Trends in health of pahautea and Hall's totara in relation to possum control in central North Island

SCIENCE FOR CONSERVATION: 52

Geoff Rogers

Published by
Department of Conservation
P.O. Box 10-420
Wellington, New Zealand

Science for Conservation presents the results of investigations contracted to science providers outside the Department of Conservation. Reports are subject to peer review within and outside the Department.

ISSN 1173-2946
ISBN 0-478-01900-9

This publication originated from work done under Department of Conservation contract 1717 carried out by Geoff Rogers, Manaaki Whenua - Landcare Research, Private Bag 3127, Hamilton. It was approved for publication by the Director, Science and Research Division, Department of Conservation, Wellington.

Cataloguing-in-Publication data

Rogers, Geoffrey Malcolm.
Trends in health of pahautea and Hall's totara in relation to possum control in central North Island / Geoff Rogers. Wellington, N.Z. : Dept of Conservation, 1997.
1 v. ; 30 cm. (Science for conservation, 1173-2946 ; 52.)
Includes bibliographical references.
ISBN 0478019009
1. Defoliation- -New Zealand. 2. Trichosurus vulpecula- -Control- - New Zealand. 3. Podocarpus hallii. 4. Libocedrus bidwillii. I. Title. II. Series: Science for conservation (Wellington, N.Z.) ; 52.
581.52230993 20
zbn97-067002

CONTENTS

Abstract

This study took a multifaceted approach to understanding the role of possums in the deteriorating health of pahautea-Hall's totara forest by assessing the diet of possums, and rates of possum population recovery after a poison programme, assessing ground-based techniques for measuring crown condition of the emergent conifers, measuring the benefits to tree health and regeneration accruing from possum control, mapping crown health and tree density changes over time from aerial photos, and analysing forest structure along environmental gradients to assess stand turnover and vulnerability to animal modification.

The study highlights the palatability of pahautea and its vulnerability to possum browse and confirms the widely suspected vulnerability of Hall's totara to prolonged defoliation. Proportionately small amounts of pahautea foliage compared to that of Hall's totara appear to be removed from trees. Hall's totara showed rapid foliar recovery after possum control, but not pahautea, and this may be partly related to their different resprouting capabilities. The Foliar Browse Index developed by Manaaki Whenua - Landcare Research can be applied effectively and confidently to Hall's totara despite its needle-leaved form, but not to the scale leaves and tall conical profile of pahautea.

Defoliation, dieback, and collapse of pahautea and Hall's totara are widespread in montane forests of Egmont National Park, Hihitahi Forest Sanctuary, and the Ruahine Range. Between 50% and 80% of emergent canopies show severe dieback and collapse. Although it is difficult to apportion the damage between natural stand turnover and possum defoliation, the evidence points to possum defoliation as the major influence.

The patterns of stand structure, landform and site stability, community composition, and climatic gradients apparently correlated with pahautea dieback and collapse are similar to those reported for the southern rata and kamahi forests of Westland. Dieback is much less severe in young cohort stands, on stable sites of lower soil fertility, where these conifers co-occur with non-preferred species, and in wetter and colder climates.

1. Introduction

A great deal of research has implicated brush-tailed possums in the collapse of rata-kamahi forest in the South Island, including landscape-scale patterns of dieback, factors predisposing stands to dieback, and community adjustments following dieback. Although possums are suspected of defoliating Hall's totara (*Podocarpus hallii*) (New Zealand Forest Service 1982), little is known about the vulnerability of pahautea[1] (*Libocedrus bidwillii*), the stand and

---

[1] Allen (1961), Beever (1987), and the Landcare Research Ethnobotanical Database list the Maori name for *Libocedrus bidwilli* as "pahautea". "Kaikawaka", and its variant "kawaka", apply to the northern *species L. plumosa*. The present publication seeks to highlight the incorrect usage of the Maori name "Kaikawaka" that has crept in over recent decades, and to re-establish the traditional name bestowed by the tangata whenua.

environmental factors that predispose the species to defoliation, and crown and recruitment recovery rates following possum control.

This project was undertaken between 1993 and 1996 by Landcare Research, Hamilton, to map canopy condition in pahautea and Hall's totara forest of the lower North Island, to explain dieback in terms of environmental factors, and to assess rates of foliar response to possum control. A ground-based method for monitoring change in tree health after possum poisoning operations is reviewed.

2. Background

Pahautea and Hall's totara are compositional dominants in upper montane forests of the wetter mountains of the central and lower North Island. J.L. Nicholls, in his forest class mapping series 6 (see, for example, New Zealand Forest Service 1970), included forests where these two conifers are compositional dominants in his *Highland and Steepland Softwoods-Hardwoods* class. The two species are conspicuous in upper montane forest on the southern slopes of the Pouakai Range and around much of the Mt Taranaki cone, around the western slopes of Mt Ruapehu and Hauhungatahi in Tongariro National Park, on high plateaus of Moawhango Ecological District, and in the north-western, western, and southern Ruahine Range. Pahautea is absent from the Tararua Range, but Hall's totara is prominent in the north in the non-beech (*Nothofagus*) belt. Stand health varies widely within these forests, but where it is poor, it has apparently dramatically deteriorated in the last 50 years, particularly in parts of Egmont National Park, at Hihitahi Forest Sanctuary in Moawhango Ecological District, and in the north-western and southern Ruahine Range.

Although possums defoliate Hall's totara (Nugent *et al.* 1997) they have yet to be convincingly implicated as defoliators of pahautea. Natural regeneration behaviour is well documented for pahautea, and to a smaller extent for Hall's totara, but the existing models do not appear to fit the synchronicity, geographic extent, and intensity of illthrift of pahautea (e.g., Hihitahi — Rogers 1989; southern Ruahine Range — Rogers & Leathwick, 1997), particularly the collapse and non-replacement of stands of uneven age. The outcomes of catastrophic collapse in upper montane conifer forest are uniform in a generic sense, in that the emergent pahautea — and to a less extent Hall's totara — virtually disappear, and lower tiers become simpler in structure and composition, often dominated by possum-palatable wineberry (*Aristotelia serrata*) and possum-unpalatable horopito (*Pseudowintera colorata*), toetoe (*Cortaderia fulvida*), bush tussock (*Chionochloa conspicua*), small-leaved coprosmas, or bush rice grass (*Microlaena avenacea*).

Research apportioning stand collapse in rata-kamahi forest to either natural turnover or to possum use has highlighted the influence on both processes of stand structure, stand composition, and geomorphology. If possums are the primary cause of stand collapse in pahautea-Hall's totara forest, then their use of this habitat may be similarly regulated, but this has yet to be thoroughly researched. This project was primarily concerned with the immediate health of the two target species and the benefits of possum control, but a full understanding of the long-term impacts of introduced animals and the induced state of compositional and structural disequilibrium requires a wider and more comprehensive community approach.

Upper montane conifer forest of the central North Island has been included in large-scale poisoning operations against possums in Egmont National Park, Hihitahi Forest Sanctuary, and the northwestern Ruahine Range, partly in the absence of a scientific understanding of the animals' role in the unhealthy state of these two conifers or an established method of "performance" monitoring, as opposed to "operational" monitoring, for conservation goals in the community. "Operational" monitoring addresses the efficiency of possum control operations, with percentage kill rates a common method. "Performance" monitoring, however, addresses the effectiveness of pest control in terms of habitat or ecosystem benefits. The Foliar Browse Index was developed by Landcare Research for the Department of Conservation to monitor possum related damage to trees and shrubs. Emergent trees and those with needle or scale leaves are difficult to visually rate. Nevertheless, in this study the method was trialled extensively against pahautea and Hall's totara in its "foliar density", "dieback", and "browse" components.

The study took a multifaceted approach to understanding the role of possums in the deteriorating health of pahautea-Hall's totara forest by assessing the diet of possums, rates of possum population recovery after a poison programme, assessing ground-based techniques for measuring crown condition of the emergent conifers, measuring the benefits to tree health and regeneration accruing from possum control, mapping crown health and tree density changes over time from aerial photos, and analysing forest structure in relation to environmental gradients and animal habitat quality.

3. Objectives

- Aerially map visually conspicuous canopy dieback in pahautea and Hall's totara forest and estimate its extent and severity in Egmont National Park, Hihitahi Forest Sanctuary, and the Ruahine Range (June 1995).
- Measure recovery rates of possum populations after 1080 poison operations at Hihitahi (June 1995, 1996).
- Determine and map environmental gradients correlated with degree of crown defoliation, dieback, and collapse of pahautea and Hall's totara at all three sites (June 1995).
- Assess rates of foliar response of both species to aerial 1080 possum control operations and to exclusion of possums by trunk banding (June 1996).

4. Methods

4.1 POSSUM POPULATION

Possum abundance was assessed from the catches recorded on a permanently marked kill-trap line immediately before and for two years after an aerially applied 1080 poison operation in May 1993 at Hihitahi Forest Sanctuary. Lured Lane's Ace gin traps were located 20–60 m apart at permanent sites along a transect for three consecutive nights for each of six sample periods. The population was first trapped one month before the drop (April 1993), and on five occasions over the next two years (December 1993, February 1994, May 1994, January 1995, and May 1995). The transect was aligned radially, southwest to northeast, commencing 400 m from the boundary, ending near the centre of the sanctuary, and subdivided into three sections along the gradient from forest margin to forest centre (margin, intermediate, interior). The transect spanned a gently-sloping plateau surface, rising in altitude from 960 m near the margin to 1116 m at the centre. The total catch over three nights was used as an index of possum abundance, with catch presented as percent catch ± 95% C.I. Repeat trapping of the same line during the experiment may have influenced rates of post-poison recovery, but by how much is unknown.

4.2 POSSUM DIET

Although microhistological analysis of faeces has been a popular method for dietary studies in the past, macroscopic analysis of stomach contents is now regarded as superior as it removes bias due to differential digestion, most plant species are readily identifiable, and estimates of dry weight can be obtained. Stomachs were collected from animals trapped to monitor possum abundance along the three sections of the permanent transect and from each of the first five sample periods — April 1993 to January 1995. Dietary differences and trends were determined over three seasons, throughout the 22-month sample period, along the radial transect, and before and after the poison drop. Between 20 and 30 stomachs were collected per sample, and 140 overall. Seasons were classed as: summer — December to February; autumn — March to May; and winter — June to August. There were no samples in spring. Possum stomachs were removed whole and frozen as soon as practicable.

Methods for macroscopic analysis were based on Nugent (1983). The layer separation technique of sampling possum stomachs (Nugent *et al.* 1997) was not used because the animals were obtained by trap-catch, rather than with potassium cyanide poison. When no pahautea fragments were found in samples that passed through 2 mm and 1.4 mm sieves, a modified technique (Appendix 1) was adopted to quantify separately the pahautea component of the diet. This involved initially separating out by hand any fragments of pahautea and determining their dry weight as a proportion of the total gut weight.

4.3 FOREST COMPOSITION

The emergent pahautea and Hall's totara component of Hihitahi Forest Sanctuary has suffered considerable dieback and collapse in the last 55 years, particularly in the central, western, and southern sectors (G. Rogers, unpubl. data). Stand density and health are variable in the western sector, where foliage biomass of the forest was assessed. Foliage cover estimates are considered to provide a quick and relatively accurate estimate of foliage biomass (e.g., Spurr & Warburton 1991). In December 1995 the RECCE method for describing vegetation (Allen 1992) was used to estimate the percent foliage cover of each species within a 2 m radius of each plot centre in predefined height strata: 0–0.5, 0.6–2.0, 2.1–4.0, 4.1–9.0, 9.1–13.0, and >13.1 m. A total of 191 plots were spaced at approximately 20 m intervals along the transect used to sample possum guts — 59 plots on the forest margin sector, 76 on the middle sector, and 56 on the forest centre sector. Small herbaceous species, such as bush rice grass (*Microlaena avenacea*), *Uncinia* spp., *Nertera* spp., and introduced grasses were amalgamated into a single cover class of herbs; the ground ferns *Asplenium gracillimum*, *Blechnum fluviatile*, *Hypolepis millefolium*, and *Polystichum vestitum* were similarly amalgamated into a single fern class. Percent cover scores were weighted by relative heights of strata to obtain estimates of total foliar abundance by species for each plot. Mean proportional abundance was then determined for each species for each of the three sections of the transect, and also for all 191 plots.

4.4 FOLIAGE PREFERENCES

Preference indices (PIs) are used to express the relationship between the relative use (% in diet) with availability (% foliage available) (Owen & Norton 1995). The index is based on the difference between the herbivores' proportional use of a plant and the proportion of that plant in the habitat. The preference index was assessed using a method similar to that used by Nugent (1990), and is calculated as: PI = (% in diet − % available) ÷ (% in diet + % available). PI values potentially range from −1 (present on vegetation plots but not in stomachs) to +1 (the converse), with a zero value when food use equals availability. Estimates are for foliage only.

4.5 MONITORING POSSUM DEFOLIATION OF CONIFERS

The recovery of needle-leaved Hall's totara and scale-leaved pahautea in upland conifer forest was assessed after possum control operations in Egmont National Park and Hihitahi Forest Sanctuary. An aerial 1080 poison operation was undertaken in early winter 1993 at Hihitahi Forest Sanctuary and on the Pouakai Range, Egmont National Park, and one year later throughout the remainder of Egmont National Park. The "Foliar Browse Index" developed by Landcare Research for the Department of Conservation, as a method to monitor possum related damage to forests and rare or endangered plant species, was tested on both conifers over a 2-year period. In addition, both species were monitored on Ohutu Ridge in the northwest Ruahine Range where no recent possum poisoning operations have been undertaken.

Monitoring transects were established on the Mangorei, Puffer, Razorback, and Veronica tracks of Egmont National Park, the west and east sides of Hihitahi Forest Sanctuary, and on Mangaohane Station and the Awarua/Aorangi Block of Ohutu Ridge, northwest Ruahine Range. Included in the sample of 193 pahautea and 140 Hall's totara were a wide range of crown foliar densities in each regional sample for both species, partly to assess their respective resilience to defoliation and dieback. The response variables assessed were crown foliar density, the age, position, and degree of dieback in the crown, evidence of browse or hedging of buds and new shoots, and stem damage. For both species results for crown foliar density, the incidence and severity of dieback, browse or hedging, and trunk use are provided. Summary statistics for diameter (dbh) distributions, tree architecture, species abundance, age and position of dieback, and the incidence of flowers and fruit are not reported here, but are available from the author. Trees with crown foliar densities as low as 5% were included to assess the resilience of severely defoliated trees. Transects were established in November–December 1994 and remeasured in January 1996.

The trunks of a further 10 Hall's totara and 39 pahautea were banded with aluminium sheet to assess foliar responses following exclusion of possums, and as a method of comparing the foliar responses of banded trees with those where possum poisoning had or had not been undertaken. McNemar's Chi-square Test with continuity correction and Manova (multivariate analysis of variance) tests were used to test for significant differences in the defoliation response variables.

Response of the conifers to release from browsing disturbance is an expression of their resilience. Of the four measures of resilience recognised by Westman & O'Leary (1986), two apply readily to the duration of the present experiment, and are tested here. "Elasticity" is the rate of recovery following disturbance, and "amplitude" is the threshold of disturbance beyond which recovery to the original state does not occur.

4.6 MAPPING DIEBACK AND STAND COLLAPSE

Broad spatial patterns of dieback and stand collapse of pahautea and Hall's totara in montane conifer forest were assessed qualitatively by comparing recent and historical aerial photos of Egmont National Park, Hihitahi, and parts of the Ruahine Range. Existing recent aerial photos of Egmont National Park were used, but a separate contract was let for the compilation of colour stereo airphotos of the western and southern Ruahine Range for this study. In the Ruahine Range the areas covered were the entire area south of the Oroua River, the Whanahuia Range in the central west, and Ohutu Ridge in the north-western sector. Visibly dead crowns of the conifers and collapse of their trunks from the canopy were classified into three categories, after the method of Rogers & Leathwick, 1997 (based on Rose *et al.* 1992), except that the aerial verification of stem loss and assessment of replacement vegetation was not undertaken: light or relatively intact (<10% loss of stems); light to moderate (11-65% loss of stems); heavy to severe (> 66% loss of stems).

The proportion of forest collapse evident on the modern photographs was scored by comparing present-day vegetation with that on the historical photographs. The replacement vegetation of canopy gaps proved to be readily distinguishable from the crowns of tall forest. The mapping units were the individual tributary catchments of major streams and all rivers. Many mapping units had variable condition of forest canopies and for these the dominant stem density change prevailed. For the southern Ruahine Range, results are adapted from Rogers & Leathwick (in press). Moderate to severe collapse is accompanied by replacement with horopito, wineberry, tree ferns (*Cyathea smithii*), bush tussock, and tupari (*Olearia colensoi*). The orange-brown coloration of horopito and the vivid green of tupari are conspicuous in polychrome airphotos.

This method attempts to assess present mortality and density reductions from canopy collapse over the aerial photo monitoring period. No regional-scale studies of stand modification exist for North Island forests, especially those in a post-dieback phase — southern Ruahine Range forests are the most advanced example (Batcheler 1983). Historical and anecdotal accounts note conspicuous dieback of pahautea in Egmont National Park in the 1950s. Possum populations were expanding in that period (L. Pracy, unpubl. data). However, natural senescence, snow-break, windthrow, mass movement, drought, and insect outbreak are all known to fragment forest canopies and produce dieback symptoms. These factors in triggering natural stand turnover must therefore have accounted for a proportion of grey and dead crowns in historical aerial photos and for subsequent changes in stem density. Furthermore, not all grey crowns of pahautea are evidence of illthrift. Flag-formed trees, particularly on Egmont, and older stag-headed trees throughout the study areas have a grey appearance in vertical aerial photos.

These climate- and age-related conditions caution against attributing all crown death and stem loss to possum defoliation. Nevertheless, the widespread and largely synchronous replacement of pahautea and Hall's totara and several lower canopy dominants with species unpalatable to possums points strongly to a breakdown in normal stand replacement processes. I suggest that introduced animals account for a large proportion of the profound compositional shifts evident in post-peak upland conifer forest of the central North Island. Animals other than possums may also be involved; deer and goats have strongly modified understoreys in the southern Ruahine Range (Batcheler, 1983), and insects and fungi are secondary pathogens in possum-debilitated canopies (Payton 1988).

4.7 STAND STRUCTURE AND REGENERATION

The regeneration behaviour of pahautea, particularly in response to catastrophic disturbance, is well understood. Mass movement and wind throw stimulate regeneration of even aged stands, leading to forests composed of overlapping patches of different aged cohorts. Nevertheless, there were striking contrasts in stand structure, regeneration mode, and stand collapse at three sites along a west-east gradient on similar landforms in the northwestern Ruahine Range. At Hihitahi Forest Sanctuary, canopy dieback, standing dead stems, and fallen trunks appeared to form a high proportion of the pahautea and Hall's totara population and, for pahautea,there were few seedlings, saplings, and poles in c. 2000 ha of conifer forest. At Ohutu Ridge there was a marked contrast between the similarly unhealthy state of old-growth pahautea forest and the healthy stands of fire-regenerated pahautea unaffected by dieback and collapse. In the far east, at Ruahine Corner, dieback was absent and, in any one small area of forest, all stem size classes were present, including abundant juveniles.

A preliminary investigation into stand structure, regeneration regime, and susceptibilty to dieback was undertaken at all three study sites using variable-area plots ranging in radius from 10 m to 45 m. The diameter (diameter at 1 m) of all conifer stems was recorded, as was the number of seedlings and saplings, along with ratings for a range of site or environmental factors, including altitude, slope, aspect, and soil drainage. The species, direction of fall, and state of decomposition in three classes was rated for all fallen stems originally rooted in the plots. Stumps were also recorded, but not those associated with adjacent fallen stems. There were 37 plots installed at Hihitahi, 18 in the fire-regenerated stand and 15 in the old-growth stand at Ohutu Ridge, and 49 at Ruahine Corner. Excluding seedlings and saplings, a total of 727 stems were recorded at Hihitahi, 608 and 257 in the fire-regenerated and old-growth stands at Ohutu Ridge, and 1476 at Ruahine Corner. Mean density and basal area statistics were compiled for all conifer species in the classes: "healthy", "dead-standing", "stump", and "fallen".

5. Results

5.1 POSSUM POPULATION RECOVERY

Trap-catch frequency was moderately low (11.7%) before the poison drop (Table 1), relative to a recent figure from montane podocarp-broadleaved forest at Waihaha (18.6–24.7%) (Nugent *et al.* 1997). Intensive commercial trapping ceased in 1989 at Hihitahi (L. Abernethy pers. comm. 1994) and the population had probably been undergoing a slow increase in the three to four years before the poison drop in May 1993. No apparent reduction in possum abundance as indicated by catch success occurred after the poison drop, nor for the following 12 months, but in the second year the population dramatically increased to well above previous levels. However, pre and post 1080 control monitoring by the Department of Conservation using 6 traplines showed a percent reduction of 74.5 ± 25.4 (95% CI) (C.C. Ogle pers. comm. 1996). Weather does influence trap-catch rates. Although it was wet over the fourth sample period, there was no reduction in trapping success when compared with the fifth sample. There were no consistent trends in possum abundance along the transect from forest margin to forest centre that might indicate what contribution reinvasion from adjoining farms made to the dramatic population recovery. There was a high proportion of adolescent animals in the trapped sample (G. Rogers, unpubl. data), consistent with a rapidly recruiting population. Thomas (1993) recorded an 18% initial reduction in trap-catch success at Waipoua after a 1080 poison operation and an approximately 6% increase in a three year post-poison period.

TABLE 1. NUMBER OF TRAP NIGHTS, NUMBER AND PERCENT FREQUENCY (IN PARENTHESES) OF CATCHES, AND BINOMIAL ERROR LIMITS AT 95% CI OF PERCENT CATCHES ALONG A PERMANENT TRANSECT DIVIDED INTO THREE SECTIONS TO MONITOR POSSUM ABUNDANCE AT HIHITAHI FOREST SANCTUARY OVER A 22-MONTH PERIOD. A POISON DROP OCCURRED IN MAY 1993.

	TRAP NIGHTS				CATCH			
	MARGIN	MIDDLE	INTERIOR	TOTAL	MARGIN	MIDDLE	INTERIOR	TOTAL
Apr. 1993	74	70	19	163	7(9.5)4-18	9(12.9)6-22	3(15.8)4-39	19(11.7)7-18
Dec. 1993	46	41	46	133	5(10.9)4-23	8(19.5)9-36	2(4.3)2-16	15(11.3)6-17
Feb. 1994	48	103	90	241	5(10.4)3-22	12(11.7)7-20	14(15.6)8-25	31(12.9)9-17
May 1994	70	60	49	179	7(10.0)3-20	10(16.7)8-29	8(16.3)7-30	25(14.0)8-21
Jan. 1995	27	48	18	93	13(48.1)32-68	23(47.9)35-62	5(27.8)11-52	41(44.1)34-54
May 1995	24	27	12	63	9(37.5)19-60	14(51.9)33-72	5(41.7)13-75	28(44.4)32-57

Because the sample is small the results, and any interpretation, should be treated with caution. However, the population appears to have responded to control with rapid recruitment in the second year, perhaps fostered by increased forage availability. Reductions in the population from one year's trapping may have depressed the success of subsequent catches because traps were permanently located. As measures of possum abundance, the trap-catch results are therefore conservative. A possum pellet frequency of 26.8% was recorded on a permanent transect in Hihitahi monitored in autumn 1996 (J. Barkla, pers. comm.). An apparently rapid rate of population recovery following control has been recorded from a 200 ha remnant of lowland broadleaved forest surrounded by farmland in Hawke's Bay (K. Briden, pers. comm. 1994).

5.2 POSSUM DIET

Thirty-one food items and food groups were identified in the diet of possums over the 22-month monitoring period. With five different species included in the food groups "herb species" and "fern species", the total number of species recorded in the diet was 39, which is comparable with the 33 identified from silver beech (*Nothofagus menziesii*) forest in the Haast valley (Owen & Norton 1995) but many fewer than the 102 identified from montane podocarp-broadleaved forest at Waihaha, Hauhungaroa Range (Nugent *et al.* 1997). The four most abundant — wineberry, fern species, Hall's totara, and herb species — constitute a substantial 67% of annual diet (Appendix 2) and, with pahautea and *Rubus cissoides* included, the top six form 81% of annual diet. Other studies have noted a similar reliance on two to four food items in possum diets (Owen & Norton 1995), even in apparently diverse forest communities (Nugent *et al.* 1995, unpubl. Landcare Research contract report). Fuchsia (*Fuchsia excorticata*) was the next most abundant foliage item, but is probably substantially reduced as fodder after its near elimination from the forest in the last 50 years (G. Rogers, unpubl. data).

Prominent in the category herbaceous species are *Trifolium* spp., *Hydrocotyle* spp., *Hypochoeris radicata*, and *Nertera* spp., species of low abundance on the forest floor. Bush rice grass is by far the dominant herb over a range of light conditions on the forest floor, but is absent from possum diets. By contrast, the dominant ground ferns *Hypolepis millefolium* and *Polystichum vestitum* feature prominently in the diet. Foliage comprises 87.6% of the total diet, with shrubs the most important group ahead of conifers, lianes, and broadleaved trees (Appendix 2). The three main tall broadleaved trees — *Pseudopanax simplex*, putaputaweta (*Carpodetus serratus*), and papauma (*Griselinia littoralis*) — are unimportant in diets, whereas the ground stratum of herbs and ferns forms a large 30% of annual diet. Fruit is also important at 9.78%, followed by insects at 1.85%, and flowers, bark, and wood all at less than 1%. Use of putaputweta and horopito fruit substantially exceeded the use of their foliage.

Marked seasonal fluctuations in diet are evident (Appendix 2). Possum browsing of pahautea and Hall's totara is concentrated in summer, the period of shoot extension, although Hall's totara is also important in early winter diets. The lianes — *Muehlenbeckia australis*, *Clematis foetida*, and *Rubus cissoides* — are used principally in winter, as are the ground herbs, ferns, and lacebark (*Hoberia populnea*). Fruit availability and use is highly seasonal, constituting 11–12% of the diet in summer and autumn and only 2.5% in winter. Possums rely heavily on wineberry in the autumn (55% of total diet), reflecting the pulse of shoot and leaf extension in early to mid summer. Overall, there was a consistent reliance on foliage throughout the year (64–76%).

There were few consistent trends in dietary components throughout the 22-month monitoring period corresponding to recovery of the possum population following poisoning (Appendix 3), probably because seasonal fluctuations mask dietary shifts attributable to increasing population density. There was also little variation or trend in diet along the radial transect from forest margin to forest centre (Appendix 4).

Where pahautea and Hall's totara foliage appeared in possum stomachs they frequently formed the bulk of that night's feeding. The energy expended in climbing a tree 20 m+ tall may therefore result in a concentrated period of feeding on what are usually emergent and isolated crowns.

At 10% of summer and 7.8% of diets, pahautea is an important food item at Hihitahi, suggesting that possums are a major factor in its widespread decline. Possums have previously not been strongly implicated in the decline of pahautea (e.g., Batcheler 1983), although pahautea has appeared at low levels in other dietary studies. Two factors may have contributed. Firstly, only terminal buds are eaten and, at 1–2 mm in length, this damage is inconspicuous on the scale-leaved branchlets. Possums mostly avoid young vigorous trees (pers. obs.), and browse sign is mostly inconspicuous on loftier emergent specimens. Second, traditional sieving techniques in dietary studies lose the masticated fragments of terminal bud in the washing process. The revised laboratory procedure developed here overcomes this problem (Appendix 1).

5.3 FOREST COMPOSITION

Wineberry foliage is the most abundant, followed closely by horopito (Table 2), to the extent that much of Hihitahi is, strictly speaking, a low forest of wineberry and horopito. As a deciduous species wineberry has low foliar abundance in late winter, with a flush in early to mid summer. Emergent pahautea and Hall's totara each comprise less than 10% mean cover and foliar biomass, yet visually they dominate forest composition. Pahautea exists almost entirely in the upper two tiers as emergent trees in the absence of juvenile and seedling classes. Hall's totara, on the other hand, is more evenly distributed in all tiers, but is edaphically concentrated along exposures of capping limestone about the plateau surfaces. The broadleaved tree-dominated lower canopy is composed mainly of putaputaweta and papauma, the latter progressively being eliminated by recruitment failure.

TABLE 2. MEAN PERCENT COVER AND FOLIAR BIOMASS IN ALL TIERS FOR SPECIES WITH >2% COVER AT HIHITAHI FOREST SANCTUARY.

	MEAN COVER (%)	FOLIAR BIOMASS (%)
Aristotelia serrata	38.4	41.5
Herbaceous species	38.4	5.9
Pseudowintera colorata	22.5	14.3
Fern species	9.3	1.7
Carpodetus serratus	7.6	6.1
Libocedrus bidwillii	7.5	9.9
Podocarpus hallii	7.4	7.8
Griselinia littoralis	3.7	2.9
Moss	3.5	0.5
Hoheria populnea	1.9	1.4

Only 28 species and species groups were recorded. The category ferns, in approximate order of cover abundance, comprised *Hypolepis millefolium*, *Polystichum vestitum*, *Blechnum fluviatile*, *Asplenium gracillimum*, and *Blechnum procerum*. Common herbs are bush rice grass, *Uncinia uncinata*, and *Uncinia gracilenta*, none of which appeared in possum diets. Other common herbs with much lower biomass are *Urtica incisa*, *Hydrocotyle* spp., *Cardamine* sp., and *Nertera villosa*. At approximately 36, the total species count compiled from RECCE plots is low relative to the 100+ in podocarp-broadleaved forest at Waihaha (Nugent *et al.* 1997), but compares closely to that from a Haast silver beech forest (Owen & Norton 1995).

Hihitahi conifer forest is similar to that of the lower-altitude section of montane conifer forest in the adjoining western and southern Ruahine Range, but the higher-altitude stands of the range differ because mountain toatoa (*Phyllocladus alpinus*) and pink pine (*Halocarpus biformis*) replace Hall's totara in the conifer component. Throughout this montane belt, emergent pahautea is the key emergent element although, in terms of canopy cover other coniferous species such as pink pine and mountain toatoa, and broadleaved trees such as putaputaweta, papauma, wineberry, and horopito in combination, exceed the cover of emergent pahautea. Upland conifer forest of Egmont National Park differs from that elsewhere in the central North Island in the greater abundance of kamahi and mountain fivefinger (*Pseudopanax colensoi*), rare species in Ruahine Range conifer forests north of the Pohangina River. Montane conifer forest in western Tongariro National Park (not studied here) has wide compositional mixes of pahautea, mountain toatoa, pink pine, papauma, silver pine (*Manoao colensoi*), Hall's totara, rimu (*Dacrydium cupressinum*), and mountain beech (*Nothofagus solandri* var. *cliffortioides*) on various combinations of elevation, landform, and soil parent material.

5.4 FOLIAGE PREFERENCES

Thirteen of the 18 foliage foods were preferred by possums in at least one season of the survey (Appendix 5). Overall, *Muehlenbeckia australis*, large-leaved coprosmas, *Rubus cissoides*, *Fuchsia excorticata*, ferns, and fungi were highly preferred. These were also abundant foods in possum diets (Appendix 2). Pahautea was moderately preferred in summer, but much less so in autumn and winter, whereas Hall's totara was moderately preferred in summer and winter, but not autumn. Ferns were highly preferred in all seasons, but the preference for herbs declined in autumn when fruits increased. Despite its dominant presence in possum diets, wineberry was less preferred in two seasons — this reflects its overwhelming biomass in this forest. Preference scores were not calculated for non-foliage food items such as fruits, flowers, and insects consumed by possums.

Until now, the relationship between possum diet and vegetation has not been studied in detail in pahautea-Hall's totara forest. A distinctive feature of this study is the proportionately large contribution that the most preferred tree species — wineberry, Hall's totara, and pahautea — make to forest biomass, in contrast to other studies where these species have featured. The relatively low species diversity results in reliance on just a few palatable foods, in this instance the structural dominants of the forest. This is reflected in the proportion that the four most preferred food types contribute to foliage biomass — 67% at Hihitahi and between 25% and 55% in podocarp-broadleaved forest elsewhere. As an extreme example, the four main food species in silver beech forest at Haast contribute <5% of foliage biomass (e.g., Owen & Norton 1995).

5.5 MONITORING POSSUM DEFOLIATION OF CONIFERS

5.5.1 Foliar browse index and tree morphology

The Foliar Browse Index is a method of monitoring possum-related damage to trees and shrubs, and as such can be used to monitor the benefits to plant health accruing from possum control. It is best applied to large-leaved shrubs and low trees (I. Payton, pers. comm. 1995), and has practical limitations when applied to both tall and small-leaved trees. This study has indicated that the method can be confidently applied to needle leaved species such as Hall's totara. The generally even and diffuse arrangement of totara foliage allows confident assessment of crown foliar densities, whilst the colour contrast between new shoots and mature leaves on the margins of crowns permits reliable estimation of browse or hedging. Viewing positions differ for the two ratings, either beneath the crown for foliar density or outside for browse or hedging. Dieback assessment often requires viewing from both positions. Trunk use can also be confidently rated. However, the thin flaky bark retains run and bark-biting evidence for many years, and accordingly, reductions in possum use of trunks may not be immediately apparent. Not all trunk use is direct evidence of possum access to crowns for roost sites or fodder; rather, scratching and bark biting on trunk bases appear to be part of ground based territorial behaviour.

Possum defoliation of Hall's totara, as with many tree species, is concentrated on marginal buds and shoots. Sustained periods of browse lead to a greying of crowns, the result of dead twigs and branchlets appearing as mature leaves die and of increased lichen growth accompanying illthrift. Complete removal or death of subtended foliage does not necessarily result in the death of branchlets and branches because Hall's totara is able to resprout from latent buds along woody tissue, after a release from browsing pressure (pers. obs.).

Pahautea, on the other hand, poses inherent difficulties for the Foliar Browse Index method because of its scale-leaved foliage and tall conical outline. Nevertheless, for lack of immediate practical alternatives, the technique was thoroughly trialed on this species. Close inspection suggests that possum defoliation is confined to the 2–3 mm long terminal bud of each branchlet, and seldom occurs on the mature scale leaves subtending the bud. Given the small size and lack of morphological contrast between terminal buds and mature leaflets it is difficult from the ground to discriminate and rate browse or hedging consistently. Truncated branchlets are evident only by close inspection although, in due course bud scales (if they remain) brown off, increasing the evidence. Eventually the entire branchlet of mature scale leaves dies of old age, and branch dieback develops as first a browning and then a greying of the remaining foliage. As on several other tree species, e.g., northern rata (*Metrosideros robusta*), possums consistently browse isolated branches, and dieback progresses as the apparently random death of a sequence of branches. Changes in crown foliar density result, not so much from consumption of individual shoots but from the death of entire branchlets after removal of the terminal bud. Progressive death of individual branches is conspicuous on stag-headed and overmature trees but somewhat camouflaged on younger trees, with their tighter conical profiles. Both foliar profiles are difficult to rate consistently for crown foliar density and a viewing position well outside the crown is often necessary to judge the dispersion and degree of dieback.

As with Hall's totara, evidence of trunk use of pahautea remains for many years in the thick excorticating bark because claw and tooth marks penetrate multiple layers. Pahautea are popular roost trees for possums because their trunks tend to become hollow, and evidence of trunk use may appear on trees with no apparent defoliation.

Pahautea is slow-growing. This is reflected in its slow vertical growth rates (pers. obs.) and radial wood increments of <1 mm per annum (Rogers 1989). It also appears to have low foliar biomass/total biomass quotients, at least in older trees, although these were not measured. Close observation over two years of the foliage of several banded trees at Hihitahi east also suggests that branchlets have little or no capacity to resprout from their woody portions and a very limited capacity to resprout from their green leaflets when damaged. In almost all instances, bud removal appeared to initiate a slow and irreversible decline of the subtending mature leaves as they aged.

Given the probably high levels of observer inconsistency in the data, results from the Foliar Browse Index method applied to pahautea and interpretations thereof should be treated with caution.

5.5.2 Crown foliar densities

Despite the comparatively short monitoring interval, the ratings for crown foliar density of Hall's totara increased significantly (by 10–20%) at all sites where possums had been poisoned except Ohutu Ridge where the rating declined slightly (Appendix 7). There was an inverse relationship between foliar recovery and stem size class, possibly corresponding to the physiological vigour of trees. There were also significant differences in the foliar responses of the different size classes of Hall's totara. The percentage recovery was similar for banded trees and those in areas where possums had been controlled. Crown foliar density of pahautea showed inconsistent changes over the two years, with virtually no change overall, but increasing slightly in the smaller size classes and also overall at North Egmont, and declining or stable for other size classes and at all other sites. The control trees at Ohutu Ridge declined in foliar density, while those banded or at sites where possums had been poisoned increased slightly. Overall, there was a significant difference between the positive response of Hall's totara and the stable or declining foliar density of pahautea over the two years.

Several pahautea with crown densities below 25% at the commencement of monitoring, banded to exclude possums, and in all three size classes, declined rapidly over the next two years.

5.5.3 Dieback

The proportion of Hall's totara trees in the entire sample that showed visible symptoms of dieback changed very little between the two surveys (Appendix 7). Nevertheless, the proportion of trees with dieback in the two larger size classes declined by 11–15%, in contrast to the smallest size class, which showed an increase in dieback. The reduction of dieback in the larger size classes suggests that resprout following a release from browsing pressure is masking previous evidence of dieback. There were no other substantial changes except at Ohutu Ridge, where the incidence of dieback increased in the area with no possum control. The incidence of dieback in monitored pahautea remained stable across all sites.

5.5.4 Degree of dieback

There were no statistically significant reductions in the ratings for degree or severity of dieback for Hall's totara over the entire dataset (Appendix 7). There were, however, significant reductions in the severity and age of dieback on trees on the Pouakai Range and the severity of dieback in the eastern and western Hihitahi populations. The degree of dieback also declined for all size classes of Hall's totara, for the banded population, for the population at poisoned sites, and also (surprisingly) for the control population. The only population of pahautea to show a substantial reduction in the degree of dieback was the >70 cm dbh size class; for the rest of the subsamples the degree of dieback was constant or increased slightly.

5.5.5 Browsing or hedging

There were significant reductions in the ratings for browse or hedging in all populations of Hall's totara except the control population (Appendix 7). The ratings for all populations of pahautea, except the control, also declined significantly.

5.5.6 Trunk use

There were significant reductions in the ratings for trunk use in all populations of both species, except their control populations (Appendix 7).

5.6 MAPPING REGIONAL PATTERNS OF MORTALITY AND STAND COLLAPSE

Changes in stem density as a measure of the collapse of conifer stems over the period spanned by the aerial photo sets were determined for Hihitahi, Ohutu Ridge, Whanahuia Range, and the southern Ruahine Range. Two additional maps are presented for Egmont National Park showing the stem density separately for 1959 and 1994 aerial photos, effectively separating dense cohort stands resulting from past catastrophic disturbance from scattered trees reflecting tree-fall gap regeneration.

5.6.1 Egmont National Park

Pahautea and Hall's totara are important components of upper montane forest of parts of the Pouakai Range and Mt Taranaki above kamahi-dominant mid-montane forest and below tupari scrub and shrubland (Clarkson 1986). On Mt Taranaki, pahautea is conspicuously absent from the southeastern sector above Dawson Falls and from the Stony River to Kahui Bog sector, an absence believed to be related to recent volcanic disturbance. The two conifers may occur outside the mapped zones, but they are a minor component of other montane forests. Pahautea also occurs as scattered low trees through lower-altitude subalpine scrub, where it displays wide regional variation in browse and dieback impacts.

In 1959, pahautea and Hall's totara were more or less continuous around two major sectors of the park (Fig. 1). Light to moderate proportions of both species were dead in several areas, for instance on the southern flanks of the Pouakai Range, on the Kokowai Stream fan, and from Kokowai Stream south to Little Maketawa Stream. High-density stands covered approximately 40% of the area of conifer-dominated forest. By 1994, the area had substantially reduced (Fig. 2),

FIGURE 1. PATTERN OF STEM DENSITY CLASSES FOR PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST IN EGMONT NATIONAL PARK IN 1959 AS MAPPED FROM MONOCHROME AIRPHOTOS. FOR AN EXPLANATION OF CLASSES SEE SECTION 4.6.

particularly in the eastern, southern and southwestern sectors of Mt Taranaki. Some areas had thinned to low density and, in others, the conifers had virtually disappeared. Large areas of low density in 1959 had also disappeared by 1994. The areas of greatest loss are the southern and eastern flanks of the Pouakai

Range fronting Ahukawakawa Swamp, the extensive Kokowai-Kaiauai fan, ridges and gullies from Kokowai Stream south to Little Maketawa Stream, and in

FIGURE 2. PATTERN OF STEM DENSITY CLASSES FOR PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST IN EGMONT NATIONAL PARK IN 1994 AS MAPPED FROM POLYCHROME AIRPHOTOS. FOR AN EXPLANATION OF CLASSES SEE SECTION 4.6.

the south from Hasties Hill to just west of Lake Dive. Overall, density reduction is greatest on spur slopes. An estimated 25% reduction in the total area of pahautea and Hall's totara-dominant forest has occurred in the last 35 years.

The amount of stem collapse between 1959 and 1994 is mapped in three classes: light, <10%; moderate, 11–65%; heavy, >66% (Fig. 3). Extensive areas of heavy collapse dominate the southern and eastern Pouakai Range and lower-altitude stands from Hasties Hill to Waiaua Stream, representing approximately 25% of existing forest. Of the remainder, the greater proportion has moderate stem collapse. The eastern sector from North Egmont to Jackson's Lookout has a large proportion of intact stands when compared with the remainder of the park.

FIGURE 3. PATTERN OF FOREST COLLAPSE CLASSES OF PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST IN EGMONT NATIONAL PARK IN 1994.

FIGURE 4. PATTERN OF FOREST COLLAPSE CLASSES OF PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST AT HIHITAHI STATE FOREST SANCTUARY IN 1978 AS MAPPED FROM MONOCHROME AIRPHOTOS.

5.6.2 Hihitahi Forest Sanctuary

Approximately 75% of this sanctuary is classed as having moderate or severe dieback and stand collapse (Fig. 4). Only the north-eastern sector and isolated smaller areas elsewhere, all characterised by flat topography, remain relatively intact. Pahautea and Hall's totara appear to be equally affected. Mortality and collapse appear in two forms. On steeper slopes a single phase of mortality affects all emergent conifers, resulting in their disappearance from post-dieback scrub and low forest, except for scattered juvenile totara in understoreys. A "salt and pepper" pattern of dieback characterises stands on more gentle topography and at the advancing front of modification that correlates with increasing altitude in an easterly direction. Fuchsia, lacebark, and ribbonwood (*Plagianthus regius*) appear to be similarly affected by possums, and are reduced to low levels from previous abundance (G. Rogers, unpubl. data).

Parallel areas of moderate and severe dieback in the west are separated topographically, with moderate dieback on flatter interfluves and severe on steeper valley slopes.

At lower altitudes in the west and south, pahautea and Hall's totara intergraded with podocarps and broadleaved hardwoods. As pahautea and Hall's totara disappear from these communities, rimu (*Dacrydium cupressinum*), miro (*Prumnopitys ferruginea*), and matai (*Prumnopitys taxifolia*) remain as scattered emergents, as seen with rimu and miro following the collapse of kamahi and northern rata (*Metrosideros robusta*) in the southern Ruahine Range. The hardwoods black maire (*Nestegis cunninghamii*), tarata (*Pittosporum eugenioides*), and lacebark appear moderately palatable to possums, and disappear at intermediate rates.

In terms of canopy cover, Hihitahi is wineberry-horopito scrub-low forest (Section 5.3). Despite its palatability and prominence in possum diets, wineberry does not die back and collapse. Size classes of wineberry suggested a rapidly expanded cohort from scattered parents approximately 20 to 30 years ago, perhaps correlating with the disappearance principally of fuchsia in the peak possum phase. With its 30–40 year life expectancy and disturbance or light-requiring regeneration needs, wineberry is expected to decline in favour of shade-tolerant horopito, despite the palatability to possums of the latter's fruit. Broadleaf or papauma is also declining, this time by deer-browsing of juveniles, a trend apparently uninterrupted by a dramatic reduction in deer density since hunter access was improved in the late 1980s (H. Dorrien, pers. comm.). A further degradational step is evident at a local and small scale with deer-induced turfs of *Hydrocotyle* spp., exotic grasses, and bush rice grass replacing wineberry or ribbonwood, particularly in apparently more fertile gullies.

The comparison of 1939 and 1980 aerial photos highlights the dramatic reduction in density of emergent pahautea and Hall's totara. Textural changes in the lower canopy of broadleaved trees also point to compositional shifts from fuchsia, mountain five-finger, and papauma to wineberry and horopito.

5.6.3 Northwestern Ruahine Range and Ohutu Ridge

Pahautea dominates upper montane conifer forest over the southern portions of the limestone-capped sedimentary plateaus of Mangaohane-Potae and Ohutu Ridge. Pink pine and mountain toatoa co-dominate, with Hall's totara a minor element at lower altitudes (details of distribution and composition appear in Rogers 1989). Defoliation or dieback symptoms on pahautea are absent in the Ruahine Corner-Potae-Waiokotore area, for which no map is provided. Even with the loss of mountain fivefinger (*Pseudopanax colensoi*), astelias, and some ferns in the 1930–40 period from deer browsing (A.P. Druce, pers. comm. 1983), these forests are highly representative of extensive pahautea forests that dominated the wet western plateaus of Moawhango Ecological District before forest clearance in the early Polynesian era.

Patterns of pahautea health and density changes west of Ohutu Ridge are similar to those at Hihitahi, with extensive areas of moderate to severe dieback at lower altitudes and on steeper slopes around Aorangi and the Ohutu Stream catchment (Fig. 5). There is a broadly inverse relationship between degree of collapse and altitude. Relatively intact forests border the subalpine scrub-low

FIGURE 5. PATTERN OF FOREST COLLAPSE CLASSES OF PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST ON OHUTU RIDGE IN 1980 AS MAPPED FROM MONOCHROME AIRPHOTOS. IN ADDITION TO THREE HEALTH CLASSES FOR OLD-GROWTH PAHAUTEA FOREST, FIRE-REGENERATED PAHAUTEA FOREST, RED BEECH FOREST, AND SUBALPINE SCRUB ARE MAPPED.

forest along the summit of Ohutu Ridge. Red beech (*Nothofagus fusca*) is slowly invading the lower-altitude extent of scrub hardwood species that have replaced the dead conifers and associated species (Rogers 1989), albeit at rates of 6–10 m per century. The dieback breaks the previously intact altitudinal sequence of forest, from podocarps bordering the Rangitikei River to tupari (*Olearia colensoi*) scrub on the Ohutu Ridge summit.

In general terms, dieback is restricted to old-growth forests, and is entirely absent from fire-regenerated stands, for instance a 40 ha stand on Ohutu Ridge which dates to a fire approximately 450 years ago (Fig. 5), and to stands marginal to the manuka (*Leptospermum scoparium*) scrub and exotic grass grasslands along the north face of Aorangi. Where pahautea occurs at higher altitudes with abundant unpalatables such as pink pine, mountain toatoa, *Coprosma* sp. (t) (Eagle 1982), *Pittosporum rigidum*, and bush tussock, defoliation and dieback are virtually absent.

5.6.4 Central Ruahine Range including Whanahuia Range

In the central Ruahine Range, pahautea-Hall's totara forest is concentrated along the treeline of the three subordinate western ranges — the Mokai Patea, Hikurangi, and Whanahuia ranges. Similar forest occurs on the Ngamoko Range, part of the main range to the south, but this area is included in analysis for the southern Ruahine Range. On the three western ranges, conifer forest occupies an altitudinal belt of approximately 100 m between red beech forest below and subalpine scrub of inaka, bog pine, and tupari above. Pink pine and mountain toatoa are also prominent in the conifer belt. The altitudinal width of conifer forest on the western ranges increases southwards from the Mokai Patea Range to the Whanahuia Range, probably corresponding to a gradient of increasing humidity and decreasing insolation.

The Whanahuia Range was chosen as a representative sample of stand and canopy health for the three western ranges. Aerial photos from February 1996 were compared with those from December 1950. The pahautea-Hall's totara belt forms the treeline for all but a small sector in the northeastern corner, where red beech forms the treeline (Fig. 6). The altitudinal width of the conifer belt is less in the east than in the west, conforming again to a climatic gradient of increasing insolation and decreasing humidity eastwards across the range. Fires concentrated in the subalpine scrub and alpine tussock grassland zones have altitudinally truncated the conifer belt to a greater extent in the east than in the west.

Severe stand collapse has occurred throughout the southeastern and eastern sectors (Fig. 6). Similar severe collapse is evident in the eastern Ngamoko Range just to the southeast. Severe collapse is much less evident in the western Whanahuia Range, where it is restricted to isolated areas at low to intermediate altitudes, mainly on northerly aspects. Moderate collapse has affected the wide altitudinal belt of forest types G6 and G2 (J. Nicholls, unpubl. data; for a definition of forest types referred to in the text see Appendix) in the central west and along the northern treeline zone. In general terms, in the west the degree of canopy collapse appears worse at low altitude than at the treeline. The remaining approximately 35% of the conifer belt on the Whanahuia Range is intact. There appear to be no environmental gradients to explain the spatial pattern of health classes. In the absence of broad environmental gradients, site fertility, stand structure, and community composition are the most likely factors to have influenced the apparent possum-related dieback.

5.6.5 Southern Ruahine Range

Pahautea and Hall's totara are conspicuous components of montane forests of the southern Ruahine Range in association with beech north of the Pohangina River and kamahi to the south (Fig. 7). In the conifer-broadleaved forests without beech south of the Pohangina, pahautea and Hall's totara dominated forest type G2 (for forest type descriptions see Appendix 12) west of the summit ridge, whereas only Hall's totara was important in forest type G1 (not

FIGURE 6. PATTERN OF FOREST COLLAPSE CLASSES OF PAHAUTEA AND HALL'S TOTARA IN MONTANE CONIFER FOREST ON THE WHANAHUIA RANGE IN 1996 AS MAPPED FROM POLYCHROME AIRPHOTOS.

mapped) east of the summit ridge. Conifer density in the G2 belt varied in relation to site stability, with dense stands concentrated on steep sites of recent catastrophic disturbance and on flatter topography with impeded drainage and reduced soil fertility.

In broad terms, none of forest type G2 remains relatively intact when compared to its condition in 1946 aerial photos (Rogers & Leathwick 1997) (Fig. 7). Of

FIGURE 7. PATTERN OF FOREST COLLAPSE CLASSES IN SOUTHERN RUAHINE RANGE. FOREST CLASSES AS MAPPED BY J. NICHOLLS (UNPUBL. DATA) ARE: G2, OCCASIONAL TO FREQUENT HALL'S TOTARA AND PAHAUTEA OVER ABUNDANT KAMAHI (*Wienmannia racemosa*) AND PAPAUMA (*Griselinia littoralis*); J3, OCCASIONAL PAHAUTEA AND ABUNDANT RED BEECH (*Nothofagus fusca*); J4, OCCASIONAL HALL'S TOTARA AND PAHAUTEA AND ABUNDANT RED BEECH AND MOUNTAIN BEECH (*Nothofagus solandri* VAR. *cliffortioides*).

the 3156 ha, approximately 20% was judged to show light to moderate collapse and 79.7% had suffered severe collapse. The modification and collapse extend into the western Ngamoko Range. Replacement vegetation is dominated by horopito, bush tussock, and on recent slips, toetoe (*Cortaderia fulvida*). There are several notable areas of light to moderately modified G2 forest where comparatively dense pahautea forest remains, for instance on a summit dome 3 km west of the Takapari Trig between the Pohangina River and Centre Creek. As in other pahautea-dominated forest of the western Ruahine Range, lower-altitude stands, often on steeper topography, are highly degraded, whereas stands at higher altitude and on flatter topography are often relatively intact. A greater loss of forest canopies on warmer northerly and westerly aspects than cooler and more humid easterly aspects is probably related to animal habitat preferences. Greater forest survival on gentle slopes reflects site stability and older, less fertile, and often poorly drained soils, whereas steep slopes promote landslide and windthrow rejuvenation of soils (Stewart & Harrison 1987). As several other studies have documented, stable sites with nutrient-poor soils are less prone to possum modification than nutrient-rich soils and vegetation (Batcheler 1983; Payton 1987; Stewart & Rose 1988). Because of the abundance and mix of animal-preferred species, the non-beech conifer-broadleaved forests south of the Pohangina River were highly susceptible to introduced herbivores. They are now post-dieback forests considerably modified by a long history of possums, deer, and goats and, in terms of composition and structure at a regional scale, represent one of the more extreme examples of animal modification in New Zealand.

In the beech-dominated forests north of the Pohangina River pahautea and Hall's totara were prominent in upper montane types J3 and J4 (J. Nicholls, unpubl. data), concentrated about the treeline of the main range and the northern Ngamoko Range. Of the 1856 ha of forest type J3, 40 % shows light to moderate collapse and 33 % severe collapse. Of the 376 ha of forest type J4, 12 % shows light to moderate collapse and 33% severe. Although the overall extent and intensity of canopy collapse is less than in G2 forests to the south (Fig. 7), the collapse of kamahi, pahautea, and Hall's totara elements has been disproportionately greater than the collapse of the beech component. In these J3 and J4 forests, stands in close proximity to non-beech vegetation, such as subalpine scrub, have also suffered disproportionately more collapse than areas further removed.

Throughout the rest of the Ruahine Range, pahautea and Hall's totara exist only as a minor element of mountain beech and red beech forests. Edaphically and climatically they are restricted to the more humid high-altitude beech-dominated stands on well drained soils or to small bogs and seepages without beech, where they show densities and size classes indicative of tree-fall gap regeneration. General observation suggests that these stands are healthier overall than in the western conifer forests.

5.7 STAND STRUCTURE AND REGENERATION

5.7.1 Hihitahi

Stem diameter and health class distributions for pahautea at Hihitahi suggest that stand structure is a mosaic of catastrophic disturbance-induced cohorts (Appendix 8A). The small number of stems in the two smallest size classes points to very limited disturbance in recent decades. A large 43% of basal area and 52% of stems for pahautea are dead-standing (Table 3), with a relatively even proportion of these in all size classes except the two smallest. Although pahautea is the dominant emergent tree in this forest, surprisingly there were no pahautea seedlings or saplings recorded in 8.01 ha of plots, a condition apparently fully representative of this 2500 ha old-growth forest (pers. obs.). Seedlings and saplings do occur, however, around the fire-disturbed margin of this forest.

Hall's totara differs from pahautea in displaying a size class distribution close to that typical of a semi-shade-tolerant gap-phase recruiter (Appendix 8B). Hall's totara is in worse condition than pahautea with an average 65% of stems and 64% basal area dead-standing (Table 3) in a relatively even proportion across the diameter classes (Appendix 8B). There are varying proportions of fallen stems by size class, with the smallest and largest classes not represented. Seedlings and saplings, although present, are not abundant (Table 4).

5.7.2 Ohutu Ridge old growth forest

There has also been very little pahautea regeneration in recent decades in the old-growth forest at Ohutu Ridge (Appendix 9A) but, in contrast to Hihitahi, it has a smaller dead-standing component. Although only 16% of stems are dead-standing (Table 3), this represents 35% of basal area and is concentrated in the larger size classes (Appendix 9A). Although basal area of live stems is comparable at Ohutu Ridge and Hihitahi (Appendix 8E, 9E), stem density is much greater at Ohutu Ridge, pointing to a higher frequency of recent disturbance-induced regeneration. In contrast to Hihitahi, frequent seedlings and small numbers of saplings are present (Table 4). Hall's totara is again in much worse condition than pahautea in all size classes (Appendix 9B) at Ohutu Ridge relative to Hihitahi, with no live stems in the largest diameter class and 65% of overall basal area dead (Table 3). Uncommon mountain toatoa has a high proportion of dead stems in the large size class, probably reflecting natural mortality (Appendix 9C).

5.7.3 Ohutu Ridge fire-regenerated forest

Only 16% of stems and 3% of basal area of pahautea is dead-standing in the fire-regenerated forest at Ohutu Ridge (Table 3, Appendix 10A), in an ostensibly similar environment to the adjacent old-growth forest. The density distribution of live stems suggests that the stand owes its origin to a single fire, and detailed investigation of stem ages date the fire at approximately 450 years ago (Rogers 1989). Natural thinning apparently accounts for most of the mortality because all dead-standing stems and the greater proportion of stumps occur in the smaller size classes. Live basal area of pahautea is double that in the adjacent old-growth forest and also double that at Hihitahi, with only small amounts dead-standing or as stumps (Appendix 10F, Table 3). There are also very few seedlings and saplings (Table 4) in the dark understorey of this dense stand. Shade-tolerant pink pine has a relatively even distribution of stems, with an interpreted gap or tree-fall scale regeneration regime (Appendix 10B). Mortality is concentrated in the smaller size classes. Remarkably, there are no dead-standing pink pine in the sample, suggesting that once dead they soon fall. Some thinning has occurred, mostly in the small size classes and its seedlings are common (Table 4). Only juvenile Hall's totara occur in this fire-regenerated stand (Appendix 10C).

5.7.4 Ruahine Corner

Pahautea at Ruahine Corner has a density distribution suggesting a combination of catastrophic and tree-fall gap regeneration (Appendix 11A). Dead-standing stems, fallen trunks, and stumps are relatively regularly distributed. Although dead-standing stems account for 25% of total stem density, they represent only 9% of standing basal area (Table 3) and evidence of possum-induced dieback is largely absent. Pink pine and mountain toatoa have similar density distributions, indicative of tree-fall gap regeneration (Appendix 11B, 11C). Pahautea, pink pine, and mountain toatoa all have similar density and basal area proportions in each health class (Table 3), suggesting similar stand turnover rates. There are also similar numbers of seedlings and saplings for all three species (Table 4). Although pink pine is present in moderate numbers (Appendix 11D), its total basal area, and that of mountain toatoa (Appendix 11E), show that this is very much a pahautea-dominant forest.

6. Conclusions

6.1 POSSUM POPULATION RECOVERY

Rapid population recovery was recorded in the second year after an aerial poison operation at Hihitahi, suggesting that enhanced recruitment in the residual population boosted population growth after control.

6.2 POSSUM DIET AND PREFERENCES

Possums feed on a small range of food types in a montane pahautea-Hall's totara forest at Hihitahi in comparison to montane podocarp-broadleaved forest at Waihaha. The small number of food types, and the possums' reliance for 80% of diet on just six food groups — wineberry, ground ferns, Hall's totara, ground herbs, pahautea, and bush lawyer — reflect the species depauperate state of this community and the foliar dominance of these few preferred species. Pahautea and Hall's totara are consumed mainly in summer, when buds and immature shoots are expanding. Pahautea and Hall's totara are confirmed as important dietary components. Whereas defoliation by possums appears to be

TABLE 3. MEAN PERCENT STEM DENSITY AND BASAL AREA IN HEALTH CLASSES FOR CONIFER SPECIES DERIVED FROM VARIABLE AREA PLOTS AT HIHITAHI, OHUTU RIDGE, AND RUAHINE CORNER. FIGURES FOR HEALTHY AND STANDING-DEAD ARE PERCENTAGES OF STANDING STEMS, WHILE THOSE FOR FALLEN ARE PERCENTAGES OF FALLEN AND STANDING STEMS COMBINED.

	PAHAUTEA		HALL'S TOTARA		PINK PINE		MOUNTAIN TOATOA		RIMU	
	STEM DENSITY	BASAL AREA	STEM DENSITY	BASAL AREA	STEM DENSITY	BASAL AREA	STEM DENSITY	BASAL AREA	STEM DENSITY	BASAL AREA
Hihitahi										
Healthy	49.09	56.61	34.77	35.9					78.62	55.73
Dead standing	51.91	43.39	65.23	64.1					21.38	44.32
Fallen	25.13	28.3	20.31	18.43					24.86	44.48
Ohutu old-growth										
Healthy	83.74	64.95	39.98	36.11			100	100		
Dead-standing	16.26	35.05	60.02	63.89						
Fallen	21.72	36.11	18.56	44.89			33.92	54.31		
Ohutu fire stand										
Healthy	83.93	97.23	62.3	41.55	100	100	69.37	78.81		
Dead-standing	16.07	2.77	37.7	58.45			30.63	21.19		
Fallen	48.66	17.19	27.38	45.07	29.75	29.43	38.97	25.22		
Ruahine Corner										
Healthy	74.51	90.81			77.66	80.03	72.67	83.96		
Dead-standing	25.49	9.19			22.34	19.97	27.33	16.04		
Fallen	39.0	27.74			38.13	39.88	31.54	38.58		

TABLE 4. MEAN DENSITIES PER ha OF SEEDLINGS AND SAPLINGS OF CONIFER SPECIES, AS RECORDED IN VARIABLE AREA PLOTS.

	PAHAUTEA		HALL'S TOTARA		PINK PINE		MOUNTAIN TOATOA	
	SEEDLING	SAPLING	SEEDLING	SAPLING	SEEDLING	SAPLING	SEEDLING	SAPLING
Hihitahi	-	-	42.83	21.6				
Ohutu – old growth	185.14	8.92	93.69	31.23				
Ohutu – fire-regenerated	19.97	2.85	84.14	85.57	45.64	12.84	346.55	98.4
Ruahine Corner	352.62	174.21			272.96	142.07	320.48	204.02

contributing to their demise, wineberry as another preferred species and structural dominant appears much less threatened.

A revised laboratory procedure for possum dietary analysis is offered to overcome the likely previous under-representation of pahautea in such studies, resulting principally from loss in the sieving process.

6.3 FOLIAR BROWSE INDEX

Despite its needle-leaves, Hall's totara can be reliably rated by all elements of the Foliar Browse Index. Its crown foliar density increased significantly over two years at three sites after possums had been poisoned. Evidence of dieback also declined in the larger size classes but increased in the smallest class. The amount of browse or hedging also significantly declined. Defoliation of Hall's totara is conspicuous from the ground, as removal of the light green terminal buds and shoots produces a hedged appearance in affected trees. This species demonstrates considerable resilience as defined by elasticity, a measure of the rate of recovery following disturbance, and low amplitude, the threshold of disturbance beyond which recovery to the original state does not occur. Mean foliar density improvements of 10–20% were recorded in two years and the species can recover from crown foliar densities as low as 5–15% with a release from browsing pressure. A longer monitoring interval than two years, and perhaps as much as four years, seems desirable to fully "performance" monitor the outcome of a single successful possum control operation on the condition of Hall's totara.

Overall, the scale-leaved foliage and tall conical profile of pahautea render it somewhat unsuitable for rating by the Foliar Browse Index. Recognition and full detection of possum defoliation of pahautea is difficult from the ground, removal of terminal buds or scale leaves manifesting as a browning and then a greying of subtended foliage. Whereas possums appear to hedge the entire foliar profile of Hall's totara, they damage pahautea in a branch-by-branch progression.

Results from several banded trees suggest that if pahautea is reduced to a crown foliar density less than 25% it continues to decline, even in the absence of further defoliation. This and other tentative results suggest that pahautea has low elasticity or rates of foliar recovery from defoliation, and higher amplitude than Hall's totara as a measure of the threshold of disturbance beyond which recovery to the original state does not occur.

6.4 REGIONAL PATTERNS OF FOREST HEALTH

Between 1959 and 1994 approximately 25% of the area of pahautea-Hall's totara-dominant forest in Egmont National Park disappeared. Severe levels of crown death affect a further 25% of surviving forests, and another 50% shows light to moderate crown death. However, within these broad-scale ratings considerable variation in crown health and stem density occurs. The eastern sector of Mt Egmont from North Egmont to Jackson's Lookout has more healthy trees than the rest of the park.

Approximately 75% of pahautea and Hall's totara in Hihitahi Forest Sanctuary has moderate and severe levels of dieback and collapse. North-eastern forests are less affected. Comparable old-growth forest at Ohutu Ridge is also in poor condition, and deterioration is progressing to higher altitudes. In sharp contrast, pahautea at Ruahine Corner is intact. There are no predictable geographical gradients in the health of pahautea-Hall's totara forest throughout the Mokai Patea, Hikurangi, and Whanahuia ranges. Stands are relatively intact in the fire-disturbed Mokai Patea and less fire-disturbed Hikurangi ranges, but only about 35% remains intact on the Whanahuia Range. In the southern Ruahine Range all the pahautea and Hall's totara-dominant forest has deteriorated to some degree, 80% of it's area with severe collapse. Where the two species co-occur with beech, between the Oroua and Pohangina rivers, 70% of the area of conifer forest has suffered some degree of collapse. Pahautea and Hall's totara have clearly deteriorated dramatically in both health and density across a wide geographical range, but not all of this can be attributed to the impacts of browsing animals.

6.5 STAND STRUCTURE AND HEALTH

Stand health of old-growth pahautea and Hall's totara at Hihitahi and Ohutu Ridge indicate that both species are in steep decline, with standing-dead stems in greater proportions than are to be expected from natural stand turnover. Despite at least 50 years of possum damage and compositional shifts in the lower canopy by deer, modification continues apace, particularly the progressive loss of emergent pahautea and Hall's totara, converting a tall conifer forest to a low broadleaved forest of wineberry and horopito. In contrast, at Ruahine Corner natural stand turnover can account for the proportions of dead-standing stems of pahautea, which are comparable to those for unpalatable pink pine and mountain toatoa. Differences in stand structure, the interpreted regeneration mode, stand composition, and altitude are correlated with vulnerability to dieback and collapse. Hihitahi, at mid montane elevations, appears to have a catastrophic or windthrow-induced regeneration regime, with no pahautea seedlings and saplings present in the old-growth component of this 2500 ha forest. Ruahine Corner, on the other hand, is upper montane and shows a combination of large-scale and tree-fall gap-sized disturbance promoting recruitment.

6.6 PATTERNS OF DIEBACK

Patterns of pahautea defoliation, dieback, and canopy collapse in the central North Island demonstrate some parallels with patterns of modification in southern rata-kamahi forest of the western South Island. North Island pahautea stands containing large numbers of possum-preferred species such as mountain fivefinger, kamahi, Hall's totara, wineberry, ferns, lacebark, and fuchsia in the canopy and subcanopy, and are more disposed to dieback than stands dominated by unpalatable species such as bush tussock, small-leaved coprosmas, pink pine, and mountain toatoa. Stand age and perceived site fertility are also major influences on dieback severity, with dieback less pronounced in young, even-aged stands and those on more stable and relatively infertile sites. In summary, a combination of persistent wetness and cold temperatures, community composition, and site infertility have buffered the most eastern and high-altitude stands in the Ruahine Range against possum damage.

6.7 EFFICACY OF ANIMAL CONTROL

Assuming that the least fragmented remnants of pahautea-Hall's totara forests have intrinsic values worthy of protection, one of the components of priority setting for pest control would be the question of their resilience or restoration potential (Holloway 1993). Mature stands of these forests partly opened up by possum browse are not buffered against further deterioration caused by wind, fungi, and insects (Payton 1988). Wind causes mechanical damage and desiccation of forest understoreys, and fungi and insects are secondary pathogens of trees in a debilitated state. An inspection of areas of existing partly collapsed forest south of the Pohangina River confirmed continuing deterioration irrespective of present levels of apparent possum defoliation. Estimation of critical possum population thresholds above which control is necessary are based on the assumption that the forest ecosystem as a whole will retain its integrity (Peterson *et al.* 1994). However, this condition is clearly not met in some pahautea-Hall's totara forests. Resilience thresholds and directions and rates of recovery following animal control have yet to be investigated in such forests, and will vary in terms of forest type, condition, and environmental gradients. Just as possum population thresholds and damage thresholds will influence future animal control programmes, resilience thresholds should also feature in the efficacy and benefit analysis of animal control.

7. Recommendations

The scarcely perceptible decline of pahautea in its remote and high-altitude locations has resulted in less recognition of its plight than has been accorded the more conspicuously palatable species — rata, kamahi, totara, and pohutukawa (*Metrosideros excelsa*) — in New Zealand forests. Remaining stands in the three study sites are conservation priorities, but rationalisation of possum control and optimal intervention require further knowledge:

- Detailed stand-level analysis, in order to corroborate the conclusions from aerial photographs and to predict rates and directions of change in deteriorating and improving pahautea-Hall's totara forests.
- Resilience thresholds and directions and rates of recovery following animal control, particularly in terms of forest type, condition, and environmental gradients. Resilience thresholds should feature in the efficacy and benefit analysis of animal control.
- Remote sensing techniques to help assess crown health of forests with measures of defoliation and successional changes resulting from animal modification.

Performance monitoring of possum control programmes in upland conifer forest in Egmont National Park, at Hihitahi, and the northwest Ruahine Range should include Hall's totara. Finally, the implications of this study extend beyond central North Island when causal mechanisms for illthrift are considered. Possum defoliation, secondary factors associated with stand fragmentation, and natural stand turnover all require evaluation, singly or in concert. Stands on Banks Peninsula and above Dunedin city are conspicuous candidates for such evaluation.

8. Acknowledgements

Several people made substantial contributions to this study. I warmly thank Bill Fleury of DoC Wanganui for lengthy discussions on the topic and for access to archival material, John Leathwick and Patrick Whaley of Landcare Research Hamilton for considerable computational and mapping help, respectively, and Philip Suisted of Landcare Research Lincoln for the exacting task of possum diet analysis. John Barkla provided aluminium plate for sheathing tree trunks. The respective owners of Matai, Motukawa, and Mangaohane stations and the Awarua/Aorangi Block kindly permitted access and provided accommodation. Bruce Clarkson, Ian Payton, Colin Ogle, and Geoff Walls kindly reviewed drafts of this report.

9. References

Allan, H.H. 1961. Flora of New Zealand. Vol. 1. Wellington, Collins.

Allen, R.B. 1992. RECCE — an inventory method for describing New Zealand vegetation. *Forest Research Institute bulletin no. 176.* Forest Research Institute, Christchurch.

Batcheler, C.L. 1983. The possum and rata-kamahi dieback in New Zealand: a review. *Pacific science* 37, 415-426.

Beever, J. 1987. A dictionary of Maori plant names. *Auckland Botanical Society Bulletin no. 16.*

Clarkson, B.D. 1986. Vegetation of Egmont National Park, New Zealand. Wellington, DSIR Science Information Publishing Centre.

Eagle, A. 1982. Eagle's trees and shrubs of New Zealand. 2nd ed. Auckland, Collins.

Holloway, J.S. 1993. Conservation pests: how can national values and objectives be quantified. *New Zealand journal of ecology* 20, 285-293.

New Zealand Forest Service 1970. Forest Service Mapping Series 6: Sheet No. 13, Ruahine Forest Class Map. Wellington, New Zealand Forest Service.

New Zealand Forest Service 1982. Totara dieback. *What's new in forest research, no. 110.*

Nugent, G. 1983. Deer diet estimation by rumen or faecal analysis: an evaluation of available techniques. *Forest Research Institute bulletin no. 24.* Forest Research Institute, Christchurch.

Nugent, G. 1990. Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains, Otago. *New Zealand journal of ecology 13*, 83-95.

Nugent, G., Fraser, K.W., Sweetapple, P.J. 1997. Comparison of red deer and possum diets and impacts in podocarp-hardwood forest, Waihaha catchment, Pureora Conservation Park. Department of Conservation *Science for Conservation 50.*

Owen, H.J., Norton, D.A. 1995. The diet of introduced possums *Trichosurus vulpecula* in a low-diversity New Zealand *Nothofagus* forest and possible implications for conservation management. *Biological conservation* 71, 339-345.

Payton, I.J. 1987: Canopy dieback in the rata (*Metrosideros umbellata*)-kamahi (*Weinmannia racemosa*) forests of Westland, New Zealand. In: Human impacts and management of mountain forests. Proceedings of the 4th International Union of Forest Research

Organisations workshop P1.07-00, 1987, eds. Fugimori, T., Kimura, M. Forestry and Forest Products Research Institute, Ibaraki, Japan, pp. 123–136.

Payton, I.J. 1988: Canopy closure, a factor in rata (*Metrosideros*)-kamahi (*Weinmannia*) forest dieback in Westland, New Zealand. *New Zealand journal of ecology* 11, 39–50.

Peterson, D.R., Blaschke, P., Gibbs, D., Gordon; B., Hughes, P. 1994. Possum management in New Zealand. Office of the Parliamentary Commissioner for the Environment, Wellington.

Rogers, G.M. 1989. Beech and conifer forest interactions in Moawhango Ecological Region, North Island, New Zealand. *New Zealand journal of ecology* 12, 47–61.

Rogers, G.M., Leathwick, J.R. 1997. Factors predisposing forests to collapse in the southern Ruahine Range, New Zealand. *Biological conservation*. 80, 325–338.

Rose, A.B., Pekelharing, C.J., Platt, K.H. 1992. Magnitude of canopy dieback and implications for conservation of southern rata-kamahi (*Metrosideros umbellata-Weinmannia racemosa*) forests, central Westland, New Zealand. *New Zealand journal of ecology* 16, 23–32.

Spurr, E.B., Warburton, B. 1991. Methods of measuring the proportions of plant species present in forest and their effect on estimates of bird preferences for plant species. *New Zealand journal of ecology* 15, 171–175.

Stewart, G.H., Harrison, J.B.J. 1987. Plant communities, landforms, and soils of a geomorphically active drainage basin, Southern Alps, New Zealand. *New Zealand journal of botany* 12, 47–61.

Stewart, G.H., Rose, A.B. 1988. Factors predisposing rata-kamahi (*Metrosideros umbellata-Weinmannnia racemosa*) forests to canopy dieback, Westland, New Zealand. *Geojournal* 17, 217–223.

Thomas, M.D. 1993. Changes in possum abundance in Waipoua Forest Sanctuary after 1080 poisoning. Unpublished Landcare Research contract report LC9394/15.

Westman, W.E., O'Leary, J.F. 1986. Measures of resilience: the response of coastal sage scrub to fire. *Vegetatio* 65, 179–189.

Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge.

APPENDIX 1

Method for analysis of possum diet at Hihitahi

Assessing the proportion of pahautea

- weigh gut with contents (a)
- remove and weigh gut (b)
- isolate pahautea and weigh (c)
- mix the remaining gut constituents ("other") in a dish. Remove a subsample, and weigh (d)
- dry pahautea sample and weigh (e)
- dry "other" subsample and weigh (f)
- retain remaining "other" sample for 100-point analysis

Weights/equations

$(a)-(b)$ = (A) total food content; wet weight
(c) = pahautea content; wet weight
$(A)-(c)$ = (B) other food content; wet weight
$((f)\div(d))\times(B)$ = (C) other food content; dry weight
$((e)\div((e)+(C)))\times100$ = (D) percentage of pahautea in gut

Establishing "other" gut constituents

- sieve remaining "other" sample using 2 mm seive
- float in shallow tray containing 100 regularly spaced dots
- select and remove the fragment closest to each dot
- identify and group the 100 fragments
- dry, then weigh grouped fragments (gi, gii, giii, giv...)
- calculate proportions of each species, i.e., (gi)÷(gi + gii...) etc.
- use proportions to calculate total proportions of "other" species in gut. N.B., Remember to adjust by $((C)\div((C)+(e)))\times100$, given that the above are proportions of "other" food constituents only.

APPENDIX 2

Mean percent dry weight of food types in possum diets by season at Hihitahi Forest Sanctuary in 1993–95, n=140.

FOLIAGE	SUMMER	AUTUMN	WINTER	ANNUAL
Total woody species	**63.82**	**76**	**69.9**	**66.36**
Total conifers	**31.1**	**7.36**	**12.67**	**17.04**
Total broadleaved trees	**1.02**	**9.3**	**4.13**	**4.82**
Total lianes	**5.01**	**0.02**	**19.27**	**8.1**
Total shrubs	**18.45**	**57.5**	**23.27**	**33.07**
Libocedrus bidwillii	9.88	5.25	1.39	7.81
Podocarpus hallii	21.23	2.1	11.28	17.16
Aristotelia serrata	16.61	54.86	17.13	21.32
Rubus cissoides	4.54	0.03	15.68	5.97
Fuchsia excorticata	0.32	9.3	-	1.34
Coprosma species	0.73	2.41	2.96	1.33
Herbaceous species	8.64	1.81	13.52	8.68
Muehlenbeckia australis	0.41	-	2.97	0.81
Carpodetus serratus	0.05	-	-	0.03
Clematis foetida	-	-	0.62	0.11
Hoheria populnea	0.24	-	4.13	0.9
Griselinia littoralis	0.41	-	-	0.29
Leucopogon fasiculata	0.65	-	-	0.46
Parsonsia heterophylla	0.06	-	-	0.04
Neomyrtus pedunculata	0.01	-	-	0.01
Myrsine divaricata	0.04	0.24	0.22	0.1
Moss species	0.23	0.1	0.14	0.2
Fern species	**20.13**	**9.83**	**25.25**	**19.8**
Fungus species	1.36	1.59	0.59	1.25
Bark and wood	0.84	0.36	0.06	0.64
Insects	**2.22**	-	**1.6**	**1.85**
Fruits	**11.21**	**12.11**	**2.47**	**9.78**
Coprosma species	0.37	5.89	0.78	1.11
Pittosporum eugenioides	0.09	1.85	-	0.29
Pseudowintera colorata	2.46	3.2	0.09	2.13
Carpodetus serratus	8.03	0.86	1.6	6.03
Unknown	0.26	0.31	-	0.22
Flowers	**0.19**	-	-	**0.14**
Myrsine divaricata	0.08	-	-	0.06
Coprosma species	0.11	-	-	0.08

APPENDIX 3

Mean percent dry weight of food types in possum diets over five sampling periods at Hihitahi Forest Sanctuary in 1993–95, n=140.

FOLIAGE	4/93	12/93	2/94	5/94	1/95
Total conifers	**7.36**	**45.23**	**23.48**	**12.67**	**23.94**
Total broadleaved trees	**9.3**	**0.06**	**2.36**	**4.13**	**0.76**
Total lianes	**0.03**	**1.32**	**9.22**	**19.27**	**4.86**
Total shrubs	**57.51**	**11.36**	**25.57**	**23.27**	**19.06**
Libocedrus bidwillii	5.25	21.85	1.97	1.39	5.11
Podocarpus hallii	2.1	23.38	21.51	11.28	18.84
Rubus cissoides	0.03	1.21	8.78	15.68	4.02
Fuchsia excorticata	9.3	-	0.33	-	0.62
Coprosma species	2.41	0.23	0.64	2.96	1.33
Herbaceous species	1.81	5.34	14.8	13.52	6.31
Muehlenbeckia australis	-	0.11	0.25	2.97	0.84
Carpodetus serratus	-	-	-	-	0.14
Clematis foetida	-	-	-	0.62	-
Hoheria populnea	-	-	0.77	4.13	-
Griselinia littoralis	-	0.06	1.25	-	-
Leucopogon fasiculatus	-	1.89	-	-	-
Parsonsia heterophylla	-	-	0.19	-	-
Neomyrtus pedunculata	-	0.02	-	-	-
Myrsine divaricata	0.24	0.09	-	0.22	0.03
Aristotelia serrata	54.86	9.01	24.68	17.13	16.86
Moss species	0.1	0.31	-	0.14	0.37
Fern species	9.84	2.88	15.1	25.25	41.97
Fungus species	1.59	2.53	0.9	0.59	0.6
Bark and wood	0.36	0.61	0.81	0.06	1.09
Insects	-	0.57	5.59	1.6	0.8
Fruits					
Coprosma species	5.89	0.9	0.18	0.78	-
Pittosporum eugenioides	1.85	0.26	-	-	-
Pseudowintera colorata	3.2	6.1	1.16	0.09	-
Carpodetus serratus	0.86	22.4	1.07	1.6	-
Unknown	0.31	-	-	-	0.75
Flowers					
Myrsine divaricata	-	0.25	-	-	-
Coprosma species	-	0.33	-	-	-

APPENDIX 4

Mean percent dry weight of food types in possum diets along a radial transect from forest margin to forest interior at Hihitahi Forest Sanctuary in 1993–95, n=140.

FOLIAGE	MARGIN	MIDDLE	INTERIOR
Total conifers	**23.81**	**24.95**	**27.01**
Total broadleaved trees	**3.09**	**0.17**	**4.55**
Total lianes	**8.4**	**4.02**	**7.96**
Total shrubs	**22.68**	**24.43**	**25.82**
Libocedrus bidwillii	9.4	5.05	8.39
Podocarpus hallii	14.41	19.90	18.63
Rubus cissoides	7.51	2.76	7.17
Fuchsia excorticata	2.36	0.16	1.01
Coprosma species	1.87	0.60	1.29
Herbaceous species	8.39	7.30	10.83
Muehlenbeckia australis	0.82	0.82	0.79
Carpodetus serratus	0.08	-	-
Clematis foetida	-	0.36	-
Hoheria populnea	-	-	3.53
Griselinia littoralis	0.65	0.01	-
Leucopogon fasiculatus	0.00	1.49	-
Parsonsia heterophylla	0.04	0.08	-
Neomyrtus pedunculata	0.01	-	-
Myrsine divaricata	0.09	0.11	0.10
Aristotelia serrata	19.90	21.41	23.64
Moss species	0.26	0.08	0.24
Fern species	21.22	18.41	19.00
Fungus species	1.63	1.72	0.04
Bark and wood	0.76	0.47	0.63
Insects	1.99	1.21	2.35
Fruits			
Coprosma species	0.62	2.36	0.44
Pittosporum eugenioides	0.15	0.51	0.25
Pseudowintera colorata	0.83	4.89	1.05
Carpodetus serratus	6.34	10.10	0.61
Unknown	0.49	-	-
Flowers			
Myrsine divaricata	-	0.19	-
Coprosma species	0.18	-	-

APPENDIX 5

Seasonal preference index (pi) scores for food types sampled in the vegetation survey at Hihitahi Forest Sanctuary in 1995. (pi>0 = preferred, pi<0 = less or not preferred).

FOOD TYPE	SUMMER	AUTUMN	WINTER	TOTAL
Libocedrus bidwillii	-0.001	-0.31	-0.76	-0.12
Podocarpus hallii	0.46	-0.57	0.19	0.38
Rubus cissoides	0.63	-0.95	0.88	0.71
Fuchsia excorticata	0.17	0.95	0.99	0.71
Coprosma species	0.79	0.93	0.94	0.87
Herbaceous species	0.19	-0.53	0.39	0.19
Muehlenbeckia australis	0.91	0.99	0.98	0.96
Carpodetus serratus	-0.98	-1.0	-1.0	-0.99
Clematis foetida	-1.0	-1.0	0.25	-0.54
Hoheria populnea	-0.71	-1.0	0.49	-0.23
Griselinia littoralis	-0.75	-1.0	-1.0	-0.82
Leucopogon fasiculata	0.71	-1.0	-1.0	0.61
Parsonsia heterophylla	0.09	-1.0	-1.0	-0.01
Myrsine divaricata	-0.73	-0.06	-0.01	-0.47
Aristotelia serrata	-0.43	0.14	-0.47	-0.32
Moss species	-0.36	-0.67	-0.57	-0.43
Fern species	0.85	0.71	0.88	0.85
Fungus species	0.99	0.99	0.99	0.99

APPENDIX 6

Preference index (pi) scores for food types along a radial transect from forest margin to forest interior at Hihitahi Forest Sanctuary in 1995. (pi>0 = preferred, pi<0 = less or not preferred).

FOOD TYPE	MARGIN	MIDDLE	INTERIOR	TOTAL
Libocedrus bidwillii	-0.03	-0.32	-0.08	-0.12
Podocarpus hallii	0.3	0.44	0.41	0.38
Rubus cissoides	0.76	0.46	0.75	0.71
Fuchsia excorticata	0.82	-0.18	0.63	0.71
Coprosma species	0.9	0.73	0.86	0.87
Herbaceous species	0.18	0.11	0.3	0.19
Muehlenbeckia australis	0.95	0.95	0.97	0.96
Carpodetus serratus	-0.97	-1.0	-1.0	-0.99
Clematis foetida	-1.0	-0.01	-1.0	-0.54
Hoberia populnea	-1.0	-1.0	0.42	-0.23
Griselinia littoralis	-0.63	-0.99	-1.0	-0.82
Leucopogon fasiculata	-1.0	0.86	-1.0	0.61
Parsonsia heterophylla	-0.12	0.24	-1.0	-0.01
Myrsine divaricata	-0.52	-0.42	-0.45	-0.47
Aristotelia serrata	-0.35	-0.32	-0.27	-0.32
Moss species	-0.32	-0.71	-0.35	-0.43
Fern species	0.86	0.84	0.84	0.85
Fungus species	0.99	1.0	0.83	0.99

APPENDIX 7

Summary statistics from the foliar browse index, as applied to pahautea and Hall's totara in Egmont National Park, Hihitahi, and Ohutu Ridge. Refer to text for explanation. P = pahautea; H = Hall's totara.

		CROWN FOLIAR DENSITY (%)		INCIDENCE OF DIEBACK (%)		DEGREE OF DIEBACK		BROWSE OR HEDGING		TRUNK USE	
		1994	1996	1994	1996	1994	1996	1994	1996	1994	1996
Species	Pahautea	63.81	65.47	88.08	89.12	2.22	2.04	2.05	0.61	1.63	0.44
	Hall's totara	55.07	64.38	80.14	80.82	2.47	1.89	2.53	0.48	1.88	0.45
Stem size class (d1m) (cm)	P, 0-30	53.0	57.5	80.0	80.0	2.44	2.25	2.25	0.55	1.6	0.5
	H, 0-30	45.52	54.48	79.3	84.5	2.52	1.96	2.55	0.45	2.16	0.36
	P, 31-70	56.51	60.21	90.4	91.8	2.35	2.16	2.15	0.55	1.62	0.38
	H, 31-70	59.93	70.67	76.1	67.53	2.39	1.77	2.58	0.51	1.82	0.55
	P, >70	75.0	75.0	88.0	89.0	2.1	0.67	1.94	0.67	1.64	0.46
	H,>70	65.95	71.67	95.23	81.0	2.55	2.06	2.33	0.48	1.29	0.33
Site											
Ohutu Ridge	Pahautea	69.88	69.38	82.93	85.36	2.29	2.34	2.07	0.78	2.1	0.46
	Hall's totara	48.85	46.54	84.61	92.3	2.27	2.0	3.08	1.39	2.31	0.62
Hihitahi east	Pahautea	72.06	70.88	88.24	88.24	2.33	2.03	1.94	0.41	1.59	0.21
	Hall's totara	52.69	75.0	84.62	76.92	2.91	1.89	2.62	0.15	1.69	0.15
Hihitahi west	Pahautea	70.26	69.04	87.72	89.47	1.98	1.86	1.9	0.81	1.46	0.6
	Hall's totara	61.0	67.89	80.0	77.77	2.69	1.91	2.44	0.56	1.62	0.53
Mangorei, Pouakai Range	Pahautea	-	-	-	-	-	-	-	-	-	-
	Hall's totara	53.54	65.73	80.49	80.49	2.12	1.85	2.2	0.34	1.95	0.49
North Egmont	Pahautea	49.1	56.48	91.8	91.8	2.34	2.0	2.25	0.43	1.49	0.39
	Hall's totara	52.35	60.88	76.47	82.35	2.5	1.86	2.82	0.32	2.03	0.32
Treatment											
Poisoning	Pahautea	60.93	63.43	88.57	90.0	2.21	1.96	2.04	0.61	1.47	0.46
	Hall's totara	56.09	65.94	79.69	79.69	2.46	1.86	2.48	0.41	1.83	0.45
Banding	Pahautea	69.48	75.34	86.2	86.2	2.36	2.28	2.14	0.31	2.12	0.1
	Hall's totara	51.67	60.0	100.0	100.0	2.17	1.5	2.26	0.33	2.33	0.4
Control	Pahautea	73.75	65.42	87.5	87.5	2.14	2.19	2.04	0.96	1.83	1.67
	Hall's totara	45.83	45.0	75.0	80.0	2.78	2.4	3.08	2.33	2.17	2.67

APPENDIX 8

Mean stem densities by stem size and health classes for individual conifer species as derived from 37 variable area plots in an old-growth conifer stand at Hihitahi Forest Sanctuary. Mean total stem density and basal area by health class for each conifer species are also shown.

APPENDIX 9

Mean stem densities by stem size and health classes for individual conifer species as derived from 15 variable area plots in an old-growth conifer stand at Ohutu Ridge, northwest Ruahine Range. Mean total stem densty and basal area by health class for each conifer species are also shown.

APPENDIX 10

Mean stem densities by stem size and health classes for individual conifer species as derived from 18 variable area plots in a fire-regenerated conifer stand at Ohutu Ridge, northwest Ruahine Range. Mean total stem density and basal area by health class for each conifer species are also shown.

APPENDIX 11

Mean stem densities by stem size and health classes for individual conifer species as derived from 49 variable area plots in an old-growth conifer stand at Ruahine Corner, northwest Ruahine Range. Mean total stem density and basal area by health class for each conifer species are also shown.

APPENDIX 12

Description of forest types in the southern Ruahine Range referred to in the text (for full list and derivation see Rogers & Leathwick, 1997).

Code	Forest type
G1	*Podocarpus hallii-Weinmannia racemosa-Griselinia littoralis*
G2	*Podocarpus hallii-Libocedrus bidwillii-Weinmannia racemosa Griselinia littoralis*
G6	*Griselinia littoralis-Carpodetus serratus-Fuchsia excorticata*
J3	*Nothofagus fusca-Libocedrus bidwillii*
J4	*Libocedrus bidwillii-Podocarpus hallii-Nothofagus fusca-Nothofagus solandri*