

6. Discussion

6.1 TRENDS IN MAJOR CANOPY SPECIES

There were some changes in forest species composition that were common to several of the five study areas. Shorter trees, especially horopito, and, to a lesser extent tawheowheo, became more common over time in the study areas. In contrast, taller trees either remained unchanged throughout census periods (kamahi and southern rata) or decreased (Hall's totara). Our study presents clear evidence of high mortality, in three central Westland study areas, of Hall's totara, which is known to be browsed by possums (Coleman et al. 1985). In all of these study areas, there was a marked decline in its basal area, stem density, and biomass (Appendix 1, Tables A1.4, A1.5, and A1.7), especially of larger trees (>35 cm, Figs. 10 and 11). Widespread death of Hall's totara has been observed in other studies in Westland (Wardle et al. 1983), including the Taramakau River valley (Rose et al. 1988, Pekelharing and Batcheler 1990, Smale et al. 1993). Long-term census data from the Copland River valley (including the plots in Architect Creek used in our study) provided firm evidence of high mortality of Hall's totara in two of three sites (Stewart 1992), and those two sites were the ones which had the longest history of possum presence (Pekelharing and Reynolds 1983). Our study shows mortality of large Hall's totara to be a general phenomenon of central Westland montane rainforests, and possums are present in all the Westland study areas we examined. Regeneration of Hall's totara in the three central Westland sites does occur but at a low rate, which may be insufficient to offset losses of canopy trees (Appendix 2, Tables A2.2, A2.3, and A2.5).

Further measurements of permanent forest plots in a variety of other forests of which Hall's totara is a component (e.g. upland beech-conifer forests) would determine how general is the decline that we have shown in this study. In lowland warm temperate rainforests in the Waitakere Ranges, Hall's totara was severely browsed by possums and showed the highest mortality among tree species during a recent 2-year census (5.6% per annum, Ogden and Carlaw 1997). In a recent aerial survey of upland beech-conifer forests of eastern Mount Aspiring National Park, Hall's totara canopies were found to be in poor condition, although mortality was low (Smale et al. 1996).

Southern rata is susceptible to widespread canopy mortality in montane rainforests in central Westland (e.g., Stewart and Rose 1988, Rose et al. 1992). It is known to be susceptible to sustained browsing by possums (e.g. Fitzgerald & Wardle 1979, Leutert 1988), and this is intimately connected with age structure, i.e. stands of larger-sized, and presumably older, trees are most vulnerable (Payton 1983). Possum browse probably combines with the effects of wind, fungi, and insects to increase the likelihood of death (Payton 1988), and may thus merely aggravate, or possibly accelerate, a natural population process for southern rata.

Southern rata declined in biomass in only one of our three central Westland sites (Copland), but its apparent decline there may reflect the sampling pattern,

Figure 14. Spars of Southern rata that died between 1979 and 1995, and characteristic patterns of widespread mortality of that species in the valley beyond. Blue Duck Creek, upper Kokatahi Valley, Hokitika River, Westland, February 1995.



as plots were located in forests where a decline in canopy condition of southern rata was anticipated. Perhaps surprisingly, in Taramakau, where plots were located in the same manner as in Copland, data from censuses of trees showed very little change in southern rata. In Kokatahi, southern rata was a major component of forests that had undergone dieback (Chavasse 1955, Allen and Rose 1983), and this dieback of southern rata continued during the census period in some higher altitude areas (e.g. in one plot all southern rata stems died between 1979 and 1995, Fig. 14), but biomass of southern rata increased in some lower altitude plots (Fig. 4). At least at higher altitudes in Kokatahi, the long-term prospects for southern rata are probably poor. In the central Westland catchments, seedlings and saplings of southern rata were rare. Therefore, while the decline of adults is gradual in Copland, and patchy in Kokatahi, an insidious decline (over several decades) of southern rata may be occurring involving the gradual death of adults, especially of larger trees, that is unmatched by commensurate recruitment of juveniles.

Kamaha is known to be susceptible to wide-spread mortality when it is a dominant canopy species. This has occurred in the southern Ruahine Ranges, including the Pohangina River valley (Elder 1965, Cunningham 1979), and the Kokatahi River valley (Chavasse 1955, Allen and Rose 1983). As in the case of Hall's totara and southern rata, widespread mortality of kamaha has been attributed to possums (e.g., McKelvey 1995), although moisture stress brought about by combined fungal and insect debilitation may also contribute (Payton 1989). Kamaha was common in the three central Westland sites in our study,

and unlike southern rata or Hall's totara, showed no substantial decline in tree populations at any of these sites.

Kamaha is not a current component in the Pohangina plots where it formerly constituted the canopy (Fig. 2). The process of widespread mortality of kamaha where it is a dominant canopy species was still occurring in Cattle Creek in early 1996 (Fig. 3). Sites such as this could be useful in evaluating the etiology of canopy mortality in kamaha; it is unlikely that possums have invaded this area recently. In *Nothofagus*-dominant forests of Cattle Creek, we found no evidence of decline of kamaha over 21 years (1975-1996); moreover our study plots were in forest close to where there either had been or was presently widespread death of canopy species, including kamaha. Longer-term monitoring of the Cattle Creek site would allow a critical evaluation of the hypothesis advanced by Rogers and Leathwick (1997) that *Nothofagus*-dominant forests of the southern Ruahine range are likely to experience widespread mortality of canopy species because of their proximity to forests either currently or formerly dominated by kamaha.

6.2 MORTALITY OF CANOPY TREES AND PATCH DYNAMICS

The type of forest change that occurs as a result of widespread mortality of canopy trees requires an appropriate scale for observation in time and space (Peet 1992). Dieback of forests is not an event that takes place over a narrow window of time. In Kokatahi, mortality of canopy trees has now been taking place for at least 45 years, and probably longer (cf. Chavasse 1955 and this study). This is probably a significant portion of the normal lifespan of many trees that comprise these communities (e.g. mahoe, horopito, tawheowheo). Neither has mortality occurred at a whole catchment level; rather it has progressed in patches, especially in the upper Kokatahi River valley, and particularly at higher altitude (Fig. 14). At a landscape level, it is appropriate to consider the 'dieback' of tall forest communities and their replacement by short forests, as has occurred in Pohangina and Kokatahi, in terms of patch dynamics (*sensu* Levin and Paine 1974). Investigations of dieback of *Metrosideros polymorpha* forests in Hawai'i at a broad spatial and temporal scale (Akashi and Mueller-Dombois 1995) have refuted single explanations for the phenomenon, which had projected a complete demise of these forests. To better understand the influence of possums on forest dynamics, future studies of forest structure and ecosystem function should examine patches of different size over time, in terms of biotic influences (e.g. possum populations, tree population size structures) and abiotic influences (e.g. events such as mass movement) that may influence vegetation dynamics. These investigations should include examination of catchment-level dynamics of declining species, such as Hall's totara.

In future assessments, the temporal and spatial scale of mortality of canopy trees and their probable life histories must be considered. Records from permanent plots, such as used in this study, are required to yield accurate mortality rates and allow comparisons among species. However, the magnitude of dieback is often assessed at a single point in time (e.g. Rose et al. 1992). For example, in a site in northern Westland, 12% of stems of southern rata and 20%

of stems of Hall's totara were dead in the forest types in which they were most common (Coleman et al. 1980). In two major forest types in Westland, as many as 44% of plots contained dead southern rata and/or dead Hall's totara stems (Reif and Allen 1988). However, these apparently high mortality levels cannot be related readily to mortality rates because standing stems of these species decay very slowly; upright specimens of dead southern rata may persist in montane rainforests for decades (Coleman et al. 1980, Allen and Rose 1983, Reif and Allen 1988), while in drier climates of montane eastern South Island dead stems of Hall's totara may persist for centuries (Wardle 1991). Consequently, assessment of mortality in forests based on single assessments may overestimate mortality of species like southern rata that remain dead *in situ* for long periods, and underestimate mortality of species such as kamahi that decay rapidly.

6.3 DEVELOPMENT AND DYNAMICS OF COMMUNITIES SINCE DIEBACK

All plots in Pohangina and three plots in Kokatahi were established in areas where the former canopy had died at least 10 years before. In Pohangina, these communities are now dominated by tree ferns, with a significant contribution from short trees such as mahoe and horopito. In the three Kokatahi plots, horopito, papaumu, and tawheowheo dominated areas where former canopy species have died (e.g. Allen and Rose 1983).

There was little substantial change in the composition of post-dieback communities in both Pohangina and Kokatahi during long census periods (more than 20 years), although papaumu became extinct in plots in Pohangina (Fig. 13 and Appendix 1, Table A1.1). In Kokatahi, although there was no change over 23 years in relative basal area or stem density of the most abundant species (horopito>papaumu>tawheowheo), total basal area in these three plots more than doubled during the census period (14.5 m²/ha in 1972 cf. 31.6 m²/ha in 1995) and stem density increased nearly fourfold (2091 stems/ha in 1972 cf. 9125 stems/ha in 1995). These communities are undergoing substantial change in size class distribution, with constant recruitment. For the three most abundant species, much of the recruitment is vegetative, by root and shoot sprouts in the case of horopito and tawheowheo, and by basal sprouts in the case of papaumu. In 1995, total basal area in these communities was still substantially less than the mean over the whole catchment, while total stem density was substantially greater. Over time we may expect thinning of these stands, with increasing biomass accumulated among survivors. Future evaluation of these plots is needed, and a greater number of permanent plots are required to assess dynamics in these communities.

There was no evidence that forest communities of the five study areas were becoming more similar to each other over time. Even where substantial 'dieback' of canopy species took place during the census period, and plots changed in classification (Fig. 13), there was usually an element of the flora retained that conferred a local distinctiveness to these new communities, e.g. tawheowheo was unique to Taramakau and Kokatahi.

6.4 ROLE OF TREE FERNS

Tree ferns are often a significant contributor to total stand composition and biomass in lowland and lower montane rainforests in New Zealand, but their contribution is frequently overlooked. We have data on tree ferns from Pohangina, Orongorongo, and Kokatahi. Tree ferns were an especially important component of forests in Pohangina, where they were the major contributor to total basal area, stem density, and biomass; *Cyathea smithii* alone contributed more than all woody gymnosperms and angiosperms combined (Appendix 1, Table A1.1). Their contribution to stem density in Orongorongo was also substantial (Appendix 1, Table A1.3), and in this site four common tree ferns increased in basal area, stem density, and biomass over 25 years. Tree fern populations may be similarly dynamic at other sites where they are common (e.g. Pohangina and Kokatahi), but we lack data on changes in their populations over time. Changes in populations of tree ferns over time may also have implications for the relative abundance of trees that regenerate frequently on tree fern trunks. In forests in which tree ferns contribute significantly to forest composition, far more attention needs to be paid to their total contribution, long-term dynamics and life history, including establishment, height growth rates, recruitment, and mortality.

6.5 CHANGES IN BIOMASS

In areas where dieback of forest canopies has occurred, an expected consequence is appreciable loss of biomass (e.g. Hall and Hollinger 1997), and consequent loss of stored carbon (the mass of which is usually estimated as half the stem biomass, Waring and Schlesinger 1985). However, in only one area, Copland, was there a substantial decrease in biomass (Table 3). In Kokatahi, where widespread mortality of canopy trees occurred during the census period in some plots, it is perhaps surprising that on average there was only a small decline in biomass (Table 3). We may expect that changes in live biomass in communities where dieback occurs may proceed so that an initial large decline later stabilises about a mean as dense regeneration occurs in post-dieback communities (Fig. 15). An indication of what catchment-level biomass in Kokatahi may have been before the start of widespread mortality of canopy trees can be gained from a comparison with the nearby Whitcombe River valley. Total biomass in Kokatahi was 35% lower than the Whitcombe River valley at the start of the census period. This may reflect a real overall loss that occurred before the establishment of plots; at least one-third of the plots in Kokatahi were established in areas in which dieback had already taken place and none of the former canopy trees remained alive. We might expect that the same process occurred in Pohangina, where live stem biomass is now very low compared with other sites (Table 3). Thus even though the census periods of growth data for our study areas are long, changes in biomass may occur at a catchment level over even longer time intervals, and the degree of biomass change detected will reflect the period at which catchment-level dieback is sampled (Fig. 15).

Although live biomass may have declined in Kokatahi before our census period, we have shown that even by very conservative estimates, a substantial

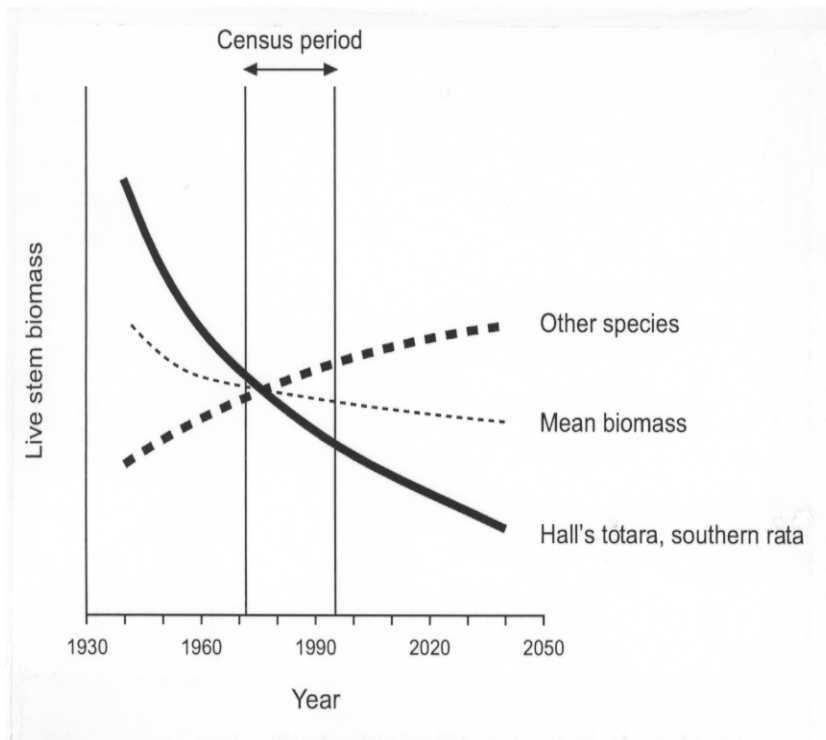


Figure 15. Schematic diagram of possible changes in live stem biomass at a catchment level in Kokatahi. The census period for permanent plots in the catchment is shown.

contribution to total woody mass in Kokatahi is made by dead standing stems of southern rata in areas where dieback has occurred, and these stems may persist for over 40 years after tree death. When the contribution to total biomass made by dead standing stems and living biomass are combined, it appears that a consequence of dieback has been a net increase in total woody mass, and of carbon stored in wood. In contrast, in Pohangina, where widespread mortality of trees occurred c. 30 years before plots were established, no dead stems of former canopy trees remained. To date, the little research on the contribution of coarse woody debris to total forest mass in New Zealand forests has focussed largely on forests dominated by *Nothofagus* species (Beets 1980, Stewart and Burrows 1994). More accurate assessments are needed of how total woody mass changes during forest development, of the contribution of dead woody mass to montane forests with widespread death of canopy trees, and of decomposition rates of dead stems of dominant tree species. Assessments of changes in below-ground biomass are also needed.

6.6 REGENERATION OF CANOPY SPECIES

In stands where dieback occurred either before or during census periods, former canopy species often did not regenerate, implying a major change of dominance. However, we can only assess this as significant if the species normally regenerates under its own canopy. This is sometimes the case for species such as kamahi (but see Smale and Kimberley 1989), but is not normally the case for southern rata. For species which seldom regenerate beneath their own canopies, we need to consider their regeneration at a landscape level, as part of a process of patch dynamics.

In Kokatahi, kamahi did regenerate in areas where it had formerly constituted part of the canopy (Appendix 2, Table 4). In Pohangina, the absence of

seedlings of kamahi in areas where canopy trees had died decades earlier is puzzling. It seems unlikely that herbivores alone would suppress regeneration, as species known to be palatable to ungulates and possums, e.g. mahoe and pate (*Schefflera digitata*), regenerated readily there (Appendix 2, Table 1). Likewise, kamahi regenerated in Westland sites where possums and ungulates are also present. Establishment and onward growth of seedlings of kamahi on tree ferns is well-documented (Pope 1926, Stewart and Burrows 1989, Smale and Kimberley 1993). Although we did not record regeneration on tree ferns in Pohangina, we believe it is unlikely that if kamahi were present on tree ferns it would have been completely absent from terrestrial plots (cf. comparative data among microsites in Kokatahi; Appendix 2, Table 4). As kamahi regenerates in a wide range of sites and is dispersed over long distances by wind (Wardle 1991), it would be appropriate to investigate what other factors may limit its regeneration in Pohangina, perhaps by monitoring the onward growth of transplanted seedlings.

Small-seeded species such as kamahi and southern rata typically require specialised microsites for establishment. Southern rata frequently regenerates on bare surfaces such as moraines and landslides (Wardle 1971, Stewart and Veblen 1982). Our sampling frequency in all study areas is inadequate to assess special sites such as landslides. Future studies on the regeneration of these species should examine sites such as landslides, especially in areas where they do not appear to be regenerating in forests. Small-seeded species often also require elevated microsites (e.g. tip-up mounds and logs) for establishment (Putz 1983, Nakashizuka 1989, Lusk 1995). The sample design employed in the four study areas where seedling plots were established (all but Orongorongo) followed a regular pattern (Allen 1993) that may be inadequate to represent the full range of less common, but potentially important, microsites within a plot. The data from a single survey of microsites in Kokatahi shows significantly different proportions of species occur in different microsites, but the current sampling designs can not show how seedlings of different species grow or change in relative abundance in different microsites over time in the different study areas (cf. Stewart and Burrows 1989). Finally, although our plots yield important data on changes in relative abundance of seedlings and saplings of different species over time, nothing is known about the relative survivorship of individuals. For example, although species such as southern rata may be rare as seedlings, the survivorship of single individuals may be greater than that of species such as horopito that have abundant seedlings. Studies involving repeated measures of tagged individual seedlings would yield demographic data that could complement data for tagged adults in the permanent plots.

Species highly palatable to red deer, such as papaumu (e.g. Wardle 1984, Stewart et al. 1987) have become an increasingly important component of the central Westland montane rainforests over time, especially in Kokatahi and Copland (Appendix 1, Tables 5 and 7, and Appendix 2, Tables 3 and 5). Usually deer numbers need to be very low for regeneration of papaumu to occur (e.g. Wardle 1984), so that although ungulates still occur in the central Westland catchments, sustained hunting pressure on deer in these catchments appears to be sufficient to enable the regeneration of such species. Very little sign of ungulates was seen during the 1995 remeasurements in Kokatahi (cf. earlier very large numbers, especially of red deer, McKelvey 1995). However, should numbers of ungulates increase in these catchments, a consequence might be

less diverse communities developing after death of canopy trees. In contrast to the Westland study areas, in Pohangina plots papaumu trees became extinct during the census period, and very little recruitment of seedlings or saplings occurred (Appendix 2, Table 1). Numbers of red deer in Pohangina may still be sufficiently high to prevent its regeneration. Alternatively, its recruitment may be suppressed by low light levels under dense tree fern canopies as reported for another North Island forest (Smale et al. 1997), but both hypotheses require experimental investigation.

6.7 EFFECTIVENESS OF AERIAL POISONING OF POSSUMS

Possoms have been subject to some control in all study areas, but the timing of aerial control operations with respect to the census periods varied considerably. Some areas were poisoned several times (e.g. Kokatahi), while others (e.g. Copland) were poisoned only once (Table 2). In judging the effectiveness of aerial poisoning of possums, we may consider the three central Westland study areas and the populations of two species that are palatable to possums, i.e. southern rata and Hall's totara. Hall's totara declined more or less concurrently among all three study areas, at a roughly similar level (i.e. at least a 30% reduction in biomass during the census periods, Fig. 10). This decline was independent of the timing of poisoning (6 years before the census period in Kokatahi; 4 years before in Taramakau; in the middle in Copland). Southern rata declined in biomass most substantially in Copland (poisoned during the census period), and least in Taramakau (poisoned long before). Furthermore, possums were poisoned in Copland soon after their establishment, i.e. when poisoning would be expected to show the greatest benefit (Pekelharing and Batcheler 1990). Thus we conclude that aerial poisoning operations against possums in the three Westland catchments have had little obvious impact on the health of populations of these two palatable tree species.

In a study that examined the effects of control of possums in a warm-temperate rainforest, Payton et al. (1997) concluded that to obtain changes in health of palatable tree species, possum populations need to be held at very low densities because residual low populations are sufficient to prevent the recovery of palatable species. The lack of sustained control operations in any of these and other study areas may explain the decline of species such as Hall's totara in Westland. Pekelharing and Batcheler (1990) stated that to prevent decline of species palatable to possums in conifer/broad-leaved rainforests, control was necessary before the possum population peaked; it is too late to achieve this in any of the study areas as peak possum densities have already been reached (Table 2), in many areas several decades ago.

6.8 COMPARISON OF SAMPLING METHODS BETWEEN STUDY AREAS

Of the study areas, the random location of plots at a large spatial scale in Kokatahi allowed the strongest interpretation of observed patterns in terms of the patch dynamics of forests in this catchment. Our results from Kokatahi

underscore the value of catchment-wide assessments of these forests that include an adequate sample of site attributes such as altitude, along which tree species vulnerable to browsing by possums (e.g. southern rata) can exhibit different responses. When sampling is biased to include only forests of a certain age or composition (as in Taramakau or Copland) it is not possible to extrapolate the dynamics within these stands to forest dynamics in the whole catchment. The advantages of an unbiased sample are shown in comparing changes in live stem biomass of southern rata (Fig. 9). In the random sample in Kokatahi, the proportion of plots that showed an increase in southern rata biomass was the same as that in which there was a decrease in biomass. By contrast in Copland, where only mature forest stands were sampled, no plots showed an increase in southern rata biomass. A random sample would be required to understand catchment-scale patch dynamics in Taramakau and Copland. That Hall's totara showed the same major decline in biomass at a catchment scale in Kokatahi as it did in the more biased sample in Taramakau and Copland (Fig. 10) increases our confidence that the nature of its decline in Westland is widespread. Plots in Pohangina have the advantage of the sampling technique as Kokatahi, but would be strengthened by a larger overall sample. Orongorongo has the poorest spatial coverage because it has only one, large plot; therefore it may be difficult to extrapolate the compositional changes observed there to elsewhere in the catchment.

7. Conclusions

- Although each of the five study areas had distinctive vegetation, we could generalise about population trends of six of seven common tree species.
- Hall's totara, which is palatable to possums, declined in basal area and live stem biomass in all study areas in which it was common. The basal area and live stem biomass of other tree species palatable to possums remained unchanged during census periods.
- Communities that developed after the dieback of former canopies changed little in tree composition over time, but showed great increases in stem density and basal area.
- At a catchment level, dieback events are not simultaneous, and proceed over at least 50 years. Consequently, censuses over long periods and at a catchment level are needed to assess changes in populations of palatable species, e.g. southern rata and kamahi.
- Even in catchments where dieback is conspicuous, there was no net change in above-ground live stem biomass.
- After dieback, dead stems of a former canopy may remain visually conspicuous for decades, and make a significant contribution to total biomass and to the amount of carbon stored. They also bias aerial estimates of mortality rates.

- Regeneration of kamahi occurred in some areas where it was formerly a canopy species, but not in others. Other former canopy species, e.g. southern rata, require specific microsites for establishment that have probably not been sampled adequately in this study.
- Concurrent with decline of some species, shorter tree species, e.g. horopito, became more abundant in the study areas.
- Changes common among study areas, especially the decline of Hall's totara, have occurred over a similar period and have not been affected by different histories of possum control operations among the study areas.

8. Recommendations

- The rate of decline of Hall's totara is concerning; if the current rate of decline continues, adults of this species will be very rare in the study areas within 50 years. Better knowledge is required of how possums and other factors control the vulnerability of Hall's totara individuals and stands. Future studies should focus on catchment-level ecology of Hall's totara, including its regeneration ecology, its ecophysiology (including water and nutrient use), pathogens, and whether the species is vulnerable to possum browse at all stages of its life history, so that management may be targeted at Hall's totara populations most at risk.
- Given that infrequent poisoning operations at catchment level have been apparently ineffective in arresting the decline especially of Hall's totara, we believe it is appropriate to concentrate sustained poisoning management in one area to determine whether control of possums prevents further deterioration. A catchment such as Copland would be suitable because it has been poisoned recently and has been invaded relatively recently by possums.
- Detailed catchment-level studies are needed to determine the regeneration of species such as southern rata that require specialised microsites for regeneration; the permanent plots we have used are inadequate to detect these microsites. More detailed investigations are needed of the regeneration of former canopy constituents in areas where dieback has occurred. Investigations are needed of the survivorship and onward growth of seedlings of palatable species using repeated measurements of tagged individuals.
- More information is required about the dynamics of kamahi, a species palatable to possums. Kamahi has shown widespread mortality in some areas, especially Pohangina, but little change in others. Investigations of why kamahi is not regenerating in areas such as Pohangina are needed.
- We advocate 5- to 10-yearly monitoring of the permanent plots used in this study, and in other areas with podocarp/broad-leaved forests with permanent forest plots (e.g. Pureora and Stewart Island), to better understand the nature of dieback events among canopy species and the onward development of communities that arise after dieback of former

canopies. We can best determine the onward development of these communities using existing permanent plots (Bakker et al. 1996). Our study has demonstrated the benefits of long-term measurements of plots over observations at a single point in time. The NVS database curated by Landcare Research contained the historic datasets used in this study, and contains data from other permanent plots that could be remeasured to extend the findings in our study. Best results will be obtained from catchment-wide assessments using sufficient numbers of randomly located plots. There are insufficient numbers of plots in some study areas (e.g. Pohangina) to make robust predictions. Greater density of plots would be desirable.

- To better understand the total biomass dynamics of these systems, better information is needed of the contribution of dead woody mass, and of the rate of decay of species once they die. These data should complement data collected on the dynamics of living stems.

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Appendix 1

TREE DENSITIES

TABLE 1. STUDY AREAS WHERE LONG-TERM CHANGES IN COMPOSITION AND STRUCTURE WERE EXAMINED IN CONIFER/BROAD-LEAVED RAINFORESTS.

STUDY AREA	LOCALITY	ECOLOGICAL DISTRICT	LATITUDE	GEOLOGY	ELEVATION RANGE (m)	RAINFALL (mm)
Pohangina Valley	Ruahine Ranges	Ruahine, North Manawatu Gorge	40° 03' S	Greywacke/Argillite	460-760	c. 1500
Orongorongo Valley	Rimutaka Ranges	Tararua	41° 20' S	Pleistocene gravels	130	c. 2500
Taramakau Valley (Hut Creek)	Westland	Whitcombe	42° 44' S	Schist	505-720	6000-8000
Kokatahi Valley	Westland	Whitcombe	42° 55' S	Schist	315-780	6000-10000
Copland Valley (Architect Creek)	Westland	Glaciers	43° 35' S	Schist	630-780	6000-10000

STUDY AREA	DOMINANT TREE SPECIES (BASAL AREA)	NUMBER OF PLOTS	PLOT TYPE	YEARS MEASURED
Pohangina Valley	<i>Cyathea smithii</i>	6	20 m × 20 m	1975, 1984, 1996
Orongorongo Valley	<i>Meliccytus ramiflorus</i> <i>Dacrydium cupressinum</i>	1	2.25 ha	1969, 1978, 1985, 1994
Taramakau Valley (Hut Creek)	<i>Metrosideros robusta</i> <i>Elaeocarpus dentatus</i> <i>Laurelia novae-zelandiae</i>	8	20 m × 20 m	1978, 1984, 1992
Kokatahi Valley	<i>Metrosideros umbellata</i> <i>Podocarpus hallii</i> <i>Weinmannia racemosa</i>	21	20 m × 20 m	1972, 1979, 1995
Copland Valley (Architect Creek)	<i>Cyathea smithii</i> <i>Metrosideros umbellata</i> <i>Podocarpus hallii</i> <i>Griselinia littoralis</i>	14	20 m × 20 m	1978, 1984, 1992

TABLE A1.1 MEAN STEM RELATIVE BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF DOMINANT WOODY SPECIES (≥ 5 cm dbh) ON 6 PERMANENT PLOTS IN POHANGINA MEASURED IN 1975, 1984, AND 1996. VALUES IN PARENTHESES INCLUDE TREE FERNS.

SPECIES	BASAL AREA (%)				DENSITY (%)				BIOMASS (%)					
	1975	1984	1996	(1996)	1975	1984	1996	(1996)	1984	1996	(1996)			
<i>Melicytus ramiflorus</i>	59.6	46.9	46.1	(15.9)	64.7	60.0	39.5	(17.5)	41	53	(18.3)			
<i>Dacrydium cupressinum</i>	13.5	17.8	17.3	(6.0)	0.4	0.9	0.6	(0.3)	22	13	(4.6)			
<i>Knighitia excelsa</i>	12.2	9.7	9.2	(3.2)	0.9	0.9	0.6	(0.3)	12	10	(3.4)			
<i>Pseudowintera colorata</i>	1.8	1.8	2.2	(0.8)	9.0	10.5	10.4	(4.7)	1	2	(0.7)			
<i>Griselinia littoralis</i>	4.7	1.7	0.0	(0.0)	2.2	1.3	0.0	(0.0)	2	0	(0)			
<i>Hedycarya arborea</i>	2.3	1.5	2.3	(0.8)	5.9	3.9	6.3	(2.8)	2	2	(0.8)			
<i>Schefflera digitata</i>	1.5	1.8	2.0	(0.7)	4.0	3.1	7.2	(3.2)	2	2	(0.6)			
<i>Olearia rani</i>	1.1	1.7	3.3	(1.1)	3.2	3.5	5.7	(2.5)	1	3	(1.0)			
<i>Carpodetus serratus</i>	0.0	0.3	4.0	(1.4)	0.0	1.7	13.7	(6.1)	<1	3	(1.2)			
<i>Podocarpus hallii</i>	0.1	0.1	0.2	(0.1)	0.9	0.9	0.9	(0.4)	<1	<1	(<0.1)			
<i>Cyathea smithii</i>				(56.2)				(47.3)			(56.0)			
<i>Dicksonia squarrosa</i>				(5.5)				(6.5)			(4.6)			
<i>Cyathea dealbata</i>				(3.0)				(1.6)			(3.5)			
<i>Dicksonia fibrosa</i>				(0.7)				(0.3)			(0.6)			
<i>Cyathea cunninghamii</i>				(0.1)				(0.1)			(0.1)			
Other species	1.6	15.6	12.0	(3.9)	2.5	7.6	8.2	(3.3)	18	12	(4.4)			
Total	(m ² /ha)	18.0	23.4	24.9	(72.0)	(no./ha)	920	950	1753	(3145)	(Mg/ha)	52	43	(124)

TABLE A1.2 MEAN STEM RELATIVE BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF DOMINANT WOODY SPECIES (≥ 100 cm dbh) ON ONE 2.25 ha PERMANENT PLOT IN ORONGORONGO MEASURED IN 1969, 1978, 1985, AND 1994. VALUES IN PARENTHESES INCLUDE TREE FERNS.

SPECIES	BASAL AREA (%)					DENSITY (%)					BIOMASS (%)				
	1969	1978	1985	1994	(1994)	1969	1978	1985	1994	(1994)	1969	1978	1985	1994	(1994)
<i>Metrosideros robusta</i>	28.6	21.3	25.3	24.7	(20.7)	1.5	1.2	1.3	1.3	(0.9)	30.9	23.4	27.8	27.5	(25.4)
<i>Elaeocarpus dentatus</i>	18.3	20.7	20.5	21.2	(17.7)	5.3	5.4	6.0	6.6	(3.1)	17.3	19.9	19.8	20.7	(19.1)
<i>Laurelia novae-zelandiae</i>	18.1	21.3	18.4	19.8	(16.5)	5.0	5.0	5.1	5.3	(3.0)	22.0	26.4	22.7	24.8	(22.9)
<i>Hedycarya arborea</i>	10.3	11.7	11.8	12.3	(10.3)	38.4	38.0	38.8	39.3	(22.6)	5.9	6.7	6.9	7.3	(6.7)
<i>Melicytus ramiflorus</i>	8.1	9.1	8.4	8.8	(7.4)	20.6	19.3	19.4	19.2	(12.1)	3.9	4.4	4.1	4.4	(4.1)
<i>Knightia excelsa</i>	3.6	4.0	3.9	3.7	(3.1)	2.6	2.0	2.0	2.0	(1.5)	5.0	5.6	5.5	5.4	(5.0)
<i>Dacrydium cupressinum</i>	2.7	2.3	2.5	2.3	(1.9)	<0.1	<0.1	<0.1	<0.1	(<0.1)	5.1	4.3	4.8	4.4	(4.1)
<i>Prumnopitys ferruginea</i>	1.7	1.4	1.1	1.1	(0.9)	0.5	0.3	0.4	0.4	(0.3)	2.0	1.7	1.3	1.4	(1.3)
<i>Weinmannia racemosa</i>	1.3	0.8	0.7	0.7	(0.6)	1.8	0.5	0.5	0.4	(0.2)	1.2	0.8	0.8	0.8	(0.7)
<i>Cyatbea dealbata</i>					(6.7)					(10.3)					(3.8)
<i>Cyatbea smithii</i>					(5.6)					(17.9)					(2.3)
<i>Dicksonia squarrosa</i>					(2.1)					(8.8)					(0.6)
<i>Cyatbea cunninghamii</i>					(1.9)					(4.2)					(0.9)
<i>Cyatbea medullaris</i>					(0.4)					(0.5)					(0.2)
Other species	7.3	7.4	7.4	5.4	(4.2)	24.1	28.2	26.4	25.4	(14.2)	6.7	6.6	6.4	3.3	(2.9)
Total	(m ² /ha) 72.3	73.5	76.3	79.0	(94.5)	(no/ha) 656	783	789	833	(1480)	(Mg/ha) 372	373	386	394	(427)

TABLE A1.3. STEM BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF TREE FERNS (≥ 100 cm dbh) ON ONE 2.25 ha PLOT IN ORONGORONGO, MEASURED IN 1969, 1978, 1985, AND 1994.

SPECIES	BASAL AREA (m ² /ha)				STEM DENSITY (no./ha)				BIOMASS (Mg/ha)			
	1969	1978	1985	1994	1969	1978	1985	1994	1969	1978	1985	1994
<i>Cyathea dealbata</i>	4.9	6.1	6.0	6.3	115	143	148	152	12.4	16.6	15.9	16.1
<i>Cyathea smithii</i>	3.8	4.8	5.0	5.3	200	249	259	258	7.0	9.0	9.4	10.0
<i>Dicksonia squarrosa</i>	1.5	2.0	2.0	2.0	98	147	168	170	2.1	2.8	2.6	2.8
<i>Cyathea cunninghamii</i>	1.4	1.8	1.8	1.8	47	64	70	67	3.0	3.7	3.7	3.7
<i>Cyathea medullaris</i>	0.6	0.4	0.5	0.4	10	6	7	8	1.4	0.8	1.1	0.9
Total (all woody species)	83.9	88.3	91.1	94.5	1116	1386	1434	1480	396	404	417	427

TABLE A1.4. MEAN STEM RELATIVE BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF DOMINANT WOODY SPECIES (≥ 5 cm dbh) ON 8 PERMANENT PLOTS IN TARAKAU MEASURED IN 1978, 1984, AND 1992.

SPECIES	BASAL AREA (%)			DENSITY (%)			BIOMASS (%)		
	1978	1984	1992	1978	1984	1992	1978	1984	1992
<i>Metrosideros umbellata</i>	52.4	53.8	55.1	11.1	10.9	11.1	65.1	66.5	68.1
<i>Podocarpus hallii</i>	19.6	16.5	14.9	5.5	4.6	4.6	15.1	12.9	10.9
<i>Weinmannia racemosa</i>	16.2	16.6	16.9	38.5	38.4	38.8	12.9	13.1	13.3
<i>Quintinia acutifolia</i>	8.3	9.3	10.0	27.2	29.1	30.0	4.7	5.3	5.8
<i>Griselinia littoralis</i>	1.6	1.8	1.4	9.1	8.4	7.3	0.8	0.9	0.8
<i>Prumnopitys ferruginea</i>	0.8	0.8	0.9	0.5	0.5	0.5	0.8	0.8	0.8
<i>Raukaua simplex</i>	0.5	0.5	0.4	3.5	3.4	2.5	0.2	0.2	0.1
<i>Pseudowintera colorata</i>	0.2	0.2	0.2	3.2	3.2	4.0	0.1	0.1	0.1
<i>Myrsine divaricata</i>	<0.1	<0.1	<0.1	0.4	0.4	0.4	<0.1	<0.1	<0.1
<i>Carpodetus serratus</i>	<0.1	<0.1	<0.1	0.3	0.3	0.1	<0.1	<0.1	<0.1
Other species	0.4	0.5	0.2	0.7	0.8	0.8	0.3	0.2	0.1
Total	(m ² /ha) 136.0	132.1	131.5	(no./ha) 2425	2443	2262	(Mg/ha) 631	617	61

TABLE A1.5. MEAN STEM RELATIVE BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF DOMINANT WOODY SPECIES (≥ 5 cm dbh) ON 21 PERMANENT PLOTS IN KOKATAHI MEASURED IN 1972, 1979, AND 1995. VALUES IN PARENTHESES INCLUDE TREE FERNS.

SPECIES	BASAL AREA (%)				DENSITY (%)				BIOMASS (%)			
	1972	1979	1995	(1995)	1972	1979	1995	(1995)	1972	1979	1995	(1995)
<i>Metrosideros umbellata</i>	34.7	33.8	30.4	(26.1)	6.2	5.5	3.1	(2.7)	47.8	47.9	44.1	(40.7)
<i>Weinmannia racemosa</i>	29.4	28.8	27.7	(23.7)	21.5	18.8	14.1	(12.3)	28.9	28.5	27.1	(25.0)
<i>Griselinia littoralis</i>	11.6	12.5	15.6	(13.4)	12.1	10.9	9.5	(8.3)	7.7	8.5	12.1	(11.2)
<i>Podocarpus hallii</i>	8.7	7.9	4.0	(3.5)	3.9	3.0	1.5	(1.3)	6.7	6.2	4.0	(3.7)
<i>Pseudowintera colorata</i>	4.1	5.9	8.1	(6.9)	30.0	37.0	42.1	(36.8)	1.5	2.3	3.8	(3.5)
<i>Quintinia acutifolia</i>	4.4	3.5	5.1	(4.3)	4.7	4.1	7.2	(6.3)	3.6	2.7	3.8	(3.5)
<i>Carpodetus serratus</i>	2.8	3.2	3.5	(3.0)	3.3	3.6	4.5	(3.9)	1.7	2.0	2.3	(2.2)
<i>Melicytus ramiflorus</i>	1.0	1.2	1.2	(1.0)	5.4	4.9	3.6	(3.1)	0.5	0.6	0.7	(0.6)
<i>Coprosma ciliata</i>	0.5	0.6	0.9	(0.8)	3.3	3.5	3.8	(3.4)	0.1	0.2	0.2	(0.2)
<i>Cyathea smithii</i>				(13.9)				(12.2)				(7.6)
<i>Dicksonia squarrosa</i>				(0.4)				(0.5)				(0.2)
Other species	2.8	2.8	3.5	(3.0)	9.6	8.7	10.6	(9.2)	1.4	1.2	1.7	(1.6)
Total	(m ² /ha) 57.8	60.1	58.2	(67.9)	(no./ha) 1657	1928	2472	(2830)	(Mg/ha) 194	197	175	(189)

TABLE A1.6 COMPARISON OF BASAL AREA, STEM DENSITY AND ABOVE-GROUND LIVE STEM BIOMASS OF SELECTED COMMON SPECIES (≥ 5 cm dbh) (NOT INCLUDING TREE FERNS) IN TWO RIVER VALLEYS IN THE HOKITIKA RIVER CATCHMENT IN 1972.

	BASAL AREA (%)		STEM DENSITY (%)		BIOMASS (%)	
	KOKATAHI	WHITCOMBE	KOKATAHI	WHITCOMBE	KOKATAHI	WHITCOMBE
<i>Metrosideros umbellata</i>	34.7	21.9	6.2	4.6	47.8	33.2
<i>Weinmannia racemosa</i>	29.4	16.4	21.5	17.8	28.9	17.5
<i>Griselinia littoralis</i>	11.6	5.8	12.1	6.3	7.7	5.1
<i>Podocarpus hallii</i>	8.7	20.8	3.9	9.4	6.7	18.8
<i>Pseudowintera colorata</i>	4.1	0.4	30.0	3.4	1.5	0.2
<i>Quintinia acutifolia</i>	4.4	7.3	4.7	13.1	3.6	6.0
<i>Melicytus ramiflorus</i>	1.0	0.1	5.4	0.2	0.5	>0.1
Other species		6.1		16.2		19.2
Total	(m ² /ha) 57.8	79.5	(no./ha) 1657	2328	(Mg/ha) 194	262

TABLE A1.7. MEAN STEM RELATIVE BASAL AREA, DENSITY, AND ABOVE-GROUND LIVE STEM BIOMASS OF DOMINANT WOODY SPECIES (≤ 5 cm dbh) ON 14 PERMANENT PLOTS IN COPLAND MEASURED IN 1978, 1984, AND 1992.

SPECIES	BASAL AREA (%)			DENSITY (%)			BIOMASS(%)		
	1978	1984	1992	1978	1984	1992	1978	1984	1992
<i>Metrosideros umbellata</i>	58.6	59.0	61.0	10.3	9.4	9.3	74.0	74.5	75.7
<i>Podocarpus hallii</i>	21.2	19.4	14.2	8.1	7.4	6.5	14.4	13.1	9.7
<i>Griselinia littoralis</i>	5.9	6.3	7.5	17.2	17.2	17.4	4.2	4.5	5.5
<i>Raukaua simplex</i>	3.2	3.4	3.9	24.9	25.5	26.2	1.3	1.4	1.7
<i>Weinmannia racemosa</i>	3.5	3.8	4.2	5.4	5.5	5.6	2.9	3.2	3.5
<i>Myrsine divaricata</i>	0.9	1.0	1.3	8.5	8.7	8.9	0.2	0.2	0.2
<i>Pseudowintera colorata</i>	0.3	0.4	0.5	3.3	3.7	4.6	0.1	0.1	0.2
<i>Coprosma ciliata</i>	0.1	0.1	0.2	1.4	1.4	1.6	<0.1	<0.1	<0.1
Other species	6.3	6.6	7.3	20.9	21.2	19.9	2.9	3.0	3.5
Total	(m ² /ha) 125.1	119.9	110.0	(no./ha) 2257	2307	2246	(Mg/ha) 547	525	455

Appendix 2

SEEDLING AND SAPLING DENSITIES

TABLE A2.1. MEAN SEEDLING (>15 cm TALL BUT <135 cm TALL) AND SAPLING (\geq 135 cm TALL BUT <5 cm dbh) DENSITY (no./100m²) OF DOMINANT WOODY SPECIES ON 6 PERMANENT PLOTS IN POHANGINA MEASURED IN 1984 AND 1996.

	SEEDLING DENSITY		SAPLING DENSITY	
	1984	1996	1984	1996
<i>Melicytus ramiflorus</i>	16	7	1	4
<i>Dacrydium cupressinum</i>	1	0	1	<1
<i>Knightia excelsa</i>	3	0	0	<1
<i>Prumnopitys ferruginea</i>	0	1	0	<1
<i>Pseudowintera colorata</i>	30	20	8	9
<i>Griselinia littoralis</i>	0	0	1	<1
<i>Hedycarya arborea</i>	22	10	4	8
<i>Pseudowintera axillaris</i>	7	8	3	9
<i>Schefflera digitata</i>	26	12	3	14
<i>Olearia rani</i>	16	18	1	3
<i>Nestegis cunninghamii</i>	5	5	<1	<1
<i>Brachyglottis repanda</i>	17	9	16	44
<i>Carpodetus serratus</i>	6	2	5	4
<i>Podocarpus ballii</i>	0	0	<1	<1

TABLE A2.2. MEAN SEEDLING (>15 cm TALL BUT <135 cm TALL) AND SAPLING (\geq 135 cm TALL BUT <5 cm dbh) DENSITY (no./100m²) OF DOMINANT WOODY SPECIES ON EIGHT PERMANENT PLOTS IN TARAMAKAU MEASURED IN 1978, 1984, AND 1992.

	SEEDLING DENSITY			SAPLING DENSITY		
	1978	1984	1992	1978	1984	1992
<i>Metrosideros umbellata</i>	6	9	10	<1	<1	<1
<i>Podocarpus ballii</i>	19	18	23	<1	<1	1
<i>Weinmannia racemosa</i>	46	55	88	4	4	4
<i>Quintinia acutifolia</i>	149	207	369	4	4	19
<i>Griselinia littoralis</i>	7	15	54	1	1	1
<i>Prumnopitys ferruginea</i>	0	0	1	<1	<1	<1
<i>Raukaua simplex</i>	54	72	100	1	<1	12
<i>Pseudowintera colorata</i>	19	19	31	3	5	6
<i>Myrsine divaricata</i>	15	23	31	<1	<1	<1
<i>Carpodetus serratus</i>	1	1	4	<1	0	<1

TABLE A2.3. MEAN SEEDLING (>15 cm TALL BUT <135 cm TALL) AND SAPLING (\geq 135 cm TALL BUT <5 cm dbh) DENSITY (no./100m²) OF DOMINANT WOODY SPECIES ON 21 PERMANENT PLOTS IN KOKATAHI MEASURED IN 1979 AND 1995.

SPECIES	SEEDLING DENSITY		SAMPLING DENSITY	
	1979	1995	1979	1995
<i>Metrosideros umbellata</i>	2	4	1	2
<i>Weinmannia racemosa</i>	18	20	2	9
<i>Griselinia littoralis</i>	38	50	2	27
<i>Podocarpus hallii</i>	7	10	1	4
<i>Pseudowintera colorata</i>	70	62	41	44
<i>Quintinia acutifolia</i>	8	10	<1	3
<i>Carpodetus serratus</i>	6	6	1	3
<i>Melicytus ramiflorus</i>	3	1	<1	1
<i>Coprosma ciliata</i>	36	43	3	8

TABLE A2.4. MEAN WOODY SEEDLING (>15 cm) DENSITY (no./100m²) MEASURED IN 1982 IN 1 m² SUBPLOTS ON THE GROUND, ON TREEFERNS AND ON LOGS IN 2 PLOTS IN KOKATAHI AT 500 m AND 700 m ELEVATION. TREE FERNS OCCURRED ONLY IN THE 500 m PLOT.

SPECIES	500 m			700 m	
	GROUND	TREE FERN	LOG	GROUND	LOG
<i>Metrosideros umbellata</i>	0	0	0	0	0
<i>Weinmannia racemosa</i>	11	43	7	2	0
<i>Griselinia littoralis</i>	14	52	26	25	126
<i>Podocarpus hallii</i>	0	0	0	0	6
<i>Pseudowintera colorata</i>	19	2	3	105	42
<i>Quintinia acutifolia</i>	46	505	105	0	2
<i>Carpodetus serratus</i>	14	11	0	0	0
<i>Melicytus ramiflorus</i>	16	8	0	0	0
<i>Coprosma ciliata</i>	2	2	0	175	123

TABLE A2.5. MEAN SEEDLING (>15 cm TALL BUT <135 cm TALL) AND SAPLING (\geq 135 cm TALL BUT < 5 cm dbh) DENSITY (no./100 m²) OF DOMINANT WOODY SPECIES ON 14 PERMANENT PLOTS IN COPLAND MEASURED IN 1978, 1984, AND 1992.

	SEEDLING DENSITY			SAPLING DENSITY		
	1978	1984	1992	1978	1984	1992
<i>Metrosideros umbellata</i>	0	0	0	<1	<1	<1
<i>Podocarpus balli</i>	3	2	2	<1	1	1
<i>Griselinia littoralis</i>	1	5	4	2	2	1
<i>Raukaua simplex</i>	25	29	30	7	5	6
<i>Weimannia racemosa</i>	1	3	1	1	1	<1
<i>Myrsine divaricata</i>	2	5	15	2	1	1
<i>Pseudowintera colorata</i>	5	3	6	2	1	2