

TABLE 2. DATES OF POSSUM COLONISATION, POPULATION PEAKS AND CONTROL OPERATIONS IN THE STUDY AREAS.

STUDY AREA	COLONISATION	PEAK OF POPULATION	CONTROL BY AERIAL POISONING
Pohangina	1883 ¹	1950s ⁶	1959-1977 ⁸
Orongorongo	1890s ²	1940s ²	1959 ⁹
Taramakau	1950s (?) ³	1970s ³	1970, 1974 ¹⁰
Kokatahi	1923 ⁴	1950s ⁴	1959, 1961, 1966 ¹¹
Copland	1924, 1930 ⁵	1970s ⁷	1986 ¹²

¹ Pracy (1962); ² Brockie (1992); ³ Bamford (1972); ⁴ James *et al.* (1973); ⁵ in Westland National Park: Fraser (1979), Pekelharing and Reynolds (1983); ⁶ Cunningham (1979); ⁷ Fraser (1988); ⁸ McKelvey (1995); ⁹ immediately south of the study area: Batcheler *et al.* (1967), L.T. Pracy and P.E. Cowan, pers. comm.; ¹⁰ Pekelharing (1979); ¹¹ Batcheler *et al.* (1967) and C.J. Pekelharing, pers. comm.; ¹² D. Morgan (1987), unpublished FRI contract report, cited in Stewart (1992).

Reynolds 1983). In Taramakau and Kokatahi, no data are available for changes in chamois populations over time. Himalayan thar (*Hemitragus jemlabicus*) are also present in Copland and rarely in Kokatahi. Among the Westland sites, numbers of ungulates between 1992 and 1996 were lower in Taramakau and Kokatahi than in Copland (116 ungulates, Taramakau; 131, Kokatahi; 601, Copland; based on recreational and commercial hunter returns 1992-1996, J. Brennan, pers. comm.).

4.2 DATA COLLECTION

In Pohangina and Kokatahi, 400-m² plots were located along randomly located transects. In Pohangina, plots were located at 120-m intervals along each transect; in Kokatahi, plots were located at random intervals along the transects. In Taramakau and Copland, permanent 400-m² plots were located in areas where southern rata was dominant (cf. Stewart 1992). In Orongorongo, data were collected from one 2.25-ha plot in lowland rainforest on a fan near the river (Campbell 1990).

For a comparison among similar catchments with and without advanced canopy dieback, we compared live stem biomass estimates from Kokatahi, where in at least part of the catchment dieback had already occurred, with concurrent estimates from the nearby Whitcombe River valley (both rivers are part of the Hokitika River catchment) where dieback had not occurred (James *et al.* 1973). Twenty-six 400-m² plots were located in the Whitcombe River valley, near Kokatahi, between Price River and Frew Creek (265-1000 m; 43° 05' S). Plots were located in the same way as in Kokatahi and measured concurrently with the first measurement in Kokatahi.

Kamahi, which features frequently in possum diets (e.g. Fitzgerald 1976) and is a major component of most forests in this study, is absent from plots in Pohangina, but still occurs in nearby forest dominated by red beech (*Nothofagus fusca*), in which it forms an understorey. We investigated the dynamics of kamahi in such forest near Pohangina by sampling four 400-m² plots in the western side of the headwaters of Cattle Creek, c. 5 km east-south-east of

the other Pohangina plots. This forest adjoins an area formerly dominated by kamahi and northern rata, which have mostly died and been replaced by shorter trees, especially horopito (*Pseudowintera colorata*), and another area where widespread death of kamahi was evident in early 1996 (Fig. 3).

For each plot, we collected data on:

- **Trees** These are stems ≥ 5 cm (diameter at breast height (dbh), 135 cm) in all study areas except Orongorongo, where they are ≥ 10 cm (Campbell 1990). At each census, all trees in each plot were identified, tagged, and dbh was measured. In three of 5 study areas (Kokatahi, Orongorongo, Pohangina) data were collected for tree ferns in at least the most recent censuses, but these data are lacking for Taramakau and Copland.
- **Saplings** These are stems < 5 cm dbh and > 135 cm tall. All saplings were identified and counted. Saplings were not measured at Orongorongo.
- **Seedlings** These are stems of woody species that are > 15 cm tall and < 135 cm tall. Data for seedlings were collected from 24, 0.75-m² circular subplots located at regular intervals on a grid (Allen 1993). All woody seedlings were identified and counted. In Kokatahi, specific seedling regeneration sites were sampled in 1982 in two plots of 54 × 36 m. Data were collected for seedlings that established terrestrially, on tree fern trunks, and on logs (cf. Stewart and Burrows 1989). Seedlings were not measured at Orongorongo.

4.3 DATA ANALYSIS

Data from permanent plots were summarised using the programs PC-DIAM (Hall 1994a) and PC-USTOREY (Hall 1994b). For each census in each study area we analysed the following data for trees, saplings, and seedlings.

4.3.1 Trees

Density, basal area, and above-ground stem biomass were computed on a per hectare basis, without correction for slope (see Harcombe et al. 1998). We report relative values (i.e. as a percentage of total) for all major tree species (those having greater than 1% relative basal area). Stem biomass was calculated from the volume of each stem and its density using the methods of Hall and Hollinger (1997). Volumes for stems were derived from diameter measurements for each stem and height derived from the stand mean top height (predominant height of the top of the canopy, Harcombe et al. 1998). For Pohangina, biomass data are presented from only the two most recent censuses because we lacked accurate height data for the earliest census (1975). Volumes for stems of each species were then estimated using species-specific height/diameter curves (Ker and Smith 1955) and the parabolic volume equation of Whittaker and Woodwell (1968). Individual volumes were converted to biomass using the basic wood density for a given species (Entrican et al. 1951, Hinds and Reid 1957, Harris 1986, Clifton 1990). Volumes for tree ferns were computed as cylinders from diameters multiplied by the stand mean top height, and biomass estimates were computed from density values for each species.

For Kokatahi, diameter measurements for standing dead southern rata were used to estimate their mass in two temporary plots in an area of post-dieback forest measured in 1982 (R.B. Allen and A.B. Rose, unpublished data). We

Figure 3. Canopy dominated by kamahi, now mostly dying or recently dead, with occasional healthy miro interspersed. Upper Cattle Creek, Pohangina Valley, Ruahine Ranges, March 1996.



assumed the average height of these stems to be the same as the average height of live southern rata stems measured in nearby plots in 1994. As we lack data on the density of dead southern rata, we have taken a conservative estimate that the wood of dead stems has half the density of living stems, i.e. is 400 kg/m^3 .

To test whether population trends for individual species were similar among study areas, we compared changes during the census periods in basal area, stem density, and biomass of seven species common in at least two study areas, i.e. at least 3% of total stem density in each study area. These species are: Hall's totara (*Podocarpus hallii*), horopito, kamahi, mahoe (*Melicactus ramiflorus*), papaumu (*Griselinia littoralis*), southern rata, and tawheowheo (*Quintinia acutifolia*). Of these species, Hall's totara, kamahi, mahoe and southern rata are known to be browsed by possums (e.g. Fitzgerald and Wardle 1979, Leathwick et al. 1983, Coleman et al. 1985, Brockie 1992). In study areas in which they were common, we summarised diameter distributions for each of these species and assessed changes in total number of stems and total live stem biomass (Mg/ha) during the census periods. We also computed the percent change in biomass between the earliest and most recent censuses for each of the seven species in each plot (except Orongorongo, where there is only one large plot). Changes in biomass for tree ferns reflect only mortality and recruitment since diameter changes are not expected over time, and we lack height increment data for tree ferns for any of our study areas.

We used an annualised percentage change to allow comparisons of change among study areas where census periods were different, and where initial stem densities, basal areas, and live stem biomass were different. Annualisation of interval percentage change was conducted using a compound interest formula (McCune and Cottam 1985, Runkle 1990) to allow comparisons on a relative basis. If changes for a given species exceeded 1% compounded per annum, that species was deemed to be an 'increaser' if the change was positive and a 'decreaser' if the change was negative; where changes were less than 1% compounded per annum during the census period, species were considered 'unchanged'.

Only Kokatahi had a sufficiently widespread network of plots to evaluate whether changes among tree species were related to altitude. We compared changes in stem density and basal area of common species over time between plots at lower altitude (<570 m) and those at higher altitude (>570 m).

We compared forest types among study areas using a TWINSPAN classification (Hill 1979) of plots based on the total basal area of each tree species in each plot (we divided the Orongorongo plot into contiguous subplots of 30 m × 30 m). To examine whether composition changed over time, and whether forest types of study areas became more similar to each other over time, we used data from both the earliest and most recent census of each plot in a single classification.

4.3.2 Saplings and seedlings

We computed sapling and seedling density (no./100 m²) for all tree species to determine whether seedling and sapling regeneration reflected abundance of present or former canopy species. We compared density between the earliest census in which seedling data were recorded (1984 in the Pohangina and 1979 in the Kokatahi) and the most recent census. To examine whether regeneration of particular tree species was related to particular microsites, we summarised the proportion of seedlings growing on the ground, on tree ferns, and on logs in one study area, Kokatahi, in 1982.

5. Results

5.1 CHANGES IN STAND BASAL AREA, DENSITY, AND LIVE BIOMASS OVER TIME

There were substantial differences in basal area, stem density, and biomass among the study areas (Table 3). For example, basal area and live biomass values in Taramakau and Copland, in stands dominated by large, dense-wooded southern rata were nearly an order of magnitude greater than in Pohangina, where stands had developed after the dieback of former canopies. This confounds comparisons among study areas, so we concentrate on changes in basal area, density and biomass within sites. The relatively low stem density in Orongorongo probably reflects the greater minimum stem size for inclusion in the censuses than in the other study areas.

The total basal area of trees remained relatively constant in most study areas throughout their census periods (Table 3). The exception was Pohangina, where basal area increased by more than 1% compounded per annum, but note that the absolute magnitude of increase for this site was small (Table 3). In contrast, stem density increased in most study areas over time (Table 3), except in Taramakau and Copland, both of which had comparatively high densities throughout. Biomass, on the other hand, decreased or remained relatively unchanged in all of the study areas (Table 3).

TABLE 3. ASSESSMENT OF OVERALL CHANGES IN (a) BASAL AREA (m²/ha), (b) DENSITY (stems/ha), (c) BIOMASS (Mg/ha), FOR TREES, EXCLUDING TREE FERNS. ABSOLUTE VALUES FOR EACH SITE ARE TABULATED WITH DATES OF THE EARLIEST AND MOST RECENT CENSUS IN PARENTHESES.

STUDY AREA	INCREASED ¹	UNCHANGED ²	DECREASED ³
(a) Basal area (m²/ha)			
Pohangina	18-25 (1975-1996)		
Orongorongo		72-79 (1969-1994)	
Taramakau		136-131 (1978-1992)	
Kokatahi		58-58 (1972-1995)	
Copland		125-110 (1978-1992)	
(b) Density (stems/ha)			
Pohangina	920-1753 (1975-1996)		
Orongorongo	656-833 (1969-1994)		
Taramakau		2425-2262 (1978-1992)	
Kokatahi	1657-2472 (1972-1995)		
Copland		2257-2246 (1978-1992)	
(c) Biomass (Mg/ha)			
Pohangina			52-43 (1984 ⁴ -1996)
Orongorongo		372-392 (1969-1994)	
Taramakau		631-615 (1978-1992)	
Kokatahi		194-175 (1972-1995)	
Copland			547-455 (1978-1992)

¹ an annual increase of more than 1% compounded;

² an annual change (increase or decrease) at less than 1% compounded;

³ an annual decrease at more than 1% compounded.

⁴ Pohangina 1975 measurements lacked height estimates to allow conversion of basal area to biomass.

The apparent paradox of a decrease in total biomass in Pohangina and Copland while basal area remained more or less constant or increased (Appendix 1, Tables A1.1 and A1.7) reflects a large increase in numbers of shorter species of lower wood density (e.g. horopito), and loss of infrequent, taller species of higher wood density (e.g. southern rata and papaumu). In Kokatahi, the large increase in total stem density was a result of recruitment of mostly short species of lower wood density at a rate that was sufficient to maintain total basal area at a constant level throughout the 23-year census period.

Changes in total basal area, density, and biomass considered in Table 3 ignore the contribution of tree ferns, but in three study areas (Pohangina, Orongorongo, Kokatahi) tree ferns contribute substantially to total forest composition. Tree ferns, especially *Cyathea smithii*, are a particularly important component of the Pohangina forests, where they comprise more than half the basal area, stem density, and biomass (Appendix 1, Table A1.1). In Kokatahi, tree ferns were a significant component of lower altitude forests (<570 m; Appendix 1, Table A1.5), and in Orongorongo they are a particularly important contributor to stem density (41% of stem density at the most recent (1994) census; Appendix 1, Table A1.2). Long term data for tree ferns exist only from Orongorongo, where *Cyathea cunninghamii*, *C. dealbata*, *C. smithii* and *Dicksonia squarrosa* were all increasers in basal area, stem density, and

Figure 4. Spars of southern rata that died during the 1950s and 1960s emergent over a lower canopy of trees including horopito, tawheowheo, and papaumu. Upper Kokatahi Valley, Hokitika River, Westland, May 1995.



biomass (i.e. rates of increase all exceeded 1% per annum compounded, Appendix 1, Table A1.3; see also Campbell 1990). *Cyathea medullaris*, which was comparatively rare in Orongorongo (Appendix 1, Table A1.3) declined in basal area, stem density, and biomass over 25 years, but less than 1% compounded per annum.

5.1.1 Contribution of dead wood to total woody mass

The changes we present in biomass over time reflect only the contributions of **living** stem biomass. In areas where there has been high mortality, the contribution of **dead** woody debris may also be important to the total mass. In a restricted area of the Kokatahi catchment where there had been high mortality of canopy trees in the 1950s, the contribution of dead southern rata stems from two plots was 576 ± 171 (standard error of the mean) Mg/ha (cf. total living biomass at the most recent census was 175 Mg/ha for the catchment). It should be noted that our calculation of dead southern rata woody mass is very conservative, and that such woody mass may remain on site for many years after stems die (Fig. 4).

5.1.2 Mortality differences between similar catchments

Forests in Kokatahi, part of which had already been affected by widespread mortality of canopy trees, were compared with forests in the nearby Whitcombe River valley, where widespread mortality had not occurred. In 1972, total basal area in Kokatahi was 38% less, total stem density 40% less, and total biomass 35% less than in the Whitcombe Valley (Appendix 1, Table A1.6). Total basal area and biomass in Kokatahi forests in 1995 were also substantially less than that in Whitcombe in 1972, but total stem density in Kokatahi in 1995 was similar to that in Whitcombe in 1972 (cf. Appendix 1, Tables A1.5 and A1.6).

Among the larger canopy trees, southern rata and kamahi had higher basal area, stem density, and biomass at all censuses in Kokatahi than in the 1972 census in Whitcombe (Appendix 1, Table A1.6), but Hall's totara had substantially lower

basal area, stem density, and biomass in Kokatahi than in Whitcombe. Among smaller trees, papaumu was similar in the two areas, but tawheowheo was a more important component of Whitcombe forests than in Kokatahi, while the opposite was true for horopito.

5.2 CHANGES IN INDIVIDUAL TREE SPECIES OVER TIME

5.2.1 Increasers

(a) Horopito (*Pseudowintera colorata*) (Fig. 5)

Horopito was common in Pohangina, Taramakau, and Kokatahi, where it was an ‘increaser’ both in stem numbers and total stem biomass. This was especially the case in Kokatahi, where stem numbers and total biomass of horopito more than doubled during the 23-year census period, in both higher and lower altitude plots. The few plots in Kokatahi that lost substantial biomass of horopito were affected by landslides during the census period (two of 21 plots were affected severely). In Taramakau most plots retained a similar biomass of horopito during the census period. While a few plots gained more than 100% biomass of horopito, the same number of plots lost as much as 60%. In Pohangina, horopito increased in biomass substantially in most plots.

The size class distribution in all three sites was a ‘reverse J’ (heavily skewed to smaller stems) typical of continuous recruitment. Only in Taramakau did the size class distribution change slightly over the census period toward a greater proportion of larger stems, i.e. growth into larger size classes was not matched by recruitment into the smallest size class—the rate of population increase was smaller in Taramakau than in Pohangina or Kokatahi.

(b) Tawheowheo (*Quintinia acutifolia*) (Fig. 6)

Tawheowheo was found only in the study areas of central Westland, i.e. Taramakau and Kokatahi, and was common in both. The Copland study area is south of its southern natural limit in montane forests. Overall, tawheowheo can be considered an ‘increaser’, i.e. in stem density in Kokatahi and in biomass in Taramakau. The rate of increase of tawheowheo was greater at lower altitudes than at higher altitudes in Kokatahi.

In Taramakau, at an individual plot level, biomass of tawheowheo either remained constant or increased, in a few cases by as much as 80%. Most plots in Kokatahi had substantial (>100%) increases in biomass of tawheowheo. However, total biomass of tawheowheo decreased very slightly during the census period. This is because a few plots lost most of their tawheowheo biomass; this was probably the result of large trees being destroyed by landslides.

Tawheowheo had a ‘reverse J’ distribution in both Taramakau and Kokatahi. Numbers of stems in Taramakau remained high during the 14-year census period, and the changes in size class distribution over time suggest growth of smaller stems into larger size classes without compensatory recruitment into the smallest size class. In contrast, stem numbers in Kokatahi more than doubled during the census period, and the size class distribution became progressively more skewed to the smallest size class.

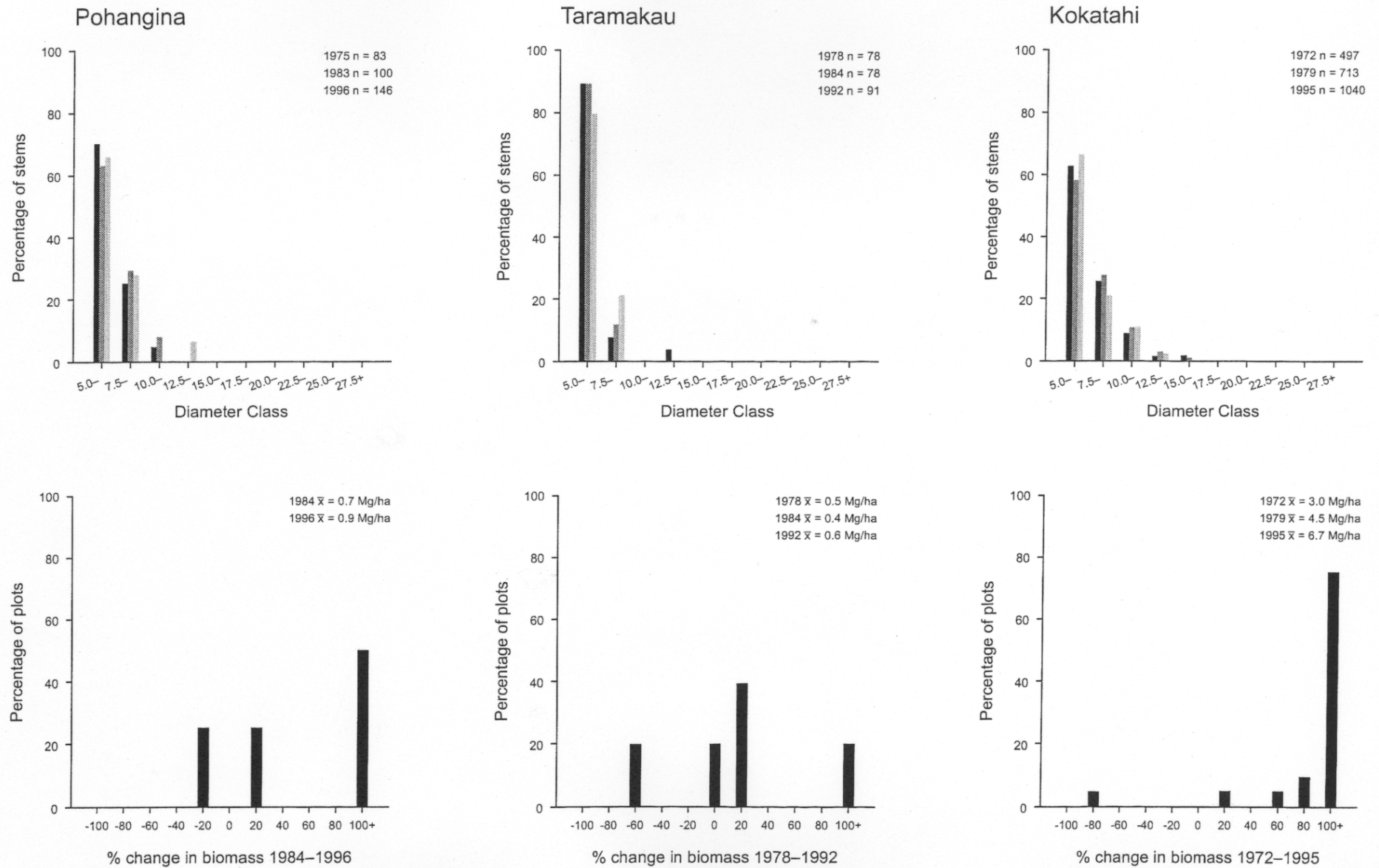


Figure 5. changes over time in stem size-class distribution and in biomass for horopito (*Pseudowintera colorata*) in three study areas. The size class distribution is shown as percentage of stems in 2.5 cm diameter size-class intervals. Within each size class, bars in the histograms show the earliest census at the left and the most recent census at the right. Total numbers of stems at each census are shown. The percentage of plots exhibiting change in biomass of horopito during the census period are shown, in intervals of 20% change in biomass. Total biomass at each census is shown (note 1975 biomass could not be calculated for Pohangina).