SOUTHERN RATA (*METROSIDEROS UMBELLATA* CAV.) MORTALITY

IN WESTLAND, NEW ZEALAND

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ABSTRACT

Defoliation was used to test the hypothesis that young southern rata trees, because of a greater ratio of green to non-green tissue, may be better able to withstand browsing than more mature trees. Three factors emerged as being important: (1) the timing and (2) extent of leaf loss, and (3) the age of the tree. Partial defoliation at all stages of the growing season depressed growth more in old than in young trees. Total defoliation before budbreak markedly depressed growth in old and young trees, but did not result in the death of shoots. All shoots totally defoliated immediately after budbreak died over winter. Conversely, shoots totally defoliated in late autumn survived. Only those of one young tree however put on any measureable growth the next season. The role of possums (*Trichosurus vulpecula* Kerr) in mortality of southern rata in Westland coniferous-broadleaf forests is discussed in the light of these results.

INTRODUCTION

New Zealand's flora evolved in the virtual absence of vertebrate grazing pressure, although the moas, an extinct group of large flightless birds (Order Dinornithiformes), may have browsed quite heavily on the native vegetation (Bull and Whitaker 1975). As a result, the introduction of a wide range of grazing and browsing herbivores during the colonisation of New Zealand by Europeans in the 18th and 19th centuries (Wodzicki 1950), has led to the severe modification of many plant communities and the virtual elimination of some (McCaskill 1973).

In the higher rainfall areas of the South Island west of the Southern Alps, coniferous-broadleaf forests occupy much of the steep and relatively unstable mountainlands associated with the Alpine Fault, a major geological faultline (Fig. 1). This forest community reaches its maximum extent in central Westland, where beech (*Nothofagus*) species are absent (Wardle 1963, 1964, Willett 1950).

Over much of their range, these coniferous-broadleaf forests are experiencing extensive mortality of several of the major canopy species, notably southern rata (*Metrosideros umbellata**),

*** nomenclature follows Allan (1961) except where otherwise indicated.
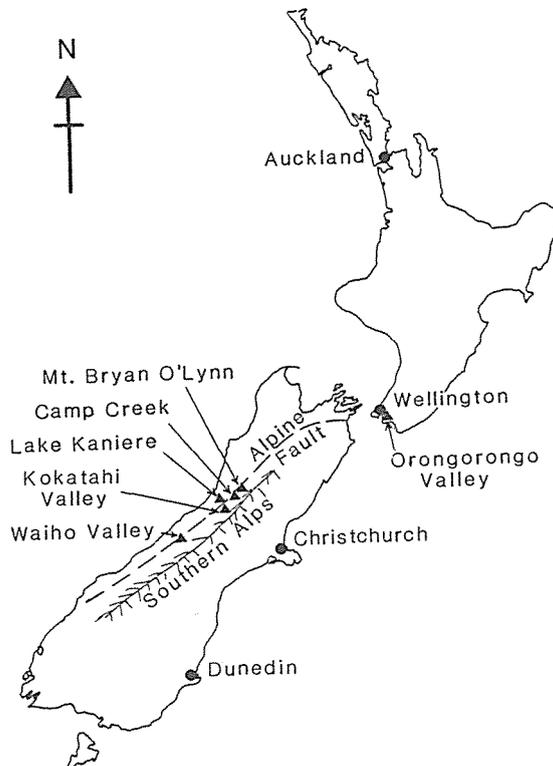

Figure 1. Map of New Zealand showing localities in the text.

kamahi (*Weinmannia racemosa*), Hall's totara (*Podocarpus hallii*) and mountain cedar (*Libocedrus bidwillii*). Although a variety of possible causes have been advanced, most published studies have been linked increases in mortality, at least of southern rata and kamahi, to the buildup of populations of the Australian brush-tailed possum (*Trichosurus vulpecula* Kerr) (Fitzgerald and Wardle 1979, J. Wardle 1974, P. Wardle 1971). This animal was liberated at numerous localities in Westland between 1895 and 1930 to establish a fur industry (Pracy 1962). The emphasis on possum damage has recently been questioned by Stewart and Veblen (1982a, b) and Veblen and Stewart (1982)
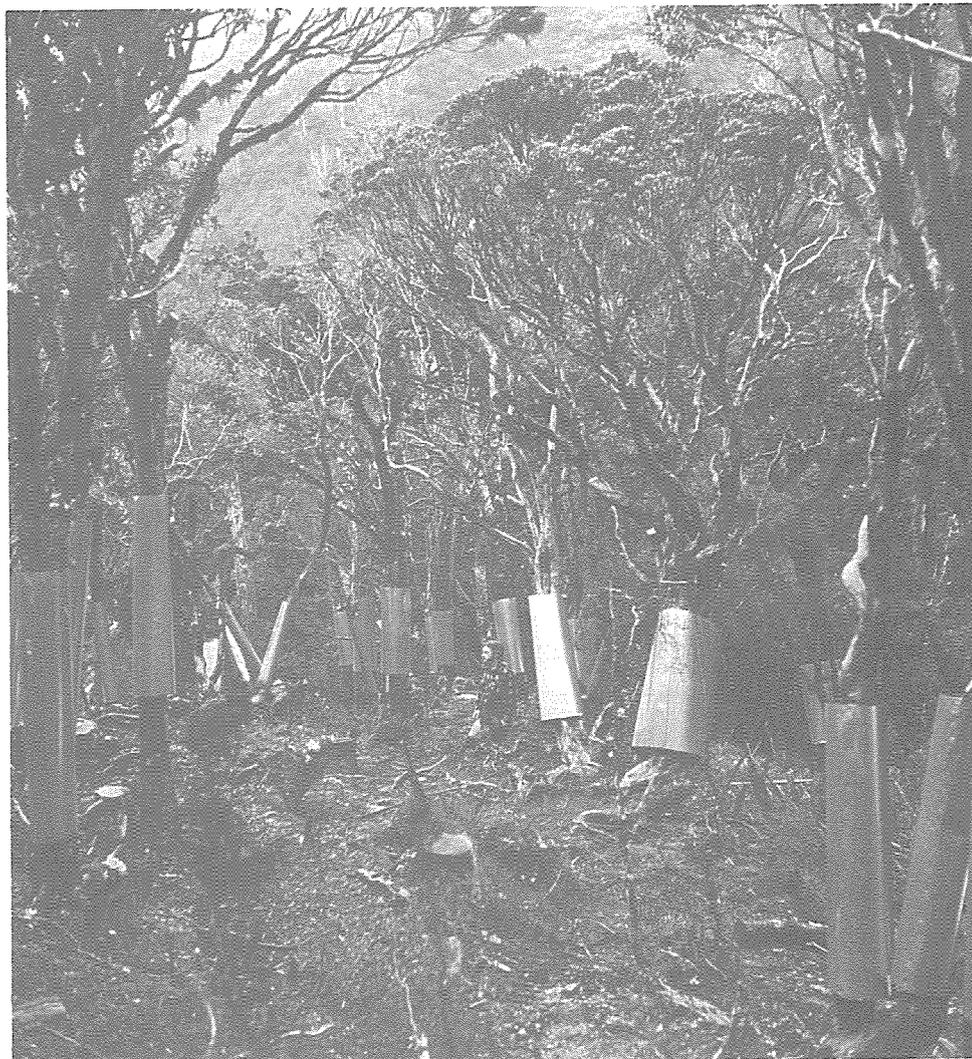
Figure 2. Experimental trees at the 800 m site with the metal bands used to exclude possums. Photo. M. Clark.

who argue that possums may merely hasten existing natural stand processes.

All three tree-forming *Metrosideros* species in New Zealand (*M. excelsa*, *M. robusta* and *M. umbellata*) are extensively browsed by possums. However direct experimental evidence that sustained possum browsing results in death is available only for *M. robusta* (Meads 1976). In Westland, mortality of southern rata (*M. umbellata*) considered to be associated with the buildup of possum populations appears to be confined initially to larger (older) individuals (P. Wardle 1971), despite trees of all size (age) classes being browsed.

Woody perennials undergo a reduction in the ratio of leaf tissue (net energy producing) to stem and root tissue (net energy utilising) with increasing age (Larcher 1975). Hence net energy

surpluses can be expected to be greater in young than in older trees. Payton (1983) examined the hypothesis that young southern rata trees, because of a greater ratio of green to non-green tissue (and therefore a more positive carbon balance), may be better able to withstand defoliation than older trees. Results from measurements of the effects of artificial defoliation in the season of defoliation (1981-82), supported the hypothesis. Measurement of these effects over the two seasons after defoliation (1981-82, 1982-83) are presented in this paper, with a discussion of their relevance to the role of possums in the mortality of southern rata in Westland.

Experimental Methods

Old and young trees of southern rata were artificially defoliated at two sites in the Camp Creek catchment, Alexander

Range, Westland (Lat. 42°40', Long. 171° 32'), to determine their response to foliage loss at different stages of the growing season. Both sites are on a north-facing slope in the upper forest zone (800 m and 1000 m a.s.l.), with the higher site being at the upper altitudinal limit for southern rata in Camp Creek.

Three major criteria influenced the choice of sites: (1) if a carbon balance concept operates, it is likely to be most obvious at or near the environmental limits of the species; (2) both sites are in areas where possum densities are still low (one to two animals/hectare), so that browsing by possums can be eliminated as a significant factor already affecting the survival of the sample trees; (3) the crown size and height of trees at these sites are small enough for hand defoliation to be a practical proposition.

All experimental trees at the 800 m site were banded with sheet tin, and the surrounding foliage was cleared away to prevent access by possums (Fig. 2). At the 1000 m site, the low canopy height (2-3 m) and the twisted nature of the stems made this impractical. Basal stem diameter measurements at the 1000 m site ranged from 14.0 to 30.0 cm (mean 19.3 cm) for old trees and 4.5 to 8.3 cm (mean 6.8 cm) for young trees. Diameters at the 800 m site ranged from 37.2 to 62.0 cm (mean 47.1 cm) for old trees, and 8.0 to 13.5 cm (mean 9.8 cm) for young trees. With the exception of old trees at 800 m, where because of the size of the task major branches were used, whole trees were defoliated. At both sites, three defoliation treatments were imposed on both old and young trees during the 1981-82 growing season: 0%, 50% (one of each pair of leaves removed) and 100%. Two replicates were defoliated before budbreak (mid September - mid December), two immediately after budbreak (mid January - mid February), and one at the end of the growing season (late April - early May).

Measurements of bud length, twig length and leaf area (800 m site only) of canopy foliage, were used to assess the effects of defoliation over the 1981-82 and 1982-83 seasons. Bud and twig measurements were made on three shoots (or pairs of shoots) in each of three canopy branches per tree/branch . Destructive sampling (five shoots per tree/branch) was used to determine leaf area of current season's foliage. In addition, dendrometer bands were used during the 1982-83 and 1983-84 growing seasons to measure diameter increment of trees with a basal diameter ⩾ 7.5 cm.

RESULTS

Growth of Nondefoliated Trees

Southern rata produces a single seasonal shoot from one or both of a pair of terminal buds produced the previous autumn (Fig. 3). Where both buds flush, the dichotomous branching pattern characteristic of the species is produced (Dawson 1968).
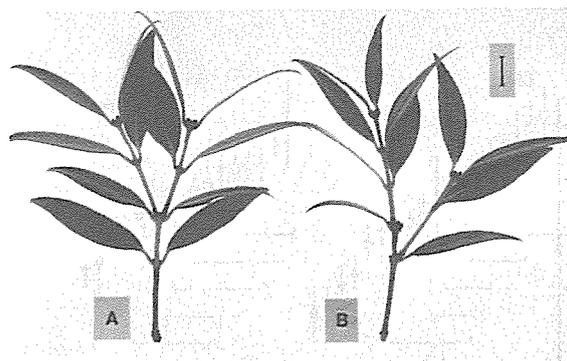

Figure 3. Normal growth (A) and growth after partial post-budbreak defoliation (B) in terminal shoots of southern rata. Scale = 1 cm.

In the 1981-82 growing season, little bud movement was detected before early November (late spring) at the 800 m site. The commencement of growth was delayed by about 2 weeks at the 1000 m site. Rapid bud elongation occurred at both sites during December, with leaf buds flushing in early January (mid summer). Twig elongation, much of which took place before the leaves had expanded sufficiently for it to be measured, had ceased at both sites by mid March (early autumn) (Fig. 4 *in* Payton 1983). Leaf growth (expressed in terms of area) continued well into April at the 800 m site. Diameter growth rates at both sites were low (< 1.0 mm/annum) in both seasons measured (1982-83 and 1983-84). Some nondefoliated trees at 1000 m produced no measurable growth (< 0.1 mm) over a season.

In the second season (1982-83), bud growth at both sites began about 2 weeks later than in the previous season. Because of lower than average temperatures throughout the growing season, buds did not flush until early-mid February at 800 m and late February-early March at 1000 m. Twig growth was completed by late March at 800 m and by early April at 1000 m. Leaf growth (measured at the 800 m site) however, continued into early May.

Values for bud and twig growth (mean ± S.E.) for all experimental trees are given in Figures 4 and 5. For both sites and over both seasons, variability in bud length between nondefoliated trees was attributable to differences between individual trees rather than to differences between young and old trees. These differences are likely to have been accentuated by the closeness of the final measurement to actual budbreak as bud growth is rapid immediately before flushing (Fig. 4 *in* Payton 1983). At neither site were there significant seasonal differences in bud length. Twig length values followed a similar pattern, with significant differences being between individual trees rather than between young and old trees. Twig growth for all treatments however was significantly depressed
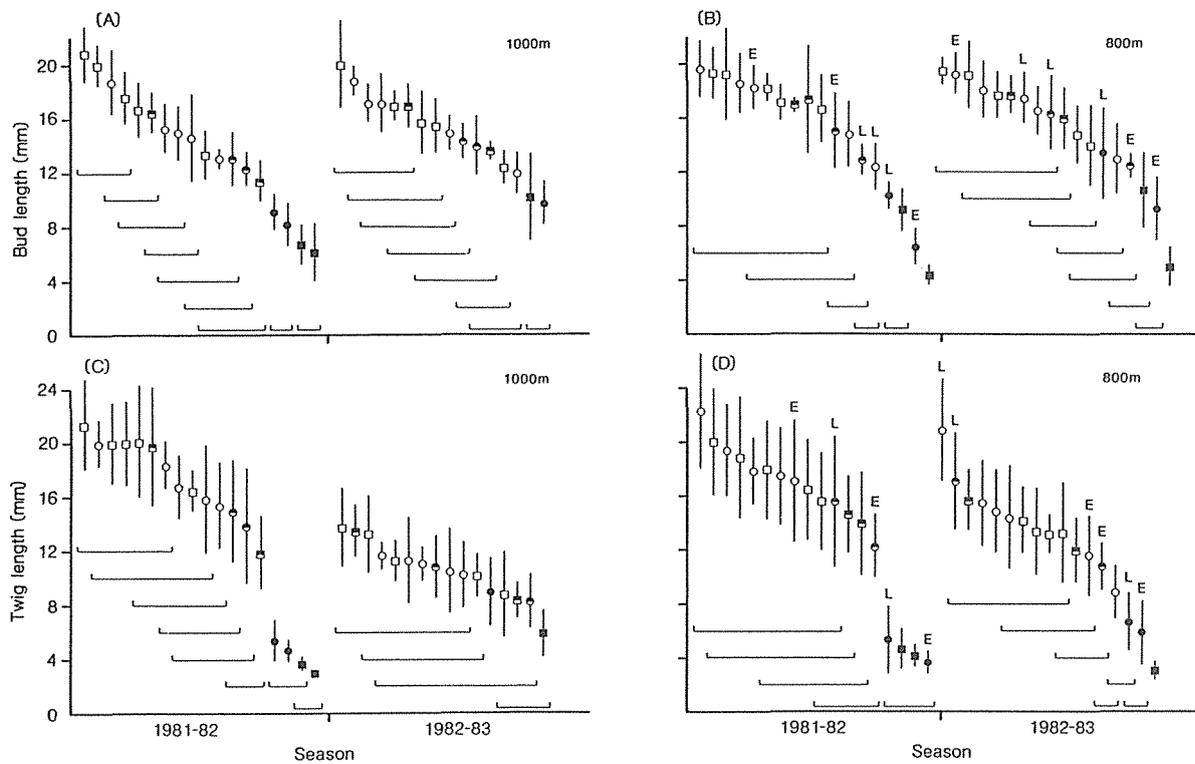
Figure 4. Maximum seasonal extension (bud and twig) in prebudbreak defoliated shoots of old (O) and young (□) rata trees over the next 2 seasons.
(Levels of defoliation 0% O □ , 50% ⊖ ⊟ , 100% ● ▣ ; values not significantly different (P<0.01) are joined by a solid line; where major branches were defoliated (old trees at 800 m) upper case letters denote within-tree treatments for old trees defoliated before budbreak in early (E) and late (L) spring. All other trees at both sites were subject to only one defoliation treatment.)

(P<0.01) at both sites during the 1982-83 season, which was colder than normal.

Pre-budbreak Defoliation

Defoliation before budbreak had the immediate effect of slowing down bud elongation. This is most easily seen in the two old trees at the 800 m site where individual branches within the trees were defoliated (Fig. 4B). In the earlier defoliated tree (E), bud length was significantly depressed both in the branch partially defoliated in early-mid October (P<0.05), and in the branch totally defoliated in mid-September (P<0.01). In the old tree defoliated closer to budbreak (L, defoliated late November-early December), bud length was significantly depressed (P<0.01) only in the totally defoliated branch. In both these trees this pattern continued into the 1982-83 season, with defoliated branches on the earlier stripped tree (E) still showing a more marked depression in bud growth than those on the tree stripped closer to bud-break. The growth of buds in both young trees at 800 m partially defoliated before

budbreak (early-mid October and early-mid November) remained within the range of that for young nondefoliated trees over both seasons. As for old trees, total defoliation significantly depressed bud growth (P<0.01) in both seasons, but did not result in death.

A similar pattern of depressed bud growth after defoliation occurred at 1000 m (Fig. 4A). Here again, particularly for partially defoliated trees, the timing of the defoliation was important. Bud length values for the pair (one old, one young) of trees partially defoliated in mid-late November fell just outside the range of values for nondefoliated trees, and did not differ significantly from one another. The effects of partial defoliation closer to budbreak (mid-December) were more evident in the old tree than in the young tree. Bud growth was significantly depressed (P<0.01) in all four trees (two old, two young) totally defoliated at the 1000 m site before budbreak. In the season after defoliation (1982-83), bud length values for partially defoliated trees fell within
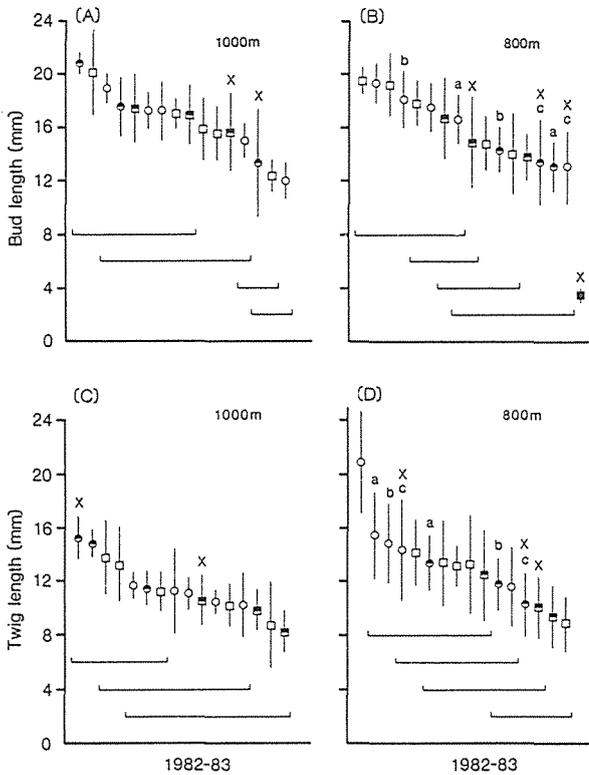
The response of twig growth to defoliation at 1000 m (Fig. 4C) mirrored that of bud growth in 1981-82, the season of defoliation. Twig growth in all trees at this site was markedly depressed (P<0.01) during the 1982-83 season, with the result that few significant differences could be detected between defoliation treatments.

The effects of defoliation on leaf area were investigated at the 800 m site. Mean leaf area per shoot was significantly greater (P<0.01) in young than in old nondefoliated trees in both seasons. Both old and young trees showed a significant reduction (P<0.01) in the leaf area of current season's foliage in the 1982-83 season as cool summer temperatures delayed budbreak. Although pre-budbreak defoliation did not affect the timing of budbreak, it did affect the size of the leaves subsequently produced (Fig. 6). Partial defoliation before budbreak resulted in a significant decrease in the leaf area of current season's foliage (P<0.05) in both old trees, but only in the season of defoliation (1981-82). Partial defoliation did not result in a significant reduction in leaf area in young trees. In contrast, total pre-budbreak defoliation significantly reduced leaf size (P<0.01) in old and young trees over both the season of defoliation (1981-82) and the following season (1982-83). It did not however result in the death of shoots.

Figure 5. Maximum seasonal extension (bud and twig) in the season after post-budbreak and end-of-season (x) defoliation. (Lower case letters denote within-tree treatments; see Fig. 4 for symbol details.)

the range of values for nondefoliated trees at this site. They remained significantly depressed (P<0.01) in totally defoliated trees.

Pre-budbreak defoliation depressed twig growth in a similar manner. For old trees at 800 m (Fig. 4D), twig growth in both partially and totally defoliated branches was depressed more in the earlier defoliated tree (E) than in the tree defoliated closer to budbreak (L), in the season of defoliation (1981-82). This trend was reversed in partially defoliated branches of old trees in the season after defoliation (1982-83) when twig growth was significantly depressed (P<0.01) only in the tree defoliated closer to budbreak (L).

Partial defoliation did not significantly depress twig growth in young trees at 800 m in either season. Total pre-budbreak defoliation however, significantly depressed twig growth (P<0.01) in both old and young trees in both seasons at this site.
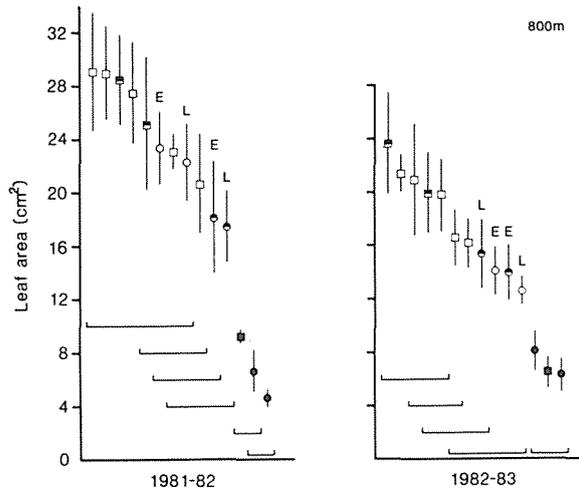
Figure 6. Leaf area of shoots produced at 800 m over the 2 seasons after pre-budbreak defoliation. (Values given are for both surfaces of four-leaf shoots; see Fig. 4 for letter and symbol details.)

The new foliage produced after total defoliation proved palatable to several insect species which restripped the trees (branches) in mid-late February 1982 (Payton 1983). As a result, canopy measurements were discontinued in several of the totally defoliated trees.

Partial defoliation before budbreak tended to depress the already low rates of diameter increment in both old and young trees at both sites. No radial increment was found in any totally defoliated trees or branches at either site.

Post-budbreak Defoliation

In southern rata, the period of maximum twig elongation occurs during and immediately after budbreak (Payton 1983). Thus by the time the leaves have unfolded sufficiently for post-budbreak defoliation to be possible, much of the current season's twig growth has been completed. Partial defoliation after budbreak did not lead to a significant change in size of the remaining leaves.

Partially defoliated shoots set normal terminal buds and overwintered satisfactorily. In most of these shoots however, only the terminal bud with an adjacent leaf expanded the following season (1982-83). The first pair of lateral buds developed in the same way (Fig. 3). On nondefoliated shoots, these buds remain dormant. In the few examples where both terminal buds flushed, the shoot developing adjacent to the leaf was consistently the larger.

In the season after defoliation (1982-83) at both sites, bud and twig growth of the two young trees which had been partially defoliated immediately after budbreak was not significantly different from that of some or all of the young nondefoliated trees (Fig. 5). The same was true of old trees at the higher (1000 m) site. For old trees at 800 m, where branches rather than whole trees had been defoliated, a within-tree comparison was possible. Here partial post-budbreak defoliation depressed bud growth in the next season at the one percent level in one old tree and at the five percent level in the other. Twig growth in the season after defoliation (1982-83) was significantly depressed (P<0.01) only in the former tree.

Shoots totally defoliated after budbreak appeared healthy during autumn 1982, but died over winter. The only exceptions were buds with an adjacent intact leaf and the subcanopy branches of old trees at 800 m, where there was limited bud survival. Where whole trees were defoliated, regrowth was limited to small clusters of epicormic shoots well down the stem and at the base of the trunk.

End-of-season Defoliation

Where whole trees were partially defoliated at the end of the growing season, shoot growth (bud and twig) in the following season fell within the range of that for nondefoliated trees (Fig. 5, X). However twig growth in the partially defoliated branch of the old tree at 800 m (Fig. 5D, c) was significantly depressed (P<0.01).

In trees totally defoliated at thé end of the growing season, most undamaged buds survived the winter. Only in the young tree at 800 m however, were there any signs of bud growth the following spring. In this tree, some 50-60% of terminal buds grew slowly through spring and early summer, but died before budbreak (Fig. 5B). By June 1984, total end-of-season defoliation in 1982 had resulted in the canopy death of old and young trees at both sites. All however show some epicormic growth on the lower part of the stem.

DISCUSSION AND CONCLUSIONS

Results presented in this paper, which cover the 2 seasons after defoliation, confirm and extend the conclusions drawn by Payton (1983) from the measurements taken in the season of defoliation (1981-82). Three factors emerge as being important in determining the response of southern rata to leaf loss; (1) the timing and (2) extent of defoliation, and (3) the age of the tree.

At both experimental sites the growth of nondefoliated rata trees was very slow, with minimal wood increment. This by itself suggested a tight energy budget. Defoliation in effect removed all or part of the photosynthetic tissue, and with it the ability to fix energy. Thus the effect of defoliation on subsequent growth provided an indication of the extent to which stored energy reserves and/or current photosynthate were important in the seasonal growth of southern rata.

Where defoliation was carried out before budbreak it had the immediate effect of slowing down bud growth. Thus the closer to budbreak the defoliation, the less its impact. The effect of defoliation on bud growth was most marked in totally defoliated shoots, where subsequent bud growth was minimal. This suggested that spring bud growth is largely dependent on current photosynthate.

Defoliation after budbreak did not affect shoot growth that season. Where shoots were partially defoliated, terminal buds with an adjacent leaf during the latter part of the season of defoliation (1981-82) grew normally the next season (1982-83). Buds lacking an adjacent leaf over this period survived only where other leaves were present on the twig. By contrast, twigs totally defoliated at the end of the growing season survived winter 1982, but were able to put on little or no growth the next season (1982-83). This suggested that overwinter bud survival is closely linked to the ability to build up carbohydrate (energy) reserves after flushing (Kramer and Kozlowski 1979) and further supported the view that the survival and growth of these buds in the next season is largely dependent on current season's photosynthate.

Where there was a differential response of age to defoliation, young trees proved more resilient to foliage loss than old trees in the 2 seasons after defoliation (Fig. 4). This was most evident at 800 m. At the 1000 m site, where growth rates in nondefoliated trees were low, age was less of a factor governing the response to defoliation. This site is at the upper altitudinal limit of southern rata in the Camp Creek catchment.

Both experimental sites were located in low fertility, mixed-aged stands showing little or no evidence of recent disturbance (J. Harrison, pers. comm.). On such relatively stable sites depletion of soil nutrients may also be a factor affecting tree vigour. Where young even-aged stands of southern rata have established after landslides, a common regeneration mode in the steep hill country of Westland (Stewart and Veblen 1982a), the increased vigour of such stands resulting from the greater fertility of these fresh surfaces could be expected to increase the differential response of old and young rata trees to defoliation by an agent such as the possum.

Recent studies by Fitzgerald and Wardle (1979) in the Waiho Valley and Coleman (unpubl. data) on Mt Bryan O'Lynn show that foliage of both southern rata and kamahi constitutes the bulk of the diet of possums in Westland coniferous-broadleaf forests.

The response of southern rata to browsing by possums closely follows that observed by Meads for northern rata (*Metrosideros robusta*). Meads (pers. comm.) found that possums browsed current season's shoots, beginning late summer-early autumn when the shoots had fully expanded. Heavy possum browsing over three consecutive years was sufficient to kill mature trees of northern rata in the Orongorongo Valley, near Wellington (Meads 1976). In southern rata, browsing is largely confined to the current season's foliage of canopy shoots (J. Coleman pers. comm., I. Payton unpubl. data). While the extent of browsing that southern rata will tolerate has not yet been determined, it is likely to be similar to that for northern rata, as canopy shoots of southern rata retain their leaves for 3-4 years. Work aimed at determining this is currently underway in the Camp Creek catchment, Westland.

Widespread mortality of southern rata coincident with the buildup of possum populations has been observed in Westland coniferous-broadleaf forests since the early 1940's (Chavasse 1955, Wardle 1971). As possum populations build up, at least the initial mortality is mainly confined to larger (or older) trees, while younger trees, which the present study suggests are more resilient to defoliation, remain healthy. Several early botanical observers, among them Kirk (1920) and Perham (1924), described this pattern of mortality in Westland forests, but did not recognise it as being possum related. The

characteristic patchwork nature of possum-induced mortality was not recognised until much later. For northern rata, Elder (1965) and Meads (1976) noted that individual trees could be killed or almost completely defoliated by possums while neighbouring trees were almost untouched. For southern rata, the patchwork nature of the mortality and the tendency for larger (older) trees to be more affected that less mature trees has been commented on by Chavasse (1955), Wardle (1971) and Fitzgerald and Wardle (1979).

The importance of the role of possums in the current extensive mortality in Westland coniferous-broadleaf forests has recently been questioned by Stewart and Veblen (1982a, b) and Veblen and Stewart (1982). They argue that browsing by the possum may be merely a contributary factor to the demise of already over-mature stands, and point to the continued existence of vigorous young stands of rata and kamahi in areas of dieback. Such young stands however, as the present study indicates, can be expected to be more vigorous, and therefore better able to withstand externally imposed pressures such as possum browsing, than more mature stands. Moreover recent evidence suggests that in areas such as the Kokatahi catchment, which have sustained high possum populations for some time, ultimately even these young stands may succumb.

Dead standing trees are a common feature of New Zealand forests, even where these forests have not been subject to external pressures such as those imposed by the introduction of grazing or browsing mammals. There are however, no indications that such mortality was ever as extensive as that seen today, or that species such as southern rata were being eliminated as major components of the forest (Allen and Rose 1983). Until such time therefore as there is substantial evidence to the contrary, it would be unwise to underestimate the contribution of the possum to the accelerated rates of mortality that have been observed in Westland's coniferous-broadleaf forests over the last few decades.

ACKNOWLEDGEMENTS

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