Defoliation as a Means of Assessing Browsing Tolerance in Southern Rata (*Metrosideros umbellata* Cav.)[1]

I. J. Payton[2]

ABSTRACT: Old and young trees of southern rata (*Metrosideros umbellata*) were artificially defoliated to examine their response to foliage loss. Partial (50%) or total defoliation before budbreak depressed shoot growth more markedly in old than in young trees. Fifty percent leaf loss shortly after budbreak or at the end of the growing season did not significantly impair shoot growth in either age class. By contrast, total postbudbreak defoliation resulted in the death of most shoots in both old and young trees. While the terminal buds of both old and young trees totally defoliated in late autumn showed good overwinter survival, only in the young trees were there sufficient energy reserves to enable some of these shoots to flush the following season. Young trees proved to be more resilient to foliage loss, suggesting a more positive carbon balance (energy surplus) in young trees than in older trees.

SOUTHERN RATA (*Metrosideros umbellata*) is a widespread tree species throughout areas of high rainfall on the South Island of New Zealand. In Westland, particularly in areas lacking one or more of the beech (*Nothofagus*) species, it is a major canopy species of mid- to high-altitude forests (Wardle 1971, 1977). These forests frequently occur on steep and relatively unstable hillsides associated with the major geological fault line that traverses Westland.

Between 1895 and 1930, numerous introductions of the Australian brush-tailed possum (*Trichosurus vulpecula*) were made throughout Westland to establish a fur industry (Pracy 1962). Since the early 1940s, widespread mortality of southern rata has been observed as possum numbers have built up (Coleman, Gillman, and Green 1980, Wardle 1971). Direct experimental evidence for a link between possum browsing and southern rata mortality such as Meads (1976) has produced for northern rata (*M. robusta*) is not yet available. However, considerable circumstantial evidence exists for such a link,

since the numbers of dead rata crowns increase as possum numbers grow (Fitzgerald and Wardle 1979, Pekelharing 1979, Wardle 1974). In areas where possums are browsing southern rata, at least the initial mortality is primarily confined to large (or old) trees, while adjacent younger stands remain healthy (Wardle 1971). However, examination of the canopies of these trees reveals that both old and young trees are browsed.

Over the life-span of woody perennials, the ratio of leaf (net energy-producing) tissue to stem and root (net energy-utilizing) tissue is progressively reduced. Young trees have a large crown relative to the amount of stem and root tissue, resulting in substantial reserves being available for growth (Larcher 1975). Much of this surplus carbon is channeled into wood production (Waring 1980). As maturity approaches, this increase in biomass, with its corresponding increase in respiratory losses, is accompanied by a static or declining crown size. This progressively moves the tree toward a nil energy balance where energy inputs balance energy requirements (Figure 1).

Defoliation results in a loss of leaf (net energy-producing) tissue. This paper examines the hypothesis that young rata trees, because of a greater ratio of green/nongreen
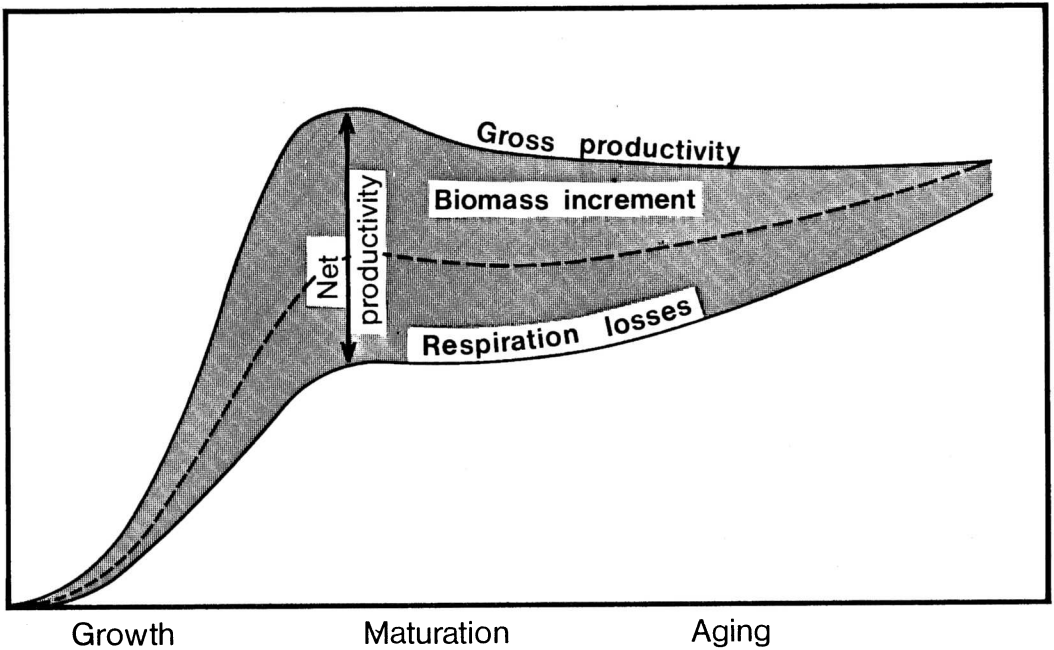
FIGURE 1. Changes in gross productivity (upper line), net productivity (shaded area), biomass increment (area above the dashed line), and respiratory losses (lower line) occurring over the life-span of a tree. (Adapted from Larcher 1975.)

tissue (and therefore a more positive carbon balance), may be able to withstand defoliation better than more mature trees.

Young and old trees of southern rata were artificially defoliated to examine the degree of their tolerance to defoliation and the importance of the stage of the growing season at which defoliation occurs. The experimental work was carried out at two sites in the Camp Creek catchment, Alexander Range, Westland. Both are on a north-facing slope in the upper rata zone (800 m and 1000 m) with the higher site at the upper altitudinal limit of southern rata for this area (Figure 2). The sites were chosen for several reasons: (1) If a carbon balance does operate, it is likely to be most obvious at or near the environmental limits of the species. (2) Both sites are in areas of low possum density (1–2 animals per hectare), so that possum browsing can be eliminated as an important factor already affecting survival of the sample trees. (3) The crown size and height of trees at these sites is such that hand defoliation is a practical proposition.

This paper describes results for the 1981–1982 growing season from the lower (800 m) defoliation site. Data from both sites covering the two seasons after defoliation are currently in preparation.

METHODS

At the 800-m site, all experimental trees were banded with sheet tin and the surrounding foliage cleared away to prevent possums from gaining access to the trees (Figure 3). Three defoliation treatments were imposed on both old and young trees during the 1981–1982 growing season: 0%, 50% (one of each pair of leaves removed), and 100%. Because of the size of the task for old trees, major branches rather than whole trees were defoliated. Whole young trees were defoliated. Two replicates were defoliated before budbreak, two after budbreak, and one at the end of the season after measurable growth had stopped.

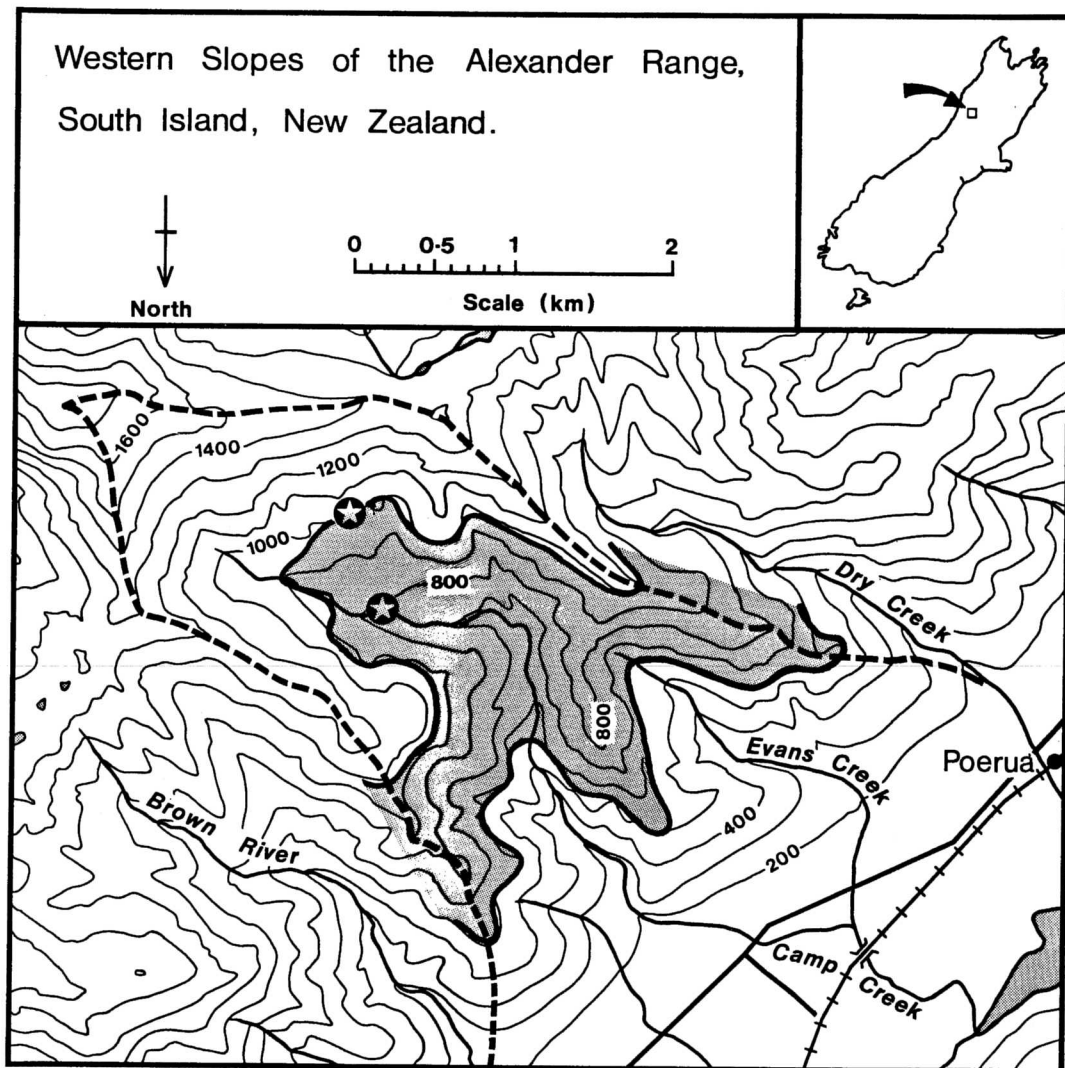Stem diameter was used to determine "old" and "young" trees. For the 800-m site, basal

FIGURE 2. Camp Creek catchment, Alexander Range, Westland, showing the experimental sites and the extent of forest with a major rata component (shaded area).

stem diameters of old trees ranged from 37 to 62 cm (mean 47.1 cm), while those of young trees ranged from 8 to 13.5 cm (mean 9.8 cm).

Measurements of bud length, twig length, and leaf weight were used to assess the effects of defoliation. 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 or branch) was used to determine

leaf weight of the current season's foliage. At the conclusion of measurements, samples of stem tissue will be taken to determine the effects of defoliation on diameter increment.

RESULTS

Growth of Nondefoliated Trees

During the 1981–1982 growing season, little bud movement was detected at the

FIGURE 3. Old and young ratas, at the lower defoliation site, banded with sheet tin to prevent access by possums.

experimental site before late spring (November). Buds elongated rapidly during December, with budbreak occurring during the early part of January (midsummer). Twig elongation, much of which took place before the leaves expanded sufficiently for it to be measured, had ceased by early autumn (mid-March) (Figure 4). However, leaf growth continued well into April (Figure 5).

Differences in bud and twig growth were nonsignificant and occurred between individual trees rather than between old and young trees (Figure 4), with the exception of one old tree that had a growing season

several weeks ahead of all other trees and a growth rate significantly greater than any other tree.

Prebudbreak Defoliation

Defoliation of old rata trees before budbreak had the immediate effect of slowing down bud elongation. In the old tree stripped in spring (100% defoliation, mid-September; 50% defoliation, early–mid-October), bud length was significantly reduced at the time of budbreak ($P < 0.01$ after total defoliation and $P < 0.05$ on the partially stripped
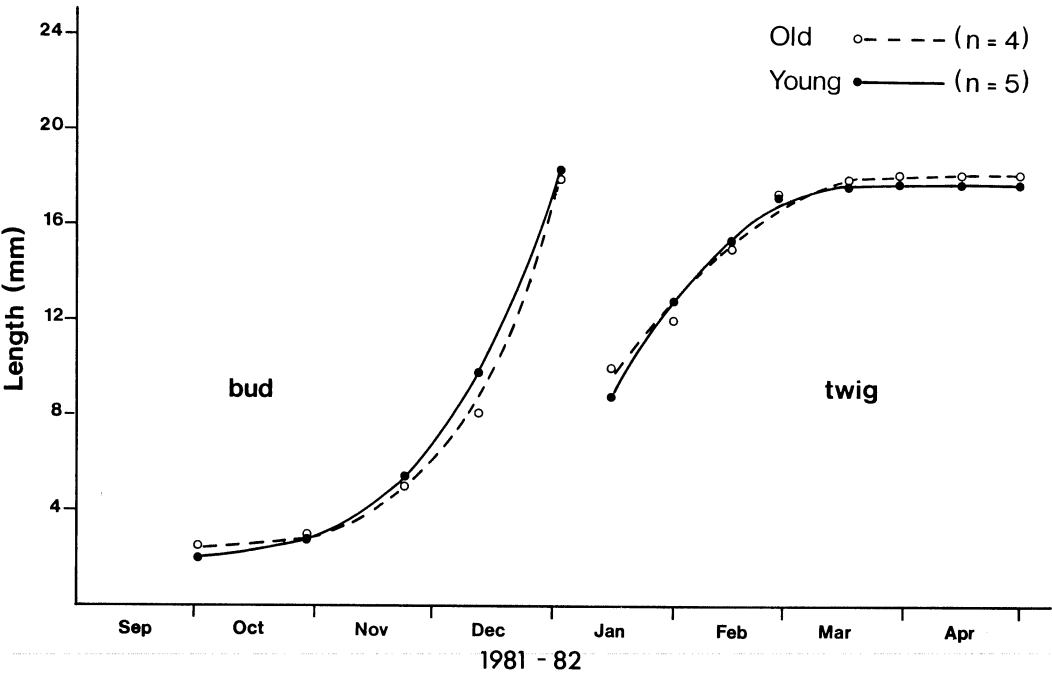
FIGURE 4. Bud and twig growth in nondefoliated ratas during the 1981–1982 growing season.
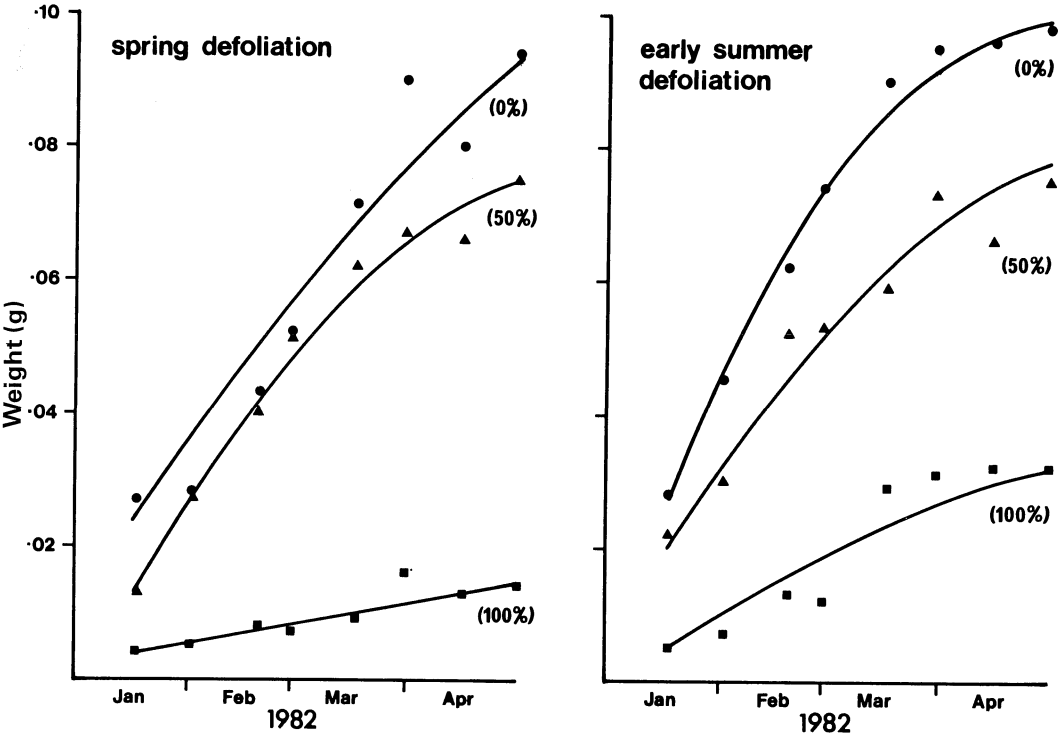

FIGURE 5. Effects of defoliation before budbreak on the weight of the current season's foliage in old trees (values given are for the second pair of leaves and are the mean of five replicates).
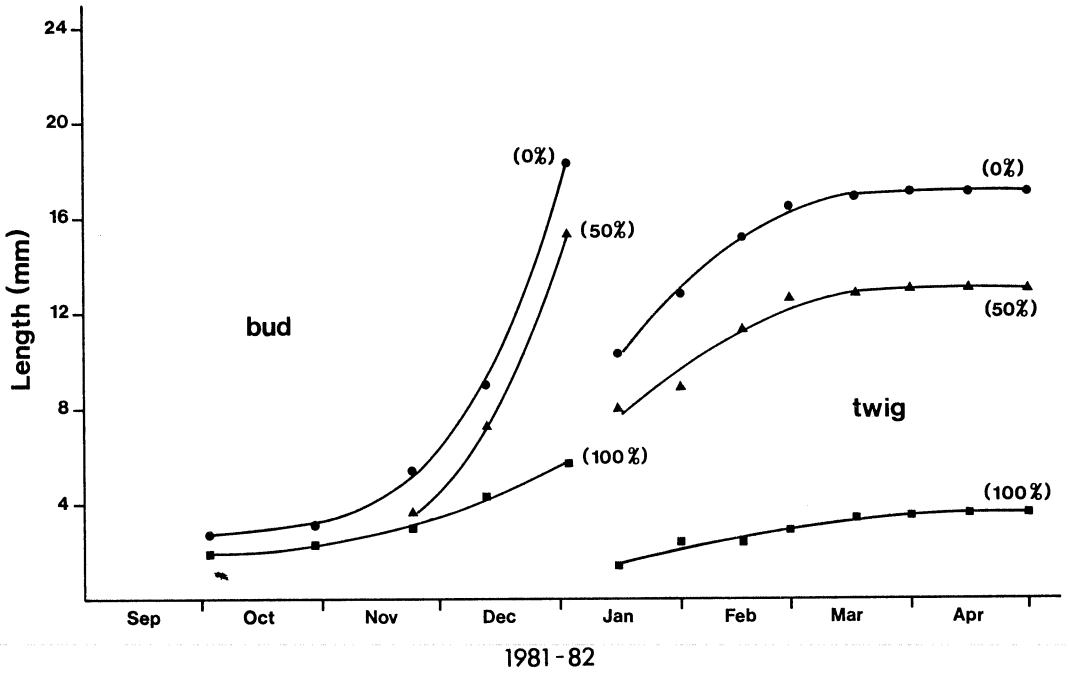
FIGURE 6. Effects of defoliation before budbreak on bud and twig elongation in an old tree.
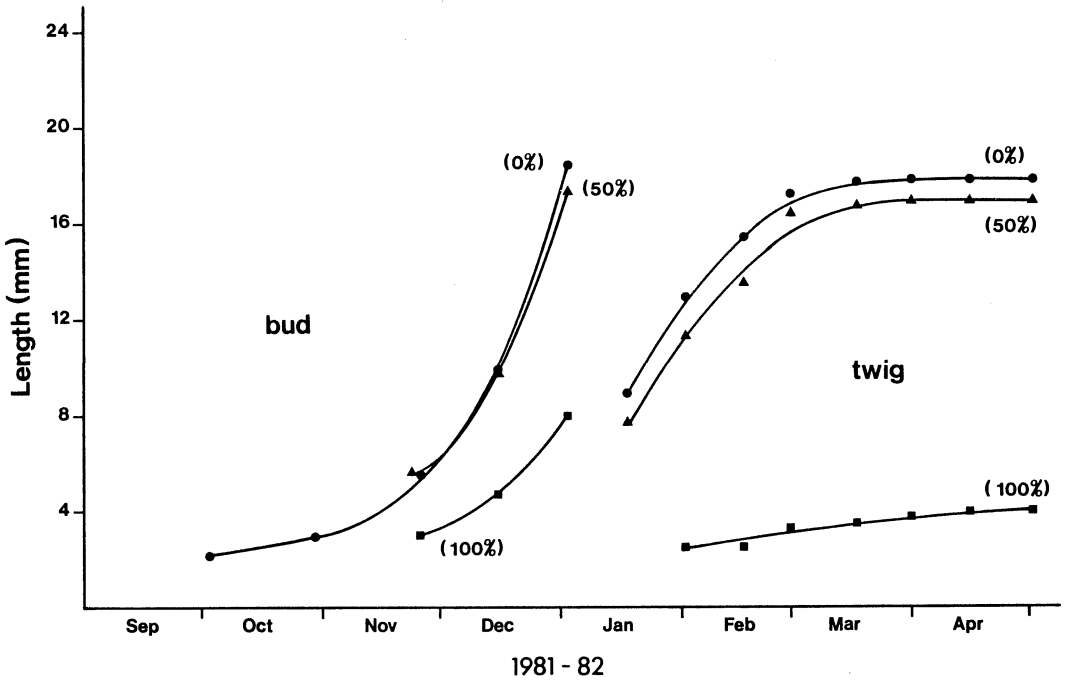

FIGURE 7. Effects of defoliation before budbreak on bud and twig elongation in young trees.

branch; see Figure 6). However, differences in bud length at budbreak were much smaller in the tree defoliated in early summer (late November and early December), being non-significant after 50% defoliation and significant at the 5% level in the totally stripped branch.

Neither timing nor extent of defoliation affected the timing of budbreak (Figure 6), but both factors influenced the weight of the new leaves (Figure 5). While partial leaf loss did not significantly depress the weight of new foliage in either tree, the slower bud growth after total defoliation resulted in a greater reduction in the weight of new foliage in the earlier stripped tree ($P < 0.01$) than in the tree defoliated closer to budbreak ($P < 0.05$).

Differences in twig growth between all three treatments were significant at the 1% level in the earlier stripped tree (Figure 6). In the partially defoliated branch of the later stripped tree, the difference was significant at the 5% level.

Young rata trees defoliated in early summer (early–mid-November) showed a similar, although less marked, response to defoliation (Figure 7). A 50% loss of foliage had little effect on the bud and twig growth of the plants. As in old trees, 100% foliage removal set the plants back significantly ($P < 0.01$) but did not kill them.

Intact shoots produced after total prebudbreak defoliation set terminal buds, overwintered satisfactorily, and grew normally—albeit more slowly than those of nondefoliated plants—the following season (1982–1983). However, in both old and young rata trees, this foliage proved very palatable to several insects, including a tortricid (*Tenopseustis obliquana*) and a geometrid (*Pseudocoremia* sp.). In late summer (mid–late February 1982), they virtually restripped whole canopies in the space of a few days. Both old and young trees attempted to replace the leaf loss by producing copious epicormic shoots, both in the canopy and well down the stem (Figure 8). Shoots developing late in the season after insect defoliation did not usually set terminal buds before the onset of winter. Rather, the growing point kept producing small leaves, a growth habit
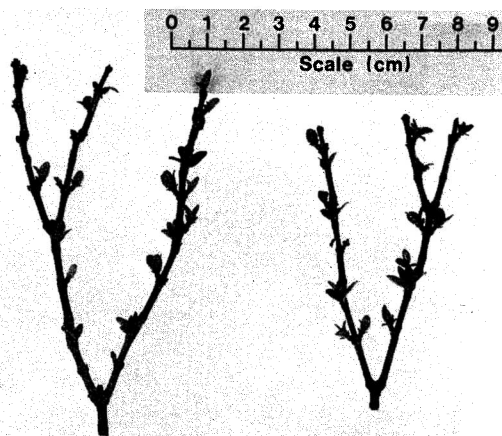

FIGURE 8. Production of epicormic shoots, after insect defoliation of trees artificially defoliated before budbreak.

characteristic of the establishment phase of rata seedlings, when height growth is all-important (Wardle 1971, Payton unpubl. data).

Postbudbreak Defoliation

By the time the leaves have unfolded sufficiently for postbudbreak defoliation to be possible, much of the current season's twig growth has been completed (Figures 4, 6, 7). However, by this stage, the pair of terminal buds that will produce the following season's growth are present. The effects of defoliation on these plants therefore did not show up until the following spring (September 1982).

In partially defoliated trees (old and young), the terminal bud adjacent to the leaf was consistently the larger of the pair. The same was true of the first pair of lateral buds. This size differential was maintained through the following season. Where both terminal buds flushed, the shoot adjacent to the leaf was consistently the larger.

In old and young trees totally defoliated after budbreak, all the terminal buds, which had been healthy in autumn, died during the winter. In most cases the twigs also died back. The only exceptions were buds with an adjacent intact leaf and the occasional bud tucked well in under the canopy. Where

whole young rata trees were defoliated, the trees appear to be dead. Where branches rather than whole trees were used (old trees), there is evidence of a little epicormic growth on some stems.

End-of-Season Defoliation

Partial defoliation in late autumn (late April–early May), after measurable growth had ceased, did not have a marked effect on the performance of either old or young trees during the following growing season. As in trees partially defoliated shortly after bud-break, buds with an adjacent leaf grew more vigorously than those without.

The terminal buds of both old and young trees totally defoliated at the end of the growing season showed a fairly good survival rate over winter. Apart from buds damaged during defoliation, most were quite healthy the following spring (early September 1982). Terminal buds of the old tree, with the exception of a few tucked well in under the canopy, died during spring and early summer 1982. The few surviving buds have shown no signs of growth. Conversely, in the young tree, the survival of terminal buds during the 1982–1983 growing season was of the order of 50–60%. At the time of writing, the majority of these buds appear healthy and have put on some growth, albeit fairly slowly. Where terminal buds in the young tree died, lateral buds on year 1 and 2 wood flushed in the season after defoliation.

DISCUSSION AND CONCLUSIONS

Partial or total defoliation before bud-break depressed shoot growth more markedly in old trees than in young ones, but did not result in death. By contrast there was little difference in the response of old and young trees to defoliation soon after budbreak. Partial leaf loss after budbreak did not seriously impair shoot growth in either age class, while total defoliation resulted in almost complete shoot death in both old and young trees. The terminal shoots of both old and young trees totally defoliated in autumn,

after measurable growth ceased, showed a good survival rate over winter. However, only in the young tree have there been sufficient energy reserves to enable some of these shoots to flush.

When there was a different response to defoliation with age, young trees proved more resilient, suggesting a more positive carbon balance (energy surplus) in young trees than in older trees. While we do not yet have data on the relationship between crown size and total biomass for southern rata, work by Grier and Waring (1974), Rogers and Hinckley (1979), and others, on a range of tree species, has shown that young trees have a greater ratio of green to nongreen tissue than older trees.

On shoots partially defoliated after bud-break, the bud adjacent to the leaf was the more vigorous of the pair. Where all leaves were removed, both buds and twigs died during the winter. By contrast, when complete defoliation followed the cessation of growth, the buds survived. Thus, the ability for over-winter bud survival appears linked to the presence of leaves during the period after budbreak, suggesting that a buildup of carbohydrate reserves before the onset of growth dormancy is involved (Mooney 1972). Such reserves act both as an energy source and by increasing the resistance of shoots to frost damage during winter (Kramer and Kozlowski 1960).

In the present experiment, the current season's foliage produced after total prebudbreak defoliation proved very palatable to insects. Foliage produced after no or partial defoliation was not palatable, which suggests that in addition to restricting growth, defoliation may also affect the defense mechanisms of the plant. There is now considerable evidence that secondary compounds—in particular, tannins and other phenolic compounds—act as a "broad-spectrum" defense mechanism against herbivores (Feeny 1970, Levins 1971). The production of such substances is relatively energy-demanding and does not appear to have a high carbon allocation priority during the growing season (Mooney and Chu 1974).

Major branches of old trees were defoliated

rather than whole trees. This did not result in substantial movement of carbon between branches in an attempt to counter the effects of leaf loss. Rather, major branches appeared to act independently in the movement of carbon, which is in line with the observation that browsed rata trees often have both healthy and dead branches.

While possum browsing is evident on both old and young rata trees, younger trees appear better able to withstand the effects of defoliation. Thus, at least in the prepeak stages of colonization by possums, mortality of southern rata appears largely confined to more mature trees. This is most obvious in stands originating after catastrophic disturbances, which tend to be even-aged. In areas such as the north bank of the Kokatahi catchment, however, which have sustained high possum populations for a long time, the elimination of southern rata is almost complete (Allen and Rose, this issue).

Whether by preventing the buildup of high possum numbers we can hope to retain southern rata as a substantial component of these forests, albeit perhaps with a younger age structure, requires a more detailed knowledge of the browsing habits of the possum. Studies are currently underway in Camp Creek. Based on the conclusions of Meads (1976) from his studies of possum browsing in northern rata, the answer may well be found in the habit of a possum (or possums) staying with a tree until death do them part, which makes sights of healthy and dead ratas side-by-side not at all uncommon.

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