

The impact of defoliation on the foliar chemistry of southern rātā (*Metrosideros umbellata*)

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Published on-line: 20 March 2006

Abstract: Brushtail possums (*Trichosurus vulpecula*) tend to eat young canopy foliage in southern rātā (*Metrosideros umbellata*), and browsing tends to be concentrated on only a few trees. Samples collected as part of an artificial defoliation experiment were analysed for NPK (nitrogen, phosphorus, and potassium), carbohydrate, and polyphenolic concentrations to determine whether changes in foliar chemistry associated with defoliation provide an explanation for these patterns of browsing. In non-defoliated trees, NPK concentrations were highest in young leaves and declined with age, while concentrations of carbohydrates and polyphenolics were independent of leaf age. Nitrogen, phosphorus and polyphenolic concentrations were consistently higher in canopy (sun) versus subcanopy (shade) foliage regardless of leaf age, a trend that was reversed for potassium. Partial (50%) defoliation had little effect on foliar chemistry, regardless of its timing. Total (100%) defoliation stimulated NPK concentrations and depressed condensed tannin concentrations of new foliage produced by the surviving shoots. These results suggest that brushtail possums may focus their feeding on only a few trees because of nutritional changes to leaves as a result of browsing.

Keywords: brushtail possums; carbohydrates; defoliation; NPK; nutrients; secondary metabolites; southern rātā.

Introduction

Southern rātā (*Metrosideros umbellata* Cav., Myrtaceae) is a major component of conifer-broadleaved forests in the high rainfall areas of the South and Stewart Islands of New Zealand (Wardle, 1971, 1991). Over much of their range, these predominantly evergreen trees are browsed by introduced brushtail possums (*Trichosurus vulpecula* Kerr) (Payton, 2000). Within stands, browsing is usually patchy with individual trees killed or almost completely defoliated while neighbouring individuals remain essentially untouched—a pattern not readily explicable in disturbance–fertility terms (Chavasse, 1955; Wardle, 1971; Payton, 1987; Reif and Allen, 1988) and anecdotally attributed to behavioural characteristics of possums (Elder, in Wardle, 1971; Payton, 1983). In Westland forests, foliage of southern rātā is a major component of possum diet throughout the year with browsing heaviest in winter and lowest in summer (Fitzgerald and Wardle, 1979; Coleman *et al.*, 1985); evidence suggests that possum browsing is largely confined to young leaves (Monks and Efford, in press)

on canopy shoots (sun foliage), and that older leaves and subcanopy (shade) foliage are largely ignored (Payton, 1985; Leutert, 1988).

Carbon and nutrient availability are important determinants of both the feeding behaviour of mammalian herbivores and the defence mechanisms of the plants they eat (Bryant *et al.*, 1983). While energetic and nutritional explanations have been useful for understanding the foraging patterns of grazing mammals in grassland ecosystems, the avoidance of plant chemical defences (Bryant *et al.*, 1991a, b) and the trade-off between optimising intake of nutrients and minimising consumption of toxic plant secondary metabolites (Dearing *et al.*, 2000) have proved more useful for predicting the feeding behaviour of browsing mammals in forest ecosystems.

Most studies on the feeding behaviour of browsing mammals focus on an evolved relationship between folivore and food source. For example, the intake of *Eucalyptus* foliage by folivorous Australian marsupials in their native environment is regulated by concentrations of a specific group of phenolic diformylphloroglucinols in the leaves (Lawler *et al.*,

1998). New Zealand's early separation from the Gondwanan landmass resulted in a flora that evolved in the absence of mammalian herbivory (Fleming, 1979). Brushtail possums, which were first introduced successfully into New Zealand in 1858 (Pracy, 1974) and have subsequently spread to most parts of all three main islands and many lesser ones (Clout and Ericksen, 2000), thus encountered a flora that had evolved in the presence of avian and invertebrate herbivory, but not mammalian herbivores.

The present study used samples, collected as part of an artificial defoliation experiment (Payton, 1983, 1985), to determine whether, in the absence of specific co-evolved plant secondary metabolites, changes in foliar chemistry associated with defoliation provide an explanation for the observed patterns of browsing by brushtail possums on southern rātā. Specifically, we were interested in the following questions: 1) How do levels of foliar constituents that are generally regarded as attractive (nutrients, carbohydrates) or deterrent (polyphenolics) differ in foliage of non-defoliated southern rātā depending on foliage type, leaf age, and season; 2) How does the level and timing of defoliation influence levels of these foliar constituents in new foliage; 3) Do changes in foliar chemistry and shoot survival as a result of defoliation provide an adequate explanation for observed possum browsing patterns and/or forest damage.

Methods

Southern rātā is a canopy-forming evergreen tree species that occurs over a wide altitudinal (sea level to c. 1100m) and latitudinal (35° 20'S – 51°S) range within the New Zealand region (Wardle, 1971; Ogle and Bartlett 1980). Canopy trees produce a single annual flush of growth, which is limited to the expansion of leaf primordia present in overwintering buds. Shoots normally bear two to three pairs of leaves, but may have as few as one pair, or as many as five pairs. Leaves are retained for three to seven years, with subcanopy shoots tending to retain leaves longer than canopy shoots (Payton 1989).

Experimental defoliation

Large and small trees of southern rātā were artificially defoliated at a site in Camp Creek, a small (approximately 6 km²) steep-sided catchment on the northwestern slopes of the Alexander Range, Westland (42° 42'S, 171° 34'E), to determine their response to foliage loss at different stages of the growing season. The study site was located on a piedmont fan (800 m a.s.l.) with heavily leached soils (Harrison, 1985; Stewart and Harrison, 1987), near the upper altitudinal limit of southern rātā-dominated forest in the catchment

(Payton, 1983, 1989). The site was selected because possum densities, determined by the point-distance nearest-neighbour technique (Batcheler 1971, 1975), were low (1–2 animals per hectare) meaning that browsing by possums could be eliminated as a significant factor already affecting the survival of the trees; and the crown size and height of individual trees were such that hand defoliation was a practical option. Canopy height at the site was seven metres (Payton, 1989).

All experimental trees were banded with galvanized iron sheeting and the surrounding foliage was cleared away to prevent access by possums. Three defoliation treatments were imposed on both large (37–62 cm diameter at breast height, dbh) and small (8–14 cm dbh) trees during the 1981–82 growing season: 0%, 50% (one of each pair of leaves removed), and 100%. Entire small trees and major branches of large trees were defoliated. Where major branches, as opposed to whole trees, were defoliated, growth data show that large trees were less resilient to foliage loss than young trees (Payton 1983, 1985), indicating that non-defoliated parts of the tree did not lessen the effect of defoliation. Two replicates of each size class were defoliated before budbreak (mid-September to mid-December), two immediately after budbreak (mid-January to mid-February), and one after measurable growth had stopped (late April to early May). A further two replicates of each size class were defoliated before budbreak in the 1982–83 growing season. In total, 21 small trees and major branches from seven large trees were either non- (0%), partially (50%) or totally (100%) defoliated.

Foliage sampling and analyses

Samples for chemical analysis were collected from all experimental trees during the 1982–83 growing season. Both canopy (full sun) and subcanopy (shade) foliage was sampled from large trees. Foliage sampling on small trees, which lacked a well-defined subcanopy layer, was restricted to the canopy. Bud scale scars were used to identify the leaf age. Foliage samples were collected at two- (seasonal trends) or three- (defoliation effects) monthly intervals. Sampling was carried out at the end of the month. All samples were collected between 9.00 a.m. and noon, and frozen in dry ice within 15 minutes of collection. In the laboratory foliage samples were freeze-dried, ground in a Wiley Mill to pass through a 40-mesh screen, and held in airtight containers until required for analysis.

Samples were analysed for NPK (nitrogen phosphorus, potassium) and carbohydrate (soluble sugars, starch) concentrations, as well as a generalised measure of carbon-based secondary metabolites as represented by polyphenolic (condensed tannins, total phenolics) concentrations. Samples analysed for NPK

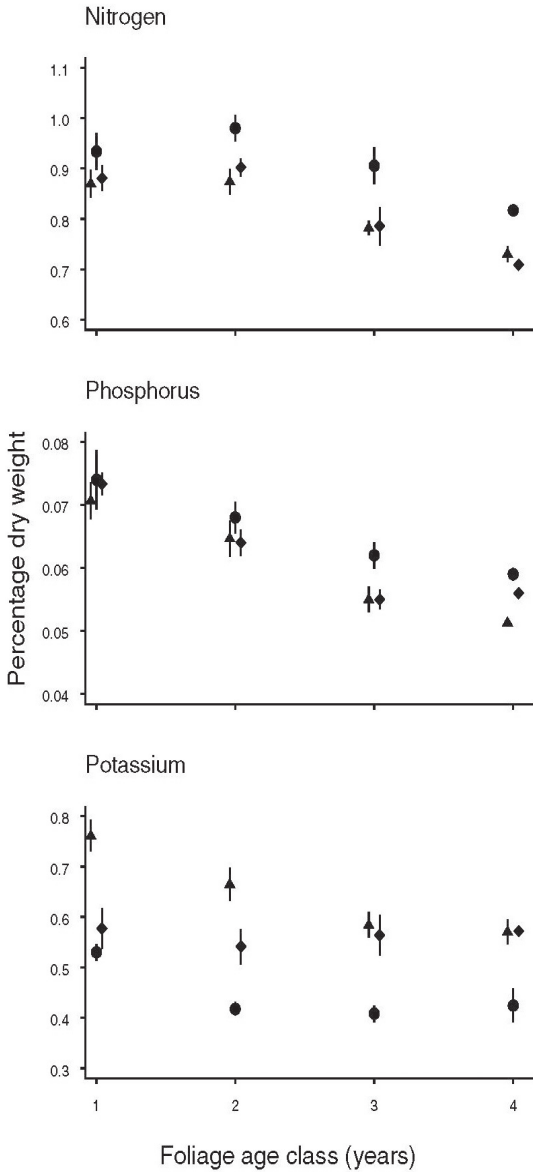


Figure 1. Trends in nitrogen, phosphorus, and potassium concentrations of canopy (large and small trees) and subcanopy (large trees) foliage of non-defoliated southern rātā trees as a function of leaf age, at Camp Creek, Westland, October 1982. Data are means \pm 1 SE from three replicates. Missing error bars are within the symbol. ● Large tree, canopy foliage; ▲ Large tree, subcanopy foliage; ◆ Small tree, canopy foliage.

were digested with sulphuric acid/hydrogen peroxide using a block digester (Nicholson, 1984). Nitrogen and phosphorus concentrations in the digest were determined by automated colorimetric methods (using the N-indophenol blue method and P-vanadomolybdophosphoric yellow method respectively), and potassium by atomic absorption spectroscopy. Concentrations of soluble sugars and starch were determined colorimetrically: sugars following extraction of the plant material with 62.5% (v/v) methanol (Haslemore and Roughan, 1976), and starch following extraction of the resulting residue with 0.5M sodium hydroxide (Dekker and Richards, 1971). Concentrations of condensed tannins, measured as catechin equivalents (Broadhurst and Jones, 1978), and total phenolics, measured as tannic acid equivalents (Price and Butler, 1977), were also determined colorimetrically following extraction of the plant material with 50% (v/v) acetone.

Data analysis

Foliar chemistry comparisons by leaf age and tree size/ foliage type were made using two-way ANOVA. The data on seasonal trends and the defoliation experiments were obtained by longitudinal sampling of the experimentally manipulated trees and were analysed using linear mixed models (Pinheiro and Bates, 2000). Tree was included as an additive random effect in all of these models. Year, tree size, level of defoliation (where applicable), and collection date were modelled

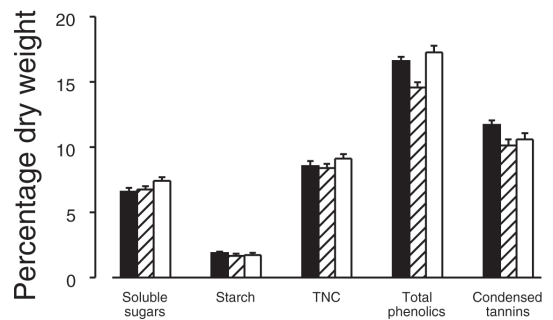


Figure 2. Trends in soluble sugar, starch, total nonstructural carbohydrate (TNC), total phenolic, and condensed tannin concentrations of large tree canopy (solid bars), large tree subcanopy (hashed bars), and small tree canopy (open bars) foliage of non-defoliated southern rātā trees. Trends in the concentrations of these components were independent of leaf age thus data from four foliar age classes (1, 2, 3, or 4 or more years old) were combined. Data are means \pm 1 SE from 12 replicates, three from each of four foliar age classes.

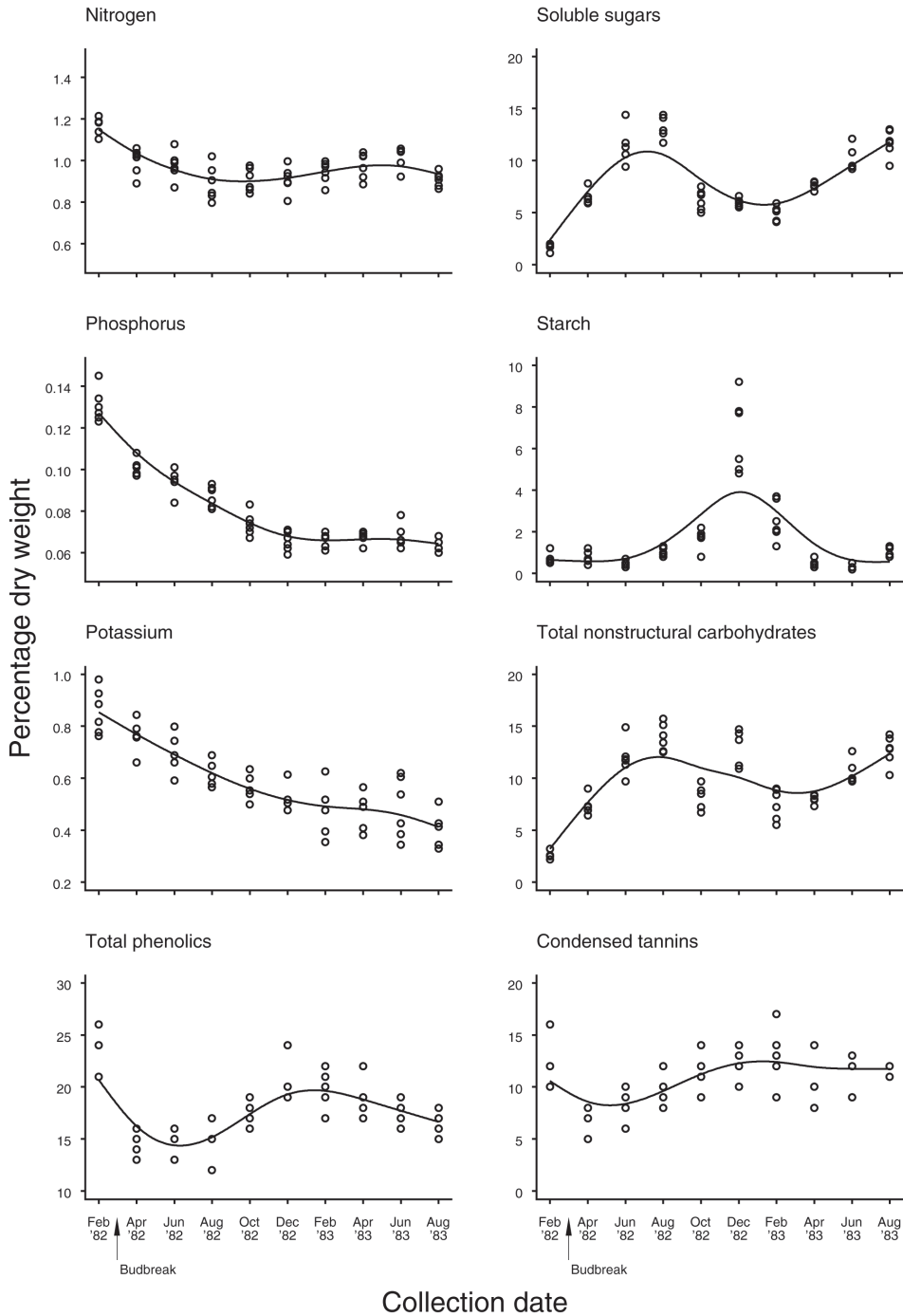


Figure 3. Seasonal trends in foliar chemistry concentrations in young (less than two years old) canopy foliage of non-defoliated southern rātā trees. The trend lines are 4° splines (all $P < 0.005$) for six trees, three large and three small. The number of circles differ because some replicates had the same value.

Table 1. *F* statistics from analyses of variance of the effects of foliage type (large-tree canopy, small-tree canopy, large-tree subcanopy) and leaf age (1, 2, 3, 4 or more years old) on foliar chemistry of non-defoliated southern rātā at Camp Creek, Westland, October 1982. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

Term	df	N	P	K	Soluble sugars	Starch	Nonstructural carbohydrates	Total phenolics	Condensed tannins
Foliage type	1	15.65***	4.90*	48.19***	4.65*	1.49	1.94	13.87***	0.77
Leaf age	1	23.29***	31.09***	8.47***	3.11*	0.36	3.60*	1.98	0.19
Foliage type × leaf age	2	0.46	0.51	2.43	0.83	1.55	1.08	0.75	1.53

as fixed effects. For visual presentation (see Fig. 3), trends in the nutrient levels of young leaves over time were modelled with 4° splines. Analyses were performed in S-Plus 6.2 (Insightful Corp., Seattle, WA).

Results

Influence of foliage type

NPK concentrations declined with increasing leaf age in non-defoliated trees, with the exception of potassium in small-tree foliage (Fig. 1). Concentrations of starch, total phenolics, and condensed tannins were independent of leaf age (Table 1). In large trees, canopy foliage had higher concentrations of phosphorus than subcanopy foliage of the same age (Table 1; Fig. 1). The same pattern was observed for condensed tannins and total phenolics (Table 1; Fig. 2). Canopy foliage from large trees also had higher concentrations of nitrogen and lower concentrations of potassium compared with foliage of the same age from either the subcanopy or from the canopy of small trees. Foliage from the canopy of small trees had lower concentrations of potassium (Table 1; Fig. 1) and higher concentrations of total phenolics (Table 1; Fig. 2) than subcanopy foliage of large trees. However, there were no significant

differences in overall NPK, carbohydrate, and polyphenolic concentrations between small and large trees in the foliage type (canopy) and age class (less than one year old) favoured by possums; canopy and subcanopy foliage in this age class differed only in potassium concentration (*t*-test: *P* < 0.001; Fig. 1).

Seasonal trends

In young (less than two years old) foliage of non-defoliated trees, all foliar components analysed varied seasonally during the first 18 months of growth (all *P* < 0.001; Fig. 3). NPK concentrations were highest in small leaves immediately after budbreak. For phosphorus and potassium, concentrations remained above those of one-year-old foliage throughout autumn and winter. Nitrogen concentrations, however, were similar to those of one-year-old foliage within two months of budbreak, when twig elongation and leaf growth had ceased (Payton, 1985). Concentrations of soluble sugars were lowest at budbreak, increased steadily through autumn and winter, and then decreased in spring. Concentrations of starch were constant through the year except for a peak in late spring (December) when cooler than average temperatures delayed the onset of growth (Payton, 1989). The trend in concentrations of total carbohydrates mirrored that of soluble sugars. Concentrations of total phenolics

Table 2. *F* statistics from analyses of variance of the effects over time of pre-budbreak defoliation on foliar chemistry of current-season (less than one-year-old) foliage of southern rātā. Twelve small trees and major branches from six large trees received one of three defoliation treatments (0%, 50%, or 100%), during either 1981 or 1982. Foliage samples were collected at three-monthly intervals over one year from the beginning of the 1982-83 growing season. No 100% defoliated small trees were analysed for soluble sugars, starch, or total nonstructural carbohydrates thus a tree size × defoliation interaction was not possible for these terms. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

Term	df	N	P	K	Soluble sugars	Starch	Nonstructural carbohydrates	Total phenolics	Condensed tannins
Tree size	1	2.08	6.85*	2.37	0.00	13.77**	0.01	0.97	0.77
Year	1	0.43	2.06	2.97	0.26	0.01	0.39	0.01	0.06
Collection date	3	3.27*	186.89***	95.33***	162.81***	37.27***	113.30***	39.02***	44.72***
Defoliation level	2	11.98**	13.33**	2.41	1.68	1.96	1.62	0.68	6.84*
Year × defoliation	2	2.52	2.38	4.69*	0.61	0.42	0.63	0.69	0.19
Tree size × defoliation	2	0.22	0.33	0.15	—	—	—	0.68	1.53

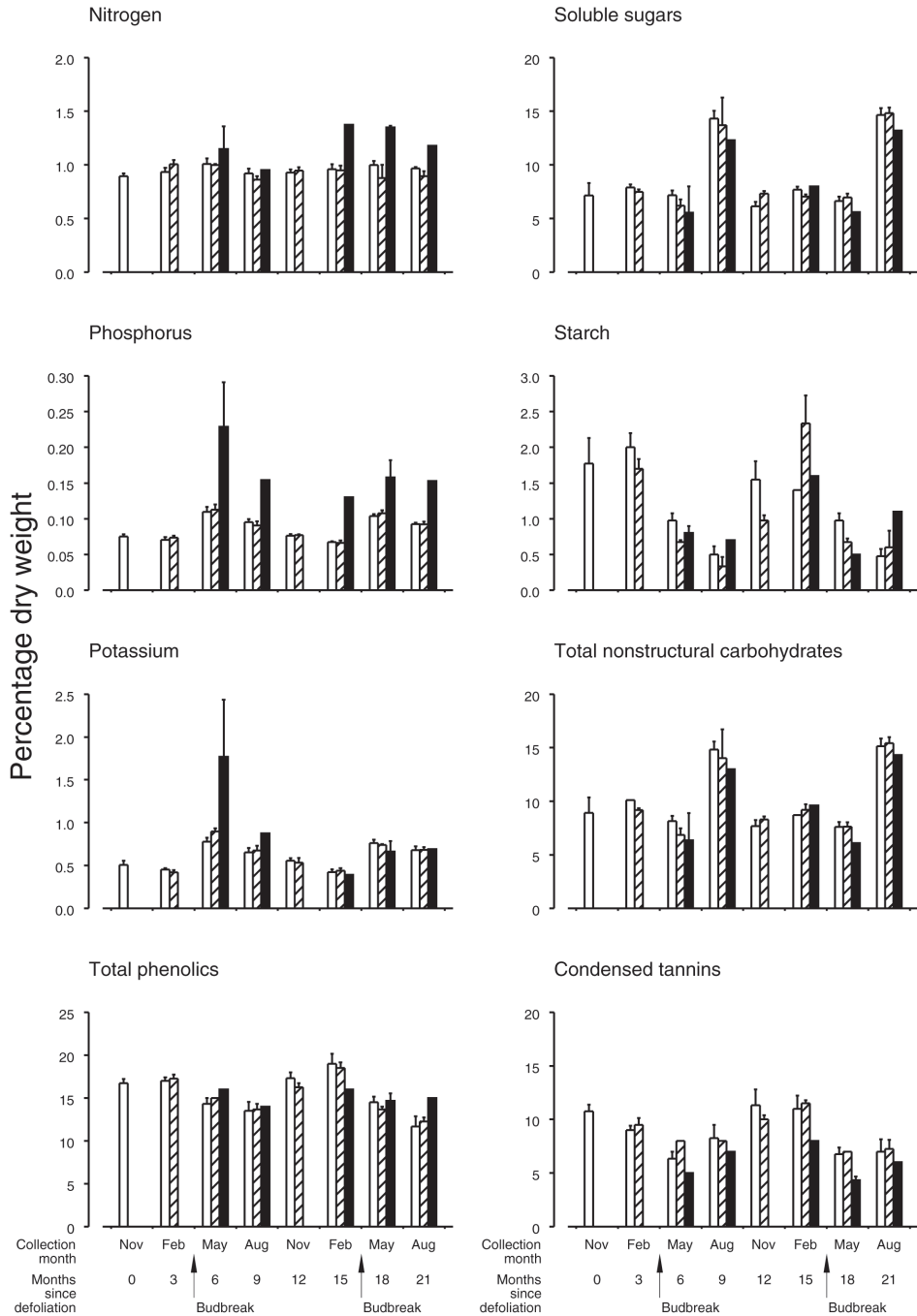


Figure 4. Effects of pre-budbreak defoliation on foliar chemistry of current-season (less than one year old) foliage of southern *rata*. Foliage was sampled every 3 months for 21 months following defoliation treatment. Missing bars indicate no data available. Data are means \pm 1 SE from four replicates, two large trees and two small trees non- (open bars), partially (hashed bars), or totally (solid bars) defoliated.

Table 3. *F* statistics from analyses of variance of the effects over time of post-budbreak and end-of-season defoliation on the foliar chemistry of current-season (less than one-year-old) foliage of southern rātā. Six small trees and major branches from two large trees received one of three post-budbreak defoliation treatments (0%, 50%, or 100%). Three small trees and major branches from one large tree received the same defoliation treatments at the end of the season. All defoliations occurred during the 1981–82 growing season. Foliage sampling occurred during the 1982–83 growing season at three-monthly intervals corresponding to 9, 12, 15, and 18 months for post-budbreak defoliations and 6, 9, 12, and 15 months post-defoliation for end-of-season defoliations. The youngest available leaf cohort was sampled during each period. Trees and branches that were totally defoliated died over winter and thus were not included in the analyses. Analysis of tree size×defoliation interactions was not possible for end-of-season defoliations. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Term	df	N	P	K	Soluble sugars	Starch	Nonstructural carbohydrates	Total phenolics	Condensed tannins
<i>Post budbreak</i>									
Tree size	1	1.08	0.83	0.04	2.75	10.34*	7.23	5.10	3.75
Collection date	3	3.90*	1.70	1.75	46.97***	81.49***	25.22***	5.09*	5.15*
Defoliation level	1	0.01	0.11	0.61	0.09	0.29	0.12	0.35	0.10
Collection × defoliation	3	0.36	0.65	0.15	11.44***	0.12	5.76**	0.50	0.24
Tree size × defoliation	1	0.00	0.05	2.01	0.22	0.23	0.43	0.69	2.80
<i>End of season</i>									
Tree size	1	1.08	1.26	4.70	13.99	28.95	14.65	0.11	19.25
Collection date	3	20.71**	3.26	1.29	10.81**	88.64***	3.87	11.86**	3.11
Defoliation level	1	22.19	2.91	10.42	0.62	1.85	0.93	0.11	0.33
Collection × defoliation	3	1.89	0.54	0.68	0.14	0.30	0.11	1.57	0.06

were highest at budbreak, and then dropped rapidly to the lowest levels over the next two months and remained below those of one-year-old foliage through winter. Concentrations of condensed tannins followed a similar pattern except that at budbreak, concentrations were similar to those of one-year-old foliage.

Effects of pre-budbreak defoliation

Foliage samples from trees defoliated before budbreak in 1981–82 (two replicates) and in 1982–83 (two replicates) allowed the effects of pre-budbreak defoliation on leaf chemistry to be followed over 21 months since defoliation. Partial (50%) defoliation had little effect on any of the measured chemical parameters of foliage from the current season (Fig. 4). However, new leaves produced after shoots had been totally defoliated had significantly higher concentrations of nitrogen, phosphorus, and potassium and lower concentrations of condensed tannins than those of non- or partially-defoliated shoots (Table 2). The increase in potassium was short-lived, and concentrations were similar to non- and partially-defoliated shoots within 6–9 months of budbreak (significant year-of-defoliation by defoliation-level interaction; Table 2). However, nitrogen and phosphorus concentrations remained above and condensed tannin concentrations remained below those of non- or partially-defoliated shoots throughout the 21 months following defoliation. Foliage sampled from small trees totally defoliated before budbreak was insufficient for carbohydrate testing. The new

foliage produced after total defoliation proved palatable to several insects, including a geometrid (*Pseudocoremia* sp.) and a tortricid (*Ctenopseustis obliquana* Walker) moth, that restripped the trees (branches) in mid- to late February 1982 (Payton, 1983). As a result, foliage sampling was discontinued from two of the totally-defoliated trees.

Effects of post-budbreak defoliation

Except for some vigorous seedlings, shoot growth in southern rātā is limited to the expansion of leaf primordia present in overwintering buds (Payton, 1989). Shoots totally defoliated after budbreak appeared healthy during autumn 1982, but died over winter (Payton, 1985). Where small trees were totally defoliated, regrowth was limited to small clusters of epicormic shoots well down the branch and at the base of the trunk. Foliage from trees (or branches) partially defoliated after budbreak in 1981–82 was sampled throughout the 1982–83 growing season, 9–18 months after defoliation. While NPK, starch, and polyphenolic concentrations in these samples were similar to those of non-defoliated shoots, soluble sugar and total nonstructural carbohydrate concentrations showed a significant time × treatment interaction (Fig. 5; Table 3).

Effects of end-of-season defoliation

As with shoots partially defoliated immediately after budbreak, the foliar chemistry of shoots defoliated at the end of the 1981–82 growing season was not

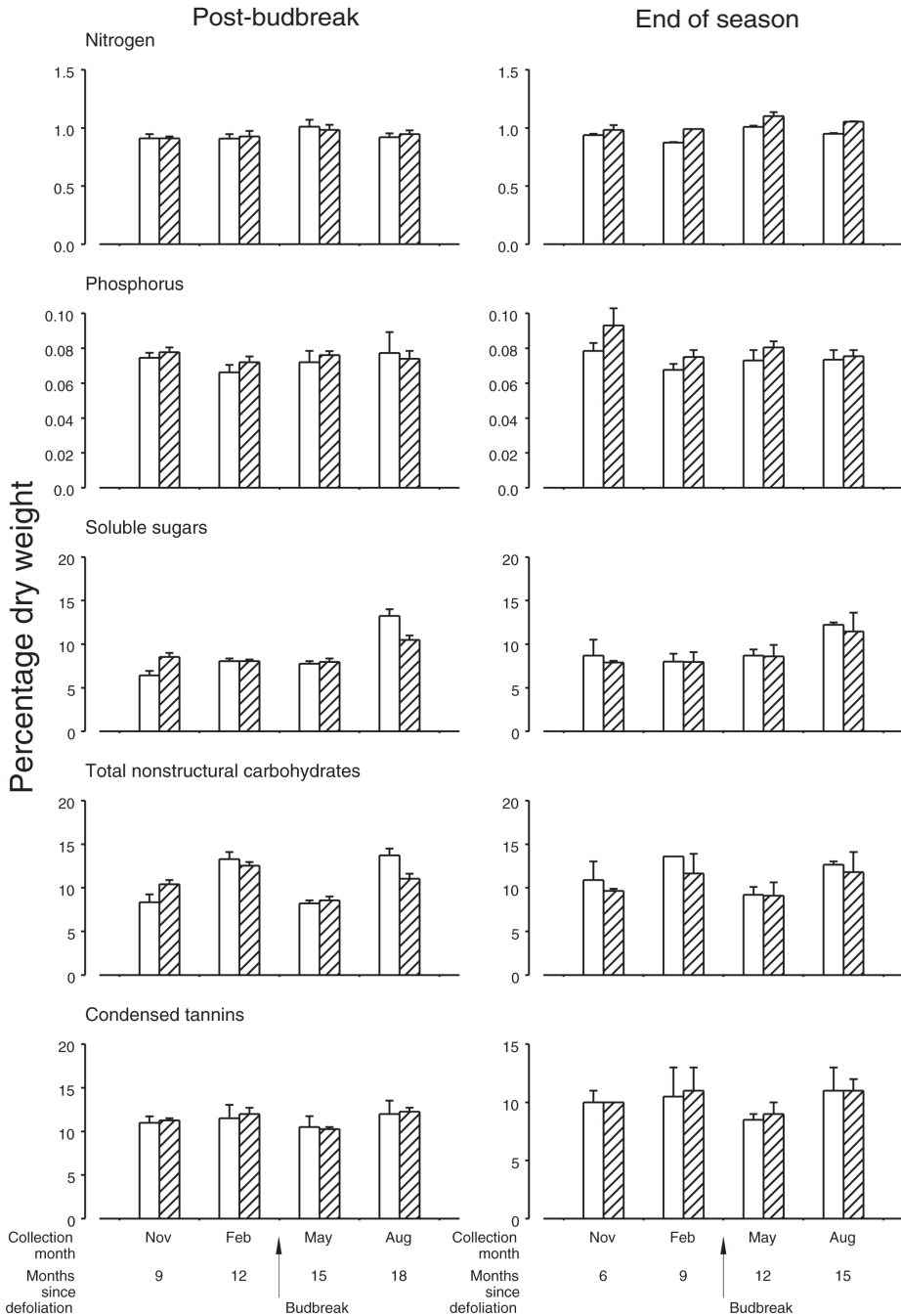


Figure 5. Effects of post-budbreak and end-of-season defoliation on foliar chemistry of current-season (less than one year old) foliage of southern rātā. Post-budbreak data are means \pm 1 SE from four replicates, two large trees and two small trees; end-of-season data are means \pm 1 SE from two replicates, two large trees and two small trees non- (open bars) or partially (hashed bars) defoliated. Trees that were completely defoliated after budbreak died. Concentrations of potassium, starch, and total phenolics were unaffected by defoliation regardless of timing thus data are not presented.

measured in the same growing season as defoliation. At the beginning of the next growing season (1982–83), concentrations of all measured foliar components in partially-defoliated shoots were similar to those of non-defoliated shoots (Fig. 5; Table 3). In trees totally defoliated at the end of the growing season, most undamaged buds survived the winter. Only the small tree totally defoliated in 1981–82 showed any signs of bud growth the following spring, with 50–60% of terminal buds growing slowly through spring and early summer, but dying before budbreak. By June 1984, total end-of-season defoliation in 1981–82 had resulted in the death of all canopy shoots in large and small trees alike. However, all showed some epicormic growth on the lower part of the branch.

Discussion

Seasonal changes in leaf chemistry reflect changing demands for carbohydrates and nutrients resulting from normal growth and differentiation processes (Waring, 1959; Moorby and Wareing, 1963). The maximum quality of foliage for herbivores generally occurs early in the growing season, when the nutritional status of new leaves is highest and concentrations of condensed tannins and other carbon-based secondary metabolites are low (Bryant *et al.*, 1983). Consistent with this expectation, we found that concentrations of nitrogen, phosphorus, and potassium were highest in southern rātā leaves immediately after budbreak, and gradually declined thereafter. This pattern was reversed for carbohydrates, where concentrations were lowest in newly emerged leaves and increased with the completion of leaf expansion and the onset of winter. NPK concentrations of mature (fully expanded) leaves declined slowly but significantly with age, while concentrations of carbohydrates and polyphenolics were independent of leaf age. The declining concentrations of NPK with leaf age seems to match the expected pattern of possum preference; in the only study to have measured preference for young and old leaves, possums ate more than eight times as much current-season foliage as they did older (two years old or more) southern rātā leaves (Monks and Efford, *in press*).

Our data show that total defoliation of southern rātā increases the nutritional quality of new leaves in the next growing season. Increased foliar concentrations of NPK following defoliation are consistent with previous findings for other species (Bryant *et al.*, 1991a; Danell and Huss-Danell, 1985; Haukioja *et al.*, 1990; Irons *et al.*, 1991; Neuvonen and Danell, 1987; Oksanen *et al.*, 1987) and may reflect a reversal of physiological aging in defoliated trees (Waring, 1959; Kramer and Kozlowski, 1979; Moorby and Wareing,

1963). Leaves of physiologically older plants typically have lower concentrations of NPK and higher concentrations of polyphenolics than their physiologically younger counterparts, with the result that they are less palatable to herbivores (du Toit *et al.*, 1990; Bryant *et al.*, 1991c). Where browsing or pruning allows physiological aging to be reversed, foliar NPK concentrations in young leaves increase relative to those in young leaves of unbrowsed/unpruned individuals of the same species. This process provides a mechanism that explains why brushtail possums often systematically defoliate one or a few trees, while leaving neighbouring individuals of the same species largely untouched. Those trees that are browsed repeatedly die (Meads, 1976).

Systematic defoliation of native New Zealand trees by brushtail possums was first reported by Perham (1924) who observed that while many southern rātā and fuchsia [*Fuchsia excorticata* (Forster et Forster f.) L. f. (Onagraceae)] trees on Mt Tuhua, Westland, were dead or dying, others remained healthy. More recently, this pattern (“salt-and-pepper dieback”) has been observed in other indigenous New Zealand tree species (Payton, 2000). In the present study, partial defoliation had little effect on foliar chemistry, regardless of the timing of the defoliation. By contrast, total defoliation at any stage during the growing season or after growth had ceased caused significant levels of shoot death (Payton, 1985), stimulated concentrations of NPK, and depressed concentrations of condensed tannins in new foliage produced by the surviving shoots. Our data show that defoliation of individual trees during winter and early spring (i.e. after the cessation of growth in autumn and before budbreak the following summer) results in young leaves produced during the following growing season that are more nutritious than those on surrounding trees that have not been defoliated. Hence, although possums may also favour trees for other reasons (e.g. microsite fertility, behavioural characteristics of possums), changes in foliar chemistry after heavy defoliation gives one explanation as to why possums tend to browse repeatedly the same trees.

In the present study, the impact of defoliation on foliar chemistry may have been exacerbated by infertile soils at the experimental site (Harrison, 1985; Stewart and Harrison, 1987), and the evergreen habit of southern rātā. For evergreen species growing in nutrient-limited habitats, growth is restricted relative to photosynthesis, leading to the accumulation of carbon that is then available for incorporation into carbon-based secondary metabolites (Bryant *et al.*, 1991a). Secondary metabolite production is energy demanding and has a low carbon-allocation priority relative to growth (Mooney and Chu, 1974). Thus, when carbon is removed as by defoliation, reduced allocation to carbon-based defences might be expected to result in the

production of more palatable leaves in the next growing season (Karban and Myers, 1989).

Secondary metabolites, especially condensed tannins, act as broad-spectrum antifeedants against browsing herbivores (Feeny, 1970; Levins, 1971). In our experiment, concentrations of both condensed tannins and total phenolics were independent of leaf age. Moreover, while we did find higher concentration of total phenolics and condensed tannins in sun (canopy) than shade (subcanopy) foliage, similar to the findings of Waterman *et al.* (1984) for *Barteria fistulosa* (Passifloraceae), a deterrent effect is not reflected in observed possum browsing preferences (sun > shade), which are better explained in nutritional (e.g. nitrogen, phosphorus) terms. However, concentrations of condensed tannins were reduced in new foliage following defoliation, a finding consistent with repeated browsing of previously browsed trees. The available foliar chemistry data for southern rātā (summarised in Brooker *et al.*, 1963; Cambie, 1976, 1996) sheds little light on the nature of other possible deterrent agents. Recent bioassay-guided experiments using caged brushtail possums have found a high-molecular-weight, water-soluble fraction from southern rātā with significant antifeedant properties (I. Payton and L. Boul, unpubl. data). The identity of the component responsible for the antifeedant effect is yet to be confirmed.

The preference of brushtail possums for young rātā leaves frequently results in damage to or loss of the terminal buds on browsed shoots. In these cases, the survival of the shoot depends on the ability of one or more axillary buds to replace the damaged growing point. Where shoot damage occurs after normal bud growth has commenced and axillary buds flush late in the growing season, the new foliage typically suffers frost damage and the shoot seldom survives (Payton, 1989). Reduced concentrations of soluble sugars, which build up as growth slows in autumn and act both to increase the frost tolerance of the plant (Kramer and Kozlowski, 1960) and as an energy source for early-season growth (Mooney, 1972), may provide an explanation for lowered bud survival of defoliated trees over winter and the reduced growth of surviving shoots (Payton, 1985). Similarly, lower concentrations of condensed tannins, which are often the product of late-season photosynthate from the previous year (Bryant *et al.*, 1983), may also reflect reduced carbohydrate availability associated with defoliation.

Our data suggest that changes in foliar chemistry after total defoliation provide an explanation for observed patterns of browsing by brushtail possums on southern rātā. Defoliation results in higher concentrations of NPK and lower concentrations of condensed tannins in the next cohort of young leaves, changes typically associated with increased palatability

to mammalian herbivores. Left to play out, this feedback loop will ultimately lead to tree death (e.g. Meads 1976).

While brushtail possums have an adverse impact on the health of individual southern rātā trees, their role in forest dieback at larger scales is less clear, with studies suggesting a range of factors that influence the predisposition of stands to dieback, the triggering of dieback, and the acceleration of the dieback process. For Westland rātā-kāmahi forests, the extent to which forest communities are predisposed to dieback is a function of their floristic composition. Forest stands with an abundance of seral shrub hardwoods, which are characteristic of recently disturbed, relatively fertile sites, are most vulnerable to dieback. Conversely, dieback is rare or absent in communities where the species composition reflects long-term stability and subsequent soil infertility (Wardle, 1977; Basher *et al.*, 1985; Payton, 1987; Reif and Allen, 1988). Stand structure is also an influential factor to rātā-kāmahi dieback (Wardle, 1971; Stewart and Veblen, 1983). While young even-aged pole stands initially prove resilient to dieback, their inability to replace the loss of larger-crowned individuals once the natural thinning process is complete renders them vulnerable to damage from accelerating factors such as wind, insects, and fungal pathogens (Payton, 1988). Biotic agents (e.g. insects and fungal pathogens) have not been shown to trigger dieback in rātā-kāmahi forests, but are important in accelerating the process in already affected stands (Hoy, 1958; Wardle, 1971).

The ability to determine the type (predisposing, triggering, accelerating) and relative importance of the factors involved in the canopy dieback process has important implications for forest managers. An understanding of the factors predisposing stands to dieback provides a basis to recognise those forest communities most at risk. Similarly, a knowledge of the factors triggering and accelerating the dieback process can provide a basis to determine the need, or otherwise, for some form of intervention. In this study, we have shown that heavy defoliation as by possum browsing is expected to elicit further browsing on the same tree and that extensive browsing late in the season contributes to shoot death and potential dieback of individual trees.

Acknowledgements

The authors thank staff of the former New Zealand Forest Service who helped defoliate the trees and collect the foliage samples. The foliage samples were analysed by Carl Kelland (NPK), Graeme Rogers (carbohydrates), and Linda Hill (polyphenolics). Bruce Warburton provided the possum density data. Valuable

feedback was provided by Mark Smale, Jim Coleman, Graham Nugent, Phil Cowan, Emma Sayer, David Coomes, Peter Bellingham, Roger Dungan, and an anonymous reviewer. This research was supported by a Landcare Research postdoctoral fellowship (JMK), and the New Zealand Foundation for Research, Science and Technology under Contract C09X0209.

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