

MINERAL ELEMENT CONCENTRATIONS IN FOLIAGE OF DIVARICATE AND NON-DIVARICATE *COPROSMA* SPECIES

Summary: The levels of mineral elements in foliage of 10 *Coprosma* species growing in secondary forest in Dunedin were compared using canonical discriminant analysis. The results revealed distinctive patterns of nutrient accumulation separating divaricating and non-divaricating growth forms. Foliar concentrations of N, P and Na were higher in divaricating species, particularly those with small, membranous leaves, compared with small- and large-leaved non-divaricating species. The results are discussed in relation to herbivory and the current ecological niche of the different *Coprosma* species.

Keywords: mineral elements; leaves; *Coprosma*; Rubiaceae; herbivory; Dunedin; New Zealand.

Introduction

The importance of the divaricating growth form in the woody flora of New Zealand, and its apparent rarity in other countries, has led biologists to look for an explanation in some unique feature of the New Zealand environment. Characteristic features of divaricating shrubs, notably the interlocking branches which diverge at a wide angle, small leaf size, and a concentration of leaves on the inner part of the plant, have traditionally been considered primarily as adaptations to extremes of climate, particularly wind and temperature. Evidence for this view has been given recently by McGlone and Webb (1981), who suggest that divaricating plants evolved in New Zealand as one of the responses of a sub-tropical flora, isolated from sources of arctic-, alpine- and desert-adapted plants, to the onset of harsh glacial climates.

Greenwood and Atkinson (1977) have developed the alternative theory that divergent and interlaced branching, the woody exterior, the tough stems and the dispersed growing points of these plants are adaptations developed in response to browsing by moas (*Dinornithiformes*). These herbivorous ratite birds, now extinct, were the only large browsing animals in New Zealand throughout the Tertiary and Quaternary period. According to Greenwood and Atkinson the distinctive morphological features of divaricates would have discouraged browsing and ensured plant survival.

Lowland forests on fertile soil frequently contain many divaricating shrubs (Greenwood and Atkinson, 1977). In this habitat we examined the 'moa browsing' hypothesis by comparing the nutrient value of foliage of divaricate and non-divaricate species growing under similar conditions. If divarication functioned primarily as a protection against herbivory, it could be expected that amongst closely related species it

would be broadly correlated with species of high nutritive value. Non-frugivorous, herbivorous birds usually select foliage high in N and P, frequently associated with new growth (Moss, 1972; Owen, 1975; Mills and Mark, 1977). Lowry (1980) has suggested that moas would have preferentially selected young plant growth containing easily available nutrients as they probably lacked a specialised cellulose-digesting system.

Coprosma, a genus of mainly shrub and small-tree species, contains the largest number of divaricating species of any New Zealand genus (Greenwood and Atkinson, 1977). It also includes many non-divaricating species, several of which are small-leaved. Species with both growth forms co-exist in the understorey of secondary forest around Dunedin, where the study was undertaken.

Study Area and Methods

All samples were collected covertly from remnants of broadleaved-kanuka (*Leptospermum ericoides*) forest in the Dunedin Town Belt. The main broadleaved species, *Melicytus ramiflorus*, *Pittosporum eugenoides*, *Griselinia littoralis*, *Fuchsia excorticata* and *Carpodetus serratus*, overtop a dense understorey of mainly *Coprosma* species. Ten *Coprosma* species were selected for study (Table 1) based mainly on their regular occurrence together in the area. A range of divaricating and non-divaricating species was sampled at four sites in the Town Belt, one at 14 m a.s.l. on alluvium and the other three at 110 m a.s.l. on weakly to moderately gleyed yellow-grey earths, formed on loess, and intergrades with brown, granular loams derived from basalt (Tomlinson, Kennedy and Leslie, 1978).

Separate samples of leaf material were collected

Table 1: Growth form and habitat of the ten *Coprosma* species studied

Species	Growth form	Habit
<i>C. rubra</i>	weakly divaricate shrub to 3m	forest on alluvial soil
<i>C. rotundifolia</i>	erect shrub to 4m; branches spreading to divaricate	moist forest interior
<i>C. areolata</i>	erect shrub to 5m; branches fastigiate or divaricate	forest interior and margins
<i>C. rhamnoides</i>	divaricating bushy shrub to 2m	forest interior and margins
<i>C. propinqua</i>	divaricating bushy shrub to 2-4m	forest margins
<i>C. crassifolia</i>	rigid divaricating shrub 2-3m	dry sites in open forest
<i>C. linariifolia</i>	small tree to 6m, non-divaricating but small leaved	dry open forest or margins
<i>C. grandifolia</i>	small erect non-divaricating tree to 6m, with large leaves	forest interior
<i>C. robusta</i>	bushy non-divaricating shrub 3-4m tall, with large leaves	forest margins
<i>C. lucida</i>	non-divaricating shrub 3-4m tall, with large leaves	forest interiors or margins

from five individual plants of each species on 22 March 1983 and oven-dried for 48 hrs at 100°C before being ground to a powder. Major elements were determined by the methods outlined in Williams et al. (1976).

To summarise and compare the nutrient balances between species canonical discriminant analysis was used. This multivariate technique, available in the statistical package TEDDY BEAR (Wilson, 1975) is explained and used in a recent plant nutrient study by Lechowicz and Shaver (1982). Canonical discriminant analysis deals with observations in groups. In this case the species were treated as groups with each observation comprising different measurements i.e. the different element concentrations at each site. The analysis transforms individual nutrient concentrations for each species to a single point in few dimensional spaces, in a way that maximises the differences in nutrient balance between species. Canonical coefficients enable the contribution of each nutrient to the arrangement

of species on each canonical axis to be assessed, the magnitude of the coefficient indicating relative importance of any individual nutrient.

Analysis of variance and Duncan's (1955) new multiple range test were used to test significance.

Results

Foliar element concentrations for ten *Coprosma* species are shown in Table 2. Nutrients differ in their variability between species, with the majority (N, P, S, Ca and K) showing approximately a twofold range in concentration between the lowest and highest values. For magnesium the spread of values was relatively small (0.37-0.59%), whereas Na exhibited the largest differences between species (0.02-0.33%).

Few species stand out with foliar nutrient levels significantly ($p < 0.05$) different from all other species. The two exceptions are *C. rubra* and *C. grandifolia* which have significantly higher

Table 2: Mean foliar element concentrations (% dry weight) of ten *Coprosma* species. Within each column, figures sharing a common letter do not differ significantly ($p < 0.05$). Species are listed according to their position on the first canonical axis.

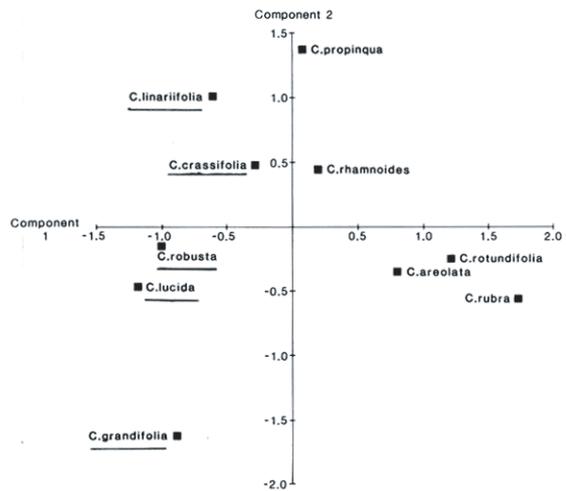
Species	Elements						
	N	S	P	Mg	Ca	Na	K
<i>C. rubra</i>	2.80 a	0.25 bcd	0.22 a	0.43 ab	1.91 ab	0.27 a	1.77 b
<i>C. rotundifolia</i>	2.34 b	0.29 abc	0.21 a	0.52 ab	1.56 abcd	0.30 a	1.48 bc
<i>C. areolata</i>	2.26 b	0.35 ab	0.16 b	0.52 ab	1.44 bcd	0.30 a	1.22 bcd
<i>C. rhamnoides</i>	1.80 c	0.33 abc	0.15 b	0.34 b	1.32 cd	0.33 a	1.23 bcd
<i>C. propinqua</i>	1.60 cd	0.21 cd	0.14 bc	0.48 ab	2.00 a	0.22 ab	0.78 d
<i>C. crassifolia</i>	1.65 cd	0.22 cd	0.13 bc	0.59 a	1.53 bcd	0.29 a	1.36 bcd
<i>C. linariifolia</i>	1.29 e	0.14 d	0.13 bc	0.40 ab	1.49 bcd	0.12 bc	1.06 cd
<i>C. grandifolia</i>	1.69 cd	0.39 a	0.17 b	0.40 ab	1.13 d	0.08 c	2.39 a
<i>C. robusta</i>	1.44 de	0.27 abc	0.12 bc	0.37 ab	1.66 abc	0.02 c	1.60 bc
<i>C. lucida</i>	1.39 de	0.29 abc	0.11 c	0.47 ab	1.21 cd	0.05 c	1.44 bc

N(2.80%) and K(2.39%) concentrations, respectively, than any other species.

For each major nutrient the following species had the highest mean concentration: N, 2.80%, *C. rubra*; S, 0.39%, *C. australis*; P, 0.22%, *C. rubra*; Mg, 0.59%, *C. crassifolia*; Ca, 2.00%, *C. prapinqua*; Na, 0.33%, *C. rhamnoides*; K, 2.39%, *C. grandifolia*.

The canonical discriminant analysis was carried out using all the elements together and the results are shown in Figure 1.

The first axis, which accounted for 68.0% of the variance between the species, contrasts *C. rubra*, *C. rotundifolia* and *C. areolata*, all of these being divaricating species with small,



Correlation coefficients between each variate and the component

Element	Component	
	1	2
Nitrogen	0.8790	-0.3703
Sulphur	0.0165	-0.6066
Phosphorus	0.6854	-0.3688
Magnesium	0.1260	0.0467
Calcium	0.3384	0.3859
Sodium	0.6455	0.2173
Potassium	-0.0825	-0.7613
% Variation in raw data accounted for	68.0	16.4
Statistical significance	p < 0.001	p < 0.001

Figure 1: Results of a canonical discriminant analysis of mineral element levels in leaves of six divaricate and four non-divaricate (underlined) *Coprosma* species.

membranous leaves, with the large-leaved non-divaricating species *C. lucida*, *C. robusta* and *C. grandifolia*. *C. linariifolia*, the only small-leaved non-divaricating species studied, is segregated with this latter group and the axis therefore clearly distinguishes divaricating species (centre and right-hand side of Fig. 1) from all non-divaricating species (far left of Fig. 1). The elements responsible for this separation are mainly N, P and Na which occur in higher concentrations in foliage of divaricating species. These differences are highly significant ($p < 0.01$) when the element concentrations are compared separately in the different growth forms (Table 3). There is also a tendency for higher Ca and lower K concentrations in divaricating species (Table 3) but this is only weakly expressed in the canonical discriminant analysis.

The second component is influenced largely by K and S; high foliar concentrations of these elements are indicated by high negative values on the second axis. It can be seen that *C. grandifolia* has high concentrations, whereas a group of mainly micro-sclerophyllous species (*C. propinqua*, *C. linariifolia*, *C. crassifolia*) in contrast had very low K and S concentrations, and generally higher levels of Ca.

Table 3: Comparison of foliar element levels of divaricating ($n = 6$) and non-divaricating ($n = 4$) *Coprosma* species. (ns = not significant).

Element	Element concentrations (% dry weight)		Significance level p <
	Divaricating	Non-divaricating	
N	2.08	1.45	.01
S	0.28	0.28	ns
P	0.17	0.14	.01
Mg	0.48	0.42	ns
Ca	1.63	1.37	.05
Na	0.29	0.07	.01
K	1.31	1.63	.05

Discussion

The pattern of nutrient accumulation in leaves of *Coprosma* species is different for divaricating and non-divaricating growth forms. Divaricating species typically have higher foliar concentrations of N, P and Na, and lower concentrations of K, than non-divaricating species. The functional significance of these differences in relation to the species' habitat preferences, and their possible

importance for herbivory can only be tentatively discussed here, because mineral element levels can only be interpreted adequately when nutrient allocation patterns and requirements, and growth and assimilation rates are known. Likewise, nutrient levels in leaves are only one aspect of herbivory; secondary anti-herbivore compounds and the ability of the plant to recover following defoliation are also important. Further, the study uses only a small sample number, assumes homogeneity of each site, and compares dissimilar leaf sizes and types.

Foliar mineral element levels may reflect plant adaptations for specific habitats. Species such as *C. rubra* and *C. rotundifolia* which grow on moist fertile sites would be expected to have high concentrations of N and P. Similarly, small thick-leaved species (*C. propinqua*, *C. crassifolia*, *C. linariifolia*), with a higher proportion of structural tissue, should have higher Ca and Mg concentrations than others. High tissue concentrations of Na are frequently found in shrubs with coastal affinities (Marrs, 1978), but there is little evidence to suggest that this is the case here. Na increases succulence in crop plants and may have an important role in improving drought resistance (Russell, 1973). Divaricating species are generally more tolerant of exposed, dry sites than other *Coprosma* species and Na may assist them in these conditions.

Amongst *Coprosma* species, those with the divaricating form have more nutritious and probably more readily digestible foliage than non-divaricating species. This suggests that they would be preferentially browsed by herbivores, which are well known for selecting plant material of high nutritive value. It is, therefore, not surprising that divaricating species have been recorded from fossilised moa gizzards (Burrows, 1980). However, having small leaves, protected on the inner shoots of the plant canopy, would assist in minimising the impact of browsing herbivores.

The reasons for high N and P concentrations in foliage of divaricate *Coprosma* species are not known, but slow growth rates and high photosynthetic activity may be involved. Amongst these divaricating forms there were pronounced differences in foliar nutrient levels. This is, perhaps, not too surprising given that "divarication" is fairly loosely defined, has arisen by a diversity of morphological processes (Tomlinson, 1978), and includes species tolerant of a variety of ecological niches.

The low quality of non-divaricating foliage

would make it less attractive to herbivores.

Nutrient balances in plants may also be a mechanism for deterring herbivores. Chapin, Johnson and McKendrick (1980) have postulated that low Na/K ratios in many arctic vascular plants could act as a defence against herbivores because of the high Na requirement of most animals. Na produced the cleanest separation of any element in this study between the two growth forms. In non-divaricating plants Na/K ratio was 0.051:0.04, which was significantly ($p < 0.01$) lower than for divaricating species (0.231: 0.05).

The fact that divarication appears to be associated in *Coprosma* with species with high N, P and Na concentrations provides some support for Greenwood and Atkinson's (1977) hypothesis. However, other corroborating evidence is required, including further comparative analyses of mineral element levels and studies of the effect of simulated browsing on the growth of divaricating and non-divaricating species, before the theory can be more fully accepted.

Acknowledgements

We are grateful to Dr Rex Dolby and staff of the Invermay Agricultural Research Centre, Ministry of Agriculture and Fisheries for determining element levels in foliage samples. Gillian Rapson and Dr J. Bastow Wilson, Botany Department, University of Otago, kindly assisted with the statistical analyses. Our colleagues, Dr Matt McGlone and Dr Ian Atkinson, provided helpful comments on early drafts of the manuscript.

The idea of undertaking this study arose following a conversation with Dr Gerry McSweeney on, inter alia, foliar nutrient levels of juvenile plants of indigenous podocarp species.

References

- Burrows, C. J. 1980. Some empirical information concerning the diet of moas. *New Zealand Journal of Ecology* 3: 125-30.
- Chapin, F. S.; Johnson, D. A.; McKendrick, J. D. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *Journal of Ecology* 68: 189-200.
- Duncan, D. B. 1955. Multiple range and multiple F tests. *Biometrics* 11: 1-42.
- Greenwood, R. M.; Atkinson, I. A. E. 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. *Proceedings of the New Zealand Ecological Society* 24: 21-33.

- Lechowicz, M. J. & Shaver, G. R. 1982. A multivariate approach to the analysis of factorial fertilization experiments in Alaskan arctic tundra. *Ecology* 63: 1029-38.
- Lowry, J. B. 1980. Evolution of divaricating plants in New Zealand in relation to moa browsing. *New Zealand Journal of Ecology* 3: 165.
- Marrs, R. H. 1978. Seasonal changes and multivariate studies of the mineral element status of several members of the Ericaceae. *Journal of Ecology* 66: 533-45.
- McGlone, M. S.; Webb, C. J. 1981. Selective forces influencing the evolution of divaricating plants. *New Zealand Journal of Ecology* 4: 20-8.
- Miller, G. R. 1968. Evidence for selective feeding on fertilized plots by red grouse, hares and rabbits. *Journal of Wildlife Management* 32: 849-53.
- Mills, J. A.; Mark, A. F. 1977. Food preferences of takahe in Fiordland National Park, New Zealand, and the effect of competition from introduced red deer. *Journal of Animal Ecology* 46: 939-58.
- Moss, R. 1972. Food selection by red grouse [*Lagopus lagopus scoticus* (Lath.)] in relation to chemical composition. *Journal of Animal Ecology* 41: 411-28.
- Owen, M. 1975. Cutting and fertilizing grassland for winter goose management. *Journal of Wildlife Management* 39: 163-7.
- Russel, E. W. 1973. *Soil conditions and plant growth* 10th ed. Longman Group Limited, London.
- Tomlinson, P. B. 1978. Some qualitative and quantitative aspects of New Zealand divaricating shrubs. *New Zealand Journal of Botany* 16: 299-309.
- Tomlinson, P. R.; Kennedy, N. M.; Leslie, D. M. 1978. *Soil map of Dunedin City and Environs, New Zealand. Scale 1:31680*. N.Z. Soil Bureau Map 107 Part of Soil Survey Report 37.
- Williams, P. A.; Cooper, P.; Nes, P.; O'Connor, K. F. 1976. Chemical composition of tall-tussocks in relation to the diet of the takahe (*Notornis mantelli* Owen), on the Murchison Mountains, Fiordland, New Zealand. *New Zealand Journal of Botany* 14: 55-61.
- Wilson, J. B. 1975. TEDDYBEAR - statistical system. *New Zealand Statistician* 10: 36-42.