

## The architecture of New Zealand's divaricate shrubs in relation to light adaptation

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**Abstract** The divaricating shoot habit is typified by a suite of architectural traits, quantified here using phylogenetic independent comparisons of three pairs of congeners, with or without the habit. We consider the hypothesis that the habit evolved as a structural photoprotection mechanism that maximises potential carbon fixation by minimising photoinhibition. Plants were grown in pots in full sun, or behind vertical screens transmitting c. 25, 52, or 73% sunlight. When shaded, all species shifted partitioning of biomass from stem thickening to leaf area expansion and occupied a larger crown volume for a given shoot biomass. Leaf numbers per stem length of divaricates and non-divaricates were greater in the lower and upper canopies, respectively, consistent with the view that in divaricates outer branches protect inner leaves. However, leaf numbers per stem length showed no response to variation in high light receipt. Divaricates showed some traits typical of plants adapted to sunny habitats: smaller effective leaf size, lesser fractional partitioning of biomass to leaves, and greater foliage densities. Other traits of divaricates were typical of plants adapted to shaded habitats: lesser stem diameters, stem biomass per unit stem length, leader dominance, leaf area index,

and heights relative to crown diameters; and more horizontal twig orientations. Compensation for high costs of support of photosynthetic area in divaricates (leaf area per unit shoot biomass c. 1.3 m<sup>2</sup>kg<sup>-1</sup>) compared with non-divaricates (c. 5.5 m<sup>2</sup>kg<sup>-1</sup>) would require a larger enhancement of net canopy photosynthesis than is likely to arise from avoidance of photoinhibition.

**Keywords** divaricate; morphological plasticity; penumbra; photoprotection; support costs

### INTRODUCTION

In New Zealand, the “divaricating” shoot habit is generally considered an example of convergent evolution in response to either past climatic extremes (Cockayne 1911; McGlone & Webb 1981; Kelly & Ogle 1990; McGlone & Clarkson 1993; Kelly 1994; Bannister et al. 1995; Darrow et al. 2001, 2002), or browsing by giant flightless birds (Greenwood & Atkinson 1977; Burrows 1980; Atkinson & Greenwood 1989; Bond et al. 2004).

The divaricating habit has also been considered adaptive for light harvesting (Day 1998a; Howell et al. 2002). It has been proposed that the habit is a structural photoprotection mechanism that maximises potential carbon fixation by minimising photoinhibition (Howell et al. 2002). Photoinhibition is the light-dependent inhibition of the light-dependent reactions of photosynthesis which results from over-excitation of photosystem II (Osmond 1994). It occurs when photon absorption by the light-harvesting pigment protein complexes is in excess of the capacity for dissipation of the resultant excitation energy via photosynthetic electron transport. Dynamic photoinhibition occurs in unstressed sun-grown plants, whereas chronic photoinhibition can occur in shade-grown plants following exposure to photon fluxes in excess of those encountered during growth or under conditions which impair photosynthetic function (i.e., stress; Osmond 1994). Howell et al. (2002) exposed the inner shoots by

pruning outer shoots and found a c. 20–30% reduction in the ratio of variable to maximal chlorophyll fluorescence. This study is controversial (Lusk 2002; Turnbull et al. 2002) because of issues such as the lack of acclimation of shaded inner leaves exposed to a sudden increase in irradiance, lack of accounting for whole crown variation in light interception and photosynthesis, difficulty in measuring rates of photosynthesis per unit leaf area using gas exchange for small-leaved shoots, and the extent to which measured responses reflect changes in the maximal quantum efficiency of photosynthesis.

Previously, the conceptual framework of Horn (1971), in which architectural traits are related to the light-saturation of photosynthesis, has been used to speculate on the functional significance of the divaricating habit for light harvesting. In divaricating shrubs, small leaf sizes and relatively long internodes, particularly in the outer canopy, have been suggested to facilitate avoidance of umbral shadows and sub-saturating irradiances for photosynthesis (Kelly 1994). Day (1998a,b) proposed that (i) in heteroblastic species the juvenile divaricating stage is adaptive for the optimisation of light harvesting in forest understories and (ii) in divaricating shrubs the habit is adaptive in open habitats. The canopy of divaricating plants was suggested to be multilayered, and it was predicted that in heteroblastic species, canopy diameter-to-height ratios and leaf area index (LAI) decrease with ontogeny. Day (1998a) proposed that plasticity of form has allowed development of a “denser” canopy in the open, discharging the apparent contradiction between (i) and (ii).

Phenotypic plasticity may be adaptively important in providing a capacity to respond opportunistically to changes in environmental conditions, including increases in irradiance, and may be more adaptively significant than deterministic form (Fisher & Hibbs 1982; Valladares et al. 2000; Bloor & Grubb 2004). However, the morphological and physiological plasticity of species varies for different traits and can not be generalised according to species’ forest regeneration, shade tolerance, or successional status (Valladares et al. 2000; Yamashita et al. 2002). It is thought that architectural plasticity in response to light environment is an important aspect of the divaricate habit in some species (McGlone & Webb 1981). In New Zealand, plasticity may have been important for species survival during glacial-interglacial climates (Mildenhall 1980).

To understand the influence of photoinhibition on the evolution of different crown structures, we must consider its influence on relative fitness, and

on carbon allocation as well as carbon gain. In the structural photoprotection hypothesis (Howell et al. 2002), greater relative fitness in divaricating species is implicitly assumed to result because of allocation of resources to structures and functions which maximise the net rate of energy capture (Givnish 1986, 1988), carbon-gaining capacity, and growth (Mooney & Gulmon 1979; Raven 1994). This advantage must have occurred relative to divaricates’ historic nondivaricating competitors, and requires a net benefit to whole plant carbon gain over and above the costs of construction and maintenance of the habit. Furthermore, if structural photoprotection involves trade-offs between benefits to carbon gain and costs of carbon allocation, we would expect two things: firstly, that in species investing in these structural mechanisms investment would be reduced when excess photon receipt is relieved; secondly, the relative advantage of divaricates should be greatest under conditions of greatest excess irradiance.

The divaricating habit, like other convergent life forms, is characterised by a suite of traits which makes defining diagnostic characters and finding a single adaptive explanation difficult (Böcher 1977; Kelly 1994). In comparative studies of the adaptive significance of such traits incorporation of phylogenetic information may be crucial, but it has been lacking for divaricates. Where phylogenies are uncertain, a standard approach is to make comparisons of pairs of species that have a common ancestor not shared with any other pair (Felsenstein 1985). During the course of evolution of species, forms with a divaricating habit can be assumed to have diverged from an ancestral form lacking the habit. For species coexistence in a two-species system intraspecific competition must be greater than interspecific competition (Chesson 2000). Increasing intensity of intraspecific competition versus interspecific competition would be expected as species diverged ecologically. Therefore, we assume that divaricate species’ non-divaricate congeners are the best extant analogues of their most important historic competitors.

We set up a common-garden experiment to quantify the benefit to net carbon gain and structural costs of the divaricating habit in shrubs acclimated to different levels of excess irradiance, using phylogenetically controlled comparisons with shrubs lacking the habit. Here we investigate shoot architecture, morphology, and biomass partitioning and consider these traits in relation to light harvesting under conditions of excess irradiance. Elsewhere, we intend to document the variation in carbon gaining capacity and growth of plants.

## MATERIALS AND METHODS

### Plant material

Three species (*Aristolelia fruticosa* Hook., *Coprosma propinqua* A.Cunn., and *Corokia cotoneaster* Raoul), described as having a divaricating habit in the mature phase (Kelly 1994), were each compared with a congener (*Aristolelia serrata* J.R.Forst. et G.Forst, *Coprosma robusta* Raoul, *Corokia budleioides* A.Cunn.) lacking the habit. We selected genera from three widely divergent dicotyledonous families (Elaeocarpaceae, Rubiaceae, Grossulariaceae, respectively; Angiosperm Phylogeny Group II 2003), in each of which the divaricate habit can be assumed to have arisen independently. Evidence for a shared progenitor is provided by nuclear ribosomal DNA sequences from wild populations of *C. propinqua* and *C. robusta* (Wichmann et al. 2002) and the occurrence of fertile hybrids in the other two congeneric pairs (Allan 1961 and references therein).

In late June 2001, plants 9–14 months old were purchased from local nurseries. All plants of each species were grown from a single source of local

seed (*Aristolelia* and *Coprosma*) or cuttings (*Corokia*). Plants were repotted in potting mix (Tree & Shrub mix, 12–14 month Osmocote, 7 kg m<sup>-3</sup>) in 5-litre pots and held in a shadehouse until being moved to the experimental plots on 1 November 2001. Pots were marked and their azimuth was maintained throughout.

### EXPERIMENTAL DESIGN

We used a split-plot, factorial pot trial. Two parallel, east-west aligned blocks each consisted of a line of 24 experimental plots (4.25 m E–W × 0.85 m N–S). Shade treatments were three-sided (N, W, and E) vertical screens (1.7 m high) bearing shade cloth transmitting c. 25, 52, or 73% of incident sunlight, or no shade cloth (i.e., 100% sunlight). A restricted randomisation was used to allocate six species and four shade treatments to plots within blocks, and six harvests to positions within plots (Table 1). Plants were blocked according to size (height followed by crown diameter). Plants were watered daily using an automated system.

### BIOMETRIC MEASUREMENTS

Here we present data from the first two harvests (i.e., 48 plants each). The order of measurement of plants at each harvest was in accordance with the experimental design (Block 1, Plot 1; Block 1, Plot 2; Block 1, Plot 3; ... Block 2, Plot 24).

Harvest 1 (mean date 16 September 2001) was conducted after six weeks growth in our nursery. For each plant, following Ackerly & Donoghue (1998), we measured shoot dimensions, including primary stem length measured along the trunk to the uppermost growing tip, and total length of the trunk and all branches. Major and minor crown diameters and depths were measured using a 100 cm × 100 cm horizontal grid of adjustable height. A north-facing leaf from the outer canopy on the north side of the plant was tagged; the midrib angle relative to the horizontal was measured *in situ* with a protractor and shot line; the length, width, and lamina thickness were measured with Vernier calipers; and the leaf was photographed and its area measured using image analysis software (ImageProPlus, Version 4.5.0.19, Media Cybernetics, Inc.). For the whole shoot (i.e., all above-ground plant parts): fresh weights of leaves and of stems plus petioles, and leaf areas (LiCor 3100 area meter, Lincoln, Nebraska, USA) were

**Table 1** Analysis of variance table for full split-plot experimental design with Block structure: Block/Plot/Position, and Treatment structure: Shade\*Genus\*Habit\*Harvest. There were two blocks, 24 plots within blocks to which four shading treatments and three congeneric species pairs of divaricates and non-divaricates were allocated, and six positions within plots to which six harvests were allocated.

Source of Variation	d.f.
<b>Block Stratum</b>	1
<b>Block.Plot Stratum</b>	
Genus	2
Habit	1
Shade	3
Genus.Shade	6
Habit.Shade	3
Genus.Habit.Shade	6
Residual	25
<b>Block.Plot.Position Stratum</b>	
Harvest	5
Genus.Harvest	10
Habit.Harvest	5
Shade.Harvest	15
Genus.Shade.Harvest	30
Habit.Shade.Harvest	15
Genus.Habit.Shade.Harvest	30
Residual	130
<b>Total</b>	287

measured. Roots were washed, and all plant parts were dried at 70°C for 72 hours and then weighed.

Harvest 2 (mean date 15 March 2002) was conducted four and half months after plants were moved to the experimental treatments. Methods were similar to harvest 1. Some measurements were made for all treatment combinations, and some were made only on the 24 plants grown under 25% and 100% sunlight (as indicated in the figures and tables). For plants grown under 25% and 100% sunlight an extended set of architectural measurements was made on five shoot samples from the crown of each plant. Since plants had different absolute crown dimensions, to sample according to relative position in the crown we defined a box with axes (dep, majD, minD) parallel to the crown depth and major and minor diameters, respectively. Ten relative positions, with values of 0.05, 0.15, 0.25, ... 0.95 quantifying their position along the axis as a proportion of its total length, gave a total of  $10^3$  possible 3-D co-ordinate sets. If no shoot was present within a 50 mm radius of a randomly selected co-ordinate set a new set was randomly selected without replacement. The co-ordinate set location (or the point nearest to it on a stem) was used as the midpoint of a stem sample, with the length of the stem sampled being 25 mm basal and 25 mm apical to this point. *In situ*, we measured the basal and apical diameters, and angle from the horizontal of this proximal stem sample. This sample and all the attached distal branches and leaves were removed. *Ex situ* we measured stem lengths, leaf numbers and areas, and fresh and dry weights of leaves and of stems plus petioles.

### Derived parameters

For each plant, the LAI was calculated as the total leaf area (one-sided) divided by the projected (elliptical) crown area. Crown volume was estimated as an ellipsoid. Total number of leaves was estimated as the total leaf area divided by the area of the tagged leaf. Foliage density was calculated as the total number of leaves divided by the projected crown area. Leader dominance was estimated from length of the primary stem relative to the total stem length minus the primary stem length. The cost of stems was estimated as stem dry mass per length (Wagner et al. 1998).

### Data analyses

Data from each harvest were analysed separately using GenStat (5th ed., releases 4.2 & 7.2, VSN International). Notation for factorial models is as in Wilkinson & Rogers (1973). Analyses of variance

were used to examine the significance of fixed effects (Genus\*Habit\*Shade) at the plant (Block. Plot) level. Data were transformed where necessary to homogenise the variance. Data presented are means and least significant difference (LSD), or backtransformed means and 95% confidence intervals, for the highest order factor interactions that were significant ( $P < 0.05$ ) for global ( $F$ ) tests, except for means presented in Table 1 which are the treatment level means.

The effect of relative position within the crown on the architecture and morphology of shoot samples was examined for six traits: angle from the horizontal of stems ( $\alpha_s$ , °); average area of individual leaves ( $A_L$ , cm<sup>2</sup>); stem diameter at the base ( $D_s$ , mm); number of leaves per unit stem length ( $f_L$ , mm<sup>-1</sup>); leaf area ratio, the ratio of leaf area to shoot dry mass (LAR, m<sup>2</sup> kg<sup>-1</sup>); and specific leaf area, the ratio of leaf area to leaf dry mass (SLA, m<sup>2</sup> kg<sup>-1</sup>). The ordinate values for position relative to crown depth (dep) were 0.05, 0.15, 0.25, ... 0.95 as above. The ordinate values for horizontal position on the two axes, majD and minD, were transformed by subtracting 0.5 and taking the absolute value, to yield majR and minR, respectively, with values of 0.05, 0.15, 2.5, ... 0.45 describing the relative position along the crown diameter from the centre to the edge. Linear mixed models were fitted using restricted maximum likelihood estimation (Patterson & Thompson 1971). We examined the fixed effects of explanatory variates describing within-crown position (dep, majR, minR), and treatment factors (Genus, Habit, Shade) on each of the six traits. Effects of treatment factors, covariates, and all possible two-way interactions were first modelled (random effects: Block/Plot/Sample). Terms were then successively deleted from nested submodels where changes in deviance tests ( $\chi^2$  test) were not significant ( $P < 0.05$ ), to arrive at the most parsimonious sub-model. Marginal predicted values of the response variates were estimated for given values of the explanatory variates as in Welham & Thompson (1997).

## RESULTS

### Leaf and stem morphology

The area and width (Table 2) of single leaves were greater in non-divaricates than divaricates, and in *Aristotelia* compared with other genera. Overall mean widths were 2.8 mm for divaricates and 31.8 mm for non-divaricates. Genera differed in the ratios of leaf

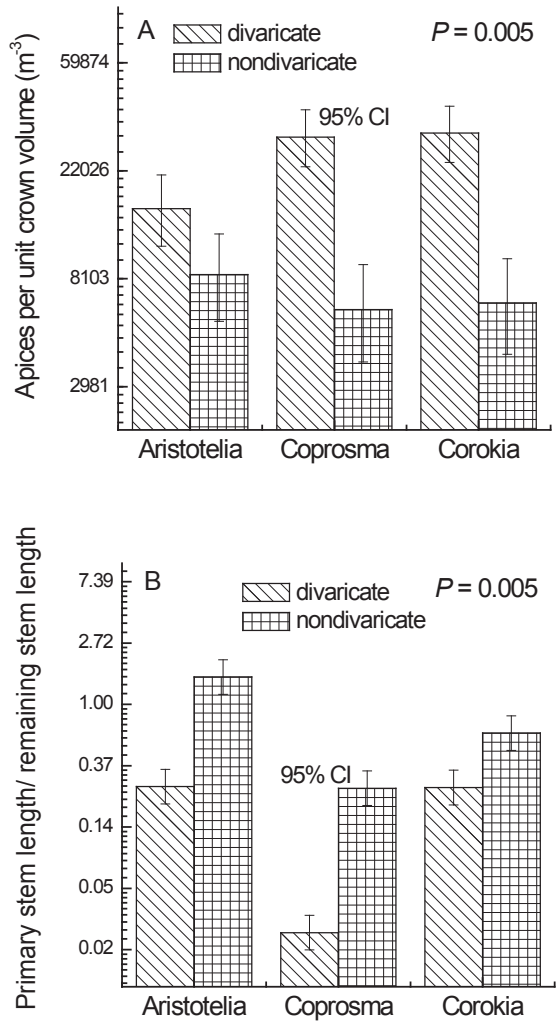
**Table 2** Architectural traits of divaricate and non-divaricate congeners of *Aristotelia*, *Coprosma*, and *Corokia* measured prior to (harvest 1), or after 4½ months growth in full sun (100% sunlight) or behind shadecloth transmitting 25, 52, or 73% sunlight (harvest 2). Traits were measured for either a north-facing tagged leaf from the outer canopy on the north side of the plant, randomly selected shoot samples, or the whole shoot. The data presented are the predicted treatment level means for the appropriate ANOVA model. The highest order factor interactions that were significant are indicated with the appropriate LSD for comparisons of the means at that level.

Trait	Subject	Significant effects ( <i>P</i> ; LSD)	sunlight (%)	Aristotelia		Coprosma		Corokia	
				divaricate	non	divaricate	non	divaricate	non
ln(leaf area (cm <sup>2</sup> ))	tagged leaf	Genus (<0.001; 0.331), Habit (<0.001; 0.270)	25	-1.190	3.531	-2.804	2.568	-2.062	1.931
			52	-1.137	3.050	-1.822	2.969	-2.133	2.624
			73	-0.843	4.030	-2.590	2.807	-2.427	1.974
ln(leaf width (mm))	tagged leaf	Genus.Habit (0.006; 0.2148)	100	-1.350	3.580	-2.784	2.042	-2.451	2.469
			25	1.546	4.017	1.017	3.399	0.968	2.819
			52	1.54	4.005	1.033	3.294	0.878	2.99
leaf length/leaf width	tagged leaf	Genus.Habit (<0.001; 0.2592)	73	1.655	4.444	0.379	3.299	0.728	2.818
			100	1.363	4.219	0.564	3.213	0.826	3.013
			25	2.511	1.409	2.546	2.112	3.772	4.200
ln(10 + leaf angle (°))	tagged leaf	Genus.Habit (0.024; 0.556)	52	2.265	1.409	3.067	1.934	3.428	4.209
			73	2.925	1.258	3.291	2.172	3.839	4.020
			100	2.693	1.286	2.756	1.948	3.529	4.376
ln(stem diameter (mm))	shoot samples	Genus.Habit (0.023; 0.231), Shade (0.037; 0.133)	25	2.996	3.387	3.107	3.734	3.198	4.094
			52	4.08	3.276	3.107	4.206	3.565	4.003
			73	4.195	3.687	3.454	3.689	2.649	4.211
bifurcation angle (°)	whole shoot	Genus.Habit (<0.001; 0.412)	100	3.951	3.8	4.007	4.401	3.902	4.401
			25	0.476	0.895	0.353	0.838	-0.152	0.905
			100	0.586	1.113	0.303	1.068	0.13	1.064
ln(number of shoot apices/ primary stem length (mm))	whole shoot	Genus.Habit (0.009; 19.2)	harvest 1	57.5	55.6	75.6	45.6	82.8	37.5
			harvest 1	-2.27	-3.197	-0.261	-2.554	-1.819	-2.866
			harvest 1	5.332	5.501	5.056	5.794	5.794	5.361
ln(number of shoot apices/ total stem length (mm))	shoot samples	Genus.Habit (<0.001; 0.256)	25	0.574	0.452	0.639	0.611	0.56	0.461
			100	0.398	0.454	0.773	0.644	0.517	0.462
			harvest 1	4.187	3.265	4.325	5.317	2.288	4.775
(total leaf number/total stem length (mm)) <sup>1/3</sup>	whole shoot	Genus.Habit (<0.001; 0.679)	harvest 1	4.187	3.265	4.325	5.317	2.288	4.775
			harvest 1	4.187	3.265	4.325	5.317	2.288	4.775
			harvest 1	4.187	3.265	4.325	5.317	2.288	4.775

Continued over page

**Table 2** (continued)

Trait	Subject	Significant effects ( <i>P</i> ; LSD)	sunlight (%)	Aristotelia	Coprosma	Corokia
				divaricate	non	divaricate
				divaricate	non	divaricate
ln(height (cm))	whole shoot	Genus.Habit (<0.001; 0.141), Shade (0.015; 0.15)	25	4.309	4.215	4.042
				4.248	4.494	4.343
				4.513	4.407	4.117
				4.19	4.329	3.98
(shoot DW/crown volume (kgm <sup>-3</sup> ) <sup>1/2</sup> )	whole shoot	Genus (0.047; 0.076)	25	0.637	0.531	0.67
				0.782	0.786	0.943
				0.482	1.218	0.817
(LAI) <sup>1/2</sup>	whole shoot	Genus (0.034; 0.249), Habit (<0.001; 0.203)	25	0.461	1.294	0.564
				-5.899	-4.742	-4.699
				-5.939	-4.377	-6.479
ln(leaf DW (kg)/stem length (m))	shoot samples	Genus.Habit.Shade (0.002; 0.4716)	100	0.414	1.07	-7.025
				-6.105	-4.691	



**Fig. 1** **A**, effect of Genus by Habit interaction on the number of shoot apices per unit of crown volume at harvest 1. Analysis of variance was for cube-root transformed data; **B**, effect of Genus by Habit interaction on the length of the primary stem relative to the length of the remaining stems at harvest 1. Analysis of variance was for natural logarithm transformed data. Data presented are back-transformed means and 95% confidence intervals for the highest order factor interactions that were significant ( $P < 0.05$ ) for global ( $F$ ) tests. Data were for the whole shoot of all species.

lengths to widths (Table 2), and there was greater relative elongation of leaves in divaricates from genera with wider, less elongated leaves, enabling these species to achieve a smaller effective leaf size for a given leaf area. The specific leaf area of

tagged leaves (square-root transformed data) showed no significant effect of any of the treatment factors (backtransformed mean and 95% CI: 81.4 (69.3, 96.2) cm<sup>2</sup> g<sup>-1</sup>). Leaf angles (Table 2) were steeper in non-divaricates than divaricates for *Coprosma* and *Corokia*, but not *Aristotelia*.

Stem diameters (Table 2) were greater in non-divaricates than divaricates (overall means 2.61 and 1.33 mm, respectively), and were largest in *A. fruticosa* and smallest in *C. cotoneaster* among divaricates. Diameters were greater in 100% than in 25% sunlight. Stem display was more horizontal in divaricates than non-divaricates (respective means: 32.8° and 64.6°; LSD = 9.9). At harvest 1, stem bifurcation angles were greatest in *Corokia cotoneaster* and least in *C. buddleioides*, but there was little difference with habit in *Aristotelia* (Table 2).

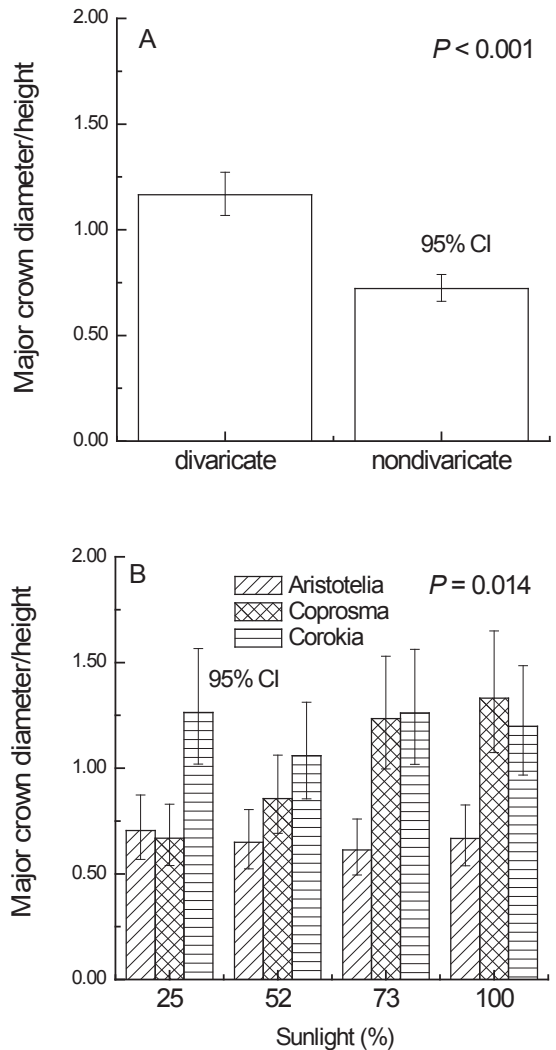
The number of leaves per stem length (Table 2) was greater for *Coprosma* than *Corokia* or *Aristotelia*, but did not differ with habit or shading. *Aristotelia* and *Coprosma* have opposite leaves and *Corokia* has alternate leaves, thus, mean internode lengths were approximately 20 mm for *Aristotelia*, 6.7 mm for *Coprosma*, and 8.3 mm for *Corokia*. The ratio of total stem length to total leaf area of samples was greater in divaricates than non-divaricates (means 9.8 and 1.8 m<sup>-1</sup>, respectively, LSD = 1.82).

### Crown morphology

Divaricates had more shoot apices per unit crown volume than non-divaricates, and this difference was least in *Aristotelia* (Fig. 1A). The same pattern was shown for the ratio of number of shoot apices to stem biomass (data not presented). Leader dominance (Fig. 1B) was greater in non-divaricates than divaricates, and greatest in *Aristotelia* and least in *Coprosma*.

Trunk diameters were greatest in *C. robusta* and least in *C. cotoneaster* but differed little with habit in *Aristotelia* (Table 2). Plant heights were greatest in *A. serrata* and least in *C. cotoneaster* (Table 2). Ratios of the major crown diameter to height (Fig. 2) were greater in divaricates than non-divaricates. *Corokia* and *Aristotelia* showed little response to shading and maintained the highest and lowest ratios, respectively. *Coprosma* switched from horizontal spread in high light to vertical spread in lower light.

Shoot biomass to crown volume ratios were greater in 100% than 25% sunlight (Table 2). Foliage densities were lower in nondivaricates (Fig. 3A) than divaricates (backtransformed means of 0.11 and 1.88 leaves cm<sup>-2</sup>, respectively); and were highest in

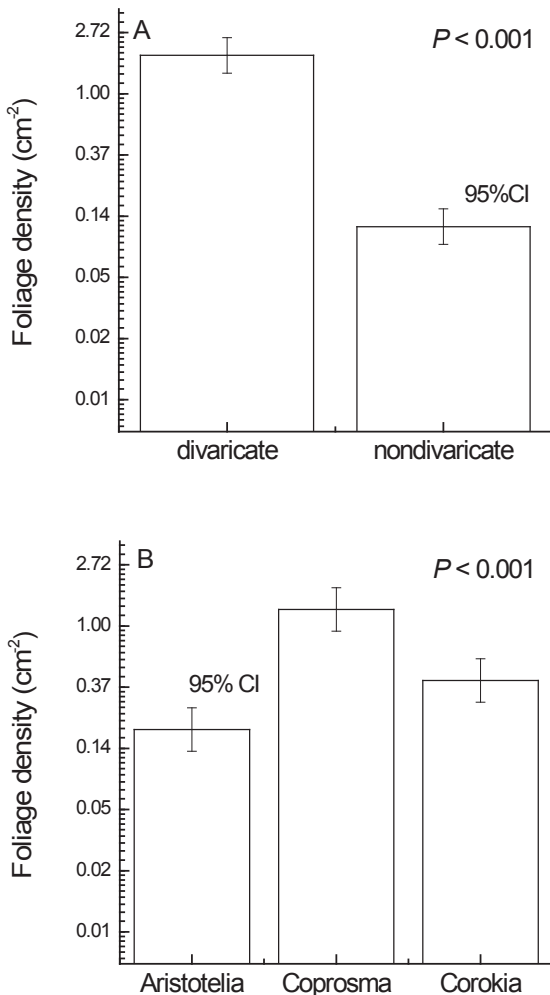


**Fig. 2** Effects of **A**, Habit and **B**, Genus by Shade interaction on the ratio of major crown diameter to height at harvest 2. Analysis of variance was for natural logarithm transformed data, presentation as in Fig 1. Data were for the whole shoot of all species under all shading treatments.

*Coprosma* and lowest in *Aristotelia* (Fig. 3B). Leaf area indices (Table 2) were lower in divaricates than non-divaricates, and were least in *Corokia* and greatest in *Coprosma*.

### Costs of supporting leaf area

There was more leaf area per shoot dry mass in non-divaricates (Fig. 4A; backtransformed mean 5.5 m<sup>2</sup> kg<sup>-1</sup>) than divaricates (1.3 m<sup>2</sup> kg<sup>-1</sup>), and in 25% than in 100% sunlight (Fig. 4B). The cost of



**Fig. 3** Effects of **A**, Habit and **B**, Genus on the foliage density at harvest 2. Analysis of variance was for natural logarithm transformed data, presentation as in Fig. 1. Data were for the whole shoot for all species and two (25% and 100% sunlight) shading treatments.

stems was lower in divaricates than non-divaricates, and differences with habit were greatest in *Corokia* and least in *Aristotelia* (Fig. 4C). The cost of stems was greater in high light (Fig. 4D). The dry mass of leaves per unit stem length (Table 2) was higher in non-divaricates than divaricates, especially for *Corokia*, and shading responses were species-specific.

#### Within-crown heterogeneity

Of the six response variables for which effects of position within the crown were modelled, only number

of leaves per unit stem length showed a significant effect of habit on the slope of the relationship (Table 3). The number of leaves per unit stem length differed with genus, increased exponentially towards the periphery (horizontal plane) of the crown in all plants, and increased exponentially with increasing depth within the crown in divaricates but decreased exponentially with increasing depth in non-divaricates (Fig. 5). The average area of individual leaves differed with genus and habit, increased exponentially with increasing depth within the crown, and increased exponentially towards the centre of the crown (horizontal plane) especially in shaded plants (Table 3). The angle from the horizontal of stems differed with habit, and decreased at the periphery (horizontal plane) of the crown especially in high light. The diameter of stems differed with habit, increased exponentially with increasing depth in *Corokia*, and decreased exponentially towards the periphery (horizontal plane) of the crown, in high light. The LAR (model not presented; see Fig. 4A,B) and SLA (model not presented) showed no significant variation with position in the crown.

## DISCUSSION

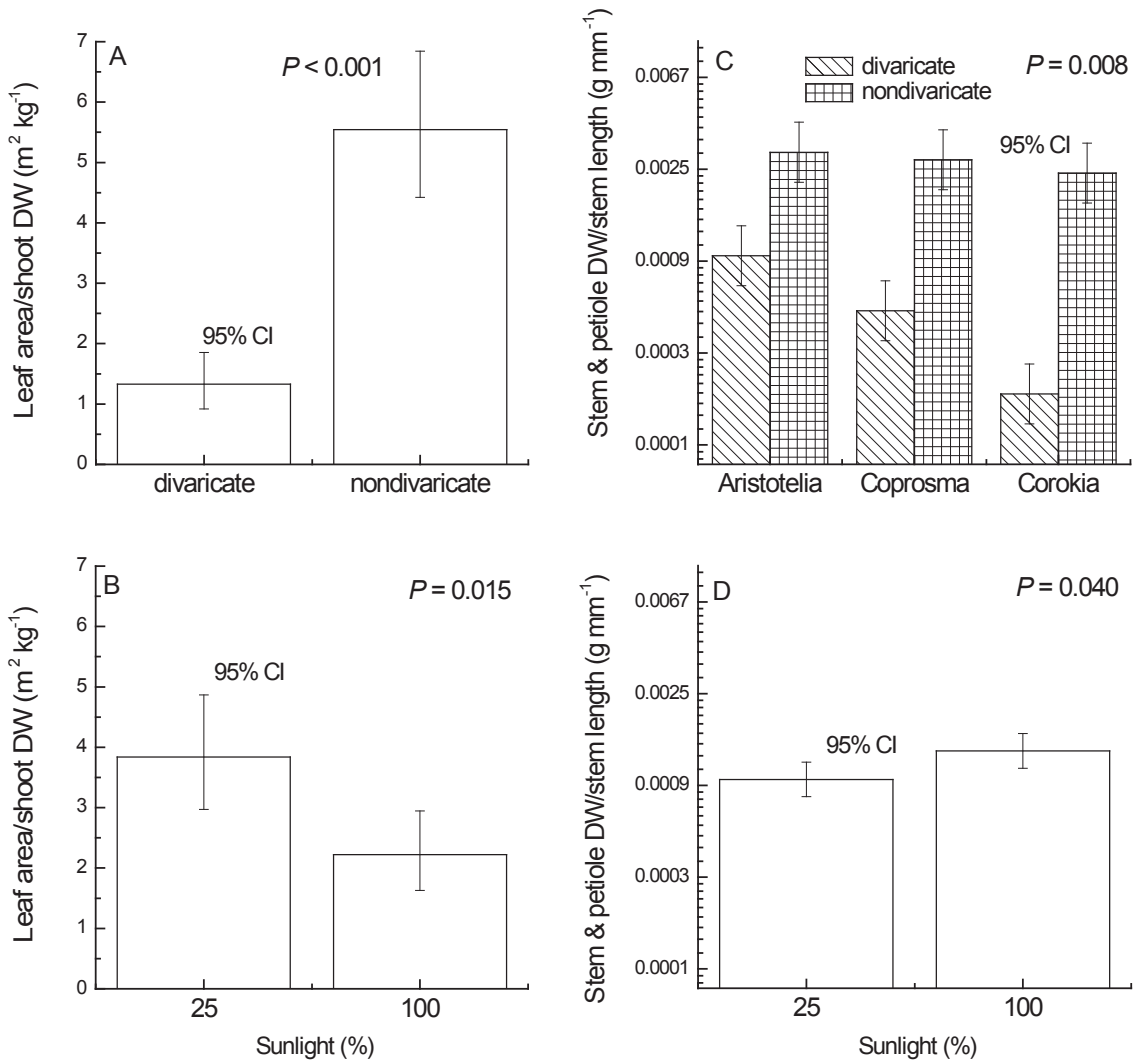
### Defining traits of the habit

Small leaves (e.g., Bulmer 1958) and interlaced branches (e.g., Cockayne & Allan 1934) were good descriptors of the divaricate habit (see also Kelly 1994). In divaricates, weak apical control (Brown et al. 1967) leading to interlaced branches (Went 1971) was expressed as lesser leader dominance and more apices per unit crown volume compared with non-divaricates (consistent with Day 1998b,c). Wide bifurcation angles were absent in *A. fruticosa*, supporting the view that branch angles are a poor diagnostic trait of the syndrome in many species (Wardle & McGlone 1988).

### Acclimation to high irradiance

We found no evidence that divaricates differed from non-divaricates in the way that high irradiance affected investment in shoot structures. The view that divaricates differ from non-divaricates in their lability of form in response to light environment (McGlone & Webb 1981; Day 1998a,b) may hold only for dense shade. Although our vertical screens provided relatively high asymmetric light this may be more representative of the forest margin, cliff, and riverbank habitats where divaricates are presently





**Fig. 4** Effects of **A**, Habit and **B**, Shade on the ratio of leaf area to shoot biomass at harvest 2. Analysis of variance for each variate was for cube-root transformed data. Effects of **C**, Genus by Habit interaction and **D**, Shade on the biomass cost of stems per unit length at harvest 2. Analysis of variance was for natural-logarithm transformed data. Presentation is as in Fig. 1. Data were for shoot samples of all species and two (25% and 100% sunlight) shading treatments.

common (McGlone & Webb 1981) than spatially homogeneous shading (Fisher 1983).

Responses to shading were expressed, at the between-plant level in all species, as a shift in the partitioning of biomass from support to light-harvesting functions (i.e., increased ratio of leaf area to shoot dry mass, reduced stem diameter, and reduced stem biomass relative to stem length). Shaded plants may require a lesser capacity for water transport

and assimilate retranslocation and less secondary thickening, and more economic use of the available carbon may be more critical (Bloor & Grubb 2004; Niinemets et al. 2004a). Shading also resulted in more horizontal orientation of branches, as in other studies (Fisher 1983). These responses resulted in occupation of a larger crown volume for a given shoot biomass, increasing opportunities for light interception.

### Within-crown heterogeneity

The perceived "insideoutness" of divaricates compared with non-divaricates was explained by increasing number of leaves per unit stem length, suggestive of shorter internode lengths, in the lower canopies of divaricates and in the upper canopies of non-divaricates. Patterns for divaricates are consistent with previous descriptions for shrubs (Kelly 1994). Our shading treatments did not affect the vertical leaf distribution in any species, suggesting little plasticity of this trait in response to varying degrees

of excess irradiance. In contrast, greater and inverse responses to deep shade have been found in the juvenile divaricating stage of heteroblastic species; LAI increased from lower to upper layers in plants under closed canopies and was constant between layers for plants growing in canopy gaps (Day 1998a). Establishing the effects of these differences in vertical leaf distribution on whole canopy photosynthesis requires modelling; other studies have found only minor (and negative compared with a homogeneous distribution) effects (Chen et al. 1994).

**Table 3** Within-crown variation in architectural traits of samples of the shoots of divaricate and non-divaricate species measured after four and a half months growth (harvest 2) under shading treatments:  $A_L$ , average area of individual leaves ( $\text{cm}^2$ );  $\alpha_s$ , angle from the horizontal of stems ( $^\circ$ );  $f_L$ , number of leaves per unit stem length (mm);  $D_s$ , stem diameter at base (mm). Linear mixed models fitted using restricted maximum likelihood estimation describe the variation in the traits of samples with increasing depth (mdep) through the canopy, and with increasing horizontal distance from the centre of the major (majR) and minor (minR) crown diameters.

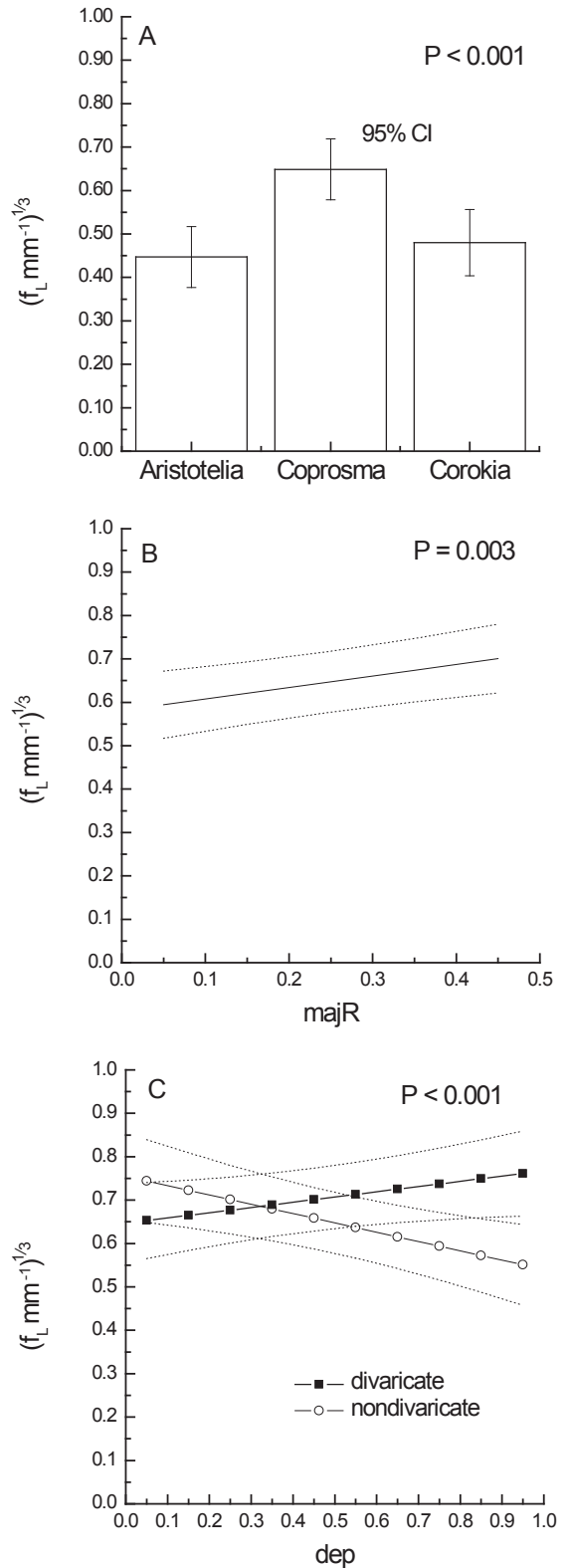
Response	Genus	Habit	Sunlight (%)	intercept	slope. [mdep]	slope. [majR]	slope. [minR]	slope. [majR].[minR]
$\ln(A_L)$	<i>Aristotelia</i>	divaricate	25	-1.75	0.49	-2.18		
$\ln(A_L)$	<i>Aristotelia</i>	nondivaricate	25	2.73	0.49	-2.18		
$\ln(A_L)$	<i>Coprosma</i>	divaricate	25	-2.73	0.49	-2.18		
$\ln(A_L)$	<i>Coprosma</i>	nondivaricate	25	1.75	0.49	-2.18		
$\ln(A_L)$	<i>Corokia</i>	divaricate	25	-2.63	0.49	-2.18		
$\ln(A_L)$	<i>Corokia</i>	nondivaricate	25	1.85	0.49	-2.18		
$\ln(A_L)$	<i>Aristotelia</i>	divaricate	100	-2.59	0.49	-0.25		
$\ln(A_L)$	<i>Aristotelia</i>	nondivaricate	100	1.89	0.49	-0.25		
$\ln(A_L)$	<i>Coprosma</i>	divaricate	100	-3.57	0.49	-0.25		
$\ln(A_L)$	<i>Coprosma</i>	nondivaricate	100	0.91	0.49	-0.25		
$\ln(A_L)$	<i>Corokia</i>	divaricate	100	-3.46	0.49	-0.25		
$\ln(A_L)$	<i>Corokia</i>	nondivaricate	100	1.02	0.49	-0.25		
$\text{abs}(\alpha_s)$		divaricate	25	32.87		-37.58	-22.98	240.50
$\text{abs}(\alpha_s)$		nondivaricate	25	62.95		-37.58	-22.98	240.50
$\text{abs}(\alpha_s)$		divaricate	100	53.78		-37.58	-97.13	240.50
$\text{abs}(\alpha_s)$		nondivaricate	100	83.86		-37.58	-97.13	240.50
$(f_L)^{1/3}$	<i>Aristotelia</i>	divaricate		0.43	0.01	0.27	0.43	
$(f_L)^{1/3}$	<i>Aristotelia</i>	nondivaricate		0.39	-0.02	0.27	0.39	
$(f_L)^{1/3}$	<i>Coprosma</i>	divaricate		0.63	0.01	0.27	0.63	
$(f_L)^{1/3}$	<i>Coprosma</i>	nondivaricate		0.59	-0.02	0.27	0.59	
$(f_L)^{1/3}$	<i>Corokia</i>	divaricate		0.46	0.01	0.27	0.46	
$(f_L)^{1/3}$	<i>Corokia</i>	nondivaricate		0.42	-0.02	0.27	0.42	
$\ln(D_s)$	<i>Aristotelia</i>	divaricate	25	0.39	0.13	-0.65	0.38	
$\ln(D_s)$	<i>Aristotelia</i>	nondivaricate	25	1.02	0.13	-0.65	0.38	
$\ln(D_s)$	<i>Coprosma</i>	divaricate	25	0.36	-0.11	-0.65	0.38	
$\ln(D_s)$	<i>Coprosma</i>	nondivaricate	25	0.98	-0.11	-0.65	0.38	
$\ln(D_s)$	<i>Corokia</i>	divaricate	25	-0.15	0.65	-0.65	0.38	
$\ln(D_s)$	<i>Corokia</i>	nondivaricate	25	0.48	0.65	-0.65	0.38	
$\ln(D_s)$	<i>Aristotelia</i>	divaricate	100	0.83	0.13	-0.65	-0.77	
$\ln(D_s)$	<i>Aristotelia</i>	nondivaricate	100	1.45	0.13	-0.65	-0.77	
$\ln(D_s)$	<i>Coprosma</i>	divaricate	100	0.79	-0.11	-0.65	-0.77	
$\ln(D_s)$	<i>Coprosma</i>	nondivaricate	100	1.42	-0.11	-0.65	-0.77	
$\ln(D_s)$	<i>Corokia</i>	divaricate	100	0.29	0.65	-0.65	-0.77	
$\ln(D_s)$	<i>Corokia</i>	nondivaricate	100	0.91	0.65	-0.65	-0.77	

Increases in leaf size in the canopy interior were also consistent with previous descriptions of divaricates (Kelly 1994), but were not restricted to divaricates, were apparent in all six species and treatments, and are typical of sun to shade transitions (Vogel 1968).

**Shade tolerance**

The suite of traits found in divaricates was typical of neither sun- nor shade-adaptation. Allometric studies of woody species suggest that dynamic strategies of light harvesting in the understorey are related to a suite of correlated traits consisting of positive associations between trunk diameter, projected crown area, and total leaf area (when adjusted for height; Ackerly & Donoghue 1998). Divaricates and non-divaricates show positive associations for the first two traits but not the third. More horizontal display of branches and greater crown diameters relative to heights in divaricates than in non-divaricates suggested greater investment in horizontal and vertical extension, respectively. The narrower crowns in non-divaricates were associated with greater leader dominance and larger leaf size, consistent with the view that species with large leaves economise on investment in stem support through greater investment in vertical growth rather than lateral branches (Givnish 1987; King 1991). Greater relative investment in horizontal extension in divaricates will enhance light interception when the sun is near its zenith (e.g., midday, summer), and may facilitate persistence in understorey habitats where light is limiting. Greater relative investment in vertical extension in non-divaricates will enhance interception of light at low solar angles (e.g., early morning, late afternoon, winter) and may facilitate opportunistic escape and prevention of overtopping in crowded stands (King 1981, 1997; Givnish 1987, 1988). Lesser leaf height in divaricates compared with non-divaricates will be exacerbated by divaricates' increase and non-divaricates' decrease in leaf number per unit stem length with depth through the crown.

**Fig. 5** Predicted values of cube-root transformed number of leaves per stem length ( $f_L \text{ mm}^{-1}$ ) for given relative positions within the crown, for the models given in Table 3. Dotted lines show the 95% confidence intervals in all cases. **A**, effect of Genus for samples of nondivaricates at the mean values of dep and majR (i.e., relative depth and relative distance from the centre of the major crown diameter, respectively); **B**, effect of majR for *Coprosma robusta* (nondivaricate) at the mean value of dep; **C**, effect of dep by Habit interaction in *Coprosma* at the mean value of majR.



Patterns of adaptation and acclimation to light are often thought to be similar, with sun plants exhibiting higher LAI, more erect twig orientations, and lower fractional partitioning of biomass to leaves than shade plants (Givnish 1988). In our study, species with either growth habit exhibited traits which are a mix of these. This view of light adaptation has been challenged by studies of carbon allocation in seedlings in response to deep shade (Walters & Reich 1999), which have proposed that tolerant species have traits (including low respiration rates, long leaf life spans, and low leaf area ratios) which maximise retention of biomass and seedling survival. According to this view, lower leaf area ratios in divaricating than in non-divaricating congeners may be indicative of greater shade tolerance. An alternative proposal is that while non-divaricates are adapted to maximise relative fitness by maximising resource acquisition and growth, divaricates are adapted to maximise relative fitness by maximising resource retention and survival (Grime & Hunt 1975; Grime 1977; Mooney & Gulmon 1979; Raven 1994; Hunt & Cornelissen 1997).

#### **Influence of leaf & stem size on microclimate**

Leaf size has been found to be independent of shade tolerance in woody species (Ackerly & Donoghue 1998). More favourable radiative heat exchange has been invoked to explain the more frequent occurrence of species with smaller leaves in exposed habitats (Niinemets & Kull 1994; Bragg & Westoby 2002). Smaller effective leaf sizes in divaricates compared with non-divaricates should enhance convective heat transfer and boundary layer conductance and may result in closer coupling of leaf and air temperatures (Gates 1980). This is consistent with reported greater minimum and lesser maximum temperatures of divaricate compared with non-divaricate foliage of heteroblastic species (Kelly & Ogle 1990).

In understorey habitats where light is limiting, greater self-shading in small-leaved divaricating species may be costly. Studies of isolated leading shoots of other broad-leaved woody species support this argument (Falster & Westoby 2003). However, within-shoot self-shading of this type may be functionally similar to "clumping" of leaves on shoots in gymnosperms (Oker-Blom et al. 1989; Cescatti & Zorer 2003) and poplar (Niinemets et al. 2004b), which increases light penetration deep in the crown compared with randomly distributed foliage and may be beneficial when photosynthesis is considered at whole-crown scale.

The thin stems and small leaves of divaricating shrubs would be expected to enhance penumbral effects (Horn 1971; Kelly 1994). The probability of an object casting penumbral shadows on a target increases with decreasing object width and increasing target distance. In sunny conditions, of high beam irradiance, the object's umbral shadow length is theoretically 108 times the object's effective diameter (Horn 1971). In divaricates compared with non-divaricates, shorter umbral shadows of leaves (c. 30 and 340 cm, respectively) and stems (c. 14 and 28 cm, respectively) will be more easily avoided. In deep canopies with small leaves penumbral shading between shoots evens out the distribution of direct sunlight within the crown. Because the photosynthetic light response is curvilinear, this enhances the rate of photosynthesis by avoidance of both limiting and saturating (or photoinhibitory) irradiance (Stenberg 1995). Penumbral effects are greater in high-LAI canopies, under high beam fraction, when top-of-the-crown irradiance is super-saturating, and when the convexity of the photosynthetic light response approaches one (Stenberg 1998). Penumbral effects may be enhanced in non-divaricates by their higher LAI, relatively taller crowns, and the positioning of leaves relatively higher in the canopy. A selective advantage mediated by penumbral effects may explain why tree forms which exhibit divarication are heteroblastic, routinely exhibiting divarication in the juvenile and not the adult stage, and often exhibit a gradient of increasing leaf size with increasing height.

#### **Allometric measures of light interception**

Despite having high foliage densities, divaricates had low LAIs, and shoot biomass to crown volume ratios showed no significant habit effects. Therefore, for only one of three measures can it be said that divaricate shrubs have "dense" canopies (Day 1998a,b).

The lower LAI in divaricates than non-divaricates can be interpreted as indicating less leaf overlap and self-shading, making divaricates and non-divaricates better adapted to low and high radiation environments, respectively (Horn 1971). This is largely the conclusion of studies of the juvenile divaricating and adult non-divaricating stages of heteroblastic species (Day 1998b). However, partly contradicting this, Day (1998b) argued that the divaricating stage is multilayered, and LAI (and diameter to height ratio) decreases with ontogeny. We found that diameter to height ratios, but not LAIs, of divaricate and non-divaricate shrubs fitted these predictions. For our

shrubs, non-divaricates were more appropriately described as multilayered than divaricates, for which LAIs were c. 0.3, similar to values for divaricating juveniles of a heteroblastic species (Day 1998b).

### Costs of support of leaf area

A low ratio of leaf to shoot biomass in the divaricating juvenile stage of a heteroblastic species has been suggested to result in high costs of light capture (Day 1998c). Our lower ratios of leaf area to shoot biomass, leaf biomass to stem length, and stem biomass to length in divaricating compared with non-divaricating shrubs indicate that divaricates invested a large amount of biomass in stem elongation to support a relatively small photosynthetic leaf area. The greater investment in shoot biomass per unit photosynthetic leaf area, and lower LAI in divaricates than non-divaricates, are consistent with lower leaf area per unit of supporting biomass in monolayers compared with multilayers (Horn 1971), and increases in the costs of support of leaf area with increasing branch order (Borchert & Tomlinson 1984) and decreasing leaf size (Givnish 1978).

Assuming partitioning of biomass to roots is similar for divaricates and non-divaricates, a greater whole-plant relative growth rate arising from enhanced photosynthesis would require rates per unit leaf area in divaricates that were sufficiently high to offset the four-fold greater investment in leaf area per unit shoot biomass in non-divaricates. Typically, studies of diurnal photoinhibition in acclimated shoots show reductions in daily net photosynthesis of around 10% in comparison with a hypothetical photoinhibition-proof state (Ögren & Sjöström 1990; Werner et al. 2001). This figure is well short of the enhancement needed for divaricates to outperform non-divaricates.

Howell et al. (2002) found that following removal of outer branches of divaricating shrubs, the species (*A. fruticosa*) that was most affected by this treatment showed a two-fold greater number of leaves which abscised (69% cf. 36%) and a reduction in net photosynthesis per unit photosynthetic area of shoots of c. 50%, compared with controls. If reductions in photosynthetic area were also two-fold this suggests that the maximum effect of sudden exposure to excess irradiance was a 75% lower net photosynthesis for the shoot compared with controls. To resolve debate over this study (Lusk 2002; Turnbull et al. 2002) we need to (i) resolve difficulties in measuring rates of photosynthesis per unit leaf area using gas exchange for small-leaved shoots, (ii) measure the maximal quantum efficiency of

photosynthesis, (iii) measure whole-crown variation in light interception and photosynthesis, (iv) know if adverse effects on exposed leaves were offset by alleviation of light limitation deeper in the crown, (iv) determine whether these short-term responses to pruning reflect only a lack of acclimation in shaded inner leaves exposed to a sudden increase in irradiance, and (v) get comparable estimates for historic competitors (i.e., nondivaricate congeners).

Furthermore, a linked understanding of carbon gain and carbon allocation is needed. We must ascertain whether higher costs of leaf area support and greater relative investments in stem-plus-petiole biomass in divaricates compared with non-divaricates could be offset, not just by higher rates of photosynthesis, but by other traits. We hypothesise that these may include (i) lesser investments in leaf veins (Givnish 1986; Niinemets 1998, 2004), (ii) petioles that are more resistant to mechanical failure, and longer-lived leaves (Chazdon 1986), or (iii) longer-lived stems. Our third hypothesis is supported by greater tensile strength and resistance to mechanical failure in stems of divaricate than non-divaricate shoots of heteroblastic species (Bond et al. 2004).

### CONCLUSION

Patterns observed for New Zealand shrubs from diverse phylogenetic lineages in this study showed that divaricates possess traits which may be advantageous in avoiding photoinhibition, (i) an upper canopy with fewer leaves per stem length than the lower canopy and (ii) smaller leaf and stem diameters, consistent with the view that the divaricate habit will result in enhanced penumbral effects. However, traits of divaricates showed no distinctive response to high irradiance compared with their congeners, suites of traits possessed by divaricates were not typical of plants adapted to high irradiance, and costs of leaf area support were so high that they are likely to more than offset benefits to net carbon gain arising from photoinhibition avoidance.

To test the hypotheses that enhanced penumbral effects and/or leaf clumping in divaricating forms with small leaves and twigs result in a more even distribution of light through the crown, photoinhibition-avoidance, and enhanced net crown photosynthesis under high beam irradiance, modelling approaches (like those of Stenberg (1995, 1998), Valladares & Pearcy (1998), or Werner et al. (2001) need to be used to quantify the effect of architectural traits on whole crown light interception and photosynthesis.

Estimates of net carbon assimilation for the whole canopy are crucial and an important question is whether the stems of divaricate shoots are photosynthetically competent.

#### ACKNOWLEDGMENTS

This research was supported by a grant (UOC001-2001) from the Marsden Fund, administered by the Royal Society of New Zealand. We gratefully acknowledge the assistance of Landcare Research, Lincoln, in making available a field site. We thank Peter Bellingham, Richard Holdaway, Ülo Niinemets, Karl Niklas, John Raven, and two referees for their comments. The hypothesis that the divaricating shoot habit may enhance penumbral effects and avoidance of photoinhibition was first proposed by Marilyn Ball (pers. comm. 1993). Raewyn Young and Meredith McKay provided technical assistance.

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