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Architecture of a clonal population of *Muehlenbeckia astonii* Petrie (Polygonaceae), a divaricating shrub endemic to New Zealand

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Abstract *Muehlenbeckia astonii* Petrie is a compact, divaricating shrub. It produces both orthotropic and plagiotropic shoots but after a period of time the orthotropic shoots revert to a plagiotropic form. Orthotropic shoots differ from plagiotropic ones in that the internodes are longer, the shoots more erect and much straighter for the first 10–15 internodes. A clonal population of two-year-old cuttings, taken from a female plant, was grown outdoors in pots. Those cuttings supplied with a balanced nutrient solution were more vigorous and produced more second-order orthotropic shoots than those not provided with nutrient. However, nutrient level did not affect the ultimate divaricating nature of the shoots. The vigour of the shoots varied. Generally, a shoot grew vigorously for the first season producing many other shoots of higher orders; then extension of the second-order axis ceased and further growth was restricted to the higher-order laterals. Most of the growth was carried out by shoots initiated in the current growing season. To a large extent the number and vigour of the orthotropic shoots determined the overall form of the plants. These shoots sometimes arose below or close to ground level but often in older plants also developed as laterals on second- or third-order shoots some distance above the ground. Plagiotropic shoots did not increase the overall height of the shrub to any great extent, but orthotropic ones were important in that they placed shoots at a higher elevation and thus increased the volume of space occupied by the plant.

Keywords *Muehlenbeckia astonii*; divaricating shrub; branching; growth form; response to nutrient; Polygonaceae

INTRODUCTION

Muehlenbeckia astonii Petrie (Polygonaceae) is a dioecious divaricating shrub which grows up to 2 m in height (Allan 1961). Only one plant, albeit a very large one, (Tom Moss pers. comm.) could be found near the type locality, NZMS 260 R28 668 776. This is of concern from the point of view of continued survival there, bearing in mind the dioecious nature of the plant and the recent fires in the area. There are several species in the genus, of which *M. astonii* is the most divaricating. Divaricating plants are described as small-leaved shrubs with interlaced, wide-angled branches (Cockayne 1912; Taylor 1975; Tomlinson 1978). *M. astonii* is characteristic of divaricating shrubs in that it has flexuous, wide angled branches which interlace. It also produces “canes” from the base (Allan 1961) and to that extent it is a typical shrub (Guédès 1981). However, Bøcher (1977) argues that “divaricatness is difficult to define unequivocally, and it may be questioned whether a limit can be set to distinguish divaricate and non-divaricate structures.” Wardle & McGlone (1988) argue that divarication is a “second-order characteristic” and that divaricating plants are part of a much larger group of plants showing a “reduction syndrome” (reduced leaf and bud dimensions but with the retention of relatively long internodes); wiry twigs being the best characteristic of this sub-set.

Although the origin of the divaricating form in shrubs has attracted a great deal of speculation (e.g., Cockayne 1912; Rattenbury 1962; Dawson 1963; Greenwood & Atkinson 1977; McGlone & Webb 1981), there have been few detailed descriptive and analytical studies of growth. Form is determined to a large extent by the number and position of apical meristems and the degree to which they grow (Cutter 1965). This paper describes the development of the main branch systems on two-year-old cuttings of *M.*

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astonii and assesses the response of the shoot systems to nutrient level over a 15-month period. Older plants were used to study the overall form of the plant and to compare the location and vigour of orthotropic shoots (canes) and plagiotropic shoots.

MATERIALS AND METHODS

Fourteen two-year-old *Muehlenbeckia astonii* plants grown from cuttings were obtained from Platt's Nursery, Albany, Auckland in March 1982. They originated from a single female plant from the grounds of the University of Auckland. Thus, the plants were a clonal population and were also uniform in overall size and extent of branching. The main shoot of the cuttings was classified as first order and subsequent shoots were given successively higher order values. Most of the plants had five orders of shoots. The plants were grown outside on a scoria bed in 200 mm diameter pots for 6 months before transfer to 450 mm pots in October 1982. The growing medium was a mixture of pine bark, peat, and sand with a little pumice. Rock phosphate was in the original medium when the plants were obtained. Plants were ranked in pairs of plants with equal vigour and divided into two groups of seven. From October 1982 one group of plants received additional nutrient (high-nutrient) and the other did not (low-nutrient). The plants were arranged in a randomised block. Each week 300 ml of 1.5 times full strength Bollard's nutrient solution (Bollard 1966) were applied to each plant in the high nutrient treatment. Low nutrient plants received an equivalent volume of water.

Non-destructive measurements of the above-ground shoot systems were made in June, September and November 1982, and January, June and

September 1983. On each occasion the position and length of each shoot, the individual internode lengths of all shoots and the point of branching of each shoot were recorded. Schematic drawings of the entire shoot system were made for each plant on each occasion so that diagrams of the development of the branching pattern could be produced.

In 1985 the plants had grown substantially and were transferred to a shadehouse where they would be more protected. A further set of recordings was made of the points of origin, orientation, and location of each shoot in relation to the overall architecture of the plant. Shoots were classified as plagiotropic (growing predominantly horizontal or generally at an acute angle to the ground) or orthotropic (growing erect or nearly so for the first 10–15 nodes). Detailed recordings of internode positions and lengths were made in order to quantify the relationship between shoot type and the vigour of extension growth.

Observations were also made of mature plants of *M. astonii* growing in the grounds of Old Government House, University of Auckland and at the type locality at Palliser Bay (Allan 1961).

RESULTS

Nutrient effects on shoot production and growth

In June 1982, the plants had a mean of about two second-order shoot systems (Table 1). The number of second-order shoots subsequently increased, principally during spring, to 3.8 and 3.5 for the two groups of plants. The effect of the nutrient treatment was evident within two months of the first application; the rate of increase in the mean number of second-order shoots was maintained in plants in the high-nutrient treatment whereas there was no increase in those under low-nutrient conditions. By November

Table 1 The production of second-order shoots by plants of *Muehlenbeckia astonii* grown under high and low nutrient conditions (\pm s.e. of the mean). Seven plants in each nutrient treatment.

Time of measurement	Nutrient level	
	High	Low
1982		
June	2.2 \pm 0.2	2.1 \pm 0.2
Sept	2.5 \pm 0.2	2.1 \pm 0.2
Nov	3.8 \pm 0.4	3.5 \pm 0.4
1983		
Feb	4.1 \pm 0.6	3.5 \pm 0.4
June	4.5 \pm 0.3	3.5 \pm 0.4
Sept	4.7 \pm 0.4	3.5 \pm 0.4
Nov	5.5 \pm 0.4	3.5 \pm 0.4

Table 2 The effect of nutrient level on the production of third and higher order shoots on the second-order shoots present before June 1982 (original) and on second-order shoots produced after that date (new). Data for the 14 plants are expressed as numbers of shoots produced during each period between recordings, (\pm s.e. of the mean); $n = 7$ in each treatment.

Time of measurement	High nutrient		Low nutrient	
	Original	New	Original	New
Jun 1982	23.5 \pm 0.3	0.0	30.3 \pm 3.2	0.0
Nov 1982	8.3 \pm 2.7	0.0	13.1 \pm 1.2	0.0
Jun 1983	28.4 \pm 9.8	44.9 \pm 14.9	12.9 \pm 3.0	15.6 \pm 4.4
Sept 1983	22.8 \pm 7.8	113.1 \pm 2.6	6.5 \pm 3.8	3.8 \pm 1.5

1983 there was a significantly ($P < 0.05$) greater number of second-order shoots in nutrient-treated plants. The second-order shoots, in turn, produced shoots of third and higher orders. Substantially more shoots were produced by plants grown under high than low-nutrient treatment (Table 2). It was also obvious that in the high-nutrient treatment most of the higher-order shoots were produced by the new second-order shoots with relatively little contribution from the second-order shoots that had arisen before June 1982. Production of higher-order shoots was sparse both on the original and the new second-order shoots under low nutrient conditions (Table 2).

The development of second-order shoots during a 15 month period is shown in Fig. 1. These plants were selected because each had three second-order shoots at the time of first recording, increasing to five at the end of the period. The approximate positions where the second-order shoots arise are presented (Figs 1B and 1D) for the high and low-nutrient-treated plant, respectively. Most of the second-order shoots produced before June 1982 were plagiotropic, although some were orthotropic for a short length before becoming plagiotropic. However, a number of the new second-order shoots, especially in the high-nutrient plants, e.g., shoots 4 and 5 (Fig. 1A) were orthotropic.

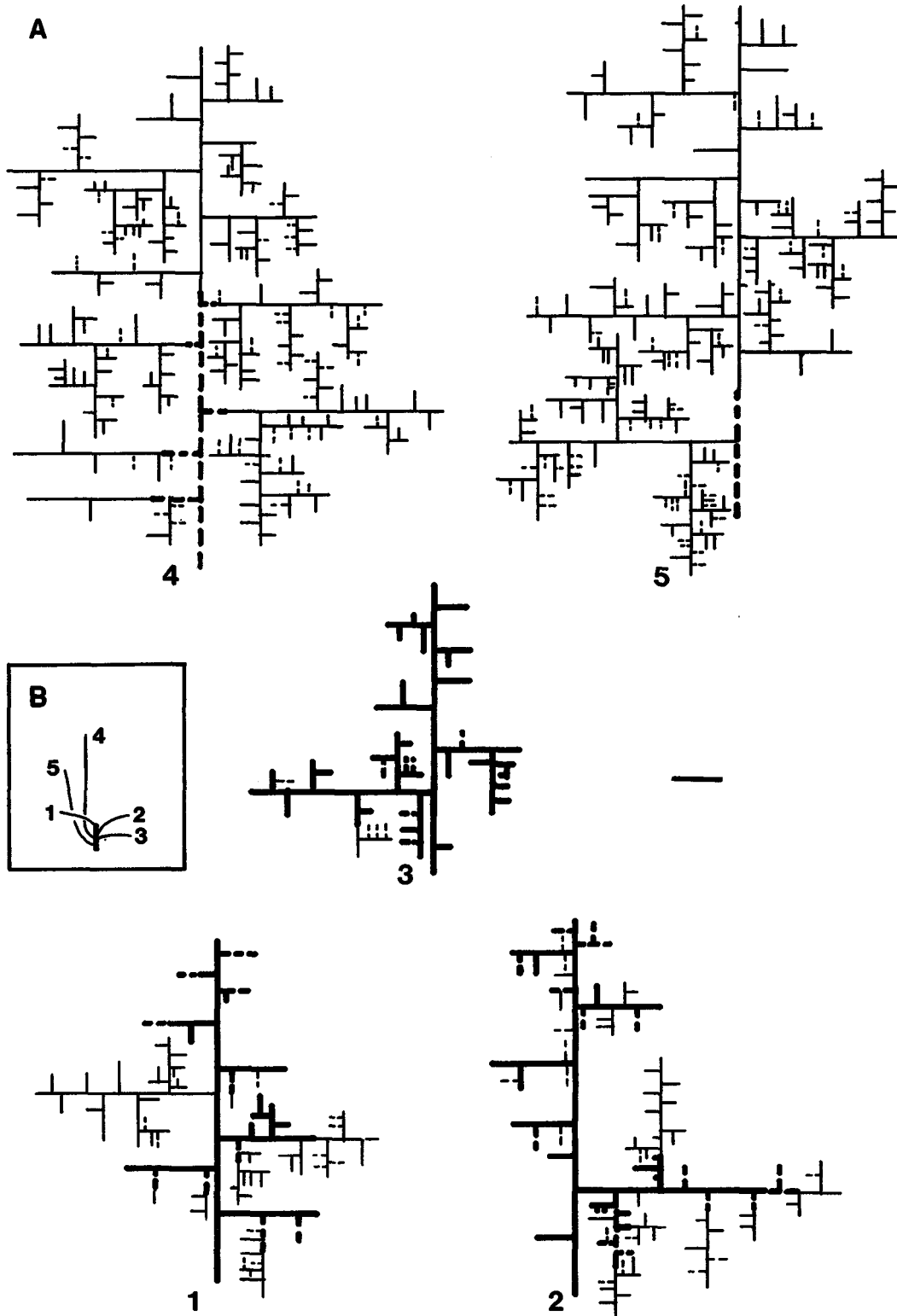
At the time of the first recording, June 1982, both plants possessed three second-order shoots (numbered 1, 2, 3) with up to three further orders of branching, i.e., to fifth-order shoots, (these shoot systems are indicated by the thick, solid line). By November 1982 two additional second-order shoots (numbered 4, 5) had been produced by each plant. Those on the high-nutrient plant had grown more vigorously, with the beginning of third-order shoot production (Fig. 1A) whereas the low-nutrient plant had produced only two short second-order shoots (Fig. 1C). During the period between June and November there was a relatively modest amount of

higher order shoot development on the three original second-order shoots on each plant. There was a marked contrast in the growth of the high- and low-nutrient-treated plants between November 1982 and June 1983. Although no additional second-order shoots were produced, up to five further orders of shoots were recorded on the two new second-order shoots of the high-nutrient-treated plant (Fig. 1A) whereas those of the low-nutrient-treated plant had one (in shoot 4) and three further orders (in shoot 5), respectively (Fig. 1C). However, most of the development was on the new second-order shoots irrespective of the nutrient treatment. The very extensive growth of the new branch systems on the high-nutrient-treated plant was in marked contrast to the much lesser growth on localised parts of the older second-order branch systems (Fig. 1A). No additional shoots developed during the winter of 1983 in the low-nutrient plant but substantial numbers of short, higher order shoots appeared on the new second-order branch systems on the high-nutrient plant, with fewer numbers on the older ones. In both branching systems this growth could be defined as "infilling." All plants were divaricate; nutrient level only affected the overall form in that there was a greater number of orthotropic shoots. These erect second-order shoots grow straight for up to ten nodes and therefore increase the overall height of the plant. However, the higher-order shoots produced by them have the characteristic angled growth pattern as does the main axis of the second-order shoot after the initial phase when it grew straight.

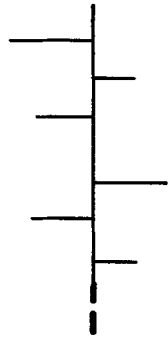
Orthotropic and plagiotropic shoots, and overall growth form

Recordings made on six-year-old plants in December 1986 showed that two types of second-order shoot systems (orthotropic and plagiotropic) were present. Orthotropic shoots were either erect or close to vertical initially and then became plagiotropic. In

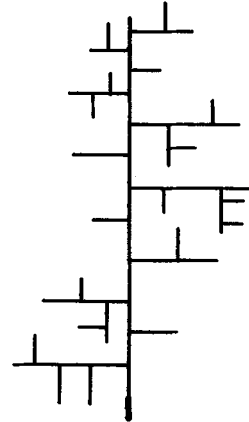
Fig. 1 The development of the second-order shoots of each of two plants of *Muehlenbeckia astonii* from June 1982 to September 1983. The recordings were taken on June 1982, thick solid line; November 1982, thick broken line; June 1983, thin solid line; September 1983, thin broken line. The internodes are to scale and the points of origin of the higher order shoots are accurate but the angles of outgrowth are all drawn at right angles in order to display all of the shoots without any overlapping. The oldest second-order shoots, present in June (winter 1982) are numbered 1, 2 and 3 and the newer second-order shoots (originating in spring and first recorded in November 1982) are numbered 4 and 5. The plants selected are typical in that they show marked differences in total numbers of higher order shoots between the high and low nutrient-treated plants and also the characteristic localisation of higher order shoot production on the newer second-order shoot systems in the high nutrient plants. The points of insertion of the second-order shoots are shown on the diagrams (inset). A. High nutrient status. Second-order shoots 4 and 5 commenced growth as orthotropic shoots before becoming plagiotropic, scale bar represents approximately 70mm; B, location of second-order shoots; C, low nutrient status; D, location of second-order shoots, scale bar represents approximately 50mm.



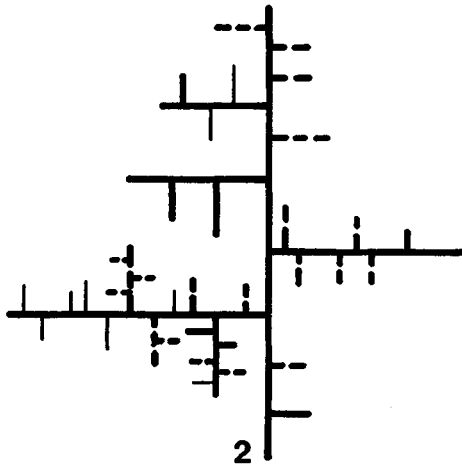
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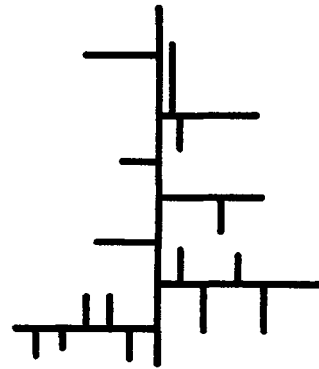
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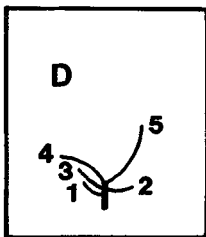
5



2



3



D

4
3
1
2
5



1

the orthotropic phase the second-order shoots grew more or less straight for about 10 nodes. Plagiotropic second-order shoots showed a typically divaricating form throughout, with angling of the stem at the nodes, and grew horizontally or at an acute angle to the ground. Orthotropic shoots produced a greater number of nodes, had a greater mean internode length and a longer shoot length in the second-order shoot between the point of origin on the first-order shoot and the first substantial third-order branch than did plagiotropic shoots (Table 3). The first 15 internodes were significantly longer ($P < 0.05$) in the second-order orthotropic shoots than in plagiotropic ones (Fig. 2) although both types showed a decrease in mean internode length over the first 15 internodes. After 15 nodes the internode length was about 20 mm on both types and the orthotropic shoot had become plagiotropic.

Attempts were made to characterise the overall growth form of the *M. astonii* plants. This presented difficulties because of the complex nature of the plant and because of the plant to plant variability. However, certain basic features could be recognised. The area closest to the ground was taken up by the plagiotropic shoots which branched throughout their length. Sometimes two or three second-order plagiotropic shoot systems interwove at their boundaries and occupied the whole of this level. Strongly-growing, erect, second-order shoots, initiated at or close to ground level, grew through the layer of plagiotropic shoots and overtopped them. These orthotropic shoots subsequently ceased to grow straight, and became branched and plagiotropic. Prolific higher-order branching on these shoots then resulted in the infilling of the layer above the lowermost region of plagiotropic shoots. All of the second-order shoots had a restricted period of

extension growth. Under low-nutrient conditions there is a strong tendency for fewer orthotropic shoots to be produced and thus a low-growing shrub develops.

In older plants the new orthotropic shoots may develop either from the base of the first-order shoot or be initiated as third-order shoots from second-order shoots higher up the canopy. In this way the plant increases in height and the growth pattern repeats itself. Observations of mature plants in the University grounds showed that it may take four or five orthotropic shoots originating at successively higher levels in the canopy to achieve an overall plant height of 2 m or more. Leaves are borne on short shoots and also on the long shoot axes. The majority of the leaves are present on the vigorous new shoots, which tend to be those that overtop the older shoots. Severe pruning of one plant in the University grounds resulted in the prolific production of canes from the base.

Although all of the recordings in the present study are from cuttings taken from a single female plant, we have rooted cuttings from plants of both sexes and followed the general growth form over a five-year period. All plants were divaricating and the growth form of male and female plants was identical.

DISCUSSION

The divaricating habit is present in many genera in New Zealand (Wardle 1963; Went 1971). Some species are divaricate during the juvenile phase but not as adults, e.g., *Sophora microphylla*, whereas others, like *M. astonii*, remain divaricate throughout. The most striking feature of *M. astonii* is the restricted period of vigour of each major branch system. This is due mainly to the limited duration of extension growth of the main axis (e.g., the second-order shoot axis) which does not extend beyond one growing season. The consequence of this is that further growth of the system is restricted to higher-order laterals. At any given time in three-year-old plants it was found that only the current season's second-order branch systems vigorously produced higher order shoots. Second-order branch systems produced earlier were much less vigorous, with both absence of apical extension and great reduction of production of lateral shoots. New developments on these older second-order shoots were restricted to the production of minor higher order shoots which did not contribute to the gross framework of the plant but had an important "infilling" role. New second-order shoot systems were often at the same level or higher than

Table 3 Characteristic morphological features of orthotropic and plagiotropic second-order shoots. The total second-order shoot length was recorded from the point of origin on the first order shoot to the first major third order shoot which developed on it. The number of nodes and the mean internode lengths between these two points were also measured. Recordings were taken in December 1986, (\pm s.e. of the mean, sample size in parentheses).

Characteristics of second order shoot	Shoot type	
	Orthotropic	Plagiotropic
Nodes (number)	5.2 \pm 0.4 (12)	4.2 \pm 1.1 (6)
Shoot length (mm)	263 \pm 24 (12)	168 \pm 32 (6)
Mean internode length (mm)	51.4 \pm 1.5 (64)	38.4 \pm 2.6 (6)

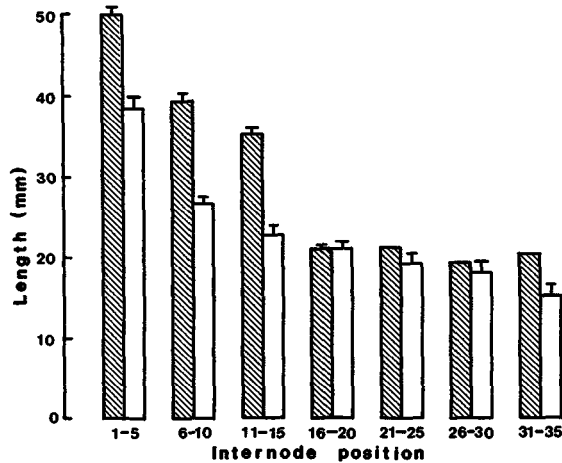


Fig. 2 Mean internode lengths (\pm s.e. of the mean) for groups of five internodes from base (1) to apex (35) of orthotropic (hatched) and plagiotropic (unhatched) second-order shoots. Sample size (number of internodes in each group) for orthotropic branch systems, 60, and for plagiotropic ones, 25. Numbers declined above node 20 because of the varying length of the second-order shoots.

the older ones in young plants. Similarly, in mature plants, newly produced orthotropic shoots tended to overtop the rest of the plant. Since the current season's shoots were the most vigorous and bore substantial numbers of leaves it is clear that a significant proportion of the leaves of the plant will normally be at or close to the periphery of the plant with a lesser proportion on the inside of the shrub.

The shape of the shrub and the arrangement of branches and leaves are important in light interception, rate of transpiration loss, and also susceptibility to browsers. Lowry (1980) noted that the dispersal of a plant's extension growth effort into a large number of small and spatially separated units would make browsing less rewarding energetically.

Some workers have suggested that the divaricating plants in New Zealand, in general, encase the leaves in a network of largely leafless twigs. This is said to be a response to browsing by moas—large flightless raptures—(Greenwood & Atkinson 1977) or a way of coping with specific sorts of environments (Cockayne 1912; Rattenbury 1962). In a number of ways *M. astonii* does not fit the moa-browsing model. The new shoot systems tend to be the most vigorous, bear large numbers of leaves and overtop the older shoot systems on the shrub. Thus, many leaves will be on the outside of the shrub giving better overall light

interception but affording less protection against browsing.

The overall architecture of *M. astonii* is determined primarily by the number, vigour and point of origin of the orthotropic shoots and secondarily by their vigour after they revert to a plagiotropic form. In many species branching patterns are not stationary, being affected by branch loss and possible subsequent outgrowth of branches. Steingraeber (1982) notes that differences are often noted within trees, with leader shoots differing from lower branches. Branching pattern may be affected by light, e.g., in sugar maple (a non-divaricating tree), open grown saplings have a higher bifurcation ratio, i.e., fuller crowns and more profuse branching, than forest grown ones (Steingraeber et al. 1979). Increased nitrogen levels often affect the extent of branching, e.g., in *Pinus radiata* (Will 1977). Unfortunately, there is little quantitative evidence for the effect of environmental factors on the growth and form of New Zealand's divaricating species. Philipson (1964) argues that in divaricate shrubs the direction of branch growth appears to be more definitely related to the parent axis than to the environment. Consequently some branches of second, third, and higher orders will grow into and through the densely shaded centre of the shrub. Morphological and anatomical studies of *M. astonii* will be reported in subsequent papers which will help to explain the development and control of branch angles and shoot architecture.

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