

# MULGA RESEARCH CENTRE

## annual report 1978

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## CHEMICAL CONTENTS OF THE FOLIAGE OF MULGA

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Introduction

The chemistry of mulga foliage is of interest for two reasons. Firstly there is the problem of variation within the species *Acacia aneura* and secondly the degree of palatability is of interest to the pastoralist in terms of drought reserves, and, also to the question of long term persistence of the plant in defined areas.

The phyllodes of *Acacia aneura* are variable between individuals. They may differ in length, breadth, colour and general shape, and possibly in their internal anatomy as well. The question of variation in size of phyllodes within individual plants is discussed elsewhere in this volume. To some extent it must be assumed that between tree variation will comprise elements related to age (size), season and the moisture availability of the habitat. The fact that in many localities individuals with different phyllode types are found adjacent to each other suggests that if there are genetical differences then perhaps hybridisation leading to the production of intermediate forms is frequent.<sup>7</sup> The chemical constituents of *Acacia* phyllodes may provide some evidence for taxonomic differences.

In a general paper on *Acacia* taxonomy Pettigrew and Watson<sup>11</sup> used the group 'phenylalanine or tyrosine alkaloids' with the following six members successfully splitting taxonomic groups on the basis of presence or absence:

1. phenethylamine
2. N-methylphenethylamine
3. tyramine
4. N-methyltyramine
5. N,N-dimethyltyramine
6. candicine

Information to these authors was not available for this group in relation to *Acacia aneura*, nor was it available for the other block of tryptophane-derived alkaloids also used as taxonomic indicators (tryptamine, N-methyltryptamine, dimethyltryptamine, and N-methyltetrahydroharman).<sup>11,14</sup>

Palatability

The foliage of mulga is not tasty and it would be presumptuous to suggest that kangaroos (the only significant indigenous herbivores) would normally include it in their diet. The introduced animals are another matter. Wilcox<sup>17</sup> suggests that there are conflicting reports on the palatability of young seedling mulgas, with rabbits definitely known to eat them, and also heavy grazing pressure by cattle in some instances. Observations at Mileura suggest that goats will browse at least terete foliage on young seedlings. Horse browsing has been noted at the Lake Mason/Yeelirrie common boundary and cattle have been observed to selectively browse

both terete and broad phyll bushes (see below). A number of observations have been made in relation to the use of mulga foliage as sheep fodder in times of drought.<sup>3,7,8,9,10,16,17</sup>

A theory on palatability was proposed by Melville<sup>7</sup> in his investigation of the drought pastures of the Murchison district (based on Boolardy) in 1937. Melville observed variations in palatability in feeding experiments with sheep. He observed that leaves with a shiny, varnished appearance were inedible. The shiny appearance is due to a resinous exudate encasing the leaf which inhibits moisture loss.

Melville related palatability to the 'ether extract' of the leaves. The extract, which contained the resinous exudate, showed a close negative relationship with palatability. This correlation was based on an analysis of six 'varieties' of mulga in one paddock and of five in another. The sheep in these paddocks showed a distinct order of preference, the most palatable trees were completely stripped before the animals proceeded to individuals of the next variety.

The quantity of resinous material was suggested as being related to:

variety;  
seasonal conditions;  
age.

All varieties were said to contain a greater amount of exudate in drought conditions and when young, with young plants in drought conditions showing maximum secretion. This however is perhaps rather controversial as many young plants tend to assume a stressed appearance in drought, whereas, particularly with the terete leaf forms, a dark resinous secretion often seems to be more evident on young actively growing foliage.

The secretion comes from glands on trichomes. Melville suggests that the secretion encases the foliage in a resinous shell which maintains it in a state of dormancy. Because of the excessive secretion even the more edible varieties are inedible when young. Melville<sup>7</sup> believes that the exudate from young plants has a different composition than the exudate of mature plants. A bitter principle in the young plant is more evident than in the mature plant. No attempt was made to determine the nature of the bitter principle.

The work of Melville is also discussed by Nichols<sup>9</sup> who gives the following values for seven edible and four inedible mulgas: total ash, average 4.8%, calcium just under 2% CaO, and P<sub>2</sub>O<sub>5</sub> average 0.25% for edible and 0.16% for inedible types. Also relatively high crude protein figures for the mulgas were noted with the average for edible types 10.4, and for inedible 8.4%. In the case of young mulga, Nichols quotes Melville to the effect that seedlings less than four inches in height, even of the most edible varieties, are definitely distasteful to stock. Often it is not until the tree is out of reach of sheep that it can be considered edible. Nichols<sup>10</sup> gives further notes on the same series of observations, viz (p.68)

"Now, botanically, mulga is *Acacia aneura* - one species - but the sheep is a sensible animal with considerable powers of discrimination. It recognises a number of mulgas".

Wilcox<sup>16</sup> reported a cutting of mulga trial at Albion Downs. The experiments reported were commenced in 1956 and 1957. His observations suggest that mulga palatability is not influenced by age, but is a lifetime characteristic of the plant.

Data is available (with D.G. Wilcox at the Department of Agriculture) for 20 different mulga labelled E1-E20 analysed by Melville for ether extract, crude protein and crude fibre. Unfortunately descriptions of the phyllodes cannot be found for these.

Similar analyses were done by Wilcox of the fallen mulga phyllodes in his trials. Wilcox<sup>17</sup> reviewed a number of papers on palatability of shrubs to sheep. He notes that Melville<sup>8</sup> ascribed differences in palatability to the level of ether extractable constituents in the phyllodes which may rise to 12% in unpalatable varieties. Wilcox reports that in his Albion Downs trial 'at no time did seed fall exceed 2 kg/ha'. The fallen leaf contained an average of 8.5% crude protein and 29.1% fibre - this is said to be adequate for maintenance but not reproduction in sheep. Leaf value would also fall off with age, due to weathering and termite activity.

A useful account of the crude protein and oxalate content of other shrubs available to sheep is given by Wilson<sup>18</sup>. He also refers to several references which give values for ash, and its sodium chloride content.

Everist<sup>3</sup> gives the following values for mulga in terms of 'crude chemical composition analyses moisture free %':

crude protein	11.7
crude fat	2.7
crude fibre	29.0
N.F.E.	49.6 (nitrogen free extract)
ash	1.29
phosphorus	0.07

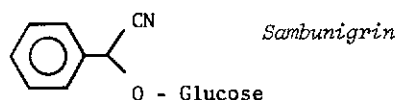
In general, of course, most of the analyses are expressed as percentage of dry weight with the difference between fresh weight and dry weight being assumed to be mainly due to the water present in the foliage.

Rogers and Davies<sup>12</sup> examined the chemical composition of four grass species. They looked at Ca, Mg, P, K using X-ray fluorescence spectrometry and N with Kjeldahl. There was correlation of K, N and Mg with soil oxygen concentration, suggesting that under different conditions these herbage species would contain different nutritive values. Seasonal trends in values for Ca, P, ash, crude fat, crude protein and crude fibre have been shown for a number of Oregon range forage plants<sup>6</sup>. Seasonal variation has also been examined for trees of the same general sort of vegetation as the W.A. Mulga

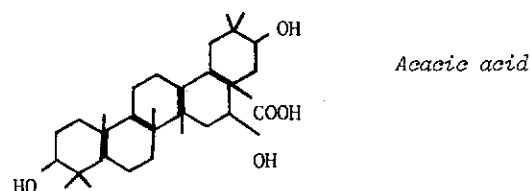
Zone by Ernst<sup>4</sup> in central Africa. He examined Ca, Cl, Cu, Fe, K, Mg, Mn, Na, Ni, Al, N, and P and found that levels of K, Mg, N and P are highest in young leaves and these elements are reabsorbed to some extent prior to leaf fall. Al, Ca, Fe and Mn increase in content with ageing of the leaves, while Cu and Zn show no regular trend.

A comparative phytochemical survey of varieties may lead to an explanation of the variations in palatability. There are many phytochemicals which are bitter, and if present in the leaves may discourage grazing. The types of compounds which may affect palatability include terpenoids, saponins, flavanoids, cyanogenic glucosides and many others.

Cyanogenic glucosides, which release HCN, have been found in a number of acacias including *A. deanei* spp. *pucijuga*, *A. cunninghamii*, *A. giraffae*, *A. parramattensis*, *A. pulchella*\* and *A. farinosa*<sup>13</sup>. The structures of the cyanogenic glucosides differ, but a typical example is sambunigrin.



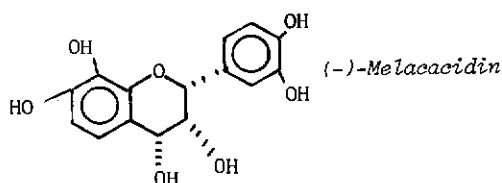
Saponins, which are triterpenoids with glucosidic attachments, have soap-like properties and may discourage grazing. An example of a saponin is acacic acid which has been found in a number of acacias<sup>1</sup> including *A. concinna*.



The sugar unit is attached through the 3-hydroxyl group, and can be any one of a number of sugars.

Extensive work has been carried out on the flavanoid content of the heartwood and bark of many species of *Acacia*.<sup>2,14,15</sup> The purpose of these studies was to classify the different species according to flavanoid content. Mulga was divided into two sub-species, one being *A. aneura* var. *aneura*, and the other *A. aneura* var. *latifolia*. Both varieties were shown to contain 3', 4', 7, 8-tetrahydroxyl flavanoids, which are similar to (-)-Melacacidin and have 3', 4', 7, 8-hydroxylation pattern.

\* This species is widely browsed by kangaroos in the south-west of Western Australia.



However, no work was done to compare the flavanoid content of the different varieties of mulga.

#### Methods

Fresh foliage was collected from 10 plants at Yeelirrie Station in an area stretching east of Altona through Mugs Bore to the eastern boundary with Albion Downs. Earlier observations at Sherwood suggested preferential grazing by cattle and the Yeelirrie set encompassed the range observed at Sherwood. Samples were collected in July and air dried for one week prior to testing. The following tests were performed.

##### 1. Detection of cyanogenic glucosides

Picric acid papers were prepared by dipping pieces of filter paper into saturated aqueous picric acid (150 ml), previously neutralized with sodium bicarbonate. The papers were allowed to dry and then cut into small strips.

About 2 g of ground leaves was placed in a test tube containing two drops of toluene and one drop of water. A strip of picric acid paper was suspended at the top of the test tube by means of a cork. The tubes were incubated at 40°C for two hours to test for the enzymic release of HCN. The tubes were then left for two days at room temperature to test for the non-enzymic release of HCN. Loquat seeds were used as a control.

##### 2. Detection of saponins

About 2 g of ground leaves was shaken with 5 ml of aqueous ethanol (1:1). An estimate of saponin content was made by comparing the amount and persistence of the foam formed.

##### 3. Flavanoid content

Leaves previously extracted with n-pentane (see item 4) were ground and extracted with hot 95% ethanol. The extraction was repeated until all colouring material had been removed from the leaves. The combined ethanol extracts were concentrated to about 20-25 ml on a steam bath.

Samples of the ethanol extracts were spotted on Whatman No. 1 chromatography paper and developed in two dimensions using a descending technique. The paper was first developed using B.A.W. (butanol, acetic acid, water, 4:1:5 top layer) for sixteen hours and then using 15% acetic acid in water for four hours. The chromatograms were air dried and examined under

U.V. light.

##### 4. Wax extraction

Exactly 5.00 g of leaves was continuously extracted with re-distilled n-pentane for 4-5 hours using a soxhlet extractor. The leaves were not ground since only surface material was being extracted. The material was extracted into a weighed flask, taken to dryness and re-weighed.

The material extracted was dissolved in pentane and a small quantity of the solution was evaporated on sodium chloride I.R. plates. The infra-red spectrum was recorded using a Perkin-Elmer 157 spectrometer.

A small quantity of the solution was spotted on an activated silica gel plate. This was developed using toluene/petroleum ether (BP 70-90) (1:1) and the spots were located using iodine vapour.

##### 5. Ether extraction

Exactly 5.00 g of leaves was extracted with re-distilled diethyl ether using the procedure in section 4. After weighing, the extracted material was dissolved in ether and dried over magnesium sulphate. A sample of the dried solution was evaporated into sodium chloride plates and the infra-red spectrum recorded.

##### 6. Terpene analysis using gas liquid chromatography (G.L.C.)

About 5.0 g of leaves was ground and extracted with n-pentane. The combined extract (50 ml) was concentrated to 5 ml. Any solid material in the extract was removed by centrifugation. The samples were analysed on a G.L.C. using the following conditions.

G.L.C.	Varian 1440
Column	3 m 5% Carbowax 20 m
Temperature column	90°C $\xrightarrow{15^\circ/\text{min}}$ 200°C
Injector	200°C
Detector	250°C
Volume	1 $\mu\text{l}$
Carrier Gas	N <sub>2</sub> 25 ml/min.
Recorder	Rikadenki
Attenuation	1 x 10 <sup>-10</sup>
Chart Speed	20 mm/min.

##### 7. Preparative G.L.C.

About 90 g of sample XI was ground using a mortar and pestle. The coarse powder was extracted with n-pentane overnight. The extract (300 ml) was concentrated to 5 ml by a series of concentration and centrifuge steps to remove precipitated material. The extract was passed through the G.L.C. using the following conditions.

Column 1.5 m 12% 0.25" OD SE 30  
 Temperature column 90°C  $\xrightarrow{700/\text{min.}}$  240°C  
 Injector 220°C  
 Detector 285°C  
 Collector 245°C  
 Carrier Gas N<sub>2</sub> 80 ml/min.  
 Volume 500 µl

Component 1 was collected using an ice bath.

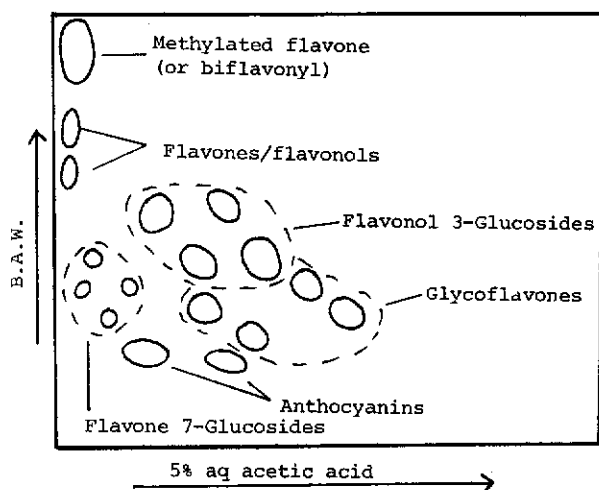


Fig. 1 Location of flavanoids.

## Results

### A. Observations at Sherwood

An area within Big Paddock, near Murchison Downs Road at the south end of Sherwood Station was visited in November 1977. Here a number of cattle were present and recent browsing damage was noted on mulga trees of intermediate size (Table 1).

This set of observations indicates distinct segregation between the broad leaf (variety *latifolia*) and terete forms as edible on the one hand versus the narrow leaf forms as inedible on the other hand.

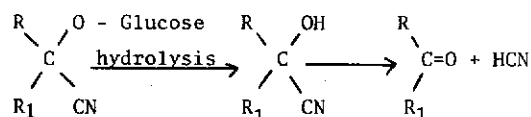
### B. The Yeelirrie samples

Using the same terminology as in Table 1 the ten Yeelirrie samples may be categorised as in Table 2.

This order of apparent edibility clearly relates only to a direct comparison of the Sherwood samples, that is as regards cattle browsing preference.

#### 1. Cyanogenic glucosides

Many plants contain cyanogenic glucosides which release small quantities of HCN when the plant tissue is damaged. The release can either be enzymic or non-enzymic and occurs by the following mechanism.



The HCN released gives the plant material a bitter taste and hence prevents grazing.

The tests carried out on the ten varieties of mulga were negative to both enzymic and non-enzymic release of HCN, which means there are no cyanogenic glucosides in the leaves.

#### 2. Saponins

Saponins are present in many plants and occur in various parts including the leaves, roots and seeds. Saponins are triterpenoids and steroids with glucosidic attachments. The presence of saponins in plant material may dis-

TABLE 1 Big Paddock Sherwood 500 m<sup>2</sup> Plot.

Collection No.	Leaf Type		Status		
			Eaten	Not Eaten	Total
1080	short terete	}	1	0	1
1078	long terete		6	0	6
1082	var. <i>latifolia</i> *(blue)	b	1	0	1
1081	long, narrow, curved	c	0	2	2
1079	long, broader, green/grey	d	0	8	8

\* Many others of this type in the vicinity, all heavily browsed.



courage grazing because of their soap-like properties.

TABLE 2 Yeelirrie Sample Characteristics.

Sample	Leaf Type	Leaf Colour	Assumed Edibility*
C1	long, terete	green	edible $\equiv$ a
H1	long, terete	green	edible $\equiv$ a
B1	var. <i>latifolia</i> (tree)	grey/blue	edible $\equiv$ b
G1	var. <i>latifolia</i> (small bush)	grey/blue	edible $\equiv$ b
E1	long, narrow, curved	light green	intermediate $\equiv$ c
F1	short, narrow, curved	green/grey	intermediate
X1	long, narrow, curved	dark green	intermediate $\equiv$ c
D1	long, broader, curved	green/grey	inedible $\equiv$ d
A1 +	long, broader, straight (small bush)	green/yellow	inedible
A2 +	long, broader, straight (tree)	green/yellow	inedible

\* a, b etc. as in Table 1. + These two specimens are from a 'black mulga' probably *Acacia* aff. *coolgardiensis*.

Semiquantitative analysis of the leaves for saponin content indicated that there were saponins present and in varying amounts. Results are given in Table 3. A number of samples formed only a very small amount of foam (+) suggesting that little or no saponins were present. Sample A2 ++++ contained significantly higher amounts of saponin than any other sample.

### 3. Flavanoids

It is possible to identify a number of flavanoid classes using paper chromatography. The location of flavanoids on a two-way chromatogram is shown in Fig. 1.

Flavanoids can be subdivided into a number of smaller classes including anthocyanins, flavones, flavanols and biflavonyls. Flavanoids are phenolic compounds, an example of one found in mulga heartwood is (-)-Melacacidin.<sup>14</sup> They are pigments and co-pigments and may discourage grazing by imparting a bitter taste to the plant.

Variations occurred though the differences in chromatogram pattern were difficult to interpret. Suffice it to report here that more flavanoid spots occurred on the chromatogram for specimen A1 than for A2 and more for that of G1

than for B1.

### 4. Wax

Examination of the leaves under a microscope showed there were globules of wax on the leaf surface. This wax could discourage grazing, hence palatability may be related to the amount of wax on the leaves.

A n-pentane extraction was carried out to determine the wax content of leaves. The results are shown in Table 3.

The waxes were a mixture of eight to ten compounds which, when separated by G.L.C., ranged in  $R_f$  from 0.03 to 0.97. Infra-red spectrums of the samples were recorded and all gave similar spectrums indicating that the waxes were largely fatty esters.

### 5. Ether extracts

Melville related palatability to the amount of ether extractable material on the leaves.<sup>7</sup> His results indicated that there was an inverse relationship between palatability and the ether extract. An ether extraction was carried out on the ten samples and the results are given in

Table 3.

The infra-red spectrum showed a strong carbonyl peak at 1710  $\text{cm}^{-1}$ , and a broad hydroxyl peak for all samples. This indicates that the ether extracted both waxes and free acids on the leaf surface.

#### 6. Terpenes

The n-pentane soluble constituents, which are mainly terpenes, were analysed using G.L.C. The aim was to compare, without necessarily identifying, the terpenes present. With the exception of two components, which were present in B1, F1, G1 and X1 but not in the other samples (Table 3) the chromatograms were almost identical. Component 1 had a retention time of 11.8 minutes and was the major constituent. The amount of 1 was especially high in F1 and X1. Associated with the major component was a second constituent (2) which had a retention time of 12.0 minutes. Because of their occurrence together and similar retention times, components 1 and 2 could be structurally similar. Component 1 presence in B1, G1 indicates that it was not related to palatability.

An attempt was made to identify component 1. By using preparative G.L.C., 98 mg of component 1 was isolated from an extract obtained from 90 g of X1. The substance isolated contained about 80-85% of component 1 and 15-20% of component 2 and had a melting point of 31-33°C. The infra-red spectrum of the mixture indicated that component 1 was an aliphatic ketone. A mass spectrum of the mixture showed there was a major constituent with a mass of 195.

#### Discussion

The results suggest that there are definite differences in the chemical constituents of the leaf types sampled. Of particular interest is the indication of confirmation of earlier work in respect of differences within a type with age. Both B1 and G1 (*Acacia aneura* var. *latifolia*) and A1 and A2 (*A. aff. coolgardiensis*) results suggest that younger plants may be less palatable than older (larger) ones of the same leaf type. Flavanoids are more evident from the younger samples for both while the broad leaf mulga young plant examined had much greater saponin and a higher proportion of ether extract than the other edible mulga types examined. There are no indications of *A. aff. coolgardiensis* being palatable at all though the lack of saponins and comparatively high ether extract for the small specimen suggest that changes with age may be a common feature for a number of species. It would be interesting to examine this with a set of samples from different sized plants of the same leaf type at one location, and also for phyllodes of different age from the same specimen.

Of the tests undertaken that for terpenes shows most promise in terms of delineating possible varieties. The classification by gross morphology (Table 2) coincides very well with presence of two components and of a high level for component 1 (Table 3). The wax proportion is likely to be most variable within a particular plant and may not be of much value in gross terms, though there may well be differences in constituents.

TABLE 3 Results of Chemical Analysis.

Sample	Saponin	Terpenes	Wax % w/w	Ether Extract % w/w
C1	++		4.6	7.6
H1	++		5.4	8.6
B1	(+)	1, 2	3.8	8.4
G1	+++	1, 2	3.2	9.8
E1	(+)		2.0	6.2
F1	+++	1*, 2	3.0	14.2
X1	+++	1*, 2	7.4	27.0
D1	(+)		2.2	6.6
A1	(+)		1.6	8.0
A2	++++		1.4	4.4

1\* component 1 particularly high (see text).

Though specimens F1 and X1 were classified as intermediate in Table 2, the high levels of ether extract coupled with high saponin content and (possibly) the particular high level for terpene component suggest that 'inedible' may more accurately describe the narrow (non-terete) leaf forms.

#### Acknowledgements

The advice and guidance of Dr. R.I Kagi and Dr. R. Alexander (Chemistry Department, W.A.I.T.) are gratefully acknowledged.

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POT TRIALS WITH *Acacia saligna*

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Introduction

*Acacia saligna* is an aggressive, vigorous shrub. In the metropolitan area of Perth it is capable of growing on bare sand alongside roads and has been planted to stabilise verges in some places. Preliminary observations had suggested that competition sets in early with 1 plant in a pot of 3 or more showing dominance within a few months of germination.

Similarly waterlogging tests suggested that pots with *A. saligna* given water to excess produced narrower phyllodes than those not so treated.

This note reports the results of experiments to measure competition and to observe the effects of an abundance of moisture on this important species. Some observations were also made on varying nitrogen levels.

Methods

Seeds of *Acacia saligna* obtained from the W.A. Forests Department were treated with hot water and then placed in petri dishes in a growth cabinet (dark) at  $21 \pm 1^\circ\text{C}$ . After 7 days 90% germination was achieved and seedlings were planted out on 1st August 1978.

Competition

A soil mix composed of two thirds coarse sand and one third nursery potting mixture (fine sand and compost) was prepared and 28 pots of 15 cm diameter were filled to 12 cm depth. Seven pots

each received 4, 3, 2 and 1 seedling(s) per pot. This allowed five harvest dates with two pots of each seedling set as spares. Harvests were at 36, 50, 64, 85 and 99 days from planting. Pots were watered approximately every third day.

Waterlogging

A set of 24 pots were planted using the same soil mixture and planting densities as above, with half the pots placed on saucers maintained with water. Three harvests were set at 36, 71 and 92 days from planting. All plants were watered every third day, the control pots lost excess water by direct drainage.

Nutrition

A set of 60 pots (plus some spares) were filled with a modified U.C. Soil Mix B<sup>1</sup> substituting coarse sand for fine sand and omitting nitrogen. Each pot received one seedling and then sets of 15 pots were given nitrogen as ammonium sulphate in multiples of the standard mix level of .22 g  $\text{L}^{-1}$  as follows:-

control	0
$\frac{1}{2}$ normal	.11
normal	.22
2 x normal	.44
3 x normal	.66

Plastic saucers were placed under the pots to prevent leaching of fertilizers. Five harvests were set at 36, 50, 64, 85 and 99 days from planting, allowing three plants to be harvested at each date. The watering regime was as described above.

Results

At each harvest all plants were directly weighed for fresh weight and after drying at  $50^\circ\text{C}$  for 48 hours for dry weight. Observations were also taken on the extent of nodule formation. The results are presented in tabular form.

TABLE 1 Competition experiment *Acacia saligna* - Weights of plants at five harvest times (g)

Harvest (Days)	No. per pot	Fresh Wt.		Dry Wt.		Mean FW/DW Ratio
		Total	Mean	Total	Mean	
36	1	-	.144	-	.017	8.5
	2	.300	.150	.028	.014	10.7
	3	.437	.146	.046	.015	9.5
	4	.640	.160	.067	.017	9.6
50	1	-	.350	-	.035	10.0
	2	.280	.140	.033	.017	8.5
	3	.721	.240	.081	.027	8.9
	4	.913	.228	.130	.033	7.0
64	1	-	.304	-	.050	6.1
	2	.473	.237	.083	.042	5.7
	3	.708	.236	.101	.034	7.0
	4	1.624	.406	.238	.060	6.8
85	1	-	.566	-	.070	8.1
	2	.672	.336	.114	.057	5.9
	3	2.011	.670	.298	.099	6.8
	4	2.743	.686	.426	.107	6.4
99	1	-	1.100	-	.150	7.3
	2	1.882	.941	.290	.145	6.5
	3	4.360	1.453	.580	.193	7.5
	4	6.278	1.570	.754	.189	8.3

TABLE 2 Waterlogging experiment *Acacia saligna*.  
Weights of plants at three harvest times (g)

Harvest (Days)	No. per pot	Fresh Wt.		Dry Wt.		Mean FW/DW Ratio
		Total	Mean	Total	Mean	
(a) <u>Plants watered to excess</u>						
36	1	-	.150	-	.015	10
	2	.303	.152	.033	.017	8.9
	3	.444	.148	.046	.015	9.9
	4	.940	.235	.086	.022	10.7
71	1	-	.560	-	.071	7.9
	2	.794	.397	.087	.044	9.0
	3	1.527	.509	.158	.053	9.6
	4	1.379	.345	.162	.041	8.4
92	1	-	2.513	-	.433	5.8
	2	1.042	.521	.152	.076	6.9
	3	3.276	1.092	.449	.150	7.3
	4	4.143	1.036	.503	.126	8.2
(b) <u>Control plants</u>						
36	1	-	.254	-	.022	11.5
	2	.333	.167	.030	.015	11.1
	3	.429	.143	.050	.017	8.4
	4	.605	.151	.077	.019	7.9
71	1	-	.380	-	.036	10.6
	2	.534	.267	.063	.032	8.3
	3	1.018	.339	.108	.036	9.4
	4	1.204	.301	.122	.031	9.7
92	1	-	.514	-	.049	10.5
	2	1.567	.784	.133	.067	11.7
	3	3.192	1.064	.451	.150	7.1
	4	1.987	.497	.288	.072	6.9

TABLE 3 Nitrogen level experiment *Acacia saligna*.  
Weights of plants at five harvest times (g)

Nitrogen level	Harvest time (days)					
	36	50	64	85	99	
0	Fresh wt.	.126	.185	.312	.206	.550
	Dry wt.	.013	.018	.034	.027	.055
	FW/DW ratio	10.1	10.6	9.2	7.6	10.0
$\frac{1}{2}$	Fresh wt.	.087	.197	.198	.388	.513
	Dry wt.	.011	.024	.019	.055	.078
	FW/DW ratio	7.9	8.2	10.7	7.1	6.6
1	Fresh wt.	.118	.172	.180	.887	.816
	Dry wt.	.012	.018	.015	.151	.130
	FW/DW ratio	9.8	9.6	12.4	5.9	6.3
2	Fresh wt.	.108	.261	.194	.555	.860
	Dry wt.	.011	.036	.017	.104	.105
	FW/DW ratio	9.8	7.3	11.8	5.3	8.2
3	Fresh wt.	.087	.290	.425	.772	.786
	Dry wt.	.011	.035	.042	.099	.115
	FW/DW ratio	8.3	8.3	10.2	7.8	6.8

## Discussion

### Competition

A comparison with the 1977 observations is confounded by different growing conditions. The original set of pots were planted on the 3rd October 1977 and harvested 64 days later on 6th December. In the 1978 experiment reported here the last harvest was 99 days after planting on 7th November 1978. The 64 day harvest was made on 3rd October, at the time the previous set was started. Better growing conditions further into summer probably accounted for the accumulation of heavier dry weights and for the more direct expression of competition than achieved in 1978. A comparison of harvests on a relative basis is as follows:-

1977 No. in pot	Maximum (64 days)	Mean
1	100	100
2	204	118
3	118	77
4	119	56

1978 No. in pot	Maximum (64 days)	Mean
1	100	100
2	166	84
3	202	68
4	476	120

and for the final harvest:

1978 No. in pot	Maximum (99 days)	Mean
1	100	100
2	193	97
3	387	129
4	503	126

Thus the tendency for total dry matter production to peak at two per pot and trail off at higher densities is not confirmed in the present experiments. Similarly the mean dry weight per plant had not begun to fall off at increasing plant density by the time the experiment had terminated. All four densities were similar (Fig. 1). However some indications of the onset of competition may be noted, with due allowances made for a lack of replication. Thus the mean fresh weight/dry weight ratio for all plants harvested at each harvest date tended to decline through the course of the

experiment (Fig. 2). Bearing in mind the seasonal effects mentioned earlier it is presumed that the 99 day harvest included a burst of enhanced growth so that to some extent the last harvest may be atypical. Similarly days 55-64 were dry and warm, possibly accounting for a rapid decline in fresh weight/dry weight ratio for the third harvest.

The relative growth rate (RGR) was calculated as follows:

$$RGR = \frac{\ln w_2 - \ln w_1}{t_2 - t_1}$$

where  $w_2$  is dry weight at time 2 ( $t_2$ );

$w_1$  is dry weight at time 1;

$t_2 - t_1$  is time between harvests;

so that RGR is expressed in  
 $g\ g^{-1}\ day^{-1}$ .

Six RGR calculations are plotted on Fig 3. It is evident that towards the end of the experiment RGR at lower densities was both rising and at a higher level than for the higher densities. Much of the difference is due to lower starting dry weights (Table 1) and clearly a longer time period would be desirable to confirm the trends illustrated.

Table 4 summarises dry weight ratios within treatments. The ratio largest/mean shows a general tendency to increase with time and density and the levels achieved are not dissimilar to the single set of measurements for 1977. When the ratio of largest to smallest is examined it is apparent that though competition is clearly present, at no stage did the experiment reach the extreme level achieved in the previous year. The 99 day harvest set of 4 in a pot appears to belie the general trend, but this may be an anomalous record.

Nodules formed between the second and third harvests. At the day 64 harvest all pots had some nodules present on the roots. In the singleton nodules occurred at 3 cm into the pot whereas in the others they tended to be closer to the surface. There was no consistent pattern of depth of nodulation with later harvests however and average depth per pot ranged from 1 to 9 cm with a number just at the surface. Nodules ranged in size from 1 to 5 mm and were most numerous in the 4 plant pots at the day 85 and 99 harvests.

TABLE 4 *Acacia saligna* competition.  
Ratios of dry weights within treatments

No. per pot	Harvest (days)					1977 set
	36	50	64	85	99	64
Largest in pot/mean per pot						
2	1.3	1.1	1.2	1.2	1.1	1.7
3	1.2	1.1	1.2	1.8	1.7	1.5
4	1.4	1.9	1.6	2.6	1.1	2.1
Largest/smallest						
2	1.8	1.2	1.4	1.4	1.2	6.3
3	1.5	1.2	1.9	5.6	3.3	3.8
4	2.2	3.4	3.1	6.3	1.4	45.2

#### Waterlogging

Plants supplied with excess water generally had higher fresh weights and dry weights than those watered adequately (Table 2). Paired treatments are plotted in Fig 4. This may be compared directly with the competition results (Fig. 1). Dry weight differences were consistent across the range of plant densities used. Surprisingly fresh weight/dry weight ratios for plants receiving abundant water were generally lower (except for the first harvest) than the controls. This trend was also evident when considering all plants at a given harvest, though the treatments were more even if the pots with one plant are excluded *viz*:

Harvest Date	Overall Ratio		Excluding 1 per pot	
	Excess	Control	Excess	Control
36	10.2	9.1	10.2	8.7
71	8.9	9.5	9.1	9.4
92	7.1	7.9	7.7	7.7

It may be tentatively noted then that *Acacia saligna* can take advantage of abundant water and increase net growth more rapidly than with what may be considered adequate moisture. This is not inconsistent with examples of roadside growth where the plants clearly benefit from water-shedding.

By the time the experiment was terminated only a few phyllodes had been produced. However at the final harvest waterlogged plants had a total of 9 phyllodes compared with only three in the control set; these were formed on 7 and 3 (out of ten) seedlings respectively.

Root nodules were evident by the day 71 harvest. They were twice as abundant in the pots receiving excess water as they were in control pots. The waterlogged pots tended to have larger individual nodules and also to have them at shallower depths than in the control pots.

#### Nutrition

Plants which had no nitrogen in the potting mixture put on less dry weight than those receiving nitrogen (Table 3). There was little difference between treatments for the first three harvests (Fig. 5) and dry weight difference levels did not reach significance (1 way analysis of variance) for the first and third harvests. However at the last (day 99) harvest differences were significant between zero N and  $\frac{1}{2}$ , 1, 2 and 3X and also between  $\frac{1}{2}$  and 1X, despite little difference in fresh weight between these latter.

Nodulation was observed by day 64 and reached greater development in the higher nitrogen treatments.

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Mean dry weight per plant

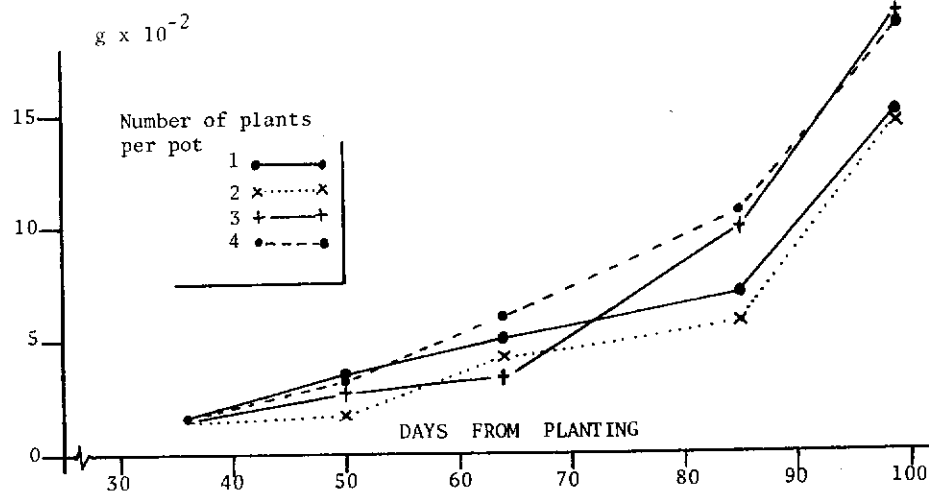


Fig. 1 Mean dry weights competition experiment *Acacia saligna*.

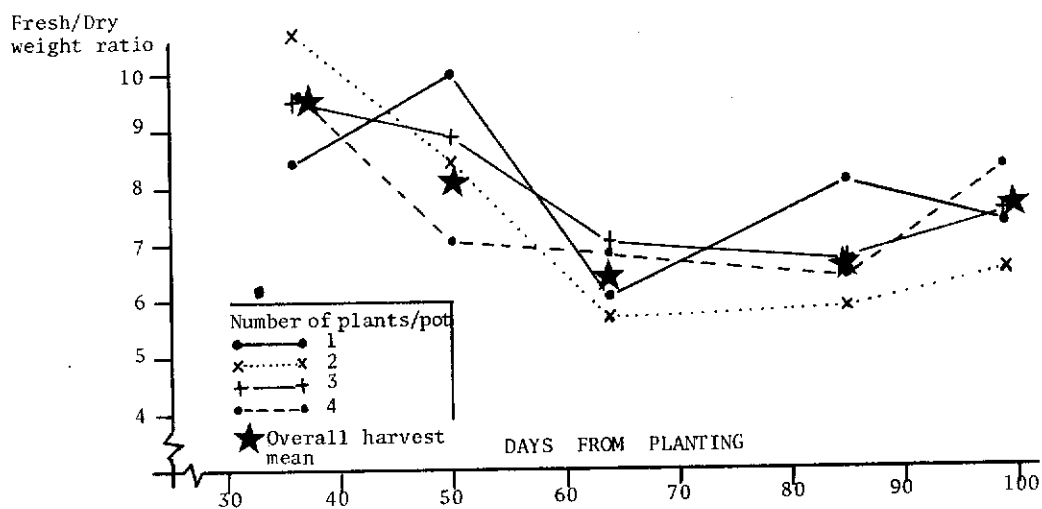


Fig. 2 Fresh weight/dry weight ratio competition experiment *Acacia saligna*.

Relative growth rate  
g g<sup>-1</sup> day<sup>-1</sup> x 10<sup>-2</sup>

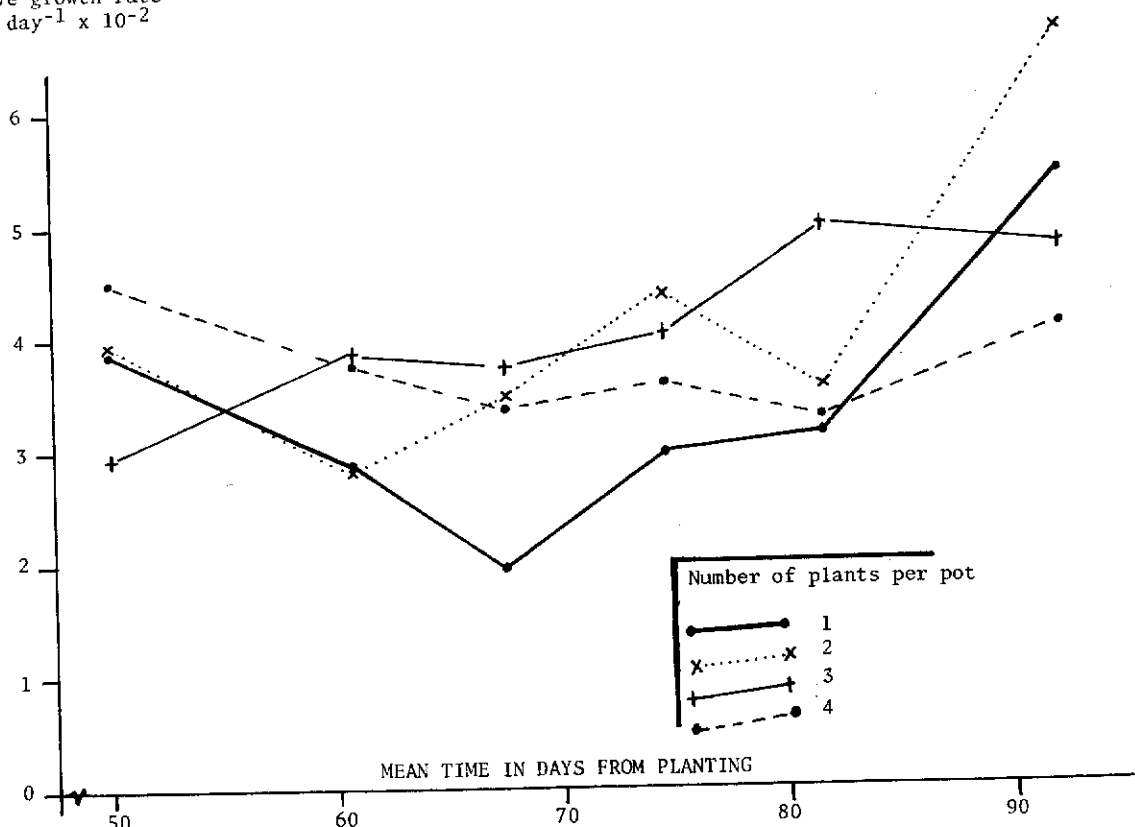


Fig. 3 Relative Growth Rates for *Acacia saligna*. Values calculated from harvests using the first three harvests twice and the latter two three times.

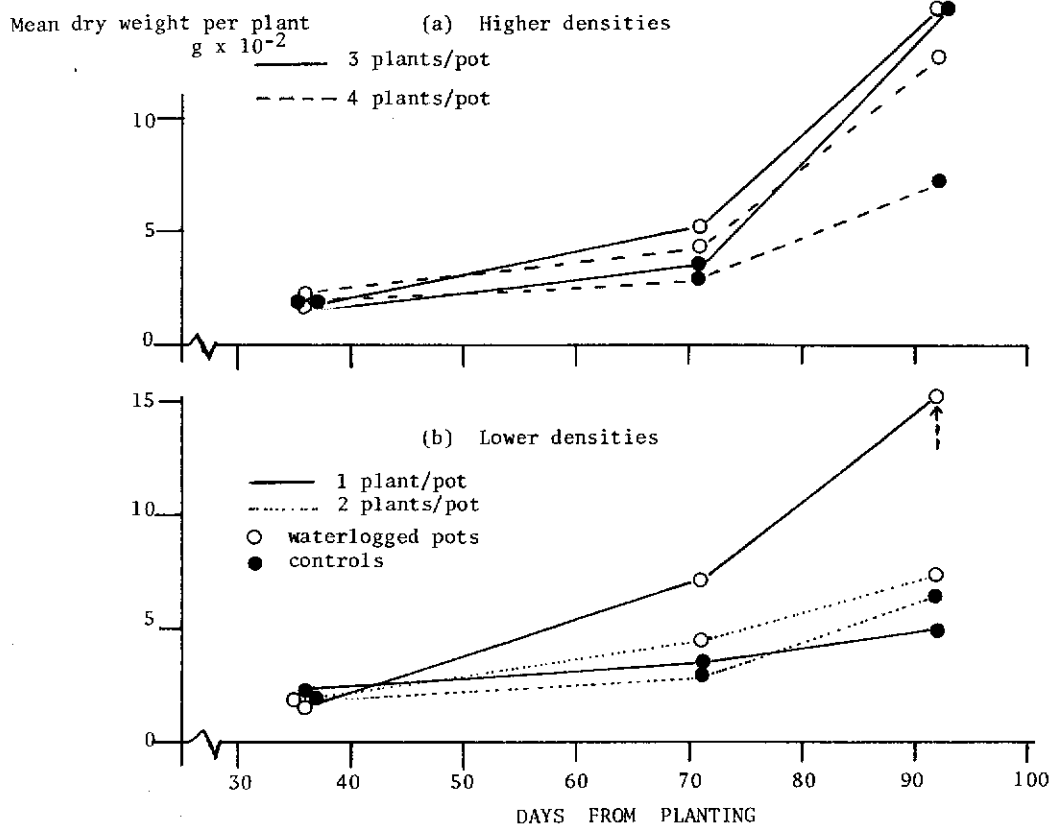


Fig. 4 Mean dry weights in waterlogging experiment with *Acacia saligna*.

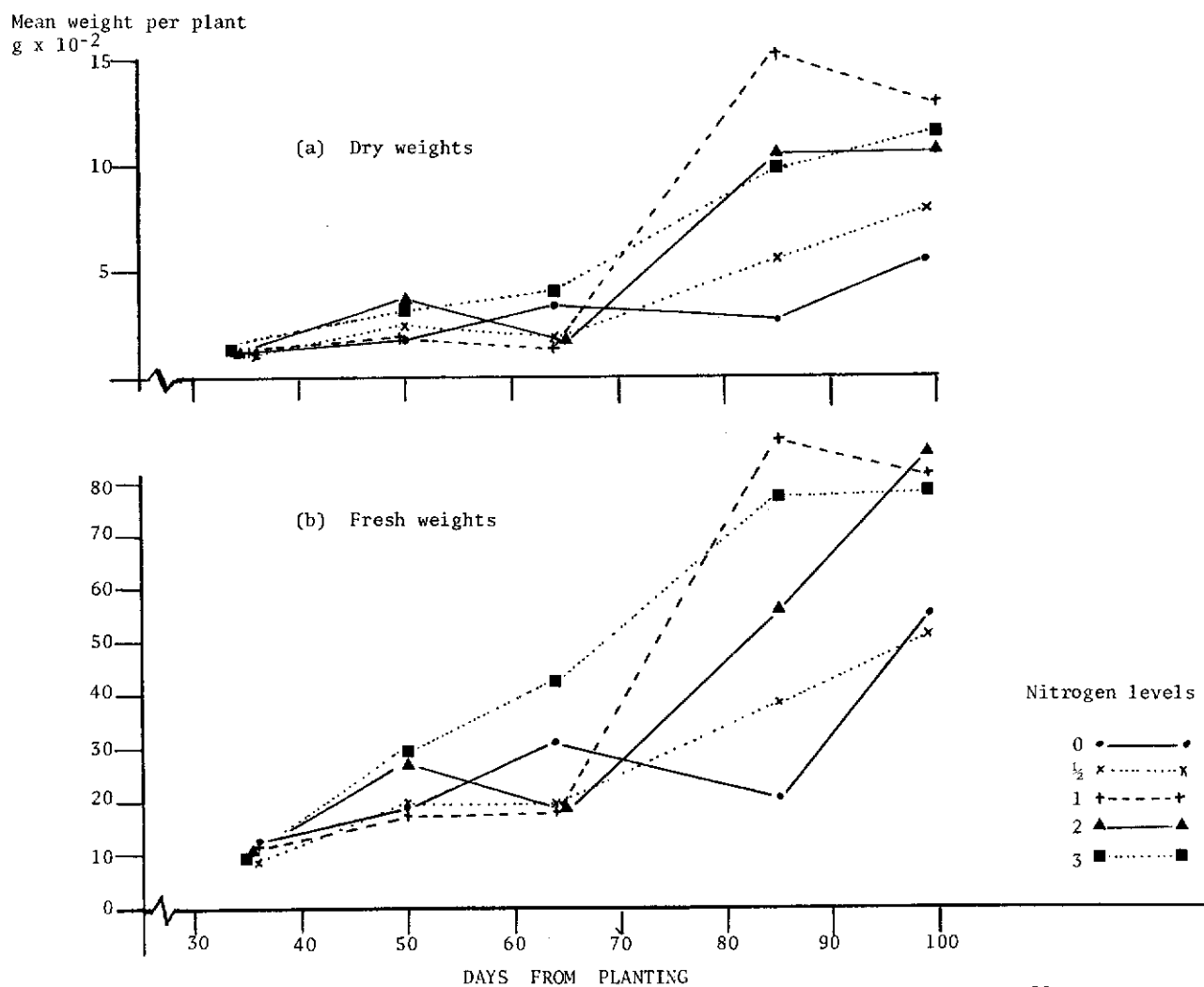


Fig. 5 Nitrogen experiment *Acacia saligna* mean weights per plant at different nitrogen levels.

# EXTRAFLOREAL NECTARIES IN AUSTRALIAN PLANTS, WITH SPECIAL REFERENCE TO *Acacia*.

Byron Lamont

## Taxonomic Distribution

Table 1 indicates that extrafloral nectaries in south-western Australia are only well represented in the legumes (perhaps universal in the highly speciated *Acacia* genus). Were more sub-tropical genera in north-western Australia (*Capparis*, Malvaceae, *Passiflora*, *Clerodendrum*) to be examined then no doubt this list would be extended considerably (Bentley, 1977). Systematic studies of living plants (to verify exudation) of other genera in Australia are still lacking. These are unlikely to change the initial impression: unlike tropical floras, the sclerophyll vegetation of Australia is deficient in species with extrafloral nectaries.

## Morphology

The extrafloral nectaries of the genera in Table 1 can be conveniently divided into three morphological types: *sunken* (e.g. *Acacia aneura*, Plate 1C), *sessile* (e.g. *A. iteaphylla*, Plate 1A, B) and *stipitate* (e.g. *A. pulchella*, Plate 1D). While stipitate nectaries appear to be restricted to a few spiny members of the series *Pulchellae* in *Acacia* (Maslin, 1975), both sunken and sessile nectaries occur in the two Australian sections now recognized in this genus (Pettigrew and Watson, 1975). In all genera examined the gland is always achlorophyllous, and capped by smooth secretory tissue devoid of stomates (Plate 1). The secretory tissue of *Hardenbergia comptoniana* is unusual in occupying much of the *abaxial* surfaces of the stipules and stipels.

## Function

Of all hypotheses proposed to explain the adaptive significance of extrafloral nectaries, protection from herbivores by ants attracted to the nectaries is now receiving almost universal support (Bentley, 1977). The phenology of two mulgas (terete morph) in relation to nectary exudation and ant activity were therefore studied over 12 months (Fig. 1). As already demonstrated (Lamont, 1978), exudation was closely associated with the presence of open inflorescences on the plants. Hence, visitation by ants was greatest when exudation and anthesis also reached their peak - though there is a clear indication of a time lag by the ants, which is not necessarily due to their lack of activity on the ground.

Of greater significance however are the indications that a) exudation may be very low at times when young leaves and flower buds are abundant on the plant (early summer and winter), and b) ants are present for only four months (late summer, autumn) of the nine month period for which protection would be required. In contrast was *Acacia iteaphylla* nearby which flowered in June-July, with no exudation or ant visitation, and produced abundant vegetative growth in August-September with much exudation by the young glands and visitation by crusader

bugs, but not ants. On the other hand, exudation from the eophylls of young seedlings of *A. aneura* has been observed by the author under shadehouse conditions (though not of the same order as the nectaries of *Albizia lophantha* seedlings of the same age in the same pots). Ants may be important then at the establishment stage in mulga, but not at the mature stage, when the synchrony between exudation and vegetative growth is almost lost.

On grounds that a) the Australian ant fauna is among the most diverse and abundant in the world (Taylor, 1972) (despite Bentley's (1977) assertion to the contrary that it is in tropical regions), and b) "Australia is the world's .. prime and indisputable .. centre for ant-dispersed plants" (Berg, 1975) - there are 59 myrmecorous genera in the south-west region alone, we would have expected far more species with extrafloral nectaries and their association with ants and protection from herbivores to be more obvious. We must look to the increasing aridity of the continent which gave rise to an essentially sclerophyllous (xerophytic) flora during Tertiary and Quaternary times as an evolutionary explanation. While elaiosomes are a minimal water and nutrient drain on the plant, extrafloral nectaries are potentially the reverse - they are clearly a vestige of tropical (mesophytic) ancestors. In support of this, the species with greatest extrafloral nectar production in south-western Australia, *Albizia lophantha*, is a vicariad of an essentially south-east Asian species and restricted here to moist forested valleys. Most taxa have developed alternative, sap-conservative devices for discouraging herbivory, including the novel synthesis of poisonous monofluoroacetates in some sclerophyllous legumes (Oliver *et al* 1977).

In contrast, the extrafloral nectaries of *Adenanthos* (and South African Proteaceae e.g. *Leucospermum cordifolium*, *Leucadendron lauratum*) seem to be an advanced character - the associated plants are very hairy and unpalatable, they occur on the tips of rigid leaves and are often positioned close to, and exuding synchronously with, open flowers. Their association with bird and mammal pollinators, rather than ant bodyguards, would seem more likely. This possibility has already been raised with respect to mulga (Lamont, 1978) and other sclerophyllous acacias (Ford and Ford, 1976) though the present author has only seen small butterflies and moths visit the specimens of mulga charted in Fig. 1, whereas honeyeaters occasionally visit specimens of *Adenanthos cygnorum* nearby.

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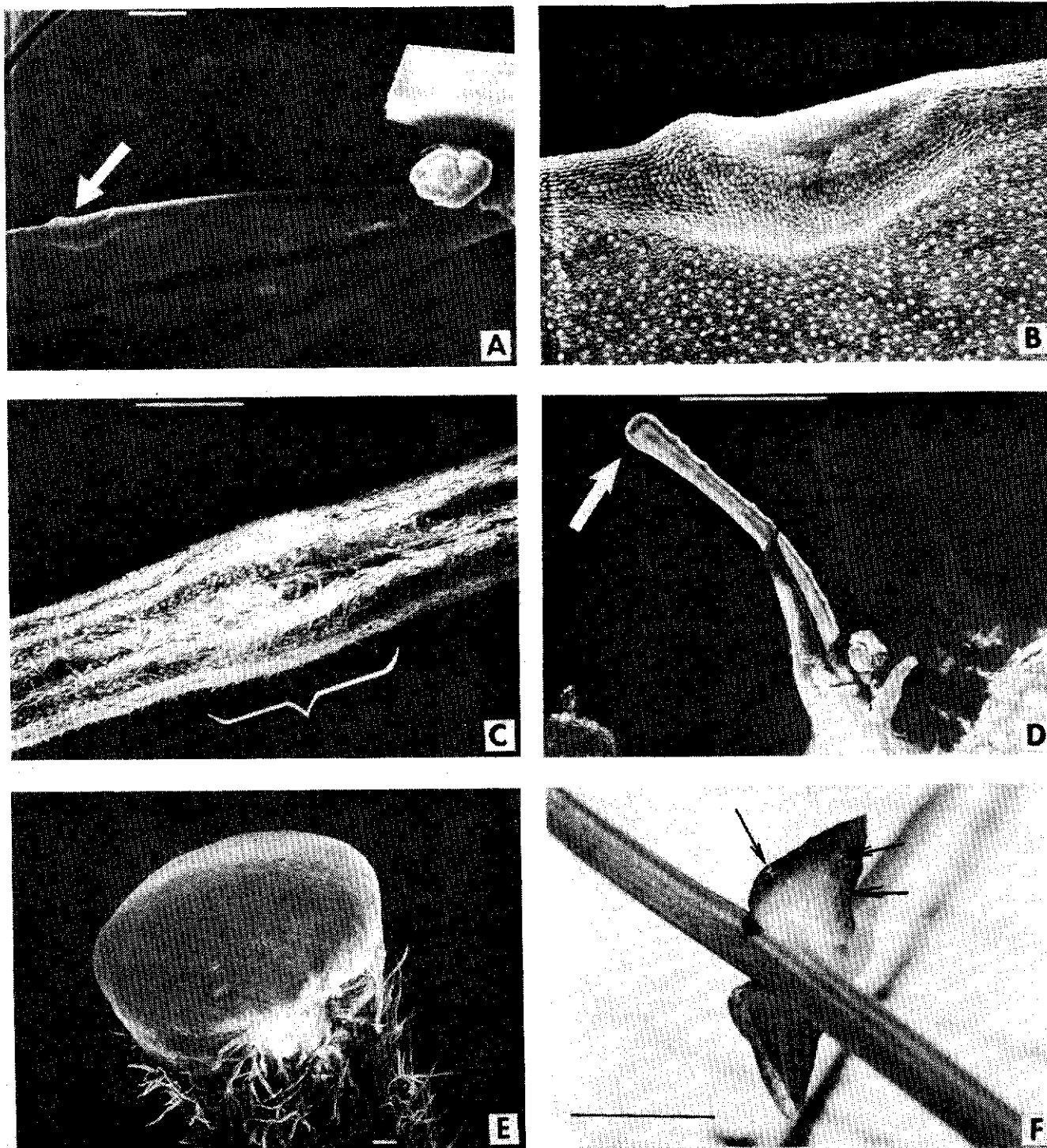
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TABLE 1 Examples of Western Australian species which bear extrafloral nectaries. (observations by author)

Species	Family	Subtribe or Section	Location on Plant	Type	Visitors
<i>Acacia aneura</i>	Mimosaceae	Heterophyllum*	phyllode, adaxial, lower rachis	sunken	ants
<i>A. pentadenia</i>	Mimosaceae	Heterophyllum*	cpd leaf, adaxial, all nodes of rachis	sessile	?
<i>A. pulchella</i>	Mimosaceae	Heterophyllum*	cpd leaf, tip of rachis	stipitate	?
<i>A. iteaphylla</i>	Mimosaceae	Uninervae*	phyllode, adaxial, lower rachis	sessile	?
<i>A. lasiocalyx</i>	Mimosaceae	Uninervae*	phyllode, adaxial, petiole	sunken	?
<i>A. saligna</i>	Mimosaceae	Uninervae*	phyllode, adaxial, lower rachis	sessile	ants
<i>Adenanthos cygnorum</i>	Proteaceae	Adenanthinae <sup>♂</sup>	some cpd leaves, tips of segments	stipitate	wasps
<i>Albizia lophantha</i>	Mimosaceae	-	cpd leaf, adaxial, tip of rachis, also lower rachis	sessile	ants
<i>Cassia desolata</i>	Caesalpinia-ceae	-	cpd leaf, adaxial, all nodes of rachis	sessile	?
<i>C. nemophila</i>	"	-	cpd leaf, adaxial, all nodes of rachis	sessile	?
<i>Hardenbergia comptoniana</i>	Fabaceae	Phaseoleae	cpd leaf, adaxial, stipules stipels	sessile	ants
<i>Stylidium brevicaupum</i>	Stylidiaceae	-	simple leaf, tip	stipitate	?
<i>Pteridium esculentum</i>	Dennstaedtiaceae	-	fronds, nodes of (lower) pinnae, adaxial	sessile	ants

\* After Pettigrew and Watson (1975).

♂ After Johnson and Briggs (1975).



## PLATE 1

A - Scanning electron micrograph (SEM) of base of phyllode of *Acacia iteaphylla*. The sessile extrafloral nectary is arrowed. Scale = 1 mm. B - SEM enlargement of extrafloral nectary of *A. iteaphylla*. Scale = 100  $\mu$ m. C - SEM of pore of sunken extrafloral nectary (bracketed) of *A. aneura* (terete morph). Note the T-shaped protective hairs on the ridges and in the pore and the bulbous glandular hairs in the crevices. Scale = 1 mm. D - SEM of stipitate extrafloral nectary (arrowed) of *A. pulchella*. Note raised stomates on stipe. Closest pinna has been removed to show origin of nectary (apex of rachis). E - SEM of stipitate extrafloral nectary of *Adenanthos cygnorum*. The lateral bright spot indicates a vestigial nectary. F - micrograph of the abaxial surface of a pair of stipules of *Hardenbergia comptoniana*. Three droplets of nectar exuding from the glandular surface have been arrowed. Scale = 5 mm.

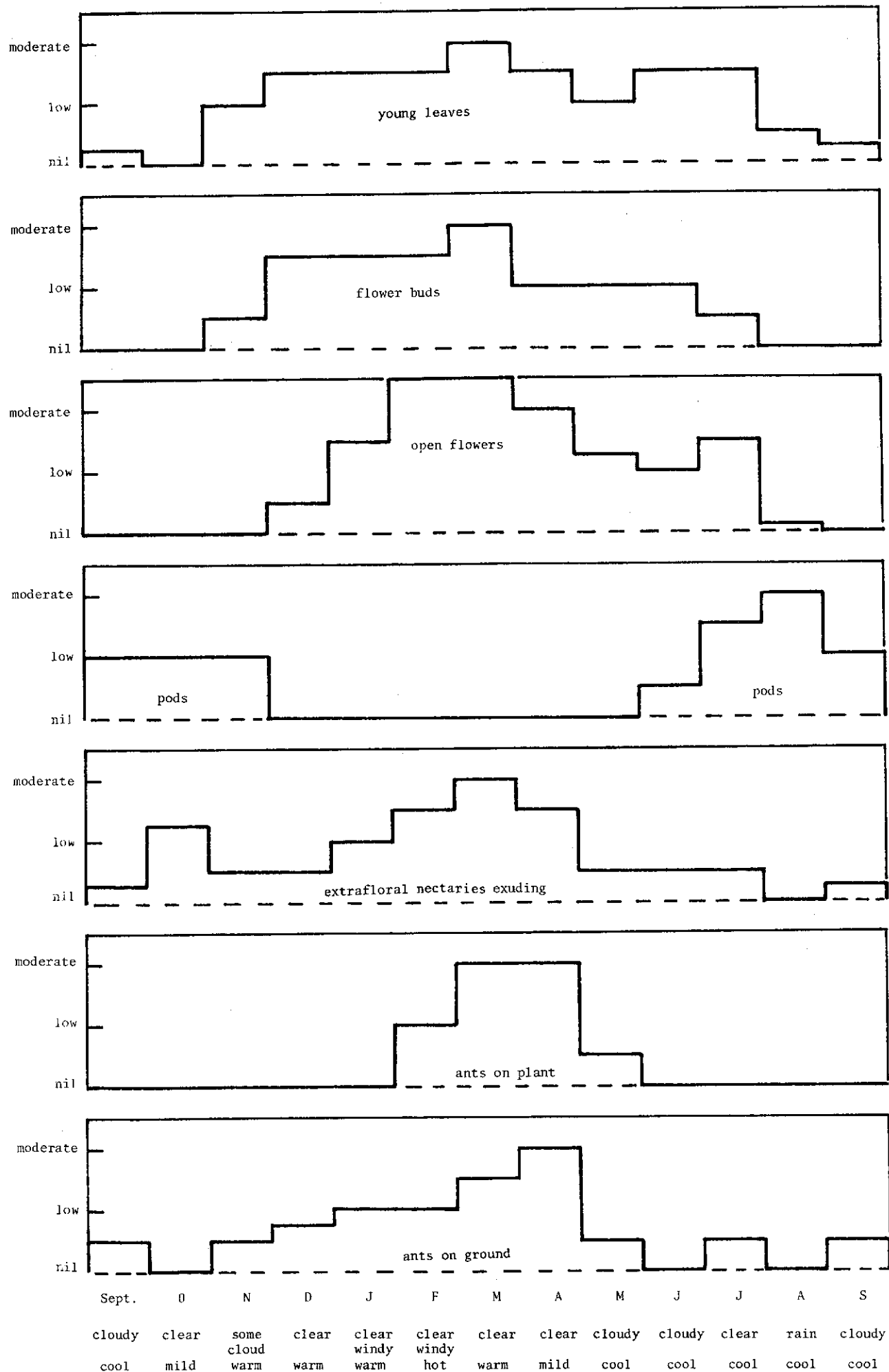


Fig. 1 Mean phenology of two naturalized specimens of *Acaacia aneura* (terete morph) in Perth in relation to exudation by extrafloral nectaries and ant activity. The weather on the day of observation (first week of each month) is given at the bottom of the Figure.

# VARIATION IN PHYLLODES WITHIN INDIVIDUALS OF *Acacia aneura*

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## Introduction

There is considerable variation in leaf (phyllode) shape between individuals of *Acacia aneura*.<sup>2</sup> It may be anticipated that individual plants will exhibit different phyllode sizes between the seedling and adult stages. Attempts at defining variation within the species as a whole may rely on a knowledge of the extent of differences within individual plants.

Foliage sampling within a crown at different times is likely to give varied proportions of leaf sizes. For example Maconochie notes that *A. aneura* gains foliage during periods of summer rain and also after good winter rain with temperatures rising.<sup>3</sup> He observed peaks of foliage loss during late summer-early autumn when

water stress prevailed. Heavy foliage loss appears to occur after heavy rain following a long period of drought stress.<sup>5,6</sup> Thus at any given time an abundance of senescing phyllodes or a comparatively high proportion of new ones may be present. Differences in size may also be related to flowering.

This account reports the extent of variation in foliage between positions in the crown from three individual trees at Mileura Station. The samples were taken in early December 1976, at which time only 62 mm of rain had fallen in the preceeding 13 months.

## Sampling Technique

Two trees were selected in the 'Trifid' study area, Lat. 26° 15'S, Long. 117° 11'E and one at Ejah 18 km to the south, at 26° 25'S, 117° 12'E.

A ladder was erected into the crown of each tree and three branchlets were marked at three vertical positions within the crown. The vertical positions were designated 'top', 'middle' and 'bottom'.

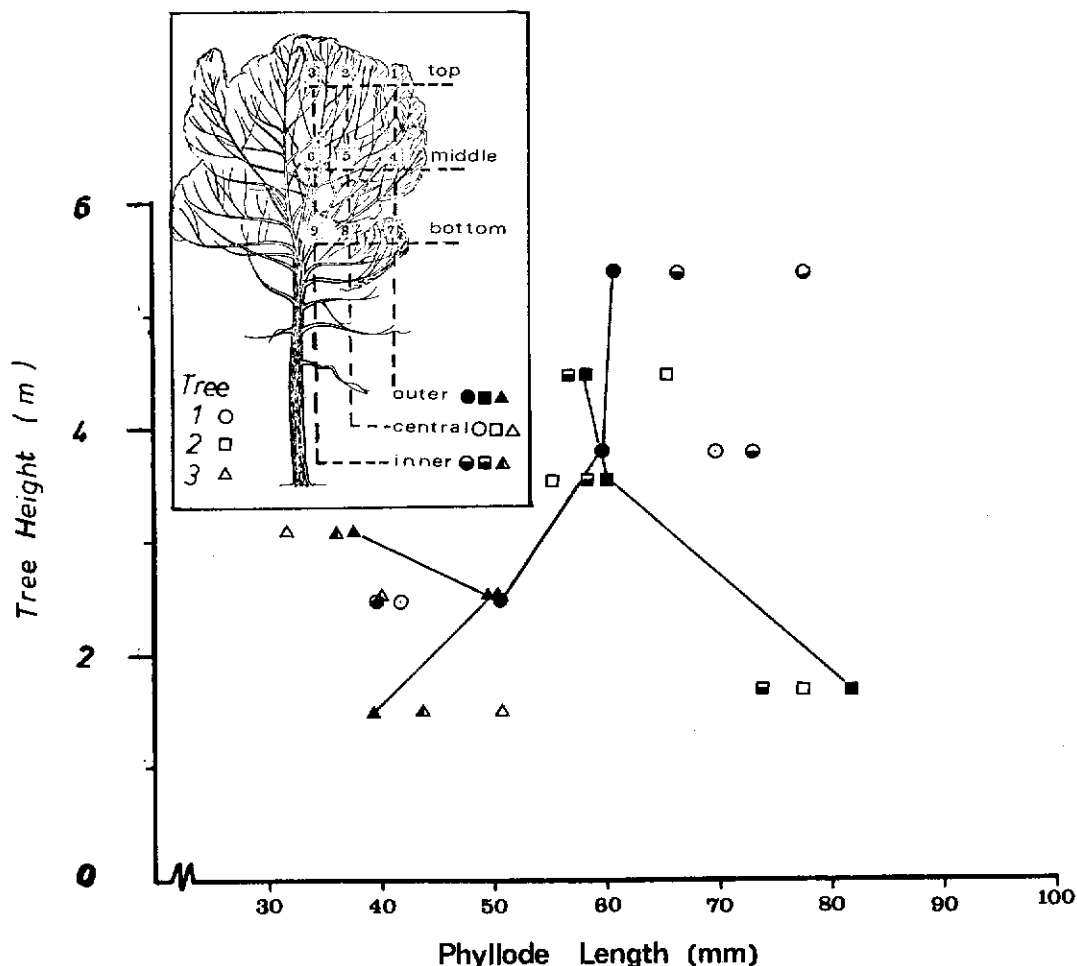


Fig. 1 Phyllode Length at Different Crown Positions. Three trees at Mileura Station, December 1976. Solid lines join 'outer' samples for each tree.

'bottom'. The three equi-horizontal points at each level were designated 'outer', 'central' and 'inner' in relation to the bole (see inset to Fig. 1).

All phyllodes on each designated branchlet were stripped off and placed in numbered specimen bottles for later measurement.

It must be emphasised that the three vertical levels between specimen trees were different and that phyllodes were stripped from individual branchlets to constitute the separate sub-samples. Collection was not therefore random as in a study reported by Pressland.<sup>4</sup> In the collection of botanical specimens from trees with foliage commencing at about head height one would normally cut off a sample for pressing from the outer, bottom crown (position 7 of Fig. 1). If however the plant is shorter and the whole crown is within easy reach then the outer, bottom position will rarely be sampled. For short trees or bushy forms of mulga sampling would most frequently cover the outer, middle or top of the crown (positions 4 and 1 of Fig. 1).

Each tree is discussed separately below. In the laboratory the phyllodes for each sub-sample were measured for length to the completed millimetre (mm) and run through a planimeter (courtesy of C.S.I.R.O.) for area to the completed square millimetre (mm<sup>2</sup>).

#### Tree 1 Profile

This specimen is the tallest of the three at 8.3 m high. The vertical samples were taken at 5.4 m (top), 3.8 m (middle) and 2.5 m (bottom). The tree is narrower in the crown than the other two, with a crown diameter taken from north to south of 5.3 m. It has one major stem at 1.3 m from the ground, with a stem diameter at this height of 16.35 cm.

Leaf shape may be categorised as narrow, lanceolate. The tree is growing in a favourable site, transect line 5 in the 'Trifid' study area (reported on elsewhere). A number of tall *Grevillea striata* are found in the immediate vicinity and the abundance of well formed mulga contrasts sharply with the stoney plains around the 'Trifid'.

A total of 157 phyllodes were measured from Tree 1. The following summarises the mean values for length and area at the nine sampled positions and for those grouped vertically and horizontally as illustrated in Fig. 1.

It may be noted (see also Fig. 1) that the levels show no consistency in trend across the tree profile apart from a decline in mean size from the top downwards. Fig. 2 gives a graphical presentation of the phyllode profile for Tree 1.

Emin tested position values for significant differences using the Kruskal-Wallis analysis of ranked differences between medians.<sup>1</sup> This gave the following results for phyllode lengths:

bottom samples: the outer set significantly greater than central and inner sets.

central samples: the top set significantly

#### PROFILE

##### TREE 1

n =	21	24	23	top 68
$\bar{x}$ length	66.5 mm	77.7	61	68.6
$\bar{y}$ area	81.6 mm <sup>2</sup>	85.3	83.4	83.6
position				
	10	12	15	middle 37
	73	69.8	59.7	66.6
	84.3	81.9	69.2	77.4
	13	24	15	bottom 52
	39.9	41.8	50.5	43.8
	37.9	50.1	54.1	48.2
	inner 44	central 60	outer 53	TREE 157
	60.1	61.7	57.7	59.9
	69.3	70.6	71.1	70.4

greater than the middle, the middle set significantly greater than the bottom.

inner samples: the middle set significantly greater than the top, the top significantly greater than the bottom.

Other positions showed no significant differences. Similar tests for leaf area suggested that the bottom set showed no significant differences, the central set was similar to the pattern for length and:

outer samples top > middle > bottom, all significantly different.

inner samples (top = middle) > bottom.

A sample collection taken from position 4 (outer, middle) would have correlated well with the overall tree profile while one from position 7 would have underestimated the overall mean size. In Fig. 2a position 4 falls at the centre, with position 7 displaced to the lower left. The greatest range in phyllode length (75 mm) was at position 1 (outer, top) from 28-103 mm. The smallest length range was at position 4 (39 mm) (outer, middle) from 38-77 mm. Range in phyllode area was greatest at position 6, from 20-144 mm<sup>2</sup> and smallest at position 1, from 51-126 mm<sup>2</sup>. Extreme values for leaf area at each crown position are shown in Fig. 2a.

Linear regressions were calculated as follows:

Whole tree Area = -10.57 + 1.35 length,  $r = .918$

Position 4 Area = -37.32 + 1.78 length,  $r = .965$

Position 7 Area = -62.12 + 2.30 length,  $r = .983$

As anticipated above the regression for position 4 underestimated the leaf area (70.4 mm<sup>2</sup>) corresponding to mean phyllode length (59.9 mm) by only 1.6%. The regression for position 7 underestimated mean leaf area by 7.5%. The balance of Fig. 2 consists of histograms illustrating leaf size distributions for top, middle, bottom, outer, central and inner positions. Only the shapes of these histograms should be compared as each set is adjusted to a total frequency of 100.



### Tree 2 Profile

This tree is a little shorter than Tree 1 at 6.6 m. Vertical samples were taken at 4.5 m (top), 3.5 m (middle) and 1.7 m (bottom). The crown is larger than Tree 1, at 6.1 m across and there are two main stems at 1.3 m from the ground with diameters of 13.6 and 11.3 cm. Leaf shape may be categorised as narrow, broader (broader than that of Tree 1). Tree 2 is 19 m away and down the gradient from Tree 1.

A total of 146 phyllodes were measured from Tree 2. The following summarises the mean values for length and area at the nine sampled positions and for those grouped vertically and horizontally:

#### PROFILE

##### TREE 2

n =	13	21	16	top 50
$\bar{x}$ length	57	65.7	58.6	61.2
$\bar{y}$ area	125.3	138.8	122.7	130.1
position				
	30	17	12	middle 59
	58.2	55.3	60.1	57.8
	119.6	85.3	104.4	106.6
	10	16	11	bottom 37
	74	77.5	82	77.9
	213.8	198.7	242.5	215.8
	inner 53	central 54	outer 39	TREE 146
	60.9	65.9	65.7	64
	138.8	139.7	150.9	142.3

In this tree the bottom set is clearly larger than the top and middle sets with position 2 (central, top) most closely approaching the overall mean (Fig. 3a).

Tests of position differences using the Kruskal-Wallis analysis ( $q.v.$ ) gave the following results for phyllode lengths:

outer samples: bottom set significantly greater than top and middle sets.

central samples: bottom set significantly greater than the top and the top significantly greater than the middle set.

inner samples: as for outer set.

Other positions showed no significant differences and similar tests for leaf area showed that for outer central and inner samples the bottom sets were significantly greater than the top sets which, in turn, were significantly greater than the middle sets.

A sample taken from position 4 would have underestimated length and grossly underestimated area, while one from position 7 would have overestimated the overall mean size (Fig. 3a). The greatest range in phyllode length was 58 mm for position 8 (central, bottom) from 47-105 mm. Position 2 had the smallest range in length from 50-84 mm. Greatest area range was at position

7, from 95-343 mm<sup>2</sup>, while the smallest area range, of 38-161 mm<sup>2</sup> was at position 5. Extreme values for leaf area at each crown position are shown in Fig. 3a.

Linear regressions were calculated as follows:

Whole tree Area = -115.16 + 4.02 length,  $r = .905$

Position 4 Area = -94.7 + 3.31 length,  $r = .885$

Position 7 Area = -244.06 + 5.93 length,  $r = .954$

The latter two underestimate leaf area (142.3 mm<sup>2</sup>) of the mean leaf length (64 mm) by 18 and 13% respectively.

### Tree 3 Profile

This specimen is the shortest of the three examined. It is 4.2 m tall and samples were taken at 3.1 m (top) 2.5 m (middle) and 1.5 m (bottom). Tree 3 has the largest crown diameter of the 3 individuals sampled at 7.1 m. There are 4 major stems at 1.3 m from the ground and these have stem diameters of 13.5, 12.7, 10.5 and 9.9 cm. This bulk of bole-wood suggests that Tree 3 is the oldest of the three sampled despite its shorter height.

Leaf shape for Tree 3 is terete. The tree is growing on a site less favourable than the other two. Distance between neighbouring trees is greater than in transect line 5 in the 'Trifid' area, and the specimen tree is one of the tallest in the general area. It is just east of the Ejah breakaway and north of the C.S.I.R.O. field station.

The number of phyllodes measured was 207. Mean values are shown here:

#### PROFILE

##### TREE 3

n =	17	22	22	top 61
$\bar{x}$ length	36.1	31.8	37.4	35
$\bar{y}$ area	31.5	33.2	32.7	32.5
position				
	19	36	19	middle 74
	50.1	40	49.3	45
	46.3	32.8	47	39.9
	24	29	19	bottom 72
	43.8	50.6	39.6	45.4
	44.6	54.6	31.2	45.1
	inner 60	central 87	outer 60	TREE 207
	43.6	41.5	41.9	42.2
	41.4	40.2	36.7	39.5

Overall means are lower than for Trees 1 and 2 with largest leaves tending to be concentrated in the middle and inner central part of the crown. Tests of position differences using the Kruskal-Wallis analysis ( $q.v.$ ) showed many more significant differences than for Trees 1 and 2 with only the top set reasonably homogeneous:

Fig. 2 Phyllode Profile, Tree No. 1

a - summary for whole tree - numbers refer to crown positions as in Fig. 1; diagonal line is regression

Area =  $-10.57 + 1.35$  length;

bars refer to standard deviation of mean (dotted, inner) and extreme values recorded (solid, outer); irregular dashed line joins extreme values for leaf area at each crown position number.

t, m, b, o, c, i are phyllode length percentage histograms for top, middle, bottom, outer, central and inner phyllodes respectively, as in Fig. 1.

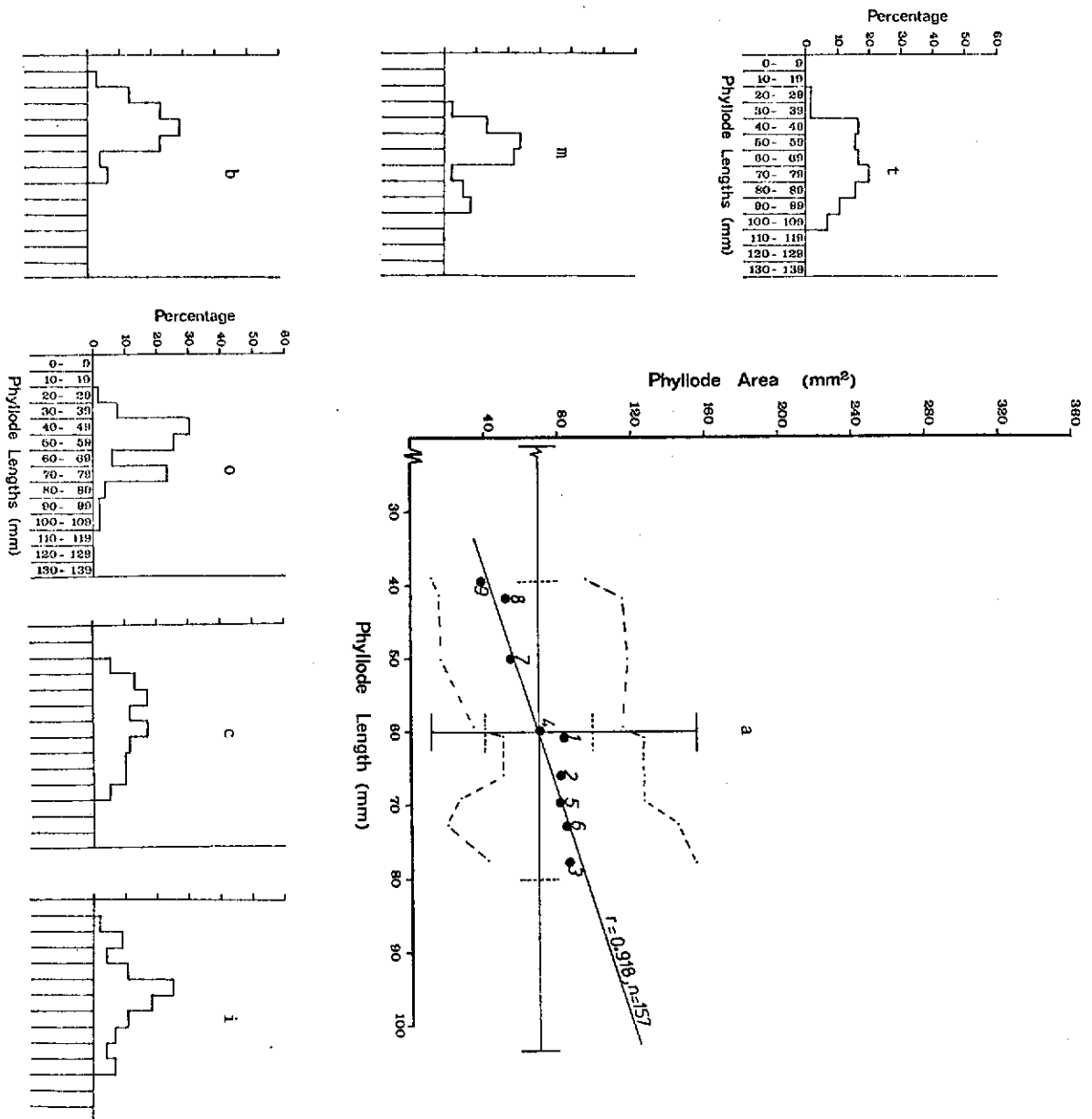


Fig. 3 Phyllode Profile, Tree No. 2

a - summary for whole tree - numbers refer to crown positions as in Fig. 1; diagonal line is regression  
 $\text{Area} = -115.16 + 4.02 \text{ length}$ ;  
 bars refer to standard deviation of mean (dotted, inner) and extreme values recorded (solid outer); irregular dashed line joins extreme values for leaf area at each crown position number.

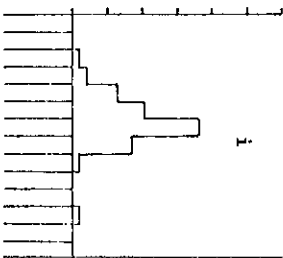
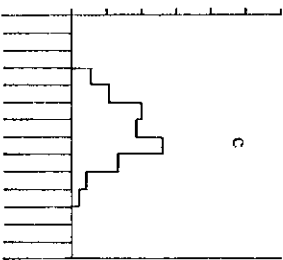
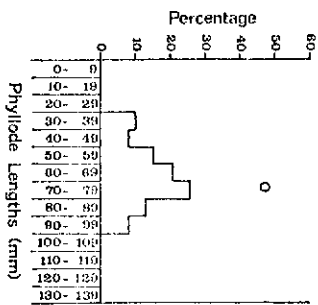
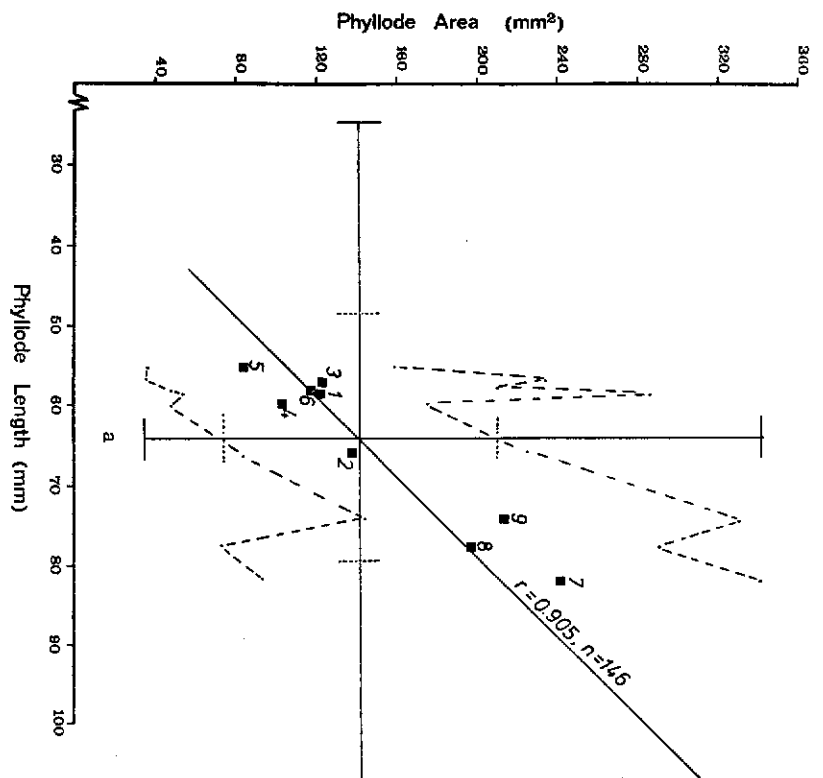
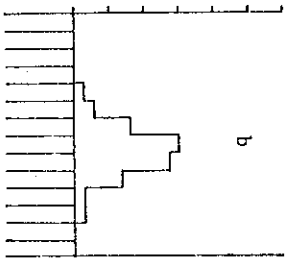
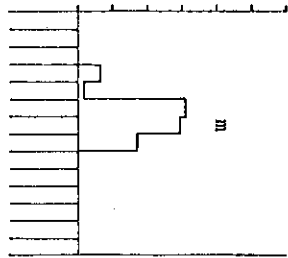
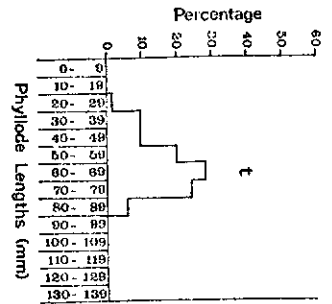
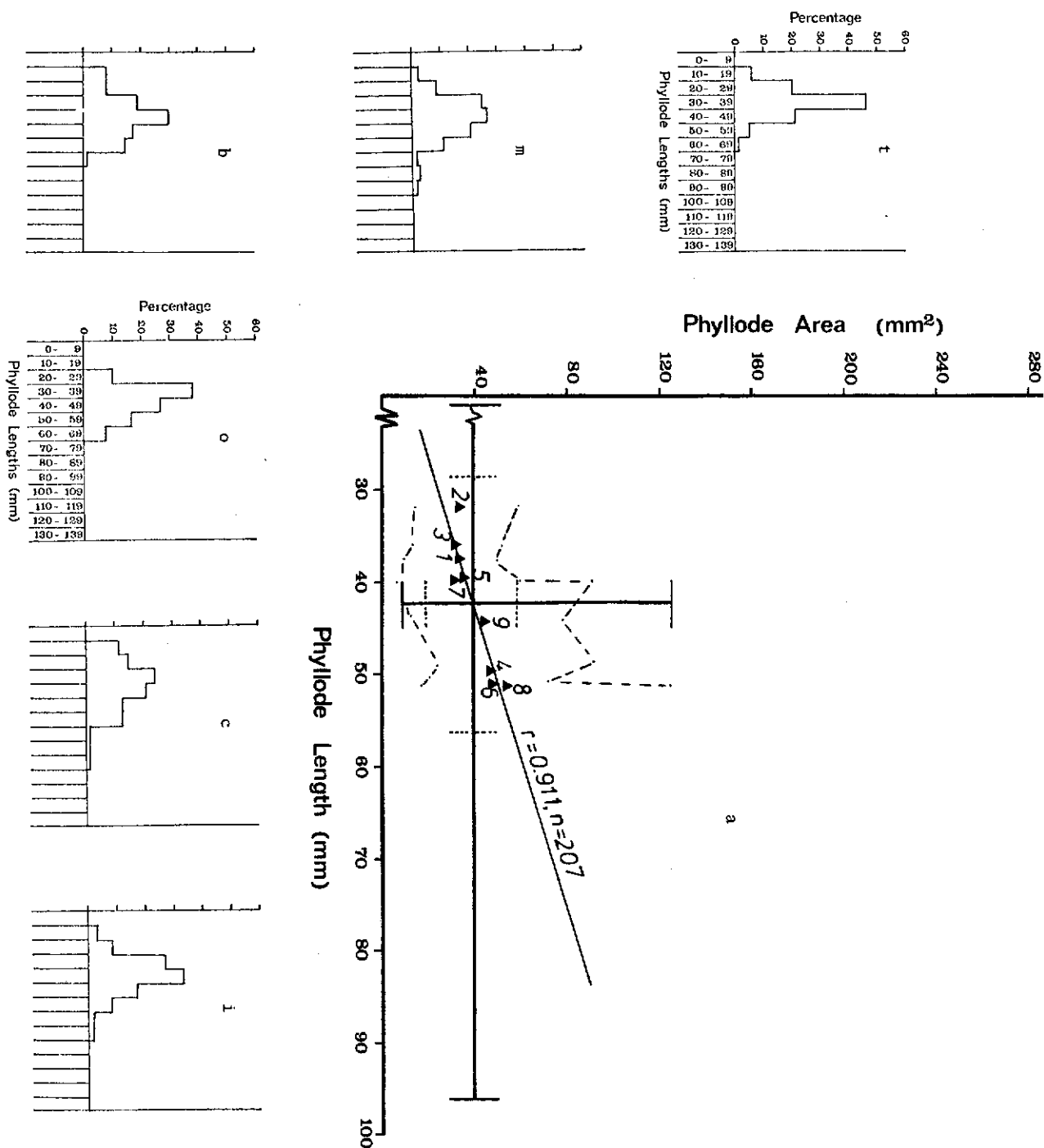


Fig. 4 Phyllode Profile, Tree No. 3

a - summary for whole tree - numbers refer to crown positions as in Fig. 1; diagonal line is regression  
 $\text{Area} = -12.72 + 1.24 \text{ length}$ ; bars refer to standard deviation of mean (dotted, inner) and extreme values recorded (solid, outer); irregular dashed line joins extreme values for leaf area at each crown position number.  
 t, m, b, o, c, i are phyllode length percentage histograms for top, middle, bottom, outer, central and inner phyllodes respectively, as in Fig. 1.



middle samples (outer = inner) > central  
 bottom samples central > inner > outer  
 outer samples middle > (top = bottom)  
 central samples bottom > middle > top  
 inner samples (middle = bottom) > top

Exactly the same pattern resulted with tests on leaf area.

A sample taken from position 4 would have overestimated size while a sample from position 7 would have underestimated size. Perhaps the closest to the mean was position 9 (inner, bottom), not one that would be commonly selected (Fig. 4a).

Despite smaller average phyllode length the ranges in length at different canopy positions were greater on the whole than those for Tree 2 and for several positions in Tree 1. This however was more a function of the numbers of comparatively short phyllodes on Tree 3. Range in both length and area was greatest at position 8 (central, bottom) from 18-96 mm and 17-125 mm<sup>2</sup> respectively. Position 3 had the shortest length range 17-49 mm, and the smallest area range at 14-52 mm<sup>2</sup>. Extreme values for leaf area at each canopy position are shown in Fig. 4a.

Linear regressions were calculated as follows:

Whole tree Area = -12.72 + 1.24 length;  $r = .911$

Position 4 Area = -19.97 + 1.36 length;  $r = .955$

Position 7 Area = -34.88 + 1.67 length;  $r = .798$

The regressions for 4 and 7 underpredict the leaf area corresponding to the mean leaf length of 42.2 mm by 2.08 and 3.41 mm<sup>2</sup> respectively.

#### Anatomical Features

Drawings based on sections taken through the mid-points of typical phyllodes are illustrated in Figs. 5 and 6. Position 1 of Tree 1 is illustrated in Fig. 5a, b (outer, top). The flattened lateral shape is illustrated well and it can be seen that 26 vascular bundles occur in this section. The palisade layer and the pith are both 0.3 mm across. Guard cells occur in the outer epidermis with a resinous layer containing trichomes peripheral to them. The stomate illustrated is recessed into the palisade tissue.

The number of vascular bundles observed in specimen phyllodes from all 9 sampling positions of Tree 1 varied from 17 (position 7, outer, bottom) to 29 (position 5, central, middle) with a mean of 24. Position 5 is illustrated in Fig. 5c, d. In addition to more vascular bundles this specimen had a deeper palisade layer (0.4 mm) than all other positions examined for Tree 1. Its outer epidermis is more convoluted than that for position 1, and its general tissue arrangement was repeated in specimens from positions 6, 7, 8 and 9 (except that these had a palisade layer of only 0.2 mm). All other positions showed overall structure more similar to that of position 1 (i.e. Fig. 5a).

Fig. 5e, f illustrate position 1 of Tree 2. Phylls are much broader than in Tree 1 with this illustration showing one > 3 mm across. 39 vascular bundles occurred here compared with a range in Tree 2 from 26 (position 4) to 43 (positions 6 and 9). The palisade at position 1 was slightly deeper than for the other 8 position samples: 0.3 mm compared with 0.2, with the pith 0.2 mm. Pith was generally much shallower in Tree 2 than Tree 1 with most samples 0.1 mm deep (only position 1, 0.2 mm; and position 8, 0.3 mm being deeper).

The phyllode illustrated in Fig. 6a, b is from position 3 of Tree 2. This sample though not as broad as shown in Fig. 5e, had more vascular bundles and these are smaller and narrower. Phylls from other positions resembled one or other of Fig. 5e or 6a though the sample from position 5 had a more contorted cuticle and epidermis not dissimilar to that illustrated in Fig. 5c.

Terete phyllodes from Tree 3 are illustrated in Fig. 6 (c-h). Most sections were similar to that of position 3 (Fig. 6c, d) with 16-18 vascular bundles and a palisade layer 0.2 to 0.5 mm deep, with an inner pith of 0.7 to 1 mm. The sample taken from position 4 (outer middle) had many more (27) vascular bundles and a deeper pith than most specimens with a distinctly flattened shape. The upper main vascular bundle shown as prominent in Fig. 6e also occurred in samples from positions 5 and 6.

Finally Fig. 6g, h illustrates a specimen from Tree 3, position 1 (outer, top) collected in July 1977 eight months after all phyllodes had been stripped from the particular branchlet on which it grew. It therefore represents a 'young' phyllode of  $\frac{1}{2}$  8 months of age. The main distinguishing features from the older phyllodes illustrated are the comparatively small proportion of pith and the elongated bundles.

#### Conclusions

Foliage of the three mulga trees discussed and enumerated here clearly differs between trees. Differences within a tree are not considered to be such as to unduly distort classification by sampling providing samples are taken consistently in a representative manner. In summary it may be noted that:

a) Tree 1 Leaf length has a range of 88 mm with the smallest 15 mm and the largest 103 mm. Similarly leaf area has a range of 144 (11-155 mm<sup>2</sup>). The longest phyllodes occurred at positions 1, 2, 3, 5, and 6; while the shortest were found at positions 7, 8 and 9. Of the 10 length classes into which the samples fell 15% were less than 40 mm; 66% were more than 50 mm and 68% were between 40 and 79 mm in length.

b) Tree 2 Leaf length 25-114 (89) mm; area 161-343 (182) mm<sup>2</sup>. Longest at positions 7, 8, 9; shortest at positions 3, 5, 6. 10 length classes. 82% > 50 mm; 7% < 40 mm and 68% 50-79 mm.

c) Tree 3 Leaf length 14-96 (82) mm; area 6-125 (119) mm<sup>2</sup>. Longest at positions 8 and 9, though some of the shortest phylls also found

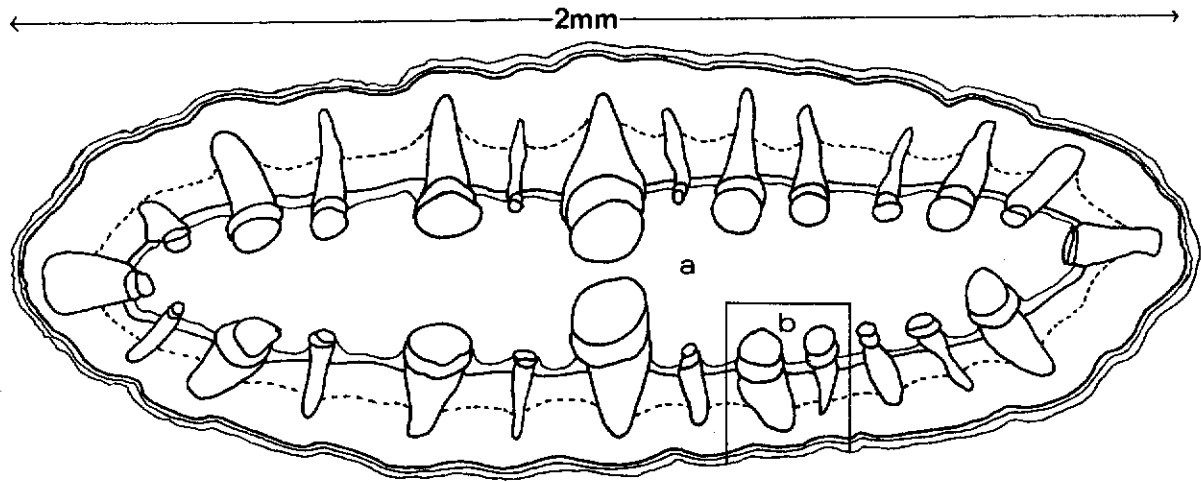
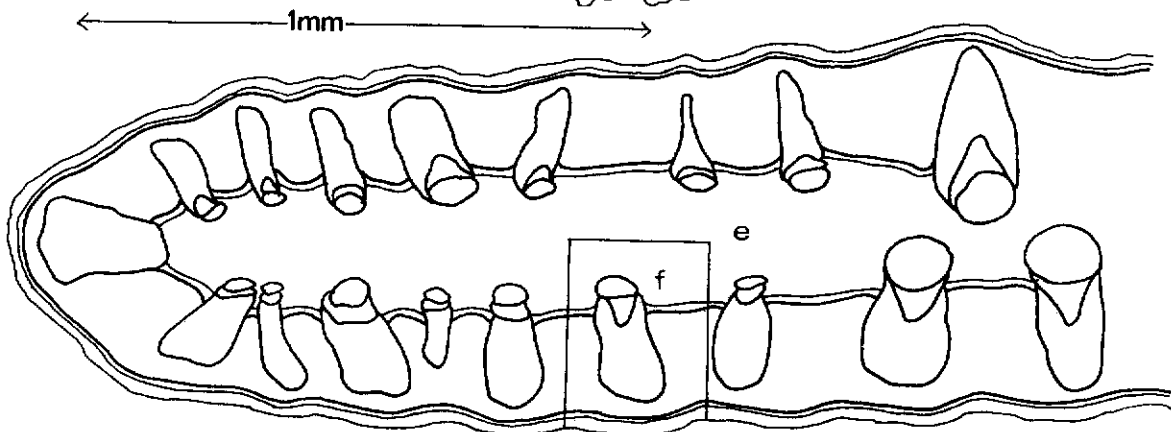
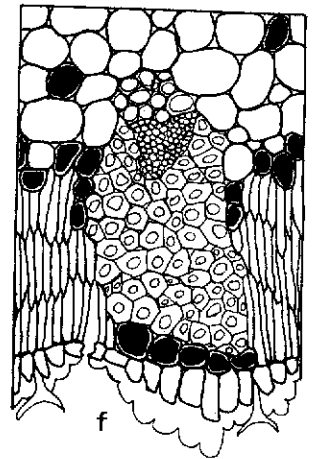
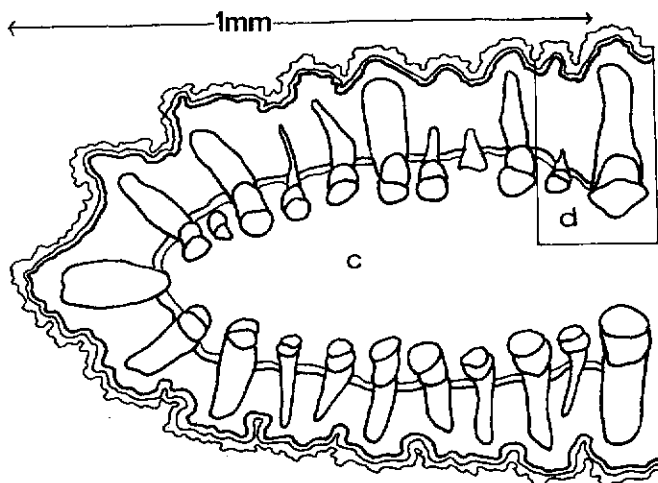
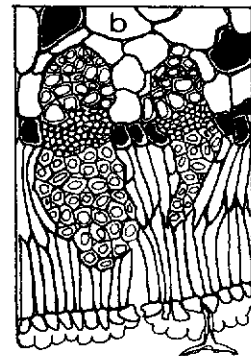
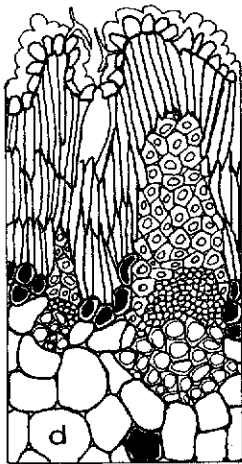


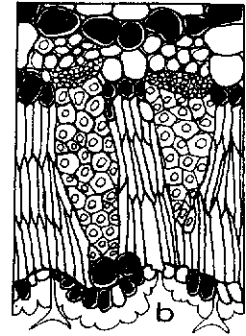
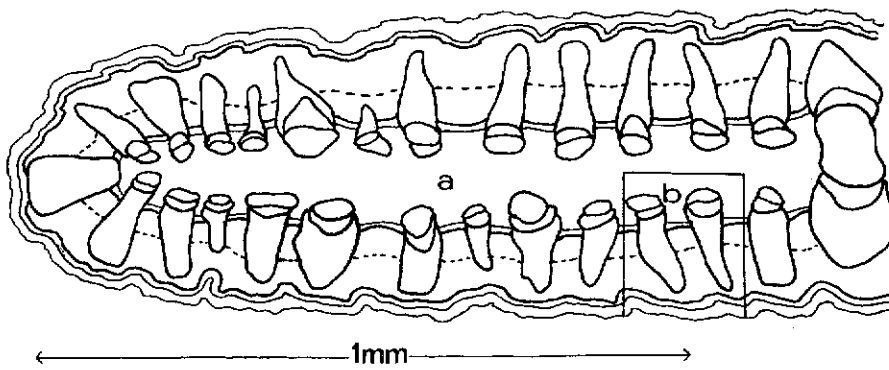
Fig. 5 Anatomical Features

Phyllode Sections, Tree 1  
Mileura Station.a, b Position 1, outer top  
c, d Position 5, central middleTree 2

e, f Position 1, outer top.

(Drawn by S. Downes)





1.5mm

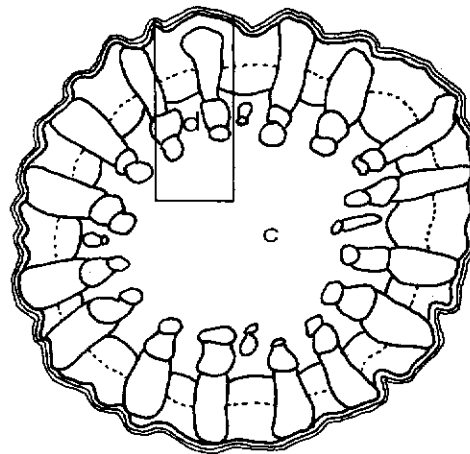
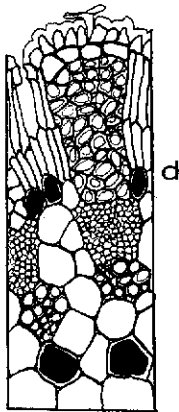


Fig. 6 Anatomical Features

Phyllode Sections Tree 2

a, b Position 3 (inner top)

Tree 3

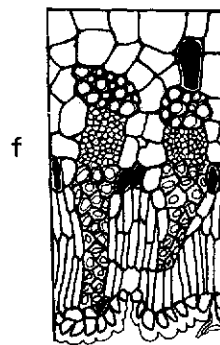
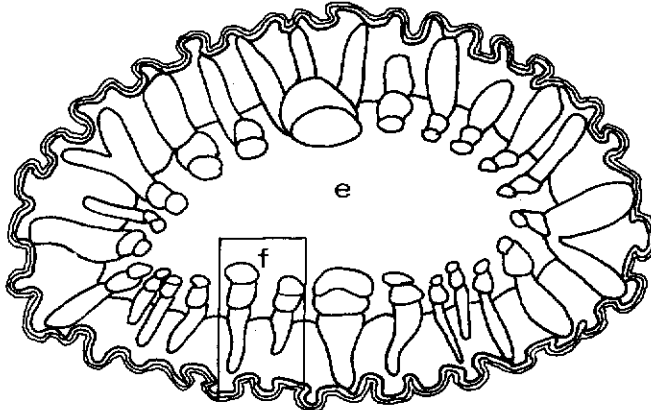
c, d Position 3 (inner top)

e, f Position 4 (outer middle)

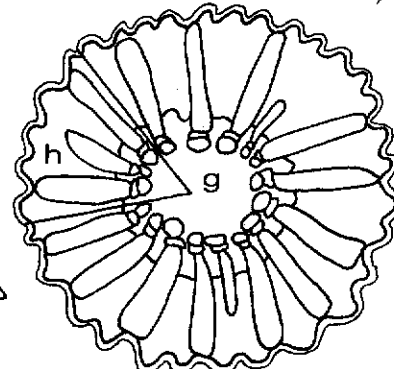
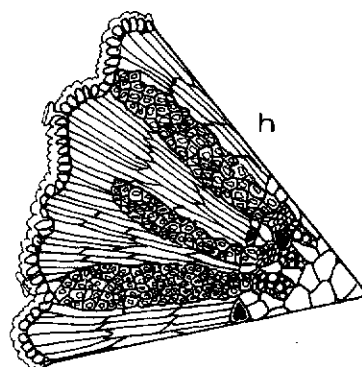
g, h Position 1 (outer top) aged 8 months.

(Drawn by S. Downes)

1.5mm



1.5 mm



at these positions. 9 length classes. 27% > 50 mm; 46% < 40 mm and 70% 30-59 mm.

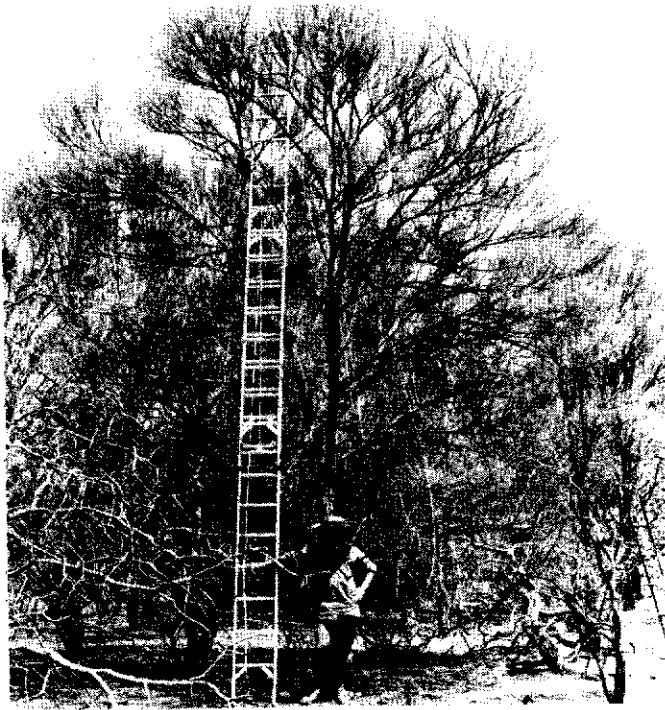
By comparison it is noted that Pressland's sample of 1200 random leaves from a number of trees were considerably larger in area than the 510 leaves taken from three trees at Mileura:

Area mm <sup>2</sup>	Pressland <sup>4</sup> %	Mileura %
< 195	19.9	94.1
196-293	47.5	5.3
294-391	24.1	0.6
392-489	6.3	-
490-587	1.9	-
> 587	0.3	-

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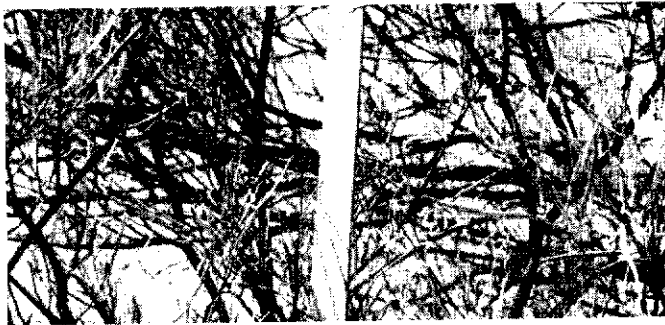
a



b



c



d



e



f

PLATE 1 Variation in phyllodes within individuals of *Acacia aneura*. Whole tree and close-up of foliage.

a, b Tree 1      c, d Tree 2      e, f Tree 3



# THE POSSIBLE PROTECTIVE FUNCTION OF EXTRAFLORAL NECTARIES OF *Acacia saligna*

J.D. Majer

## Introduction

It is well documented that extrafloral nectaries are common and taxonomically widespread in the plant kingdom.<sup>2</sup> These nectaries are frequently associated with attendance by insects, the ants in particular. There are two schools of thought regarding the roles of extrafloral nectaries. The 'exploitationist' school believes that the glands primarily serve some physiological function, such as removal of surplus carbohydrates, salts or water, and that ant attendance is incidental, conferring no benefit on the plant.<sup>9</sup> The 'protectionists' claim that these nectaries form the basis of a mutualistic relationship, with the ant obtaining nutrition or water from the glands while at the same time protecting the plant from herbivores.<sup>1</sup> The consideration of herbivores has generally been directed towards invertebrates although Brown<sup>4</sup> suggests that browsing mammals could also be repelled by aggressive ants. He draws support for this hypothesis from the fact that, atypically for this genus, extrafloral nectaries and other myrmecophytic structures are uncommon amongst Australian *Acacia* species where there is a paucity of browsing mammals. Elsewhere, the frequently ant attractive *Acacia* species are found along with potential mammalian herbivores.

A further suggestion for the role of extrafloral nectaries is made by Ford and Forde<sup>5</sup> for the Australian *Acacia pycnantha*. Here nectaries on the base of petioles, only active at the time of flowering, may attract bird pollinators.

Bentley<sup>2</sup> states that for the protectionists' hypothesis to hold, ants must be present on the plant and be aggressive towards, and potential predators of, potential herbivores. The plant must also be vulnerable, and subject, to herbivore attack. For efficient operation of the relationship, nectar flow should vary directly with herbivore activities.

This paper reports some preliminary observations and experiments designed to investigate the protectionists' hypothesis using *Acacia saligna* as an example.

The endemic Western Australian wattle, *A. saligna* (series *Uninerves-Racemosae*) is conspicuous for its actively secreting glands. It generally occurs west of a line connecting Murchison River, around Ajana, to Mount Ragged, 150 kilometres north-east of Esperance.<sup>7</sup> It grows as a dense shrub or tree, normally ranging from 2 to 6 metres in height. Solitary glands are situated on the upper margin of the linear or lanceolate phyllodes, at or near the distal end of the pulvillus. Glands are oblong to circular ranging from 1 to 2 centimetres in diameter. This species flowers between August and October and mature seeds are produced between November and January.<sup>7</sup>

## Methods

Investigations were performed at two sites: Yalgorup National Park south of Mandurah (115° 22'E 32° 40'S) where *A. saligna* occurs extensively along roadsides, and Manning, Perth (115° 52'E 32° 01'S) where scattered plants grow on vacant land.

Forty *A. saligna* plants were tagged and numbered along roadsides at Yalgorup in March 1977. One branch of each plant was selected for detailed observation and the distal 20 phyllodes were marked with a small dot of white acrylic paint. Plants were examined at approximately monthly intervals between March 1977 and February 1978. Notebook records of herbivore abundance and new phyllode damage were made. The ants on each labelled branch were collected for later identification and counting. The glands on the 20 marked phyllodes of each plant were inspected and scored for presence or absence of fluid. Each shoot was then assigned the following score: 0, no glands secreting; 1, 1 to 5 glands secreting; 2, more than 6 glands secreting. An index of gland activity was obtained by taking the mean score for all 40 trees.

In September 1977 20 plants in the Manning plot were selected for investigation. They had recently flowered but had not yet set seed. Plants were paired on the basis of size and proximity and designated experimental or control trees. The height of each plant was measured as was the crown diameter along the north-south axis. On 13 September 1977 a 0.87 square metre column of each plant canopy was sampled for invertebrates using a beating tray and by hand collecting. Sampling was always performed on the north side of the canopy. Invertebrates were transferred into vials of 70 percent alcohol and returned to the laboratory for counting and identification to species level in the case of ants and, where possible, family level for other taxa. On 16 September 1977 the ants of the experimental plants were excluded by banding the stem at the 15 centimetre level with Stickem<sup>®</sup> and by removing the vegetation which formed bridges between the plant and ground or adjacent vegetation. The control and experimental plants were resampled for invertebrates, by the original method, 4, 11, 25, 39 and 53 days after the ant exclusion operation. Canopy diameter and plant height were re-measured after the final sampling date.

## Results

### Gland activity

Glands of the Yalgorup plants were extremely active in autumn at the beginning of the observation period (Fig. 1). Activity decreased considerably during winter and rose in the following spring. Gland activity appeared to drop in the summer although this may well have been due to rapid evaporation of the fluid.

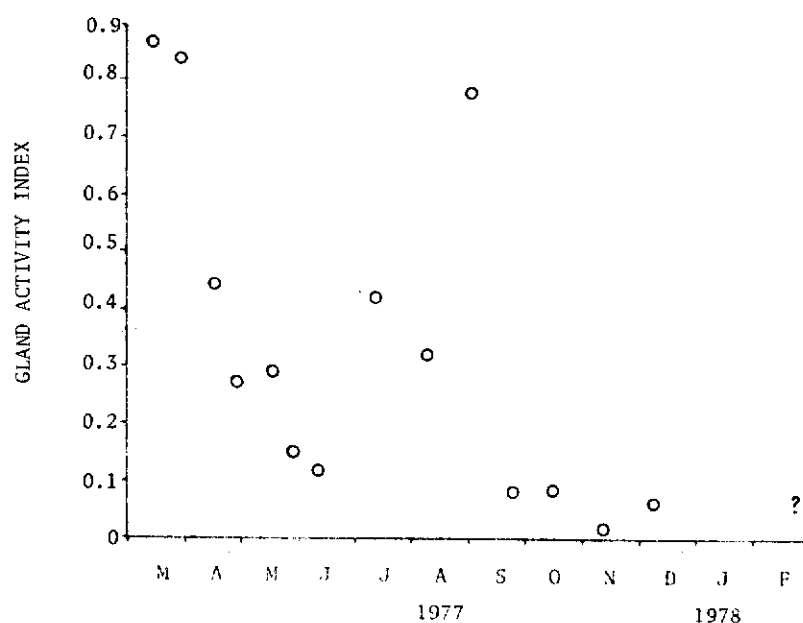


Fig. 1 Variation in gland activity index for 40 plants observed at Yalgorup between March 1977 and February 1978. The February 1978 reading is unavailable.

It should be noted that as the marked leaves matured, the more recently extended leaves had higher gland activity rates.

#### *Herbivores on A. saligna*

Table 1 shows the invertebrates obtained from the 10 Manning control plants over the 6 successive samplings. They are ranked on the basis of total sampled and of frequency out of 60 samples; ants are not included in this Table. Of the 112 non-ant species sampled, 69 were herbivores. Virtually all of the most abundant and frequently occurring species were herbivores, namely sap-sucking Hemiptera and leaf feeding Coleoptera. Most herbivores were species associated with leaves and stems. The predators largely comprised of Araneae, reduviid bugs and coccinellid beetles. A number of parasitic or predatory wasps and flies were also present.

The herbivore records gathered from Yalgorup indicate that the main period of herbivore activity in *A. saligna* is spring when growth is greatest, followed by a smaller peak in autumn. The Manning samples were taken during the peak herbivore period.

#### *Ants on A. saligna*

Table 2 shows the species of ants which have been noted on *A. saligna* at Yalgorup and at Manning. Specific names are given where possible, otherwise codes used in the W.A.I.T. collection are used. Members of all five common sub families forage on this species of plant.

The totals and frequencies of ants collected by beating the 10 Manning control trees over 6 successive samples are given in Table 3. Some

relevant points are apparent from the Table. Two species of ants, *Iridomyrmex* sp. J.D.M. 384 and *Diceratoctinea* sp. J.D.M. 211, were more numerous on *A. saligna* than was any other invertebrate and the former was also the most frequently sampled species of invertebrate (cf. Table 1). It is also noteworthy that the most numerous ants on this plant are all members of the Dolichoderinae and are probably all omnivorous. With the possible exception of *Camponotus* (*Colobopsis*) sp. J.D.M. 417, all of the ants listed in Table 3 nest in the ground or in dead wood lying on the ground.

Fig. 2 shows the mean number of ants per shoot for the repeated observations made at Yalgorup. The times of occurrence of each species and their mean number per shoot over the entire observation period are also given. The data reaffirms the prominence of *Iridomyrmex* spp. and *Diceratoctinea* sp. J.D.M. 211 as foragers on *A. saligna*. Three genera which were not found on the Manning plants are represented by the species *Crematogaster* sp. J.D.M. 33, *Monomorium* sp. J.D.M. 39 and *Prolasius* sp. J.D.M. 441. The first mentioned species nests in woody cavities of plants such as *A. saligna*<sup>8</sup> and is probably associated with some of the larger, more woody plants at Yalgorup.

The overall ant foraging pattern on Yalgorup plants was high in summer, decreasing in autumn to a winter trough followed by a subsequent increase in the following spring. It is tempting to relate this trend to gland activity since, if the probably unreliable late spring and summer gland activity index values are excluded, ant activity closely followed gland activity (Figs. 1 and 2). The relationship of glands and ants may not be causal however since ant forag-

TABLE 1 Species sampled by beating foliage of 10 Manning control trees over 6 successive samples showing their totals, frequency out of 60 samples, and various aspects of their biology.

Code	Class	Order	Family or Superfamily	Winged	Adult	Immature	Feeding habit*	Total	Frequency
A14	Insecta	Hemiptera	Coreidae	+	+		H	50	24
A45	"	Lepidoptera	indet.	-		+	H	37	18
A6	"	Coleoptera	Curculionidae	+	+		H	34	18
A46	Arachnida	Araneae	Salticidae	-	+		P	32	17
A44	Insecta	Coleoptera	indet.	-		+	H	29	14
B5	"	Hemiptera	Psyllidae	-		+	H	25	16
A4	"	Lepidoptera	indet.	-		+	H	24	15
A12	"	Hemiptera	Psyllidae	-		+	H	23	15
A19	"	Hemiptera	Psyllidae	+	+		H	20	16
A48	"	Coleoptera	Chrysomelidae	+	+		H	20	13
A23	"	Diptera	Sciaridae	+	+		H	18	8
A43	"	Hemiptera	Cicadellidae	+	+		H	17	16
B43	"	Lepidoptera	indet.	-		+	H	17	10
C1	"	Coleoptera	Belidae	+	+		H	16	9
B33	"	Coleoptera	Curculionidae	+	+		H	15	8
B22	"	Hymenoptera	Platygasteridae	+	+		P	15	6
A22	"	Hemiptera	Derbidae	-		+	H	15	6
A42	"	Hemiptera	Coreidae	-		+	H	13	8
A27	Arachnida	Araneae	Clubionidae	-	+		P	12	11
A24	Insecta	Coleoptera	Coccinellidae	+	+		P	12	9
A15	Arachnida	Araneae	Clubionidae	-	+		P	9	8
A26	Insecta	Coleoptera	Chrysomelidae	+	+		H	8	7
C42	"	Hemiptera	Coreidae	-		+	H	8	6
A11	"	Coleoptera	Cerambycidae	+	+		H	8	6
B40	"	Coleoptera	indet.	-		+	H	8	4
A8	"	Hemiptera	Membracidae	-		+	H	7	7
B8	"	Lepidoptera	indet.	-		+	H	7	6
B19	"	Coleoptera	Bruchidae	+	+		H	7	4
B32	"	Hemiptera	Nogonidae	+	+		H	5	5
B10	"	Orthoptera	Gryllacrididae	+	+		H	5	5
A13	"	Lepidoptera	indet.	-		+	H	5	5
B30	"	Lepidoptera	indet.	-		+	H	5	4
A39	Arachnida	Araneae	indet.	-	+		P	4	4
B6	Insecta	Lepidoptera	Tineoidea	+	+		H	4	4
B45	"	Coleoptera	Coccinellidae	+	+		P	4	3
C5	Arachnida	Acarina	indet.	-	+		P	4	1
A10	"	Araneae	Araneidae	-	+		P	3	3
A33	Insecta	Blattodea	Blattidae	-		+	D	3	3
C39	"	Neuroptera	indet.	-		+	P	3	3
B34	"	Coleoptera	Cleridae	+	+		P	3	3
B29	"	Coleoptera	indet.	-		+	H	3	3
B13	"	Lepidoptera	indet.	-		+	H	3	3
B47	Arachnida	Araneae	Clubionidae	-	+		P	3	2
B31	Insecta	Coleoptera	Sarabaeidae	+	+		H	3	2

Code	Class	Order	Family or Superfamily	Winged	Adult	Immature	Feeding habit*	Total	Frequency
C6	Insecta	Lepidoptera	indet.	-		+	H	3	2
A31	"	Orthoptera	Acrididae	-		+	H	2	2
A37	"	Orthoptera	Acrididae	-		+	H	2	2
A18	"	Mantodea	Mantidae	-		+	P	2	2
C23	"	Hemiptera	Cicadellidae	-		+	H	2	2
C33	"	Hemiptera	Piesmididae	+	+		H	2	2
A21	"	Neuroptera	indet.	-		+	P	2	2
B9	"	Coleoptera	Carabidae	+	+		H	2	2
B24	"	Coleoptera	Coccinellidae	+	+		H	2	2
B44	"	Coleoptera	Chrysomelidae	+	+		H	2	2
C11	"	Coleoptera	Scarabaeidae	+	+		H	2	2
C19	"	Coleoptera	Chrysomelidae	+	+		H	2	2
C48	"	Coleoptera	Scarabaeidae	+	+		H	2	2
A30	"	Diptera	Ephydriidae	+	+		H	2	2
A7	"	Coleoptera	indet.	-		+	H	2	1
A9	Arachnida	Araneae	Oxyopidae	-	+		P	1	1
A40	"	Araneae	Clubionidae	-	+		P	1	1
A50	"	Araneae	Salticidae	-	+		P	1	1
B12	"	Araneae	Theridiidae	-	+		P	1	1
B18	"	Araneae	Salticidae	-	+		P	1	1
B36	"	Araneae	Thomisidae	-	+		P	1	1
C3	"	Araneae	Araneidae	-	+		P	1	1
C10	"	Araneae	Araneidae?	-	+		P	1	1
C47	"	Araneae	Thomisidae	-	+		P	1	1
D13	"	Araneae	Salticidae	-	+		P	1	1
B7	Collembola	Collembola	Entomobryidae	-	+		D	1	1
C16	"	Collembola	Entomobryidae	-	+		D	1	1
B41	"	Collembola	Sminthuridae	-	+		H	1	1
A35	Insecta	Blattodea	Blattidae	-		+	D	1	1
A36	"	Blattodea	Blattidae	-		+	D	1	1
D14	"	Blattodea	Blattidae	-		+	D	1	1
B35	"	Orthoptera	Acrididae	+	+		H	1	1
C12	"	Psocoptera	Peripsocidae	+	+		H	1	1
C49	"	Psocoptera	indet.	-		+	H	1	1
B3	"	Hemiptera	Pentatomidae	+	+		H	1	1
B14	"	Hemiptera	Margarodidae	-		+	H	1	1
B26	"	Hemiptera	Psyllidae	+	+		H	1	1
C20	"	Hemiptera	Aphididae	+	+		H	1	1
C30	"	Hemiptera	Lygaeidae	+	+		H	1	1
C34	"	Hemiptera	Reduviidae	+	+		P	1	1
C35	"	Hemiptera	Membracidae	+	+		H	1	1
C50	"	Hemiptera	Delphacidae	+	+		H	1	1
B42	"	Neuroptera	Hemerobiidae	-		+	P	1	1
A1	"	Coleoptera	Chrysomelidae	+	+		H	1	1
A5	"	Coleoptera	indet.	-		+	H	1	1
A28	"	Coleoptera	indet.	-		+	H	1	1

Code	Class	Order	Family or Superfamily	Winged	Adult	Imma- ture	Feeding habit*	Total	Frequency
B50	Insecta	Coleoptera	Carabidae	+	+		P	1	1
C17	"	Coleoptera	Scarabaeidae	+	+		H	1	1
C36	"	Coleoptera	Chrysomelidae	+	+		H	1	1
B1	"	Diptera	Culicidae	+	+		P	1	1
B4	"	Diptera	Drosophilidae	+	+		H	1	1
B49	"	Diptera	Drosophilidae	+	+		H	1	1
B38	"	Diptera	Chironomidae	+	+		P	1	1
B13	"	Diptera	Sciomyzidae	+	+		P	1	1
C18	"	Diptera	Cecidomyiidae	+	+		H or D	1	1
C21	"	Diptera	Chironomidae	+	+		P	1	1
C45	"	Diptera	Drosophilidae	+	+		H	1	1
A3	"	Lepidoptera	indet.	-		+	H	1	1
A16	"	Lepidoptera	indet.	-		+	H	1	1
A32	"	Lepidoptera	indet.	-		+	H	1	1
B37	"	Lepidoptera	indet.	-		+	H	1	1
B48	"	Lepidoptera	indet.	-		+	H	1	1
D7	"	Lepidoptera	indet.	-		+	H	1	1
A25	"	Hymenoptera	Scelionidae	+	+		P	1	1
C43	"	Hymenoptera	Scelionidae	+	+		P	1	1
B46	"	Hymenoptera	Encyrtidae	+	+		P	1	1
C31	"	Hymenoptera	Cynipidae	+	+		P	1	1
C32	"	Hymenoptera	Scelionidae	+	+		P	1	1

\* H, herbivores; P, predators or parasites; D, decomposition associated species.

TABLE 2 Checklist of ant species found on *A. saligna* plants at Yalgorup National Park or at the Manning plot.

Myrmeciinae	Melophorini
Myrmeciini	<i>Melophorus</i> sp. J.D.M. 52
<i>Myrmecia</i> sp. J.D.M. 1	<i>Prolasius</i> sp. J.D.M. 441
<i>Myrmecia chasei</i>	
Ponerinae	Dolichoderinae
Ectatommini	Dolichoderini
<i>Rhytidoponera violacea</i>	<i>Diceratoclinea</i> sp. J.D.M. 211
Myrmicinae	Tapinomini
Crematogastrini	<i>Iridomyrmex glaber</i>
<i>Crematogaster</i> sp. J.D.M. 33	<i>I.</i> sp. J.D.M. 9
Metaponini	<i>I.</i> sp. J.D.M. 22
<i>Monomorium</i> sp. J.D.M. 39	<i>I.</i> sp. J.D.M. 200
	<i>I.</i> sp. J.D.M. 217
	<i>I.</i> sp. J.D.M. 354
	<i>I.</i> sp. J.D.M. 384
Formicinae	
Camponotini	
<i>Camponotus</i> sp. J.D.M. 27	
<i>C.</i> sp. J.D.M. 199	
<i>C. (Colobopsis)</i> sp. J.D.M. 417	

TABLE 3 Totals and frequencies of ants collected by treating the 10 Manning control trees over 6 successive samples.

	Total	Frequency
<i>Iridomyrmex</i> sp. J.D.M. 384	279	32
<i>Diceratoctinea</i> sp. J.D.M. 211	89	11
<i>Iridomyrmex</i> sp. J.D.M. 22	39	17
<i>Iridomyrmex</i> sp. J.D.M. 9	32	6
<i>Iridomyrmex glaber</i>	6	4
<i>Myrmecia</i> sp. J.D.M. 1	4	3
<i>Myrmecia chasei</i>	3	3
<i>Camponotus (Colobopsis)</i> sp. J.D.M. 417	2	2
<i>Rhytidoponera inornata</i>	2	1

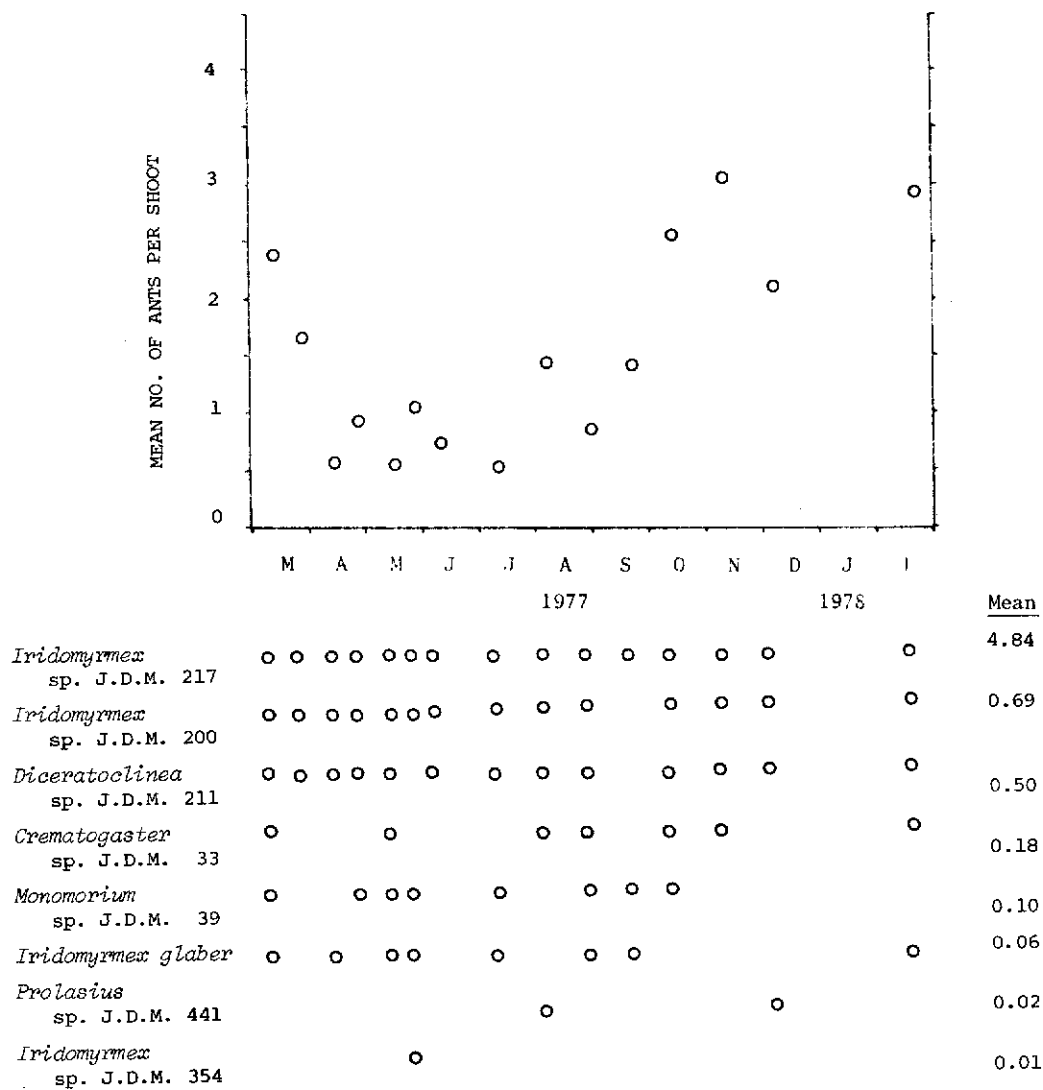


Fig. 2 Mean number of ants per labelled shoot for 40 plants observed at Yalgorup between March 1977 and February 1978. The times of occurrence of individual species and their mean number per shoot over the total observation period are also shown.



ing on plants closely followed the seasonal trend of ground foraging observed at the nearby localities of Perth (Reabold Hill) and Dwellin-gup (Majer, unpublished data). The relationship between ant attendance levels and gland activity rates merits more detailed investigation.

#### *Ant exclusion experiment*

The banding of plants is likely to interfere with the traffic of wingless invertebrates onto the plant. Analysis of results is therefore basically confined to winged species in order to avoid this confounding factor. Invertebrate data are bulked since ants are not generally likely to distinguish between, say, herbivores and predators when disturbing or attacking animals.

Fig. 3 shows the mean and standard deviations of total number of winged species and winged individuals on the control and experimental trees for the one pre- and 5 post-ant exclusion samples. The high values for the pre-exclusion samples indicate that beating of plants has subsequently depleted the fauna. This is unlikely to bias the data since control and experimental trees were equally affected.

Initially, control group trees supported a greater number of individuals and species of invertebrates than did the experimental trees (Fig. 3). The difference was less in the first post-exclusion sample and reversed in subsequent samples. The only exception was the penultimate sample in which species richness was higher on control plants. The number of species

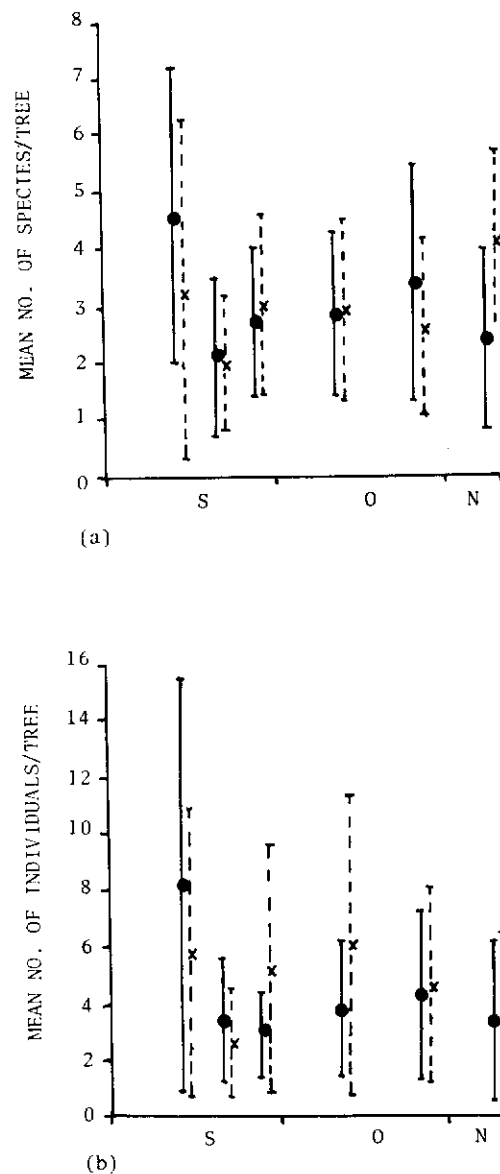


Fig. 3 Mean number of winged insect species (a) and individuals (b) per tree for the Manning control (●) and experimental (x) plants for the pre-ant exclusion and 5 post-ant exclusion samples. The bars represent standard deviations.

and individuals on control and experimental plants were compared for each sample date using Wilcoxon's Signed Ranks test. In view of the high variance exhibited by the data, only species richness values for the second and fifth post-exclusion sample were significantly different ( $p < 0.1$ ).

It was only possible to compare a few individual species on the two plants groups in view of their low numbers and frequencies. The winged Cicadellidae (A43), Psyllidae (A19) and Cerambycidae (A11) and the larvae of one Psyllidae (A12), and two Lepidoptera (A4 & A13), were all significantly more numerous on the ant excluded trees when data for the 5 post-exclusion samples were bulked ( $p < 0.1$ , using Wilcoxon's Signed Ranks test).

The mean and standard deviation of plant height and canopy area before and at the end of the exclusion experiment are shown for both groups of plants in Table 4. There was a considerable variance in the data due in part to the insensitivity of the method of measurement so no differences were significant. The data do suggest, however, that plants on which ants were excluded grew less in height during the study period and actually suffered some contraction of canopy diameter; presumably due to leaf damage. The changes in height and diameter of the two plant groups are consistent with the data on invertebrates, namely the more herbivores on the plant, the less growth there is.

#### Discussion

*A. saligna* presents a situation where the protectionists' hypothesis might apply. It supports

a diverse and abundant range of herbivores which cause damage to the plant, aggressive ants are present and the spatial and temporal patterns of gland activity are appropriate for maximising any protective effect of ants. These points are now discussed in greater detail.

The range of herbivores on *A. saligna* is more diverse and abundant than that found on other *Acacia* species observed by the author in the south-west of Western Australia. While complying with the conditions of the hypothesis, this suggests that ants are poor or ineffective agents for reducing herbivory. It should be noted, however, that *A. saligna* is often found in highly disturbed areas, as were the two study sites, so herbivore levels may here be abnormally high due to clearing or some other environmental disturbance. Even if herbivores were this abundant on *A. saligna* in its natural environment, there would still be advantage in the plant possessing devices which allow ants to reduce herbivore levels by even a minor extent.

This species is certainly attended by a sufficient density of ants to have an impact on the herbivore fauna. The range of ant species on *A. saligna* (8 and 9 species at Yalgorup and Manning respectively) suggests that it is only attractive to certain species since both areas would be inhabited by at least 50 ant species (Majer, unpublished data). Some of the species present on the plant are aggressive (e.g. *Myrmecia* spp. and *Rhytidoponera inornata*) and others are omnivorous (e.g. *Iridomyrmex* spp.) so the plant supports species which are capable of reducing herbivore levels.

Certain *Iridomyrmex* species have characteristic

TABLE 4 Mean and standard deviation of plant heights and crown canopy areas for the Manning control and experimental plants, measured before and 54 days after ant exclusion.

#### (a) Height of plant (m)

	12 Sep 1977	9 Nov 1977	Percentage change
Control trees	1.76 $\pm$ 0.45	1.87 $\pm$ 0.42	+6.5%
Ant excluded trees	1.76 $\pm$ 0.39	1.78 $\pm$ 0.45	+1.3%

#### (b) Area of crown canopy (m<sup>2</sup>)

	12 Sep 1977	9 Nov 1977	Percentage change
Control trees	3.18 $\pm$ 2.11	3.64 $\pm$ 2.2	+14.5%
Ant excluded trees	2.61 $\pm$ 1.59	2.53 $\pm$ 1.2	- 3.06%

foraging patterns on *A. saligna*. Workers systematically move between adjacent phyllodes, visiting glands near the base and then detouring to the tip of each phyllode before passing to the next gland. Such a strategy would be most efficient for detecting stem and phyllode living herbivores.

The temporal and spatial pattern of gland activity is also appropriate for maximising efficiency of a protectionist relationship. The high gland activity on new leaves, which are particularly susceptible to herbivores, might attract more ants or encourage them to spend a greater amount of time where they are most needed. This pattern of gland activity has also been noted for other species of plant such as cotton (literature reviewed in 2).

Glands appear to be most active in spring and autumn when the threat of herbivory is greatest. This might also have the effect of encouraging ants at a time most important to the plant. Whether this is the case or not has not been resolved, as ants are also abundant on the plants in summer (although glands may also be very active then). Also, ant foraging on plants closely reflects the temporal ground foraging pattern so this time relationship may be fortuitous.

The ant exclusion experiment was subject to a number of limitations. Firstly the banding operation influenced the presence of other groups such as lepidoptera larvae which took refuge in the litter layer during the daytime. Banding therefore directly altered the composition of the fauna on *A. saligna* with consequent uncertainty in effects on plant damage, growth and invertebrate interactions. Secondly the variation in invertebrates present on individual plants was high thus making statistical detection of trends difficult. Thirdly, most species were infrequent, or present in low numbers, on plants so comparison at the individual species level of control and experimental trees was only possible for a limited number of taxa.

The data nevertheless do suggest acceptance of the protectionists' hypothesis since exclusion leads to partly statistically demonstrated increases in species richness and abundance of bulked winged invertebrates and in the numbers of 6 individual herbivorous insects. These encouraging results suggest that the experiment merits repeating using a greater number of study plants and more sensitive methods of measuring plant growth parameters. If further findings confirm these early results then *A. saligna* would be added to the two existing cases, *Bixa orellana*<sup>5</sup> and *Helianthella*<sup>6</sup>, where ants attracted to extrafloral nectaries have been demonstrated to have a protective effect on the plant.

#### Acknowledgements

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\* Original not seen. Quoted in Bentley, 1977a.



## A GENERAL ACCOUNT OF THE TRIFID SITE, MILEURA.

J.E.D. Fox

Introduction

'Trifid' is a botanical adjective meaning divided into 3 lobes. In this account a landscape feature at Mileura Station (at Lat. 26° 15'S, Long. 117° 11'E) is described which has three distinctive arms (Fig. 1), two tributary creeks and an exit creek. Elsewhere a description of phyllode characteristics is given for two trees of *Acacia aneura* F. Muell ex Benth. whose locations within the Trifid are shown on Fig. 1.

My attention was drawn to the site in mid 1976 by Stephen Davies who showed me sites examined earlier by John Mott. Despite the lack of mulga regeneration within the locality<sup>7</sup> several features suggested that it would be of interest in a study of the mulga in a long term sense. The most important of these was the work undertaken by Mott 9,10,11,12,13,14,15 at Mileura on three annuals, to be referred to below. The second feature was the stark contrast between the central parts of the area, the 'arms' of the Trifid, and the surrounding landscape, as seen from the top of Mileura Hill just to the east. The third feature of interest was the occurrence of *Grevillea striata* R.Br., 'beefwood' as a large tree within the area in contrast to its virtual absence over great areas of land in the overall vicinity. A number of larger *G.striata* tree positions are illustrated in Fig. 1. In sum a fascination was engendered and the area was selected as a study site within the overall context of the aims of the Mulga Research Centre.\*

A set of five transects was set out in December 1976. These straddle the area with three crossing the Trifid arms and two running along the tributary arms. All perennial shrubs were measured for height and crown diameter along the transects and a number of soil samples were taken for examination.<sup>8</sup>

Eleven perennial species were encountered along the transects. These were classified as:

<i>Acacia aneura</i>	
<i>Acacia kempeana</i>	F. Muell.
<i>Acacia tetragonophylla</i>	F. Muell.
<i>Cassia helmsii</i>	Symon
<i>Eremophila fraseri</i>	F. Muell.
<i>Eremophila longifolia</i>	F. Muell.
<i>Eremophila spathulata</i>	W.V. Fitzg.
<i>Grevillea striata</i>	
<i>Pittosporum phillyraeoides</i>	DC.
<i>Santalum lanceolatum</i>	R.Br.
<i>Scaevola spinescens</i>	R.Br.

While these form a small proportion of the spectrum of shrub and tree species recorded for Mileura<sup>3</sup>, nevertheless the more common Trifid species (Table 1) are representative of much of the station. *Pittosporum phillyraeoides* is 'off-site' being a typical tree of creek edges and of salt-bush flat margins. *Acacia kempeana* does not flourish at Mileura and has not been observed to produce much seed.<sup>6</sup> Only two specimens of *Scaevola spinescens* were recorded. This species appears to fruit only after prolonged periods of favourable summer moisture conditions and is correlated with high summer rainfall.<sup>6</sup> It is rather localised at Mileura.

Mott has described the vegetation of the central creek, transect 4 (his rocky creek - no 'rocks' seen so the present study refers to 'creek') and the adjacent plain (his rocky plain, equal to 'stony plain' in this account).<sup>9</sup> The first he referred to as a low woodland and as Community 15 *Acacia aneura*-*A. craspedocarpa* of Speck's system (A.R. 1, M.R.C. 1977, p25). However as no *A. craspedocarpa* is present the nearest community in that system is No. 13 *Grevillea striata*-*Acacia aneura*-*A. tetragonophylla*. The plain was described as a tall open shrubland, as Community 21 *Acacia aneura*; as will be seen below it may more appropriately be described as Community 23 *Acacia aneura*-*Eremophila spathulata*. In the list of species of shrubs found in the area, Mott (page 284)\* includes *Eremophila hastiana* R.Br. and *E. leucophylla* Benth. which collectively\* presumably represent that classified as *E. spathulata* in the present study. Several collections of the plant referred to herein as *E. spathulata* have been given the name *E. macmillaniana* C.A. Gardn. by the W.A. State Herbarium. These two differ little. The former has a hairy ovary the latter not. As most specimens taken have been sterile it may well be that the 'species' referred to in this account is in fact a complex of several species. For the present purposes however it is assumed that the smaller *Eremophila* bushes with rounded, spoon shaped leaves are all referable to *E. spathulata*. *E. hastiana* is not listed by Davies<sup>5</sup> and the description of *E. leucophylla* given by Wilcox and Morrissey<sup>16</sup> does not fit the plants of the Trifid area.

A second common *Eremophila* in the general area is *E. longifolia* also described by Mott. Several collections representing the plant referred to by this name in the present account have been named as *E. freelingii* F. Muell. by the State Herbarium and the same strictures must be applied as to *E. spathulata*. Certainly these plants are not like the *E. longifolia* of Wilcox and Morrissey.<sup>16</sup>

Mott noted two *Cassia* species in the area of the Trifid study site. These were *Cassia artemisioides* Gaud. and *C. desolata* F. Muell. The former I have not seen in the area, the latter is very similar to *Cassia helmsii* the name used in this account, though it is not as common as *C. helmsii*. At Mileura it has been reported in the general

\* See p1 Annual Report 1, Mulga Research Centre 1977. (Abbreviated subsequently to A.R. 1, M.R.C. 1977).

+ Page numbers refer to reference number 9.  
\* These species may be conspecific. See 'How to Know Western Australian Wildflowers' Part IV by B.J. Grieve and W.E. Blackall, 1975, p631.

TRIFID CREEK  
SITE S.W. of  
MILEURA HILL

Fig. 1 Transects and Topography

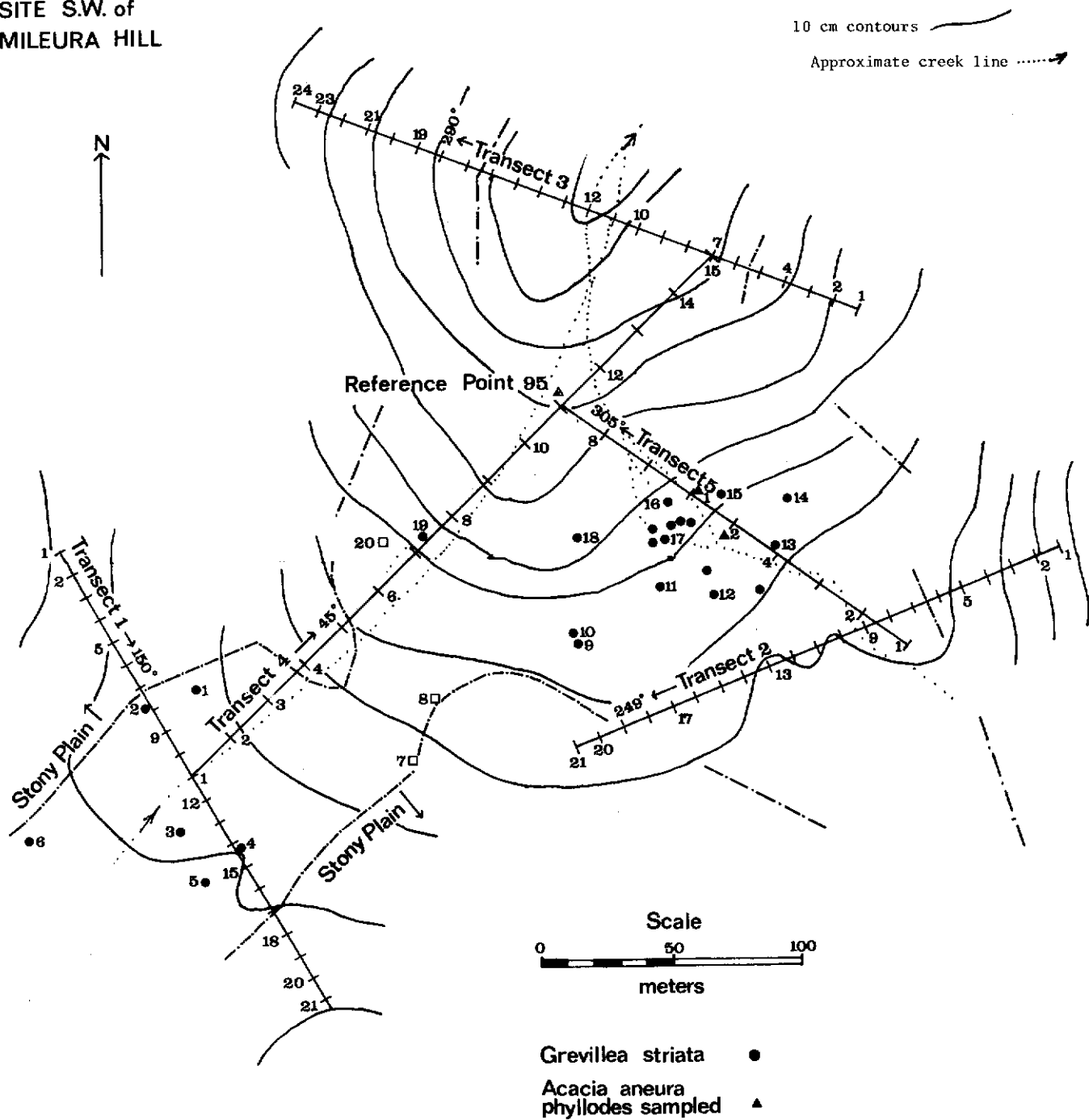


TABLE 1 Stand table Transects 1-5 combined, Trifid Site, Mileura.  
Numbers of plants in height classes by species.

	Height Classes (m)									Total
	.1-.49	.5-.99	1-1.99	2-2.99	3-3.99	4-4.99	5-5.99	6-6.99	7+	
<i>Acacia aneura</i>	1	8	6	11	16	19	29	18	21	129
<i>Acacia kempeana</i>					5	1				7
<i>Acacia tetragonophylla</i>		5	9	28	26	16	6	1		91
<i>Cassia helmsii</i>	2	10	6	4						22
<i>Eremophila fraseri</i>	2	2	11	11	11	3	2			42
<i>Eremophila longifolia</i>	1	15	12	3						31
<i>Eremophila spathulata</i>	4	26	47	32	5					114
<i>Grevillea striata</i>							2	2	9	13
<i>Pittosporum phillyraeoides</i>						1				1
<i>Santalum lanceolatum</i>				5	4					9
<i>Scaevola spinescens</i>				1	1					2
TOTAL	10	66	92	95	68	40	39	21	30	461

TABLE 2 Density and frequency of species, Trifid Site, Mileura.  
Values based on presence in 20 x 20 m quadrats (0.04 ha).

Species	Transect	1	2	3	4	5	$\Sigma$	Density	Frequency	Ratio
<i>Acacia aneura</i>	Plants	17	11	33	39	29	129	2.35	71	3.30
	Quadrats	6	4	9	13	7	39			
<i>A. kempeana</i>	Plants	4		1	2		7	.13	11	1.15
	Quadrats	3		1	2		6			
<i>A. tetragonophylla</i>	Plants	11	12	21	36	11	91	1.66	73	2.27
	Quadrats	6	6	8	13	7	40			
<i>Cassia helmsii</i>	Plants	3	1	10	6	2	22	.40	29	1.38
	Quadrats	3	1	5	5	2	16			
<i>Eremophila fraseri</i>	Plants	2	10	5	15	10	42	.76	34.5	2.21
	Quadrats	2	2	3	8	4	19			
<i>E. longifolia</i>	Plants	5	6	1	15	4	31	.56	29	1.94
	Quadrats	2	3	1	7	3	16			
<i>E. spathulata</i>	Plants	43	23	13	26	9	114	2.07	56	3.70
	Quadrats	11	8	6	10	6	31			
<i>Grevillea striata</i>	Plants	2	3		3	5	13	.24	23.6	1.00
	Quadrats	2	3		3	5	13			
<i>Pittosporum phillyraeoides</i>	Plants		1				1	.02	1.8	1.00
	Quadrats		1				1			
<i>Santalum lanceolatum</i>	Plants	2	1		5	1	9	.16	12.7	1.29
	Quadrats	2	1		3	1	7			
<i>Scaevola spinescens</i>	Plants			1	1		2	.04	3.6	1.00
	Quadrats			1	1		2			
Number of quadrats in transects		11	9	12	14	9	55			

Density - mean number of plants per 0.04 ha

Frequency - percentage of 0.04 ha quadrats occupied

Ratio - density/frequency  $\times 10^2$ ; and equivalent to density of occupied quadrats

area.<sup>6</sup> Where *Cassia* is referred to herein it is possible that *C. desolata* and *C. helmsii* are lumped together - the two are not readily distinguishable in the field.

All the other species noted by Mott (page 284) are in agreement though the desert poplar *Codonocarpus cottonifolius* (Desf.) F. Muell. noted by Mott as rare on the stony plain seems an unlikely candidate for that general site.

Two of the three annuals studied by Mott occur in the Trifid, viz. the summer germinating grass *Aristida contorta* F. Muell. and the winter germinating daisy *Helipterum craspedioides* W.V. Fitzg.<sup>11</sup> These desert annuals are not ephemerals in terms of moisture availability within a year. They exhibit seasonal germination which is temperature dependant. However failure of rain in a given season may mean that few plants germinate that year, in this sense they are ephemeral.<sup>14</sup> Annuals have been scarce over the period covered by this report.

### Environmental Variables

#### Topography

The general area falls on the Koonmarra land system (A.R. 1, M.R.C. 1977 ppl7, 22). The total area encompassed by the transects is about 16 ha and the combined transect length is 1070 m. The area sampled and represented in tables herein totals 2.32 ha, comprised of 58 quadrats of 20 x 20 m (Table 2).<sup>\*</sup> The central creek area varies from about 100 m wide where transects 1 and 2 cross the arms of the Trifid to a broader zone at the confluence and narrower strips further to the south west and south east than transects 1 and 2 and again north east of the confluence.

Fig. 1 shows 10 cm contour intervals across the study area based on levels taken along the transects (comparative levels for each transect are shown in Fig. 2). Slopes are 1 in 300 along transect 4 and 1 in 350 along transect 5. On the stony plain surrounding the drainage channels slopes tend to be rather gradual on the outer flanks, e.g. 1 in 500 on the north and south segments of transect 1. The western side of transect 3 has a slope of 1 in 220 while the eastern side has a slope of 1 in 250. The most severe slope in the study area is at the eastern side of transect 2. This is a very stony area with little vegetation, being the extremity of a large plain extending west from Mileura Hill. At the hill itself the slope is very steep, the land falls gradually across the plain (traversed by the road from Mileura to Beringarra) and then there is a sharper slope of 1 in 170 where transect 2 cuts the edge of the plain. The drainage channels are ill defined on the ground though the presence of shallow water scoured areas reveal the lower lying surfaces. Point 10 of transect 3 lies in one such scoured area which retains water for some time after rain. At this point there is only 5 cm of soil over hardpan (Fig. 3). These scoured areas are interspersed with mounds of a more sandy nature (see below). Erosion does not appear to be proceeding at a rate which could cause changes over short term periods.

<sup>\*</sup> 3 quadrats unoccupied 2 in T2, 1 in T3, all at eastern ends on barren stony plain.

Above ground termite workings are most evident in the more wooded parts of transect 5. Subterranean workings are much more common and it is difficult to take a soil sample which shows no old termite workings in it.

Mott<sup>11</sup> has emphasised the high proportion of annual productivity in the run-on areas. Seed from most plants in the study area remains on the soil surface after shedding, though in the summer of 1970/71 Mott observed germination of *Aristida contorta* from 2 cm depth. This was related to loss of light sensitivity over the three years that it had been present. On the whole very little of the annual seed is carried over from a season conducive to good germination<sup>10,11</sup> though this may not be true of hard-seeded *Acacia* species. The question of seed pools needs examination as also the role, if any, of ants in burying seed.

#### Climatic Influences

Davies has discussed climatic variables of the general area of Mileura<sup>2,5</sup> and in this account features of interest related to the potential reproductive capacity of the plants found at the Trifid site are drawn from his work. Firstly there tends to be repetition, in different parts of the landscape, of shrub species. That is a species occurring on the flanks of a minor creek is also likely to occur in the same topographical position in relation to a larger creek. This pattern for 10 species has been illustrated.<sup>4</sup> Secondly although some flowering and fruiting of many shrubs may be noted through the year<sup>4</sup> there is strong seasonality and definite correlations of successful seed maturation with the quantity of rainfall in particular seasons.<sup>6</sup> Thirdly creeks and drainage channels concentrate and store water to some extent. Plants in or near the channels have access to much more, available, water than annual rainfall averages would suggest. In addition there are temperature differences on the broad scale, between higher and lower positions in the landscape. The higher ground provides less extreme habitats than lower lying creeks.<sup>4</sup>

The present account seeks to establish a detailed statement of what this particular study area has in the way of perennials and how these are positioned within the landscape. In addition to those described in detail the presence of *A. victoriae* Benth. is mentioned here. This occurs as an individual tree at the edge of the stony plain south east of point 4, transect 4. Another *Acacia*, recorded as equivalent to sp. nov. HA 251274<sup>5</sup> (possibly *A. quadrangulata* F. Muell., recorded by Mott (p284) for this site) is found to the north of transect 4 at point 6.

The dry period<sup>7</sup> preceeding the establishment of transects (62 mm of rain in the 13 previous months) may account for the absence of small mulga regeneration (indeed no recent regeneration of any of the perennials has been observed in the general area 1976-1978) and certainly for the lack of any seed pods on the mulga trees.<sup>2</sup> Davies has examined a total of 21 shrubs for correlation between environmental factors and phenology<sup>6</sup> (his Table 4) finding relations between successful fruit production and rainfall for the majority. This examination included



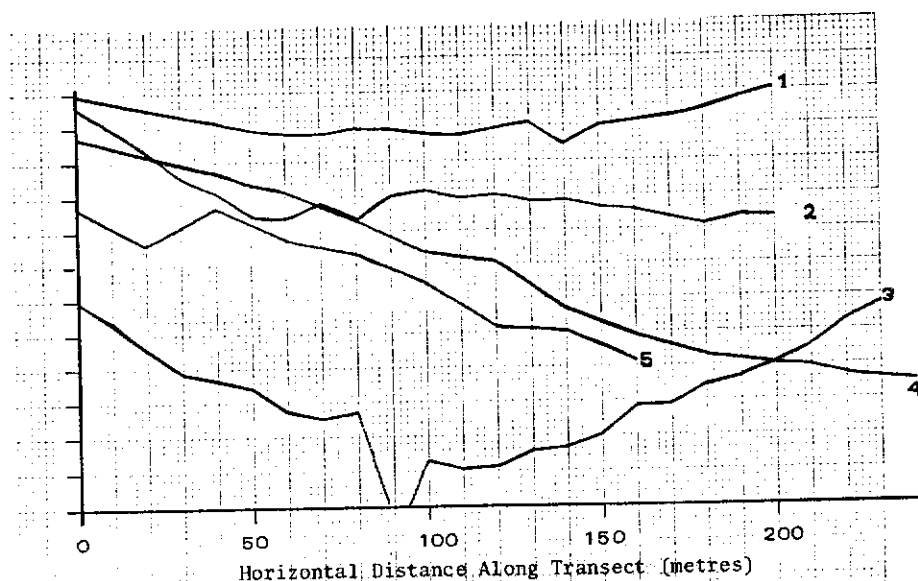


Fig. 2 Comparative levels for all five transects. Vertical intervals equivalent to 10 cm height differences i.e. start of Transect 1 is 1.2 m above lowest point of T3.

individuals of the species found in the Trifid transects, with the exceptions of *Eremophila longifolia*, *E. spathulata*, *Grevillea striata* and *Pittosporum phillyraeoides*.

The third feature raised by Davies' work is perhaps the most relevant to the present account. Clearly perennial plants persist at a site because they are able to tolerate the local environment at that site. What may be possible is to attempt to formulate a relationship of 'capability' in terms of maximum stature. The *Grevillea* trees of same size may represent an opportunity to develop this theme in more detail later on. It is probable that more mulga seed is matured in the central Trifid area than on the flanks and while pods may be blown out of the trees by wind<sup>2</sup>, water movement acts to concentrate propagules within the lower lying areas. This is less true of lighter seeds and re-deposition is of importance in maintaining populations of annuals.<sup>13</sup> The data of Davies suggest that reproductive efficiency in *Acacia tetragonophylla* may be related to both temperature and rainfall. Frost damage has been noted to foliage in a low valley site where seed production was greatest in years of high winter rainfall whereas elsewhere fruit production seems to be greatest in years of heavy summer rainfall.<sup>6</sup>

Summer thunderstorms of <10 mm wet the soil surface for only 10-15 hours. In the winter at least 30 mm of rain is required to maintain the surface soil moisture on flatter areas for more than five days.<sup>10</sup> Mott has shown that the grass *Aristida* requires at least 24 hours to reach 50 percent germination and the daisies he examined some 3-5 days so that it is probable that little germination occurs unless heavy rain falls. Propagules of the annuals, at least, can imbibe moisture rapidly but will also dehydrate quickly; light falls of rain may posi-

tion seed to better advantage for later heavy falls.<sup>12</sup> Soil surface temperatures (taken at 0.5 cm below surface) show strong diurnal ranges.<sup>10</sup> After rainfall maximum surface temperatures fall dramatically, as much as 32°C in summer and 20°C in winter<sup>11</sup> from levels of 80°C and 27°C (mean monthly values).<sup>10</sup>

Over the period 1969-1971 *Helipterum craspedioides* germinated between early May and early June with 3-4 weeks to flower initiation and 6½ to a little over 8 weeks to anthesis, with mean times of 27 and 55 days respectively. *Aristida contorta* germinated in early February of 1971 and flowered 42 days later.<sup>14</sup>

The presence of established shrubs ameliorates temperature conditions at the micro-topographic level. Mott noted soil surface temperatures in winter differed under bushes compared with adjacent open sites viz. mean maximum 6°C lower; mean minimum 3-5°C higher (page 117). This reduction was similar after rain with sites under shrubs showing diurnal ranges of 12-18°C compared with 12-23°C in the open.

#### Soils

The soils of the area are red earths, generally sandy loams or sandy clay loams overlying an impervious siliceous hardpan.<sup>13</sup> On the stony plain white quartz rocks lie on the surface, these are sharply angular but not usually more than 10 cm across. Depth of soil to hardpan is considered an important factor in perennial distribution and attained size, mainly because the higher ground has shallower soil over hardpan (Figs. 3 and 4) and moisture values tend to remain higher in the run-on sites than on the plain for a longer time after rainfall. This logically suggests a greater water storage due to greater soil depth even though soil-moisture characteristics are generally similar.<sup>11</sup> When

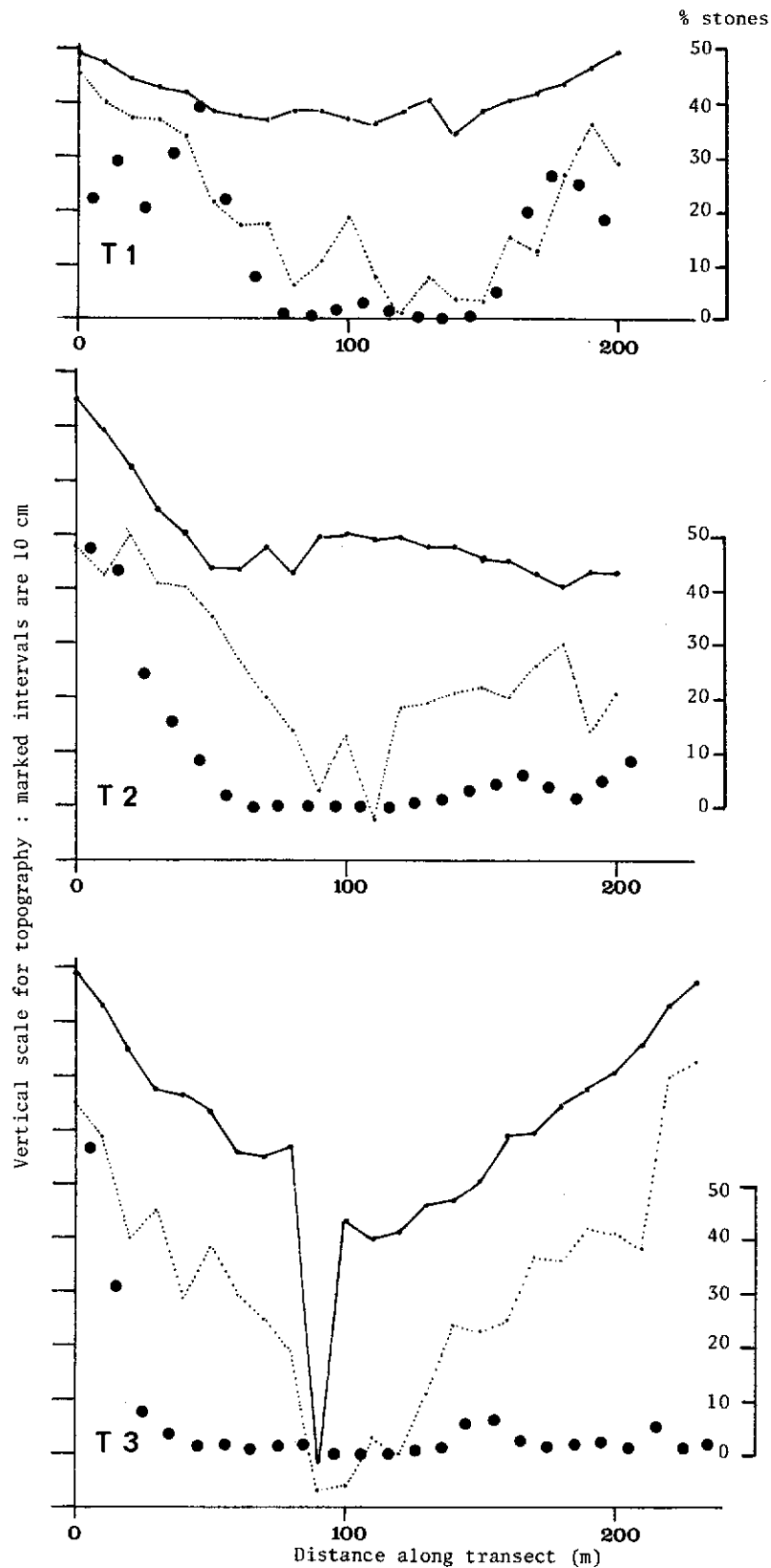


Fig. 3 Topography, depth to hardpan and surface stoniness of three transects starting on stony plain and traversing the Trifid arms. Bold line represents surface topography, dotted line depth to hardpan, solid circles percentage stones on soil surface.

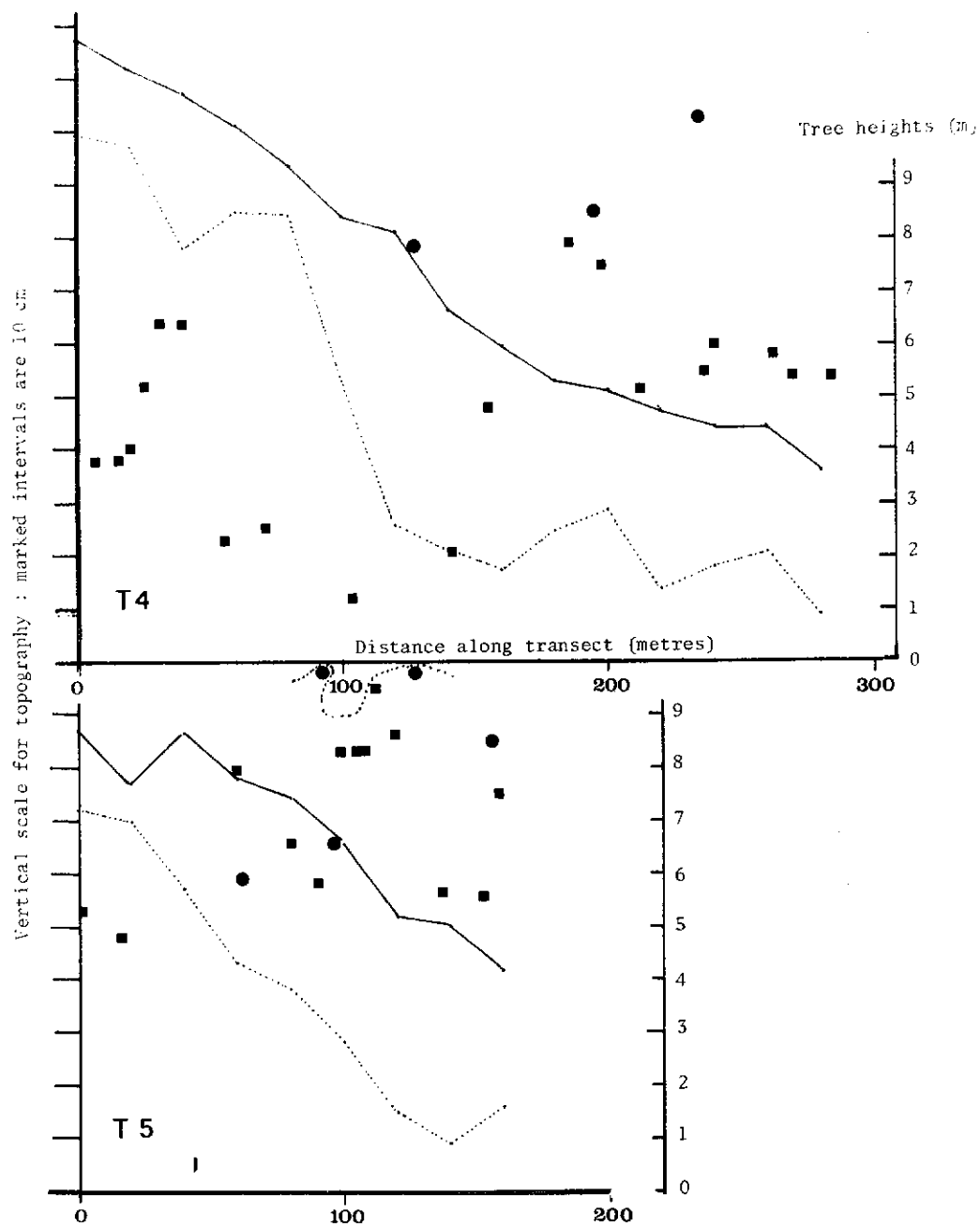


Fig. 4 Topography and depth to hardpan, transects 4 and 5 at Trifid site, Mileura. Heights of the two largest species are shown along each:

- *Acacia aneura*
- *Grevillea striata*

the surface has dried out the soil just above the hardpan may still have reasonable levels of soil moisture.

In addition there is a micro-topographic effect described for the Trifid by Mott (his Site A) who observed that on slight mounds annuals carried more seed, were larger and occurred in greater numbers than the same species in intervening depressions.<sup>13</sup> In the case of *Aristida contorta* artificial seeding suggested lower germination occurred in depressions due to ponding after cyclonic rains. The mounds and depressions are generally elongated in the direction of water flow the mounds being 3-5 m long and 1-3 m wide with depressions  $6.4 \pm 1.3$  cm below crests of adjoining mounds. There is a small increase in depth of soil to hardpan under the mounds, such that soil depth under mounds is of the order of 16 cm greater than in the depressions. Shrubs occurred on mounds, rarely in depressions and Mott suggests that formation of a hollow (dishing effect) in the hardpan surface seems to be associated with the larger *Acacia* plants.<sup>13</sup>

There appears to be little variation in particle size or in soil moisture capacity between mounds and depressions.

#### Particle Fractions (after Mott and McComb<sup>13</sup>)

Depth (cm)	Mound		Depression	
	0-3	18-22	0-3	18-22
Silt	10	9	7	10
Clay	19	12	25	22
Fine sand	33	37	33	37
Coarse sand	41	39	38	31

However soil moisture remains above wilting point marginally longer in the mounds. The mounds have higher nutrient levels (except for available nitrogen) than the depressions largely because their surface soils contain more litter, and Mott concludes that better growth on mounds is due to a combination of moisture storage and availability of nutrients. Nutrient accumulation is clearly related to presence of plants and their associated litter fall.

Soils of the stony plain have more large fragments than those of the creek and have less clay, particularly at depth. The average values for clay reported by Mott<sup>9</sup> are as follows (percentages):

Depth	Surface	20 cm
Plain	14	17
Creek	18	24

(page 36)

This difference is sufficient to class the sub-surface creek soil as sandy clay loam, whereas the other soils are sandy loams. As noted above however clay has tended to accumulate more in the depressions within the creek sites. Soil moisture levels were followed over the period 1969-1971 by Mott<sup>9</sup> with samples taken at 0-2 cm, 25-30 cm, 40-45 cm, 55-60 cm and 75-80 cm or until the hardpan was reached. Of particular interest is 'available moisture': that between field capacity (at -0.3 bars) and wilting point (-15 bars). For these levels Mott reported the following:

#### Water as % Dry Weight

Location	-15 bars	-0.3 bars
Plain*	5.6	12.9
Creek*	6.0	12.8
Mound $\phi$	6.2	12.3
Depression $\phi$	6.5	12.8

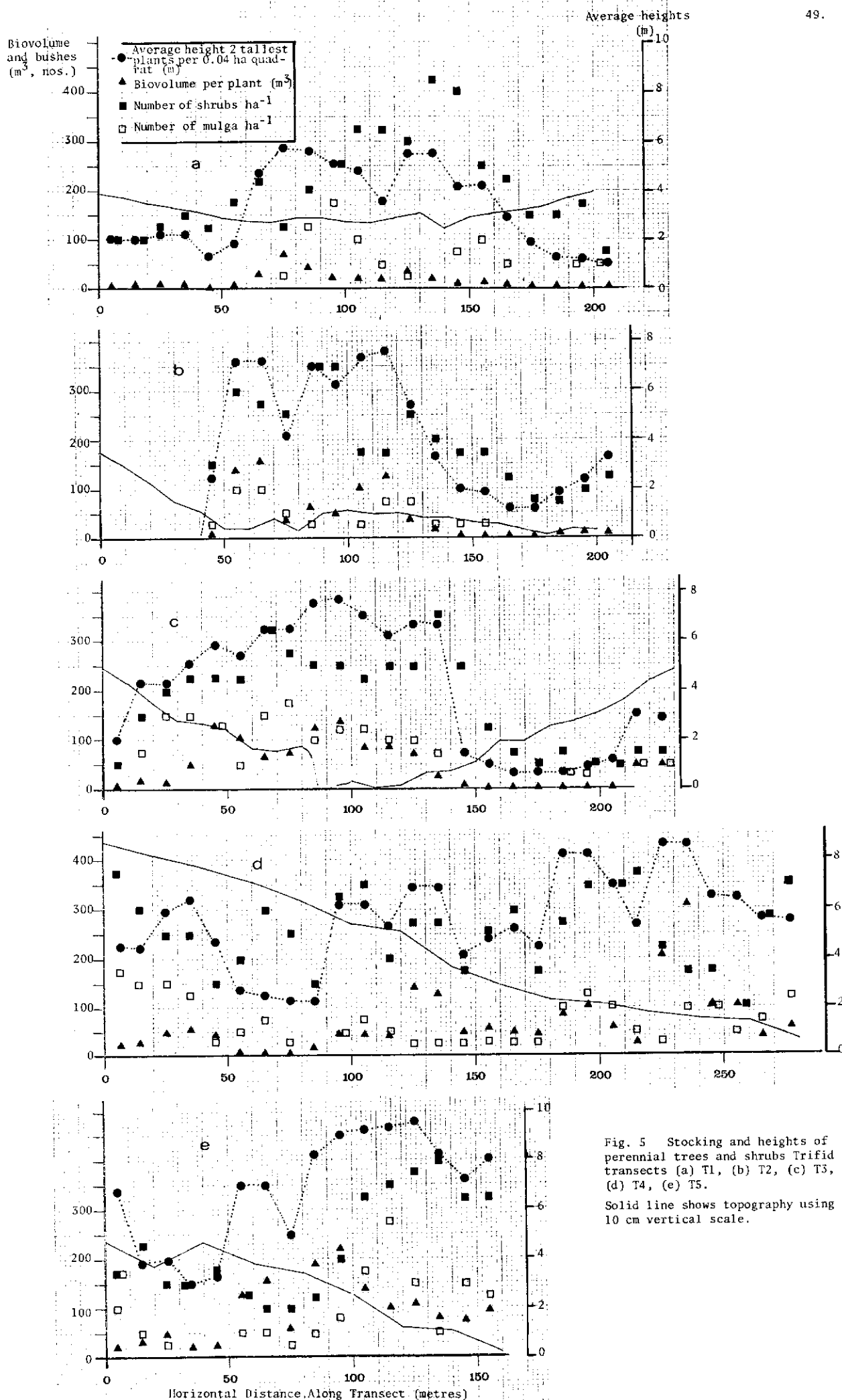
\*<sup>9</sup>  $\phi$ <sup>13</sup>

Thus a maximum of 7.3% is the value suggested for available moisture. For the plain surface soil moisture was generally well below permanent wilting point (page 39) in the range of 0-3% with slightly higher levels in the creek (page 38). At 45 cm depth surface soil moisture exceeded PWP on 7/23 occasions for plain samples and 13/21 occasions for creek samples. Tests on the annuals showed that exposure to soil water potential of -15 bars (using fine silty loam) was lethal in five days.<sup>15</sup> Annuals do not flower more rapidly under conditions of moisture stress. Survival of the perennials from year to year must be related to a combination of competition and available soil moisture.

#### Description of Transects

Along each transect the perennials have been summarised for those occurring within 10 m either side of the line of the transect (Table 1) while in the descriptions of transects which follow (Figs. 3-6, Tables 3-7) data is presented for overlapping 20 m x 20 m quadrats along the lines. The distinction may be made by noting whether points on transects are reported in multiples of 10 or 20 m ending with zero (original data) or ending in 5 (overlapping averages). For example in Fig. 3 topography and depth to hardpan are presented as original data while 'percentage stones' is plotted on the overlapping average system.

The ratio of density/frequency may be taken as a measure of dispersion.<sup>1</sup> This is shown for all transects combined in Table 2. *Acacia tetragonophylla* occurs in 73% of the 0.04 quadrats covered by transects with an average density of 1.66 and has a lower ratio than *Acacia aneura* and *Eremophila spathulata* which both occurred in fewer quadrats with higher average densities.



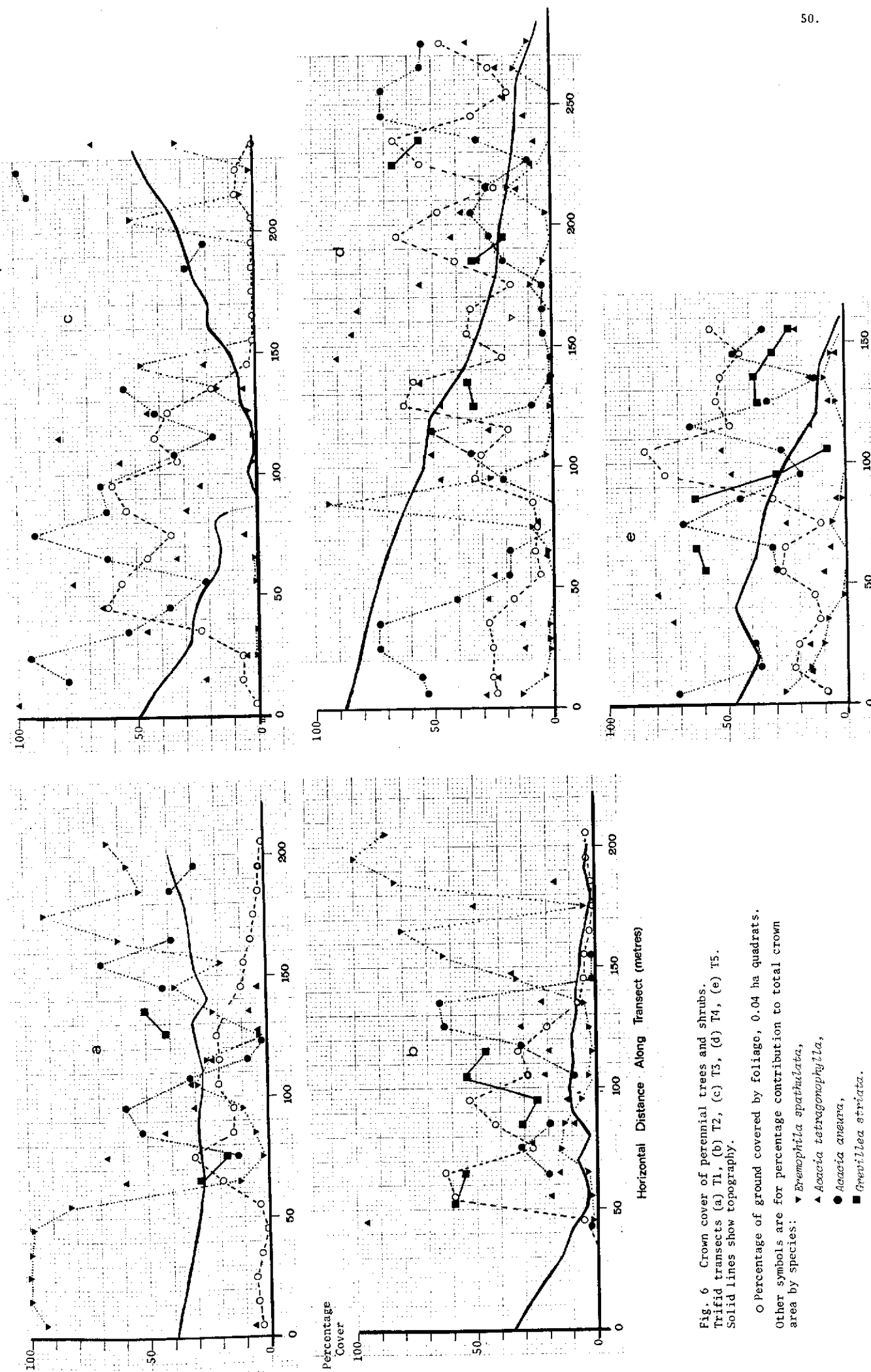


Fig. 6 Crown cover of perennial trees and shrubs. Trifid transects (a) T1, (b) T2, (c) T3, (d) T4, (e) T5. Solid lines show topography.

○ Percentage of ground covered by foliage, 0.04 ha quadrats. Other symbols are for percentage contribution to total crown area by species:

- ▼ *Eremophila spathulata*,
- ▲ *Acacia tetragonophylla*,
- *Acacia aneura*,
- *Grevillea striata*.

*Grevillea striata* mainly a large tree is well dispersed at this scale of aggregation with 13 trees in 13 different quadrats. The total of perennials recorded was 461 with an average quadrat density of 8.38 or 209.5 ha<sup>-1</sup>.

Original field measurements of perennials consisted of height, crown diameter and stem diameter at 1.3 m. Crown diameter has been used to derive crown area in m<sup>2</sup> (Table 3 etc.), percentage ground covered and percentage contribution to crown area by species (Fig. 6). 'Biovolume' is here defined as crown area x height in m<sup>3</sup> and is shown per perennial by quadrat in Fig. 5 and tabulated with percentage contribution by species in Table 3 etc. Depths to hardpan are the mean of three recordings at each point. Points were established at 10 m sections along transects 1-3 and 20 m sections along transects 4 and 5. In both Figs. 5 and 6 the bold lines represent surface topography. Soil pH was determined for 14 soil samples from 0-10 cm depth along transects 1 and 2 in December 1976. The average value was 7.0 (6.5-7.5).

#### Transect 1

This transect cuts across the highest part of the study area (Fig. 2) with 11 points falling on the stony plain and 10 in the south western arm of the creek system. On the plain the average percentage of stones is 16 compared with 1% in the creek, whereas the average depths to hardpan are 13 and 33 cm respectively. The lowest point is 140 m from the start (Fig. 3) and this is probably the site of the main surface flow though there is nothing to indicate this on the ground and a strong possibility that run off from the west would be concentrated in one or other of the lower lying areas at 70 or 110 m along the transect. The change from >20% stones on the surface to lower proportions from each end of this transect is most marked and neatly coincides with increased soil depth and shallower slopes. Soil depth varies from <10 cm at 0, 10, 20, 30 and 40 m to a maximum of 37 cm at 120 m along the line.

Soil moisture was sampled in December 1976, July 1977 and November 1978, in the first two instances along the entire transect and in the latter between 50 and 100 m. Samples were taken from the surface 0-10 cm. In December 1976 the range was 0.38% (180 m) to 1.14% (20 m) with all values less than permanent wilting point (as previously defined) which was calculated as between 3.1% (120 m) and 5.5% (30 m).<sup>8</sup> At this time there was no difference between points on stony ground and in the creek area. In July 1977 the range was 0.41 to 2.26% with the average and range for points on the stony plain 0.86 (.41-1.78) and in the central creek 1.35 (.59-2.26). The six central points sampled in November 1978 averaged 2.67% with the highest value 4.17% at 70 m coinciding with a pronounced trough in soil depth (Fig. 3). In this transect 4 trees exceed 5 m in height, two each of *Acacia aneura* and *Grevillea striata*. The tallest being a *G. striata* at 6.8 m height 134 m along the line in a dip in surface topography where the soil is comparatively deep (Fig. 3). The other member of this species is 5.2 m in height at 68 m along the line just at the break between stony plain and creek sites. The taller *A. aneura* (6.2 m)

also occurs in a trough at 78 m while the other (5.3 m) is on level ground with a locally relatively shallow depth to hardpan at 100 m along the line. This may not be a useful observation as this tree lies nearly 10 m from the point at which topography and hardpan were measured. Fig. 5 shows the averaged heights of the two tallest plants per 0.04 ha across the transect. The trend suggests an inverse relation with percentage stones on the surface and an apparent (untested) correlation with depth to hardpan. Heights are lowest in this transect compared with the other four, as also are average biovolumes per bush and crown cover. There is a distinct contrast between the two basic land forms:-

	Plain	Creek
Average heights	1.0-2.9	3.6-5.7 m
Biovolume per bush	1.1-8.3	7.7-70.1 m <sup>3</sup>
Percent crown cover	0.6-5.9	9.9-31.1%

Not only are dimensions lower in the stony plain parts of the transect but fewer shrubs (i.e. more widely spaced perennials) contribute to the means with 2-9 perennials per quadrat compared with 7-17 in the central creek section. *Acacia aneura* is absent from the north western segment of stony plain (though individuals do occur scattered across its lower flanks outside the transect) where *Eremophila spathulata* is the most frequent plant as also at the other end of the line (Fig. 6, Table 3). *Acacia aneura* reaches a maximum frequency of 175 ha<sup>-1</sup> at 95 m along the line occurring in only 6 quadrats compared with *E. spathulata* in all quadrats. Overall the latter has the highest density/frequency ratio in transect 1. Both *Cassia helmsii* and *Eremophila fraseri* are uncommon and scattered in this area but *A. kempeana* is more frequent than elsewhere in the Trifid (Table 2). Organic matter in the top 0-10 cm from 7 points along transect 1, sampled in December 1976 averaged 1.8% (1.3-2.1).<sup>8</sup>

#### Transect 2

This line commences to the east of the area and traverses the south eastern arm of the Trifid. Its eastern-most side has a comparatively sharp slope across the stony flank of Mileura Hill. This is virtually barren despite an apparently deeper soil to hardpan than at the extremities of transect 1 (Fig. 3). The first 40 m falls on the stony plain where the average depth to hardpan is 18 cm. The section 50-80 m covers an irregularly scoured area of pronounced mounds and depressions suggesting that flow may occur throughout. The other low area indicated, at 180 m, may receive run off from the south. Soil depth varies from 9 cm at 50 m to 52 cm at 110 m along the transect. Soil moisture levels recorded were as follows:-

	Dec 1976	Jul 1977	Nov 1978
Max.	3.28	2.15	1.81
Min.	.55	.53	.23
Mean	.89	1.12	.95

TABLE 3 Summary of Transect Data T1.

Distance (m)	Crown Area (m <sup>2</sup> )	Biovolume (m <sup>3</sup> )	Percentage Biovolume Contributed by Species								
			A.a.	A.k.	A.t.	C.h.	E.f.	E.L.	E.s.	G.s.	S.l.
5	13.1	25			3				97		
15	19.8	33							100		
25	22.2	39							100		
35	13.3	27					< 1		99		
45	3.9	6					< 1		99		
55	15.0	22		12					88		
65	77.0	254		1	50				5	43	
75	124.5	491	21		56				1	22	
85	58.7	332	46		52				2		
95	58.4	202	71		23				6		
105	82.6	259	43	6	31	< 1			20		
115	80.7	226	10	35	26	< 1	8	< 1	19		
125	84.0	383	1	28	1		5	< 1	1	63	< 1
135	69.4	330		13	2			< 1	11	73	1
145	41.5	124	62		2			< 1	29		7
155	39.6	127	85					< 1	8		7
165	23.7	53	59						41		
175	9.5	14				8			92		
185	8.6	10	44			11			45		
195	11.3	12	35			12			53		

TABLE 4 Summary of Transect Data T2.

Distance (m)	Crown Area (m <sup>2</sup> )	Biovolume (m <sup>3</sup> )	Percentage Biovolume Contributed by Species								
			A.a.	A.t.	C.h.	E.f.	E.l.	E.s.	G.s.	P.p.	S.l
5	No perennials present										
15	"	"									
25	"	"									
35	"	"									
45	19.9	44	<1	99					<1		
55	238.4	1651	14	7					<1	78	
65	254.1	1696	13	6	<1	3			<1	76	
75	107.5	360	43	22	<1	23			12		
85	169.5	865	18	6		13	<1		6	57	
95	211.1	697		8		17	<1		3	70	
105	113.9	733	8	8		5			<1	78	
115	132.8	880	26	9					<1	65	<1
125	83.1	352	76	22			<1		<1		1
135	31.7	115	87	11			1		1		
145	20.7	35	<1	36		23	3		37		
155	16.3	27	1			30	2		67		
165	5.9	7					12		88		
175	2.5	3		71			27		2		
185	7.7	14		15					85		
195	14.8	32							100		
205	13.6	33							78		22



TABLE 5 Summary of Transect Data T3.

Distance (m)	Crown Area (m <sup>2</sup> )	Biovolume (m <sup>3</sup> )	Percentage Biovolume Contributed by Species							
			A.a.	A.k.	A.t.	C.h.	E.f.	E.l.	E.s.	S.s.
5	4.1	8			100					
15	25.8	98	90		10					
25	30.0	112	99		<1				<1	
35	96.5	427	60		40				<1	
45	248.0	1141	42		58					
55	227.1	951	26	2	72				<1	
65	181.9	868	85	2	12	<1	<1		<1	
75	142.4	782	98		2	<1	<1			
85	217.6	1221	78		14		8			
95	238.5	1390	79		12		7			2
105	132.2	729	40		55				<1	5
115	170.9	848	21		79				<1	
125	147.8	718	55		38		5		2	
135	73.1	318	78		1	<1	13	<1	7	
145	14.5	17			24	10	4	11	51	
155	2.2	2				100				
165	0.8	<1				100				
175	1.1	<1				100				
185	1.5	1	28			72				
195	2.1	2	13			87				
205	3.4	4				48			52	
215	30.8	144	99						1	
225	29.4	142	99						<1	
235	2.0	<1			57				43	

TABLE 6 Summary of Transect Data T4.

Distance (m)	Crown Area (m <sup>2</sup> )	Biovolume (m <sup>3</sup> )	Percentage Biovolume Contributed by Species									
			A.a.	A.k.	A.t.	C.h.	E.f.	E.l.	E.s.	G.s.	S.l.	S.s.
5	102.6	328	61		27	1			10			
15	107.2	353	63	14	20	1			2			
25	104.0	462	81	11	8			< 1	< 1			
35	110.2	529	87		8			5	< 1			
45	66.6	266	66		18			9			7	
55	21.9	44	23		15	5		2			43	12
65	34.2	58	27		2	3		57	1			9
75	27.1	42			12	2		78	8			
85	35.7	81				1		< 1	98			
95	132.1	603	30		55		< 1	1	14			
105	120.8	616	42		54	1	< 1	1	< 1			
115	76.9	333	62		25	2	< 1	2			9	
125	252.1	1541	9		41		5	< 1	< 1	44	2	
135	235.5	1412	< 1		46		6		< 1	48		
145	86.5	345	< 1		94		6					
155	144.3	598	5		88	1	6	< 1				
165	139.7	586	5		87	2	6	< 1				
175	71.7	308	3		68		23		6			
185	164.9	937	23		18		7		2	49		
195	262.4	1424	34		26		8			32		
205	191.7	825	50		29		17	3	1			
215	97.7	341	41		11		8	7	13		20	
225	221.5	1844	8		4				2	82	4	
235	267.2	2178	23		4		4			70		
245	134.4	736	80		7		12					
255	76.0	422	84		13		3					
265	107.3	454	71	4	15		< 1		10			
275	189.4	771	69	2	22		< 1		6			

TABLE 7 Summary of Transect Data T5.

Distance (m)	Crown Area (m <sup>2</sup> )	Biovolume (m <sup>3</sup> )	Percentage Biovolume Contributed by Species							
			A.a.	A.t.	C.h.	E.f.	E.l.	E.s.	G.s.	S.l.
5	36.5	170	90		< 1			10		
15	90.4	292	53	10	< 1	28		8		
25	83.0	283	55	11		29		5		
35	47.8	123		84			10	6		
45	57.3	149		88	4		8	< 1		
55	109.8	641	35	4	1					60
65	103.5	633	36	4						61
75	42.9	235	82	15				3		
85	121.3	949	35	1				< 1		50
95	306.9	1778	23	30		4				44
105	337.5	1817	41	39		9				10
115	193.1	1405	78	13		9				
125	218.4	1644	37	2		7	1	1	52	
135	211.6	1298	13	5		7	3	4	66	2
145	178.9	1010	44	3		1	1	3	46	3
155	226.4	1219	36	13		11	2		38	

The point 70 m along the transect was consistently the lowest in these sets. This point, interestingly, is on a pronounced rise compared with the surrounding land surface (Fig. 3). The highest record for 1976 was at 180 m, a shallow area; for 1977 at 130 m and for 1978 at 80 m, another shallow area. Permanent wilting point for samples from transect 2 varied between 3.5 (70 m) and 5.0% (200 m).<sup>8</sup> Six trees exceed 5 m in height along this transect, three each of *Acacia aneura* and *Grevillea striata*. Each of the latter is 9.3 m tall. These six occur in the central part of the line between 56 and 118 m where the ground level is relatively flat and the soil is at least 20 cm to hardpan (50-60 m) but generally in excess of 40 cm deep. The largest *G. striata* is at 56 m along the line, this has a stem diameter at 1.3 m of 78.4 cm and a crown diameter of 13.3 m. Although the soil is not deep at this point it represents the break in slope of a considerable area to the east which presumably provides run-off moisture when rain occurs. Average heights are greatest in the central part and biomass per plant reflects the major contribution of the *G. striata* trees (Fig. 5). *Acacia aneura* is less frequent in this transect than in transect 1 (Table 2) reaching a maximum frequency of 100 ha<sup>-1</sup> at 55-65 m and with the lowest density/frequency ratio throughout the sample area despite the omission of three unoccupied quadrats at the eastern extremity of the line in Table 2. *A. tetragonophylla* is more frequent in terms of occupied quadrats but *E. spathulata*, occurring in 8/9 is almost as frequent as in transect 1, forming the bulk of biovolume and crown cover from 145-205 m along the line (Table 4, Fig. 6). This line is also distinguished by the presence of the single *Pittosporum phillyraeoides* at 214 m along the line, and by a high density/frequency ratio for *Eremophila fraseri* with the main concentration at 80-100 m. Organic matter in the top 0-10 cm of soil from 7 points along transect 2, sampled in December 1976 averaged 2.0% (1.6-3.1).

#### Transect 3

This line cuts the exit creek at the lowest point of the study area, starting from about the same topographical point on the stony plain to the east as does transect 2. Both extremities have steeper slopes than transect 1 but although the western most section runs onto the plain fewer stones are present on the surface. The central section of profile is atypical (Fig. 3) in that the scour channel featured is one of the deepest in the Trifid area and if the line had been a few metres either side this feature would not have been illustrated. The profiles of surface topography and soil depth at each of transects 1, 2, 3 suggest a skewed effect and that a more detailed analysis of these two features to illustrate a three dimensional representation could be useful. That is soil depth appears to be slightly out of phase with surface topography. Soil depth is shallowest at the western end of the transect - 13 cm at 220 m and 15 cm at 230 m, and deepest at 100 m where it is 49 cm. Soil moisture levels recorded were as follows:

	December 1976	July 1977
Max.	1.46	3.92
Min.	.54	.33
Mean	.82	1.05

Highest values in 1976 were at 60, 70, 80 and 150 m (all over 1%) and of these only that at 80 m exceeded 1% in 1977 when the highest values were at 90 and 110 m. However the general trend was for the central area, in proximity to the main channel, and also incidentally relatively well-shaded, to have higher soil moisture levels.

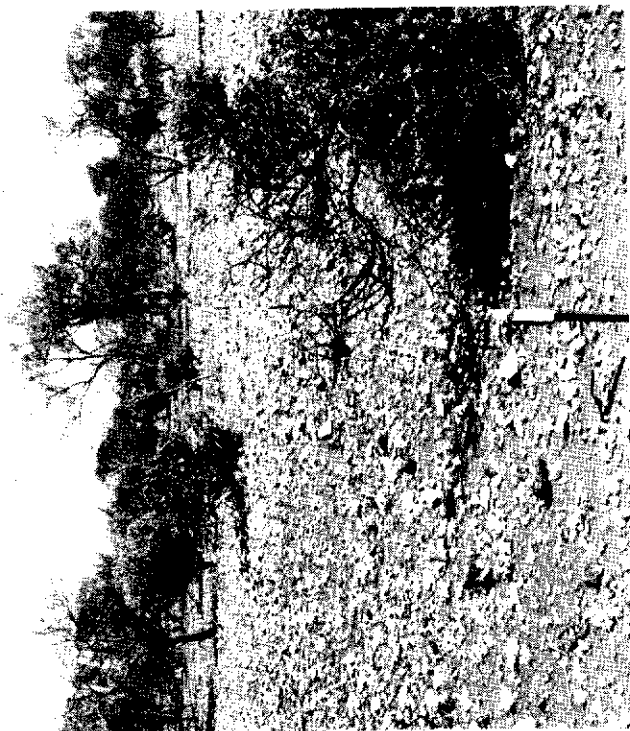
The tallest trees in transect 3 are all *Acacia aneura*, with *Grevillea striata* being notably ab-



c

PLATE 1 A general account of the Trifid site, Mileura.

- a From the south eastern end of transect 1 looking north west along the line.
- b From the most easterly point of transect 3 looking east towards Mileura Hill. The low shrubs are *Acacia grasbyi* Maiden, common on the slopes of Mileura Hill but not present in the Trifid.
- c From the south eastern end of transect 5 looking north west into the central creek area. The large tree is *Grevillea striata*.



a



b

sent. 20 individuals exceed 5 m in height with the tallest 6 of these (>6.8 m ht) between 72 and 128 m along the transect, in the lowest lying area sampled (Fig. 2). Density of *A.aneura* is highest on the ledge at 60-80 m (Fig. 5) at 150-175 ha<sup>-1</sup>, but remains in excess of 100 ha<sup>-1</sup> between 25 and 125 m apart from an aberration at 55 m. Soil depth to hardpan generally exceeds 30 cm for this stretch (Fig. 3). The tallest *A.tetragonophylla* (5.8 m) occurs at 114 m along the transect where the soil is 40 cm to hardpan in a distinct trough. Overall stocking is greatest at 135 m with 350 stems ha<sup>-1</sup>.

In contrast to transects 1 and 2 *Acacia aneura* contributes the bulk of biovolume and crown cover (Table 5, Fig. 6) to much of the first half of the line. One quadrat is omitted as unstocked from the bottom line of Table 2, leaving *A.aneura* with a 75% frequency (9/12) and a higher density/frequency ratio than for transects 1 and 2. This is probably a reflection of the lower position of this transect in the landscape and the proximity of the eastern end to the Trifid confluence. *Acacia tetragonophylla* also has a higher density and frequency in this transect than in 1 and 2, with its most frequent representation at 15, 40, 90 and 115 m along the line, all possibly areas where soil depth to hardpan is dished (Fig. 3). *Santalum lanceolatum* is absent, *Eremophila longifolia* scarce, and *E.spathulata* much less frequent than in transects 1 and 2. The transect has one of the two *Scaevola spinescens* recorded at 101 m and has the highest number of *Cassia helmsii* in all transects, located mainly between 150 and 160 m along the line.

#### Transect 4

Transect 4 does not exactly follow the line of drainage which is indicated approximately on Fig. 1. Because of this and also probably the scour and dish effect noted above there is some variation in soil depths along the line. However both this and transect 5 (Fig. 4) show a distinct contrast from the first three transects in the general overall trend of depth to hardpan slope following surface soil topography. Percentage stones on the surface are not illustrated for this transect though at 60, 80 and 260 m stones were present. These points coincide with some of the lowest soil depths to hardpan along the line viz. 16, 9 and 23 cm respectively against an overall average of 28 cm with a maximum of 55 cm at 120 m. This area is at about the position sampled by Mott though the presently noted soil depths are much shallower than his. Soil moisture levels recorded were as follows:-

	December 1976	November 1978
Max.	1.24	8.60
Min.	.52	0.71
Mean	.82	3.59

These differ little for 1976 from transect 3 and show no trend of interest for that period. The highest value at the 1978 sampling date was for 160 m along the transect where the soil depth was 43 cm and a definite trough in depth to

hardpan occurs (Fig. 4). While not all positions were sampled in 1978 it is interesting to note that for 1976 the highest value for percentage moisture was at the start of the transect i.e. the highest point in the landscape of this line. The same thing occurred in transect 5. Individuals of *Acacia aneura* and *Grevillea striata* lying close to the transect line are represented by heights in Fig. 4. Only 3 *G.striata* occur in this line and they show an increase in height down slope, with height not directly related to depth of soil to hardpan. The tallest tree is 10.3 m high with a stem diameter at 1.3 m of 72.8 cm and a crown diameter of 13.7 m. Twenty individuals of *A.aneura* exceed 5 m in height (average 6.1 m) along this line. Fig. 4 suggests a trend of height with depth of soil (untested). Other species exceeding 5 m in height are *Acacia tetragonophylla* 4 trees <6 m at 101, 131(2) and 171 m along the line where soils are deepest; and one *Eremophila fraseri* at 129 m. Average heights and biovolumes per plant fluctuate along the line (Fig. 5) with an underlying trend of increase down slope. Total stocking is greatest at 5 and 215 m along the transect with 375 stems ha<sup>-1</sup> and numbers of *A.aneura* are highest at 5 m with 175 ha<sup>-1</sup>. *Acacia tetragonophylla* occurs at highest density and frequency in this transect with some tendency to aggregation. Of the 36 stems recorded 5 lie between 130 and 142 m, 5 between 160 and 172 m, and 10 between 186 and 214 m along the line. The major contribution of this species to crown cover and biovolume is between 145 and 175 m (Fig. 6, Table 6). *Eremophila fraseri* and *E.longifolia* are both also at highest density and frequency in this transect with one patch of 5 bushes of the latter at 60-70 m. Apart from this they tend to occur in smaller aggregations along the transect. One *Scaevola spinescens* occurs at 64 m. The transect is also distinguished by the presence of 5 of the 9 *Santalum lanceolatum* shrubs (Table 2), 1 at 47 m, 2 at 120 m and 2 at 220 m, all positions where the depth to hardpan shows apparent dish-ing (Fig. 4).

#### Transect 5

This transect commences in an area of surface scour just past that mentioned for transect 2. Here considerable differences exist in both depth to hardpan and surface topography. Readings taken show that the transect passes through surface scour at the 0 and 20 m points (Fig. 4) thereafter the line while not following the main drainage channel precisely does have a more consistent soil profile depth of between 26 and 41 cm, mean depth 34.6 cm. Soil moisture records were similar to those for transect 4:-

	December 1976	November 1978
Max.	1.21	3.92
Min.	.43	0.41
Mean	.73	1.29

Not all positions were sampled in 1978. The highest value at the 1976 period was at 0 m along the line whereas in 1978 the highest value was recorded at 100 m, where the third highest value occurred in 1976. Both parts were at slope

positions both on the surface and with respect to hardpan (Fig. 4). A total of 31 trees in this transect exceed 5 m in height, that is 46% of the total (Table 1). More *G. striata* occur in this line than elsewhere (5) including the tallest recorded at 10.4 m (off the scale on Fig. 4). Representative heights of tallest trees are shown on Fig. 4. These suggest an increase in height down slope for the first 100 m of transect whereafter heights tend to level off, declining towards the end of the line (Fig. 5) where the transect moves west of the main drainage arm (Fig. 1). In addition to 23 *Acacia aneura* > 5 m (average 7.35) there are two *A. tetragonophylla* and one *Eremophila fraseri* exceeding this height. Average biovolumes per plant range from 20.5 at 35 m along the line to 222.3 m<sup>3</sup> at 95 m. Biovolume is greatest in the stretch 95-155 m where trees are also more densely packed. Numbers of *A. aneura* ha<sup>-1</sup> achieve the highest level in this transect with 275 at 115 m. *Acacia tetragonophylla* is comparatively scarce though reasonably well distributed, *Eremophila spathulata* is also scarce with the lowest density/frequency ratio in this transect. *E. fraseri* is mainly concentrated at the western end of the transect with 6 of the 10 individuals present between 114 and 133 m along the line.

#### Conclusions

The present description of vegetation of the Trifid site and review of previous findings in the area will serve as a basis for further studies on growth persistence and regeneration of perennials. While the sampling program and analysis undertaken to date allows little to be stated in the way of firm conclusions, it is considered that the material presented can be elaborated and tested further. Reasons for the presence of large *Crevillea striata* trees to occur at certain locations require further deliberation. Is it possible to predict which microsites can support large growth? Are mounding and dishing geomorphic features or of biological origin? Is the spacing of shrubs directly related to absolute soil volumes or a combination of rooting space and moisture availability?

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# PRELIMINARY STUDIES OF WATER RELATIONS OF SOME TREE SPECIES AT YEELIRRIE

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## Introduction

During the mining of the Western Mining Corporation's uranium deposit at Yeelirrie it will be necessary to reduce water table levels to enable extraction of the ore. The company is concerned that as a consequence of the reduction in water table the native vegetation (particularly trees) in the areas surrounding the mine site will be adversely affected. The impact of the lowering of the water table on the vegetation will be one factor influencing whether the mining procedure will be modified to reduce the regional effects of water table reduction.

Comprehensive ecological surveys including vegetative type mapping are being carried out by consultants to characterize the vegetation of the lease area. In the area of principal concern the vegetation consists of an open, grassy woodland. The principal tree species are *Casuarina cristata* Miq., *Acacia aneura* var. *latifolia* F. Muell. ex Benth., *Eucalyptus clelandii* (Maiden) Maiden, *Eucalyptus trivalva* Blakely and a *Melaleuca* sp. Mixed grasses dominate the ground layer but there are considerable areas of bare soil.

The climate is arid with an average annual rainfall of 218 mm. At the time of this study no rain had fallen for 18 months. Soils in the study area were calcareous red sandy earths (Churchwood, pers. comm.). A typical profile consisted of a red sandy loam to a depth of between 20-40 cm overlying a calcareous clay. The clay was of variable density but typically was hard and compact. Depth to water table in the study area varied from 4-6 m. T.D.S. content of this water ranged from 3,000 to 7,000 p.p.m.

Plants have evolved numerous mechanisms to enable them to grow and survive in arid regions. The literature on the subject is large and has been comprehensively reviewed by Parker (1968). The particular type of mechanism used by a plant to survive in an arid environment will influence its capacity to withstand additional disturbance to the environment. A variety of classifications have been proposed to categorize arid zone plants. The simplest and most pertinent (to this study) system divides drought resistant plants into ephemerals, water savers and water spenders. Water savers are plants which have evolved mechanisms which reduce water loss (for example, thick cuticle development, reduction in leaf size and number etc.). They may also have adaptations which allow them to resist permanent damage even when subjected to large plant water deficits. Water spenders survive in arid environments by ensuring maximum use of stored water. The most common adaptation of these plants is extensive lateral and vertical root development.

The ability of the vegetation at Yeelirrie to withstand lowering of the water table will depend to a degree on whether the plants have become

one physiologically dormant to avoid drought (i.e. water savers) or whether they are obtaining stored water (i.e. water spenders). Plants in the latter category are likely to be severely affected by a reduction in the water table level as they are unlikely to have mechanisms which allow conservation of water and they would not be adapted to the very high plant water deficits which would develop.

Thus, a rapid assessment can be made of the impact of the reduction in water table by investigating whether the plants are consuming water and if rooting systems are present which are tapping the existing water table.

## Methods

### Temperature

Wet and dry bulb temperatures were recorded throughout the period of measurement.

### Measurement of Stomatal Resistance

Stomatal resistance is a measure of the resistance to water vapour diffusion from the interior of the leaf to the atmosphere. Resistance is related primarily to stomatal aperture. Although it is not simply related to water loss per unit area of leaf there is an inverse correlation between water loss and resistance.

Measurements of stomatal resistance of the major tree species present was carried out over a 24 hour period on the 29th and 30th March 1977, at four hourly intervals. Stomatal resistance was measured with a diffusive resistance meter (Kanemasu et al, 1969) on 4 leaves of two trees of each species.

### Xylem Pressure Potential

Xylem pressure potential is a measure of the tension at which water is held in the plant. It is a balance of the rate of water loss from the plant and the rate of supply from the soil. Xylem pressure potential was determined for each tree using the Scholander (1964, 1975, 1966) pressure bulb technique at the same time that leaf resistance measurements were made.

### Root Excavations

A backhoe was used to excavate a trench approximately 3 m deep adjacent to one tree each of *E. trivalva*, *E. clelandii* and *Casuarina cristata*. In addition, a specimen of *Melaleuca* sp. was excavated. The sides of the trenches were excavated by mechanical and hydraulic methods to determine if vertical roots were present.

### Soil Moisture and Soil Potential

Since no rainfall had occurred for 18 months it could be assumed that the surface soil had no "available water". If available water was present in the surface soils then water consumption by the trees would not necessarily have indicated dependence on water stored at depth. Soil samples were taken adjacent to each excavation tree at 0-20 cm, 100 cm, and 200 cm. The samples were placed in containers and sealed and

TABLE 1 Yeelirrie Study - Data Summary.

A. Species *Casuarina cristata*

Time	Approximate Leaf Temperature	Corrected T	Resistance	Stomatal Conductance	Xylem Pressure Potential
0900	24	554	15.4	6.5	-31.2
1200 (i)	28	559	15.6	6.4	-24.4
(ii)	30	574	16.4	6.1	
1600	29	966	31.8	3.1	-28.6
1800	26	—*	—*	—*	-25.2

\* Note: resistance too high (conductance too low) to be measured.

B. Species *Acacia aneura* var. *latifolia*

Time	Approximate Leaf Temperature	Corrected T	Resistance	Stomatal Conductance	Xylem Pressure Potential
0900	24	*	*	*	-68
1200	28				-68
1300	30				-68
1600	29				-68
1800					-68

\* Leaf resistances could not be obtained as they were too large to be recorded by the instrument.

C. Species *Eucalyptus trivalva*

Time	Approximate Leaf Temperature	Corrected T	Resistance	Stomatal Conductance	Xylem Pressure Potential
0800	20	352	7.0	14.2	-25.2
1100 (i)	29	403	9.2	10.9	-30.6
(ii)	29	434	10.5	9.5	-30.6
1500	29	541	15.0	6.7	-26.5
1800	27	2139	78.0	1.2	-24.4

D. Species *Eucalyptus olelandii*

Time	Approximate Leaf Temperature	Corrected T	Resistance	Stomatal Conductance	Xylem Pressure Potential
0900	22	576	16.5	6.1	-44.8
1200 (i)	29	703	21.8	4.6	-44.2
(ii)	29	961	32.5	3.1	
1500	30	1234	42.5	2.4	-43.8
1800	26	1604	56.0	1.8	-41.4

Resistance in seconds/cm. Conductance in cm/sec  $\times 10^{-2}$ . Xylem pressure potential in bars.



TABLE 2 Soil Moisture Readings.

Depth (cm)	Soil Type	Moisture Content on 30.3.77	Moisture Content at 15 bars
0-20	Sandy loam	1.9%	10.3
100	Clay	11.7%	16.6
200	Clay	16.7%	23.6

their water moisture content was determined at a later date in the laboratory by gravimetric methods. Soil moisture content at 15 atmospheres was determined for each soil type using the pressure membrane apparatus (Richards and Weaver, 1943).

#### Results

Stomatal resistance, stomatal conductance (the inverse of resistance) and xylem pressure potential data for each of the species is recorded in Table 1A, 1B, 1C and 1D. Mean soil moisture content at 0-20 cm, 100 cm, and 200 cm and the moisture content of these soils at 15 bars is shown in Table 2.

*E. clelandii*, *E. trivalva*, *C. cristata* and the *Melaleuca* sp. had root systems which had a pronounced vertical component. *E. clelandii* had strong vertical roots developed from horizontal laterals within two metres of the tree stump. These penetrated to at least a depth of 2.5 m which was the limit of the excavation. Extensive proliferation of roots in the clay occurred almost throughout the exposed profile. There was also evidence of the formation of vertical roots from horizontal laterals at least 6 m from the tree stump.

No vertical root development could be detected adjacent to the stump of *E. trivalva*. However, a major lateral was excavated for a distance of 15 m from the base of the tree where a major vertical root was located. The root extended approximately 2 m to the bottom of the pit and through a less compacted zone of calcareous clay. At the base of the pit at least one of the vertical roots was 5 cm in diameter and there was no indication that its vertical extension was about to be terminated. (During excavation of this tree severed roots were observed to yield considerable quantities of water).

The root system of *Casuarina cristata* was similar to that of *E. clelandii* although vertical root development was not as strong and diameters of the vertical roots were less than those of the two eucalypts. However, vertical root extension and proliferation to a depth of at least 2.5 m was observed. The *Melaleuca* sp. had similar root characteristics to the *Casuarina*.

#### Discussion

Despite the preliminary nature of the study the results obtained were clear-cut. The species examined can be clearly separated into two dis-

tinct groups on the basis of their inferred water consumption rates. The high pressure potential and leaf resistance of *A. aneura* indicates that this species is a drought-evader and is not using stored water. Hence, its ability to survive is not likely to be affected by reduction of the water table.

*E. trivalva*, *E. clelandii* and *C. cristata* were using significant quantities of water. Levels of stomatal conductance during the morning (i.e.  $6 - 14 \times 10^{-2} \text{ cm sec}^{-1}$ ) indicate only low to moderate resistance to the loss of water vapour. The sharp decrease in conductance through the afternoon (i.e. below  $2 \times 10^{-2} \text{ cm sec}^{-1}$ ) indicates a very significant reduction in the rate of water vapour loss coinciding with stomatal closure. Stomatal closure was accompanied by an increase in xylem pressure potential. These species are able to sufficiently restore water balance after stomatal closure and overnight to enable a period of transpiration in the morning. They can, therefore, be classified as "water spenders".

Soil moisture contents in the upper 2 m of the profile are lower than or equivalent to the soil moisture contents corresponding to 15 bars. This level of soil potential is generally considered to indicate the lower level of water availability. Thus, since there are not significant amounts of available water for plant use in the upper 2 m of the profile these species must be extracting considerable amounts of water stored at depth in the soil profile.

The root excavations, although limited, were sufficient to demonstrate that these three species had an extensive vertical root system which would be sufficient to transport water from depths.

#### Conclusions

This study indicates that several of the tree species growing on the Yeelirrie lease are using water stored at depth in the soil profile. It is, thus, likely that they will be adversely affected by a drop in the water table. The severity and rapidity of the effect is difficult to predict as it would depend on climatic conditions, the rate at which the water table is reduced and the level to which it is dropped.

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