

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.² 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.⁹ 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.¹ The consideration of herbivores has generally been directed towards invertebrates although Brown⁴ 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 Forde⁵ for the Australian *Acacia pyrantha*. Here nectaries on the base of petioles, only active at the time of flowering, may attract bird pollinators.

Bentley² 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.⁷ 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.⁷

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[®] 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.

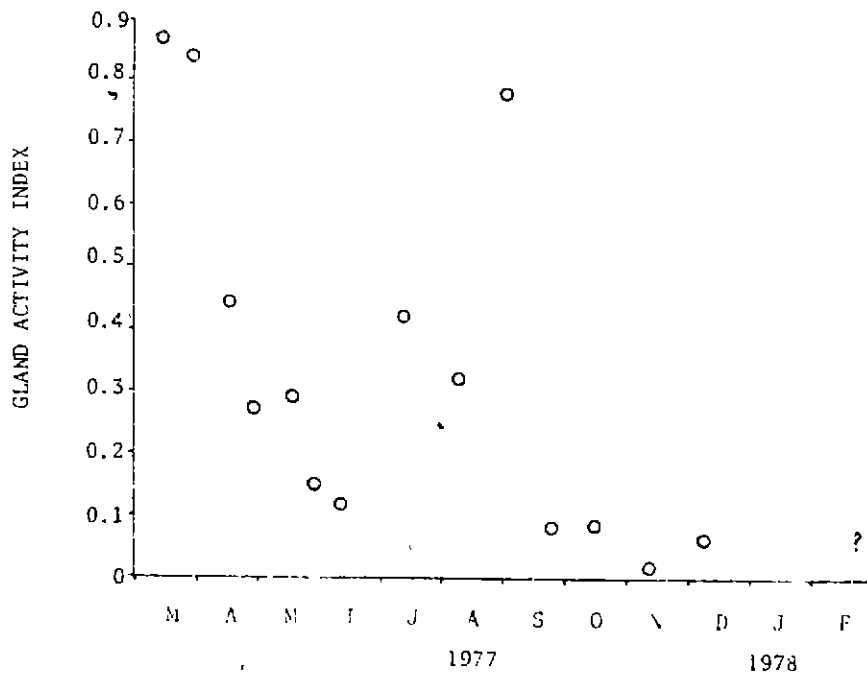


Fig. 1 Variation in gland activity index for 40 plants observed at Yalgorup between March 1977 and February 1978. The February 1978 reading is unavailable.

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 *Diceratoclinea* 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 *Diceratoclinea* 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*⁸ 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
C25	"	Hemiptera	Cicadellidae	-		+	H	2	2
C33	"	Hemiptera	Piesmidae	+	+		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	Immature	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>Prolastus</i> sp. J.D.M. 441
<i>Myrmecia chasei</i>	
Ponerinae	Dolichoderinae
Ectatommini	Dolichoderini
<i>Rhytidoponera violacea</i>	<i>Dioeratoalinea</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

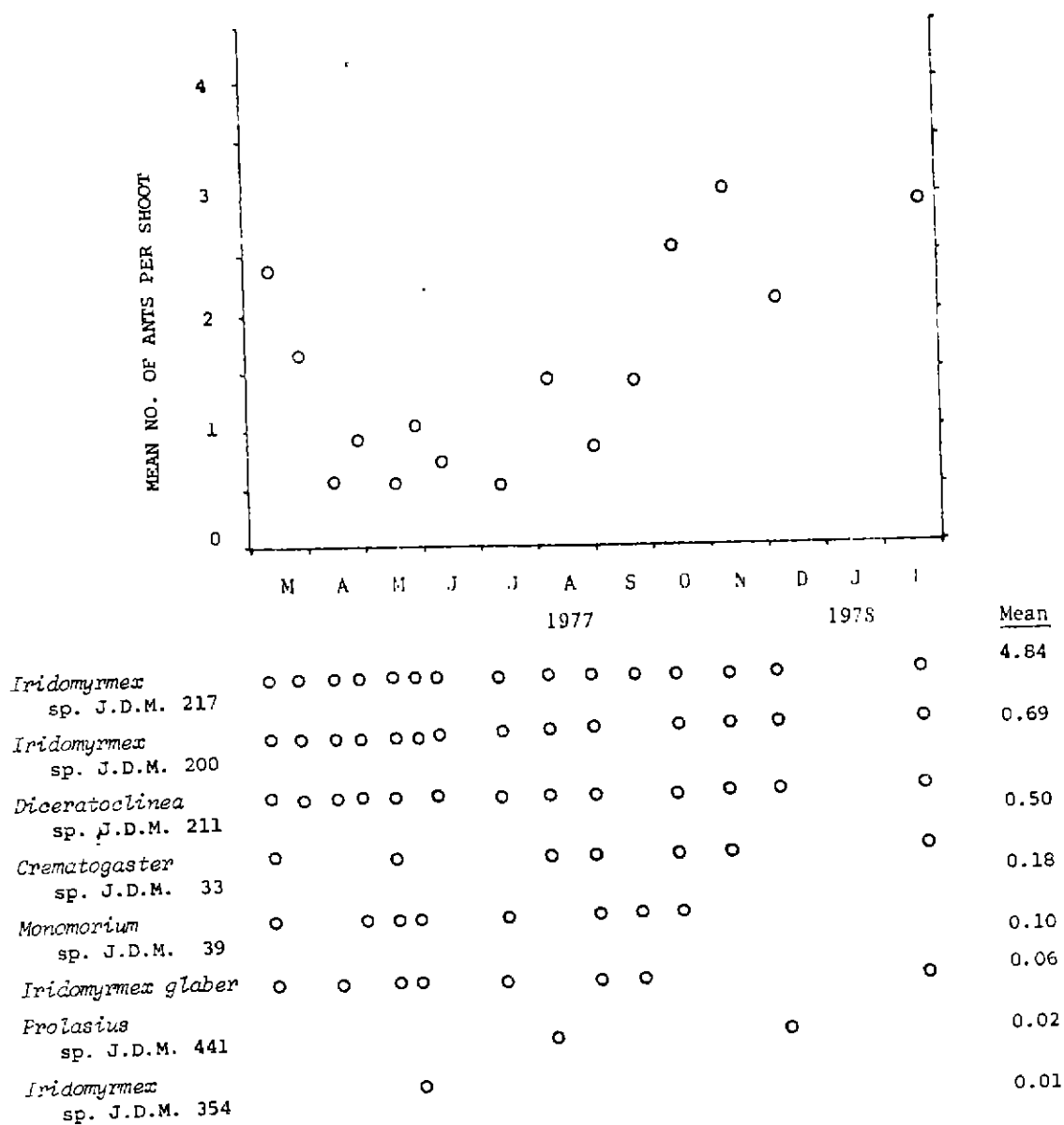


Fig. 2 Mean number of ants per labelled shoot for 40 plants observed at Yalgorup between March 1977 and February 1978. The times of occurrence of individual species and their mean number per shoot over the total observation period are also shown.

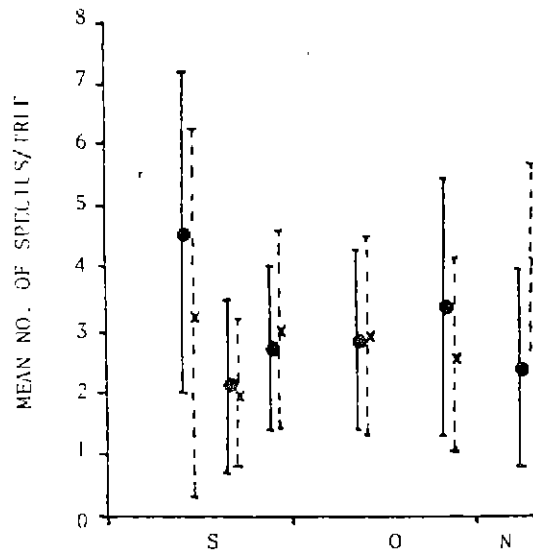
ing on plants closely followed the seasonal trend of ground foraging observed at the nearby localities of Perth (Reabold Hill) and Dwellin-gup (Majer, unpublished data). The relationship between ant attendance levels and gland activity rates merits more detailed investigation.

Ant exclusion experiment

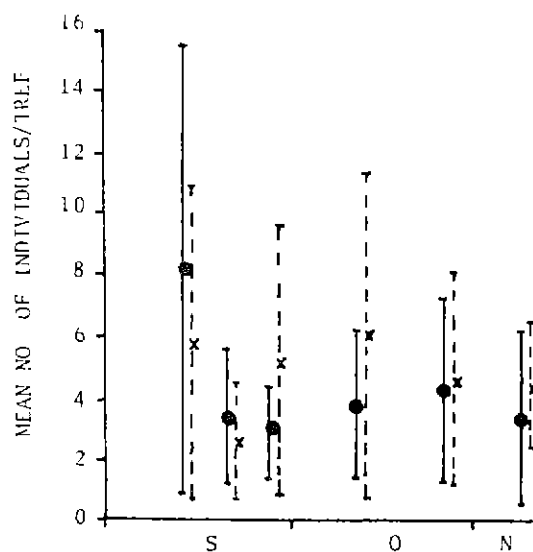
The banding of plants is likely to interfere with the traffic of wingless invertebrates onto the plant. Analysis of results is therefore basically confined to winged species in order to avoid this confounding factor. Invertebrate data are bulked since ants are not generally likely to distinguish between,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



(a)



(b)

Fig. 3 Mean number of winged insect species (a) and individuals (b) per tree for the Manning control (●) and experimental (×) 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 (m²)

	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 uncertain 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*³ and *Helianthella*⁶, where ants attracted to extrafloral nectaries have been demonstrated to have a protective effect on the plant.

Acknowledgements

The author thanks Wayne Mitchell, Nigel Robertson and John Penniket for assistance in gathering the data. This work was funded by a grant from the W.A.I.T. Academic Staff Development Fund. Barbara York Main determined the spiders to family level.

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