

The effects of ants on herbivory and herbivore numbers on foliage of the mallee eucalypt, *Eucalyptus incrassata* Labill.*

DUNCAN A. MACKAY

School of Biological Sciences, Flinders University, Bedford Park, SA 5042, Australia

Abstract

Although there has been much recent interest in ant-plant mutualisms, few data are available on the effects of foraging ants on herbivore numbers and levels of herbivory on plants that do not offer specific inducements to attract ant visitation. In forestry plantations and tropical crops, ants have erratic but sometimes dramatic effects on the numbers of insect herbivores but, in more natural habitats, their effects on levels of herbivory appear to be largely unknown. In Australia, where ants and Eucalyptus woodlands are ubiquitous and abundant and where considerable debate has occurred regarding levels of herbivory in Eucalyptus forests, very little work has been done to examine the effects of ants on densities of insect herbivores on eucalypts.

In this study, ants were experimentally excluded from mature and immature foliage of saplings of the mallee *Eucalyptus incrassata* in South Australia, and herbivore numbers and levels of leaf herbivory were assessed during the next 6 months. No significant differences in herbivory were found between ant-access and ant-exclusion treatments. In spring and early summer, ants were found in associations with aggregations of eurymelid bugs on young foliage, and the effects of ants on bug densities were experimentally investigated. Bug densities decreased rapidly in ant-exclusion treatments compared with ant-access controls. Ants also quickly removed seeds of *E. incrassata* from experimental caches.

The potential of ants to limit the numbers of insect herbivores on eucalypts seems limited given their tendency to form mutualistic associations with sap-feeding Homopterans and because of a lack of other herbivores that are particularly vulnerable to ant predation.

Introduction

Associations between ants and plants that provide ants with specialized rewards such as nectar, food bodies or nest sites are now known to be quite common and widely distributed, both geographically and across ant and plant taxonomic groups (Buckley 1982; Beattie 1985; Hölldobler & Wilson 1990 and references therein). Such associations have long been thought to be mutualisms, with ants benefiting the plants that attract them by foraging over the plant surface and repelling plant herbivores. This hypothesis has now been experimentally tested in many ant-plant associations and, in most (but by no means all) such studies, it has been found that ants do in fact benefit the plants from which they obtain rewards (op. cit.)

Ants are, of course, ubiquitous animals. Hölldobler and Wilson (1990) state that:

Recent measurements suggest that about one-third of the entire animal biomass of the Amazonian *terra firma* rain forest is composed of ants and termites, with each hectare of soil containing in excess of 8 million ants and 1 million termites... Although comparable biomass measurements have not yet been made elsewhere, it is our subjective impression that the eusocial insects, ants foremost among them, are comparably abundant in most other principal habitats around the world.

Given the high densities of ants in many habitats, it seems reasonable to ask whether foraging ants may reduce the densities of herbivores on those plants that do not attract ants by providing nectar or other rewards.

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Several examples of such an effect have been provided by studies of the *Formica rufa* group of wood ants in European forests (reviewed by Adlung (1966)). Ants from nests of *F. rufa* appear to be capable of suppressing the numbers of insect pests on trees over an area of several thousand square metres. However, Adlung (1966) concluded in his review that 'An objective analysis of the published information shows only one clear, unambiguous case where the ants are of value in controlling a forest pest'. Adlung showed that ants commonly preyed upon non-harmful or beneficial insects and that, particularly on broad-leaved trees, they protected harmful sap-sucking aphids. More recently, Skinner and Whittaker (1981) and Fowler and MacGarvin (1985) studied the interactions between *Formica* ants and insect herbivores in forest canopies. These authors also concluded that the overall effects of ants on the trees were complex because ants tended sap-sucking insects as well as preying on other herbivores.

Examples of ants reducing the numbers of insect pests on tropical plantation crops such as cocoa and coconuts are also known (Room 1971; Majer 1976 a, b) although, again, the tendency of ants to tend sap-sucking homopterans on some tree crops has been observed in these habitats (Way 1954).

Beattie (1985) pointed out the paucity of studies of ant protection on plants without ant attractants in natural communities. He hypothesized that, in pristine habitats, homopteran densities may not reach destructive levels, or damage caused by ant-tended homopterans might be outweighed by the beneficial effects of ants in reducing herbivory by other insect pests.

This hypothesis has remained almost completely untested. Grant and Moran (1986), however, examined the effects of ants on herbivores and levels of herbivory on three tree species in an undisturbed South African savannah woodland. Ants were experimentally excluded from some trees with sticky bands around the trunks, and numbers of herbivores and levels of herbivory were subsequently measured on banded and unbanded control trees during a 21-month period. Grant and Moran found that on all three tree species, numbers of sap-sucking Homoptera such as coccids, aphids and leaf-hoppers tended to de-

crease when ants were excluded. Levels of foliar herbivory were low during this study (usually less than 1% of leaf area) although there was a weak and often statistically insignificant tendency for control trees to suffer less herbivory than ant-exclusion trees. These authors concluded that 'plant protection as a consequence of ant-insect interactions appears minimal in the savannah ecosystem'.

In Australia, eucalypts are a dominant and widespread component of the flora. Although eucalypts do not appear to offer specific inducements to ants, ants may be commonly observed ascending the trunks of many eucalypt species or foraging in their foliage. Although the extent of herbivory in natural eucalypt communities has been the subject of intense study and debate in the past decade or so (Fox & Morrow 1983, 1986; Ohmart *et al.* 1983; Morrow & Fox 1989) and some ecological work has been done on the insect faunas of eucalypts in natural settings (e.g. Morrow 1977; Springett 1978; Lowman & Heatwole 1987), almost nothing is known about the ecological effects of ants on such faunas. The present study was undertaken to test the hypothesis that ants may have a significant effect on herbivore numbers and herbivory levels on eucalypts in natural communities.

Methods

Study site and plant species

This study was undertaken in the Monarto Conservation Park, approximately 85 km ESE of Adelaide, South Australia. The climate of this area is semi-arid and the vegetation in the park consists of an open mallee scrubland. The most common mallees in the park are the ridge-fruited mallee (*Eucalyptus incrassata*) and the red mallee (*E. socialis* F. Muell. ex Miq.), and the former was chosen for the present study.

Experimental ant-exclusions from mature and immature foliage

In the Spring of 1986, experiments were set up to investigate the effects of ants on numbers of insect herbivores and leaf damage levels on both immature and mature foliage. For the mature foliage experiment, 20 pairs of saplings

or small trees were chosen so that the members of each pair were separated by a distance of no more than 10 m. One member of each pair was assigned at random to the ant-exclusion treatment, the other being designated as a control. Ants were excluded from exclusion saplings by smearing a layer of sticky Tanglefoot resin on a band of masking tape that was placed around the trunk of the sapling. Trunks of control (i.e. ant-access) saplings were simply banded with masking tape. Two branches of mature foliage of similar size on each sapling were then tagged and the 10–15 terminal leaves on these branches were individually numbered and examined for herbivores and herbivore damage. (Mature leaves are clearly distinguishable from immature leaves, being harder and a darker green in colour.)

For the immature foliage experiment, 20 new saplings were selected and, on each sapling, two branches bearing immature leaves were chosen. One branch chosen at random was banded with masking tape and Tanglefoot (the ant-exclusion treatment) and the other branch (the ant-access control) was banded with masking tape only.

The experimental branches in both experiments were then assessed for damage levels and herbivores at approximately monthly intervals during the next 6 months. At each census, the numbers of leaves on the experimental branches (NLVS) were counted and each leaf was assigned three damage scores on a 0 to 8 scale, where 0 represented no damage, 1 represented up to one-eighth of the leaf damaged and so on up to 8, which represented 100% damage. The first score, MARGIN, estimated the proportion of the leaf margin that was missing; the second, CHEWING, estimated the proportion of the total leaf area that was missing and the third, DAMAGE, estimated the proportion of the remaining leaf area that was damaged by feeding spots, necrosis or galls. The names of these scores are rather arbitrary—both the MARGIN and CHEWING scores would largely reflect damage caused by chewing insects, for example. Landsberg (1989) compared visual estimates of defoliation of individual eucalypt leaves with measurements made with a digitizing tablet, and found very high correlations ($r^2 = 0.99$) between these methods, although visual estimates tended to overestimate proportional

damage. On each census, the numbers of insect herbivores on experimental branches were also recorded.

Comparisons of numbers of leaves and the three herbivory indices between ant-access and ant-exclusion treatments were performed using multivariate repeated measures or profile analysis (Morrison 1976; Potvin *et al.* 1990), as repeated census counts and measurements were taken from the same experimental units. Analyses did not include data taken on the days the experiments were set up. The nature of the replicates used in statistical analyses was determined by the way in which the Tanglefoot treatments were applied. In the immature foliage experiment, in which treatments were applied to branches, individual replicates consisted of damage and density values averaged across the leaves on a branch. Because the design of this experiment employed paired branches on saplings, statistical analyses were conducted on the differences between ant-access and ant-exclusion branches. The null hypothesis of no difference in ant-access and ant-exclusion branches was therefore tested by determining whether the averaged (across censuses) mean difference was significantly different from zero.

For the mature foliage experiment, in which treatments were applied to whole saplings, individual replicates consisted of means taken across the leaves on the two branches surveyed on each sapling. The statistical analysis of these data followed standard procedures for two-sample profile analysis (e.g. Timm 1975, p. 244). First, the null hypothesis of parallelism in the profiles (across censuses) of the ant-access and ant-exclusion treatments was tested with a multivariate test and, if the null hypothesis was accepted, a univariate test of the null hypothesis of equality of ant-access and ant-exclusion group means was then tested.

In March 1987, towards the end of the study, a branch was clipped from each of the ant-access and ant-exclusion saplings in the mature foliage experiment and quickly placed in a plastic garbage bag and sprayed with synthetic pyrethrin insecticide. These branches were later removed from the bags in the laboratory and examined for insect herbivores and other arthropods. The leaves on the branches were then removed, and the leaves and remaining

twigs were oven-dried and weighed so that insect densities could be expressed on a per gram of dry leaf weight basis.

Experimental ant-exclusions from bug aggregations

In Spring and early Summer, while surveying the saplings in the ant-exclusion experiments described above, we saw ants tending aggregations of nymphs and adults of the eurymelid bug *Ipoella porriginosa* (Signoret) on the young foliage of other saplings in the area. The family Eurymelidae is endemic to Australasia and most species feed on eucalypts; the nymphs of these bugs are gregarious and apparently are always tended by ants (Evans 1931; Woodward *et al.* 1970). A further experiment was conducted to examine specifically this ant-bug interaction and its effects on eucalypt leaf damage levels. In October 1987, 20 small (less than 2 m tall) eucalypt saplings with at least two bug aggregations on separate branches were selected. Pairs of branches with similarly sized eurymelid aggregations were chosen on each sapling and the numbers of ants, bugs and leaves on these branches were counted. One branch was then selected at random and banded with masking tape and Tanglefoot to exclude ants; the other was banded with masking tape to serve as an ant-access control. The numbers of ants and bugs were then counted at least once a week until the bugs had disappeared or the experiment terminated in mid-December. When observations on a branch ceased, the branch was clipped from the sapling and returned to the laboratory for final determination of leaf numbers and leaf damage levels. Data on bug survivorship on ant-access and ant-exclusion branches were analysed using the SURVIVAL program of the SPSSx statistical software package.

Seed removal experiment

Apart from their possible effects on foliar herbivores, ants may have a significant effect on the lifetime fitness of eucalypt trees by acting as seed predators. Wellington and Noble (1985) reported that ants quickly removed 65–100% of newly fallen seeds of *E. incrassata* in

Wyperfeld National Park, Victoria and an experiment was conducted in late October 1988 to determine whether ants were also significant agents of seed removal at Monarto. In October, 1988, seeds were collected from fruits of *E. incrassata* at Monarto. Under the canopy of each of 20 *E. incrassata* trees, four plastic petri dishes were placed, each containing 20 *E. incrassata* seeds and each being subjected to one of four exclusion treatments. Each petri dish was glued on to a stand consisting of a piece of plywood on a cork pedestal about 2–3 cm high. The stands were employed so that ants could be excluded from some dishes while still allowing vertebrate access. Four holes about 5 mm in diameter were also pierced through the walls and lid of each petri dish. The treatments used were:

(1) Allow ant and vertebrate access. Petri dish placed on its stand without a lid.

(2) Allow ant, deny vertebrate access. Lid placed over the petri dish and secured with masking tape.

(3) Exclude ants, allow vertebrate access. Petri dish placed on the stand without a lid; cork pedestal ringed with a band of Tanglefoot.

(4) Exclude ants and vertebrates. Petri dish placed on the stand with a lid secured with masking tape, pedestal of the stand ringed with Tanglefoot. This treatment served as a control for the effects of wind and rain in removing seeds.

The weather at Monarto Conservation Park is often very windy, so to reduce losses of seeds caused by wind and rain, each group of four petri dishes was placed under a semi-cylindrical canopy of plastic on a wire mesh frame, approximately 50 cm in diameter and height, and about 1 m in length. This may have reduced vertebrate access to the seed trays. A test-tube pitfall trap containing 70% alcohol was placed next to each group of petri dishes to sample the ant fauna active on the ground during the experiment. Data on seed losses after a week were analysed by a two-factor randomized block analysis of variance, with each group of four petri dishes under a tree canopy constituting a block, one factor being the application (or not) of Tanglefoot on the pedestal (ant exclusion), the other being the application (or not) of the petri dish lid (vertebrate exclusion).

Results

Ant and herbivore densities

The densities of insect herbivores and other arthropods in eucalypt foliage were recorded during censuses of the immature and mature foliage experiments, and from clipped branches at the close of the mature foliage experiment. To facilitate analyses and comparisons with other studies, insect herbivores were categorized as being either sap-sucking or chewing. The former category comprised various Hemiptera such as psyllids and leaf-hoppers, and the latter comprised mainly beetles and various lepidopteran larvae. The numbers of insect herbivores seen in the monthly censuses were quite low, always being less than an average of one per branch; the total number of insect herbivores did not differ significantly between ant-access and ant-exclusion treatments of either the mature or immature foliage experiments on any census (Mann-Whitney *U* test, $P > 0.05$ in all comparisons).

Ants were by far the major component of the insect fauna on the experimental saplings, and most ants seen in mallee foliage belonged to a species group in the genus *Iridomyrmex* that also dominated the ant community on the ground. The relative numbers of ants and insect herbivores on the experimental saplings are shown in Fig. 1a. Yen (1989) examined the invertebrate fauna in the canopies of three mallee species, including *E. incrassata*, on the fringe of the Big Desert in north-western Victoria. Yen sampled canopy invertebrates by beating foliage over a tray, rather than by clipping branches or from censuses, but he also found that ants constituted by far the largest component of the invertebrate fauna (66–92%) on all three mallee species (Fig. 1b).

Herbivory in immature foliage experiment

The mean numbers of leaves on ant-access and ant-exclusion branches over the course of the experiment were compared using profile analysis. The average number of leaves was initially slightly greater on ant-exclusion branches but, by the time of the following census and thereafter, ant-access branches had a greater mean number of leaves than ant-

exclusion branches (Fig. 2). Such a trend is consistent with the ant protection hypothesis but the overall difference between ant-access and ant-exclusion treatments was not statistically significant ($F_{1,13} = 0.53$, $P = 0.48$). Tests on the three indices of leaf damage also failed to reveal a significant effect of ants in affecting levels of foliar herbivory (MARGIN: $F_{1,12} = 3.91$, $P = 0.07$; CHEWING: $F_{1,12} = 0.78$, $P = 0.39$; DAMAGE: $F_{1,10} = 1.89$, $P = 0.20$; Fig. 2).

Herbivory in mature foliage experiment

The null hypothesis of parallelism between ant-access and ant-exclusion sapling censuses could not be rejected for any of the three leaf herbivory indices or for the number of leaves on experimental branches (Fig. 3; multivariate *F*-tests of interactions; $P > 0.13$ in all cases). Comparisons of these variables (averaged across censuses) between ant-access and ant-exclusion treatments were also not significant (NLVS: $F_{1,30} = 0.01$, $P = 0.91$; MARGIN: $F_{1,30} = 0.07$, $P = 0.79$; CHEWING: $F_{1,30} = 0.69$, $P = 0.41$; DAMAGE: $F_{1,30} = 0.21$, $P = 0.65$; Fig. 3).

Ant-eurytomelid experiment

At the beginning of the experiment, prior to application of Tanglefoot barriers, all eurytomelid aggregations consisted entirely of nymphs, almost all in first or second instar. Aggregations contained between 2 and 39 bugs (median = 7) and were tended by up to 70 *Iridomyrmex* ants (median = 8.5), there being no significant initial correlation between ant and bug numbers ($r = 0.14$, $n = 40$, $P = 0.39$). This lack of correlation may simply have reflected the failure of ants to have found a few recently hatched aggregations at that time. The barriers on seven ant-exclusion branches were broached by wind-blown sand and twigs: these branches were not included in subsequent statistical analyses.

The survivorship of bugs on ant-access and ant-exclusion branches was significantly different (Lee-Desu statistic = 9.904, 1 d.f. $P = 0.002$) with bug numbers decreasing more rapidly on branches from which ants were excluded (Fig. 4). The median survival time for

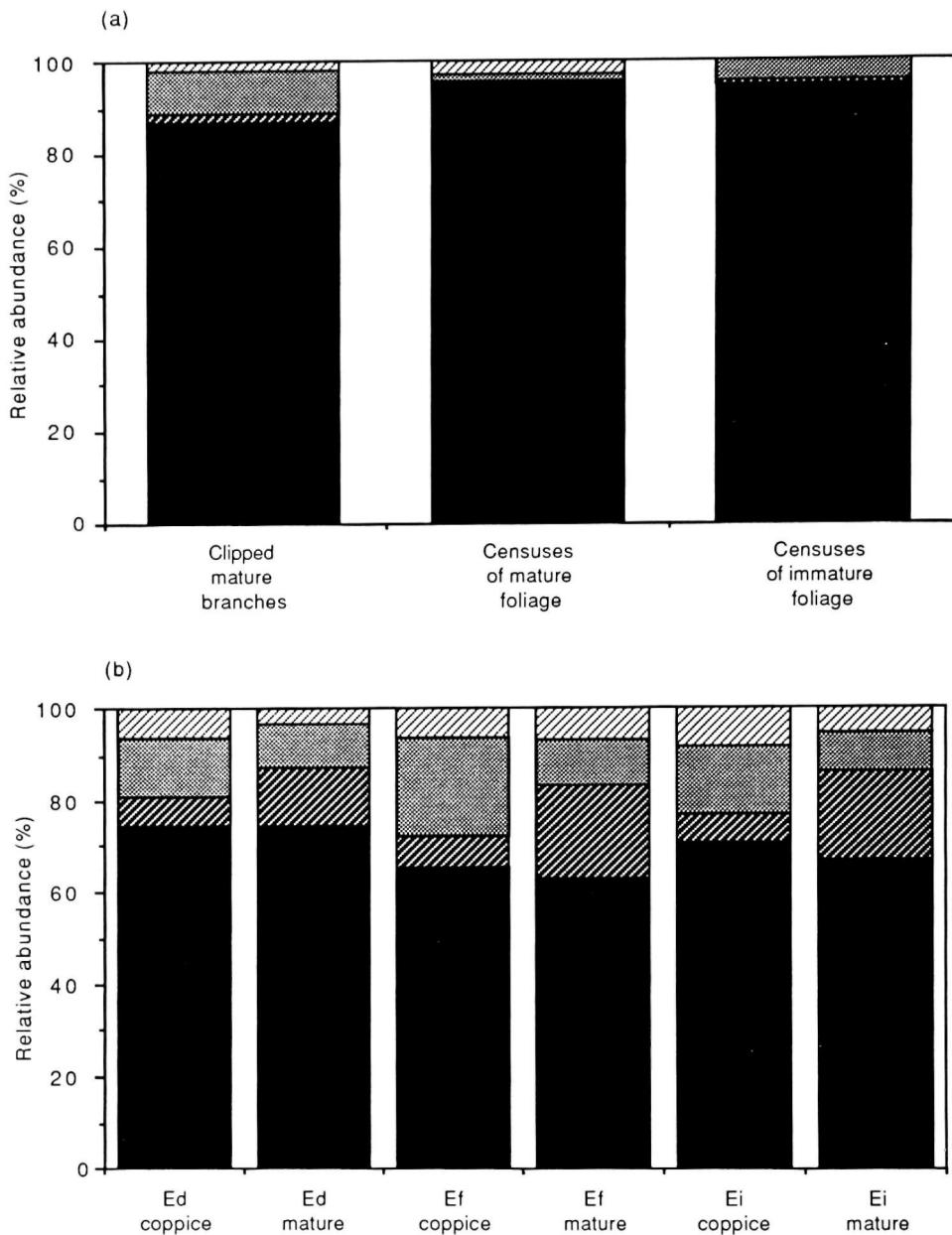


FIG. 1. Relative abundances of (▨) chewing insects, (▨) sucking insects, (▨) spiders and (■) ants in the canopies of mallee eucalypts. Data in (a) were obtained in the present study. Percentages for clipped mature branches were derived from weights of arthropods per kg of dry leaf weight on 15 ant-access branches; those for mature foliage censuses were derived from 95 observations of ant-access branches and those for immature foliage censuses from 87 observations of ant-access branches. Data in (b) were derived from Yen (1989). Ed coppice = *E. dumosa* coppice foliage, $n = 859$ insects; Ed mature = *E. dumosa* mature foliage, $n = 647$; Ef coppice = *E. foecunda* coppice foliage, $n = 1086$; Ef mature = *E. foecunda* mature foliage, $n = 562$; Ei coppice = *E. incrassata* coppice foliage, $n = 650$; Ei mature = *E. incrassata* mature foliage, $n = 597$.

bug aggregations on ant-access branches was estimated at 42 days and that for bug aggregations on ant-exclusion branches at 19 days. Aggregations without ants were also seen to

produce fewer adults than aggregations with ants (Table 1; G-statistic of independence with Williams' correction (Sokal & Rohlf 1981, p. 737) = 5.29, 1 d.f., $P = 0.02$), and ag-

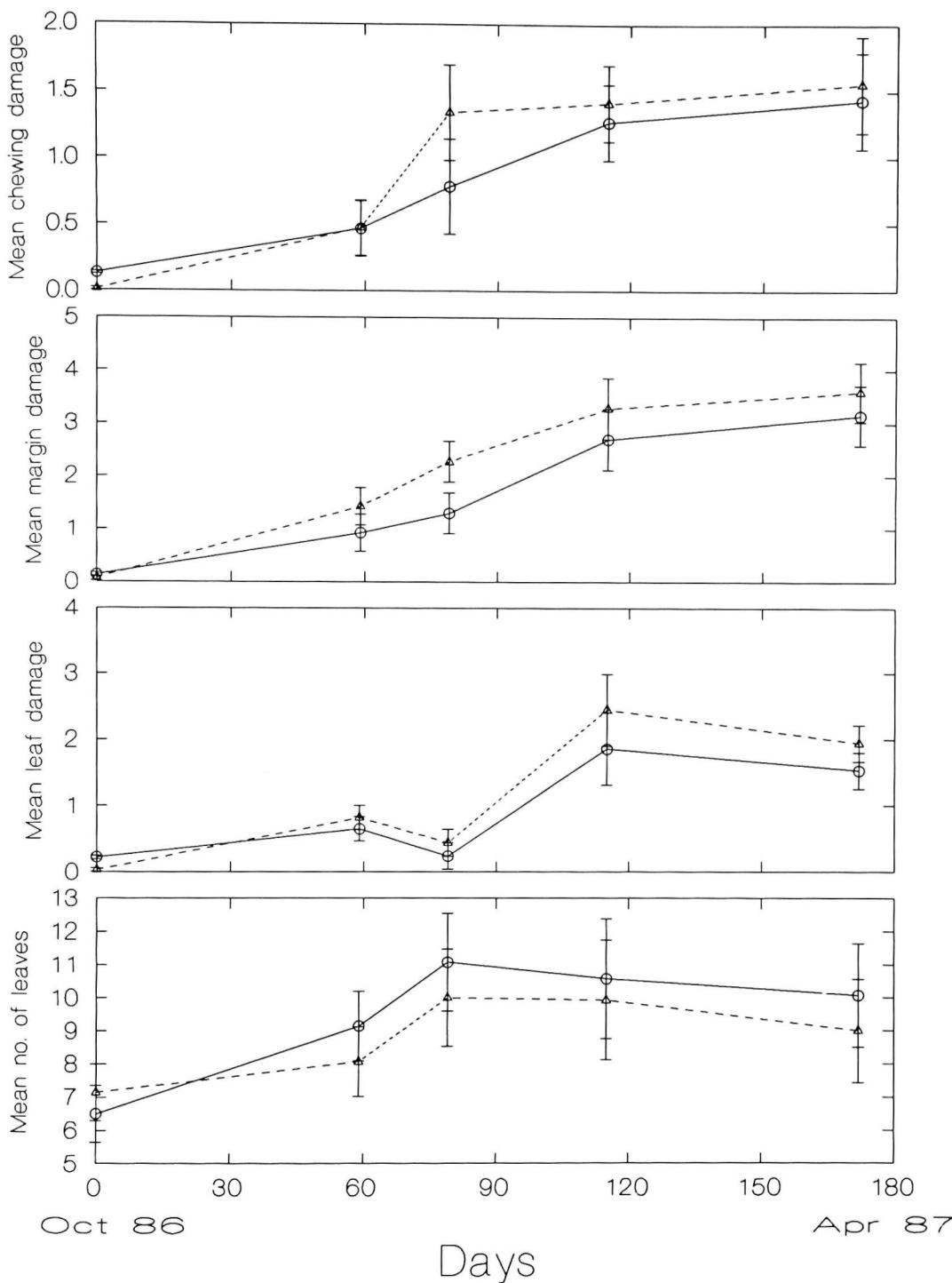


FIG. 2. Means of the CHEWING, MARGIN and DAMAGE leaf damage scores and of the number of leaves on (—) ant-access and (---) ant-exclusion branches at censuses of the immature foliage experiment. Error bars are standard errors.

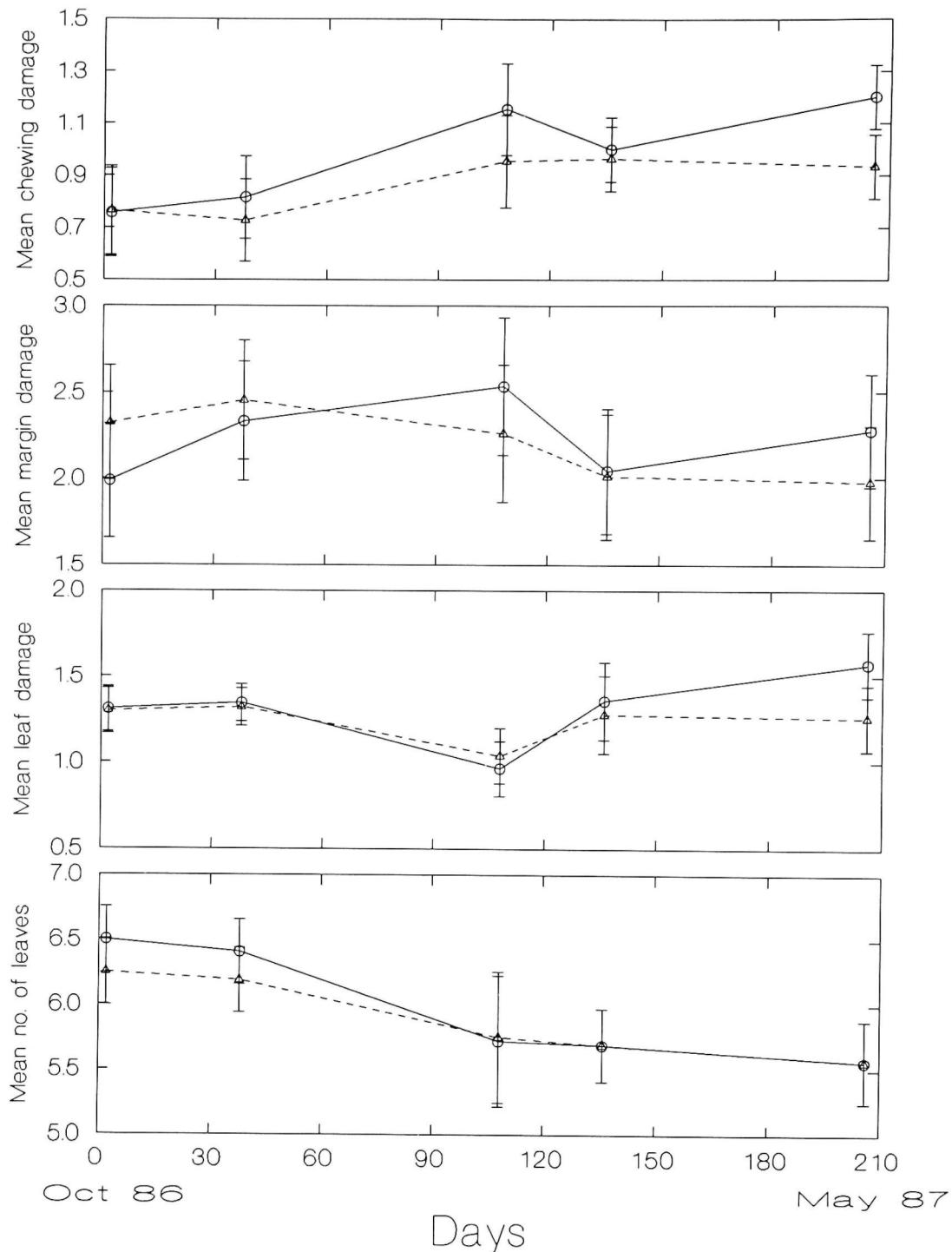


FIG. 3. Means of the CHEWING, MARGIN and DAMAGE leaf damage scores and of the number of leaves on (—) ant-access and (---) ant-exclusion branches at censuses of the mature foliage experiment. Error bars are standard errors.

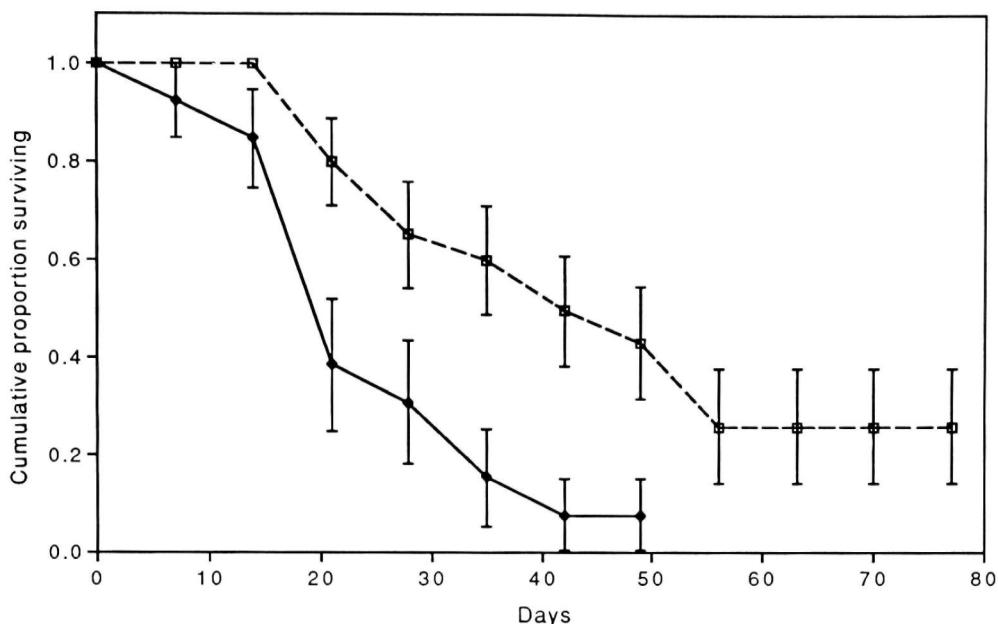


FIG. 4. Estimated survivorship of bug aggregations on (---) ant-access and (—) ant-exclusion branches of experimental saplings. Error bars are standard errors.

TABLE 1. Production of adults by eurymelid aggregations

Treatment	Seen to produce adults	Not seen to produce adults	Total
Ant access	11	9	20
Ant exclusion	2	11	13
Total	13	20	33

TABLE 2. Change in size of eurymelid aggregations

Treatment	No. increasing	No. not increasing	Total
Ant access	14	6	20
Ant exclusion	0	13	13
Total	14	19	33

TABLE 3. Measures of plant growth and herbivory in ant-eurymelid experiment

	Ant-access branches*	Ant-exclusion branches*	Mann-Whitney <i>U</i> statistic, <i>P</i>
% new growth	86.4 ± 10.3	72.5 ± 13.3	149.0, 0.33
Leaf damage	2.8 ± 0.2	3.1 ± 0.3	105.5, 0.49

*Mean \pm standard error.

gregations without ants never increased from their initial size, whereas aggregations tended by ants frequently increased in numbers (Table 2; $G = 19.58$, 1 d.f., $P < 0.001$).

At the end of the experiment, levels of leaf damage and the percentage change (from initial measurements) in the number of new buds and leaves were measured on ant-access and

ant-exclusion branches. Levels of new growth were actually slightly higher, and levels of damage slightly lower, on ant-access branches compared with ant-exclusion branches, although neither difference was statistically significant (Table 3).

Seed removal experiment

The effect of the ant-exclusion treatment on numbers of *E. incrassata* seeds taken over a week was highly significant, whereas the effect of the vertebrate exclusion was not, nor was the interaction between ant and vertebrate exclusions (Fig. 5; Table 4). Approximately 63% of seeds were removed from ant-access dishes at the end of the week, compared with 11% from ant-exclusion dishes. Two of the 20 pitfall traps were dug up by unknown agents during the experiment. A total of 1632 ants in nine genera were collected in the remaining 18 traps, the most common four genera (*Iridomyrmex* (94.3%), *Pheidole* (3.5%), *Camponotus* (0.8%) and *Melophorus* (0.7%)) accounting for more than 99% of the total.

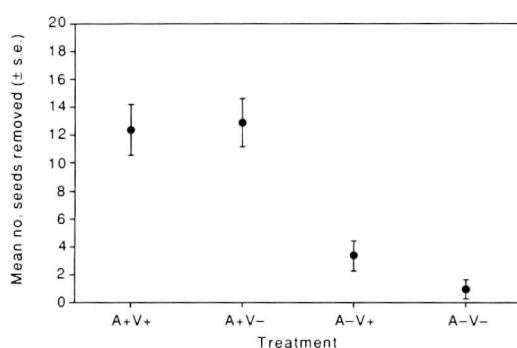


FIG. 5. Numbers of *E. incrassata* seeds removed (of 20) from petri dishes of the seed removal experiment. Treatment codes: A + V + = ant and vertebrate access; A + V - = ant access, vertebrate exclusion; A - V + = ant exclusion, vertebrate access; A - V - = ant and vertebrate exclusion.

Discussion

Although comparative data are not extensive, it appears that the relative and absolute densities of ants found in mallee eucalypt canopies by Yen (1989) and in this study are considerably higher than those reported from studies on non-mallee eucalypts elsewhere in southern Australia. Ohmart *et al.* (1983), for example, sampled the arthropod communities in the canopies of three sub-alpine forests 50 km west of Canberra that were dominated by *Eucalyptus delegatensis*, *E. dives* and *E. pauciflora* respectively. On a per kg of dry foliage basis, the densities of the arthropod groups found in their study and in the present study respectively are: spiders (13–28 and 10), sap-sucking insects (5–14 and 49); chewing insects (10–15 and 12) and ants (0 and 469). Woinarski and Cullen (1984) clipped branches to sample the invertebrate fauna of 156 plant species, including 34 species of *Eucalyptus*, the latter including *E. incrassata* and several other mallee species. Insect densities were expressed on a per m² of leaf area basis; these data indicated that ants comprised only a minor (< 10%) component of the canopy faunas on eucalypts. However, these authors excluded all invertebrates less than 3 mm in length from their estimates of densities and this procedure may well have led to an underestimate of ant densities. Majer and Recher (1988) reported results of chemical knockdown and branch clipping censuses of invertebrates in the canopies of three species of Western Australian eucalypts, wandoo (*E. wandoo*), jarrah (*E. marginata*) and marri (*E. calophylla*). They found that ants were usually the most abundant animals in knockdown samples, constituting up to 48% of invertebrate numbers, although they generally comprised a smaller fraction of the total invertebrate biomass (up to 12%) or of numbers of invertebrates on clipped branches

TABLE 4. Analysis of variance of number of *E. incrassata* seeds taken from dishes of seed removal experiment

Source of variation	d.f.	Mean square	F	P
Ant exclusion (A)	1	2125.500	79.782	0.000
Vertebrate exclusion (V)	1	17.338	0.651	0.423
A*V interaction	1	43.286	1.625	0.208
Canopy (block)	19	80.977		
Error	55	26.641		

(up to 28%). Majer (1990) indicated that 'the use of trees in southern Australia by tree- or ground-nesting ants is generally not high, although ants are locally abundant on trees where conditions are optimal.'

Yen (1989) noted that the abundance of ants on three mallee species was not correlated with the abundance of sucking insects and he attributed the relatively high ant densities in mallee canopies to the suitability of the mallee habitat as a whole for ants, rather than to indirect ant–arthropod–plant interactions. Observations made in the present study were consistent with this view: very high densities of foraging ants were observed on the ground and the high numbers of arboreal ants may simply reflect the low stature of mallees. Although densities of arboreal ants were high, no significant effects of ants on total herbivore numbers or levels of foliar herbivory were revealed in ant-exclusion experiments. The results of these experiments are therefore similar to those of Grant and Moran (1986) in that ants were not found to have a major role in protecting the plants that they foraged on.

In the experiment conducted to examine specifically the interactions between ants, eurymelid bugs and eucalypts, it was found that ants had a marked effect on bug survivorship, with ant-tended bug aggregations showing significantly higher survivorship than non-tended aggregations. Buckley (1990) found that *Iridomyrmex* ants significantly increased the survivorship of eurymelid aggregations on *Eucalyptus* and *Melaleuca* saplings by reducing nocturnal spider predation. The only instance of predation seen in the present study was an attack by an unidentified spider on a nymph in a non-tended aggregation. Presumably, ants enhanced bug survivorship by protecting aggregations from predators and parasites. No nocturnal observations were made in this study. Because only ant-tended aggregations increased more than their initial sizes, it may be that ant protection is particularly important for the survival of eggs or early instar nymphs. Levels of leaf damage and of new foliage production did not differ significantly between ant-access and ant-exclusion branches. Because bug numbers and survivorship were enhanced on ant-access branches, the reason for the lack of difference in herbivory is unclear. Small aggregations of

bugs may produce as much apparent damage as large aggregations, or saplings may compensate for low levels of herbivory by an increased production of new tissue. Alternatively, herbivores other than eurymelids may cause more damage on ant-exclusion branches than on ant-access branches, although such an effect was not seen in the immature and mature foliage experiments.

The results of the seed removal experiment are consistent with those obtained by Wellington and Noble (1985), indicating that seed-harvesting ants are capable of removing most newly fallen *E. incrassata* seeds within a week. Wellington and Noble considered that harvested seeds are unlikely to contribute to future mallee recruitment. If so, this loss probably represents a way in which the activities of ants negatively affect mallee fitness.

In summary, the effects of ants on the survival and reproduction of the mallee eucalypt, *E. incrassata*, were found to be neutral or negative. Ants were not observed to reduce significantly insect herbivore numbers or levels of leaf herbivory on immature or mature foliage. On the other hand, ants were shown to be capable of increasing the densities and survivorship of a sap-sucking herbivore and ants were also shown to be significant agents of seed removal. The few other studies performed in natural communities on the effects of ants on plants that lack specific ant attractants have also shown that ants are at best sporadic or minimal defenders against herbivory. The results from studies in natural habitats are similar to those performed in disturbed or agricultural settings, which have found that the effects of ants on plant fitness are very complex. Positive effects caused by ants deterring herbivores are potentially counterbalanced by their negative effects in tending sap-sucking Homoptera or in harvesting seeds. These results, therefore, do not support the view that plant protection by ants is more beneficial in natural communities than in agricultural or forestry situations.

Effective plant protection by ants appears likely when herbivores vulnerable to ant attack become numerous, or when ants that are effective against herbivores dominate the vegetation (Mackay & Whalen 1991). Adlung (1966) noted that wood ants in European forests specialized on pests undergoing popu-

lation outbreaks. He also noted that lepidopteran larvae were preferred prey. Soft-bodied exterior-feeding caterpillars may be particularly susceptible to ant defence. Such insects were very rarely observed on *E. incrassata*: most lepidopteran larvae observed were covered in long hairs or spines, or they fed in shelters that they constructed by rolling or sticking leaves together.

In the context of the failure of ants to protect mallee eucalypts from herbivory, it is interesting that members of another common and widely distributed plant genus in Australia, *Acacia*, frequently possess extra-floral nectaries. Acacias and eucalypts frequently occur in the same habitats. It is not yet known whether most of the nectaries on acacias are effective in attracting ants or whether this is their chief function but, if they are, the question arises as to why acacias should find it worthwhile attracting ants when eucalypts do not. It would be interesting to determine whether the herbivore faunas on co-occurring eucalypts and acacias were different and whether the provision of nectar by acacias enabled them to preferentially attract ants that were effective as defensive agents.

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