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Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential antiherbivore agents

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Summary. *Qualea grandiflora* is a typical tree of Brazilian cerrados (savanna-like vegetation) that bears paired extrafloral nectaries (EFNs) along its stems. Results show that possession of EFNs increases ant density on *Q. grandiflora* shrubs over that of neighbouring non-nectariferous plants. Frequency of ant occupancy and mean number of ants per plant were much higher on *Qualea* than on plants lacking EFNs. These differences resulted in many more live termite-baits being attacked by foraging ants on *Qualea* than on neighbours without EFNs. Termites were attacked in equal numbers and with equal speeds on different-aged leaves of *Qualea*. The greatest potential for herbivore deterrence was presented by *Camponotus* ants (*C. crassus, C. rufipes* and *C.* aff. *blandus*), which together attacked significantly more termites than nine other ant species grouped. EFNs are regarded as important promoters of ant activity on cerrado plants.

Key words: Ant foraging – Extrafloral nectaries – *Qualea* – Cerrado vegetation – Ant-plant mutualism

Extrafloral nectaries (EFNs) are nectar-secreting organs not directly involved with pollination functions (Delpino 1875). Such nectaries are extremely variable in structure and location, and occur in many plant taxa, especially in tropical regions (Elias 1983). Ants are by far the most frequent visitors of EFNs, and many recent field studies have demonstrated that these insects can effectively protect the plant against herbivore damage (Koptur 1984; Barton 1986; and citations therein).

Despite the relatively high frequencies that plants with EFNs may reach in some areas of cerrado vegetation (Oliveira and Leitão-Filho 1987), the ecological function of these glands has never been investigated in this vegetation type. The cerrados cover approximately 25% of Brazil and present several intergrading physiognomic forms within their distribution, ranging from forest with more or less merging canopy ('cerradão') to open grassland with scattered shrubs ('campo sujo'). The cerrado *sensu stricto* consists of a dense scrub of shrubs and trees (Goodland 1971). *Qualea grandiflora* Mart. (Vochysiaceae) is a typical cerrado tree that reaches high abundances in southeast Brazil (Gibbs et al. 1983). This species, as others in the genus *Qualea,* has paired EFNs along its stems, next to the insertion of leaves. Ants of several species are frequently observed on *Q. grandiflora,* and actively search for extrafloral nectar on all plant branches.

This paper investigates the following questions concerning the interaction between ants and *Q. grandiflora:* (1) Does the presence of EFNs increase ant visitation on *Qualea* over that on non-nectariferous plant species? (2) Do ant visitors find and attack animals (i.e., potential herbivores) on plant leaves? (3) Is there a differential foraging and protection by ants on different-aged leaves of the plants?

Materials and methods

Field work was undertaken from January to April 1985, in an area of cerrado *sensu stricto* at Itirapina (22°15′S, 47°49′W), state of São Paulo, southeast Brazil.

One hundred pairs of experimental plants were tagged in the cerrado of Itirapina. These pairs consisted each of a shrub of *Q. grandiflora* (0.6–1.2 m tall) and the nearest similar-sized plant species without EFNs. Neighbouring plants having honeydew-producing homopterans were not included since these insects and EFNs can sometimes have very similar ecological functions (Messina 1981). To see whether EFNs increased ant density over that on non-nectariferous plants, the number of ants present on each plant of experimental pairs was recorded upon our arrival. The behavior of foraging ants toward potential herbivores was evaluated by using live workers of the termite *Armitermes euamignathus* as baits (i.e., simulated herbivores) for ants on experimental plant pairs. Live baits have already been used in the field to evaluate patterns of ant predation (Jeanne 1979; Barton 1986). Three termite-baits were placed simultaneously on three different-aged leaves (upper, middle and lower portions of branches) of a plant, totalling 300 baits for each class (i.e., with and without EFNs) of experimental plants. Live termites were glued by the dorsum (agitating legs upwards) on the basal third of leaf blades. Ants were neither attracted to nor repelled by the adhesive (Cascolar® plastic glue, Alba Química, Brasil). Once baiting was completed on an experimental plant pair, attacks by foraging ants on termites were monitored simultaneously, each minute during a 15 min period, for both plants of the pair. The number of ants of each species attacking (biting and/or stinging) the termites was registered within this period. Due to the small number of baits attacked on non-nectariferous neighbours, only data from *Qualea* were ana-

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Table 1. Differences in ant visitation and ant attacks on termites, between *Qualea grandiflora* and non-nectariferous nearest-neighbours in cerrado vegetation

Variable	*Qualea grandiflora* ($N=100$)	Nearest neighbour ($N=100$)	Significance of difference
Number of plants occupied by ants	92	8	$P<0.001$ (χ^2 test)
Ants per plant ($\bar{X} \pm 1$ SD)	4.42 ± 4.28	0.14 ± 0.53	$P<0.001$ (t test)
Number of baits (3 per plant) attacked in 15 min	191	6	$P<0.001$ (χ^2 test)

lysed for ant patrolling activity. The scores of three abundant *Camponotus* species (*C. crassus*, *C. rufipes* and *C.* aff. *blandus*) are treated together due to the difficulty in distinguishing these agile ants from one another in the field. Ant censuses and bait-experiments on plant pairs were carried out intermittently, in sunny days, between 0800 and 1200 h.

Results

The proportion of *Qualea grandiflora* plants occupied by ants greatly surpassed that of neighbouring plants without EFNs (Table 1). The number of ants on experimental plant pairs ranged from 0 to 35 for *Qualea* ($\bar{X}=4.42$) and from 0 to 3 for nearest neighbours ($\bar{X}=0.14$). At least five ants were present on 44% of the *Qualea* shrubs censused. Ants attacked significantly more termites on *Qualea* than on nearest neighbours ($P<0.001$, Table 1).

Twelve ant species were observed attacking termites on *Qualea*; three abundant *Componotus* species (*C. crassus*, *C. rufipes* and *C.* aff. *blandus*) together attacked significantly more termites than nine other species grouped ($P<0.001$, Table 2). Once finding a termite, *Camponotus* ants (size 0.5–1.0 cm) attacked it fiercely with several bites, readily removing the entire prey item. Other ants (e.g., *Zacryptocerus*, *Pseudomyrmex*), besides being only occasional visitors to the EFNs of *Qualea*, were either less alert and aggressive toward the termites, or too small to subdue and transport the prey item as promptly as *Camponotus*.

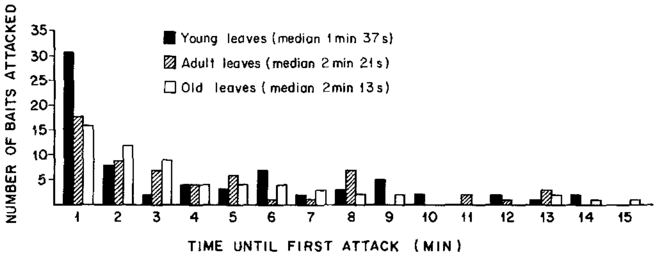

Fig. 1. Temporal distribution of ant attacks on termite-baits placed on different-aged leaves of *Qualea grandiflora* shrubs. Each leaf age-class received 100 baits, totalling 300 baits for all shrubs monitored ($N=100$). The distributions are statistically similar (Kruskal-Wallis test, adjusted $H=0.4938$, $P>0.5$). See also Table 2

Attacks on termites by foraging ants were uniformly distributed among different-aged leaves of *Qualea* (Table 2), indicating a spatial homogeneity of ant patrolling activity within the plant crown. The temporal distributions of ant attacks are also statistically similar among leaf age-classes ($P>0.5$); termites are attacked at equal rates irrespective of leaf age (Fig. 1).

Discussion

The results strongly support the hypothesis that possession of EFNs increases ant density on *Qualea grandiflora* over that of non-nectariferous plants. Both the frequency of ant occupancy and mean number of ants per plant are much higher on *Qualea* than on neighours lacking EFNs. These differences in ant visitation levels clearly resulted in many more termites being attacked by foraging ants on *Qualea* than on plants without EFNs, and strengthens the suggestion that ants could act as effective antiherbivore agents of *Qualea* in cerrado vegetation. Similar results were obtained by Barton (1986) in Florida (USA) with *Cassia fasciculata*, a herbaceous legume bearing EFNs on petioles: ants occupied 61.4% of the *Cassia* individuals censused (averaging 3.7 ants per plant), against less than 10% of non-nectariferous plants. Using *Drosophila* larvae as simulated herbivores, Barton (1986) also showed that the removal rate of larvae by ants was significantly higher on *Cassia* than on non-nectariferous neighbours.

Termites were attacked in equal numbers and with equal speeds on different-aged leaves of *Qualea* shrubs. Differential foraging by ants on leaves of different ages has been shown to occur in plants that maintain obligate mutualisms with ants (Janzen 1967; McKey 1984). In the swollen-thorn

Table 2. Distribution of attacks by ants on termite-baits placed on different-aged leaves of *Qualea grandiflora* in cerrado vegetation. Ant attacks are independent of leaf age ($\chi^2=0.097$, $P=0.95$, NS). *Camponotus* ants attacked significantly more termites than all other species together ($\chi^2=107.1$, $P<0.001$)

Ant species	Number of baits attacked			
	young leaves ($N=100$)	adult leaves ($N=100$)	old leaves ($N=100$)	all leaves ($N=300$)
Camponotus spp. (*C. crassus*, *C. rufipes* and *C.* aff. *blandus*)	63	51	53	167
Nine other species	9	8	7	24
Total	72	59	60	191

Acacia cornigera, the greater patrolling activity of ant inhabitants on shoot tips, as contrasted with older foliage, appears to be correlated with greater production of extrafloral nectar and food bodies on young leaves (Janzen 1967). In facultative ant-plant mutualisms (Boucher et al. 1982), plants bearing EFNs are expected to allocate more nectar both to portions of the plant and to time periods more vulnerable to herbivore attack (cf. Bentley 1977). In trees of *Q. grandiflora* (≈15 m tall) the farther an EFN is located from shoot tips the darker (brown) and less frequently visited by ants it becomes, due presumably to the low quantity of secreted nectar. On the other hand all shrubs of *Q. grandiflora* monitored in this study (up to 1.2 m tall) had EFNs active, green, and intensively visited by ants, irrespective of their location within the plant. Therefore the spatial uniformity of ant patrolling activity on the shrubs could be related to the uniform distribution of extrafloral nectar within the plant foliage. Although we have not measured extrafloral nectar production by either shrubs or trees of *Qualea*, it seems that nectar distribution within the foliage changes as the plant grows larger.

As several authors have already demonstrated, many ants tend to behave aggressively toward phytophagous insects found on EFN-bearing plants, but their effectiveness as antiherbivore agents clearly varies among different ant species (cf. Schemske 1980; Koptur 1984). Although all ant species recorded on *Qualea* leaves attacked the termites, the greatest potential for herbivore deterrence was clearly presented by the larger, more common and aggressive *Camponotus* ants (*C. crassus, C. rufipes* and *C.* aff. *blandus*). The study conducted by Morais (1980) on the arboreal ant community of cerrado vegetation showed that *Camponotus rufipes* and *C. crassus* are the most abundant species of this vegetation type, foraging intensively on foliage. In fact, these two ant species occur in almost all regions of Brazil (Kempf 1972) and their distributions correspond quite well with the geographical range of Brazilian cerrados.

This is the first study to provide evidence for the ecological significance of EFNs in cerrado vegetation. The results suggest that EFNs are very important in promoting ant activity on cerrado plants, and enhance the potential of these insects as antiherbivore agents in neotropical savannas. Future research will attempt to elucidate more precisely the nature of the interactions between ants and *Qualea*. The wide taxonomic distribution and relatively high abundance of EFNs in cerrado vegetation (Oliveira and Leitão-Filho 1987) certainly stimulate well-designed experiments aiming to assess the relevance of these glands for this vegetation type.

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