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The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae)

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Summary

1. Shrubs of *Caryocar brasiliense* are intensively visited by many ant species in the cerrado vegetation of south-east Brazil. Ants collect nectar from the extrafloral nectaries (EFNs) located on the buds at the apex of the plant.
2. The proportion of *C. brasiliense* shrubs occupied by ants greatly surpassed that of neighbouring plants without EFNs and this resulted in many more termites being attacked and removed on this plant than on plants lacking EFNs. Ant attacks on *Caryocar* were more frequent near the EFNs.
3. Ant-exclusion experiments with *Caryocar* shrubs revealed that ants significantly reduce the infestation levels by the butterfly *Eunica bechina*, the sucking bud *Edessa rufomarginata*, the bud-destroying fly *Prodiplosis floricola* and by a stem-galling wasp. Ants had no effect on the infestation by a leaf-galling wasp.
4. Control (ants present) and treatment (ants excluded) plants produced equal numbers of buds but flower and initial fruit production was significantly greater for ant-visited plants. Higher abortion rates of initial fruits by control plants resulted in similar final fruit and seed sets for plants in either experimental category.
5. The extremely low fertility of cerrado soils is suggested as a possible factor constraining the ability of *Caryocar* shrubs to provide the resources necessary for growth and development of their heavy fleshy fruits. Higher production of initial fruits by ant-visited shrubs would be neutralized by competition among developing fruits and subsequent abortion.
6. Possible ant-derived benefits to *C. brasiliense* include: protection of vegetative tissues during plant growth, larger floral display and increased attractiveness to bat pollinators, increased male contribution to fitness through pollen donation and selective abortion of genetically inferior progeny as the maternal investment is adjusted to match available resources.

Key-words: Ant–plant interaction, cerrado vegetation, fruit abortion, fruit set, mutualism

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Introduction

Ants may interact with plants in a variety of ways and in the past decades a number of experimental field studies have evidenced the high frequency with which such associations are mutualistic (reviews in Beattie 1985; Koptur 1992; Davidson & McKey 1993). The role of ants as anti-herbivore agents of many plant species has been repeatedly demonstrated in facultative and obligate ant–plant mutualisms, both in temperate and tropical environments (Janzen 1967; Bentley 1977; Inouye & Taylor 1979; Koptur 1979; Schemske 1980; McKey 1984; Fonseca 1994). Ant visitation to extrafloral nectaries (EFNs) has been shown to increase plant fitness by deterring leaf

herbivores (Koptur 1979; Stephenson 1982; Smiley 1985), flower herbivores (Schemske 1980; Horvitz & Schemske 1984) and seed predators (Inouye & Taylor 1979; Pickett & Clark 1979; Keeler 1981). Ant protection, however, is not universal and several other studies have also demonstrated that visiting ants may not benefit EFN-bearing plants (O'Dowd & Catchpole 1983; Heads & Lawton 1984; Whalen & Mackay 1988; Rashbrook, Compton & Lawton 1992). Extrafloral nectar is a generalized food source that attracts a wide variety of ant taxa and the non-specialized nature of ant–plant mutualisms mediated solely by the supply of nectar has been stressed by several authors (Schemske 1983; Addicott 1984; Beattie 1985; Koptur 1992). Therefore the benefits to the

plants vary both geographically and temporally, and depend largely on the protective abilities of the ant visitors and the corresponding capacity of specialized herbivores to circumvent the ants' deterring traits (Koptur 1992, and included references).

Plants bearing EFNs are widely distributed amongst the woody flora of the 'cerrado' woodland of Brazil; up to 25% of the local species may have EFNs and together they may account for 31% of the woody individuals in a given cerrado area (Oliveira & Leitão-Filho 1987; Oliveira & Oliveira-Filho 1991). The ant fauna associated with EFNs in the cerrado is taxonomically diverse (see Oliveira & Brandão 1991; Oliveira, Klitzke & Vieira 1995) and experimental field studies have shown that visiting ants can act as anti-herbivore agents and reduce leaf damage on trees of *Qualea grandiflora* Mart. (Vochysiaceae) (Oliveira, Silva & Martins 1987; Costa, Oliveira-Filho & Oliveira 1992). Moreover, Del-Claro, Berto & Réu (1996) have recently demonstrated that ant visitation to *Qualea multiflora* Mart. not only reduces herbivore damage to both leaves and reproductive parts (buds and flowers) but also increases fruit set in this plant species.

The present field study examines the anti-herbivore effect of ants visiting the EFNs of *Caryocar brasiliense* Camb. (Caryocaraceae), a plant producing heavy fleshy fruits (see below), and its possible influence on the plant's reproductive output in a cerrado area in south-east Brazil. Four questions were addressed: (1) does the presence of EFNs increase ant visitation to *C. brasiliense* over that of non-nectariferous plants; (2) do ant visitors behave aggressively towards other organisms (i.e. potential herbivores) on the plants and is aggression more pronounced near the EFNs; (3) does ant visitation to EFNs reduce the infestation levels by the principal insect herbivores of *C. brasiliense*; (4) does herbivore deterrence affect the reproductive output of *C. brasiliense*?

THE PLANT, THE ANT VISITORS AND THE HERBIVORES

Caryocar brasiliense is a main representative of the cerrados, growing wherever this vegetation type is found from north to south Brazil (Prance & Freitas da Silva 1973). In the nuclear area of its distribution the species appears as a large tree but it may also occur as a shrub in the southern limit of the cerrados (Barradas 1972). In south-east Brazil the inflorescences are racemes of one to 27 hermaphroditic flowers (mean \pm SD = 12.2 ± 4.6 , $n=70$) located at the apex of the stem and positioned outside of the shrub's foliage. The fruits are drupes weighing up to 400 g and containing one to four seeds coated by woody endocarp and a fleshy mesocarp. The species is bat-pollinated and self-compatible, and an account of its floral biology and breeding system in central Brazil is given by Gribel & Hay (1993).

Shrubs of *C. brasiliense* are intensively visited by many ant species which actively collect extrafloral

nectar on the outer surface of the bud sepals and at the margins of shoot tips. Extrafloral nectar sugar concentrations (sucrose equivalent) in *C. brasiliense* range from 10.5 to 14% (Oliveira 1988). A total of 34 ant species was recorded visiting the plant's EFNs, with a clear daily turnover in ant species composition and a marked dominance of the formicine genus *Camponotus* (a detailed account of the ant fauna associated with the EFNs of *C. brasiliense* is given by Oliveira & Brandão 1991).

Shrubs of *C. brasiliense* are infested by five principal insect herbivores. (1) *Eunica bechina magnipunctata* Talbot (Lepidoptera: Nymphalidae): eggs are laid singly on young leaves and shoot tips (87% and 10%, respectively; $n=141$); larvae feed preferentially on young leaves (Oliveira & Freitas 1991; Freitas & Oliveira 1992). (2) *Edessa rufomarginata* (De Geer) (Hemiptera: Pentatomidae): adults mate on the plant and batches consist of six to 14 eggs; nymphs and adults feed on buds and fruits. (3) *Prodiplosis floricola* (Felt) (Diptera: Cecidomyiidae): females oviposit on exposed developing buds which are destroyed by the larvae. (4) Unidentified stem-galling wasp (Hymenoptera: Chalcidoidea): induces galls along the stem; heavily attacked branches are deprived of leaves and reproductive organs. (5) Unidentified leaf-galling wasp (Hymenoptera: Chalcidoidea): induces galls over the leaf blade; heavily attacked leaves fall prematurely.

Materials and methods

Fieldwork was carried out from 1985 to 1987 in an area of cerrado vegetation near Itirapina ($22^{\circ} 15' S$, $47^{\circ} 49' W$), State of São Paulo, south-east Brazil. The vegetation consists of a dense scrub of shrubs and trees, which corresponds to the cerrado *sensu stricto* of Goodland (1971a). The climate of the region is characterized by a dry/cold season (May to September) and warm/rainy season (November to March). *Caryocar brasiliense* is one of the most abundant shrubs in the area, occurring at a density of nearly 300 individuals per ha.

The pattern of ant visitation on the vegetation was evaluated by tagging 60 experimental plant pairs, each consisting of a shrub of *C. brasiliense* (1–1.5-m tall) and the nearest similar-sized plant species without EFNs. Neighbouring plants hosting honeydew-producing homopterans were avoided because these insects and EFNs can sometimes have very similar ecological functions (Messina 1981). To see whether EFNs increased ant density over that expected on non-nectariferous plants, the number of ants present on each plant of a pair was recorded upon my arrival. To evaluate whether foraging ants would attack potential herbivores on the plants, live workers of the termite *Armitermes euamighnathus* Silvestri (Termitidae) were used as bait on experimental plant pairs. Live bait has already been used in the field to evaluate

patterns of ant predation on ant-visited plants (Barton 1986; Oliveira *et al.* 1987; Freitas & Oliveira 1996). Six live termites were placed simultaneously on both plants of a pair. Shrubs of *C. brasiliense* were baited with two termites on the inflorescence, two on young leaves and two on adult leaves (one termite per leaf). Similarly, plants without EFNs had equal numbers of termites placed on young, adult and old leaves. Live termites were glued by the dorsum (agitated legs upwards) with a fast-drying adhesive (Cascolar® palstic glue, Alba Química, Brasil) which apparently had no effect on ant behaviour. Attacks on termites by foraging ants were monitored simultaneously for both plants of a pair during a 15-min period. Ant censuses and bait-experiments on plant pairs were carried out during October and November 1985. Thirty plant pairs were monitored during sunny days (08.00–12.00 h) and 30 during clear nights (19.00–24.00 h). A given plant pair was used only once.

The protective role of visiting ants against herbivores of *C. brasiliense* was tested through ant-exclusion experiments. By August 1986, before the beginning of the wet season, 40 randomly chosen control plants and 40 treatment plants of *C. brasiliense* (0.5–1.5-m tall) were tagged, all of which were still without leaves or inflorescences. Ants were prevented from climbing on treatment plants by applying a sticky barrier of tree Tanglefoot (Tanglefoot Co., Grand Rapids, MI, USA) to the base of their trunks every 2 weeks. Grass bridges providing ants with a barrier-bypass to the trunk of treated plants were regularly pruned. Ants had free access to control plants.

The presence of eggs and larvae of the butterfly *E. bechina*, and egg batches of the sucking bug *E. rufomarginata* were regularly monitored on control and treated plants. Herbivore infestation and the phenological state of experimental shrubs of *C. brasiliense* were determined every 1–2 weeks from September 1986 to January 1987. Plant size was estimated as the number of leaves on each plant; the number of inflorescences, buds, flowers, young and mature fruits were also counted for each plant. To account for differences in plant size, the number of ovipositions and herbivores on a plant was divided by the number of leaves. The same oviposition or individual herbivore

were never re-counted on successive censuses (doubtful cases were ignored).

To investigate the influence of visiting ants on the bud-destroying fly *Prodiplosis floricola*, 70 shrubs of *C. brasiliense* (different from the ones described above) bearing young inflorescences were tagged in October 1986. Experimental inflorescences were still covered by involucre bracts (bud diameter <2 mm). Ants were prevented from climbing on randomly chosen treatment inflorescences ($n=36$) by applying Tanglefoot at the base of the trunk. Ants had free access to control inflorescences ($n=34$). After 2 weeks of exposure in the field, all inflorescences (bud diameter 4–8 mm) were collected and the number of *P. floricola* larvae infesting the buds in each experimental category was counted.

The effects of ants on the infestation by leaf-galling and stem-galling wasps was evaluated for 30 control and 30 treatment shrubs of *C. brasiliense*. The two largest branches of the plants that were tagged in August 1986 (see above) were marked and randomly assigned for future evaluation of either leaf- or stem-galling by the end of January 1987. Levels of infestation were estimated as the percentage of leaves galled on one branch and the per cent extension of the stem infested on the other branch.

Results

PATTERNS OF ANT VISITATION AND ANT PREDATION

During both day and night the proportion of *C. brasiliense* shrubs occupied by ants greatly surpassed that of neighbouring plants without EFNs (Table 1). Greater ant densities on *C. brasiliense* resulted in many more live termites being attacked and removed from this plant than from plants lacking EFNs (Table 1). A total of 20 ant species from 12 genera were recorded attacking termites on shrubs of *C. brasiliense*, all of which were also seen collecting extrafloral nectar on the plants. Seven *Camponotus* species together accounted for 52% of the attacks on termites; other common genera such as *Pheidole*, *Zacryptocerus*, *Wasmannia* and *Brachymyrmex* comprised 36% of the attacks on termites (further details are given in Oliveira & Brandão 1991).

Table 1. Differences in ant visitation, and ant predation of termites, between *Caryocar brasiliense* and neighbouring plants lacking extrafloral nectaries (EFNs) in cerrado vegetation

Variable	No. of plants occupied by ants ($n=30$ plant pairs)		Ants per plant (mean \pm SD)		No. of termites attacked (six per plant)	
	Day	Night	Day	Night	Day	Night
<i>Caryocar brasiliense</i>	22 (73.3%)	21 (70.0%)	1.97 \pm 1.61	1.80 \pm 1.58	54 (30.0%)	49 (27.2%)
Plants lacking extraflora nectaries	6 (20.0%)	6 (20.0%)	0.58 \pm 1.51	0.28 \pm 0.64	10 (5.6%)	17 (9.4%)
Significance of difference	$P < 0.001^*$	$P < 0.001^*$	$P < 0.001^{**}$	$P < 0.001^{**}$	$P < 0.001^*$	$P < 0.001^*$

* *G*-test; ** Mann–Whitney *U*-test.

Ant activity within the foliage of *C. brasiliense* shrubs was significantly different from that recorded for plants without EFNs, as expressed by the spatial distribution of ant attacks on termites (Fig. 1). Upon climbing on *C. brasiliense*, ants usually walked straight to the apex of the plant and gathered at the EFNs on the inflorescences and leaf buds. This tendency made the termites on the apical portion of the plants more likely to be found and removed by foraging ants. While descending the plant, however, ants frequently walked on leaves and eventually found the termites on lower parts of *C. brasiliense*. On plants lacking EFNs ant attacks tended to be more frequent on lower parts of the plant (Fig. 1).

EFFECTS OF ANTS ON INFESTATION LEVELS BY HERBIVORES

Both the butterfly *E. bechina* and the sucking bug *E. rufomarginata* presented higher infestation levels on ant-exclusion shrubs than on control shrubs of *C.*

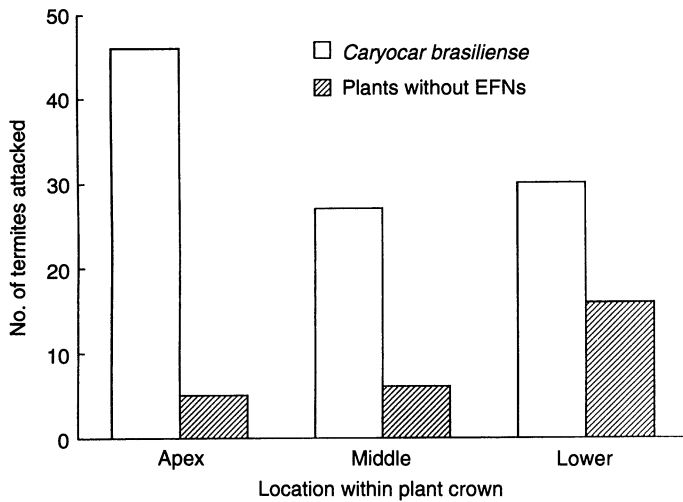


Fig. 1. Distribution of attacks by ants on termite-baits placed on different parts of the crown of *Caryocar brasiliense* (extrafloral nectaries on buds, at the apex of the plant) and on neighbouring plants lacking extrafloral nectaries. Thirty plant pairs were used during the day and 30 during the night. Six live termites were placed simultaneously on both plants of a pair (two per plant location). The distribution of ant attacks within the plant crown is statistically different between plant types; $G=9.379, P<0.01, df=2$.

Table 2. Infestation levels by the butterfly *Eunica bechina* and the sucking bug *Edessa rufomarginata* on control (ants present) and treatment (ants excluded) shrubs of *Caryocar brasiliense* in cerrado vegetation. Values are means \pm SD

Herbivore species	Control plants (ants present) (n=40)	Treatment plants (ants excluded) (n=40)	Significance of difference*
<i>Eunica bechina</i>			
Eggs per leaf	0.14 \pm 0.44	0.40 \pm 0.62	$P<0.001$
Larvae per leaf	0.06 \pm 0.13	0.19 \pm 0.28	$P<0.01$
<i>Edessa rufomarginata</i>			
Eggs per leaf	0.02 \pm 0.08	0.25 \pm 0.34	$P<0.001$

* Mann-Whitney U-test.

brasiliense (Table 2). Foraging ants were never observed removing the eggs of either type of herbivore; *Eunica* caterpillars, however, can be attacked and removed by several ant species on *C. brasiliense* (Freitas & Oliveira 1992, 1996). Ant predation on a hemipteran nymph was recorded once. Field observations suggest that interference from foraging ants is likely to affect egg-laying by the sucking bug *E. rufomarginata*. Most of the egg batches (80%, $n=21$) were found on the woody stem of the main branch, which is the principal route taken by ants toward the apical inflorescences. On many occasions adult bugs were seen moving away from the stem as a result of intense ant traffic towards and away from the apical EFNs. Bugs (nymphs and adults) were also seen moving away from ants while feeding on the buds or fruits of *C. brasiliense*.

Ant-excluded inflorescences of *C. brasiliense* were significantly more infested by the bud-destroying fly *P. floricola* than control inflorescences (Table 3).

The effect of visiting ants on the infestation levels by stem- and leaf-galling wasps is summarized in Fig. 2. Although ants had a significant deterrent effect against stem-gallers, branches in either experimental class were equally infested by leaf-galling wasps.

EFFECT OF VISITING ANTS ON PLANT REPRODUCTION

The reproductive output of ant-excluded and control shrubs of *C. brasiliense* is shown in Table 4. Plants in either category produced equal numbers of buds but flower and initial fruit production was significantly greater for control plants. Higher abortion rates of initial fruits by control plants resulted in similar fruit and seed sets for plants in either experimental category.

Discussion

The data confirmed that possession of EFNs increases ant density on *C. brasiliense* over non-nectariferous plants, resulting in many more termite-baits being attacked by ants on *Caryocar* than on plants without EFNs. Similar results were reported for *Q. grandiflora* in cerrado vegetation (Oliveira *et al.* 1987) and *Cassia fasciculata* in Florida, USA (Barton 1986). In comparison with non-nectariferous vegetation, ant-patrolling activity within the crown of *Caryocar* was more pronounced on the upper part of the shrubs (inflorescences with EFNs), where larger numbers of termites were attacked by foraging ants. A correlation between ant foraging and the spatial production of extrafloral nectar has also been recorded within the foliage of other plant species (O'Dowd 1979; Koptur 1984; McKey 1984; but see also Oliveira *et al.* 1987). Plants receiving protection by ants typically provide food rewards for the ant visitors both at time periods when, and on plant parts where, the plants are more vulnerable to herbivore attack (Bentley 1977). Ant

visitations to EFNs located on or near reproductive structures have been demonstrated to provide protection against herbivore damage to buds, flowers, fruits and seeds of several plant taxa (see Koptur 1992, and included references). In fact, developing inflorescences of *Caryocar* with free ant access were significantly less damaged by the fly *P. floricola* than ones from which ants had been excluded and plants with ants produced twice as many flowers than plants without ants (Tables 3 and 4).

Table 3. Infestation levels by the bud-destroying fly *Prodioplosis floricola* on control (ants present) and treatment (ants excluded) inflorescences of *Caryocar brasiliense* in cerrado vegetation

Variable	Control (ants present) (n = 34)	Treatment (ants excluded) (n = 36)	Significance of difference
Percentage of buds infested	9.4% (40/425)	17.6% (75/427)	$P < 0.001^*$
No. of larvae per inflorescence (mean \pm SD)	8.97 \pm 19.46	16.39 \pm 27.23	$P < 0.05^{**}$

* G-test; ** Mann-Whitney U-test.

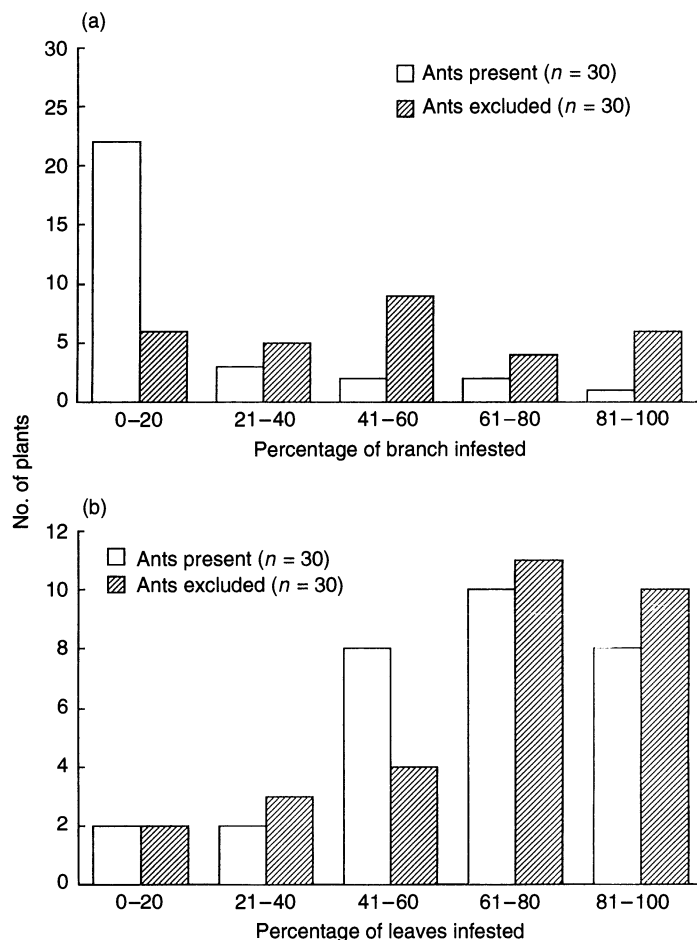


Fig. 2. Infestation levels by (a) stem- and (b) leaf-galling wasps on control (ants present) and treatment (ants excluded) shrubs of *Caryocar brasiliense*. Ants had a significant deterrent effect against stem-gallers ($P < 0.001$) but did not affect the infestation by leaf-galling wasps ($P > 0.6$). Mann-Whitney U-tests.

Observations of ant movements on *C. brasiliense* suggest that the lower infestation on control plants by *E. rufomarginata*, *P. floricola* and the stem-galling wasp is related to the apical location of EFNs within the plant crown, resulting in strong interference by foraging ants at the oviposition sites of these herbivores. Intense ant activity on the inflorescence by nectar-gathering ants presumably disturbs *P. floricola* flies during oviposition on developing buds, consistent with observations of other plants bearing EFNs on reproductive organs (Inouye & Taylor 1979; Schemske 1980). Similarly, because *E. rufomarginata* and the stem-galling wasp oviposit on the main route taken by ants while collecting extrafloral nectar, they too are exposed to strong interference by ants during egg laying. In fact, on many occasions the sucking bugs were seen avoiding contact with ants on the plants, both on the stem and on buds and fruits. Such avoidance behaviour by the bugs may reduce predation by aggressive ants, which was observed once. The more intense foraging activity by ants on the stem and buds of *Caryocar* probably explains why the infestation levels by leaf-galling wasps were unaffected in the ant-exclusion experiment (Fig. 2). Although not measured quantitatively, at any given moment the number of ants per unit area appeared far greater on the stem (main route of ants) and buds (EFNs present) than on the broad leaves of *Caryocar*, and this presumably makes leaf-galling wasps less vulnerable to ant interference during oviposition.

Oviposition by herbivores on ant-occupied plants is inhibited either by the ants' chasing behaviour towards ovipositing females (Janzen 1967; Inouye & Taylor 1979; Schemske 1980) or from egg removal by the ants (Letourneau 1983). Visual avoidance of ant-occupied plant locations by ovipositing females has recently been demonstrated to restrict egg laying by *E. bechina* on *C. brasiliense* (Freitas & Oliveira 1996). Damage to young leaves by caterpillars, although not quantified, appeared to be severe. The highest infestation level by *E. bechina* occurs between September and October when most *Caryocar* leaves are still young, soft and red in colour (Oliveira 1988). Pereira-Neto & Hay (1986) showed that the young leaves of *Caryocar* are the most photosynthetically valuable to the plant (see also Coley 1980), a fact that probably increases the cost of being infested by *Eunica* larvae. Caterpillars are frequently attacked and removed from *Caryocar* by several ant species and the mortality owing to ant predation has been shown to depend both on larval size (early instars are more vulnerable) and the level of ant visitation to the host plant (Freitas & Oliveira 1992, 1996; see also Tilman 1978; Smiley 1986).

The current study demonstrated that ant visitation to the EFNs strongly affects the infestation levels by four out of five of the principal herbivores of *C. brasiliense*. Although these results are in accordance with most studies reporting herbivore deterrence by

ants on ant-inhabited and ant-visited plants (Koptur 1992, and included references), they also corroborate data showing that within a given plant–ant system some herbivores may be less vulnerable to the ants' deterring traits and therefore can utilize the plant despite the ants (Janzen 1967; Koptur 1984; Heads & Lawton 1985; Barton 1986; Freitas & Oliveira 1996).

By contrast with several other studies that have demonstrated a positive effect of reduced herbivore damage on the fecundity of EFN-bearing plants (reviewed by Koptur 1992), the current study with *Caryocar* showed that an increase in the number of flowers and juvenile fruits in control plants does not affect final fruit set in this plant species (see also O'Dowd & Catchpole 1983; Kelly 1986). As stressed by several authors, the outcome of mutualistic interactions are inherently variable and strongly dependent on several ecological factors (Thompson 1988; Cushman & Addicott 1991; Rashbrook *et al.* 1992; Bronstein 1994). Although recent experimental evidence with EFN-bearing *Q. multiflora* indicates that herbivore deterrence by visiting ants can increase plant fitness in the cerrado (Del-Claro *et al.* 1996), differences in plant habit and fruit type between *Qualea* and *Caryocar* may possibly account for the observed discrepancy in the outcome of these two ant–plant systems.

Contrary to *Qualea* trees which produce many dry fruits each containing 10–18 wind-dispersed seeds (Del-Claro *et al.* 1996), shrubs of *C. brasiliense* produce only one to four heavy fruits containing one to four large seeds (Oliveira 1988) and the fleshy mesocarp is consumed by birds and mammals which are the main dispersal agents (Gottsberger & Silberbauer-Gottsberger 1983; Gribel & Hay 1993). Sutherland (1986) showed that plants producing 'cheap' dry fruits tend to have a higher fruit set than plants with 'expensive' fleshy fruits, and further suggested that resource limitation can be an important factor increasing juvenile fruit abortion in plants producing expensive fruits. The extremely low fertility of cerrado soils is well documented (Eiten 1972; Goodland 1971b) and the lack of soil nutrients is known to affect final seed set in plants negatively (Willson & Price 1980; Stephenson 1981). It is possible that the low soil fer-

tility in the cerrado constrains the ability of *Caryocar* shrubs to provide the resources necessary for growth and development of fruits. Consequently, the potential benefit afforded by ants as expressed by initial higher numbers of flowers and fruits (as compared with ant-excluded plants, Table 4) would be neutralized later on by competition among developing fruits and subsequent abortion. Resource limitation (water stress) has already been implied as a possible factor affecting the reproductive output in EFN-bearing plants protected by ants (Kelly 1986). Moreover, the production of food rewards, a trait mediating protection by ant inhabitants in myrmecophytic *Cecropia*, has recently been shown to depend on the nutrient levels under which the plants are grown (Folgarait & Davidson 1994). The confirmation of low soil fertility as a factor limiting final fruit set in ant-protected *Caryocar*, however, would require soil-enrichment experiments with fertilizers similar to those performed by Willson & Price (1980).

If ant deterrence of important herbivores is not translated into greater fecundity by *Caryocar*, how are EFNs maintained and what other possible advantages may EFNs confer to this plant species in the cerrado? It is possible that the cost of extrafloral nectar production in *Caryocar* is so low that selection against it would be weak (see O'Dowd 1979). Ant-derived benefits related to fecundity, however, may vary greatly both in space and time, and selective pressure to maintain EFNs may be intense only at certain habitats and/or periods (O'Dowd & Catchpole 1983, Barton 1986; Kelly 1986). This study was conducted at the southern limit of the distribution of *C. brasiliense* (Prance & Freitas da Silva 1973), so it may be that the experimental shrubs were growing under sub-optimal conditions (see Begon, Harper & Townsend 1990). It is therefore possible that fecundity-related benefits from ants would only be detected in fully grown plants (i.e. trees). It would be worthwhile to test whether ant protection would affect fruit set at the core of the cerrado distribution in Brazil, where *C. brasiliense* grows as a large tree (Eiten 1972; Prance & Freitas da Silva 1973). However, even if not translated into an increased reproductive output, protection of vegetative tissues may allow shrubs of *C. brasiliense* to overcome periods of intensive herbivore attack better as the plant grows larger. Finally, the surplus number of flowers and juvenile fruits observed in ant-visited control plants may be advantageous for *Caryocar* shrubs in three ways. First, a large floral display may increase the plant's attractiveness to pollinators, this being particularly relevant at periods of low pollinator availability (Augspurger 1980; Udovic 1981). Indeed, Gribel & Hay (1993) report that *C. brasiliense* trees bearing increased numbers of flowers are more attractive to potential bat pollinators in central Brazil. Second, production of surplus hermaphroditic flowers increases male contribution to fitness through pollen donation (Willson & Price

Table 4. Reproductive output by control (ants present) and treatment (ants excluded) shrubs of *Caryocar brasiliense* in cerrado vegetation. Values are means \pm SD

Variable	Control plants (ants present) (n = 40)	Treatment plant (ants excluded) (n = 40)	Significance of difference*
No. of buds per plant	25.20 \pm 17.77	21.22 \pm 21.7	P = 0.23, NS
No. of flowers per plant	2.60 \pm 4.17	1.17 \pm 2.69	P = 0.01
No. of young fruits per plant	2.13 \pm 3.67	1.12 \pm 2.67	P = 0.02
No. of mature fruits per plant	0.37 \pm 0.84	0.35 \pm 0.83	P = 0.81, NS
No. of seeds per plant	0.55 \pm 1.20	0.47 \pm 1.21	P = 0.74, NS

* Mann–Whitney U-test.

1977). Third, given that offspring may differ in some quality related to fitness (e.g. pollen parentage), the production of surplus fruits and seeds may allow the plant to abort selectively genetically inferior progeny (Janzen 1977) as the maternal investment is adjusted to match available resources (Lloyd 1980). As stressed by Stephenson (1981), these three factors may operate alone or simultaneously and their relative importance may depend on other variables, such as the plant taxa and habitat.

In conclusion, although ant–plant interactions have been intensively studied in the past three decades and a number of cases have been described in which herbivore deterrence by ants has a positive effect on plant fitness, the present study with *Caryocar* shows that several other aspects need to be taken into account when examining a particular ant–plant system. Mutualistic systems are strongly conditioned by the ecological settings in which they occur and viewing species interactions as a continuum would lead us to expect a range of possible outcomes (Bronstein 1994). Therefore, focusing on the variation characterizing such species associations should give a more precise picture of the processes operating within populations and communities.

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