

Dual ant attraction in the Neotropical shrub *Urera baccifera* (Urticaceae): the role of ant visitation to pearl bodies and fruits in herbivore deterrence and leaf longevity

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Summary

1. This study investigated the protective role of ants against phytophagous insects on *Urera baccifera* (L.) Gaudich. Ants (22 species) visit shrubs of *U. baccifera* throughout the year and forage especially on leaves, where they harvest pearl bodies, and on fruiting branches, where they collect fleshy fruits. The main leaf herbivores are the butterflies *Smyrna blomfieldia* (Fruhstorfer) and *Urbanus esmeraldus* (Butler), and the moth *Pleuroptya silicalis* (Guené).

2. The proportion of vegetative (no flowers or fruits) individuals of *U. baccifera* occupied by ants greatly surpassed that of neighbouring plant species lacking food rewards, consistent with the hypothesis that pearl bodies act as ant attractants. Ant visitation to vegetative individuals of *U. baccifera* increased larval mortality of *S. blomfieldia*, suggesting that ants attracted to pearl bodies reduce herbivore survival. Fruits were also demonstrated to play an important role in ant attraction by *U. baccifera*. Ant visitation to pearl body-producing shrubs of non-mycorrhizal *Piper amalago* L. with *U. baccifera* fruits attached was significantly higher than to *P. amalago* plants with an attached leaf of *U. baccifera*.

3. Ant-exclusion experiments showed that ants effectively reduce the incidence of lepidopteran larvae on the plants. In both 2003 and 2004, herbivores were more abundant on ant-excluded than on ant-visited shrubs of *U. baccifera*. Additionally, in both years ant-excluded plants had significantly faster leaf abscission rates compared with ant-visited plants.

4. So far, all ant–plant systems with dual food rewards involve extrafloral nectar as one of the attractants. This study with *U. baccifera* is the first to report food bodies and fruits as ant attractants in a non-symbiotic ant–plant interaction. This facultative system is also unique in that herbivore deterrence caused by pearl body- and fruit-harvesting ants can also add to leaf longevity.

Key-words: ant–plant interaction, ant–fruit interaction, food bodies, herbivory, leaf abscission, leaf longevity, mutualism

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Introduction

Mutualistic systems involving ants and plants fall within a continuum from very loose associations to obligate symbiosis (Heil & McKey 2003). Although mutualism is defined as an interaction between two species that is beneficial to both, some mutualisms can be understood only in the context of the community, and by assessing the influence of other species and other trophic levels on the pairwise relationship (Bronstein & Barbosa 2002).

A combination of positive and negative effects among participating species determines the outcome of these interactions, and recent studies have shown that the results of ant–plant–herbivore interactions may vary widely in space and time (Rico-Gray *et al.* 1998). Temporal and spatial variations may modulate the strength of the association between ants and their partners, a phenomenon termed conditional mutualism (Cushman & Addicott 1991; Del-Claro & Oliveira 2000).

Perhaps due to the overemphasis of studies on obligate ant–plant mutualisms relative to facultative ones (reviewed by Heil & McKey 2003), the relation between conditionality and type of food reward offered to ants has

been largely ignored in ant–plant systems. For instance, in Mexican sand dunes the plant community offers a variety of food rewards that differ in quality and quantity throughout the year, and this in turn can mediate the outcomes of facultative ant–plant associations in the dune environment (Díaz-Castelazo *et al.* 2004; Rico-Gray *et al.* 2004). Several unrelated plant species attract ants by providing food rewards such as extrafloral nectaries (Oliveira & Leitão-Filho 1987; Koptur 1992); fruit pulp or elaiosomes (Lu & Mesler 1981; Cuautele & Rico-Gray 2003); and food bodies (O’Dowd 1982; Fiala *et al.* 1994). Pearl bodies are food rewards with a lustrous pearl-like appearance that are produced on leaves and stems of plants (O’Dowd 1982). Plants bearing pearl bodies

occur over a wide range of taxa, and the harvesting of pearl bodies by ants has long been reported in the literature (Risch & Rickson 1981; O’Dowd 1982 and references therein). However, the role of pearl bodies in mediating plant protection remains largely overlooked (Schupp & Feener 1991; Marquis & Braker 1994). Most studies dealing with ant–pearl body systems investigated highly specialized and symbiotic ant–plant associations and showed that pearl body-harvesting ants may benefit the plant through protection against herbivores (Letourneau 1983; Fiala *et al.* 1994; Heil *et al.* 2001).

While the role of pearl bodies in symbiotic ant–plant interactions is well documented, few studies have directly investigated the outcomes for facultative, non-symbiotic ant–plant interactions mediated by pearl bodies (but see Fiala *et al.* 1994; Heil *et al.* 2001). Likewise, although numerous ant species consume fallen fleshy fruits on the floor of tropical forests (Pizo & Oliveira 2000; Passos & Oliveira 2003), ants are hardly seen harvesting fruit material directly from the plant crown (but cf. Wheelwright 1985). Here we study the interaction between ants and the Neotropical nettle *Urera baccifera* (L.) Gaudich. (Urticaceae). This ant–plant system is peculiar in that the nettle offers two distinct food rewards to visiting ants: pearl bodies and fleshy fruits (Fig. 1a,b) (Schupp & Feener 1991; Machado & Freitas 2001). We document via observations and experiments the dynamics of the facultative mutualism involving ants and *U. baccifera*, and examine the role of pearl bodies and fruits in mediating this interaction system. Five questions were addressed. (1) What is the pattern of ant visitation to *U. baccifera* throughout the year? (2) Does the presence of pearl bodies or fruits increase ant visitation to *U. baccifera* over non-rewarding, background vegetation? (3) Does ant visitation to pearl bodies reduce herbivore infestation levels on the plant, and (4) does it affect leaf longevity? (5) Do ant-derived benefits to *U. baccifera* vary temporally?

Materials and methods

STUDY AREA AND ORGANISMS

Field work was carried out from 2000 to 2004 in the Santa Genebra Reserve at Campinas, south-east Brazil (22°49’45’’ S, 47°06’33’’ W). The climate is warm and wet, with a dry winter from May to October and a wet summer from November to April. The average annual rainfall is 1381.2 mm and the mean annual temperature is 21.6 °C. Most of the reserve is covered by semi-deciduous mesophytic forest (Morellato 1995). The experiments were performed with *U. baccifera* shrubs located along a 1200-m trail within the forest.

Urera baccifera is a thin-stemmed nettle distributed from Mexico to Brazil, and is normally found in secondary environments. The plant starts to abscise its leaves during the fruiting season (early April to late June), sprouting again in August. Individuals of *U. baccifera* (1.5–2 m tall) produce a few hundred small, white, single-seeded



Fig. 1. Ant foraging and food rewards in *Urera baccifera*. (a) Worker of *Pachycondyla villosa* transporting a recently collected fruit (note fruit cluster in right foreground); arrows show scattered pearl bodies over the leaf surface. (b) Workers of *Acromyrmex* sp. acting as primary dispersers by removing entire fruits directly from the plant.

fruits (width 0.54 ± 0.06 cm; length 0.56 ± 0.05 cm; weight 0.07 ± 0.02 g; mean \pm SE; $N = 50$ fruits). The fruits are spongy and watery, and rich in carbohydrates (79.6% of fruit dry mass) and proteins (16.3% of fruit dry mass; Dutra 2003). Although capuchin monkeys (*Cebus apella*) and seven bird species are the main seed dispersers of *U. baccifera* in the study area (Galetti & Pedroni 1994; Galetti & Pizo 1996), up to 50 ant foragers can be seen collecting fresh fruits on a single shrub (Fig. 1a,b) (Machado & Freitas 2001) and many also gather fallen fruits beneath the parent plants (Dutra 2003). Ants appear to be less relevant as seed dispersers of *U. baccifera* compared with frugivorous vertebrates, and a study on fruit-gathering behaviour and seed displacement by ants is in preparation (H.P.D., P.R. Guimarães and P.S.O.).

Ants also forage intensively on vegetative individuals of *U. baccifera* in search of pearl bodies, which are found on stems, leaves and stalks of flowers and fruits. Plants accumulate thousands of pearl bodies that are promptly removed by foraging ants, or are easily detached from the plant. Water and carbohydrates are the main constituents of the pearl bodies of *U. baccifera*; no lipids or proteins were detected. Carbohydrates represent $\approx 67\%$ of the dry mass, and the main components are glucose (16%) and sucrose (4%) (Dutra 2003).

Three species of Lepidoptera are the main herbivores of *U. baccifera*: *Smyrna blomfildia* (Fruhstorfer) (Nymphalidae: Nymphalinae); *Urbanus esmeraldus* (Butler) (Hesperiidae: Pyrginae); and *Pleuroptya silicalis* (Guené) (Crambidae: Pyraustinae). These shelter-building caterpillars are specialist insect herbivores of *U. baccifera*, and a single fully grown larva can defoliate the entire plant. Other moths and grasshoppers were seen only occasionally (two to three times) on *U. baccifera* during the entire study period.

PATTERNS OF ANT VISITATION AND HERBIVORE INFESTATION

The seasonality of ant visitation to *U. baccifera* was evaluated by regular ant censuses (every 15–20 days) on 17 plants bearing only one branch (≈ 1.5 m tall), from May 2000 to April 2001. In each census the whole plant was searched for 40 s, and ants were classified according to their location (stem, leaves, flowers or fruits). We also recorded the number of *S. blomfildia* larvae on the plant. All censuses were carried out between 12.00 and 14.00 h.

PEARL BODIES: ANT ATTRACTION AND HERBIVORE SURVIVAL

To access whether pearl bodies in *U. baccifera* increased ant density over that expected on non-rewarding plants, 76 plant pairs were tagged. Each pair consisted of a vegetative (no flowers or fruits) individual of *U. baccifera* (1–2 m tall) and a neighbouring shrub species of similar size and height. Neighbour shrubs possessing ant attractants such as extrafloral nectaries, pearl bodies,

flowers or fruits, or hosting honeydew-producing insects, were avoided. The number of ants present on each plant of a pair was recorded upon our arrival. Ant recruitment to plants was compared using a Wilcoxon test. The number of plants occupied by ants in each plant group was compared using a χ^2 test, assuming the expected ratio of 1 : 1 to *U. baccifera* and plants without ant attractants.

We carried out an ant-exclusion experiment to evaluate if ant visitation to pearl bodies reduces herbivore survivorship on *U. baccifera*. We avoided using fruiting plants in this experiment to ensure that pearl bodies were the only ant attractants. We used 80 similarly sized plants (1–2 m tall) and randomly assigned them as control or treatment. Treatment plants had ants excluded by applying a sticky barrier of tree Tanglefoot (Tanglefoot Co., Grand Rapids, USA) to the base of their stem every 15 days. Grass bridges providing aerial access of ants to treated plants were pruned regularly. Control plants received Tanglefoot on only one side of the stem, so that ants could still have free access to plant foliage. We chose *S. blomfildia* for this experiment because it was the most abundant herbivore when we conducted the experiment in February 2003. Ant effects on the mortality of *S. blomfildia* larvae were evaluated by placing one larva (1st or 2nd instar) on the first fully grown leaf (4th to 6th relative to the plant apex) of each plant in either experimental group. Test larvae were obtained from plants not used in the experiments, or in the censuses of organisms. To ensure that larvae were securely established on experimental plants, we waited until they built their frass chains (a stick-like refuge constructed at leaf margins; Freitas & Oliveira 1996; Machado & Freitas 2001). Ant predation on larvae was evaluated as the number of larvae that disappeared after 4 days. Larval survival on experimental plant groups was compared using χ^2 tests.

FRUITS AS ANT ATTRACTANTS

We tested the role of *U. baccifera* fruits as ant attractants experimentally by adding fruits of this plant species to shrubs of non-mycophytic *Piper amalago* L. (Piperaceae). This species was chosen because it produces pearl bodies (Burger 1971) and is similar in architecture and size to *U. baccifera*. We tagged 74 vegetative (no flowers or fruits) individuals of *P. amalago*, each designated as a treatment or control plant by the flip of a coin. Treatment plants received 10–15 fresh fruits of *U. baccifera* that were strung together with a polyester sewing line (20–30 cm long) and tied to a branch. Control plants received a leaf of *U. baccifera* (≈ 20 –30 cm long) strung with a similar sewing line and tied to a branch. Experimental plants were established in the morning and ants were censused at 1-h intervals from 1300 to 1700 h. Samplings consisted of recording the number of ants during 20 s. Ant activity on experimental plants along successive censuses was analysed by repeated-measures ANOVA after $\log(x + 1)$ transformation on the data.

ANT EFFECTS ON HERBIVORE INFESTATION AND ON LEAF LONGEVITY

The protective role of ants against herbivores of *U. baccifera* was tested with ant-exclusion experiments in 2003 and 2004. Before the beginning of the fruiting period, we tagged similarly sized (0.6–2.0 m tall) *U. baccifera* individuals in the same phenological state (no flowers or fruits). We assigned them randomly as control or treatment (29 and 24, respectively, in 2003; 30 and 26, respectively, in 2004). Two distinct sets of plants were used each year. Ants were excluded from treatment plants by applying a sticky barrier of Tanglefoot to the trunk base. Ants had free access to control individuals of *U. baccifera*, which had Tanglefoot on only one side of the trunk. Each plant had one branch selected for records of herbivores. Infestation levels by *S. blomfieldia*, *U. esmeraldus* and *P. silicalis* were determined by counting the number of larvae of each species present on tagged branches. As herbivory may affect leaf abscission (Blundell & Peart 2000), we also counted the initial number of leaves and the number of abscised leaves of tagged plants. We conducted weekly herbivore and leaf censuses during 7 weeks in both 2003 and 2004. Herbivore infestation levels and leaf abscission rates on experimental plant groups along successive censuses in

2003 and 2004 were analysed by a three-way repeated-measures ANOVA after $\log(x + 1)$ transformation on the data. Between-year comparisons of herbivore abundance on *U. baccifera* were performed using a two-way ANOVA; *post hoc* Tukey tests evaluated differences among herbivore species.

Results

PATTERNS OF ANT VISITATION TO *URERA BACCIFERA*

The ant assemblage foraging on shrubs of *U. baccifera* comprises a total of 22 ant species in eleven genera: *Camponotus* (seven species); *Pheidole* (four species); *Crematogaster* and *Pseudomyrmex* (two species each); *Acromyrmex*, *Atta*, *Cephalotes*, *Linepithema*, *Pachycondyla*, *Solenopsis* and *Tapinoma* (one species each). Large ant species acted as primary seed dispersers by climbing onto the plant and removing entire fruits to their nests (Fig. 1a,b). Except for the fungus-growers *Acromyrmex* and *Atta*, which were only seen collecting fruits, all other ants exploited both pearl bodies and fruits of *U. baccifera*, and behaved aggressively toward lepidopteran larvae on leaves (Machado & Freitas 2001).

Ants were present on plants throughout the year except during the period of leaf fall (July–August). On average 0.39 ± 0.02 (SE) ants were seen per plant. We recorded a seasonal variation in the number of ants visiting *U. baccifera*, with an increase in ant visitation during the fruiting period, May–June 2000 and April 2001 (Fig. 2a). Ants foraged on all aerial vegetative and reproductive structures, but especially on leaves. Ants were also observed harvesting pearl bodies produced on the stems and pedicels of inflorescences. During the fruiting season ants were mostly found feeding on fruit pulp (Fig. 2b). Larvae of *S. blomfieldia* were present on plants from September 2000 to April 2001 (Fig. 2a), averaging 0.85 ± 0.06 caterpillars per plant. During the fruiting period of 2000 we did not observe a single larva foraging on shrubs of *U. baccifera*, although they were present on non-fruiting plants.

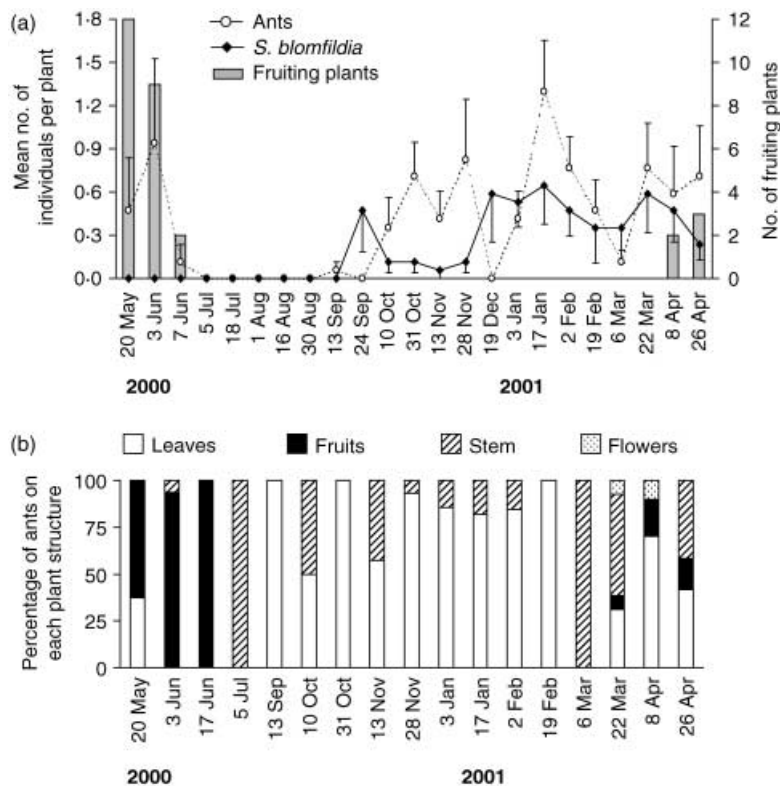


Fig. 2. (a) Ant visitation and larval infestation by *Smyrna blomfieldia* on shrubs of *Urea baccifera* in a semi-deciduous forest in south-east Brazil. Censuses were carried out every 15–20 days on 17 plants; data are means \pm SE. (b) Percentage of ants visiting vegetative and reproductive structures of *Urea baccifera* (ants were absent in August 2000).

PEARL BODIES: ANT ATTRACTION AND HERBIVORE SURVIVAL

The mean number of ants visiting vegetative shrubs of *U. baccifera* (0.50 ± 0.12) was significantly higher than on neighbouring plants without ant attractants (0.07 ± 0.03 ; Wilcoxon's $z = -3.51$, $P < 0.001$). Ants occupied nearly 30% of the *U. baccifera* individuals (21 out of 74) against less than 7% (five out of 74) of the neighbouring plants ($\chi^2 = 11.95$, $df = 1$, $P < 0.001$). These results are consistent with the hypothesis that pearl bodies are effective ant attractants, although uncontrolled traits of neighbouring plants such as plant architecture and leaf pubescence cannot be discarded for differences in ant attendance.

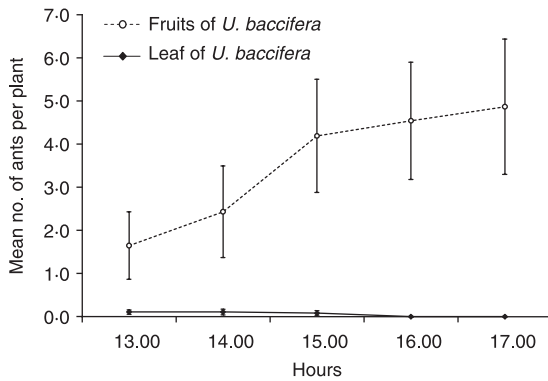


Fig. 3. Role of fruits and leaves of *Urera baccifera* as ant attractants when attached to shrubs of *Piper amalago*. Treatment *P. amalago* plants ($N = 37$) received 10–15 fresh fruits of *U. baccifera*; control plants received one leaf of *U. baccifera*. Ant visitation to *P. amalago* is affected by the presence of *U. baccifera* fruits (repeated-measures ANOVA: $F_{1,72} = 14.70$, $P < 0.0001$). Data are means \pm SE.

The ant-exclusion experiment demonstrated that larval mortality is affected by ant presence ($\chi^2 = 6.24$, $df = 1$, $P < 0.05$). After 4 days, 55% of the *S. blomfieldia* larvae had disappeared from the ant-visited branches, whereas only 26.5% were removed from the ant-excluded ones, indicating that visiting ants have a

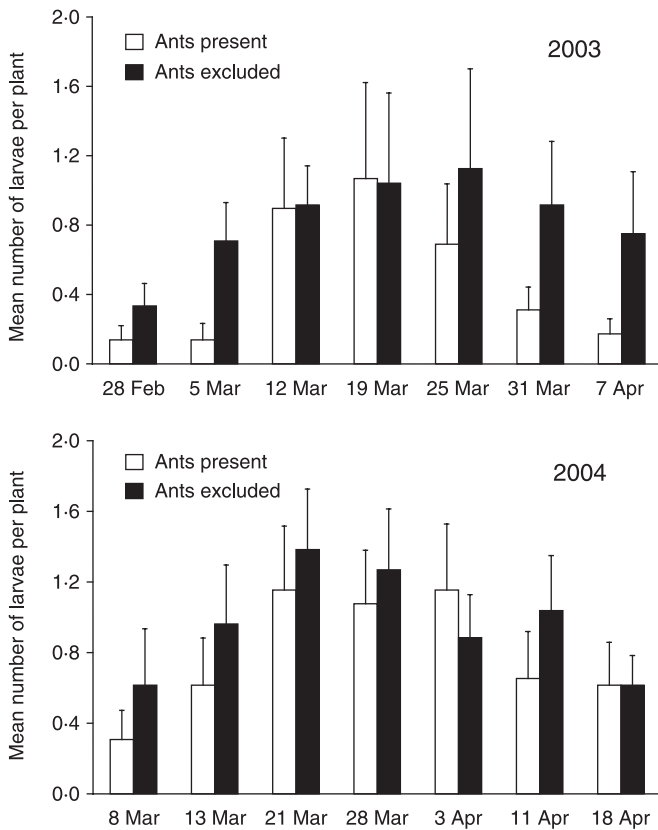


Fig. 4. Infestation levels by larvae of *Smyrna blomfieldia*, *Urbanus esmeraldus* and *Pleuroptya silicalis* (Lepidoptera) on experimental plant groups of *Urera baccifera* over time in 2003 and 2004. Herbivore activity is affected by ant treatment in both years (Tables 1 and 2). Data are means \pm SE.

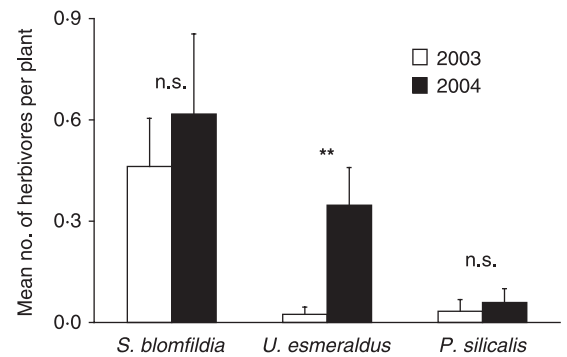


Fig. 5. Abundance of *Smyrna blomfieldia*, *Urbanus esmeraldus* and *Pleuroptya silicalis* on shrubs of *U. baccifera* in 2003 and 2004. **, Statistically different according to a *post hoc* Tukey test; ns = not significant. Data are means \pm SE (Tables 2 and 3).

negative impact on *S. blomfieldia* larval survival on shrubs of *U. baccifera*.

FRUITS AS ANT ATTRACTANTS

Ant activity on shrubs of *P. amalago* with fruits of *U. baccifera* attached was significantly higher than on *P. amalago* plants with an attached leaf of *U. baccifera* (Fig. 3; repeated-measures ANOVA: $F_{1,72} = 14.70$, $P < 0.0001$). During the censuses we recorded up to 33 ants per *P. amalago* plant with *U. baccifera* fruits attached.

ANT EFFECTS ON HERBIVORE INFESTATION AND ON LEAF LONGEVITY

In both 2003 and 2004, herbivores presented higher infestation levels on ant-excluded than on control shrubs of *U. baccifera*, indicating that ants were effective in reducing the incidence of lepidopteran larvae on this plant (Fig. 4; Table 1). *Smyrna blomfieldia* accounted for most of the herbivore records in both years, but in 2004 we observed a significant increase in the number of *U. esmeraldus* larvae (Fig. 5; Tables 2 and 3). In both years we recorded low infestation levels of the moth *P. silicalis* (Fig. 5; Tables 2 and 3).

Predation on *U. esmeraldus* larvae by the large ponerine ant *Pachycondyla villosa* was recorded twice. We also observed once the formicine *Camponotus crassus* preying on *S. blomfieldia* larva. In all predation events, the larvae (1st to 3rd instar) were feeding on leaves outside their leaf shelters. On many occasions, while feeding on leaves, larvae of *S. blomfieldia* and *U. esmeraldus* were seen taking refuge inside their shelters on the approach of an ant, as already recorded for other nymphalid caterpillars on ant-visited plants (Freitas & Oliveira 1992, 1996).

In both 2003 and 2004 a significant interaction between ant treatment and time was detected for leaf longevity, indicating that ant-excluded plants had faster leaf abscission rates than ant-visited ones (Fig. 6; Table 1).

Table 1. Three-way repeated-measure ANOVAs on herbivore infestation levels and leaf longevity in shrubs of *Urera baccifera* for the ant-exclusion experiments of 2003 and 2004

Source	SS	df	MS	F	P
Herbivore infestation					
Between subjects					
Ant treatment	0.644	1	0.644	4.034	0.047
Year	0.487	1	0.487	3.055	0.083
Ant treatment × year	0.015	1	0.015	0.092	0.762
Error	16.751	105	0.160		
Within subjects					
Time	1.557	6	0.260	6.645	<0.001
Time × ant treatment	0.160	6	0.027	0.681	0.665
Time × year	0.015	6	0.003	0.065	0.999
Time × ant treatment × year	0.083	6	0.014	0.353	0.909
Error	24.605	630	0.039		
Leaf abscission					
Between subjects					
Ant treatment	882.111	1	882.111	0.570	0.452
Year	14076.063	1	14076.063	9.095	0.003
Ant treatment × year	5.209	1	5.209	0.003	0.954
Error	162509.554	105	1547.710		
Within subjects					
Time	102805.084	6	17134.181	175.600	<0.001
Time × ant treatment	2361.644	6	393.607	4.034	0.001
Time × year	2458.708	6	409.785	4.200	<0.001
Time × ant treatment × year	495.676	6	82.613	0.847	0.534
Error	61472.394	630	97.575		

Analyses were performed on $\log(x + 1)$ -transformed data (see Figs 4 and 6).

Table 2. Levels of infestation by three lepidopteran herbivores (*Smyrna blomfieldia*, *Urbanus esmeraldus* and *Pleuroptya silicalis*) on control (ants present) and treatment (ants excluded) shrubs of *Urera baccifera* in 2003 and 2004 (see Fig. 5)

Herbivore species	Control plants (ants present)	Treatment plants (ants excluded)
2003		
	<i>N</i> = 29 plants	<i>N</i> = 24 plants
<i>S. blomfieldia</i>	0.46 (±0.11)	0.81 (±0.14)
<i>U. esmeraldus</i>	0.03 (±0.01)	0.02 (±0.01)
<i>P. silicalis</i>	0.09 (±0.03)	0.02 (±0.01)
All herbivores	0.49 (±0.11)	0.83 (±0.14)
2004		
	<i>N</i> = 30 plants	<i>N</i> = 26 plants
<i>S. blomfieldia</i>	0.39 (±0.06)	0.55 (±0.09)
<i>U. esmeraldus</i>	0.30 (±0.06)	0.40 (±0.06)
<i>P. silicalis</i>	0.04 (±0.02)	0.02 (±0.01)
All herbivores	0.73 (±0.10)	0.97 (±0.11)

Discussion

This study supports the hypothesis that possession of pearl bodies enhances ant visitation to *U. baccifera*. The attraction of a wide ant assemblage to *U. baccifera* indicates a low specificity and illustrates the facultative character of this ant–plant system (but cf. Fiala & Maschwitz 1992; Fiala *et al.* 1994). Ants respond positively to larger food resource concentrations (Koptur 1984; McKey 1984) and the efficacy of ant attraction is usually enhanced when pearl bodies are offered together with other food rewards (Fiala & Maschwitz

Table 3. Two-way ANOVA on herbivore abundance on shrubs of *Urera baccifera* in 2003 and 2004

Source	SS	df	MS	F	P
Year	8.85	1	8.85	0.54	0.46
Herbivores	690.19	2	345.10	20.97	<0.0001
Year × herbivore species	163.26	2	81.63	4.96	<0.01
Error	5283.57	321	16.46		

Lepidopteran caterpillars: *Smyrna blomfieldia*, *Urbanus esmeraldus*, *Pleuroptya silicalis* (see Fig. 5).

1991). Our study reinforces this tendency by characterizing an ant–plant system mediated by two distinct food rewards: pearl bodies and fruits. The energy-rich pearl bodies and fruits of *U. baccifera* probably play an essential role, increasing the diversity of ant visitors to the plant and adding to plant protection. Although not addressed in the current study, production of pearl bodies by *U. baccifera* may also serve as an additional attractant to ants that act mainly as seed dispersers rather than plant protectors (H.P.D., P.R. Guimarães and P.S.O., unpublished). A similar, complex system involving *Turnera ulmifolia* and omnivorous ants (25 species) has recently been described in Mexican sand dunes. By simultaneously offering extrafloral nectaries and elaiosome-bearing seeds to ants, *T. ulmifolia* promotes frequent ant visitation throughout the year and adds to both plant defence and seed dispersal (Cuautle & Rico-Gray 2003; Cuautle, Rico-Gray &

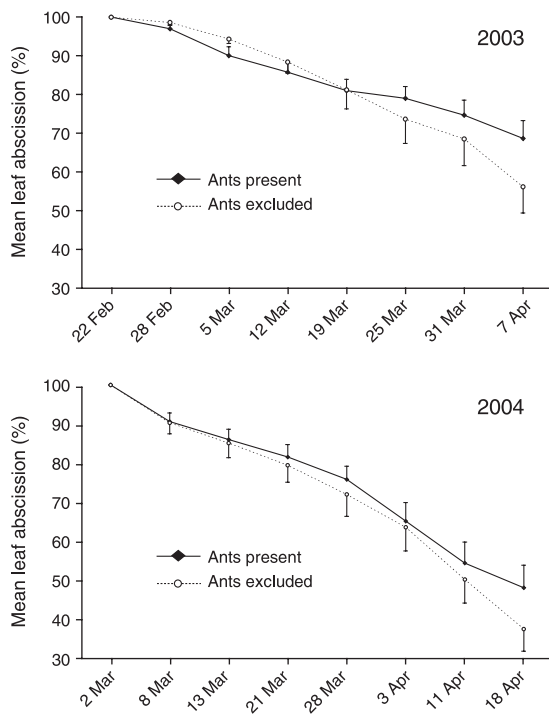


Fig. 6. Survivorship curves of leaves of ant-visited and ant-excluded *Ureba baccifera* in 2003 and 2004. In both years ant-excluded plants have faster leaf abscission rates than ant-visited ones (Table 1). Data are means \pm SE.

Díaz-Castelazo 2005). Our censuses on *U. baccifera* showed that ants were present on the plants during most of the year. Harvesting of pearl bodies by ants is particularly conspicuous when *U. baccifera* produce new leaves and pearl bodies accumulate on the leaf surface. Ant activity ceases during leaf abscission, as pearl body production drops considerably.

Machado & Freitas (2001) showed that ant visitation to *U. baccifera* decreases the residence time of live termites and reduces *S. blomfieldia* larval survival, but the isolate attraction effects of pearl bodies and fruits remained untested. Our data demonstrate that fruits of *U. baccifera* do encourage ant visitation to plants, and during the fruiting period there are almost no larvae occupying shrubs of *U. baccifera* (Fig. 2). Moreover, ant-exclusion experiments showed that ant visitation to pearl bodies *per se* reduced the survival of *S. blomfieldia* caterpillars as well as decreased overall herbivore abundance on the plants. These results confirm the deterrent capacities of pearl body-attracted ants on non-symbiotic systems (Fiala *et al.* 1994). The reduced herbivore numbers on shrubs without ants could be explained by four non-exclusive factors: (1) aggressive and/or interference behaviour towards ovipositing females (Schemske 1980; Oliveira 1997; Oliveira *et al.* 1999); (2) host-plant choice by adult lepidopterans (Freitas & Oliveira 1996; Freitas *et al.* 1999); (3) egg removal by ants (Letourneau 1983; Barton 1986); or (4) larval predation by ants on highly visited plants

(Freitas & Oliveira 1992, 1996; Oliveira & Freitas 2004).

In 2004 we registered a 15-fold increment in the occurrence of *U. esmeraldus* compared with the previous year, and an overall increase in herbivore infestation (Fig. 5; Tables 2 and 3). Despite increased herbivore abundance in 2004, ant-visited plants still had fewer herbivores compared with ant-excluded ones, suggesting that ants provide a consistent defence system against herbivores. Additionally, our results show that ant-derived protection to *U. baccifera* may affect leaf longevity, as expressed by faster leaf abscission rates in ant-excluded compared with ant-visited plants in both 2003 and 2004 (Fig. 6; Table 1). Indeed, herbivory can induce leaf abscission (Núñez-Fárfan & Dirzo 1989; Blundell & Peart 2000), and Fonseca (1994) showed for a myrmecophytic plant that ant exclusion increased both herbivore infestation and leaf abscission rates.

Ant-plant interactions are extremely diverse, and are mostly mediated by plant-derived food resources (Rico-Gray *et al.* 1998). More recently, the role of pearl bodies as ant attractants has received increased attention (Fiala *et al.* 1994; Heil *et al.* 2001). On the other hand, few studies have reported ants climbing onto plants to collect vertebrate-dispersed fleshy fruits (Wheelwright 1985), suggesting that this type of interaction is largely overlooked (but cf. Cuautle *et al.* 2005). This study demonstrates that the simultaneous offer of nutritious pearl bodies and fleshy fruits by *U. baccifera* promotes ant visitation, which reduces herbivore infestation. Most studies on protective ant-plant mutualisms mediated by pearl bodies involve myrmecophytic plant species (Heil & McKey 2003), and so far all ant-plant systems with dual food rewards involve extrafloral nectar as one of the attractants. Although a protective role of pearl body-harvesting ants has already been documented for facultative systems in Asian forests (Fiala *et al.* 1994; Heil *et al.* 2001), this study with Neotropical *U. baccifera* is unique in showing that herbivore deterrence caused by intense activity of pearl body- and fruit-harvesting ants can also add to leaf longevity. An assessment of the ecological roles played by each visiting ant species (plant defence, seed dispersal) should improve our understanding of the dynamics of this system.

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