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PLANT MEDIATION OF ANT-HERBIVORE ASSOCIATIONS: THE ROLE OF STICKY RINGS FORMED BY BOERHAVIA SPICATA

Y. McClellan[1] and W. J. Boecklen

Department of Biology, Box 30001, New Mexico State University, Las Cruces, NM 88003, USA
(Correspondence to: W. J. Boecklen)
1 Present address: P.O. Box 5800, Sandia National Laboratory, Organization No. 7731, Albuquerque, NM 87185, USA.

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Abstract. The ability of plants to interfere with ant-homopteran associations has received relatively little attention in studies of ant-homopteran-plant interactions. Given the potential of significant negative impacts to plant fitness from ant-herbivore mutualisms, one might anticipate that some plants have evolved defensive countermeasures. Here, we experimentally examined the role of sticky rings formed by *Boerhavia spicata* Choisy (Nyctaginaceae) in plant defense against ant-herbivore associations. We randomly assigned 67 plants to one of two treatments: sticky rings covered with diatomaceous earth and controls. Treatment plants (no rings) supported significantly higher densities of aphids ($p=0.045$) and ants ($p=0.056$) than did controls. Ants, predominantly *Myrmecocystus depilis* (Hymenoptera: Formicidae), attained significantly ($p= 0.030$) higher abundances on a per aphid basis on treatment plants than on controls. Densities of nonmyrmecophilous herbivores did not differ significantly between treatment groups. Sticky rings appear to disrupt the establishment of ant-aphid associations in *Boerhavia spicata*..

Introduction

Ants are known to form mutualistic relationships with a variety of herbivorous insects including cynipid wasps (Washburn 1984, Abe 1988), lepidopterans (Ross 1966, Atsatt 1981, Horvitz and Schemske 1984, Maschwitz *et al.* 1984), membracids (Messina 1981, Fritz 1982, Buckley 1983), coccids (Bradley 1973, Hill and Blackmore 1980, Bach 1991), and aphids (Banks 1958, Takeda *et al.* 1982, Dixon 1985). Ants receive nutrient-rich honeydew and occasionally consume erstwhile mutualists. In exchange, ants provide protection from natural enemies, transport to suitable hosts, brood care, and removal of fouling honeydew (reviewed by Way 1963, Buckley 1987).

The impact to plants that harbor ant-herbivore mutualisms ranges from detrimental to beneficial (Carroll and Janzen 1973, Buckley 1987) depending on, among other things, the population size and feeding rates of ant-tended herbivores (Buckley 1983, Horvitz and Schemske 1984), transmission of viral pathogens by myrmecophilous insects (Maramorosch 1963, Conti 1985, Nault 1985), and ant protection of (Fritz 1983) or aggressiveness to nonmutualistic herbivores (Stout 1979, Messina 1981, Temple 1983, Boecklen 1984, Strauss 1987, Horvitz and Schemske 1990, Bach 1991). Plants benefit from ant-herbivore mutualisms only if there is a reduction in nonmutualist herbivory that outweighs the negative impacts of myrmecophilous herbivores.

The variable nature of ant-herbivore interactions has motivated much recent interest in host plant mediation of ant-herbivore mutualisms (Buckley 1987, Becerra and Venable 1989, Cushman 1991). Most of this interest has focused on the roles of extrafloral nectaries (Thompson 1982, Becerra and Venable 1989 1991, Fiala 1990), plant nutritional status (Buckley 1987, Cushman 1991), or other measures of plant quality, such as plant height (Breton and Addicott 1992). Little attention has been given to the role of plant physical defenses in plant-ant-herbivore interactions.

Plants possess a variety of physical defenses that could deter or mediate ant-homopteran associations (see Campbell *et al.* 1980, Tingey 1985). These include plant hairs (Levin 1973, Johnson 1975, Woodman and Fernandes 1991), glandular trichomes (Duffey 1986, Tingey and Laubengayer 1981, Shade and Kitch 1983), and sticky rings, glutinous bands that develop at the internodes of some plants (Levinson 1982). The effectiveness of plant hairs and glandular trichomes as a defense against herbivores is well established (*e.g.* Tingey and Laubengayer 1981, Shade and Kitch 1983, Woodman and Fernandes 1991). In contrast, the role of sticky rings in herbivore defense is largely unknown.

Here we examine the defensive role of sticky rings formed by *Boerhavia spicata* Choisy. We demonstrate through field experiments that sticky rings function to reduce densities of aphids and ants. The rings appear to deter the establishment of ant-aphid associations.

Materials and Methods

Organisms and study site

Boerhavia spicata Choisy (Nyctaginaceae) is an annual herb widespread in the Sonoran and Chihuahuan deserts of Southwestern United States and Northern Mexico. The plant usually has 3 to 5 slender branches that radiated from the base and is supported by a thin taproot. Leaves occur at the base of the plant; main stems (20 to 60 cm) and all subsequent emerging lateral stems terminate with inflorescences (Wooton and Standley 1915, Spellenberg et al. 1986). Sticky rings occur at the internodes of all main and lateral stems from above the leaves to the flower blossoms (Fig. 1).

We examined a population of *Boerhavia spicata* from mid-July through mid-October, 1988, at a 5 km^2 site approximately 10 km east of Las Cruces, Dona Ana County, New Mexico, USA. The population of *B. spicata* was growing in sandy red clay soil located near Tortugas Mountain. Germination and establishment occurred shortly after the onset of summer rains in early July. Plants were withered and dried by the end of October.

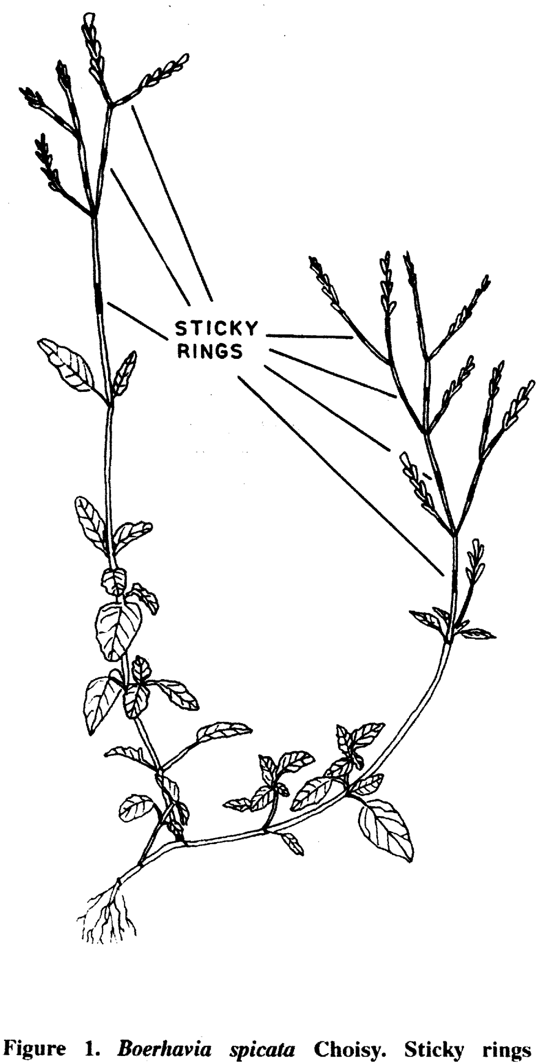

Figure 1. ***Boerhavia spicata*** **Choisy. Sticky rings are depicted as black bands (after Parker 1958).**

Hypotheses and experimental design

Based on preliminary observations of *Boerhavia spicata, Anulocaulis annulatus,* and *A. gypsogenus* (Nyctaginaceae), we hypothesized that sticky rings may act as a physical defense against aphids and may prevent ants from establishing mutualistic associations with aphids. The sticky rings on *Boerhavia spicata* are similar in appearance and texture to Tanglefoot, a sticky commercial product often used in ant exclusion experiments (e.g. Faeth 1980, Boecklen 1984, Washburn 1984).

To determine the function of sticky rings, we randomly assigned 80 newly emerged plants to one of two treatments: 40 plants were treated with diatomaceous earth to cover the sticky rings, and 40 plants were controls. We removed all vegetation within a 10 cm radius around each plant. Diatomaceous earth was reapplied daily to the sticky rings of the treatment plants, twice daily when rain removed the diatomaceous earth. Over a six week period, counts were made daily of numbers and types of insects (ants, aphids, and other herbivores). During the course of the experiment, several ($N = 13$) plants from both experimental groups died and were excluded from the analyses.

Statistical analyses

We compared abundances of ants, aphids, and other herbivores on treatment and control plants with one-factor, repeated measures univariate analyses of variance (ANOVA). We averaged densities (individuals/plant) over six weekly intervals and transformed densities by square root ($X+1$). We excluded 6 experimental plants and 1 control plant from the analysis of ant abundances - the plants never had aphids and could not be expected to attract ants. We controlled for multiple testing by using Sidak's multiplicative inequality (see Sokal and Rohlf 1981):

$$\alpha = 1 - (1 - \alpha)^{1/k,}$$

where α is the familywise error rate and k is the number of comparisons. We were testing *a priori* hypotheses that ants and aphids would increase on experimental plants. We evaluated these hypotheses using one-tailed tests. We had no expectation regarding abundances of other herbivores and used a two-tailed test.

To determine whether sticky rings interfered with ant access to aphids, we compared abundances of ants on a per-aphid basis on experimental and control plants with a one factor analysis of covariance using cumulative abundance of ants ($\sum_{1}^{6} (X+1)^{0.5}$) as the dependent variable and cumulative abundance of aphids as the covariate. We then estimated separate linear regressions for both experimental groups.

Table 1. Mean densities (individuals/plant) and standard errors (SE) of ants, aphids, and nonmyrmecophilous herbivores on 34 treatment and 33 control plant of Boerhavia spicata over a six week sampling period in 1988.

Week		Ants		Aphids		Herbivores	
		X	SE	X	SE	X	SE
1	Control	0.27	0.09	2.60	0.86	0.05	0.03
	Treatment	.30	0.13	2.02	1.06	0.04	0.03
2	Control	0.52	0.18	1.31	0.49	0.54	0.24
	Treatment	1.11	0.32	1.50	0.57	0.02	0.01
3	Control	0.37	0.12	2.14	0.60	0.07	0.03
	Treatment	0.76	0.25	4.82	2.37	0.04	0.02
4	Control	0.21	0.10	3.24	0.98	0.09	0.02
	Treatment	0.60	0.30	8.19	2.79	0.03	0.01
5	Control	0.12	0.07	1.25	0.51	0.13	0.04
	Treatment	0.08	0.06	9.65	3.73	0.07	0.02
6	Control	0.00	0.00	5.46	2.07	0.19	0.84
	Treatment	0.07	0.61	11.80	2.94	0.24	0.06

Results

Aphids were the most common insects on both treatment and control plants (Table 1). Aphids averaged 6.3 individuals per plant on treatment plants (no rings) and 2.6 individuals per plant on controls. Control plants averaged fewer numbers of ants, 0.25 individuals per plant, than did treatment plants, 0.49 individuals per plant, over the six week sampling period. The most common ant on the study site was the formicine, *Myrmecocystus depilis*. This ant was quite active in tending aphids. Non-mutualistic herbivores averaged only 0.10 individuals per plant on controls and 0.07 individuals per plant on treatment plants. The sphingid, *Hyles lineata*, was the most common of the nonmyrmecophilous herbivores. Predatory and parasitic hymenopterans, particularly chalcids and eulophids, were present at the study site, as were coccinellids.

Treatment plants supported significantly (p= 0.045) higher densities of aphids than did control plants as indicated by analysis of variance (Table 2). Aphid densities also varied significantly ($p < 0.001$; two-tailed test) among weeks, reaching highest densities for both groups in week 6 (Fig. 2). There was a marginally significant (p= 0.057; two-tailed test) interaction effect for aphid densities, with aphids increasing more rapidly over time on treatment plants than on control plants.

Analysis of variance indicated marginally significant (p= 0.057) differences in ant abundances between treatment and control plants over the six week period sampling period (Table 2). Ant densities were generally higher on treatment plants. There were highly significant ($p < 0.001$; two-tailed test) differences among weeks in mean ant densities (Fig. 2). Densities for both treatment groups were highest in week 2, but by week 5 ants were largely absent from both groups. There was no significant (p= 0.290) treatment-by-week effect for ant densities.

Densities of nonmutualistic herbivores, predominantly *Hyles lineata*, did not differ significantly (p= 0.781) between treatment groups. Densities did vary significantly ($p < 0.001$) among weeks, with densities steadily increasing over the six week sampling period (Table 1). There was no significant (p= 0.900) interaction effect for nonmutualistic herbivore densities.

Analysis of covariance indicated significant differences (partial $F_{1,63}= 6.198$; p= 0.030) between treatment and control plants in the relationship between cumulative ant and aphid abundances (Fig. 3). Individual regressions indicated a highly significant ($p < 0.001$) positive relationship for treatment plants, but not for control plants (p= 0.442).

Table 2. Comparison of treatment (no sticky rings) and control plants on the basis of three insect categories. Treatment effects for ants and aphids are based on one-tailed tests; all other effects are based on two-tailed tests. All tests have been adjusted for familywise error. Analyses are based on square root (X+1) transformations.

ANOVA - Aphids	d.f.	F	p
Treatment	1, 65	4.90	0.045
Weeks	5, 325	5.95	<0.001
Treatment x Weeks	5, 325	2.73	0.057
ANOVA - Ants			
Treatment	1, 58	4.51	0.056
Weeks	5, 290	9.29	<0.001
Treatment x Weeks	5, 290	1.82	0.290
ANOVA -Other Herbivores			
Treatment	1, 65	0.73	0.781
Weeks	5, 325	5.76	<0.001
Treatment x Weeks	5, 325	0.82	0.900

Discussion

Densities of aphids and aphid-tending ants increased on plants without operational sticky rings. Aphid densities generally increased throughout the sampling period, increasing faster on treatment plants than on control plants. In contrast, ant densities peaked early (week 2) and declined thereafter. By week 5, ants were largely absent from experimental and control plants. Densities of nonmyrmecophilous herbivores were unaffected by the experimental removal of sticky rings. This suggests that ant- aphid associations did not confer a net increase in protection against nonmutualistic herbivores to *Boerhavia spicata*.

The decrease in ant abundances after week 2 is puzzling. Two hypotheses seem plausible. First, ant-homopteran associations have been reported to exhibit age-dependent effects (Wood 1982, Cushman and Whitham 1989), with the strength of association diminishing through time. Second, ants are known to drop low- value items from their diets as higher valued items become available (Addicott 1978, Becerra and Venable 1989). Perhaps *Myrmecocystus depilis* has a limited dietary requirement for honeydew that is satisfied early in the growing season of *Boerhavia spicata*. We will investigate these hypotheses in future field experiments.

Our experimental results are consistent with a hypothesis that sticky rings function as a plant defense against the establishment of ant-aphid associations. Sticky rings could be effective in one or more modes of operation. First, sticky rings could act against aphids directly through entrapment, and in this way function like glandular trichomes (see Tingey and Laubengayer 1981, Shade and Kitch 1983, Tingey 1985). Aphids were found trapped in sticky rings on control plants. Sticky rings could also act to compartmentalize aphids, increase crowding, and trigger a variety of density-dependent effects that retard aphid population growth. Crowding in aphids is known to increase the production of alatae (Lees 1967, Shaw 1970, Watt and Dixon 1981,

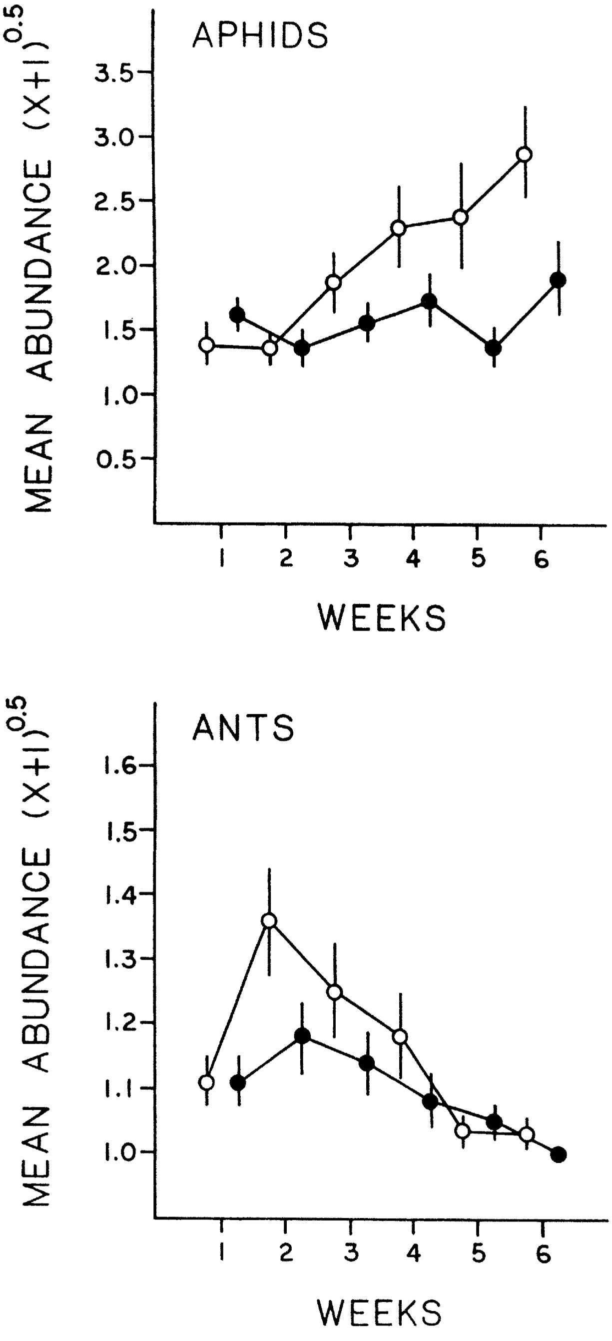

Figure 2. Mean abundances (individuals/plant) of aphids and ants on treatment (open circles) and control plants over a six week sampling period. Vertical bars are standard errors. Data are transformed by square root (X+1).

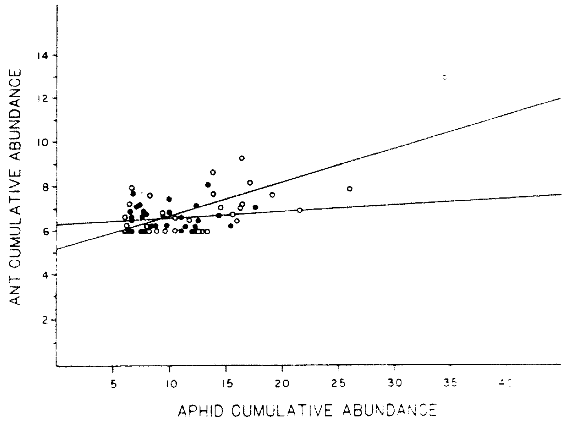

Figure 3. Relationship between cumulative abundance of ants ($(X+1)^{0.5}$) and cumulative abundance of aphids for treatment (open circles) and control plants summed over a six week sampling period. Half-open circle represents 7 plants at coordinates (6.0,6.0). Individual relationships are $Y = 6.322 + 0.025X$ for controls ($F_{1,31} = 0.607$; $p = 0.0442$) and $Y = 5.101 + 0.153X$ ($F_{1,32} = 34.512$; $p < 0.001$) for treatment plants.

Dixon 1985), and to reduce adult weight (Way and Banks 1967, Dixon 1971, Dixon 1985) and fecundity (Dixon 1971, Whitham 1980). Sticky rings may also prevent aphids from moving within plants to preferred feeding sites (see Shade and Kitch 1983). Compartmentalization was not a focus of the present study and will be tested in future field experiments.

An alternative, but not mutually exclusive, mode of defense is exclusion of aphid-tending ants. Recall that cumulative abundances of ants exhibited a positive relationship with cumulative abundances of aphids in experimental plants, but no relationship was found for control plats (Fig. 3). We did not measure the effects of ant tending on aphid performance, so a defensive mechanism of ant exclusion must be viewed as speculative. Nevertheless, unattended aphids are subject to at least two sorts of effects that could reduce population growth. First, ant-tending is known to increase aphid feeding rates (Banks and Nixon 1958, Way 1963, Takeda *et al.* 1982), growth (El- Zaidy 1960, Dixon 1985), reproduction (El-Zaidy 1960, Way 1963), and colony persistence (Dixon 1985). Second, unattended aphids often suffer greater rates of predation than do ant-tended aphids (reviewed by Way 1963, Buckley 1987). Predators and natural enemies can have devastating impacts on aphid populations. For example, Liao *et al.* (1985) tested a variety of chrysopid and coccinellid predators on populations of the blackmargined pecan aphid (Monellia caryella) under laboratory conditions and observed average consumption rates of 25 to 60 aphids per day. Thus, sticky rings might function not only to reduce initial aphid colonization, but to mitigate subsequent impacts of aphid colonization, as well.

There is at least one alternative hypothesis for the function of sticky rings in *Boerhavia spicata* - capture of nutrients from entrapped insects. The importance of carnivory for plants in resource-limited environments is widely studied and well documented (*e.g.* Benzing *et al.* 1977, Dixon *et al.* 1980). Several species of plants are capable of absorbing nutrients from insects trapped by glandular trichomes (see Dixon *et al.* 1980). At present, we have no evidence that *Boerhavia spicata* is capable of absorbing nutrients through its sticky rings. We will test this hypothesis in future laboratory experiments. Of course, sticky rings may contribute both to plant nutrition and plant defense as the two functions are not mutually exclusive.

The proposition that plants should defend against ant-homopteran mutualisms requires further exploration. In a recent paper, Becerra and Venable (1989) suggested that extrafloral nectaries may function in just such a capacity. The Ant-Distraction Hypothesis (Becerra and Venable 1989) maintains that extrafloral nectar substitutes for honeydew and entices ants to abandon myrmecophilous homopterans (see also Thompson 1982). The Ant- Distraction Hypothesis has been challenged empirically (Fiala 1990) and lacks experimental evidence (Becerra and Venable 1991). We have presented experimental evidence that sticky rings formed by *Boerhavia spicata* may interfere with the establishment of ant- aphid associations. These results suggest that plant physical defenses also can play a critical role in complex ant-homopteran- plant interactions.

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