ORIGINAL ARTICLE

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Induced responses to herbivory in the Neotropical ant-plant association between *Azteca* ants and *Cecropia* trees: response of ants to potential inducing cues

Abstract Plant defense against herbivores often involves constitutive and inducible mechanisms of resistance. Obligate ant-plants, which provide food and housing for ants, are thought to primarily rely on ants for defense against herbivores. This form of plant defense has largely been viewed as static. We have been investigating the dynamic nature of *Azteca* ants as an inducible defense of *Cecropia* trees. Ants rapidly recruit to and patrol sites of foliar damage. We propose that *Azteca* ants can be viewed as an inducible defense for *Cecropia* trees because of their sensitivity to cues associated with herbivory, their rapid and aggressive recruiting ability, and their reclaimable and redeployable nature as a plant defense. In this study, we examine ant behavior following plant damage, and the potential cues that induce ant recruitment. We found that ants present on leaves when the plant is damaged leave the damaged leaf and recruit other ants to it, presumably by laying recruitment trails. Volatile leaf cues associated with herbivory were important in eliciting an induced response in two experiments. However, we found that cues associated with a congeneric plant elicited a much stronger ant response than conspecific cues. Although the type of leaf damage (gaping wounds versus leaf edge wounds) did not affect the level of ant recruitment, the extent of damage did. Leaves with one hole punched showed a 50% increase in ants, while leaves with five holes punched in them elicited a 100% increase in ant numbers. In sum, it appears that multiple plant-related cues associated with herbivory are involved in induction of ant recruitment in the *Cecropia*-*Azteca* system. We discuss the generality of ant responses to herbivory in obligate ant-plant systems, and in facultative ant-plant associations, which may be more common.

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Introduction

Ant-plants, plants that provide food and/or housing for ants, are conspicuous members of tropical plant communities, in part because their putative plant defenses are visible on the outside of the leaves as opposed to being hidden inside. Many ant-removal studies have demonstrated that ants protect plants against herbivory and competing plants (Janzen 1966, 1969; Schupp 1986; Vasconcelos 1991; Fisher 1992; Fonseca 1994; Del-Claro et al. 1996; Gaume et al. 1997; Oliveira 1997), and have led to the hypothesis that ants are functionally equivalent to chemical defenses (Janzen 1966, 1969; Rehr et al. 1973; McKey 1984, 1988; Davidson and Fisher 1991). Ants are similar to chemical defenses in that their numbers (concentrations) are dependent on various environmental conditions (Agrawal and Rutter, in press). In addition, several authors have suggested that plant defense by ants is not as simple as the presence/absence of ants, and that the dynamic behaviors of ants may be an important factor in their effectiveness (Letourneau 1983; Madden and Young 1992; Rocha and Bergallo 1992; Gaume et al. 1997, Agrawal, in press; Agrawal and Rutter, in press).

Some plant defenses are induced by herbivory. Induced phytochemical and physical responses following herbivory have been well documented in temperate plants (Tallamy and Raupp 1991; Karban and Baldwin 1997). Few studies have investigated plant responses to herbivory in tropical plants. Young (1987) found that giraffe herbivory resulted in increased length of newly formed thorns on African *Acacia drepanolobium*.

Milewski et al. (1991) further demonstrated that this increase in thorn length resulted in reduced subsequent grazing. Ants have also been studied as an inducible plant defense (Fiala and Maschwitz 1990; Madden and Young 1992; Rocha and Bergallo 1992; Cronin 1998; Agrawal, in press). Belt (1874) was one of the first naturalists to document that disturbance to myrmecophytic plants resulted in aggressive biting, stinging, and swarming of the ants living inside ant-plants. The general biology of ants makes them well suited for use as an inducible plant defense: (1) they have acute sensory mechanisms to detect disturbance and chemical cues, (2) they are often aggressive and have well-developed defense mechanisms (e.g., biting and stinging), (3) they have recruiting mechanisms which make them rapidly deployable and also reclaimable, and (4) individual ants will give their life in defense of the colony or its resources (Hölldobler and Wilson 1990).

We have been studying the aggressive behavior of *Azteca* spp. ants that inhabit Neotropical *Cecropia obtusifolia* trees. Leaf damage resulted in a tripling of the number of ants patrolling damaged leaves compared to undamaged controls (Agrawal, in press), and ant number is positively associated with resistance against herbivores in *Cecropia* trees (Rocha and Bergallo 1992). In this study, we extend our previous results and examine several potential cues which may serve as signals that ants use to recruit to damaged leaves. Our goal is to understand how ants respond to leaf damage, and whether their response is largely due to signals produced by the plant, or to other cues associated with herbivory such as disturbance and leaf damage.

Our previous work suggested that volatiles associated with *C. obtusifolia* may be important in the induction process and that the type of damage may also influence the level and persistence of ant patrolling. In this study we asked: what is the behavioral mechanism of ant induction on damaged leaves? It is important to distinguish between a plant-wide ant response to herbivory and active "recruitment" of ants at the damage site. Our study is the first to specifically test for ant recruitment per se to damaged leaves. We then conducted experiments to determine the effects of (1) plant chemicals specific to *C. obtusifolia*, (2) the type of leaf damage, and (3) the extent of leaf damage.

Methods

Study site and natural history

This study was conducted at the Organization for Tropical Studies La Selva Biological Station, near the town of Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica (10°26′N and 84°00′W). La Selva is located in a lowland tropical wet forest on the Costa Rican Caribbean slope and receives approximately 4000 mm of rainfall each year. Detailed information about the site and climate is provided in McDade et al. (1994). We conducted the field work in December 1997–January 1998 during the beginning of the dry season.

Of the early successional Neotropical flora, the genus *Cecropia* (Urticaceae; Judd et al. 1994) contains over 100 species, most of which have associations with symbiotic ants. *Azteca* spp. (Formicidae: Dolichoderinae) ants inhabit most of the *C. obtusifolia* trees at La Selva Biological Station. The mutualism between *Cecropia* spp. and *Azteca* spp. has been intensively studied (Skutch 1945; Janzen 1969, 1973; Schupp 1986; Jolivet 1988, 1990; Longino 1989, 1991; Davidson and Fisher 1991; Rocha et al. 1992; Folgarait and Davidson 1995; Vasconcelos and Casimiro 1997; Yu and Davidson 1997). Like almost all members of the genus, *C. obtusifolia* develops hollow stems in which ant colonies nest. *C. obtusifolia* also produces glycogen-containing Müllerian food bodies and pearl bodies, which may contain carbohydrates, lipids, and proteins (Rickson 1971, 1973; O'Dowd 1982; A.A. Agrawal, personal observation). *Azteca* ants consume the food bodies, patrol the plant and, in many cases, successfully reduce herbivory and increase the fitness of plants relative to conspecifics without ant protectors (Schupp 1986; Rocha and Bergallo 1992; Vasconcelos and Casimiro 1997). Schupp (1986) demonstrated that when its ant inhabitants were removed, *C. obtusifolia* experienced higher herbivory, increased vine cover, and significantly stunted growth. We studied young *C. obtusifolia* trees inhabited by *Azteca xanthocroa* or *Azteca constructor*. Both ant species are extremely aggressive obligate mutualists that defend *Cecropia* spp. and are difficult to distinguish from each other without examining the queen (J. Longino, personal communication). Worker ants were sampled from each tree to make sure that the ants were not *Azteca alfari*, the apparently less aggressive and less defensive species of *Azteca* ant that inhabits *Cecropia* spp. (Longino 1991; but see Vasconcelos and Casimiro 1997). *A. alfari* can be easily distinguished by examining workers (J. Longino, personal communication).

Recruiting behavior

Our previous studies of induction in the *Cecropia-Azteca* system demonstrated that leaf damage caused a fivefold increase in the number of *Azteca* spp. ants on damaged leaves of *C. obtusifolia* compared to that on disturbed but undamaged control leaves on the same tree (Agrawal, in press). Although we initially attributed this differential accumulation of ants on the damaged leaf to induction of ant "recruitment," we did not have data on the mechanism of induction. Wilson (1971) defined recruitment as communication between nestmates that results in movement of ants towards an area where work is required. Recruitment can be triggered by a variety of mechanisms, of which chemical trail communication is the most prevalent (Hölldobler and Wilson 1990). As an alternative to recruitment per se, ants may respond systemically to the induction cues and simply accumulate on damaged leaves. To determine if the ants were indeed recruiting to sites of foliar damage, we conducted experiments where we inflicted leaf damage (five holes from a standard hole puncher, approximately 30 mm^2 each) to individual leaves of plants and intensively observed ant activity. We recorded every ant that came onto or left the leaf at the leaf-petiole juncture. Similarly, we recorded every ant that came onto or left the petiole at the petiole-stem juncture (see Fig. 1). These measurements were taken simultaneously for 2 min prior to the leaf damage and for 12 min following leaf damage. We recorded ant numbers at the end of every 30-s period during this time so that we could construct a 30-s flux index for the net change in the number of ants. We conducted these observations on five trees and report the results of a representative tree since the results were consistent among trees. We performed a paired *t*-test on the mean number of pre-damage ants and the total number of ants 12 min after damage. Twelve minutes post-damage was previously determined to be the peak time of ant activity following damage (Agrawal, in press).
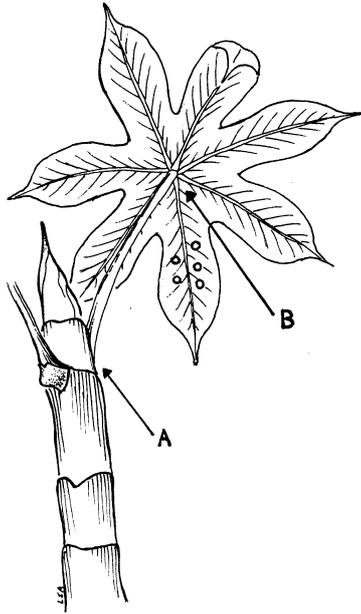
Fig. 1 Schematic diagram of the experimental design used to test for the behavioral responses of ants to leaf damage. *A* represents the petiole-stem juncture and *B* represents the leaf-petiole juncture. Points *A* and *B* were 30–60 cm apart

Inducing signals

To test for the effects of various cues associated with herbivory on inducing ant recruitment, we monitored ant numbers on control and treatment *C. obtusifolia* leaves using a paired-leaf design, with each tree having a treatment and a control leaf. For each experiment we selected 10–20 young trees between 1.5 and 2.5 m tall, lacking signs of recent herbivory, and with established colonies of *A. xanthocroa* or *A. constructor*. On each tree, we chose two of the youngest, fully expanded leaves coming off of the main stem (about 1–2 m apart) and randomly assigned one to the "treatment" and one to the "control" group. We censused the number of ants on the leaves prior to imposing the treatment and at 4, 8, 12, and 16 min after damage. The specific manipulations follow:

(1) To test for effects of leaf volatiles on ant recruitment, we augmented the treatment leaf with a freshly cut *C. obtusifolia* leaf disc (9 cm^2, cut from a different tree), and the control leaf with a disc of paper cut to the same size ($n = 13$ pairs).
(2) To test for the effect of conspecific versus heterospecific leaf volatiles, we augmented one leaf with a freshly cut *C. obtusifolia* leaf disc (9 cm^2, cut from a different tree) and the other leaf with a leaf disc cut from a another myrmecophytic *Cecropia* species common at La Selva Biological Station, *C. insignis* ($n = 19$ pairs). At La Selva, *C. insignis* (like *C. obtusifolia*) is often inhabited by *A. xanthocroa* and *A. constructor*.
(3) As an additional test of the importance of leaf volatiles, we tested for the effects of a methanol extract of *C. obtusifolia* on ant recruitment. We extracted 15 g of fresh *C. obtusifolia* foliage by cutting the foliage into approximately 1-cm^2 pieces and soaking them in 100 ml of methanol for 24 h; after 24 h, the leaf pieces were removed. Methanol generally extracts both polar and non-polar components of the foliage. On each of 19 trees we added five drops of the *C. obtusifolia* extract to the treatment leaf and five drops of methanol onto the control leaf.
(4) Previous results suggested that the type of leaf damage may be important in the strength and/or persistence of ant recruitment (Agrawal, in press). In this experiment, we at-

tempted to create two types of damage with an equal amount of leaf tissue damage, but differing in the visual cues left behind. On one leaf of each of 20 plants we punched 15 holes (30 mm^2 each), to create approximately 30 linear cm of damaged leaf and leaving behind gaping holes. On the paired leaf of each hole-punched leaf we damaged 30 linear cm of leaf by removing (using scissors) a thin (less than 0.5-cm) strip of leaf tissue following the outline of the leaf perimeter.
(5) To determine the importance of the extent of damage in ant recruitment, we conducted experiments in which paired leaves of ten trees received either one or five hole punches.

Statistical analysis

All analyses were conducted using the MGLH routine in Systat (Wilkinson et al. 1992). All experiments were conducted with a paired design, where each tree or experimental unit had both treatments, with no replication within each unit. Repeated-measures analysis of variance procedures were used to test for treatment effects in all experiments. Treatments were considered fixed effects and tree was considered a random effect. In such designs, the between-subjects (remainder) mean square and degrees of freedom is used in the denominator to calculate the *F*-statistic (Zar 1996, p. 267).

Results

Recruiting behavior

In Fig. 2, we present the mean change in ant numbers every 30 s at the leaf-petiole and the petiole-stem junc-
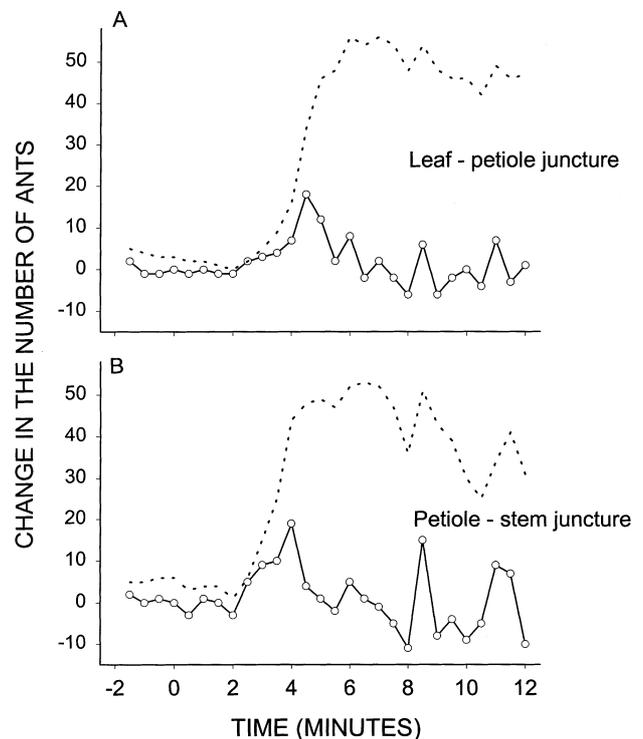

Fig. 2a–b The net change in numbers of ants at the leaf-petiole (**A**) and the petiole-stem (**B**) juncture every 30 s (*solid line*). Five hole punches were imposed on the leaf at time 0. The *dashed line* represents the total (cumulative) number of ants that were on the leaf at any given time

ture for a representative damaged plant. The observed pattern indicates a net decrease in the number of ants at each juncture prior to each major influx of ants. For example, prior to the first major influx of ants to the damaged leaves, in every sampled tree we observed two to five ants leave the leaf-petiole juncture and also leave the petiole-stem juncture. In all cases, this outflow of ants was almost immediately followed by a large net inflow onto the leaves. We interpret this behavior as "recruitment;" it appeared that ants needed to leave the leaves and travel all the way down the petiole off to the stem before there was a influx of ants to the leaf. This experiment also confirmed our previous results indicating a net increase in the number of ants 12 min after damage (mean number $\pm$ SE of ants per leaf: pre-damage $= 10.0 \pm 2.1$, post-damage $= 34.0 \pm 5.3$; $t = 6.303$, $df = 4$, $P = 0.003$).

Inducing signals

Azteca ants responded to plant volatiles and responded differently to conspecific and heterospecific volatiles. Volatiles from *C. obtusifolia* (leaf disc experiment) caused significant induction of ant recruitment relative to paper controls (Fig. 3A, Table 1). In the methanol extract experiment, it appears that methanol alone re-
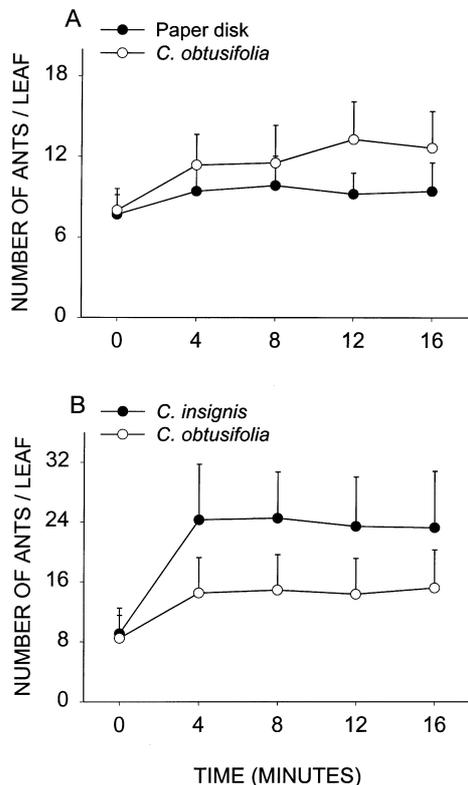

Fig. 3a–b Recruitment of ants to paired leaves that were treated with a paper disc versus a leaf disc of *Cecropia obtusifolia* (**A**), or a leaf disc of *C. obtusifolia* versus a leaf disc of *C. insignis* (**B**). Data shown are the mean + SE

pelled the ants, and that the *C. obtusifolia* extract tempered that response (Fig. 4, Table 1). Volatiles from conspecific plants of *C. obtusifolia* resulted in approximately 30% more ants than on control leaves in both experiments. Heterospecific volatiles from *C. insignis* induced much greater ant recruitment (165%) than volatiles from *C. obtusifolia* (Fig. 3B, Table 1).

The type of damage (gaping wounds vs leaf edge wounds) did not influence ant response to damage, and in both treatments, ant numbers approximately tripled following damage (Fig. 5A, Table 1). Extent of damage had a significant effect on the level of *Azteca* ant recruitment (Figure 5b, Table 1). On leaves with one hole punch ant numbers increased approximately 50%, while on leaves with five hole punches, ant numbers increased just over 100%.

Discussion

Induced responses to herbivory are common in most groups of plants including annual and perennial species and both terrestrial and aquatic species (Karban and Baldwin 1997). Plant responses to herbivory can take the form of phytochemical changes such as increases in proteinase inhibitors, oxidative enzymes, and alkaloids following wounding in solanaceous plants (Green and Ryan 1972; Baldwin 1991; Duffey and Stout 1996; Stout et al. 1996). Plant responses can also take the form of increased density or size of physical resistance mechanisms such as thorns, spines, and trichomes (Young 1987; Baur et al. 1991; Myers and Bazely 1991; Young and Okello 1998; A.A. Agrawal, unpublished data). Induced responses have also been reported in ant-plants, most often as changes in extrafloral nectar volume or composition following herbivory (Mound 1962; Stephenson 1982; Koptur 1989; Smith et al. 1990; Agrawal and Rutter, in press). These examples of nectar responses following herbivory were all found in non-obligate ant-plant species, and ant responses were not quantified in these studies. In more obligate systems, there have been observations of ant responses to disturbance and herbivory, although the mechanisms are unknown in each case (*Crematogaster-Macaranga*: Fiala and Maschwitz 1990; *Camponotus-Macaranga*: Federle et al. 1998; *Crematogaster-Acacia*: Madden and Young 1992; *Azteca-Cecropia*: Rocha and Bergallo 1992; Agrawal, in press; *Pseudomyrmex-Acacia*: Cronin 1998). For example, Fiala and Maschwitz (1990) found that ants on Asian *Macaranga* trees showed a strong numerical response to leaf damage and increased in numbers for up to 3 h following damage. Similarly, we have shown in our previous work with *Cecropia* trees that leaf damage per se was an important cue for induction of ant recruitment, and that disturbance alone caused minimal induction (Agrawal, in press). Induction of ants in these obligate systems does not appear to be associated with induction of ant rewards such as nectar or food bodies.

Table 1 Repeated-measures analysis of variance tables for the effects of various stimuli on recruitment of *Azteca* ants on *Cecropia obtusifolia* trees. Probabilities corrected for sphericity are provided using the Greenhouse-Geisser correction (*G-G*)

Experiment	Source	df	MS	F	P	G-G
Leaf disc vs paper						
	Treatment	1	238.784	4.418	0.05	
	Tree	18	747.947	13.838	< 0.001	
	Error	18	54.051			
	Time	4	72.039	9.718	< 0.001	< 0.001
	Time × treatment	4	19.771	2.667	0.039	0.071
	Time × tree	72	21.787	2.939	< 0.001	< 0.001
	Error	72	7.413			
C. obtusifolia vs C. insignis						
	Treatment	1	1794.531	5.531	0.037	
	Tree	12	3232.869	9.964	< 0.001	
	Error	12	324.464			
	Time	4	582.873	17.469	< 0.001	< 0.001
	Time × treatment	4	97.204	2.913	0.031	0.061
	Time × tree	48	81.294	2.436	0.001	0.009
	Error	48	33.366			
Extracts						
	Treatment	1	188.005	5.409	0.032	
	Tree	18	1541.714	44.352	< 0.001	
	Error	18	34.761			
	Time	4	13.592	1.103	0.362	0.346
	Time × treatment	4	20.913	1.697	0.160	0.195
	Time × tree	72	17.095	1.387	0.084	0.156
	Error	72	12.321			
Type of damage						
	Treatment	1	389.205	1.379	0.255	
	Tree	19	9778.792	34.655	< 0.001	
	Error	19	282.173			
	Time	4	3029.683	45.061	< 0.001	< 0.001
	Time × treatment	4	32.793	0.488	0.745	0.588
	Time × tree	76	322.219	4.792	< 0.001	< 0.001
	Error	76	67.235			
Extent of damage						
	Treatment	1	784.000	13.972	0.005	
	Tree	9	1141.107	20.337	< 0.001	
	Error	9	56.111			
	Time	4	563.840	44.031	< 0.001	< 0.001
	Time × treatment	4	43.250	3.337	0.019	0.032
	Time × tree	36	57.207	4.467	< 0.001	< 0.001
	Error	36	12.806			

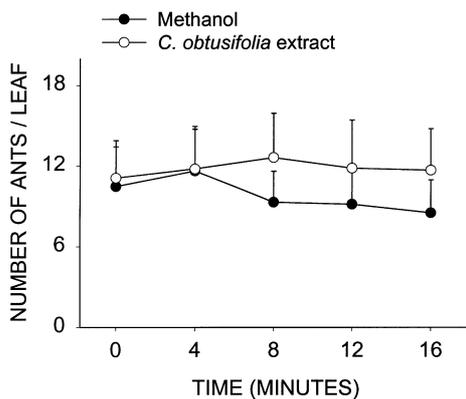It is generally thought that inducible defenses increase plant fitness in the presence of herbivores, but

Fig. 4 Recruitment of ants to paired leaves that were treated with five drops of a methanol extract of *C. obtusifolia* versus methanol alone. Data shown are the mean + SE

have costs, so that induction decreases plant fitness in the absence of herbivores (Harvell 1990; Karban and Baldwin 1997; Agrawal 1998a). Such a cost-benefit trade-off, if genetically based, may constrain the evolution of inducible defenses. For ant-plant systems, especially those that are facultative, i.e., where plants offer an inducible reward to ants following herbivory (see above), such cost-benefit models may be appropriate. However, in obligate systems where ants may "induce themselves," alternative hypotheses need to be considered (Agrawal and Rutter, in press). In many of these obligate systems, the ants remove herbivores from plants, but do not consume them. In such systems, it is not clear who or what regulates the induction, the ants or the plants. Ants do not appear to directly benefit from inducing recruitment and removing herbivores. However, if herbivory affects plant performance and ant fitness is tightly coupled to plant performance, then ants may "induce themselves" in response to herbivory and may not be responding to plant cues (Agrawal and
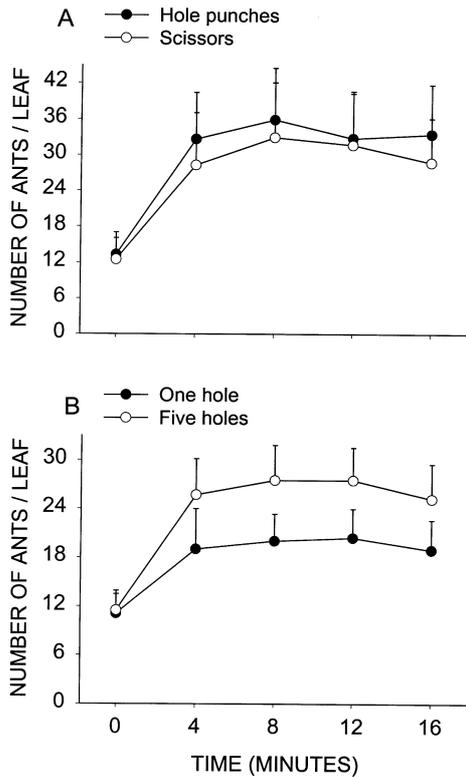
Fig. 5a–b Recruitment of ants to paired leaves that were treated with hole punches versus scissors clipping around the perimeter of the leaf (equal amount of linear length of leaf damage in both treatments) (**A**), and one hole punch versus five hole punches (**B**). Data shown are the mean + SE

Rutter, in press). In such cases, the plant may not offer additional rewards to induce ant recruitment. Our investigations of the *Cecropia-Azteca* system have focused on how the ants respond to damage and what the inducing cues may be.

Azteca ants appear to respond to foliar damage by alarming nestmates and show a numerical increase primarily due to some form of recruitment. In our observations of ant behavior, the ants present on the leaves at the time of damage immediately became excited and began swarming around the damaged leaf and investigating the damaged sites. Ant numbers on the leaf, however, did not increase for a few minutes, and the increase was always preceded by a fraction of the ants on the leaf leaving and travelling all the way off the petiole to the stem. These ants were often observed walking with a curled gaster, perhaps indicating that the ants were releasing alarm substances or trail pheromones (P.S. Ward, personal communication, see also Wheeler et al. 1975). The alternative to the "recruitment hypothesis" is that ants not present on the damaged leaf respond to plant cues that emanate from damaged leaves. This is unlikely because volatile damage cues are likely to diffuse and not reach the rest of the colony. Consistent with this, in a previous experiment in which we removed damaged and undamaged *C. obtusifolia*

leaves and used them to elicit ant recruitment on another tree, we observed no difference in recruitment of ants to leaves adjacent to damaged leaves compared to recruitment on leaves adjacent to undamaged leaves (Agrawal, in press).

Azteca ants responded to host plant volatiles. These volatiles may serve as a cue that herbivores are present on the plant. Fiala and Maschwitz (1990) also reported ant responses to host plant cues in the *Crematogaster-Macaranga* system. Interestingly, they observed the greatest ant response to conspecific cues from water extracts of the foliage, compared to extracts from congeneric and unrelated plants. However, ants also respond to plant cues in order to "prune" competing plants and encroaching vines (Janzen 1969; Davidson et al. 1988). Fiala and Maschwitz observed the strongest "pruning" response to non-host plant leaves. Our results can be interpreted consistently with the observations of Fiala and Maschwitz (1990): we found that ants responded to host plant volatile cues (extract, and leaf disc experiments), but that they had a stronger response to heterospecific cues in the leaf disc experiment. The stronger response of ants to *C. insignis* may be due to the ants' perception of this plant as a competitor which they were attempting to prune. Alternatively, *C. insignis*, which is an ant-plant which also has an association with *A. xanthocroa* and *A. constructor*, may produce similar alarm signals that are stronger than those present in *C. obtusifolia*. Further work on volatile leaf cues from various related and unrelated species will be instructive in resolving how ants recognize host plant wounding versus competitor encroachment. In addition, this effect of the ants' apparent response to plant cues may also be related to the territoriality of arboreal ants (see Davidson et al 1988; Adams 1994).

The current study indicates that visual or tactile cues are less important than chemical cues. In previous experiments we had hypothesized that visual and/or tactile cues were important. Treating a *C. obtusifolia* leaf with several hundred pin wounds induced significant ant recruitment beyond the recruitment observed on paired leaves that were disturbed but not damaged (Agrawal, in press). However, the magnitude and persistence of this recruitment was much weaker than that observed following hole punch damage. This led us to the hypothesis that gaping holes associated with hole punching were important cues not present in the pin-wounding treatment. Our experiments with leaf discs and methanol extracts resulted in ant responses to conspecific volatiles even though treatment and control leaves had the same visual and tactile cues. Furthermore, ants showed similar numerical responses to clipping of the leaf perimeter and hole punching when the linear length of damage was controlled for. Our previous results may have been caused by a difference in the actual area of leaf tissue that was damaged in the pin-wounding versus hole-punching experiments.

Extent of damage appears to be an important determinant of the ant response to damage. Induced phyto-

chemical responses also appear to be positively associated with the level of herbivory (Karban 1987; Lin et al. 1990, Bodnaryk 1992; Baldwin and Schmelz 1994). In our experiments, we found that the ant response to five hole punches was twice that of the response to one hole punch. This result has two implications. First, the amount of damage can have a quantitative effect on ant recruitment. We observed ant responses to the single hole punch (Fig. 5b), indicating that both our experimental levels of damage fell above the threshold of damage necessary to cause induction. Rocha and Bergallo (1992) additionally found that the extent of *Azteca* responses to herbivores was positively correlated with subsequent resistance to herbivores. The second implication of our result is that ant responses do not appear to be simply additive with regard to the level of damage. A fivefold increase in damage only caused a twofold increase in ant recruitment. Detailed studies on the importance of the extent of damage will be needed to characterize the density-dependent relationship between herbivory, induced responses, and induced resistance to herbivores.

Conclusion

Resident *Azteca* ants on *C. obtusifolia* trees respond to volatile plant cues associated with herbivory. Such volatile cues may be released in a fashion that is density dependent with the level of damage. Excited ants recruit nestmates to damage sites. Induction of ant recruitment in this system is likely to serve as a mechanism of induced resistance to herbivores.

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