

## MINI- REVIEW

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# Dynamic anti-herbivore defense in ant-plants: the role of induced responses

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We compare the dynamic nature of anti-herbivore defense in ant-plants to other plant-herbivore systems. Previous studies have neglected the dynamic nature of defense in ant-plants. Changes in environmental cues can trigger modifications in a plant's defensive strategy (induced responses). In ant-plants, many cues and signals controlled by the plant and the environment can enhance defense by influencing recruitment, patrolling, and persistence of ants. Leaf damage may trigger plant signals such as the release of plant sap or green leaf volatiles that attract ant defenders. Similarly, disturbance and mammalian breath may themselves induce ants to recruit.

We also review studies that have looked for changes in extrafloral nectar production induced by herbivory. Induced responses to herbivory that stimulate changes in nectar volume, sugar concentration, and amino acid concentration of extrafloral nectar have been reported. This should increase patrolling by defending ants. We propose that non-nectary mediated ant recruitment should also occur, but may be restricted to tightly linked ant-plant systems. We suggest that induced responses to herbivory are common in ant-plants.

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Plants have a variety of defensive strategies against herbivores. Chemical, physical, and biotic defenses can reduce herbivory and increase plant fitness. Most plants employ multiple defenses, which vary in intensity and effectiveness, and can operate over different temporal and spatial scales against different attackers. For example, the leaves of some solanaceous plants have trichomes which exude toxins (Duffey 1986), as well as suites of interacting

constitutive and inducible chemical compounds that are assumed to confer resistance against various herbivores (Duffey and Stout 1996). Trichomes provide a physical hazard, while constitutive chemical defenses may be poisonous or anti-nutritive. Induced responses boost the defensive phenotype and may produce an unpredictable environment for herbivores (Karban and Myers 1989, Karban and Baldwin 1997, Agrawal 1998a).

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Some ant-plants (e.g., neotropical *Cecropia*) have a combination of chemical (tannins and phenolics), physical (leaf toughness), and biotic (Müllerian and pearl bodies as food for ants) defenses (Coley 1986, Davidson and Fisher 1991, Folgarait and Davidson 1995). Although it is currently recognized that most plants probably have multiple and dynamic defenses, these patterns are still being uncovered, especially in ant-plant systems. Studies which incorporate a multifaceted approach looking at various defenses over different scales will be more likely to define the nature, trade-offs, and constraints of plant defenses. In this paper we focus on the factors that may influence ants as defenders of myrmecophytic plants and specifically on induced plant responses in ant-plant systems. We conclude that in facultative ant-plant associations plants may actively recruit ant defenders, while in more obligate associations, ants may themselves be responsible for induction of recruitment.

### Defense in ant-plant systems

Ant-plants provide food and/or domicile for ants. Research on anti-herbivore defenses of ant-plants has focused on the ants as plant protectors (Janzen 1967, Schemske 1980, O'Dowd and Catchpole 1983, Koptur 1984, 1992, Schupp 1986, Davidson and McKey 1993; but see Coley 1986, Folgarait and Davidson 1995). Direct evidence that ants defend plants comes from experiments which show that ant removal increased herbivory and decreased plant fitness (Janzen 1967, Schemske 1980, Koptur 1984, 1992, Schupp 1986, Vasconcelos 1991, Fisher 1992, Del-Claro et al. 1996, Oliveira 1997, Letourneau 1998, and see reviews in Beattie 1985, Huxley and Cutler 1991, Davidson and McKey 1993). Although observations suggest a gradation in the nature of ant-plant associations from incidental to obligate, the actual benefits are best quantified by an experimental approach, as the tactics of biotic defenders may not always be obvious (Letourneau 1983, 1998, O'Dowd and Catchpole 1983, Rashbrook et al. 1991, Koptur 1992, Gaume et al. 1997).

Indirect evidence for the defensive role of ants in ant-plant systems comes from the study of defensive characters among closely related plant taxa. Rehr et al. (1973) found that leaves of non-ant *Acacia* spp. contained cyanogenic glycosides, which have been implicated in defense, while these compounds are absent in ant-*Acacia* spp. (but see Seigler et al. 1978, Seigler and Ebinger 1987). Further indirect evidence for a cost of maintaining ant defense was found by Janzen (1973). Production of Müllerian food bodies is almost completely lacking in *Cecropia* species in Puerto Rico, where ants do not inhabit the trees. Thus, it can be hypothesized that where some defenses are ineffective

they may be selected against. Such "costs" are a crucial assumption of proposed trade-offs between plant defenses (Herms and Mattson 1992). A general pattern of trade-offs between defenses, especially in highly obligate ant-plant systems, is consistent with the notion that ants protect plants in these systems (see also other examples of trade-offs in plant defenses: Björkman and Anderson 1990, Twigg and Socha 1996). McKey (1988) and Davidson and Fisher (1991) generalized this idea and suggested that there should be a lack of redundancy of defenses that act over the same temporal, spatial, and/or herbivore scales.

An absolute (presence/absence) trade-off between defense systems, however, is not always found (e.g., Waterman et al. 1984, Steward and Keeler 1988, reviewed by Herms and Mattson 1992). A general model for allocation to different defenses in ant-plant systems should take into account the relative effectiveness of each defense, since no single defense is likely to eliminate damage by all herbivores. In highly mutualistic and obligate associations such as that between neotropical *Acacia* trees and *Pseudomyrmex* ants (Janzen 1967) there are examples of trade-offs: plants with defending ants have no obvious chemical defenses (Janzen 1966, 1967, Rehr et al. 1973), although both Central American and African *Acacia* have large thorns which may defend against large mammalian herbivores (Young 1987, Milewski et al. 1991, Gowda 1996). Ant and thorn defenses may act independently depending on the environment (Madden and Young 1992). Induction of increased thorn length stimulated by simulated herbivory in an African *Acacia* was not accompanied by changes in phenolics or tannins, which are putative chemical defenses (Gowda 1997).

In associations like that between *Cecropia* trees and *Azteca* ants, plants may employ several defensive tactics (see above, Folgarait and Davidson 1995), and adjust each of them as necessary to the environmental conditions. For example, *Cecropia* trees employ non-ant defenses (chemical and physical) in greater quantity as juveniles before ants inhabit them (Coley 1986, Martinelli et al. 1993, Folgarait and Davidson 1995, D. Schemske pers. comm.). Martinelli et al. (1993) observed that adult leaves of ant-inhabited *Cecropia* trees were found to be overwhelmingly more palatable to generalist orthopterans than were leaves from juvenile plants without ants. This suggests that leaves of ant-less plants were better defended by chemical or physical agents. Where ants are geographically unavailable (i.e., high elevation), myrmecophytic plants typically enhance other anti-herbivore defenses (e.g., Bentley 1977a). Koptur's (1985) classic study on multiple defense strategies of *Inga* found that upland plants employed "a novel complex of facultative defenses in the absence of protection by ants", including higher concentrations of defensive phenolics. At the interspecific level, Fiala et al. (1994) have found that Asian

*Macaranga* species exhibit a range of associations with ants from facultative to obligate. Their studies indicate that extrafloral nectaries are especially effective as attractants of generalist ants and parasites of herbivores, while food bodies may be an adaptation to more obligate ants (Fiala and Maschwitz 1990, 1991, 1992, Fiala et al. 1994).

Many plant species with extrafloral nectaries and defending mutualist ants also employ a diverse array of other defensive tactics. For example, many *Gossypium* species have well developed extrafloral nectaries known to attract biotic defenders (Maxwell et al. 1976, Treacy et al. 1987) as well as suites of constitutive and inducible chemical and physical defenses (Karban and Carey 1984, Brody and Karban 1992, Gershenson and Croteau 1992, Matthews and Tunstall 1994, Bi et al. 1997, Thaler and Karban 1997). Many, if not most, ant-plant associations are facultative, and in such cases, biotic defense in plants with extrafloral nectaries or ant domatia may be minimal or difficult to detect (O'Dowd and Catchpole 1983, Rashbrook et al. 1991, Koptur 1992). Intraspecific expression of extrafloral nectaries is sometimes variable depending on the presence of ants (e.g., Bentley 1977a), while in other cases, nectaries are present and secrete nectar even in the absence of ant protectors (e.g., Koptur 1985). In facultative associations it is not known if having so-called "adaptations" for biotic defenses is incidental, due to phylogenetic inertia, or if these "adaptations" only function in certain environments (see also Mithen et al. 1995). The majority of anti-herbivore defense in such plants may be unrelated to ants.

The less effective a particular defense, the more effective the alternative strategies should be. For example, Letourneau and Barbosa (1998) found that plants of myrmecophytic *Endospermum labios* had new leaves with denser trichomes on plants with evidence of stem-borer damage. The authors postulate that this pubescence may be an induced plant response (sensu Baur et al. 1991) in individual plants with poor ant defense. Similarly, the high concentrations of phenolics found in high elevation *Inga* plants (without ants), compared to lower elevation plants with ants, may have been induced by initial herbivory. Further evidence for plasticity of multiple defenses in ant-plants comes from studies of African ant-*Acacias* in which thorn length and density have been demonstrated to be inducible traits affecting resistance to mammalian herbivores (Young 1987, Milewski et al. 1991, Gowda 1996, 1997). This pattern suggests that aggressive ants may be less effective defenders against large ungulates, and thorns compensate for this (see Madden and Young 1992). It should be emphasized that there are alternative explanations to the apparently adaptive plant responses outlined above; however, plants may still benefit due to such shifts in

defense allocation. We predict that our extension of McKey's (1988) and Davidson and Fisher's (1991) verbal model should not only apply across different species of plants, but across ontogenetic changes (within individuals) or environments (between individuals) where each defense has a different effectiveness. We also predict that there will rarely be an absolute presence/absence trade-off between multiple defenses because the myriad attackers are themselves dynamic.

## Induced biotic defenses

There has been considerable interest in measuring the costs and benefits of ant defense in ant-plant systems. This approach answers two important questions: (1) how effective are biotic defenders? and (2) what pattern of costs or trade-offs are responsible for the maintenance of variation for a given defense? The defensive phenotype for biotic defense is often measured as the number of food bodies or other ant rewards produced by the plant (O'Dowd 1980, Risch and Rickson 1981, Davidson and Fisher 1991, Koptur 1992, Folgarait et al. 1994, Folgarait and Davidson 1995, Frias and Dirzo 1996, Heil et al. 1997). Alternatively, studies measure the net effectiveness of ant presence by ant removal (e.g., Janzen 1967, Schemske 1980, Schupp 1986, Fisher 1992, Letourneau 1998). These studies do not consider short-term dynamics of the ants. It has been known anecdotally for over one hundred years (e.g., Belt 1874) that ant activity is not static on ant-plants. For example, disturbance has been known to excite, and induce biting and stinging in the ant inhabitants of many ant-plants (e.g., Madden and Young 1992). Apparently passive behavior by non-aggressive ants may also be quite deceptive and observations alone may not be suggestive of the dynamic defenses (Letourneau 1983, 1998, Gaume et al. 1997). What is the significance of dynamic behavior and potentially induced ant responses?

Induced responses in non-ant-plant systems have been characterized extensively, and reduced performance and/or preference of herbivores on damaged plants has been documented for over 100 systems (reviewed in Karban and Baldwin 1997). The occurrence of induced resistance demonstrates that plant defenses are more dynamic than once thought, and present changing defensive phenotypes which should complicate herbivore strategies (Karban et al. 1997). Ants, being spatially and temporally mobile and having developed mechanisms for recruitment, are an ideal candidate for deployment as induced defenses. Table 1 lists some of the potential mechanisms that can influence the location and persistence of ant patrolling. Inducing ant recruitment may be an important way

of manipulating the level of defense in ant-plant systems. Most previous studies of costs and benefits of biotic defense have neglected the dynamic nature of biotic defenses. Below we review the current state of knowledge about nectary and non-nectary mediated induced responses in ant-plants.

### Extrafloral nectar induction

Induced responses to herbivory that result in changes in the quality and/or quantity of extrafloral nectar have been reported in several systems (Table 2). Stephenson (1982) noted that *Catalpa* leaves damaged by caterpillars produced more sugar (and/or dissolved solutes) in extrafloral nectaries, and Smith et al. (1990) found increased amino acid contents in the extrafloral nectar of artificially damaged *Impatiens* leaves. Amino acids are known to be important to potentially beneficial nectary visitors (see Smith et al. 1990). Other studies on *Gossypium* species have noted

increases in nectar volume stimulated by herbivory by various herbivores (Table 2). Such responses in *Gossypium herbaceum* and *Ricinus communis* appear not to be "herbivory-specific" as similar responses in extrafloral nectar production were noted following caterpillar damage and artificial damage. Finally, in promising experiments by Swift and colleagues (Swift and Lanza 1993, Swift et al. 1994), *Passiflora* vines were found to have locally inducible extrafloral nectar (volume). In field experiments, damaged plants were found more quickly and maintained higher numbers of ants than undamaged controls. Although few other studies measured ant activity in response to damage and nectar flow, the studies listed in Table 2 suggest that plants under attack may recruit biotic defenders by increasing the quality and/or quantity of extrafloral nectar. Other studies have demonstrated significant increases in ant patrolling with increased nectar flow (Bentley 1977a, b, Tilman 1978).

The physiological mechanisms underlying induced extrafloral nectar responses to herbivory are completely unknown. Herbivory can physiologically alter the source-sink and carbon-nutrient balance relationships in many systems (e.g., Bryant et al. 1991, Larson and Whitham 1991, 1997, Reichardt et al. 1991, Inbar et al. 1995) and such alterations could result in channeling of excess carbohydrates through extrafloral nectaries (Bentley 1977b, Koptur 1992). This has been termed the "sap-valve" hypothesis. The sap-valve function of extrafloral nectaries could potentially explain induction of increased nectar volume or concentration, although no real evidence exists to support this (see also Baker et al. 1978). Alternatively, plants have several distinct biochemical pathways that regulate wound induced responses and induced responses to other plant parasites (Bennett and Wallsgrave 1994, Hammerschmidt and Schultz 1996). Sophisticated changes in the composition and amino acid contents of extrafloral nectar (e.g., Smith et al. 1990) are less likely to be explained by the sap-valve mechanism, and may be regulated by such pathways.

A new form of induced "nectary" responses to herbivory has recently been reported by Young et al. (1997). The African *Acacia drepanolobium* has an apparently mutualistic relationship with several species of ants in four genera. When the trees are inhabited by *Crematogaster nigriceps* they have significantly more active nectaries than trees inhabited by other species of ants. The mechanism behind this phenomenon appears to involve *C. nigriceps* chewing the shoots, which causes new growth with increased numbers of nectaries. This bizarre behavior may be common in plant-ants (see Yu and Pierce 1998). It is not known at this stage whether grazing mammals also cause this induction of new foliage with more active nectaries.

Table 1. Potential cues that influence the location, aggressiveness and persistence of ant patrolling on ant-plants.

Cues	References
Age of plant tissue	Downhower 1975, McKey 1984, Madden and Young 1992, Moog et al. 1998
Colony size	Rocha and Bergallo 1992, Agrawal 1998b
Damaged plant tissues	Fiala and Maschwitz 1990, Jolivet 1996, Agrawal 1998b
Density of conspecific worker ants	Way 1963, Agrawal 1998b
Disturbance	Young et al. 1990, Madden and Young 1992, Cronin 1998, Federle et al. 1998
Food bodies	Janzen 1966, 1967, O'Dowd 1980
Green leaf volatiles (e.g., hexanal)	Agrawal 1998b
Insect exudates	Way 1963, Buckley 1987, Koptur 1992, Cushman et al. 1994
Mammalian breath (CO <sub>2</sub> ?)	Agrawal and Rutter pers. obs., T. P. Young pers. comm.
Nectaries and nectar production	Bentley 1977a, b, Tilman 1978, Koptur 1992
Plant sap	Fiala and Maschwitz 1990, Jolivet 1996, Agrawal 1998b, J. Longino pers. comm.
Presence of herbivores	Fiala and Maschwitz 1990, Rocha and Bergallo 1992, Cronin 1998, Agrawal 1998b, Moog et al. 1998
Presence of foreign conspecific ants	Fiala and Maschwitz 1990
Time of day	Bentley 1977a, b, Cronin 1998, M. Heil pers. comm., R. Marquis pers. comm.

Table 2. Studies to date that have investigated changes in extrafloral nectar following leaf damage.

Species	Environment	Damage type	Measurement	Effect	Reference
<i>Gossypium barbadense</i>	field	whitefly	nectar droplet size	positive	Mound 1962
	field	jassid thrips	nectar droplet size	positive	Mound 1962
	field		nectar droplet size	n.s.	Mound 1962
<i>Catalpa speciosa</i>	field	caterpillar	nectar concentration	positive	Stephenson 1982
<i>Vicia sativa</i>	greenhouse	scissors	nectar volume	positive	Koptur 1989
<i>Ipomea carnea</i>	field	scissors	nectar volume	n.s.	Koptur 1989
<i>Inga brenesii</i>	field	scissors	nectar volume	n.s.	Koptur 1989
<i>Inga punctata</i>	field	scissors	nectar volume	n.s.	Koptur 1989
<i>Impatiens sultani</i>	greenhouse	scissors	amino acid concentration	positive	Smith et al. 1990
			nectar volume	n.s.	Smith et al. 1990
			nectar concentration	n.s.	Smith et al. 1990
<i>Campis radicans</i>	field	simulated	nectar volume	positive	Stevens 1990
<i>Passiflora</i> spp.	Greenhouse	simulated	nectar volume	positive	Swift and Lanza 1993
<i>Passiflora incarnata</i>	field	Simulated	time to discovery/ant attendance	positive	Swift et al. 1994
<i>Hibiscus tiliaceus</i>	field	hole puncher	nectar volume	n.s.	Agrawal and Rutter, unpubl.
			ant visitation	n.s.	
<i>Acacia drepanolobium</i>	field	Ants eating shoots	number of nectaries	positive	Young et al. 1997
<i>Gossypium herbaceum</i>	greenhouse	caterpillar	nectar volume	positive	Wunderlin et al. 1997, Waeckers et al. unpubl.
		artificial	nectar volume	positive	
<i>Ricinus communis</i>	greenhouse	caterpillar	nectar volume	positive	
		artificial	nectar volume	positive	
		artificial	nectar volume sugar composition/concentration	positive n.s.	
<i>Macaranga tanarius</i>	field	natural (various)	nectar volume	positive	M. Heil pers. comm.

n.s. = no significant effect.

### Non-nectary mediated interactions

Young et al. (1990) showed that the activity of *Pseudomyrmex spinicola* and *P. flavicornis* inhabiting *Acacia* trees more than doubled when the trees were disturbed. Cronin (1998) extended this work on the *Pseudomyrmex-Acacia* interaction by demonstrating that ant activity can be induced by the arrival of the herbivores. In experiments with katydids, he found that ant activity increased in the presence of herbivores and disturbance. Furthermore, Cronin found an intriguing species by time interaction, whereby different species of *Pseudomyrmex* ants responded to herbivore presence differently at various times of the day. Nectar flow and the associated ant activity often have diurnal variation (e.g., Bentley 1977a), and in Asian *Macaranga* increased flow of nectar at dusk is correlated with the nightly emergence of herbivores (M. Heil pers. comm.). Repeatable differences in ant activity over even short temporal scales are consistent with our analysis of

plasticity in ant defense. Rocha and Bergallo (1992) have shown that *Azteca* ants inhabiting Brazilian *Cecropia* trees recruited to the presence of a herbivorous beetle. Induction of ant recruitment was positively correlated with colony size and the larger the recruitment event, the shorter was the time to removal of the herbivore. Finally, Fiala and Maschwitz (1990) demonstrated that protective *Crematogaster* ants recruited to leaf damage, leaf extracts, and foreign conspecifics when patrolling *Macaranga* trees. Similar results have recently been reported from *Camponotus* ants inhabiting *Macaranga puncticulata* (Federle et al. 1998). Although more studies are needed, it appears that induced responses commonly influence the patrolling patterns of ants on ant-plants.

We have found that in the neotropical *Cecropia-Azteca* system, ants recruit heavily to herbivores and local sites of leaf damage (Agrawal 1998b). *Azteca* ants do not consume the herbivores to which they recruit, but rather drop them off the plant. On average, ant

numbers increased 400% on leaves artificially damaged with a hole puncher. The induced recruitment and subsequent patrolling of foliage began within four minutes after the damage and continued for several hours. As *Cecropia* do not have extrafloral nectaries, nectar production cannot be the mechanism for induced recruitment in this system. Furthermore, it seems improbable that production of food bodies could account for the rapid and localized induced recruitment. To test for alternative cues that could be inducing the ant recruitment, we have measured ant recruitment responses to abiotic disturbance, plant sap, and a green leaf volatile (hexanal). Each of these factors appeared to induce a mild level of short term ant recruitment, but did not induce persistent recruitment for hours, as did leaf damage.

In non-ant-plant systems several examples have been reported in which foliar damage induces attraction of predators and parasites of herbivores. This interaction may result from volatile cues released locally from damage sites or systemically throughout the plant (Turlings et al. 1990, Pare and Tumlinson 1996, Rose et al. 1996, Takabayashi and Dicke 1996, Shimoda et al. 1997). For example, foliar wounds served as a cue for tachinid parasitoids to oviposit on damaged red oak leaves (Embree and Sisojevic 1965). Wilcox (1996) found that damaged stems of bush lupine attracted formicine ants to sites of damage and significantly increased ant density on damaged bushes within 24 h as compared to undamaged bushes. Such responses often only occur when herbivore saliva contacts leaf wounds (e.g., Turlings et al. 1990, Alborn et al. 1997), and leaf damage or herbivore presence alone may not produce the response. Lastly, plant wounds themselves can result in the attraction of natural enemies which may drink plant sap at the "nectary-like" site of damage (Embree and Sisojevic 1965, Jolivet 1996, G. Gentry pers. comm.). For example, Naganuma and Hespeneheide (1988) observed high levels of herbivore natural enemy visitation to insect created wounds on *Baccharis sarothroides* bushes.

Why might ant-plants employ an inducible defense system? If ants serve a defensive function, more should be better. Indirect evidence suggests that housing and feeding ant defenders may be costly and divert resources from plant growth (Janzen 1973, Rehr et al. 1973). Although ant-plants such as *Piper* withhold food body production until ant occupation (Risch and Rickson 1981, Letourneau 1990), others such as *Cecropia* do not, and uninhabited plants can be found with dropping food bodies (Agrawal pers. obs. but see Folgarait et al. 1994). Similarly, although most untended extrafloral nectaries produce nectar, without nectar removal, nectaries often become clogged and secretion may stop (Bentley 1977b, pers. obs.).

In addition to the allocation cost argument, which suggests that plants employ induced defenses to save

diversion of resources, other hypotheses exist. High densities of patrolling ants may be a host-finding signal for specialist herbivores. In addition, ants could be "autotoxic" to the plants. The presence of aggressive ants could lead to fewer pollinators visiting the flowers of ant-plants (Janzen 1966, Buys 1990, Jolivet 1996, Willmer and Stone 1997). Consistent with this idea, Bentley (1977a) reported that extrafloral nectar production dropped off when the flowers of *Bixa orellana* were open, and resumed during fruit maturation. Willmer and Stone (1997) demonstrated that ant activity on the flowers of African *Acacia* trees was quite dynamic over two temporal scales: 1) during the course of a day, ant activity on flowers was the lowest during peak pollinator visitation, and 2) over the phenology of flowers (unopened through dehiscence), high ant activity kept unopened flower buds pristine, low activity on open flowers allowed for pollination, and finally returning high ant activity protected developing seeds from seed predators. Willmer and Stone argue that the plant mediates this dynamic ant behavior through the use of ant deterring volatiles. Although there are several hypotheses to explain why plants may employ induced responses in general (see Agrawal and Karban 1998), none of the hypotheses has been well explored empirically.

### Why ants might be self-inducing

Patrolling and defending plants can be a relatively dangerous activity, and occupies ant workers that might otherwise be tending larvae or gathering food (Oster and Wilson 1978). As a result, it may be in the best interest of the ant colony to minimize the time workers spend externally patrolling leaves. We speculate that, in some cases, this may be the driving force behind the inducible nature of ant recruitment to damaged leaves or disturbance. Many non-plant-ants forage in this inducible manner, and this may be a pre-adaptation for induction of recruitment in ant-plants (Hölldobler and Wilson 1990). A basal constitutive defense of a few patrolling ants can become an induced swarm of hundreds of workers as soon as the colony is alerted to the presence of damage or a herbivore. The result is an effective defense with a minimal continuous defense. This explanation leads to the critical question: why should cues related to plant damage provoke any recruitment response from the ant colony?

There are three explanations for this behavior. First, if the herbivore is a recognized food source, the induced response may be nothing more than a foraging expedition by the ants (e.g., the biotic responses in many non-myrmecophytic plants reviewed

by Takabayashi and Dicke 1996). Secondly, as described above, the plant may have secreted a reward substance that recruits more ants to the vicinity of the herbivores (Table 2). The ants then opportunistically attack the herbivores, but the induced response was a result of plant-controlled changes. Finally, the ants may be responding to prevent further plant damage that would lead to a decline in the quality of resources offered by the plant (see Frias and Dirzo 1996).

We suggest that this final explanation, driven by ants suffering from diminished plant vigor, will be stronger for obligate (for both partners) mutualistic associations. If ants are not able to easily relocate to another host plant, and they depend on the plant for nearly all resources, any decrease in plant quality may have detrimental effects on the ant colony. In this situation, selection will favor ant colonies which respond to damage cues regardless of any stimulus from the plant itself. Our observations of the *Cecropia* system are consistent with the idea of rapid response without induced reward production. In several other systems, obligate ants recruit to disturbance or damage without any apparent rewards (Fiala and Maschwitz 1990, Madden and Young 1992, Rocha and Bergallo 1992, Cronin 1998, Federle et al. 1998). In these systems, the ants do not eat the herbivores that they vigorously attack. Additional information regarding our hypothesis was presented by Frias and Dirzo (1996), who found that 40% defoliation had no measurable effect on the long-term production of food bodies in *Cecropia obtusifolia*. Although in the case of *C. obtusifolia* most of the ant inhabitants are obligate associates of the plant, it did not appear that damage to the plant affected vigor enough to reduce food body production. Thus, our notion about obligate systems and ant-controlled induced responses remains a hypothesis.

In contrast, when individual plants are interchangeable to the ants (as is the case in many facultative mutualisms), ants may avoid or abandon lower quality plants. To "induce" an ant response (recruitment) in such cases, a plant will have to increase the rewards it provides. In summary, our hypothesis predicts that dynamic ant responses to damage should largely be controlled by the plant in facultative interactions, but be predominantly mediated by the ants in obligate interactions. Although data are currently scant, the observations of non-nectary mediated ant recruitment in *Acacia* and *Cecropia* (see above) and nectar induction in several facultative systems (Table 2) appear consistent with our predictions. An additional approach to test this hypothesis may include observations of the behavior of facultative versus obligate ant species inhabiting plants without reward-based induced responses.

## Talking trees and talking ants

Plants attacked by herbivores and pathogens may provide cues or signals that affect the defensive phenotype and response of neighboring plants (Baldwin and Schultz 1983, Rhoades 1983, Farmer and Ryan 1990, Shulavev et al. 1997). However, these studies of "inter-plant communication" were rarely conducted in the field and there has been some question regarding their validity (Fowler and Lawton 1985). Two studies on ant-plants have provided some evidence for induction of ant recruitment on undamaged trees neighboring damaged trees (Janzen 1967, Agrawal 1998b). In Janzen's study of the *Acacia-Pseudomyrmex* interaction, he reported that on trees downwind of a tree with a riled up ant colony (i.e., disturbed by humans or deer) the ants became more active. In a more controlled experiment, Agrawal (1998b) reported that *Cecropia* leaves next to damaged conspecific leaves on another plant accumulated significantly more *Azteca* ants than did leaves next to disturbed but undamaged control leaves. The mechanism of this neighbor induction remains unknown and may lie in plant-released volatiles or ant-released pheromones.

## Conclusion

Although anecdotal evidence abounds, quantitative data are only now being collected to indicate the dynamic nature of anti-herbivore defense in ant-plant systems. Recent studies show that various mechanisms, including induced changes in extrafloral nectar quality and/or quantity, may be responsible for inducing ant recruitment. In other systems, ant fitness may be so tightly linked to plant vigor that there is no need for a direct reward for recruiting to sites of damage. What seems clear is that ant-plants capitalize on the recruitment behavior of ants. Ants are agile, highly mobile, and reclaimable defenses. Organismal defense of food sources and domicile are obvious throughout nature; the benefit to the plants in ant-plant associations probably ranges from coincidental to highly evolved. In either case, many ant-plants, from facultative to highly obligate, are likely to employ induced defenses. These dynamic defenses may benefit the plants by reducing various costs of defense and by presenting changing defensive phenotypes to herbivores. As in non-ant-plant systems, future assessment of the various costs and benefits of defenses will need to account for inducible defenses. Future studies should also consider the multiplicity of function of the various defenses employed, and the temporal, spatial, and herbivore scales upon which the defenses operate. How phenotypically plastic are the various defenses in the face of ontogenetic or environmental changes (Martinelli et al. 1993, Letourneau and Barbosa 1998)? And how has the geo-

graphic mosaic of interactants (sensu Thompson 1994) affected defensive strategies of ant-plants across the range of widely distributed taxa such as *Cecropia* and *Acacia* (Janzen 1973)?

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## References

- Agrawal, A. A. 1998a. Induced responses to herbivory and increased plant performance. – *Science* 279: 1201–1202.
- Agrawal, A. A. 1998b. Leaf damage and associated cues induced aggressive and recruitment in a neotropical ant-plant. – *Ecology* (in press).
- Agrawal, A. A. and Karban, R. 1998. Why induced defenses may be favored over constitutive strategies in plants. – In: Tollrian, R. and Harvell, C. D. (eds), *The ecology and evolution of inducible defenses*. Princeton Univ. Press, Princeton, NJ (in press).
- Alborn, H. T., Turlings, T. C. J., Jones, T. H., Stenhagen, G., Loughrin, J. H. and Tumlinson, J. H. 1997. An elicitor of plant volatiles from beetle armyworm oral secretion. – *Science* 276: 945–949.
- Baker, D. A., Hall, J. L. and Thorpe, J. R. 1978. A study of the extrafloral nectaries of *Ricinus communis* [Castorbean]. – *New Phytol.* 81: 129–137.
- Baldwin, I. and Schultz, J. 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. – *Science* 221: 277–279.
- Baur, R., Binder, S. and Benz, G. 1991. Nonglandular leaf trichomes as short-term inducible defense of the gray alder, *Alnus incana* (L.), against the chrysomelid beetle, *Agelastica alni* L. – *Oecologia* 87: 219–226.
- Beattie, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. – Cambridge Univ. Press, Cambridge.
- Belt, T. 1874. *The naturalist in Nicaragua*. – Dent & Sons, London.
- Bennett, R. N. and Wallsgrave, R. M. 1994. Tansley review no. 72. Secondary metabolites in plant defence mechanisms. – *New Phytol.* 127: 617–633.
- Bentley, B. L. 1977a. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). – *J. Ecol.* 65: 27–38.
- Bentley, B. L. 1977b. Extrafloral nectaries and protection by pugnacious bodyguards. – *Annu. Rev. Ecol. Syst.* 8: 407–427.
- Bi, J. L., Murphy, J. B. and Felton, G. W. 1997. Antinutritive and oxidative components as mechanisms of induced resistance in cotton to *Helicoverpa zea*. – *J. Chem. Ecol.* 23: 97–117.
- Björkman, C. and Anderson, D. B. 1990. Trade-off among antiherbivore defenses in a South American blackberry (*Rubus bogotensis*). – *Oecologia* 85: 247–249.
- Brody, A. K. and Karban, R. 1992. Lack of a trade-off between constitutive and induced defenses among varieties of cotton. – *Oikos* 65: 301–306.
- Bryant, J. P., Danell, K., Provenza, F., Reichardt, P. B., Clausen, T. A. and Werner, R. A. 1991. Effects of mammal browsing on the chemistry of deciduous woody plants. – In: Tallamy, D. W. and Raupp, M. J. (eds), *Phytochemical induction by herbivores*. John Wiley, New York, pp. 135–154.
- Buckley, R. 1987. Ant-plant-homopteran interactions. – *Adv. Ecol. Res.* 16: 53–85.
- Buys, B. 1990. Relationships between argentine ants and honeybees in South Africa. – In: Vander Meer, R. K., Jaffe, K. and Cedeno, A. (eds), *Applied myrmecology: a world perspective*. Westview Press, Boulder, CO, pp. 519–524.
- Coley, P. D. 1986. Costs and benefits of defense by tannins in a neotropical tree. – *Oecologia* 70: 238–241.
- Cronin, G. 1998. Between-species and temporal variation in *Acacia*-ant-herbivore interactions. – *Biotropica* 30: 135–139.
- Cushman, J. H., Rashbrook, V. K. and Beattie, A. J. 1994. Assessing benefits to both participants in a lycaenid-ant association. – *Ecology* 75: 1031–1041.
- Davidson, D. W. and Fisher, B. L. 1991. Symbiosis of ants with *Cecropia* as a function of light regime. – In: Huxley, C. R. and Cutler, D. F. (eds), *Ant-plant interactions*. Oxford Univ. Press, Oxford, pp. 289–309.
- Davidson, D. W. and McKey, D. 1993. The evolutionary ecology of symbiotic ant-plant relationships. – *J. Hy-menop. Res.* 2: 13–83.
- Del-Claro, K., Berto, V. and Reu, W. 1996. Effect of herbivore deterrence by ants on the fruit set of an extrafloral nectary plant, *Qualea multiflora* (Vochysiaceae). – *J. Trop. Ecol.* 12: 887–892.
- Downhower, J. F. 1975. The distribution of ants on *Cecropia* leaves. – *Biotropica* 7: 59–62.
- Duffey, S. S. 1986. Plant glandular trichomes: their partial role in defence against insects. – In: Juniper, B. and Southwood, R. (eds), *Insects and the plant surface*. Edward Arnold, London, pp. 151–172.
- Duffey, S. S. and Stout, M. J. 1996. Antinutritive and toxic components of plant defense against insects. – *Arch. Insect Biochem. Physiol.* 32: 3–37.
- Embree, D. G. and Sisojevic, P. 1965. The bionomics and population density of *Cyzenis albicans* (Fall.) (Tachinidae: Diptera) in Nova Scotia. – *Can. Entomol.* 97: 631–639.
- Farmer, E. E. and Ryan, C. A. 1990. Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. – *Proc. Natl. Acad. Sci. USA* 87: 7713–7716.
- Federle, W., Maschwitz, U. and Fiala, B. 1998. The two-partner ant-plant system of *Camponotus* (Colobopsis) sp. 1 and *Macaranga puncticulata* (Euphorbiaceae): natural history of the exceptional ant partner. – *Insectes Soc.* 45: 1–16.
- Fiala, B. and Maschwitz, U. 1990. Studies on the South East Asian ant-plant association *Crematogaster borneensis*/*Macaranga*: adaptations of the ant partner. – *Insectes Soc.* 37: 212–231.
- Fiala, B. and Maschwitz, U. 1991. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. – *Biol. J. Linn. Soc.* 44: 287–306.
- Fiala, B. and Maschwitz, U. 1992. Food bodies and their significance for obligate ant-association in the tree genus *Macaranga* (Euphorbiaceae). – *Bot. J. Linn. Soc.* 110: 61–75.
- Fiala, B., Grunsky, H., Maschwitz, U. and Linsenmair, K. E. 1994. Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. – *Oecologia* 97: 186–192.
- Fisher, B. L. 1992. Facultative ant association benefits a neotropical orchid. – *J. Trop. Ecol.* 8: 109–114.
- Folgarait, P. J. and Davidson, D. W. 1995. Myrmecophytic *Cecropia* – antiherbivore defenses under different nutrient treatments. – *Oecologia* 104: 189–206.

- Folgarait, P. J., Johnson, H. L. and Davidson, D. W. 1994. Responses of *Cecropia* to experimental removal of Müllerian bodies. – *Funct. Ecol.* 8: 22–28.
- Fowler, S. V. and Lawton, J. H. 1985. Rapidly induced defenses and talking trees: the devil's advocate position. – *Am. Nat.* 126: 181–195.
- Frias, R. and Dirzo, R. 1996. Effects of defoliation on Müllerian bodies in *Cecropia obtusifolia* in Los Tuxtlas, Veracruz. – *Bull. Ecol. Soc. Am.* 77: 150.
- Gaume, L., McKey, D. and Anstett, M. C. 1997. Benefits conferred by “timid” ants: active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. – *Oecologia* 112: 209–216.
- Gershenzon, J. and Croteau, R. 1992. Terpenoids. – In: Rosenthal, G. A. and Berenbaum, M. R. (eds), *Herbivores: their interactions with secondary plant metabolites*, 2nd ed, Vol. I: The chemical participants. Academic Press, San Diego, CA, pp. 165–219.
- Gowda, J. H. 1996. Spines of *Acacia tortilis*: what do they defend and how? – *Oikos* 77: 279–284.
- Gowda, J. H. 1997. Physical and chemical response of juvenile *Acacia tortilis* to browsing: experimental evidence. – *Funct. Ecol.* 11: 106–111.
- Hammerschmidt, R. and Schultz, J. C. 1996. Multiple defenses and signals in plant defense against pathogens and herbivores. – In: Romeo, J. T., Saunders, J. A. and Barbosa, P. (eds), *Phytochemical diversity and redundancy in ecological interactions*. Plenum Press, New York, pp. 121–154.
- Heil, M., Fiala, B., Linsemair, K. E., Zotz, G., Menke, P. and Maschwitz, U. 1997. Food body production in *Macaranga triloba* (Euphorbiaceae): a plant investment in anti-herbivore defence via symbiotic ant partners. – *J. Ecol.* 85: 847–861.
- Hölldobler, B. and Wilson, E. O. 1990. *The ants*. – Belknap Press, Cambridge, MA.
- Hermes, D. A. and Mattson, W. J. 1992. The dilemma of plants: to grow or defend. – *Q. Rev. Biol.* 67: 283–335.
- Huxley, C. R. and Cutler, D. K. (eds), 1991. *Ant-plant interactions*. – Oxford Univ. Press, Oxford.
- Inbar, M., Eshel, A. and Wool, D. 1995. Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. – *Ecology* 76: 1506–1515.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. – *Evolution* 20: 249–275.
- Janzen, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. – *Univ. Kans. Sci. Bull.* 47: 315–558.
- Janzen, D. H. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. – *Biotropica* 5: 15–28.
- Jolivet, P. 1996. *Ants and plants*. – Backhuys, Leiden.
- Karban, R. and Carey, J. R. 1984. Induced resistance of cotton seedlings to mites. – *Science* 225: 53–54.
- Karban, R. and Myers, J. H. 1989. Induced plant responses to herbivory. – *Annu. Rev. Ecol. Syst.* 20: 331–348.
- Karban, R. and Baldwin, I. T. 1997. Induced responses to herbivory. – Univ. of Chicago Press, Chicago.
- Karban, R., Agrawal, A. A. and Mangel, M. 1997. The benefits of induced defenses against herbivores. – *Ecology* 78: 1351–1355.
- Koptur, S. 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. – *Ecology* 65: 1787–1793.
- Koptur, S. 1985. Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. – *Ecology* 66: 1639–1650.
- Koptur, S. 1989. Is extrafloral nectar production an inducible defense? – In: Bock, J. H. and Linhart, Y. B. (eds), *The evolutionary ecology of plants*. Westview Press, Boulder, CO, pp. 323–339.
- Koptur, S. 1992. Extrafloral nectary-mediated interactions between insects and plants. – In: Bernays, E. (ed.), *Insect-plant interactions IV*. CRC Press, Boca Raton, FL, pp. 81–129.
- Larson, K. C. and Whitham, T. G. 1991. Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions. – *Oecologia* 88: 15–21.
- Larson, K. C. and Whitham, T. G. 1997. Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. – *Oecologia* 109: 575–582.
- Letourneau, D. K. 1983. Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. – *Oecologia* 60: 122–126.
- Letourneau, D. K. 1990. Code of ant-plant mutualism broken by parasite. – *Science* 248: 215–217.
- Letourneau, D. K. 1998. Ants, stem-borers and fungal pathogens: experimental tests of fitness advantages in *Piper* ant-plants. – *Ecology* 79: 593–603.
- Letourneau, D. K. and Barbosa, P. 1998. Ants, stem-borers, and pubescence in *Endospermum* in Papua New Guinea. – *Biotropica* (in press).
- Madden, D. and Young, T. P. 1992. Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*. – *Oecologia* 91: 235–238.
- Martinelli, T., Hormiga, G., Dirzo, R., Lambert, J., Messier, S., Rettig, J. and Schultz, K. 1993. Ontological changes in defense against herbivory in *Cecropia* sp. – In: Greig, N. and Blake, J. G. (eds), *Tropical biology: an ecological approach (OTS 93-1)*. OTS, Durham, pp. 48–50.
- Mathews, G. A. and Tunstall, J. P. (eds), 1994. *Insect pests of cotton*. – CAB International, Wallingford.
- Maxwell, F. G., Schuster, F., Meredith, W. R. and Laster, M. L. 1976. Influence of the nectariless character in cotton on harmful and beneficial insects. – *Symp. Biol. Hung.* 16: 157–161.
- McKey, D. 1984. Interactions of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. – *Biotropica* 16: 81–99.
- McKey, D. 1988. Promising new directions in the study of ant-plant mutualisms. – In: Greuter, W. and Zimmer, B. (eds), *Proceedings of the XIV International Botanical Congress*. Koeltz, Königstein/Taunus, pp. 335–355.
- Milewski, A. V., Young, T. P. and Madden, D. 1991. Thorns as induced defenses: experimental evidence. – *Oecologia* 86: 70–75.
- Mithen, R., Raybould, A. F. and Giamoustaris, A. 1995. Divergent selection for secondary metabolites between wild populations of *Brassica oleracea* and its implications for plant-herbivore interactions. – *Heredity* 75: 472–484.
- Moog, J., Drude, T. and Maschwitz, U. 1998. Protective function of the plant-ant *Cladomyrma maschwitzi* to its host, *Crypteronia griffithii*, and the dissolution of the mutualism (Hymenoptera: Formicidae). – *Sociobiology* 31: 105–129.
- Mound, L. A. 1962. Extra-floral nectaries of cotton and their secretions. – *Emp. Cotton Grow. Rev.* 39: 254–260.
- Naganuma, K. and Hespeneide, H. A. 1988. Behavior of visitors at insect-produced analogues of extrafloral nectaries on *Baccharis sarothroides* Gray. – *Southwest. Nat.* 33: 275–286.
- O'Dowd, D. J. 1980. Pearl bodies of a neotropical tree *Ochroma pyramidale*: ecological implications. – *Am. J. Bot.* 67: 543–549.
- O'Dowd, D. J. and Catchpole, E. A. 1983. Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp. – ant interactions. – *Oecologia* 43: 233–248.
- Oliveira, P. S. 1997. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocarpus brasiliense* (Caryocaraceae). – *Funct. Ecol.* 11: 323–330.
- Oster, G. F. and Wilson, E. O. 1978. *Caste and ecology in the social insects*. – Princeton Univ. Press, Princeton, NJ.
- Pare, P. W. and Tumlinson, J. H. 1996. Plant volatile signals in response to herbivore feeding. – *Fl. Entomol.* 79: 93–103.
- Rashbrook, V. K., Compton, S. G. and Lawton, J. H. 1991. Bracken and ants: why is there no mutualism? – In: Hux-

- ley, C. R. and Cutler, D. F. (eds), *Ant-plant interactions*. Oxford Univ. Press, Oxford, pp. 231–237.
- Rehr, S. S., Feeny, P. P. and Janzen, D. H. 1973. Chemical defence in Central American non-ant-acacias. – *J. Anim. Ecol.* 42: 405–416.
- Reichardt, P. B., Chapin, F. S. I., Bryant, J. P., Mattes, B. R. and Clausen, T. P. 1991. Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. – *Oecologia* 88: 401–406.
- Rhoades, D. 1983. Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromone sensitivity of willows. – *Am. Chem. Soc. Symp. Series* 208: 55–68.
- Risch, S. J. and Rickson, F. R. 1981. Mutualism in which ants must be present before plants produce food bodies. – *Nature* 291: 149–150.
- Rocha, C. F. D. and Bergallo, H. G. 1992. Bigger ant colonies reduce herbivory and herbivore residence time on leaves of an ant-plant: *Azteca muelleri* vs. *Coelomera ruficornis* on *Cecropia pachystachya*. – *Oecologia* 91: 249–252.
- Rose, U. S. R., Manukian, A., Heath, R. R. and Tumlinson, J. H. 1996. Volatile semiochemicals released from undamaged cotton leaves. – *Plant Physiol.* 111: 487–495.
- Schemske, D. W. 1980. The evolutionary significance of extrafloral nectar production by *Costus woodsonii* (Zingiberaceae): an experimental analysis of ant protection. – *J. Ecol.* 68: 959–967.
- Schupp, E. W. 1986. *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. – *Oecologia* 70: 319–385.
- Seigler, D. S. and Ebinger, J. E. 1987. Cyanogenic glycosides in ant-acacias of Mexico and Central America. – *Southwest. Natl.* 32: 499–503.
- Seigler, D. S., Dunn, J. E., Conn, E. E. and Holstein, G. L. 1978. Acacipetalin from six species of *Acacia* of Mexico and Texas. – *Phytochemistry* 17: 445–446.
- Shimoda, T., Takabayashi, J., Ashihara, W. and Takafuji, A. 1997. Response of predatory insect *Scolothrips takahashii* toward herbivore-induced plant volatiles under laboratory and field conditions. – *J. Chem. Ecol.* 23: 2033–2048.
- Shulaev, V., Silverman, P. and Raskin, I. I. 1997. Airborne signalling by methyl salicylate in plant pathogen resistance. – *Nature* 385: 718–721.
- Smith, L. L., Lanza, J. and Smith, G. C. 1990. Amino acid concentrations in extrafloral nectar of *Impatiens sultani* increase after simulated herbivory. – *Ecology* 71: 107–115.
- Stephenson, A. G. 1982. The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. – *Ecology* 63: 663–669.
- Stevens, J. A. 1990. Response of *Campsis radicans* (Bignoniaceae) to simulated herbivory and ant visitation. – M.S. Thesis, Univ. of Missouri-St. Louis.
- Steward, J. L. and Keeler, K. H. 1988. Are there trade-offs among antiherbivore defenses in *Ipomoea* (Convolvulaceae)? – *Oikos* 53: 79–86.
- Swift, S. and Lanza, J. 1993. How do *Passiflora* vines produce more extrafloral nectar after simulated herbivory? – *Bull. Ecol. Soc. Am.* 74: 451.
- Swift, S., Bryant, J. and Lanza, J. 1994. Simulated herbivory on *Passiflora incarnata* causes increased ant attendance. – *Bull. Ecol. Soc. Am.* 75: 225.
- Takabayashi, J. and Dicke, M. 1996. Plant-carnivore mutualism through herbivore-induced carnivore attractants. – *Trends Plant Sci.* 1: 109–113.
- Thaler, J. S. and Karban, R. 1997. A phylogenetic reconstruction of constitutive and induced resistance in *Gossypium*. – *Am. Nat.* 149: 1139–1146.
- Thompson, J. N. 1994. *The coevolutionary process*. – Univ. of Chicago Press, Chicago.
- Tilman, D. 1978. Cheries, ants, and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. – *Ecology* 59: 686–692.
- Treacy, M. F., Benedict, J. H., Walmsley, M. H., Lopez, J. D. and Morrison, R. K. 1987. Parasitism of bollworm (Lepidoptera: Noctuidae) eggs on necaried and nectariless cotton. – *Environ. Entomol.* 16: 420–423.
- Turlings, T. C. J., Tumlinson, J. H. and Lewis, W. J. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. – *Science* 250: 1251–1253.
- Twigg, L. E. and Socha, L. V. 1996. Physical versus chemical defence mechanisms in toxic *Gastrolobium*. – *Oecologia* 108: 21–28.
- Vasconcelos, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmecophytic melastome and one of its ant inhabitants: ant protection against insect herbivores. – *Oecologia* 87: 295–298.
- Waterman, P. G., Ross, J. A. M. and McKey, D. B. 1984. Factors affecting levels of some phenolic compounds, digestibility, and nitrogen content of the mature leaves of *Barteria fistulosa* (Passifloraceae). – *J. Chem. Ecol.* 10: 387–401.
- Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. – *Annu. Rev. Entomol.* 8: 307–344.
- Wilcox, C. 1996. Ant response to insect herbivory, and the potential for community-wide indirect effects. – *Bull. Ecol. Soc. Am.* 77: 481.
- Willmer, P. G. and Stone, G. N. 1997. How aggressive ant-guards assist seed-set in *Acacia* flowers. – *Nature* 388: 165–166.
- Wunderlin, R., Keller, F. and Waeckers, F. L. 1997. A comparison between *Spodoptera littoralis* (Boisduval) damaged and undamaged *Gossypium herbaceum* (L.) with respect to sugar composition and concentration of extrafloral nectar. – In: Sommeijer, M. J. and Francke, P. J. (eds), *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.)*, Vol. 8. Netherlands Entomological Society, Amsterdam, pp. 189–192.
- Young, B. E., Kaspari, M. and Martin, T. E. 1990. Species-specific nest site selection by birds in ant-*Acacia* trees. – *Biotropica* 22: 310–315.
- Young, T. P. 1987. Increased thorn length in *Acacia drepanolobium* – an induced response to browsing. – *Oecologia* 71: 436–438.
- Young, T. P., Stubblefield, C. H. and Isbell, L. A. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. – *Oecologia* 109: 98–107.
- Yu, D. W. and Pierce, N. E. 1998. A castration parasite of an ant-plant mutualism. – *Proc. R. Soc. Lond. B* 265: 375–382.