Ant Defense Versus Induced Defense in *Lafoensia pacari* (Lythraceae), a Myrmecophilous Tree of the Brazilian Cerrado

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ABSTRACT

We compared the effects of ant presence at extrafloral nectaries of *Lafoensia pacari* St. Hil. on herbivore damage and silicon accumulation. Plants that were accessible to ants experienced lower herbivory levels over the first 3 mo of the experiment. After 3 mo, most leaves were fully expanded with inactive extrafloral nectaries; by 6 mo there was no effect of ant access on herbivore damage. Along with experiencing higher herbivory, plants in the ant-exclusion treatment had significantly higher silicon levels in their leaves, suggesting that silicon serves as an induced defense in this ant–plant–herbivore interaction.

RESUMO

Foi analisado o efeito da presença de formigas visitantes sobre a herbivoria e acúmulo de silício em *Lafoensia pacari* St. Hil. Nas plantas com formigas observamos menores níveis de herbivoria com três meses de experimento. Depois de três meses a maior parte das folhas estavam completamente expandidas e com nectários inativos e aos seis meses a presença de formigas não teve influência sobre a herbivoria. Juntamente com uma maior herbivoria, as plantas apresentaram significativamente maiores concentrações de silício nas folhas, sugerindo que silício sirva como defesa induzida nesta interação formiga-planta-herbívoro.

Key words: Cerrado; extrafloral nectaries; herbivory; induced defense; *Lafoensia pacari*; silicon.

In response to herbivores, plants have developed a great variety of defensive strategies, such as chemical (presence of alkaloids, tannins, and other substances), physical (presence of thorns, trichomes, leaf toughness), and biotic defenses (association with animals, mainly ants) that can reduce herbivory, consequently increasing plant fitness (Crawley 1983, Del-Claro *et al.* 1996, Goussain *et al.* 2002).

Extrafloral nectaries (EFNs) are nectar-producing glands that are not involved with pollination, but instead attract ants (Bentley 1977, Del-Claro & Oliveira 1993). Some authors have demonstrated that associations between ants and EFNs are beneficial for the plants (see Del-Claro *et al.* 1996, de la Fuente & Marquis 1999, and references therein). Ants protect the plants against the action of several herbivores, which they prey upon or drive away (e.g., Bentley 1977, Horvitz & Semske 1984, Koptur 1984, Fuente & Marquis 1999). Although the benefits to ants have been rarely studied, authors generally assume that the interaction has positive effects on ant fitness because ants obtain resources like sugars, amino acids, and water from the plants they protect (Buckley 1987a, b; Cushman & Beattie 1991; see also Davidson *et al.* 2003).

Until recently, it was believed that plant defenses against herbivores were mainly constitutive (e.g., always expressed and present in the plant; Karban & Baldwin 1997). Today, it is known that plants can respond to herbivore damage in ways that reduce herbivore performance and/or the preference of the herbivores for the plant, including modification of the plant’s chemical composition (e.g., an increase in secondary compounds) or reduction in the plant’s tissue quality (see extensive review in Karban & Baldwin 1997). Although silicon (Si) is the second-most common element in the Earth’s crust, its role in plant defense has been infrequently explored. Current data suggest that Si could be an important antiherbivore agent in agricultural systems (Korndörfer & Datnoff 1995, Goussain *et al.* 2002). Most existing data on Si’s role in plant defense have been limited to grasses (McNaughton *et al.* 1985). The objective of this study was to analyze the effectiveness of ants in reducing herbivory and the possible existence of induced defense in a tree, *Lafoensia pacari* (Lythraceae).

We selected 40 individuals of *L. pacari*, of approximately the same size and phenological state, in the cerrado (cerrado—*stricto sensu* Goodland 1971, see also Oliveira & Marquis 2002) of the Panga Ecological Station (Uberlândia, Minas Gerais State, 18° 57’ S, 48° 12’ W). We applied an ant-exclusion treatment to 17 of the plants, in which we manually removed all ants and coated the base of each tree with Tanglefoot® (The TangleFoot Company, Grand Rapids, MI, U.S.A.). The remaining 23 individuals were maintained in natural conditions as a control treatment.

*Lafoensia pacari* is a deciduous tree, and individuals at the beginning of the experiment only had leaf buds; thus the mean level of initial herbivory for each individual was considered zero. Mean herbivory was estimated twice, at 3 and 6 mo after application of the ant-exclusion treatment. For herbivory measurements, we selected nine leaves per plant per treatment (three leaves from the most apical branch, three from a middle branch, and three from the lowest branch of each plant). Measurements of herbivory rates on leaves were assessed by placing them on a transparent grid (divided into...
EFNs were active (first 3 mo), but not after these glands lost function (ants (control group) exhibited a significantly reduced level of herbivory while crassus trees with (white bars) and without (black bars) ant access. (a) Plants with EFNs of L. pacari are active in all new leaves, remaining green and producing nectar until full leaf expansion (20 d). EFNs were visited by ants during most of the first 3 mo of the experiment. The most common visitors were in the genera Camponotus (C. crassus) and Cephalotes (C. puillus). However ants from other genera were also observed on the plants, including Cremaatogaster, Pheidole, Brachymyrmex, Wasmannia, Ectatomma, and Solenopsis.

Visiting ants had a significant effect on the herbivory level. After 3 mo, herbivore damage was significantly greater in the ant-exclusion treatment than in the control ($F = 6.0918; df = 1, 32; P = 0.01$, Repeated-measures ANOVA, Fig. 1a). After 3 mo, leaves were fully developed and toughened and the EFNs were no longer active. In this second 3-mo period few ants visited the plants, presumably due to the absence of nectar. Thus after 6 mo the statistical analyses showed no significant difference in herbivory between groups ($F = 0.2648; df = 1, 32; P = 0.61$, Repeated-measures ANOVA, Fig. 1a).

Although control plants had higher herbivory damage in the first 3 mo, the total number of herbivores observed on control plants was not significantly different between the control and ant-exclusion plants ($U = 145; P = 0.2342$, Mann–Whitney $U$ test). Plants with ant access accumulated significantly lower amounts of Si in their leaves than plants without ant access ($U = 45.5; P = 0.01$, Mann–Whitney $U$ test, Fig. 1b).

Different ant-herbivory tactics can be useful to plants under different selective pressures. The system involving L. pacari, its herbivores and ants, clearly illustrates conditional outcomes in a facultative mutualistic interaction (Bronstein 1994, 1998). Our data show that ants provide effective defense against chewing herbivores during leaf expansion in this Lythraceae species. However, after leaves have expanded and EFNs cease to be active, ants no longer protect the plants against herbivores. Compared to controls, plants in our ant-exclusion treatment experienced a significantly higher level of leaf herbivory in the first 3 mo of the experiment and exhibited significantly higher Si content 6 mo after the start of the experiment. These results suggest that Si accumulation in L. pacari is an induced response to herbivory.

McNaughton et al. (1985) viewed Si as an ant-herbivore defense that was quantitatively inductible in grass shoots. Si accumulation in leaves can increase leaf toughness and thus potentially reduce herbivory damage (McNaughton et al. 1985, Korndörfer & Datnoff 1995). In African grasslands, McNaughton et al. (1985) showed that grasses with a higher level of Si had a lower level of herbivory and that artificial herbivory produced in laboratory conditions also verified a Si accumulation in plants with more herbivory damage. Korndörfer and Datnoff (1995) also have shown that Si accumulation in plants increases the resistance of cell walls against the attack by fungi and other diseases.

Many plant species with EFNs and defending ants also employ a diverse array of other defensive tactics (Treacy et al. 1987, Agrawal & Rutter 1998). Some ant plants have a combination of chemical, physical, and biotic defenses, and the intensity and effectiveness of each defense varies over different temporal and spatial scales against different attackers (Agrawal & Rutter 1998). We suggest that both biotic and physical defenses are important to the plants in different conditions. Some authors have even found that allocation of resources to multiple defenses is common in plants that need to defend against many different types of herbivores (Dyer et al. 2001). Seasonal variation in climatic conditions can produce variation in the abundance of herbivores, predators, and parasitoids in the field (Del-Claro & Oliveira 2000, Oliveira & Del-Claro 2005). This variation can also be responsible for variation in the herbivore pressure on plants. In the leaf expansion stage of L. pacari, EFNs are likely its most effective defense against herbivory, depending on the abundance and behavior of ants and associated herbivores. However, with the increase in herbivory levels, our data suggest that

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<th>Herbivory (%)</th>
<th>Control Group (ant present)</th>
<th>Treatment Group (ant excluded)</th>
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<tr>
<td>3 months</td>
<td>20</td>
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**FIGURE 1.** Herbivory and silicon accumulation in Lafoensia pacari (Lythraceae) trees with (white bars) and without (black bars) ant access. (a) Plants with ants (control group) exhibited a significantly reduced level of herbivory while EFNs were active (first 3 mo), but not after these glands lost function (*Repeated-measures ANOVA, $P < 0.01$). (b) Silicon analyses (mean ± 1 SD) revealed that plants with ant access accumulated significantly lower amount of Si in their leaves than plants without ant access (Mann–Whitney $U$ Test, $P < 0.01$).
these plants can employ an induced defense, accumulating Si and perhaps other chemical compounds. For *L. pacari*, both biotic and induced defenses can have an important role in the defense against herbivores. The relative effectiveness of these two defenses is likely conditional on plant phenology, ant visitation, and the intensity of herbivore attack.

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**LITERATURE CITED**


