

RELAXATION OF INDUCED INDIRECT DEFENSES OF ACACIAS FOLLOWING EXCLUSION OF MAMMALIAN HERBIVORES

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Abstract. Many plants offer rewards to attract ants that provide indirect defense against herbivores. These rewards include nectar and swollen thorn domatia, and their production can be inducible. Theory predicts that costly rewards should be relaxed if the risk of herbivory is reduced, although this has not been previously demonstrated. *Acacia drepanolobium* trees in East Africa produce two ant rewards, extrafloral nectar and swollen thorns. We compared the rewards offered by trees experimentally protected from mammalian browsing for seven years with those offered by unprotected trees. Protected trees produced 25% fewer nectaries per leaf and 25% fewer swollen thorns than did trees in browsed plots. Relaxation of indirect defenses when trees are protected from herbivores is consistent with the dual hypotheses that inducible defenses are dynamic and that plants can save costs by relaxing these defenses when they are not needed. Among trees exposed to mammalian herbivores, trees that were browsed within roughly the past year provided rewards for ants similar to those provided by trees exposed to herbivores but not browsed within the past year. This result suggests that relaxation of indirect defenses only occurs following more than one year of protection from mammalian herbivory.

Key words: *Acacia drepanolobium*; ant–plant interactions; East Africa; indirect defense; induced response; Kenya; mammalian herbivory; mutualism; nectaries; relaxation; swollen thorns.

INTRODUCTION

Long-lived plants are attacked by a shifting assemblage of herbivores. They defend themselves against these attackers by employing constitutive defenses that are fixed or preformed and induced defenses that are produced or activated following attack. Plants produce their own direct defenses, which include secondary compounds such as anti-nutritive chemicals and morphological deterrents such as spines and trichomes. They also produce indirect defenses such as nectaries and domatia, which provide rewards to facilitate the predators, parasites, and other antagonists of their herbivores.

Induced plant responses to herbivory by invertebrates and mammals are widespread in nature (Bryant et al. 1991, Karban and Baldwin 1997). They are assumed to enable plants to match their defenses to current attackers. This matching of the defense with the herbivore threat may enable plants to maximize fitness in the presence of herbivores while minimizing costs. If the plant cannot quickly induce defenses when herbivores are present and relax (or reduce) expensive defenses when herbivores are absent, the induced system will be much less effective and cost efficient (e.g., Levins 1968, Edelstein-Keshet and Rausher 1989, Pa-

dilla and Adolf 1996). Many studies of induced defenses have documented the speed of induction, but much less is known about whether induced defenses are relaxed when herbivores are no longer present, or about the timing of such relaxation (Karbon and Baldwin 1997). Observing relaxation is often more difficult and time consuming than observing induction, so few workers have examined this process (for exceptions involving direct defenses, see Underwood 1998, Young and Okello 1998, Gómez and Zamora 2002, Young et al. 2003). No published study has looked for evidence of relaxation of indirect defenses.

Plants may reduce their losses to herbivory by facilitating the enemies of their herbivores. For instance, many plants attract predators and parasites of herbivores by releasing volatiles that serve as cues to these enemies (Turlings et al. 1990, De Moraes et al. 1998, Dicke and van Loon 2000). Plants also attract ants and other antagonists of herbivores by providing nectar or other sources of food (Bentley 1977, Agrawal and Rutter 1998) as well as domatia (Davidson and McKey 1993, Walter 1996, Agrawal and Rutter 1998). Experimental removal of these plant defenders increased levels of herbivory and decreased plant fitness (Janzen 1967, Agrawal and Karban 1997).

Acacia drepanolobium has been a model system for the study of the induction and relaxation of woody spines, a direct defense against mammalian herbivores. Spines were ~27% longer on branches that were

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browsed by mammals than on unbrowsed branches (Young 1987), and experimental removal of *A. drepanolobium* spines caused a threefold increase in mammalian browsing of new leaves (Milewski et al. 1991). Length of newly produced spines relaxed by 20% after two years of complete protection from mammalian browsing and by 35–40% after five years of protection (Young and Okello 1998, Young et al. 2003). Spines are particularly effective against mammalian herbivores, the primary taxon considered in this study. Other defenses may be used to deter insect herbivores; however, they were beyond the scope of this study.

At Mpala Ranch, our study site, virtually every *Acacia drepanolobium* tree is inhabited by one of four species of resident ants that are obligately associated with these, or closely related, trees (Young et al. 1997). These aggressive ants reduce feeding times and leaf loss by mammalian browsers and increase the survivorship of their host trees (Madden and Young 1992, Stapley 1998; M. Stanton, *personal communication*). *Acacia drepanolobium* typically produces a single nectar gland near the leaf base, where ants sip nectar, and hollow swollen thorns, which ants use for shelter (Hocking 1970, Young et al. 1997). The most common resident ant species is *Crematogaster mimosae*, which occupies 40–60% of mature trees and appears to be a “true mutualist,” protecting the tree against herbivores (Young et al. 1997, Palmer et al. 2000). The second most common ant species is *C. nigriceps*, which also defends the tree against herbivores, but prunes most axillary and some terminal shoots, perhaps simulating mammalian herbivory (Young et al. 1997, 2003). Trees inhabited by this ant do not relax thorn length even when protected from mammalian herbivory, suggesting that trees cannot differentiate ant pruning from herbivore browsing (Young et al. 2003). Some trees are also inhabited by two other ant species, *Tetraponera penzigi* and *C. sjostedti*. Swollen thorns are produced from the spines, so they may simultaneously serve as direct defenses similar to spines and indirect defenses similar to galls that house ants. The ratio of swollen thorns to spines is variable and the regulation of production of swollen thorns is unknown.

In this study, we compare production of indirect defenses (nectaries and swollen thorns) in trees experiencing mammalian herbivory with trees that have been protected from herbivory for the past seven years. Specifically, we ask the following questions: (1) Does *A. drepanolobium* relax its investment in rewards for indirect defense (number of nectaries, number of swollen thorns, maximum size of swollen thorns) when protected from mammalian herbivores? (2) Does *C. nigriceps* prevent the relaxation of these rewards by simulating browsing by large mammals?

METHODS

The research was conducted in Laikipia, Kenya, at Mpala Research Centre (1800 m above sea level; 0°17'

N, 37°52' E, northwest of Mount Kenya on the Laikipia Plateau) at the Kenya Long-Term Exclosure Experiment (KLEE; Young et al. 1998). The exclosure experiment is located on wooded grassland on a black cotton soil, where *Acacia drepanolobium* forms almost monospecific stands constituting up to 97% of woody cover (Young et al. 1997). The KLEE experiment consists of three blocks of large plots (200 × 200 m each) that use electrified and visual barriers to exclude several combinations of different native mammalian herbivores and cattle (Young et al. 1998). For the purpose of this experiment, we were interested in the plots that either excluded all native large mammalian herbivores or allowed access to all native large mammalian herbivores. Native large mammalian herbivores that consume *A. drepanolobium* include elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), elands (*Taurotragus oryx*), and Grant's gazelles (*Gazella granti*). The native large mammalian herbivore treatment was crossed with a cattle treatment as part of the larger KLEE design. Because cattle do not consume *A. drepanolobium* (Young and Okello 1998), this design provided two replicates of native herbivore treatment per block, for a total of 12 plots (two treatments × two replicates × three blocks = 12 plots). The exclosure experiment was established in September 1995, and this study was conducted in August 2002, so the acacias in the treatment plots had been protected from large-mammal herbivory for seven years. We restricted our study to the two most common ant species, *Crematogaster mimosae*, which is a true mutualist, and *C. nigriceps*, which may simulate mammalian herbivory by pruning branch tips.

To determine whether protected acacias were relaxing their investment in indirect defenses, we measured three potential rewards for their ant defenders on trees located as follows. Four posts marked the corners of the inner hectare of each 4-ha plot. We chose three of these posts per plot haphazardly and located the nearest two trees inhabited by each ant species (*Crematogaster mimosae* and *C. nigriceps*), for a total of 12 trees per plot (three posts × two trees × two ant species = 12 trees), and 144 trees overall. At each tree, the condition of nectaries on each of five leaves haphazardly selected from branch ends at chest height was denoted as either active (e.g., nectaries consisting of green or red tissue) or inactive (e.g., damaged or absent nectaries). On the same tree, we then selected four chest-height branches, one in each cardinal direction, and counted the number of swollen thorns on the most distal 15 cm of each branch. The number of swollen thorns for all four branches was summed. We also measured the maximum diameter of the largest swollen thorn on each of the measured branch segments.

We used MANOVA to evaluate the effects of native mammalian herbivory, ant species, treatment location (block), and cattle herbivory on the three response variables. The overall MANOVA was significant and in-

licated significant effects of native mammalian herbivory and of ant species on response variables. There was no block effect, so it was excluded from further analyses, although including block in the models did not markedly influence our results. The effect of cattle herbivory was examined to confirm that the differences between mammalian herbivory treatments were not driven by competition between acacias and herbaceous vegetation (cattle drastically reduce herbaceous vegetation but do not eat *A. drepanolobium*; Young and Okello 1998). There was no effect of cattle, so this factor was excluded from further analyses. We performed protected univariate ANOVAs on each response variable. Maximum diameters of the largest swollen thorns were log-transformed to meet model assumptions. All analyses were performed using JMP 4.0.4. (SAS Institute 2000).

To better understand the timing of relaxation, we examined the number of nectaries and the number of swollen thorns in 24 trees adjacent to our plots that were occupied by *C. mimosae* and exposed to mammalian herbivores. Half of the trees showed evidence of recent mammalian herbivory (branches with evidence of fresh wounds from chewing within the previous year) and half did not. If trees that were exposed to herbivores but had no evidence of recent herbivory showed signs of relaxing their ant rewards, this would suggest that relaxation occurs over a relatively short time span (approximately one year).

RESULTS

The experimental removal of mammalian herbivores over the past seven years influenced the investment in indirect defenses by *Acacia drepanolobium* (for the overall MANOVA Wilks' lambda, $F = 9.16$, $df = 10, 34$, $P < 0.0001$; for block, $F = 1.143$, $df = 4, 34$, $P = 0.35$; for the exclusion of mammalian herbivores, $F = 16.73$, $df = 2, 17$, $P < 0.0001$; for ant species, $F = 58.83$, $df = 2, 17$, $P < 0.0001$; for the exclusion of mammalian herbivores $\times$ ant species, $F = 1.57$, $df = 2, 17$, $P = 0.24$).

Acacia trees that were protected from large mammalian browsers were less likely to invest in nectaries or swollen thorns. Active nectaries were 25.4% less abundant in plots from which large mammals had been excluded than in plots to which large mammals had access ($F_{1,20} = 12.31$, $P = 0.002$; Fig. 1A). Swollen thorns on distal tree branches were 24.8% less abundant in protected plots than in plots where trees were browsed ($F_{1,20} = 21.97$, $P < 0.0001$; Fig. 1B). However, acacias protected from large mammalian browsers did not produce significantly smaller swollen thorns. Maximum swollen thorn diameter was, on average, 7% smaller in protected plots, but this trend was not statistically significant ($F_{1,20} = 2.39$, $P = 0.14$; Fig. 1C).

The relaxation of indirect defenses in trees protected from mammalian herbivores does not appear to be driven by competition with surrounding herbaceous plants.

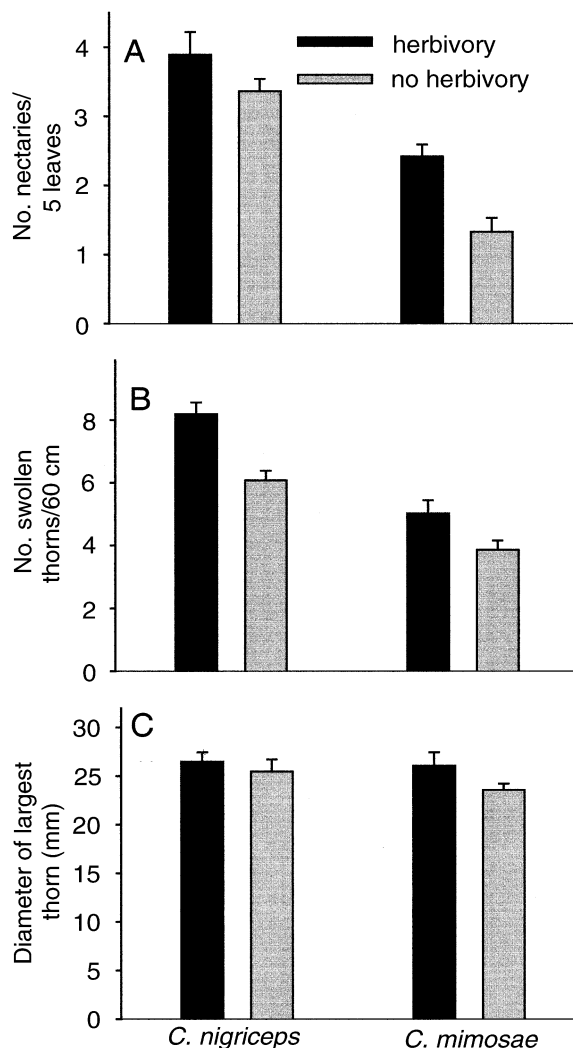


FIG. 1. Rewards (mean $\pm$ 1 SE) offered to ants by trees inhabited by either *Crematogaster nigriceps* or *C. mimosae* in plots that experienced herbivory by large mammals and plots that have received no herbivory by large mammals for the past seven years. (A) Number of active nectaries on five new leaves. (B) Number of swollen thorns on the distal 15 cm of four branches. (C) Diameter of the largest swollen thorn.

Although the cover of herbaceous plants differs considerably between plots with and without cattle (T. P. Young, *unpublished data*), there was no difference between the indirect defense response variables between those plots (MANOVA Wilks' lambda, $F = 0.14$, $df = 2, 21$, $P < 0.87$).

The level of investment by *A. drepanolobium* in indirect defenses depended strongly on the ant species inhabiting the tree. Acacia trees inhabited by *Crematogaster nigriceps* provided more nectar rewards per leaf than did trees occupied by *C. mimosae*. Provisioned nectaries were 93% more abundant on leaves of trees inhabited by *C. nigriceps* than *C. mimosae* ($F_{1,20} = 58.11$, $P < 0.0001$). Acacias inhabited by *C. nigri-*

ceps were also more likely to invest in swollen thorns. Distal tree branches on trees inhabited by *C. nigriceps* had 61% more swollen thorns ($F_{1,20} = 59.40$, $P < 0.0001$). Trees inhabited by *C. nigriceps* did not detectably alter their investment in larger swollen thorns compared to trees inhabited by *C. mimosae* ($F_{1,20} = 1.79$, $P = 0.20$).

We hypothesized that the destruction of axillary and terminal shoots by *C. nigriceps* would prevent acacias in plots protected from large mammalian herbivores from relaxing their indirect defenses. Consequently, we expected a significant interaction between exclusion of mammalian herbivores and ant species. Trees inhabited by *Crematogaster nigriceps* did appear to relax their indirect defenses less than trees inhabited by *C. mimosae*, although our power to detect a difference was low (see previous MANOVA results; Fig. 1A–C; in all cases, $\beta \leq 0.25$). Trees inhabited by *C. mimosae*, the true mutualist, produced 45% fewer nectaries in the absence of browsing mammals, whereas trees inhabited by *C. nigriceps*, the ant species that prunes shoot tips, produced only 14% fewer nectaries ($F_{1,20} = 1.46$, $P = 0.24$). Similarly, trees inhabited by *C. mimosae* produced 23% fewer swollen thorns, whereas trees inhabited by *C. nigriceps* produced only 16% fewer swollen thorns ($F_{1,20} = 1.82$, $P = 0.19$). Maximum swollen thorn diameters were 9.5% smaller on trees occupied by *C. mimosae*, compared to only 3.8% smaller for *C. nigriceps* ($F_{1,20} = 0.16$, $P = 0.69$).

In order to assess the timing of relaxation, we compared trees that were all exposed to large mammalian herbivores for the past seven years, but had different recent histories of herbivory. Trees exposed to, but not attacked by, browsers within approximately the past year showed no evidence of beginning to relax their rewards. The rewards offered by recently browsed trees (browsed within approximately the past year) were similar to those offered by trees exposed to mammalian herbivores but not recently browsed (for the number of nectaries, $F_{1,22} = 0.08$, $P = 0.78$; for the number of swollen thorns, $F_{1,22} = 1.28$, $P = 0.27$; for the maximum diameter of swollen thorns, $F_{1,22} = 0.55$, $P = 0.47$; see Fig. 2A–C).

DISCUSSION

Many plants offer rewards that attract ants and indirectly provide defense against herbivory (Bentley 1977, Agrawal and Rutter 1998). These indirect defenses have been shown to be inducible in a few cases. For example, production of extrafloral nectar, an indirect defense, increased for leaves of *Catalpa speciosa*, *Macaranga tanarius*, and *Vicia faba* after damage by herbivores (Stephenson 1982, Heil et al. 2000, Mondor and Addicott 2003). Increased production of extrafloral nectar may, in turn, cause an increase in ant attendance. For instance, ant attendance was strongly positively correlated with production of extrafloral nectar by leaves of *Catalpa bignonioides* (Ness 2003).

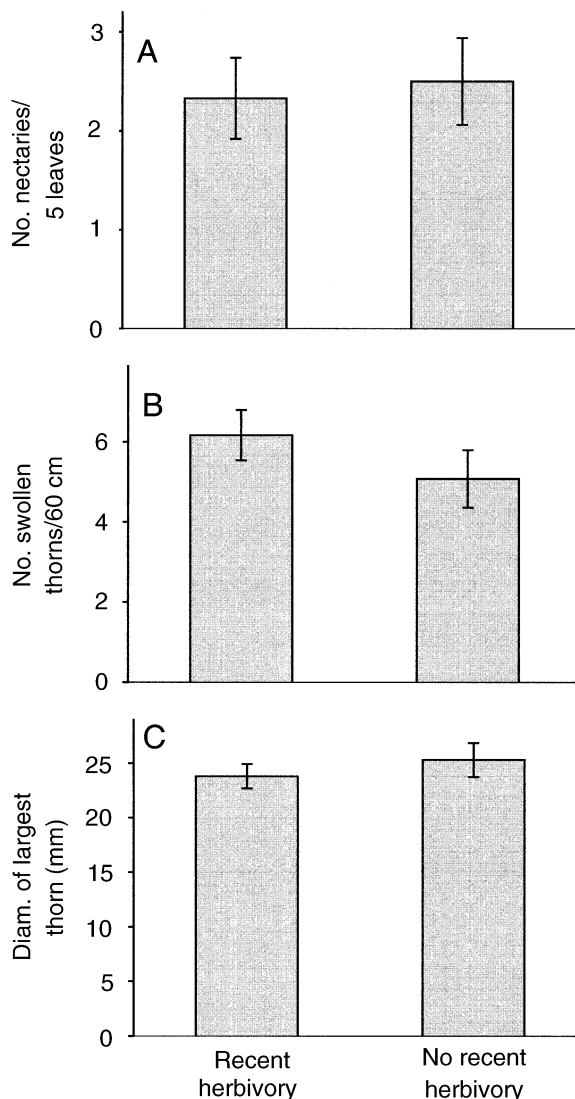


FIG. 2. Rewards (mean $\pm$ 1 SE) offered to ants by trees that have been recently damaged by large mammalian herbivores and those that have not been recently damaged in plots where large mammalian herbivores have had access to trees for the past seven years. All trees were occupied by *Crematogaster mimosae*. (A) Number of active nectaries on five new leaves. (B) Number of swollen thorns on the distal 15 cm of four branches. (C) Diameter of the largest swollen thorn.

Furthermore, herbivory or its signals may cause an increase in aggressive ant activity. Leaf damage to *Cecropia obtusifolia* caused a rapid, fivefold increase in the local number of aggressive ants (Agrawal 1998). The induced ant response has the potential to reduce herbivory. Aggressive ants on *Acacia drepanolobium* significantly reduced the feeding time of juvenile giraffes (Madden and Young 1992) and repelled browsing by goats (Stapley 1998). In the dynamic process of ant defense, a reduction in herbivory should lead to a relaxation of these induced defenses.

In this study, we found that *Acacia drepanolobium* relaxed nectar and swollen thorn rewards offered to ants for indirect defense after seven years without mammalian herbivory. Over time, older nectaries stop producing nectar and swollen thorns often crack and break apart (Hocking 1970; T. M. Palmer and T. P. Young, *personal observations*), so lower production of new nectaries and swollen thorns probably indicates a biologically meaningful reduction in investment by the trees in indirect defense.

If expressing defenses is costly to the plant, we would expect the plant to relax induced defenses when herbivores no longer make indirect defenses beneficial. Such costs of defense can take several forms, such as allocation and ecological costs (Karban and Baldwin 1997). Allocation costs are incurred when investment in defense diverts resources from plant growth and reproduction. These costs are difficult to demonstrate and have not been found uniformly (Strauss et al. 2002). Ecological costs are incurred when a strategy that works as a defense attracts nonbeneficial organisms as well. Ecological costs are more commonly demonstrated and are certainly possible in the case of *Acacia drepanolobium*. For example, the production of extrafloral nectar may attract not only ant defenders but also insect herbivores. In addition, the swollen thorns used by ants also provide protection for many nonbeneficial insects (Hocking 1970). Finally, the nectar and swollen thorn rewards of *A. drepanolobium* also attract ant inhabitants that do not provide a net benefit to the acacias. *Crematogaster nigriceps*, one of the four species that inhabits the swollen thorns and feeds at leaf nectaries, defends against herbivores but essentially sterilizes the plant (Young et al. 1997, Stanton et al. 1999). Producing food and shelter rewards when ants are not providing an important defensive service may thus be ecologically costly.

Acacia drepanolobium trees offered fewer rewards to *Crematogaster mimosae*, an obligate, true ant mutualist, than to *C. nigriceps*, an obligate ant species that chews axillary and terminal shoot tips. Thus, *C. nigriceps* appears to be able to manipulate the rewards offered by *A. drepanolobium*, presumably by simulating mammalian herbivory through the chewing of new shoot tips. However, among trees occupied by *C. nigriceps*, those trees protected from large mammalian herbivores nonetheless had lower investment in ant rewards. This suggests that the overall levels of these indirect defenses are due to additive or multiplicative effects of large mammal herbivory and ant pruning. Our results are roughly consistent with the hypothesis that the effects are multiplicative (in the absence of mammalian herbivory, trees occupied by *C. mimosae* had 45% fewer green nectaries per leaf and 23% fewer swollen thorns, whereas trees occupied by *C. nigriceps* had only 14% fewer green nectaries per leaf and 16% fewer swollen thorns; Fig. 1A, B). However, small sample sizes gave us very little statistical power to detect

the difference in the interaction between large-mammal herbivory and ant species occupant, and the differences are not statistically significant. These results contrast with the pattern of relaxation of spines, a direct defense, at the same site. Thorn length relaxed after protection from large-mammal herbivory in trees occupied by *C. mimosae*, the true mutualist, but not by *C. nigriceps*, the pruning ant, suggesting that ant pruning alone was sufficient to maintain this direct defense (Young et al. 2003).

The differences in rewards offered by the trees occupied by *C. mimosae* and *C. nigriceps* are unlikely to be due to inherent differences in the trees themselves. Changes in the ant species occupying individual trees are common (Young et al. 1997, Palmer et al. 2000). In addition, many phenotypic traits that characterize trees occupied by different ant species are altered when ant occupancy changes (T. M. Palmer and T. P. Young, *personal observations*). Thus, these differences in rewards appear to be caused by the ant occupants themselves.

Comparing trees with different recent histories of natural herbivory provided some preliminary information on the time scale of relaxation in *A. drepanolobium*. Trees that had been browsed by mammalian herbivores recently (within approximately the last year), as well as those that had been exposed to mammalian herbivores for the past seven years but had not been browsed recently (both are included in the control treatment in Fig. 1A, B), offered more rewards than those that had been protected for the past seven years. Trees that were browsed recently offered rewards similar to those of trees that were exposed to mammalian herbivores but not recently browsed (Fig. 2A–C). This suggests that trees must remain unattacked for more than one year before they detectably relax their indirect defenses. The speed of relaxation favored by natural selection should be heavily influenced by the probability of herbivory in a given time period. If a plant is highly likely to be attacked in the time period, but no attacks occur, the plant should begin relaxing costly defenses rapidly. However, if a plant is unlikely to be attacked in the time period, despite a high likelihood of being attacked in a subsequent time period, then the plant should not relax its defenses immediately. In one study, when the rates of herbivore attack were ~80% per year, shrubs relaxed their investment in a direct defense, spines, by 40–50% after just one year of protection (Gómez and Zamora 2002). Because the probability that an individual *A. drepanolobium* tree that is exposed to mammals will actually get browsed is only 10–20% per year at our study site (Young and Okello 1998), it makes sense for the tree to be conservative about relaxing its defenses (Young et al. 2003).

Our results demonstrate that *Acacia drepanolobium* relaxes indirect rewards offered to ant defenders when the threat of mammalian herbivory has been excluded for seven years. This is the first evidence that plants

may reduce their investment in indirect defenses following the removal of an herbivore threat. Thus, trees with induced traits that attract aggressive ants appear to be dynamic in their ability to relax these traits. This relaxation is variable and is influenced by the specific ant inhabitant. Relaxation of indirect defenses suggests that maintaining these defenses is costly to the plant.

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LITERATURE CITED

- Agrawal, A. A. 1998. Leaf damage and associated cues induce aggressive ant recruitment in a neotropical ant-plant. *Ecology* **79**:2100–2112.
- Agrawal, A. A., and R. Karban. 1997. Domatia mediate plant–arthropod mutualisms. *Nature* **387**:562–563.
- Agrawal, A. A., and M. T. Rutter. 1998. Dynamic anti-herbivore defense in ant-plants: the role of induced responses. *Oikos* **83**:227–236.
- Bentley, B. L. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* **8**:407–427.
- Bryant, J. P., F. D. Povenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. du Toit. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* **22**:431–446.
- Davidson, D. W., and D. M. McKey. 1993. The evolutionary ecology of symbiotic ant–plant relationships. *Journal of Hymenoptera Research* **2**:13–83.
- De Moraes, C. M., W. J. Lewis, P. W. Paré, H. T. Alborn, and J. H. Tumlinson. 1998. Herbivore-infested plants selectively attract parasitoids. *Nature* **393**:570–573.
- Dicke, M., and J. J. A. van Loon. 2000. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata* **97**:237–249.
- Edelstein-Keshet, L., and M. D. Rausher. 1989. The effects of inducible plant defenses on herbivore populations. I. Mobile herbivores in continuous time. *American Naturalist* **133**:787–810.
- Gómez, J. M., and R. Zamora. 2002. Thorns as induced mechanical defense in a long-lived shrub (*Hormathophylla spinosa*, Cruciferae). *Ecology* **83**:885–890.
- Heil, M., B. Fiala, B. Baumann, and K. E. Linsenmair. 2000. Temporal, spatial and biotic variations in extrafloral nectar secretion by *Macaranga tanarius*. *Functional Ecology* **14**:749–757.
- Hocking, B. 1970. Insect associations with the swollen thorn acacias. *Transactions of the Royal Entomological Society of London* **122**:211–255.
- Janzen, D. H. 1967. Interaction of the bull's thorn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *University of Kansas Science Bulletin* **47**:315–558.
- Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.
- Madden, D., and T. P. Young. 1992. Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*. *Oecologia* **91**:235–238.
- Milewski, A. V., T. P. Young, and D. Madden. 1991. Thorns as induced defenses: experimental evidence. *Oecologia* **86**:70–75.
- Mondor, E. B., and J. F. Addicott. 2003. Conspicuous extrafloral nectaries are inducible in *Vicia faba*. *Ecology Letters* **6**:495–497.
- Ness, J. H. 2003. *Catalpa bignonioides* alters extrafloral nectar production after herbivory and attracts ant bodyguards. *Oecologia* **134**:210–218.
- Padilla, D. K., and S. C. Adolph. 1996. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evolutionary Ecology* **10**:105–117.
- Palmer, T. M., T. P. Young, M. L. Stanton, and E. Wenk. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* **123**:425–435.
- SAS Institute. 2000. JMP 4.0.4. SAS Institute, Cary, North Carolina, USA.
- Stanton, M. L., T. M. Palmer, T. P. Young, A. Evans, and M. L. Turner. 1999. Sterilization and canopy modification of a swollen thorn acacia tree by a plant–ant. *Nature* **401**:578–581.
- Stapley, L. 1998. The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias. *Oecologia* **115**:401–405.
- Stephenson, A. G. 1982. The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. *Ecology* **63**:663–669.
- Strauss, S. Y., J. A. Rudgers, J. A. Lau, and R. E. Irwin. 2002. Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution* **17**:278–285.
- Turlings, T. C. J., J. H. Tumlinson, and W. J. Lewis. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* **250**:1251–1253.
- Underwood, N. C. 1998. The timing of induced resistance and induced susceptibility in the soybean–Mexican bean beetle system. *Oecologia* **114**:376–381.
- Walter, D. E. 1996. Living on leaves—mites tomenta, and leaf domatia. *Annual Review of Entomology* **41**:101–114.
- Young, T. P. 1987. Herbivory induces increased thorn length in *Acacia drepanolobium*. *Oecologia* **71**:436–438.
- Young, T. P., and B. N. Okello. 1998. Relaxation of an induced defense after exclusion of herbivores: spine length in *Acacia drepanolobium*. *Oecologia* **115**:508–513.
- Young, T. P., B. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: A long-term, large-scale herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* **14**:94–102.
- Young, T. P., M. L. Stanton, and C. E. Christian. 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* **101**:171–179.
- Young, T. P., C. H. Stubblefield, and L. A. Isbell. 1997. Coexistence among obligate acacia ants. *Oecologia* **109**:98–107.