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MUTUALISM AS RECIPROCAL EXPLOITATION: AFRICAN PLANT-ANTS DEFEND FOLIAR BUT NOT REPRODUCTIVE STRUCTURES

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Abstract. The foundation of many plant–ant mutualisms is ant protection of plants from herbivores in exchange for food and/or shelter. While the role of symbiotic ants in protecting plants from stem- and leaf-feeding herbivores has been intensively studied, the relationship between ant defense and measures of plant fitness has seldom been quantified. We studied ant aggression, damage by herbivores and seed predators, and fruit production among *Acacia drepanolobium* trees occupied by four different acacia-ant species in an East African savanna. Levels of ant aggression in response to experimental disturbance differed strongly among the four species. All four ant species recruited more strongly to new leaf growth on host plants following disturbance, while recruitment to developing fruits was on average an order of magnitude lower. Host plants occupied by more aggressive ant species suffered significantly less vegetative damage from leaf-feeding insects, stem-boring beetles, and vertebrate browsers than host plants occupied by less aggressive ant species. However, there were no differences among fruiting host plants occupied by different ant species in levels of seed predation by bruchid seed predators. Fruit production on host trees was significantly correlated with tree stem diameter but not with the identity of resident ants. Our results demonstrate that defense of host plants may differ substantially among ant species and between vegetative and reproductive structures and that fruit production is not necessarily correlated with high levels of aggression by resident ants.

Key words: Acacia drepanolobium; *ant–plant interactions; antiherbivore defense; biotic defense;* Crematogaster; *herbivory; mutualism; myrmecophyte seed predators.*

Introduction

Ant–plant protection relationships are a prominent example of mutualism (Bronstein 1998). Typically, plants provide a number of potential benefits to ants, including food rewards and/or nesting space (Janzen 1966, 1975, Vasconcelos 1991). In return, ants may provide protection from herbivory (e.g., Janzen 1966, Davidson and McKey 1993, Fonseca 1994, Federle et al. 1998, Heil et al. 2001) or pathogens (Letourneau 1998, Heil et al. 1999), pruning of neighboring plants (Janzen 1966, Benson 1985, Davidson and McKey 1993, Federle et al. 1998), and nutrient enrichment (Janzen 1966, Treseder et al. 1995, Sagers et al. 2000; but see Fischer et al. 2003). Of these services, protection from herbivory is the best documented; plants without ants generally suffer higher levels of herbivory than conspecifics with ants present (reviewed in Davidson and McKey 1993, Heil and McKey 2003). Although it is reasonable to expect that strong ant defense of plants should translate into higher plant reproductive output, relatively few studies have explicitly examined the relationship between ant defense and plant reproduction within obligate ant–plant symbioses (e.g., Janzen 1966, Vasconcelos 1991, Letourneau and Dyer 1998, Gaume et al. 2005*b*).

There are several reasons to examine ant defense of both vegetative (e.g., leaves and stems) and reproductive (e.g., flowers and seeds) plant parts. First, because ant–plant associations are reassembled in each successive generation (i.e., "horizontally transmitted"), there may be no selection for ants to defend plant reproductive structures, potentially leaving host plants vulnerable to attack by specialist insects such as predispersal seed predators. Predispersal seed predators are common in many flowering plant communities (reviewed in Crawley 1992) and may strongly influence plant reproductive success (Louda and Potvin 1995), but their impact on ant-plants has not been examined. Second, while higher levels of folivory can decrease plant reproductive performance (e.g., Coleman and Leonard 1995), the two are not always negatively correlated (e.g., Marquis 1988, 1992). For example, Letourneau (1998) found no correlations between foliar damage and reproductive output for *Piper* plants occupied by the ant *Pheidole bicornis*. A more careful examination of the links between ant defense and plant reproductive output will help to clarify the full scope of costs and benefits within ant–plant protection mutualisms.

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In this study, we examined relationships between resident ant aggressive behavior and levels of herbivory, seed predation, and fruit production on *Acacia drepanolobium* trees in Laikipia, Kenya. In our study system, individual *A. drepanolobium* trees were occupied by one of four mutually exclusive acacia-ant species. Here, we quantified levels of aggression toward intruders by each of the four resident ant species and addressed four questions: (1) Do defending ants recruit equally to different plant parts (e.g., new leaves vs. developing fruits) following disturbance? (2) Do trees occupied by more aggressive ant species suffer lower levels of three types of damage to vegetative structures from stem-boring beetles and invertebrate and vertebrate browsers? (3) Do trees occupied by more aggressive ant species incur lower losses to bruchid seed predators? (4) Do trees occupied by the most aggressive ant species have the highest levels of fruit production?

Study System and Methods

Our research was conducted in the semi-arid Laikipia ecosystem (37° E, 0° N; 1800 m elevation) in north-central Kenya at the Mpala Research Center. In our study area, *A. drepanolobium* accounts for over 97% of canopy cover, forming a virtual monoculture in the overstory (Young et al. 1997). *Acacia drepanolobium* is a small tree defended by stipular spines (Milewski et al. 1991, Young et al. 1997, Young and Okello 1998), symbiotic ants (Madden and Young 1992, Young et al. 1997), and leaf chemistry (Ward and Young 2002). A pair of straight, sharp spines is produced at each node. Approximately one node out of every 10–20 has a swollen structure up to 5 cm in diameter located at the base of the spine pair that houses resident ants that feed in part from extrafloral nectaries at the leaf bases (Hocking 1970). Virtually all trees more than 1 m tall have a single resident ant colony, although a colony may occupy multiple trees.

Four species of acacia-ants are the principal symbionts of *A. drepanolobium* (Hocking 1970, Young et al. 1997). *Tetraponera penzigi*, *Crematogaster nigriceps*, and *C. mimosae* depend entirely on the interiors of swollen thorns for nesting space and are specialists on *A. drepanolobium* within this ecosystem. *Crematogaster nigriceps* is a castration parasite (an organism whose activities preclude a host from reproducing; Stanton et al. 1999), and host plants occupied by this species at our primary study site are virtually never found fruiting. However, this ant species does not completely sterilize host plants at a nearby study site. *Crematogaster sjostedti* nests are principally within stems hollowed out by longhorn beetle larvae (Cerambycidae), but its workers may also occupy swollen thorns. More details on the study system can be found in Palmer et al. (2000).

Browsing mammals that occur in the study area and feed on *A. drepanolobium* are Grant's gazelle (*Gazella granti*), eland (*Taurotragus oryx*), steinbuck (*Ramphicerus campestris*), oryx (*Oryx beisa*), and elephant (*Loxodonta africana*). Invertebrate herbivores and predators include grasshoppers (Orthoptera), cerambycid beetles (Cerambycidae), weevils (Cucurlionidae), and bruchid beetles (Bruchidae), a predispersal seed predator of *A. drepanolobium*.

Assessing levels of ant aggression and herbivore damage

To assess overall levels of resident ant aggression and levels of herbivore damage on *A. drepanolobium*, we selected 24 similarly sized trees (1.5–2.2 m in height) occupied by each of the four acacia ant species along four 200-m linear transects running in a north–south direction. At the start of each transect, we identified the nearest tree of the appropriate height occupied by one of the four acacia ant species. We then located the nearest 1.5–2.2 m high trees occupied by each of the three other ant species. Because strong termite-generated gradients in soil fertility influence ant–plant associations in this habitat (Palmer 2003), we selected only focal trees that were >20 m from termite mound edges. After each set of four trees had been identified and measured, we then proceeded 30 meters southward along the transect and repeated the process until a total of 24 sets of trees were measured.

For each focal tree identified, we performed a number of measurements. First, we arbitrarily chose two branches at a height of ~1.5 m, one on the south side of the canopy and one on the north. An observer wearing a leather glove then grasped the branch tip and raked the first 15 cm of the branch three times in rapid succession. Prior observations indicated that this simulation mimics a typical ungulate browser feeding bout in both duration and intensity of disturbance. We then recorded the number of ants swarming onto the leather glove during a 30-second period for both branches. The mean of these two numbers was used as an index of overall ant aggression for each focal tree.

Second, we scored each tree for the presence and number of stem scars inflicted by stem-boring beetles (Cerambycidae). To assess levels of damage to trees by vertebrate browsers, we examined all branches on each focal tree for characteristic signs of browsing, including bite marks, nipped branch tips, and signs of bark stripping. We did not distinguish among these different signs of browsing. We then recorded the number of damaged branches and the total number of branches per tree.

Third, to assess general levels of invertebrate damage to foliage, we arbitrarily removed five leaves from branches occurring at a height of 1–2 m around the entire circumference of focal trees. Leaves were selected from within the first 10 cm of new growth on branch tips. We then visually estimated the percentage of leaflets bearing signs of insect damage (including both missing and chewed leaflets), assigning each leaf to one of four damage categories (1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). We used the mean value of each damage class in analyses.

Quantifying ant recruitment to different plant parts following disturbance

We chose 12 fruiting host plants between 1.5 and 2.25 m in height occupied by each of the four ant species and where new growth was present on at least one branch. On each host plant, two observers each arbitrarily selected a branch bearing either developing fruits or newly opened leaves and then chose a single developing fruit or a single new leaf on those branches. Both observers then simultaneously disturbed the focal branches at a point equidistant to the fruit and leaf and counted the number of workers coming into contact with the developing fruit or new leaf during the following 60 seconds. Prior observations indicated that resident ants reliably recruit to disturbed areas on host plants. Our goal here was not to mimic browsing, but to test whether ant recruitment to different plant structures varied following generalized disturbances to an area equidistant from those structures.

Assessing fruit production for host plants occupied by different ant species

We censused 500 *A. drepanolobium* trees along randomly oriented 4 m wide belt transects at our primary study site to assess the relationship between the number of fruits produced per tree, ant occupant, and host plant diameter (a surrogate for plant age; T. Palmer, M. Stanton, and T. Young, *unpublished data*). Because *C. nigriceps*-occupied host plants do not fruit at this study site, we did not include this species in our analysis.

Quantifying damage by bruchid seed predators

We assessed fruit production by *A. drepanolobium* and the number of seeds and fruits attacked by bruchid beetle predators on separate focal trees at two sites. At our primary study site, we surveyed host trees occupied by *C. sjostedti*, *C. mimosae*, and *T. penzigi*. *C. nigriceps* effectively sterilizes trees at this site (Young et al. 1997, Stanton et al. 1999) and so was excluded from these analyses. However, at a secondary site fewer than 5 km distant (Palmer et al. 2003), trees occupied by *C. nigriceps* occasionally fruit, allowing us to determine the efficacy of this ant species in defending host trees from attack by bruchid seed predators. At each study site, we surveyed 20 fruiting *A. drepanolobium* trees occupied by each ant species. Fruiting trees were chosen as they were encountered along parallel linear transects run by two or three observers (secondary and primary study sites, respectively). For each fruiting tree, we arbitrarily selected up to 10 fruits from within the canopy to score for seed and fruit predation. In cases where fewer than 10 fruits were present on trees, we scored all fruits present for damage. Each fruit was opened, and the seed pod and seeds within were examined for bruchid beetle exit holes. In some cases, fruits had dehisced and seeds were missing. In cases where bruchid exit holes were found on locations on pods corresponding to missing seeds (pod chambers), the missing seed was scored as damaged. Missing seeds with undamaged corresponding pod chambers were not included in our analyses.

All measures of ant aggression, vertebrate and invertebrate herbivory, cerambycid beetle damage, and bruchid fruit predation were conducted between June and August 2004. The survey of fruit production, host plant stem diameter, and ant occupant was conducted in January of 2007, following unusually late rains in December 2006.

Statistical analyses

We compared overall levels of aggression among ant species using ANOVA and contrasted differences in recruitment among the four species to developing fruits vs. new leaves using a nested ANOVA and planned contrasts. MANOVA was used to determine whether overall differences in damage by beetles, leaf-chewing invertebrates, and vertebrate herbivores existed between host plants occupied by the four acacia-ant species. We then used ANOVA to assess whether differences existed in each measure of damage among host plants occupied by the four ant species, adjusting significance levels for multiple comparisons using a sequential Bonferroni correction (Rice 1989). We analyzed the relationship between fruit production and tree diameter and ant occupant using ANOVA. The number of fruits per host plant was log-transformed to normalize variance. The proportion of seeds attacked per fruit by bruchid seed predators was analyzed using ANOVA, with the total number of fruits per tree included as a covariate.

Results

Interspecific variation in ant aggression

The four acacia ant species differed strongly in overall levels of aggression in response to simulated browsing; *Crematogaster mimosae* and *C. nigriceps* recruited strongly to disturbances, whereas responses by *C. sjostedti* were an order of magnitude lower, and responses by *Tetraponera penzigi* were intermediate (Fig. 1; ANOVA $F_{3,92} = 65.58$, $P < 0.0001$).

Variation in levels of recruitment to different plant parts

There were significant differences among the four ant species in overall levels of recruitment to new leaves and developing fruits following disturbance (Fig. 1B; nested ANOVA, $F = 13.27$, $df = 3$, $P < 0.0001$). Within species, recruitment to new leaves following disturbance was on average an order of magnitude higher than recruitment to developing fruits (Fig. 1B; nested ANOVA, $F = 16.91$, $df = 4$, $P < 0.0001$).

Relationships between fruit production and plant diameter, and ant occupant

Fruit production was significantly correlated with plant diameter (Fig. 2; ANOVA, $F = 174.02$, $df = 1$, $P < 0.0001$) but not with the species of ant occupant in

residence ($F = 0.02$, df = 2, $P = 0.98$). There was no significant interaction between plant diameter and ant occupant on the number of fruits produced per tree (diameter × ant species, $F = 2.07$, df = 2, $P = 0.13$).

Variation in cerambycid beetle damage, insect and vertebrate herbivory, and bruchid attack

Overall levels of damage by stem-boring beetles and vertebrate and insect browsers differed significantly among host plants occupied by the four different ant species (MANOVA, Wilks' lambda = 0.46, df = 9, $P < 0.0001$). Leaves on host plants occupied by *C. sjostedti* had significantly higher levels of invertebrate damage than leaves on host plants occupied by the other acacia-ant species, whereas *C. nigriceps*-occupied host plants had the lowest levels of invertebrate leaf damage (Fig. 3A; ANOVA, $F_{3,92} = 17.87$, $P < 0.0001$). Cerambycid damage to host plant stems was significantly greater on *C. sjostedti*-occupied trees relative to host trees occupied by the other three acacia-ant species (Fig. 3B; ANOVA, $F_{3,92} = 14.68$, $P < 0.0001$). The proportion of shoots browsed on host plants occupied by *C. sjostedti* was significantly greater than on host plants occupied by the other three ant species (Fig. 3C; ANOVA, $F_{3,92} = 10.58$, $P < 0.0001$). There was no significant effect of ant identity (Fig. 3D; ANOVA, $F = 0.54$, df = 3, $P = 0.66$) or the number of fruits per tree (ANOVA, $F = 0.41$, df = 3, $P = 0.52$) on the proportion of seeds attacked by bruchid beetle seed predators.

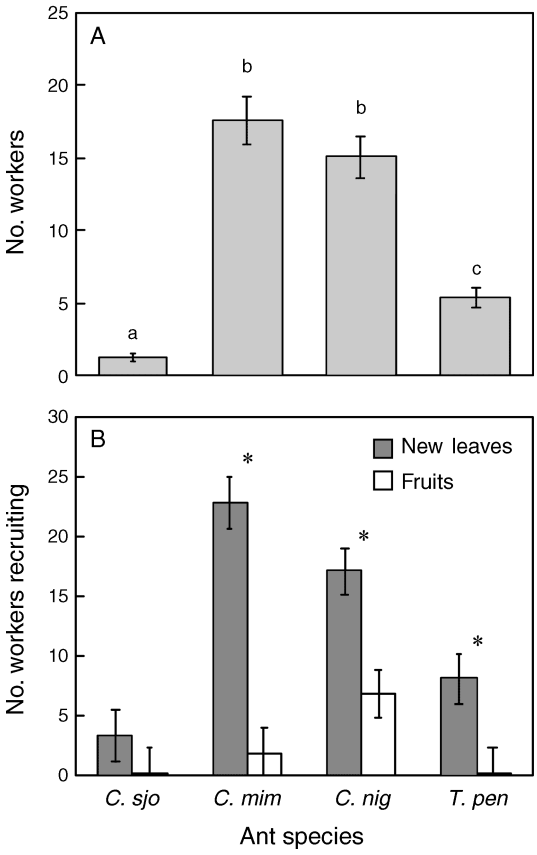

FIG. 1. (A) The number of ants swarming aggressively in response to simulated browsing of branch tips for host plants occupied by four acacia ant species (mean ± SE). Lowercase letters above bars show means that differ significantly from one another in Tukey-Kramer hsd tests. (B) The number of ants recruiting to new leaves vs. fruits following disturbance (mean ± SE). Asterisks show significant differences ($P < 0.05$) within each ant species from planned contrasts of the number of workers recruiting to new leaves vs. fruits. Species abbreviations are: *C. sjo*, *Crematogaster sjostedti*; *C. mim*, *C. mimosae*; *C. nig*, *C. nigriceps*; *T. pen*, *Tetraponera penzigi*.

DISCUSSION

Our goal in this study was to examine variation in herbivory, seed predation, and fruit production on *Acacia* trees occupied by four different ant species that vary strongly in levels of host plant defense. While host plants occupied by more aggressive ant species had lower levels of damage by vertebrate and invertebrate herbivores, there were no significant differences in seed predation by bruchid beetles among *Acacia* trees occupied by the four different ant species. Moreover, while we expected fruit production to be highest on trees occupied by the most aggressive ant species, we found no significant relationship between ant occupant and host plant fruiting. Instead, fruit production was significantly correlated with the size of the host plant. Our results highlight that the relationships between resident ant aggressiveness and measures of host plant performance are not always straightforward.

The inverse relationship we observed between ant aggression and herbivore damage to host plant stems, shoots, and leaves demonstrates that the four acacia ant species differ markedly in their protection of vegetative structures on their host plants. While we did not demonstrate a mechanism for these correlated responses through an ant removal experiment (made intractable by the size of our focal trees), it seems likely that low levels of ant aggression toward herbivory would result in higher levels of leaf herbivory by both mammalian and invertebrate browsers. Preliminary data from an ongoing ant-removal study on smaller host plants (T. Palmer, M. Stanton, T. Young, J. Goheen, and R. Karban, *unpublished manuscript*) demonstrate that while removal of *Crematogaster mimosae* and *C. nigriceps* increases rates of longhorn beetle attack on host trees, removal of *C. sjostedti* strongly reduces damage to trees by these longhorn beetles (whose tunnels *C. sjostedti* uses for nest space), indicating active facilitation of cerambycids by this ant species.

By contrast, the absence of differences among host plants occupied by these species in levels of bruchid predation on seeds and the relatively high levels of seed predation (≈30% across all ant-occupied trees) suggests that ant protection of reproductive structures is minimal for all of the ant partners within this symbiosis. Our experiments examining ant recruitment in response to artificial disturbance suggest that ants preferentially

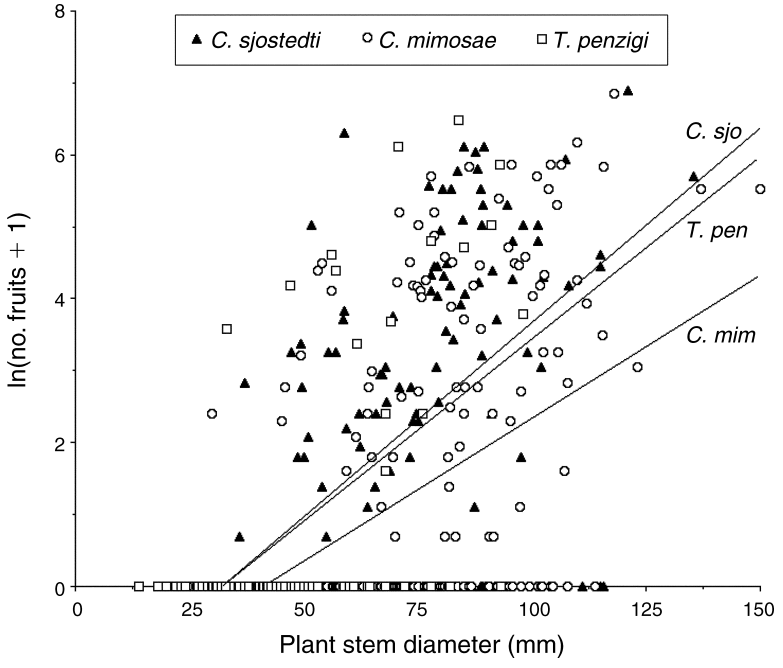

FIG. 2. Relationship between stem diameter and the number of fruits produced by host plants occupied by three different ant species.

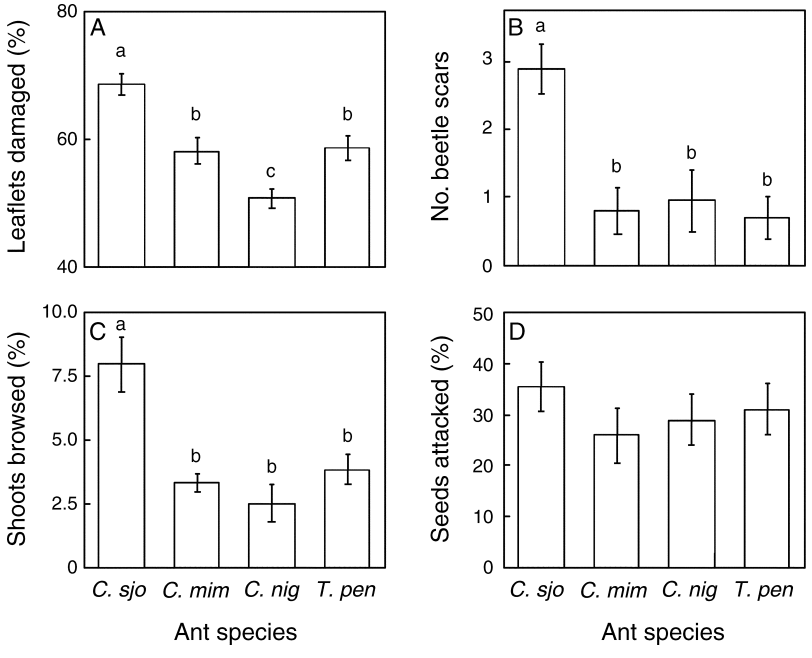

FIG. 3. Levels of damage by plant enemies to host plants occupied by four acacia ant species: (A) percentage of leaflets damaged by invertebrate herbivores, (B) number of stem-boring beetle scars per tree, (C) percentage of shoots browsed by mammalian herbivores, and (D) percentage of seeds attacked by bruchid beetle seed predators. Lowercase letters above bars show means that differ significantly from one another in Tukey-Kramer hsd tests. Species abbreviations are: *C. sjo*, *Crematogaster sjostedti*; *C. mim*, *C. mimosae*; *C. nig*, *C. nigriceps*; *T. pen*, *Tetraponera penzigi*. Error bars show ±SE.

protect growing shoots, while recruiting weakly or not at all to developing fruits. That plant-ants may vigorously defend new growth on vegetative structures of host plants while ignoring reproductive structures is consistent with the characterization of mutualisms as "reciprocal exploitations" (Axelrod and Hamilton 1981, Thompson 1982, 1994): because ant–plant symbioses are reassembled in each successive generation, ants should defend only those structures that will directly (e.g., swollen thorn domatia, new leaves bearing productive extrafloral nectaries) or indirectly (e.g., leaves and stems, which support photosynthesis) contribute to colony performance.

A number of studies have demonstrated interspecific differences in ant protection of the same species of host plant (e.g., Janzen 1975, Yu and Pierce 1998, Gaume and McKey 1999, Mody and Linsenmair 2004, Raine et al. 2004, Frederickson 2005, Gaume et al. 2005*a, b*). Our report corroborates this growing literature on the variability of partner benefits in multispecies ant–plant symbioses and extends the literature by demonstrating that mutualists which vigorously defend host plant vegetative parts may be poor defenders of reproductive structures. Contrasting with our results, Willmer and Stone (1997) found a positive correlation between *Crematogaster* ant abundance and fruit set on individual branches in *A. zanzibarica* (a close relative of *A. drepanolobium*). Their results suggest that ants may protect developing fruits in this system, although they did not continue their observations of ant activity through fruit dehiscence nor report bruchid damage to fruits that were produced. For obligate myrmecophytes, relatively few studies have explicitly examined the consequences of ant protection for plant reproduction (e.g., Janzen 1966, Vasconcelos 1991, Letourneau and Dyer 1998), and none of these have examined the influence of ant associates on predispersal seed predators.

These correlative results should be interpreted with appropriate caution. Alternative explanations for the patterns we observed include variation in herbivore attack on plants for reasons not related to ant occupancy. For example, a spurious correlation could be obtained if herbivory on plants varies among microsites, and there are persistent associations between host plants in these microsites and particular ant species. This alternative explanation is unlikely for several reasons. First, the study site habitat is remarkably uniform with respect to topography and abiotic variables, and care was taken to ensure that focal trees were chosen from areas with similar topography. Second, competition among ant species for host plants is intense at the study site. Interspecific turnovers in ant occupancy are as high as 7–8% of marked trees during a 6-month period (e.g., Palmer et al. 2000), making persistent associations between particular ant species and host plants within uniform habitat unlikely. Finally, anecdotal behavioral observations suggest that although aggressive species such as *C. mimosae* and *C. nigriceps* show strong behavioral responses to both vertebrate and invertebrate herbivores, we have rarely observed these ant species patrolling fruits or behaving aggressively toward seed predators present on fruits. On *Acacia drepanolobium* trees, ant aggressive behavior is strongest on the newest growth where nectaries are highly productive (T. Palmer and M. Stanton, *unpublished data*) and declines with distance from these active nectaries. We measured levels of insect and vertebrate herbivory on new growth, where defense by ant associates is strongest. In contrast, most fruits are located on older growth where nectaries are inactive, where defense is likely to be low.

Breakdowns in ant–plant cooperation with respect to plant reproduction may be a widespread feature of obligate ant–plant systems. For example, castration parasites have been reported in this and a number of other ant–plant associations (Yu and Pierce 1998, Stanton et al. 1999, Izzo and Vasconcelos 2002). In our study system, fruits on host plants occupied by all four ant species suffered similar and relatively high levels of bruchid predation. In the absence of factors that might select for better protection of plant reproductive output within these horizontally transmitted mutualisms (e.g., strong spatial structure and local dispersal; Christy 1995, Doebeli and Knowlton 1998), there may be few opportunities for plants to effectively manipulate ant protection of host plant reproduction.

Interestingly, we did not find a direct relationship between antiherbivore aggression by resident ants and host plant fruit production at our primary study site. *Crematogaster nigriceps*, while highly aggressive toward simulated herbivory in our assays, is a castration parasite of its host plants and greatly restricts host plant flowering (Stanton et al. 1999). For host plants occupied by the other three ant species, fruit production by *A. drepanolobium* was correlated only with host plant size, suggesting that older trees produce more fruit irrespective of the identity of their resident ants. Because the lifespan of individual ant colonies is likely significantly shorter than the lifespan of their host plants (*A. drepanolobium* has a lifespan of ~150–200 years; T. Palmer, M. Stanton, T. Young, and J. Goheen, *unpublished data*), larger and older trees have probably hosted multiple ant colonies of several different species over their lifetimes (T. Palmer, *unpublished data*). The reproductive fitness of these trees may therefore integrate the antiherbivore effects of multiple ant colonies over much longer timescales than a single year, potentially decoupling the effects of the current ant resident on fruiting in a given year.

Another study of fruit production in *A. drepanolobium* (Goheen et al. 2007) reported that trees occupied by *C. sjostedti* were marginally more likely to produce fruit than trees occupied by *C. mimosae*. The authors hypothesized that low nectar production by *C. sjostedti*-occupied trees (T. Palmer, *unpublished data*) might allow

for increased allocation to reproduction relative to trees occupied by *C. mimosae*. While we did not find significantly higher reproduction for *C. sjostedti*-occupied host trees, our results showed the same basic trend; for any given host tree diameter, *C. sjostedti*-occupied trees had higher (albeit not significantly) fruit production than trees occupied by *C. mimosae* (see Fig. 2).

It is important to note that fitness in these long-lived iteroparous plants depends on both annual fruiting success and longevity. Although fruit production did not differ significantly for host plants occupied by different ant species in this study, there are striking differences in mortality for host plants occupied by the different ant species.

In another study, Palmer et al. (*unpublished manuscript*) report that host plants occupied by *C. sjostedti* suffer doubled mortality relative to host plants occupied by the other three acacia-ant species. Thus, although *C. sjostedti*-occupied acacias may successfully fruit in a given year, their lifetime reproductive output may be lower relative to trees occupied by more beneficial ant associates, highlighting the importance of long-term measures of reproduction and mortality in longer lived species of ant-plants (see also Heil et al. 2001).

A thorough accounting of the benefits of ant associates to host plants should include their efficacy in defending both vegetative and reproductive structures, and the long-term consequences of ant occupancy for host plant fitness. Our study demonstrates that ant symbionts, which vary strongly in their defense of host plant vegetative structures, may not vary in their defense of plant reproductive propagules from seed predators. Further, despite strong differences in antiherbivore protection, fruit production in a single year in this long-lived tree species was correlated only with host plant size and was not related to the aggressiveness of its ant associates. These results highlight the importance of examining multiple aspects of plant fitness over appropriate timescales in assessing costs and benefits within ant–plant symbioses.

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