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Influence of neighboring plants on the dynamics of an ant–acacia protection mutualism

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Abstract. Ant–plant protection symbioses, in which plants provide food and/or shelter for ants in exchange for protection from herbivory, are model systems for understanding the ecology of mutualism. While interactions between ants, host plants, and herbivores have been intensively studied, we know little about how plant–plant interactions influence the dynamics of these mutualisms, despite strong evidence that plants compete for resources, that hosting ants can be costly, and that host-plant provisioning to ants can therefore be constrained by resource availability. We used field experiments in a semiarid Kenyan savanna to examine interactions between the ant-plant *Acacia drepanolobium*, neighboring grasses, and two species of symbiotic acacia-ants with divergent behaviors: *Crematogaster mimosae*, an aggressive symbiont that imposes high costs to host trees via consumption of extrafloral nectar, and *Tetraponera penzigi*, a less-protective symbiont that imposes lower costs because it does not consume nectar. We hypothesized that by competing with acacias for resources, neighboring grasses (1) reduce hosts' ability to support costly *C. mimosae*, while having little or no effect on the ability of hosts to support low-cost *T. penzigi*, and (2) reduce sapling growth rates irrespective of ant occupant. We factorially manipulated the presence/absence of grasses and the identity of ant occupants on saplings and evaluated effects on colony survivorship and sapling growth rates over 40 weeks. Contrary to prediction, the high-cost/high-reward nectar-dependent mutualist *C. mimosae* had higher colony-survival rates on saplings with grass neighbors present. Grasses appear to have indirectly facilitated the survival of *C. mimosae* by reducing water stress on host plants; soils under saplings shaded by grasses had higher moisture content, and these saplings produced more active nectaries than grass-removal saplings. Consistent with prediction, survival of low-cost/low-reward *T. penzigi* did not differ significantly between grass-removal treatments. Saplings occupied by low-cost/low-reward *T. penzigi* grew 100% more on average than saplings occupied by high-cost/high-reward *C. mimosae*, demonstrating that mutualist-partner identity strongly and differentially influences demographic rates of young plants. In contrast, contrary to prediction, grass neighbors had no significant net impact on sapling growth rates. Our results suggest that neighboring plants can exert strong and counterintuitive effects on ant–plant protection symbioses, highlighting the need to integrate plant–plant interactions into our understanding of these mutualisms.

Key words: Acacia (Vachellia) drepanolobium; *ant-plant; costs and benefits; defense investment; facilitation; herbivory; Kenya; mutualism; plant defense; tree–grass interactions.*

Introduction

Cooperative interspecific partnerships, mutualisms, are among the most widespread and economically important species interactions on Earth (Bronstein 2015). Obligate ant–plant protection mutualisms occur throughout the world's tropical ecosystems (Davidson and McKey 1993) and were the first coevolved mutualisms to be intensively studied by ecologists (Janzen 1967). Within these symbiotic exchanges, ant-plants (myrmecophytes) provide resources (e.g., nest space, food) in exchange for protection of the host plant from enemies. At a proximate level, most ant–plant protection mutualisms evolved (from the plant's perspective) as a mechanism for protection from natural enemies, primarily herbivores and pathogens (Davidson and McKey 1993, Letourneau 1998), which has led to a strong focus in the literature on the interplay among resident ants, host plants, and plant consumers. But ultimately, these mutualisms evolved by acting on (and increasing) host plants' fitness, which depends not only on interactions between ant-plants and their consumers, but also on interactions with plant neighbors.

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Yet there is a striking paucity of studies examining how neighboring plants affect the dynamics of ant–plant interactions (but see Janzen 1967, 1969, Frederickson et al. 2005). This gap is potentially significant given that resource availability (e.g., nutrients, light, moisture) can influence host-plant provisioning of ant rewards (Folgarait and Davidson 1994, 1995, Heil et al. 2001), which are often energetically costly to host plants (Heil et al. 1997, Linsenmair et al. 2001, Stanton and Palmer 2011, Frederickson et al. 2012). Further, the quantity and quality of host rewards can influence both the identity of ant-mutualist partners (Palmer et al. 2008, Heil et al. 2009, Archetti et al. 2011, Heil 2013) and the efficacy of mutualistic protection (Palmer et al. 2008, Heil et al. 2009, Pringle et al. 2013). Because plant neighbors have the potential to influence myrmecophytes both directly (e.g., through competition) or indirectly (e.g., facilitation via modifications of environmental conditions), they may play important roles in both the evolutionary (e.g., see Janzen 1966) and ecological dynamics of these widespread associations.

In this study, we examined interactions among *Acacia (Vachellia) drepanolobium*, its ant symbionts, and neighboring grasses in an East African savanna. *Acacia drepanolobium* is a myrmecophytic tree that is broadly distributed and locally abundant on clay-rich "black cotton" savannas throughout East Africa (Herlocker 1974, Stapley 1998), frequently comprising >90% of total woody plant cover (Young et al. 1998). Across this range, trees host single colonies (at any given time) of between one and four sympatric symbiotic ant species, each of which imposes different costs and confers different benefits to its host plant (Palmer and Brody 2007, Palmer et al. 2010). This ant–plant association has a strong impact on ecological dynamics and landscape architecture: trees without defensive ants suffer high mortality (Palmer et al. 2010, Palmer and Brody 2013, Riginos et al. 2015, Pringle et al. 2016), because ants provide protection to trees from elephants and other herbivores (Palmer and Brody 2007, 2013, Goheen and Palmer 2010, Pringle et al. 2015). However, the behavior of different coexisting ant species in this system, and hence their energetic costs and protective benefits to host trees, varies considerably. Here we focus on two species that associate with *A. drepanolobium* throughout much of its range and differ dramatically in multiple traits that affect mutualism outcomes. *Crematogaster mimosae* is a costly mutualist that relies strongly on plant-provided extrafloral nectar and aggressively defends host plants from herbivory (Palmer et al. 2008); *Tetraponera penzigi* is a comparatively low-cost mutualist that does not consume nectar, providing less-aggressive and less-effective defense against herbivores (Palmer and Brody 2007, Stanton and Palmer 2011). Whereas *C. mimosae* obtains proteins and lipids by foraging off host trees for insect parts and prey, *T. penzigi* does not forage off of host plants, instead gleaning pollen from plant surfaces (T. Palmer, *personal observation*) and cultivating fungus within swollen-thorn domatia (Visiticao 2011, Baker et al. 2017).

Acacia drepanolobium's nearest plant neighbors in this system are typically perennial bunchgrasses, with five species (*Pennisetum stramineum*, *P. mezianum*, *Lintonia nutans*, *Themeda triandra*, and *Brachiaria lachnantha*) accounting for >90% of herbaceous cover at our study site (Young et al. 1998). Tree–grass interactions are fundamental in governing the structure of savanna ecosystems in general (Bond 2008), and grass competition has been shown to sharply reduce growth rates across life stages from saplings to adults in *A. drepanolobium* specifically (Riginos and Young 2007, Riginos 2009). However, the impact of tree–grass interactions on the dynamics of *A. drepanolobium*'s multi-species ant-protection mutualism has not previously been investigated.

In our field experiments, we manipulated both grass neighbors and ant occupants to investigate their independent and interactive effects on colony survival and host plant performance. First, we evaluated whether the presence/absence of grass neighbors and the energetic costs imposed by different symbiotic ant species influenced the survivorship of young colonies on *A. drepanolobium* saplings. Because the presence of grasses also modifies the abiotic conditions experienced by saplings and their resident colonies, we also measured soil moisture at the base of experimental plants in the field and heat tolerance for both *C. mimosae* and *T. penzigi* in the lab. For this part of the experiment, we hypothesized that colony identity and presence/absence of grass neighbors would have an interactive effect on colony survivorship: if neighboring grasses compete with saplings and thereby reduce host plant nectar production, then survivorship of the energetically costly, nectar-dependent *C. mimosae* should be lower in the presence of grass neighbors; in contrast, survivorship of the low-cost *T. penzigi* should not depend on the presence/absence of grass neighbors. This prediction assumes that *C. mimosae* on saplings cannot compensate for carbohydrate deficiencies arising from reduced nectar availability, which is likely because small *C. mimosae* colonies are not known to exploit alternative sources of carbohydrates (unlike mature colonies, which sometimes tend hemipteran associates; Young et al. 1998). Second, we examined the effect of grass neighbors and ant-associate identity on rates of sapling growth over a 40-week period. We hypothesized that both ant-occupant identity and presence/absence of grass neighbors affect sapling growth rates, with lower growth rates for saplings occupied by the energetically costly *C. mimosae* and lower growth rates for saplings occupied by both species in the presence of grass neighbors.

METHODS

Study site

We conducted our field work at the Mpala Research Centre (MRC), on the Laikipia Plateau in central Kenya (0°17′ N, 36°52′ E), between July 2012 and May 2013. Annual precipitation at MRC was 657 ± 194 mm/yr from 1999 to 2013 (mean ± SD; median = 646, interquartile range = 532–817), typically falling in a weakly tri-modal annual pattern, with a short dry season from December to March; rainfall during the experimental period was ~25% higher than the average annual rainfall (821 mm). *Acacia drepanolobium* produces hollow swellings at the base of some of its stipular thorns that serve as domatia (housing) for symbiotic ants (Monod and Schmitt 1968, Hocking 1970), and extrafloral nectaries on the petioles of most leaves secrete carbohydrate-rich nectar (Rudolph and Palmer 2013). Trees begin producing domatia and nectar (henceforth "ant rewards") early in their ontogeny (~3 month old saplings) and continue throughout their lives. Across its range, *A. drepanolobium* interacts with up to four native acacia ant species (*Crematogaster mimosae*, *C. nigriceps*, *C. sjostedti*, and *Tetraponera penzigi*). These ant species compete strongly for host trees (Palmer et al. 2000) and are mutually exclusive such that a single species occurs on any given acacia tree. While these species vary in their levels of aggression toward herbivores, they all confer fitness (survivorship and/or reproduction) benefits to host plants, both individually and collectively over a plant's lifetime (Palmer et al. 2010, Tarnita et al. 2014). Ants have a particularly large impact on plant survivorship by deterring catastrophic whole-tree destruction by elephants (Goheen and Palmer 2010, Palmer and Brody 2013). Ant species also vary in their use of host plant resources; while *C. sjostedti*, *C. mimosae*, and *C. nigriceps* consume nectar, *T. penzigi* destroys all nectaries (Palmer et al. 2002). Maintaining the nectar-consuming *Crematogaster* species appears to be particularly costly, at least for mature host plants: adult trees occupied by these ants had substantially lower growth and reproduction, and attained only one-half the gains in biomass over a 5-yr period, relative to plants on which colonies were removed, despite higher rates of herbivory on ant-removal trees. In contrast, removal of *T. penzigi* did not result in changes in adult plant growth or reproduction over the five-year study period (Stanton and Palmer 2011), although demographic models of lifetime fitness suggest that *T. penzigi* confers fitness advantages to host plants by increasing survival of early plant life stages (Palmer et al. 2010). Here, we focus on *C. mimosae* and *T. penzigi*, which differ strongly in both the costs and benefits they confer to mature host plants, and on juvenile (sapling) host plants, which have been less intensively studied in the context of this mutualism. The sapling stage is likely particularly critical to the demography of *A. drepanolobium*, as long-term population growth rates for this species are highly sensitive to the survival of small trees (Palmer et al. 2010).

Experimental methods, part 1: evaluating ant species and grass neighbor effects on colony survival

Sapling survey.—We located 243 saplings along a 600 × 50 m belt transect. Saplings were defined as plants 15–70 cm in height, and <1.5 cm in diameter, that had not yet fully emerged from the grass layer. Each plant was tagged and numbered. Early-stage colonies were identified by the presence of "nanitic" workers, which are roughly one-half the size of workers from mature colonies, and emerge from the foundress queen's domatia typically 2–4 months after queens establish on a sapling (Stanton et al. 2002). Such young colonies typically only occupy a single sapling (Palmer et al. 2013).

Establishing experimental saplings.—Natural patterns of ant occupancy on saplings may reflect underlying variation in sapling quality and/or the surrounding environment, particularly if patterns of queen colonization and establishment are non-random. To avoid possible confounds between ant species occupancy and environmental factors, we experimentally transplanted *C. mimosae* and *T. penzigi* colonies onto existing saplings from which we had removed resident ant colonies. From our sapling survey, we randomly selected 80 to be "recipient" plants in our experiment, subject to the criterion that each was at least 2 m from any neighboring *A. drepanolobium* plants (to minimize the likelihood of takeover of host plants by larger neighboring colonies). These experimental plants were measured for total branch and stem length, number of swollen thorns, and basal stem diameter (because much of the stem growth on small *A. drepanolobium* is lateral, total branch and stem length and basal stem diameter are more reliable measures of plant growth than is height). Each sapling was fogged using a short-lived pyrethrin-based insecticide (0.6% alpha-cypermethrin, half-life of 2–3 d in full sunlight; World Health Organization 2013) to kill the resident colony. We then randomly assigned each of four consecutive trees along the transect to one of two competition treatments, grass present (+ Grass) or grass removal (– Grass), and one of two ant treatments (either *C. mimosae* or *T. penzigi*), so that each set of four trees had one of each of the four treatment combinations in our 2 × 2 factorial design. Sets of four consecutive trees were not necessarily spatially aggregated, and so we did not include a blocking variable in our study design.

Transplanting nanitic colonies.—From the remaining saplings in our initial survey, we randomly chose 40 similarly sized nanitic colonies each of *C. mimosae* and *T. penzigi* to be used as "donor" colonies. For each colony, we disturbed the sapling by tapping all swollen thorns with a pencil in a standardized way, and then counted the maximum total number of workers seen patrolling the sapling immediately following the disturbance. Only colonies with ~25–75 workers (typical of early stage colonies within the first several months of establishment) responding to disturbance were chosen for transplants, which were conducted four weeks after insecticide application. After ant activity reverted to predisturbance levels, we severed saplings at the base of the stem and immediately transferred each dead sapling and its live colony to one of the 80 experimental saplings discussed above. In a prior pilot study, we confirmed that young colonies transferred all workers, brood, and reproductives from the domatia of dead saplings to those of living saplings, typically within 1–3 d.

Grass-removal treatments.—To establish grass-removal treatments, we clipped all herbaceous vegetation in a 1-m radius around each experimental plant and used a brush to apply glyphosate (Roundup; Monsanto, St. Louis, Missouri, USA) to the cut stems to kill grass roots (experimental saplings were carefully wrapped in plastic during this treatment to protect them from the herbicide). All clipped vegetation was removed from the site. Because grass removal could potentially influence the local availability of insect prey of the acacia ants, and ants forage to distances >2 m from hosts (A. Evans, *personal observation*), 1 m radius grass-removal circles were also created at a distance of 2 m from all + Grass saplings as a procedural control. Root competition between saplings and grasses is likely to be low at this distance, as field dissections of sapling root systems indicated that they seldom extended laterally beyond 1 m from the stem.

Because grass removal can increase the apparency of small plants to mammalian herbivores (Louthan et al. 2014), all experimental saplings were enclosed within 1 × 1 × 1 m herbivore-exclosure cages (constructed of rebar and wire mesh with 2.5-cm diameter openings) after treatments had been imposed. This was done to ensure that the effects of competition with grass were not confounded with the effects of mammalian herbivory on saplings.

We maintained these treatments for 40 weeks, checking saplings every two weeks to assess colony and sapling survivorship. Colonies were noted as either present or absent. When saplings were found to be devoid of ants, we presumed that the colony had died.

Evaluating effects of treatments on soil moisture.—We measured soil moisture near the base of each sapling at the experiment's end in late May, following the long rains. Volumetric soil moisture was measured at 4 points around the base of each sapling using a Spectrum Technologies Field Scout TDR-100 soil moisture meter with a 3-inch probe (1 inch = 2.54 cm), at the "High Clay" soils setting.

Evaluating effects of grass neighbors on sapling nectary production.—For each *C. mimosae*-occupied sapling, we counted the number of active nectaries (which is in turn correlated with nectar production; Palmer et al. 2008) on each of five fully expanded leaves per sapling at the end of the 40-week experiment. Active nectaries were defined as nectaries consisting of green or red tissue, whereas inactive nectaries have a brown and dried appearance (Palmer et al. 2008). While the secretion of extrafloral nectar from nectaries has been shown to vary depending on both environmental and ecological (e.g., ant partner) factors (Heil et al. 2009, Heil 2011), prior study in our system (Palmer et al. 2008) has shown that nectaries on *A. drepanolobium* classified as "inactive" do not secrete nectar ($N = 55$), while nectaries classified as "active" reliably secreted at least some nectar over a 48-h period (197.3 ± 30.6 μg of sugars [mean ± SE], $N = 39$ nectaries; Palmer et al. 2008). We surveyed active nectaries only on *C. mimosae*-occupied plants, as *T. penzigi* destroys all host plant nectaries (Palmer et al. 2002).

Assessing heat tolerance in C. mimosae *and* T. penzigi.—Because the removal of grass neighbors may have increased the heat and desiccation stress (and subsequent mortality) experienced by small colonies via a loss of shade, we tested whether the two ant species differed in their ability to withstand high heat stress. We collected 40 workers of each species from non-experimental saplings in the field, and placed each into its own plastic vial with three holes in the tops to allow gas exchange. Vials were randomly arranged in a tray and placed into a drying oven (Lab Line Model 100) at 50°C (a temperature commonly experienced by tropical ants within the boundary layer on unshaded branches: Spicer et al. 2017) for 70 min. We removed vials at 10-min intervals to check for ant mortality before placing them back into the oven.

Experimental methods, part 2: evaluating ant-species and grass-neighbor effects on sapling performance

To evaluate the relative impact of ant species identity, grass neighbors, and their interaction on sapling growth and survival, it was necessary to ensure that all saplings hosted colonies of the designated ant species for the entire duration of the experiment. Thus, when colonies died before the end of 40 weeks, we replaced them with new colonies of the same species using the methods described above; these new colonies were not included in the analyses of colony survival. New colonies were transplanted immediately when a sapling's original colony was found to have died, such that all experimental plants were effectively continuously occupied by either *C. mimosae* or *T. penzigi* for the entire 40-week duration of the experiment. At the experiment's end, we surveyed all surviving saplings for new growth (i.e., changes in the total length of all new growth on branches and the primary stem). New growth can be identified in this species by the presence of pubescent green or green-brown tissue that had not yet fully lignified.

Statistical analysis

We analyzed survivorship of initially transplanted colonies on saplings using parametric survival analysis with a Weibull distribution (Pinder et al. 1978). Our model included ant species, grass neighbor, and ant species × grass neighbor as main effects, and initial diameter of saplings as a covariate; survivorship was right-censored at 40 weeks corresponding to the termination of the experiment. Differences in heat tolerance (i.e., individual survival) between the two ant species were analyzed using a parametric survival analysis with a Weibull distribution, censored at 70 min. We analyzed the effects of ant-species identity and grass neighbors on host plant growth using a generalized linear model (normal distribution, identity link), with initial plant diameter as a covariate. The number of active nectaries on *C. mimosae*-occupied host plants with and without grass neighbors, and the effects of ant-species identity, grass neighbors, and their interaction on soil moisture, were likewise analyzed using a generalized linear model with normal distribution and identity link. We evaluated the strength of the relationship between soil moisture and active nectaries on host plants by calculating a Pearson correlation coefficient (*r*). All statistical analyses were performed in JMP Pro 12 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Effects of grass neighbors and ant species identity on colony survivorship

Both ant-species identity and grass-neighbor treatment interacted to affect colony survivorship (Fig. 1; ant-species × grass-neighbor $\chi^2 = 5.56$, 1 df, $P = 0.018$). Contrary to our predictions, presence of grass neighbors enhanced *C. mimosae* survival at the experiment's end by >500% relative to − Grass treatments. *Tetraponera penzigi* colony survival was roughly equivalent in both the presence and absence of grass neighbors (Fig. 1) and was intermediate between the two *C. mimosae* treatments. Survival of all colonies declined most strongly in the first four months of the experiment. Initial plant diameter had no significant effect on colony survival ($\chi^2 = 2.79$, 1 df, $P = 0.10$).

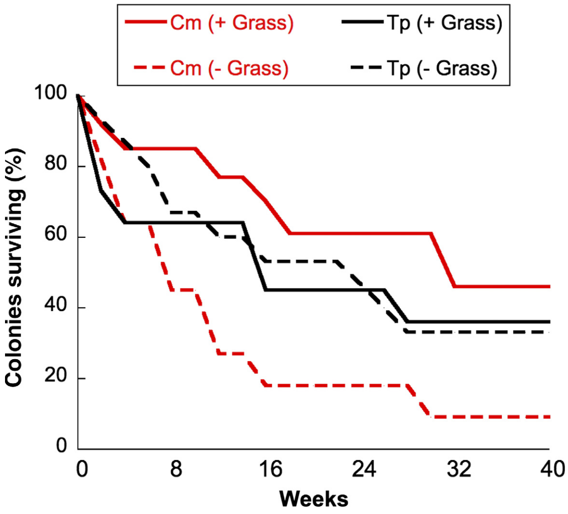

FIG. 1. Colony survivorship of transplanted *Crematogaster mimosae* (Cm, red lines) and *Tetraponera penzigi* (Tp, black lines) on *Acacia drepanolobium* saplings in the presence (solid lines) and absence (dashed lines) of grasses over a 40-week period. [Color figure can be viewed at wileyonlinelibrary.com]

Effects of grass neighbors on soil moisture

Soil moisture was 33% higher under saplings with grass neighbors than those without (mean soil moisture 16.8% vs. 13.2% for + Grass and − Grass, respectively, Fig. 2; $\chi^2 = 25.22$, df = 1, $P < 0.0001$), while neither ant species identity, ant × grass interaction, nor initial plant diameter had a significant effect on soil moisture ($\chi^2 = 0.70$, df = 1, $P = 0.40$; $\chi^2 = 1.06$, df = 1, $P = 0.30$, $\chi^2 = 0.80$, df = 1, $P = 0.40$, respectively). The number of active nectaries on plants occupied by *C. mimosae* was positively correlated with soil moisture ($r = 0.64$).

Heat tolerance of C. mimosae *vs.* T. penzigi

Workers of *C. mimosae* were significantly more heat tolerant than *T. penzigi*; at the end of the 70-min trial, 82.5% of *C. mimosae* workers were still alive, compared to only 30% of *T. penzigi* workers (Fig. 3; $\chi^2 = 25.85$, df = 1, $P < 0.0001$).

Effects of grass neighbors and ant species identity on sapling performance

Ant-species identity significantly affected sapling growth rates (Fig. 2; $\chi^2 = 7.18$, df = 1, $P = 0.007$);

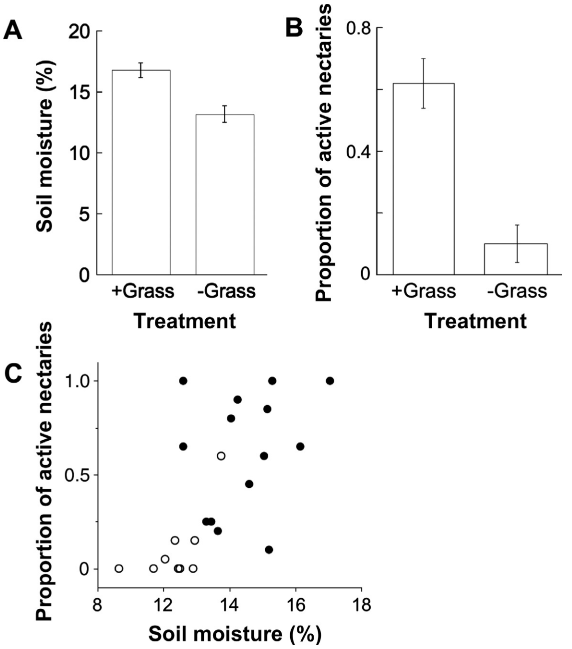

FIG. 2. Effects of the grass-removal treatment on (A) soil moisture (mean ± SE) and (B) the proportion of active nectaries (mean ± SE) on experimental saplings; (C) correlation between soil moisture and the proportion of active nectaries for *Crematogaster mimosae*-occupied host plants with (solid circles) and without (open circles) grass neighbors.

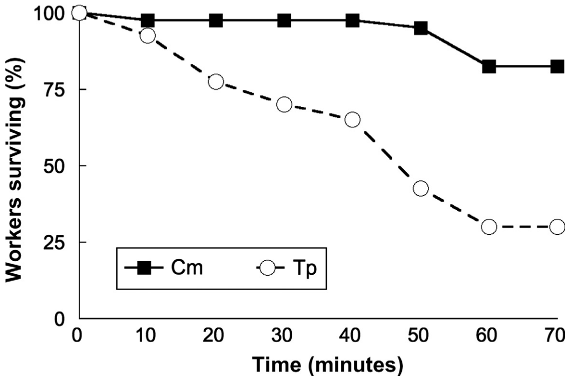

FIG. 3. Survival of *Crematogaster mimosae* (Cm) and *Tetraponera penzigi* (Tp) workers at 50°C over 70 m.

T. penzigi-occupied host plants had ~100% greater total branch growth than did *C. mimosae*-occupied trees. In contrast, we found no significant effects of grass-neighbor treatment ($\chi^2 = 2.11$, df = 1, $P = 0.15$), ant species × grass neighbor interaction ($\chi^2 = 0.29$, df = 1, $P = 0.59$), or initial plant diameter on sapling growth ($\chi^2 = 5.37^{e-5}$, df = 1, $P = 0.99$). *Crematogaster mimosae* host plants with grass neighbors produced six-fold more active nectaries than did *C. mimosae*–occupied plants with grass neighbors removed ($\chi^2 = 14.52$, df = 1, $P < 0.0001$).

DISCUSSION

Our results show that grass neighbors facilitate the establishment and persistence of a highly defensive, yet costly, mutualist partner (*C. mimosae*), contrasting with our prediction that grasses would exert a negative effect on this ant species. This facilitative effect by grasses is unlikely to be a result of reduced heat stress on the ants themselves (resulting from shading by grasses), because *C. mimosae* had a much higher tolerance for heat stress than *T. penzigi* did, yet suffered much higher rates of colony failure on saplings without grass neighbors. Instead, grasses appear to ameliorate physical stress on the host plant itself (not the ants directly) by reducing evaporative water loss from the soil and allowing saplings to produce higher levels of liquid carbohydrate rewards for this energetically demanding mutualist. When grass neighbors were removed, soils around all saplings had lower water content and *C. mimosae*-occupied saplings produced many fewer active nectaries, which appears to contribute to a high level of colony failure for this protective but costly symbiont.

The ability of saplings to successfully host persistent colonies of *C. mimosae* may be important in areas where herbivores are abundant, since the aggressive *C. mimosae* is more effective than *T. penzigi* at defending (adult) host plants from both invertebrate and vertebrate herbivores (Stanton and Palmer 2011). Although we do not yet know whether *C. mimosae* and *T. penzigi* differ in efficacy of defense on saplings, worker recruitment to simulated disturbance on small saplings is ca. 3.5× higher for *C. mimosae* than *T. penzigi* (T. Palmer, *unpublished data*), suggesting that the more costly mutualist likely provides higher levels of protection to *A. drepanolobium* at this vulnerable life-stage.

Further, the consequences for saplings of the loss of *C. mimosae* colonies are likely to be strongly negative where herbivores are present. Unoccupied *A. drepanolobium* have high mortality rates (Palmer et al. 2010), and unoccupied saplings suffer 30% more vertebrate herbivory than occupied saplings (Riginos and Young 2007). The window of vulnerability experienced by saplings after losing a colony of any ant species is substantial; empty saplings must first be colonized by queens, which typically take 2–4 months to produce first workers, and only about 15% of colonizing queens ultimately survive to produce workers (Stanton et al. 2002). The loss of defensive mutualists is likely to affect population dynamics of these trees, because long-term *A. drepanolobium* population growth rates are highly sensitive to the survival of plants in the smallest size classes (Palmer et al. 2010). This result further illuminates our recent finding (Pringle et al. 2016) that *A. drepanolobium* saplings typically fail to establish on nearby sandy soils at our site, where *A. drepanolobium* does not occur naturally and where understory cover is patchier and ground temperatures are hotter (Goheen et al. 2013): saplings transplanted into these sandy soils suffered high herbivore-induced mortality, even following experimental addition of colonies of *C. nigriceps* (which like *C. mimosae* is a highly nectar-dependent and aggressive defender). Pringle et al.'s (2016) hypothesis that host trees in sandy soils could not adequately provision defensive ant colonies is consistent with our finding that grass cover helps trees sustain nectar-reliant ants.

While competition between trees and grasses is common in savannas (Scholes and Archer 1997, Bond 2008, Riginos 2009), there is a growing appreciation for the potential role of facilitation in mediating coexistence between these life forms (Belsky 1994, Dohn et al. 2013, Moustakas et al. 2013). Prior work has demonstrated that trees may facilitate grasses by increasing soil nutrients and/or decreasing thermal stress (Belsky et al. 1989, Belsky 1994, Riginos 2009), increasing soil moisture through hydraulic lift (e.g., Dawson 1993, but see Ludwig et al. 2004), and providing refuge from herbivory (O'Connor 1995, Coverdale et al. 2016). Although fewer studies have investigated the facilitative effects of grass on trees, several studies have shown that grasses can increase the growth (Anthelme and Michalet 2009) and survival (Berkowitz et al. 1995, Meli and Dirzo 2013) of tree seedlings, and protect saplings and seedlings from herbivores (Riginos and Young 2007, Anthelme and Michalet 2009). Our study suggests the potential for a novel mechanism of facilitation between these two plant life forms, mediated by the enhanced survival of an aggressive mutualist defender: grasses may indirectly facilitate *A. drepanolobium* if the costs of hosting aggressive *C. mimosae* (which result in slower growth of saplings) are offset by increases in sapling survival as a result of more effective protection from herbivory. In other plant species, facilitation has been shown to occur indirectly via interactions with a shared mutualist, such as when co-flowering species attract a greater number and/or diversity of pollinators (Rathcke 1983, Ghazoul 2006, Carvalheiro et al. 2014).

In contrast to *C. mimosae*, *T. penzigi* colony persistence was not affected by grass neighbors. This was likely because *T. penzigi* does not use host-plant nectar, and thus is likely to perform better than *C. mimosae* on water-stressed trees (Stanton and Palmer 2011). Rather than feeding on nectar, *T. penzigi* gleans small food items such as pollen from the surfaces of the host (T. Palmer, *personal observation*) and also appears to cultivate fungus within swollen thorn domatia (Visiticao 2011, Baker et al. 2017). On larger trees, *T. penzigi* provides lower levels of defense than *C. mimosae*, giving this species the appearance of an inferior mutualist (Palmer and Brody 2007). However, at the sapling stage, persistence of *T. penzigi* colonies was much higher than for *C. mimosae* colonies under environmentally stressful conditions (i.e., grass-removal treatments). Thus, this species may be a particularly persistent mutualist partner when plants are strongly resource limited, including during periods of prolonged drought, or in areas of high tree density where resource competition is intense. On a neighboring property where tree densities are very high and large mammalian browsers are absent, a large proportion of trees are occupied by *T. penzigi* (T. Palmer, *personal observation*). In this case, both the absence of large browsers (which results in a gradual reduction of nectar production over 5–10 yr, Huntzinger et al. 2004, Palmer et al. 2008) and inter-tree competition may reduce the ability of host plants to sustain the more metabolically demanding *Crematogaster* species, resulting in a shift in community dominance toward *T. penzigi*. By interacting with a suite of mutualist partners that vary in environmental tolerances, as well as costs and benefits, populations of mutualist species such as *A. drepanolobium* may be better buffered from spatiotemporal environmental variation than they would if they interacted with only one mutualist partner (Bond 1994, Ollerton et al. 2007, Palmer et al. 2010, Stat et al. 2013).

Our results further suggest that the energetic investment made by saplings into ant rewards (i.e., extrafloral nectar) may serve as a “partner screening” (Archetti et al. 2011) mechanism whereby mutualists on *A. drepanolobium* saplings are passively “screened” (or “filtered”) by environmental conditions. In this case, differential mortality of *C. mimosae* on saplings under resource-poor conditions creates opportunities for the establishment and persistence of *T. penzigi*, which has higher survivorship when saplings are stressed. Mutualist pairs are thereby “matched” on the basis of the energetic status of the sapling, potentially reducing opportunities for exploitation of host plants by ants (e.g., see Heil 2013). Such screening mechanisms have the potential to stabilize mutualisms at evolutionary timescales, without invoking the need for partner recognition or active partner selection by the host plant (Archetti et al. 2011).

Differences in sapling growth rates among treatments experimentally confirm that the vital rates of *A. drepanolobium* host plants are strongly influenced by the identity of their ant partner, as previously suggested by long-term observational data and demographic modeling (Palmer et al. 2010). Over 40 weeks, plants continuously occupied by *T. penzigi* grew ~200% more in total length than saplings continuously occupied by *C. mimosae* (Fig. 4). Lower growth rates for saplings occupied by *C. mimosae* likely reflect the high metabolic demand of these nectar-feeding ant associates, and suggest that the costs of nectar production are high for small plants, as has been shown for adult *A. drepanolobium* (Stanton and Palmer 2011).

Because our experiments excluded mammalian herbivores, our results reflect the costs of the mutualism while holding anti-herbivore benefits constant (i.e., near 0). While the net benefits to saplings of associating with *C. mimosae* vs. *T. penzigi* are not yet known, it is likely that these benefits depend strongly on environmental context, as has been shown for other ant–plant mutualisms (Trager et al. 2010). Where herbivores are abundant, the benefits of associating with the more aggressively defensive *C. mimosae* may outweigh the high costs of supporting this mutualist, as has been shown for adult trees (Goheen and Palmer 2010, Palmer and Brody 2013). Contrastingly, the higher growth rates of *T. penzigi*-occupied saplings may allow for more rapid escape of the grass layer, which could be advantageous in savannas with frequent fire. We are currently conducting experiments examining the context-dependent benefits and costs to saplings of occupation by different ant species. Although studies of ant–plant interactions (and mutualism more broadly) have historically focused primarily on benefits (Bronstein 2001), understanding the

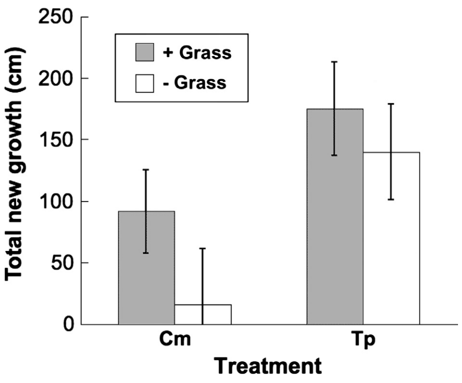

FIG. 4. Total new-shoot growth (mean ± SE) over a 40-week period for saplings occupied by *Crematogaster mimosae* and *Tetraponera penzigi* in the presence and absence of grass neighbors.

costs of mutualism is critical to predicting context-dependent outcomes in these widespread relationships.

The absence of any significant main or interactive effect of grass neighbors on sapling growth rates contrasts with prior work on *A. drepanolobium* in this system. For example, Riginos and Young (2007) showed that saplings with grass neighbors removed had double the shoot growth of saplings grown in the presence of grass neighbors. While the reasons for the contrasting effects of grass neighbors on sapling growth in these two studies are not yet clear, several differences between them may have contributed to the discrepancy. First, as noted above, all saplings in our study were caged, removing the potential effect of browsing, which has been shown elsewhere to stimulate shoot growth in saplings in African savannas (Scogings 2003, O'Kane et al. 2011). In Riginos and Young (2007), saplings with grass neighbors removed were more heavily browsed, although the authors found no significant relationship between browse intensity and growth at the level of individual saplings. Second, our study was conducted in a relatively wet year (821 mm over the 40-week period, relative to an average rainfall in this area of ~650 mm/yr), while Riginos and Young's (2007) experiments were conducted over two drier-than-average years (mean rainfall for the two-year period = 485 mm). It is possible that during wetter years, resource competition is lessened during the rainy season, allowing the facilitative effects of microhabitat amelioration (i.e., reduced evaporation) by grasses to predominate during the dry season. Irrespective of the mechanism, the contrasting effects of grass on *A. drepanolobium* sapling growth during different years is consistent with the spatiotemporally shifting balance between competitive and facilitative effects between neighboring species reported for many natural systems (Callaway et al. 2002, Kikvidze et al. 2006, Sthultz et al. 2007, Soliveres et al. 2010, Louthan et al. 2014). Whether neighboring plant species exert a net negative or positive effect on the maintenance of the *A. drepanolobium*–ant mutualism over the long term, and in the presence of mammalian herbivory, requires further study.

The natural history of other ant–plant associations suggests that interspecific competition with non-ant plants may play strong roles in shaping the eco-evolutionary dynamics of these mutualisms. For example, Janzen (1967, 1969) found that *Pseudomyrmex* and *Azteca* ants attack plants surrounding their host trees in Central America, thereby reducing shading, liana infestation, and likelihood of mortality in fires. And within Amazonian "Devil's gardens," *Myrmelachista schumanni* clears neighboring vegetation of *Duroia hirsuta*, providing space for host plants to recruit, which in turn ensures abundant nest sites for the ants (Frederickson and Gordon 2007). While these studies suggest an important role for direct myrmecophyte–plant interactions in shaping the dynamics of ant–plant mutualisms, many questions about potential indirect effects remain unanswered. For example, how frequently, to what extent, and in what ways do neighboring plants influence the performance of mutualistic ants, their effects on host plants, and the stability of these associations? Similarly, does the presence, density, or identity of plant neighbors affect the quantity or quality of resources or services exchanged by partners within ant–plant protection mutualisms, and if so, by what mechanisms (e.g., resource competition, facilitation, variation in herbivore loads/visitation)? Evaluating the interactions between host plants, their symbiotic ant partners, and neighboring plants presents an opportunity to improve our understanding of the interplay between mutualisms and the broader communities in which they are embedded (Palmer et al. 2015).

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