Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*

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Abstract. In African savannas, vertebrate herbivores are often identified as key determinants of plant growth, survivorship, and reproduction. However, plant reproduction is likely to be the product of responses to a suite of abiotic and biotic factors, including nutrient availability and interactions with antagonists and mutualists. In a relatively simple system, we examined the role of termites (which act as ecosystem engineers—modifying physical habitat and creating islands of high soil fertility), vertebrate herbivores, and symbiotic ants, on the fruiting success of a dominant plant, *Acacia drepanolobium*, in East African savannas.

Using observational data, large-scale experimental manipulations, and analysis of foliar N, we found that *Acacia drepanolobium* trees growing at the edge of termite mounds were more likely to reproduce than those growing farther away, in off-mound soils. Although vertebrate herbivores preferentially used termite mounds as demonstrated by dung deposits, long-term exclusion of mammalian grazers did not significantly reduce *A. drepanolobium* fruit production. Leaf N was significantly greater in trees growing next to mounds than in those growing farther away, and this pattern was unaffected by exclusion of vertebrates. Thus, soil enrichment by termites, rather than through dung and urine deposition by large herbivores, is of primary importance to fruit production near mounds.

Across all mound–herbivore treatment combinations, trees that harbored *Crematogaster sjostedti* were more likely to fruit than those that harbored one of the other three ant species. Although *C. sjostedti* is less aggressive than the other ants, it tends to inhabit large, old trees near termite mounds which are more likely to fruit than smaller ones.

Termites play a key role in generating patches of nutrient-rich habitat important to the reproductive success of *A. drepanolobium* in East African savannas. Enhanced nutrient acquisition from termite mounds appears to allow plants to tolerate herbivory and the reduced defense by a relatively ineffective ant partner. Our results underscore the importance of simultaneously examining top-down and bottom-up effects to understand those factors most important to plant reproductive success.

Key words: Acacia drepanolobium; ant symbionts; direct and indirect effects; ecosystem engineers; termites; top-down and bottom-up effects; vertebrate herbivores.

Introduction

The interactions among species, both above- and belowground, can have profound impacts on plant performance. In East African savannas, as in temperate grasslands, large vertebrate herbivores can be critically important to population-, community-, and ecosystem-level processes (Georgiadis 1989, Côté et al. 2004, Pringle et al. 2007). Indeed, vertebrate herbivores are arguably the most conspicuous zoological component of savanna ecosystems and can have significant positive (Augustine and McNaughton 1998, Goheen et al. 2004, Riginos and Young 2007) as well as negative (Goheen et al. 2007, Young and Augustine 2007) impacts on plant performance. Although the direct importance of herbivory in removing leaf tissue and affecting plant performance is obvious, the indirect effects of herbivores in creating heterogeneous soils that, in turn, scale up to a growth or fitness response in plants have yet to be fully explored (Steinauer and Collins 2001, Augustine 2003*a*, *b*, Augustine et al. 2003, Sankaran and Augustine 2004).

Like vertebrates, termites are ubiquitous in East Africa and elsewhere. However, many termites are subterranean, inconspicuous, and are often overlooked as important drivers of habitat quality. Yet the effects of

termites on soil character and quality may rival or exceed that of vertebrate herbivores. Through their mound-building activities, termites enrich soils, contribute to both large- and small-scale habitat heterogeneity, and provide critical resources to a diverse suite of species on many continents (e.g., West Africa, Konate et al. 1999, Ndiaye 2004; Australia, Black and Okwakol 1997; Europe, Wolters 2000; and North America, Nash and Whitford 1995, Fox 2003). How these potential "islands of fertility" (Schlesinger et al. 1996, Lavelle et al. 1997, Dawes-Gromadzki 2007) created by termite mounds affect measures of plant fitness is largely unknown. In addition, the effects of soil enrichment by termites might be enhanced or diminished by vertebrate herbivores that preferentially graze on mound grasses and deposit nutrients in dung and urine.

Here, we examined the direct and indirect effects of termites and vertebrate herbivores on the reproductive success of *Acacia drepanalobium*, the whistling thorn acacia. *Acacia drepanalobium* is the numerically dominant tree within grasslands on the Laikipia plateau of central Kenya and across large areas of savanna on black cotton soils in upland east Africa, in some areas creating an almost single-species canopy (Coe and Beentje 1991, Young et al. 1997). While at first glance these *Acacia* grasslands appear homogeneous, on closer inspection one finds a mosaic of habitat patches created by termites (order Isoptera: *Odontotermes* spp.). In our study site and elsewhere (Loveridge and Moe 2004), termitaria soils are enhanced in minerals including nitrogen (N), phosphorous (P), and carbon (C) as compared to surrounding, matrix soils (this study and T. M. Palmer, *unpublished data*). In addition, the soils of the mounds are less clay rich and exhibit enhanced plant–water relations compared to surrounding soils. However, the degree to which rich termitaria soils affect reproductive success of plants in general, and *A. drepanolobium* specifically, has been unexplored.

We were primarily interested in how termites and ungulate herbivores affected the reproductive success of *A. drepanalobium*. However, these effects could be altered by the plant's interactions with other mutualists and antagonists. Each *A. drepanolobium* tree harbors one of four species of arboreal ant (*Crematogaster sjostedti, C. mimosae, C. nigriceps, and Tetraponera penzigi*; Young et al. 1997, Palmer et al. 2000), which vary in their effectiveness as defenders of host plants (Young et al. 1997, Stanton et al. 1999, Palmer and Brody 2007). Trees growing next to termite mounds have an increased likelihood of harboring the behaviorally dominant (sensu Schoener 1983) ant, *Crematogaster sjostedji* (Palmer 2003), which is not particularly effective at defending its host (Palmer and Brody 2007). Therefore, the reproductive success of a given tree could be affected by both its proximity to rich mound soils and the ant species it harbors.

Here, we asked three overarching questions: (1) To what extent is fruit production of *A. drepanolobium* correlated with proximity to termite mounds? (2) What is the relative contribution of nutrient enhancement by termites vs. that from herbivores to tree reproduction? (3) Do the species of ant inhabitants, which differ in their degree of protection, help explain patterns of reproduction? Our results demonstrate that proximity to termite mound, independent of herbivores and protection from ants, is the strongest predictor of fruiting success for *A. drepanolobium*.

MATERIALS AND METHODS

Study system

Our work was conducted on the Laikipia plateau (37° E, 8° N; 1800 m elevation) in north-central Kenya near the Mpala Research Centre. Approximately 43% of the Laikipia plateau (Taiti 1992), and much of upland East Africa, is underlain with poorly drained, high-clay "black cotton" vertisol soils that support *Acacia drepanolobium* wooded grassland (see Plate 1). Black cotton soils, characterized by heavy clay and high levels of calcium carbonate, have impeded drainage and shrink and swell, creating deep cracks that enhance evaporation during dry periods reducing water availability to plants (Taita 1992, Young et al. 1998).

Termites (order Isoptera) are one of the most conspicuous and ubiquitous modifiers of habitats in the grasslands of central Kenya. Through their mound-building and foraging activities, termites directly modify grassland ecosystems. Within the black cotton savannas, *Odontotermes* sp. (the species is yet undescribed, and hereafter referred to as "*Odontotermes*"; see Plate 1) create highly productive, nutrient-rich "hotspots" above their subterranean mounds that contrast with less productive surrounding habitat. *Odontotermes* mounds are low lying, generally 10–20 m in diameter, but no more than 0.5 m high (Darlington and Bagine 1999), and predominantly treeless (Fig. 1). The spatial pattern of mounds is stable, persisting over hundreds of years through repeated re-colonization of established nest sites (Watson 1967, Darlington 1985). Mounds are readily distinguishable from the surrounding area during the rainy season by their bright green vegetation, high densities of the grass *Pennisetum stramineum* (Fig. 1; also see Palmer 2003), and absence of woody vegetation.

On black cotton soils of Laikipia, *A. drepanolobium* trees are abundant. Each tree is inhabited by one of four species of ant (*Crematogaster sjostedti, Crematogaster nigriceps, Crematogaster mimosae* [see Plate 1], and *Tetraponera penzigi*), and violent takeovers among neighboring ant colonies are relatively common (Stanton et al. 1999, Palmer et al. 2000, 2002). Ant species vary in the degree to which they benefit their host tree. One of the four ants (*C. nigriceps*), while aggressive in its response to intruders, sterilizes the tree by removing axillary and apical meristems. Another species of ant, *C. sjostedti*, is not particularly aggressive in defending its host (Young et al. 1997, Stanton et al. 1999, Palmer and Brody 2007). *Crematogaster sjostedti* is more likely to
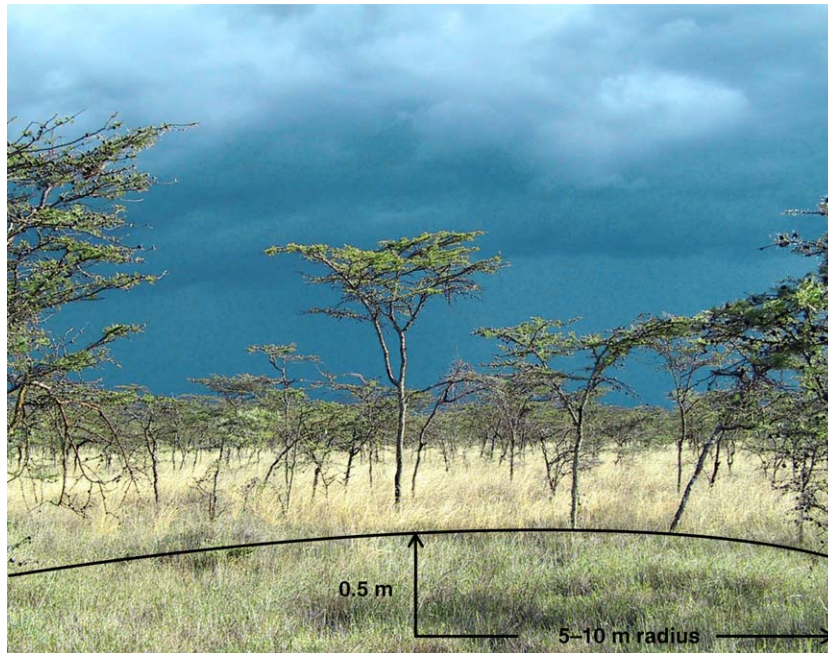
FIG. 1.   An *Odontotermes* sp. (termite) mound showing topography and vegetation structure in Kenya. Note the distinct mound edge beyond which *Acacia drepanolobium* begin.

inhabit trees growing next to termite mounds (Palmer 2003). Thus, the reproductive reward from a tree's ability to garner resources from mounds may be compromised by increased herbivory on relatively unprotected trees.

Effects of termite mounds and species of ant inhabitant on Acacia drepanolobium

To determine if fruit production in *A. drepanolobium* was correlated with proximity to termite mounds, in October of 2003 we ran three parallel 200-m transects and scored the fruiting status of all trees within 1 m of each side of the transects. For each tree, we recorded whether the tree was growing at the edge of a termite mound (see Fig. 1), measured tree height, determined which ant species inhabited the tree, and counted the number of fruits present. We analyzed these data in two ways. First, we used logistic regression to determine if whether or not a tree was fruiting (yes/no) could be explained by proximity to a termite mound (scored as on a mound edge or not), ant species identity, and tree height. We used a fully crossed model in the first analysis and subsequently eliminated those interactions that were nonsignificant. To reduce bias toward finding an "ant" effect, we excluded trees inhabited by *C. nigriceps* because this species reproductively sterilizes its host plants and none of the trees inhabited by *C. nigriceps* were in fruit. In the second analysis, we asked if proximity to a mound, ant inhabitant, and height explained a significant amount of the variance in the number of fruits produced, including only those trees that produced fruit. We analyzed these data using an

ANCOVA with edge of termite mound (yes/no) and ant species as categorical predictor variables and tree height as a covariate. Again, we used a fully crossed model and eliminated nonsignificant interactions in the final analysis. Fruit number was the response variable, which was square-root transformed to homogenize variances.

Effects of resource enhancement by vertebrates

To examine whether preferential use of termite mounds by vertebrate herbivores might enhance or diminish *A. drepanolobium* fruiting, we quantified dung densities in 2003 along transects across 60 haphazardly selected mounds that represented a range of mound sizes and were located throughout the study area. Dung censuses were conducted along transects that began at the center of the mound and extended to twice the radius of the mound. All dung piles that fell within two meters of either side of the transect were identified to species and recorded. Dung data were regressed against distance from mound centers, using both a simple linear and polynomial regression model, incorporating a second-order quadratic term for the latter. We analyzed these data by species, as different herbivore guilds (e.g., browsers vs. grazers) are likely to partition the landscape in different ways (Bell 1970). All analyses were performed in JMP (version 4.04; SAS Institute 2001).

To separate the effects of termites and herbivores on reproductive success of *A. drepanalobium*, we compared fruiting success of trees at mounds in open areas to the fruiting success of trees at mounds where herbivores had been excluded for the past 8 years. These comparisons were made in October of 2003, using the Kenya Long-

TABLE 1. Results of logistic regression analysis for effects of ant species, tree height, and proximity to a termite mound on the probability of producing fruits (yes/no) for *Acacia drepanolobium* trees.

Source	df	χ^2	P
Mound	1	14.4	0.001
Ant	2	30.64	<0.0001
Height	1	66.74	<0.0001

Note: A total of 451 trees were measured; of those, 89 were fruiting.

term Exclosure Experiment (KLEE) established in 1995 (by T. P. Young). The exclosures consist of six experimental treatments or plots, replicated in three blocks identified as "North," "Central," and "South." Each exclosure, or treatment plot, is four hectares (200 × 200 m). To disentangle the effects of vertebrates and termites, we measured the fruiting success of trees associated with termite mounds in two of the plots in each of the three blocks: the fully fenced plots ("O") where no large vertebrates are allowed and the plots that allow wildlife and cattle access ("WC") but exclude mega-herbivore browsers such as elephants and giraffes. Our initial fruiting census was conducted in the area adjacent to exclosures where all animals have access. Thus, any potential effects of mega-herbivores on fruiting trees would be revealed by comparing fruiting success of trees outside to those within the exclosures. Here, by examining only trees growing next to termite mounds, with and without access by vertebrate herbivores, we sought to address whether the presence of vertebrate herbivores influences the probability of fruiting for *A. drepanolobium* growing at the edge of termite mounds.

We located 10–15 mounds in each experimental plot and measured up to 10 trees growing on the edge of each mound. Some mounds were relatively small and had <10 trees on their edges. Others were large, and for those we haphazardly chose 10 trees evenly spaced around the mound periphery. Again, we measured tree height, recorded which ant was present, and counted the number of fruits. These data were analyzed using a randomized block design with block (North, Central, and South) and "O" and "WC" as categorical variables. Mean height of all trees measured for each mound was included as a covariate. All analyses were conducted using JMP (version 4.04; SAS Institute 2001).

To further examine the role of termite enhancement vs. vertebrate enhancement of soils, we sampled N concentration (dry mass percentage N [%N]) of leaves from trees growing near and far from mounds (<5 m and >25 m from mound edge, respectively) where herbivores were allowed ("WC" plots), and where herbivores were excluded ("O" plots). Sampling occurred in July 2008 (with 58.7 mm rainfall). We selected three mounds within the each of North, Central, and South KLEE "WC" and "O" plots, for a total of 18 mounds and 36 composite samples (near and far from

mounds). All *A. drepanolobium* leaf samples were a composite; each sample was composed of the newest fully unfurled leaves from three nearest neighbor trees, irrespective of occupant ant species (there is no significant effect on ant *A. drepanolobium* percentage N; K. Fox-Dobbs, *unpublished data*). We sampled mature trees that were all 2–4 m in height. Immediately after collection we dried the leaf samples in an oven at 60°C until they reached a constant mass. We ground the samples into a coarse powder with a mortar and pestle, and weighed ∼5 mg of powders into tin boats for percentage N analysis in the Geochemistry Analytical Laboratory, University of Wyoming (Laramie, Wyoming, USA). Based upon results from replicates of an acetanilide standard we determined that instrument error for percentage N was <0.3%.

In addition to collecting leaf tissue, we sampled plant-available nutrients (N and P) from soils on and off 15 termite mounds in June of 2008. All of these mounds were accessible to herbivores, and all of these mounds were included in the initial fruiting and dung censuses. To do so, we took 2.2 cm diameter soil cores from a depth of 5–30 cm below the ground surface. The soils were homogenized across the core and sieved to remove organic material. For total extractable N analysis, 5 g of fresh soil was mixed with 50 mL of 2 mol/L KCl and incubated for 2 hours, shaken periodically. The solution was filtered through Whatman 42, medium porosity filter paper. Extracts were frozen, then transported to the International Council for Research in Agroforestry (ICRAF; Nairobi, Kenya) for analysis. A series of KCl solution "blank" samples ($n = 8$) were also analyzed, and a mean blank extractable-N value (1.01 mg/kg) was used in the calculations of soil sample extractable N. A subsample of the homogenized soil core was dried to a constant mass, placed in a sealed bag, and submitted to ICRAF for total extractable P analysis (via the Olsen method; sodium bicarbonate extraction with molybdenum blue detection).

RESULTS

Effects of termite mounds and species of ant inhabitant on Acacia drepanolobium

Outside the large mammal exclosures, *Acacia drepanolobium* growing adjacent to termite mounds were significantly more likely to fruit than those growing farther away from mound edges: 30.7% of those trees growing adjacent to a mound produced fruits, while only 13.9% of those growing further away from a mound fruited (Table 1). Trees harboring *Crematogaster sjostedti* were more likely to fruit than those harboring *C. mimosae* or *Tetraponera penzigi* (50.0% vs. 23.0% and 20.0%, respectively; Fig. 2A, Table 1). Taller trees were also more likely to produce fruits than shorter ones. Within the subset of *A. drepanolobium* that produced fruits, there was no significant effect of proximity to a termite mound, ant species, or tree height on mean fruit
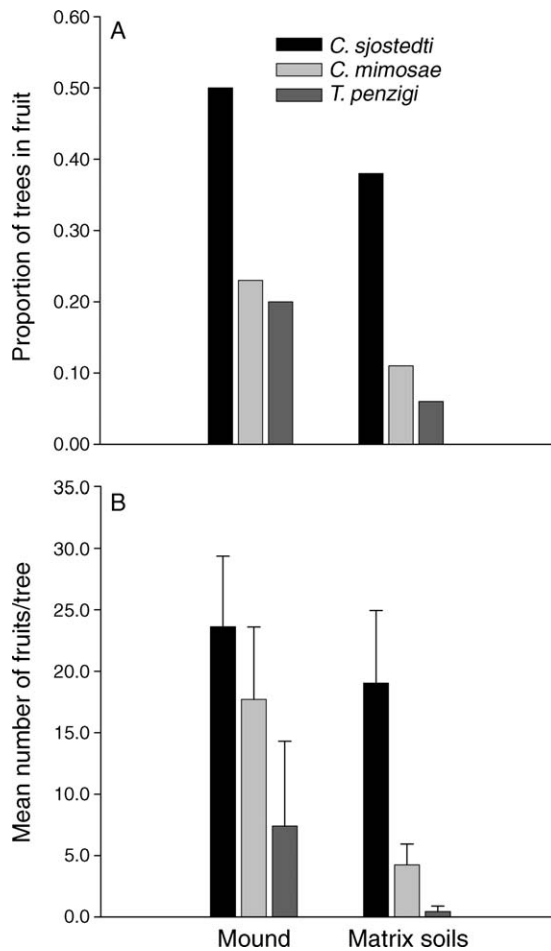
TABLE 2. Results of an ANCOVA for effects of ant species, tree height, and proximity to a termite mound on the mean number of fruits (square-root transformed) produced by *A. drepanolobium* trees.

Source	df	Sums of squares	F	P
Mound	1	32.11	2.24	0.138
Ant	2	6.75	0.24	0.791
Height	1	4.55	0.32	0.575
Error	83	1190.01		

Notes: Tree height was used as the covariate. Only trees that produced fruits were included.

mean number of fruits produced in plots where herbivores were allowed access to trees in comparison with plots where all large vertebrates were excluded (Table 3, Fig. 3A).

Ant species and tree height significantly influenced which trees produced fruits: 67.9% of trees inhabited by *C. sjostedti* fruited, whereas only 28.6% and 25.9% of trees occupied by *C. mimosae* and *T. penzigi,* respectively, set fruit (Fig. 3A). Within the exclosures, trees that harbored *C. sjostedti* produced more fruits than trees with *C. mimosae* or *T. penzigi* (Fig. 3B).
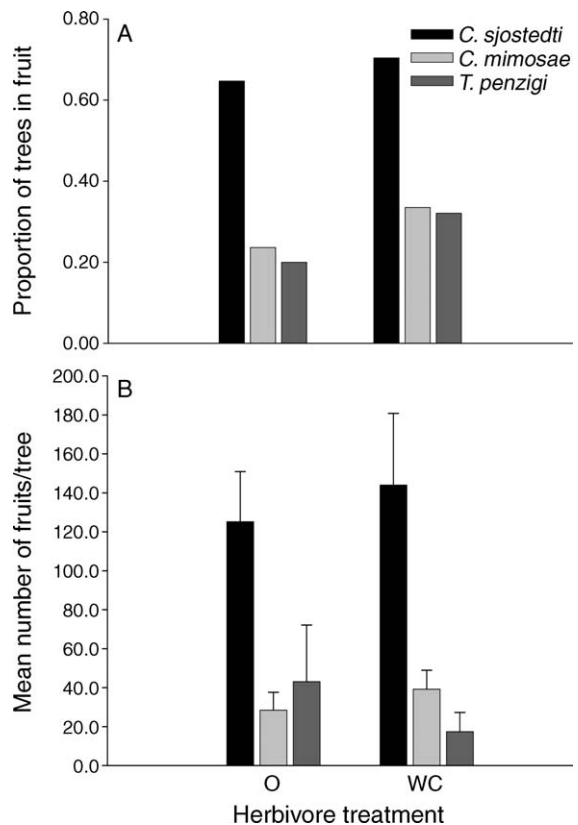

FIG. 2. (A) The probability of fruiting based on proximity to a termite mound and ant species inhabitant for *A. drepanolobium* trees. $N = 451$ trees. (B) The mean ($\pm$SE) number of fruits produced by trees growing adjacent to mounds (<0.5 m from edge of mound), or farther away in matrix soils, and inhabited by one of three species of acacia ants (*Crematogaster sjostedti*, *C. mimosa*, and *Tetraponera penzigi*). $N = 47$ trees adjacent to mounds; $N = 41$ trees not adjacent to a mound.

production (Fig. 2B, Table 2), nor were there any significant interactions among these variables.

Effects of resource enhancement by vertebrates

Of the 100 dung piles found and identified, there was a significant negative linear relationship between distance from mound center and the number of dung piles for steinbuck ($F_{1,21} = 4.81$, $P = 0.039$; Fig. 4A) and eland ($F_{1,23} = 14.65$, $P = 0.0009$; Fig. 4A), and a significant second-order quadratic relationship for Grant's gazelle ($F_{2,25} = 3.99$, $P = 0.032$), zebra ($F_{2,27} = 34.33$, $P < 0.0001$), and cattle and buffalo ($F_{2,30} = 16.72$, $P < 0.0001$; Fig. 4B).

Within the herbivore exclosure treatments, we only sampled trees adjacent to termite mounds. The was no difference in either the probability of fruiting or the

FIG. 3. (A) The probability of fruiting based on presence (WC) or absence (O) of vertebrate herbivores and ant species inhabitant for *A. drepanolobium* trees. (B) The mean ($\pm$SE) number of fruits produced by those trees that reproduced. A total of 727 trees were sampled at 10–15 mounds per treatment per block. Of those, 654 trees were in fruit.
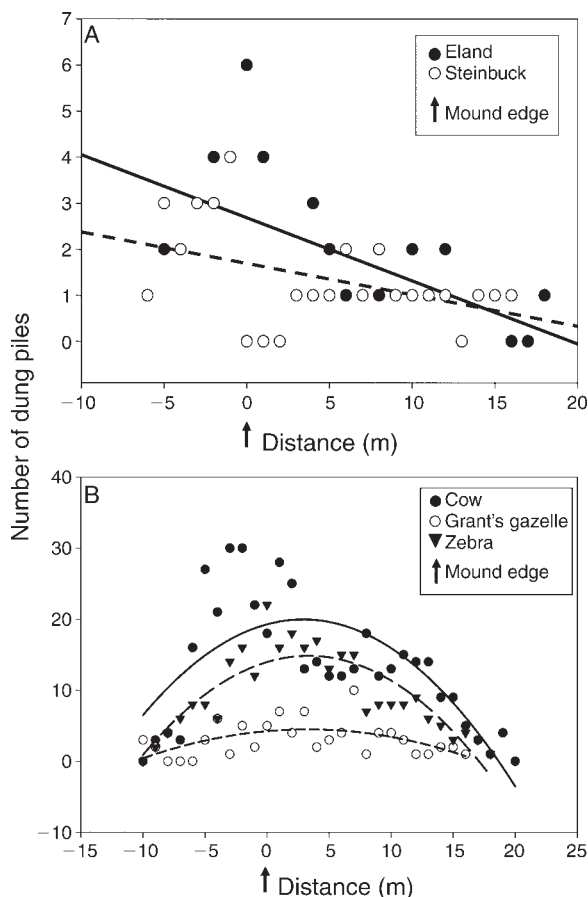
FIG. 4. Dung density as a function of distance from termite mound center. (A) For eland and steinbuck, a linear fit explained 39.9% and 18.6% of the variance, respectively. (B) For Grant's gazelle, zebra, and cow, a second-order polynomial explained 25.8%, 73.3%, and 54.4% of the variance, respectively. In all cases the first term was not significant, while the second term was highly significant ($P < 0.01$).

Averaged over all trees, the mean number of fruits (± 1 SE) produced in plots where wildlife and cattle were allowed was 73.8 (± 12.9) vs. 56.1 (± 12.2) fruits in plots where all large vertebrate herbivores were excluded ($F_{1,76} = 0.608$, $P = 0.438$).

Leaves of *A. drepanolobium* were significantly higher in percentage N when growing adjacent to termite mounds than when farther away ($F_{1,32} = 58.9$, $P < 0.0001$; Table 4). The presence of vertebrate herbivores, however, had no significant effect on leaf percentage N ($F_{1,32} = 0.59$, $P = 0.44$; Table 4). Soils collected on mounds where herbivores were allowed were significantly higher in N and P than paired off-mound soils ($F_{1,29} = 4.43$, $P = 0.04$ and $F_{1,29} = 24.68$, $P < 0.0001$, respectively; Table 4).

DISCUSSION

The activities of *Odontotermes* termites appears to play a key role in the reproductive success of *Acacia drepanolobium*. *Odontotermes* activities could enhance the reproductive success of *A. drepanolobium* through several direct and indirect mechanisms. First, by directly affecting soil chemistry and physical properties, termites may create environments that enhance plant growth. Second, the productive and better drained mound soils may support higher microbial biomass, resulting in more rapid rates of nutrient turnover in these productive areas (e.g., Myrold et al. 1989; but see Sankaran and Augustine [2004] for a review of the idiosyncratic relationships between grazers, plant production, and microbial communities). Third, *A. drepanolobium* at termite mounds may host larger populations of symbiotic mycorrhizae, and we are currently examining these associations. Regardless of which, or all, of these factors is driving the effect of proximity to mounds on fruiting, there is a significant resource-driven, or bottom-up (Hunter and Price 1992), effect of termites on the reproductive success of *A. drepanolobium*.

The influence of termite mounds on soil nutrients and nitrogen fixation by *A. drepanolobium* is extensive across the black cotton ecosystem (Fox-Dobbs et al. 2010). Trees growing close to mound-enriched soils fix significantly less atmospheric nitrogen than those growing farther away (Fox-Dobbs et al. 2010). Our results suggest that the energy savings associated with the uptake of nitrogen from soils rather than the fixation of atmospheric N appears to translate, directly or indirectly, into enhanced reproduction.

The interactions among termites and acacia trees don't occur in isolation, and our results do not rule out the importance of herbivory, or protection by ants, on *A. drepanolobium*. Although we found no significant direct effect of nutrient input by herbivores on tree-fruit production near mounds, the effects could be exerted in other stages of the life history. For instance, *Acacia drepanolobium* competes with grasses during seedling establishment (Riginos and Young 2007), and dense grasses, particularly those on termite mounds, harbor rodents which likely prey on *A. drepanolobium* seeds (Goheen et al. 2004). The lack of trees growing on termite mounds might be attributable to seedlings being outcompeted by the dense grasses on mounds and/or by enhanced herbivory and seed predation on mounds, although these effects remain to be tested. After

TABLE 3. Results of logistic regression analysis for effects of presence/absence of vertebrate herbivores, ant species, and tree height on the probability of producing fruits (yes/no) for *A. drepanolobium* trees.

Source	df	χ^2	P
Vertebrates	1	3.36	0.067
Height	1	11.39	0.0007
Ant species	2	85.89	<0.0001
Ant × height	2	27.43	<0.0001

Notes: All trees were growing in proximity to termite mounds. Herbivores species included all grazers, but not browsers.

PLATE 1. Hypothesized determinants of the fruiting success of *Acacia drepanolobium* examined here. Clockwise from upper left: Buffalo (*Syncerus caffer*), a common grazer in savanna ecosystems; the acacia-ant *Crematogaster mimosae*; a silhouetted limb of *Acacia drepanolobium*, bearing both crescent-shaped fruits and swollen-thorn ant domatia; *Odontotermes* termites within their fungal comb. Photo credits (clockwise): T. M. Palmer (top panels), A. K. Brody, and D. F. Doak.

establishment, mineral-rich mound soils may mitigate competition between grasses and *Acacia* while also enhancing predation on seeds or seedlings (for reviews of *Acacia*–grass interactions, see Sankaran et al. [2004], Riginos and Young [2007], Seymour [2008]).

Thus, the fruiting success of *A. drepanolobium* is likely to be determined by a suite of direct and indirect effects of enhanced nutrient access via proximity to mounds, degree of browsing, density of nearby grasses, and protection from damage by ants. By utilizing exclosures

TABLE 4. Soil N and P total extracts (mg/kg; mean $\pm$ SE) taken from on and off 15 *Odontotermes* mounds.

Treatment	Herbivores allowed			Herbivores excluded
	Soil N	Soil P	Leaf N (%)	Leaf N (%)
ON mound	31.68 $\pm$ 4.456	5.68 $\pm$ 0.463	3.02 $\pm$ 0.071	2.94 $\pm$ 0.039
OFF mound	18.69 $\pm$ 4.268	3.09 $\pm$ 0.296	2.53 $\pm$ 0.052	2.54 $\pm$ 0.065

Notes: Soil samples were taken from mound center (ON) or 30 m from center (OFF). Leaf percentage N samples were taken from trees growing within 5 m of the edge of a mound (ON) or 30 m from center (OFF) from nine mounds in each treatment combination. Leaf samples were composites of three leaves per plant and averaged over three trees per sampling location.

where ungulate grazers had been excluded for nearly a decade, we could tease apart the nutrient-enhancement effects of herbivores from termites. Although we found significant differences in leaf percentage N for trees growing adjacent to mounds vs. those growing farther away, there was no effect of excluding vertebrates on leaf percentage N, and the absence of herbivores did not significantly reduce the reproductive success of *A. drepanolobium* adjacent to termite mounds. To varying degrees, herbivores feed on *A. drepanolobium* and reduce its fecundity (Goheen et al. 2004, 2007). In 2004 and 2005, trees protected from vertebrate herbivores had greater reproductive success than those exposed to herbivores (Goheen et al. 2007). However, the trees in Goheen et al. (2007) were sampled without regard to proximity to termite mounds. Thus, it appears that termites more than compensate for the negative effects of herbivory on trees by generating higher fertility substrate for *Acacia* fruit production and/or defense (see *Results* and Fox-Dobbs et al. 2010).

Not surprisingly, these bottom-up effects are not the only factor important in predicting the reproductive success of *A. drepanolobium*. *Acacia drepanolobium* trees harbor ant symbionts and the effect of occupancy by different ant species was apparent in two ways. First, trees inhabited by *Cremanogaster nigriceps* did not fruit, as found in other studies as well (Young et al. 1997, Stanton et al. 1999). Second, trees inhabited by *C. sjostedti* were significantly more likely to produce fruits than those inhabited by *C. mimosae* or *T. penzigi*. This result is intriguing since *C. sjostedti* is a poor defender of its host, and other studies have demonstrated positive relationships between ant defense and host plant vigor (e.g., Gaume and McKey 1999, Lapola et al. 2003, Bruna et al. 2004). We propose two interpretations of this result. One, because *C. sjostedti* is a twig nester that excavates nest space within the trunk and branches of host plants, trees occupied by this species may be under significant stress, senescing more rapidly and potentially shunting a greater proportion of their resources toward reproduction (cf. Kozlowski and Pallardy 2002). Alternatively, many trees occupied by *C. sjostedti* are older than those occupied by the other species. Large, old trees may fruit with greater frequency and these tend to be occupied by *C. sjostedti* as a result of competition–colonization tradeoffs within this highly competitive ant guild (Palmer et al. 2000, Stanton et al. 2002).

Understanding the relative importance of top-down vs. bottom-up effects (Hunter and Price 1992) and the role of indirect effects in species interactions (Wootton 2002) has been a long-standing goal in ecology. In addition, understanding the influence of particular, key species within communities is crucial in linking community structure with local and regional biodiversity (Chapin et al. 1997, Simberloff 1998, Soulé et al. 2003). We are currently pursuing the links between termites and plant and invertebrate diversity of the region. Here, we demonstrate that termite activities affect the reproductive status of *A. drepanolobium*, a dominant tree in many areas throughout East Africa. Further, we show that the effects of more conspicuous species (e.g., symbiotic ants and large vertebrate herbivores) on plant reproduction can only be fully understood in the context of one of Africa's strongest habitat modifiers, termites.

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