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NET EFFECTS OF LARGE MAMMALS ON *ACACIA* SEEDLING SURVIVAL IN AN AFRICAN SAVANNA

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Abstract. Trees of the genus *Acacia* are widespread and important components of savanna ecosystems. Factors or organisms that influence the survival of *Acacia* seedlings are likely to affect tree recruitment and therefore community and ecosystem dynamics. In African savannas, large mammals, especially elephants, have been considered the most important agents of mortality for adult trees, but their impacts on tree seedlings are not well known. We investigated the effects of large mammals on *Acacia* seedling survival by excluding large mammals from replicated 4-ha plots. Approximately twice as many seedlings were killed in plots with large mammals absent as on plots with large mammals present. Rodents and some invertebrates were more abundant on plots without large mammals and were responsible for these higher predation rates. Seedlings in areas with large mammals were more likely to die of desiccation; however, net seedling survival was approximately twice as high in the presence of large mammals. Our results indicate that large mammals may indirectly increase *Acacia* seedling survival and thus accelerate, rather than inhibit, tree recruitment.

Key words: Acacia; *herbivory; rodent; savanna; seedling; seedling predation; small mammal; tree recruitment; ungulate.*

INTRODUCTION

In African savannas, large herbivorous mammals such as elephants, giraffes, and various antelopes, are known to kill and damage trees via browsing, uprooting, and trampling (Dublin et al. 1990, Mwalyosi 1990, Sinclair 1995). Because these direct, negative impacts are obvious, it is tempting to conclude that the overall effect of large herbivores is a reduction in survival or performance of individual trees and in biomass or stem density of woody vegetation. However, at least three pathways exist by which large herbivores could facilitate growth of tree populations or biomass. One is by dispersing fruits or seeds in dung (Coe and Coe 1987, Miller 1994). A second is by increasing germination via nutrient inputs (Augustine and McNaughton 1998). The final potential mechanism, which has received only scant attention, is the suppression of other, smaller herbivores, which could have a stronger direct, negative impact than do the large herbivores.

We have documented compensatory increases in abundance of herbivorous small mammals following exclusion of large mammalian herbivores (Keesing 1998, 2000, Metz and Keesing 2001); these increases were driven by a near doubling in populations of the numerically dominant species, the pouched mouse (*Saccostomus mearnsi*). Some herbivorous insects also appear to increase in abundance when large mammalian herbivores are excluded (D. Ogada and F. Keesing, *unpublished data*). Smaller consumers (e.g., small mammals, insects) are known to influence recruitment of woody species via seed and seedling predation in a number of ecological communities (Sullivan 1979, Andersen and Lonsdale 1990, Miller 1994, Harju and Tahvanainen 1997, Weltzin et al. 1998, Manson et al. 2001). In African savannas, the reported role of small mammals in influencing tree recruitment ranges from potentially important (e.g., Miller 1994) to negligible (e.g., Barnes 2001), although interactions involving small mammals have been understudied relative to other groups of consumers. Further, in recent studies, insects have been shown to be major sources of damage to tree seeds and seedlings (Miller 1994, Mucunguzi 1995, Okello 2002, Shaw et al. 2002).

We expected large mammals to impose a negative direct effect on tree seedling survival via trampling or consumption, but to have a positive indirect effect on seedling survival by suppressing populations of small-mammal and insect herbivores. We designed a study, therefore, to test the net effects of large mammalian herbivores on seedling survival by monitoring fates of seedlings planted inside and outside large-mammal exclusion plots (see Young et al. 1998). We focused on *Acacia* seedlings because trees of the genus *Acacia* are dominant woody species in savanna ecosystems of Af-

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rica, Australia, and the Middle East. Population dynamics of these trees in savanna ecosystems strongly influence many community and ecosystem processes (Belsky et al. 1989, Georgiadis 1989, Weltzin and Coughenour 1990, Belsky 1994).

Materials and Methods

Study site

We conducted fieldwork from March–July 2002 at the Mpala Research Centre (MRC) in the Laikipia District of central Kenya (0°17′ N, 36°53′ E). The study site is characterized by savanna woodland on ‘‘black cotton’’ soil. Rainfall in this area is highly seasonal, with peaks in April–May and, to a lesser extent, October–November. Average annual precipitation at MRC is 539 mm, with approximately half of this falling April–July. Precipitation April–July 2002 was 235 mm (M. Ogada, *unpublished data*).

Acacia drepanolobium is the dominant tree species at the study site, accounting for >98% of the overstory vegetation (Young et al. 1998). *A. mellifera*, *Balanites aegyptica*, *Cadaba farinosa*, *Lycium europium*, and *Rhus natalensis* are other woody species present. The grasses *Brachiaria lachnatha*, *Lintonia nutans*, *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra*, and the forbs *Aerva lanata*, *Commelina* spp., *Dyschoriste radicans*, and *Rhinacanthis ndorensis* comprise the majority of herbaceous species at the study site (Young et al. 1998). Large mammalian herbivores common at the study site include African elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Grevy's zebras (*Equus grevyi*), Burchell's zebras (*E. burchelli*), Grant's gazelles (*Gazella granti*), steinbucks (*Raphicerus campestris*), and domestic cattle (*Bos taurus*; Young et al. 1998). Small-mammal populations have been monitored continuously at the study site since 1995 (Keesing 1998); species occurring during our study included *S. mearnsi*, *Mus minutoides*, *Mastomys natalensis*, *Dendromus melanotis*, and *Crocidura* spp. (F. Keesing, *unpublished data*).

Our experiment was conducted in conjunction with the Kenya Long-term Exclusion Experiment (KLEE). This study was established in 1995 to examine interactions between native ungulates and livestock (Young et al. 1998). KLEE consists of three 400 × 600 m (24 ha) blocks, each consisting of six 200 × 200 (4 ha) treatments. Each treatment excludes a particular combination of large mammals. For our experiment, we used only the plots to which all large mammals had access and the plots from which all large mammals were excluded. In the latter, large mammals were excluded via 2.4 m high game fencing with 11 strands of wire electrified at 5000 volts.

Seedling transplanting

We collected *A. drepanolobium* seeds from trees at MRC. Seeds were planted outdoors in 1-L nursery bags filled with black cotton soil, with five seeds planted per bag. Seeds were watered three times per week, and began to germinate after two weeks. Throughout the germination period, we attempted to standardize seedling condition and size by culling those that suffered insect damage or desiccation, and by culling those that were noticeably taller or shorter than the majority of other seedlings. Seedlings were covered with hardware cloth to minimize herbivore damage prior to transplanting.

Seedlings were transplanted to the study site 23 April–26 April 2002. Seedlings measured 3–7 cm at the time of planting, and all seedlings had 2–4 leaves. Only seedlings with no foliage or cotyledon damage were planted, and care was taken to minimize disturbance of roots while transplanting. Seedlings were transplanted into holes ~10 cm deep. To avoid scent contamination, we wore latex gloves when handling seedlings and soil. Seedlings were watered with ~250 mL immediately after transplanting.

Ninety-six seedlings were planted in each of the three large-mammal exclusion and three control plots, for a total of 576 seedlings across the six plots. Seedlings were planted in clusters of four, with each cluster consisting of two caged and two uncaged seedlings (Fig. 1). Caged seedlings were covered by a cylinder of 0.6-cm mesh hardware cloth to prevent access by small mammals and large invertebrates. Cages were anchored to the ground by two wire clips. Cages were permeable to the majority of invertebrate species at MRC, and invertebrates were noted regularly inside the cages (J. Goheen, *personal observation*). In contrast, all consumers in a plot had access to uncaged seedlings. Seedlings within a cluster were spaced 1 m apart, and clusters within a plot were spaced 25 m apart (Fig. 1).

Seedlings were censused weekly following transplanting and monitored for damage. Specifically, each seedling was categorized as (1) alive, no damage; (2) alive, some leaf or cotyledon damage; (3) alive, major damage (stalk stripped of both leaves and cotyledons or stalk clipped at the base); (4) dead due to predation; or (5) dead due to desiccation.

Rodent and invertebrate sampling

To assess abundances of two groups of consumers, we sampled rodents and invertebrates in both large-mammal exclusion and control plots. Rodents were trapped from 30 May–20 June 2002 in conjunction with ongoing research to assess the impact of megaherbivores (elephants, giraffe), other native ungulates, and cattle upon small-mammal community dynamics (Keesing 1998, 2000). A detailed description of trapping methods and research rationale is given in Keesing (1998). Briefly, a trapping grid is associated with each plot. Trapping was conducted for three consecutive nights on each 10 × 10 grid with 10 m spacing between traps. At each trap station, we placed a large Sherman folding trap baited with a peanut butter/oat mixture.

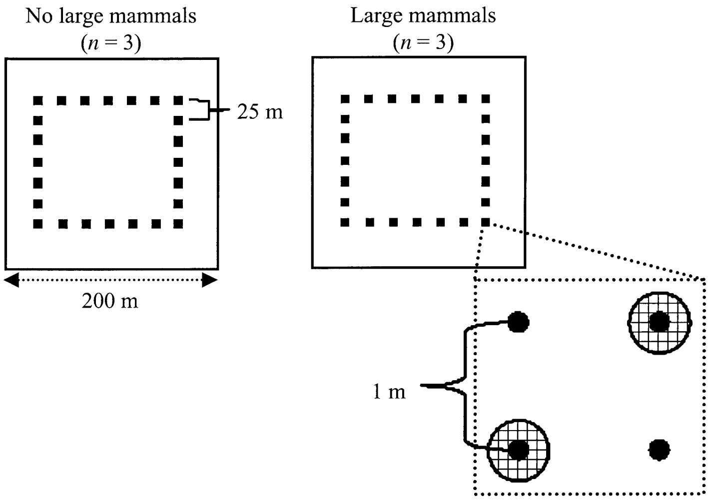

FIG. 1. The experimental design for the *Acacia* seedling experiment. Within each of three replicates of two large-mammal treatments (with all large mammals and without all large mammals), we planted 24 two-by-two seedling grids, with two seedlings caged in each grid (see *Methods*).

Traps were checked every morning between 06:00 and 09:00, closed, and reset in the late afternoon. *S. mearnsi* accounted for 85% of all small mammals captured.

Invertebrates were sampled via pitfall trapping and sweep net sampling from 23 June–6 July 2002. On each plot, one array of four pitfall traps was opened for three days. Invertebrates were collected from pitfall traps at the end of the third day. Sweep-netting was used to sample invertebrates along a 100-m transect in each plot. Invertebrates from both sampling methods were pooled and identified to order. We focused our attention on individuals from the orders Coleoptera, Homoptera, and Orthoptera, which comprise the most abundant orders of invertebrate herbivores at the study site (D. Ogada and F. Keesing, *unpublished data*).

Statistical analyses

We used three separate repeated-measures split-plot ANOVAs to examine the proportion of seedlings within each plot experiencing: (1) major damage or mortality due to predation, (2) mortality due to desiccation, and (3) mortality due to either predation or desiccation.

The analysis was conducted across six two-week time periods, using the cumulative proportion of seedlings experiencing major damage or death due to predation at each time step as the response variable. We lumped the major damage and mortality due to predation for the first analysis because 89.6% of seedlings suffering major damage died by the end of the study. To be conservative, each plot of 96 seedlings was analyzed as a single unit for each time step. Plot type (large-mammal exclusion or control) was analyzed as the whole plot treatment, while caged/open status was analyzed as the subplot treatment for the first and third analyses. We included block as a main effect in the model, and tested for interactions between time and plot type and time and caged/open status (first and third analyses only).

We used a series of independent samples t tests to assess effects of large-mammal exclusion upon the abundance of coleopterans, homopterans, orthopterans, and total numbers of all invertebrates. We also tested for effects of large-mammal exclusion upon the abundance of rodents. For all t tests, we used Levene's test to ensure assumptions of equal variances were not violated. We then conducted a series of backwards multiple regression analyses to assess the impact of consumer abundances upon the proportion of caged and open seedlings depredated across plots. All factors were included in assessing the proportion of open seedlings depredated; rodent abundance was not used in predicting the proportion of caged seedlings killed. Finally, we attempted to better gauge the influence of seedling predation by rodents by regressing the difference between caged and uncaged seedlings against abundance of rodents. This allowed us to isolate the effects of rodents on seedling survival by accounting for the impact of invertebrates.

RESULTS

We observed significant effects of both large-mammal exclusion ($P < 0.0001$) and caged/uncaged status ($P < 0.0001$) with respect to seedling predation (Fig. 2A, Table 1). Seventy-five percent (±4.2%) of uncaged seedlings in plots from which large mammals were excluded died or were heavily damaged by the end of the experiment. In contrast, only 45% (±17.7%) of seedlings exposed to all herbivores, including large mammals, suffered mortality or major damage via herbivory by the end of the experiment.

There was no evidence that any seedlings were consumed by large mammals; however, a single seedling was trampled by a large mammal and subsequently died. Rodents and the largest invertebrates were responsible for most mortality due to herbivory in plots both with and without large mammals. Caging seed-

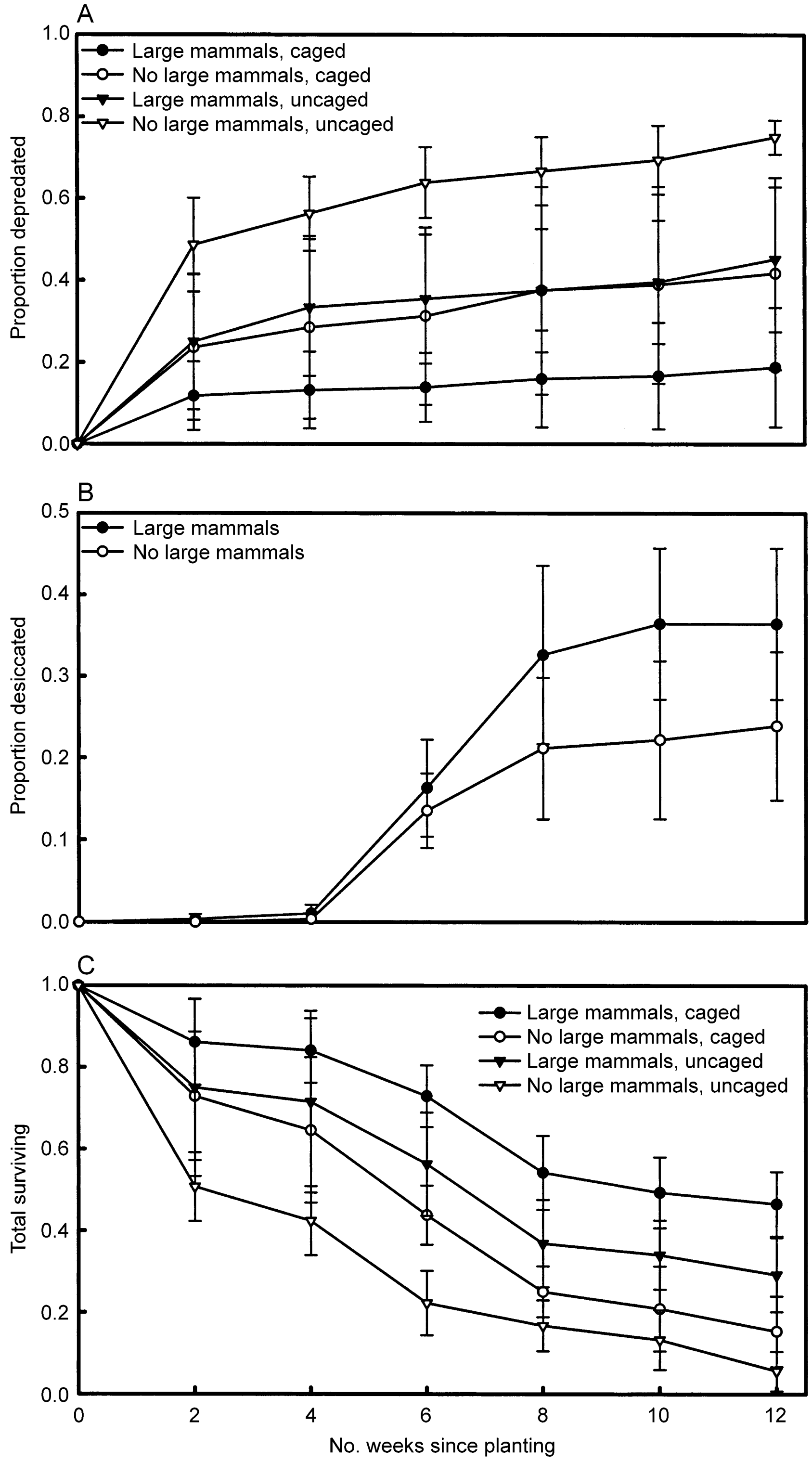

FIG. 2. (A) Proportion of seedlings depredated, (B) proportion of seedlings desiccated, and (C) total proportion of seedlings surviving as a function of plot treatment and caged/uncaged status. Error bars represent ±1 SE.

TABLE 1. Effects of large-mammal exclusion and caged/uncaged status on *Acacia* seedling predation in Kenya, Africa.

Source	df	Mean square	F	P
Model	25	0.124	12.43	<0.0001
Error	46	0.010		
Plot	1	0.945	94.05	<0.0001
Caged/Open	2	0.596	59.26	<0.0001
Time	5	0.049	4.83	0.0012
Block	2	0.350	34.85	<0.0001
Time × Plot	5	0.004	0.41	0.836
Caged/Open × Plot	10	0.002	0.21	0.994

lings, which excluded rodents and large invertebrates, reduced seedling mortality and major damage in both control (54 caged vs. 130 uncaged seedlings died or were heavily damaged) and large-mammal exclusion (120 caged vs. 216 uncaged seedlings died or were heavily damaged) plots.

Desiccation-induced mortality varied significantly (repeated-measures ANOVA, $F = 20.56$, df = 13, 58, $P < 0.0001$), with plot type, time, and block as statistically significant factors (Fig. 2B). Total desiccation-induced mortality was significantly higher in control plots ($P < 0.01$) and increased with time ($P < 0.0001$). Block was also a significant factor in predicting the total desiccation-induced mortality ($P < 0.0001$). There was no significant interaction between time and plot type (the rate of desiccation of seedlings in control plots did not differ from that in large-mammal exclusion plots) although this approached statistical significance ($P = 0.06$). Results from the analysis of total seedling survival were similar to those for seedling predation, in that large-mammal exclusion, caged/uncaged status, time, and block were important predictors of the total proportion of seedlings surviving ($P < 0.0001$ for all; Fig. 2C). Overall, 30.9% of seedlings in plots with large mammals survived, compared to only 17.4% in plots without large mammals. We detected no significant interactions between time and plot type or time and caged/uncaged status.

The assumption of equal variances was not violated for any group of consumer (Levene's test, $P > 0.05$ for all groups). Densities of rodents were higher on large-mammal exclusion plots ($t = -3.21$, df = 4, $P = 0.03$), where they averaged 51.67 ± 9.61 individuals/ha as compared to 31.67 ± 4.93 individuals/ha on control plots (Fig. 3). Similarly, abundance of homopteran insects was higher on large-mammal exclusion plots ($t = -2.90$, df = 4, $P = 0.04$), with 78.0 ± 24.02 and 30.33 ± 15.31 individuals/ha occurring on large-mammal exclusion plots and on control plots, respectively (Fig. 3). The Cicadellidae comprised the most abundant family of homopterans on both plots to which large mammals had access and plots from which large mammals had been excluded (D. Ogada and F. Keesing, *unpublished data*). We detected no significant effects of excluding large mammals on abundances of orthopterans, coleopterans, or all invertebrates combined (Fig. 3).

The proportion of open seedlings killed by predators on each plot increased strongly with increasing abundance of rodents ($R^2 = 0.77$, df = 5, $P = 0.02$; Fig. 4A). However, no relationship was noted between the abundance of rodents on each plot and the difference in predation between caged and uncaged seedlings ($R^2 = 0.15$, df = 5, $P = 0.46$; Fig. 4B). Multiple regression of coleopteran, orthopteran, homopteran, and total invertebrate abundances against the proportion of caged seedlings killed by predators revealed an insignificant relationship (adj. $R^2 = 0.68$, df = 2, 3, $P = 0.08$). Partial correlations for the abundance of homopterans ($r = 0.90$, $P = 0.04$; Fig. 4C) against the proportion of caged seedlings killed and the abundance of all invertebrate species ($r = -0.80$, $P = 0.10$) against the proportion of caged seedlings killed occurred in opposite directions. No strong collinearity was detected between these predictors (tolerance = 0.54, variance inflation factor = 1.84).

DISCUSSION

Overall, approximately three times as many uncaged seedlings survived when large mammalian herbivores were present, with 5.6% of uncaged seedlings surviving on plots without large mammals as compared to 15.3% on plots to which large mammals had access. Large mammals indirectly facilitated seedling survival by suppressing populations of other herbivores (rodents and insects). High densities of rodent and insect herbivores caused the increase in mortality on plots without large mammals, killing or severely damaging 75.0% of uncaged seedlings on plots without large mammals as compared to 45.1% on plots to which large mammals had access. Seedlings on plots with large mammals were more likely to die of desiccation, probably because these plots have lower herbaceous cover

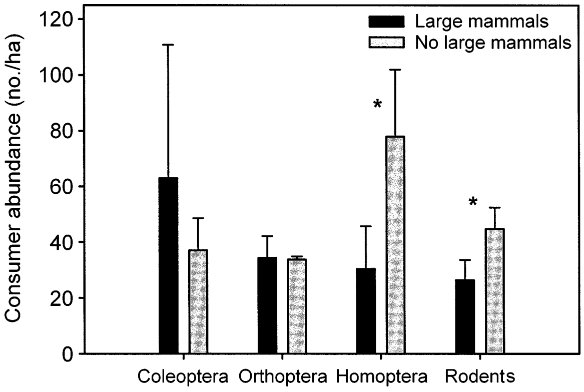

FIG. 3. Mean (+1 SE) abundance of small consumers (arthropods and rodents) as a function of plot treatment. Asterisks above error bars indicate significant differences in abundance ($P < 0.05$).

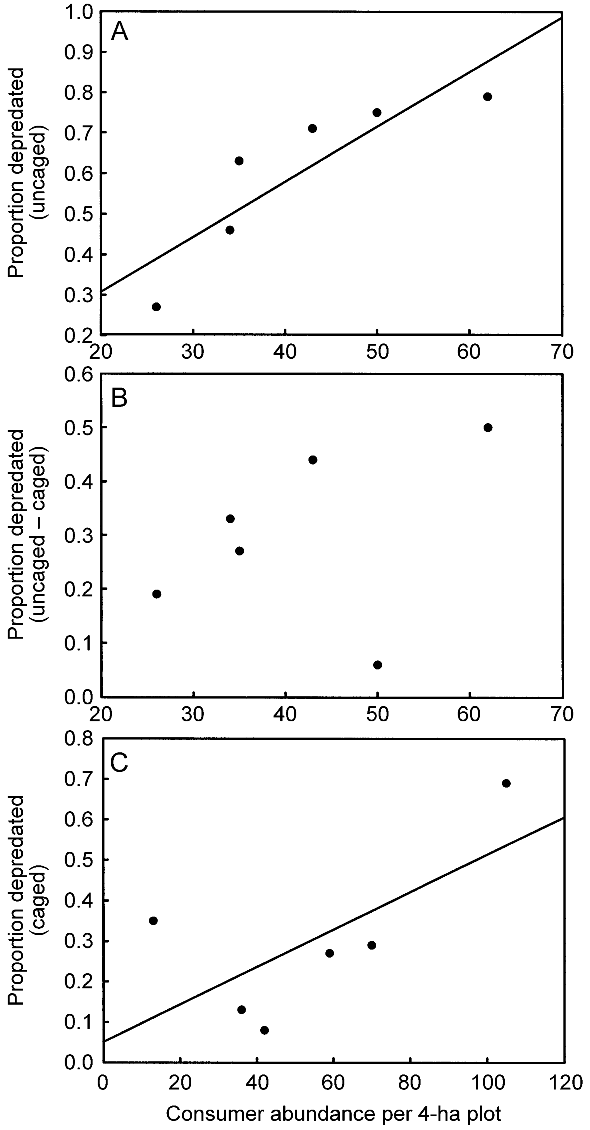

FIG. 4. Partial regressions of (A) the proportion of uncaged seedlings depredated by rodent abundance, (B) the proportion of uncaged seedlings depredated − caged seedlings depredated by rodent abundance, and (C) the proportion of caged seedlings depredated by homopteran abundance.

(T. P. Young and F. Keesing, *unpublished data*). However, differential mortality due to desiccation was not enough to override differences in herbivore-induced mortality. Large mammalian herbivores indirectly assisted performance of *A. drepanolobium* seedlings by limiting populations of smaller, more important seedling herbivores.

Herbivory by both insects and rodents was an important determinant of *A. drepanolobium* seedling survival. Caged seedlings experienced approximately half the herbivory-induced mortality of open seedlings. The proportion of caged seedlings killed was not significantly related to the abundance of invertebrates on each plot. In contrast, the proportion of uncaged seedlings killed was strongly related to the abundance of rodents on each plot. However, the proportion of caged seedlings killed subtracted from the proportion of uncaged seedlings killed was not related to the abundance of rodents on each plot. This suggests that insects might have compensated for the exclusion of rodents with regard to caged seedlings. In this scenario, rodents were the primary consumers of open seedlings, but the exclusion of rodents from caged seedlings led to an increase in herbivory by insects on these seedlings.

We may underestimate the long-term effects of herbivory and desiccation. Although desiccation-induced mortality had tapered off by the end of our experiment, total mortality (driven by herbivory) was still increasing. There may also be strong temporal variability in the overall effects of different consumers on seedling survival. A recent study of seedling herbivory at our study site (Shaw et al. 2002) failed to detect differences in seedling survival as a function of the presence or absence of large mammalian herbivores, although seedlings exposed only to rodents and insects suffered mortality at a faster rate. Using techniques similar to ours, Shaw et al. (2002) found insects to be the most important agents of *A. drepanolobium* seedling mortality. However, this study was conducted during a drought period at MRC when rodent densities numbered less than five per hectare.

A major challenge for the future is to assess the importance of seedling mortality, relative to sapling or adult mortality, to the population dynamics of *Acacia* trees in savanna ecosystems. Specifically, we know little about the number of seedlings necessary for successful regeneration of *A. drepanolobium* woodlands, or the size at which seedlings are effectively safe from predation by smaller herbivores. Further, given that rodent populations exhibit temporal variability, the survival and subsequent establishment of *A. drepanolobium* seedlings should be dependent largely upon those factors that influence rodent abundances. Finally, we do not know whether direct damage and/or mortality incurred by adult trees via large mammals is strong enough to override the positive, indirect benefits to seedlings we documented.

In other ecological systems, small mammals and insects have been shown to strongly influence the abundance and dynamics of a multitude of plant species (Brown and Heske 1990, Howe and Brown 2001, Gomez and Gonzalez-Megias 2002). Experiments conducted in conjunction with long-term monitoring have revealed intricate and often unanticipated relationships between disparate groups of consumers, their resources, and abiotic factors (Ernest and Brown 2001, Trotter et al. 2002, Meserve et al. 2003), thus highlighting the importance of experimental manipulations coupled with long-term observations in understanding networks of interactions. Our results revealed negligible direct impacts of large mammalian herbivores on seedling survival and strong, positive indirect impacts mediated by the suppression of smaller mammalian and insect herbivores. The net effect, therefore, of large mammals was to enhance seedling survival. Given the importance of dominant consumer species in driving complex interactions (Jones et al. 1998, Brown et al. 2001), it is likely that future research will demonstrate the cascading effects of the herbivores that influence *A. drepanolobium* dynamics in east African savannas.

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