

Herbivory on *Acacia* seedlings in an East African savanna

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Trees critically affect the functioning of savanna ecosystems through their effects on nutrient cycling, water availability, and patterns of space use by wildlife. Therefore, whatever factors influence successful recruitment of tree seedlings are important filters controlling savanna ecosystem function. In African savannas, large mammals have been considered the most important agents of mortality for adult trees, but their impacts on tree seedlings are not well-known. Similarly, the effects of rodents and invertebrates as seedling predators are largely unstudied in Africa. To assess the relative roles of large mammals, rodents, and invertebrates as predators of *Acacia* seedlings in an African savanna, we conducted two experiments in which we exposed *Acacia drepanolobium* seedlings to different guilds of herbivores. In the first experiment, seedlings exposed to rodent and invertebrate herbivores did not suffer greater damage than did seedlings exposed only to invertebrates, suggesting that invertebrates caused most of the damage to the seedlings. In the second experiment, 63% of seedlings exposed to all herbivores (large mammals, rodents, and invertebrates) suffered major damage or mortality in 14 days. Seedlings exposed to only rodents and invertebrates, however, suffered damage at a faster rate than did seedlings exposed to rodents, invertebrates, and large mammals, suggesting that small herbivores (rodents and invertebrates) might be compensating for the removal of large herbivores. Certain specific types of damage, such as cotyledon removal, were significantly more common in areas from which large mammals had been excluded, suggesting that the invertebrate herbivore community may differ between areas with and without large mammals. Overall, invertebrates caused the greatest damage to seedlings while rodents had relatively little effect and no seedlings were consumed or trampled by large mammals. Our results indicate that invertebrates can have a pronounced influence on seedling survival for a dominant savanna tree, which in turn may influence tree recruitment and ecosystem function.

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Trees are critical to the functioning of savanna ecosystems. Due to their complex root structures and the ability of many savanna trees to fix atmospheric nitrogen, they increase water infiltration and nutrient cycling in the soil (Belsky et al. 1993, Belsky 1994). As a consequence, trees can increase spatial heterogeneity by concentrating nutrients and water in sub-crown tree environments (Belsky et al. 1989, 1993). Trees also can increase faunal diversity by providing forage, shade, and protective cover for animals (Belsky et al. 1989). Therefore, factors that determine the successful recruit-

ment of woody plants into savannas are important determinants of savanna ecosystem function.

Recruitment is likely to be limited by survival of tree seedlings, since plants are usually most vulnerable to herbivores at this stage (Crawley 1983). African savannas host a diversity of herbivores, including large native ungulates such as elephants (*Loxodonta africana*) and antelopes, domestic livestock, rodents, and a vast array of invertebrates. The impacts of this array of herbivores on tree seedling survival is not well-known, though several studies have speculated on the effects of individ-

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ual herbivore species on savanna tree recruitment (Laws 1970, Belsky 1984, Dublin 1995, Sinclair 1995) and the profound effects of ungulates, particularly elephants, on trees >1 m in height are well-documented (Laws 1970, Dublin 1995, Sinclair 1995). In other ecosystems, the impacts of smaller seedling predators have been studied more extensively. For example, rodents have found to be critical seedling consumers in both temperate forest (Ostfeld and Canham 1993, Ostfeld et al. 1997) and temperate grassland (Hulme 1996) habitats, and invertebrates have been found to be important seedling predators in some areas (Meiners et al. 2000). In African savannas, however, the impacts of rodents and invertebrates as seedling predators are largely unknown.

In parts of central Kenya, the dominant tree is the whistling thorn tree, *Acacia drepanolobium*, which accounts for >98% of the overstory vegetation in some areas (Young et al. 1998). The goal of our study was to examine the magnitude of herbivory on *A. drepanolobium* seedlings and the identity of the most important herbivores, including large mammals, small mammals, and invertebrates. We conducted two experiments to assess the magnitude of herbivory and identify the herbivore taxa responsible for it. In the first experiment, we planted *A. drepanolobium* seedlings in areas to which rodents and invertebrates had access and in control areas from which rodents had been excluded. To more accurately determine the identity of different herbivores, and to incorporate the role of ungulates in seedling predation, we conducted a second experiment in which we planted *A. drepanolobium* seedlings in a nested enclosure design. In both experiments, we monitored seedlings for damage and mortality over a multi-week period following planting.

Methods

Study site

Our experiments were conducted at the Mpala Research Centre (MRC) in the Laikipia District of central Kenya (0°17'N, 36°53'E) between December 1999 and January 2001. The study site was in *A. drepanolobium* woodland/savanna on 'black cotton' soil. Rainfall in this area is highly seasonal, averaging 500–600 mm per year, with the greatest precipitation typically occurring during April–July and October–November. The least rainfall typically occurs during January–March. Both experiments were conducted early in the dry season (December–January). In addition to the normal dry season, the region experienced an extended drought during the time of these experiments; rainfall in 1999 and 2000 was approximately

30% below the long-term average (M. Ogada, unpubl.).

Woody vegetation at the study site is dominated by the trees *A. drepanolobium*, which accounts for >98% of the overstory, *A. mellifera* and *Balanites aegyptiaca*, and the shrubs *Cadaba farinosa*, *Lycium europeum*, and *Rhus natalensis* (Keesing 1998). Herbaceous vegetation is dominated by the grasses *Brachiaria lachnatha*, *Lintonia nutans*, *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra*, and the forbs *Aerva lanata*, *Commelina* spp., *Dyschoriste radicans* and *Rhinacanthus ndorensis* (Young et al. 1998).

Large mammal herbivores at the study site include elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), cape buffalos (*Syncerus caffer*), elands (*Taurotragus oryx*), Grevy's zebras (*Equus grevyi*), Burchell's zebras (*Equus burchelli*), Beisa oryx (*Oryx beisa*), Jackson's hartebeests (*Alcelaphus buselaphus jacksoni*), Grant's gazelles (*Gazella granti*), steinbucks (*Raphicerus campestris*) and domestic cattle (Young et al. 1998). Large mammal biomass averages 44 kg/ha in the Laikipia ecosystem (Keesing 2000). Small mammals found at the study site include *Saccostomus mearnsi*, *Arvicanthus nairobae*, *Mus minutoides*, *Mastomys natalensis*, *Dendromus melanotis* and *Crocidura* spp. (Keesing 1998). Small mammal biomass at the time of the study varied from ~1 kg/ha in December 1999 to <0.5 kg/ha in January 2001, with densities ranging from ~12/ha to ~5/ha. The only herbivorous small mammal present during the study was the pouched mouse (*Saccostomus mearnsi*) (F. Keesing, unpubl.). Although we made no systematic attempt to capture and identify invertebrate herbivores, we observed several species of grasshoppers, leafhoppers, ants, and beetles on and around the seedling grids. Further descriptions of the Laikipia ecosystem are available in Young et al. (1998).

Both experiments were conducted within the Kenya Long-term Exclusion Experiment (KLEE) which was established in 1995 (Young et al. 1998). KLEE was designed as a longitudinal study of herbivory by six different combinations of cattle and native large mammals, including megaherbivores (giraffes and elephants), and consists of three blocks, each measuring 400 × 600 m (24 ha). Within each of the three blocks, there are six separate exclusion treatments, each measuring 200 × 200 m (4 ha) and excluding a particular combination of large mammals. For our experiments, we used the plots allowing access by all large mammals and the plots excluding all large mammals. The total large mammal exclusion plots were surrounded on all sides by 2.4 m high standard game fencing with 11 strands of wires electrified at 7,500 volts. The control plot, to which all large mammals had access, was unfenced.

Seedling germination and transplanting

Acacia drepanolobium seeds were collected from trees on black cotton soil at MRC and then germinated outdoors in individual 1 l bags of black cotton soil approximately 1 month prior to the initial transplant. To prevent herbivory by mammals before transplanting, we covered the seedlings with chicken-wire cages. During this growing period, seedlings were watered approximately every other day, but they were not fertilized. At the time of planting, only seedlings showing foliage with no previous herbivory were utilized, and all seedlings still possessed intact cotyledons. Aboveground height of seedlings ranged from ~6 to 9 cm, with all seedlings possessing at least two branches.

All seedlings were planted in holes ~10 cm deep. To avoid scent contamination, we wore latex gloves when working with the soil and manipulating the seedlings. After transplanting, seedlings were watered with approximately 250 ml. Seedlings were again watered with ~250 ml two days after the initial transplant and then every three days for 14 days.

Experiment 1

To determine the magnitude of herbivory by small mammals, especially rodents, we conducted an experiment in which we planted seedlings in two types of locations – one to which rodents had access and one to which they did not. To exclude small mammals, we took advantage of a series of small-mammal exclusion fences established in 1995 inside the large mammal exclusion plots (Keesing 2000). Each fence measures 3 × 7 m and is composed of 0.6 cm mesh hardware cloth that is buried into the ground a depth of 0.5 m to prevent rodents from burrowing under. Aboveground, the fences are 0.5 m tall, with aluminum flashing, attached by rivets, covering the top 25 cm to prevent rodents from climbing over. Three small-mammal enclosures were established in each of the three large-mammal exclusion plots, for a total of nine enclosures.

Five meters from each of these nine small-mammal enclosures, we planted a line of seven *Acacia* seedlings 20 cm apart; these seedlings were accessible to both rodents and invertebrates. To assess herbivory by invertebrates only, we planted a line of four seedlings, 20 cm apart, inside each small-mammal exclusion fence. We censused the seedlings on days 2, 5, 7, 14, 21, and 28 and recorded any damage observed.

Experiment 2

We conducted a second experiment to determine the magnitude of predation by different guilds of seedling predators. For this experiment, seedlings were planted

in grids within the two types of large-mammal plots (with and without all large mammals). Two seedling grids were established in each of the three replicates of the two types of large-mammal plots, for a total of six grids on plots without large mammals and six grids on plots with large mammals. Each seedling grid consisted of a 90 × 90 cm grid of 4 parallel rows of 4 seedlings each, with 30 cm between seedlings and rows. Seedling grids were >150 m from other seedlings planted within the same plot and >45 m from the edges of the exclusion plots. Within the clusters, seedlings were assigned one of five herbivore exclusion treatments, which were designed to isolate damage by individual guilds of herbivores and are described in detail below. Seedlings in the plots excluding large mammals were assigned one of four herbivore treatments and were placed in the same relative positions on each grid (Fig. 1). Seedlings in the plot allowing access by all herbivores, including large mammals, represented the fifth herbivore treatment. All seedling clusters consisted of 16 seedlings. However, only four seedlings per grid were censused on the plots where large mammals had access; the other twelve seedlings on these grids were used to equalize the densities of seedlings in the clusters on all experimental grids (Fig. 1).

Seedlings were censused 2 days after the initial transplant and every three days following. With every check, each seedling was categorized as:

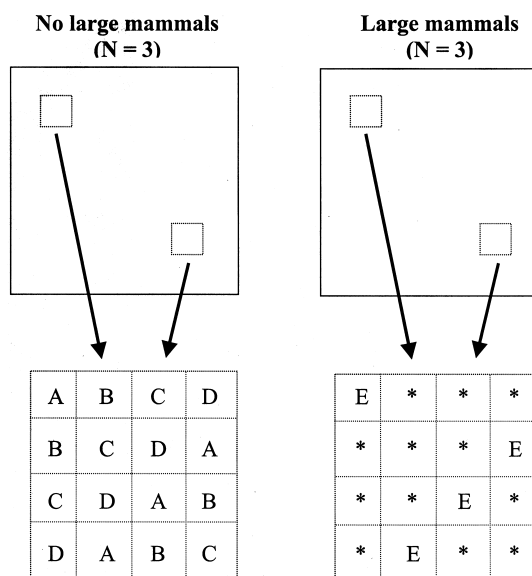


Fig. 1. Layout of seedling herbivory design for Experiment 2. Within each of the three replicates of the two types of large mammal treatments, there were two grids of 16 seedlings. Letters represent particular seedling exclusion treatments (e.g. "A" and "E" seedlings were not caged; "B" seedlings were covered with a wire mesh cage). "*" seedlings were not censused, but were planted to equalize densities among seedling grids (see Methods).

- Alive: No herbivory
- Alive: Minor leaf or cotyledon damage
- Alive: Major epicotyl, branch or foliage damage
- Dead: All photosynthetic material removed, either clipped at hypocotyl or photosynthetic material stripped from the leaves to the hypocotyl
- Dead: No herbivory; mortality assumed to be a consequence of transplanting or drought

In addition to these categories of damage, we documented particular types of damage within each category. For example, some seedlings had both cotyledons removed; others had their branches stripped of leaves. After 14 days, a final damage assessment was made and the seedlings were removed. Because the “major damage” category included loss of all photosynthetic tissue except stems and branches, we lumped major damage with outright mortality for most analyses.

The five herbivore treatments were designed to distinguish between the damage caused by ungulates, rodents, large invertebrates, crawling invertebrates, and flying or hopping invertebrates. The first herbivore treatment assessed the combined impacts of all of these herbivores and consisted of the seedlings planted in plots allowing access by large mammals and all other herbivores. The other four treatments excluded particular herbivores and were placed in the seedling grids on the plots from which large mammals were excluded. The second herbivore treatment, therefore, allowed access by all herbivores other than large mammals, and consisted of an uncaged seedling. The third treatment, which excluded large and small mammals and large invertebrates, consisted of a seedling covered by a 10 × 21 cm cylindrical cage of 0.6 cm mesh hardware cloth, in which ~ 15 one cm-diameter holes had been cut. The fourth treatment consisted of a cage identical to that in the third treatment, but with the addition of an acetate ring, 4 cm wide, and covered on both sides with Tanglefoot®, surrounding the base of the wire mesh cage. This excluded mammals and large invertebrates, as in treatment 3, but also excluded crawling invertebrates; only flying or hopping invertebrates had access to these seedlings. The fifth treatment consisted of a cylindrical cage, as in the previous two treatments, but with the addition of mosquito netting covering the cage and anchored to the ground by metal pegs. This effectively excluded all herbivores and served as a control. Overall, there were four replicates of each type of herbivore exclusion in each of the six replicates of the seedling grids (Fig. 1), for a total of 24 seedlings experiencing each type of herbivore exclusion.

Statistical analysis

Experiment 1. We examined the proportion of seedlings within each treatment that suffered major damage or

mortality. The replicates of each of the two exclusion types (with both rodents and invertebrates, and with only invertebrates) within each seedling cluster were analyzed as one unit. We conducted a repeated measures analysis of variance (rmANOVA), with exclusion type as the independent variable and the angularly-transformed proportion of seedlings suffering major damage or mortality after 14 and 28 days as the dependent variables.

Experiment 2. We examined the proportion of seedlings within each treatment that were damaged following the damage categories described previously. The four replicates of each exclusion type within each seedling grid were analyzed as one unit. Therefore, with four replicates of each exclusion type, seedlings examined in each grid could experience 0%, 25%, 50%, 75%, or 100% damage. After angular transformation, these values were used as the dependent variables in Analysis of Variance (ANOVA), with exclusion type as the independent variable. To test whether patterns of predation in the different exclusions varied over time, we conducted rmANOVAs using the same dependent and independent variables. We also analyzed the specific types of damage suffered by seedlings using a multivariate ANOVA (MANOVA), with the angularly-transformed proportion of seedlings undergoing each specific type of damage (e.g. branch stripping, cotyledon removal) as the dependent variables and herbivore treatment as the independent variable. All analyses were conducted using SYSTAT 7.0 (SPSS 1997).

Results

Experiment 1

Thirty percent ($\pm 10\%$ standard error) of seedlings to which rodents and invertebrates had access suffered major damage or mortality in 14 days; 44% ($\pm 11\%$) suffered major damage or mortality in 28 days. When rodents were excluded, damage was reduced to an average of 8.3% ($\pm 5.9\%$) in 14 days and 16.7% ($\pm 11.0\%$) in 28 days, though the differences between the percentage of seedlings consumed in the two treatment types were not significantly different, based on a rmANOVA ($P = 0.18$; Table 1). We did observe a significant effect of time on the proportion of seedlings damaged ($P = 0.04$), but there was no significant interaction between time and treatment ($P = 0.88$; Table 1).

Experiment 2

Sixty-three percent of seedlings to which all herbivores had access suffered major damage or death within 14 days (Fig. 2). Of these, all were damaged by invertebrates; none were damaged by rodents or ungulates.

Table 1. ANOVA table (Experiment 1) for the effect of treatment and time on the proportion of seedlings experiencing major damage or mortality after 14 and 28 days since planting.

Source of variation	df	MS	F	P
Between subjects				
Treatment	1	0.006	2.012	0.175
Error	16	0.003		
Within subjects				
Time	1	0.003	4.882	0.042
Treatment × time	1	0.000	0.025	0.877
Error	16	0.001		

When large mammal herbivores were excluded, the number of badly damaged or killed seedlings increased to 75% (Fig. 2), though these differences between treatments with and without large mammals were not statistically significant. Of the seedlings badly damaged or killed when large mammals were excluded, almost 90% were damaged by invertebrates, while only ~10% were damaged by rodents.

In the treatment exposed to all herbivores, 17% of seedlings experienced direct mortality; all of these seedlings were killed by invertebrates. In the treatment where large mammals were excluded, the percentage of seedlings killed more than doubled (42%), though the differences between treatments with and without large mammals were not statistically significant based on a post-hoc Bonferroni test ($P = 0.69$). Of the 42% killed in the absence of ungulates, ~80% were killed by invertebrates, and ~20% were killed by rodents.

The exclusion of additional herbivore guilds through caging significantly reduced the number of seedlings experiencing major damage or mortality ($P \ll 0.01$; Table 2; Fig. 2). Post-hoc Bonferroni analyses of ANOVA results indicated that control seedlings – those covered with both a wire cage and mosquito

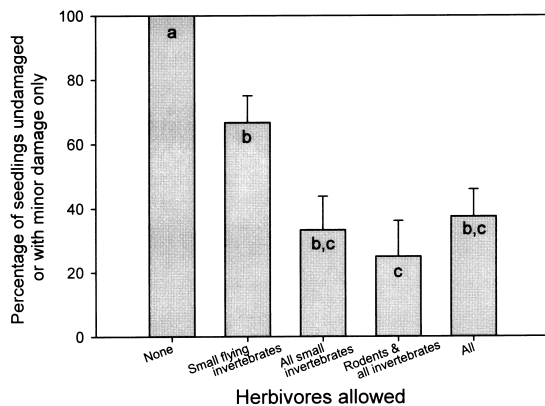


Fig. 2. Percentage of seedlings in each herbivore exclusion treatment that were undamaged or suffered only minor damage at the conclusion of the 14-day study. All seedlings exposed to herbivores suffered significantly more major damage or mortality than did control seedlings exposed to no herbivores.

Table 2. ANOVA table (Experiment 2) for the effect of treatment on the proportion of seedlings experiencing major damage or mortality after 14 days.

Source of variation	df	MS	F	P
Treatment	4	0.023	24.237	0.000
Error	25	0.001		

netting – suffered significantly less herbivory than did seedlings exposed to any of the groups of herbivores. Seedlings exposed to only small flying invertebrates suffered significantly less major damage or death than did seedlings exposed to small mammals and all invertebrates ($P = 0.03$; Fig. 2).

We observed a significant interaction between the number of days since planting and the amount of damage inflicted by different herbivore guilds ($P \ll 0.01$; Table 3), with the most rapid damage occurring to the seedlings to which only rodents and invertebrates had access (Fig. 3). Seedlings to which all herbivores had access suffered damage at a slower rate (Fig. 3).

Though there was no difference in the overall amount of damage to seedlings in plots with and without large mammals, certain specific types of damage occurred more frequently if large mammals were absent, based on the results of the MANOVA (Table 4). Where large mammals were absent, cotyledons were completely removed from virtually all seedlings, while on plots with large mammals, only ~1/3 of seedlings suffered this type of damage (Fig. 4). Similarly, on plots without large mammals, 25% of seedlings were found to have had half a cotyledon removed at some point during the 14-day experiment, while no seedlings suffered this type of damage where large mammals were present.

Discussion

In woodlands and temperate forests, rodents have been found to be the primary herbivores affecting tree recruitment through their consumption of tree seedlings (Ostfeld and Canham 1993, Hulme 1996, Ostfeld et al. 1997), while in tropical savannas, ungulates have been

Table 3. ANOVA table (Experiment 2) for the effect of treatment and time on the proportion of seedlings experiencing major damage or mortality after 2, 5, 7, and 14 days since planting.

Source of variation	df	MS	F	P
Between subjects				
Treatment	4	292.722	25.243	0.000
Error	25	11.596		
Within subjects				
Time	4	75.293	36.235	0.000
Treatment × time	16	10.381	4.996	0.000
Error	100	2.078		

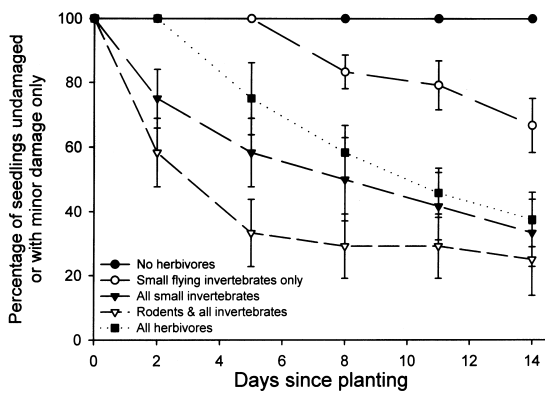


Fig. 3. Percentage of seedlings through time that were undamaged or suffered only minor damage. Seedlings exposed to only rodents and invertebrates experienced damage at a faster rate than did seedlings exposed to rodents, invertebrates, and large mammals.

identified as critical filters on tree regeneration (Dublin 1995, Sinclair 1995). Our results provide evidence that in African savannas, invertebrates may account for the majority of serious herbivory on *Acacia* seedlings while mammalian herbivores have much less of an impact. In our first experiment, in which we compared seedling predation with and without small mammals, we found that the removal of small mammals did not significantly reduce seedling predation, suggesting that the majority of damage and death of seedlings was caused by invertebrates. In our second experiment, invertebrates caused over 90% of major damage or mortality of *Acacia* seedlings within a period of 14 days. Rodents consumed only 10% of seedlings, while no seedlings were damaged by ungulates through either consumption or trampling during the course of the study.

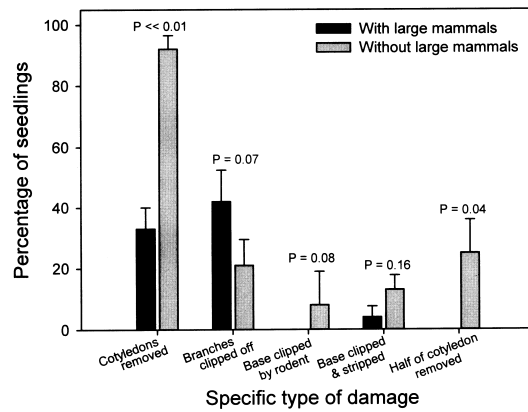


Fig. 4. Percentage of seedlings experiencing specific types of damage with and without large mammals present. Though overall damage did not differ significantly when ungulates were present compared to when they were not, certain types of specific damage were more common in areas from which ungulates were excluded.

We considered our category of major damage, which involved the removal of virtually all photosynthetic tissue, to be so severe that it would likely to lead to the death of the seedling. Some of the seedlings suffering major damage subsequently died during the course of the experiment, and none of the others refloresced leaves. Therefore, the assumption that major damage is tantamount to mortality seems justified.

Our exclusion design sequentially removed each guild of herbivores (i.e. rodents and large invertebrates excluded; rodents, large invertebrates and flying/hopping invertebrates excluded; rodents and all invertebrates excluded). To estimate the damage to seedlings caused by specific guilds of herbivores, we subtracted the mag-

Table 4. Multivariate analysis of variance (MANOVA) table Experiment 2 for categories of specific damage to seedlings in Experiment 2.

	F-statistic	df	P	
Multivariate test statistic				
Wilks' Lambda	2.91	36, 61	0.00	
Univariate F tests	df	MS	F	P
Half cotyledon removed	4	23.47	2.94	0.04
Error	24	7.97		
Whole cotyledon removed	4	68.17	13.23	0.00
Error	24	5.15		
Branches clipped off	4	25.51	2.45	0.07
Error	24	10.43		
Clipped at base by rodent	4	3.31	2.38	0.08
Error	24	1.39		
Clipped at base & shredded	4	10.33	1.45	0.25
Error	24	7.15		
Clipped at base & stripped	4	6.84	1.79	0.16
Error	24	3.83		
Major leaf damage	4	15.53	1.80	0.16
Error	24	8.62		
Minor leaf damage	4	3.94	0.35	0.84
Error	24	11.15		

nitudes of damage in each individual exclusion treatment. By this method, 44% of major damage or death was caused by small crawling invertebrates, and 45% was caused by small flying or hopping invertebrates. Rodents and large invertebrates accounted for the remaining 11%. On the other hand, outright mortality was primarily caused by large invertebrates (31%) and small crawling invertebrates (40%). This method of calculating the effects of particular guilds of herbivores assumes that the exclusion of some herbivores did not lead to compensatory herbivory by those that still had access. If herbivores did compensate, our method would overestimate the importance of herbivores that maintained access to seedlings after other herbivores were excluded.

We predicted that the treatment allowing access to the seedlings by all herbivores would suffer the greatest damage, but this was not the case. Seedlings exposed to all herbivores did not suffer significantly more damage than did seedlings from which large mammals had been excluded. However, there may be differences in invertebrate herbivore communities in areas with and without large mammals, given the differences we found in certain types of specific damage (Fig. 4). Putative differences in species composition of invertebrate herbivores when ungulates are excluded could be due to the increased biomass of herbaceous vegetation, which provides increased cover and a lower-light microhabitat, that has developed on these plots (F. Keesing, unpubl.).

Seasonal patterns of *A. drepanolobium* seed germination and seedling establishment are not well known. In three years of biannual vegetation surveys, no *A. drepanolobium* seedlings were recorded despite the occurrence of abundant seed production and precipitation (F. Keesing, unpubl.). Therefore, it is difficult to determine the appropriate timing for seedling predation experiments. We expected young seedlings having germinated during the rainy season to be present early in the dry season, matching the timing of our experiments. However, we do not know how representative of other seasons the levels of herbivory we observed might be. Some guilds of herbivores vary numerically and behaviorally in response to seasonal changes in the plant community, but whether this results in variation in *A. drepanolobium* seedling mortality is unknown. Moreover, the relative importance of other mortality agents, including seed predation and drought, is unknown for any season. Nevertheless, the high rate of heavy damage and mortality occurring in a relatively brief period suggests that herbivory by invertebrates has strong demographic consequences.

Persistence of savanna habitats requires the successful recruitment of *Acacia* seedlings. This study demonstrates that invertebrates are a major, but largely overlooked, component affecting seedling sur-

vival in African savannas. Damage inflicted on seedlings by invertebrates could surpass that caused by more conspicuous mammalian herbivores, especially ungulates. Because our study focused on young seedlings, our results suggest that invertebrate herbivores may be a crucial filter for trees when they are small; only those trees that escape this herbivory can become available to larger herbivores. Further studies are needed to understand the demographic consequences of herbivory for *Acacia* woodlands and savannas.

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References

- Belsky, A. J. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. – *Afr. J. Ecol.* 22: 271–279.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. – *Ecology* 75: 922–932.
- Belsky, A. J., Amundson, R. G., Duxbury, J. M. et al. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. – *J. Appl. Ecol.* 26: 1005–1024.
- Belsky, A. J., Mwonga, S. M., Amundson, R. G. et al. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. – *J. Appl. Ecol.* 30: 143–155.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. Studies in Ecology, Volume 10. – Univ. of California Press.
- Dublin, H. T. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. – In: Sinclair, A. R. E. and Arcese, P. (eds), *Serengeti II: dynamics, management, and conservation of an ecosystem*. Univ. of Chicago Press, pp. 71–90.
- Hulme, P. E. 1996. Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. – *J. Ecol.* 84: 43–51.
- Keesing, F. 1998. Impacts of ungulates on the demography and diversity of small mammals in central Kenya. – *Oecologia* 116: 381–389.
- Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. – *BioScience* 50: 205–215.
- Laws, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. – *Oikos* 21: 1–15.
- Meiners, S. J., Handel, S. N. and Pickett, S. T. A. 2000. Tree seedling establishment under insect herbivory: edge effects and inter-annual variation. – *Plant Ecol.* 151: 161–170.
- Ostfeld, R. S. and Canham, C. D. 1993. Effects of meadow vole population density on tree seedling survival in old fields. – *Ecology* 74: 1792–1801.
- Ostfeld, R. S., Manson, R. H. and Canham, C. D. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. – *Ecology* 78: 1531–1542.

- Sinclair, A. R. E. 1995. Equilibria in plant-herbivore interactions. – In: Sinclair, A. R. E. and Arcese, P. (eds), Serengeti II: dynamics, management, and conservation of an ecosystem. Univ. of Chicago Press, pp. 91–113.
- SPSS 1997. SYSTAT® 7.0: Statistics. – Chicago, Illinois.
- Young, T. P., Okello, B., Kinyua, D. and Palmer, T. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. – *Afr. J. Range Forage Sci.* 14: 92–104.