Oecologia (1998) 115:508–513

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Relaxation of an induced defense after exclusion of herbivores: spines on *Acacia drepanolobium*

Received: 29 September 1997 / Accepted: 26 February 1998

Abstract Descriptive and experimental evidence suggests that spine length is an inducible defense, with longer spines being produced by branches experiencing greater levels of herbivory. Here we present results from a replicated, controlled herbivore exclusion experiment in which cattle, wildlife (large mammalian herbivores), and megaherbivores (elephants and giraffes) were independently manipulated. Experimental wildlife barriers virtually eliminated herbivory on *Acacia drepanolobium* branches at all heights. Megaherbivore barriers reduced herbivory on branches more than 1.75 m from the ground by up to 80%, and reduced herbivory on lower branches by 40%. These patterns of herbivory were matched by patterns of relaxation of spine length that occurred in response to the treatments. After 22 months of herbivore exclusion, the lengths of newly produced spines were 19% shorter on branches protected from large mammal herbivory than on trees in control plots. On low branches, there was a steady increase in spine length from total exclusion plots (shortest spines) to plots with wildlife to plots with both megaherbivores and wildlife (longest spines). On higher branches, new spines were shorter in total exclusion plots and wildlife plots than in plots in which megaherbivores were allowed. This is the first replicated, controlled experimental demonstration that browsing by free-ranging herbivores is associated with greater spine lengths. Examination of trees incidentally protected from herbivory for several years suggests that reduction in spine length in the experimental plots will eventually exceed 70%. Initially slow relaxation of spine length may represent a cautious adaptive strategy in an environment where a given branch is likely to escape herbivory in a given growth season, even when herbivores are present.

Key words Kenya · Spinescence · Induced resistance · Herbivore exclusion · *Acacia drepanolobium*

Introduction

Plants not only defend themselves with fixed (constitutive) defenses, but can also increase their (inducible) defenses in the face of active herbivory. It is suggested that it is adaptive to match defenses to herbivore challenge in the short term. However, recent models offer alternative explanations for the adaptive value of induced defense (Milewski et al. 1991; Adler and Karban 1994; Karban et al. 1997) which imply different predictions about the relative rates at which defenses are initially induced and then relaxed after the cessation of herbivory. The timing of induction and relaxation are critical to determining the effects of induced responses on herbivores and on plants. However, data on the relative timing of induction and relaxation are in short supply (Karban and Baldwin 1997).

Induced chemical defenses have been the most studied (reviewed in Karban and Baldwin 1997), but these are relatively difficult to measure and manipulate, and direct evidence of their effects on herbivores is rare. Physical defenses such as spines provide an ideal model system for the study of induced defense for several reasons. First, they are easy and inexpensive to measure in the field. Second, they can be readily manipulated on the plant, especially when they consist of dead tissue. Third, their defensive function has been experimentally demonstrated clearly and repeatedly (Cooper and Owen-Smith 1986; Milewski et al. 1991; Gowda 1996; Cooper and Ginnett 1997).

Naturalists have long noted the absence of long spines on branches not subject to mammalian herbivory (e.g., Abrahamson 1975). Only recently, however, have such natural patterns been the subject of quantitative

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analysis (Young 1987; White 1988; Myers and Bazely 1991; Bazely et al. 1991; Milewski et al. 1991). Young (1987) and Milewski et al. (1991) described patterns of greater spine length on (lower) branches within the reach of browsers, and shorter spines on branches above the foraging heights of browsers. In addition, Milewski et al. (1991) documented significant differences in spines length among sites differing in herbivore density. Experimental approaches have also been used. Simulated herbivory (hand pruning of shoots) was associated with increased prickle density in brambles (Bazely et al. 1991) and greater biomass of spines in *A. tortilis* (Gowda 1997). Obeso (1997) took advantage of a 1-year-old exclosure to document a decrease in holly spinescence. However, there has not yet been a controlled, replicated experimental demonstration that actual herbivory by native browsers is associated with changes in spine length, for any spinescent species. Here we use a series of controlled, replicated experiments in which different guilds of mammalian herbivores are independently manipulated to examine the existence and rate of relaxation of physical defense (spine length) in *Acacia drepanolobium*.

Methods

Study site

This research was carried out from 1995 to 1997 at the Mpala Research Centre in Laikipia, Kenya. Rainfall averages ~600 mm per year, in a complex seasonal pattern that may be best described as tri-modal (although any of the "modes" may fail in a given year). The study area is located in the southwestern corner of the property at an elevation of 1800 m above sea level (asl) (0°17′N, 37°52′E). The vegetation at the study plots is *A. drepanolobium* bushed grassland, characteristic of heavy clay "black cotton" soils of impeded drainage (Ahn and Geiger 1987; Taiti 1992). The understory is dominated by five species of grasses. The dominant tree, *A. drepanolobium*, accounts for > 95% of the woody vegetation (Young et al. 1997).

This research is part of a multi-disciplinary project (KLEE: Kenya Long-term Exclosure Experiment) that is examining the interactions between livestock and native biodiversity with a series of herbivore barriers. The study plots were established in September 1995. We use a series of "semi-permeable" barriers (including electric game fencing) to exclude different combinations of large mammalian herbivores (see Hoare 1992; Thouless and Sakwa 1994). There are six different treatments, based on the herbivores that are allowed. "Megaherbivores" refers to elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). "Wildlife" refers to large mammalian herbivores, but not giraffes and elephants. In particular, the wildlife exclusion plots excluded the following browsers of *A. drepanolobium*: Grant's gazelles (*Gazella granti*), elands (*Taurotragus oryx*), steinbucks (*Ramphicerus campestris*), and oryx (*Oryx beisa*).

1. No large mammalian herbivores allowed (O)
2. Only cattle allowed (C)
3. Only wildlife (less megaherbivores) allowed (W)
4. Only wildlife (less megaherbivores) and cattle allowed (WC)
5. Wildlife and megaherbivores allowed (MW)
6. Cattle, wildlife, and megaherbivores allowed (MWC)

Each of these six treatments is represented by three 4-ha replicates, one in each of three blocks. Treatment plots within each block were arranged in a stratified random design. Further details of the study ecosystem can be found in Young et al. (1995, 1997).

A. drepanolobium

A. drepanolobium is a small single-stemmed tree that occurs in East Africa on soils of impeded drainage. It is defended by stipular spines (Young 1987; Milewski et al. 1991), symbiotic ants (Madden and Young 1992; Young et al. 1997), and perhaps leaf chemistry (tannins currently being analyzed) . At the study sites it can reach heights of 6 m. Its size structure is L-shaped, implying healthy recruitment (Young et al. 1997). There is a pair of straight sharp spines up to 6 cm (exceptionally, up to 10 cm) long at each node. Approximately one node in five has a swollen structure up to 5 cm in diameter at the base of the spine pair that usually houses resident ants, which feed in part from extrafloral nectaries at the leaf bases (Young et al. 1997). Spines are produced along with their attendant shoots during periods of rainy weather (Isbell, in press). Within a few weeks, the spines are fully lignified and contain no living tissue; by then their length is fixed. Old spines remain on branches for several years.

Herbivory measurements

We surveyed *A. drepanolobium* trees in the study plots for mammalian herbivory. In each of the 18 plots, 30 trees of different sizes were permanently tagged in March 1996. On each tree, five shoots were individually tagged and measured. These trees were surveyed again in June 1996. The proportion of new shoots eaten was calculated for each tree, and these values were averaged over all trees of each of two heights (0.50–1.74 and ≥1.75 m) within each plot. Within each block, there were three pairs of plots that differed only in the presence of cattle (O and C, W and WC, and MW and MWC). Because cattle do not feed on *A. drepanolobium* (see below), mean herbivory rates and mean spine lengths for these pairs of plots were averaged, leaving three treatment combinations per block.

Spine measurements

In July 1997, in each of the 18 experimental plots, we surveyed eight different trees near each of five central posts, set 50 m apart. (These posts are used to demarcate subquadrats in these large plots.) Each of these posts was also at least 50 m from the nearest herbivore barrier. At each post, we divided the area into four cardinal quarters. In each quarter, we selected a tree on which there were branches 1.0 ± 0.3 m from the ground, and a tree on which there were branches 2.2 ± 0.3 m from the ground. We selected the nearest trees that were at least 3 m from the post (to reduce the risk of past disturbance to the trees). For each tree, we chose three branches closest in height to 1.0 m or 2.2 m, but not sampling branches with obvious mammalian herbivory on recent (< 8 weeks) shoots.

On each selected branch, we measured five cm from the shoot tip, and then sampled the next node more proximate to the tree. If this was a swollen spine, it was skipped and the next node measured. Swollen spines (ant domatia) invariably have longer straight portions than their unswollen neighbors, regardless of whether they are occupied by ants (T.P. Young, personal observations). We do not know whether this is a physiological/developmental consequence of the mechanisms by which the swellings are produced. In any case, we controlled for this source of variation by measuring only unswollen spines.

At each node, one of the pair of spines was measured to the nearest mm. If the two spines were very different in size, the one most vertical was measured. If this was ambiguous ($\ll 1\%$ of all measurements), both were measured and an average was recorded. If no spine was visible at a node, a value of 0.0 cm was recorded.

We also recorded the identity of the person measuring each spine, the height of each sampled tree, the average height of the sampled branches, and the identity of the ant species that inhabited the tree. In total, we sampled 60 spines on 20 trees at each of two heights in each of 18 plots, for a total of 2160 spines on 720 trees.

We also visited four nearby sites (within 35 km) which had been completely protected from large mammal browsing for at least 5 years (a wheat field, a private yard, a quarantine livestock paddock, and a breeding livestock paddock). At these sites, we measured spine lengths on high and low branches as described above on a total of ten trees.

Statistical analysis

For statistical analysis, we took the mean of all three spine measurements for each tree. Because these means were right-skewed, they were ln-transformed for normality before statistical analysis. Because cattle do not eat *A. drepanolobium*, and because spine lengths were similar between plots with and without cattle across treatments and blocks (Table 1), we lumped data from pairs of plots within each block that differed only in the presence of cattle. This left us with three treatment classes: no browsers, (non-megaherbivore) wildlife browsers, and wildlife browsers including megaherbivores. We carried out analysis of spine length and herbivore treatment using a Model I ANOVA with branch height classes, blocks, and wildlife treatments as effects. Because there were significant differences in mean spine lengths among trees occupied by different ant species, we did a similar analysis of spines using only those trees occupied by the most abundant ant, *C. mimosae* (on 415 of 720 trees; no other ant occurred on more than 137 trees, see Table 1).

Mean coefficients of variation in (untransformed) spine length were calculated for adjacent nodes on the same branch (90 trees), for three different branches on the same tree (720 trees), and for different trees in the same plot (mean spine length on each of 20 trees for both high and low branches, for each of the 18 plots), and the latter separately for trees inhabited by each of the four ant species. For all but the first category, we used the data described earlier. For the variation between adjacent nodes on single trees, we used a data set that was collected separately in the same month (as part of a different study): In each plot, four trees were identified with accessible branches at ~1 m: one with each of the four ant species. An additional tree was selected with branches at ~2.2 m, occupied by *C. mimosae*. On each of these five trees, four branches were measured. On each of these four branches, we measured one of the spines at the first node below 5 cm from the shoot tip (as above). We also measured one of the spines at the next node along the branch, using similar criteria.

Results

The herbivore barriers were effective in greatly reducing herbivory by the targeted species of large mammalian herbivores between March and June 1996 (Fig. 1). Browsing on both low and high *A. drepanolobium* branches was virtually absent inside the wildlife exclosure (treatments O and C). The new shoots of 10% of the lower branches inside the megaherbivore exclosures (treatments W and WC) were eaten, and this increased to 16% in the total access plots (treatments MW and MWC). Herbivory on the new shoots of higher branches was reduced by more than 63% inside the megaherbivore exclosures. In two out of three blocks, this reduction was more than 80%. The residual herbivory on higher branches inside the megaherbivore exclosures could have been due to either eland reaching higher than 1.75 m, or to herbivory during the rare fence breaks. Cattle do not eat *A. drepanolobium* (there was no herbivory in the "cattle only" plots).

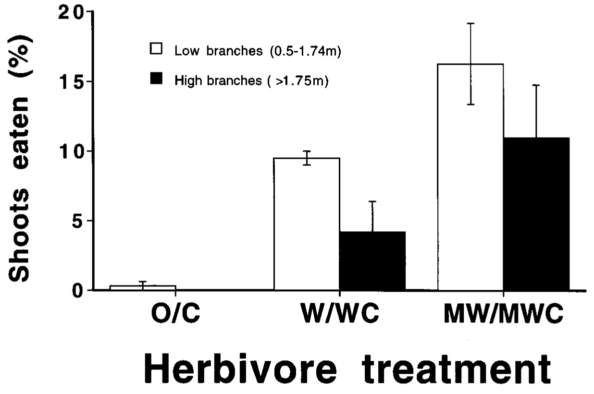

Fig. 1 Rates of shoot herbivory (% shoots eaten) between March and June 1996 across experimental herbivore treatments. *Bars* are standard errors, based on three blocks. Herbivore treatment classes are based on the large herbivores allowed: *0* no large mammalian herbivores, *C* cattle, *W* native large mammalian herbivores (less megaherbivores), *M* megaherbivores (giraffes and elephants). Analysis of variance shows significant effects of treatment ($F = 21.7$, $P < 0.001$) and branch height ($F = 4.80$, $P < 0.05$) on browse rates

The mean length of unswollen spines was 1.62 cm, and the range was 0.0–8.3 cm. Only 14 (< 0.7%) of 2160 spines were longer than 5.0 cm, and only 4 (< 0.2%) were longer than 6.0 cm. The straight thin portions of the swollen spines housing ants were generally longer than their unswollen counterparts (authors, personal observations); the longest we have seen in the area was 10.1 cm long (shown to us by T. O'Connor).

Spines in plots without cattle were on average 6% longer than spines in plots with cattle (Table 1), but this difference was not significant ($F = 1.96$, $P = 0.17$), and we lumped data across plots within blocks that differed only in the presence of cattle (see Methods). Spines on lower in branches were consistently longer (by an average of 20%) than were spines on higher branches, in all plots (Table 1, Table 2).

There were strong and significant effects on spine length from branch height, wildlife treatment, and block (Table 2). Overall, new spines in plots from which browsers were excluded were 19% shorter than spines in plots exposed to all browsers (Fig. 2). On low branches, there was a steady increase in spine length from total exclusion plots to plots that allowed wildlife to plots with both megaherbivores and wildlife. For branches at least 2 m from the ground, new spines were similar in length in total exclusion plots and plots that allowed wildlife, but were longer in plots in which megaherbivores were allowed. Similar (significant) patterns are evident when analysis is limited to trees occupied by *C. mimosae*. Spines on trees in the four (uncontrolled) nearby sites which had been completely protected from large mammal herbivory for several years had exceedingly short spines both on low (0.65 ± 0.15 cm) and high (0.44 ± 0.08 cm) branches. These mean values were 70–75% lower than those in the experimental plots accessible to all herbivores.

The three main effects in the ANOVA model accounted for more than 87% of the variation in mean spine length (ln transformed) across plots and branch heights. However, there was considerable variation in spine length within plots that was not attributable to treatment effects (Table 3). Mean coefficients of variation in length were large for spines across different branches at the same height within trees (47%), and across trees within plots, both on low (53%) and high (40%) branches. Mean coefficients of variation for adjacent nodes within branches (23%) were about half as great. Some of the variability among trees was related to the species of ant occupant (Table 1), with spines being 20% shorter (Tukey-Kramer HSD, $P < 0.05$) on lower branches of trees occupied by *Crematogaster nigriceps* than on lower branches of trees occupied by *C. mimosae* (across all four ant species: $F = 2.50$, $P < 0.06$). Similar differences were found on upper branches, but these were not statistically significant ($F = 0.98$, $P = 0.40$).

Table 1 Mean spine lengths of *Acacia drepanolobium* trees subject to different experimental and random effects. Although samples sizes (and standard errors) here are based on the total number of trees, sample size for the statistical analyses of variance reported in the text (and in Table 2) was three blocks, and spines lengths were log-transformed

	Low branches (0.7–1.3 m)	High branches (2.0–2.5 m)
All trees (both $n = 360$ trees)	1.80 ± 0.04	1.44 ± 0.04
Cattle (all $n = 180$ trees)		
Present	1.74 ± 0.06	1.39 ± 0.06
Absent	1.85 ± 0.06	1.49 ± 0.06
Ant occupant		
Crematogaster nigriceps	1.54 ± 0.09 (54)	1.14 ± 0.10 (27)
C. sjoestedti	1.71 ± 0.09 (55)	1.48 ± 0.08 (82)
Tetraponera penzigi	1.81 ± 0.11 (57)	1.56 ± 0.25 (21)
C. mimosae	1.90 ± 0.06 (192)	1.46 ± 0.06 (223)

Table 2 Analysis of variance for mean spine length (ln transformed) on *A. drepanolobium* trees with respect to block, branch height, and wildlife treatment. When included, no interaction term was significant

Effect	*df*	SS	MS	*F*	*P*
Branch height	1	0.355	0.355	46.84	< 0.0001
Wildlife treatment	2	0.108	0.054	7.13	< 0.01
Block	2	0.157	0.089	10.36	< 0.005
Error	12	0.091	0.0076		

Discussion

Karban and Myers (1989) suggest three criteria for a plant response to be considered an induced defense. First, the response must be caused by herbivory. Second, the response must result in lower levels of herbivory. Third, the resultant lower herbviory must result in greater plant fitness. We show here for the first time in replicated, controlled experiments that variation in mean spine length on *A. drepanolobium* is positively associated with variation in browsing by natural herbivores. This is supported by the work of Gowda (1997), in which experimental pruning increased both the relative and absolute biomass of spines on *A. tortilis* in Tanzania (spine lengths were not measured). Previous controlled, replicated experiments have shown that spine removal in *A. drepanolobium* and other acacia species reduces herbivore bite rates (Cooper and Owen-Smith 1986; Gowda 1996; Cooper and Ginnett 1997), and overall branch herbivory (Milewski et al. 1991; Gowda 1996). However,

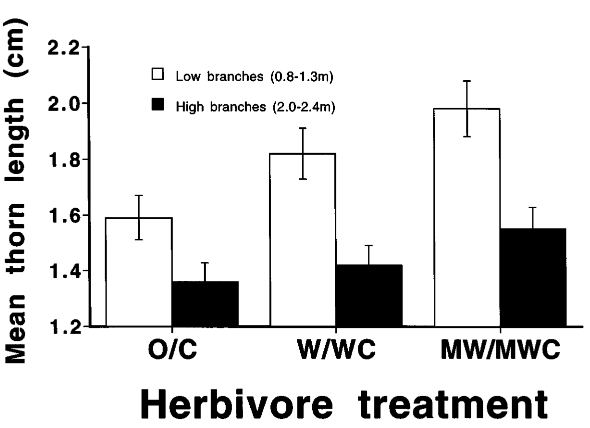

Fig. 2 Mean (untransformed) spine lengths of low (~1.0 m, *open bars*) and high (~2.2 m, *filled bars*) branches on *Acacia drepanolobium* trees accessible to different herbivores. Note scale of vertical axis. *Bars* are standard errors, based on 120 trees. For statistical analysis, sample size per treatment was 3 (blocks), and the spine lengths were log-transformed. Herbivore treatment classes are based on the large herbivores allowed: *0* no large mammalian herbivores; *C* cattle, *W* native large mammalian herbivores (except megaherbivores), *M* megaherbivores (giraffes and elephants)

Table 3 Mean coefficients of variation for (untransformed) spine length within different sampling classes

Class	Mean CV	Sample
Across adjacent nodes (same branch)	23%	Two spines on each of 360 (low) branches
Across branches within a tree	47%	One spine on each of three branches on each of 720 trees
Across trees within a plot (low branches)	53%	Mean spine length (of 3) on each of 20 trees in each of 18 plots
Across trees within a plot (high branches)	40%	Mean spine length (of 3) on each of 20 trees in each of 18 plots

we still do not have experimental evidence on the effects on more moderate variation in spine length on herbivory rates. There has been insufficient mortality or reproduction thus far in the experimental plots to assess whether reduced herbivory is associated with increased evolutionary fitness, but data on natural variation in herbivory by giraffes on *A. tortilis* and subsequent survival imply high costs of herbivory on plant fitness (Pellew 1983).

Spine length in *A. drepanolobium* seems to be tracking herbivory rates (compare Figs. 1 and 2). Lower branches experience greater herbivory and have longer spines than higher branches. Among lower branches, there is a steady increase in both herbivory and spine length as one moves from plots lacking large mammalian herbivores to plots allowing the presence of non-megaherbivore wildlife to plots allowing the presence of both wildlife and megaherbivores. Among higher branches, both herbivory and spine lengths remain low in plots without megaherbivores, but both herbivory and spine lengths are greater when giraffes and elephants are allowed access.

The rate of relaxation of defense (shorter spines on new shoots) is apparently gradual. After 22 months of herbivore exclusion, spine lengths have been reduced by 19% (less than a third of the total reduction we expect to occur eventually). Similarly, Obeso (1997) found an approximately 20% reduction in spinescence in holly leaves after a year of protection from herbivory. A review of chemical induced defenses and the success of insect herbivores suggests that rapid induction and gradual relaxation may be a common pattern (Karban and Baldwin 1997). The lag in response represented by a gradual relaxation is a necessary component of some induced defense models of cyclic insect outbreaks (Karban and Baldwin 1997).

One expects some lag between herbivore exclusion and plant response in this system because there must first be a growth season (first rainy season after exclusion) during which there are differences in herbivory on fresh shoot tips (there is far less herbivory on older shoot tips), and then a second growth season in which the next generation of new shoots can respond by producing shorter spines. Even if leaf herbivory alone (on older shoots) can trigger a response, there would still be the lag until the next season of shoot and spine production. We are currently conducting experiments on the cues the plants use to assess herbivory and trigger increased spine length.

Since the exclosures were erected in September 1995, there have been four or five growth periods at the study site (depending on how they are separated), sufficient for an induced response in spine lengths. The initially small response recorded here may be appropriately cautious. In a system where a given shoot has only a 10–15% chance of being eaten in a given season (see Fig. 1), even several consecutive seasons without herbivory would be an unreliable predictor of the cessation of herbivory. Therefore, a slow relaxation of plant defense would be an adaptive strategy (for a similar argument, see Karban and Adler 1996). In contrast, one might expect that the induction of a defensive response (in this case, increased spine length) would be relatively rapid, as has been shown in other systems (reviewed in Karban and Baldwin 1997). Experiments currently underway will test this prediction. The data of Gowda (1997) indicate a doubling in spine biomass within 2 months of simulated shoot herbivory.

If we confirm that defenses are quickly induced but are only slowly relaxed, it may help our understanding about the selective pressures involved in the evolution of induced defense. Recent alternative models of induced defense suggest that it may have evolved for reasons other than simple economic efficiency under temporally variable herbivore pressure. Although not explicitly explored by the authors, each model implies certain patterns in the induction and relaxation of defense. Milewski et al. (1991) suggest that when there is predictable spatial variation in herbviory (e.g., lower branches are at far greater risk of herbivory), herbivory itself may be the best indictor of the position of a branch or leaf. If so, then once a defense has been induced, it should remain in place indefinitely. Adler and Karban (1994) suggest that having a different defense from one's neighbors may be selectively advantageous in itself, in which case again once a defense has been induced, it should remain in place indefinitely. Karban et al. (1997) suggest that alternating between high and low defense might be adaptive even under fairly constant herbivory, in which case the rates of relaxation and inducement of defense need not differ at all.

Surveys of *A. drepanolobium* trees at four different sites within 35 km of the experimental plots that had been incidentally protected from browsing for several years revealed that mean spine lengths were less than 0.7 cm on low branches and less than 0.5 cm on high branches. We predict that the current pattern of relaxation of spine length will continue in the experimental plots, and that eventually new shoots will consistently produce spines that are similarly short, which would represent a reduction in mean spine length of >70%.

Even after controlling for variation due to significant treatment, block, and branch height effects (and ant effects), there is tremendous variation in the length of unswollen spines among trees within plots, among branches on a given tree, and within a given branch. One possible reason for the remaining variation is that having long spines at every node is energetically wasteful or otherwise not selectively advantageous. In addition, we suggest that some of the variation in spine length represents the "ghost of herbivory past" in a system where, once increased spine length has been induced, it is fixed in those spines and only slowly relaxed in later spines. Branches (and sections of branches; i.e., different growth seasons) that had experienced more herbivory prior to shoot production should exhibit longer spines than branches that had not. It may eventually be possible to read the recent history (last few years) of herbivory on individual trees and even on individual branches, using inducible spine length as a key, much as tree rings in the temperate zone reveal past growth.

Acknowledgements This research was supported by the Smithsonian Institution (James Smithson grant to the late Alan P. Smith); the National Geographic Society (grant 4691-91), the University of California at Davis, Fordham University, Mpala Farm, the Mpala Research Centre, the University of California Research Expeditions Program (UREP) to T. Young; a Citibank Mpala Fellowship and an International Federation of Science grant to B. Okello; and NSF grant BSR 93-07477 to L. Isbell. Field assistance was provided by F. Erei, D. Kinyua, B. Okello, J. Lemboi, S. Talbot, F. Olmstead, J. Olmstead, A. Dickens, J. Dickens, H. Eggleston, T. Palmer, N. Patterson, K. Radzilkowski, L. Harrell, J. Martin, A. Stewart, and D. Tortelli. Special thanks to George Small and John Wreford-Smith. The manuscript was greatly improved by comments from L. Isbell, A. Agarwal, R. Karban, S. Cooper, P. Stiling, T. Palmer and an anonymous reviewer.

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