Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya

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We present experimental evidence supporting the hypothesis that increased spine length in acacia species is a defense induced by herbivory. *Acacia drepanolobium* is the dominant tree over large areas of East Africa. Each individual tree is occupied by one of four ant species at our study site. Using two types of electric fences, we have effectively controlled herbivory by megaherbivores (elephants and giraffes) and other large mammalian herbivores at a field site in Laikipia, Kenya since 1995. Mean spine lengths of new spines on trees occupied by the most abundant ant species (presumed to be a defensive mutualist) have shown a slow and steady decline over the first five years of the experiment on branches protected from these herbivores. This reduction has been 35–40%, or approximately half of the reduction in spine length that we anticipate will eventually occur, based on trees that have been protected from herbivory for many years. In contrast, trees occupied by a resident ant species that systematically prunes shoots have shown no reduction in spine length associated with herbivore exclusion treatments. Experimental pruning of shoots similar to that carried out by this ant species resulted in longer spines on seedlings in a greenhouse setting. Simulated large mammal browsing in the field rapidly (re-)induced greater spine lengths on trees that had been protected from large mammals for five years. The slow relaxation of spine length in the absence of herbivory, contrasted with its rapid induction after simulated browsing, suggests that there is a difference in the reliability of these two signals. Spine length responses to herbivory were extremely local (limited to individual branches). These branch-specific responses are consistent with the hypothesis that induced defense in this system evolved in the context of within-tree spatial variation in herbivore pressure, in particular variation in branch height.

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When herbivory is variable in space or time, it may be adaptive to adjust levels of defense to rates of herbivory (induced defense). Induced chemical defenses have been the most studied plant defenses (reviewed in Karban and Baldwin 1997), and there is evidence that such defenses while potentially costly (Agrawal et al. 1999) can enhance the fitness of plants exposed to herbivore attack (Agrawal 1998). In contrast, less attention has been paid to inducibility of physical defenses such as spines and thorns, despite the ease with which they can be measured and manipulated in the field. The defensive function of spinescence has been demonstrated clearly and repeatedly. Herbivores prefer individual plants that are less spinescent (Bazley et al. 1991, Gowda 1996, Obeso 1997, Gomez and Zamora 2000). The experimental removal of spines or prickles significantly increased rates of herbivory and total tissue loss to herbivores in *Acacia drepanolobium* and other species (Cooper and Owen-Smith 1986, Milewski et al. 1991, Young and Smith 1994, Cooper and Ginnett 1998).

There is considerable inferential evidence that variation in plant spinescence is caused by variation in past herbivory, but little of this evidence has been the result of controlled experiments (see review by Myers and Bazley 1991). Plant spinescence has been associated with (sometimes inferred) natural variation in herbivory, in the form of less browsed (higher) branches having less spinescence than more browsed (lower) branches (O'Rourke 1949, Abrahamson 1975, Young 1987, White 1988, Milewski et al. 1991). In natural (uncontrolled) experiments comparing areas with and without herbivores, *Acacia* spp. plants protected from browsing exhibited less spinescence than browsed plants (Gowda 1996, Obeso 1997, Rohner and Ward 1997, Takada et al. 2001). Controlled, replicated experiments have also shown that protection from herbivory by large mammals results in relaxation of spine length in *A. drepanolobium* (Young and Okello 1998) and spine density in *Hormathophylla spinosa* (Gomez and Zamora 2002). The only other controlled experimental studies we have found showed that simulated herbivory increased spinescence in *A. tortilis* (Gowda 1997), *Opuntia stricta* (Myers and Bazley 1991, and *Rubus fruticosus* Bazley et al. 1991). No previous study has examined both the relaxation and induction of spinescence in the same controlled, replicated experimental system.

Spatial or temporal variation in herbivory may select for inducible defense systems (Karban and Baldwin 1997, Karban et al. 1997). Defenses that are locally induced and expressed may be advantageous in systems where certain portions of the plant are consistently at greater risk for herbivory. For example, locally inducible increased spine length in *Acacia* spp. may have evolved because upper canopy branches are consistently out of reach of herbivores.

Here, we report on controlled and replicated experiments demonstrating that changes in simulated and natural herbivory are associated with changes in spine length. In a previous paper, we showed a 20% reduction in spine length in *Acacia drepanolobium* after two years of herbivore exclusion (Young and Okello 1998). We report on continued slow reductions in spine length after five years of herbivore exclusion, show that these changes can be modified by resident acacia-ants, and show that simulated herbivory rapidly induces longer spines in both field and greenhouse experiments.

Study sites and methods

Study site

The field research was carried out from 1995 to 2001 at the Mpala Research Centre in Laikipia, Kenya (1800m asl; 0°17′N, 37°52′E). Rainfall averages 500–600 mm per yr. 1997–98 was an extremely wet El Nino yr, and 1999–2000 was an extremely dry La Nina yr. The vegetation at the study plots is *Acacia drepanolobium* bushed grassland (Taiti 1992), characteristic of heavy clay "black cotton" soils of impeded drainage (Ahn and Geiger 1987). Further details of the study ecosystem can be found in Young et al. (1997, 1998).

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 (Young et al. 1998). Eighteen 4-ha study plots were established in September 1995. Electric game fencing (Hoare 1992, Thouless and Sakwa 1995) and control of cattle herds exclude different combinations of large mammalian herbivores. 'Megaherbivores' in this study system are elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). 'Wildlife' here refers to other large mammalian herbivores (>15 kg). In particular, the wildlife exclusion plots excluded the following browsers of *A. drepanolobium* in addition to elephants and giraffes: Grant's gazelles (*Gazella granti*), elands (*Taurotragus oryx*), and oryx (*Oryx beisa*). Non-megaherbivore wildlife feed almost exclusively on leaves less than 2 m from the ground; megaherbivores feed at all heights up to several meters above the ground (Young and Isbell 1991, Young and Okello 1998, Young et al. 1998)

Exclosures create six combinations of access by cattle (C), wildlife (W), and megaherbivores (M): O (Control), C, W, WC, MW, MWC. Each treatment is represented by three 4-ha replicates, one in each of three blocks. Treatment plots within each block were assigned in a stratified random design. Further details of the exclosure experiment can be found in Young et al. (1998) and at http://envhort.ucdavis.edu/young/index.htm.

Acacia drepanolobium

Acacia drepanolobium is a small (up to 6 m) single-stemmed tree that occurs in East Africa on soils of impeded drainage (Coe and Beentje 1991). In our study area, most individuals are less than 3 m tall. They are defended by stipular spines (Young 1987, Milewski et al. 1991), symbiotic ants (Madden and Young 1992, Young et al. 1997, Stapley 1998), and perhaps leaf chemistry (Ward and Young 2002). A pair of straight sharp spines up to 6 cm long (exceptionally, up to 10 cm) exists at each node. Spines are produced along with their attendant terminal shoots during growth periods of rainy weather (Isbell 1998). 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. There are also short axillary shoots ("cushions") located at the nodes of branches up to several years old. During growth seasons, these produce new leaves, flowers and fruits, and some of them produce new branch shoots.

Approximately one node in five has a hollow swollen structure up to 5 cm in diameter at the base of the spine pair. These swollen thorns usually house one of four species of resident plant-ants. The most common ant species is *Crematogaster mimosae*, which occupies 40–60% of mature trees (Young et al. 1997, Palmer et al. 2000). It appears to be a true defensive mutualist, protecting the tree against herbivores and epiphytes in exchange for housing and nectar. A less common ant, *C. nigriceps*, also lives in the swollen thorns and feeds on the extrafloral nectaries, but systematically prunes most axillary shoots and many of the terminal shoots, often effectively sterilizing the tree (Young et al. 1997, Stanton et al. 1999). Two additional ant species (*C. sjoestedti* and *Tetraponera penzigi*) are also much less common than *C. mimosae*, and may also be essentially parasitic (Young et al. 1997, T. Palmer, pers. comm.; TPY, MLS, pers. obs.).

Spine measurements

We use spine lengths as a measure of mechanical defense. In August 2000, in each of the 18 experimental plots, we surveyed four different trees near each of nine central posts, set 50 m apart. These posts are used to demarcate 50×50 m sub-quadrats in these large plots (Young et al. 1998). Each of these posts was also at least 50 m from the nearest herbivore barrier. At each post, we sought out the nearest four trees that had branches at both 1.0 ± 0.3 m from the ground and 2.1 ± 0.3 m from the ground. For each tree, we chose three branches closest in height to 1.0 m or 2.1 m and with living shoots tips; we did not sample branches with obvious mammalian herbivory on recent (< 8 weeks) shoots. We sampled branches at 1 m because they were well within the reach of all large mammals, and branches at 2.1 m because they were within reach only to elephants and giraffes, while still being readily accessible to us. For this part of the study we only sampled trees occupied by the most common acacia ant, *Crematogaster mimosae*, because trees with different ant occupants have different characteristic spine lengths (Young and Okello 1998).

On each selected branch, we measured five cm from the growing shoot tip, and then sampled the next three nodes more proximate to the tree (to reduce allometric sources of spine length variation; Midgley and Ward 1996). If any of these was a swollen spine, it was skipped and the next node measured. At each node, one of the pair of spines was measured to the nearest mm. If the two spines were very different in size, 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 sampled 36 trees at each of two heights in each of 18 plots, for a total of 3888 spines on 648 trees.

We also separately sampled trees occupied by the less abundant *C. nigriceps*, which systematically prunes both axillary and terminal shoots on its host trees (Stanton et al. 1999). In each block, we sampled 10–12 trees in each of the total exclusion plot ("O") and the total access plot ("MWC"), again using the central posts as sampling points. We sampled 64 trees with trees with branches at 1 m and 64 trees with branches at 2 m. Trees occupied by *C. nigriceps* are much less abundant than trees occupied by *C. mimosae*, especially in the taller height classes (Young et al. 1997, Palmer et al. 2000). Therefore we sometimes sampled two different trees close to each other in order to get branches at both 1 and 2m. On each sampled branch, spines were measured as described above. We measured 384 spines on 128 branches.

Simulated browsing- greenhouse

A simulated herbivory experiment offered the opportunity to identify the cues to induce the production of longer spines. In December 1999, fifty seeds of *A. drepanolobium* collected from the field were planted into UC mix, a soil-less planting medium, into 15 cm pots in a greenhouse in Davis, CA, USA. They were provided drip irrigation with a dilute fertilizing solution, and given natural light. In April 2000, forty healthy seedlings were randomly assigned to one of four treatments in a 2×2 factorial design: 1) control (no manipulation); 2) growing shoot tips removed every two weeks; 3) axillary meristem cushions removed every two weeks; and 4) removal of both apical meristems and lateral meristems. Treatments were carried out April–June 2000. To mimic the behavior of *C. nigriceps*, axillary meristems were not removed from nodes bearing swollen spines, and were not removed from still-green stem nodes produced within the past week.

In September 2000 we measured spines on 8–9 remaining trees from each treatment class. On each tree, we sampled the three most mature branches. On each branch we sampled three distal spines using the same methods outlined above. These spines were on shoots produced at least six weeks after treatments had ceased. To measure the effects of treatment on growth contemporary with simulated herbivory, we also measured three spines further down the branch, starting at 5 cm above its last major fork.

Simulated herbivory, field experiments

In July 2000, we located seven trees in each of the three blocks, all in the total exclosure treatments. We wanted to control for the variation among ant species in mean spine length (Young and Okello 1998, Gadd et al. 2001), and to examine possible increases in spine length

Table 1. Analysis of variance for mean spine length on *A. drepanolobium* trees with respect to block, branch height, and wildlife exclusion treatment.

Effect	d.f.	SS	MS	F	p
Branch height	1	0.734	0.734	55.45	<0.0001
Wildlife treatment	2	0.827	0.414	31.23	<0.0001
Branch ht × Treatment	2	0.202	0.101	7.61	<0.01
Block	2	0.042	0.021	1.58	0.25
Error	10	0.132	0.0013		

associated with simulated herbivory. Therefore, we chose trees inhabited by *Crematogaster mimosae*, with short spine lengths, and with several branches approximately 1 m off the ground (mean, 108 cm). On each tree, we identified a forked branch, and randomly assigned one fork for shoot removal, and one as a same-branch control. We also selected a second control branch on the opposite side of the canopy. On all three shoots, we measured their length, and the length of the spines on the distal three nodes, excluding the distal 5 cm of the branch (as above). We measured 189 spines on 63 branches of 21 trees. Initial spine lengths were similar across blocks ($p = 0.28$) and across treatment classes ($p = 0.75$). We then removed the distal 2–4 cm of the shoot removal branch (mean, 2.9 cm) from each experimental shoot using pliers in an action similar to being coarsely clipped by large mammalian herbivores, and remeasured its length. In June 2001, we resurveyed the experimental and control branches, measuring spine length in the same way on any growth since June 2000. On shoot removal branches, this new growth arose from an axillary bud just below the damaged shoot tip.

Statistical analysis

For statistical analysis of the exclosure study, we took the mean of all three spine measurements for each branch, and then calculated the grand mean within each plot. 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 did not distinguish pairs of plots within each block that differed only in the presence of cattle. This left us two replicates of each of with three treatment wildlife classes in each block: 1) no browsers ("O" and "C"), 2) non-megaherbivore browsers ("W" and "WC"), and 3) all browsers, including megaherbivores ("MW" and "MWC"). 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. We also went back to the data collected in 1997 (Young and Okello 1998), and separately analyzed the spine length patterns for trees occupied by *C. mimosae* and *C. nigriceps*.

In the greenhouse simulated pruning study, we calculated the mean spine length for both distal and proximate sections of each branch, and averaged across the three branches to get two means for each tree. Mean spine lengths were normally distributed. We carried out a two way ANOVA testing the effects of treatment and spine location on spine length.

In the field simulated herbivory study, we compared mean spine lengths before and after simulated herbivory, and between spines on experimental and control branches, using one-way ANOVAs.

Results

Relaxation of spine lengths in exclosure plots

On trees occupied by *C. mimosae* in August 2000, mean spine length was strongly affected by wildlife treatment and branch height and was independent of block (Table 1). Overall, new spines in plots from which browsers were excluded were 35–40% shorter than spines in plots exposed to all browsers (Fig. 1). On low branches (1 m from the ground), spine lengths were low in total exclusion plots, and longer in plots that allowed wildlife and plots with both megaherbivores and wildlife. On higher branches (2.1 m from the ground), recently produced spines were similar in length in total exclusion plots and plots that allowed wildlife, but were longer in plots in which megaherbivores were allowed. This
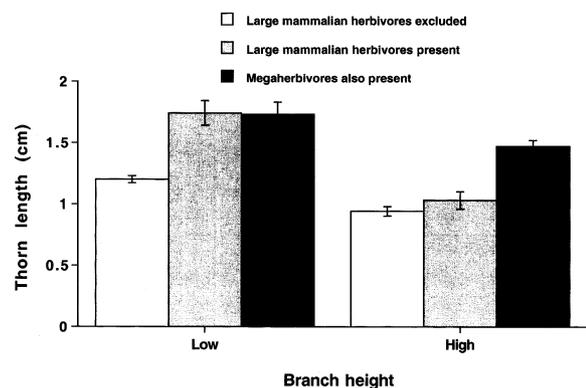

Fig. 1. Mean spine lengths of low ($\sim$1 m) and high ($\sim$2 m) branches on *A. drepanolobium* trees accessible to different herbivores. Only trees occupied by the ant *C. mimosae* were sampled. Bars are standard errors, based on three blocks. For complete sample sizes, see text. Herbivore treatment classes are based on the large herbivores allowed (see Methods).
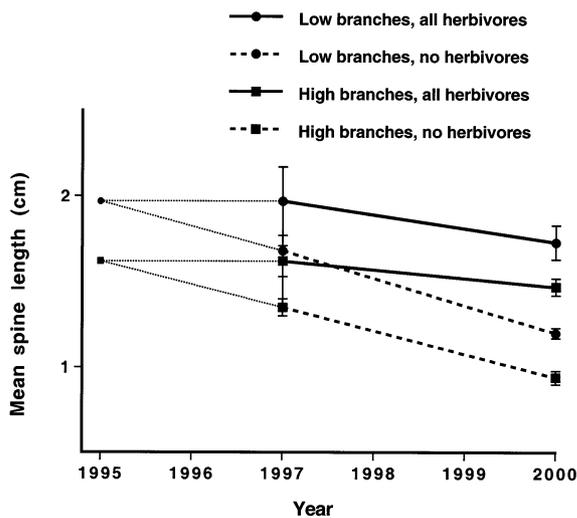
Fig. 2. Changes in mean spine length through time since the erection of the exclosure plots for *Acacia drepanolobium* trees occupied by *C. mimosae*. Initial (1995) spine lengths were inferred from mean 1997 spine length in plots accessible to herbivores, for illustrative purposes only. Bars are standard errors, based on three blocks. For low branches, "no herbivores" includes treatments O and C (see text); for high branches, "no herbivores" includes treatments O, C, W and WC.
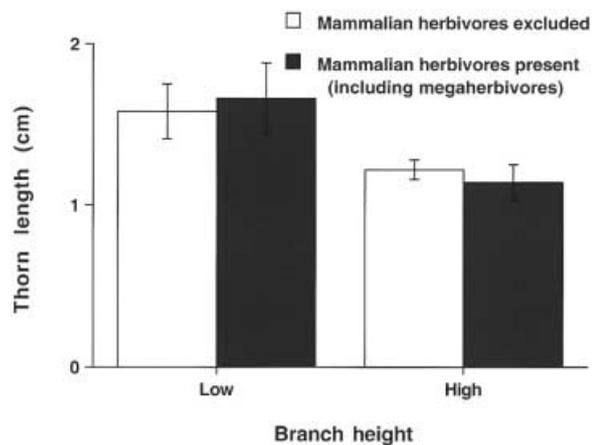

Fig. 3. Mean spine lengths on trees occupied by the pruning ant *C. nigriceps* in two treatments: exclusion of all large mammalian herbivores, and plots open to all herbivores. N = 31–33 for each sample, but standard errors bars are based on three blocks. A reanalysis of the 1997 data showed similar patterns.

height-specific response (Fig. 1) resulted in a significant branch height by wildlife treatment interaction (Table 1). When combined with the results from 1997 (Young and Okello 1998), these results suggest a steady decline in spine length over the five years of herbivore exclusion, while mean spine lengths in the control plots remained essentially unchanged (Fig. 2). Spines on lower branches remained 20% longer than spines on taller branches, even in the absence of herbivory (Fig. 1 and 2).

On trees occupied by *C. nigriceps* in August 2000, there were no significant differences between trees subject to large mammal browsing ("MWC") and trees protected from such browsing ("O") since 1995 (p = 0.99, Fig. 3). A reanalysis of the spine lengths measured in 1997 (in which 77 of the sampled trees were occupied by *C. nigriceps*) also showed no significant effects of herbivore treatment on spine lengths (p = 0.40). In both of these data sets, spines on lower branches were ∼30% longer than spines on higher branches (1997, p = 0.01; 2000, p = 0.006).

Induction of spine lengths in a greenhouse experiment

In the greenhouse experiment, spine lengths differed significantly among treatment classes (Fig. 4, Table 2, p = 0.0013). An a posteriori test (Tukey-Kramer HSD)

indicated that the spines on control plants were significantly shorter than the spines on any of the pruning treatments, with the effect being most pronounced for the plants on which only terminal shoots were pruned. Spines were 50–66% longer on plants subjected to simulated pruning than on control plants. Basal spines, produced during the treatment period, were 20% longer than distal spines, produced at least six weeks after the treatments ended (p = 0.029; Table 2).
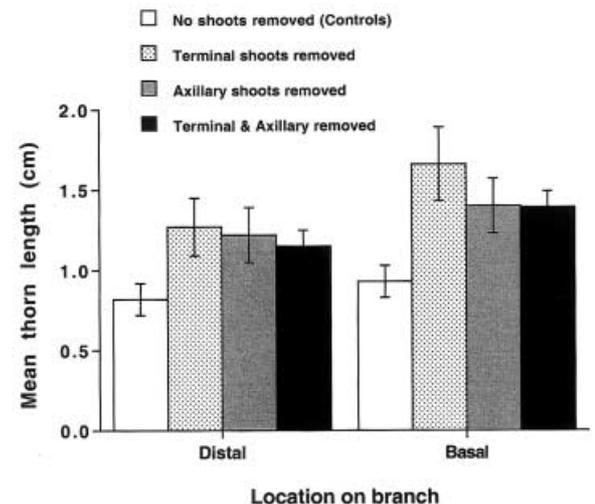

Fig. 4. Mean spine lengths on trees grown in a greenhouse (without either acacia ants or mammalian herbivores) and subjected to different treatments meant to simulate the pruning of axillary and terminal shoots carried out by *C. nigriceps*. Bars are standard errors.

Table 2. Analysis of variance for mean spine length on greenhouse *A. drepanolobium* trees with respect to simulated herbivory treatment and spine location (distal versus basal on the branch).

Effect	d.f.	SS	MS	F	p
Herbivory treatment	3	3.22	1.07	5.92	0.0013
Spine location	1	0.90	0.90	4.98	0.029
Treatment × Location	3	0.17	0.05	0.32	0.81
Error	60	10.89	0.18		

Induction of spine lengths in a field shoot removal experiment

In June 2001, we found 20 of the 21 experimental shoot removal trees in the exclosures. Overall, 60% of the marked branches exhibited no new growth (and no new spines) over the previous year, and were not remeasured for spine length. Shoot removal branches were no more or less likely to exhibit subsequent growth than were controls. Changes in spine length did not differ between the two control branch types (a fork of the experimental branch and a branch on the opposite side of the canopy, paired t-test, $t = 0.82$, $F = 0.67$, $p = 0.43$), and they were combined for further analysis. On the 23 branches that did grow and produce new shoot length during the previous year, the shoot removal branches produce significantly longer spines than did the control branches ($t = 3.44$, $F = 11.81$, $p = 0.0025$). Spine length increased more than 3-fold on the shoot removal branches (Fig. 5), attaining values similar to those on trees continuously

exposed to herbivory (Fig. 1, Young and Okello 1998).

Discussion

The field data presented here show a continued slow and steady reduction of spine length associated with experimental exclusion of wildlife browsers (Fig. 2). Spine length variation in *A. drepanolobium* canopies closely tracks browsing patterns. Browsing on branches 1 m from the ground was greatest in plots open to all herbivores, slightly lower in plots from which megaherbivores were excluded, and virtually non-existent in total exclosure plots. Browsing on branches 2 m from the ground was limited to plots accessible to megaherbivores (Young and Okello 1998, Young et al. 1998). Where only megaherbivores were excluded, the taller branches only they could reach produced smaller spines. Where all large mammalian herbivores were excluded, this spine length relaxation occurred on both low and high branches. Previous surveys indicated that in trees continually protected from browsing, mean spine lengths were less than 0.7 cm on low branches and less than 0.5 cm on high branches (Young et al. 1998). Using these figures as targets, five years of herbivore exclusion have resulted in approximately 50% of the spine length reduction that should eventually occur. The slight declines in mean spine length in control plots between 1997 and 2000 (Fig. 2) may have been related to the severe drought of 1999–2000, or merely to sampling error.

Relaxation of spine length due to exclusion of mammalian browsers was absent among trees occupied by the pruning ant *C. nigriceps*. We limited our main survey only to trees occupied by *C. mimosae* because we knew that the identity of ant occupant was associated with differences in mean spine length (Young and Okello 1998). It was during the current survey that we noticed the apparent lack of relaxation among trees occupied by *C. nigriceps*. Accordingly, in 2000 we resurveyed some of the plots for trees occupied by this ant (see Methods), and reanalyzed the data collected in 1997. Among *C. nigriceps* trees in both of these data sets, spine length remained long in all trees, even those protected from mammalian
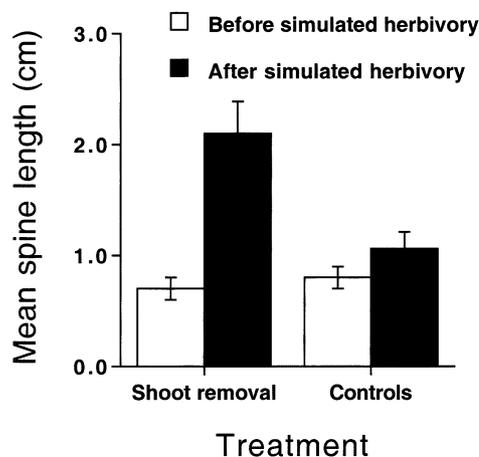
Fig. 5. Reinduction of spine length in simulated herbivory experiments on trees that had been protected from large mammalian herbivory for five years. Spine lengths before (open bars) and one year after (solid bars) simulated herbivory. Control branches were a) on a paired fork on the same branch and b) on a branch on the opposite side of the tree crown. Experimental shoot removal resulted in new spine three times longer than before the experiment, but no significant response on other branches on the same tree. Bars are standard errors.

176

browsing. This ant species uniquely engages in extensive pruning of both axillary and terminal shoots of *A. drepanolobium* (Young et al. 1997, Stanton et al. 1999). Based on the field data, we hypothesized that pruning by *C. nigriceps* produces an induced response similar to that produced by browsing of large mammals, perhaps because the tree cannot distinguish between ant pruning and mammalian herbivory. Trees induced in this way are likely to be better defended against mammalian herbivores (Milewski et al. 1991), but not against pruning by this ant species. Although this pruning may incidentally reduce herbivory by large mammals, it comes with a massive fitness cost – the pruned meristems do not produce any flowers or fruits, and trees occupied by *C. nigriceps* have greatly reduced reproduction (Young et al. 1997, Stanton et al. 1999).

Simulated herbivory like that of the pruning ant species was associated with greater spine length. In the greenhouse experiment, both terminal shoot removal and axillary shoot removal resulted in similar increases in spine length, and the combination of both treatments did not increase spine length further. These shoot removal techniques were specifically intended to simulate the pruning carried out by *C. nigriceps*. They therefore represent not only a general test of the effects of herbivory on spine length, but specifically a confirmation of our hypothesis that ant pruning maintains longer spines on trees occupied by *C. nigriceps*.

While pruning by *C. nigriceps* appears to induce the production of longer spines, mean spine length in trees occupied by this species were shorter on average than those on trees occupied by other ants (Young and Okello 1998). We hypothesize that although pruning by ants does maintain longer spines than would have been produced in the absence of herbivores, trees occupied by this species are protected from herbivory by large mammals by their unique architecture, including a high density of spines (Stanton et al. 1999). This protection might then prevent the even greater induction of spine length seen in trees occupied by *C. mimosae* and exposed to large mammals.

In our field studies, spines on higher branches were consistently shorter than spines on lower branches (Young 1987, Milewski et al. 1991, Young and Okello 1998). One possibility is that a decline in browsing with branch height results in less induction on higher branches. However, this difference is maintained even five years after the removal of herbivores, and in trees incidentally protected from herbivory for many years (Young and Okello 1998, see also above). This difference also exists in trees occupied by *C. nigriceps*, which appears to prune shoots at all branch heights. An alternative explanation is that this difference in spine lengths at different heights may be part of a more constituitive defense strategy that evolved under long-term historical patterns of greater browsing on lower branches. Other spinescent species exhibit greater spinescence on taller individuals than on shorter individuals (*Gleditsia*, O'Rourke 1949; *Aralia*, White 1988),

In a previous shoot removal experiment (Gadd et al. 2001), we failed to demonstrate a significant increase in spine length after shoot removal. However, that experiment was done after only two years of herbivore exclusion, and base spine lengths were still relatively long. In addition, there is considerable variation in spine length among trees, and our earlier sampling design may have been powerful enough to discern a treatment effect. We therefore decided to limit our field simulated herbivory experiment to trees in the total exclosure plots that had already relaxed spine length appreciably.

In our field experiment, we show here for the first time that simulated large mammal browsing induces greater spine length on trees that had relaxed spine length after several years of herbivore exclusion (Fig. 5). This induction occurred rapidly, in contrast to the slow relaxation that occurs after the exclusion of herbivores (Fig. 1). We propose that this difference is due to the different reliability of two kinds of signal. Experiencing herbivory should be a reliable signal that a given shoot is at risk from herbivory, and so the response is immediate and large. On the other hand, in systems where normal herbivory rates are low (10–20% of the shoots of *A. drepanolobium* are eaten each year; Young and Okello 1998, Young et al. 1998), the absence of herbivory in a given year or short series of years is not a reliable signal that a given shoot will not experience herbivory in the future. In such a situation, one might expect that the relaxation of spine length would be relatively conservative and gradual. In *Hormathophylla spinosa*, where herbivory rates were higher ($\sim 80\%$) and therefore more reliable indicators, relaxation of spine density was much faster (50% in two years) after the exclusion of herbivores (Gomez and Zamora 2002).

The induction of increased spine length was extremely local. Even branches on adjacent forks did not respond to experimental shoot removal with increased spine lengths. In addition, spines on taller branches respond to browsing independently from lower branches, even on the same tree (Fig. 1; Young 1987, Milewski et al. 1991, Young and Okello 1998). Although individual modules on plants are often relatively autonomous, one would think that it would be adaptive to have a more systemic response to herbivory, at least if variation in herbivory were predictable at the scale of entire trees. If instead herbivory were variable on finer spatial scales, the branch-specific responses would be more appropriate.

Localized, branch-specific induction of increased spine length suggests that this response may not have evolved under the selective pressure of temporal variation in the presence or absence of herbivores (Adler and Karban 1994, Karban and Adler 1996). Instead, the main variation in natural browsing may be associated with escape in space from browsers by production of branches beyond the reach of browser, as trees grow (Young 1987, Milewski et al. 1991). Perhaps the best source of information about whether an individual branch is out of reach of herbivores is the long-term absence of herbivory itself. We suggest that it is this escape from herbivory by individual branches high above the ground (or interior to the canopy) may have been a driving force in the evolution of the inducibility of spine length in *Acacia* spp.

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