

Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna

Corinna Riginos · Truman P. Young

Received: 1 December 2006 / Accepted: 19 June 2007 / Published online: 28 July 2007
© Springer-Verlag 2007

Abstract Plant–plant interactions can be a complex mixture of positive and negative interactions, with the net outcome depending on abiotic and community contexts. In savanna systems, the effects of large herbivores on tree–grass interactions have rarely been studied experimentally, though these herbivores are major players in these systems. In African savannas, trees often become more abundant under heavy cattle grazing but less abundant in wildlife preserves. Woody encroachment where cattle have replaced wild herbivores may be caused by a shift in the competitive balance between trees and grasses. Here we report the results of an experiment designed to quantify the positive, negative, and net effects of grasses, wild herbivores, and cattle on *Acacia* saplings in a Kenyan savanna. *Acacia drepanolobium* saplings under four long-term herbivore regimes (wild herbivores, cattle, cattle + wild herbivores, and no large herbivores) were cleared of surrounding grass or left with the surrounding grass intact. After two years, grass-removal saplings exhibited 86% more browse damage than control saplings, suggesting that

grass benefited saplings by protecting them from herbivory. However, the negative effect of grass on saplings was far greater; grass-removal trees accrued more than twice the total stem length of control trees. Where wild herbivores were present, saplings were browsed more and produced more new stem growth. Thus, the net effect of wild herbivores was positive, possibly due to the indirect effects of lower competitor tree density in areas accessible to elephants. Additionally, colonization of saplings by symbiotic ants tracked growth patterns, and colonized saplings experienced lower rates of browse damage. These results suggest that savanna tree growth and woody encroachment cannot be predicted by grass cover or herbivore type alone. Rather, tree growth appears to depend on a variety of factors that may be acting together or antagonistically at different stages of the tree’s life cycle.

Keywords *Acacia drepanolobium* · Woody encroachment · Competition · Positive interactions · Tree–grass interactions

Communicated by Alan Knapp.

C. Riginos (✉) · T. P. Young
Department of Plant Sciences,
University of California,
Mail Stop 1, One Shields Avenue,
Davis, CA 95616, USA
e-mail: criginos@ucdavis.edu

C. Riginos · T. P. Young
Mpala Research Centre,
P.O. Box 555, Nanyuki 10400, Kenya

T. P. Young
Center for Population Biology,
University of California, Davis, CA 95616, USA

Introduction

Increasingly, plant–plant interactions are recognized to be a complex mixture of positive and negative interactions (Dickie et al. 2005; Lortie et al. 2004; Maestre et al. 2005). The strength and net direction of these interactions can depend on numerous factors, including abiotic conditions, herbivory, life stage, and the particular species involved (Bertness and Callaway 1994; Rebollo et al. 2002; Riginos et al. 2005; Rousset and Lepart 2000; Tewksbury and Lloyd 2001). Recent empirical and theoretical work on positive interactions has focused largely on the role of abiotic stress (Bertness and Callaway 1994; Bertness and

Ewanchuk 2002; Callaway et al. 2002; Holmgren et al. 1997), while the role of herbivory has received relatively less attention. In savanna systems, large ungulate herbivores are considered to be major drivers of vegetation dynamics. Large herbivores can have multiple and potentially contrasting effects on savanna vegetation. First, they can directly reduce the abundance of the tree, grass, and forb species that they eat. Second, they can alter the competitive interactions between trees and grasses by reducing the abundance of one or the other guild (Scholes and Archer 1997; Skarpe 1992). Lastly, some positive interactions between plants may only be expressed in the presence of herbivores, as when one species protects another from herbivory (Rebollo et al. 2002). However, the effects of large herbivores on tree–grass interactions have rarely been studied in an experimental context.

In African savannas, intense cattle grazing is commonly associated with an increase in woody vegetation (Roques et al. 2001; van Vegten 1984), while wild browsing ungulates, especially elephants, can have the opposite effect (Dublin et al. 1990; Western and Maitumo 2004). “Woody” or “bush” encroachment can have profound negative consequences for native fauna (Dean et al. 1999; Scholes and Archer 1997) and rangeland productivity (Tobler et al. 2003). Woody encroachment is thought to occur via both direct and indirect mechanisms. Where cattle, which are primarily grazers, have replaced the diverse complement of grazing and browsing wild herbivores, trees may benefit from the reduction in browsing pressure (direct effect of browser absence). At the same time, increased grazing pressure may allow trees to escape from competition with grasses (indirect effect of cattle presence). Moreover, where wildlife and cattle coexist, as they do in large regions of sub-Saharan Africa, the presence of wild browsers may offset the effects of cattle on the tree–grass competitive balance (Augustine and McNaughton 2004).

Despite the importance of understanding how different land-use practices affect savanna dynamics and stability, an explicit experimental comparison of the effects of cattle and wild herbivores on tree–grass interactions has not yet been made. Here, we examine the effects, both positive and negative, of cattle, wild herbivores, and the grass layer on tree saplings. Saplings of African *Acacias* can persist within the grass layer for many years. These saplings represent a tree “bank” that, if released, may contribute substantially to woody encroachment (Midgley and Bond 2001; O’Connor 1995).

Saplings have the potential to be affected in multiple ways by herbivores and the grass layer, both separately and in combination. For example, browsing pressure and competition with grasses may combine to keep saplings within the grass layer when wild herbivores are present. Alternatively, grass may benefit saplings, for example by

maintaining a more moist soil microenvironment, or by concealing saplings from browsing herbivores (Western and Maitumo 2004). These positive effects may offset or supercede the negative (competitive) effects of grass on sapling growth, so that the net effect of grass on trees is neutral or even positive. Although anecdotal evidence suggests that positive and negative interactions between *Acacia* saplings and the grass layer depend on the types of large herbivores present, this has not been studied in an experimental context (Midgley and Bond 2001).

Here, we report the results of a grass removal experiment on *A. drepanolobium* saplings under four replicated experimental herbivore regimes in the “black cotton” savanna ecosystem in Kenya. Herbivore regimes were: cattle only, wild herbivores only, both cattle and wild herbivores, and neither cattle nor wild herbivores. In conducting this study, we posed the following questions:

1. Do cattle and wild herbivores have different effects on sapling growth?
2. Does grass have a negative effect on sapling growth?
3. Does grass affect the degree to which saplings are browsed?
4. Do the effects of grass on saplings differ under different herbivore regimes?
5. How do grass and herbivores affect the colonization or abandonment of saplings by symbiotic ants?

Methods

Study site and species

This study was conducted at the Mpala Research Centre (36°52′E, 0°17′N; mean annual rainfall \approx 550 mm), in the Laikipia district of central Kenya. Here, the poorly drained, high clay content “black cotton” soil supports a highly productive savanna system (5–10 T dry biomass/ha year; Otieno 2004). The whistling thorn acacia (*A. drepanolobium*) comprises 97% of the woody cover in this system and five species of grasses make up over 90% of the herbaceous cover (Young et al. 1998). All of the dominant grass species are perennial bunchgrasses. Although the herbaceous layer includes small quantities of several forb species, we will hereafter use the term “grass” to refer to all herbaceous understory species.

Acacia drepanolobium is one of the most abundant and widespread tree species in eastern Africa (Coe and Beentje 1991). It is typically found on impeded-drainage black cotton soils, where it forms nearly monospecific stands over hundreds of kilometers. It has been identified as one of Africa’s most serious rangeland invaders (Angassa 2005; Pratt and Gwynne 1977). At the Mpala Research Centre,

numerous saplings of *A. drepanolobium* persist within the grass layer for many years, growing minimally in height or not at all relative to larger individuals (T.P. Young, T.M. Palmer, and M.L. Stanton, unpublished data). Trees of *A. drepanolobium* are characterized by swellings at the base of some, but not all, thorns. These swollen thorns are produced inherently by the plant itself, regardless of exposure to insects or mammalian herbivores (Hocking 1970), even in greenhouse settings (Young et al. 2003). Trees are typically occupied by one of four species of symbiotic ants, *Crematogaster mimosae*, *Crematogaster nigriceps*, *Crematogaster sjostedti*, or *Tetraponera penzigi* (Palmer et al. 2000; Young et al. 1997). Small saplings, however, are often not occupied by ants. Here, we focus on saplings that are unoccupied by ants and saplings occupied by *C. mimosae*, *C. nigriceps*, or *T. penzigi*, since these are the four occupancy states most commonly seen among the smallest trees.

The Mpala Research Centre is managed both for domestic cattle production and for wildlife conservation. Within the Research Centre, the Kenya Long-term Exclusion Experiment (KLEE) provides a unique opportunity to examine the effects of wild and domestic ungulate herbivores on savanna community dynamics. KLEE, a set of large-scale (4-ha) herbivore exclosures replicated in three blocks, was established in 1995 (Young et al. 1998). Here, we focus on four of the KLEE herbivore regimes: cattle only, wild herbivores only, both cattle and wild herbivores, and neither cattle nor wild herbivores. Cattle densities in the plots are moderate in comparison to other commercial cattle operations, but high in comparison to the total wildlife density in the landscape (Young et al. 2005). Wild herbivores common at this site include grazers, namely plains zebras (*Equus burchelli*), hartebeest (*Alcelaphus buselaphus*), buffalos (*Syncerus caffer*), and oryx (*Oryx gazella*), as well as browsers and mixed feeders, namely elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Grant's gazelles (*Gazella granti*), and eland (*Taurotragus oryx*). Common smaller mammalian herbivores not excluded by the exclosure fences include steinbuck (*Raphicerus campestris*), hares (*Lepus capensis*), and rodents (mostly *Saccostomus mearnsi*).

Experimental design

Within each of the 12 plots ($n = 3$ for each of four herbivore regimes), we randomly selected 28 saplings of *A. drepanolobium* in transects roughly 50×200 m, for a total of 336 trees. All saplings were at least 15 cm tall (smaller saplings and seedlings are very rarely encountered) and less than 70 cm tall (the approximate height of the grass layer). In each plot, we selected six saplings occupied by each of three species of symbiotic ant (see above) and ten

saplings unoccupied by ants. Half of the saplings of each ant occupancy type within each plot were randomly assigned to a grass-removal treatment, and the remaining saplings were assigned to a control treatment.

In July of 2004, we clipped and sprayed with glyphosate (Roundup[®], Monsanto Co, St. Louis, MO, USA) all herbaceous vegetation in a 50 cm radius around each grass-removal sapling. Trees were wrapped in plastic while the herbicide was being applied. All grass clippings were removed. Initial measurements of sapling size included height, basal diameter, and the number of swollen thorns. Basal stem diameter has been shown to correlate well with biomass for *A. drepanolobium* ($r^2 = 0.96$; Okello et al. 2001). Total stem length also provides a highly sensitive measure of tree size, but it is very laborious given the highly branched architecture of the larger saplings. To test the efficacy of number of swollen thorns as a proxy for stem length, we measured the total stem length (including the main stem(s) and all branches) and counted the swollen thorns for all saplings in one block of the experiment in August 2005 and examined the correlation between these two measures. The height, basal diameter, and number of swollen thorns for all saplings were recorded in August 2005 and in August 2006. In both 2005 and 2006 we randomly selected ten stems on each tree (or all stems if there were fewer than ten) and counted the proportion of stem tips that had been bitten off (browsed). We could not quantify the number of individual leaves browsed, since it is not possible to distinguish between leaves that have been removed by browsers and leaves that have been dropped due to drought stress or senescence. Saplings were also monitored for change in ant occupancy state. Finally, for each experimental sapling we counted the number of trees (almost exclusively conspecifics) within a 3-m radius around the sapling.

Data analysis

We focus on basal diameter and number of swollen thorns as the main measures of change in sapling size. Number of swollen thorns proved an accurate, efficient, and unbiased measure of total stem length for *A. drepanolobium* trees of this size. Total number of swollen thorns was closely correlated with total stem length ($r^2 = 0.72$, $P < 0.001$, $n = 102$). This relationship was independent of herbivore regime, grass treatment, and ant occupancy (Table 1). Height, on the other hand, was a poor measure of sapling size, exhibiting a logarithmic relationship with total stem length and basal diameter and changing minimally over the course of the experiment. Considerable stem growth was lateral. Consequently, we present results only for basal diameter and number of swollen thorns. Both variables were log-transformed to meet ANOVA assumptions of

Table 1 Regressions for number of swollen thorns by total stem length, within each experimental treatment

	<i>n</i>	Slope	<i>r</i> ²	<i>P</i>
Grass present				
No large herbivores	14	0.06	0.88	<0.0001
Cattle	10	0.05	0.37	0.06
Wildlife	10	0.07	0.78	<0.001
Cattle + wildlife	13	0.09	0.73	<0.001
Grass removed				
No large herbivores	13	0.08	0.80	<0.0001
Cattle	14	0.07	0.75	<0.0001
Wildlife	14	0.06	0.71	<0.001
Cattle + wildlife	13	0.09	0.91	<0.0001
Ant occupancy				
No ants	19	0.07	0.52	<0.001
<i>C. mimosae</i>	21	0.08	0.68	<0.0001
<i>C. nigriceps</i>	21	0.07	0.82	<0.0001
<i>T. penzigii</i>	20	0.06	0.64	<0.0001

Fitted lines did not differ depending on treatment (no significant interaction between total stem length and treatment in an ANCOVA for number of swollen thorns when all classes were combined: $F = 1.27$, $P = 0.27$), nor did they differ depending on ant occupancy (no significant interaction between total stem length and ant occupancy in an ANCOVA for number of swollen thorns when all classes were combined: $F = 1.50$, $P = 0.22$)

homogeneity of variances. Trees that died or died back and subsequently coppiced ($n = 45$ out of 336) were excluded from all analyses. The proportion of such trees did not differ significantly with respect to either herbivore or grass treatment.

The effects of the grass and herbivore treatments on basal diameter, number of swollen thorns, and proportion of stem tips browsed were analyzed as a split-plot ANOVA, with cattle presence/absence and wild herbivore presence/absence as whole-plot effects and grass presence/absence as the sub-plot effect. For growth traits, initial size (initial basal diameter and number of swollen thorns, respectively) was used as a covariate to control for differences in sapling size at the start of the experiment. Subsequent models included the number of neighboring trees as a covariate to examine possible effects of neighborhood tree density on sapling growth.

In addition, we examined the changes in ant occupancy state that occurred over the experimental period. Differences among treatments in final ant occupancy were analyzed using Pearson's χ^2 . The effects of final ant occupancy status on sapling growth and browse damage were examined by including ant occupancy as an effect in the above ANOVAs. Tukey's tests revealed that growth and browse damage were related to whether saplings were occupied by ants or not, but did not depend on the particular species of

ant. We therefore reduced ant occupancy to a two-factor effect, occupied versus unoccupied, preserving degrees of freedom to test for interactions between ant occupancy and other factors.

Initially, we analyzed the data from the first year of the experiment (2004–2005) separately from the data from the second year of the experiment (2005–2006). Although the effects of the grass and herbivore treatments differed in magnitude between the two years, the results were not qualitatively different. Therefore, we present cumulative growth and average browse damage over the two-year experimental period.

In all ANOVA and ANCOVA models, block was treated as a random factor, and wildlife, cattle, and grass treatment were treated as fixed factors. All data were analyzed using SAS (Version 9.1, SAS Institute, Inc, Cary, NC, USA).

Results

Sapling browse damage

Browse damage to saplings was strongly affected by both herbivore regime and grass treatment (Fig. 1). While cattle presence did not affect the degree of browse damage ($F = 0.29$, $df = 1$, $P = 0.61$), wild herbivore presence did ($F = 20.79$, $df = 1$, $P = 0.004$). Trees in the wild herbivores and cattle + wild herbivore regimes were browsed 86% more, on average, than trees in the no-herbivore and cattle-only regimes.

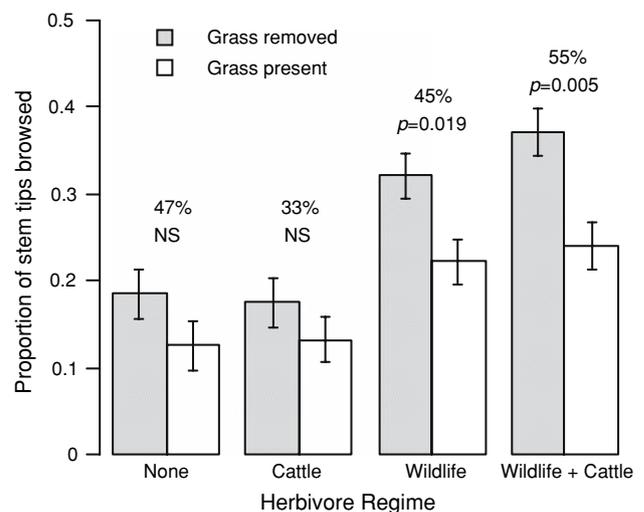


Fig. 1 Mean (\pm SE) proportion of stems browsed among saplings in four herbivore regimes and with or without the surrounding grass removed. Percent differences and *P* values for pairwise comparisons between grass-removal and grass-present saplings are presented for each herbivore regime

Grass removal resulted in an average of 45% more browse damage to saplings (Fig. 1; main effect of grass treatment: $F = 18.71$, $df = 1$, $P < 0.0001$). The effect of grass removal on browse damage did not differ significantly across herbivore regimes; no interaction between cattle presence or wildlife presence and grass treatment was detected (cattle: $F = 0.05$, $df = 1$, $P = 0.83$; wildlife: $F = 2.83$, $df = 1$, $P = 0.09$), and within each herbivore regime the percent difference in browse damage for grass-removal trees relative to control trees was similar (Fig. 1). This suggests that the effects of wild herbivores and grass removal on browse damage were additive. Overall, saplings were browsed most where wildlife were present and grass absent, and least where wildlife were absent and grass present.

Sapling growth

Herbaceous vegetation strongly suppressed sapling growth. After two years, grass-removal trees had, on average, a total stem length 108% greater and a diameter 16% greater than control saplings (Fig. 2; stem length: $F = 39.21$, $df = 1$, $P < 0.0001$; basal diameter: $F = 11.47$, $df = 1$, $P < 0.001$). Grass removal benefited sapling growth similarly in all herbivore regimes; no significant interactions between cattle presence or wild herbivore presence and grass treatment were detected.

While herbaceous vegetation suppressed sapling growth, the presence of wild herbivores had a positive effect on saplings. Cattle presence did not affect stem growth ($F = 0.19$, $df = 1$, $P = 0.68$) but wild herbivore presence did ($F = 8.21$, $df = 1$, $P = 0.029$); after two years, trees in the plots accessible to wild herbivores and to cattle + wild herbivores had accrued, on average, 25% more total stem length than trees in the no-herbivore and cattle-only regimes (Fig. 2a). Although the effect of wild herbivores on basal diameter was not significant ($F = 2.09$, $df = 1$, $P = 0.19$), basal diameter exhibited a trend in the same direction as stem length in response to wild herbivores (Fig. 2b). Overall, saplings grew most where wild herbivores were present but grass absent, and least where wild herbivores were absent and grass present.

The effect of wild herbivores on sapling stem growth was in part correlated with differences in neighborhood tree density across herbivore regimes. Number of neighboring trees was a significant covariate when included in the ANCOVA of sapling stem growth ($F = 6.45$, $df = 1$, $P = 0.012$) and substantially reduced the variance in sapling growth explained by wildlife presence ($F = 8.21$ and $P = 0.029$ when neighbors were not included as a covariate, versus $F = 4.55$ and $P = 0.077$ when neighbors were included). A two-way ANOVA with block and herbivore regime as the main effects revealed that saplings in the cattle + wild herbivores regime had 43% fewer neighbors than saplings in the plots without wild herbivores (Fig. 3).

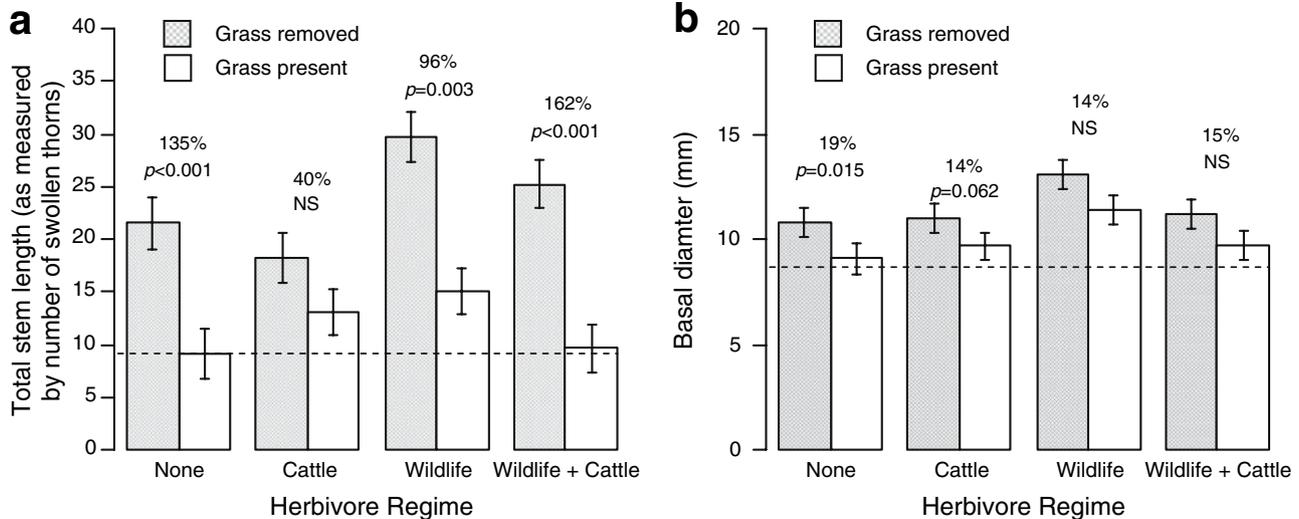


Fig. 2a–b Mean (\pm SE) growth among saplings in four herbivore regimes and with or without the surrounding grass removed. Growth is measured as **a** number of swollen thorns (a proxy for total stem length), when holding the initial number of swollen thorns constant, and **b** basal diameter, when holding the initial basal diameter constant. Percent differences and P -values for pairwise comparisons

between grass-removal and grass-present saplings are presented for each herbivore regime. *Dashed lines* represent the mean size of saplings across all treatments at the start of the experiment. Mean initial sizes were very similar in magnitude among the eight treatments

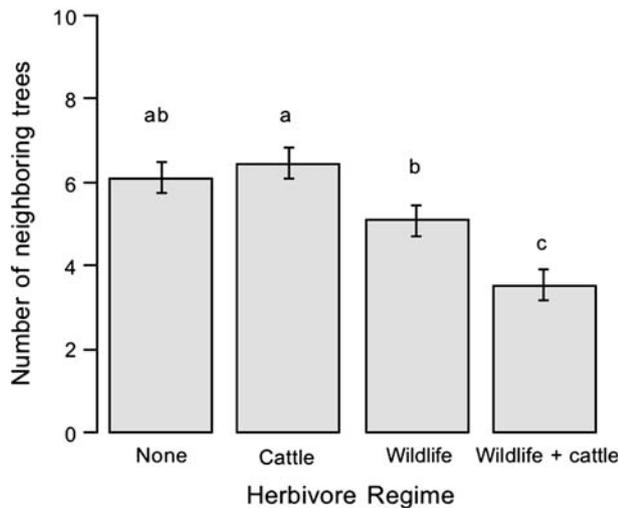


Fig. 3 Mean (\pm SE) number of neighboring trees in a 3-m radius around focal saplings in four herbivore regimes. Significant differences ($P < 0.05$, Tukey's HSD) among herbivore regimes are indicated with letters

The wild herbivores-only regime showed a similar pattern, with 18% fewer neighboring trees than the cattle-only plots and 16% fewer than in the herbivore exclusion plots, although the latter comparison was not statistically significant.

Relationship between growth and browse damage

Across herbivore and grass treatments, sapling growth showed similar patterns to browse damage (Figs. 1, 2). One might infer that herbivores induced or responded to this increased growth (within each herbivore regime). However, within each treatment, individual tree growth (measured as the change in total stem length or basal diameter over the two-year experimental period) was not correlated with browse damage to that tree (Table 2). Moreover, neither measure of growth explained a significant amount of variation when included as a covariate in ANCOVAs of sapling browse damage (stem length: $F = 1.92$, $df = 1$, $P = 0.17$; basal diameter: $F = 0.16$, $df = 1$, $P = 0.69$). These findings were consistent even when we considered growth and browse damage within each year of the experiment. Taken together, these results suggest that there was no direct relationship between an individual trees' growth and browse damage.

Ant occupancy

Sapling ant occupancy status changed markedly over the course of the experiment (Fig. 4). After two years, saplings

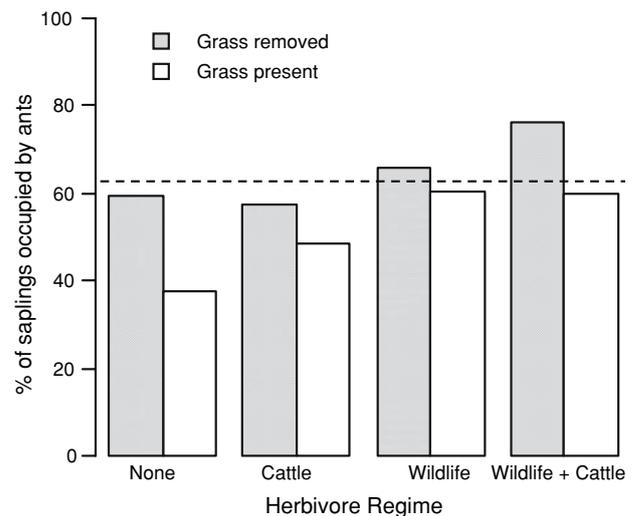


Fig. 4 Percent of saplings occupied by symbiotic ants after two years in each of four herbivore regimes, with or without the surrounding grass removed. The dashed line represents the percent of saplings occupied by ants at the start of the experiment (by design, 27 out of 42, or 64% of saplings in each plot). See "Results" for χ^2 comparisons among treatments

in the grass-removal treatment were, on average, 30% more likely to be occupied by ants than saplings in the control treatment ($\chi^2 = 4.66$, $df = 1$, $n = 276$, $P = 0.031$). There was also a significant effect of wildlife presence ($\chi^2 = 6.17$, $df = 1$, $n = 276$, $P = 0.013$), but not cattle presence ($\chi^2 = 0.51$, $df = 1$, $n = 276$, $P = 0.48$), on ant occupancy. Saplings in the wildlife and cattle + wildlife herbivore regimes were more likely to be occupied by ants than saplings in the cattle and no large herbivores regimes. These differences reflect both abandonment of saplings in the absence of wildlife as well as colonization, particularly by the ant *Crematogaster mimosae*, in the presence of wildlife.

Sapling ant occupancy status, in turn, was associated with differences in both browse damage and growth. Saplings not occupied by ants were browsed 30% more than saplings occupied by ants ($F = 8.31$, $df = 1$, $P = 0.004$). This effect was consistent across grass and herbivore treatments. Ant presence was also related to sapling growth. After two years, trees occupied by ants had a total stem length 87% greater and basal diameter 30% greater than trees not occupied by ants (stem length: $F = 115.51$, $df = 1$, $P < 0.0001$; basal diameter: $F = 39.40$, $df = 1$, $P < 0.0001$). For both measures of growth, there was a significant interaction between ant occupancy and grass treatment (stem length: $F = 4.05$, $df = 1$, $P = 0.045$; basal diameter: $F = 6.61$, $df = 1$, $P = 0.011$); saplings that were not occupied by ants did not respond to grass removal, whereas those occupied by ants grew significantly more when their surrounding grass was removed. In general, ant

Table 2 Regressions for growth (change in total stem length and change in basal diameter) by browse damage, within each experimental treatment

	<i>n</i>	Slope	<i>r</i> ²	<i>P</i>
<i>Stem growth</i>				
Grass present				
No large herbivores	31	−0.004	0.04	0.25
Cattle	35	−0.001	0.01	0.56
Wildlife	35	−0.000	0.00	0.90
Cattle + wildlife	34	−0.002	0.01	0.54
Grass removed				
No large herbivores	31	−0.003	0.08	0.12
Cattle	32	−0.002	0.02	0.41
Wildlife	34	−0.001	0.03	0.32
Cattle + wildlife	33	0.002	0.04	0.28
<i>Diameter growth</i>				
Grass present				
No large herbivores	31	0.011	0.02	0.46
Cattle	35	−0.002	0.00	0.83
Wildlife	35	0.007	0.02	0.47
Cattle + wildlife	34	−0.009	0.02	0.51
Grass removed				
No large herbivores	31	0.001	0.00	0.91
Cattle	32	0.002	0.00	0.81
Wildlife	34	0.012	0.09	0.06
Cattle + wildlife	33	0.001	0.00	0.85

These results suggest that there is no relationship between growth and browse damage for individual trees

occupancy status was closely correlated with sapling growth, both for individual trees and across the different experimental treatments.

Discussion

Cattle grazing, separately as well as in combination with other factors such as CO₂ fertilization, climatic changes, and fire suppression, has been associated with an increase in woody vegetation in savannas all over the world (Archer 1995; Archer et al. 1995; Bond et al. 2003; Roques et al. 2001; van Auken 2000; van Vegten 1984). In African savannas, this woody encroachment has generally been attributed to trees escaping from competition with grasses and browse pressure where cattle have replaced wildlife as the predominant herbivores. However, experimental tests of these hypotheses have been few. Using a large-scale, long-term experiment, we tested the effects of grass, cattle, and wild herbivores on *A. drepanolobium* saplings. As expected, grass had a net negative effect on saplings, even though its presence also reduced herbivory on these trees. Contrary to our expectations, wild herbivores had a net

positive effect on sapling growth, even though they directly hindered saplings by browsing them.

Positive and negative effects of grass

Saplings that were not surrounded by grass were browsed much more than saplings that were surrounded by grass (Fig. 1). This positive effect of grass, however, was far outweighed by the negative effects of grass on saplings. After two years, grass-removal trees were, on average, more than twice the size of control trees in terms of total stem length (Fig. 2a). Control trees grew minimally or not at all (Fig. 2). Thus, grass appears to have had a strong competitive effect on sapling growth.

The close concordance between the effects of grass treatment on net sapling growth and browse damage can be explained by at least three hypotheses. First, greater growth among grass-removal saplings may have attracted greater browse pressure. Second, since trees of this species are capable of fully compensatory growth following browse damage (Gadd et al. 2001), it is possible that greater browse damage resulted in greater growth among grass-removal saplings (over-compensation). A third explanation is that there was no causal relationship between growth and browse damage, but rather that the presence of grass deterred herbivores from browsing the saplings. We suggest that the latter is most likely to be operating in this system. If either of the first two hypotheses were driving the relationship between mean growth and mean browse damage, we would expect there to be a positive relationship between the growth and browse damage experienced by individual trees within each of the grass-removal and control treatments. We found no evidence for such a relationship (Table 2). Moreover, Gadd et al. (2001) found no evidence for over-compensation in this species. In contrast, we know from first-hand experience that saplings can be extremely well concealed within the grass layer, but easily spotted when the surrounding grass is removed. We suggest that grass in this system facilitates saplings by concealing them from herbivores, even as it competes with them in terms of growth.

The competitive effects of grass on *A. drepanolobium* saplings, however, did not track patterns of aboveground herbaceous biomass. In the KLEE exclosures, herbaceous vegetation has the lowest aboveground biomass where cattle are present and the highest biomass where all large herbivores are excluded (Young et al. 2005). A logical hypothesis is that removing grass where cattle are present (and grass biomass is lowest) would have a lesser effect on tree growth than removing grass where cattle are not present. Here, however, grass removal had the greatest relative effect on the growth of saplings in the no large

herbivores and cattle + wild herbivores regimes (Fig. 2), the herbivore regimes with the highest and lowest grass biomass, respectively. Thus, it appears that the intensity of grass effects on trees is not directly linked to aboveground biomass. It is likely that grass–sapling competitive interactions occur belowground or depend on grass productivity, rather than biomass. Unfortunately, we do not have reliable estimates of grass primary productivity in the KLEE exclosures.

Regardless of the mechanisms, the results of this study clearly demonstrate that grass can have strong effects on trees, both positive and negative. Although the positive effects of trees on understory vegetation (via mechanisms such as soil nutrient enrichment, shading, and hydraulic lift) have received much attention (Belsky 1994; Belsky et al. 1993; Callaway et al. 1991; Ludwig et al. 2003; Vetaas 1992), few studies have considered the potential for grasses to benefit trees (Lauenroth and Aguilera 1998). In a grass removal experiment on *A. xanthophloea* seedlings, Western and Maitumo (2004) also found evidence that grass concealed trees from browsers and that this positive effect was only seen where large wild herbivores were present. Our results further suggest that grasses can have positive effects on small *Acacia* trees, supporting the hypothesis that associational-defense facilitation among plants is more important where herbivore pressure is greater (Bertness and Callaway 1994; Rebollo et al. 2002).

As expected, however, the net effect of grass was negative. Despite the common perception that grass suppresses tree seedlings and saplings in savanna systems, few studies have explicitly tested the competitive effects of grass on trees (Midgley and Bond 2001). Knoop and Walker (1985) demonstrated that grass can suppress larger *A. tortilis* and *A. nilotica* trees. O'Connor (1995) tested the hypothesis that grass competition suppresses the establishment of *A. karroo* seedlings, but found no evidence to support this, at least in the first year of growth. Neither of these studies considered the role of herbivores in affecting this competition. Western and Maitumo (2004) found, contrary to our findings, that competitive suppression of seedlings by grasses had a statistically significant but biologically negligible effect on seedlings relative to the effects of browsing herbivores on seedling survival. In their study, the density of herbivores, especially elephants, was very high, and many seedlings were consumed by elephants. At our study site, herbivore densities are not nearly as high, and only one out of 336 experimental saplings was killed by the direct effects of large herbivores. Thus, our results demonstrate that grass can have a substantial effect in suppressing the growth of prereproductive trees where trees are exposed to a moderate density of large herbivores.

Positive and negative effects of wild herbivores

It has been suggested that *Acacia* saplings persisting in the grass layer represent a sapling “bank” that, if released, will contribute substantially to woody encroachment (Midgley and Bond 2001; O'Connor 1995). However, the effects of cattle grazing on sapling growth, as opposed to the effects of mixed grazing and browsing by wild herbivores, have not previously been investigated. We expected that saplings would exhibit the greatest growth in the cattle-only herbivore regime due to less browsing pressure and less competition from grasses as compared to the other herbivore regimes. Contrary to these expectations, we found that saplings of *A. drepanolobium* did not grow more where cattle were present. In fact, saplings grew more where wild herbivores were present, despite being browsed more. The latter is not surprising, given that cattle hardly ever browse on *A. drepanolobium* (Odadi et al. 2007). These results suggest that wild herbivores had an indirect positive effect on saplings, even while they had a direct negative effect on them.

There are a number of hypotheses that could explain these results. One hypothesis is that smaller herbivores not excluded by the KLEE exclosures (e.g., small mammals and arthropods) browsed more on saplings where wild herbivores were absent. Unfortunately, it is not possible to distinguish between leaves or leaflets lost due to browsing by small herbivores and those lost due to senescence or desiccation. Small mammal abundances, however, do not support the hypothesis that small mammals overcompensate for larger mammals in terms of browse damage. Steinbuck and hares do not appear to differ in their densities among the KLEE treatments (T.P. Young, unpublished data). Rodents persist at much higher densities in plots that exclude all large herbivores, but they exhibit similar densities in the cattle-only, wild herbivores-only, and cattle + wild herbivores regimes (Goheen et al. 2004; Keesing, in preparation). Thus, it is unlikely that rodents overcompensate for the absence of wild herbivores but not cattle in terms of browse damage to saplings. Some insect herbivores may respond to the KLEE treatments (Misurelli 2002; Pringle et al. 2007); however, they appear to have only minor effects on *A. drepanolobium* (T.P. Young, personal observation).

A second hypothesis is that differences in soil fertility have developed among the KLEE treatments since the exclosures were established. When *A. drepanolobium* seedlings were used in a bioassay experiment, however, no differences in soil fertility were found (C. Riginos, unpublished data).

A third hypothesis is that neighborhood competition among plants is higher where wild herbivores are absent. As noted above, cattle, not wild herbivores, play the

greatest role in reducing grass biomass and potential tree–grass competition in this system. Thus it is unlikely that neighborhood grass competition alone explains our results. Neighborhood tree density, however, was 16–43% lower in the plots accessible to wildlife than in the plots that excluded wildlife. The density of neighboring trees around saplings was a significant covariate in explaining sapling stem growth and its inclusion in statistical models substantially reduced the amount of variation explained by wild herbivore presence. This suggests that lower neighborhood tree density—and consequently less intraspecific competition—may offer a partial explanation for the greater growth of *A. drepanolobium* saplings in plots accessible to wild herbivores.

The present differences in tree density have arisen since the start of the KLEE experiment; tree density among herbivore regimes was similar when the plots were established in 1995 (T.P. Young, unpublished data). By 2005, however, density was significantly reduced in the plots accessible to wild herbivores relative to plots that exclude wild herbivores (Pringle et al. 2007; Goheen, in preparation). This change in density probably reflects an increase in elephant density in the region (T.P. Young, personal observation). Tree trunk breakage, almost certainly due to elephants, is significantly higher in plots that allow access to wild herbivores than in plots that exclude wild herbivores (Goheen, in preparation). Thus, it is possible that elephants are having an indirect positive effect on the growth of *A. drepanolobium* saplings by reducing the overall level of intraspecific competition they experience. However, it remains unclear why (a) tree density is lower in the wild herbivores-only plots relative to the cattle + wild herbivores plots if elephants are the main agents of tree destruction, and (b) why sapling growth is equivalent across these two herbivore regimes despite differences in neighborhood tree density. We are currently conducting experimental manipulations of tree density to quantify the effects of intraspecific competition on *A. drepanolobium* growth relative to other determinants of tree growth in this system.

Effects of symbiotic ants

A. drepanolobium is well known for hosting several species of symbiotic ants (Palmer et al. 2000; Young et al. 1997). Only seedlings and small saplings of this species tend not to be occupied by ants. However, the processes leading to ant colonization of saplings and the role of colonization in sapling escape from the grass layer are poorly understood. Here, saplings that were colonized or not abandoned were browsed substantially less than unoccupied saplings, despite growing more. These results match results seen

among larger *A. drepanolobium* trees. Ants occupying *A. drepanolobium* are known to defend larger trees against browsing herbivores (Madden and Young 1992; Stapley 1998). The association between prior tree vigor and subsequent likelihood of colonization or takeover by competitively dominant ant species has also been well documented (Palmer et al. 2000). Ants appear to respond to tree vigor at this temporal scale, rather than cause it. Thus, differences in ant occupancy among our experimental treatments (Fig. 4) probably developed because ants were tracking differences in tree vigor among grass and herbivore treatments. Occupied saplings, however, clearly benefited from reduced browse damage. Ant species composition among saplings in the grass-removal and wild herbivore treatments also shifted towards relatively higher occupancy by *Crematogaster mimosae*, one of two symbiotic ant species (along with *C. nigriceps*, which is not considered here) that is associated with relatively lower levels of browse damage among *A. drepanolobium* trees (Palmer and Brody 2007). Thus ant occupancy may confer additional fitness advantages to saplings in these treatments, perhaps accelerating their recruitment into the larger size classes.

Conclusions and implications for woody encroachment

The results presented here provide some insight into the complex set of mechanisms underlying woody encroachment. *A. drepanolobium* itself is a serious encroacher in East Africa (Angassa 2005; Pratt and Gwynne 1977). Our experimental study of this species demonstrates that grass can substantially suppress sapling growth. This in turn suggests that heavy cattle grazing could indirectly benefit sapling growth and recruitment into the reproductively active size classes. In many areas where woody encroachment is severe, cattle virtually eliminate the grass layer throughout much of the year, similar to our grass removal treatment. However, the moderate levels of cattle grazing at our study site could not be linked directly to differences in sapling growth. It remains unclear how much cattle would need to drive down the density and/or productivity of grasses to release trees from grass competition.

Although we found no effects of cattle on *A. drepanolobium* saplings, we found a positive effect of wild herbivores on sapling growth. At first glance this appears to contradict the idea that cattle grazing and wildlife extirpation combine to cause woody encroachment. However, the net effect of wild herbivores over the ten years since the KLEE enclosures were established has been to reduce the density of neighboring trees. In fact, this reduction may be partly responsible for the greater vigor of saplings in the wildlife-accessible plots. Additionally, it remains to be seen whether the relatively short-term growth differences

observed in the present study translate to differences in adult recruitment. Continued monitoring of experimental trees will help to illuminate the longer term effects of grass and herbivore treatments on *A. drepanolobium* saplings.

We have demonstrated that the herbaceous layer can have both positive and negative effects on tree saplings and that these effects can combine with other factors, such as the presence or absence of wild herbivores, retention and colonization by symbiotic ants, and possibly neighborhood tree density, to suppress or release sapling growth. These represent factors that have rarely, if ever, been considered in the study of tree–grass interactions. Our results contribute to the growing recognition that plant–plant interactions can vary greatly in time and space, depending on the environmental and community contexts. An understanding of these contexts and their effects on tree–grass interactions, both in the short term and the long term, is essential to effective and sustainable management of African savannas and the unique megafauna they support.

Acknowledgments We would like to thank Frederick Erii, John Lochikuya, Jackson Ekadeli, and Patrick Etelej for their invaluable assistance in the field. We also thank the Mpala Research Centre staff for their logistical support. We are grateful to Maureen Stanton and Kevin Rice for productive conversations, and to Jacob Goheen, Kari Veblen, Todd Palmer, Niall Hanan, Alan Knapp, and one anonymous reviewer for their comments on earlier versions of this manuscript. The enclosure plots were built and maintained by grants from the James Smithson Fund of the Smithsonian Institution (to A.P. Smith), The National Geographic Society (4691–91), The National Science Foundation (LTREB BSR-97-07477 and 03-16402) and the African Elephant Program of the U.S. Fish and Wildlife Service (98210-0-G563) (to T.P. Young). This research was additionally funded by a National Science Foundation Graduate Research Fellowship and a Jastro-Shields fellowship to C. Riginos. All research was carried out in accordance with the laws of the government of Kenya.

References

- Angassa A (2005) The ecological impact of bush encroachment on the yield of grasses in Borana rangeland ecosystem. *Afr J Ecol* 43:14–20
- Archer S (1995) Tree–grass dynamics in a *Prosopis*-thornscrub savanna parkland—reconstructing the past and predicting the future. *Ecoscience* 2:83–99
- Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion—land-use, climate, or CO₂. *Clim Change* 29:91–99
- Augustine DJ, McNaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J Appl Ecol* 41:45–58
- Belsky AJ (1994) Influences of trees on savanna productivity: tests of shade, nutrients, and tree–grass competition. *Ecology* 75:922–932
- Belsky AJ, Mwonga SM, Amundson RG, Duxbury JM, Ali AR (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *J Appl Ecol* 30:143–155
- Bertness MD, Callaway RM (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- Bertness MD, Ewanchuk PJ (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132:392–401
- Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Glob Change Biol* 9:973–982
- Callaway RM, Nadkarni NM, Mahill BE (1991) Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72:1484–1499
- Callaway RM, Brooker RW, Choler P, et al. (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848
- Coe M, Beentje H (1991) A field guide to the acacias of Kenya. Oxford University Press, Oxford
- Dean WRJ, Milton SJ, Jeltsch F (1999) Large trees, fertile islands, and birds in arid savanna. *J Arid Environ* 41:61–78
- Dickie IA, Schnitzer SA, Reich PB, Hobbie SE (2005) Spatially disjunct effects of co-occurring competition and facilitation. *Ecol Lett* 8:1191–1200
- Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J Anim Ecol* 59:1147–1164
- Gadd ME, Young TP, Palmer TM (2001) Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *Oikos* 92:515–521
- Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 85:1555–1561
- Hocking B (1970) Insect associations with the swollen thorn acacias. *Trans R Entomol Soc Lond* 122:211–255
- Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975
- Knoop WT, Walker BH (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *J Ecol* 73:235–253
- Lauenroth WK, Aguilera MO (1998) Plant–plant interactions in grasses and grasslands. In: Cheplick GP (ed) *Population biology of grasses*. Cambridge University Press, Cambridge, pp 209–230
- Lortie CJ, Brooker RW, Choler P, et al. (2004) Rethinking plant community theory. *Oikos* 107:433–438
- Ludwig F, Dawson TE, Kroon H, Berendse F, Prins HHT (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia* 134:293–300
- Madden D, Young TP (1992) Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*. *Oecologia* 91:235–238
- Maestre FT, Valladares F, Reynolds JF (2005) Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *J Ecol* 93:748–757
- Midgley JJ, Bond WJ (2001) A synthesis of the demography of African acacias. *J Trop Ecol* 17:871–886
- Misorelli DL (2002) Large ungulate impacts on bird populations in an East African savanna. State University of New York, Albany, NY, p 79
- O'Connor TG (1995) *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103:214–223
- Odadi W, Young TP, Okeyo-Owuor JB (2007) Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. *Rangeland Ecol Manage* 60:179–185
- Okello BD, O'Connor TG, Young TP (2001) Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *For Ecol Manage* 142:143–153
- Otieno SG (2004) Effects of domestic and wild herbivore utilization on herbaceous layer aboveground primary production in a central Kenya grassland. University of Nairobi, Nairobi

- Palmer TM, Brody AK (2007) Mutualism as reciprocal exploitation: African plant-ants defend foliar but not reproductive structures. *Ecology* (in press)
- Palmer TM, Young TP, Stanton ML, Wenk E (2000) Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* 123:425–435
- Pratt DJ, Gwynne MD (1977) Rangeland management and ecology in East Africa. Hodder and Stoughton, London
- Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc Natl Acad Sci USA* 104:193–197
- Rebollo S, Milchunas DG, Noy-Meir I, Chapman PL (2002) The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. *Oikos* 98:53–64
- Riginos C, Milton SJ, Wiegand T (2005) Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland. *J Veg Sci* 16:331–340
- Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J Appl Ecol* 38:268–280
- Rousset O, Lepart J (2000) Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). *J Ecol* 88:401–412
- Scholes RJ, Archer SR (1997) Tree–grass interactions in savannas. *Annu Rev Ecol Syst* 28:517–544
- Skarpe C (1992) Dynamics of savanna ecosystems. *J Veg Sci* 3:293–300
- Stapley L (1998) The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias. *Oecologia* 115:401–405
- Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425–434
- Tobler MW, Cochard R, Edwards PJ (2003) The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *J Appl Ecol* 40:430–444
- van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annu Rev Ecol Syst* 31:197–215
- van Vegten JA (1984) Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetation* 56:3–7
- Vetaas OR (1992) Micro-site effects of trees and shrubs in dry savannas. *J Veg Sci* 3:337–344
- Western D, Maitumo D (2004) Woodland loss and restoration in a savanna park: a 20-year experiment. *Afr J Ecol* 42:111–121
- Young TP, Stubblefield CH, Isbell LA (1997) Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 109:98–107
- Young TP, Okello BD, Kinyua D, Palmer TM (1998) KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr J Range Forage Sci* 14:94–102
- Young TP, Stanton ML, Christian CE (2003) Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101:171–179
- Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biol Conserv* 122:351–359