

# Regulation of shrub dynamics by native browsing ungulates on East African rangeland

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## Abstract

1. Herbivores, edaphic features and fire are primary factors regulating the balance between woody and herbaceous vegetation in savannas. Many observational studies have evaluated the potential effects of browsing herbivores on woody plant dynamics in African savannas, but few experimental studies have compared the dynamics of African savannas with and without browsers.

2. A replicated herbivore exclusion experiment was used to assess the role that native ungulates play in regulating woody plant dynamics on commercial rangeland in central Kenya, where the indigenous fauna have been allowed to coexist with cattle.

3. Exclusion of native browsing ungulates for just 3 years showed that they have dramatic effects at every scale from individual twig growth rates to overall rates of woody biomass accumulation in the ecosystem.

4. At the scale of individual *Acacia* twigs, browsers significantly reduced leaf density, leaf biomass and growth rates of twigs < 50 cm above-ground (within the foraging height of dik-diks *Madoqua kirkii*), but browsers had no effects on twig leaf density or leaf biomass at a height of 1.0–1.25 m above-ground.

5. Reductions in the growth rate of twigs within the foraging height of dik-diks was associated with a 6-fold reduction in the rate at which shrubs < 0.5-m tall were recruited into the 0.5–1.5 m height class. This reduced recruitment combined with measured rates of shrub mortality in larger height classes shows that browsers reduced the rate of increase in shrub density nearly to zero ( $7.1 \pm 10.2$  shrubs  $\text{ha}^{-1} \text{year}^{-1}$ ) compared to the rapid rate of increase in the absence of browsers ( $136.9 \pm 13.6$  shrubs  $\text{ha}^{-1} \text{year}^{-1}$ ).

6. Damage to shrub canopies by elephants *Loxodonta africana* caused large, significant reductions in cover of *A. mellifera* and *Grewia tenax*, but lesser reductions in cover of *A. etbaica*. For *Acacias*, elephant damage was focused on shrubs > 2.5 m tall, such that *Acacias* in intermediate height classes (0.5–2.5 m) experienced minimal browser impacts. Elephants influenced shrubland dynamics by altering shrub height-class distributions, shifting species composition from broad-leaved *Grewia tenax* to fine-leaved *Acacia* species, and suppressing woody biomass accumulation; but elephants had little influence on changes in shrub density.

7. *Synthesis and applications.* Our results suggest that a community of native browsers that includes both small, selective species (e.g. dik-diks) and large, bulk-feeding species (elephants) can provide an important ecosystem service by suppressing shrub encroachment on commercial rangeland.

*Key-words:* *Acacia* savanna, *Aepyceros melampus*, dik-dik, elephant, Laikipia, *Loxodonta africana*, Kenya, *Madoqua kirkii*, shrub encroachment, wildlife conservation.

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## Introduction

Perceived antagonistic relationships between wild ungulates and livestock have led humans to reduce drastically the distribution and abundance of wild ungulates on rangelands world-wide. In the past century, rangeland ecosystems have also experienced widespread increases in woody plant abundance and associated declines in the suitability of rangeland for cattle production (van Vegten 1983; Adamoli *et al.* 1990; Archer 1995; van Auken 2000; Roques, O'Connor & Watkinson 2001). Shifts from grassland to shrubland have been variously attributed to changes in climate (Neilson 1986), fire frequency and grazing intensity (Dublin, Sinclair & McGlade 1990; Roques *et al.* 2001), and browsing pressure (Dublin *et al.* 1990; Weltzin, Archer & Heitschmidt 1997). The degree to which browsing pressure regulates woody plant dynamics has significant implications for the conservation and management of savannas where human activities continue to influence herbivore distribution and abundance. In many protected areas of Africa where livestock are excluded, woodlands and shrublands have declined in the past half century, often coincident with a concentration of elephants into protected areas as a result of human activities on surrounding land (Laws 1970; Croze 1974; Field & Ross 1976; Barnes 1983; Dublin *et al.* 1990; Ben-Shahar 1996; van de Vijver, Foley & Olf 1999). In contrast, increasing shrub abundance has been a major concern on African rangelands managed for livestock production (van Vegten 1983; Roques *et al.* 2001).

Unfortunately, the importance of browser effects on woody plant dynamics in African savannas remains unclear. For decades, ecologists have documented temporal fluctuations in woody plant abundance and distribution in African savannas and discussed the potential role of browsing ungulates, particularly elephants (Caughley 1976; Jachmann & Bell 1985; Dublin *et al.* 1990; Ruess & Halter 1990; Jachmann & Croes 1991; Prins & van der Juegd 1993; Ben-Shahar 1996; Jeltsch *et al.* 1997; van de Vijver *et al.* 1999; Roques *et al.* 2001), but these studies have relied on observational and modelling analyses. In some regions of Africa, variation in browser abundance is not associated with rates of shrub increase (Oba & Post 1999; Roques *et al.* 2001), and studies conducted at the twig level have reported no negative browser effects on twig growth rates (du Toit, Bryant & Frisby 1990; Gowda 1996; Gadd, Young & Palmer 2001). In contrast, several other studies suggest browsers can significantly suppress shrub growth. Prins & van der Juegd (1993) noted that pulses of shrub encroachment in Lake Manara National Park coincided with anthrax epidemics that depressed impala *Aepyceros melampus* populations. Dublin *et al.* (1990) estimated that elephant densities in the Maasai Mara reserve during the 1980s were sufficient to prevent an increase in shrub abundance, and Belsky (1984) concluded that small browsers

suppressed shrub growth rates in the Serengeti National Park. Despite these variable interpretations of browser effects on shrub dynamics and the potential economic importance for managed savannas, replicated experiments assessing the effects of native browsers on shrub dynamics in African savannas are lacking.

In the Laikipia district of central Kenya, approximately 6500 km<sup>2</sup> of savanna are managed for commercial livestock production. Important changes have occurred with respect to both shrubland habitats and native ungulate populations in Laikipia over the past half century, but the implications of these changes for rangeland condition and economic potential are unclear. One important change in Laikipia's rangelands has been increasing shrub encroachment, primarily by *Acacia* species. Prior to 1900, Maasai pastoralists occupied Laikipia and early European travellers through the district reported mostly open grass plains (Hohnel 1894; Patterson 1910). The Maasai were displaced by European settlers following a treaty with the British in 1911 (Young, Partridge & Macrae 1995). Since that time, most of Laikipia has been managed by ranchers of European descent who have actively suppressed wildfires. Analyses of aerial photos from 1961 and 1969 (D.J.A., pers. obs.) combined with reports from long-term residents of the district indicate shrub cover has increased substantially over the past half century, reaching an average cover of 28% in north-central Laikipia in 1998 (Augustine 2003b).

A second important trend on Laikipia's rangeland has been improved incentives to maintain and even increase native wildlife populations. In 1992, the Kenya Wildlife Service (KWS) legalized harvests of wildlife in Laikipia on an experimental basis, and game meat now contributes significantly to the local economy. Although no formally protected natural areas exist in Laikipia, wildlife on private land has also become important for ecotourism. Until the 1970s, elephants were largely absent from Laikipia, but were resident in Samburu district to the north (Thouless 1995). The development of long-distance elephant migrations from Samburu to Laikipia since the 1970s has been attributed largely to the transition from grassland to shrubland and to improved security in Laikipia (Thouless 1995). Elephants now migrate into Laikipia's commercial rangeland during June–October each year, and can reach wet-season densities of 2.9–5.1 per km<sup>2</sup> (Augustine 2002). Both elephants and other native ungulates (particularly dik-dik and impala), could play an important role in reducing and even reversing shrub encroachment in the region.

We evaluated the effects of native ungulates on shrub dynamics using a set of replicated, 0.5-ha herbivore exclosures at the Mpala Ranch and Research Centre in north-central Laikipia, Kenya. Our first objective was to evaluate whether browsers affect twig growth of the dominant *Acacias* in this ecosystem, and whether browser effects at the twig level scale up to effects on shrub population dynamics. Our second objective was to

evaluate how browsers differentially affect shrub species, and relate these effects to shrub defences against herbivores (e.g. spinescent, fine-leaved *Acacia* spp. vs. non-spinescent, broad-leaved *Grewia* spp.) and long-term patterns in shrub community composition. Thirdly, we examine the implications of current browser effects on the shrub community for long-term patterns of shrub encroachment.

One additional factor affecting shrub distribution in many African savannas is the presence of nutrient-rich patches (typically c. 1 ha in size) that are created by the abandonment of overnight cattle enclosures (Stelfox 1986; Blackmore, Mentis & Scholes 1990; Reid & Ellis 1995; Young *et al.* 1995; Augustine 2003a). In Laikipia, these nutrient-rich patches occupy only c. 1% of the total landscape, but they are dominated by short, nutrient-rich grasses and are important concentration areas for medium-sized ungulates such as eland *Taurotragus oryx* and impala (Augustine 2002). The absence of shrubs in these nutrient-rich glades is surprising because abandoned livestock enclosures in northern Kenya are focal points for recruitment and rapid growth of *Acacia tortilis* (Reid & Ellis 1995). We hypothesized that mixed-feeding ungulates such as impala suppress shrub invasion into glades by consuming and preventing the establishment of shrub seedlings. In other words, the nutrient-rich soils of these glades may indirectly suppress shrub invasion and growth by attracting ungulate herbivores. A fourth objective of this study was therefore to compare browser effects on shrub dynamics in the relatively nutrient-poor bushland habitat, which dominates most of the landscape, to browser effects on shrub invasion into nutrient-rich glades. Because glades and bushland study sites were located on the same soil type (both contain 75% sand; Augustine 2003a) and at the same topographic position, they provide a unique opportunity to examine how nutrient enrichment can affect shrub–browser interactions.

### Study area

All research was conducted at the Mpala Research Centre and associated Mpala ranch (MRC) which encompasses 190 km<sup>2</sup> of semi-arid savanna within the Laikipia district of central Kenya (37° 53' E, 0° 17' N). The study area is underlain by moderate to very deep,

friable sandy loams developed from metamorphic basement rocks (Ahn & Geiger 1987). Topography consists of gently rolling hills and occasional granitic inselbergs. Mean annual rainfall during 1972–2000 was 508 mm (1 SD = 226 mm; CV = 0.44). Rainfall occurs in a trimodal fashion with wet seasons typical during April–May, August and October, and a consistent dry season during January–March. The bushland community (99% of the landscape) consists of a discontinuous layer of perennial grasses (*Digitaria milaniana*, *Cynodon dactylon*, *Pennisetum mezianum* and *P. stramineum*) and a shrub layer dominated by *A. mellifera*, *A. etbaica*, *A. brevispica*, and *Grewia tenax* (Young *et al.* 1995). Nomenclature follows Polhill (1972, 1974, 1982). Glades (1% of the landscape) are dominated by a short-grass lawn of *Cynodon plectostachyus* and glade soils contain 1.6 times more total carbon (C) and nitrogen (N) and 8.6 times more phosphorous (P) than surrounding bushland soils (Augustine 2003a). Fire may have been an important component of Laikipia's savannas previously, but has been actively suppressed since European settlement.

Since the early 1900s, most of Laikipia, including MRC, has been privately owned rangeland. At MRC, cattle are managed for market production using traditional pastoral (Maasai and Turkana) herding methods. The most common native browsing and mixed-feeding ungulates are impala, dik-dik and elephant (Table 1). Eland, giraffe *Giraffa camelopardalis* and greater kudu *Tragelaphus strepsiceros* are also present at densities < 0.5 km<sup>-2</sup> (Augustine 2002).

### Methods

In 1999, two paired 0.5-ha (70 × 70 m) plots were established at each of three glade and three bushland study sites located in central and southern MRC. For each pair of 0.5-ha plots, one was randomly selected and protected with an 11-strand, 3-m tall electrified fence (three fences at glade sites and three fences at bushland sites; six in total) that excluded all large herbivores ranging in size from dik-diks to elephants. Fences followed the design of Young *et al.* (1998), with additional mesh and electrified wires from 0 to 0.5 m in height. Fence condition and voltage were monitored and maintained weekly throughout the study. With the

**Table 1.** Densities of cattle and native browsers and mixed-feeders within the study area, and <sup>13</sup>C content of dung (means with 1 SE in parentheses) from those species in wet and dry seasons. The <sup>13</sup>C content of dung indicates the amount of grass in the diet because all grasses at Mpala use the C<sub>4</sub> photosynthetic pathway. Values for cattle are indicative of grazers that only occasionally consume shrubs and forbs, while values for dik-dik are indicative of pure browsers that do not consume grasses

Species	Density			$\delta^{13}C$ of dung	
	kg km <sup>-2</sup>	Animals km <sup>-2</sup>	(± 95% CI)	Wet season	Dry season
Cattle	2280	12.2	–	–15.1 (0.33)	–15.8 (0.23)
Elephant	2882	1.7	(0.8–3.4)	–23.6 (0.43)	–26.2 (0.26)
Impala	813	20.3	(14.3–29.0)	–21.0 (1.21)	–23.7 (0.52)
Dik-dik	693	139	(124–156)	–25.6 (0.48)	–25.5 (0.46)

exception of several incursions by dik-dik into the exclosures during the first 3 months after construction, fences were effective in excluding all large herbivores throughout the 3-year study. Effects of browsers on shrub growth and community dynamics were evaluated by monitoring (i) *Acacia* leaf density and biomass, (ii) *Acacia* twig growth, (iii) sapling recruitment, and (iv) whole-shrub growth rates of different species inside and outside these electrified exclosures. *Acacia* leaf density and twig growth were only studied at the three bushland sites, while sapling recruitment was examined at both bushland and glade study sites. The three glade study sites each consisted of a 0.5–1.0 ha short-grass lawn that was surrounded by *Acacia* bushland. The glade boundary was defined by the spatial extent of the dominant grass species, *Cynodon plectostachyus*. Both the exclosure and the control plot at each glade site contained approximately one-third of the short-grass lawn and extended into the surrounding bushland. This design was used to examine whether browsers influenced the rate at which shrubs invaded the short-grass glades.

At bushland sites, we monitored leaf density, leaf biomass and twig growth of *A. etbaica* and *A. mellifera*. To evaluate growth differences among twigs accessible to different ungulate species, we monitored twigs within the foraging height of dik-diks plus larger ungulates (twigs  $\leq 0.5$  m from the ground on small shrubs that were 0.25–0.75 m tall) and twigs that were above the foraging height of dik-diks but accessible to all other native ungulates (twigs that were 1.0–1.25 m above-ground on larger shrubs that were 1.25–3.0 m tall). For this study, a 'twig' was defined by measuring 30 cm from the apical bud along the primary stem, and including all lateral stems originating from that 30 cm length of the primary stem. At each site, we used a stratified-random procedure to select 15 large and 15 small shrubs of each *Acacia* species both inside and outside the exclosure. We marked and monitored two twigs per shrub for twigs  $< 0.5$  m above-ground and 4 twigs per shrub for twigs 1.0–1.25 m above-ground. During March 2000 (late dry season when shrubs had no leaves), we marked each twig with a plastic tag located 30 cm from the apical bud, and measured the basal diameter and length of the primary stem plus any lateral stems. We remeasured the basal diameter and length of the primary and any lateral stems in March 2001 and March 2002. In March 2001, twigs that had died or been consumed during the previous year were replaced with new twigs. From August 2000–August 2001, we also counted the number of leaves on each twig at monthly intervals. Each month, we recorded any damage to twigs due to consumption by elephants (identified by roughly broken stems and/or major damage to the entire shrub), trampling by cattle (identified by tracks at the point of stem breakage), consumption by hares (stems cleanly severed at a 45° angle), or drought and insect damage (stems withered and leafless, and/or with clear insect damage to the bark).

Finally, during August, September and October of 2000, we examined the effects of browsers on *Acacia* leaf mass. For each site, browsing treatment, *Acacia* species, and shrub size class, we collected leaves from five shrubs (two twigs per shrub). For each twig, we collected and counted all leaves, dried the leaves in an oven at 70 °C for 3 days, and then weighed the leaves to the nearest milligram. Measurements of twig lengths and diameters were converted into woody biomass estimates based on regression equations derived from twigs that were measured, clipped, oven-dried and then weighed (*A. mellifera*:  $y = 0.0143x + 0.0732$ ,  $r^2 = 0.98$ ; *A. etbaica*:  $y = 0.0175x + 0.1359$ ,  $r^2 = 0.88$ ; where  $y = g$  woody biomass, and  $x =$  twig volume calculated as the volume of a cone with the twig's length and basal diameter).

To evaluate the effects of browsers on shrub population and community dynamics, we mapped and measured every individual shrub  $> 0.5$  m tall within the central 50 × 50 m area of each control and exclosure plot at the time of fence construction in May–June 1999. For each shrub, we recorded the species and its  $x$  and  $y$  coordinates within the plot. We then measured canopy diameter in each of the cardinal directions, shrub height and the diameter of each stem 15 cm above ground level. Lianas (*Craibia* spp. and *Kleinia* spp.) were not included in the census. We remeasured all shrubs 3 years later during May–June 2002, including any new shrubs that exceeded 0.5 m in height. Shrub sapling recruitment was defined as the recruitment of shrubs  $< 0.5$  m tall into the 0.5–1.5-m height class during the 3-year period.

When elephants forage on shrubs, two types of damage can occur. First, twig consumption results in the loss of small, outer twigs on the order of the size of twigs that we marked and monitored in this study. Secondly, elephants can chew and strip bark from the shrub's main branches, which generally results in major damage to all or part of the shrub. During shrub measurements in 1999, we recorded any stems with bark-stripping damage by elephants, and in 2002 we noted any stems with new bark-stripping damage on control plots.

During 1999, we collected five dung groups from each of the dominant herbivore species at MRC (impala, elephant, cattle and dik-dik) during wet and dry seasons. Each dung group was collected from a different herd. Dung was oven-dried at 70 °C for 3 days, and analysed for  $^{13}\text{C}$  content by the Staple Isotope Laboratory at the University of California at Davis. Due to major differences in the  $^{13}\text{C}$  signature of  $\text{C}_4$  grasses vs.  $\text{C}_3$  dicots and the fact that all grasses at MRC possess the  $\text{C}_4$  photosynthetic pathway, this measurement provides an index of the degree to which grasses contribute to a given ungulate's diet (Cerling, Harris & Passey 2003). Analyses of plants from East African savannas (including MRC) showed that  $\text{C}_3$  dicots have a  $\delta^{13}\text{C}$  signature of  $-25$  to  $-29$ , while  $\text{C}_4$  grasses have a  $\delta^{13}\text{C}$  signature of  $-11$  to  $-14$  (Cerling *et al.* 2003).

Deshmukh (1992) reviewed regression equations for estimating total woody biomass of *Acacia* spp. and other shrubs in East African savannas. He concluded that the relationship derived by Epp, Herlocker & Peden (1982), where mass in kg =  $[7.49 \times (\text{crown diameter in m}) - 7.76]$ , provided intermediate estimates compared to all other reported equations for Kenyan shrublands, so we used this equation to estimate woody biomass at Mpala. Our estimate of canopy diameter for each shrub is the mean of two measurements (in the north–south and east–west directions). Note that this regression equation does not include biomass of any shrubs with canopy diameter less than 1.04 m. We calculated whole-plot changes in above-ground live woody biomass inside and outside fences using Epp *et al.*'s (1982) regression. Net accumulation of woody biomass was also calculated without subtracting the biomass of shrubs that died during the study. Because most of the woody biomass from dead shrubs was still present in 2002, this latter estimate provides a closer approximation of above-ground net ecosystem biomass production on the study plots over the 3-year period (Randerson *et al.* 2002).

Effects of browsers on shrub leaf density, shrub leaf biomass, and twig growth rates were evaluated with split-plot ANOVAs where the experimental treatment (browsed vs. unbrowsed) was applied at the whole-plot level, and differences among shrub species (*A. mellifera* vs. *A. etbaica*) and shrub size class (above or below dik-dik browsing height) were evaluated at the subplot level. When significant interactions were detected between shrub size/species and browsing treatment, planned contrasts of simple effects (i.e. comparisons between two levels of browsing for a given shrub size) were based on standard errors and degrees of freedom calculated for split-plot designs following Keuhl (2000: pp. 477–478). For variables that were measured over a series of months (leaf density and mass of *Acacia* twigs), we tested for time  $\times$  treatment interactions following Meredith & Stehman (1991). Briefly, we evaluated split-plot ANOVAs for linear, quadratic, and in some cases cubic combinations of the monthly leaf measurements, which is a test for any treatment effects on temporal trends (Meredith & Stehman 1991). In the absence of time  $\times$  treatment interactions, we evaluated treatment effects on leaf characteristics averaged over all months of measurement. Sapling recruitment rates were evaluated within a split-plot design with community (glade vs. bushland) as the whole-plot factor and browsing as the subplot factor. If significant community  $\times$  browsing interactions were detected, planned contrasts for the simple effect of browsing within each community were based on appropriate standard errors and degrees of freedom for a split-plot design (Keuhl 2000). Browser effects on whole-shrub growth rates for larger size classes and net ecosystem production were only analysed for the bushland sites, and hence were based on paired *t*-tests. Given the low power of statistical tests (d.f. = 2 in most tests), we considered  $\alpha \leq 0.1$  as statistically significant.

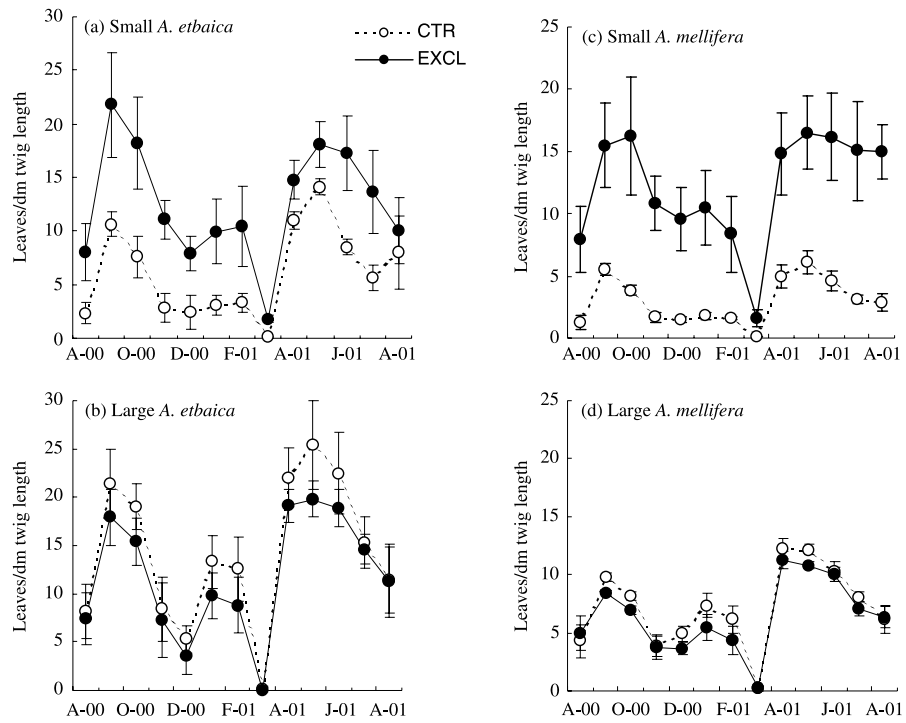
## Results

Previous studies showed that dik-dik, impala, and elephant dominated the community of native browsing and mixed-feeding ungulates at MRC during 2000–02 (Augustine 2002, Table 1). Analyses of  $\delta^{13}\text{C}$  of dung samples showed that dik-dik were browsers year-round, while elephant were pure browsers during dry seasons and included a minor component of grass in the diet during wet seasons. Impala were mixed feeders; they primarily consumed  $\text{C}_3$  plants during dry seasons (dung  $\delta^{13}\text{C}$  slightly less negative than dik-diks), but the contribution of grass to the diet increased during wet seasons to a level that was intermediate between cattle and dik-dik (Table 1).

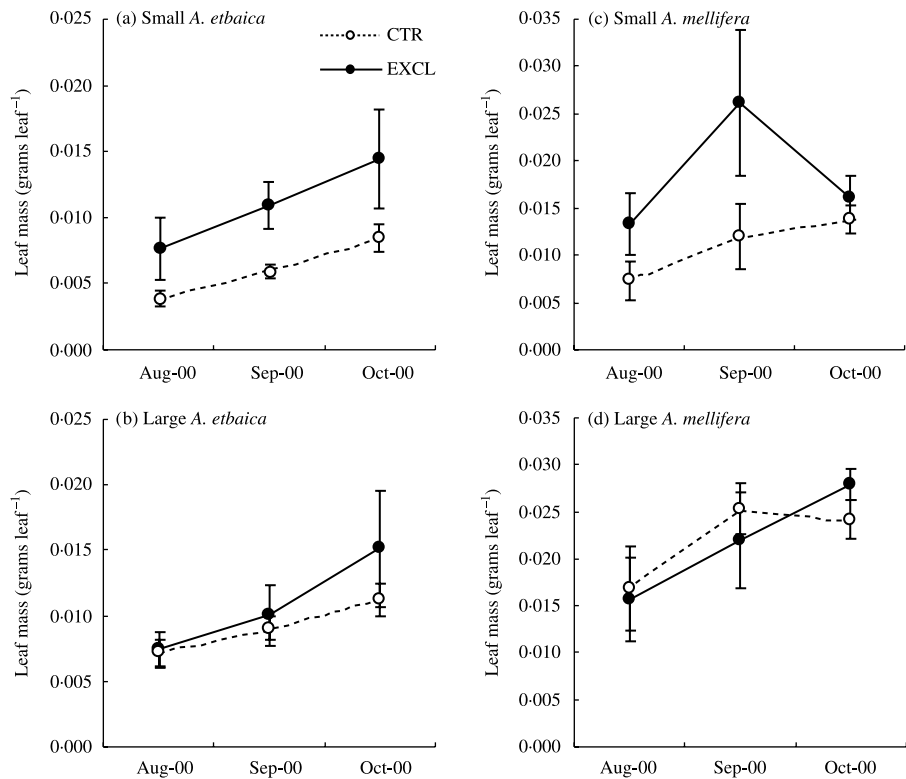
### SHRUB LEAF AND TWIG MEASUREMENTS

Browsers significantly reduced leaf density on *Acacia* twigs during growing seasons in 2000 and 2001, but their effects were contingent on twig height (Fig. 1). Leaf density peaked 1–2 months after major rainfall events in August of 2000 and April–May of 2002, and reached a near-zero minimum at the end of the long dry season in March of 2001. Temporal changes in leaf density were similar for both *Acacia* species, both twig height classes, and both browsing treatments (Fig. 1). We found no significant interactions between time and browsing, twig height, or shrub species ( $P > 0.1$  for all main and interaction effects). The effect of browsing was contingent on twig height (browsing  $\times$  twig height interaction:  $F_{1,12} = 55.3$ ,  $P < 0.0001$ ), but we found no browsing  $\times$  size  $\times$  species interaction ( $F_{1,12} = 0.20$ ,  $P = 0.66$ ) and only a marginal browsing  $\times$  species interaction ( $F_{1,12} = 2.94$ ,  $P = 0.11$ ). For twigs within the reach of dik-dik ( $< 0.50$  m above-ground), browsers reduced leaf density of *A. etbaica* and *A. mellifera* by an average of 63% ( $t = 6.18$ ,  $P < 0.001$ , Fig. 1). In contrast, browsers had no detectable effect on leaf density of twigs above the foraging height of dik-dik (1.0–1.25 m above-ground;  $t = 1.28$ ,  $P = 0.25$ , Fig. 1).

In addition to the large reduction in leaf density on twigs  $< 0.5$  m high, browsers also reduced mean leaf mass ( $\text{mg leaf}^{-1}$ ) on twigs that were accessible to dik-diks. Over the 3 months of measurements (Fig. 2), there were no significant interactions between time and browsing treatment, twig height, or shrub species (linear model: time  $\times$  species,  $F_{1,12} = 0.58$ ,  $P = 0.46$ ; time  $\times$  shrub size,  $F_{1,12} = 2.05$ ,  $P = 0.18$ ; time  $\times$  browsing,  $F_{1,2} < 0.01$ ,  $P = 0.97$ ; overall quadratic model:  $F_{12,12} = 0.71$ ,  $P = 0.71$ ), although leaf mass increased linearly from August to October (linear model:  $F_{1,12} = 49.2$ ,  $P < 0.0001$ ). There were also no significant browsing  $\times$  species  $\times$  twig height ( $F_{1,12} = 0.06$ ,  $P = 0.82$ ) or browsing  $\times$  species ( $F_{1,12} = 0.73$ ,  $P = 0.41$ ) interactions. Again, browser effects depended on twig height ( $F_{1,12} = 9.24$ ,  $P = 0.010$ ). For twigs  $< 0.5$  m above-ground (within reach of dik-diks), browsers reduced mean leaf mass by 42% ( $t = 2.26$ ,  $P = 0.086$ ). Browsers had no effect on



**Fig. 1.** Variation in leaf density on twigs of *A. etbaica* and *A. mellifera* in relation to browsing and twig height at Mpala, Kenya. Twigs on small shrubs were < 0.5-m above ground level and hence accessible to dik-diks plus large ungulates. Twigs on large shrubs were 1.0–1.25 m above ground level and hence accessible only to large ungulates. Error bars show  $\pm 1$  SE.

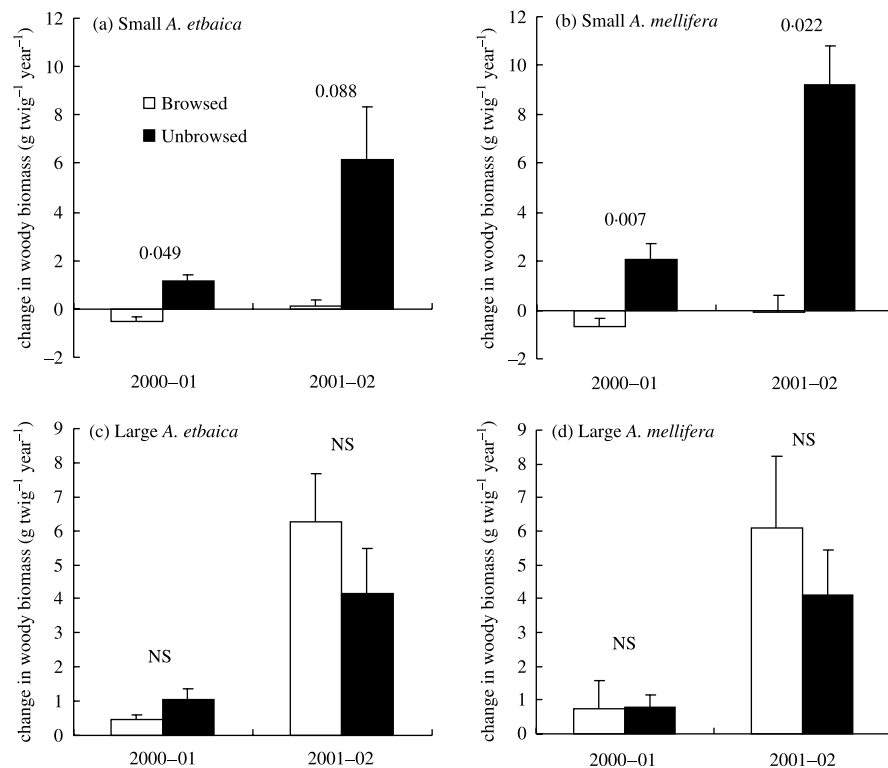


**Fig. 2.** Variation in leaf mass (g leaf<sup>-1</sup>) of *A. etbaica* and *A. mellifera* in relation to browsing and twig height at Mpala, Kenya. Twigs on small shrubs were 0.25–0.5 m above ground level and hence accessible to dik-diks plus large ungulates. Twigs on large shrubs were 1.0–1.25 m above ground level and hence accessible only to large ungulates. Error bars show  $\pm 1$  SE.

leaf mass of large shrubs ( $t = 0.36$ ,  $P = 0.74$ ; Fig. 2). Combining the results for mean leaf density per twig length and mean mass per leaf during August–October 2000, browsers reduced leaf biomass per twig (grams

per dm twig length) by 76% for *A. etbaica* and 83% for *A. mellifera*.

The way browsers affected leaf density was in turn reflected in their effects on net twig growth rates. During



**Fig. 3.** Effects of browsers on net twig growth rates during a drought (2000–01) and a wet year (2001–02) at Mpala, Kenya. Error bars show  $\pm 1$  SE. Numbers above pairs of bars for browsed vs. unbrowsed treatments are  $P$ -values evaluating the effect of browsing. NS indicates no significant difference ( $P > 0.1$ ).

the drought year (2000–01), we detected a significant twig height  $\times$  browsing interaction ( $F_{1,12} = 7.49$ ,  $P = 0.018$ ), but no species  $\times$  twig height  $\times$  browsing interaction ( $F_{2,12} = 0.84$ ,  $P = 0.46$ ), indicating that browsers had similar effects on both *Acacia* species, but those effects were contingent on twig height. Analysis of the simple effects showed browsers reduced net growth rates of twigs within the reach of dik-dik, but had no detectable effect on twigs above that height (Fig. 3). Similar patterns were also observed in the high-rainfall year, with a significant twig height  $\times$  browsing interaction ( $F_{1,12} = 25.8$ ,  $P < 0.001$ ) but no species  $\times$  twig height  $\times$  browsing interaction ( $F_{2,12} = 0.65$ ,  $P = 0.54$ ). Browsers again significantly reduced net woody biomass growth of twigs within the reach of dik-dik, but not above that height (Fig. 3). In addition, major differences in twig growth rates were observed between the drought and the high-rainfall year. For all shrub species, size classes and browsing treatments, mean twig growth rates increased 7-fold from the drought (grand mean =  $0.64$  g woody biomass accumulation twig<sup>-1</sup> years<sup>-1</sup>) to the high rainfall year (grand mean =  $4.51$  g twig<sup>-1</sup> year<sup>-1</sup>).

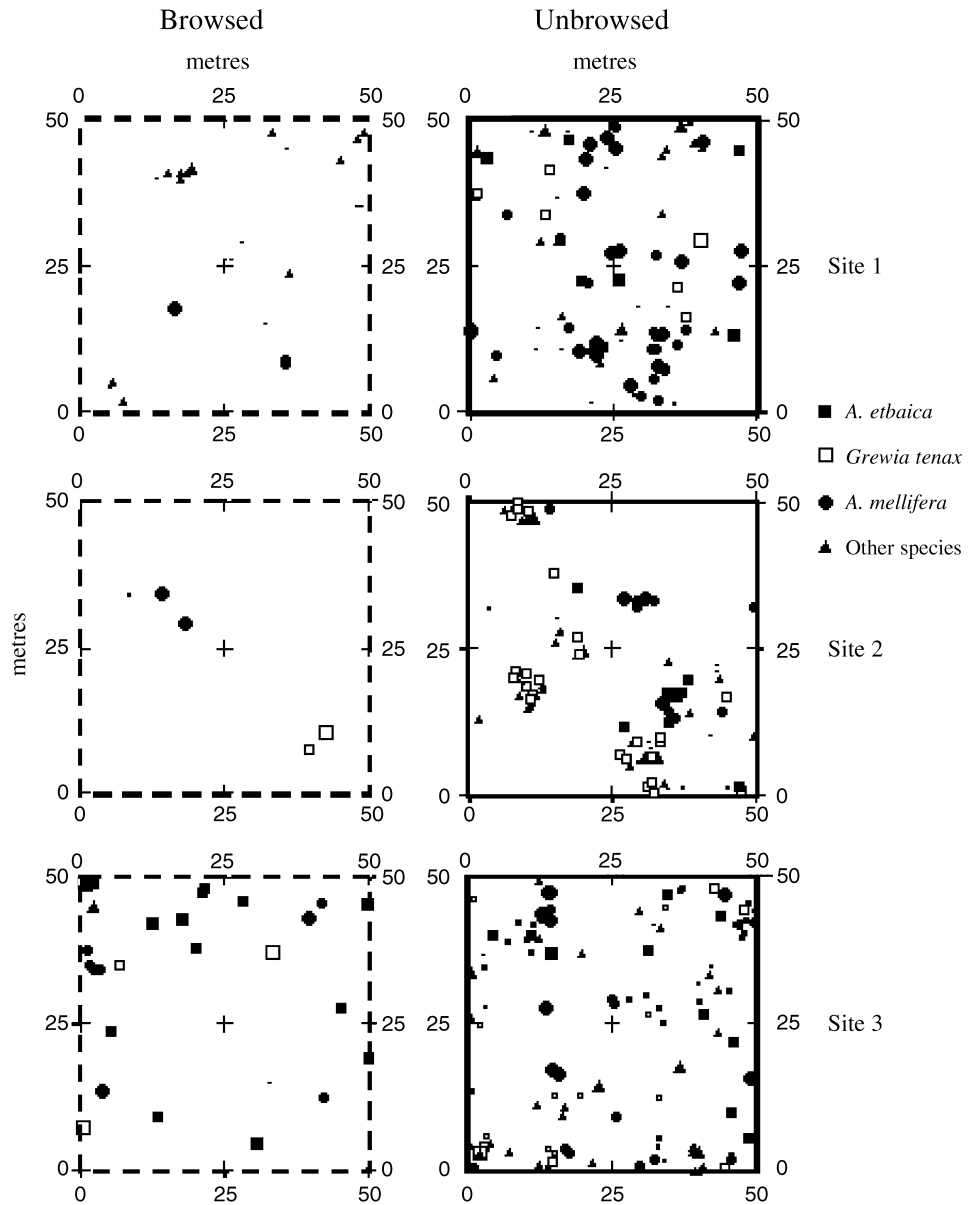
The browser-induced reduction in twig growth rates can largely be attributed to reduced leaf density and leaf mass because rates of complete twig mortality due to trampling or consumption were low. For twigs  $< 0.5$  m above-ground, mean annual mortality rates due to elephant consumption were only 4.5% and 6.1% for

*A. mellifera* and *A. etbaica*, respectively; corresponding mortality rates were 5.0% and 3.3% due to insect/drought damage, and 1.1% and 3.8% due to hare consumption and trampling damage. A reanalysis of twig growth rates excluding those affected by elephant consumption, trampling and hare consumption yielded similar results to those shown in Fig. 3, again with lower growth rates for small but not large shrubs (2000–01: size  $\times$  treatment interaction,  $F_{1,12} = 8.21$ ,  $P = 0.014$ , browsing reduced twig growth by  $2.04$  g twig<sup>-1</sup> on small shrubs and did not affect large shrubs; 2001–02: size  $\times$  treatment interaction,  $F_{1,12} = 24.76$ ,  $P < 0.0001$ , browsing reduced twig growth by  $7.38$  g twig<sup>-1</sup> on small shrubs and did not affect large shrubs).

#### WHOLE-PLOT SHRUB DYNAMICS

Persistent negative browser effects on leaf biomass and growth rates of twigs  $< 0.5$  m above-ground were associated with major browser effects on shrub sapling recruitment from the  $< 0.5$  m height class into the  $0.5$ – $1.5$  m height class (Fig. 4). In the bushland community, browser exclusion increased shrub recruitment rates nearly 6-fold, and significantly increased recruitment rates of all shrub species including the 3 dominant species (Fig. 4 and Table 2).

In contrast, changes in shrub density at glade sites were slow and unaffected by exclusion of large herbivores (Table 2). Moreover, very few shrubs  $< 0.5$  m

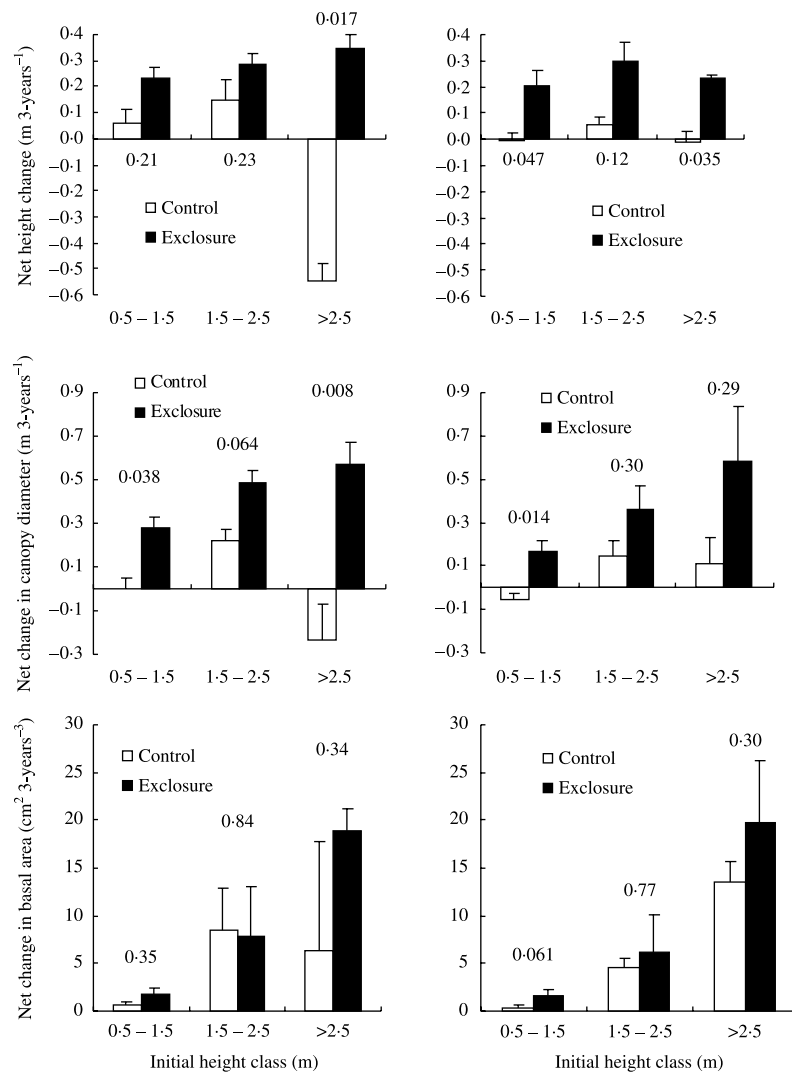


**Fig. 4.** The distribution and density of shrubs recruited from the < 0.5 m height class into the 0.5–1.5 m height class between 1999 and 2002 for browsed and unbrowsed treatments at Mpala, Kenya. Large symbols show shrubs with a canopy diameter > 1 m, intermediate sized symbols show shrubs with a mean canopy diameter of 0.5–1.0 m, and the smallest symbol size shows shrubs with a canopy diameter of 0–0.5 m.

**Table 2.** Rates of shrub sapling recruitment from the < 0.5-m height class into the 0.5–1.5 m height class (mean number of new shrubs ha<sup>-1</sup> year<sup>-1</sup> with 1 SE in parentheses) in browsed and fenced treatments in glade and bushland communities at Mpala, Kenya. Due to significant community × browsing interactions for each species and for all species combined ( $F_{1,4} > 8.82$ ,  $P < 0.04$  for all ANOVAS),  $P$ -values are presented for simple effects of browsing on shrub recruitment rates in each community. Note that standard errors reflect among-site variation, while the test for browser effects reflects the within-site effect of browsing

	Bushland			Glades		
	Browsed	Fenced	$P$	Browsed	Fenced	$P$
<i>A. etbaica</i>	7.1 (7.1)	27.1 (13.3)	0.011	0.7 (0.7)	1.8 (0.9)	0.83
<i>A. mellifera</i>	5.8 (2.5)	41.8 (6.5)	0.003	0.0	1.5 (1.5)	0.80
<i>G. tenax</i>	2.7 (1.3)	28.9 (9.6)	0.012	0.0	0.0	–
Other species	10.2 (8.9)	48.0 (8.1)	0.015	1.5 (1.5)	2.3 (1.3)	0.94
All species	25.8 (7.3)	145.8 (8.3)	< 0.001	2.2 (2.2)	5.6 (1.7)	0.81





**Fig. 5.** Effects of browsers on growth rates of (a–c) *A. mellifera* and (d–f) *A. etbaica* in three different height classes at Mpala, Kenya. Numbers above or below each pair of bars show *P*-values testing for the significance of the browser effect. Error bars show +1 SE and reflect among-block variation.

tall were observed in the glades (either inside or outside exclosures) throughout the 3-year study.

Although browsers strongly affected sapling recruitment of all 3 dominant shrub species, browser effects on larger shrubs depended on both shrub size class and species. For *A. mellifera*, browsers had no effect on height and basal area growth of shrubs in 0.5–1.5 m and 1.5–2.5 m height classes, but did significantly reduce growth of shrubs > 2.5 m tall (Fig. 5). On browsed plots, *A. mellifera* in > 2.5-m height class decreased 55 cm in mean height and 23 cm in mean canopy diameter. Inside exclosures, *A. mellifera* in the > 2.5-m height class increased 35 cm in mean height and 57 cm in mean canopy diameter (Fig. 5). Browsers did not significantly reduce basal area of the largest *A. mellifera* size class (Fig. 5), reflecting the fact that elephants typically consumed or damaged large portions of *A. mellifera* canopies, but rarely killed shrub stems.

Of the 3 dominant shrub species, browser effects were least severe for *A. etbaica* (Figs 5 & 7). Browsers had no

effect on growth (in terms of height, canopy diameter, or basal area) of *A. etbaica* in the 1.5–2.5-m height class. Browsers did negatively affect growth in the 0.5–1.5-m height class, which is in contrast to the lack of browser effects on *A. etbaica* twig growth rates in this height class (Fig. 3c). At one site where browser effects on 0.5–1.5 m tall *A. etbaicas* were most severe, we directly observed elephants feeding on those *A. etbaicas* late in 1999; by 2002 none of those damaged shrubs had died but none returned to their original size. Browsers affected growth of *A. etbaica* in the > 2.5 m height class to a far lesser degree than they affected *A. mellifera* in that height class (Fig. 5). Browsers slightly reduced the height of *A. etbaicas* > 2.5 m tall, but had no significant effect on canopy diameter or basal area.

Differences in the magnitude of browser impacts on *A. mellifera* vs. *A. etbaica* were reflected in the distribution of elephant bark-stripping damage across height classes of the two species. For *A. mellifera*, 69% of all shrubs > 2.5 m in height on control plots experienced

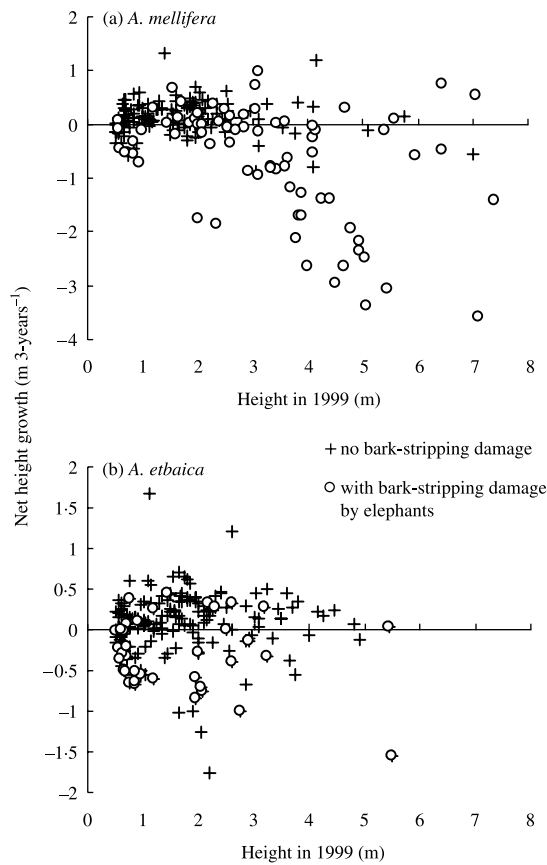


Fig. 6. The distribution of bark-stripping damage by elephants for (a) *A. mellifera* and (b) *A. etbaica* in relation to shrub height at Mpala, Kenya.

bark-stripping damage and net height growth was negative for 76% of those elephant-damaged shrubs during the study (Fig. 6a). Mean net height growth of large (> 2.5 m tall) *A. mellifera* that experienced bark-stripping damage averaged  $-0.88 \pm 0.11$  m ( $\bar{x} \pm 1$  SE) across the 3 study sites, which was significantly less than zero ( $P = 0.02$ ). In contrast, elephants damaged only 14% and 24% of *A. mellifera* in the 0.5–1.5 m and 1.5–2.5 m height classes, respectively. For *A. etbaica*, bark-stripping damage occurred at a lower frequency and was more evenly distributed across shrub height classes (20%, 14% and 23% of shrubs in the 0.5–1.5 m, 1.5–2.5 m and > 2.5 m height classes, respectively; Fig. 6b).

Finally, browsers severely reduced all measures of growth for *Grewia tenax*. Because large *G. tenax* individuals were rare (mean height across all study sites = 1.18 m; median height = 0.95 m), analyses of growth rates were not stratified by height class. For all *G. tenax*, net height and canopy diameter growth was negative and net basal area growth was nearly zero on browsed plots. All three measures of growth were positive on fenced plots (Fig. 7). The larger effect on height and canopy diameter relative to basal area again reflects elephant removal of *G. tenax* canopies without killing basal stems.

Shrub mortality rates were low despite a severe drought in 2000, averaging only 1.12% per year for all

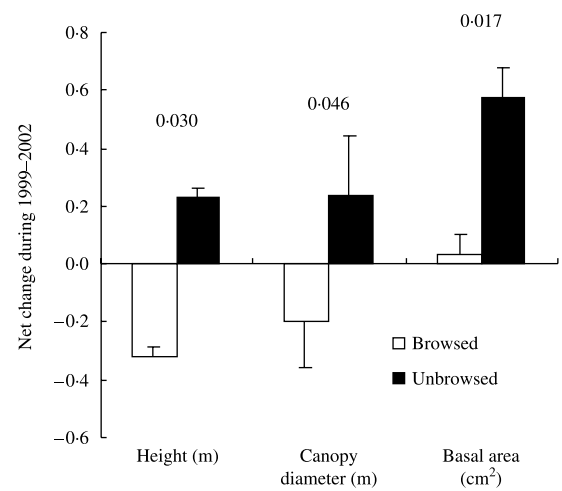


Fig. 7. Effects of browsers on growth rates of *Grewia tenax* at Mpala, Kenya. Numbers above each pair of bars show  $P$ -values testing for the significance of the browser effect. Error bars show  $+1$  SE and reflect among-block variation.

shrubs > 0.5 m tall. Furthermore, shrub mortality rates were independent of shrub height when evaluated for 0.5–1.5 m, 1.5–2.5 m, and > 2.5 m height classes ( $\chi^2 = 4.06$ , d.f. = 2,  $P = 0.13$ ). Browsers had no detectable effect on mortality rates of *A. etbaica*, *G. tenax* and all shrub species combined, and only a minor effect on mortality of *A. mellifera* (Table 3). When shrub mortality rates are expressed in terms of shrub deaths  $\text{ha}^{-1} \text{year}^{-1}$  (Table 3) and compared to recruitment rates (Table 2), browsers clearly have a profound effect on shrub density. The rate of change in shrub density was slightly positive ( $\bar{x} = 7.1 \text{ ha}^{-1} \text{ year}^{-1}$ ) and indistinguishable from zero (1 SE = 10.2) on browsed plots, and rapidly increasing on fenced plots ( $136.9 \pm 13.6 \text{ ha}^{-1} \text{ year}^{-1}$ ; Table 4). Differences in the rate of increase for browsed vs. unbrowsed plots were greatest for *G. tenax* ( $39.1 \text{ shrubs ha}^{-1} \text{ year}^{-1}$ ), intermediate for *A. mellifera* ( $25.3 \text{ ha}^{-1} \text{ year}^{-1}$ ) and least for *A. etbaica* ( $20.4 \text{ ha}^{-1} \text{ year}^{-1}$ ; see Tables 2 and 3).

Several additional measures of shrub dynamics at the whole-plot scale emphasize the strength of browser effects over this 3-year period alone. At the beginning of the study in 1999, mean shrub cover across all plots ( $\bar{X} \pm 1$  SE) was  $33.5 \pm 1.7\%$ . Browsers significantly reduced the rate of change in shrub cover, which increased by 5.8% on fenced plots and decreased by 2.2% on browsed plots over 3 years (Table 4). In 1999, live woody biomass on study plots ( $\bar{X} \pm 1$  SE) was  $8226 \pm 474 \text{ kg ha}^{-1}$ . During 1999–2002, browsers switched net rates of live woody biomass accumulation from positive to negative (Table 4). Because this measurement does not include the biomass of shrubs that died during the study period (but most of the wood from dead shrubs was still present), we also calculated woody biomass accumulation after correcting for shrub mortality to better estimate above-ground net ecosystem production (ANEP; see Randerson *et al.* 2002). Browsers

**Table 3.** Mortality rates of browsed and unbrowsed shrubs > 0.5 m tall (means with 1 SE in parentheses) at bushland study sites at MRC. *P*-values are for paired *t*-tests comparing fenced and unfenced treatments at the three study sites. Mortality rates are also expressed in terms of density (deaths ha<sup>-1</sup> years<sup>-1</sup>) for comparison to shrub recruitment rates in Table 2

	Annual mortality rate (% year <sup>-1</sup> )			Shrub deaths ha <sup>-1</sup> year <sup>-1</sup>	
	Browsed	Fenced	<i>P</i>	Browsed	Fenced
<i>A. etbaica</i>	0.73 (0.44)	0.44 (0.23)	0.69	1.8 (0.9)	1.3 (0.8)
<i>G. tenax</i>	2.41 (1.37)	1.07 (0.58)	0.41	2.2 (1.2)	3.1 (1.6)
<i>A. mellifera</i>	1.67 (0.56)	0.64 (0.32)	0.07	5.3 (2.0)	2.2 (1.2)
Other species	2.26 (0.96)	0.15 (0.15)	0.18	9.3 (5.6)	2.2 (2.2)
All species	1.68 (0.33)	0.56 (0.09)	0.10	18.7 (1.5)	8.8 (2.7)

**Table 4.** Effects of browsers on whole-plot measures of shrub dynamics (means with 1 SE in parentheses) at MRC. Measures of shrub density, basal area and cover are for all shrubs > 0.5 m tall. *P*-values are for paired *t*-tests comparing fenced and unfenced treatments at the three study sites

Response variable	Treatment		
	Browsed	Fenced	<i>P</i>
Rate of change in shrub density (individuals ha <sup>-1</sup> year <sup>-1</sup> )	7.1 (10.2)	136.9 (13.6)	0.026
Net change in shrub cover (% per year)	-0.75 (0.30)	1.92 (0.91)	0.049
Net live woody biomass accumulation (kg above-ground ha <sup>-1</sup> year <sup>-1</sup> )	-111 (22)	898 (290)	0.083
Net ecosystem production (kg above-ground ha <sup>-1</sup> year <sup>-1</sup> )	-26 (62)	962 (257)	0.086

significantly reduced ANEP, again causing a switch from a positive to a negative value (Table 4).

## Discussion

Our results show that browsers exert strong effects on shrub dynamics in savannas at scales ranging from the growth rates of individual twigs to the accumulation of woody biomass at the ecosystem level. Findings at each of the hierarchical scales in this study (twigs, shrub populations, the shrub community and the ecosystem) have significant implications for the role browsing mammals can play in the dynamics of savannas.

### SHRUB TWIG GROWTH RATES

At the scale of individual twigs, browsers dramatically reduced leaf density and biomass on twigs within the foraging height of dik-diks. Mean net growth rates of these twigs in browsed treatments were negative in 2000–01 and zero in 2001–02 (Fig. 3). Our results are in contrast to findings for browsers such as goats, impala and giraffe in other savannas where browsing either stimulated or had no negative effect on twig growth rates (Pellew 1983b; du Toit *et al.* 1990; Gowda 1996; Oba & Post 1999; Gadd *et al.* 2001). At Mpala, several factors suggest dik-diks are the primary browser reducing twig growth rates. Despite relatively high impala densities within the study area (averaging 20 km<sup>-2</sup>), ungulates had no effect on leaf biomass or growth of twigs that exceeded the height of dik-dik but were still accessible to impala. Impala are mixed feeders that increase consumption of grasses during wet seasons (Table 1, Klein

& Fairall 1986; Meissner, Pieterse & Potgieter 1996), while dik-dik are pure browsers throughout the year (Table 1, Boshe 1984). Elephants contributed minimally to the suppression of twig growth, and browser effects on twig growth were still highly significant when twigs consumed by elephants were removed from the analysis. While larger browsing ruminants such as impala, goats and giraffe often remove shoot ends while feeding and hence have a pruning effect (Pellew 1983b; du Toit *et al.* 1990; Gowda 1996), dik-dik are small and highly selective feeders that nimbly remove leaves between *Acacia* thorns and do not prune twig ends. Furthermore, dik-dik density did not decline during the drought in 2000 (Augustine 2002). Effects of dik-dik browsing may therefore be more similar to the type of severe, chronic defoliation often caused by insects, rather than the pruning effect of larger ungulates (du Toit *et al.* 1990).

### SHRUB RECRUITMENT

Browser suppression of the growth of twigs < 0.5 tall was associated with a 6-fold reduction in the rate at which shrubs < 0.5 m tall were recruited into the 0.5–1.5 m height class in the bushland community. This reduced recruitment combined with low rates of shrub mortality in larger height classes indicates that browsers reduced the rate of change in shrub density nearly to zero. In contrast, shrub density increased rapidly inside exclosures.

Browsers dramatically reduced recruitment rates of all three dominant shrub species, despite variation among those species in the degree and type of thorn defences. This may again reflect the ability of dik-dik to selectively remove leaves between *Acacia* thorns and to

maintain high population densities through extended dry seasons. Our results emphasize the generally overlooked potential for small mammalian browsers to regulate woody vegetation dynamics in savannas (Weltzin *et al.* 1997). Small browsers could be particularly important on commercial rangelands such as in Laikipia, where cattle are the primary livestock species and shrub encroachment reduces cattle access to grass forage. Differences between the results of this study and those involving or simulating goat browsing (Gowda 1997; Oba & Post 1999) also suggest that dik-dik may more effectively suppress twig and sapling growth than domestic goats.

In contrast to the strong browser effects on shrub recruitment in the bushland community, browsers had no detectable effects on shrub invasion into nutrient-rich glades. We originally hypothesized that impala prevented shrub establishment in glades, but results indicate no interaction between the effects of browsers and nutrient enrichment on shrub recruitment. The lack of shrub invasion inside glade exclosures suggests other factors such as glade soil chemistry or the dispersal, predation and germination of shrub seeds may be related to the long-term persistence of glades as short-grass lawns. It is important to note that our study did not focus on seedling germination or growth, and factors influencing seedling germination will certainly have an important effect on long-term patterns of shrub encroachment. In 2001, we did observe extensive germination of *A. mellifera* seedlings between and beneath shrub canopies and in both browsing treatments, but we did not observe germination of other species. Experiments focused on seedling survival in glade vs. bushland soils may provide greater insight to the relationship between landscape-scale patchiness in shrubs and soil nutrients observed in many African savannas (Blackmore *et al.* 1990; Reid & Ellis 1995; Young *et al.* 1995).

#### SHRUB POPULATION AND COMMUNITY DYNAMICS

In the bushland community, *Acacias* that escaped above the foraging height of dik-dik then entered a second phase where browser impacts were low. Browsers had no effect on growth rates of twigs above 0.5 m (Fig. 3), minimal effects on growth of shrubs in the 0.5–1.5 m height class, and no effects once shrubs reached the 1.5–2.5 m height class (Fig. 5). The lack of impala effects on *Acacia* twig growth despite high impala densities may reflect the fact that shrubs are also abundant, covering an average of 28% of this savanna (Augustine 2003b), and impala increase grass consumption during the wet season (Table 1). Elephants also occasionally damaged shrubs in the 0.5–2.5 m height classes, but caused negative growth rates for only a small proportion of those shrubs (Fig. 6).

Shrubs taller than 2.5 m experienced increased rates of damage by elephants, particularly *A. mellifera*.

Although elephants may forage intensively on shrub seedlings and saplings in some savannas (Dublin *et al.* 1990), elephant impacts are primarily focused on large *Acacias* in savannas with high shrub and tree density (Fig. 6, Pellew 1983a; Ruess & Halter 1990; Ben-Shahar 1996; van de Vijver *et al.* 1999). Elephant browsing significantly reduced shrub height and canopy diameter, but not basal area, because elephants typically foraged on canopies without killing the main stems. Thus elephants do not appear to influence the population dynamics of *Acacias* significantly, but do reduce mean shrub size, overall shrub cover, and the rate of woody biomass accumulation in this ecosystem. Similar elephant effects on shrub size class distribution have been reported for some East African parks, where the loss of large, spreading *Acacia* canopies was a major concern with respect to tourism (Pellew 1983a; van de Vijver *et al.* 1999). At Mpala, this damage to large shrub canopies created greater access for cattle to grasses growing beneath shrubs.

Browsers also had significant effects on the species composition of the shrub community. In contrast to the minimal damage observed for *Acacias* in the 0.5–2.5 m height classes, browsers negatively affected growth of the broad-leaved *Grewia tenax* in all height classes (Fig. 7). Most *G. tenax* individuals were in the 0.5–1.5 m height class, and even canopies of these smaller plants were often severely damaged by elephants. Similar effects were also observed for the broad-leaved shrub *Rhus natalensis*, but *Rhus* only occurred at two of the three study sites and could not be analysed statistically. Both *Rhus* and *Grewia* lack thorn defences, and the strong negative browser effects on recruitment and growth of these two broad-leaved shrubs suggest they are highly palatable. Growth rates observed inside exclosures suggest that in the absence of browsers, *G. tenax* would be a dominant shrub in this ecosystem. In addition, elephant effects were more severe for *A. mellifera*, which possesses only short, recurved thorns, than for *A. etbaica*, which is defended by long straight thorns and recurved thorns (Figs 5 and 6). These results suggest that native browsers shift the species composition of this savanna from dominance by palatable, broad-leaved shrubs to dominance by thorny, fine-leaved *Acacias*, particularly *A. etbaica*. A similar shift toward dominance of unpalatable shrub species occurred in a West African savanna with similar elephant densities to MRC (Jachmann & Croes 1991). Results from MRC provide community-scale experimental support for the idea that the spinescence and dominance of many *Acacias* in African savannas are a consequence of ungulate browsing pressure (Young 1987; Gowda 1996; Young & Okello 1998).

#### SHRUBLAND ECOSYSTEM DYNAMICS

At the ecosystem scale, browsers reduced total shrub cover, suppressed the accumulation of woody biomass and switched net ecosystem production from positive

to negative (Table 4). These results show native browsing ungulates can indeed dramatically reduce rates of shrub encroachment on managed rangelands, with dik-dik and elephants apparently exerting the most important effects. Given that reductions in woody cover typically increase grass biomass and productivity (O'Connor 1985; Scholes *et al.* 2002), the presence of native browsers could provide important benefits on commercial rangeland, particularly in regions such as Laikipia where high variability in annual rainfall makes fire an unattractive option for shrub control.

Large, bulk-feeding species (elephants) play an important role by reducing shrub cover and woody biomass accumulation, thereby increasing access of grazers to herbaceous forage beneath large shrubs. However, elephants primarily damaged large shrubs and had minimal effects on the rate of shrub density increase. These findings are consistent with the predictions of Dublin *et al.* (1990) that elephants are unlikely to switch shrub population growth rate from positive to negative unless fire reduces shrubs to low initial density. Similarly, studies from other bushland or woodland habitats where large shrubs and trees are abundant suggest that elephants primarily affect the size structure of woody plant populations, with minimal effects on density (Pellew 1983a; Ruess & Halter 1990; Ben-Shahar 1996; van der Vijver *et al.* 1999).

Small, selective browsers (dik-diks in particular) play a major role by regulating the rate of sapling recruitment, which largely determines the rate at which shrub density can increase. At the same time, shrub density still increased at low but positive rates in the presence of browsers. Results therefore suggest that in the absence of changes in browsing pressure or fire management policy, shrub populations may still continue to increase slowly. Due to the effects of elephants, these shrubs will primarily occur in intermediate height classes with increasing dominance of *Acacia etbaica*. Conversely, loss or removal of native browsers from the system could result in the rapid development of dense *Acacia* thickets with far greater woody biomass and cover, and increasing dominance of broad-leaved shrubs. Clearly, such a change in the shrub component would have major consequences for cattle forage production and accessibility. Native browsers can thus provide an important ecosystem service by suppressing rates of shrub encroachment on commercial rangeland.

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