Did the elephant and giraffe mediate change in the prevalence of palatable species in an East African *Acacia* woodland?

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Abstract: We report on a 2009 survey of *Acacia* woodlands in the Seronera area of central Serengeti, Tanzania, and compare the results to previous surveys from the 1970s–1980s. We document a substantial change in woodland structure and composition. From 1978 to 2009, woody plant density (mean $\pm$ SD) declined from 255 ± 35 trees ha^{-1} to 147 ± 14 trees ha^{-1}. Canopy cover declined from $15.1 \pm 1.9\%$ to $5.7 \pm 0.6\%$. Canopy volume declined from 1810 ± 207 m^3 ha^{-1} to 1410 ± 121 m^3 ha^{-1}. A 19% increase in the relative canopy volume of *Acacia robusta*, a species avoided by the giraffe, represents a sharp decline in the quality of the giraffe's food supply, which was last comprehensively assessed in 1978. We examine these changes in the context of Pellew's 1983 woodland dynamics model describing the impacts of elephant, giraffe and fire on an *Acacia tortilis* tree population and determine that our data are qualitatively consistent with this model. We hypothesize that selective elephant and giraffe browsing has contributed to an increase in the relative dominance of unpalatable species, consistent with Pellew's predictions.

Key Words: Acacia, African elephant, giraffe, Serengeti, vegetation impacts, unpalatable species

INTRODUCTION

The elephant (*Loxodonta africana* Blumenbach) and giraffe (*Giraffa camelopardalis* Linnaeus) are two important large browsers of African savanna woodlands. Elephants break branches and stems, strip bark and uproot mature trees, at times causing considerable damage (Beuchner & Dawkins 1961, Croze 1974a, Lamprey *et al.* 1967). In contrast, giraffes strip leaves and unlignified shoots from stems, the main impact of which is to retard plant growth (Birkett 2002, Birkett & Stevens-Wood 2005, Norton-Griffiths 1979, Pellew 1983a, Ruess & Halter 1990). Pellew's seminal studies in Serengeti National Park, Tanzania, in the 1970s contributed greatly to our understanding of giraffe browsing behaviour and the potential impacts of elephant, giraffe and fire on the Serengeti woodlands (Pellew 1981, 1983a, b, c, d, 1984a, b). In the current study, we revisit the locations of Pellew's studies to determine the extent of woodland change in Seronera, central Serengeti, and whether or not it is qualitatively consistent with his predictions.

In particular, we explore and develop the hypothesis that giraffe browsing has contributed to the suppression of palatable woody plant species, such that the giraffe may have reduced the quality of its own food supply. Previous work suggests that large-herbivore browsing activity can increase the relative dominance of chemically defended, unpalatable species relative to palatable species (Augustine & McNaughton 1998). For example, by browsing on more palatable competitors, moose (*Alces alces*) on Isle Royale, Michigan, may have led to increases in the relative abundance of white spruce (*Picea glauca*) (McInnes *et al.* 1992), and, in Burkina Faso, heavy elephant browsing suppressed palatable shrub species to the advantage of unpalatable species (Jachmann & Croes 1991).

First, we evaluate changes in the structure and composition of the Seronera woodlands and consider the possible impact of elephant and giraffe browsing. We test the hypothesis that unpalatable species have increased in relative dominance while preferred species have decreased. We also consider whether selective giraffe browsing could drive an increase in the dominance of the unpalatable species *Acacia robusta* Burch. (synonym: *Acacia clavigera* E. Mey) relative to the more palatable *Acacia tortilis* (Forssk.) Hayne (Pellew 1981). Second, we test the hypothesis that the quantity and quality of the giraffe's food supply have recently changed, by

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comparing data from 2009 with 1978 (Pellew 1983c). Finally, we qualitatively assess the predictive power of Pellew's woodland dynamics model (Pellew 1983a), which predicts the number of mature *A. tortilis* trees in the Seronera woodlands as a function of elephant and giraffe impact and fire frequency.

STUDY SITE

The Serengeti ecosystem covers $25\,000\,km^2$ of northern Tanzania and southern Kenya, loosely bounding the path of the migrating wildebeest (*Connochaetes taurinus* Burchell) (Sinclair 1979a). The area is subject to seasonal rains with a June–October dry season. Annual rainfall is highest in the north-west ($>1000\,mm\,y^{-1}$) and decreases toward the south-eastern plains ($500\,mm\,y^{-1}$) (Sinclair 1979b).

Fire and herbivores are critical drivers of woodland-grassland dynamics in the Serengeti (Dublin 1995, Dublin *et al.* 1990, Norton-Griffiths 1979, Pellew 1983a, Shaw *et al.* 2010, Sinclair *et al.* 2008). For example, following the elimination of the rinderpest virus in the early 1960s, wildebeest numbers climbed from $<300\,000$ to over one million in just over a decade (Sinclair & Norton-Griffiths 1982). Resultant heavy grazing reduced fires, in turn fostering the regeneration of *Acacia* woodland in the 1970s and 1980s (Sinclair *et al.* 2008).

This study focuses on an area of *c.* $120\,km^2$ around Seronera, central Serengeti, roughly bounded by the Seronera and Sangere Rivers to the west and east and the Wandamu River to the south (Croze 1974a, Pellew 1983c, Ruess & Halter 1990). Rainfall averages $\sim800\,mm\,y^{-1}$ (Pellew 1983c). We surveyed the woodlands in 2009 and compare the results with prior surveys completed in 1971 (Croze 1974a), 1978 (Pellew 1981, 1983a, b, c) and in 1982 (Ruess & Halter 1990). To draw parallels with these earlier studies, we focus on the possible roles of the elephant and giraffe in driving local woodland change.

Elephants and giraffes utilize most of the principal tree species of Seronera, such as *Acacia tortilis*, roughly in proportion to their availability (Croze 1974a, Pellew 1984b, Ruess & Halter 1990). Notably, however, they avoid two relatively common woody species: (1) *Acacia robusta*, a medium-sized tree with lush foliage and relatively short stipular spines and (2) *Commiphora trothae* Engl., a small tree with pungent foliage. The giraffe avoids *A. robusta* year-round and consumes *C. trothae* only during its short foliated phase (Pellew 1981, 1984b). The elephant consumes these plants infrequently, stripping the bark of *A. robusta* and consuming the bark and roots of *C. trothae* (Croze 1974a, b; Lamprey *et al.* 1967, Ruess & Halter 1990). In contrast, preferred species, particularly *Acacia senegal* Willd. and *Acacia xanthophloea* Benth. have been subject to heavy browsing pressure, especially from

the elephant (Croze 1974a, b, Pellew 1984b, Ruess & Halter 1990).

Elephant and giraffe abundance in Serengeti have fluctuated substantially over the last several decades. The earliest description of the elephant in the Serengeti is from 1955 (Lamprey *et al.* 1967) but thereafter density rapidly increased, reaching ~0.2 elephants km^{-2} in the early 1970s (Norton-Griffiths 1979). In central Serengeti, bull elephants were first reported in 1963–1964 (Croze 1974b, Lamprey *et al.* 1967) and cow-calf groups appeared several years later (A.R.E. Sinclair, pers. comm.). From 1975–1977, elephant density (mean $\pm$ SD) in the Seronera woodlands was 0.2 ± 0.16 elephants km^{-2} (Pellew 1983a). From 1977–1986, poaching drastically reduced the elephant population inside the Park to <0.04 elephants km^{-2} (Dublin 1995). However, the population subsequently recovered, approaching 1970s densities (Sinclair *et al.* 2008). Early studies of elephant-tree interactions in Seronera focused on the rapid destruction of mature trees by bulls (Croze 1974b, Lamprey *et al.* 1967).

Giraffe density has likewise fluctuated. In the mid-1970s, there were 1.47–2.64 giraffes km^{-2}, with the population increasing at a rate of 5–6% y^{-1} in response to the concurrent increase of young *Acacia* trees (Pellew 1983d). However, giraffe numbers have since declined, possibly beginning in the 1980s. In Seronera, giraffe density (mean $\pm$ SE) fell from 1.47 ± 0.27 giraffes km^{-2} in 1975–1976 (Pellew 1983d) to 0.28 ± 0.03 giraffes km^{-2} by 2008–2010 (Strauss *et al.*, unpubl. data).

Small and medium-sized mammals also feed on woody vegetation in Seronera, including dikdik (*Rynchotragus* (*Madoqua*) *kirkii* Günther), eland (*Taurotragus oryx* Pallas), impala (*Aepyceros melampus* Lichtenstein), Grant's gazelle (*Gazella granti* Brooke) and Thomson's gazelle (*G. thomsoni* Günther), however, we do not consider their browsing impacts.

METHODS

Measurements of woodland structure and composition

To enable direct comparison with previous studies, we sampled the Seronera woodlands using the point-centred quarter method (Croze 1974a, Cottam & Curtis 1956, Heyting 1968), the suitability of which has been described elsewhere (Croze 1974a, Pellew 1981, 1983c; Ruess & Halter 1990). Following Pellew (1983c), we divided the woodlands into four types based on vegetation and position in the drainage catena: (1) ridge-top and upper-slope woodland, (2) mid-slope woodland, (3) seasonal drainage woodland ('korongo woodland' in Pellew 1983c) (includes stream-beds and banks) and (4) riverine woodland (includes perennial watercourses and

banks). Areas of open grassland (<1% canopy cover) were excluded. Within each woodland type, we sited line transects of fixed direction to overlap areas surveyed in 1978 (Pellew 1983c, R. Pellew, pers. comm.) and close to areas sampled in 1971 by Croze (1974a) and in 1982 by Ruess & Halter (1990).

Along each transect, sample points were placed at even intervals of 40–50 m for ridge-top and mid-slope transects and 25 m for the more species-rich riverine and seasonal drainage areas. At each sample point, we placed a cross on the ground, dividing the area into four quarters, and located the tree or shrub in each quarter closest to the centre of the cross using a Haglöf DME measuring device. We included all woody perennials >0.5 m tall. Thus, four plants were evaluated at each sample point, recording species name, distance from the centre of the cross, total plant height, canopy diameter (the mean of two measurements taken at right angles) and canopy depth. The canopy diameter and depth measurements excluded canopy above 5.75 m, which is outside the maximum reach of an adult male giraffe.

Distance measurements were used to estimate woody plant density (plants ha^{-1}) for each woodland type and the relative density of each species, using statistics defined in Croze (1974a). We compared plant density, canopy cover (%) and volume (m^3 ha^{-1}), and species composition with Pellew's 1978 survey (Pellew 1983c). We compared tree population structures with the 1971, 1978, and 1982 surveys (Croze 1974a, Pellew 1983c, Ruess & Halter 1990).

Elephant and giraffe usage of *Acacia robusta*

To estimate current elephant and giraffe usage of common *Acacia* species, we assessed elephant and giraffe browsing/damage to *A. robusta*, *A. tortilis* and *A. drepanolobium* Harms ex Sjöstedt on trees with a canopy bottom >1.5 m from the ground, which excludes browse damage from smaller species such as impala. Browsing assessments were performed simultaneously with other routine tree measurements during the point-centred quarter survey. In addition, we visited nine even-aged stands of *A. robusta* and five even-aged stands of *A. drepanolobium* in several locations across the Serengeti. At each location we set up circular plots with a 10-m radius and recorded browsing/damage. Surveys were completed in the dry season when the majority of trees were in a deciduous phase or producing few shoots. Thus, we recorded evidence of cumulative browsing over several seasons. We sampled only living trees, which underestimates the impact of elephants. Even-aged stands of *A. robusta* are extremely dense, often covering large areas. We established plots both on the inside of stands ($n = 4$) and on stand edges ($n = 5$). We calculated the proportion of trees of each species showing evidence of elephant or giraffe browsing but did not assess the severity of browsing. Elephant usage includes browsing of leafy material, bark stripping and branch breaking.

RESULTS

Summary of changes in Seronera woodland structure and composition

Mostly, the same species were encountered in the 1978 and 2009 surveys, although *Hibiscus* spp. and *Aspilia mossambicensis* (Oliv.) Wild – small woody perennials – were encountered frequently in the riverine and seasonal drainage areas in 2009 but were unreported in 1978, despite being present elsewhere in Serengeti in the 1970s.

Woody plant density (mean $\pm$ SD) in the Seronera woodlands has decreased from 255 ± 35 plants ha^{-1} to 147 ± 14 plants ha^{-1} (Table 1), largely due to a significant decrease in plant density in the ridge-top woodland type, which supported extremely dense thickets of regenerating *Acacia* seedlings in 1978. Across all woodland habitats, significant increases in plant density in the seasonal drainage and mid-slope woodlands and an increase in the extent of mid-slope woodland have been insufficient to replace the loss of density in ridge-top areas.

Canopy volume has remained comparable to 1978 values, with the exception of the riverine sample area, which has experienced especially heavy elephant impact (Table 1). The significant decrease in canopy volume in this area reflects a loss of regenerating and mature *A. xanthophloea* trees and an increase in the relative density of smaller shrub species.

Species composition has shifted throughout the woodlands (Figure 1, Appendix 1). For example, in the seasonal drainage woodland type, smaller woody shrubs are now dominant to species of *Acacia*. In the riverine sample area, located near Downey's Dam on the Seronera River, elephants have decimated the *A. xanthophloea* population, the previous riverine dominant.

Changes observed in the relatively sparsely treed mid-slope woodland, which accounts for 55% of woodland area, contrast with those observed in the other woodland types (Table 1, Appendix 1). Woody plant density in the mid-slope woodland increased significantly ($z = 9.2$, P < 0.001, Table 1). The relative densities of the principal woody species remained almost identical to the 1978 values, with the notable exception of *A. senegal*, the preferred browse species. All principal species (as defined in 1978) aside from *A. senegal* have increased in absolute density by a factor of 5–7. Additionally, the total number of species encountered in the mid-slope woodland has almost tripled (Appendix 1).

Table 1. A comparison of the mean structure of the Seronera woodlands, Serengeti in 1978 (Pellew 1983c) and 2009, with 95% confidence limits. Woody plants <0.5 m in height were excluded. Canopy measurements include only foliage/stems below 5.75 m, the maximum reach of an adult male giraffe. To estimate per cent total area of each woodland type in 2009, we compared Pellew's woodland map to recent aerial photographs and high-resolution satellite imagery (Google Maps for 2013), using ArcMap10. P-values test the null hypothesis that woodland structure in 2009 is equivalent to 1978. *P < 0.05, **P < 0.01, ***P < 0.001.

Woodland type	No. transects	No. sample points	Total % of Seronera woodlands	Woody plant density (plants ha^{-1})	Canopy cover (%)	Canopy volume (m^3 ha^{-1})
1978						
Ridge-top	8	243	34	591 ± 99	23.4 ± 3.1	3080 ± 444
Mid-slope	4	112	51	13 ± 8	5.4 ± 2.8	438 ± 236
Seasonal drainage	4	155	6	518 ± 136	26.4 ± 7.2	5040 ± 1180
Riverine	5	136	9	179 ± 23	30.7 ± 3.1	2630 ± 312
Composite	21	646	100	255 ± 35	15.1 ± 1.9	1810 ± 207
2009						
Ridge-top	8	224	32	***154 ± 25	***7.7 ± 1.2	***2100 ± 224
Mid-slope	4	112	55	***81 ± 12	3.4 ± 0.7	*774 ± 137
Seasonal drainage	4	140	6	*716 ± 142	*17.0 ± 4.4	4340 ± 1010
Riverine	5	120	7	146 ± 33	***4.5 ± 1.4	***815 ± 208
Composite	21	596	100	147 ± 14	5.7 ± 0.6	1410 ± 121

Changes in key woody species

Across the woodlands, preferred and heavily utilized species have been reduced and unpalatable species have thrived. The unpalatable species *A. robusta* has increased in dominance relative to *A. tortilis* (Figure 1, Appendix 1) and the relative canopy volume of *A. robusta* has increased by a factor of 3.6 (Appendix 1). Figure 2 indicates that the increase in *A. robusta* canopy volume is due to a dramatic shift in the population from mostly small trees to mostly mature, large-canopied trees. The fluctuation of the *A. robusta* population between a phase with a high proportion of mature trees and a phase dominated by regeneration is consistent with pulsed growth (Figure 2d). Similar changes in structure have been observed in the *A. tortilis* and *A. senegal* populations (Figure 2a, b).

In 1978, the unpalatable species, *C. trothae*, and the preferred species, *A. senegal*, occurred at densities of 22 trees ha^{-1} and 34 trees ha^{-1} respectively, and in each species, >90% of the population was vulnerable to fire (<3 m tall) (Figure 2a, e, Appendix 1). Strikingly, *C. trothae* has not only persisted, but has increased in density and become co-dominant with *A. tortilis*: *C. trothae* has more than tripled in relative dominance in the ridge-top woodland, whereas densities of all other principal species have decreased. In contrast, *A. senegal*, once a principal species in the ridge-top woodland, has been reduced to a handful of specimens in the sample areas (Figure 1, Appendix 1). Another preferred species, *A. hockii* De Wild., has also become rare. A dominant in the seasonal drainage woodland type in 1978, *A. hockii* has decreased in density by 96% (Appendix 1).

As noted, elephants have severely reduced the population of *A. xanthophloea* trees along the upper Seronera River. In 1978, *A. xanthophloea* constituted ~90% of total canopy volume in the riverine woodland. In 2009, its contribution had shrunk to a mere 6% (Appendix 1). Many of the small *A. xanthophloea* specimens in the area today are the coppicing remnants of once larger trees. Interestingly, despite the dramatic reduction in the density of *A. xanthophloea* trees along the Seronera River, the height structure of the *A. xanthophloea* population has remained relatively stable (Figure 2c).

The absolute density of *A. tortilis* has been halved due in part to thinning and maturation of the once-dense stands of *A. tortilis* regeneration observed in the 1970s (Figure 1). However, *A. tortilis* remains the woodland dominant. The density of mature *A. tortilis* (>6 m) in the Seronera woodlands has increased by a factor of 1.6 (Appendix 1). Figure 3 shows that the population structure of *A. tortilis* is now more evenly distributed among height classes in contrast to a bimodal structure observed in 1971.

Elephant and giraffe usage of *Acacia robusta* vs. control species

In the point-centred quarter sample of *A. robusta* plants (n = 74), 23% of plants had evidence of giraffe browsing and 86% had evidence of elephant browsing/damage. This is similar to results from even-aged stands of *A. robusta*, where 32% of plants (n = 330) had evidence of giraffe browsing and 95% had evidence of elephant use. Elephant damage was occasionally severe. There was no difference in the proportion of *A. robusta* trees browsed at edge versus inside plots for the giraffe (z = 0.72, P = 0.47) or the elephant (z = 0.82, P = 0.41). In the *A. tortilis* sample (n = 179), 65% and 57% had evidence of giraffe
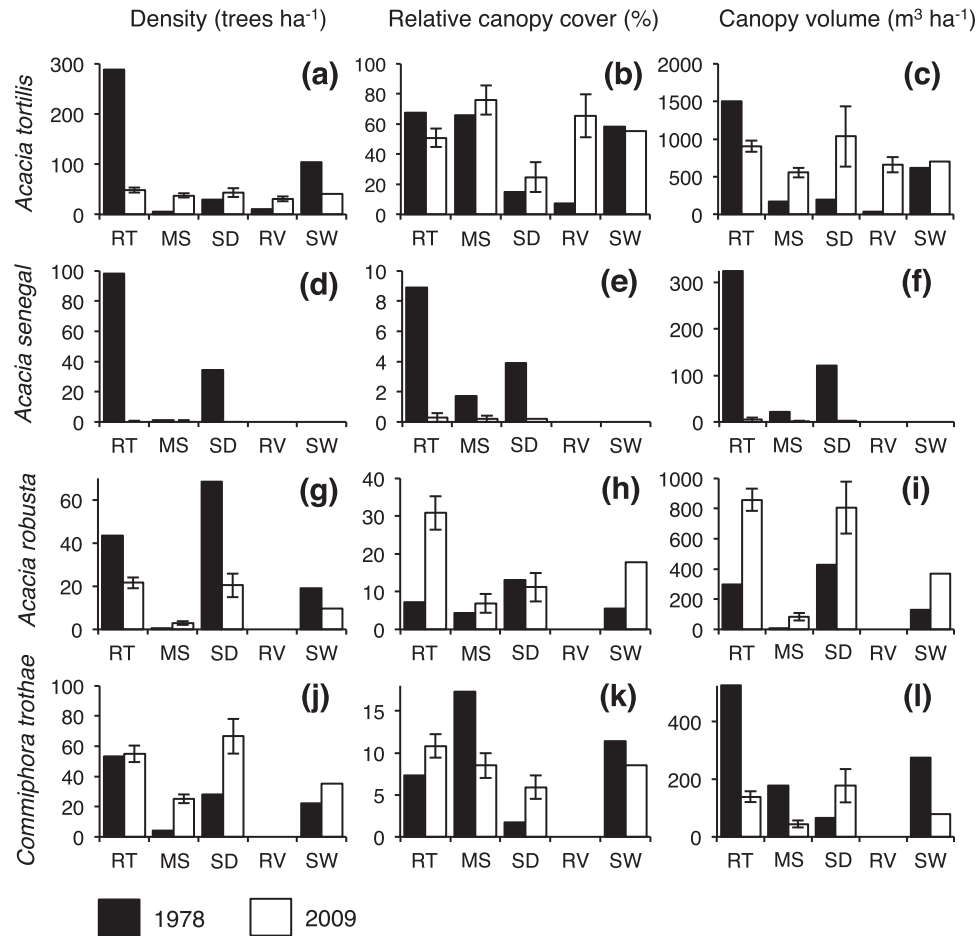
Figure 1. Changes in tree density (trees ha^{-1}, includes plants > 0.5 m tall), relative canopy cover (%) and available canopy volume (m^3 ha^{-1}) between 1978 (black bars, Pellew 1983c) and 2009 (white bars; error bars are ± SD) for: *Acacia tortilis*, *Acacia senegal*, *Acacia robusta* and *Commiphora trothae*. RT = ridge-top woodland, MS = mid-slope woodland, SD = seasonal drainage woodland, RV = riverine woodland and SW = Seronera woodlands, weighted by the % area of each woodland type. Although *Acacia tortilis* has decreased in density (a), its overall contribution to canopy cover (b) and volume (c) is similar to 1978. *Acacia senegal* has been decimated in all measures, (d), (e) and (f). *Acacia robusta* has decreased in density (g), but increased in relative canopy cover (h) and volume (i). *Commiphora trothae* has increased in density (j), although its relative canopy cover (k) and volume (l) have decreased.

and elephant use, respectively. In the *A. drepanolobium* sample (n = 114), 84% and 73% respectively had evidence of giraffe and elephant use.

Changes in the giraffe's food resource

Overall canopy volume (mean ± SD) in the Seronera woodlands decreased from 1800 ± 207 to 1400 ± 121 m^3 ha^{-1} between 1978 and 2009 (Table 1). This decrease has been particularly marked in the ridge-top and riverine areas. Canopy volume available to giraffes has dropped by two-thirds in the riverine woodland, mostly due to a > 97% reduction in *A. xanthophloea*. Another important change in the food resource is the dramatic reduction, throughout the woodlands, in the absolute density and volume of preferred species such as

A. senegal, A. hockii, and principal browse species such as the broad-leaved *Grewia* species. However, in the seasonal drainage woodland, canopy volume has not significantly declined due to an increase in *A. tortilis*, though *A. tortilis* produces few shoots (i.e. low edible biomass) in the dry season.

The total canopy volume of *A. tortilis*, the principal wet-season food, has remained stable. However, the preferred species *A. senegal* and *A. hockii* previously contributed 172 m^3 ha^{-1} but now contribute only 14 m^3 ha^{-1}. Moreover, a significant proportion of the available biomass is unpalatable. *Acacia robusta* has tripled in absolute volume and now contributes 26% of total canopy volume, up from 7% in 1978. Large, dense, monospecific stands of *A. robusta* were a notable feature at the periphery of some sample areas. Thus, *A. robusta* may contribute even more to the canopy volume of the woodlands. The
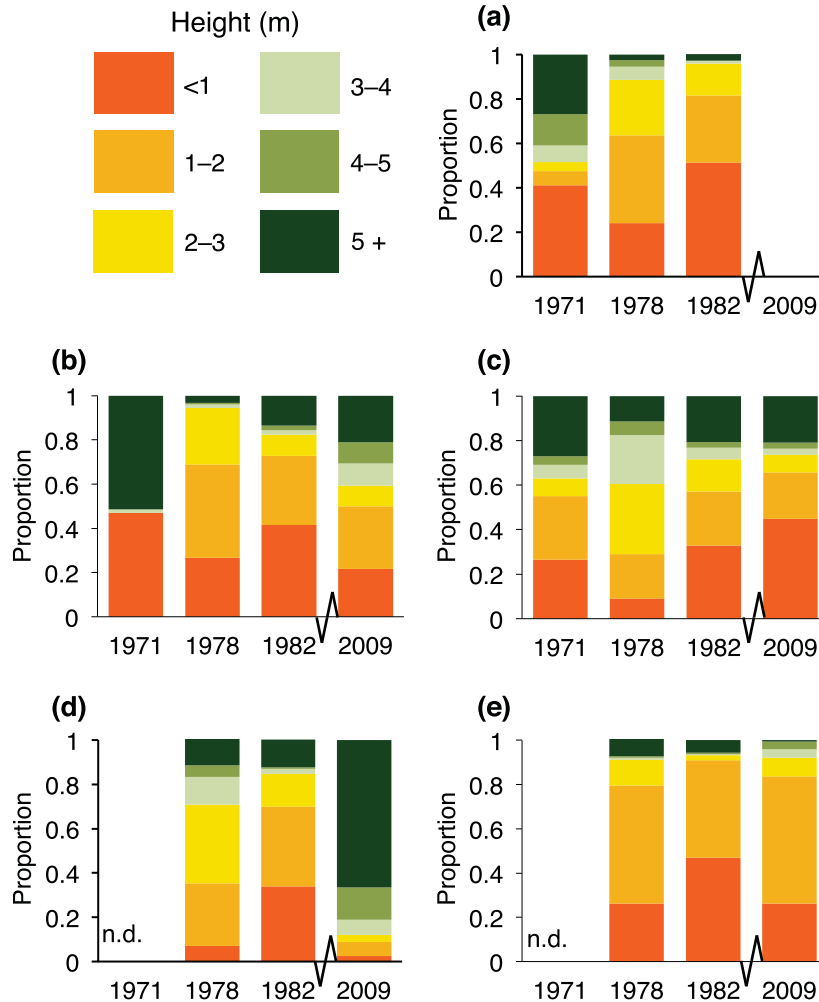
Figure 2. Temporal patterns (1971–2009) in the population structure of *Acacia senegal* (a), *Acacia tortilis* (b), *Acacia xanthophloea* (c), *Acacia robusta* (d) and *Commiphora trothae* (e) in the Seronera woodlands. Data were not available from 1971 for (d) and (e), and the sample size for (a) in 2009 was trivial. Mature trees > 5 m tall are lumped into a single height class. Height classes in orange/yellow are most vulnerable to fire, although *A. senegal* is more tolerant than *A. tortilis* at small sizes and *A. xanthophloea* can remain fire vulnerable up to a height of 7 m (Herlocker 1976). Populations of *A. senegal*, *A. tortilis* and *A. robusta* show pulsed growth: periods with a high proportion of either mature or young trees. Data are from Croze (1974a), Pellew (1983c), Ruess & Halter (1990) and the current study.

C. trothae population is made up of mostly small trees. Thus, despite an increase in density, *C. trothae* actually contributes less to canopy volume now than in 1978. Together, the unpalatable species *A. robusta* and *C. trothae* contribute 31% of canopy volume in 2009 vs. 22% in 1978 (Appendix 1).

DISCUSSION

Woodland change in Seronera

The Seronera woodlands have undergone substantial change over the last 30–40 y: we observed substantial declines in woody plant density in three of four woodland types (Table 1) and major shifts in species composition (Appendix 1). Although woodland dynamics are invariably complex, some of the changes we observed may be linked to the activities of elephant and giraffe. The elephant, for example, has clearly caused major damage to *A. xanthophloea* trees along the Seronera River, consistent with findings of the 1982 survey (Ruess & Halter 1990), which reported a 30% decline in the density of *A. xanthophloea* along the river from 1971–1982. The giraffe may also have contributed to observed changes in plant density. In the midslope woodland type, where giraffe browsing pressure was historically low (Pellew 1981, 1984b), woodland plant density increased significantly. In contrast, woody plant density declined in the ridge-top and seasonal drainage/riverine woodland types, favoured by giraffes in the wet and dry seasons respectively (Pellew 1981, 1984b).
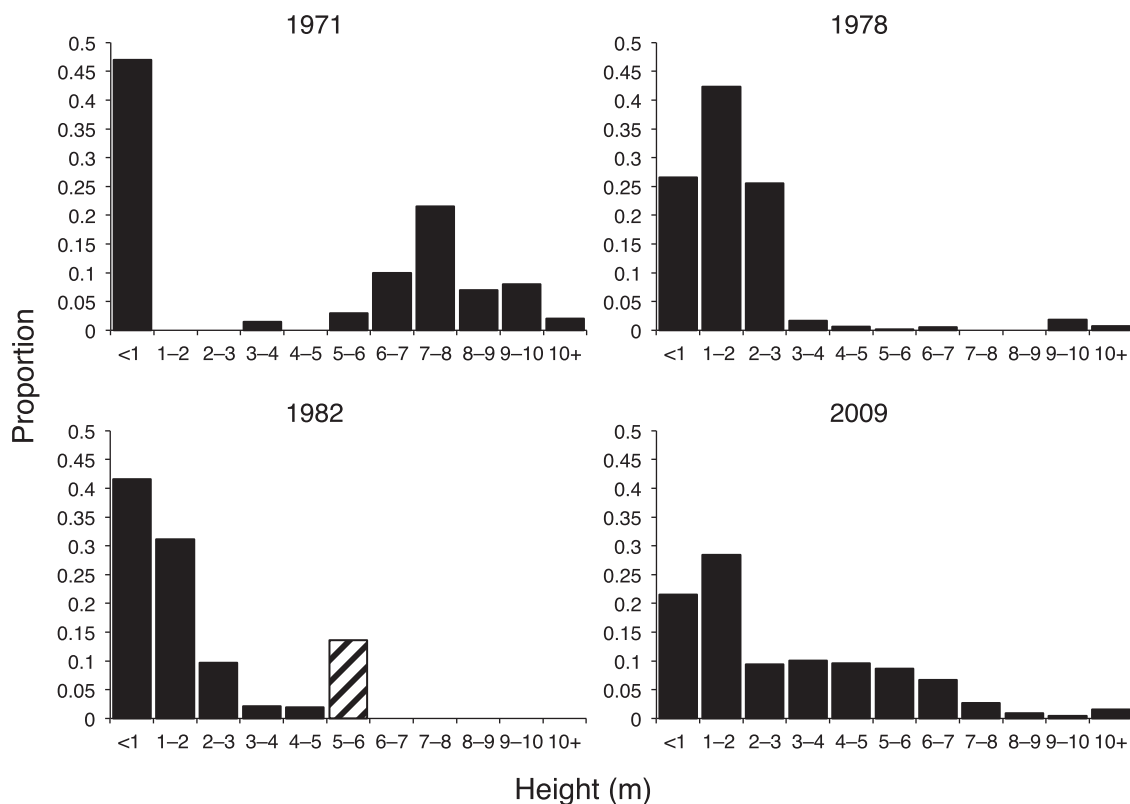
Figure 3. Temporal changes in the *Acacia tortilis* population of Seronera from 1971–2009. For 1982, trees > 5 m tall are lumped (hatched bar). The mature canopy suffered heavy elephant damage after 1963 (Lamprey *et al.* 1967), and the persistence of mature trees > 10 m, was a management priority in the 1970s (Croze 1974a, Pellew 1983a, b). By 2009, the population of *A. tortilis* trees had become more evenly distributed among height classes.

Through selective browsing, we suggest that the elephant and giraffe may also have played an important role shaping species composition, not unlike changes observed in other savanna woodlands. For example, in north-western Zimbabwe, elephant browsing likely drove a switch in the dominant woodland species from *Brachystegia boehmii* to *Pseudolachnostylis maprouneifolia* (Mapaure & Moe 2009). The interaction of heavy giraffe browsing with species tolerance also led to shifts in species composition in South African woodland savanna (Bond & Loffell 2001).

Consistent with Pellew's predictions, there has been a clear shift toward species that are unpalatable to the elephant or giraffe and a corresponding decrease in species that have been preferred or heavily utilized. Pellew (1981) predicted that giraffe avoidance of *A. robusta* would cause an increase in the dominance of *A. robusta* relative to *A. tortilis*. In the ridge-top woodland, where the vast majority (80%) of *A. robusta* trees were encountered, the ratio of *A. robusta* to *A. tortilis* trees has increased threefold over the past 30 y. We observed a similar pattern in a second species, *C. trothae*, which is unpalatable to the elephant and giraffe. The ratio of *C. trothae* to *A. tortilis* trees has increased almost fourfold in the Seronera woodlands

and *C. trothae* has become co-dominant with *A. tortilis* (Appendix 1).

In the early 1970s, *A. senegal* was considered a principal tree species in parts of Seronera (Croze 1974a, Herlocker 1976). Pellew (1981), however, predicted that the combined activity of the elephant and giraffe would rapidly reduce the dominance of this preferred species and indeed our data show that the density of *A. senegal* has been reduced from 34.2 trees ha^{-1} in 1978 to a mere 0.6 trees ha^{-1} in 2009.

The broad-leaved *Grewia* spp., which dominated seasonal drainage woodland canopy volume and giraffe dry-season diets in the 1970s (Pellew 1981, 1983c, 1984b), have more than halved in density and decreased in canopy volume by >96% from 1978 to 2009. In contrast. *A. tortilis*, which the elephant and giraffe browse roughly in proportion to its availability, remains a dominant woodland species.

Avoidance of *Acacia robusta*?

Although earlier studies suggested that the elephant infrequently utilizes *A. robusta*, Ruess & Halter (1990)

reduce seedling survival (Goheen *et al.* 2004, Pellew & Southgate 1984, Shaw *et al.* 2002). Wildebeest horning can severely damage up to 24% of small trees/shrubs inside woodland areas (Estes *et al.* 2008). Woodland dynamics in savannas result from intricate interactions between such biotic drivers and abiotic factors, such as fire, rainfall, soils and topography (Norton-Griffiths 1979, Pellew 1983a, Reed *et al.* 2009, Sankaran *et al.* 2005, Sinclair 1979b). Although our study does not provide an irrefutable causal link between the elephant, giraffe and woodland composition, careful monitoring of the impact of elephant and giraffe will likely prove valuable in understanding woodland dynamics in African savannas.

ACKNOWLEDGEMENTS

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Appendix 1. Comparison of 1978 (Pellew 1981, 1983c) and 2009 structure and composition of the Seronera woodlands, Serengeti. Table entries are mean ± SD in 2009, for four woodland types (ridge-top, mid-slope, seasonal drainage and riverine). Percentage values in parentheses indicate relative density/canopy volume for each species. The composite section combines all habitat types, weighted by the % area of each. Data are organized in decreasing order of 1978 density. Woody plants <0.5 m in height were excluded. Canopy measurements include only foliage/stems below 5.75 m, which is the maximum reach of an adult male giraffe. - represents species not encountered/not reported in one of survey years.

	Woody plant density (plants ha^{-1})		Relative canopy cover (%)		Canopy volume (m^3 ha^{-1})	
	1978	2009	1978	2009	1978	2009
Ridge-top:						
Acacia tortilis	289 (49%)	48.5 ± 4.9 (32%)	67.4	50.7 ± 6.1	1500 (49%)	907 ± 74.8 (43%)
Acacia senegal	98.2 (17%)	0.5 ± 0.3 (<1%)	8.9	0.3 ± 0.3	324 (11%)	4.7 ± 4.7 (<1%)
Commiphora trothae	53.3 (9%)	55.0 ± 5.5 (36%)	7.3	10.8 ± 1.4	528 (17%)	140 ± 19.2 (7%)
Acacia hockii	44.2 (8%)	0.3 ± 0.2 (<1%)	2.9	0.02 ± 0.01	79.6 (3%)	0.1 ± 0.02 (<1%)
Acacia robusta	43.5 (7%)	21.6 ± 2.6 (14%)	7.2	30.8 ± 4.4	296 (10%)	856 ± 73.5 (41%)
Grewia bicolor	2.8 (<1%)	0.5 ± 0.3 (<1%)	2.1	0.05 ± 0.04	211 (7%)	0.3 ± 0.15 (<1%)
Grewia fallax	1.4 (<1%)	0.2 ± 0.17 (<1%)	0.6	0.02 ± 0.02	64.1 (2%)	0.1 ± 0.0 (<1%)
All other species (12, ≥18)	59.5 (10%)	26.9 (18%)	3.6	7.4	76.1 (3%)	188 (9%)
Totals	591 (100%)	154 (100%)	100	100	3080 (100%)	2100 (100%)
Mid-slope:						
Acacia tortilis	5.3 (40%)	37.7 ± 3.9 (47%)	66.0	75.9 ± 9.7	175 (40%)	556 ± 63.7 (72%)
Commiphora trothae	4.1 (31%)	25.2 ± 2.9 (31%)	17.3	8.5 ± 1.5	179 (41%)	44.8 ± 12.1 (6%)
Acacia senegal	1.3 (10%)	0.7 ± 0.4 (<1%)	1.7	0.2 ± 0.2	21.5 (5%)	1.0 ± 0.9 (<1%)
Balanites aegyptica	0.7 (5%)	3.6 ± 0.9 (4%)	4.2	2.2 ± 0.9	35.9 (8%)	19.5 ± 9.8 (3%)
Acacia robusta	0.5 (4%)	2.9 ± 0.8 (4%)	4.4	6.9 ± 2.5	7.9 (2%)	83.3 ± 24.4 (11%)
All other species (4, ≥20)	1.5 (11%)	11.0 (14%)	6.4	6.3	19.6 (5%)	69.6 (9%)
Totals	13.4 (100%)	81.1 (100%)	100	100	438 (100%)	774 (100%)
Seasonal drainage:						
Acacia hockii	91.2 (18%)	3.8 ± 2.2 (<1%)	7.6	2.3 ± 1.6	341 (7%)	190 ± 85.5 (4%)
Acacia robusta	68.4 (13%)	20.4 ± 5.5 (3%)	13	11.2 ± 3.8	426 (9%)	806 ± 172 (19%)
Acacia gerrardii	64.3 (12%)	26.8 ± 6.5 (4%)	6	7.9 ± 2.9	286 (6%)	320 ± 84.9 (7%)
Dichrostachys cinerea	31.7 (6%)	34.5 ± 7.5 (5%)	1.1	3.0 ± 1.0	24.6 (5%)	79 ± 32.5 (2%)
Acacia tortilis	29.7 (6%)	43.5 ± 8.7 (6%)	15.1	24.7 ± 9.9	200 (4%)	1040 ± 401 (24%)
Commiphora trothae	28.0 (5%)	66.5 ± 11.4 (9%)	1.7	5.9 ± 1.4	65.8 (1%)	178 ± 58.1 (4%)
Phyllanthus sepialis	24.9 (5%)	107 ± 16.0 (15%)	2.2	1.4 ± 1.0	54.6 (1%)	14.0 ± 18.2 (<1%)
Grewia fallax	19.2 (4%)	5.1 ± 2.6 (<1%)	11.2	1.0 ± 0.9	1090 (22%)	38.0 ± 35.9 (<1%)
Grewia bicolor	15.3 (3%)	10.2 ± 3.8 (1%)	10.8	2.1 ± 1.3	1070 (21%)	59.1 ± 37.9 (1%)
Cordia ovalis	13.4 (3%)	20.4 ± 5.5 (3%)	4.5	8.4 ± 3.7	480 (10%)	476 ± 201 (11%)
Aspilia mossambicensis	–	123 ± 17.7 (17%)	–	5.6 ± 0.9	–	66.5 ± 8.1 (2%)
All other species (23, >27)	132.0 (26%)	254 (36%)	26.8	26.5	1000 (20%)	1080 (25%)
Totals	518 (100%)	716 (100%)	100	100	5040 (100%)	4340 (100%)
Riverine:						
Acacia xanthophloea	136 (76%)	7.9 ± 1.8 (5%)	87.8	12.0 ± 6.3	2360 (90%)	51.7 ± 25.9 (6%)
Phyllanthus sepialis	13.4 (8%)	20.1 ± 3.4 (14%)	0.5	3.4 ± 0.7	15.5 (<1%)	11.5 ± 1.6 (1%)
Acacia tortilis	10.1 (6%)	31.0 ± 4.7 (21%)	7.2	65.4 ± 14.2	35.8 (1%)	661 ± 102 (81%)
Acacia sieberiana	6.3 (4%)	–	1.7	–	46.5 (2%)	–
Grewia fallax	1.0 (<1%)	–	1.4	–	85.1 (3%)	–
Hibiscus spp.	–	33.1 ± 5.0 (23%)	–	2.2 ± 0.4	–	6.7 ± 0.6 (<1%)
Aspilia mossambicensis	–	19.8 ± 3.4 (14%)	–	2.6 ± 0.5	–	7.0 ± 0.7 (<1%)
All other species (17, 16)	12.3 (7%)	34.0 (23%)	1.4	14.4	85.2 (3%)	77.5 (10%)
Totals	179 (100%)	146 (100%)	100	100	2630 (100%)	815 (100%)

Appendix 1. Continued.

	Woody plant density (plants ha^{-1})		Relative canopy cover (%)		Canopy volume (m^3 ha^{-1})	
	1978	2009	1978	2009	1978	2009
Composite of Seronera woodlands:						
Acacia tortilis	103 (41%)	41.0 (28%)	58.1	55.1	614 (34%)	704 (50%)
Acacia senegal	34.2 (13%)	0.6 (<1%)	3.9	0.2	121 (7%)	2.1 (<1%)
Commiphora trothae	22.0 (9%)	35.4 (24%)	11.4	8.5	275 (15%)	80.0 (6%)
Acacia hockii	20.9 (8%)	0.5 (<1%)	1.7	0.4	50.1 (3%)	11.5 (<1%)
Acacia robusta	19.2 (8%)	9.7 (7%)	5.5	17.7	130 (7%)	368 (26%)
Acacia xanthophloea	12.3 (5%)	1.5 (1%)	7.9	1.3	213 (12%)	13.2 (<1%)
Acacia gerrardii	4.4 (2%)	1.8 (1%)	0.4	1.7	18.2 (10%)	23.9 (2%)
Balanites aegyptica	2.2 (<1%)	3.4 (2%)	2.4	1.5	33.1 (2%)	24.2 (2%)
Grewia fallax	1.9 (<1%)	0.7 (<1%)	1.4	0.2	137 (8%)	3.1 (<1%)
Grewia bicolor	1.9 (<1%)	0.9 (<1%)	1.4	0.4	100 (6%)	3.7 (<1%)
Cordia ovalis	1.6 (<1%)	3.5 (2%)	0.4	1.9	36.0 (2%)	31.6 (2%)
All other species (23, ≥36)	30.8 (12%)	48.0 (33%)	5.5	10.9	81.1 (5%)	148 (11%)
Totals	255 (100%)	147 (100%)	100	100	1810 (100%)	1410 (100%)

Appendix 2. Length of giraffe feeding bouts on *Acacia tortilis* and *Acacia robusta* trees in the Seronera woodlands. A feeding bout was defined as the time from first to last bite on a single tree. Data taken from observations of adults (ages 5+ y) and subadults (ages 1–5 y) of both sexes.

	Number of giraffe indiv. sampled	Total number of feeding bouts	Range of browse times (s) per tree	Average browse time (s) per tree ± SE
Acacia tortilis	20	96	10–908	143 ± 18.3
Acacia robusta	10	16	1–202	55.8 ± 15.2