Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya

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Abstract

Savannah ecosystems in East Africa are rarely stable and can experience rapid local changes from dense woodlands to open plains. In this 3-year study there was a reduction of 16.3% in a height-stratified sample of nearly 1000 individually marked *Acacia drepanolobium* trees. The study was carried out in an enclosed fire-free wooded grassland habitat in the Laikipia region of Kenya. The trees were monitored from 1998 to 2001, a period that included 12 months when rainfall was 60% below average. Elephants were responsible for the loss of 40% of the trees, black rhinos 33% and 27% died from the effects of the drought. Low rainfall was correlated with increased damage as elephants switched diet from grass to trees. Heavy browsing by giraffes reduced tree growth rates and increased their susceptibility to drought. Hence the combination of low rainfall and heavy browsing by elephants, black rhinos and giraffes led to the rapid tree loss. These findings have implications for research into the causes of instability in savannah ecosystems and the management of enclosed reserves.

Key words: *Acacia drepanolobium*, black rhinoceros, elephant, giraffe, rainfall, savannah

Résumé

Les écosystèmes de savane en Afrique Orientale sont rarement équilibrés et peuvent connaître de changements rapides locaux, allant de fort impénétrable aux plaines exposées et découvertes. Au cours de cette étude de trois ans, on a constaté une diminution de 16.3% dans un échantillon stratifié de presque 1000 arbres *Acacia drepanolobium* marqués individuellement. L'étude fut menée dans un habitat clos de prairie boisée, dépourvu de feu, dans la région du Laikipia, au Kenya. Les arbres furent contrôlés de 1998 à 2001, une période comprenant 12 mois où les précipitations furent 60% au-dessous de la moyenne. Des éléphants furent responsables de la perte de 40% des arbres, des rhinocéros noirs 33%, et 27% sont mort à cause de la sécheresse. Le taux bas des précipitations entraîna plus de dégâts parce que les éléphants furent obligés de manger les arbres à la place de l'herbe. Du fort grignotage par des girafes réduisi le taux de croissance des arbres et augmenta leur hypersensibilité à la sécheresse. La combinaison des précipitationslégères et du surpâturage par les éléphants, les rhinocéros noirs et les girafes a mené à la perte rapide des arbres. Ces résultats pourraient avoir des implications pour la recherche sur les causes d'instabilité dans les écosystèmes de la savane et la gestion de réserves closes.

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Introduction

Savannah ecosystems can show rapid changes in tree cover (Mistry, 2000). In East Africa the Serengeti–Mara region has fluctuated from open grassland to dense woodland and back to open grassland over a period of 100 years (Dublin, 1995). Tree cover reduction was particularly rapid in the 1950s. The precise cause of such dynamic changes has been the subject of considerable discussion. Generally studies have focused on elephant and fire impact (Dublin, Sinclair & McGlade, 1990; Ben-Shahar, 1996; Van de Vijver, Foley & Olff, 1999) but some have included the effect of giraffes (Pellew, 1983a; Ruess & Halter, 1990) and some have suggested that small herbivores may be important (Van de Koppel & Prins, 1989). Nearly all these studies have based their conclusions on retrospective analysis of tree loss. This technique suffers from the problem that the reasons for tree loss must be inferred many years after the trees are damaged.

In this study, following the approach used by Pellew (1983a), the effect of elephants, giraffes, black rhinos and rainfall has been quantified by frequent measurement of the growth rate and damage to individually marked trees in an enclosed savannah woodland system. Regular monitoring allows the precise identification of factors affecting tree growth or death.

The woodland system studied lies within an enclosed Black Rhino Reserve that has a wide range of habitats and high bio-diversity. It was set up in 1989 to protect the highly endangered black rhinoceros (*Diceros bicornis*) and eventually act as a donor site with surplus rhinos being used to stock other reserves (Brett, 1993). Hence the main purpose of the Reserve is to act as a protected breeding site for rhinos but, as the site is funded by tourism, the Reserve Management would prefer that the site's current appearance and bio-diversity be maintained. Indeed, a system of well protected reserves, linked by translocation to similar reserves, may become an important model for conservation where human disturbance is high.

Enclosed reserves suffer from a particular set of problems – animals cannot move to avoid environmental stress, populations can change rapidly and habitat can be altered quickly. However, as animal densities are known, research into the causes of instability in savannah ecosystems can be carried out in a much more controlled way in a closed reserve than in an open system. Prior to the study, damage to the *Acacia* woodland could be seen throughout the Reserve and, although it was thought that this was because of high densities of elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis reticulata*), the precise causes of the changes were unknown. Hence this study was set up to provide both new insights into the vegetation dynamics of woodland savannahs and generate information that would enhance the management of enclosed reserves where high bio-diversity needs to be maintained.

Methods

Study site

Sweetwaters Game Reserve is located in central Kenya, 230 km north of Nairobi, near Nanyuki, on the equator at longitude 36°56′E. It lies on the Laikipia plateau between Mt Kenya and the Aberdare Mountains at an altitude of 1800 m. The Reserve's black rhino population increased from 23 in 1998 to 31 (0.34 km^{-2}) at the end of the study.

These rhinos occupy well-established home ranges (Tatman, Stevens-Wood & Smith, 2000). The Reserve also has high densities of elephant (1.2 km^{-2}) and giraffe (1.4 km^{-2}). The vegetation (White, 1983) is a mosaic of open grassland, *Acacia drepanolobium* dominated wooded grassland, *Euclea divinorum* dominated scrub woodland and riverine woodland (Birkett, 2002). The *Acacia* woodland covers 39% of the 9200 ha Reserve with a mean density of 670 *A. drepanolobium* trees per hectare. These trees form a large proportion of the diet of the rhinos and giraffes (Edwards, 1998; Pinkney, 1998) as well as being eaten by elephants. Hence the wooded grassland is much more heavily browsed than the rest of the Reserve.

Tree measurements

Acacia drepanolobium tree growth and browse impacts were measured by setting up 21 variable radius plots randomly throughout the *Acacia* woodland areas of the Reserve. In each woodland plot between 40 and 60 trees were selected to give a height stratified sample of 979 trees, using a proportional sampling method (Krebs, 1989) that reflected the known tree height distribution measured in the Reserve between 1996 and 1999. In addition 96 seedlings, defined as being in two height classes <0.5 m, were tagged. The term seedling is in common usage in the literature (Dublin *et al.*, 1990; Dublin, 1995 and Ben-Shahar, 1996) to identify small trees found generally within the grass layer. Trees were classified in six height classes from 0.5 m to greater than 6 m. Two additional plots (78 trees) were located in an area from which elephants, rhinos and giraffes were excluded and acted as controls. Growth and damage to the original trees and seedlings were recorded 12 months after the initial assessment and then at 6 month intervals for a further 2 years.

Tree damage was defined as that which reduced the height of the main stem or killed the tree. Branch damage was not recorded. The agent causing the damage was easily established in the field. Elephants either pushed over trees, or broke the main stems and left the bark hanging in strips; rhinos made a clean cut of the main stem; giraffes ate the leaves and growing tips of branches and main stems. Some trees died from natural mortality agents, of which the most obvious in this study was drought. These trees were still standing but were dead with the bark peeling off and showed no evidence of disease or other damage.

Trees that had no main stem damage were used to calculate growth and were classified as 'undamaged' but

browsed by giraffes. A tree was classed as 'reversed' when a rhino or an elephant broke the main stem to such an extent that the tree moved from a higher to a lower height class but did not die. Elephant, rhino and drought impacts were measured by counting the number of trees in each height class that they killed or 'reversed'. Giraffe impact in the Reserve was measured for each height class by subtracting the mean growth of 'undamaged' trees in the Reserve from the mean growth in the Control area.

The tagging and measuring methods are given in detail in Birkett (2002). Tree height was measured to an accuracy of ±2 cm using a Dynamis Telescopic Measuring Rod (Stanton Hope, 1998) that could be extended to seven meters. Measurements were recorded in the field using a US Robotics 3Com PalmPilot Professional loaded with software supplied by the University of Kent (Pascoe, Morse & Ryan, 1998).

Tree growth rates are given as mean ± SE. Statistical tests were performed on Minitab Release 10.2.

Results

Change in the number of trees and seedlings

The original sample, selected in August 1998, consisted of 979 trees and 96 seedlings. Three years later, in September 2001, there were 788 trees and 84 seedlings – a reduction of 19%. There were 19.5% fewer trees. The 14.4% tree mortality was compounded by a net reduction of 5.1%, because reversals into the seedling class (5.4%) exceeding growth from the seedling class (0.3%). Hence the seedling class (0–0.5 m) consisted of a mixture of 'reversed' trees and new seedlings that had not yet grown into trees.

However, there were only 96 in the seedling class in the original sample, compared with the 868 that would be required to match the density measured in the acacia woodland. Growth from the seedling class would, therefore, be 3.5%, not 0.3%, and hence the reduction in tree numbers should be corrected to 16.3%. Germination of new seedlings was not measured but, based on the negative growth of tagged seedlings shown in Fig. 2, any that did germinate would not have escaped the seedling class during the 3 years of the study.

In summary, the reduction was 16.3% over 3 years giving an annual loss of 5.4% for trees 0.5 m or taller, 6.9% for trees 3 m or taller, and 9.7% for trees 4 m or

taller. This represents a very significant reduction in the woody vegetation of these woodlands where more than 76% of the trees are *A. drepanolobium*.

Change in the number of trees in each height class

The percentage change in tree numbers varied significantly between height classes (Fig. 1) compared with the mean of 16.3% (chi-square test $\chi^2 = 69$, $P < 0.005$). Most height classes were reduced, some by more than 30% (0.5–1 m and 4–6 m) but others showed no change (6 m+) or even a slight increase (2–3 m).

Browse pressures and drought impacts differ between height classes

Within each height class the effect of elephant, giraffe, rhino and drought differed. Three factors – growth, reversals and mortality – determined whether tree numbers increased or decreased (Table 1). Giraffe browsing depressed growth of 3–6 m height trees (Fig. 2). Rhinos caused more reversals of small trees than elephants (Fig. 4) and elephants and drought killed tall trees whilst rhinos killed small trees (Fig. 3). In each height class these impacts combined in different ways to produce the height class changes shown in Fig. 1.

For example (Table 1) in the 0.5–1 m height class, light giraffe browsing allowed a high number of trees to grow into and out of this height class. Just over 30% were killed and reversals out of the class exceeded reversals into the class by 16% giving a net reduction of 46.5%. Rhino browsing caused a high rate of reversals and both elephant
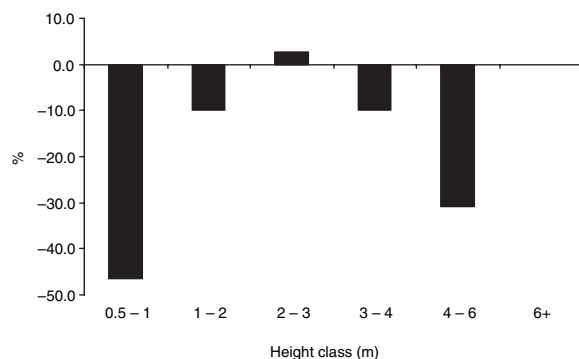

Fig 1 The percentage change in the number of trees in each height class of *Acacia drepanolobium* over 3 years

Table 1 Percentage of trees added to or removed from each class

Height class (m)	Number of trees	Growth in (%)	Growth out (%)	Reversals in (%)	Reversals out (%)	Killed (%)	Reduction (%)
0.5–1	172	19.8	20.3	11.6	27.3	30.2	46.5
1–2	251	13.9	17.1	5.2	7.6	4.4	10.0
2–3	256	16.8	3.9	2.3	5.9	6.6	−2.7
3–4	131	7.6	4.6	3.8	6.1	10.7	9.9
4–6	159	3.8	3.1	0.0	5.0	26.4	30.8
6+	10	50.0	0.0	0.0	0.0	50.0	0.0
Total	979	13.6	10.1	4.5	9.9	14.4	16.3
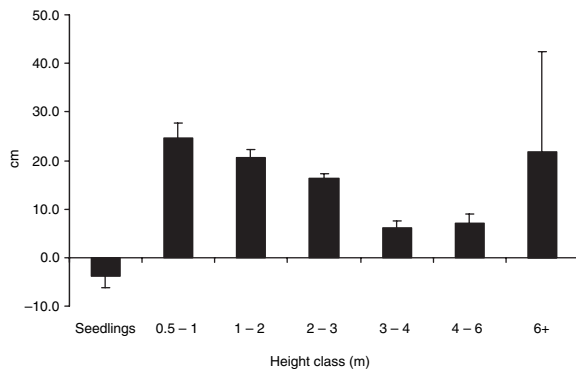
Fig 2 The growth rate (mean ± SE) of each height class of *Acacia drepanolobium* trees over 3 years
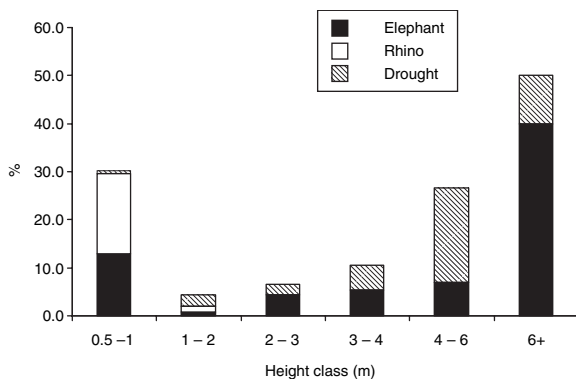
Fig 3 The percentage of *Acacia drepanolobium* trees killed in each height class over 3 years

and rhino killed trees. In the 6 m+ height class, mortality (mainly by elephants) was balanced by growth into the class as trees grew out of reach of giraffes.

In the 4–6 m height class, the high mortality, caused by drought and elephants, was not balanced by growth

because of the high level of giraffe browsing. In the 2–3 m height class light giraffe browsing allowed growth to replace losses.

Growth of undamaged trees and seedlings

The rate of growth determines how many trees and seedlings move each year from one height class to another. The mean rate of growth of the 663 trees and seedlings in the Reserve that were not damaged by elephants or rhinos during the 3 years was 14.4 ± 0.8 cm – an annual rate of only 4.8 cm.

Growth rate in the Reserve varied significantly between height classes (Fig. 2) compared with the mean of 14.4 cm (chi-square test $\chi^2 = 25.2$, $P < 0.005$). Growth was low for trees from 3 to 6 m, the height classes most heavily browsed by giraffes. Growth was highest in the 0.5–2 m height classes, so up to 14 and 17%, respectively grew out of these two classes. Mean growth was negative for seedlings.

For the same tree height distribution, the mean rate of growth for trees in the Reserve was 15.1 ± 0.8 cm compared with 47.0 ± 4.2 cm in the Control area where no giraffes browsed.

Tree mortality over 3 years

Tree mortality was 14.5% over 3 years. Mortality varied significantly between tree height classes (chi-square test $\chi^2 = 30.3$, $P < 0.005$) (Fig. 3).

There were three main causes of tree mortality. Elephants killed 5.8%, rhinos 3.3% and 5.3% appeared to have died from the effects of the drought. Elephants killed all height classes, rhinos killed trees below 2 m and drought affected taller trees. Twenty per cent of the trees that died from drought had been previously damaged by

elephants but 80% showed no other sign of damage or disease.

Seedling mortality

Nearly 65% of the original seedlings were killed or missing. Although we did not see what caused the seedlings to disappear, we can make the assumption that the browse pattern was similar to trees. Nearly 64% of the trees that were eventually reported as missing had been damaged by either elephant or rhino before they were reported as missing. Of these 62% were damaged by rhinos and 38% by elephants. If this browse pattern also applied to seedlings it would suggest that 8% per year were being removed by rhinos, 5% by elephants and 7% by other browsers or drought.

Tree reversals

A total of 9% of the original trees were 'reversed'. Elephants 'reversed' 4.9%, rhinos 2.9 and 1.2% were damaged by both herbivores (Fig. 4). The rate of reversal varied significantly with height class (chi-square test $\chi^2 = 17.8$, $P = 0.003$) Elephants 'reversed' trees in all height classes but rhinos 'reversed' mainly those in the 0.5–1 m height class.

Rainfall

The study was carried out over the 3 years from August 1998. Rainfall was significantly below average during the study (Student's *t*-te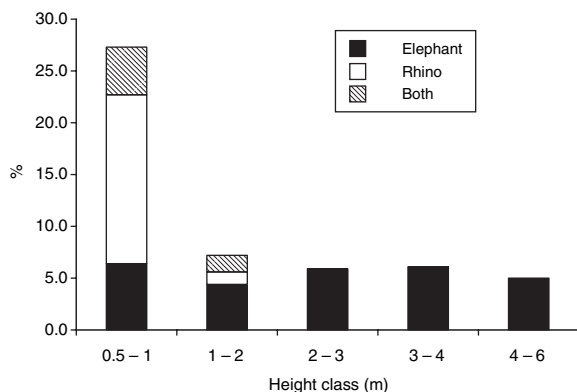st $t = 3.62$, $P = 0.0086$). Rainfall varied from a low of 27 mm per month to a high of 62 mm with a mean of 45 mm. Mean monthly rainfall over the previous 4 years was 70 mm. Hence rainfall was 36% below average for the whole period. From February 2000 to February 2001 it was nearly 60% below the average for similar periods in the previous 4 years.

Effect of low rainfall on tree growth

Trees in the Control Area were not browsed by giraffes, elephants or rhinos. These trees grew at 0.8–1.6 cm per month (mean 1.4 cm per month)(Fig. 5). Tree growth over the 3-year period was not correlated with rainfall ($r^2 = 0.25$, $P = 0.4$). However, in the 12 months prior to this study (Birkett, 2002), the same trees grew at 4.8 cm per month when rainfall was 109 mm per month. Hence tree growth does increase rapidly at high rainfall but, at the low rainfall experienced during this study, growth did not respond to rainfall and remained below 1.6 cm per month or 19 cm per annum, a very low rate of growth.

Effect of Giraffe browsing on the rate at which tree growth responds to rainfall

Tree growth in the Reserve (Fig. 5), measured for trees that had not been damaged by elephants or rhinos, but had been browsed by giraffes, followed a similar pattern to that in the Control Area, except that mean growth rate was 0.9 cm per month lower. The difference between growth in the Control area and the Reserve was positively correlated
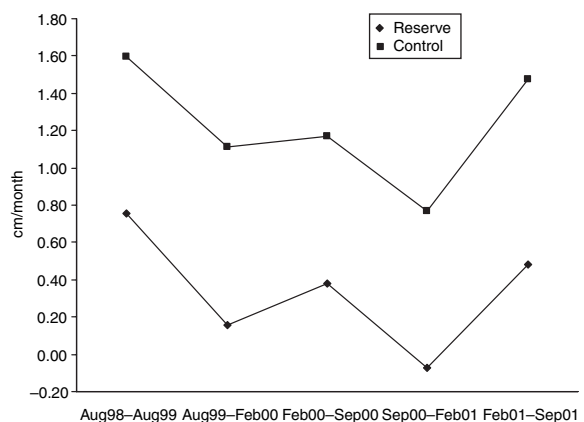

Fig. 4 The percentage of *Acacia drepanolobium* trees 'reversed' in each height class over 3 years

Fig 5 The mean monthly growth rate of *Acacia drepanolobium* trees in the Control Area and the Reserve for the five sample periods of the study
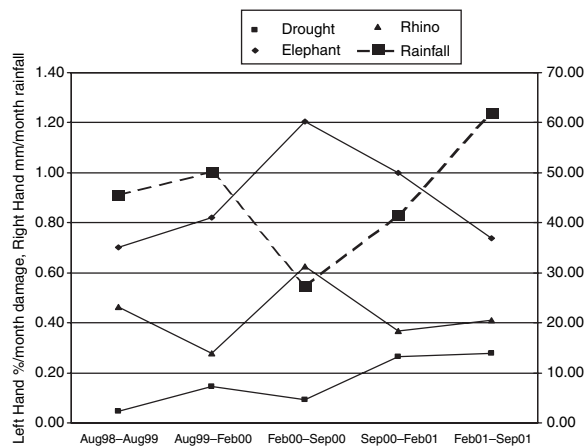
Fig 6 The mean monthly percentage of *Acacia drepanolobium* trees damaged and the mean monthly rainfall for the five sample periods of the study

with rainfall ($r^2 = 0.86$, $P = 0.022$). Although the difference is normally taken to measure the intensity of giraffe browsing it may also indicate that the trees in the Reserve have been so heavily browsed in recent years that they are in very poor condition and so cannot respond to increased rainfall. This analysis is supported by the fact that in the year before the study, when rainfall was heavy (Birkett, 2002) growth in the Reserve was only 1.13 cm per month compared with 4.87 cm per month in the Control Area. Hence the difference was 0.9 cm per month at low rainfall and 3.74 cm per month at high rainfall. Such a large difference could not be caused by giraffe browsing.

Tree damage and low rainfall

Tree damage caused by elephants increased significantly as mean rainfall decreased and fell when the rains returned (Fig. 6). The correlation between the damage rate and the mean rainfall during each study period was weak because there was a lag between rainfall change and damage change of about 3 months. Hence there was a strong inverse correlation between the rate of damage by elephants and mean rainfall for the study period advanced by 3 months ($r^2 = 0.89$, $P = 0.016$). There was no correlation between damage by rhinos and rainfall. Tree deaths that appeared to be because of drought increased steadily during the study and continued to increase even after the rains began.

Seedling losses also increased during the drought, from 2% per month to a maximum of 4.9% per month for the

period September 2000 to February 2001. Losses decreased to 1% per month after the drought.

Allocation of tree losses

Three agents were directly responsible for tree losses. Trees were either killed or reversed into the seedling class by elephants and rhinos or died from natural causes that appeared to be linked to the drought. Elephants caused 40% of the losses, rhinos 33% and drought 27%.

Discussion

Elephant density in the Reserve was 1.2 km^{-2} throughout the study. In comparison, elephant densities in the Serengeti fluctuated from 0.3 km^{-2} in the 1960s to 0.7 in the 1980s (Dublin *et al.*, 1990). Mean rhino density was 0.3 km^{-2}, similar to that estimated in Tsavo in the 1970s (Goddard, 1970). The mean giraffe density was 1.4 km^{-2}, similar to that of 1.47 km^{-2} recorded in the Serengeti in 1975–1978, when it was said to be higher than any other comparable savannah area in East Africa (Pellew, 1983b). Hence a high level of elephant, rhino and giraffe browsing, combined with a period of low rainfall produced a rapid reduction in the number of *A. drepanolobium* trees.

The reduction of 5.4% per year is comparable with several previous studies of rapid tree loss in East Africa. *Acacia* trees taller than 5 m were lost at a rate of 5% per year in the Serengeti in the 10 years prior to 1982 (Ruess & Halter, 1990). Tree loss in the Serengeti was 2.5% overall with local maxima of 6% for *Acacia tortilis* trees taller than 1 m (Croze, 1974) and 6.5% per annum over a 5-year period reported by Pellew (1983a). For trees taller than 3 m, mortality caused by elephants in the Serengeti in the 1960s and 1980s ranged from a mean of 2.5% to a maximum of 7% per year (Dublin *et al.*, 1990). In all these studies, based on large-scale retrospective analysis of photographs, tree loss was attributed to elephants. Non-elephant tree mortality was estimated to be an additional 1% per annum (Croze, 1974; Dublin, 1995).

In this study, because individual trees and seedlings were monitored regularly over 3 years it was possible to be more precise about the cause of tree loss. Rhinos and drought killed or 'reversed' almost as many trees as elephants. Losses were not balanced by growth from the seedling class. Seedlings were heavily browsed and killed by rhinos, elephants and other herbivores or died from the drought. Although only elephants and drought removed 'mature'

trees taller than 3 m, these were not replaced from lower classes because smaller trees grew too slowly under the influence of heavy giraffe browsing and low rainfall. In addition heavy giraffe browsing may have stressed mature trees to the point where they were more susceptible to death during periods of low rainfall. Therefore it was the interaction between several herbivores, magnified by the low rainfall that caused the rapid changes.

Low rainfall not only lowered the rate at which trees were replaced but also slowed grass and herb growth. Elephants eat a mixture of grass and browse in the wet season but increase the browse proportion during the dry season (Field & Ross, 1976; Dublin, 1995). Similarly, rhinos will eat more woody species (Oloo, Brett & Young, 1994) as the availability of herb species decreases during dry periods. Green grass biomass peaks within a month of the rains starting and then grass quantity and quality decline (Dublin, 1995) during the dry period. The crude protein content of grasses was reported to fall from 11 to 3% during a 3-month dry period. Woody species retain their high protein levels (Pellew, 1984). In an enclosed reserve, elephants are in competition for the available grass with other grazers such as zebras and buffaloes. Zebras in particular can browse grass to such a low height that elephants have difficulty feeding. The higher the density of competing grazers, the earlier in the dry season elephants will be forced to switch to trees and seedlings, hence the more they will damage trees. In this study six elephants died during the drought and there were clear signs that the rest had lost weight. As the drought intensified, elephants were frequently seen in woodland areas eating *A. drepanolobium*. As a result tree damage increased rapidly.

In contrast to the rapid re-growth of grass, tree growth did not increase for a full 6 months after the rains began. Deaths from drought continued to increase even 12 months later. This may be associated with the water table. Grasses have shallow roots and benefit immediately from rainfall whereas trees need the water table to be replenished before their deeper roots can benefit. One other factor may be important. The mean difference in growth rate between the Control Area and the Reserve was 0.9 cm per month or 11 cm per annum. This is a measure of the intensity of giraffe browsing. This difference did not change during the study although the giraffe population fell. This suggests that the heavy giraffe browsing of the last 10 years has caused long term damage to the trees in the Reserve and this may not be reversed unless there is a protracted period of growth under very low or no giraffe pressure.

This study, conducted during a period of severe environmental stress, has given new insights into the vegetation dynamics of woodland savannahs. If climatic change leads to longer and more frequent droughts, the type of change reported in this study may become more common with severe implications for the carrying capacity of enclosed reserves and the maintenance of fragile habitats.

Acknowledgements

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