Plant Ecology **136:** 189–194, 1998.

Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire

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Received 16 June 1997; accepted in revised form 22 February 1998

Key words: Elephants, Fire, Savanna, Seedlings, Shrubs, Trees

Abstract

Fluctuations in densities of woody plant species were monitored in plots within three northern Botswana woodland types subjected to elephant damage and burning. Woodlands dominated by *Baikiaea plurijuga* and *Colophospermum mopane* sustained significant changes occurring on an annual basis, whereas *Acacia erioloba* plots maintained a typical structure. The structure of *A. erioloba* woodlands appeared to be influenced by factors other than elephants and the occurrence of fire. Woodlands dominated by *C. mopane* plants were subjected to obtrusive elephant damage, although the densities of tall trees remained largely unchanged. The effects of fire were most prominent in *B. plurijuga* woodlands. Tree densities declined consistently and plants of lower height classes, such as shrubs and seedlings increased in densities in areas subjected to a high occurrence of fire.

Introduction

The densities of tall canopied trees within woodlands of semi-arid savannas could decline due to the impacts of large herbivorous species and fire. Many theories about the dynamics of woodlands had been proposed (Laws et al. 1975; Caughley 1976; Norton-Griffiths 1979; Croze et al. 1981; Barnes 1983; Guy 1989; Dublin et al. 1990) There is limited evidence, however, to delineate the amplitude of elephants and fire in the regulation of tree densities in savanna woodland habitats.

In northern Botswana, the resident elephant population is considered as a prominent factor influencing vegetation structure because of its abundance and high recruitment potential (Melton 1985; Calef 1988). Elephants in the region seem to prefer particular plant species and elephant damage to the vegetation is widespread throughout the region (Ben-Shahar 1993). The impact of fire on woodlands in northern Botswana is also apparent although there is some distinction between the effects of elephants and fire on different plant communities. Accordingly, woodland vegetation in the region can be viewed as a mosaic of 3 types containing (1) low elephant utilization and high fire damage, (2) high elephant impact and low fire damage and (3) minor utilization by elephants and/or minor fire damage (Ben-Shahar 1993).

The decline in woody vegetation resulting from elephant and/or fire impacts could be attributed to conspicuous biomass removal from living trees or the reduction of tree densities through tree mortality. This study describes short term changes in vegetation structure following the impacts of elephants and fire in three woodland types within northern Botswana. Some changes were consistent enough to indicate that fire precipitates the decline in densities of mature trees in woodlands subjected to frequent burning while the effect of elephants was not as conspicuous.

The study area

In this study, northern Botswana is defined as an area of more than 80 000 km^2 between 18 ° and 21 ° south and 21 ° and 26 ° east, but excluding the permanent swamps of the Okavango Delta. Rainfall ranges from 400 mm in the south and 650 mm in the north-east. Rains occur during the summer from October to April and mainly in heavy storms. Temperatures vary between a monthly mean maximum of 34 °C (October) and a mean minimum of 6 °C (June) (Bhalotra 1987).

The topography of the area is very flat and the altitude is around 950 m asl. The north easterly elongated Goha and Shinamba Hills, which rise to 150 m above the surrounding plain, form the only significant topographical feature. The area is covered with deep deposits of aeolian and alluvial sands and silts of the Kalahari beds. These soils are generally neutral or slightly acid, poor in nutrients, poorly structured and with low water holding capacity. More fertile vertisols and Molapo soils are mainly found on flood plains and in some depressions. The bedrock consists mainly of Karoo sediments, material of the Ghanzi, Kwebe and Damara formations and granitoid gneisses of the old basement complex. Bedrock is exposed in the eastern and south-eastern parts of Botswana where the sand cover is thin. In the northern, central and western parts, solid rock is obscured by loosely consolidated deposits, known collectively as the Kalahari Beds, which attain thicknesses of 300 m or more (Hutchins et al. 1976). Most of the area is covered by tree and shrub savanna, towards the north, changing into woodland and to dry deciduous forest with *Baikiaea plurijuga* dominating in the Chobe area while the south is dominated by shrub savanna, rich in *Acacia* spp. Depression areas and the edge of flood plains are often dominated by *Colophospermum mopane* woodlands.

Materials and methods

Changes in woodland structure

Changes in vegetation structure were monitored in plots within Chobe National Park and Moremi Game Reserve. Plots were allocated to cover as much as possible the existing regional range in plant damage as a result of elephant activity and the occurrence of fire. The original position of plots thus followed a stratification according to vegetation communities (Child 1968), annual estimates of elephant densities (Melton 1985; Craig 1990), and the occurrence of fire (Ben-Shahar 1993, 1996). Dominance of woody plants was defined for a plant species that contributed more than 80% of the standing biomass within a plot. I concentrated on species that dominated much of the cover abundance of tall tree woodlands throughout northern Botswana, such as *Acacia erioloba*, *Baikiaea plurijuga* and *Colophospermum mopane*.

Changes in woodland structure were derived by comparing mean plant densities in plots between 1992, 1993 and 1995. Sampling included 17 *A. erioloba*, 25 *B. plurijuga* and 47 *C. mopane* plots in total. Some of the plots, however, were not accessible for sampling every year. In each plot, squares of 10 × 10 m were allocated along four separate lines which were parallel to the direction of a nearby track. The location of re-sampled squares was as close as possible to the original sampling position and squares were independently sampled. The relocation of plots was done by odometer readings from prominent spots, such as road junctions which were the nearest to the plots. The size of plots was determined by the number of dominant plant species that were sampled. Plots with high density of woody plants were smaller in their total area in comparison to plots with scattered vegetation. The size of plots, thus varied from 200 × 100 to 300 × 600 m. The number of squares per plot was determined after initial sampling in each woodland type. Accordingly, woodlands dominated by *A. erioloba*, *B. plurijuga*, and *C. mopane* had a minimum of 75, 110, and 150 squares respectively, sampled in each plot.

In each square, the number of plants belonging to specific height classes were counted. Height classes included new seedlings ($<$0.1 m in height), seedlings ($>$0.1 and $\leq$0.25), small shrubs ($>$0.25 and $\leq$1 m), shrubs ($>$1 and $<$3 m), trees (3–10 m) and tall trees ($>$10 m), and densities were represented in terms of mean number of plants ha^{-1} (Table 1) (Ben-Shahar 1996). The category of shrubs included fallen trees, the individual branches of which were considered as shrubs if the size criteria were met. Multi-stemmed plants with stem diameters of less than 6 cm were treated as a single shrub unless a gap wider than the width of 10 cm could be distinguished between the stems. Trees were defined as plants with a stem diameter of 6 cm or more and higher than 3 m. Woody plants that corresponded to the definition of a tree and had several stems which were jointed close to the ground were considered as one tree.

The effects of elephants and fire

Damage to woody plants was estimated for individual plants within each square as being one of the three types; new elephant, old elephant, and fire. New damage is that which had occurred since the recent rainy season. Damage becomes characteristically greyish in colour after rain soaks into the exposed inner plant parts. Damage in this context is not only excessive vegetation destruction, but is all easily noticeable utilization of woody material. Plants affected by fire had

Table 1. Mean densities (and standard deviations) of new seedlings, seedlings, shrubs, trees, elephants derived from dung ball counts (Ben-Shahar 1996), and the frequency of plants affected by elephants or fire, in plots dominated by *Acacia erioloba*, *Baikiaea plurijuga* and *Colophospermum mopane* in northern Botswana.

	A. erioloba	*B. plurijuga*	*C. mopane*
New seedlings (No./ha)	42	26	312
	(149)	(103)	(896)
Seedlings (No./ha)	105	176	648
	(141)	(347)	(830)
Shrubs (No./ha)	148	498	1626
	(138)	(629)	(1140)
Trees (No./ha)	131	371	282
	(169)	(208)	(377)
Elephant density (No./km^2)	2.57	3	2.95
	(5.52)	(6.71)	(5.45)
Plants affected by elephants (%)	24.1	10.7	43.4
Plants affected by fire (%)	13.6	58.2	23.8

conspicuous scorch marks on branches and some had characteristic new growth from the base of stem of dead branches following the suppressing effects of fire. Only damage which was positively attributed to elephants or fire was recorded.

Data analysis

Standard regression techniques were applied using SAS (Schlotzhauer & Littell 1987). I assessed woodland changes by comparing the annual differences in the densities of particular height classes of plants, the number of plants affected by elephants, the number of plants affected by fire, and the number of dung balls, using multiple comparisons (*T*-test) and general linear models for samples of unequal size (at $P = 0.05$, $T = 1.96$).

A multivariate analysis supplemented the regression models and produced an overview of the associations between plots and variables related to vegetation structure, elephants and fire damage. Canonical correspondence analysis (Ter-Braak 1987), an eigenvector ordination technique for displaying variables in a two-way contingency table was used to generate ordination axes. The analysis produced axes that were linear combinations of a matrix in which plots were represented by rows and species, namely damage types and densities of plants belonging to height classes, were the columns. A matrix of variables consisted of rows for each sampling plot. Columns had 6 vegetation structure classes representing mean densities of seedlings, shrubs and trees. Additional columns had mean dung ball counts, a column of the mean proportion of plants burnt which represented fire damage, and two columns describing the percentage of plants with new and old elephant damage.

Trends representing growth or decline of woody plants were derived by comparing annual densities of plants that belonged to particular height classes in plots. It was assumed that the annual variation in the relocation of squares within plots and the occasional usage of volunteers for sampling, did not introduce considerable error to sampling. Bias from repeated sampling conducted by different observers could be caused as a result of variations in estimates between observers and existing patchiness of vegetation structure within a plot. The magnitude of bias was monitored between two plots dominated by *C. mopane*, (the most heterogeneous structure of the 3 woodland types examined). The methodology included repetitive sampling intervals by two different teams of observers who recorded 150 squares in each plot. There were no significant differences in the estimates of height classes ranging between $<$0.25 m, 1–3 m, 3–10 m and $>$10 m, the number of plants affected by recent elephant damage, and number of dung balls within the squares (T tests at $P = 0.05$, $T = 1.96$).

Results

Structure and damage types associations

Multivariate analyses performed for each woodland type separately suggested that the relationships between the densities of plants of different height classes and damage classes were species specific. Ordinations were plotted for the first two principal axes that described the maximum variation in the analyses. *Acacia erioloba* points that represented the annual state of a plot, had a tendency to aggregate according to the geographic location of plots (Figure 1). In other words, the relative homogeneity in vegetation structure and damage characteristics in plots override the annual variations among the plots. The distribution of points representing elephant and fire damage and their respective associations with points representing plots indicated that neither particular height classes nor any damage type dominated the appearance of a plot.

Ordination of *B. plurijuga* plots revealed that some plots were associated with high occurrence of elephants and high elephant damage to plants. These associations indicated that elephants frequented particular plots on an annual basis. Some plots sampled in 1995 had high abundance of low vegetation structure classes (**A**, **B**, and **C**). However, most points representing plots gravitated towards the origin of the axes and were associated with fire damage. This implies that most plots had evidence of fire damage and that the variation between plots was relatively small. Plot C'93 represented a zonal sampling extension of the designated C93 plot. The ordination indicated that the differences between these nearby plots were marginal (Figure 1). Plots of *C. mopane* were grouped around most vegetation structure and elephant related points. Some plots sampled during 1995 were closely associated with fire damage (Figure 1). However, most plots had weak associations with particular vegetation structure classes.

Changes in woodland structure

Results of multiple comparisons indicated that the most prominent trend in *B. plurijuga* plots was the decline of trees above 10 m tall, that was consistent for the entire sampling period (T tests at $P = 0.05$, $T = 1.96$). Tree density between 3 to 10 m tall appeared to be declining between 1992 and 1993, but recovered between 1993 and 1995 for the 3 woodland types examined. The annual change in the densities of *A. erioloba* trees (3 m and above) was often not

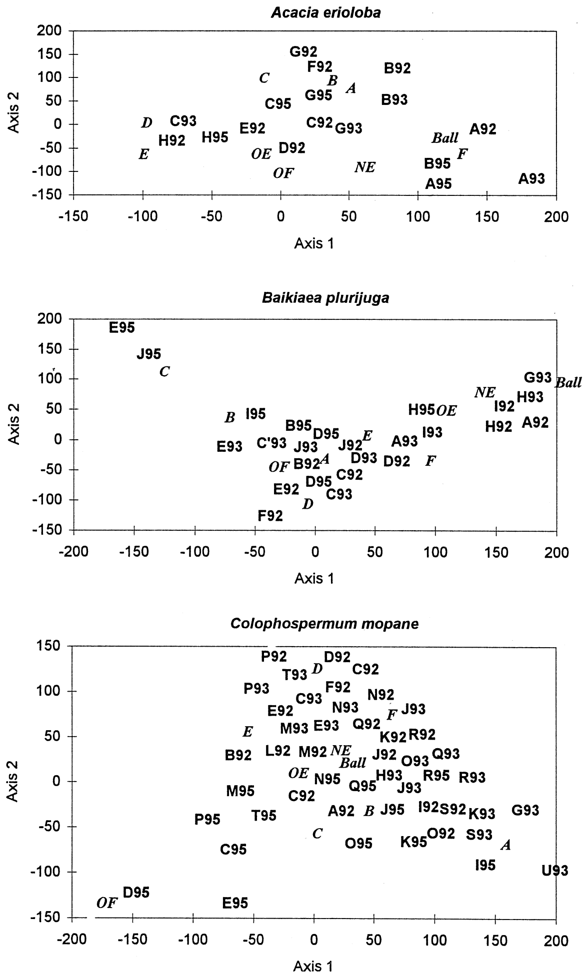

Figure 1. Ordinations of vegetation plots dominated by *Acacia erioloba*, *Baikiaea plurijuga* and *Colophospermum mopane* along the first principal axes of canonical correspondence analysis. Sample categories included (in m height) new seedlings ($0.1 < A$), seedlings ($0.1 \leq B > 0.25$) small shrubs ($0.25 \leq C \leq 1$ m), shrubs ($1 < D < 3$ m), trees ($3 \leq E \leq 10$ m) and tall trees $F > 10$ m). Sample categories included *Ball*, elephant dung densities, *NE* new elephant damage, *OE* old elephant damage and *OF*, fire damage to plants. Vegetation plots were indicated by an alphabetical letter followed by an abbreviation of the year in which the plot was sampled. For example , *C. mopane* plants that were sampled in plot **P** during 1992 were indicated as **P92**.

significant throughout the sampling period. There was however, a decline in the densities of *A. erioloba* seedlings between 1992 and 1993 which was followed by an increase between 1993 and 1995. Woodlands dominated by *C. mopane* had annual changes that were not statistically significant.

The effects of elephants and fire

Elephants ranged within all woodland types examined and dung ball counts derived from all plots suggested that elephants frequented *A. erioloba* and *B. plurijuga* woodlands more than *C. mopane* woodlands (Table 1). The extent of new elephant damage to plants varied between woodland types where *C. mopane* woodlands sustained the heaviest impact (Table 1). Evidence of new damage was significantly less in 1993 when compared to 1992 in some *C. mopane* and *A. erioloba* plots (T tests at $P = 0.05$, $T = 1.96$). The trend, however, reversed somewhat between 1993 and 1995. Elephant damage to *B. plurijuga* woodlands did not show a significant trend throughout the sampling.

The occurrence of fire, measured in terms of the number of burnt plants within a plot was the most prominent in *B. plurijuga* woodlands (Table 1). A comparison between all woodland types sampled in 1992 and 1993 indicated some plant recovery because less plants had scorch marks on the branches. This trend reversed, however, between 1993 and 1995.

Linear regression models were applied to explore some possible relationships between elephant densities, elephant damage to plants, the occurrence of fire, and the change in woodland structure. The mean scores of records from squares of each plot were used for the calculations. The number of dung balls in plots were correlated with recent and old elephant damage to plants and expressed in terms of the proportion of plants affected within a plot for each damage category. As might have been expected, the number of recently affected plants by elephants increased with rising dung ball counts (and respected elephant densities), particularly in *C. mopane* and *B. plurijuga* woodlands although, the correlation coefficients were low ($r = 0.20$ and 0.12 $P < 0.0001$ for both). The density of shrubs increased in all woodland types with the increase in fire damage. The trend was significant in *B. plurijuga* and *C. mopane* woodlands ($r = 0.6$, $P < 0.0001$ and $r = 0.58$, $P < 0.0001$, respectively), but less evident in *A. erioloba* woodlands ($r = 0.15$, $P = 0.001$).

Discussion

Structure and damage types associations

Multivariate analyses explored the spatial and temporal variations between plots of three woodland types in northern Botswana subjected to elephant damage and the occurrence of fire. As might be expected for a comparison carried over a relative short term period, the temporal differences in vegetation structure among plots did not override the variance in the analyses. Of the 3 woodlands examined, *Acacia erioloba* plots had typical structures that varied slightly each year. Moreover, the structure of *A. erioloba* woodlands appeared to be influenced by factors other than elephants and the occurrence of fire. In contrast, *B. plurijuga* woodlands were influenced mostly by the occurrence of fire than elephants. Woodlands dominated by *C. mopane* however, showed considerable spatial and temporal variations that were mostly related to the occurrence of elephants and respected damage to plants.

The effects of elephants and fire

Comparisons between mean densities of plants in *A. erioloba*, *B. plurijuga*, and *C. mopane* woodlands through univariate analyses indicated that short term changes in vegetation structure are apparent, although somewhat inconsistent. There were no indications that the prolific elephant population is inducing the decline of woodlands in northern Botswana. Furthermore, substantial impacts of both elephants and fire did not appear in any of the woodland types examined. Nonetheless, only 8.3% of *C. mopane* plants that were sampled had never been damaged by elephants before. Hence, elephants are a pivotal factor in the modification of *C. mopane* woodland structure. Accordingly, elephants should be considered within the framework of management policies aiming for the maintenance of a particular vegetation structure.

There was an apparent contradiction whereby elephant densities were significantly higher in *B. plurijuga* and *A. erioloba* woodlands that sustained less of their impact (Table 1). It seems that the proximity of water sources to sampling plots within these woodland types played a role in the determination of local elephant densities (Ben-Shahar 1993). Elephants appeared to reside in the shade of trees without utilizing the foliage or damaging the bark if the plant was not a preferred food item.

Woodlands dominated by *B. plurijuga* sustained high fire incidence particularly in the period between 1993 and 1995 (unpublished data). The frequency of affected plants identified by scorch marks on branches and bark indicated that with the increase in fire occurrence there was an increase in the density of the lower height classes such as shrubs and seedlings. Woody plants growing in semi-arid savannas which are less than 3 m high are more susceptible to fire damage than mature trees (Dublin et al. 1990). Yet, the consistent decline in densities of *B. plurijuga* trees which are above 10 m high suggests the result of accumulated fire damage. Statistical analyses indicated that the decline of tall trees was significant over a short time span. Hence, the rate of mortality of tall *B. plurijuga* trees may be high. If indeed such phenomenon is wide spread in northern Botswana, priority should be given to prevent the loss of mature *B. plurijuga* woodlands.

Acknowledgements

I thank the Office of the President and the Department of Wildlife and National Parks for a permission to do this research. Volunteers from Earthwatch Corps had a principal role in the collection of data. This project was supported and funded by Earthwatch Corps, the Disney Foundation, the National Geographic Society and the Wildlife Conservation Society.

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