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ECOSYSTEMS

Fire and Grazing Change Herbaceous Species Composition and Reduce Beta Diversity in the Kalahari Sand System

Gaseitsiwe S. Masunga,[1]* Stein R. Moe,[2] and Baipidi Pelekekae[3]

[1]*Okavango Research Institute, University of Botswana, Private Bag 285, Maun, Botswana;* [2]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432 Aas, Norway;* [3]*Department of Wildlife and National Parks, P.O. Box 131, Gaborone, Botswana*

ABSTRACT

After rainfall and soils, fire and herbivory are two of the main determinants of savanna ecosystems. Although the interactive effects of fire and herbivores on soil and vegetation are widely acknowledged few studies have addressed these two factors in concert, and none of the studies has focused on the Kalahari sand system. We experimentally studied how annual late dry season fires and grazing affect herbaceous plant species composition, above- and belowground biomass, and soil and grass nutrient concentrations in the nutrient-poor semi-arid Kalahari system in northern Botswana. Four treatments (fire, grazing, fire + grazing, and no-fire–no-grazing) were applied for two consecutive years in the late dry season. Plant species composition was affected by treatment and year. The no-fire–no-grazing treatment was distinctly different from all the other treatments in terms of species composition. Beta diversity was lower on the fire treatment and grazing treatment, but not where fire and grazing were combined. Fire and grazing alone or in combination did not have a substantial effect on biomass, soil and plant nutrients or plant species alpha diversity. Plant nitrogen was the only element that differed between treatments, with high concentrations on all the grazed treatments in the first year and low levels on the fire-alone treatment during the second year. The results show that fire and grazing mainly affect species composition and large-scale biodiversity patterns as indicated by the no-fire–no-grazing treatment being distinctly different from other treatments, suggesting the evolutionary adaptation of this dystrophic Kalahari sand system to herbivory and fire.

Key words: beta diversity; fire; herbivory; Kalahari; plant species composition; semi-arid savanna; soil nutrients.

INTRODUCTION

Frequent fires and herbivory by terrestrial vertebrates are widely recognized as major natural agents of spatial heterogeneity and modifiers of savanna ecosystems (Trollope 1984; Skarpe 1992; Bond and van Wilgen 1996; Van Langevelde and others 2003; Archibald and others 2005). Hence,

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**Corresponding author; e-mail:* gsmasunga@ori.ub.bw

fire and grazing have been studied extensively in the savannas, but often independently in spite of the fact that they regularly occur together with potential synergistic effects (McNaughton 1985; Hobbs and others 1991; Johnson and Matchett 2001; Fuhlendorf and Engle 2004; Archibald and others 2005; Midgley and others 2010).

Fire removes moribund vegetation and may create a window of opportunity for the establishment of species-rich communities that also host rare species that may otherwise have been suppressed by dominant species (Pickett and White 1985; Enright and others 1994). However, because of high sensitivity or low tolerance of rare species, frequent fires may lead to their local extinction (Brockway and others 2002). Fire may increase soil available forms of nitrogen (N), calcium (Ca), magnesium (Mg), and other mineral elements (Wan and others 2001; Lavoie and others 2010) as well as N, sodium (Na), potassium (K), and phosphorus (P) in plants (Moe and Wegge 1997). Fire has also been associated with increases in plant tissue nutrient quality (Van de Vijver and others 1999; Brockway and others 2002), plant species composition (Enright and others 1994), primary production (Hulbert 1988), plant growth rates (Gignoux and others 1997), and cover (Brockway and others 2002). However, some studies have found little or no significant effect of fire on soil, plant chemical properties or on plant species richness (Dougill and others 1999; Van de Vijver and others 1999; Jensen and others 2001; Brockway and others 2002; Dougill and Thomas 2004; Holdo and others 2011). Although repeated burning may cause increases or no changes in the concentrations of some elements (Wan and others 2001), significant losses may occur in aboveground biomass, foliar carbon (C) and N (Trollope 1984; McNaughton and others 1988; Hobbs and others 1991; Wan and others 2001), as well as in total soil N in mostly temperate soils (Kaye and Hart 1998; Deluca and Zouhar 2000).

Similarly, grazing removes aboveground grass biomass both in its green or dry state, and may in the process create gaps for recolonization of open spaces by new species or local extinction of rare and sensitive species (McNaughton 1985; Olff and Ritchie 1998). Many studies have observed grazing to stimulate growth of some grazing-tolerant plant species, and also to contribute to increased plant tissue nutrient quality, species diversity, and productivity (Frank and McNaughton 1993; Augustine and McNaughton 1998; Ritchie and others 1998; Augustine and Frank 2001). Belowground biomass can also be influenced by grazing or fire, despite the fact that vegetative organs are often protected by a soil layer from the disturbances occurring aboveground (Frost 1984; Sullivan and Rohde 2002). However, studies on belowground root biomass are generally few (Böhm 1979; De Castro and Kauffman 1998; Frank and others 2002), and those investigating effects of grazing or fire have found inconsistent results. Root biomass can be reduced by grazing as a result of more resources being allocated to the remaining aboveground tissues to compensate for the grazed tissues (Holland and Detling 1990; Ritchie and others 1998; Gao and others 2008) or it can increase or not be affected by fire or grazing (McNaughton and others 1998; Van de Vijver and others 1999; Frank and others 2002).

Interactive effects of fire and grazing have often been overlooked despite knowledge that grazers are frequently attracted to burned patches by the green and nutritive plants found in those patches (Daubenmire 1968; Moe and Wegge 1997; Archibald and others 2005; Mills and Fey 2005). In the process, grazers consume grass biomass, and with increasing grazing intensity the amount of grass that would otherwise be spared to serve as fuel load for the dry season fire is eventually reduced. Grazing, therefore, has the ability to moderate fire effects on vegetation and soils (Hobbs and others 1991). During grazing, herbivores may also deposit dung and urine that subsequently enrich the grazed patches with readily available plant nutrients (Ruess and McNaughton 1987; Hobbs 1996). Burning also removes biomass, but deposits ash and increases soil temperature, respiration, and nutrient turn-over rates (Hobbs and others 1991; Van de Vijver and others 1999; Johnson and Matchett 2001). The combined effects of fire and grazing may be additive resulting in enhanced nutrient cycling processes (McNaughton and others 1988; Johnson and Matchett 2001) or compensatory, with the strength of one factor becoming negligible or weakened by the presence of the other factor (Hobbs and others 1991). Grazing and burning thus offer alternate soil and plant nutrient enrichment pathways and have the potential to transform the plant structure, composition, and productivity in a complex manner when acting together (McNaughton 1985; Hobbs and others 1991; Mills and Fey 2005).

The objectives of this study were to experimentally test how annual fires and continuous grazing, alone or in combination affect (i) plant species composition and diversity, (ii) above- and belowground herbaceous plant biomass, and (iii) soil and grass nutrient concentrations in the Kalahari sand system in northern Botswana.

In light of the above, we predicted that (i) fire and grazing would change plant species composition (Enright and others 1994), and that (ii) plant richness and diversity would be lower in areas protected from fire and grazing by large herbivores as well as under the combined disturbance of fire and grazing, but relatively higher in burned or grazed areas. We further predicted that (iii) fire and grazing would decrease herbaceous biomass (Hobbs and others 1991; Van Langevelde and others 2003) and (iv) that fire would increase soil N, Ca, Mg, and other mineral elements (Wan and others 2001; Lavoie and others 2010), and this would be reflected in increased concentrations in emerging plant tissue materials following intake from nutrient-enriched soils (Trollope 1984; McNaughton and others 1988; Wan and others 2001). (v) Because of dung and urine deposition, and accelerated nutrient turn-over rates facilitated by grazing, vegetation in grazed plots would be higher in plant nutrient concentrations compared to vegetation in burned and unburned plots (Hobbs and Huenneke 1992; Moe and Wegge 2008), except P which is normally reduced on grazed areas (Moe and Wegge 2008; Wang and others 2011).

METHODS AND MATERIALS

Study Area

The study was done in Chobe National Park (17°49′–17°55′S, 24°50′–24°59′E), a wildlife protected area in semi-arid northern Botswana, in the open savanna woodland characterized by scattered large trees of Zambezi Teak (*Baikiaea plurijuga* Harms) and a long history of annual fires (Child 1968; Taolo 2003). The current open tree vegetation structure is attributed to frequent fires in this part of the park which reduced the density of the once dominating fire-sensitive woodlands of *Baikiaea plurijuga* (Taolo 2003). The soil is nutrient-poor Kalahari sand—a deep and poorly structured soil, with low water-holding capacity and high infiltration rates (Ben-Shahar and MacDonald 2002; Skarpe and others 2004).

Rainfall occurs only in hot summer months (October–April) with a peak in January and February (Figure 1). The maximum monthly mean temperature in summer months is 35°C. Annual average rainfall is about 650 mm. The period between May and July is cold and dry, with a mean temperature of 6°C. August to September is dry and hot (Bhalotra 1987; Ben-Shahar and MacDonald 2002). Most herbaceous plants reach their maximum growth in February and senescence in March as the rainfall intensity declines.

Annual fires are common in the dry season in the study site, occurring mainly in the dry and hot months (August–October), but fires are commonly put out in line with the no-fire policy of the park (Taolo 2003). However, some fires often manage to spread over a larger part of the park before they are put out. Records of fire incidents in the study area are poorly documented. Reports, however, indicate that the last fire recorded in this part of the area occurred in 1997 (DWNP, unpublished reports). Charred wood and charcoal remains found within 30 cm depth of the soil surface showed that fires were common in the study area.

The study site was located 300 m south of the Ngoma-Kasane tarmac road, about 10 km from the Chobe River. The dominant tree species in the study site is *Baikiaea plurijuga*. Common grass species are *Aristida congesta* R. et S, *Schmidtia pappophoroides* Stued, and *Digitaria* species (Child 1968; Taolo 2003).

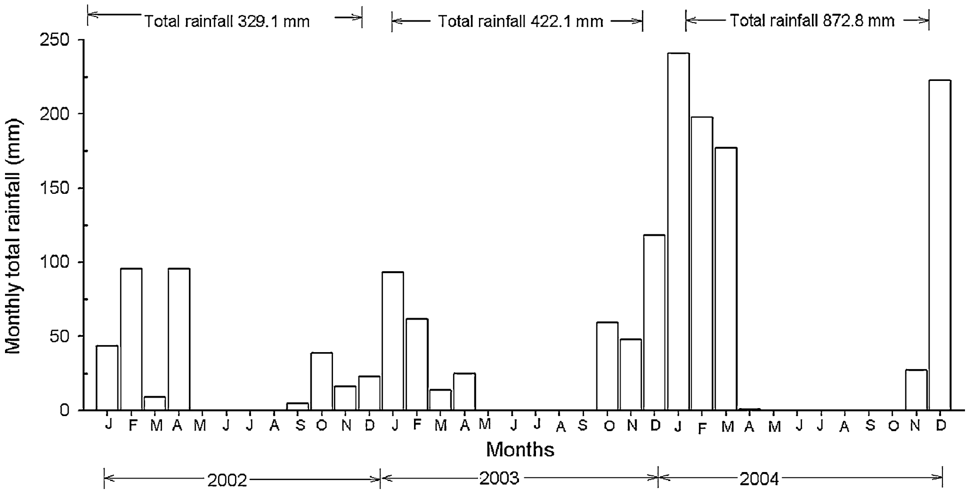
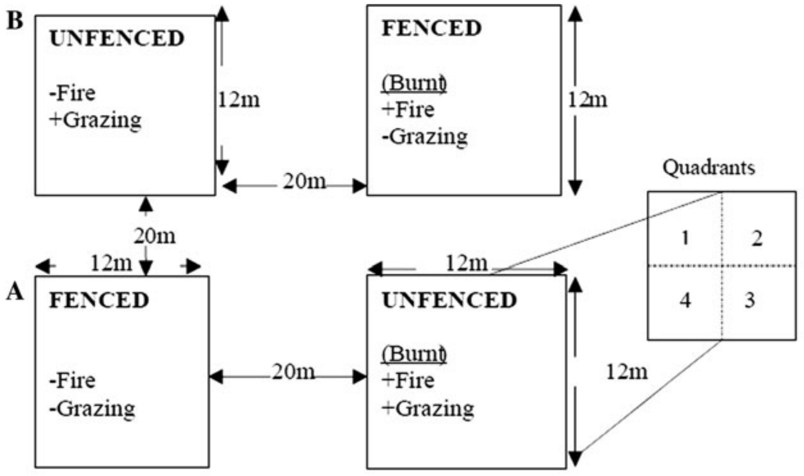


Figure 1. Monthly total rainfall in Kasane from September 2002 to April 2004. The weather station is located 11–20 km from the study sites, and is monitored daily by Botswana Government Meteorological Services Department.



Key: A positive sign (+) denotes presence, and a negative (-) denotes absence of a treatment

Figure 2. The lay-out of randomized treatment plots within an experimental block.

The site is a wet season range for a large number of wildlife species that include Cape buffalo (*Syncerus caffer* Sparrman) and African elephant (*Loxodonta africana* Blumenbach) (Taolo 2003; Skarpe and others 2004). There are about 7,000 buffalo and 80,000 elephant in the Chobe area, which is a substantial proportion of the 150,000 elephant estimated for the whole northern Botswana (Taolo 2003; DWNP 2006).

Experimental Design

A randomized block design was used for the application of four treatments: (i) fire alone (fenced plots with burning), (ii) grazing alone (unfenced plots with no burning), (iii) fire + grazing (unfenced plots with burning), and (iv) no-fire–no-grazing (fenced and no burning) (Figure 2). Treatment plots, each measuring 12 m × 12 m, were placed 20 m from each other and were replicated in eight blocks. Each block covered an area of 44 m × 44 m. The blocks were set up in homogenous open woodland within the flat to gentle depressions of undulating fossil sand dunes (Child 1968). There were two blocks per depression and blocks within one depression were 100 m distant from each other. None of the blocks had trees or large shrubs in them. The depressions were about 2–3 km apart, and are used by different wildlife species for grazing (Taolo 2003) and as a passage route to the Chobe River, the only permanent surface water source in the park (Child 1968). The selection of the sites was done in the dry season when the herb layer was dominated by dry perennial grasses. The perennial grass species were, therefore, used to confirm similarity among the block locations.

The fence used was 1.8 m high, and had a mesh size of 10 cm × 10 cm to exclude both medium and large herbivores. Large plots permitted us to avoid sampling within 1 m distance from the edge of the plots, and within one spot more than once.

Plots were marked in mid-September 2002, and the exclosures erected and completed on 12 October 2002. Prior to burning, litter was collected from four randomly placed 1 m × 1 m subplots within each treatment plot to measure litter quantity. The litter was made up of all standing dead and loose litter on the ground floor. The collected litter was taken to camp for oven drying at 60°C for 72 h prior to weighing for litter quantity. The litter was then returned and redistributed on the 1 m × 1 m subplots where it was collected before fire was applied. Litter was returned to the treatment plots to minimize disturbances to the plots and reduce loss of fuel load. Fire was applied in the late hot dry season on October 14–15, 2002 and October 15–16, 2003, in the evening between 1700 and 1900 h when air temperature and wind speed were low. When it was not possible to burn all plots in one evening, fire was applied to the remaining plots the following morning between 0600 and 0800 h.

Aboveground vegetation parameters were recorded in the wet season at the peak of the following growing seasons (February 1–15) in 2003, and in 2004. Root biomass was sampled between February 25 and March 03, 2003, and February 20–26, 2004.

Species Composition and Vegetation Cover

Species composition was recorded from four 1 m × 1 m permanent subplots which were randomly located within each treatment plot. The random location of the permanent subplots was restricted by subdividing each treatment plot with a thin thread into four quadrants of 6 m × 6 m each (Figure 2). Within each quadrant one permanent subplot was located from which a total percent areal vegetation cover was visually estimated, and plant species present as well as their individual numbers were recorded, during the 2 years of study.

Shoot and Root Biomass

Within each treatment plot, another four 1 m × 1 m temporary subplots were randomly selected for sampling of shoot and root biomasses. All live and standing dead shoot biomass was clipped at the ground level in all plots, and separated into graminoids and forbs (De Castro and Kauffman 1998). However, there was very little standing dead shoot biomass remaining from the last dry season at the time of sampling. Litter found within the quadrants on the ground surface was collected separately and oven-dried at 60°C for 72 h prior to weighing. Roots were excavated within the temporary subplots used for sampling shoot biomass. Root biomass was sampled by removing a monolith (50 cm × 50 cm, 30 cm deep) from within each subplot (Böhm 1979; De Castro and Kauffman 1998). Monolith sites within each treatment plot were at least 4 m apart. A pilot study had showed that the accumulative root biomass of the herbaceous plants in the study sites reaches 90% at 30 cm depth within 0–50-cm soil depth (data not shown). The 5–10 cm depth contributed the largest root biomass of 29%, with the 0–15 cm depth contributing 67% of the root biomass. Bulbs and large taproots were excluded.

Four blocks were randomly chosen for root sampling, and were used in both years. Monoliths were transported to the camp in firm containers where the soil was wet sieved through 1-mm wire mesh to obtain live roots (McNaughton and others 1998; Ritchie and others 1998). The roots were washed clean and separated into graminoids and forbs according to their color and morphology (McNaughton and others 1998). Roots that broke easily when bent using forceps were considered dead and discarded. All biomass samples were air-dried and then oven-dried at 60°C for 72 h before being weighed.

Soil Nutrient Concentration

Soil samples were collected at the same time as the aboveground biomass samples in both years. Four soil samples (0–10 cm depth, core diameter 5 cm) were collected randomly per treatment plot for all the eight blocks ($n = 128$). The soil was air-dried and later oven-dried at 40°C for 48 h. Total C, total N, P, K, Na, Ca, and Mg were determined for each sample. Chemical analysis was done at the Norwegian Institute for Agricultural and Environmental Research at the Norwegian University of Life Sciences. The soil was passed through a 2-mm sieve and nutrient elements extracted using ammonium lactate. Total C and N were determined by dry combustion (using 2400 CHN Elemental Analyser, Perkin-Elmer) (Nelson and Sommers 1996). Emissions of P, K, Na, Ca, and Mg were read on an optical emission spectrometer (OES Optima-5300 DV, Perkin-Elmer precisely) (Soltanpour and others 1996).

Grass Nutrient Concentration

Nutrient concentration of the live grass shoot biomass collected in 2003 and 2004 was determined for each of the subplots. The dried biomass was ground in a Wiley Mill (Arthur H. Thomas Comp, Philadelphia, USA) using a 2-mm sieve before being analyzed for N, P, K, Na, Ca, and Mg (AOAC 1995).

Aristida congesta and *Schmidtia pappophoroides* were the two dominant grass species selected to monitor monthly trends in nutrient levels following treatment application. Both *S. pappophoroides* and *A. congesta* are perennial species; though *A. congesta* can have a shorter lifespan (Gibbs-Russel and others 1990; Weber and others 2000). The two species were sampled within one continuous wet season of 2003/2004 on November 23–24, December 26, 2003, and January 25, 2004 from each treatment in the eight blocks by selecting only green foliage. The first rains of this wet season occurred on October 17, 2003 making it possible to sample green foliage a month later. Care was taken to avoid interfering with the whole plot where other mid-wet season samples were to be collected.

The grass tissue was air-dried and subsequently oven-dried at 60°C for 72 h. The tissues from each sampling period were analyzed for N, P, K, Na, Ca, and Mg at the Agricultural Research Soil and Plant Analyses Research Support laboratories (SPARS) in Sebele, Botswana. A sulfuric–selenium–salicylic acid mixture was used as the digestion reagent. The sample–reagent mixture was then heated at 330°C for 2 h before being cooled. Nitrogen was determined following the Kjeldahl process (AOAC 1995). Phosphorus was read on an UV photospectrometer (Shimadzu Corp. Japan). Potassium emission was measured on a flame photometer

(Corning 410). Calcium, Mg, and Na were measured using atomic absorption spectrophotometer (Varian Techron, Australia) (AOAC 1995).

Data Analysis

We determined relationships between species composition, treatment, and year using canonical correspondence analysis (CCA) (ter Braak 1986) within the Vegan package in the R-software version 2.11.1 (Oksanen and others 2012). We removed infrequent species with less than three occurrences, as commonly done in vegetation gradient analyses (McCune and others 2000). We used treatment, year, and their interactions as explanatory variables for species composition. The CCA runs were constrained by blocks.

We also used the generalized Morisita's similarity index (Chao and others 2008; Jost 2008), associated with 95% confidence intervals based on 200 bootstrap replications, to compare the plant compositional similarities between treatments. This index uses abundance data and it can compare multiple assemblages. The free software SPADE was used for this analysis (http://chao.stat.nthu.edu.tw/SPADE_UserGuide.pdf).

Species alpha diversity (between treatment heterogeneity) and evenness were calculated using Shannon–Wiener's indices (Magurran 2004). Species richness (number of species per plot) was also calculated. Data were either log- or arcsine square root transformed for normality and homogeneity of variance, prior to analysis of variance (ANOVA). A two-factor repeated-measure ANOVA using the General Linear Model was used to determine differences between treatments, with biomass, alpha diversity indices, and nutrient levels as response factors measured on two occasions. A two-way ANOVA was also used to determine differences within years. The Kruskall–Wallis *H* test was used when assumptions of normality and homogeneity of variance were not met when determining differences in nutrient concentrations of individual grass species between treatments and months. Means that were significantly different at $p < 0.05$ were separated by a post hoc Student–Newman Keuls method.

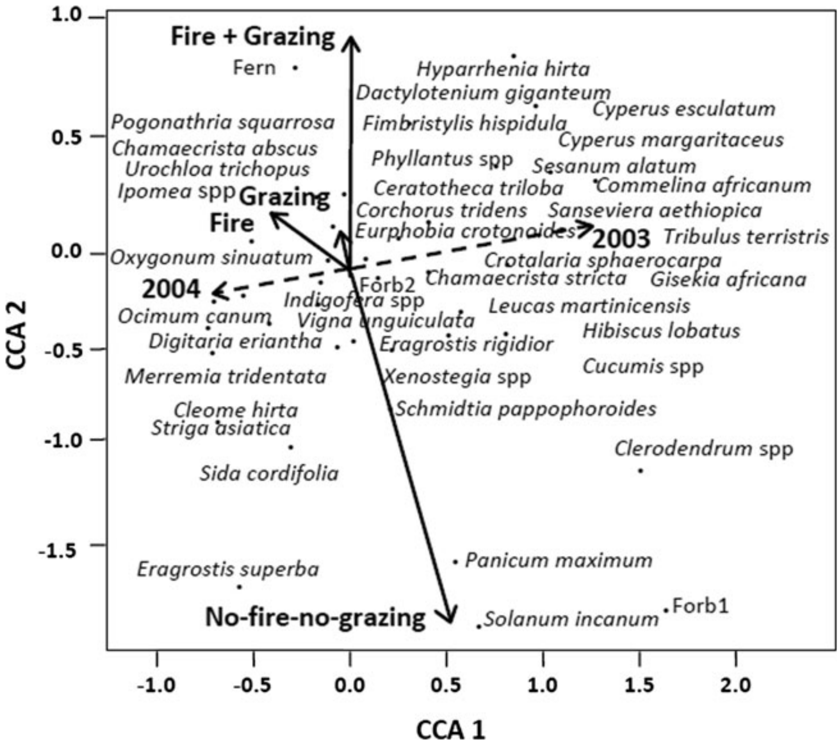


Figure 3. Canonical Correspondence Analysis (CCA) biplot diagram of herbaceous plant species composition and fire, grazing, fire + grazing, control, and years (2003 and 2004) as environmental variables. *Solid arrows* represent a gradient influenced by treatments (fire, grazing, fire +grazing, and control) and *broken arrows* represent a gradient influenced by years. For plant species that could not be identified to species level, only the genus names are written and then followed by abbreviation "spp" (for example, *Clerodendrum* spp.). Forb species that could not be identified altogether were coded as Forb1, 2, 3... and unidentified fern as Fern.

Beta diversity which is within treatment heterogeneity (Anderson 2006; Anderson and others 2006) was determined using the function betadisper in Vegan in R (Oksanen and others 2012). Tukey's HSD was used as a post hoc test to evaluate pair-wise contrasts between treatments.

RESULTS

Species Composition, Diversity, and Cover

Species composition within the plots was significantly affected by treatments ($F_{3,52} = 1.65$, $p = 0.002$) and year ($F_{1,52} = 3.25$, $p = 0.002$) (Figure 3). The CCA 1 axis mainly captured the differences between the 2 years, whereas CCA 2 axis separated the treatments. The grass species *Panicum maximum*, *Eragrostis superba* and *Schmidtia pappophoroides*, and forb species *Solanum incanum*, *Clerodendrum* species, *Sida cordifolia*, and *Striga asiatica* were associated with the no-fire–no-grazing treatment. The forb species *Oxygonum sinuatum* and *Ipomea* species were associated with fire-alone, whereas the grass species *Urochloa trichopus* and *Pogonathria squarrosa* and forb species *Eurphobia crotonoides* and *Corchorus tridens* were mostly associated with the grazing treatment. Grass species *Hyparrhenia hirta* and *Dactylotenium gigateum* and forb species *Cyperus esculatum*, *Cyperus margaritaceous*, and *Fimbristylis hispidula* were mostly associated with the fire–grazing treatment.

The species similarities among plots subjected to different combinations of grazing and fire were high (>0.9), and confidence intervals overlapped (Table 1). However, when the different combinations of fire and grazing were compared to the no-fire–no-grazing treatment similarities were less and statistically different from the comparisons between the treatments involving fire and grazing.

Species alpha diversity ($F_{3,21} = 0.61$, $p = 0.62$), richness ($F_{3,21} = 1.00$, $p = 0.41$), and evenness ($F_{3,21} = 0.85$, $p = 0.48$) did not differ between treatments, but differed between years (Tables 2, 3). Species alpha diversity and evenness were significantly higher in 2004 than in 2003. Species richness, however, was higher in 2003 than in 2004. Perennial grass species were more dominant in terms of numbers than annual grass species in both years (Perennials = 10; Annuals = 4) (Supplementary Table). Overall, forb species accounted for a larger number of the herbaceous plant species in the system in both 2003 and 2004 (forb = 38, grass = 14). The total number of individual plants of each plant species was about two-fold in 2004 compared to 2003 (data not shown). *Aristida congesta* (1600), *Digitaria eriantha* (1300), *Dactyloteniun giganteum* (900), *Pogonarthria squarrosa* (800), and *Schmidtia pappophoroides* (500) had many individuals in 2004 compared to 2003 in which the number of individuals was lower and species abundance rankings shifted (*Dactyloteniun giganteum*—559, *Aristida congesta*—492, *Pogonathria squarrosa*—433, *Schmidtia pappophoroides*—271, *Gisekia africana*—216, *Digitaria eriantha*—167).

Species beta diversity (heterogeneity within the treatments) was significantly affected by treatment (Figure 4). Fire alone (Tukey's HSD, $p = 0.03$) and grazing alone (Tukey's HSD, $p = 0.02$) had lower beta diversity compared to the control treatment. There were no differences in beta diversity between the control and the combined fire and grazing treatment.

There was no significant difference between treatments in the vegetation cover when both years were used (Repeated measures $F_{3,21} = 0.40$, $p = 0.75$), but there was a significant treatment–year interaction effect ($F_{3,21} = 4.50$, $p = 0.01$) and year-effect ($F_{1,21} = 34.1$, $p < 0.0001$). The grazing-alone and the no-fire–no-grazing treatments had a significantly higher cover in 2004 compared to the two fire treatments (Two-way ANOVA $F_{3,21} = 6.51$, $p = 0.003$) (Figure 5). There was no significant effect of treatments on the herbaceous cover in 2003 ($F_{3,21} = 0.72$, $p = 0.5$).

The litter quantity measured in the growing season was significantly different between treatments ($F_{3,21} = 12.80$, $p < 0.0001$). Treatments that were affected by fire (fire alone and fire + grazing) had less litter compared to treatments that were not

Table 1. Morisita's Similarity Indexes for Plant Species Composition Between Treatment Combinations

Pairwise comparisons	Estimate (±SE)	95% Confidence intervals
Grazing versus fire + grazing	0.942 (0.010)	0.922–0.960
Grazing versus fire	0.937 (0.012)	0.913–0.960
Fire versus fire + grazing	0.902 (0.014)	0.875–0.929
No-fire–no-grazing versus grazing	0.806 (0.015)	0.779–0.834
No-fire–no-grazing versus fire	0.735 (0.019)	0.698–0.771
No-fire–no-grazing versus fire + grazing	0.712 (0.019)	0.674–0.750

Table 2. Mean Values (±SE) of Herbaceous Layer Shoot Biomass (Live and Standing Dead), Root Biomass (Live Biomass), and Diversity Indices at the Peak of the Growing Season Across Four Treatments Applied in 2003 and 2004

	Shoot biomass (g m^{-2})				Root biomass (g m^{-3})				Diversity indices					
	Grass		Forb		Grass		Forb		Shannon–Weiner		Richness		Evenness	
Treatment (year)	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Fire	142 ± 10	162 ± 16	58 ± 9	37 ± 8	430 ± 180	91 ± 22	87 ± 36	22 ± 17	0.97 ± 0.06	1.38 ± 0.09	14 ± 1	7 ± 1	0.37 ± 0.02	0.70 ± 0.04
Grazing	139 ± 10	190 ± 16	39 ± 9	19 ± 8	173 ± 147	76 ± 18	104 ± 47	34 ± 22	0.89 ± 0.06	1.41 ± 0.09	12 ± 1	7 ± 1	0.35 ± 0.02	0.71 ± 0.04
Fire + grazing	130 ± 10	149 ± 16	60 ± 9	17 ± 8	236 ± 330	70 ± 40	48 ± 47	51 ± 22	1.02 ± 0.06	1.41 ± 0.09	13 ± 1	7 ± 1	0.40 ± 0.02	0.73 ± 0.04
No-fire–no-grazing	143 ± 10	165 ± 16	50 ± 9	18 ± 8	112 ± 147	127 ± 18	54 ± 36	55 ± 16	1.00 ± 0.06	1.24 ± 0.09	14 ± 1	7 ± 1	0.39 ± 0.02	0.66 ± 0.04

There was no significant difference between treatments.

affected by fire (no-fire–no-grazing, and grazing) in both 2003 ($F_{3,21} = 0.77$, $p < 0.0001$) and 2004 ($F_{3,21} = 16.1$, $p < 0.0001$). In general, there was more litter in 2003 (75 g m^{-2}) compared to 2004 (57 g m^{-2}) ($F_{1,21} = 6.56$, $p = 0.02$) when all treatment plots were considered.

Shoot and Root Biomass

There was no significant difference in shoot biomass or in root biomass between treatments or years (Tables 2, 3). Also, when separated into the grass and forb groups, no significant difference in the shoot biomass was found between treatments. Neither the grass root nor the forb root biomass differed between treatments (grass: $F_{3,6} = 0.65$, $p = 0.61$, forb: $F_{3,6} = 0.16$, $p = 0.92$) or years (grass: $F_{1,6} = 2.75$, $p = 0.15$, forb: $F_{1,6} = 1.85$, $p = 0.22$). However, there was a significant difference between years in the shoot biomass of the grasses ($F_{1,21} = 11$, $p = 0.003$), and of the forbs ($F_{1,21} = 34.7$, $p < 0.0001$). The shoot biomass of the grasses was higher in 2004 than in 2003, whereas that of the forbs was higher in 2003 than in 2004.

Soil and Grass Shoot Nutrients

None of the soil nutrients studied differed significantly between treatments (Tables 4, 5). There was, however, a significant difference between years in soil C, N, P, Na, K, and pH. There was a higher concentration of soil C, P, and K in 2003 than in 2004. Soil N and Na were higher in 2004 than in 2003. Soil Ca and Mg concentrations were not different between years. Soil pH was higher in 2003 than in 2004.

There was a significant difference in grass shoot N concentration between treatments ($F_{3,21} = 5.38$, $p = 0.01$) (Figure 6). In 2003, grasses that were subject to grazing alone, and to both fire and grazing had a higher concentration of N than grasses that were only burned, and those excluded from both burning and grazing ($F_{3,21} = 4.20$, $p = 0.02$). In 2004, grasses in the plots that were only grazed, burned and grazed, and not burned and grazed had a higher N concentration compared to grasses in plots that were only burned ($F_{3,21} = 6.55$, $p = 0.003$). Essentially, grazing increased plant N, whereas burning lowered plant N. Furthermore, the grass N level was significantly higher in 2003 than in 2004 ($F_{1,21} = 184$, $p < 0.0001$). There was no significant treatment–year interaction effect on the N concentration. No significant difference between treatments was observed in the concentration of P ($F_{3,18} = 0.87$, $p = 0.47$), K ($F_{3,12} = 0.13$, $p = 0.94$), Ca ($F_{3,21} = 0.41$, $p = 0.74$), Mg ($F_{3,21} = 0.94$, $p = 0.44$), and Na ($F_{3,18} = 3.09$, $p = 0.05$). Between years, the

Table 3. Analysis of Variance (ANOVA) of the Effects of Fire, Grazing, Fire + Grazing, and No-Fire–No-Grazing Treatments on Total Herbaceous Layer Shoot Biomass (Live and Standing Dead) and Root Biomass (Live), Species Diversity, Richness, and Evenness at the Peak of the Growing Season (February) in 2003 and 2004

Main effect (df)	Total shoot biomass		Total root biomass		Shannon–Weiner diversity		Species richness		Species evenness	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Repeated measures ANOVA										
Block (7)	4.41	0.004	2.80	0.13	0.96	0.48	4.74	0.003	0.78	0.61
Treatment (3)	0.80	0.51	0.60	0.64	0.61	0.62	1.00	0.41	0.85	0.48
Year (1)	0.02	0.89	2.65	0.16	49.3	<0.0001*	310	<0.0001*	238	<0.0001*
Year × treatment	2.39	0.10	0.77	0.55	1.11	0.37	1.68	0.20	0.71	0.56
Residual error	21		6		21		21		21	
Two-way ANOVA										
Within 2003										
Block (7)	7.60	0.0001	3.18	0.09	0.86	0.55	3.60	0.01	1.44	0.24
Treatment (3)	0.74	0.54	0.78	0.55	1.01	0.41	1.53	0.24	1.05	0.39
Residual error	21		7		21		21		21	
Within 2004										
Block (7)	2.88	0.03	1.11	0.41	1.16	0.37	3.25	0.02	1.11	0.40
Treatment (3)	1.59	0.22	1.74	0.24	0.81	0.50	0.86	0.48	0.69	0.57
Residual error	21		7		21		21		21	

Blocks df = 3 for total root biomass.
** Significantly different between years.*

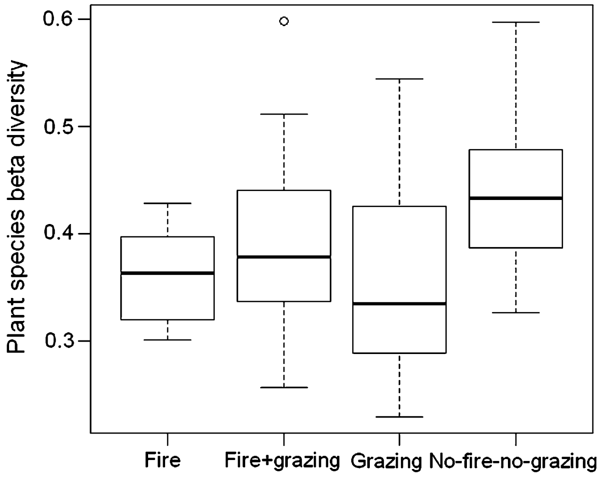


Figure 4. Box-plot of species beta diversity (heterogeneity within treatment) in relation to control, fire, fire + grazing, and grazing treatments.

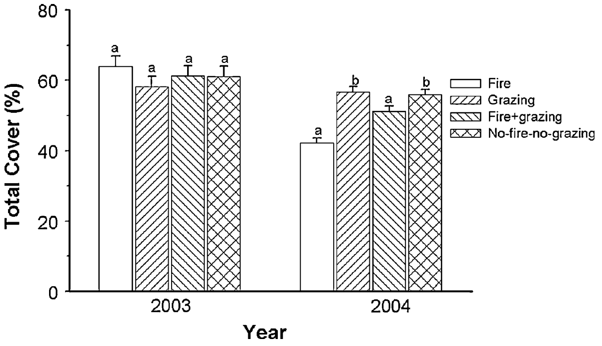


Figure 5. Mean (±SE) percent cover of the herbaceous plants in fire-only, grazing-only, fire + grazing, and no-fire–no grazing treatments in the mid-wet season of 2003 and 2004.

concentrations of P ($F_{1,18} = 41.9$, $p < 0.0001$), K ($F_{1,12} = 63.4$, $p < 0.0001$), Ca ($F_{1,21} = 12.2$, $p = 0.003$), and Mg ($F_{1,21} = 53.9$, $p < 0.0001$) were significantly lower in 2004 than in 2003.

In general, there was a significant decrease in the concentration of all nutrients ($p < 0.0001$) of *A. congesta* and *S. pappophoroides* within 3 months (November 2003, December 2003, and January 2004), except for K and Na in *A. congesta* (Figure 7a, b). The concentration of K was higher in December and January than in November (Kruskall–Wallis $H_2 = 13.7$, $p = 0.01$), whereas the concentration of Na did not differ between months (Kruskall–Wallis $H_2 = 5.53$, $p = 0.06$). There was no significant difference between treatments in the concentration of each of the nutrient elements of *A. congesta* and *S. pappophoroides* in November, December and January ($p > 0.05$), except for the Mg concentration in *S. pappophoroides*, which was slightly lower in January in the fire + grazing treatment than

Table 4. Mean Percent Concentrations (mg/100 g of soil) of the Selected Five Nutrient Elements in Soil, and Soil pH from the Fire-Alone, Grazing-Alone, Fire + Grazing, and No-Fire–No-Grazing Treatments in 2003 and 2004

Treatment (year)	Carbon ($\times 10^{-1}$)		Nitrogen ($\times 10^{-2}$)		Phosphorus ($\times 10^{-1}$)		Calcium		Magnesium		Sodium ($\times 10^{-1}$)		pH	
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
Fire	4.5 ± 0.2	4.5 ± 0.2	1.7 ± 0.1	1.7 ± 0.1	3.0 ± 0.3	3.0 ± 0.3	29.6 ± 1.1	29.6 ± 1.1	5.4 ± 0.2	5.4 ± 0.2	6.5 ± 0.4	6.5 ± 0.4	6.0 ± 0.05	6.0 ± 0.04
Grazing	4.5 ± 0.2	4.5 ± 0.2	1.8 ± 0.1	1.8 ± 0.1	2.8 ± 0.3	2.8 ± 0.3	26.7 ± 1.1	26.7 ± 1.1	5.2 ± 0.2	5.2 ± 0.2	6.1 ± 0.4	6.1 ± 0.4	6.1 ± 0.05	5.9 ± 0.04
Fire + grazing	4.7 ± 0.2	4.7 ± 0.2	1.7 ± 0.1	1.7 ± 0.1	3.2 ± 0.3	3.2 ± 0.3	28.3 ± 1.1	28.3 ± 1.1	5.2 ± 0.2	5.2 ± 0.2	6.3 ± 0.4	6.3 ± 0.4	5.9 ± 0.05	5.9 ± 0.04
No-fire–no grazing	4.5 ± 0.2	4.5 ± 0.2	2.1 ± 0.1	2.1 ± 0.1	3.2 ± 0.3	3.2 ± 0.3	27.1 ± 1.1	27.1 ± 1.1	5.1 ± 0.2	5.1 ± 0.2	6.6 ± 0.4	6.6 ± 0.4	5.9 ± 0.05	5.9 ± 0.04

There was no significant difference between treatments (see Table 5).

other treatments (Kruskall–Wallis $H_3 = 10.4$, $p = 0.02$) (Figure 7b).

DISCUSSION

Species Composition, Diversity, and Cover

Although fire and grazing are important determinants of African savannas they are rarely studied in concert. Several studies have documented the effects of fire and grazing separately and the few that studied the interaction of these two factors have found strong interactive effects (Johnson and Matchett 2001; Mills and Fey 2005). Supporting our first prediction, there were differences in plant species composition between the treatments. The most pronounced difference we have documented in this study is between the no-fire–no-grazing treatment and the other treatments. Both fire and grazing have traditionally been regarded as strong agents of savanna heterogeneity (McNaughton 1985; Skarpe 1992; Van Langevelde and others 2003). In this study, we have shown that the beta diversity (that is, within treatment heterogeneity) is higher when herbivores are excluded. The strong effects of removing fire and grazing can also be seen from the similarity indices where the no-fire–no-grazing treatment is highly different from the other treatments. Recently, in a more eutrophic savanna in Uganda, Okullo and Moe (2012) also found that beta diversity was higher when large herbivores were excluded from savanna areas. Contrary to common perceptions, Milchunas and others (1988) have argued that in areas with a long evolutionary history of grazing, excluding herbivores may be considered as a strong disturbance. This view is supported by our study as indicated by the strong effect of grazing and fire removal on species composition, and the small differences between the other three treatments. Savanna systems, in general, and our study system, in particular, are adapted to fire and grazing. The Kalahari sand system in northern Botswana is dominated by large bodied bulk feeders like elephant and buffalo. Large herds of buffalo numbering over 7,000, and a substantial part of the current population of about 150,000 elephant in northern Botswana congregate along the Chobe river system in the dry season (Taolo 2003; Skarpe and others 2004; DWNP 2006). Although elephant (4 elephants per km^2) and buffalo occur in higher densities in the study area during the dry season when grass forage is less important, these animals are also present during the wet season when grass is more important

Table 5. Analysis of Variance (ANOVA) of the Effects of Treatments (Fire, Grazing, Fire + Grazing, and No-Fire–No-Grazing) on Soil Nutrient Concentrations at the Peak of the Growing Season in February 2003 and 2004

Factor	Repeated measures ANOVA								Two-way ANOVA							
									2003				2004			
	Block		Treatment		Years		Year × treatment		Block		Treatment		Block		Treatment	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Total C	2.7	0.04	0.33	0.81	45.7	<0.0001	1.24	0.32	1.28	0.31	0.82	0.49	3.81	0.01	0.09	0.96
Total N	4.28	0.004	0.24	0.87	18.4	<0.0001	1.15	0.35	0.85	0.56	0.90	0.46	7.33	0.0002	0.64	0.59
P	6.41	<0.0001	0.29	0.83	15.9	0.001	0.89	0.46	12.5	<0.0001	0.62	0.61	3.36	0.01	0.46	0.72
K	17.3	<0.0001	2.05	0.14	24.7	<0.0001	0.85	0.48	10.7	<0.0001	3.01	0.05	12.0	<0.0001	0.31	0.82
Ca	5.83	0.001	0.36	0.78	0.18	0.68	0.56	0.65	4.21	0.005	0.12	0.95	5.31	0.001	0.75	0.53
Mg	8.30	<0.0001	0.04	0.99	0.01	0.93	0.49	0.69	6.80	0.0003	0.02	1.00	6.62	0.0003	0.23	0.87
Na	5.62	0.001	0.49	0.69	45.4	<0.0001	0.84	0.49	2.72	0.04	1.01	0.41	4.81	0.002	0.31	0.82
pH	3.47	0.12	1.24	0.32	40.4	<0.0001	1.83	0.17	2.23	0.07	1.73	0.19	4.32	0.004	1.13	0.36

Degrees of freedom (df) blocks = 7, treatments = 3, year = 1, y × t = 3, residual error = 21.

(Skarpe and others 2004). Elephant and buffalo are less selective than smaller grazers and consequently, this feeding behavior may contribute to a homogeneous herbaceous species pattern at the landscape scale.

The grass species *Panicum maximum*, *Eragrostis superba*, and *Schmidtia pappophoroides* and forb species *Solanum incanum*, *Sida cordifolia*, and *Clerodendrum* species were associated with the no-fire–no-grazing treatment. These grasses are good forage species and can tolerate light disturbances in the form of light intensity fires and grazing, but can disappear under heavy grazing and frequent fires (Sweet 1982; O'Connor 1991; Van Oudtshoorn 1992; Skarpe 1986). The three forb species are also indicators of disturbed ecosystems, though *Solanum incanum* can occur in both disturbed and undisturbed sites in climax grassland communities (Belsky 1987; Kutt and Woinarski 2007). There were many forbs and few grass species associated with the fire and grazing treatments, with the grazing-alone treatment showing less strength in species association compared to the other three treatments. Usually, forb species occur in higher frequencies in burned than in unburned and grazed areas, especially in semi-arid systems (Ruthven III and others 2000). Moisture conditions can be a critical determinant of forbs response to disturbances such as grazing. In mesic environments, grazing has been found to stimulate forb abundance (Winter and others 2012), whereas in semi-arid systems an opposite response has been observed (Ruthven III and others 2000).

Contrary to our second prediction, we did not find significant changes in alpha diversity or species richness between any of the treatments.

Plant Biomass and Cover

Neither fire nor grazing changed the plant shoot and root biomass, or concentrations of most nutrients in the open Baikiaea woodland of the Kalahari sands in semi-arid northern Botswana. This result was not in line with our prediction that fire and grazing would decrease plant biomass. Only the concentration levels of grass shoot N were affected by the treatments. Thus, the herbaceous component of the Baikiaea woodland seems to a large extent adapted to herbivory and fire, as has also been argued in other studies done in sandy semi-arid ecosystems (Dougill and others 1998, 1999; Sullivan and Rohde 2002). Because of the high frequency of fires in semi-arid systems, fine fuels do not accumulate in large quantities and fire intensities are, therefore, relatively low and

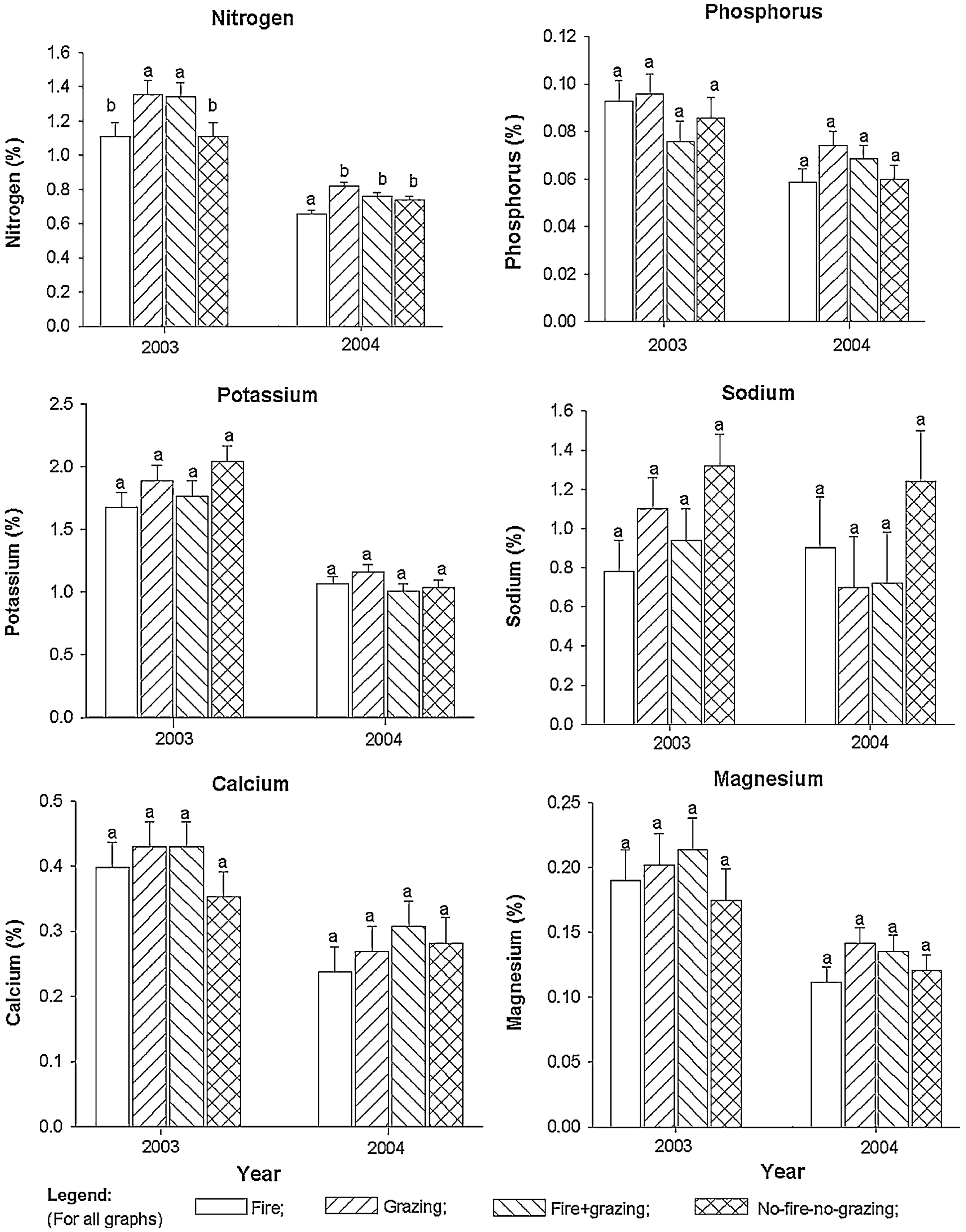


Figure 6. Mean (±SE) percent concentration of nutrient elements in live grass shoots from the fire-only, grazing-only, fire + grazing, and no-fire–no grazing treatments in 2003 and 2004. *Different lower case letters* denote significant differences between treatments within years.

consequently their impact, particularly on the herbaceous vegetation and soils is also low. It may be argued that the lack of vegetation and soil response to fire and herbivory could be a result of the short duration of the study. We do indeed acknowledge that more long-term experiments could modify our findings. However, the many inter-annual differences we did find in this study show that herbaceous vegetation does respond rapidly to changes in rainfall.

It is widely acknowledged that rainfall and soils are the primary determinants of savanna vegetation (Sankaran and others 2005), with rainfall particularly important in semi arid and arid regions (Oba and others Oba and others 2000; Fynn and O'Connor 2000; Sullivan and Rohde 2002; Sankaran and others 2005). Fires and herbivory are mainly modifiers or secondary determinants (Skarpe 1992; Fynn and O'Connor 2000; Sankaran and others 2005). Our study shows that, whereas fire and herbivory did not cause considerable change to the savanna vegetation over 2 years, variations in rainfall had a significant influence. The high amount of rainfall in 2004 as compared to 2003 probably contributed to the higher plant biomass, species diversity (see also Oba and others 2000), and evenness observed in 2004. Species richness was, however, lower in 2004 in spite of the higher rainfall received in that year. Rainfall also affected the treatments in that vegetation

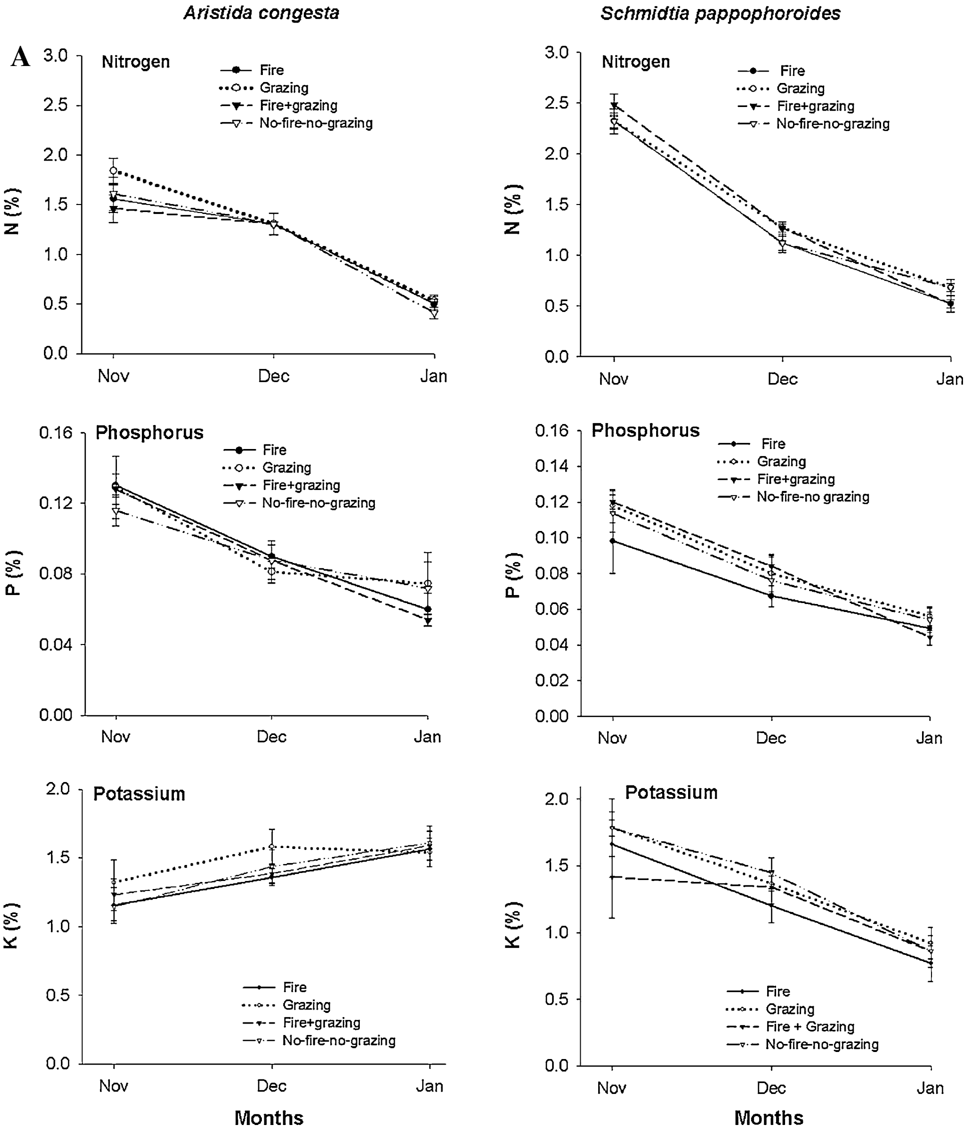


Figure 7. Mean (±SE) monthly percent concentration of **A** nitrogen, phosphorus, potassium, and **B** calcium, magnesium, and sodium in green shoot tissues of *Aristida congesta* and *Schmidtia pappophoroides* grasses in relation to fire-only, grazing-only, fire + grazing, and no-fire–no grazing (none) treatments. Fire was applied in October.

cover was different between treatments in the high rainfall year. The vegetation cover was reduced by burning but increased under grazing and in the no-fire–no-grazing treatment. Grass biomass was higher and forb biomass lower when rainfall was high, suggesting that grass suppressed forbs in years of high rainfall.

This study is not the only study that has found limited effects of fire on nutrient levels in southern African savanna systems. Frequent fires caused no significant changes to soil N mineralization, total N, and organic carbon at depths ranging from 0 to 60 cm over a 50-year period in Kruger National Park (Coetsee and others 2010; Holdo and others 2011). The lack of difference in soil organic carbon following fire was attributed to the recalcitrance of the carbon pools, which was suggested to be reinforced by fire (Holdo and others 2011).

The fuel load, a reflection of fire intensity, was within the normal ranges experienced in this particular area and in similar semi-arid systems in the region. The natural grass fuel load in Chobe National Parks commonly ranges between 2000 and 9930 kg ha^{-1} (Smith and others 2005). In our study, the total herbaceous fuel load prior to burning in 2002 was 2420 ± 280 kg ha^{-1} (mean ± SE). In 2003, 1 year after the application of the first year treatment the fuel load was 1710 ± 100 and 1940 ± 100 kg ha^{-1} (mean ± SE) for fire-alone and fire + grazing treatments, respectively. Hence, the fuel load in this study was comparable, though on the lower side, to the fuel load previously recorded in Chobe National Park (Smith and others 2005). A fuel load of about 2500 kg ha^{-1} commonly yields a fire intensity of 2000 kW m^{-1} (Trollope and others 2002).

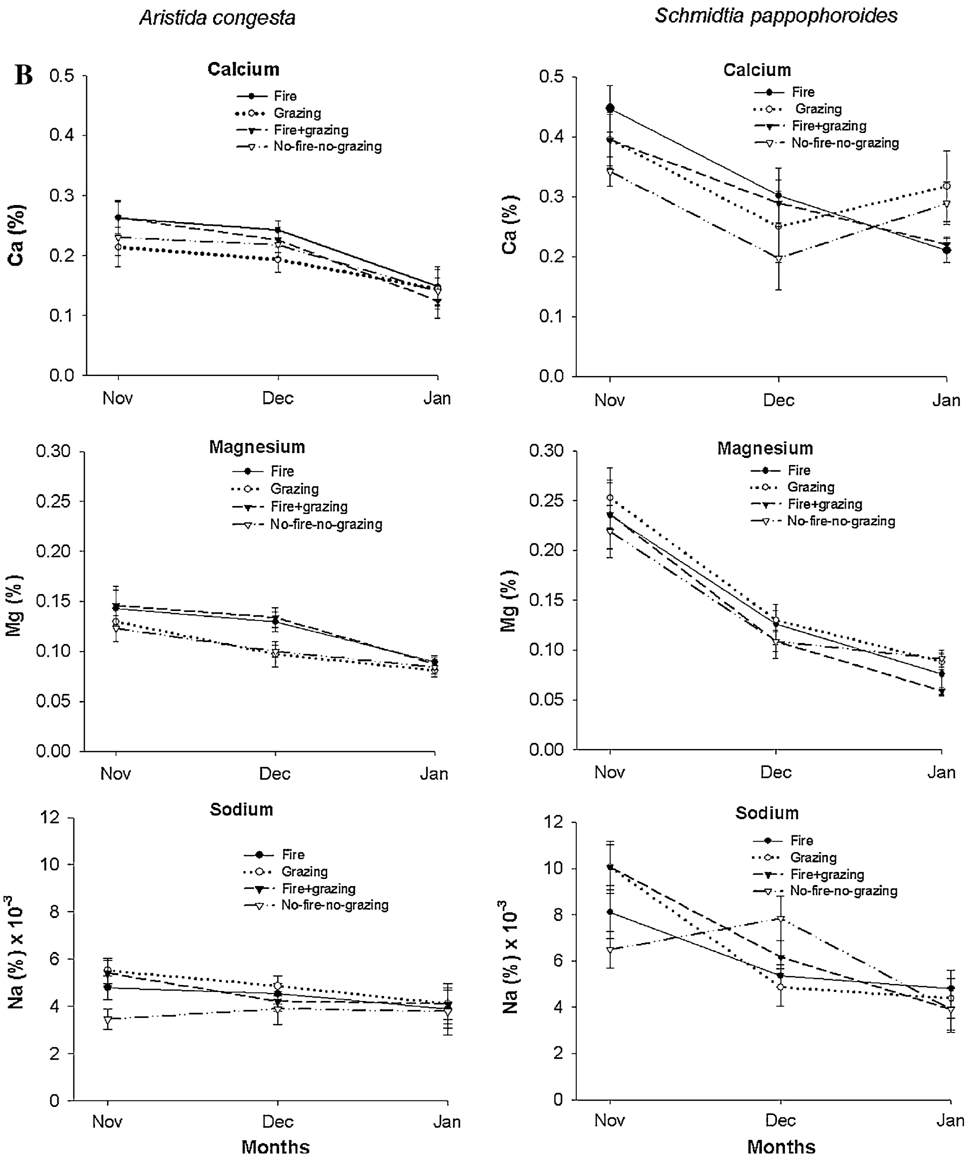


Figure 7. continued

However, the overall fire intensity in this study might have been lower than expected particularly when determined from the grass fuel load.

Similar to fire, grazing in semi-arid grassy regions often does not affect grasses adversely, particularly at the population and community level (Trollope and others 2002; Milchunas and others 1989). Although grazing intensity was not measured during this study, the number and spoors (footprints, dung and urine deposits) of elephant, buffalo, sable antelope, and kudu sighted in the area during the dry and wet seasons revealed that unfenced plots were grazed or trampled. About 3000 buffalo are estimated to use the study area during the wet season, as well as over 80,000 elephant that graze the area during the wet and the dry seasons (Taolo 2003; Skarpe and others 2004). Herds of over 15 sable antelope are common in the area. However, grazing is considered to be light during the wet season as wildlife grazers are widely distributed at this time of the year. Trampling is often heavy in the experimental area during the dry season as large herds of ungulates traverse the area to reach and congest along the Chobe River which provides a permanent supply of surface water. The dominance of perennial grass species in the experimental area further suggests that grazing was generally low. Normally, light grazing promotes growth and abundance of perennial grasses in areas receiving high rainfall (Fynn and O'Connor 2000), such as in the Chobe ecosystem. Had intense grazing occurred, it would have removed much of the perennial grasses and promoted an increase in growth of annual grasses and forbs.

Soil and Plant Chemistry

Soil chemistry showed no response to fire and grazing. Similar results have been found in previous studies of effects of grazing (Dougill and others 1998; Dougill and Thomas 2004), and of 2-year (Brockway and others 2002) and 7-year annual fires (Tongway and Hodgkinson 1992). Although there was no change in soil total N, available soil N may have changed in the upper layer of the soil. Usually when there is a change in soil N due to either fire or grazing, it occurs immediately after fire, within 0–5-cm soil depth and in the available forms of N (NH_4^+ and NO_3^-)(Ruess and McNaughton 1987; DeBano and others 1998; Dougill and others 1998; Wan and others 2001). Volatilization of N from plant matter normally occurs during combustion (Wan and others 2001), and this may have led to no transfer of N into the soil. Normally, soil total N does not change due to fire even in long-term studies (Coetsee and others 2010).

Grazing alone, and grazing and fire combined resulted in a significantly higher concentration of plant N, hence partially supporting theories that grazing stimulates an increase in plant nutrient concentrations (Singer and Schoenecker 2003) and burning decreases plant nitrogen (Hobbs and others 1991; Lavoie and others 2010). In our study, the fire-alone treatment had a lower concentration of N in grass shoots. Some studies have found that although fire can increase nutrient concentrations in plant tissues (Brockway and others 2002), the increase is not due to the soil nutrient status, but to the leaf–stem ratio and tissue rejuvenation (Daubenmire 1968; Van de Vijver and others 1999).

The nutrient concentrations of the individual grass species showed no response to fire or grazing. Van de Vijver and others (1999) have observed that although nutrient concentrations were higher in plant tissues from burned plots compared to those from unburned plots, the differences did not last for 3 months, and were not due to ash generated by fire as indicated by their ash-exclusion treatments.

In conclusion, areas subjected to fire and grazing have a distinctly different vegetation composition from that of no-fire–no-grazing, even over a 2-year period, indicating a rapid response to these treatments. Beta diversity (within treatment heterogeneity) was higher on the no-fire–no-grazing treatment compared to the fire-alone and grazing-alone treatments, indicating that herbivores and fire increases homogeneity at the landscape scale. Our results support Milchunas and others (1988) in that exclusion of herbivores, and in our case also fire, can be viewed as the disturbance factor in ecosystems that have co-evolved with large grazing and browsing herbivores as well as fire. Species diversity and concentrations of key soil and plant nutrients are maintained under fire and grazing. Thus, any changes in plant composition are unlikely to adversely affect the overall functioning of the dystrophic Kalahari sand system.

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