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Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa

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Abstract

Aims:
The long-term effects of changing fire regimes on the herbaceous component of savannas are poorly understood but essential for understanding savanna dynamics. We present results from one of the longest running (>44 years) fire experiments in savannas, the experimental burn plots (EBPs), which is located in the Kruger National Park (South Africa) and encompasses four major savanna vegetation types that span broad spatial gradients of rainfall (450–700 mm) and soil fertility.

Methods:
Herbaceous vegetation was sampled twice in the EBPs using a modified step-point method, once prior to initiation of the experiment (1954) and again after 44–47 years. Different combinations of three fire frequency (1-, 2- and 3-year return intervals) and five season (before the first spring rains, after the first spring rains, mid-summer, late summer and autumn) treatments, as well as a fire exclusion treatment, were applied at the plot level (~7 ha each), with each treatment (n = 12 total) replicated four times at each of the four sites (n = 192 plots total). The effects of long-term alterations to the fire regime on grass community structure and composition were analyzed separately for each site.

Important Findings:
Over the 44+ years duration of the experiment, fires were consistently more intense on sites with higher mean annual rainfall (>570 mm), whereas fires were not as intense or consistent for sites with lower and more variable rainfall (<510 mm) and potentially higher herbivory due to greater soil fertility. Because the plots were open to grazing, the impacts of herbivory along with more variable rainfall regimes likely minimized the effects of fire for the more arid sites. As a consequence, fire effects on grass community structure and composition were most marked for the higher rainfall sites and generally not significant for the more arid sites. For the high-rainfall sites, frequent dry season fires (1- to 3-year return intervals) resulted in high grass richness, evenness and diversity, whereas fire exclusion and growing season fires had the lowest of these measures and diverged the most in composition as the result of increased abundance of a few key grasses. Overall, the long-term cumulative impacts of altered fire regimes varied across broad climatic and fertility gradients, with fire effects on the grass community decreasing in importance and herbivory and climatic variability likely having a greater influence on community structure and composition with increasing aridity and soil fertility.

Keywords: climate • fire intensity • grass • herbivory • soil fertility

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INTRODUCTION

Savannas constitute one of the largest biomes of the world, covering ~20% of the terrestrial land surface. Savannas are unique, in that two contrasting life forms codominate, with herbaceous species (mainly grasses) forming a continuous matrix in which woody plants occur at varying densities. The dynamic coexistence of these two life forms has long interested ecologists (Belsky 1990; Huntley and Walker 1982; Sarmiento 1984), and a wealth of studies suggest that the balance between herbaceous and woody components of the community is determined by multiple factors, including climatic variability, herbivory, fire and soil fertility, interacting in complex ways (Bond and van Wilgen 1996; Bond *et al.* 2003; Sankaran *et al.* 2008; Scholes and Archer 1997). Fire is often recognized as the primary modifier of structure, function and dynamics of savannas (Bond and Parr 2010; Bond *et al.* 2003; Scholes and Walker 1993). The main effects of fire are the large-scale and episodic removal of aboveground biomass or when severe enough the death of individual plants (mainly woody species). Thus, depending on their timing and intensity, fires can range from promoting diversity and productivity to causing a decline in each and can have impacts similar to grazing or drought (Bond and Keeley 2005; Bond and van Wilgen 1996). As a consequence, the role of fires in savannas remains unclear (Bond and Keeley 2005; Bond *et al.* 2003; Scholes and Walker 1993), specifically how changes in the fire regime (season, frequency and intensity, Gill 1975) impact the balance between the herbaceous and the woody components of the community (Bond and Keeley 2005; Higgins *et al.* 2000) and compare to and interact with other important drivers, such as herbivory or climate (van Langevelde *et al.* 2003).

The herbaceous component of tropical savannas is dominated by a diverse array C_4 grasses, which contribute most to herbaceous productivity (Buis *et al.* 2009) and provide forage for ungulates and livestock. Alterations in fire regime (frequency and/or season) have been shown to have variable effects of grass diversity and composition (Belsky 1992; Everson and Tainton 1984; Fynn *et al.* 2004, 2005; Jacobs and Schloeder 2002), with grass diversity often declining in the absence of disturbance (Belsky 1992; Fynn *et al.* 2004; Jacobs and Schloeder 2002) and grass composition responding strongly to fire frequency (Furley *et al.* 2008; Fynn *et al.* 2005). While much of the research on fires in savanna ecosystems has focused on how short-term changes in fire frequency and intensity impact woody vegetation (van Wilgen *et al.* 2003; but see; Higgins *et al.* 2007; Smit *et al.* 2010), those examining impacts of multiple aspects of fire regimes on herbaceous (grass) diversity and composition are rarer, particularly those examining long-term (>10 years) alterations in fire regimes (Furley *et al.* 2008; Savadogo *et al.* 2008). This is an important gap in knowledge, given that savanna ecosystem models (e.g. Higgins *et al.* 2000; van Langevelde *et al.* 2003) suggest that changes in the grass community (composition and productivity) can impact the fire regime, patterns of herbivory and ultimately coexistence of herbaceous and woody species.

The frequency, season and intensity of the fire regime in savannas are determined by the amount of grass biomass (which is in turn related to the previous season's rainfall, van Wilgen *et al.* 2004), the moisture content of the grass fuel and weather at the time of the fire (Govender *et al.* 2006; Higgins *et al.* 2000). Therefore, alterations in grass composition can have important implications for fire regimes. Fire intensity varies in space and time as a result of variable fuel loads and differences in the season and return intervals of fires (Higgins *et al.* 2000; van Wilgen *et al.* 2003). However, with contemporary management practices, savanna fire regimes can be altered within limits (Archibald *et al.* 2009). For example, different approaches to fire management in semi-arid savannas had little impact on fire return intervals, although management did affect the season of fire and thus fire intensity (Govender *et al.* 2006; van Wilgen *et al.* 2004). Although mesic savannas may have burnt every 1–3 years historically (Smith 1992), it is unlikely that semi-arid savannas, which comprise the bulk of savannas in southern Africa, burnt this consistently or frequently (van Wilgen *et al.* 2000).

Here, we present results from a unique experiment located in the Kruger National Park (KNP), South Africa, where both the frequency and the season of fires were manipulated simultaneously for >44 years. Our goal was to assess the impacts of long-term changes in the fire regime on the understudied herbaceous plant component of savanna ecosystems across a broad climatic (~450 to 700 mm of rainfall) gradient in the park. Our study complements several others that have used the same experiment to examine the responses of the woody vegetation of these savannas to different fire regimes (Enslin *et al.* 2000; Higgins *et al.* 2007; Jacobs and Biggs 2001; Kennedy and Potgieter 2003; O'Regan 2005; Shackleton and Scholes 2000; Smit *et al.* 2010). These studies have revealed that fire frequency and season significantly impacted the size structure and standing aboveground biomass of woody plants, with the greatest reduction in woody plant size and biomass observed with the most frequent and intense fire regimes (annual return interval and dormant season burns; e.g. Higgins *et al.* 2007; Smit *et al.* 2010). Although fire exclusion had the largest overall effects on size structure and biomass of the woody plant community, the effects were most marked in areas with higher rainfall (Higgins *et al.* 2007; Smit *et al.* 2010).

Based on the responses of the woody component, we hypothesized that the long-term exclusion of fire would have the greatest impact on the herbaceous community. Specifically, we expected that grass composition would shift to more fire- or disturbance (grazing)-intolerant species and that grass diversity would decline due to dominance by a few grass species. We also hypothesized that herbaceous community structure (grass diversity and composition) of plots experiencing more frequent and/or intense fires would differ from plots with less frequent and/or intense fires, which should be more

similar to the fire exclusion treatments. We expected that these impacts would be most pronounced for the savannas in the southern portion of the park receiving the most rainfall, where fires are likely more frequent and intense, when compared to the savannas in the central and northern portions of the park, which have lower rainfall, are subjected to greater climatic variability and potentially more intense herbivory and as a result likely experience less frequent and/or intense fires (van Wilgen *et al.* 2000, 2003).

MATERIALS AND METHODS

Site description

The KNP is located in the Limpopo and Mpumalanga provinces of northeastern South Africa. The park is ~2.0 million ha in size with elevations ranging from 260 to 839 m above sea level. A distinct rainfall gradient occurs in the park; mean annual rainfall is lowest (~350 mm) in the north and highest (~750 mm) in the south. The vegetation of the park is semi-arid savanna, dominated by trees in the genera *Acacia*, *Combretum*, *Sclerocarya* and *Colophospermum*. The western half of the park is underlain by granites (relatively nutrient-poor), while the eastern half is underlain by basalts (relatively nutrient-rich).

Experimental design

The KNP's plot-based fire experiment—the Experimental Burn Plots (EBPs)—was initiated in 1954 to address a general lack of knowledge about the effects of fire (see Biggs *et al.* 2003 for details). The experiment was established at four sites that typify the major vegetation types and that encompass the broad precipitation gradient (precipitation amounts and variability) and the two major soil types (nutrient-rich basalts vs. nutrient-poor granites, Table 1) in the park. As a consequence, the four sites differ considerably in productivity (Table 1, Kennedy *et al.* 2003), abundance of woody plants (Higgins *et al.* 2007) and the levels of herbivory (Mills and Fey 2005; van Wyk 1971).

The experiment is a semi-randomized complete block design with different combinations of three fire frequency (1-, 2- and 3-year return intervals) and five season [before the first spring rains (August), after the first spring rains (October), mid-summer (December), late summer (February) and autumn (April)] treatments, as well as a control (fire exclusion) treatment. The 2- and 3-year fire frequency treatments are fully crossed with the fire season treatments, whereas the 1-year treatment is burnt only in August. Thus, there are a total of 12 fire frequency/season treatments applied at the plot (~7 ha each) level, and for each site, there are four blocks of 12 plots ($n = 4$ replicates per fire frequency/season treatment combination). Importantly, herbivores have open access to all the experimental plots, and thus, the fire frequency and season treatments cannot be assessed separately from the potential impacts of herbivores.

Although considerable effort was made to adhere to the fire treatments over the 44–47 year duration of the experiment, not every plot was burnt according to schedule—mainly due to weather, insufficient fuel or unintentional burning (Biggs *et al.* 2003). Therefore, relative fire frequency for each of the fire frequency treatments was lower than target levels for all sites and deviated more so for those plots with lower rainfall (Knobthorn–Marula, Mopane; see van Wilgen *et al.* 2007 for details). Fire intensity was estimated for experimental burns conducted only between 1982 and 2003 (Govender *et al.* 2006). The intensity of fires (Byram 1959) was calculated as $I = Hwr$, where I is the fireline intensity (kW m^{-1}), H is the heat yield of fuels (kJ kg^{-1}), w is the mass of fuel consumed (kg m^{-2}) and r is the rate of fire spread (m s^{-1}). Cumulative

Table 1: salient features of study sites located in four major vegetation types of the Kruger National Park, South Africa (Fig. 1)

					Precipitation		Standing crop	
Site	Study period	Dominant tree species	Dominant grass species	Soil type	Annual mean (mm)	CV (%)	Mean (g m^{-2})	CV (%)
Sourveld	1954–2001	*Terminalia sericea* and *Dichrostachys cinerea*	*Hyperthelia dissoluta*, *Elionurus argenteus* and *Panicum maximum*	Granite	705.5	39.4	411.7	34.3
Combretum	1954–2001	*Combretum collinum* and *C. zeyheri*	*Digitaria eriantha*, *Setaria sphacelata* and *P. maximum*	Granite	572.3	35.4	347.1	47.6
Knobthorn–Marula	1956–1998	*Acacia nigrescens* and *Sclerocarya birrea*	*Bothriochloa radicans*, *P. coloratum* and *D. eriantha*	Basalt	507.9	39.0	316.6	59.3
Mopane	1957–2000	*Colophospermum mopane*	*Enneapogon cenchroides*, *Urochloa mosambicensis* and *B. radicans*	Basalt	451.9	55.0	300.0	53.4

Mean annual precipitation and variability (%CV) were estimated using data collected between 1982 and 2003 from nearby weather stations. Average standing crop (total aboveground biomass of herbaceous material) and variability (%CV) were estimated from 27 monitoring points (within 5 km of the sites) between 1989 and 1999 (see Kennedy *et al.* 2003 for details). Nomenclature follows van Wyk and van Wyk (1997) and van Oudtshoorn (1999).

mean fire intensity of the treatments was estimated by multiplying the mean intensity of fires on a plot (where available) by the total number of fires that took place on that plot (using data from Biggs *et al.* 2003), divided by the period over which those fires occurred and averaged over all plots within the relevant treatment.

Vegetation sampling

Although the fire treatments were maintained for the duration of the experiment, herbaceous vegetation was sampled only twice, once prior to initiation of the experiment (1954) and again in 1998 (Knobthorn–Marula), 2000 (Mopane) and 2001 (Sourveld and Combretum). For both surveys, grasses were identified to species and other graminoid and forb species were combined; at the Mopane site, only grasses were sampled. Nomenclature follows van Wyk and van Wyk (1997) and van Oudtshoorn (1999).

For the pre-treatment 1954 survey, herbaceous vegetation was sampled using the point quadrat technique. A Levy Bridge with 10 metal rods arranged 5 cm apart was placed at ~6-m intervals along transects diagonally located in each plot for a total of 500 points per diagonal (1000 points per plot). The number of hits of living rooted plants was recorded for each herbaceous species. For the post-treatment surveys, herbaceous vegetation was sampled using a step-point technique. In each plot, 100 points placed ~2 m apart were sampled along two diagonal transects (~300 m) for a total of 200 points. Data were expressed as the percentage frequency of each species (calculated as 100 p/t, where p is the number of points encountered for a species and t the total number of points sampled).

Numerical methods and statistical analyses

Because sampling methods differed between the pre-treatment and the post-treatment surveys, the two surveys are not directly comparable, and therefore, we analyzed them separately. The 1954 plant species composition data were analyzed only to confirm that there were no differences in grass community structure and composition among the treatments prior to initiation of the experiment. Since no systematic differences were detected among the treatments for any of the sites (data not shown), these results are not presented. Treatment effects after 45+ years were assessed using the post-treatment surveys only by examining grass community structure and composition, as well as relative frequencies of key grass species. Non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) analyses (see below), which used community matrices that included all four sites, revealed that composition differed significantly and considerably between the sites (Fig. S1 in the online supplementary material; ANOSIM: $R = 0.743$, $P = 0.001$; see Table 1 for complete list of grass species). Thus, we examined each site separately in all subsequent analyses.

Changes in community structure were assessed using several community metrics (Magurran 2004). Richness (S), Shannon's diversity (H′), evenness (J′) and dominance (Berger–Parker index, D) were calculated for both the pre-treatment and the post-treatment communities using relative frequencies of grasses since these were the only ones identified to species. Because the fire frequency and fire season treatments were not fully crossed, we conducted separate unbalanced randomized block analysis of variance (ANOVA) analyses for the effects of the fire frequency and fire season treatments on herbaceous plant community structure. Treatment mean comparisons were made using least square means tests with multiple comparison adjustments when treatment effects were significant. ANOVA analyses were performed using SAS statistical software (GLM procedure, SAS version 9.2; SAS Institute, Inc.), with significance levels set at $P \leqslant 0.05$.

We examined changes in community composition with the different fire frequency and season treatments in three ways: (i) NMDS analysis, (ii) ANOSIM and (iii) similarity percentage analysis (SIMPER). All these were performed in Primer (v. 5.2.4, Primer-E Ltd.). Community matrices used for these analyses were constructed for the post-treatment data. These consisted of all species with relative frequencies (described above) >5%. For each site, the matrix consisted of all pairwise comparisons among plots across the four blocks based on a quantitative similarity index, Euclidean distance. We used NMDS to construct a two-dimensional ordination that best represented relationships among samples in the community similarity matrix. In NMDS ordination space, the relative distance between points reflects the degree of dissimilarity of species composition among plots.

Differences in community composition between the fire frequency and season treatments were each subsequently examined using ANOSIM, which is similar to multivariate analysis of variance, but differs, in that it is non-parametric and tests for differences among *a priori*-defined treatments in ordinate space. The R-statistic generated by ANOSIM is a relative measure of separation among the treatments, with a 0 indicating no differences among treatments and a 1 indicating all samples in a treatment are more similar to one another than any sample belonging to another treatment. When ANOSIM revealed significant differences between treatments, we used SIMPER to identify those grass species contributing most to the differences observed. We then examined how relative frequency of these grass species differed between the fire frequency and season treatments with unbalanced randomized block ANOVAs. As with the community structure analyses, tests for differences among treatment means were made using least square means tests when main effects were significant.

RESULTS

Fire intensities

Across the sites, cumulative mean fire intensities were highest with annual burning and for winter and early spring (August and October) burns, intermediate with 2- and 3-year fire frequencies and for April burns and lowest for summer (December and February) burns (Fig. 1).

Herbaceous plant community responses

The average relative frequencies of grass species found on the plots across the four sites prior to initiation of the experiment and after 44–47 years of fire manipulation are summarized in Table S1 (in the online supplementary material). Overall, the Sourveld and Combretum sites had over double the number of grass species (46 and 48 species, respectively) than the Knobthorn–Marula (24 species) and Mopane (14 species) sites.

Sourveld site

The fire treatments had significant effects on this vegetation type, with the largest effects apparent between frequent fires in the dormant (dry) season on the one hand and fires in the wet season or exclusion of fire on the other. Grass community structure, as characterized by the evenness, diversity or dominance of grass species, differed significantly among the fire frequency and season treatments after 47 years of manipulation (Tables 2 and 3). Grass diversity was consistently lowest for plots where fire was excluded and for plots burnt in mid- to late summer when the grass sward was greenest (December and February; Fig. 2). Similar patterns were observed for grass richness and evenness (data not shown). Grass richness, evenness and diversity were highest for plots burnt annually and between autumn and early spring (start

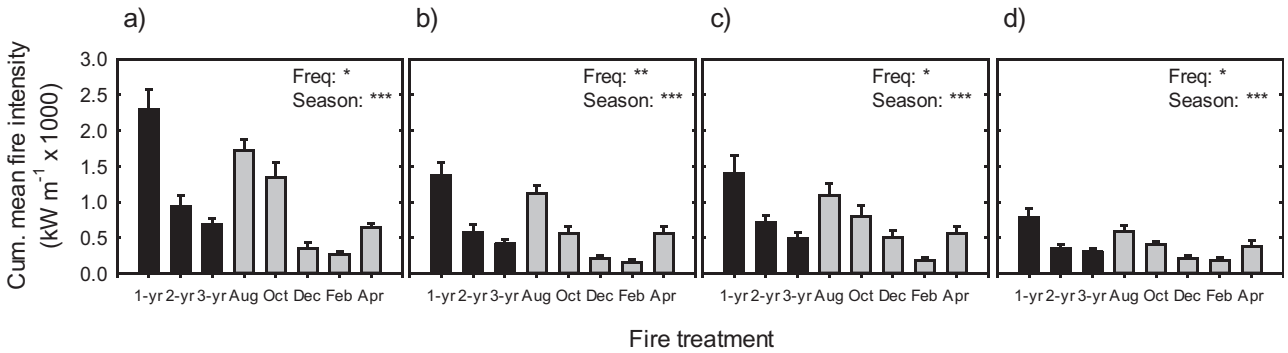

Figure 1: effects of the fire frequency and season treatments on cumulative mean fire intensity (mean intensity of all fires on a plot × number of fires/period over which those fires took place, averaged over all plots within the relevant treatment) at four sites in the Kruger National Park, South Africa. Sites are (**a**) Sourveld, (**b**) Combretum, (**c**) Knobthorn–Marula and (**d**) Mopane. UB = fire excluded for 44–47 years. Significance levels are denoted by $*P \leqslant 0.05$, $**P \leqslant 0.01$, $***P \leqslant 0.001$ for the cumulative mean fire intensities. Different letters indicate significant differences between the fire frequency or season treatments.

Table 2: analysis of variance of the long-term effects of fire frequency treatments on grass richness (S), evenness (J′), diversity (H′) and dominance (D) at four sites in the Kruger National Park, South Africa

			Richness (S)			Evenness (J′)			Diversity (H′)			Dominance (D)		
Site	Source	df	*SS*	*F*	*P*	SS	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*
Sourveld	Model	15	142.9	0.93	NS	0.23	2.30	*	2.81	2.00	*	4654.5	3.60	***
	Frequency	3	74.0	5.84	NS	0.86	5.24	*	1.16	6.39	*	2117.2	7.41	**
	Block	3	6.05	0.32	NS	0.06	3.23	NS	0.54	2.49	NS	580.6	2.10	NS
	Frequency × block	9	38.0	0.41	NS	0.05	0.80	NS	0.54	0.64	NS	854.6	1.10	NS
Combretum	Model	15	102.1	0.72	NS	0.17	0.85	NS	1.67	0.90	NS	4277.7	1.93	*
	Frequency	3	21.2	1.03	NS	0.10	5.46	NS	0.74	3.71	NS	3562.3	17.81	***
	Block	3	25.5	1.10	NS	0.03	1.34	NS	0.44	1.68	NS	151.5	0.53	NS
	Frequency × block	9	61.5	0.72	NS	0.05	0.44	NS	0.60	0.54	NS	600.0	0.45	NS
Knobthorn–Marula	Model	15	110.1	3.07	**	0.09	1.18	NS	0.82	1.43	NS	2312.4	1.18	NS
	Frequency	3	3.42	0.25	NS	0.09	0.42	NS	0.01	0.68	NS	359.6	0.71	NS
	Block	3	40.1	3.75	*	0.12	0.67	NS	0.03	2.54	NS	477.9	1.03	NS
	Frequency × block	9	37.7	1.76	NS	0.02	1.81	NS	0.04	0.85	NS	1509.7	1.20	NS
Mopane	Model	15	137.7	7.55	***	0.41	2.57	*	3.92	3.64	***	6117.5	3.96	*
	Frequency	3	34.2	6.03	*	0.04	0.61	NS	0.46	1.71	NS	569.3	1.40	NS
	Block	3	56.9	10.43	***	0.11	2.71	NS	1.63	6.54	**	2609.2	5.73	**
	Frequency × block	9	17.0	0.97	NS	0.14	1.24	NS	0.80	1.24	NS	1224.2	0.75	NS

Significance levels are denoted by $*P \leqslant 0.10$, $**P \leqslant 0.01$, $***P \leqslant 0.001$.

Table 3: analysis of variance of the long-term effects of fire season treatments on grass richness (S), evenness (J′), diversity (H′) and dominance (D) at four sites in the Kruger National Park, South Africa

			Richness (S)			Evenness (J′)			Diversity (H′)			Dominance (D)		
Site	Source	df	*SS*	*F*	*P*	SS	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*
Sourveld	Model	15	254.8	1.81	NS	0.21	2.30	**	3.24	3.43	**	4031.1	5.57	***
	Season	4	125.0	3.90	NS	0.06	3.17	NS	1.45	5.72	**	950.2	1.97	NS
	Block	3	46.5	1.93	NS	0.10	6.85	**	1.21	6.39	**	1979.0	5.55	*
	Season × block	9	96.2	1.08	NS	0.06	1.01	NS	0.76	1.27	NS	1443.9	3.16	**
Combretum	Model	15	184.7	1.10	NS	0.40	5.14	***	3.72	3.67	**	4445.4	3.33	**
	Season	4	58.3	1.61	NS	0.33	19.39	***	2.78	12.79	***	3763.7	20.28	***
	Block	3	17.7	0.65	NS	0.02	1.53	NS	0.28	1.74	NS	138.8	0.99	NS
	Season × block	9	108.7	1.03	NS	0.05	1.04	NS	0.65	1.02	NS	556.9	0.66	NS
Knobthorn–Marula	Model	15	123.7	3.39	*	0.16	2.51	NS	1.24	2.56	*	3728.5	2.22	*
	Season	4	9.37	0.55	NS	0.04	1.98	NS	0.20	0.68	NS	819.8	1.05	NS
	Block	3	65.8	5.25	*	0.04	2.32	NS	0.17	0.79	NS	494.1	0.85	NS
	Season × block	9	50.6	2.19	*	0.07	1.66	NS	0.87	2.86	*	2342.1	2.21	*
Mopane	Model	15	96.2	1.86	NS	0.10	1.54	NS	0.40	1.54	NS	6202.9	1.76	NS
	Season	4	27.9	7.35	NS	0.07	3.11	NS	0.60	7.10	NS	9.33	2.53	NS
	Block	3	55.7	18.93	NS	0.26	13.99	NS	2.54	37.83	NS	4165.8	14.77	NS
	Season × block	9	11.4	0.35	NS	0.07	0.43	NS	0.25	0.25	NS	1108.3	0.50	NS

Significance levels are denoted by $*P \leqslant 0.10$, $**P \leqslant 0.01$, $***P \leqslant 0.001$.

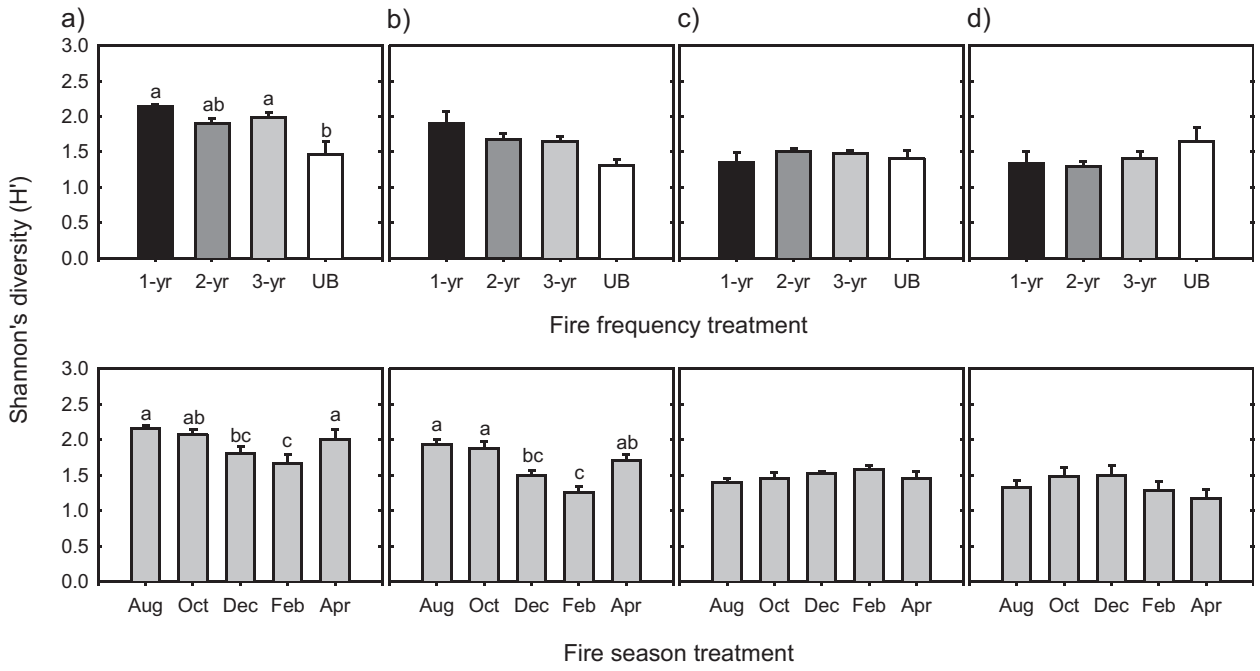

Figure 2: long-term effects of fire frequency (top; UB = fire excluded for between 44 and 47 years) and season (bottom) on grass diversity (Shannon's H′) in the (**a**) Sourveld, (**b**) Combretum, (**c**) Knobthorn–Marula and (**d**) Mopane sites in Kruger National Park, South Africa. UB = fire excluded for 44–47 years. Similar patterns were observed for grass richness and evenness (data not shown). Bars are means (±1 SE), and different letters indicate significant differences among the treatments (see Tables 2 and 3).

and end of the dormant season, April and October), irrespective of how often they burnt (see Fig. 2 for diversity; other data not shown). Grass dominance was highest when fire was excluded or when fires occurred in the late summer but was similar among the remaining treatments (data not shown).

As with community structure, fire frequency and season changed grass species composition significantly (Table 4). The plots left unburned diverged most in grass composition from others. The grass composition of burnt plots was significantly different from plots where fire was excluded but not from each other (Table 4; Fig. S2 in the online supplementary material). In terms of fire season, significant differences in grass composition were found between the winter (August) and the summer (December and February) burn plots, as well as between plots where fire was excluded and those burned either in winter or in early spring (August and October) or autumn (April).

The SIMPER analyses revealed that differences in composition of grasses between the fire frequency and season treatments were mainly caused by divergent responses of a few key grass species. Differences in composition between the fire exclusion plots and those burnt at different frequencies or during different seasons were driven primarily by increased relative frequency of *Panicum maximum* as fire frequency and intensity decreased (Fig. 3a, Table 5a; Table S1 in the online supplementary material), with maximum abundance of *P. maximum* observed in the fire exclusion plots. Relative frequency of *Heteropogon contortus* was highest with frequent and intense (dormant season) fires, whereas it was greatest for *Hyperthelia dissoluta* on plots experiencing intermediate fire frequencies and intensities (Fig. 3a, Table 5a; Table S1 in the online supplementary material).

Combretum site

Fire season resulted in a significant difference in grass community structure at the 'Combretum' site, but fire frequency only had an effect on grass dominance (Tables 2 and 3). Similar to the Sourveld site, grass dominance was highest when fire was excluded or when fires occurred during the summer (data not shown). In contrast, grass richness, evenness and diversity were lowest for plots where fire was excluded and for plots burnt during the summer growing season (December and February; see Fig. 2 for diversity; other data not shown). Grass richness, evenness and diversity were highest for plots burnt annually and between autumn and early spring (start and end of the dormant season, April and October), irrespective of how often they burnt (Fig. 2).

Table 4: ANOSIM of the long-term effects of fire frequency and season on herbaceous plant community composition at four sites in the Kruger National Park, South Africa

	Sourveld		Combretum		Knobthorn–Marula		Mopane	
	R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
Frequency	0.097	*	0.206	***	0.124	*	0.036	NS
1 year vs. 2 years	0.016	NS	0.375	**	0.044	NS	—	
1 year vs. 3 years	0.134	NS	0.704	***	−0.005	NS	—	
2 years vs. 3 years	−0.025	NS	−0.011	NS	0.005	NS	—	
1 year vs. UB	0.469	*	1.000	*	0.255	NS	—	
2 years vs. UB	0.349	*	0.257	*	0.509	**	—	
3 years vs. UB	0.426	**	0.412	***	0.524	**	—	
Season	0.15	**	0.385	***	0.180	**	−0.058	NS
August vs. October	0.038	NS	0.042	NS	0.163	NS	—	
August vs. December	0.176	*	0.319	**	0.252	*	—	
August vs. February	0.266	*	0.683	***	0.028	NS	—	
August vs. April	0.084	NS	0.114	NS	−0.060	NS	—	
February vs. October	0.149	NS	0.919	***	0.045	NS	—	
February vs. December	−0.002	NS	0.540	***	0.002	NS	—	
February vs. April	0.084	NS	0.511	***	0.083	NS	—	
April vs. October	0.103	NS	0.145	*	0.295	**	—	
April vs. December	0.062	NS	0.050	NS	0.039	**	—	
October vs. December	−0.011	NS	0.243	**	−0.033	NS	—	
August vs. UB	0.631	**	0.736	***	0.559	**	—	
October vs. UB	0.434	*	0.941	**	0.489	*	—	
December vs. UB	0.200	NS	0.737	**	0.473	*	—	
February vs. UB	0.136	NS	0.189	NS	0.461	*	—	
April vs. UB	0.397	*	0.634	**	0.564	**	—	

The *R*-statistic is a measure of the similarity of composition and reflects the degree of separation in composition between the experimental plots. The closer the *R*-statistic value is to 1, the greater the difference in composition. *P*-values are significant at the α-level of 0.05 using Bonferroni tests for each pairwise treatment comparison. Significance levels are denoted by $*P \leqslant 0.10$, $**P \leqslant 0.01$, $***P \leqslant 0.001$. UB = unburnt control treatment.

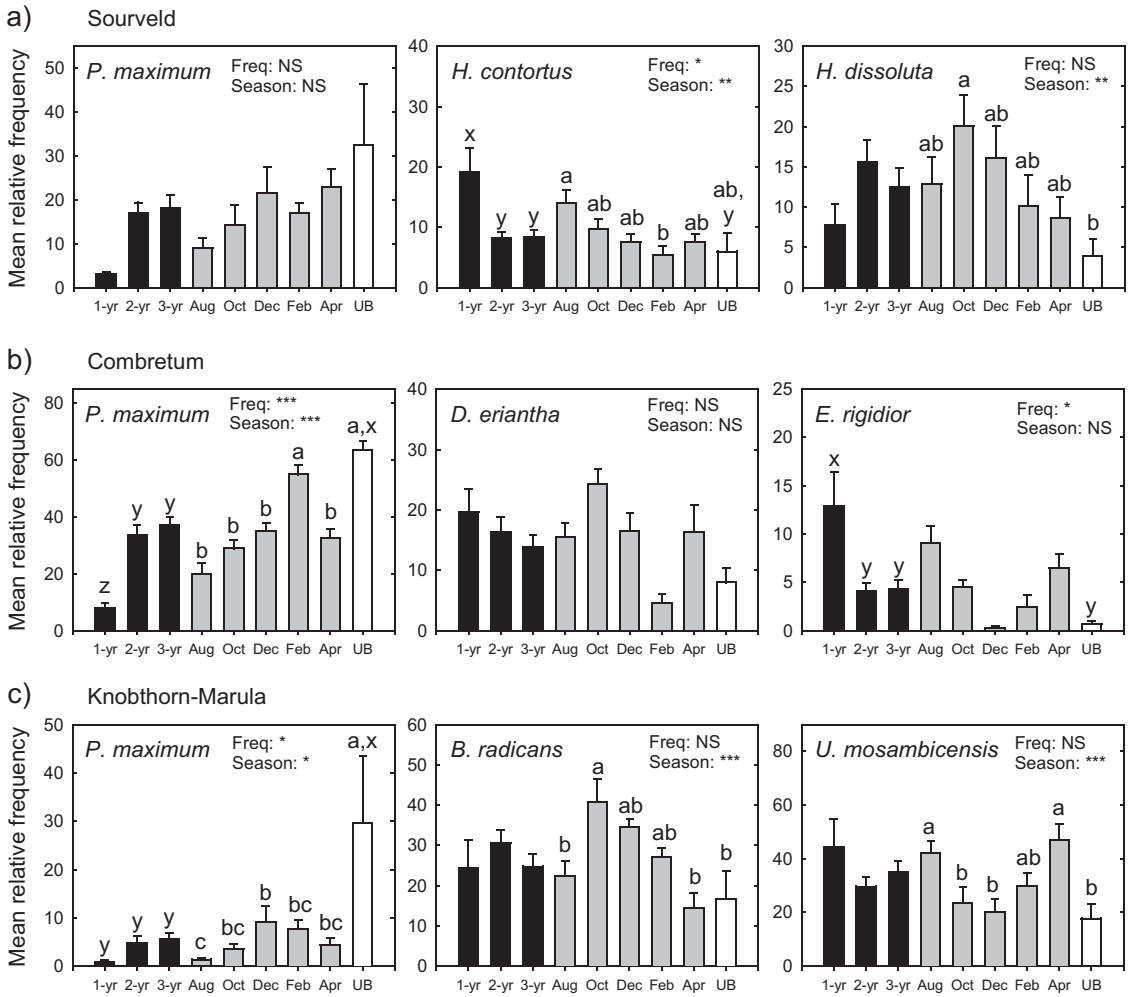

Figure 3: responses of key grass species to the fire frequency and season treatments in (**a**) Sourveld, (**b**) Combretum and (**c**) Knobthorn–Marula sites in the Kruger National Park, South Africa. UB = fire excluded 44–47 years. Data are not shown for the Mopane site because significant differences were not detected between the treatments. Bars are means (±1 SE), and different letters indicate significant differences among the fire frequency or season treatments. Significance levels are denoted by $*P \leqslant 0.10$, $**P \leqslant 0.01$, $***P \leqslant 0.001$.

Fire frequency and season treatments also significantly changed grass species composition (Table 4; Fig. S2 in the online supplementary material). As with the Sourveld site, plots left unburned for >44 years diverged most in composition (Table 4; Fig. S2 in the online supplementary material). Plots that were burnt at different frequencies differed in grass composition from those where fire was excluded, and the annual burn treatment plots diverged in grass composition from the 2- and 3-year treatments, which were similar in composition (Table 4, Fig. S2 in the online supplementary material). Grass composition was most similar between the least intense fire treatment (February) plots, and those where fire was excluded, and between plots burnt in the winter (August) and those burnt early or late in the growing season (October and April, Fig. S2 in the online supplementary material). The winter (August) burn plots differed most in grass composition from plots burnt in mid-summer or where fire was excluded.

The divergence in grass composition between the fire exclusion plots and those burnt at different frequencies, and between those burnt during summer vs. early or late in the growing season, was driven primarily by increased relative frequency of *P. maximum*, with highest abundance in plots where fire was excluded and secondarily by decreased relative frequency of *Digiteria eriantha* and *Eragrostis rigidior* (Fig. 3, Table 5b; Table S1 in the online supplementary material).

Knobthorn–Marula site

In contrast to the Sourveld and Combretum sites, grass community structure showed no significant differences among the fire frequency or season treatments for the Knobthorn–Marula site (Fig. 2, Tables 2 and 3). In terms of composition, the fire exclusion plots differed from 2- and 3-year burn frequency plots but not from those burnt annually (Table 4; Fig. S2 in the online supplementary material). The fire exclusion plots

Table 5: analysis of variance of the long-term effects of fire frequency and season treatments on mean relative frequency of key grass species in the (a) Sourveld, (b) Combretum and (c) Knobthorn–Marula sites in the Kruger National Park, South Africa

(a)		*Panicum maximum*			*Heteropogon contortus*			*Hyperthelia dissoluta*		
Source	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Model	15	5368.0	2.81	**	1110.2	4.17	**	3341.2	3.47	**
Frequency	3	1739.5	1.64	NS	466.3	6.67	*	581.3	2.99	*
Block	3	564.9	0.68	NS	380.8	5.94	**	486.7	2.51	*
Frequency × block	9	3188.5	2.78	*	209.6	1.31	NS	582.8	1.01	NS
Model	23	6149.7	1.94	*	1127.2	2.14	*	3813.6	2.51	*
Season	5	2212.0	1.90	NS	483.1	6.91	**	1025.4	5.03	**
Block	3	501.6	0.74	NS	410.0	9.27	**	1822.8	14.17	***
Season × block	15	3497.8	1.70	NS	209.8	0.61	NS	611.2	0.62	NS
b)		*Panicum maximum*			*Digiteria eriantha*			*Eragrostis rigidior*		
Source	df	SS	*F*	*P*	SS	*F*	*P*	*SS*	*F*	*P*
Model	15	7103.9	2.31	*	1517.3	1.03	NS	611.5	2.49	*
Frequency	3	6365.2	28.87	***	340.1	2.33	NS	339.8	5.19	*
Block	3	22.2	0.06	NS	265.1	1.34	NS	112.7	1.88	NS
Frequency × block	9	661.3	0.36	NS	438.3	0.49	NS	196.4	1.33	NS
Model	23	10491.9	3.45	**	3830.2	4.76	**	668.2	1.49	NS
Season	5	9518.6	31.87	***	1786.7	4.11	*	516.4	20.3	***
Block	3	64.8	0.33	NS	587.3	2.37	NS	51.0	2.69	*
Season × block	15	896.0	0.45	NS	1304.6	2.48	*	76.5	0.26	NS
c)		*Panicum maximum*			*Bothriochloa radicans*			*Urochloa mosambicensis*		
Source	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Model	15	4885.8	9.87	***	4177.8	1.65	NS	9660.0	3.72	**
Frequency	3	2322.9	3.03	*	806.2	1.03	NS	1694.7	1.38	NS
Block	3	887.2	1.66	NS	209.8	0.31	NS	2598.9	2.66	*
Frequency × block	9	2297.8	7.73	***	2341.1	1.55	NS	3672.3	2.36	*
Model	23	5429.3	11.04	***	6384.8	2.10	*		2.53	*
Season	5	2616.6	3.08	*	3928.1	8.26	**	10761.2	18.20	***
Block	3	653.1	1.38	NS	732.9	2.49	*	5552.7	18.69	***
Season × block	15	2547.6	7.95	***	1426.1	0.72	NS	4010.3	0.33	NS

Significance levels are denoted by $*P \leqslant 0.10$, $**P \leqslant 0.01$, $***P \leqslant 0.001$.

also differed most in grass composition from those burned at different seasons, whereas those burnt in autumn (April) differed in composition from those burnt in early spring (October) or summer (December, Fig. S2 in the online supplementary material).

Changes in abundance in a few grass species, notably *P. maximum*, *Bothriochloa radicans* and *Urochloa mosambicensis*, caused differences in composition between plots where fire was excluded and those burnt at different frequencies or seasons (Fig. 3, Table 5c; Table S1 in the online supplementary material). As observed with the Sourveld and Combretum sites, *P. maximum* increased in abundance in the absence of fire. In contrast, *U. mosambicensis* decreased in abundance with decreasing fire frequency. Both *B. radicans* and *U. mosambicensis* drove changes in composition with increasing fire intensity, with *B. radicans* increasing in abundance with intermediate fire intensities and *U. mosambicensis* abundance highest in plots experiencing greater fire intensities (Fig. 3).

Mopane site

Grass community structure, except for grass richness, was not significantly affected by the fire frequency or season treatments at the Mopane site. In general, the effects of the treatments on grass richness, diversity, evenness and dominance tended to be opposite to other sites, with, e.g., fire exclusion tending to enhance grass diversity (Fig. 2). No significant differences in grass composition were found for either the fire frequency or the season treatments (Table 4).

DISCUSSION

Fire regimes on the experimental plots

The design of the Kruger National Park's long-term fire experiment was aimed at imposing an identical set of fire regimes onto individual plots across the four sites with different vegetation types, soils and climate, but this was not fully achieved. The desired fire regimes had greater cumulative mean fire intensities at the Sourveld and Combretum sites because higher and more reliable rainfall resulted in correspondingly more consistent fuel loads (Table 1). For the more arid Mopane site, lower and less reliable rainfall resulted in low fuel loads that were insufficient to support spreading or intense fires. In addition, grazing pressure is generally higher on the more fertile basalt soils (van Wyk, unpublished data; Biggs *et al.* 2003), further contributing to more variable fuel loads on the

Knobthorn–Marula and Mopane sites. Thus, regular and consistent burning in these more arid sites was not possible, and consequently, the effects of other factors (rainfall and herbivory) most likely combined to have a greater effect on grass composition and structure than fire regime alone.

Fire intensity is regarded as an important feature of the fire regime (Gill 1975), but at the time that the fire experiment was established, this aspect of the fire regime was not fully recognized. Fire intensity measurements were initiated only in the early 1980s (Trollope and Potgieter 1985), following a growing recognition among fire ecologists regarding their importance. Fire intensity and fire season are closely linked, and the resultant response of herbaceous plants to timing of fires cannot necessarily be separated from the effects of fire intensity. In this study, seasonal differences in cumulative fire intensity arose primarily as a result of differences in fuel moisture content (Govender *et al.* 2006). Annual burns had the greatest cumulative intensity because they were restricted by necessity to August (unlike other treatments) when fuel moisture was lowest. However, individual burns at 1-, 2- or 3-year intervals in August did not necessarily differ in intensity (Govender *et al.* 2006). In contrast, fires occurring during the growing season when fuel moisture was highest were the least intense over time irrespective of whether they burned every 2 or 3 years.

Effects of fire regime on savanna herbaceous vegetation

Despite the recognition of fire being a primary determinant of abundance of herbaceous vs. woody vegetation in savanna ecosystems (Bond *et al.* 2003; Sankaran *et al.* 2008), few studies have examined the long-term effects of fire regime on the herbaceous (grass) community (Furley *et al.* 2008; Savadogo *et al.* 2008), and we know of no studies that have examined the impacts of altering multiple aspects of the fire regime (frequency and season/intensity) on the grass diversity and composition of savanna ecosystems across broad environmental gradients. Thus, there was a general lack of understanding prior to our study of how the grass community would respond to long-term alterations in fire regime.

Based on responses observed in the woody component of these savanna communities (Bond and Keeley 2005; Higgins *et al.* 2007), we predicted that 44+ years of fire exclusion would cause the largest shift in grass community structure and composition. It is known that that frequent fire favors grasses and that the exclusion of fire can lead to the loss of many species from grassland ecosystems (Briggs *et al.* 2002; Collins 2000; Fynn *et al.* 2004; Leach and Givnish 1996; Mistry 1998; Uys *et al.* 2004). Therefore, we predicted that grass diversity would be lowest in plots where fire was excluded and highest in plots experiencing frequent fires. Moreover, we expected grass composition would differ between plots experiencing frequent and/or intense fires and those subjected to less frequent and/or intense fires, which should be more similar to plots where fire was excluded. We generally found support for these predictions, although significant responses of grass diversity and composition to long-term alterations in fire regime were restricted to the Sourveld and Combretum sites, which experienced more consistent and intense fires and potentially lower grazing pressure due to the less fertile granite soils. For these sites, long-term exclusion of fire caused a reduction in grass diversity and richness and the greatest shift in grass composition, and grass diversity and composition with less frequent and intense (mainly growing season) fires tended to be similar to the fire exclusion plots. There is previous evidence for a decline in the species richness of the grasses with decreasing fire frequency in African savannas (Furley *et al.* 2008; Savadogo *et al.* 2008; Yeaton *et al.* 1986). In contrast, grass diversity was highest with annual burning and with the more intense, growing season (August and October) fires. Surprisingly, the fire frequency and season treatments applied over the long-term did not result significant changes in grass composition for all of the sites (Table 4) and grass diversity for the Knobthorn–Marula and Mopane sites (Fig. 2). For example, grass composition was similar irrespective of whether a plot had been burned annually or every 2 or 3 years for the Sourveld and Knobthorn–Marula sites. Moreover, many of the grass species that were common prior to initiation of the experiment remained common after 44+ years of manipulation of fire regime (Table S1 in the online supplementary material). Collectively, these results suggest that these savanna grass communities are relatively resistant to change with alterations in fire regime, except in the most extreme case of long-term fire exclusion, where both grass diversity and composition were altered to some extent for all sites.

The alterations in grass diversity and composition observed with fire exclusion and the less frequent and intense (growing season, December and February) fires were driven primarily by increased dominance by a few tall-statured grass species, in particular *P. maximum*. In contrast, changes in grass diversity and composition with the most frequent and intense fires were driven by an increase in abundance a few shorter statured grass species, such as *H. contortus* and *E. rigidior*, which are favored by frequent disturbance ('increaser II', Table S2 in the online supplementary material). Relative frequency of *P. maximum*, which is considered to increase in abundance in the absence of disturbance (i.e. 'decreaser', Table S1 in the online supplementary material), was highest with fire exclusion, irrespective of vegetation type (excluding the Mopane site). Similar responses have been observed in other savannas where the exclusion of fire or disturbance results in an increase in abundance of tall-stature grasses (Belsky 1992; Frost and Robertson 1987; Fynn *et al.* 2005). The shift in composition to increased abundance *P. maximum* with less intense fires could have broader implications. *P. maximum* tends to have higher tissue moisture content, and as this species becomes more abundant in the community, intensity of fires could further decrease, thereby providing a positive feedback for the expansion of woody vegetation with exclusion of fire.

P. maximum tends to be highly competitive, and therefore, the decline in grass diversity observed with fire exclusion may

be, in part, due to increased competition between the tall- vs. shorter stature or less common grasses, as well as due to the increase in dominance of woody vegetation (Higgins *et al.* 2007; Smit *et al.* 2010). Fire has been shown to play an important role in seed bank dynamics of semi-arid savannas (Anderson *et al.* 2012) and thus changes in grass diversity and composition observed with long-term alterations in fire regime and fire exclusion could be driven, in part, by long-term changes in demographic success. For example, abundance of *H. contortus*, which has been found to have greater germination success with fire (Campbell *et al.* 1996; Orr *et al.* 1997), was highest with the most frequent and intense fires and lowest with fire exclusion at the Sourveld site. These patterns of abundance could be due to greater germination and seedling establishment with frequent and intense fires and conversely the prevention of these with fire exclusion. *E. rigidior* also significantly increased in abundance with frequent and intense fires at the Combretum site, and given that this grass is a prolific seeder (Veenendaal *et al.* 1996), fire may also favor its germination and seedling establishment. In addition, timing of tiller emergence could be important in determining the shifts in composition observed as species that delay tillering after rains (e.g. *H. contortus*) are less vulnerable to fire than those in which tillers emergence occurs soon after rains begin (e.g. *P. maximum*; Frost and Robertson 1987). However, it is important to consider that all the plots were open to herbivores throughout the duration of the experiment, and therefore, responses of the grass community also could be due to differences in grazing intensity across the fire frequency and season treatments, with the fire excluded plots experiencing the lowest grazing pressure (Burkepile *et al.*, unpublished data.). Higher grazing pressure could promote grass diversity by preventing a few grass species, particularly those not favored by disturbance ('decreasers' such as *P. maximum*, *D. eriantha*, etc., Table S1 in the online supplementary material), from dominating and by providing opportunities for seedling recruitment, particularly when combined with frequent and intense fires (Anderson *et al.* 2012).

In contrast to the grasses, the fire treatments have been shown to have little effect on woody plant species richness and composition (Enslin *et al.* 2000; Jacobs and Biggs 2001; Kennedy and Potgieter 2003; O'Regan 2005; Shackleton and Scholes 2000). Higgins *et al.* (2007) found that tree and shrub density were unresponsive to fire regimes or fire exclusion, but tree size was reduced as fire frequency increased, and fire exclusion promoted dominance by large trees. Therefore, fire does not appear critical for the maintenance of woody plant species diversity, but it does affect structure (biomass and height) of the woody component. Although both the woody and the herbaceous communities were simultaneously measured on the EBPs, these data were collected at different spatial scales using different methodologies. Therefore, direct comparisons between responses of the woody and herbaceous components of the community could not be made. However, such comparisons are critical for ultimately understanding the effects of long-term alterations of fire regimes on herbaceous woody dynamics in these savannas. Thus, future studies are clearly needed that measures both components of the community in spatially explicit and directly comparable ways.

Fire effects and gradients of climate and soil fertility

As indicated above, the effects of fire frequency and season varied across the broad gradients in climate, soil fertility and productivity captured by the experiment. In general, we observed a much stronger effect of fire on grass diversity and composition in the more mesic sites (Sourveld and Combretum) when compared to the more arid and climatically variable sites (Knobthorn–Marula and Mopane). Similar patterns of response to fire in the same plots were found for the woody component (Higgins *et al.* 2007), as well as for ant communities (Parr *et al.* 2004), where the greatest effects of the treatments were observed for the higher rainfall sites.

We hypothesize that the apparent lack of response of the grass community to the different fire treatments in the Knobthorn–Marula savanna, despite it experiencing similar intensities of fires over the study period as the Combretum site (Fig. 1), was most likely due to heavier grazing (Biggs *et al.* 2003). The greater grazing pressure in the Knobthorn–Marula site has been attributed to higher quality forage of the community as a consequence of dominance by more palatable lawn-grass species (e.g. *U. mosambicensis*, *Panicum coloratum*; Fig. 3; Table S1 in the online supplementary material), as well as the more nutrient-rich basalt soils. In contrast, the Combretum plots are situated on nutrient-poor granite soils and dominated by *D. eriantha* and *P. maximum*. The high abundance of *D. eriantha* in particular is suggestive of lower grazing pressure as this species is highly palatable and tends to decrease with overgrazing (i.e. 'decreaser'; Table S1 in the online supplementary material). The potential for greater herbivore pressure on the Knobthorn–Marula plots may have minimized any differences between the fire frequency and season treatments, particularly if the herbivores were attracted to and concentrated on the burned plots over time. Such interactions between fire and grazing have been observed in North America grasslands, where grazers selectively reduce abundance of the dominant grass species with frequent burning (annual frequency) causing community diversity and composition to be similar to that with infrequent burning (Collins *et al.* 1998; Fuhlendorf and Engle 2001, 2004). For the Knobthorn–Marula savanna ecosystem, grazers may have been attracted to the more frequently and intensely burned plots as compared to surrounding area due to the consistent flush of new and more palatable growth (Archibald *et al.* 2005) or potentially to avoid predators (Burkepile *et al.*, unpublished data), causing community composition and structure to be similar irrespective of fire frequency or season when compared to the unburned plots. For the Mopane community, it is likely that climatic variability and/or herbivory plays a more important role in influencing grass community structure composition, given that composition was similar irrespective of whether the plots were

burned or left unburned or experienced more of less intense or frequent fires.

Thus, across the broad precipitation, fertility and productivity gradients represented in KNP (and more generally across savannas in South Africa), we hypothesize that the impacts of varying fire regime on the herbaceous community become less important as top–down control by herbivores and/or climatic means and variability become more important drivers of herbaceous community structure and composition. This emphasizes the need for future studies aimed at separately assessing the impacts of fire and herbivory in savanna ecosystems across broad gradients of climate and soil fertility.

SUPPLEMENTARY DATA

Supplementary Figs. S1 and S2 and Table S1 are available at *Journal of Plant Ecology* online.

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