Effects of fire on woody vegetation structure in African savanna

Author(s): Izak P. J. Smit, Gregory P. Asner, Navashni Govender, Ty Kennedy-Bowdoin, David E. Knapp and James Jacobson

Source: *Ecological Applications*, Vol. 20, No. 7 (October 2010), pp. 1865-1875
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/25741353
Accessed: 31/07/2014 11:07

Ecological Applications, 20(7), 2010, pp. 1865–1875

Effects of fire on woody vegetation structure in African savanna

Izak P. J. Smit,[1,3] Gregory P. Asner,[2] Navashni Govender,[1] Ty Kennedy-Bowdoin,[2] David E. Knapp,[2] and James Jacobson[2]

[1]*Scientific Services, South African National Parks, Kruger National Park, Private Bag X402, Skukuza, 1350 South Africa*
[2]*Department of Global Ecology, Carnegie Institution, 260 Panama Street, Stanford, California 94305 USA*

Abstract. Despite the importance of fire in shaping savannas, it remains poorly understood how the frequency, seasonality, and intensity of fire interact to influence woody vegetation structure, which is a key determinant of savanna biodiversity. We provide a comprehensive analysis of vertical and horizontal woody vegetation structure across one of the oldest savanna fire experiments, using new airborne Light Detection and Ranging (LiDAR) technology. We developed and compared high-resolution woody vegetation height surfaces for a series of large experimental burn plots in the Kruger National Park, South Africa. These 7-ha plots (total area ~1500 ha) have been subjected to fire in different seasons and at different frequencies, as well as no-burn areas, for 54 years. Long-term exposure to fire caused a reduction in woody vegetation up to the 5.0–7.5 m height class, although most reduction was observed up to 4 m. Average fire intensity was positively correlated with changes in woody vegetation structure. More frequent fires reduced woody vegetation cover more than less frequent fires, and dry-season fires reduced woody vegetation more than wet-season fires. Spring fires from the late dry season reduced woody vegetation cover the most, and summer fires from the wet season reduced it the least. Fire had a large effect on structure in the densely wooded granitic landscapes as compared to the more open basaltic landscapes, although proportionally, the woody vegetation was more reduced in the drier than in the wetter landscapes. We show that fire frequency and fire season influence patterns of vegetation three-dimensional structure, which may have cascading consequences for biodiversity. Managers of savannas can therefore use fire frequency and season in concert to achieve specific vegetation structural objectives.

Key words: conservation management; fire frequency; fire intensity; fire policy; fire season; Kruger National Park; protected areas; South Africa; structural diversity; structural heterogeneity.

Introduction

Fire is an important process in savannas, acting both like a generalist herbivore (Bond and Keeley 2005) and as a facilitator for the coexistence of trees and grasses (Higgins et al. 2000, Sankaran et al. 2004). The overall effect of fire on woody vegetation depends upon the interacting elements defining the fire regime, including intensity, frequency, and season (Gill 1975). Fire can influence woody vegetation biomass, composition, and structure. Studies of African savannas find that fire generally reduces woody biomass (Trapnell 1959, Kennan 1971, van Wyk 1971, Huntley 1984, Bond et al. 2005, Higgins et al. 2007). Fire does not significantly change the species composition in dry savannas (Enslin et al. 2000), although fire-sensitive species (e.g., forest species) may appear in the absence of fires in mesic savannas (Whateley and Wills 1996, Lloret et al. 2005). Finally, fire has a marked effect on the structure of woody vegetation in savanna woodlands (Enslin et al. 2000, Higgins et al. 2007), but the precise responses of the vegetation to the prevailing fire regime remains difficult to ascertain.

Higgins et al. (2007) found that fire did not influence tree density, but influenced the size structure and biomass of tree populations in savannas. The resilience of woody vegetation to fire is due to the ability of most savanna tree species to resprout from root stocks (Hoffmann and Solbrig 2003, Nefabas and Gambiza 2007). As a result, repeated fires may keep individuals small, but individuals rarely suffer mortality and large individuals are often immune to life-threatening fire damage (Enslin et al. 2000, Higgins et al. 2000). However, the utilization of large trees by elephants (*Loxodonta africana* Blumenbach, 1797) and other animals (e.g., porcupines, *Hystrix cristata* Linnaeus, 1758), especially by means of debarking, can compromise these individuals and make them more susceptible to wood borer infestation and fire damage, which may lead to them being killed or toppling over (Yeaton 1988, van Wilgen et al. 2008). Fire therefore drives variations in vegetation structure, which is important for shaping nutrient patterns (Treydte et al. 2007), animal visibility (Riginos and Grace 2008), habitat suitability, and other

Manuscript received 27 May 2009; revised 18 November 2009; accepted 13 January 2010. Corresponding Editor: J. Belnap.
[3] E-mail: izaks@sanparks.org

TABLE 1. Ecological details of the four studied landscapes (based on data extracted from Naiman et al. [2003] and van Wilgen et al. [2007]).

Landscape	Vegetation type	Dominant tree species	Geology	Mean annual rainfall (mm)	Estimated herbivore biomass (kg/ha)
Pretoriuskop	sourveld	*Terminalia sericea, Dichrostachys cinerea*	granite	705	27
Skukuza	*Combretum*	*Combretum collinum, Combretum zeyheri*	granite	572	27
Satara	knobthorn–marula	*Acacia nigrescens, Sclerocarya birrea*	basalt	507	37
Mopani	mopane	*Colophospermum mopane*	basalt	451	29

Notes: The estimated herbivore biomass is based on historical aerial census data (1980–1991) and is provided for the major land systems of Kruger (Pretoriuskop and Skukuza are both part of the "Skukuza southern granites" land system and hence have similar estimates).

cascading features affecting biodiversity (e.g., Parr and Andersen 2006).

It is well known that fire is one of the key management tools that can be used to manipulate the structure of woody vegetation in savannas. Although some papers explore the effects of long-term fire exclusion (e.g., Moreira 2000), variable fire return periods (e.g., Furley et al. 2008), or time since last fire (e.g., Harrell et al. 2001), few have resolved the interacting effects that different combinations of fire frequency and fire season have on woody vegetation structure (especially vertical structure) over the long term.

Here we present an analysis of a unique data set derived from the long-term fire experiments in the Kruger National Park (KNP), South Africa. This experiment, with different fixed-fire regimes and no-burn areas, has run uninterrupted since 1954. Numerous studies have subsequently been conducted on these experimental burn plots (synthesized by van Wilgen et al. 2007), which is generally considered one of the largest and best-known fire experiment in Africa, and one of the oldest in the world (Furley et al. 2008). Now, advances in airborne remote-sensing technology have afforded new opportunities to explore woody vegetation structure throughout the KNP experimental burn plots that were not possible previously. In particular, we developed high-resolution vegetation height surfaces from airborne Light Detection and Ranging (LiDAR) data to quantify and understand how fire frequency and season affect vertical woody vegetation structure. Previous studies on the Kruger burn plots that explored the effects of fire on woody structure (e.g., van Wyk 1971, Enslin et al. 2000, Shackleton and Scholes 2000, Kennedy and Potgieter 2003, O'Regan 2005) usually considered only specific landscapes and/or relied on field-based sampling strategies (e.g., belt transects) that identified only a subset of woody vegetation from the plots (Higgins et al. 2007) and often used height classes. This study expands on these earlier studies by considering all four landscapes and measuring woody structure wall-to-wall and in a spatially explicit manner across 168 of the 208 plots. This allows detailed, comprehensive and systematic measurements of woody vegetation structure, affording three-dimensional profiling on a near-continuous scale thereby permitting the investigation of the effects of different fire treatments at various measured heights of woody plants. The following specific questions were addressed: How does fire affect woody vegetation structure across different geologies and rainfall regimes in savannas? How do fire frequency and fire season influence woody vegetation structure? We then consider the answers to these questions in the context of fire management at the KNP and more generally in semiarid savannas.

MATERIALS AND METHODS

Study site

The Kruger National Park (KNP) covers ~1 948 528 ha within the low-lying savannas of northeastern South Africa. The vegetation in Kruger is characterized by savannas, described by 35 landscapes (Gertenbach 1983), and is dominated by knobthorn (*Acacia nigrescens*), marula (*Sclerocarya birrea*), leadwood (*Combretum imberbe*), red-bush willow (*Combretum apiculatum*), silver cluster leaf (*Terminalia sericea*), and mopane (*Colophospermum mopane*). Mean annual rainfall ranges from ~350 mm in the north to 750 mm in the south. Geologically, the park is underlain by granites and their erosion products in the west, while the eastern sector is predominantly underlain by basaltic erosion products. The flora of the park comprises 1983 species, including more than 400 tree and shrub species and more than 220 grass species.

Experimental burn plots (EBP)

Fire research formally began in KNP in 1954 with the establishment of one of the long-term fire ecology research experiments in Africa (Van der Schijff 1958). The original aim of the experiment was to study the effects of fire (frequency and season) on the vegetation of KNP under the grazing pressure of indigenous herbivores. The experiment consisted of the application of fires at varying return intervals and seasons, and protection from fire, on a series of ~7-ha plots in four of the major vegetation landscapes of the Park (Pretoriuskop, Sourveld vegetation; Skukuza, *Combretum* vegetation; Satara, knobthorn and marula vegetation; Mopani, mopane vegetation; Table 1; Gertenbach 1983). The treatments were replicated four times in each of these landscapes. These replicates are called "strings." The

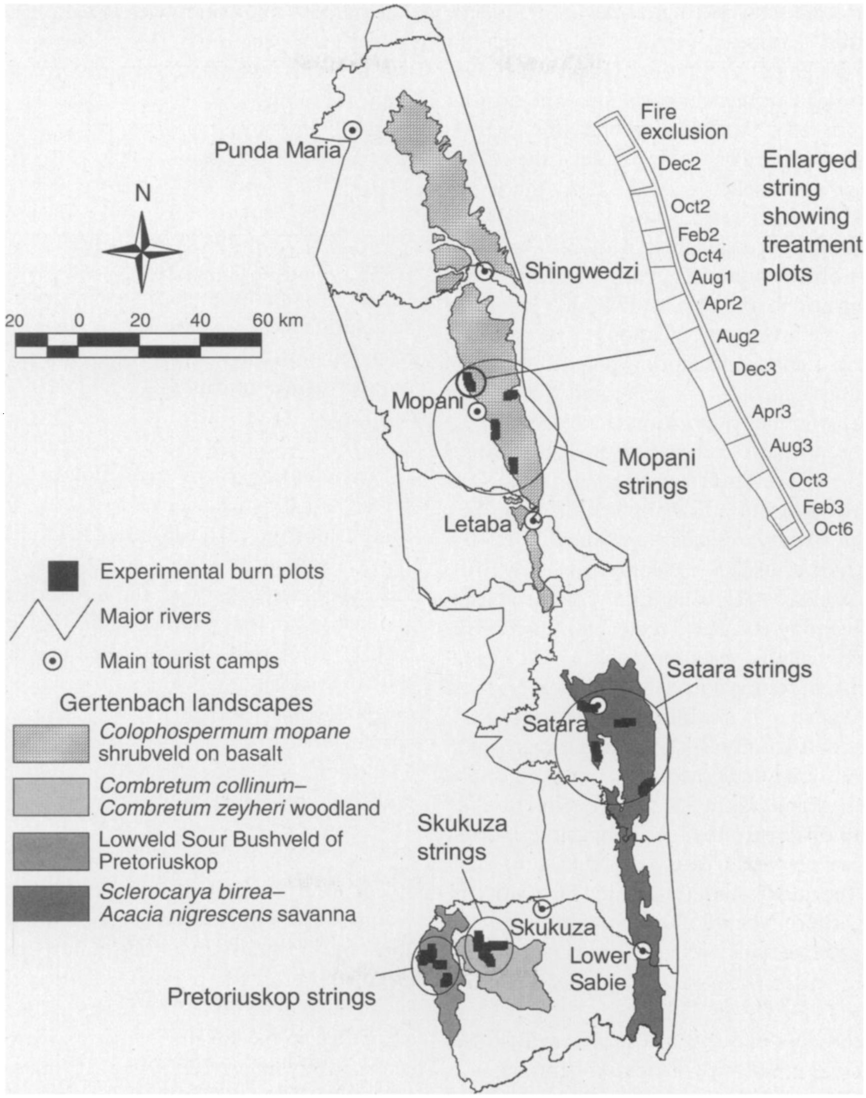

FIG. 1. The experimental burn plots (EBP) of the Kruger National Park, South Africa. The experiment consisted of four replicates (called strings) in each of four major vegetation landscapes. Within each string the different fire treatments were applied in plots (see insert for a zoomed example of a string; the letters and number in the plots indicate the season and fire return period, e.g., the Feb3 plot is burned every third year in February). The figure is adapted from Biggs et al. (2003).

resulting hierarchical organization of treatments was: plots < strings < landscapes (Fig. 1).

The treatments originally included annual winter fires in August, and biennial and triennial fires in August, October, December, February, and April. In 1976, further treatments to examine the effects of fires every four and six years in October were added to selected landscapes (Satara and Mopani) by subdividing the February treatment plots. Full details and history of the experimental design and application of treatments are available from Biggs et al. (2003).

Data collection and processing

Airborne LiDAR data were acquired over the experimental burn plots (EBP) in April 2008 using the Carnegie Airborne Observatory (CAO; Asner et al. 2007). The CAO was mounted in a twin-engine, fixed-wing aircraft flying at an altitude averaging 2000 m above ground level. For this project, the CAO LiDAR was operated at 50 kHz pulse repetition frequency and a 34-degree scanning configuration cross-track of the aircraft direction. One string in each of the Skukuza, Satara, and Mopani landscapes was not included in the survey because local soil differences made them unrepresentative of the particular landscapes (Venter 2004).

Global positioning system (GPS) and inertial motion unit (IMU) data collected with the laser ranging data were combined to determine the three-dimensional location of the laser returns. From the laser "point cloud" data, a physical model was used to estimate top-of-canopy and ground surfaces (digital elevation models; DEM) using the Terrascan/Terramatch (Terrasolid 2008) software package. Vegetation height was then estimated by differencing the top-of-canopy and ground surface DEM. In the particular flying and sensor configuration employed for this project, the CAO generated a laser spot spacing of 1.12 m. Since the beam diameter at ground level was also 1.12 m, this laser spot spacing configuration resulted in a 50% overlap between LiDAR observations. This approach produces a continuous surface in the results that decreases the likelihood of missing a vegetation canopy. The resulting canopy DEM had a spatial resolution of 1.12 m × 1.12 m. This means that a surface was generated where each 1.244-m^2 square contained the estimated height of the highest vegetation in that particular pixel. The absolute vertical resolution of the CAO waveform LiDAR is 15 cm, but following digitization and application to porous tree canopies, the effective vertical resolution is 0.2–0.5 m. The top-of-canopy surface was subset for each EBP, resulting in 168 subsets. All further analyses were based on these top-of-canopy surfaces created for each EBP, and will be called "woody vegetation cover."

Acquisition of remote-sensing data always represents a trade-off between spatial resolution and area covered. Therefore, even though the spatial resolution of the LiDAR was high, some smaller woody individuals might not be detected, resulting in an underestimation of woody cover. However, as most of the results reported in this paper compare fire treatments relative to each other and, since the underestimation would be consistent across all plots, the effect of underestimation on the emerging structural patterns was considered small.

Structural change

For each height class (0.5 m vertical increments), the difference in canopy cover was calculated between each fire treatment plot in a string and the associated fire exclusion plot from the same string (Eq. 1). We will call this the "structural change" (SC) brought about by fire. SC gives an indication of how much the canopy cover at a specific height class was altered due to the fire treatment effect, using the associated fire exclusion plot as reference (note, however, that any fire treatment could have been chosen as reference treatment):

$$\mathrm{SC}_{TSI} = \mathrm{CD}_{T_{\mathrm{excl}}SH} - \mathrm{CD}_{TSH} \qquad (1)$$

where SC_{TSH} is the structural change in woody canopy cover in height class H, for treatment T, and string S (in square meters per hectare); $\mathrm{CD}_{T_{\mathrm{excl}}SH}$ is the canopy cover in height class H, for the fire exclusion treatment T_{excl} in string S (in square meters per hectare); and CD_{TSH} is the canopy cover in height class H, for treatment T in string S (in square meters per hectare).

The sum of the SC values across all height classes in a burn plot gives an indication of how much the structure of that plot has been altered by fire. The sum of the SC will be called "total structural change" (TSC; Eq. 2). The larger TSC for a treatment, the more fire has reduced the structure of the woody vegetation canopy of that specific treatment compared to the associated fire exclusion plot:

$$\mathrm{TSC}_{TS} = \sum_{H_i}^{n_{\mathrm{H}}} \mathrm{SC}_{TSH_i} \qquad (2)$$

where TSC_{TS} is the total structural change in woody canopy cover across all height classes in treatment T of string S (square meters per hectare); SC_{TSH_i} is the structural change in woody canopy cover of treatment T of string S at height class H_i (from Eq. 1); and n_{H} is the number of height classes.

Fire intensity and total structural change

Fire intensity (FI) is a function of: (1) the rate of fire spread at the head of a fire, (2) the mass of fuel combusted, and (3) a calibrated heat yield factor (Byram 1959). Between 1982 and 2003, FI has been calculated at 956 experimental fires on the Kruger EBP (Govender et al. 2006). To test whether plots that have experienced high FI change the woody vegetation structure more or less than plots that have experienced lower FI, we correlated the average FI for a treatment to the total structural change (TSC) of the same treatment. FI and TSC were averaged for each treatment within each landscape before calculating the correlation (Fig. 2).

Relative structural change

The four study landscapes differed considerably in woody vegetation cover. This is mainly due to differences in rainfall and the underlying geology. The granitic Pretoriuskop area is a densely wooded mesic savanna that receives annual rainfall of ~705 mm, compared to the basaltic Mopani area, which is an open semiarid savanna receiving ~451 mm/yr (van Wilgen et al. 2007). The granitic Skukuza landscape is also much more wooded than the basaltic Satara landscape (and receive rainfall of 572 mm/yr and 507 mm/yr, respectively; van Wilgen et al. 2007). Due to these differences in rainfall, herbaceous biomass and woody vegetation cover between these landscapes, we decided not to only compare the absolute total structural change (TSC) brought about by fire across landscapes, but also to compare the relative structural change. We believe these two components compliment each other and are important to understanding and comparing vegetation structural responses to fire across landscapes.

Consequently, we calculated "relative structural change" (RSC) for each plot. RSC expresses the SC of a particular height class in a plot as a percentage of the canopy cover of the same height class in the associated fire exclusion plot (Eq. 3). RSC can be interpreted as the percentage of change in woody canopy cover at a specific height that is brought about by a particular fire treatment. For example, if in landscape A, the canopy cover at height class X in treatment Y is 600 m^2/ha, and

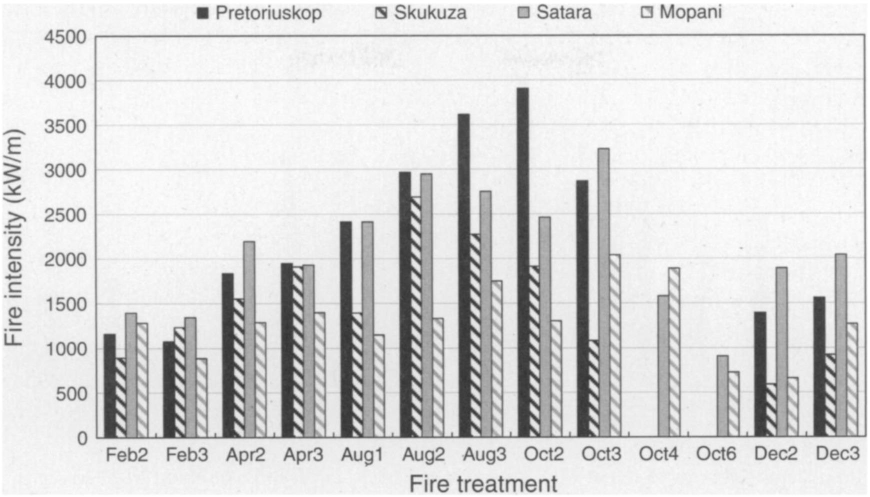

FIG. 2. Mean fire intensity (FI) per fire treatment in each landscape (derived from data collected by Govender et al. [2006]). Fire treatment abbreviations indicate the season and fire frequency, e.g., the Feb3 plot is burned every third year in February.

the canopy cover of the fire exclusion plot for the same string and height class is 1000 m^2/ha, then RSC is calculated at 40%. This means that the plot experienced a 40% decrease in canopy cover compared to the fire exclusion at that specific height class. If in landscape B, the canopy cover for the same treatment and height class as described above is 30 m^2/ha, and the canopy cover of the associated fire exclusion plot at that height class is 100 m^2/ha, RSC is 70%. Comparing the SC between landscape A and B, it is clear that fire has consumed/suppressed more woody cover at height class X in landscape A than B (400 m^2/ha vs. 70 m^2/ha), but when comparing RSC, it becomes evident that fire has in fact caused a much larger relative decrease in landscape B compared to landscape A, and landscape B is in fact in relative terms more affected by fire:

$$\mathrm{RSC}_{TSH} = \frac{(\mathrm{CD}_{T_{\mathrm{excl}}SH} - \mathrm{CD}_{TSH})}{\mathrm{CD}_{T_{\mathrm{excl}}SH}} \times 100 \qquad (3)$$

where RSC_{TSH} is the relative structural change in woody canopy cover in height class H, for treatment T in string S (percentage); $\mathrm{CD}_{T_{\mathrm{excl}}SH}$ is the canopy cover in height class H, for the fire exclusion treatment T_{excl} in string S (square meters per hectare); and CD_{TSH} is the canopy cover in height class H, for treatment T in string S (square meters per hectare).

The RSC values calculated above were analyzed for each height class using a generalized linear model (GLM). In order to balance the design, the August annual, as well as the October four and six yearly treatments were dropped from the GLM analysis. Landscape (four levels), fire season (five levels), and fire frequency (two levels) were specified as fixed factors in the GLM. All first-order interactions of these factors were also included in the model. The GLM analysis was used to ascertain whether there were any significant differences between the relative change in woody cover brought about by different long-term fire frequency and fire season regimes, as well as various combinations/interaction of these factors at different heights, and to establish whether these patterns are consistent across all the landscapes.

RESULTS

We note the following two issues that should be considered in interpreting the results: (1) The structural characteristics of the fire treatment plots reported below reflect the cumulative effects of long-term fire manipulation. (2) Even though the fire exclusion plots were used as "reference plots" (Eqs. 1 and 2), these plots should not be considered "control plots." In fact, fire exclusion is arguably the most extreme treatment in fire-driven systems where fire is a natural and desired process. Therefore, even though all the plots were referenced to the fire exclusion treatments, the interpretation should go beyond the "fire/no-fire" comparison and should consider treatment effects relative to each other.

Structural change

Fig. 3 summarizes the total structural change (TSC) in woody cover (expressed in square meters per hectare) for the 11 fire treatments, separately for each landscape. Fire changes woody vegetation structure more in the densely wooded granitic landscapes (Pretoriuskop and Skukuza) than in the open basaltic landscapes (Satara and Mopani). Furthermore, within the same geology, fire usually changes the woody vegetation structure more in the wetter than in the drier landscapes. For each of the landscapes, the total structural change in woody vegetation was least in the February triennial treatment (Feb3), and most in the August annual (Aug1) and October biennial (Oct2) treatments.

Fire intensity and total structural change.—Table 2 shows that average fire intensity (FI) and TSC are

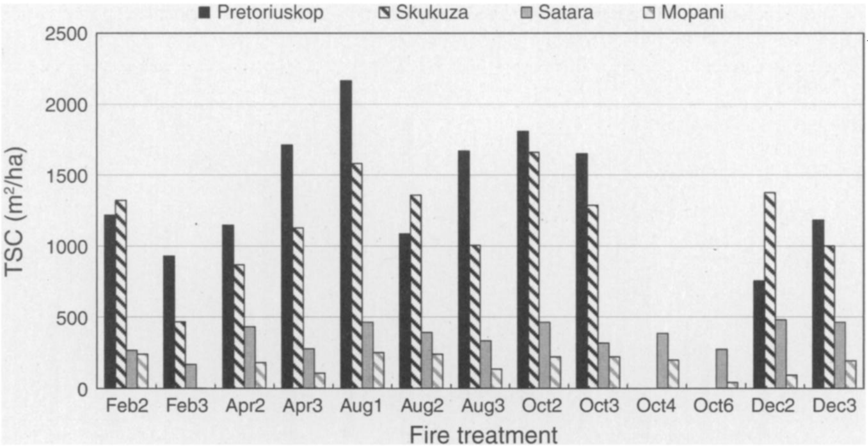

FIG. 3. The total structural change (TSC) in woody vegetation canopy cover brought about by different fire treatments when compared to fire exclusion plots. Fire treatment abbreviations indicate the season and fire frequency, e.g., Feb3 is the February triennial treatment. Note how the August annual and October biennial treatments result in the largest TSC values, and February triennial treatments result in the smallest TSC values.

positively correlated, indicating that higher intensity fires cause more structural change than do lower intensity fires (Pearson correlation coefficient, r, ranging between 0.08 and 0.60). However, by multiplying the average FI with $1/t$, where t is the number of years between successive fires, the cumulative effect of fire intensity can be considered. When exploring the cumulative effect of fire intensity, the correlations increase considerably in all four landscapes (r ranging between 0.45 and 0.78). Although FI takes fire frequency implicitly into account (i.e., increased time between fires giving rise to increased fuel accumulation, resulting in increased FI), it appears that fire frequency also needs to be explicitly taken into account.

Relative structural change

Table 3 summarizes the statistical results from the GLM analysis of relative structural change in the different vegetation height classes. Figs. 4–6 depict the main factor plots.

Fire frequency.—Fig. 4a compares the degree to which long-term biennial and triennial fires reduced the woody vegetation cover, when averaged across all five fire seasons and across all landscapes. Biennial fire treatments led to greater reduction in woody vegetation canopy cover than triennial treatments. This is especially true (and statistically significant at $\alpha < 0.1$) in the lower height classes (0.5–3.0 m), where there is ~45–48% reduction in woody cover for the biennial treatments compared to ~30–40% reduction for the triennial treatments. Although not statistically significant, the same general pattern of more reduction in woody cover for the triennial fires compared to the biennial fires appears to hold true in the taller height classes (3.0–7.5 m; Fig. 4a and Table 3).

Annual fires were only applied to August treatments (across all landscapes), and quadrennial and sexennial fires were only applied to October treatments (only across the Satara and Mopani treatments). Fig. 4b, c compares the percentage reduction that August and October fires experienced for these different fire frequencies. Generally, the same patterns emerged as in Fig. 4a: Longer fire return periods resulted in less reduction of woody vegetation cover. Woody vegetation below the 4.5-m height class was reduced by ~60–65% for the August annual treatments, compared to ~50% for the August biennial, and ~30–45% for the August triennial. October biennial treatment reduced the lower woody vegetation height classes with ~70% compared to values well below 35% for the sexennial treatments. However, when interpreting the quadrennial and sexennial October plots it must be kept in mind that these treatments were only included in 1976 (see *Experimental burn plots [EBP]*). Since the woody cover responses are cumulative through time, these differences in duration may have influenced the results for the four and six yearly October treatments.

Fire season.—Long-term dry-season fire treatments reduced woody vegetation canopy cover the most, with the October and August treatments reducing woody vegetation cover in height classes lower than 4.5 m by 47–

TABLE 2. Pearson correlation coefficients (r), and associated P values, between "average fire intensity" (AFI) and "total structural change" (TSC), as well as between AFI-adjusted and TSC.

		Correlation (AFI and TSC)		Correlation (AFI-adjusted and TSC)	
Landscape	n	r	P	r	P
Pretoriuskop	11	0.600	0.051	0.696	0.017
Skukuza	11	0.081	0.812	0.452	0.163
Satara	13	0.406	0.168	0.554	0.049
Mopani	13	0.534	0.060	0.783	0.002

Note: The number of treatments is indicated by n.

Table 3. *P* values from the generalized linear models (GLM), with relative structural change as response variable and landscape, fire frequency, and fire season as main factors.

Height class (m)	Landscape	Frequency	Season	Frequency × season	Landscape × frequency	Landscape × season
0.5–1.0		0.027				
1.0–1.5		0.047				
1.5–2.0		0.076				
2.0–2.5		0.093	0.082			
2.5–3.0	0.08	0.058	0.068			
3.0–3.5	0.01		0.029			
3.5–4.0	0.01		0.065	0.046		
4.0–4.5	0.01			0.034		
4.5–5.0	0.06					
5.0–7.5						
7.5–10.0	<0.001					
10.0–13.0	0.011					
13.0–17.0						

Notes: First-order interactions (×) were also included in the models. Empty cells indicate nonsignificance at $\alpha = 0.1$.

55% and 40–51%, respectively (Fig. 5). The wet-season fire treatment (February) reduced woody vegetation cover the least, reducing woody cover below 4.5 m by only 20–30% (Fig. 5). The effect of fire season is the most pronounced in intermediate height classes when the RSC differs statistically significantly between the plots receiving October and February fires (2.0–3.5 m) and August and February fires (3.0–3.5 m). The pattern becomes less clear in vegetation height classes above 4.5 m.

Landscape (geology and rainfall).—Fig. 6 suggests that fire reduces woody vegetation cover by a larger percentage on the drier basaltic plots than on the wetter granitic plots. Fire reduced woody vegetation in the Mopani landscape the most (52–56%) and the least in the Pretoriuskop landscape (31–33%). This pattern seems to hold relatively consistently up to about 4 m height, after which it becomes noisy. Landscape did not significantly interact with either fire frequency or fire season (Table 3), indicating that the fire frequency and season patterns observed in Figs. 4 and 5 and described in the previous two subsections can be generalized across all four landscapes.

Interaction between fire season and fire frequency.—In the 3.5–4.5 m height class, certain combinations of fire season and fire frequency create significant differences, i.e., biennial dry-season plots have significantly less woody vegetation cover than triennial wet-season plots (Table 3). For woody vegetation cover taller than 4.5 m, neither fire frequency nor fire season nor any combination of these factors is significantly different from each other.

Discussion

Broad-scale effects of fire (across geologies and rainfall gradient)

It has previously been shown that the effects of fire on woody vegetation structure can vary with differences in rainfall (van Wyk 1971, Sankaran et al. 2005, Higgins et

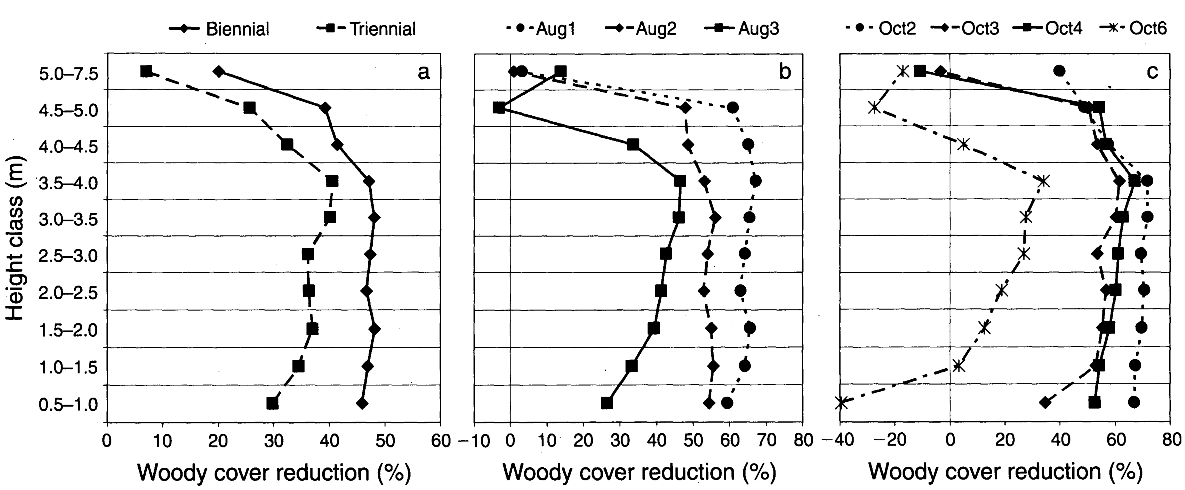

Fig. 4. Fire frequency factor plot. Average "relative structural change" (RSC) at various height classes, measured as percentage change (reduction) in woody canopy cover averaged across (a) all five seasons (n = 65 for each height class; all landscapes included), (b) August fires ($n = 13$ for each height class; all landscapes included), and (c) October fires ($n = 6$ for each height class; Satara and Mopane landscapes included). The letters and number abbreviation in the keys above panels (b) and (c) indicate the fire season and frequency: e.g., Aug1 is August annual treatment.

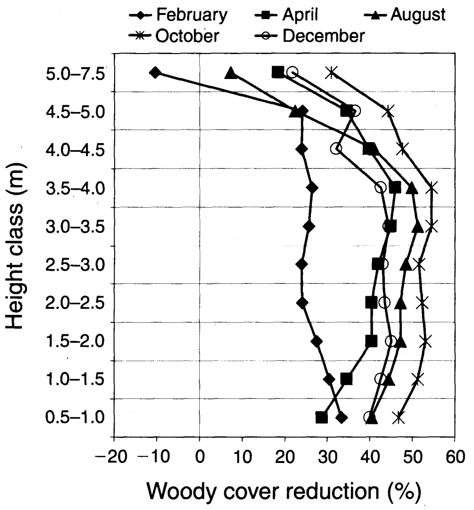

FIG. 5. Fire season factor plot. Average "relative structural change" (RSC) at various height classes, measured as percentage change (reduction) in woody canopy cover brought about by different seasons of fire treatments (late summer [February], autumn [April], late winter [August], spring [October], and mid-summer [December]; $n = 26$ for each height class, averaging biennial and triennial fires across all landscapes).

al. 2007) and geomorphology (Vigilante et al. 2004, Mermoz et al. 2005). Generally, it is expected that fire will have more of an influence on woody vegetation cover in wetter savannas than in drier savannas (Sankaran et al. 2005, van Wilgen et al. 2007). This has also been shown previously in Kruger where the increase in biomass following protection from fire at the EBP in the high-rainfall areas was two to six times greater than in plots receiving less rain (Higgins et al. 2007). The results presented in Fig. 3 further confirm this generalization, with fire changing woody vegetation cover more in the wetter than in the drier landscapes.

Fire caused a larger percentage reduction in woody vegetation cover in the more open and drier landscapes than in the wetter, more wooded landscapes. This suggests that the effects of fire on vegetation in wet and dry savannas reverses, depending on whether the focus is placed on the absolute or the relative change in woody vegetation cover. For example, when considering the effect of fire on changing carbon storage in savannas (i.e., when absolute woody vegetation cover is of concern), fire plays a more important role in the wetter savannas compared to the drier savannas since more woody biomass is removed/suppressed by fires in the wetter areas (Bond et al. 2005). When considering, for example, the availability of forage below three meters for browsers, fire reduced it by ~55% in the drier landscapes compared to ~33% in the wetter landscapes.

Our results challenge the current widely held belief that the EBP in the dry Mopani landscape have not been significantly affected by fire. Fire caused a larger percentage reduction at the Mopani EBP compared to the Pretoriuskop EBP (Fig. 6). We believe this is a significant finding that warrants a reevaluation of how fire effects are perceived and monitored across rainfall gradients. Considering the relative change in woody vegetation structure brought about by fire, we argue that the current perception that fire has more of an effect on the structure of densely wooded wet savannas than on open dry savannas may be too simplistic and even misleading in certain contexts (i.e., when considering relative vs. absolute changes). We argue that this perception is due to (1) studies usually comparing absolute change in woody cover rather than relative change, and (2) sample-based fieldwork approaches and observations often being insensitive to detect changes in landscapes with low woody cover (i.e., signal to noise ratio low for sparsely wooded landscapes). On the other hand, high-resolution LiDAR data, collected wall-to-wall on 7-ha fire plots, highlight these patterns, which may not be clearly visible and detectable using fieldwork estimation.

Fire frequency effects on woody vegetation structure

Long-term exposure to biennial fires reduced woody vegetation cover more than long-term exposure to triennial fires. This was the case across a range of height classes (Fig. 4). This result is significant since the literature does not provide clear empirical evidence whether an additional year between successive fires will result in a net increase or decrease in woody cover. Two competing hypotheses can be considered. Hypothesis 1: Areas experiencing an additional year between successive fires will experience a net increase in woody cover, due to a longer recovery period between fire events and

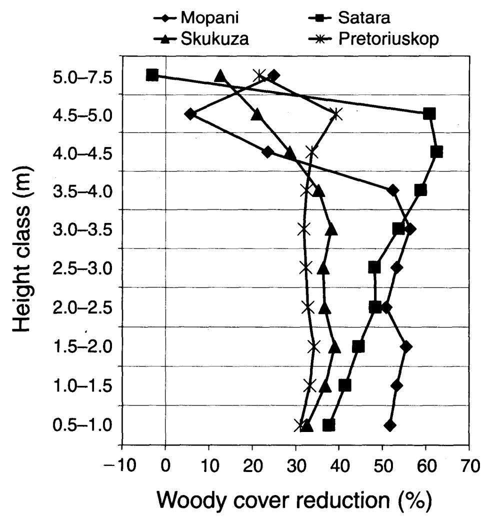

FIG. 6. Landscape factor plot. Average "relative structural change" (RSC) at various height classes, measured as percentage change (reduction) in woody canopy cover brought about by fire treatments separately for each of the four landscapes ($n = 30$ for Mopani, Satara, and Skukuza landscapes, and $n = 40$ for Pretoriuskop landscape, including biennial and triennial fires across all seasons).

hence more woody vegetation escaping the fire trap. Hypothesis 2: Areas experiencing an additional year between successive fires will experience a net decrease in woody cover, due to (1) higher intensity fires resulting from the additional year of fuel accumulation, and/or (2) increased competition with grasses for resources.

When considering Fig. 4a–c and Table 2, this study clearly supports Hypothesis 1, indicating that considerably more woody vegetation escapes if the interval between fires increase, offsetting the effects of any potential increases in resource competition with increased grass cover or increased fire intensity due to additional years of fuel accumulation. This is in line with the findings of Govender et al. (2006), who found that there were no significant difference in fire intensities between annual burns and burns at two-, three-, and four-year intervals, despite lower fuel loads in annual burns. Considering the findings of Govender et al. (2006) and the results presented here, fuel accumulation due to additional years since last fire does not significantly increase the fire intensity or decrease the woody vegetation cover. This means that woody vegetation would gain more by longer recovery periods between fire events than it would lose due to more competition with grasses or potentially higher fire intensities resulting from additional fuel accumulation. These findings challenge the commonly held perception that fires occurring after long fire-free periods will be of higher intensity and result in increased percentages of topkill due to accumulation of moribund fuel. In fact, we have demonstrated that woody vegetation across a range of rainfall conditions will be favored by longer return intervals notwithstanding any additional fuel accumulation or resource competition that may result. Govender et al. (2006) showed that fire intensity and fuel load actually decreased significantly on the sexennial plots, probably as a result of lower fuel loads resulting from decomposition and loss of plant vigor following long inter-fire periods (Midgley et al. 2006). We further corroborate this finding by showing that the woody vegetation cover was least affected by fire in the sexennial plots (Fig. 4c). This result may not hold in areas where the rates of fuel accumulation and decay differ significantly from the situation in Kruger.

Fire season effects on woody vegetation structure

Woody vegetation cover was more reduced by long-term exposure to dry-season fires than by wet-season fires. This was observed across a range of height classes (Fig. 5). This is due to the fact that fire intensity of dry-season fires is higher than the intensity of wet-season fires (Fig. 2 and Govender et al. 2006). Trapnell (1959) and Kennan (1971) reported similar results in Zimbabwe, with burning late in the dry season (October) having much more drastic effects on regeneration and regrowth of woody vegetation than burning early in the dry season (June/July). Spring fires (October) reduced woody vegetation the most, and although not statistically significantly so, these fires reduced woody vegetation more than late-winter fires (August). This may be due to a large proportion of dry and moribund herbaceous biomass still being present in October, especially if the spring rains had not fallen yet when the treatment was applied, giving rise to high-intensity fires. This agrees with Govender et al. (2006), who found that high to very high intensity fires (>4000 kW/m) were most prevalent in winter (August) and spring (October) burns, with the four most intense fires of their study occurring in spring (exceeding 10 000 kW/m). Furthermore, in October the woody vegetation comes out of dormancy and starts sprouting, transferring reserves from the roots to aboveground parts. Therefore, spring is the season when high-intensity fires can occur in the presence of sprouting woody vegetation, which may be more sensitive for fire damage than dormant winter vegetation (Shultz 2007).

Bond and Midgley (2000) stated that for some savanna woody species, the recruitment of old but small individuals (kept in a suppressed state by repeated fires) into mature size classes depends on rare escape opportunities whereby a tree attains sufficient height to escape flame damage. It is the interaction between fire frequency and fire intensity on the woody component that creates these escape opportunities for trees. Our results provide some evidence that fire frequency acts largely on the shorter height class and fire intensity on the taller height classes (Table 3).

Recently there have been many models that have been developed to explain the role of fire in shaping savanna systems and maintaining the tree–grass balance (Higgins et al. 2000, van Langevelde et al. 2003, Liedloff and Cook 2007). Hanan et al. (2008) questioned the use of aggregated savanna fire models, because these models did not realistically represent the impacts of fire on the structure and dynamics of the woody community. As such, they did not provide an adequate explanation for tree–grass coexistence or woody dynamics in savanna ecosystems. In turn, a more realistic but still simplified two-size class model that separates the savanna woody community into broad size classes (subadult and adult) based on susceptibility to fire was used to explain the role of fire in shaping savanna ecosystems (Hanan et al. 2008).

Management Implications

The results presented here suggest that managers of African savannas should consider both fire season and intensity in their fire policy as both affect woody vegetation cover at a range of heights. This study provides some evidence that the fixed-fire-regime approach, which was particularly popular during the previous century (and still is in certain areas), would homogenize woody vegetation structure. Note, however, that these structural changes are lagged, with woody vegetation profiles evolving as the immediate demographic changes caused by fires (i.e., loss of seedlings/

small individuals) are accompanied by slow demographic changes (loss of large individuals/adults) (Hanan et al. 2008).

Due to the high occurrence of nonmanagement ignited fires, van Wilgen et al. (2004) suggested that managers in Kruger have little influence on how much of the park burns on an annual basis, and that area burnt is largely dictated by rainfall of the previous two years. Because of this apparent inability to influence fire frequency in Kruger, managers are instead encouraged under the current fire policy to burn earlier in the season (i.e., lower intensity fires) in order to (1) diversify the current range of fire intensities, and (2) preempt the high-intensity fires that will follow later in the season when biomass and fuel conditions are favorable (Govender et al. 2006, van Wilgen et al. 2008). Our results suggest that this approach of encouraging cooler fires earlier in the dry season will favor woody vegetation and will probably allow more cohorts of trees to escape the fire trap and grow into larger tree classes, but potentially also allow some bush thickening in the lower height classes. Although it seems as if burning earlier in the fire season will favor tree cohorts to escape into larger height classes, it is not clear how management fires outside of the natural lightning fire season will affect other aspects of biodiversity. Furthermore, managing fire season alone without any consideration for fire frequency may result in very little area that is left unburned for relatively long periods. Long-unburned habitats may potentially act as important refugia for certain species that are fire sensitive or fire intolerant (see, e.g., O'Regan [2005] for a list of such species in southern KNP) in a similar way that habitats that are far removed from surface water are refugia for species that are sensitive to foraging and trampling (Fensham and Fairfax 2008). Long-unburned areas have thus been identified as a management priority in certain Australian savannas (Andersen et al. 2005). Kruger may also need to consider management options that will allow such long-unburned areas to occur, just as it has reestablished water remote areas by removing artificial waterholes from naturally dry landscapes (Smit and Grant 2009). This will further increase the heterogeneity in fire regime and may be critical for certain species that prefer these extreme conditions.

A fire return period with a large variance around the mean is very different from a similar mean return period with little variance. Fixed fire regimes remove the variability that is crucial in many systems to open demographic "windows" for young/small trees to pass through (Higgins et al. 2000, Hanan et al. 2008). Since the results presented in this paper are based on fixed fire treatments, it is more directly applicable to areas that experience less variable fire regimes. Future studies should focus on comparing woody vegetation structure in areas where managers aim to keep the fire variability low (e.g., rotational burning, spring fires at a fixed interval) with structure in areas where the management approach allows, or even induces, spatiotemporal variability in the fire regime (e.g., patch mosaic fires).

Acknowledgments

We thank South African National Parks for permission to conduct this study within the Kruger National Park (KNP). The team that maintained the experiment for many decades deserves special mention. We thank Brian van Wilgen, Guy Boggs, and Kate Parr for inputs and ideas during project conceptualization. Shaun Levick, Renaud Mathieu, Konrad Wessels, Jan van Aardt, and Barend Erasmus are thanked for support and advice during the project. Two reviewers provided comments that significantly improved the manuscript. I. P. J. Smit thanks the Andrew Mellon Foundation for funding a trip to the Department of Global Ecology that resulted in this paper. Airborne mapping and analysis of the KNP was funded by the Andrew Mellon Foundation. The Carnegie Airborne Observatory is made possible by the W. M. Keck Foundation and William Hearst III.

Literature Cited

Andersen, A. N., G. D. Cook, L. K. Corbett, M. M. Douglas, R. W. Eager, J. Russell-Smith, S. A. Setterfield, R. J. Williams, and J. C. Z. Woinarski. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecology 30:155–167.

Asner, G. P., D. E. Knapp, T. Kennedy-Bowdoin, M. O. Jones, and R. E. Martin. 2007. Carnegie Airborne Observatory: in-flight fusion of hyperspectral imaging and waveform light detection and ranging (wLiDAR) for three-dimensional studies of ecosystems. Journal of Applied Remote Sensing 1:1–21.

Biggs, R., H. C. Biggs, T. T. Dunne, N. Govender, and A. L. F. Potgieter. 2003. Experimental burn plot trial in the Kruger National Park: history, experimental design and suggestions for data analysis. Koedoe 46:1–15.

Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20:387–394.

Bond, W. J., and G. F. Midgley. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology 6:865–869.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. New Phytologist 165:525–538.

Byram, G. M. 1959. Combustion of forest fuels. Pages 155–182 *in* K. P. Davis, editor. Forest fire: control and use. McGraw-Hill, New York, New York, USA.

Enslin, B. W., A. L. F. Potgieter, H. C. Biggs, and R. Biggs. 2000. Long-term effects of fire frequency and season on the woody vegetation dynamics of the *Sclerocarya birrea*/*Acacia nigrescens* savanna of the Kruger National Park. Koedoe 43: 27–37.

Fensham, R. J., and R. J. Fairfax. 2008. Water-remoteness for grazing relief in Australian arid-lands. Biological Conservation 141:1447–1460.

Furley, P. A., R. M. Rees, C. M. Ryan, and G. Saiz. 2008. Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe. Progress in Physical Geography 32:611–634.

Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. Koedoe 26:9–121.

Gill, A. M. 1975. Fire and the Australian flora: a review. Australian Forestry 38:4–25.

Govender, N., W. S. W. Trollope, and B. W. van Wilgen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensities in savanna vegetation in South Africa. Journal of Applied Ecology 43:748–758.

Hanan, N. P., W. B. Sea, G. Dangelmayr, and N. Govender. 2008. Do fires in savannas consume woody biomass? A comment on approaches to modelling savanna dynamics. American Naturalist 171:851–856.

Harrell, W. C., S. D. Fuhlendorf, and T. G. Bidwell. 2001. Effects of prescribed fire on sand shinnery oak communities. Journal of Range Management 54:685–690.

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. Journal of Ecology 88:213–229.

Higgins, S. I., et al. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology 88:1119–1125.

Hoffmann, W. A., and O. T. Solbrig. 2003. The role of topkill in the differential response of savanna woody species to fire. Forest Ecology and Management 180:273–286.

Huntley, B. J. 1984. Ecological effects of fire in South African ecosystems. Pages 1–18 *in* P. De Booysen and N. M. Tainton, editors. Ecological studies 48. Springer-Verlag, Berlin, Germany.

Kennan, T. C. D. 1971. The effects of fire on two vegetation types at Matopos, Rhodesia. Proceedings: Tall Timbers Fire Ecology Conference 11:53–98.

Kennedy, A. D., and A. L. F. Potgieter. 2003. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. Plant Ecology 167:179–192.

Liedloff, A. C., and G. D. Cook. 2007. Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the Flames simulation model. Ecological Modeling 201:269–282.

Lloret, F., H. Estevan, J. Vayreda, and J. Terradas. 2005. Fire regenerative syndromes of forest woody species across fire and climatic gradients. Oecologia 146:461–468.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology 86:2705–2715.

Midgley, J. J., D. Balfour, and N. Govender. 2006. Is carry-over of grass biomass between years import in determining savanna fire regimes. African Journal of Range and Forage Science 23:81–83.

Moreira, A. G. 2000. Effects of fire protection on savanna structure in Central Brazil. Journal of Biogeography 27: 1021–1029.

Naiman, R. J., L. Braack, R. Grant, A. C. Kemp, J. T. du Toit, and F. J. Venter. 2003. Interactions between species and ecosystem characteristics. Pages 221–241 *in* J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA.

Nefabas, L. L., and J. Gambiza. 2007. Fire-tolerance mechanisms of common woody plant species in a semiarid savanna in south-western Zimbabwe. African Journal of Ecology 45: 550–556.

O'Regan, S. R. 2005. The long-term effects if fire frequency and season on woody vegetation in the Pretoriuskop sourveld of the Kruger National Park. Thesis. University of the Witwatersrand, Johannesburg, South Africa.

Parr, C. L., and A. N. Andersen. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20:1610–1619.

Riginos, C., and J. B. Grace. 2008. Tree density, wild ungulate habitat use and the herbaceous community in a Kenyan savanna: top-down vs. bottom-up effects. Ecology 89:2228–2238.

Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. Nature 438:846–849.

Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree-grass coexistence in savannas revisited: insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480–490.

Shackleton, C. M., and R. J. Scholes. 2000. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. Koedoe 43(1):75–81.

Shultz, A. E. N. 2007. Can the season of burning affect the growth of *Dichrostachys cinerea* populations? A hypothesis of phenology. Thesis. University of Cape Town, South Africa.

Smit, I. P. J., and C. C. Grant. 2009. Managing surface-water in a large semi-arid savanna park: effects on grazer distribution patterns. Journal for Nature Conservation 17:61–71.

Terrasolid. 2008. Terrascan/Terramatch. Version 8.003. Terrasolid, Jyväskylä, Finland.

Trapnell, C. G. 1959. Ecological results of woodland and burning experiments in northern Rhodesia. Journal of Ecology 47:129–168.

Treydte, A. C., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology, Evolution and Systematics 8:197–205.

Van der Schijff, H. P. 1958. Inleidende verslag oor veldbrandnavorsing in die Nasionale Krugerwildtuin. Koedoe 1:60–93.

van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. van de Koppel, N. De Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350.

van Wilgen, B. W., N. Govender, and H. C. Biggs. 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. International Journal of Wildland Fire 16:519–530.

van Wilgen, B. W., N. Govender, H. C. Biggs, D. Ntsala, and X. N. Funda. 2004. Response of savanna fire regimes to changing fire management policies in a large African national park. Conservation Biology 18:1533–1540.

van Wilgen, B. W., N. Govender, and S. MacFadyen. 2008. An assessment of the implementation and outcomes of recent changes to fire management in the Kruger National Park. Koedoe 50:22–31.

Van Wyk, P. 1971. Veld burning in the Kruger National Park: an interim report of some aspects of research. Proceedings: Tall Timbers Fire Ecology Conference 11:9–31.

Venter, F. J. 2004. An identification and evaluation of outliers in the experimental burning plots, Kruger National Park: an objective benchmarking. Internal report. South African National Parks, Skukuza, South Africa.

Vigilante, T., D. M. J. S. Bowman, R. Fisher, J. Russell-Smith, and C. Yates. 2004. Contemporary landscape burning patterns in the far North Kimberley region of north-west Australia: human influences and environmental determinants. Journal of Biogeography 31:1317–1333.

Whateley, A. M., and A. J. Wills. 1996. Colonization of a subtropical woodland by forest trees in South Africa. Lammergeyer 44:19–30.

Yeaton, R. I. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. Journal of Ecology 76:1017–1029.