EFFECTS OF FOUR DECADES OF FIRE MANIPULATION ON WOODY VEGETATION STRUCTURE IN SAVANNA

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Abstract. The amount of carbon stored in savannas represents a significant uncertainty in global carbon budgets, primarily because fire causes actual biomass to differ from potential biomass. We analyzed the structural response of woody plants to long-term experimental burning in savannas. The experiment uses a randomized block design to examine fire exclusion and the season and frequency of burn in 192 7-ha experimental plots located in four different savanna ecosystems. Although previous studies would lead us to expect tree density to respond to the fire regime, our results, obtained from four different savanna ecosystems, suggest that the density of woody individuals was unresponsive to fire. The relative dominance of small trees was, however, highly responsive to fire regime. The observed shift in the structure of tree populations has potentially large impacts on the carbon balance. However, the response of tree biomass to fire of the different savannas studied were different, making it difficult to generalize about the extent to which fire can be used to manipulate carbon sequestration in savannas. This study provides evidence that savannas are demographically resilient to fire, but structurally responsive.

Key words: carbon sequestration; fire; long-term ecological research; savanna.

INTRODUCTION

Tropical savannas are characterized by a codominance of grasses and trees. Savannas are globally important, not just because they occupy 11% of the earth's land-surface (Scholes and Hall 1996), but because they are characterized by a substantial discrepancy between the climatically defined potential biomass and observed biomass (Sankaran et al. 2005). This discrepancy between potential and realized biomass can often be attributed to the consumptive effects of fire (Bond et al. 2005). A good example of this is the Venezuelan Llanos where the total ecosystem carbon stock of burnt savannas can vary threefold from the climate potential (San Jose et al. 1998). Similarly, Australian estimates suggest that while the net ecosystem productivity in savannas without fire is 3 Mg C·ha^{-1}·yr^{-1}, it is only 1 Mg C·ha^{-1}·yr^{-1} in savannas with fire (Williams et al. 2004). It follows that the effect of fire on savannas is a significant uncertainty in the global carbon budget (Bond et al. 2005).

Fire not only influences the total biomass of savanna systems it also markedly influences the structure of savannas. Structural changes influence the microclimate and the distribution of resources such as nutrients and moisture (Ludwig et al. 2004). These changes in turn have cascading effects on biodiversity (Walker and Peet 1983, Bigalke and Willan 1984) with some organisms responding to microclimate and resource availability, while others are influenced directly by woodland structure (Raman et al. 1998, Williams et al. 2002, Skowno and Bond 2003, Ripple and Beschta 2004).

The literature reviewed in the previous paragraphs suggests that fire is an important modifier of savannas. Yet, few long term data sets document the extent to which fire can structure savannas. Most insights are derived from short-term (e.g., Andersen et al. 2005) or poorly replicated fire manipulations (see Bond et al. [2005] for a recent synthesis) and therefore provide limited insight as to how different frequencies and seasons of burning may shape savannas. In this paper, we present an analysis of a unique data set derived from an experiment initiated in 1954 that aimed to explore the role of fire frequency and fire season on the structure of savanna vegetation. A special feature of this study is its large scale and high level of replication. The experiment manipulated the frequency and season of burn in 192 7-

ha experimental plots for more than 40 years. Our primary aim is to analyze structural changes that have occurred between the initiation of the experiment in 1954 and follow-up vegetation surveys conducted between 1996 and 1999. Specifically, we ask, did fire regime lead to changes in the density of trees and in the above ground biomass of trees?

A second aim is to test a model that proposes that savanna structure is defined by the probability of trees escaping fire sensitive size classes (Higgins et al. 2000). This "demographic bottleneck model" was presented as an alternative to the rooting niche model of savanna structure (Walter 1971, Walker and Noy-Meir 1982), yet empirical tests of the model's predictions are lacking. We test this model using the data from this experiment and supplementary data on the response of trees to fire.

METHODS

Study site and experimental design

Biggs et al. (2003) provide a very useful history of the experiment and its design; we provide only a brief summary of pertinent information. The study site is the Kruger National Park, a 20 000-km^2 reserve located on the border between South Africa and Mozambique. The experimental burn trials were initiated in 1954. They are replicated in four representative savanna ecosystems (hereafter called landscapes) of the Kruger National Park. The Mopani landscapes are dominated by *Colophospermum mopane* growing on basalt-derived soils, mean annual precipitation (MAP) is 447 mm. The Satara landscapes are dominated by *Acacia nigrescens* growing on basalt-derived soils, MAP is 537 mm. The Skukuza landscapes are dominated by *Combretum* species on granite soils, MAP is 550 mm. The Pretoriuskop landscape is dominated by *Terminalia sericea* growing on granite soils, MAP is 737 mm.

The experiment is replicated 16 times, with four replicates in each of the four landscapes. Each replicate consists of 12 different experimental treatments and each treatment is implemented in a 7-ha plot. Eleven treatments manipulate the season and frequency of burning, while a 12th treatment excludes fire. The 11 burning treatments are April (early dry season) biennial and triennial; August (dry season) annual, biennial, and triennial; October (early growing season) biennial and triennial; December (early to mid growing season) biennial and triennial; February (mid to late growing season) biennial and triennial. The experimental design is unbalanced, that is not all combinations of all treatments are implemented. The experiment was laid out between 1954 and 1956. In 1979, some plots, in some landscapes were split to allow the implementation of additional treatments; we do not analyze the data emerging from these new treatments.

We analyze data emerging from two woody vegetation surveys, the first was conducted in 1956/1957 and the second between 1996 and 1999. The later survey replicated the methods used in the original survey and collected additional information on vegetation structure. The surveys recorded the size class (the size classes are defined in Appendix A), and species of each woody individual encountered on two belt transects on each experimental plot. In the second survey, the height of each individual was also recorded. The belt transects were orientated to run diagonally from corner to corner of each plot. In the initial survey, each belt transect was 305 × 1.52 m in size, in the second survey the transect width was increased to 2 m, and the transect length varied from 150 to 500 m. The shorter transect lengths are due to the splitting of two plots in each block in 1979 as described in the previous paragraph. In all cases, transect dimensions are known and are used to express the data as densities. The data from the transect pairs were pooled prior to analysis.

We will use the following terminology to describe aspects of the experimental design. "Landscape" refers to one of the four savanna ecosystems types (Mopani, Satara, Skukuza, Pretoriuskop); "string" refers to one of the 16 replicate complete blocks, four of which are found in each landscape; "plot" refers to an individual ~7-ha experimental plot on which a particular treatment was implemented.

Statistical methods

We use analysis of variance to analyze three response variables: change in tree density, change in small tree dominance, and change in biomass. Change in tree density is the change in number of trees per hectare between the first and second survey. The change in dominance of small individuals is simply the proportion of individuals that were small (<2 m in height) at the second survey minus the proportion of individuals that were small at the first survey. Change in biomass is the change in the estimated aboveground tree biomass per hectare between the first and second survey. To calculate both the change in small tree dominance and change in biomass, we need to transform the size class data collected in the first survey into height data. This transformation is explained in Appendix A. To estimate biomass (kg) from height (m) we use an allometric equation: biomass = $0.52 \times$ height$^{2.55}$; the estimation of the parameters of this equation is explained in Appendix B. Two of the response variables analyzed were Box-Cox transformed for the analyses of variance; however untransformed values are plotted in the figures. The Box-Cox parameters used are, respectively, 0.5 and 0.25 for the change in individual density and change in biomass variables.

We use two analyses of variance models to analyze these three response variables. The first considers the fixed factors fire exclusion (two levels: yes, no) and landscape (four levels: Mopani, Satara, Skukuza, and Pretoriuskop) and treats the string (16 levels) as a random effect. The fire exclusion factor groups all fire treatments into one factor level, hence this first analysis of variance model allows us to compare the effects of fire

exclusion to the effects of burning at different seasons and frequencies. The second analysis of variance model considers the fixed factors fire return interval (three levels: annual, biennial, triennial), fire season (five levels: April, August, October, December, February), and landscape (four levels: Mopani, Satara, Skukuza, and Pretoriuskop), with string (16 levels) being treated as a random effect. In this second analysis of variance model, the fire exclusion plots are excluded.

The demographic bottleneck model (Higgins et al. 2000) predicts that the intensity of fires and the topkill responses of plants to fires of different intensities should explain significant amounts of variance in savanna structure. To test whether topkill can predict the observed shifts in the structure of the tree populations on the experimental plots we use two two-stage projection matrices

$$\mathbf{N} = \begin{bmatrix} 1-g & f \\ g & 1 \end{bmatrix}$$

$$\mathbf{F} = \begin{bmatrix} 1-g(1-s_j) & f+1-s_a \\ gs_j & s_a \end{bmatrix}.$$

The projection matrix $\mathbf{N}$ describes the growth that occurs in years without fires, it states that the growth rate g defines the transition from the small to the large size class and that the parameter f defines the offspring produced per individual in the large size class. The parameters f and g are unknown; we selected f and g so that populations simulated using these matrices increase slowly. Years with fires are described by the matrix $\mathbf{F}$. This matrix modifies matrix $\mathbf{N}$ by considering the effect of the topkill rates of small $(1 - s_j)$ and large trees $(1 - s_a)$ on the rates of transition between the small and large size classes. The parameters s_j and s_a are defined by a landscape-specific logistic regression model of topkill probability, $p_L(h, I)$. The logistic regression models (see Appendix C) describe topkill probability as function of tree height (h) and fire intensity (I). The parameters s_j and s_a are defined using the topkill models as $s_j = 1 - p_L(1, I_i)$ and $s_a = 1 - p_L(3, I_i)$. The values 1 (m) and 3 (m) are chosen as the modal tree heights of the small and large size classes. I_i is the fire intensity randomly sampled (with replacement) from the empirical distribution of the landscape and treatment specific fire intensities as described by Govender et al. (2006). The median number of data points available for estimating the distributions of fire intensities was 21, the lowest number was 4, and the highest number was 54.

The stable size distributions implied by these matrices are calculated by simulation for the experiments three fire return interval cases. For plots with triennial fires, we simulated using the product $\mathbf{NNFNNFn}_t$, for biennial fires with the product $\mathbf{NFNFNFn}_t$, and for annual fires with $\mathbf{FFFFFFn}_t$ (where $\mathbf{n}_t$ is the state vector). The stable size class distributions are compared to the size distribution observed on the experimental plots at the time of the second survey.

We use a linear mixed effects model (with fixed effects expected proportion of large trees and landscape and random effect string) to test whether the expected proportion of large trees predicted by the transition matrices are significantly related to the proportion of large (>2 m tall) trees observed at the second survey.

RESULTS

Fire exclusion

Fire exclusion did not significantly influence the change in mean density of individual woody plants (Fig. 1, $F_{1, 150} = 1.83$, $P = 0.18$). However, landscape had a highly significant effect ($F_{3, 10} = 55.56$, $P < 0.001$) on the change in the density of individuals; three landscapes effected a decrease in the density of individuals (there were 1017, 1476, and 214 fewer individuals per hectare in Mopani, Satara, and Skukuza respectively), while Pretoriuskop effected an increase of 3270 individuals per hectare. Note that, in the description of the analysis of variance results, we report the treatment effects, whereas Figs. 1 and 2 plot the mean responses. For three landscapes the direction of the change in the density of individuals was as anticipated, fire exclusion lead to more of an increase or less of a decrease in the density of individuals. For the remaining landscape, Skukuza, the fire-exclusion plots lost more individuals than plots that were burned (this interaction between fire exclusion and landscape was not significant; $F_{3, 150} = 1.96$, $P = 0.12$). Field observations lead us to speculate that this is because the dominant species (*Combretum* spp.) in the Skukuza landscape cannot regenerate in the absence of fire and saplings appear to be shade intolerant.

The effects of fire on vegetation structure are explored by examining the change in dominance in size structure (Fig. 1). Analysis of variance of these data shows no significant landscape effect ($F_{3, 10} = 1.36$, $P = 0.31$), but a significant effect of fire exclusion ($F_{3, 150} = 20.59$, $P < 0.001$). The effect of fire exclusion was to reduce small tree dominance by 12%, while the effect of fire was to increase small tree dominance by 1%.

An analysis of the change in above ground biomass showed that fire exclusion plots increased significantly in above ground woody biomass (Fig. 1, $F_{1, 150} = 20.68$, $P < 0.001$). The effect of fire exclusion was to increase in biomass by 6059 kg/ha, while the effect of exposure to fire was a loss of 551 kg/ha. The landscape effect on above ground woody biomass was also significant ($F_{3, 10} = 6.11$, $P = 0.013$); with the Pretoriuskop landscapes gaining 5695 kg/ha, whereas Mopani, Satara, and Skukuza lost 2833, 1766, and 379 kg/ha, respectively.

Fire return interval and season

Neither fire return interval ($F_{2, 132} = 1.13$, $P = 0.32$) nor fire season ($F_{4, 132} = 0.69$, $P = 0.60$) had significant effects on the change in the density of individuals over the course of the experiment (Fig. 2); landscape did have a significant effect ($F_{3, 12} = 35.46$, $P < 0.001$). The Mopani, Satara, and Skukuza landscapes effected
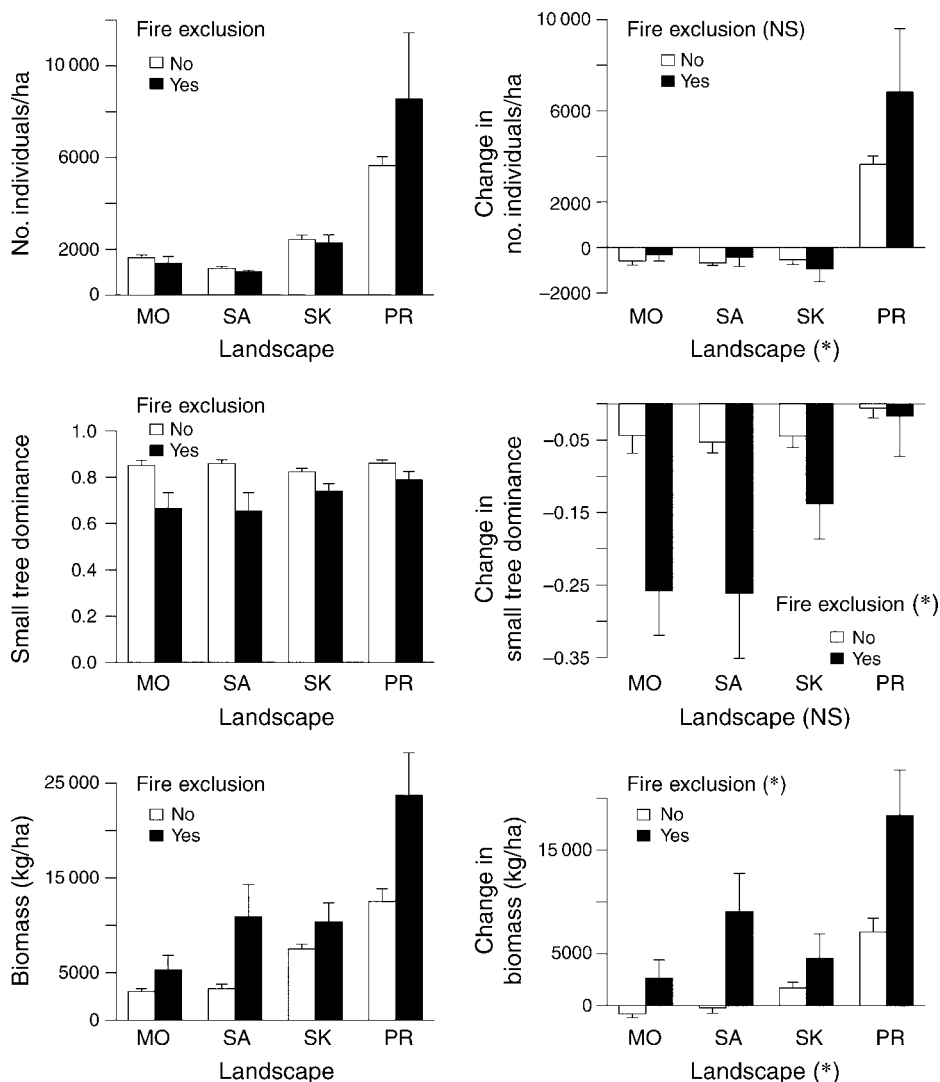
REPORTS

FIG. 1. The mean estimate at the second survey (left-hand panels) and mean change (right-hand panels) in the number of woody individuals, dominance of small trees (proportion of all trees <2 m height), and aboveground woody biomass after four decades in different landscapes (MO, Mopani; SA, Satara; SK, Skukuza; PR, Pretoriuskop). Open bars are plots that were burned in different seasons and at different frequencies; solid bars are fire-exclusion plots. Analysis of variance was used to test the effects of fire exclusion and landscape on the change response variables (right panels); factors that were not significant are indicated by NS; factors that were significant at $P < 0.05$ are indicated by an asterisk (see *Results* for details). The fire-exclusion plots on two strings were exposed to runaway wildfires (Pretoriuskop Fayi burned in 1991 and Mopani Tsende burned in 1968); these two strings are excluded from these analyses. Error bars indicate +SE.

decreases of 1361, 1064, and 924 individuals/ha; Pretoriuskop effected an increase in individual density of 3349 individuals/ha (Fig. 2).

There was a significant effect of fire return interval ($F_{2,132} = 19.66$, $P < 0.001$; Fig. 2) on the change in dominance of small trees. Annual and biennial fires had the effect of increasing small tree dominance by 9% and 2%, respectively; whereas triennial fires had the effect of decreasing small tree dominance by 4%. Fire season had a significant effect ($F_{4,132} = 2.64$, $P = 0.037$; Fig. 2) on the change in dominance of small trees. The effect of growing season fires (October, December, and Febru-

ary) was to reduced the dominance of small trees by 2%, 2%, and 1%, respectively; whereas the effect of dormant season (April and August) fires was to increase small tree dominance by 2%. Although landscape had no significant effect on the change in dominance of small trees ($F_{3,12} = 0.89$, $P = 0.47$), a significant interaction between landscape and fire-return interval ($F_{6,132} = 3.34$, $P = 0.004$) was detected. This could be attributed to the weaker effect of fire frequency on the Satara landscape.

The change in aboveground biomass was significantly influenced by fire return interval ($F_{2,132} = 5.43$, $P = 0.005$) but not by fire season ($F_{4,132} = 1.58$, $P = 0.18$). A
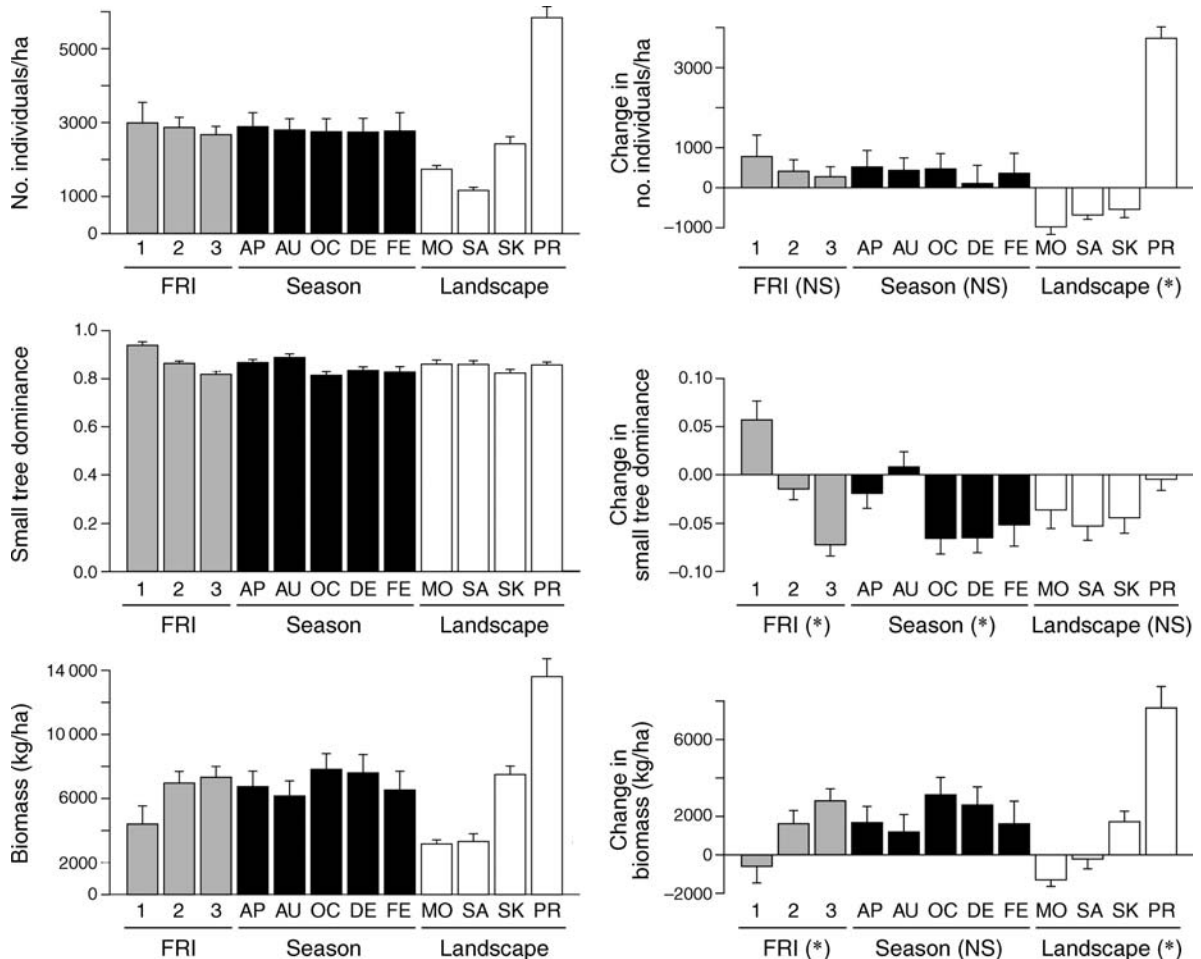
FIG. 2. The mean estimate at the second survey (left-hand panels) and mean change (right-hand panels) in the number of woody individuals, dominance of small trees (proportion of all trees <2 m height) and aboveground woody biomass after four decades in response to fire return interval (FRI; gray bars) and fire season (black bars; letters are the first two letters of the month in which fires were ignited). The mean responses in the different landscapes are indicated by the white bars (MO, Mopani; SA, Satara; SK, Skukuza; PR, Pretoriuskop). Analysis of variance was used to test the effect of the factors fire return interval, fire season, and landscape on the change response variables (right-hand panels); factors that were not significant are indicated by NS; factors that were significant at $P < 0.05$ are indicated by an asterisk (see *Results* for details). Error bars indicate +SE. Fire-exclusion plots are excluded from these analyses.

2566 kg/ha decrease in biomass could be attributed to annual fires, and 342 kg/ha decrease could be attributed to biennial fires. The effect of triennial fires was to increase biomass by 853 kg/ha (Fig. 2). Landscape had a significant effect on the change of above ground woody biomass ($F_{3,12} = 7.88$, $P = 0.004$), with the Pretoriuskop landscape effecting a gain in biomass of 5683 kg/ha, and the Mopani, Satara, and Skukuza landscapes effecting losses in biomass of 3266, 2175, and 242 kg/ha, respectively.

Topkill

The proportion of large trees present on the plots at the time of the second survey was significantly (Fig. 3; $F_{1, 159} = 15.49$, $P < 0.001$) related to the proportion of large trees at the stable size class distribution (a square-root transformation was used for this analysis). The

factor landscape did not significantly influence this trend ($F_{3,12} = 0.37$, $P = 0.77$).

DISCUSSION

Previous studies in savannas would lead us to expect decreases in tree densities in response to increases in fire frequency (Hoffmann 1999). Other studies have shown that the mortality rates of individuals (Trapnell 1959, Geldenhuys 1977, Williams et al. 1999) and individual densities (Rose Innes 1972, Russell-Smith et al. 2003) are responsive to fire season. Yet, the results of more than four decades of fire manipulation presented here show that fire frequency, fire season, and total fire exclusion do not influence the density of trees. This finding was consistent across four different savanna sites ranging from moist (737 mm rainfall/yr) to semiarid (447 mm
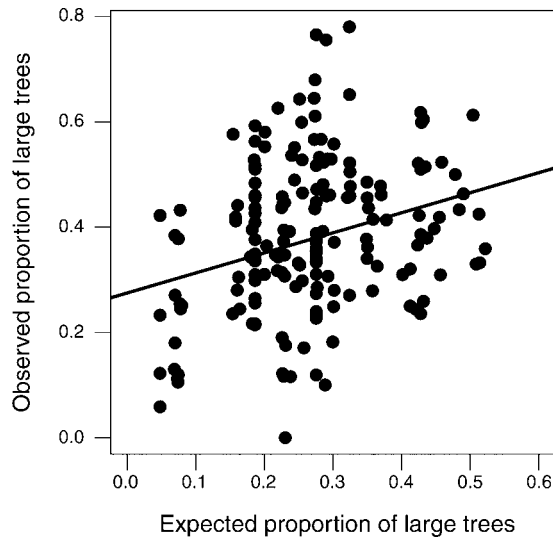
FIG. 3. The observed proportion of large (>2 m tall) trees at the second survey plotted against the proportion of large trees expected at the stable size class distribution (square-root transformed). There is a significant relationship between observed and expected ($F_{1, 159} = 15.49$, $P < 0.001$). The calculation of the stable size distributions is explained in *Statistical methods*. Fire-exclusion plots are excluded from these analyses.

rainfall/yr) and from nutrient-poor granitic soils to nutrient-rich basaltic soils. The expected trend of a decrease in tree density with increasing fire frequency was not observed, instead tree density increased (nonsignificantly) with increasing fire frequency (Fig. 2).

We interpret the results in terms of the high vulnerability of savanna trees to fire-induced stem mortality (topkill) combined with a high resilience to fire induced individual mortality. The resilience is due to the capacity of most savanna tree species to resprout after fire from root stocks and because stem mortality rates, while high (>0.9) for small (<2 m in height) stems are low (<0.05), for larger stems (Higgins et al. 2000, Hoffmann and Solbrig 2003). Hence, repeated fires can keep individuals small, but individuals rarely suffer mortality and large individuals are virtually immune from fire damage. This syndrome has been called the Oskar syndrome (after Günter Grass' character Oskar Matzerath), which emphasizes the potentially advanced age of a small individual, or the Gulliver syndrome (after Jonathan Swift's character Lemuel Gulliver), which emphasizes a tree's potential to be a giant once it escapes fire. Simulation modelling studies of the potential consequences of the Oskar/Gulliver syndrome for savannas have shown that the distribution of fire intensities at a site can shape the structure of the tree stratum (Higgins et al. 2000, Gardner 2006). Our empirical analyses support the Oskar/Gulliver hypothesis in two regards. First, we found that the density of individuals did not appear to be influenced by fire, but that structural dominance was related to fire (Figs. 1 and 2). Second, we found that sites with fire treatments that increased the probability of stems surviving fire, were more likely to be dominated by larger individuals (Fig. 3).

Although we found that fire did not influence tree density, we did find that fire influenced the size structure and biomass of tree populations. The observed shifts in structural dominance have potentially significant implications for carbon budgets of savanna ecosystems. Fire exclusion led to an average increase in aboveground woody biomass of 6059 kg/ha, while sites exposed to fire lost on average 551 kg/ha of aboveground woody biomass. Burning annually led to an average loss of 2266 kg/ha over the course of the experiment; whereas burning every three years lead to an average accumulation of 853 kg/ha. These averaged effects mask the larger changes seen at some sites (Fig. 2), which suggest that we should be cautious when extrapolating averaged responses or single-site responses to regional carbon budgets. Notable here is the mesic site (Pretoriuskop), where fire exclusion plots gained 11 754 kg/ha and even burned plots gained on average 5508 kg/ha in aboveground woody biomass over the course of the experiment. Why woody biomass increased, irrespective of burning treatment, at the mesic sites but not at the arid sites remains unclear. It has, for instance, been suggested that atmospheric CO_2 concentrations (which have increased from 310 to 375 ppm over the course of the experiment) would increase the chances of trees escaping fires (Hoffmann et al. 2000, Bond et al. 2003). While this theory could explain the trends observed at Pretoriuskop, it does not provide an explanation for why similar trends were not observed at the more arid sites in this study. This suggests either that the benefits that C_3 trees gain over C_4 grasses due to increased atmospheric CO_2 levels are small, or that they need to be considered in the context of the interactions between moisture availability, the probability of trees escaping fire, and atmospheric CO_2.

The variable response of the savannas in different landscapes to long-term burning observed in this study also emerges from the literature on long-term fire manipulations in Africa. For example Chidumayo (1988) found little structure response after 29 years of fire exclusion in Zambia, yet Brookman-Amissah et al. (1980) found structural responses to fire season and fire exclusion in Ghana as did Rose Innes (1972) in Nigeria, Ivory Coast, and Ghana. This literature and our own findings make it difficult to generalize about the influence of fire on magnitude of carbon storage in African savannas. Future work should seek to understand how soils, climate, and CO_2 interact to determine how fire structures savannas.

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APPENDIX A

Estimating tree height (Ecological Archives E088-070-A1).

APPENDIX B

Estimating tree biomass (Ecological Archives E088-070-A2).

APPENDIX C

Topkill models (Ecological Archives E088-070-A3).