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Woody cover in wet and dry African savannas after six decades of experimental fires.

Aisling P. Devine*, Iain Stott, Robbie A. McDonald and Ilya M. D. Maclean

Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, TR10 9FE, UK

***Correspondence author. E-mail:** a.p.devine@swansea.ac.uk ; aislingdevine86@gmail.com

Running headline: Effects of fire in wet and dry savannas

Summary

Fire is an integral process in savannas because it plays a crucial role in altering woody cover of this globally important biome. In this study we examine the long term effects of varying fire frequencies over a 60 year time period in South Africa. We analyse the effects of fire exclusion and of experimental burns every 1, 2 and 3 years on woody cover, tree abundance and stem structure on a wet and dry savanna. Increased fire frequency did not display a consistent effect on woody cover. The presence of fire, irrespective of frequency, was much more influential in lowering tree abundance in the wet savanna than the dry savanna. In the dry savanna, fire was more effective in greatly increasing coppicing in trees, when compared to the wet savannas. The effects of fire on three measures of savanna woody vegetation differed between wet and dry experimental sites. We suggest that vegetation responses to fire are dependent on local conditions, which are likely influenced by rainfall. Therefore we suggest that management strategies should take account of whether a savanna is a wet or dry system when implementing fire management regimes.

Key-words

disturbance, mesic savannas, plant populations and community dynamics, savannah, semi-arid savannas, vegetation dynamics, woody encroachment.

Introduction

Savannas are an ecologically and socio-economically important biome, covering approximately up to 20% of the earth's terrestrial surface and supporting one fifth of the world's human population (Parr *et al.* 2014). Savannas are characterized by the co-occurrence of trees and grasses and so woody cover is a key determinant of their properties as ecosystems (Murphy and Bowman 2012). The complexity of interactions between large-scale and local factors has hindered understanding of what regulates the co-occurrence of grasses and trees. To date, one of the most convincing explanations is that maximal woody cover is determined by rainfall but is reduced at many locations by local disturbances (Sankaran *et al.* 2005).

Making use of data from across a wide range of African savannas Sankaran *et al.,* (2005) proposed that savanna regions with annual rainfall lower then 650mm are stable systems in which woody cover is constrained by rainfall availability and in which disturbance is not required to maintain an open canopy. Consequently, rainfall higher than 650mm annually creates an increasingly unstable savanna with increased potential for woody growth. Higher mean rainfall serves to tip the balance in favour of a woodland system, though savanna can be maintained under such conditions by disturbances such as fires and livestock grazing. Understanding the mechanisms limiting woody cover on savannas is essential in order to determine current changes occurring on these systems, such as woody encroachment. More specifically, examining the extent to which the presence and frequency of disturbances limit woody cover in stable and unstable systems is crucial in order to disentangle local from larger-scale drivers that may be causing changes in woody cover.

There is disagreement about which drivers influence the extent of woody cover, especially with regards to the importance of local factors. In particular, management practices in relation to fire are acknowledged as having a major influence on African woodland and grassland ecosystems (Devineau, Fournier & Nignan 2010). Many field studies have demonstrated that the intensity and frequency of fires can affect various ecological processes and vegetation structure (Backer, Jensen & McPherson 2004; Bond, Woodward & Midgley 2005; Ryan & Williams 2011; Mitchard *et al.* 2011; Murphy & Bowman 2012; Werner & Prior 2013; Lehmann *et al.* 2014). Significant changes in fire regimes can thus be expected to have a major impact on vegetation communities. Fire increases tree seedling and sapling mortality and prolongs adult tree recruitment (Glitzenstein, Platt & Streng 1995; Bond *et al.* 2005; Werner 2012). Fire also limits tree growth by top-killing tree saplings, which do not then have enough time to resprout and grow high enough to escape the fire zone before another fire occurs (Werner & Franklin 2010). These saplings, otherwise known as “Gulliver trees”, are stuck in the fire zone for years and are unable to reproduce fully, thus limiting tree recruitment into the canopy (Werner 2012). Additionally, trees experiencing disturbance are often prone to producing multiple stems, akin to the effects of coppicing (Chidumayo 2007; Werner & Franklin 2010). Therefore savannas experiencing fire may have a higher prevalence of multi-stemmed trees, which may affect habitat structure for fauna communities, especially bird populations (Sirami *et al.* 2009) . Tree recovery after disturbance is a crucial component of fire vegetation dynamics. In populations where seed production, germination, and/or seedling survival are very low, the ability of individual established trees to resprout after disturbance is vital if a viable population is to be sustained (Bond & Midgley 2000).

The rate at which a tree can resprout and gain height after disturbance is dependent on the characteristics of the disturbance, the species and on resource availability (Bond & Midgley 2001). It is still unclear why some species are better at resprouting than others and if environmental conditions can alter this trait (Vesk & Westoby 2004). Trees in wet savannas may experience increased competition for resources due to higher population densities, but water availability is still much less of a constraint in comparison to dry savannas. In comparison to dry savannas, trees in wet savannas can potentially attain greater height after fires and therefore be more likely to escape the fire zone. Savannas experiencing lower fire frequencies will have longer periods for trees to resprout and grow enough to escape the fire zone (Bond 2008). On the other hand, a lower frequency of fires can result in more intense, destructive burns due to greater accumulations of grass fuel (Govender, Trollope & Van Wilgen 2006). More intense burns can increase tree mortality or cause more extensive damage to individual trees, which can inhibit resprouting rates, decreasing the rate of recovery. Changes in the length of recovery time or the rates of tree regrowth after a fire can be a critical determinant of the extent of woody cover.

The nature of the relationship between fire and woody cover is still not fully understood. The slow growth of woody vegetation and the effects of fire and tree composition mean that long periods of time are required before any significant change is apparent. Previous research in savanna habitats (Higgins *et al.* 2007) has examined the role of fire, and its influence on woody biomass and demographic bottlenecks in trees over a 48 year time period. In this study, we examine the effects of 60 years of experimental burning, on tree abundance, woody cover and multi-stemmed trees. Specifically, we examine these woody characteristics under different fire frequencies (fire- exclusion and fires every 1, 2 and 3 years) at two savanna sites with marked differences in annual rainfall. We determine how these differences in rainfall interact with fire frequency in altering tree abundance, woody cover and the proportion of multi-stemmed trees.

Material and methods

Study site

The study site was located on Experimental Burn Plots (EBPs) at Kruger National Park (KNP), in the Republic of South Africa (RSA). KNP is the largest national park in South Africa, covering approximately 1.9 million ha, and is also a part of the Great Limpopo Transfrontier Park spanning across Zimbabwe and Mozambique (Du Toit, Rogers & Biggs 2003). The EBPs were set up by the park authorities in 1954 and are the longest running fire experiments in Africa (Biggs *et al.* 2003). The EBPs represent the landscapes of four different regions within KNP: Mopani, Satara, Skukuza, and Pretoriuskop. Each of these four regions contains four replicate sites, within which there are 12 fire treatment plots of approximately 7 hectares. Each treatment plot was prescribed a different fire frequency treatment, which was then repeated among the four replicate sites. The fire treatments are experimental burns every 1 (annual), 2 (biennial) and 3 years (triennial) and an unburnt control.

Our study focused on two of the EBP regions, Pretoriuskop, the wet savanna and Skukuza, the dry savanna, using all replicate sites. Skukuza and Pretoriuskop are located on the Southwest part of the park, approximately 30 km apart. The Skukuza field site is a dry savanna classed as a Combretum savanna whereas Pretoriuskop is a wet savanna classed as a Sourveld savanna. Skukuza has an average annual rainfall of 572 mm, whereas Pretoriuskop is the wettest region in KNP, with an average annual rainfall of 705 mm. Thus, the two sites are on either side of the 650 mm annual rainfall threshold proposed by Sankaran *et al*. (2005). We chose Pretoriuskop and Skukuza, because these two sites (unlike Mopani and Satara) share the same underlying granite geology and so allowed the most appropriate comparison between a wet and a dry savanna. Vegetation surveys were conducted on the No-Fire Control, and the August-Annual, August-Biennial and August-Triennial treatments, the mid-dry season fires, as the aim of this study was to examine the effects of fire frequency as opposed to variation in fire seasonality (Higgins *et al*., 2007). Although KNP as a whole has a higher intensity of grazing and browsing than other non-protected savannas with a great deal of variation within the park (Smit, Grant & Devereux 2007). The grazing intensity on the field sites is predominantly evenly distributed due to the proximity of sites relative to ranges of grazing animals.

Field methods

Vegetation surveys were carried out between March and June 2012. Woody vegetation was surveyed using 2 transects per treatment plot, each 100 m in length and 2 m wide. This transect method was chosen in accordance with previous data collection methods established by the park authorities in order to ensure that the data collected were comparable to previous data (Biggs *et al.* 2003; Higgins *et al.* 2007). Trees that could not be identified in the field were sampled and later identified using resources from the Skukuza herbarium at KNP. Stem diameter was measured at standard breast height (140 cm) for each adult tree and for trees that were smaller than 140 cm basal diameter was measured instead. Trees with a basal diameter lower than 0.4 cm were classed as saplings. Each tree was classed as being single or multi-stemmed, which was then used to calculate the proportion of individual trees that were multi-stemmed per transect.

Analyses

For each transect at each plot the following measures were calculated: (1) Tree abundance, which was the total number of trees in each transect; (2) the proportion of total tree basal area to transect area, which we use as an index of ‘woody cover’; (3) the proportion of multi-stemmed trees relative to the total number of trees per transect. Logit transformations were applied to measures of woody cover and the proportion of multi-stemmed trees to ensure a continuous range of values. Multi-stem data from one of the replicate sites at Skukuza site was excluded due to an insufficient number of measured trees.

The relationship between fire frequency and savanna type on woody cover and multi-stemmed trees were examined using a linear mixed effect model with Gaussian residual variance. Tree abundance was also examined in this way as it displayed a distribution that was closer to Gaussian than Poisson (abundance was rarely close to zero), and model residuals were normally-distributed and homoscedastic. In both instances, models were fitted using Maximum Likelihood (ML) with plot modelled as a random intercept nested within treatment replication areas to account for the nested study design and concomitant variation across plots. Fixed effects were fire frequency, region (wet or dry savanna) and an interaction between fire frequency and region. Models with all possible combinations of fixed effects and a null model containing only the random effects of plot nested within area were generated. A second set of analyses was conducted, using fire presence (regardless of frequency), region, and an interaction between fire presence and region. In each case, AIC scores for each of the models were compared to identify the most parsimonious model. Analyses were performed in R (R Core Team 2013) using the nlme package (Pinheiro *et al.* 2014).

Results

Tree abundance

There were marked differences in the effects of fire on tree abundance in wet and dry savannas (Table 1). In the wet savanna, tree abundance was higher in burnt plots than in unburnt plots, whereas in the dry savanna there was little consistent variation in abundance across treatment or control plots (Fig. 1). The best model explaining variation in tree abundance was one in which fire frequency, region and the interaction between both terms were included (AIC=690.92). However, an alternative model using the presence of fire, as opposed to frequency of fire, provided a more parsimonious fit (ΔAIC=5.98). This suggests that it is the presence of fire rather than burn frequency that most influences tree abundance.

Woody cover

In common with models for tree abundance, the best models for woody cover were obtained by fitting the presence of fire, as opposed to its frequency (Table 1). The best model was obtained by fitting fire presence only (AIC=201.02), followed by fire and region combined (ΔAIC=0.22). When fitting fire frequency, the most parsimonious model was the null model (AIC=202.9). By contrast with the result for tree abundance, the model for woody cover in which an interaction between fire frequency and region was included was the poorest (ΔAIC=5.73). Although in the dry savanna, increased fire frequency did lower woody cover, the overlapping standard errors suggest a considerable degree of variability in cover across treatments. In both wet and dry savannas, woody cover was higher in control plots than in burnt plots (Fig. 2). Overall our results suggest that the effects of fire frequency had little bearing on woody cover, however the presence of fire itself did result in lower woody cover.

Multi-stemmed trees

Fire frequency, as opposed to presence, had its most marked effect on the proportion of trees that were multi-stemmed and this differed between the wet and dry savanna (Table 1). The most plausible model included both fire frequency and region and an interaction between both terms (AIC=90.57), whereas the best model fitting the presence of fire performed slightly less well (AIC=92.31). In the wet savanna the proportion of multi-stemmed trees was greater in plots subjected to annual fires. However the proportions of multi-stemmed trees were similar across the other fire frequency treatments (biennial and triennial) and the unburnt control plots (Fig. 3). In the dry savanna, the proportion of multi-stemmed trees, was higher in plots subjected to burning than in the control plots (c. 60% cf. <40%), but fire frequency appeared to be unimportant (Fig. 3).

Discussion

Previous research (Sankaran *et al.* 2005) proposes that across Africa, maximum woody cover in dry savannas, where mean annual precipitation is less than 650 mm, is constrained by, and increases linearly with, rainfall. In wetter regions, savannas are characterised as 'unstable' systems in which rainfall is sufficient for the development of woody canopy, though local disturbances can prevent this from happening. This comparative study presented a hypothesis to the effect that water availability is a key factor constraining woody vegetation in drier savannas. In wetter regions, however, tree-grass co-existence is dependent upon disturbance and changes in disturbance regimes can affect the ratio of trees to grasses. Our study has allowed the experimental comparison of savanna regions where rainfall is above and below the proposed 650 mm annual rainfall threshold (Sankaran *et al.* 2005). Our results support the hypothesis in so far as the effects of fire on tree abundance and woody cover are greater in the wetter region than in the drier region. The effects of fire on multi-stemmed tree structure also differed in wet and dry savannas.

Our study has shown that the effects of fire on woody vegetation differ by region, in relation to rainfall, emphasising the importance of the relative stability of savannas when considering the effects of fire. However an added complexity that should be considered when interpreting the results of our study is that the plots are also subject to high levels of herbivory. While it is likely that herbivory affects the overall amount of woody cover on our study sites to some extent there is no reason to suppose it acts in a way that would confound our results. If herbivory played an important role in determining woody cover one would expect greater changes in tree abundance on the dry savanna, consistent with findings in Buitenwerf *et al,* (2012).

Nevertheless, the effects of background variation in disturbance due to herbivory should be considered when implementing or interpreting the effect of fire management regimes, especially at KNP.

Increasing fire frequency did not lead to significantly lower tree abundance in the wetter savanna; the presence of fire itself rather than frequency had a greater influence on tree abundance. This has important management implications because the same outcomes for abundance can be achieved with lower burning frequency. Thus less management effort is needed to achieve the same density of trees, by extending burn intervals from annual to at least three years. However this is not to say that increased fire frequency will have no effect on other aspects of woody cover such as structure, size and species diversity. The lack of a linear decrease in tree abundance with increasing fire frequency may be due to commonly observed relationships between frequency and intensity (Govender *et al.* 2006). Higher fire frequencies often have lower burn intensity due to reduced accumulation of grass fuel load, whilst lower frequency fires can be more intense as a result of higher fuel load. It is very likely that fire regimes greater than a three-year cycle could become unmanageable due to much higher fire intensities.

Although woody cover was higher at the wet savanna than the dry savanna, proportionally larger reductions in woody cover were observed with increased fire frequency in the dry savanna. Similar findings are reported by Smit *et al.*(2010), who showed that fire caused larger reductions in the proportions of woody cover in dry savannas than in wet savannas. In our study, however, high variation in woody cover is apparent across both savanna regions and all fire frequency treatments and it would appear therefore that fire frequency had a limited additional effect. Overall, it was clear from our study that the presence of fire, irrespective of frequency, decreased woody cover. Previous research relating to the demography of trees in the Experimental Burn Plots in Kruger (Higgins *et al.* 2007; Buitenwerf *et al.* 2012) also suggests that the frequency of burning over decades has had little effect on woody cover. Interestingly, the effects of fire on tree abundance and woody cover do not correlate with each other. Woody cover is ultimately the combination of tree abundance and tree size in a given area, therefore variation in woody cover is the product of these two elements, and fire alters population and community structures (tree size distributions) as well as sizes (tree numbers). Fire decreases the presence of trees mainly by reducing the proportion of young trees that can grow to sexual maturity. This results in a disproportionate number of small trees unable to grow to maturity, but it also decreases competition among mature trees, which may lead to greater growth and survival. Therefore, repeated fires can ultimately lead to bimodal tree size distributions which may also contribute to the disparity between tree abundance and woody cover. The disparity between tree abundance and woody cover has important ecological and management implications as clearly the same fire regime could produce different outcomes in abundance versus woody cover.

Multi-stemmed trees can be prevalent in areas experiencing fire as a result of a coppicing effect after disturbance (Chidumayo 2007; Werner & Franklin 2010). The dry savanna region responded to fires by an increase in the proportion of multi-stemmed individuals, whilst in the wet savanna a similar response was observed only where burns were annual. Differences in the proportion of multi-stemmed trees may also be due to the compounding effects of water-stress, whereby trees produce multiple thinner stems rather than a single larger stem. While it also possible that this difference may be due to variation in species composition across wet and dry regions, we believe that this is unlikely as most species across both regions exhibited coppicing. Although tree composition did vary regionally, both sites also shared common species. Changes in tree structure can have implications for habitat diversity and may affect fauna communities, as well the degree of competition with grasses through changes in light regimes.

Our study can also provide insight into the ecological problem management issues associated with woody encroachment, a growing concern in African savannas (Archer, Schimel & Holland 1995). Our results lend support to the hypothesis that dry savannas are more ‘stable’ in that disturbance is not required to maintain an open savanna system. Thus, wet savannas may be more vulnerable to woody encroachment if they experience changes to management strategies that result in reduced burning. That is not say that dry savannas are not also vulnerable to woody encroachment from changes in climate or land use, which can alter water availability (Graz 2008).

Conclusions

Our study highlights the importance of local disturbance in maintaining savanna states in regions of high rainfall and supports the hypothesis of a mean annual rainfall threshold of 650mm between a stable and unstable savanna system. Though the presence of fire can alter woody vegetation on dry savannas, it is not required to permit the coexistence of trees and grasses, whilst in wet savannas disturbance is required to maintain an open system. Our study has important implications for the fire management of savanna landscapes as vegetation responses to fire differed, depending on whether it is a dry or wet savanna. Additionally the presence of fire rather than frequency was often a stronger explanatory factor in altering woody vegetation. Thus, fire frequency and savanna type should be addressed within fire management strategies.

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Data Accessibility

Data deposited in the Dryad repository (Devine *et al.*, 2014).

References

Archer, S., Schimel, D.S. & Holland, E. a. (1995) Mechanisms of shrubland expansion: land use, climate or CO2? *Climatic Change*, **29**, 91–99.

Backer, D.M., Jensen, S.E. & McPherson, G.R. (2004) Impacts of Fire-Suppression Activities on Natural Communities. *Conservation Biology*, **18**, 937–946.

Biggs, H.C., Dunne, T.T. & Govender, N. (2003) Experimental burn plot trial in the Kruger National Park : history , experimental design and suggestions for data analysis. *Koedoe*, **1**, 1–15.

Bond, W.J. (2008) What Limits Trees in C 4 Grasslands and Savannas? *Annual Review of Ecology, Evolution, and Systematics*, **39**, 641–659.

Bond, W.J. & Midgley, G.F. (2000) A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*, **6**, 865–869.

Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*, **16**, 45–51.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *The New phytologist*, **165**, 525–37.

Buitenwerf, R., Bond, W.J., Stevens, N. & Trollope, W.S.W. (2012) Increased tree densities in South African savannas: >50 years of data suggests CO2 as a driver. *Global Change Biology*, **18**, 675–684.

Chidumayo, E.N. (2007) Growth responses of an African savanna tree, Bauhinia thonningii Schumacher, to defoliation, fire and climate. *Trees*, **21**, 231–238.

Devine, A.P., Stott, I., McDonald, R.A., Maclean, I.M.D (2014) Data from: Woody cover in wet and dry African savannas after six decades of experimental fires. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.vm766

Devineau, J.-L., Fournier, A. & Nignan, S. (2010) Savanna fire regimes assessment with MODIS fire data: Their relationship to land cover and plant species distribution in western Burkina Faso (West Africa). *Journal of Arid Environments*, **74**, 1092–1101.

Du Toit, J.., Rogers, B. & Biggs, H.. (2003) *The Kruger Experience: Ecology And Management Of Savanna Heterogeneity.* (ed BH. Du Toit J.T, Rogers K.H). Island Press.

Glitzenstein, J.S., Platt, W.J. & Streng, D.R. (1995) Effects of Fire Regime and Habitat on Tree Dynamics in North Florida Longleaf Pine Savannas. *Ecological Monographs*, **65**, 441.

Govender, N., Trollope, W.S.W. & Van Wilgen, B.W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*, **43**, 748–758.

Graz, F.P. (2008) The woody weed encroachment puzzle : gathering pieces. , **348**, 340–348.

Higgins, S.I., Bond, W.J., February, E.C., Bronn, A., Euston-Brown, D.I.W., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A.L.F., Scheiter, S., Sowry, R., Trollope, L. & Trollope, W.S.W. (2007) Effects of four decades of fire manipulation on woody vegetation structure in Savanna. *Ecology*, **88**, 1119–25.

Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.S. & Bond, W.J. (2014) Savanna vegetation-fire-climate relationships differ among continents. *Science (New York, N.Y.)*, **343**, 548–52.

Mitchard, E.T.A., Saatchi, S.S., Lewis, S.L., Feldpausch, T.R., Woodhouse, I.H., Sonké, B., Rowland, C. & Meir, P. (2011) Measuring biomass changes due to woody encroachment and deforestation/degradation in a forest–savanna boundary region of central Africa using multi-temporal L-band radar backscatter. *Remote Sensing of Environment*, **115**, 2861–2873.

Murphy, B.P. & Bowman, D.M.J.S. (2012) What controls the distribution of tropical forest and savanna? *Ecology letters*, **15**, 748–58.

Parr, C.L., Lehmann, C.E.R., Bond, W.J., Hoffmann, W.A. & Andersen, A.N. (2014) Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in ecology & evolution*, **29**, 205–213.

Pinheiro, J., Bates, D., DebRoy, S., D, S. & Team, R.C. (2014) nlme: Linear and Nonlinear Mixed Effects Models.

R Core Team. (2013) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Ryan, C.M. & Williams, M. (2011) How does fire intensity and frequency affect miombo woodland tree populations and biomass? *Ecological Applications*, **21**, 48–60.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846–9.

Sirami, C., Seymour, C., Midgley, G. & Barnard, P. (2009) The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions*, **15**, 948–957.

Smit, I.P.J., Asner, G.P., Govender, N., Kennedy-Bowdoin, T., Knapp, D.E. & Jacobson, J. (2010) Effects of fire on woody vegetation structure in African savanna. *Ecological Applications*, **20**, 1865–1875.

Smit, I.P.J., Grant, C.C. & Devereux, B.J. (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, **136**, 85–99.

Vesk, P.A. & Westoby, M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology*, **92**, 310–320.

Werner, P.A. (2012) Growth of juvenile and sapling trees differs with both fire season and understorey type: Trade-offs and transitions out of the fire trap in an Australian savanna. *Austral Ecology*, **37**, 644–657.

Werner, P.A. & Franklin, D.C. (2010) Resprouting and mortality of juvenile eucalypts in an Australian savanna: impacts of fire season and annual sorghum. *Australian Journal of Botany*, **58**, 619–628.

Werner, P.A. & Prior, L.D. (2013) Demography and growth of subadult savanna trees: interactions of life history, size, fire season, and grassy understory. *Ecological Monographs*, **83**, 67–93.

Van Wilgen, B.W., Govender, N., Biggs, H.C., Ntsala, D. & Funda, X.N. (2004) Response of Savanna Fire Regimes to Changing Fire-Management Policies in a Large African National Park. *Conservation Biology*, **18**, 1533–1540.

Table

Table 1. Results from an analysis of the effects of fire, fire frequency and region upon woody vegetation characteristics at Pretoriuskop (wet savanna and Skukuza (dry savanna) in Kruger National Park, South Africa. Results are the Akaike's Information Criterion for linear mixed effect model analyses. Two sets of models are fitted, one with fire frequency as a linear covariate and the other with fire fitted as a binary, presence/absence factor

	Abundance		Woody cover		Multi-stemmed	
Model Terms	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Fire frequency						
Fire frequency + region interaction	690.92	*	208.62	5.73	90.57	*
Fire frequency + region	693.05	2.14	204.48	1.59	93.93	3.36
Region	695.24	4.33	203.22	0.32	104.72	14.15
Fire frequency	697.07	6.16	204.29	1.39	96.52	5.95
Null model	699.26	8.34	202.90	*	106.29	15.79
Fire Presence						
Fire presence + region interaction	685.03	*	203.21	2.19	92.31	*
Fire presence+ region	690.44	5.41	201.23	0.22	95.64	3.34
Region	695.24	10.21	203.22	2.20	104.72	12.41
Fire presence	694.46	9.43	201.02	*	98.15	5.85
Null model	699.26	14.23	202.90	1.88	106.29	13.98

Figures

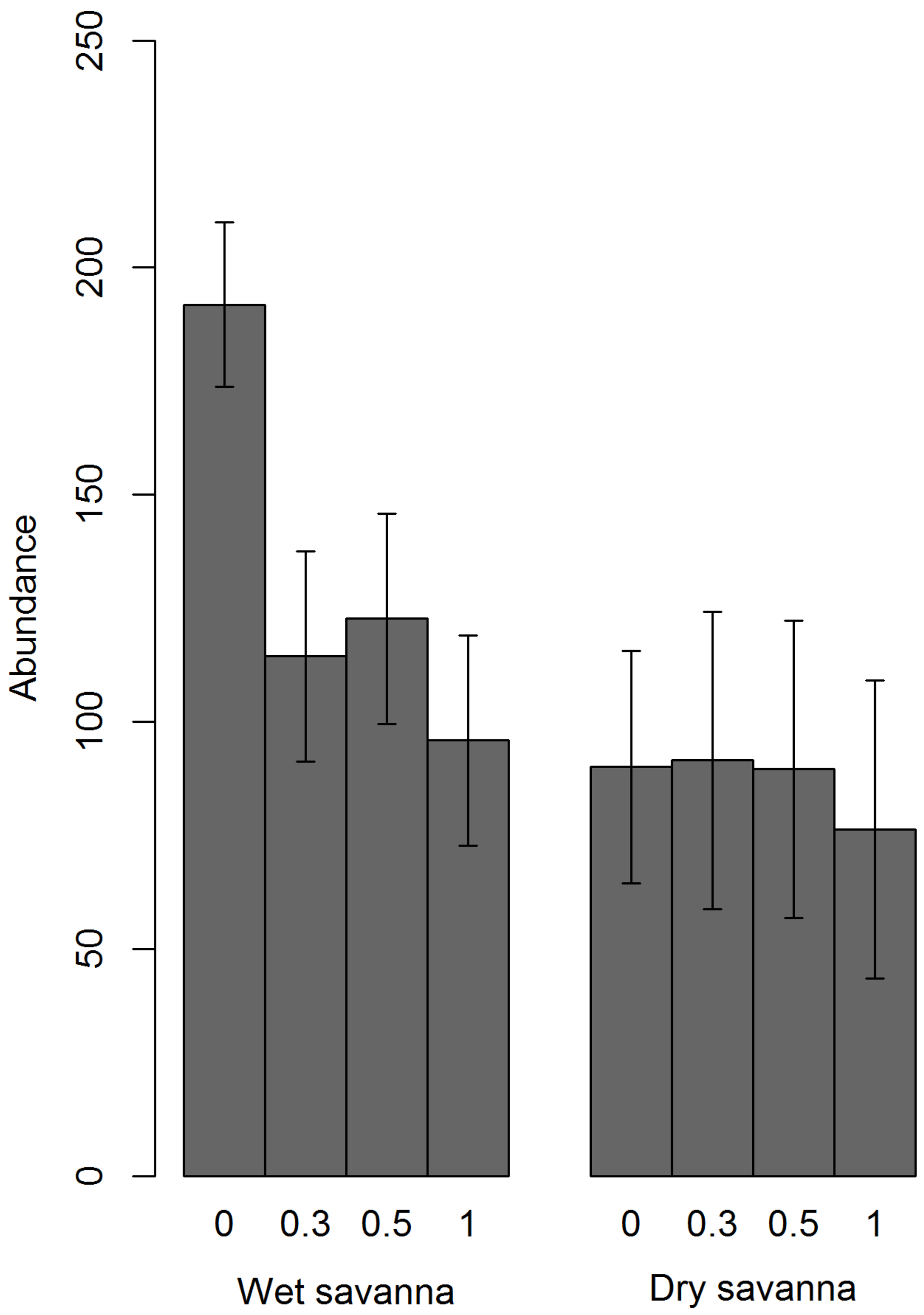

Fig. 1. Tree abundance (mean ±1 S. E.) in plots subject to different burn treatments estimated from the linear mixed effect model. Results are shown for the long-term experimental burn plots at Pretoriuskop, the wet savanna and Skukuza, the dry savanna subjected to the following burning frequencies; 0=control plot, 0.3=triennial, 0.5=biennial and 1=annual.

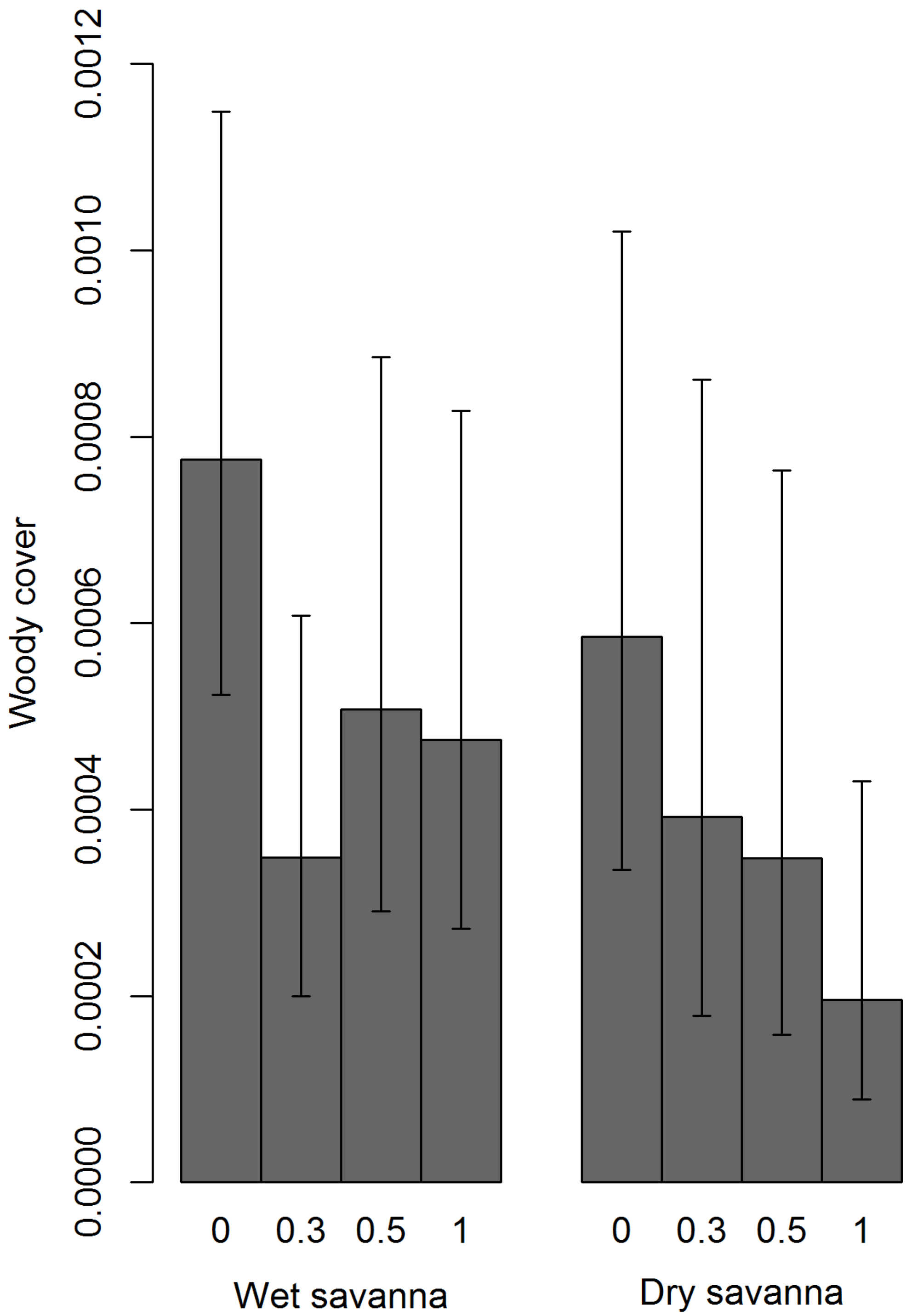

Fig. 2. Woody cover (mean ±1 S. E.) in plots subject to different burn treatments estimated from the linear mixed effect model. Results are shown for the long-term experimental burn plots at Pretoriuskop, the wet savanna and Skukuza, the dry savanna subjected to the following burning frequencies; 0=control plot, 0.3=triennial, 0.5=biennial and 1=annual.

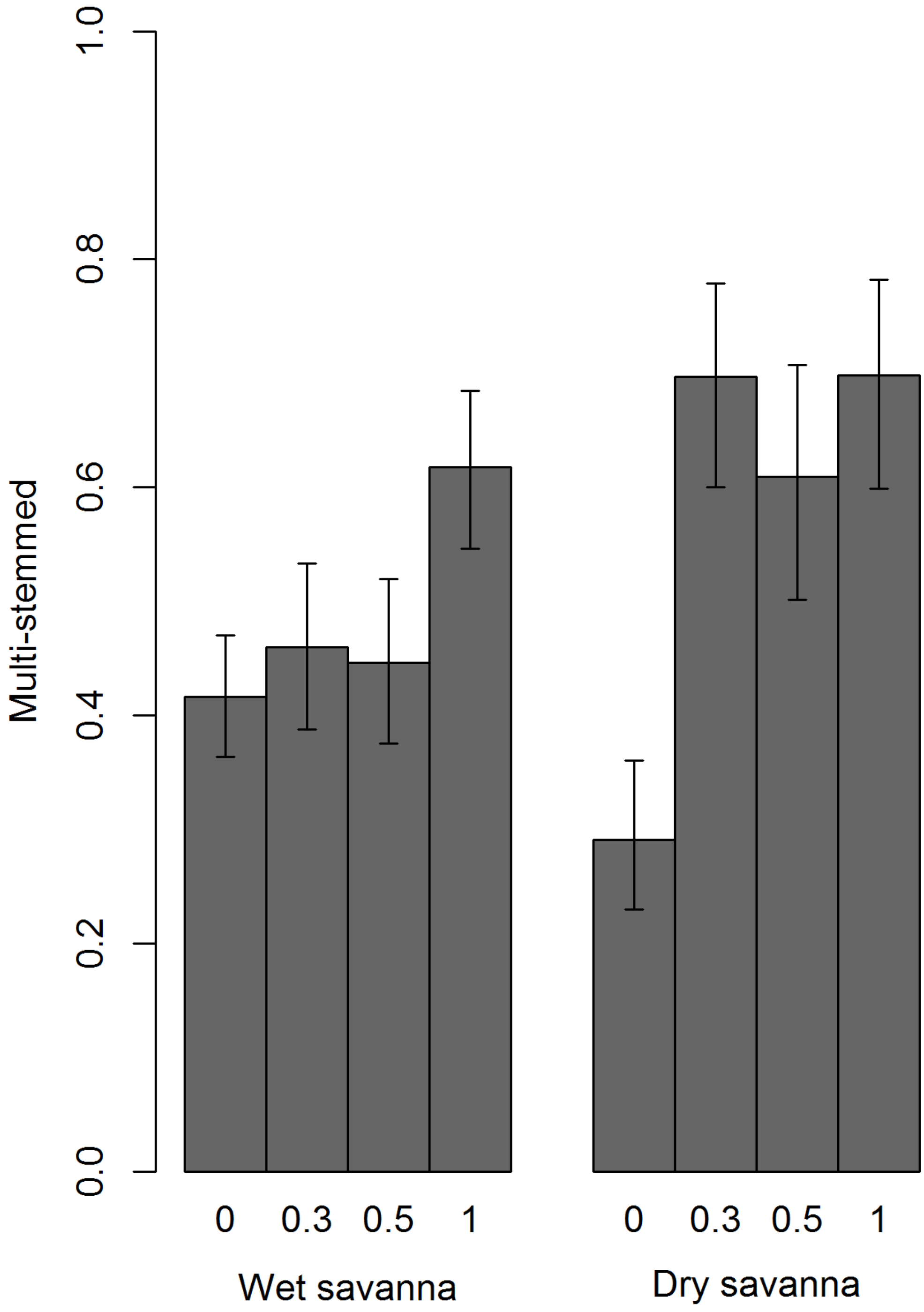

Fig. 3. The proportion of multi-stemmed trees (mean ±1 S. E.) in plots subject to different burn treatments estimated from the linear mixed effect model. Results are shown for the long-term experimental burn plots at Pretoriuskop, the wet savanna and Skukuza, the dry savanna subjected to the following burning frequencies; 0=control plot, 0.3=triennial, 0.5=biennial and 1=annual.