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Vegetation secondary succession in response to time since last fire in a broad-leaved savanna in central Namibia

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ABSTRACT

Savanna ecosystems developed as a response to frequent fires, and to date, fire plays an important role in shaping the vegetation structure of these ecosystems. Yet, little research on the effect of fire on Namibian savanna, especially at the more arid end of the rainfall gradient, has been done. This study was conducted at the Waterberg Plateau National Park, which experiences a range of fire frequencies, with the fire return period and time since last fire relatively well-known since 1976. Four fire blocks last burned 1, 2, 14 and 24 years ago prior to the study (2014) were surveyed, with the objective to assess the secondary succession after fire of perennial grasses and woody plants in terms of density, cover and species composition in a broad-leaved savanna on dystrophic sandy soils. Findings revealed that fire positively affects the grass component by increasing grass density and grass productivity ($p < 0.05$). On the other hand, as in most southern African savannas, time after fire did not result in a significant change in overall woody plant density ($p > 0.05$) but led to a steady increase in woody canopy cover and height ($p < 0.05$), thus reducing the amount of browse available for small to medium sized browsers. Overall plant species composition did not significantly change with time after fire, although when grass species were grouped into grazing value categories, species with high grazing value declined with time after fire. Recent fires thus improve grazing and browsing opportunities, without significant plant species successional changes, but rather with significant plant structural succession.

Keywords: Fire occurrence; fuel loads; grazing value; Namibia; space-for-time; vegetation secondary succession; Waterberg Plateau Park

INTRODUCTION

Fire is a megaherbivore that has been burning savanna ecosystems for millennia and has shaped their vegetation structure and floristic composition (Bond & Keeley 2005, Scholes & Walker 1993). This is attributed to the alternation of short wet periods and extended long dry periods in savannas, which make them highly prone to fire due to lightning storms and the highly flammable fuel of dry grass (Trollope 2003, Scholes & Archer 1997, Scholes & Walker 1993). The widespread occurrence of fire in Africa, especially in the savanna and grassland biomes brands it as the “fire continent” (Komarek 1971). Fire is one of many environmental drivers, including rainfall, herbivory and human activities that, in combination, shape African savanna vegetation (Burke 2006).

Fire remains a controversial issue and has seldom been researched in Namibia. There is still a knowledge gap on how fire affects vegetation dynamics, particularly in the more arid woodland savannas found in Namibia. Joubert *et al.* (2012) who focused on the effects of fire on a single encroaching species, *Acacia mellifera*, concluded that, in arid

thorn bush savanna, fire had to coincide with seedling establishment to be effective in maintaining an open savanna. In broad-leaved woodland savannas, Sheuyange *et al.* (2005) found that recent fires reduced shrub cover and promoted the herbaceous component (cover, biomass and species richness). Despite little fire research being conducted in the more arid Namibian savannas, fire regimes are being altered in different ways (Joubert *et al.* 2008), without prior and follow-up research and monitoring. For instance, fires occur in the north-eastern woodland savannas on an almost annual basis (Le Roux 2011, Sheuyange *et al.* 2005), while fires are deliberately excluded on commercial farms throughout the country (Joubert *et al.* 2008). In addition, the time of year in which fires occur has been altered in the north-eastern and central savannas from late dry season to late wet to early dry season. It is widely believed that these lower intensity fires will reduce damage to fire sensitive woody species and maximise habitat diversity (patch mosaic effect) (Beatty 2014).

Against this background, the study investigated the secondary succession of vegetation after fire in a

broad-leaved savanna occurring on dystrophic sandy soils at the arid end of the rainfall gradient in Namibia, with the aim of reducing the knowledge gap that exists in understanding the impacts of fire on vegetation dynamics.

METHODS

Study site

The study was conducted at the Waterberg Plateau National Park, in central Namibia (study site central coordinates: S 20.39°, E 17.35°) (Figure 1). The national park is an important conservation area with the main aim of protecting and breeding rare, endangered and economically important large herbivores such as African buffalo, black and white rhino, giraffe, roan antelope and sable antelope (Schneider 1993, Eco Impact Consultants 2011).

The study area experiences warm summers with temperatures reaching up to 40°C in the hottest months, while winter temperatures can drop to below -10°C (SASSCAL Weather net). The mean annual rainfall recorded at the foot of the plateau for the period 1981 to 2001 was 425.5 (±129) mm, with February being the wettest month (Erckie 2007, Mendelsohn *et al.* 2002). There seems to be no long-term rainfall data for the plateau, with the only available data recorded by the SASSCAL weather station starting from 09 September 2011, which

provided the total rainfall amounts for the years 2012, 2013, 2014 and 2015 as 664.1 mm, 395.7 mm, 838.2 mm and 81.6 mm respectively, indicating that although the study site is located between the 400-450 mm rainfall isohyets (Figure 1), actual annual rainfall is highly variable.

The Waterberg Plateau Park forms part of the “Tree Savanna and Kalahari Woodland” vegetation types of Namibia (Giess 1998, Jankowitz 1983). The mostly broad-leaved vegetation occurs on dystrophic (nutrient-poor) sandy red quartzite soils (Mukaru 2009). Common trees in this broad-leaved bushland savanna include *Acacia ataxacantha*, *Acacia fleckii*, *Burkea africana*, *Combretum collinum*, *Combretum psidioides*, *Dichrostachys cinerea*, *Grewia flavescens*, *Grewia retinervis*, *Philenoptera nelsii*, *Ochna pulchra*, *Peltophorum africanum*, *Terminalia sericea* and *Ziziphus mucronata* (Erb 1993). *Terminalia sericea* is the dominant woody species and is even considered to be encroaching the study area (Lutibezi 2016). Perennial grass species commonly occurring are *Brachiaria nigropedata*, *Aristida stipitata*, *Andropogon schirensis*, *Digitaria sericata*, *Eragrostis pallens*, *Eragrostis rigidior*, *Eragrostis jeffreysii*, *Panicum kalaharensense*, *Stipagrostis uniplumis*, *Stipagrostis hirtigluma* and *Triraphis schinzii* (Erb 1993). The nomenclature used is as in the latest Namibian plant species list published (Klaassen & Kwembeya 2013).

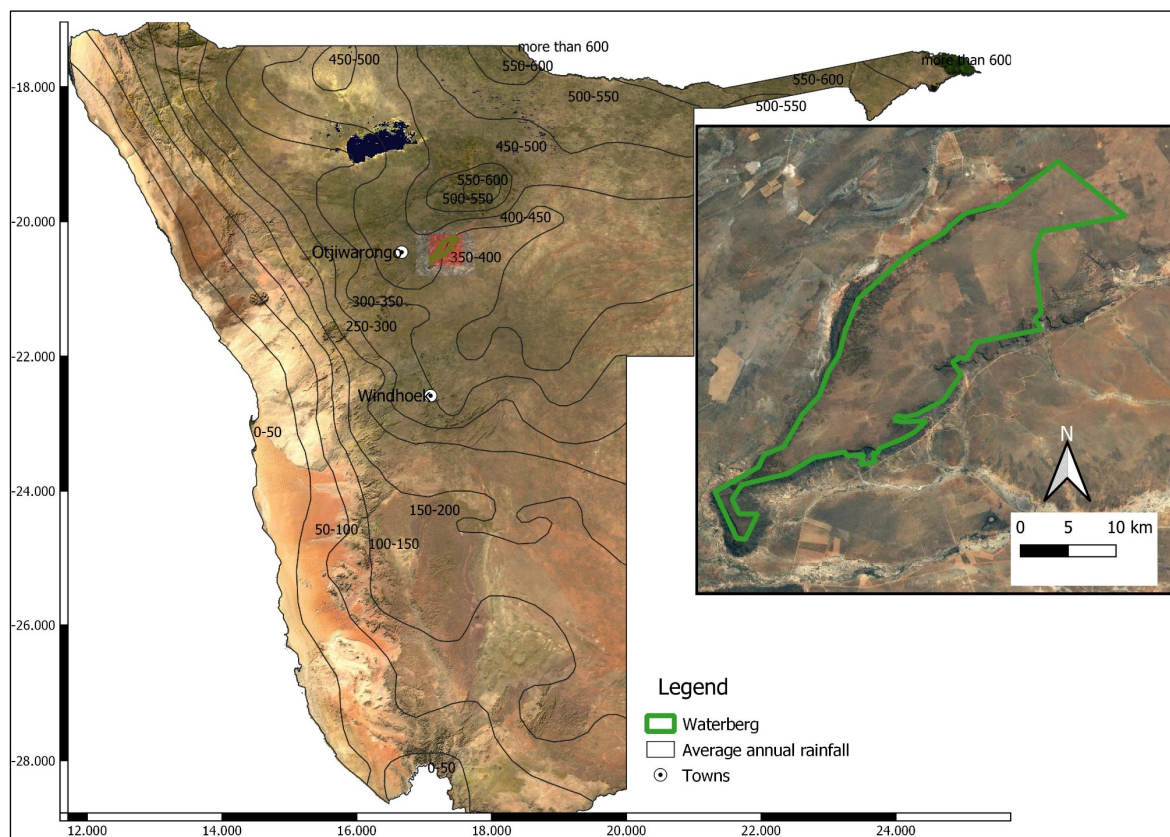


Figure 1: Location of the Waterberg Plateau Park in central Namibia.

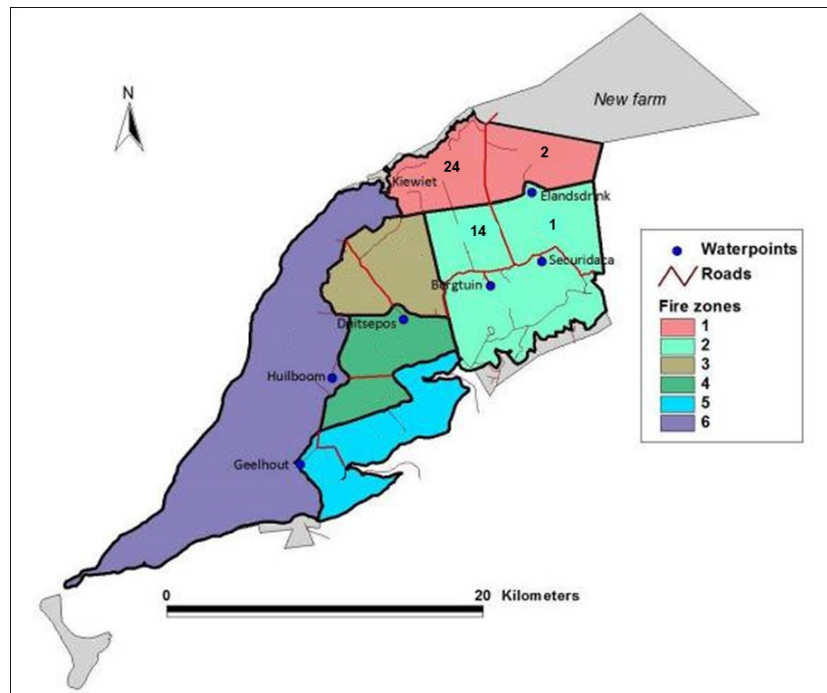


Figure 2: Location of the surveyed fire blocks, labelled according to time since last fire (1, 2, 14 and 24 years) in the Waterberg Plateau Park (Source: Eco Impact Consultants 2011).

Study design

A space-for-time (SFT) substitution technique was used for this study since the treatments were adjacent to each other (sharing the same climatic conditions) and showed no or little variation in soil texture (Ngalipo *et al.* 2018). The SFT approach has widely been used for examining vegetation community structure and composition and uses spatial variation to understand temporal dynamics (Likens 1989).

The study was carried out in four adjacent fire blocks, each approximately 2000 ha in size and burned 1 year, 2 years, 14 years and 24 years prior to the study and with mean fire return intervals of 6.2 years, 9.3 years, 9.3 years, and 18.5 years respectively (Figures 2, 13).

This study is inevitably pseudoreplicated (Hurlbert 1984) as there is only one of each fire block in the Waterberg Plateau Park. This pseudoreplication is considered acceptable, as most landscape-scale experiments rely on natural events (Davies & Gray 2015). In each fire block, six 200 m long line transects were randomly placed. Sample points were placed at 40 m intervals along each transect (5 per transect). At every sample point the following three vegetation sampling techniques were used: the modified point-centred quarter (PCQ) method (Cottam & Curtis 1956, Trollope *et al.* 2013), the Bitterlich gauge (Zimmermann *et al.* 2003) and the visual obstruction reading method (VOR) (Smith 2008, Uresk *et al.* 2009).

Data collection

The PCQ method used is an adapted version of Cottam & Curtis (1956) which overcomes the problems linked to the normal PCQ that results in oversampling small, short woody plants and under-sampling taller trees and shrubs (Trollope *et al.* 2013). In each quarter within a 20 m radius the distances to the nearest live perennial grass and woody species of <1 m, 1-2 m, 2-3 m, 3-4 m and >4 m in height were measured and recorded (Trollope *et al.* 2013), instead of just measuring the nearest woody plant in each quarter (Cottam & Curtis 1956). The basal diameter of the perennial grasses and the height of the woody plants in the different height classes were also measured. The different species being measured were also identified and recorded.

The Bitterlich gauge with a percentage factor of 5 based on its dimensions (length=75 cm and breadth=33.5 cm) was used to estimate woody canopy cover (Friedel & Chewings 1988 in Zimmermann & Mwazi 2002). Zimmermann & Mwazi (2002) found it to be an accurate method to estimate woody cover. The tip of the longer rod is held below the eye, with the other tips held horizontally in the direction of a woody canopy. If the woody canopy extends beyond the two tips, the canopy is counted and recorded as 1 (converted to a percentage by multiplying with the percentage factor of 5) and its species identified, if the two tips extend beyond the canopy then it is ignored. This procedure

was repeated until a 360° turn clockwise was made at every PCQ point along each transect.

The Visual Obstruction Reading (VOR) method was used to estimate standing grass biomass (Smith 2008, Uresk *et al.* 2009). This method requires little effort to monitor rangelands and was tested in Namibia (Joubert *et al.* 2014), including in the study area and found to adequately estimate standing biomass. Calibration in this study was conducted using 60 points in the study area. The VOR and dry weight of the grasses was used to calculate a regression equation used to convert all VORs to biomass (Figure 3).

Data analysis

All vegetation structural (grass & woody density, woody cover, grass biomass and grass tuft size) statistical tests were run with STATISTICA 12 (StatSoft 2002). The Kolmogorov-Smirnov test was used to see if data were normally distributed. The main effects analysis of variance (ANOVA) revealed that time since last fire was the driving variable contributing to significant differences rather than mean fire return interval, and hence time since last fire was considered as the driving variable for all further tests. For normally distributed data the one-way ANOVA was used. If the one-way ANOVA yielded a significant difference, Fisher's less significant difference (LSD) posthoc test was used for multiple comparisons among sites to reveal differences. If the data were not normally distributed, the equivalent non-parametric Kruskal-Wallis test was used to test for significant differences.

For plant species composition, a non-metric multidimensional scaling ordination (NMS) (Kruskal 1964), using the Sorenson distance measure, with the time of day used as the random starting parameter was performed in PC-ORD version 6.08 (McCune & Mefford 2011), separately for perennial grass species (relative density) and woody species (relative woody

cover). Based on an initial scree plot of stress versus dimensions, the ordination was done for two dimensions with axis 1 being the most relevant at the final stress of 14.343, with 200 iterations. The following environmental variables were used on the secondary matrix: time since last fire, mean fire return interval, as well as the following soil properties: percentage clay, organic carbon, phosphorus, potassium, calcium, magnesium, sodium, and total nitrogen. The soil data and the description of soil sampling procedures and analysis were obtained from a parallel study conducted in the same area that investigated soil nutrients and soil carbon in relation to time since last fire along the same transects (Nghalipo *et al.* 2018).

RESULTS

Perennial grass component

(a) Perennial grass density

Perennial grass density decreased significantly with time since last fire ($F=5.568$, $df=3$, $p<0.05$, $n=6$). The site burned 1 year ago had about three times higher perennial grass density than those burned 14 and 24 years ago (Figure 4).

(b) Grass biomass and grass tuft size

Grass biomass was significantly different ($F=4.611$, $df=3$, $p<0.05$, $n=6$) between the site burned 1 year ago and that burned 2 years ago, with the latter having about three times higher grass biomass (Figure 5). Perennial grass tuft size was significantly smaller ($F=4.017$, $df=3$, $p<0.05$, $n=6$) in the recently burned site as compared to the other sites (Figure 6).

(c) Perennial grass species composition

The NMS ordination (13.153 at final stress for two axes; 0.00000 final instability and 44 iterations) revealed that percentage nitrogen may be an influential variable for the relative density of different grass species observed in some of the sites (Figure 7).

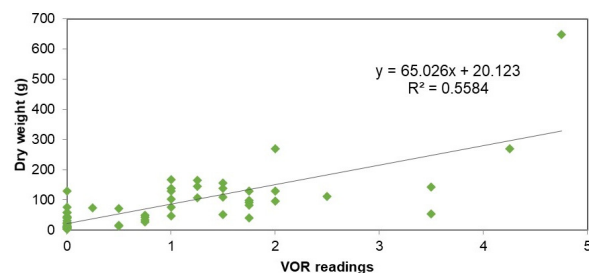


Figure 3: Regression of VOR readings and dry weight (g) of perennial grasses.

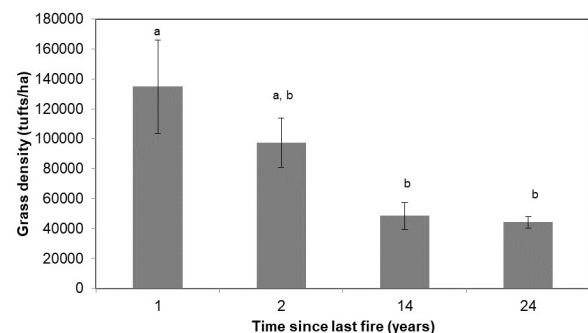


Figure 4: Perennial grass density (grass tufts/ha) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

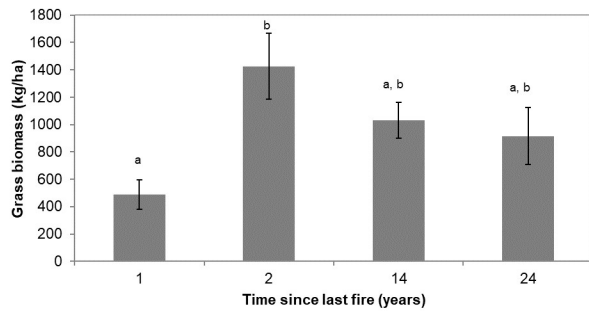


Figure 5: Grass biomass (kg/ha) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

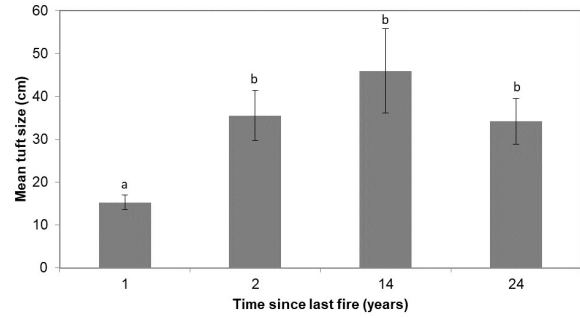


Figure 6: Perennial grass tuft size (cm) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

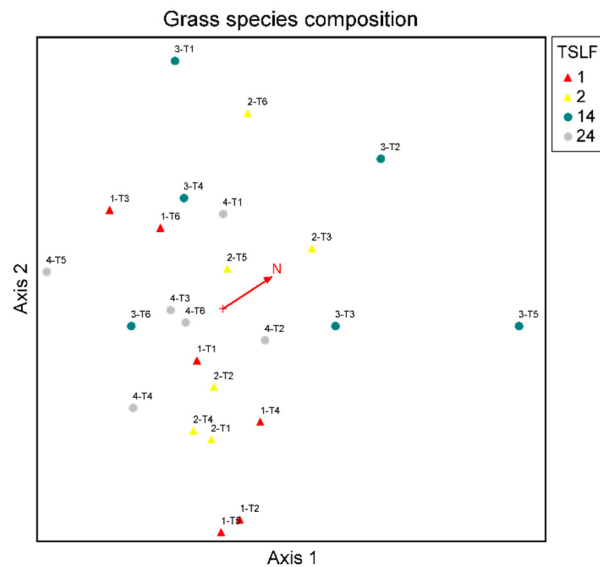


Figure 7: NMS joint plot for perennial grass species composition in relation to various environmental variables at r^2 cut off=0.1. The numbers denote the four fire blocks: 1=1 year, 2=2 years, 3=14 years and 4=24 years, while the letter & number represent the transect numbers, i.e. T1=transect 1

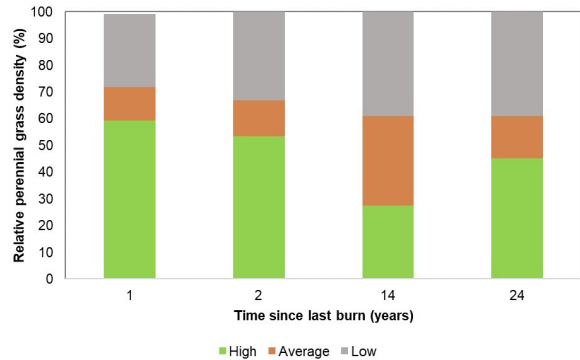


Figure 8: Proportion of relative grass density in the grazing value categories in relation to time since last fire (years).

Table 1: Relative density (%) of perennial grass species with grazing value (van Oudtshoorn 2004) in relation to time since last fire (years).

Perennial grass species	Grazing value	Time after fire (years)			
		1	2	14	24
<i>Brachiaria nigropedata</i>	High	0	9.2	0.8	0.8
<i>Digitaria seriata</i>	High	57.5	44.2	26.7	44.2
<i>Panicum maximum</i>	High	1.7	0	0	0
<i>Aristida meridionalis</i>	Average	2.5	0.8	0	0.8
<i>Eragrostis lehmanniana</i>	Average	0.8	0	1.7	0
<i>Melinis repens</i> subspecies <i>repens</i>	Average	0.8	0	2.5	1.7
<i>Panicum kalaharens</i>	Average	2.5	7.5	11.7	5
<i>Stipagrostis uniplumis</i>	Average	5	5	14.2	2.5
<i>Triraphis schinzii</i>	Average	0.8	0	3.3	5.8
<i>Aristida stipitata</i>	Low	18.3	23.3	20	22.5
<i>Eragrostis jeffreysii</i>	Low	3.3	2.5	12.5	0.8
<i>Eragrostis pallens</i>	Low	5.8	4.2	2.5	12.5
<i>Stipagrostis hirtigluma</i>	Low	0	3.3	4.2	3.3

(d) Grazing value and relative density of grass species in relation to time since last fire

Three grass species of high grazing value were encountered with *Digitaria seriata* having the highest relative density overall and mostly in the recently burned areas (Table 1). The recently burned areas had higher relative grass density of high grazing value species compared to areas burned more than 14 years ago (Figure 8).

Woody component

(a) Woody density and canopy cover

Total woody density was not significantly different ($F=1.004$, $df=3$, $p>0.05$, $n=6$) between sites with different time since last fire (Figure 9). There were however significant differences ($F=5.416$, $df=15$, $p<0.05$, $n=6$) found for woody density of <2 m and >2 m woody plants among the sites (Figures 10a and 10b). Total woody cover significantly ($H=19.698$, $df=15$, $p<0.05$, $n=6$) increased with time since last fire (Figure 11).

(b) Woody species composition

The NMS ordination (14.254 at final stress for two axes, 0.00000 at final instability and 43 iterations) revealed that time since last fire (TSLF) and mean fire return interval (MFRI) contribute to differences

in woody species composition (relative woody cover) in the different sites (Figure 12).

(c) Relative cover of woody species (Table 2)

Table 2: Relative woody cover (%) of woody species in relation to time since last fire (years)

Woody species	Time since last fire (years)			
	1	2	14	24
<i>Acacia ataxacantha</i>	16.3	13.8	20.9	23.6
<i>Acacia fleckii</i>	0	8.9	0	1.3
<i>Bauhinia petersiana</i>	1	2.9	4.1	11.9
<i>Burkea africana</i>	4	2	4.6	0.5
<i>Combretum apiculatum</i>	0	1.1	0.8	0
<i>Combretum collinum</i>	10.3	11	6.1	5
<i>Combretum psidioides</i>	10.5	7.1	15.2	3
<i>Croton gratissimus</i>	0	0	0	0.7
<i>Grewia avellana</i>	0	1.5	0	0
<i>Grewia flavescens</i>	1	0.8	2	1.6
<i>Grewia retinervis</i>	1.9	0.8	0	1
<i>Ochna pulchra</i>	1.4	2.2	2.2	5.2
<i>Peltophorum africanum</i>	11.2	0.4	2.5	0.7
<i>Philenoptera nelsii</i>	6.8	7	3.3	3.9
<i>Searsia tenuinervis</i>	0	0	1.6	0
<i>Terminalia sericea</i>	34.9	40.5	35.9	41.6
<i>Ziziphus mucronata</i>	0.6	0	0.7	0

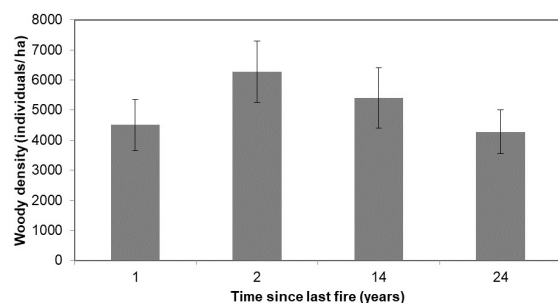


Figure 9: Total woody density (individuals/ha) in relation to time since last fire (years). The bars show standard errors.

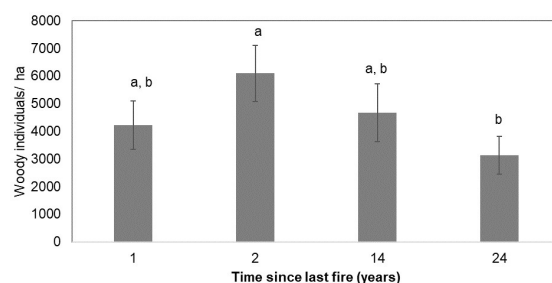


Figure 10a: Woody density (individuals/ha) of <2 m woody plants in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

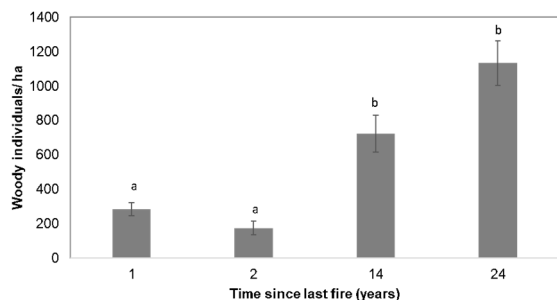


Figure 10b: Woody density (individuals/ha) of >2 m woody plants in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

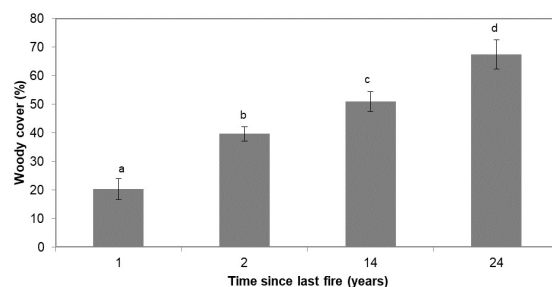


Figure 11: Total woody cover (%) in relation to time since last fire (years). Letters denote significant differences between sites, while the bars show standard errors.

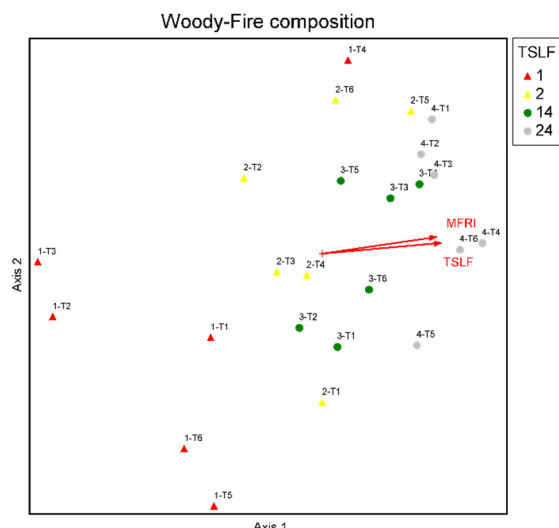


Figure 12: NMS joint plot for woody species composition in relation to various environmental variables at r^2 cut off= 0.1. The numbers denote the four fire blocks: 1=1, 2=2, 3=14 and 4=24, while the letter & number represent the transect numbers, i.e. T1=transect 1.

DISCUSSION

Perennial grass component

Perennial grass density decreased with time since last fire and was about three times higher in the recently burned site (Figure 4). The removal of moribund grass, reduced plant canopy cover and reduced competition from established plants by fire contributed to this, which supports observations from other studies (Holdo 2005, Mapiye *et al.* 2008, Zimmermann *et al.* 2010, Nepolo & Mapaire 2012, Gul *et al.* 2014). Fire stimulates the recruitment and regrowth of new grass shoots (Menke 1992, van Oudtshoorn, 2004, Gul *et al.* 2014, Roodt 2015). This is especially evident for *Digitaria seriata* where dry stolons were burned by the recent fire, resulting in the production of numerous new tillers.

The recently burned site (488.4 kg/ha) had about three and two times less grass biomass than blocks burned 2 (1425.7 kg/ha) and 14 years (1030.2 kg/ha) ago respectively (Figure 5), as well as significantly smaller grass tufts (Figure 6). The low biomass is to be expected because the recent fire burned away above-ground material of grasses causing a temporary decline in standing biomass and overall productivity and this is supported by other studies conducted in southern African savannas (Scholes & Walker 1993, van Langevelde *et al.* 2003, Goldammer & de Ronde 2004, Mbatha & Ward 2010, Zimmermann *et al.* 2010). In addition, due to the highly nutritious regrowth, herbivores utilised this block about four times more than the other blocks (Uunona 2014), resulting in even less grass biomass.

Despite the site burned 2 years ago being much more utilised than the sites burned 14 or more years ago (Uunona 2014) the grass biomass was significantly higher. This suggests that grass production and biomass recover rapidly after fire (du Toit *et al.* 2015). The post-fire regrowth of grasses and woody plants is highly nutritious and attracts herbivores that readily forage on it (Uunona 2014), allowing for other recently burned areas to rest and recover (Archibald *et al.* 2005). Grass tuft size also recovered within two years after fire (Figure 6). This could be due to reduced grazing pressure because herbivores are being attracted away from the area by other more recently burned areas nearby (Scholes & Walker 1993, Zimmermann *et al.* 2010). This is supported by Archibald *et al.* (2005), who showed that burned areas attract animals off unburned grazed patches long enough for patches to recover full grass biomass in one growing season. Besides being available forage for grazers, grass biomass is an important factor that influences fire behaviour, as fire intensity is positively related to the amount of fuel load (Scholes & Walker 1993, Trollope *et al.* 2002, Sah *et al.* 2006). Grass biomass in the study area is generally low, with 1425.7 kg/ha being the highest recorded (Figure 5), despite the above-average rainfall (913.9 mm) recorded for the 2013/2014 period (SASSCAL Weather net), prior to the study. Fuel loads tend to be sparser and more unevenly distributed in bushland savannas as compared to open savannas because of the influence of tree neighbourhoods on grass growth (Holdo 2005). In addition, *Terminalia sericea*, a species considered to be an encroacher species in the study area, is dominant in all fire blocks and is likely to compete intensively with grasses, due to its shallow root system (Hipondoka & Versfeld 2006, Lutibezi 2016).

The steady decline in perennial grass density is partially due to the build-up of competitive pressure between individuals which becomes severe enough to lead to high mortality but also moribundity which increases with time since last fire (Scholes & Walker 1993, Zimmermann *et al.* 2010, van Oudtshoorn 2004, Roodt 2015). Therefore, fire temporarily resets standing grass biomass and competitive pressure (Zimmermann *et al.* 2010). Recent fires tended to result in a higher proportion of high grazing value species (Figure 8) and an improvement in the rangeland for grazing herbivores, but according to the NMS analysis there was no significant grass species composition successional change with time since last fire (Figure 7), but rather a structural change in terms of grass density (Figure 4), grass biomass (Figure 5), and grass tuft size (Figure 6).

Woody component

Time since last fire did not significantly affect total woody density (Figure 9). This suggests that fire in

this bushland savanna is not sufficient to reduce woody plant density and maintain an open savanna. However, other factors such as fire intensity should be taken into account. High-intensity fires increase tree mortality in higher rainfall savannas such as the woodland savanna in the Kruger National Park (Govender *et al.* 2006), and thus may reduce woody density in southern African savannas (du Toit *et al.* 2003, Scholes & Walker 1993). These effects are more prevalent in higher rainfall areas such as in the miombo woodlands found in Zimbabwe and Zambia as well as the north-eastern parts of Namibia (Mendelsohn & el Obeid 2005). Therefore, high intensity fires are likely to be rare in the study area due to relatively low fuel loads (Figure 5), that may also be attributed to grazing pressure in the recently burned areas and the high density and cover of woody individuals in the unburned areas (Figure 9, 11). As in most savanna systems, fire maintains an open savanna mainly through causing a top-kill of woody stems and branches, decreasing their canopy cover (Figures 11, 13) and height to “browsable” heights (Higgins *et al.* 2000, Trollope 2003, Bothma & du Toit 2005, Joubert *et al.* 2012, Nyazika *et al.* 2017); the resulting resprout is more accessible and highly nutritious for small to medium sized browsers (Scholes & Walker 1993).

In the absence of fire woody plants grow larger and their individual canopy areas become bigger resulting in a higher woody cover (Figure 11) (Accatino *et al.* 2010, Smit *et al.* 2010) and a more closed woodland with woody plants mainly >2 m tall (Figure 10b) beyond the fire trap. Thus, the increase in woody cover is due to an increase in the size of individual canopies free of fire, rather than an increase in the

density, which also suggests very little recruitment in this bushland savanna.

Woody species composition was influenced by time since last fire and mean fire return interval (Figure 13), indicating that there may be plant species secondary succession occurring in the current time frame, but structural succession is clearly more evident and significant (Figures 10, 11, 12). This supports other studies in southern African savannas (du Toit *et al.* 2015, Trollope 2003, Bond & van Wilgen 1996) who found that the main effect of fire on woody vegetation is that it causes top-kill of above-ground plant material, forcing the plants to coppice from the base of the stem, confining woody plants in the fire trap (Holdo 2007), but fire does not significantly alter plant species composition, which indicates that savanna vegetation is well adapted and resistant to fire. This is further strengthened by a synergistic study of fire and elephant damage in a miombo woodland that revealed a complete shift in woody plant species composition, mainly a drastic reduction in woody species preferred by elephants for browsing (Mapaure & Moe 2009), suggesting that fire alone could not cause significant changes to plant species composition.

CONCLUSIONS AND FIRE MANAGEMENT IMPLICATIONS

For the study area, fire increases the availability and utilisation of the vegetation by increasing perennial grass density and biomass and reducing woody plants through top-kill to browsable heights for small to medium sized herbivores, thus maintaining an open bushland savanna. There appears to be no significant grass and woody species succession after fire, rather



Figure 13: A series of images illustrating the changing vegetation structure with time since last fire in the bushland savanna.

there is a dramatic structural change, with a steady increase in woody plant height and canopy cover leading to a more closed savanna in the absence of fire.

Based on the findings of this study, a modest increase in fire frequencies, and the burning of areas that have not been burnt in a long time (14-24 years) will have no detrimental impacts on plant species composition but will rather support grazers and small to medium sized browsers. Such fires would need to be set after high rainfall seasons, to cause a significant top-kill of woody plants and thus open up the more closed woodland sites (Figures 11, 13) and improve grass quantity & quality.

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REFERENCES

- Accatino F, De Michele C, Vezzoli R, Donzelli D, Scholes R (2010) Tree-grass co-existence in savanna: Interactions of rain and fire. *Journal of Theoretical Biology* 267: 235-242.
- Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications* 15(1): 96-109.
- Beatty R (2014) *Integrated transfrontier fire management for Liwana Partial Reserve (Angola) and Bwabwata National Park (Namibia): A proposed approach*. 321Fire, Namibia.
- Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20(7): 387-394.
- Bond WJ, van Wilgen BW (1996) *Fire and plants*. Chapman and Hall, London.
- Bothma JP, du Toit JG (2010) *Game ranch management*. 5th Edition, Van Schaik Publishers, Pretoria.
- Burke A (2006) Savanna trees in Namibia: factors controlling their distribution at the arid end of the spectrum. *Flora* 201: 189-201.
- Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution* 5(22): 5295-5304.
- du Toit JT, Rogers KH, Biggs HC (2003) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington D.C.
- du Toit JCO, van den Berg L, O'Connor TG (2015) Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. *African Journal of Range & Forage Science* 32 (1): 13-20.
- Eco Impact Consultants (2011) *Waterberg Plateau Park Management and Tourism Development Plan*. Ministry of Environment and Tourism, Windhoek, Namibia.
- Erb KP (1993) *The Roan antelope (Hippotragus equinus, Desmarest 1804), its ecology in the Waterberg Plateau Park*. M.Sc thesis: University of Stellenbosch. Unpublished.
- Erckie JB (2007) *Assessing the effects of grazing intensity by large herbivores on species diversity and abundance of small mammals at Waterberg Plateau Park, Namibia*. MSc. Thesis, University of Namibia, Windhoek. Unpublished.
- Giess W (1998) A Preliminary Vegetation Map of Namibia. 3rd edition. *Dinteria* 4: 1-112.
- Goldammer JG, de Ronde C (Ed.) (2004) *Wildland fire management handbook for Sub-Sahara Africa*. comPress, Global fire monitoring centre.
- Govender N, Trollope WSW, van Wilgen BW (2006) The effect of fire season, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748-758.
- Gul B, Islam M, Ahmad S, Gul S (2014) Effects of prescribed fire on forage production and nutritive value of the perennial grass *Saccharum griffithii*. *International Journal of Experimental Botany* 83: 415-421.
- Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.
- Hipondoka MHT, Versfeld WD (2006) Root system of *Terminalia sericea* shrubs across rainfall gradient in a semi-arid environment of Etosha National Park, Namibia. *Ecological Indicators* 6: 516-524.
- Holdo RM (2005) Stem mortality following fire in Kalahari sand vegetation: effects of frost, prior damage, and tree neighbourhoods. *Plant Ecology* 180: 77-86.
- Holdo RM (2007) Elephants, fire and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* 17(2): 558-568.
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2): 187-211.
- Jankowitz WJ (1983) *Die plantekologie van die Waterberg Platopark*. PhD Thesis. Universiteit van die Oranje Vrystaat. Unpublished.
- Joubert DF, Powell LA, Schact WH (2014) Visual obstruction as a method to quantify herbaceous biomass in southern African semi-arid savannas. *African Journal of Range and Forage Science* 32: 1-6.
- Joubert DF, Rothauge A, Smit GN (2008) A conceptual model of vegetation dynamics in the semi-arid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments* 72: 2201-2210.
- Joubert DF, Smit GN, Hoffman MT (2012) The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. *Journal of Arid Environments* 87: 1-7.
- Klaassen ES, Kwembeya EG (Ed.) (2013) *A Checklist of Namibian Indigenous and Naturalised Plants*. Occasional Contributions No. 5, National Botanical Research Institute, Windhoek, Namibia.
- Komarek EV (1971) Effects of fire on wildlife and range habitats. *Proceedings of the Prescribed Burning Symposium*, pp. 46-52.

- Kruskal JB (1964) Nonmetric Multidimensional Scaling: A Numerical Method. *Psychometrika* 29: 115-129.
- Le Roux J (2011) *The Effect Of Land Use Practices on the Spatial and Temporal Characteristics of Savanna Fires in Namibia*. PhD. Thesis, University of Erlangen-Nürnberg.
- Likens GE (ed.) (1989) *Long term studies in Ecology: Approaches and alternatives*. Springer-Verlag, New York, Inc. Pp 110-135.
- Lutibezi SP (2016) *The effect of fire history on the root carbohydrate concentration of encroaching Terminalia sericea at the Waterberg Plateau Park, Central Namibia*. Master thesis, University of Science and Technology. Unpublished.
- Mapaure I, Moe SR (2009) Changes in the structure and composition of miombo woodlands mediated by elephants (*Loxodonta africana*) and fire over a 26-year period in north-western Zimbabwe. *African Journal of Ecology* 47: 175-183.
- Mapiye C, Mwale M, Chikumba N, Chimonyo M (2008) Fire as a rangeland management tool in the savannas of southern Africa: a review. *Tropical and Subtropical Agroecosystems* 8(2): 115-124.
- Mbatha KR, Ward D (2010) The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. *Journal of Arid Environments* 74: 1294-1301.
- McCune B, Mefford MJ (2011) PC-ORD. *Multivariate Analysis of Ecological Data*. Version 6.08. MjM Software, Gleneden Beach, Oregon, U.S.A.
- Mendelsohn J, el Obeid S (2005) *Forests and woodlands of Namibia*. RAISON, Windhoek.
- Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) *Atlas of Namibia*. David Philip, Cape Town. Accessed at: http://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/ 16 October 2017.
- Menke JW (1992) Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia Journal of the California Native Plant Society* 20(2): 22-25.
- Mukaru WC (2009) *Impacts of large herbivores on vegetation and soils around water points in Waterberg Plateau Park, central Namibia*. M.Sc. Thesis, University of Namibia and Humboldt University in Berlin. Unpublished.
- Nepolo E, Mapaure I (2012) Short-term influence of fire on herbaceous composition, diversity and grass biomass production in Savanna woodland in Windhoek, Namibia. *International Journal of Ecosystem* 2(6): 154-160.
- Nghalipo E, Joubert D, Throop H, Groengroeft A (2018) The effect of fire history on soil nutrients and soil organic carbon in a semi-arid savanna woodland, central Namibia. *African Journal of Range and Forage Science* 1-8.
- Nyazika T, Gandiwa P, Chanyandura A, Muboko N, Gandiwa E (2017) Influence of fire frequency on woody vegetation structure and composition in Lake Chivero Recreational Park, northern Zimbabwe. *Tropical Ecology* 58(3): 583-589.
- Roodt V (2015) *Grasses and grazers of Botswana and the surrounding savanna*. Struik Nature, Cape Town.
- Sah JP, Ross MS, Snyder JR, Koptur S, Cooley HC (2006) Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests. *International Journal of Wildland fire* 15: 436-478.
- SASSCAL (Southern African Science Service Centre for Climate Change and Adaptive Land Management) - weather net: <http://www.sasscalweather.net.org>. Accessed: 18 October 2016.
- Schneider I (1993) *Waterberg Plateau Park, Namibia*. John Meinert, Windhoek.
- Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annual Review Ecological Systems* 28: 517-544.
- Scholes RJ, Walker BH (1993) *An African Savanna: Synthesis of the Nylsvley study*. Cambridge University Press, Great Britain.
- Sheuyange A, Oba G, Weladji RB (2005). Effects of anthropogenic fire history on savanna vegetation in north eastern Namibia. *Journal of Environmental Management* 75: 189 198.
- Smit IPJ, Asner GP, Govender N, Bowdoin TK, Knapp DE, Jacobson J (2010) Effects of fire on woody vegetation structure in African savanna. *Ecological Applications* 20: 1865-1875.
- Smith MA (2008) *Robel pole technique and data interpretation*. University of Wyoming, United States of America.
- StatSoft Inc (2002) *STATISTICA*. Tulsa, OK.
- Trollope WSW (2003) *Fire effects in African grasslands and savannas*. Department Livestock and pasture Science, University of Fort Hare, Eastern Cape, South Africa.
- Trollope WSW, Trollope LA, Goode R, de Bruyn P, van den Broeck D (2013) Assessment of veld condition using the adapted point centred quarter method for bush surveys. *Special Report- Research & Development, Working on Fire*, South Africa: 1-20.
- Trollope WSW, Trollope LA, Hartnett DC (2002) *Fire behaviour a key factor in the fire ecology of African grasslands and savannas*. Mill press, Rotterdam.
- Uunona NM (2014) *Impacts of fire on grazers and browsers utilization at the Waterberg Plateau Park, Central Namibia*. Work Integrated Learning project, Polytechnic of Namibia. Unpublished.
- Uresk DW, Mergen DE, Benzon TA (2009) Estimating standing vegetation with a modified Robel pole on meadows and grasslands in the southern black hills of South Dakota. *Proceedings of the South Dakota Academy of Science* 88: 91-97.
- van Langevelde F, van De Vijver CADM, Kumar L, van Koppel J, de Ridder N, van Andel J, Skidmore AK, Heerne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84(2): 337-350.
- van Oudtshoorn F (2004) *Guide to grasses of southern Africa*. Briza Publications, Pretoria.
- Zimmermann I, Joubert DF, Graz FP (2003) Proposed ground monitoring of bush thickening in Namibia. In *Proceedings of the VIIth International Rangelands Congress* 26th July - 1st August, Durban, South Africa, 793-795.
- Zimmermann I, Mwazi FN (2002). The effect of a prescribed burn, followed up with browsing pressure on rangeland condition in the Mountain savanna and Karstveld of Namibia. *Dinteria*, 27: 49 57.
- Zimmermann J, Higgins SI, Grimm V, Hoffman J, Linstadter A (2010) Grass mortality in semi-arid savanna: The role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 1-8.