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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 Dichrostachvs psidioides. 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 seriata, Eragrostis pallens, Eragrostis rigidior, jeffreysii, Panicum kalaharense, Eragrostis 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 (Nghalipo *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 undersampling 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 oneway 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



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

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 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 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 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 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).

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



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

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)

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



**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 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 & Mapaure 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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