



One savanna, many shapes: How bush control affects the woody layer in the southern Kalahari

N. Dreber^{a,b,*}, S.E. van Rooyen^{b,1}, K. Kellner^b

^a Department of Ecosystem Modelling, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 4, 37077 Göttingen, Germany

^b Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa

ARTICLE INFO

Article history:

Received 9 May 2019

Received in revised form 30 July 2019

Accepted 16 August 2019

Available online 30 August 2019

Edited by SJ Siebert

Keywords:

Arbicide

Biodiversity

Diversity profile

Height-class distribution

Savanna

Shrub encroachment

Species composition

Sustainable land management

Vegetation structure

Woody vegetation

ABSTRACT

Bush thickening (shrub encroachment) is a major ecological and economic threat in southern African savannas. Different types and intensities of bush control (BC) are applied to counteract and mitigate bush thickening. However, woody vegetation response to BC and possible ecological side effects can be manifold. Land users therefore require solid knowledge about the associated structural and compositional changes, helping to apply an informed BC strategy that preserves multiple ecosystem services and functions. The present study addresses this need in a South African thornbush-type savanna. We sampled 41 rangeland sites with a known history of BC in comparison to benchmark conditions. The BC treatments included a selective and non-selective herbicide application and a selective stem burning. We identified each woody species in belt transects and measured the size and canopy of all individuals. The data were used to calculate measures of diversity, cover and density and to describe the population structure of key species. Marked differences in woody species composition and abundance patterns as well as significant alterations of the horizontal and vertical woody vegetation structure clearly reflected the intensity and level of selectivity with which BC had been conducted. While population trends displayed regeneration of key species, important structural elements (large mature trees) were often at risk of being lost from the savanna ecosystem. Results suggest varying degrees of ecosystem functional integrity following the BC treatments. It is concluded that selective BC treatments should be preferred as they allow to create open and well-structured savannas in benefit of the stability and biodiversity of the system. Yet, for improved predictions further research is needed into species-specific population dynamics and trait-related plant–plant interactions. In addition, there is still uncertainty about possible long-term ecological effects associated with the use of herbicides in this type of savanna, which should receive special attention in future research.

© 2019 SAAB. Published by Elsevier B.V. All rights reserved.

1. Introduction

Bush thickening, i.e. the encroachment of indigenous trees and shrubs, is a major threat to savanna rangelands in southern Africa (O'Connor et al., 2014). Apart from local factors like overgrazing, exclusion of browsing and suppression of wildfire, it seems that elevated atmospheric CO₂ is a superior global factor that benefits bush thickening dynamics across savanna types and land uses (Stevens et al., 2017). The increase in the density and cover of woody species can affect ecosystem services and functions in various ways and at different temporal and spatial scales, with the ecological and socio-economic implications and net effects not necessarily being negative (Eldridge et al., 2011; Thomas

et al., 2018). However, for the purpose of increasing or maintaining grass production adequate to livestock farming and game ranching, it is often mandatory to manage the woody layer by controlling density (or cover) and recruiting cohorts in an appropriate way to sustain the economic viability of savanna rangelands (Harmse et al., 2016; Smit, 2004).

In semi-arid Kalahari savannas, wildfires can counteract bush thickening but they only occur sporadically due to often too low fuel loads (Donaldson, 1969). For the same reason, prescribed fires that are used for management purposes are often insufficiently hot for topkilling large shrubs and trees and can only be applied to affect the regeneration layer (Lohmann et al., 2014). Moreover, the option of prescribed fires is often not realized due to the risk of going wild (Lohmann et al., 2014; pers. comm., 2013, Kalahari farmer) and potentially decreasing grazing capacities for an economically relevant period of time (Breedt et al., 2013). To avoid any such risks caused by fire, many (commercial) land users prefer mechanical and chemical treatments of bush control (Harmse et al., 2016; Haussmann et al., 2016).

The objectives of preventing or reversing bush thickening can be manifold, so are the potential trade-offs and undesired ecological

* Corresponding author at: Department of Ecosystem Modelling, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 4, 37077 Göttingen, Germany

E-mail address: n.dreber@gmx.de (N. Dreber).

¹ Present address: Environmental Management Group, Laan Sonder Naam, Groenvlei, Bloemfontein 9300, South Africa.

side-effects of bush-control treatments (Archer and Predick, 2014; Bezuidenhout et al., 2015; Haussmann et al., 2016). In case of southern Kalahari savannas, many studies have shown that clearing or thinning-out dense woody layers is in benefit for grass forage production (e.g. Harmse et al., 2016; Meyer et al., 2001; Richter et al., 2001), while the reduced structural complexity may come at the expense of, among others, biodiversity (e.g. Blaum et al., 2007; Seymour and Dean, 2010), nutrient-enriched sub-habitats (e.g. Dougill and Thomas, 2004; Hudak et al., 2003) and ecosystem stability (e.g. Harmse et al., 2016). In order to minimize such negative effects, Smit (2004) highlighted the importance of managing the woody layer toward a well-structured configuration supporting a balanced tree:grass ratio in time. Whether this is always feasible also depends on the ecology of concerned species and prevalent environmental limitations to structural vegetation development as governed by soil properties and moisture availability (Donaldson, 1969; Smit, 2004). Hence, sustainable land management (SLM) approaches should integrate an informed bush-control strategy to preserve multiple ecosystem services and functions in the long-term and to provide reliable short-term perspectives for the land user.

From an ecological point of view, a basic and simple question is: what savanna are we actually talking about? More precisely, what is the state or transitional condition and which ecological side effects characterize the local savanna system? Local savannas in a land-use context are multifaceted, rich in shapes and different in ecosystem integrity and functioning. From the above it is apparent that SLM requires much baseline information tailored to the concerned savanna type, that helps to better evaluate the corresponding potential ecosystem impacts and economic consequences. This includes information about the structural and compositional changes that typically characterize the woody vegetation response to a particular management and type and intensity of bush control. Questions of ecological and economic relevance pertain to, for example species that are at risk of being lost from the system (with feedbacks on the biotic and abiotic environment), the likelihood of increaser species to regenerate and dominate, or time horizons of developing vegetation states with different structures and compositions (e.g. Harmse et al., 2016; Haussmann et al., 2016; Ruwanza et al., 2013; Smit, 2004).

In the present study we address the lack of basic information on post-control woody vegetation in southern Kalahari savannas. We conducted assessments in a semi-arid thornbush-type savanna, where the selective and non-selective control of trees and shrubs is commonly applied to counteract bush thickening and to maintain open savanna states. We asked:

What is the status of woody species in post-control environments in terms of abundance patterns and population structure? Are structural attributes of the woody layer like species richness, diversity, size distribution, density and canopy area characteristic for post-control environments shaped by a certain BC treatment?

The objective was to provide a baseline inventory that can be used as a reference for scientists and practitioners by providing access points for research into processes and environmental feedback mechanisms and by supporting the guidance of restoration and conservation efforts in SLM, respectively. Overall, the study adds to our understanding of vegetation dynamics in post-control environments of this and similar savanna types.

2. Methods

2.1. Study area

The study was conducted in the Molopo Bushveld (sensu Rutherford et al., 2006), a thornbush-type savanna characteristic for the semi-arid Kalahari found in the north-western part of the North West province and in the most easterly part of the bordering Northern Cape province in South Africa (Appendix A). The corresponding Molopo area is relatively flat with predominantly deep-sandy and nutrient-poor soils.

Mean annual rainfall is about 300 mm with an inter-annual coefficient of variation about 47% (Harmse et al., 2016). Despite primary productivity being highly variable in space and time due to the stochastic environment, it still allows for extensive cattle farming and game ranching if the grass layer is sustainably managed (Harmse et al., 2016; Meyer et al., 2001). Farming activities in the Molopo area became prominent in the 1950's, but inappropriate management systems and the suppression of wildfires have been repeatedly identified as likely causes of large-scale habitat transformations (Donaldson, 1969; O'Connor et al., 2014) toward the dominance of woody increaser species such as *Grewia flava*, *Senegalia (Acacia) mellifera* subsp. *detinens* and *Vachellia (Acacia) luederitzii* (Dreber et al., 2018; Harmse et al., 2016). The increase in woody cover continues extensively in the Molopo area already being affected by bush thickening (Symeonakis et al., 2016). Similar developments of extensive savanna transformation are reported from grazing lands just across the Molopo river in neighboring Botswana (Reed et al., 2015). Local land users apply a range of different bush-control treatments which vary in terms of efficiency, intensity and consequently in their ecological and economic implications (Harmse et al., 2016). Looking at the associated structural and compositional variability of the woody layer, the Molopo Bushveld appears quite heterogeneous in the Molopo area at landscape scale (compare Appendix B).

2.2. Site selection and treatments

The study included a total of 41 rangeland sites on five commercial farms (Table 1; Appendix A). The sites had either a history of bush control a few years back with partly follow-up treatments, or, for reference, were untreated with a woody layer of varying density (for details see below). Site selection followed discussions with the land owners, who were asked to identify representative portions of their rangelands in different condition with a known management history and bush-control treatment. Apart from differences in the grazing regime and the bush-control treatment applied (Table 1), the sites were considered comparable with respect to vegetation- and soil type, topography and climate. Altogether, the sites formed a cross section of woody vegetation states and transitions commonly found on rangelands within the northern Molopo area (Appendix B).

The survey allowed to differentiate four general management practices: non-selective arboricide treatment via airplane (NAT), selective arboricide treatment by hand (SAT1–3), stem burning (SB) and no treatment (NoT). Sampling sites of the latter showed a range of different tree densities, for which reason a further division into more open sites [NoTo; <600 TE ha⁻¹ (for definition of tree equivalents (TE) see below)] and sites with a denser woody layer (NoTD; >600 TE ha⁻¹) seemed appropriate. NAT was conducted in the years 2008 and 2009. The three SAT treatments included the one-time removal of undesirable woody species in favor of especially the shrub *G. flava* in the year 2008/09 (SAT1), the one-time removal of specifically the increaser shrub *Rhigozum trichotomum* and trees *V. luederitzii* and *S. mellifera* in 2000 (SAT2), as well as the same as SAT2 but with a follow-up treatment in 2012 (SAT3). For NAT and SAT1–3 a systemic, photosynthesis-inhibiting Tebuthiuron-based arboricide had been applied by the land users as described in Harmse et al. (2016). SB included the selective killing of *V. luederitzii* and *S. mellifera* by putting glowing coals around the lower basal stem area (Donaldson, 1966, 1967). SB had been conducted in 1982 and again in 2000 to control newly established plant individuals. For the purpose of this descriptive study we did not deem necessary each treatment being equally represented (compare Table 1).

2.3. Sampling

The survey was conducted in February and March 2015. Per site, a sampling unit consisted of two parallel belt transects (4 m*80 m or 4 m*100 m) about 40 m apart. They were placed in direction of the topographic gradient with a random starting point of the first transect.

Table 1

Key characteristics of the commercial rangeland systems where treatment effects on the woody savanna layer were assessed. Sampling sites of NoTO and NoTD were selected in the vicinity of the treated areas. We considered effects of browsing herbivores on woody species, especially in the recruitment layer to be low and comparable among sites due to the dominance of grazer species on the game ranch and free roaming wild (meso)herbivores in the whole area. NAT = non-selective arboricide treatment, NoTO = no treatment, open woody layer, NoTD = no treatment, denser woody layer, SAT1–3 = selective arboricide treatment, SB = stem burning.

Characteristic	NAT	SAT1	SAT2	SAT3	SB	NoTO	NoTD
Land-use type	Game ranching/cattle farming	Cattle farming	Cattle farming	Cattle farming	Cattle farming	Cattle farming	Game ranching, cattle farming
Grazing system	Open/4 camp rotational	4 camp rotational	6 camp rotational	6 camp rotational	8 camp rotational	6- and 8 camp rotational	Open, 4-, 6- and 8 camp rotational
Stocking rate	10 LSU ha ⁻¹	10 LSU ha ⁻¹	10 LSU ha ⁻¹	10 LSU ha ⁻¹	12 LSU ha ⁻¹	10–12 LSU ha ⁻¹	10–12 LSU ha ⁻¹
Treatment area	1000 ha/245 ha camp ⁻¹	245 ha camp ⁻¹	119 ha camp ⁻¹	250 ha camp ⁻¹	150 ha camp ⁻¹	146–198 ha camp ⁻¹	150–1000 ha camp ⁻¹
No. of sites	8 (4 / 4)	4	4	4	3	6	12

All living trees and shrubs rooting within the belt were identified to species level and counted. The plant height and two maximum canopy diameters (rectangular to each other) were taken. The canopy diameters were used to calculate a proxy for canopy cover using the formula for an ellipse: area = (π *length*width/4).

In order to account for differences in species composition and height class distributions across sampling sites, tree density ha⁻¹ was also standardized into an expression for phytomass by converting plant individuals into tree equivalents, where a TE is a woody plant 1.5 m in size (Teague et al., 1981). Following Dreber et al. (2014), TEs were calculated as $n*h*1.5^{-1}$, where n is the tree density ha⁻¹ and h is the mean height (m) of a species or all recorded plants within pairs of belts. Plant individuals were assigned a height class [≤ 0.5 m (recruits); > 0.5 –1 m; > 1 –2 m; > 2 –3 m; > 3 –5 m; > 5 m] and the number of plants per class (density) used to calculate the Shannon diversity index (H) as a measure of structural diversity (Seymour and Dean, 2010). Species data were used to calculate richness (S), Shannon diversity (H) and Shannon evenness (J) (Magurran and McGill, 2011) per sampling unit.

2.4. Analyses

Differences in structural attributes of the woody layer between treatments [i.e. post-control environments and benchmark sites (NoTD and NoTO)] were assessed by applying one-way ANOVA followed by post-hoc pairwise comparisons using the Tukey–Kramer test appropriate for unequal sample sizes (Quinn and Keough, 2002). Prior analyses, we tested for normality and homogeneity of variance and transformed data if necessary. We note that because some sample sizes were small, potential medium or small effect sizes may have not been detected.

We calculated diversity profiles to compare the woody plant community structure across treatments with respect to different diversity components. The diversity profiles were based on the exponential of the Rényi index family (H_α), as such being basically identical to Hill's index family (Tóthmérész, 1995). Here, a scale parameter $\alpha = 0$ corresponds to species richness (S), $\alpha = 1$ to the Shannon index (H) and $\alpha = 2$ to the Simpson index (D^{-1}), i.e. with increasing α more weight is given species abundances and their equitability. Even though not equaling evenness in the sense of diversity/richness (Tuomisto, 2012), high α is a measure of dominance with the profile shape additionally indicating how even the community structure is (Oldeland et al., 2010). In so doing, communities can be ordered in diversity with varying degrees of sensitivity to rare versus common species and their comparison does not rely on a single arbitrarily selected index. A community is truly more diverse if its diversity profile is consistently above those of other communities, whereas communities with intersecting profiles cannot be fully ordered in diversity (Oldeland et al., 2010; Tóthmérész, 1995).

We used multivariate analyses to examine the similarity of sampling sites across treatments and to summarize their variation with respect to species composition and vegetation structure. Due to the predominance

of short gradients (i.e. data were rather homogeneous), we decided for Principal Components Analysis (PCA) as a linear type of ordination method. It is appropriate for both species and environmental data when applied on a variance–covariance matrix of samples x species and a correlation matrix of samples x environmental variables (here structural attributes), respectively (Lepš and Šmilauer, 2003). Species data were log-transformed to downweight the influence of large abundance values (outliers). Generally, the dissimilarity between samples in a PCA ordination diagram refers to Euclidean distances, whereas the length of the vectors indicates the strength of association with the principal components and the angle between vectors how much correlated they are. Sample points are to be projected perpendicular to the vectors with their ordering providing an indication of a variable's value across the samples (Lepš and Šmilauer, 2003).

Population structure and trends of key species were graphically examined by plotting the mean plant density of height classes per treatment (Gordijn and Ward, 2014). In consideration of the partly extreme variation in plant numbers among height classes, density values were transformed by $\ln(x + 1)$ (Mwavu and Witkowski, 2009), improving visualization of population structure and facilitating the interpretation of population trends. Species included the two most frequent increaser shrubs *G. flava* and *S. mellifera*, as well as the trees *B. albitrunca* and *V. erioloba* both representing important structural elements in the savanna system. Interpretation of population trends follows Breebaart et al. (2001) and Rao et al. (1990): (1) reverse J-shaped size distributions indicate healthy populations with good rejuvenation and recruitment under constant conditions; (2) a weak reverse J-shape, i.e. with fewer individuals in the smaller height classes, suggests a hampered regeneration; (3) L-shaped size distributions indicate a recent recruitment event following an event of exceptional mortality of individuals across demographic stages; (4) normal distributions (hump-shaped) suggests infrequent recruitment and potentially an increased risk of population extinction; (5) uneven size distributions point toward pulsed recruitment patterns and high survival rates in disturbance-driven environments; (6) low densities or missing classes in-between height classes may either refer to limited sampling or indicate some sort of recruitment- or growth-inhibiting disturbances such as fire or browsing.

All analyses were done using PAST v.3.06 (Hammer et al., 2001).

3. Results

3.1. Species patterns

A total of 18 tree- and shrub species were recorded (Table 2). The species *G. flava* and *S. mellifera* were most frequently observed and most abundant across the study area, though their lower phytomass than density was indicative for a relatively large proportion of small individuals (Table 2). The status of *S. mellifera* as the most severe increaser and thickening species and primary target of bush-control measures was also reflected by its large range of density and phytomass

Table 2
Abundance distribution of woody species across the study area and treatments. Species are listed in decreasing order of their frequency given as the percentage of sites (sampling units), which contained the species [(total no. of sites with spp.1 / total no. of sites sampled)*100].

Species	% Frequency	Tree density (plants ha ⁻¹)		Phytomass (TE ha ⁻¹)	
		Mean (±SE)	Range	Mean (±SE)	Range
<i>Grewia flava</i>	97.56	225.96 ± 21.57	468.90	198.03 ± 18.34	466.40
<i>Senegalia mellifera</i>	90.24	179.77 ± 31.60	1128.49	116.70 ± 19.83	476.19
<i>Boscia albitrunca</i>	87.80	51.31 ± 7.33	221.95	54.86 ± 10.29	274.15
<i>Vachellia erioloba</i>	85.37	57.32 ± 8.43	225.00	65.45 ± 13.57	360.42
<i>Lycium cinereum</i>	58.54	29.43 ± 7.28	234.45	14.61 ± 3.61	120.87
<i>Ehretia rigida</i>	56.10	31.79 ± 6.84	175.06	8.73 ± 1.83	46.59
<i>Vachellia luederitzii</i>	53.66	62.29 ± 19.26	597.07	80.73 ± 26.39	824.84
<i>Searsia tenuinervis</i>	41.46	32.33 ± 13.29	425.14	9.77 ± 3.71	94.72
<i>Grewia retinervis</i>	39.02	21.27 ± 6.22	159.43	19.72 ± 7.13	202.56
<i>Lycium hirsutum</i>	36.59	10.59 ± 2.68	50.00	4.72 ± 1.28	32.09
<i>Dichrostachys cinerea</i>	31.71	42.70 ± 19.23	672.09	15.86 ± 8.61	342.82
<i>Ziziphus mucronata</i>	29.27	6.63 ± 1.92	34.39	7.35 ± 2.28	57.20
<i>Cadaba aphylla</i>	19.51	3.13 ± 1.09	18.76	0.75 ± 0.28	6.04
<i>Rhigozum brevispinosum</i>	17.07	37.21 ± 26.52	1050.34	11.60 ± 8.64	343.02
<i>Vachellia hebeclada</i>	12.20	2.21 ± 1.08	25.00	1.39 ± 0.63	11.75
<i>Terminalia sericea</i>	9.76	2.21 ± 1.15	18.76	1.21 ± 0.65	14.58
<i>Vachellia haematoxylon</i>	7.32	3.05 ± 1.84	37.50	3.42 ± 2.14	52.83
<i>Rhigozum trichotomum</i>	2.44	0.30 ± 0.30	0.00	0.29 ± 0.29	0.00

(Table 2). In contrast, frequent trees like *B. albitrunca* and *Vachellia erioloba* had in average a low density but higher phytomass (Table 2), suggesting abundant mature individuals. Among the remaining less frequent species, *Dichrostachys cinerea*, *V. luederitzii* and especially *Rhigozum brevispinosum* were relatively abundant at some locations as indicated by the standard error and range of respective plant densities (Table 2).

The PCA explained about 58% of the variability in species distribution with the first principal component (axis) separating the species-diverse from the species-poor savanna sites (Fig. 1). Most species were positively associated with the untreated, relatively dense growing woody layer (NoTD) and to a lesser extent with the non-selective treatment (NAT) and the selective treatment SAT1 (Fig. 1). Accordingly, NoTD sites were the most species diverse and evenly structured followed by NAT- and SAT1 sites (Fig. 2). The NoTD sites were characterized by

increased abundances of the tree *V. luederitzii* and a prominent shrub layer dominated by *Lycium cinereum*, *Eragrostis rigida*, *Searsia tenuinervis* and *R. brevispinosum*. Despite some within-group variation, the woody layers following NAT and SAT1 were relatively similar in species composition. The increaser species *D. cinerea*, *Grewia retinervis* and *S. mellifera* were strongly associated with respective sites (Fig. 1).

In contrast to SAT1, the selective control of increaser species showed to have the potential to also create species poor communities of low diversity as in the case of SAT2 and SAT3 (Fig. 2). Here, many species were absent and others occurred at low abundance. Accordingly, the woody layer was dominated by a few species, notably *Vachellia haematoxylon* and *V. erioloba* (Fig. 1), which are usually not treated during bush-control operations if not accidentally treated or cleared in the course of non-selective treatments (e.g. NAT). In comparison, untreated open savanna layers (NoTO) were similar in species composition to SAT2

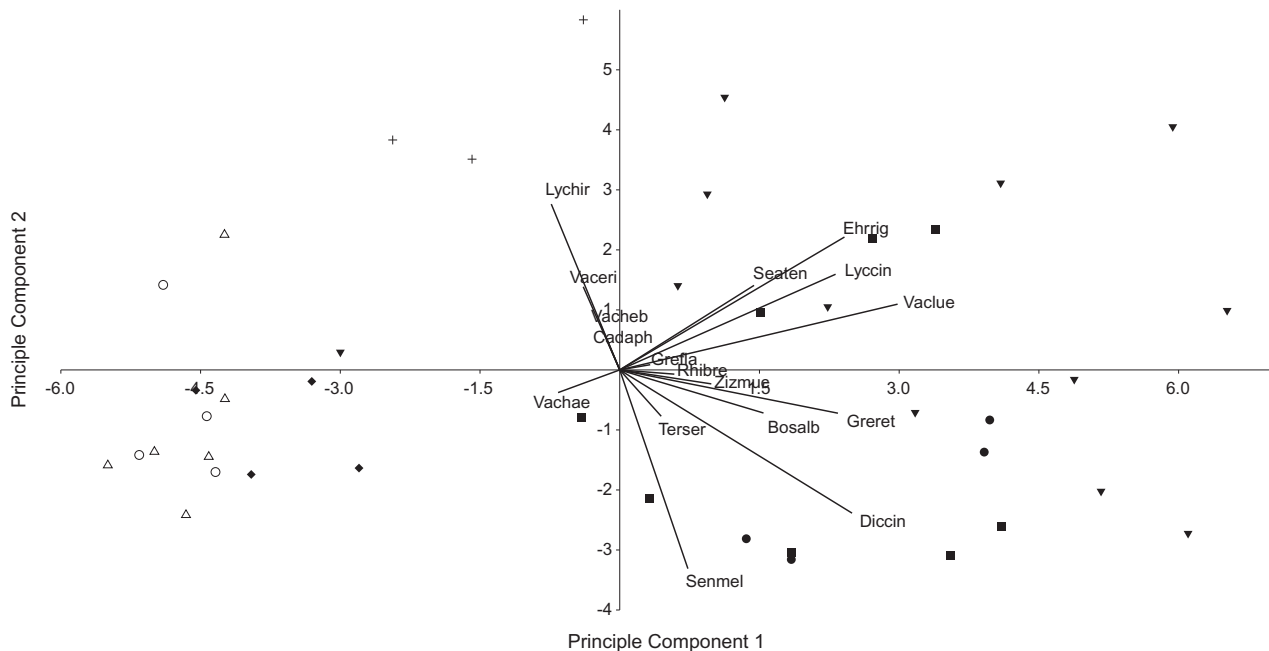


Fig. 1. Principle Component Analysis of woody plant communities across treatments. PC1 explains 57.5% and PC2 20.6% of the variance in the data set. For component loadings see Table 4. Species names (see Table 2) are abbreviated by the first three letters of genus and species. NAT = filled squares (non-selective herbicide treatment); NoTO = triangles (no treatment, open woody layer); NoTD = filled, inverse triangles (no treatment, denser woody layer); SAT1 = filled circles, SAT2 = filled diamonds, SAT3 = open circles (selective herbicide treatments); SB = pluses (stem burning).

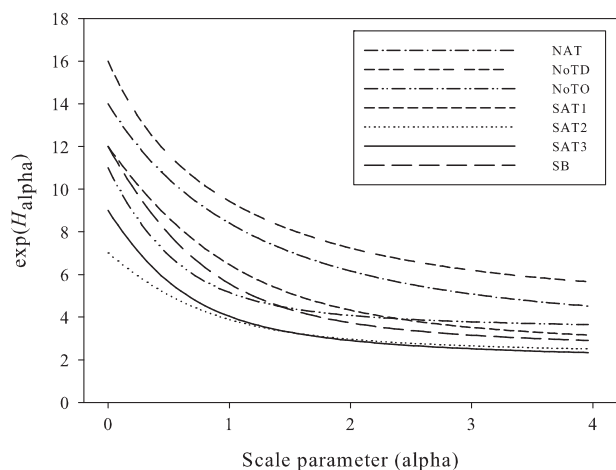


Fig. 2. Diversity profiles for the woody savanna layer across treatments. The profiles are based on the exponential of the Rényi index family. NAT = non-selective herbicide treatment; NoTO = no treatment, open woody layer; NoTD = no treatment, denser woody layer; SAT1–3 = selective herbicide treatment; SB = stem burning.

and SAT3 (Fig. 1), even though NoTO featured more species and the sites were more diverse and even in structure (Fig. 2). Stem burning (SB) resulted in a woody layer of intermediate richness and diversity (Fig. 2).

3.2. Population structure

In untreated savannas (NoTD and NoTO), the height-class distribution of the increaser shrubs *S. mellifera* and *G. flava* was uneven, and in case of the latter approximated a hump-shaped distribution in denser woody layers (NoTD). Both tree species displayed a reverse J-shaped population structure in dense savannas, whereas in the open savannas mature individuals of *B. albitrunca* were largely absent and the height-class distribution of *V. erioloba* was uneven (Fig. 3).

Following the non-selective removal of woody species (NAT), both *S. mellifera* and *V. erioloba* displayed a L-shaped population structure, but the former had a higher recruitment rate. *Grewia flava* displayed a constant decrease in height-class density and *B. albitrunca* had an uneven, concave-like height-class distribution, i.e. recruits and mature individuals were most abundant (Fig. 3).

In general, *S. mellifera* showed strong recruitment and high mortality in the larger height classes in response to the selective herbicide treatments (SAT1–3). Compared to SAT2, the follow-up control of *S. mellifera* (SAT3) further reduced the density of medium-sized individuals. The population structure of *G. flava* was hump-shaped irrespective of the SAT treatment. *B. albitrunca* displayed a reverse J-shaped height-class distribution following SAT1 but a weak J-shaped distribution following SAT2 and SAT3. The population structure of *V. erioloba* was variable across the SAT treatments displaying an uneven height-class distribution in SAT1-sites, a weak reverse J-shaped size structure in SAT2-sites and a L-shaped size structure in SAT3-sites (Fig. 3).

The double SB treatment eradicated all height classes of *S. mellifera* but recruitment occurred in the meantime. *Grewia flava* approximated a J-shaped and *B. albitrunca* a reverse J-shaped height-class distribution, at least as far as could be deduced from the number of individuals recorded at the sampling sites. In contrast, *V. erioloba* was relatively abundant across demographic stages, displaying an uneven height-class distribution (Fig. 3).

3.3. Vegetation structure

Differences in vegetation structure between treatments clearly reflected the intensity and level of selectivity with which the bush-control treatments had been applied. While all treatments

resulted in fairly open environments resembling plant densities found in NoTO sites, the selective control with follow-up treatment (SAT3) significantly lowered the standing woody phytomass (Table 3). Phytomass was also comparatively low in NAT sites and together with the highest proportion of recruits and smallest individuals in the category “<2 m” it relativized the high plant density (Table 3). Hence, contrary to the dense woody layer of NoTD sites, NAT sites were characterized by a prominent recruitment layer and overall significantly lowest structural diversity (Table 3). Comparing the non-selective (NAT) and selective treatments (SAT1–3, SB), it was apparent that they differed significantly in the height structure of a lower and upper woody stratum, whereas these strata were comparable among the selective treatments and in comparison to both untreated conditions (NoTO and NoTD) (Table 3). NoTO sites had in average the tallest tree stands with correspondingly large canopies (Table 3).

In correspondence to above described differences, the PCA of structural variables revealed not only distinct patterns between bush-control treatments and their separation from the benchmark sites, but also that there is much variation in the development of the woody layer. The first three principle components (PCs) explained about 95% of the structural variability among the sampling sites. PC1 had a large positive association with the proportion of recruits in the woody layer, as well as negative associations with average plant height and height below 2 m (Table 4). Accordingly, it separated NAT from the other treatments, where the recruitment layer was generally less strongly developed, increasing the average height of trees and shrubs (Fig. 4A). PC2 was positively associated with especially woody phytomass, plant density and structural diversity (Table 4). These variables were strongly correlated and characterized major gradients between NAT and NoTD environments (Fig. 4B). The corresponding scores of the NoTO samples and those of the selective treatments were lower, hence sample sites appeared in an intermediate stage. However, there was still some within- and between-group variation as shown by the varying distances to either sites of the major gradients (Fig. 4B). PC3 was strongly associated with mean canopy area and species evenness (Table 4), separating especially NoTO from SAT1–3 (Fig. 4B).

4. Discussion

4.1. Woody vegetation in non-selectively controlled sites

The non-selective herbicide treatment (NAT) can be considered most destructive because of its clearing-like character affecting the woody savanna layer as a whole (see Appendix B). In the present study, the corresponding loss of structural diversity also came at the expense of individuals of *V. erioloba* important for biodiversity conservation (Seymour and Dean, 2010), enriched soils and favorable microclimates (Thomas et al., 2018). The species' population structure indicated a high mortality in especially the woody stratum above 2 m (height classes 4–6) compared to the benchmark sites. In the created open savannas, only a few large solitary *B. albitrunca* trees protruded from the grass matrix (compare Appendix B), confirming the notion of Moore et al. (1985) that this species responds less sensitive to the applied Tebuthiuron-based herbicide. However, Bezuidenhout et al. (2015) pointed out that delayed effects caused by Tebuthiuron's possible accumulation, persistence and potential of groundwater contamination cannot be fully excluded. Low densities of *S. mellifera* in height class 3 and above suggest that the treatment via airplane accidentally missed some medium-sized (saplings) and larger individuals, which may vary a lot with application procedure and treatment intensity.

Following the metabolism or leach of the herbicide's active ingredient Tebuthiuron into deeper soil layers, it seems that many woody species were able to re-establish likely due to a viable seed bank, an initially competition-free environment, and thus an increased resource availability (Bezuidenhout et al., 2015; Harmse et al., 2016). The evolved transitional state showed to be the second-most species rich and diverse

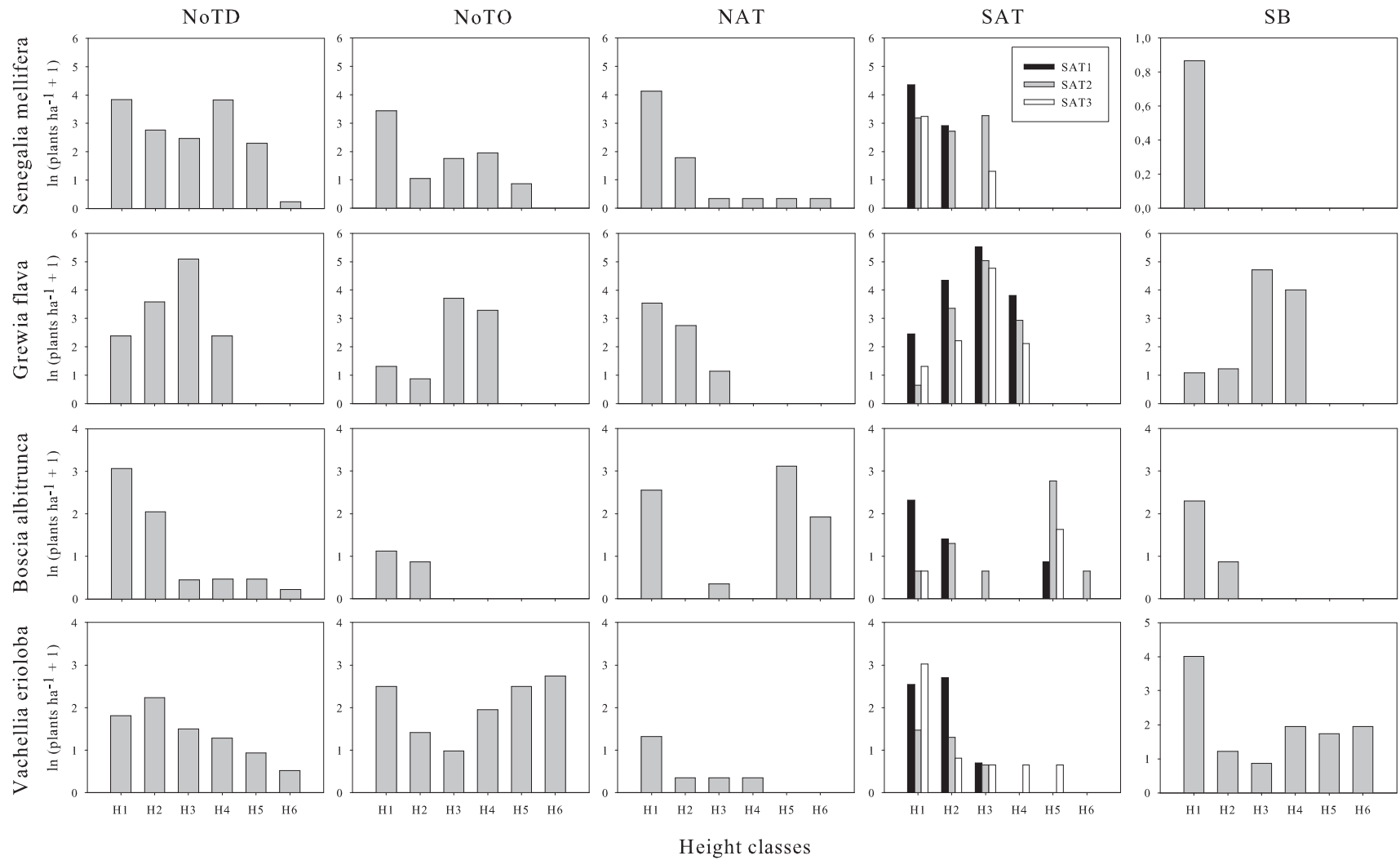


Fig. 3. Density of the four dominant species in different height classes per treatment. Height classes: H1 = ≤ 0.5 m; H2 = > 0.5 –1 m; H3 = > 1 –2 m; H4 = > 2 –3 m; H5 = > 3 –5 m; H6 = > 5 m. Treatments: NAT = non-selective arboricide treatment; NoTO = no treatment, open woody layer; NoTD = no treatment, denser woody layer; SAT1–3 = selective arboricide treatment; SB = stem burning.

Table 3

Structural attributes of the woody layer across treatments (for comparisons of species richness and species diversity refer to the Rényi diversity profiles in Fig. 2). Values are the mean \pm SE per treatment. The lowest and highest value in a row is highlighted in bold. Different superscripts indicate significant differences ($p < .05$) between treatments (Tukey–Kramer test). NAT = non-selective arboricide treatment, NoTO = no treatment, open woody layer, NoTD = no treatment, denser woody layer, SAT1–3 = selective arboricide treatment, SB = stem burning.

Attribute	Treatment						
	NAT	SAT1	SAT2	SAT3	SB	NoTO	NoTD
Density (plants ha ⁻¹)	707.26 \pm 140.32 ^{abc}	953.43 \pm 106.58 ^{ac}	431.25 \pm 58.30 ^{ab}	290.63 \pm 22.46^b	462.50 \pm 52.04 ^{ab}	437.50 \pm 52.93 ^{ab}	1365.98 \pm 216.77^c
Phytomass (TE ha ⁻¹)	341.95 \pm 32.20 ^{ac}	628.72 \pm 52.32 ^b	360.48 \pm 38.34 ^{ac}	242.83 \pm 15.07^c	437.78 \pm 25.78 ^{ab}	464.31 \pm 27.83 ^{ab}	1121.61 \pm 103.45^d
% Recruits (<0.5 m)	69.93 \pm 4.68^a	34.53 \pm 7.94 ^{ab}	18.64 \pm 6.71^b	30.18 \pm 6.95 ^b	29.98 \pm 2.30 ^b	32.96 \pm 9.12 ^b	28.80 \pm 3.41 ^b
Height (m)	0.82 \pm 0.10^a	1.01 \pm 0.10 ^{ab}	1.30 \pm 0.16 ^{ab}	1.28 \pm 0.15 ^{ab}	1.47 \pm 0.23 ^{ab}	1.71 \pm 0.22^b	1.39 \pm 0.11 ^{ab}
Height below 2 m	0.43 \pm 0.03^a	0.85 \pm 0.08 ^b	1.12 \pm 0.13^b	1.03 \pm 0.10 ^b	0.91 \pm 0.07 ^b	0.89 \pm 0.14 ^b	0.86 \pm 0.05 ^b
Height above 2 m	4.76 \pm 0.22^a	2.62 \pm 0.22^b	3.11 \pm 0.29 ^b	3.02 \pm 0.20 ^b	3.19 \pm 0.60 ^b	3.61 \pm 0.42 ^{ab}	3.07 \pm 0.11 ^b
Canopy area (m ²)	5.42 \pm 0.96 ^{abc}	2.64 \pm 0.31^a	4.28 \pm 0.39 ^{ab}	5.14 \pm 1.27 ^{abc}	6.04 \pm 1.59 ^{bc}	9.58 \pm 1.23^c	5.15 \pm 0.61 ^{abc}
Structural diversity (H)	0.87 \pm 0.09^a	1.25 \pm 0.05 ^b	1.22 \pm 0.04 ^b	1.34 \pm 0.09 ^b	1.49 \pm 0.08^b	1.37 \pm 0.07 ^b	1.47 \pm 0.03 ^b

with an evenly structured woody community forming a fairly dense recruitment layer. In this respect, the population structure of *G. flava* and *S. mellifera* indicated a recent recruitment event that must have followed a period of frequent rainfall since arboricide application eight years ago (see also discussion in Harmse et al., 2016). *Senegalia mellifera* can be a highly problematic species in Kalahari savannas. While it provides nutritious browse for game and livestock (van Rooyen et al., 2001) and contributes to the availability of nutrient-enriched subhabitats (“islands of fertility”) in these systems (Hagos and Smit, 2005; Ward et al., 2018), it suppresses herbaceous plant growth in the understorey (Ward et al., 2018) and beyond the canopy spread (Donaldson, 1969) (see also Appendix B). Further, populations of this species tend to form thickets given: (1) favorable conditions for seed production and germination, (2) a lack of fires or browsing as demographic bottlenecks, and/or (3) the overgrazing of a competitive grass layer (Donaldson, 1969; Harmse et al., 2016; Kraaij and Ward, 2006; Skarpe, 1990). Likewise, *G. flava* has the potential to increase in abundance once competition by grasses

(Skarpe, 1990) or other woody species (Hesselbarth et al., 2018) is removed (compare Appendix B).

The assessed NAT rangelands can be assumed to possess low functional integrity (sensu Ludwig et al., 2004): Results suggest that NAT is capable of effecting a long-standing change of the horizontal and vertical structural heterogeneity of the woody layer, coming along with a lowered ability of the ecosystem to retain water and accumulate nutrients in the soil and to benefit biodiversity. Moreover, while the competitive environment favors the development of a productive grass layer, the strongly developed recruitment layer indicates an increased risk of a re-thickening woody layer (compare Harmse et al., 2016). At least, the composition and diversity of the recruitment layer suggest that non-selectively treated woody communities do not necessarily have to develop into mono-dominant stands of serious increaser species (compare Appendix B) and multiple pathways are possible depending on the climatic conditions triggering recruitment events, timely follow-up treatments and an adapted post-control grazing management (compare Harmse et al., 2016; Smit, 2004).

Table 4

Component loadings of individual variables used in the Principal Component Analyses of the woody plant communities (upper part) and vegetation structure (lower part) in correspondence to Figs. 1 and 4.

Variable	Principal components		
	PC 1	PC 2	PC 3
Species			
<i>Vachellia erioloba</i>	-0.12129	0.069494	
<i>Vachellia haematoxylon</i>	-0.092163	-0.019705	
<i>Vachellia hebeclada</i>	-0.024328	0.11857	
<i>Vachellia luederitzii</i>	0.51449	0.12584	
<i>Senegalia mellifera</i>	0.14855	-0.11324	
<i>Boscia albitrunca</i>	0.18449	-0.076234	
<i>Cadaba aphylla</i>	-0.0078473	-0.038031	
<i>Dichrostachys cinerea</i>	0.24413	-0.62342	
<i>Ehretia rigida</i>	0.37906	0.16572	
<i>Grewia flava</i>	0.074136	0.094997	
<i>Grewia retinervis</i>	0.31035	-0.37533	
<i>Lycium cinereum</i>	0.41322	0.14666	
<i>Lycium hirsutum</i>	-0.08717	0.40541	
<i>Rhigozum brevispinosum</i>	0.16334	0.27085	
<i>Searsia tenuinervis</i>	0.32421	0.31241	
<i>Terminalia sericea</i>	0.016519	-0.14535	
<i>Ziziphus mucronata</i>	0.19957	0.028954	
Structural attributes			
Density (plants ha ⁻¹)	0.26785	0.38825	-0.20637
Phytomass (TE ha ⁻¹)	0.10454	0.52924	-0.085761
% Recruits (<0.5 m)	0.42169	-0.23854	0.095415
Height (m)	-0.40682	0.14652	0.26641
Height < 2 m	-0.43819	0.12303	-0.13199
Height > 2 m	0.23556	-0.26065	0.34491
Canopy area (m ²)	-0.21785	-0.072403	0.53181
Species richness (S)	0.32242	0.36349	0.050091
Shannon diversity (H)	0.27988	0.32914	0.35308
Evenness (Shannon J)	0.040765	0.15101	0.5612
Structural diversity (H)	-0.30838	0.37312	0.093035

4.2. Woody vegetation in selectively controlled sites

Compared to the newly developing woody layers in NAT sites, SAT communities were more heterogeneous in vegetation structure (see also Appendix B) but less so in species composition, i.e. species diversity was lower. In case of SAT2 and SAT3, species diversity was even lower than in the open configuration of non-treated sites (NoTO). Nevertheless, the average recruitment level of species and height structure was comparable to those of the benchmark sites (NoTO and NoTD). Unfortunately, we do not know how the initial composition looked like, and therefore could only consider the common species pool of the benchmark sites as representative for the study area. Given similar soil properties and climatic conditions across sampling sites, the very low diversity and amount of recruits characterizing SAT2 sites might be explained by either increased browsing, a weak seed bank and/or a less selective treatment of species across demographic stages. The very low tree diversity, density and phytomass characterizing SAT3 sites may depict a manifested long history of bush control toward the creation of grasslands for forage (meat) production.

Vachellia erioloba and *S. mellifera* populations were similar in that they: (1) showed a healthy recruitment comparable to conditions in benchmark sites and (2) lacked mature individuals. In case of *V. erioloba*, the absence of height classes 4–6 in SAT1 and SAT2 sites may document the threat of accidentally treating individuals of non-target species (see also Appendix B). The population structure of *G. flava* indicated infrequent recruitment and a risk of population declines. However, the comparatively low densities of recruits compared to other species in most treatments corresponds to the reported “low emergence rate and high juvenile mortality” being characteristic for this species (Tews and Jeltsch, 2004). A similar pattern was found in NoTD sites.

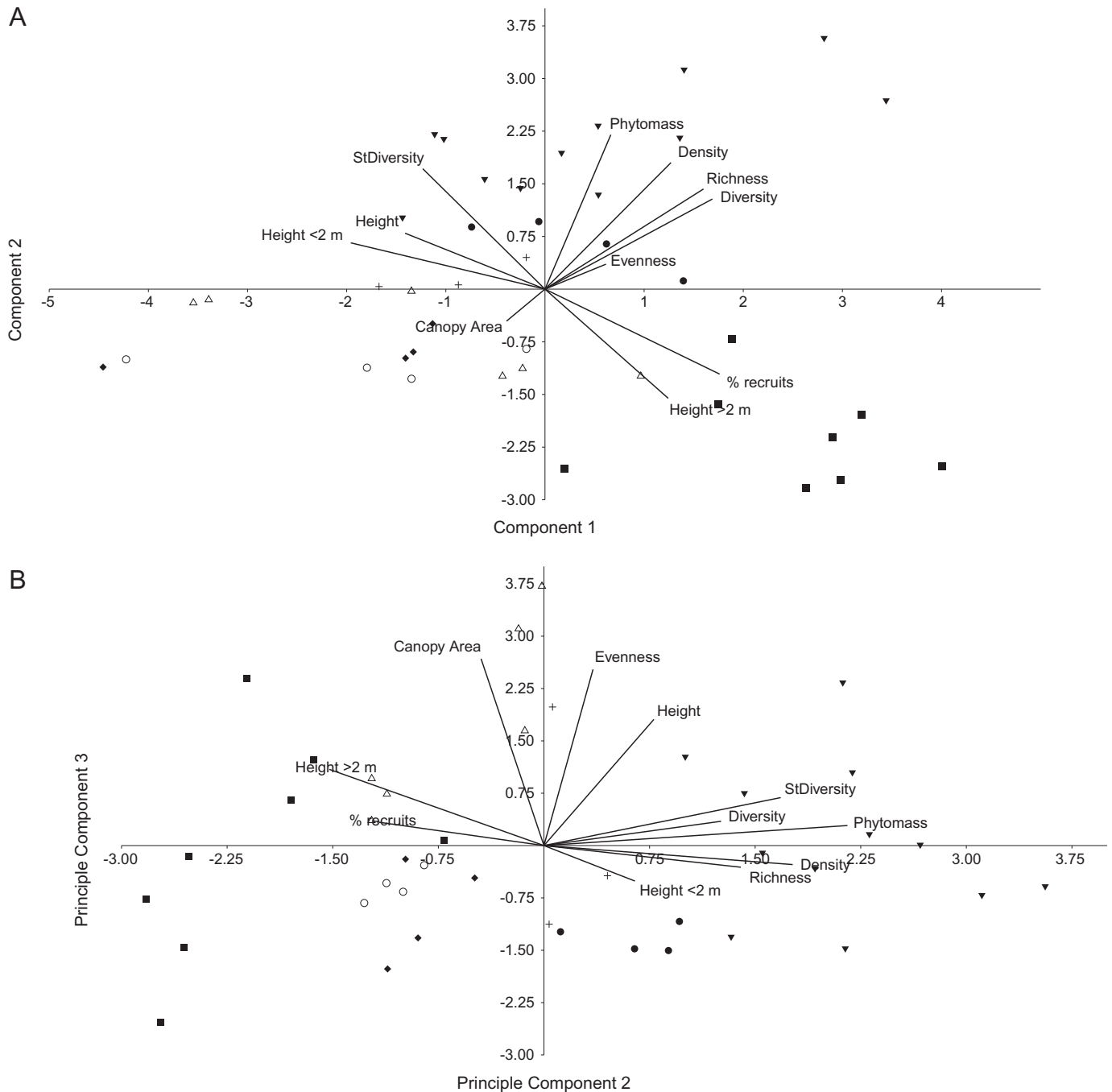


Fig. 4. Principle Component Analysis of the vegetation structure across treatments. Shown are the principal components 1 and 2 (A) and 2 and 3 (B), explaining about 41.8%, 30.8% and 22.6%, respectively, of the structural variability among sampling sites. For component loadings see Table 4. Symbol coding of treatments as in Fig. 1.

The SB treatment targeting *S. mellifera* was obviously conducted quite accurate and did not harm other species. The population structure of *S. mellifera* indicated that the treatment was effective, i.e. all height classes except H1 were absent and the observed lack of coppice shoots point toward total bud and root kill (Donaldson, 1966, 1967). The woody layer was of intermediate species richness and diversity and structurally diverse, overall pointing toward a favorable condition for biodiversity and stability (compare above and Appendix B). Thus, SB can be considered a “green” alternative to the selective bush control with chemicals. However, the effort of SB is certainly much more time- and labor-consuming. Experiments have shown that no matter which fuels for SB are used, the killing of a larger plant individual requires an effective burn of at least 3 min (Donaldson, 1967). In comparison, SAT by hand is

quickly done by dropping granules or spraying solution under the canopy (Harmse et al., 2016) and then only relies on a rainfall event transporting the herbicide into the ground.

It is often recommended that if bush-control treatments are applied, care should be taken to keep a certain proportion of trees and shrubs as fodder sources for browsing livestock and game, as habitats for a variety of plants, animals and microbes (Hagos and Smit, 2005; Harmse et al., 2016; Seymour and Dean, 2010; Thomas et al., 2018). SAT and SB allows to create such a savanna ecosystem. The option of thinning out undesirable woody species and treating individual based across demographic stages has the advantage of being able to opt for a preferred intensity and tree:grass ratio, while keeping functionally important structural elements. In order to effectuate a more stable environment, low-intensity

thinning is therefore recommended over intensive thinning, because it allows to specifically promote growth and competitive strength of some remaining trees, which can suppress the surrounding regeneration of woody increaser species (Smit, 2004). Accordingly, outcomes of selective treatments can differ to a great extent, as documented in the present survey. On the one hand, this may relate to different needs, outlooks and preferences of the land owners according to their land-use objectives. On the other hand, outcomes are sensitive to the appropriateness and carefulness of the treatment, and easily configurations are established that have undesirable side effects which are hardly reversible. Moreover, restoration and regeneration of woody communities is a slow process. This is why selective bush-control treatments should formulate clear requirements regarding woody layer density, height structure and composition before being preferably conducted by trained laborer who must have sufficient species knowledge.

4.3. General considerations concerning local bush control

The above described response patterns of different woody species and the resulting shape of the woody savanna layer documents a cross-section of different savanna states and transitions in the semi-arid Kalahari of the Molopo area in South Africa. Some of these suggest that bush control can be harmful to the local ecosystem, pointing toward the responsibility of properly applying a treatment, especially as some treatment effects may persist and change the ecosystem over an extended period of time (Bezuidenhout et al., 2015). Accordingly, good knowledge about the ecology of concerned species and solid information about the used herbicide is crucial to assess woody responses and possible directions of post-control vegetation development in a specific environmental context.

In the introduction we noted the importance of aligning the bush-control treatment with the prevailing environmental conditions and characteristics of the target woody species. Life-history strategies are of special relevance, with the species' performance, re-colonization potential and spread often being highly dependent on the quantity of a viable seed bank and dispersal ability (Donaldson, 1969), the quantity and frequency of seasonal rainfall over multiple consecutive years as determinants of successful germination and establishment (Bezuidenhout et al., 2015), as well as the species' competitive strength and ability to use windows of opportunities. For example, the coarse-structured, deep sandy and well leached soils of the surveyed water-limited Kalahari environments facilitate the establishment of woody species, whose taproot can rapidly penetrate soil into layers below the upper grass-tree competition zone (Donaldson, 1969; Kambatuku et al., 2013; Wilson and Witkowski, 1998). An additional extensive lateral root system, as in *G. flava* and *S. mellifera*, allows to effectively and efficiently exploit also the moisture resources of the topsoil (Donaldson, 1969). Accordingly, disturbances that lowers tree-tree and tree-grass competition (e.g. fire, drought, overgrazing, bush control) may initiate or accelerate the thickening up of the so-called increaser woody species (Kraaij and Ward, 2006; Skarpe, 1990, 1980). Species like *S. mellifera* shed their seeds close to the parent plant, where grass competition and risk of fires is low, giving seedlings an advantage during early life stages. In contrast, due to the zoochorous dispersal mode of *V. erioloba*, *B. albitrunca* and *G. flava*, individuals of these species often have to recruit in more competitive and fire-prone habitats, likely slowing down their establishment rate in the grass matrix (Donaldson, 1969). However, according to Tews et al. (2004), cattle browsing on fruiting *G. flava* may intensify seed dispersal and, in the long term, facilitate the development of dense stands.

Another crucial factor to consider is the species' sensitivity to the applied herbicide (Moore et al., 1985), in our case a Tebuthiuron-based chemical, and how the species interact with the active ingredient in the soil over time (du Toit and Sekwadi, 2012). This may be decisive for treatment effectiveness, plant recovery rates and potential lags in the response of some species (for related management implications in the same environmental context like the present study see Harmse

et al., 2016). In the sandy Kalahari soils with low organic matter and clay content, Tebuthiuron is quite mobile and easily leached into deeper soil layers. Hence, its effect on shallow-rooting woody species is temporary, whereas there is concern that it could remain active some time and in the long term affect slow-growing and deep-rooting species (compare Bezuidenhout et al., 2015). However, we are not aware of any study that has analyzed and monitored the fate of such an herbicide in deep sandy Kalahari soils. This seems to be long overdue also because of some conflicting views among and between scientists and land users, resulting in scientific but also economic uncertainty. Bush control with herbicides therefore requires a very thorough and foresighted planning and an ecologically responsible implementation.

5. Conclusions

The study documents how different bush-control treatments can shape the structure and alter the composition of the woody layer in a semi-arid Kalahari savanna. Intense thinning, for which there can be an economic logic, showed to create "artificial" savanna landscapes of low woody phytomass and structural diversity and with a prominent and diverse recruitment layer. Selective thinning largely resembled the structure of woody communities found in benchmark sites but still the active interference was apparent in some cases through a lower species richness, diversity and evenness. Results suggest that high intensity and/or low selectivity of bush control pose a threat to local biodiversity and landscape integrity. However, the induced changes are not permanent as recruitment occurred to varying degrees among woody species, offering different pathways in post-control vegetation development.

The results allowed us to draw some basic conclusions about the impact potential of selected bush-control treatments, whereas the total survey provides valuable baseline information that add to the available information from related descriptive and experimental studies conducted in the Molopo area (e.g. Donaldson, 1966, 1967, 1969; Harmse et al., 2016; Meyer et al., 2001; Moore et al., 1985; Richter et al., 2001). Together, this information can help land users to make appropriate management choices to prevent or mitigate negative effects of both bush thickening and its control. Moreover, it can serve as reference for decision making in similar semi-arid and deep-sandy savanna systems.

The present study should motivate to conduct more detailed comparative assessments of a larger set of bush-control treatments and samples embedded in a monitoring framework. This would allow to integrate interfering factors like grazing management and spatiotemporal rainfall patterns that are crucial determinants of woody layer dynamics and may have influenced the short-term site-specific vegetation development since bush control took place. It would also allow to assess possible long-term ecological effects associated with the use of herbicides in this type of savanna.

Still, in order to better understand recruitment, growth and mortality patterns of local woody species, more research is needed into tree-grass and tree-tree interactions (e.g. Hesselbarth et al., 2018) and species-specific population dynamics (e.g. Joubert et al., 2017). Moreover, while relationships between grass productivity and bush cover or density are relatively well established for some semi-arid Kalahari savannas, less is known with respect to changes in ecosystem functioning, especially after the application of certain bush-control treatments. Due to trait differences between woody species, it is likely that the functional consequences of thinning and thickening vary considerably with the selection of treated species and the species increasing in abundance, respectively (Linstädter et al., 2016; Randle et al., 2018). Overall, this knowledge would improve our ability to predict bush-thickening dynamics under different land-use and climate scenarios (e.g. Tews and Jeltsch, 2004), to create a suitable competitive environment within and between the vegetation layers and ultimately to align the post-control management of the woody layer accordingly (Donaldson, 1969; Smit, 2004).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.sajb.2019.08.026>.

Funding

This work was supported by the German Federal Ministry of Education and Research (BMBF) via the IDESSA project (www.idessa.org; grant number 01LL1301A).

Author contributions

K.K. and N.D. conceived the idea of this study; S.v.R. and N.D. conducted the fieldwork; N.D., with contributions from S.v.R., analyzed the data; K.K. contributed to the interpretation of findings; N.D. wrote the manuscript; K.K. and S.v.R. commented on the manuscript.

Acknowledgements

We are very grateful to all land users participating in this study by providing access to their rangelands and sharing their knowledge and rangeland management history.

References

- Archer, S.R., Predick, K.L., 2014. An ecosystem services perspective on brush management: research priorities for competing land-use objectives. *J. Ecol.* 102, 1394–1407.
- Bezuidenhout, H., Kraaij, T., Baard, J., 2015. Persistent effects of chemicals used to control shrub densification in semi-arid savanna. *Earth Sci. Res.* 4, 31–39.
- Blaum, N., Rossmanith, E., Schwager, M., Jeltsch, F., 2007. Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic Appl. Ecol.* 8, 552–564.
- Breebaart, L., O'Connor, T.G., Hughes, J.C., Morris, C.D., Rushworth, I.A., 2001. The effects of topographic variables and cultivation on the woody vegetation of Weenen nature reserve, KwaZulu-Natal. *Afr. J. Range Forag. Sci.* 18, 75–91.
- Breedt, J.A.D., Dreber, N., Kellner, K., 2013. Post-wildfire regeneration of rangeland productivity and functionality – observations across three semi-arid vegetation types in South Africa. *Afr. J. Range Forag. Sci.* 30, 161–167.
- Donaldson, C.H., 1966. Control of blackthorn in the Molopo area with special reference to fire. *Proc. Annu. Cong. Grassl. Soc. South. Afr.* 1, 57–62.
- Donaldson, C.H., 1967. Further findings on the effects of fire on blackthorn. *Proc. Annu. Cong. Grassl. Soc. South. Afr.* 2, 59–61.
- Donaldson, C.H., 1969. Bush Encroachment with Special Reference to the Blackthorn Problem of the Molopo Area. Department of Agricultural Technical Services, Vryburg, RSA.
- Dougill, A.J., Thomas, A.D., 2004. Kalahari sand soils: spatial heterogeneity, biological soil crusts and land degradation. *Land Degrad. Dev.* 15, 233–242.
- Dreber, N., Harmse, C.J., Götze, A., Trollope, W.S.W., Kellner, K., 2014. Quantifying the woody component of savanna vegetation along a density gradient in the Kalahari bushveld: a comparison of two adapted point-centered quarter methods. *Rangel. J.* 36, 91–103.
- Dreber, N., Van Rooyen, S.E., Kellner, K., 2018. Relationship of plant diversity and bush cover in rangelands of a semi-arid Kalahari savanna, South Africa. *Afr. J. Ecol.* 56, 132–135.
- du Toit, J.C.O., Sekwadi, K.P., 2012. Tebuthiuron residues remain active in soil for at least eight years in a semi-arid grassland, South Africa. *Afr. J. Range Forag. Sci.* 29, 85–90.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709–722.
- Gordijn, P., Ward, D., 2014. Fire can suppress the development of macrophyllous thickets. *Afr. J. Range Forag. Sci.* 31, 147–160.
- Hagos, M.G., Smit, G.N., 2005. Soil enrichment by *Acacia mellifera* subsp. *detinens* on nutrient poor sandy soil in a semi-arid southern African savanna. *J. Arid Environ.* 61, 47–59.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electr.* 4, 1–9.
- Harmse, C.J., Kellner, K., Dreber, N., 2016. Restoring productive rangelands: a comparative assessment of selective and non-selective chemical bush control in a semi-arid Kalahari savanna. *J. Arid Environ.* 135, 39–49.
- Hausmann, N.S., Kalwij, J.M., Bezuidenhout, S., 2016. Some ecological side-effects of chemical and physical bush clearing in a southern African rangeland ecosystem. *S. Afr. J. Bot.* 102, 234–239.
- Hesselbarth, M.H.K., Wiegand, K., Dreber, N., Kellner, K., Esser, D., Tsvurra, Z., 2018. Density-dependent spatial patterning of woody plants differs between a semi-arid and a Mesic savanna in South Africa. *J. Arid Environ.* 157, 103–112.
- Hudak, A.T., Wessman, C.A., Seastedt, T.R., 2003. Woody overstorey effects on soil carbon and nitrogen pools in south African savanna. *Austral Ecol.* 28, 173–181.
- Joubert, D.F., Rust, A., Smit, G.N., Hoffman, M.T., 2017. Growth rates and mortality patterns of *Acacia mellifera* subsp. *detinens* in the semi-arid Highland savanna, Namibia: encroachment is not as rapid as previously believed. *Namib. J. Environ.* 1, 1–5.
- Kambatuku, J.R., Cramer, M.D., Ward, D., 2013. Overlap in soil water sources of savanna woody seedlings and grasses. *Ecohydrology* 6, 464–473.
- Kraaij, T., Ward, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecol.* 186, 235–246.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, New York, USA.
- Linstädter, A., Bora, Z., Tolera, A., Angassa, A., 2016. Are trees of intermediate density more facilitative? Canopy effects of four east African legume trees. *Appl. Vegetat. Sci.* 19, 291–303.
- Lohmann, D., Tietjen, B., Blaum, N., Joubert, D.F., Jeltsch, F., 2014. Prescribed fire as a tool for managing shrub encroachment in semi-arid savanna rangelands. *J. Arid Environ.* 107, 49–56.
- Ludwig, J.A., Tongway, D.J., Bastin, G.N., James, C.D., 2004. Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. *Austral Ecol.* 29, 108–120.
- Magurran, A.E., McGill, B.J., 2011. *Biological Diversity – Frontiers in Measurement and Assessment*. Oxford University Press, Oxford, UK.
- Meyer, T.C., Richter, C.G.F., Smit, G.N., 2001. The implications of vegetation dynamics in the Kalahari Thornveld for game ranching. *North West Focus* 2, 3–10.
- Moore, A., Van Niekerk, J.P., Knight, I.W., Wessels, H., 1985. The effect of tebuthiuron on the vegetation of the thorn bushveld of the northern cape – a preliminary report. *J. Grassl. Soc. S. Afr.* 2, 7–10.
- Mwavu, E.N., Witkoswki, E.T.F., 2009. Population structure and regeneration of multiple-use tree species in a semi-deciduous African tropical rainforest: implications for primate conservation. *For. Ecol. Manage.* 258, 840–849.
- O'Connor, T.G., Puttick, J.R., Hoffman, M.T., 2014. Bush encroachment in southern Africa: changes and causes. *Afr. J. Range Forag. Sci.* 31, 67–88.
- Oldeland, J., Dreber, N., Wesuls, D., 2010. Diversity measures in comparative rangeland studies: application and advantages of species abundance distributions and diversity profiles. *Dinteria* 31, 50–66.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Randle, M., Stevens, N., Midgley, G., 2018. Comparing the differential effects of canopy shading by *Dichrostachys cinerea* and *Terminalia sericea* on grass biomass. *S. Afr. J. Bot.* 119, 271–277.
- Rao, P., Barik, S.K., Pandey, H.N., Tripathi, R.S., 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. *Vegetatio* 88, 151–162.
- Reed, M.S., Stringer, L.C., Dougill, A.J., Perkins, J.S., Athlpheng, J.R., Mulale, K., Favretto, N., 2015. Reorienting land degradation towards sustainable land management: linking sustainable livelihoods with ecosystem services in rangeland systems. *J. Environ. Manage.* 151, 472–485.
- Richter, C.G.F., Snyman, H.A., Smit, G.N., 2001. The influence of tree density on the grass layer of three semi-arid savanna types of southern Africa. *Afr. J. Range Forag. Sci.* 18, 1–7.
- Rutherford, M.C., Mucina, L., Lötter, M.C., Breidenkamp, G.J., Smit, J.H.L., Scott-Shaw, C.R., Hurter, P.J.H., 2006. Savanna Biome. In: Mucina, L., Rutherford, M.C. (Eds.), *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria, RSA.
- Ruwanza, S., Gaertner, M., Esler, K.J., Richardson, D.M., 2013. Both complete clearing and thinning of invasive trees lead to short-term recovery of native riparian vegetation in the Western cape, South Africa. *Appl. Vegetat. Sci.* 16, 193–204.
- Seymour, C.L., Dean, W.R.J., 2010. The influence of changes in habitat structure on the species composition of bird assemblages in the southern Kalahari. *Austral Ecol.* 35, 581–592.
- Scarpe, C., 1980. Observations on two bushfires in the western Kalahari, Botswana. In: Sjögren, E. (Ed.), *Studies in Plant Ecology. Acta Phytogeographica Suecica* vol. 68. Almqvist & Wiksell International, Uppsala, Sweden, pp. 131–140.
- Scarpe, C., 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *J. Appl. Ecol.* 27, 873–885.
- Smit, G.N., 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *J. Environ. Manage.* 71, 179–191.
- Stevens, N., Lehmann, C.E.R., Murphy, B.P., Durigan, G., 2017. Savanna woody encroachment is widespread across three continents. *Glob. Chang. Biol.* 23, 235–244.
- Symeonakis, E., Petroulaki, K., Higginbottom, T., 2016. Landsat-based woody vegetation cover monitoring in southern African savannas. *ISPRS – Int. Arch. Photogram. Remote Sens. Spatial Inform. Sci.* XII-B7, 563–567.
- Teague, W.R., Trollope, W.S.W., Aucamp, A.J., 1981. Veld management in the semi-arid bush-grass communities of the eastern cape. *Proc. Grassl. Soc. South. Afr.* 16, 23–28.
- Tews, J., Jeltsch, F., 2004. Modelling the impact of climate change on woody plant population dynamics in south African savanna. *BMC Ecol.* 4, 17.
- Tews, J., Schurr, F., Jeltsch, F., 2004. Seed dispersal by cattle may cause shrub encroachment of *Grewia flava* on southern Kalahari rangelands. *Appl. Vegetat. Sci.* 7, 89–102.
- Thomas, A.D., Elliott, D.R., Dougill, A.J., Stringer, L.C., Hoon, S.R., Sen, R., 2018. The influence of trees, shrubs, and grasses on microclimate, soil carbon, nitrogen, and CO₂ efflux: potential implications of shrub encroachment for Kalahari rangelands. *Land Degrad. Dev.* 29, 1306–1316.
- Tóthmérész, B., 1995. Comparison of different methods for diversity ordering. *J. Veg. Sci.* 6, 283–290.
- Tuomisto, H., 2012. An updated consumer's guide to evenness and related indices. *Oikos* 121, 1203–1218.
- Van Rooyen, N., Bezuidenhout, H., de Kock, E., 2001. *Flowering Plants of the Kalahari Dunes*. first ed. Ekotrust, Pretoria.
- Ward, D., Trinogga, J., Wiegand, K., Du Toit, J., Okubamichael, D., Reinsch, S., Schleicher, J., 2018. Large shrubs increase soil nutrients in a semi-arid savanna. *Geoderma* 310, 153–162.
- Wilson, T.B., Witkowski, E.T.F., 1998. Water requirements for germination and early seedling establishment in four African woody savanna plant species. *J. Arid Environ.* 38, 541–550.