

Restoring productive rangelands: A comparative assessment of selective and non-selective chemical bush control in a semi-arid Kalahari savanna



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ABSTRACT

The chemical control of thickened woody savanna layers is a common practice applied in southern Africa to release the grass layer from competitive pressure and restore the economic viability of rangelands. We comparatively assessed the composition, density and production of the grass layer in relation to the woody vegetation structure following the selective control of increaser woody species (SC) and non-selective control of the whole woody layer (NSC) in a semi-arid Kalahari savanna. Vegetation states associated with bush-thickening preventative range management (PRM) served as a benchmark. The SC treatment created a well-structured woody layer and favored the development of a grassy savanna state with abundant valuable forage grasses, as found under PRM. Despite a high dry matter production and density of grasses, NSC rangelands appeared to be unstable. Results indicate that NSC facilitates the development of a dense woody recruitment layer that counteracts a favorable grass layer development. We conclude that SC is conditionally more effective in restoring a relatively stable and desirable bush-grass ratio for commercial farming purposes, whereas NSC increases the risk of vegetation transition back to a bush-dominated state. While essential in combination with both treatments, NSC demands an increased effort of follow-up control of woody recruits.

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1. Introduction

The tree-grass ratio in savanna rangelands matters in both ecological and economic aspects by influencing a range of ecosystem services, which in commercial ranching systems particularly concerns forage production and environmental stability (Eldridge et al., 2011; Lukomska et al., 2014; Smit, 2004). The effective provisioning of these services depends on the grass and woody layer being in a competitive balance, and its maintenance requires a flexible management that accounts for the complex interrelated factors shaping savannas and driving resource patterns in space and time (Joubert et al., 2014). In semi-arid savannas, the

soil-water regime and inter-life form competition for moisture and nutrients are key controlling factors for this balance (Kambatuku et al., 2013; Kraaij and Ward, 2006; Smit and Rethman, 2000), which is commonly interfered with ill-adapted spatial and temporal rangeland utilization (Graz, 2008). As a consequence of removals of demographic bottlenecks to woody recruitment (high rainfall frequency, lack of fire and/or browsing herbivores), the savanna structure may then shift from a grass dominated to a woody dominated state (Joubert et al., 2008; Ward, 2005). In southern Africa, this phenomenon is commonly referred to as bush thickening, i.e. the encroachment of indigenous trees or shrubs in areas of natural occurrence, and is a major threat in extensively managed ranching systems (O'Connor et al., 2014; Smit, 2004).

The interplay of causal factors and underlying mechanisms of bush thickening are still not fully understood (Graz, 2008; Ward, 2005), having implications for how to predict rangeland dynamics prior to bush thickening and following different bush-control practices to restore a balanced bush-grass ratio and related functions (Scholes and Archer, 1997; Smit, 2004). Effects of bush thickening vary with the ecosystem and response variable

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under investigation (Eldridge et al., 2011), and likewise may the outcome of bush control differ between practices, vegetation types, and examined plant community attributes (Richter et al., 2001; Smit, 2004). Knowledge about the consequences of different bush-control practices is therefore crucial for the context-specific guidance of management responses (Joubert et al., 2014; Lukomska et al., 2014; Smit, 2005).

Management responses are either adaptive, reactive or preventative in nature, depending on whether the vegetation is in a transitional state towards bush dominance, the bush density has already crossed a critical level, or a desirable grassy state prevails (Joubert et al., 2014). Woody thickets or maturing, dense woody regeneration layers are not to be overcome by adaptive management responses alone (Joubert et al., 2014). In such cases, reactive and cost-intensive bush control becomes mandatory to restore bush-thickened savannas to a more profitable grassy state (Joubert et al., 2014; Lukomska et al., 2014), also because natural self-thinning dynamics due to interspecific competition (Scholes and Archer, 1997; Smit et al., 1999) or diebacks related to drought-stress, old age or fungal pathogens (Joubert et al., 2008) usually exceed an economically feasible time horizon.

A variety of bush-control practices exist, including the use of chemicals, prescribed fires, stem burning, and mechanical or manual treatments, each being only conditionally efficient and appropriate (Donaldson, 1966; Haussmann et al., 2016; Smit et al., 1999). Chemical control is a primary choice when the woody layer is very dense and covers extensive areas (Harmse, 2013; Smit et al., 1999). In the southern African region, the most popular chemical control practice among farmers is the use of systemic, photosynthesis-inhibiting arboricides, whose active ingredient enters the soil after rain, where it is absorbed by the roots of woody species and leads to death once carbohydrate reserves are exhausted (Bezuidenhout et al., 2015; du Toit and Sekwadi, 2012). Substituted urea arboricides, based on the non-selective Tebuthiuron as the active ingredient, are very common in use and highly effective in killing woody species at relatively low dosage rates (du Toit and Sekwadi, 2012; Moore et al., 1985). A major concern using Tebuthiuron pertains to its accumulation and persistence in the soil for several years, i.e. with potential long-lasting threats to also non-target species including herbaceous life forms. For example, du Toit and Sekwadi (2012) observed Tebuthiuron-treated soil to exclude any plant recovery for at least eight years post-application in semi-arid South African grassland. In contrast, Haussmann et al. (2016) found an immediate re-infestation of chemically cleared sites by an undesirable perennial shrub in the Highland savanna of Namibia. Moore et al. (1985) found Tebuthiuron-based arboricides to express some degree of selectivity for woody species from the semi-arid Kalahari, with obviously no detrimental effects on local grass species (Moore et al., 1985; Richter et al., 2001). The fate of Tebuthiuron in soils varies with the decomposition rate (half-life) and mobility in the soil as influenced by the content of clay particles and organic matter (adsorption), rainfall amounts (leaching), as well as soil temperatures (Bezuidenhout et al., 2015; du Toit and Sekwadi, 2012). In dryer areas with summer rain and well-drained sandy soils of low organic matter, persistence of Tebuthiuron in at least the upper soil layers can thus be expected to be of only short duration (Bezuidenhout et al., 2015), as would be the case in the Kalahari environments the present study took place.

In the southern Kalahari, bush thickening was locally recognized already in the mid-nineteenth century and emerged to be a problem about a century later (O'Connor et al., 2014). The ranching area of the geographically related Molopo savanna in South Africa was reported to have lost an estimated 1 million morgen (about 860 000 ha) of valuable rangelands to woody thicket formation by the 1960s (Donaldson, 1966). According to Donaldson (1969) and

local oral histories (G. Keyser, pers. comm., 2015), the gradual settlement of farmers in the 1940's and related sedentary grazing schemes and suppression of wildfires induced this environmental transformation. This serious situation in the Molopo area gave rise to a range of local thinning experiments testing the effectiveness of different bush-control practices (Donaldson, 1966, 1969) and their effects on the regeneration of the grass layer (Donaldson and Kelk, 1970; Moore et al., 1985; Richter et al., 2001). A recent participatory study explored which types of bush-management practices are actually applied by Molopo farmers and how they rate their particular effectiveness based on a set of biophysical and socio-economic indicators (Harmse, 2013). In terms of achieving best ecological and economic gains, an ongoing sustainable grazing management preventing bush-thickening (preventative range management (PRM)) was rated the highest. However, in areas where bush dominance precluded profitable rangeland utilization, chemical bush control was preferred to the use of fire or mechanical or manual control (Harmse, 2013). Here, two approaches with a Tebuthiuron-based arboricide were generally followed: the selective chemical bush control (SC) to thin out increaser woody species by hand and the non-selective, clearing-like bush control (NSC) by airplane (Harmse, 2013). The consequence of selective thinning as opposed to clearing is a differently structured vegetation with different net results of competitive and facilitative inter- and intra-life form interactions (Smit et al., 1999), usually in favor of a progressive development towards a more stable and productive savanna system (Smit, 2004).

In the present study, we comparatively assessed structural and compositional attributes of the grass layer in relation to the woody vegetation structure for the above-mentioned bush-management practices as applied by Molopo farmers. The main objective was to evaluate the potential of SC and NSC to restore open savanna close to a grassy state with abundant perennial grasses of high grazing value. For evaluation, the vegetation state associated with PRM was chosen to set the benchmark. In addition, bush-dominated vegetation states resulting from long-term rangeland mismanagement (RMM) were assessed, which served as a control. At the time of assessment, the selectively- and non-selectively controlled rangelands had already been under grazing management for a few years, which enabled us to explore (1) whether related states in vegetation development progress in similar directions, and (2) to which degree they deviate from the selected benchmark. In reference to information from bush-thinning studies (e.g., Smit, 2014; Smit and Rethman, 1999), we expected the deviation from benchmark conditions to be highest in the non-selectively controlled sites as a consequence of the intense removal of trees and shrubs, promoting the re-establishment of increaser woody species and counteracting a progressive development of the grass layer.

2. Material and methods

2.1. Study area

The study was conducted in the semi-arid Molopo ranching area of the North-West- and Northern Cape Provinces of South Africa. The area is located in the southeastern part of the Kalahari bordering Botswana between 25°20' and 26°50'S and 22°30' and 24°10'E, and is mainly used for large livestock farming, game ranching and eco-tourism purposes. The mean annual temperature is 19 °C and reaches 42 °C at day in the summer months (Hagos and Smit, 2005). The mean annual precipitation is about 300 mm (Fig. 1a), falling mainly from December to March but irregularly distributed and erratic (inter-annual CV = 47% for rainfall stations in Bray and Severn combined). The topography of the study area is relatively level. Soils are predominantly well-drained, deep

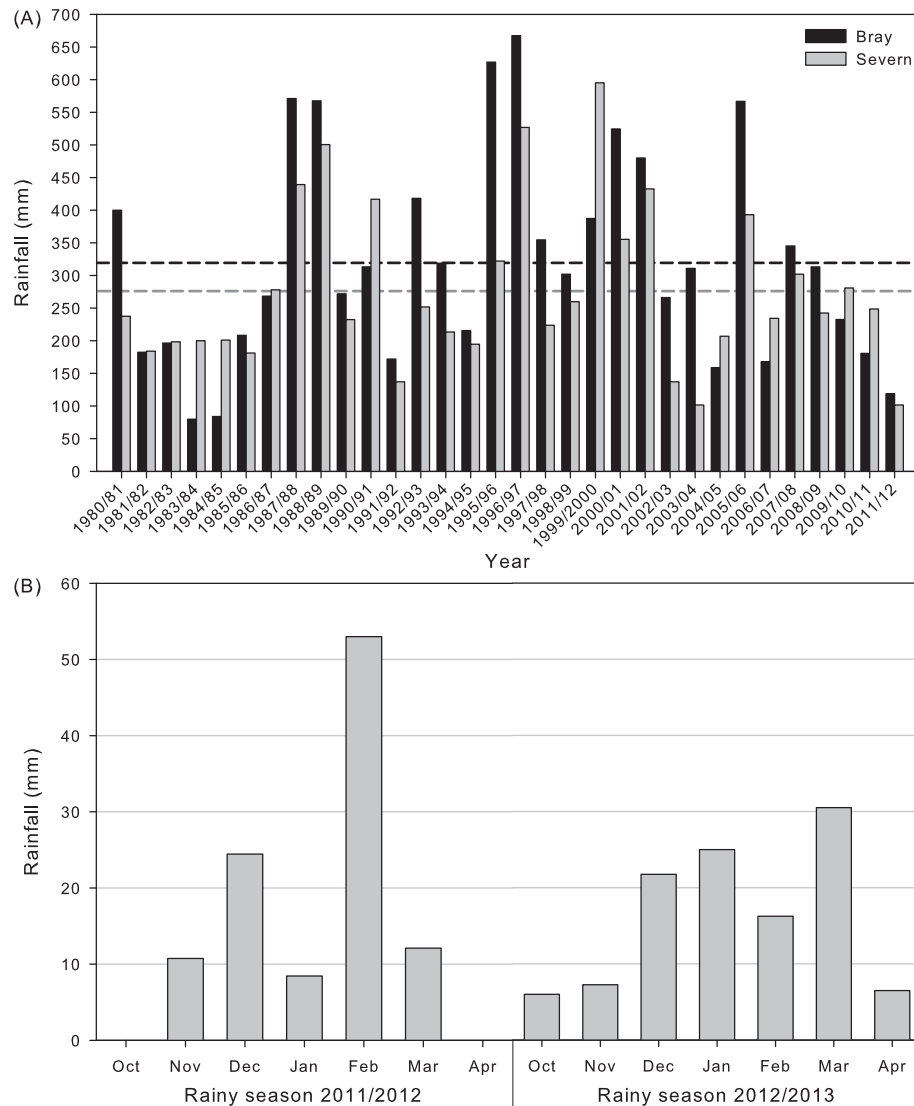


Fig. 1. Precipitation patterns in the Molopo area: (A) total annual rainfall (calculated for full rainfall seasons from October to September) recorded in the towns Bray and Severn over 32 years (dashed lines = medium-term mean per weather station). (B) Monthly rainfall averaged for Bray and Severn before grass layer assessments in March 2012 and 2013. Data source: South African Weather Service.

arenosols formed by Kalahari sands (Rutherford et al., 2006) of poor fertility with exceptionally low phosphate content (Donaldson and Kelk, 1970; Hagos and Smit, 2005).

The vegetation is an open savanna with scattered growing individuals or clusters of trees and tall shrubs and is classified by Rutherford et al. (2006) as the Molopo Bushveld of the Eastern Kalahari Bushveld Bioregion. The woody layer consists of particularly *Vachellia erioloba* and *Boscia albitrunca*, as well as the local increaser species *Senegalia mellifera* subsp. *detinens*, *Vachellia luederitzii* and *Grewia flava* (new nomenclatural combinations of African *Acacia* spp. in *Senegalia* and *Vachellia* according to Kyalangaliwa et al. (2013)). The herbaceous layer consists of a rich forb and rather poor grass component (Donaldson and Kelk, 1970) with common key grasses being *Eragrostis lehmanniana*, *Schmidtia pappophoroides* and *Stipagrostis uniplumis* (Richter et al., 2001; Rutherford et al., 2006).

2.2. Treatments and site selection

The specifications of the compared treatments were as follows:

- (1) Non-selective bush control plus grazing (NSC): Application of the herbicide Molopo 200 GG (active ingredient Tebuthiuron at 200 g kg^{-1}) via airplane, where granules were uniformly spread over larger bush thickened areas (dosage: $2.5\text{--}3 \text{ kg ha}^{-1}$). At the time of grass layer assessment, the application was 4–5 years old, and followed by either rotational cattle or open game grazing (72% grazer species) at recommended long-term stocking rates of $8\text{--}12 \text{ LSU ha}^{-1}$ (LSU = Large Stock Unit). Differential effects of herbivore-specific utilization and the two management regimes on the vegetation composition and grass cover were not obvious by sight, corresponding to findings by Britz and Ward (2007) from a similar Kalahari savanna type.
- (2) Selective bush control plus grazing (SC): Application of either Molopo 200 GG or Molopo 500 SC (solution with Tebuthiuron at 500 ml l^{-1}) under the canopy of undesirable increaser woody species (particularly *S. mellifera*, *V. luederitzii* and *Dichrostachys cinerea*). In known cases, the exact dosage was 0.2 g (granule) or 0.15 g (solution) Tebuthiuron per 0.5 m tree height. The treatment was implemented over a period of

maximum 12 years, i.e. with conditional maintenance control of woody recruits. At the time of grass layer assessment, the last application was 4–6 years ago and the subsequent grazing regimes were the same as for NSC.

- (3) Bush-thickening preventative range management (PRM): Rotational cattle grazing in multi-camp systems at recommended long-term stocking rates of 8–12 LSU ha⁻¹ that avoids overgrazing and assures resting periods for the grass layer for regrowth and reproduction. According to the interviewed land users, respective sites haven't been bush thickened before and an open, grass dominated state was constantly maintained. Hence, a side-effect of the grazing management was preventing unfavorable vegetation transitions. PRM sites were used as a benchmark for the chemically controlled sites.
- (4) Rangeland mismanagement (RMM): Group of unspecified actions that resulted in bush thickening most likely due to the combined effects of overgrazing and suppression of fires over extended time periods (see introduction). The resulting vegetation state served us as a control, which was deemed representative for local rangelands lacking a preventative range management or reactive interventions. Corresponding sites were located nearby the NSC- and SC-sites, and were selected with the assistance of the land users to assure that they matched the initial condition of the chemically treated sites as far as possible.

All four treatments were each replicated five times (total $n = 20$) and the related study sites were identified within grazing camps or larger open grazing units on at least two different farms. In order to account for spatial independence, sites sampled on the same farm were located in different camps or were minimum 900 m apart. As the treatments referred to practical operations by land users, there was a limited ability to completely control for environmental and management heterogeneity. In order to minimize the possibility of related confounding effects, site selection was based on local knowledge and scientific data gained in previous studies by Harmse (2013) and Dreber et al. (2014). Comparability among sites was facilitated by a similar topography, soil type, and topsoil pH (overall mean (SE): 5.01 (0.07) in KCl) and electrical conductivity (overall mean (SE): 0.13 (0.01) mS cm⁻¹) (soil sampled from the inter-bush matrix). Proximity to watering points was avoided (average distance 1.2 km) to exclude potential confounding effects of increased grazing and trampling pressure. To our knowledge, none of the sites had burned in at least the decade before sampling took place.

Note that pre-treatment data were generally lacking, excluding the possibility to relate assessed states to previous conditions at sampled sites and to trace treatment-related vegetation changes over time, respectively. Nevertheless, we are confident that prior herbicide application, vegetation between the chemically-treated sites and between the chemically-treated and control sites did not differ substantially. Accordingly, this comparative assessment certainly provides a reliable indication of the response potential of this type of savanna vegetation to the investigated treatments.

2.3. Vegetation assessment

At each site, the woody- and grass layer was surveyed along replicated transects, forming a single sampling unit (five per treatment and vegetation layer). Transects were laid out in homogeneous vegetation representative of the plant community and treatment, respectively, i.e. with no visual anomalies in structure and composition in an area large enough for the transects (equating to a plot size of 1 ha and 1.8 ha for the grass- and woody layer, respectively; compare below).

2.3.1. Assessment of the woody layer

The density and height structure of the woody layer was determined using the APCQ20 (adapted point-centered quarter) method as described in Dreber et al. (2014). Per site, the APCQ20-sampling unit consisted of two 160-m transects laid out 40 m apart, with a total of eight recording points, each in the centre of four sampling areas (quarters) 400 m² in size. In each quarter, the nearest rooted species >2 m, <2 m and the tallest was recorded together with its canopy height and distance to the recording point. Canopy heights were classified into six classes of varying intervals: <0.5 m, 0.5 to <1 m, 1 to <2 m, 2 to <3 m, 3 to <5 m, and ≥5 m. The variability in the canopy profile per sampling unit was determined through the coefficient of variation. Species- and height class frequencies were expressed as a percentage of the total number of plants recorded. The total woody density was calculated from plants ha⁻¹ in an upper (>2 m) and lower (<2 m) woody stratum. For improved comparability of sites with a different woody height structure, the total density was also standardized to tree equivalents per hectare (TE ha⁻¹), here referred to as woody phytomass. A tree equivalent represents a tree or shrub 1.5 m tall (Teague et al., 1981). For calculations of density and phytomass see Dreber et al. (2014). Assessments took place in late October 2012.

2.3.2. Assessment of the grass layer

The grass layer was sampled using a step-point technique along two 100-m transects in the understory of the sampled woody layer, parallel to the APCQ20-transects. At every second meter the nearest grass to the point on the transect line (in total 100 recording points) was identified to species level and the point-to-tuft distance measured as a proxy for basal cover (Hardy and Tainton, 1993). Grass species frequency was expressed as a percentage of all grass recordings along the two transects. In order to link the composition to the overall condition of the grazing ecosystem, species were also classified into three grass functional groups: GFG 1 = competitively strong, perennial grasses of high grazing value, which are sensitive to prolonged disturbances and indicate rangelands in a favorable condition; GFG 2 = weak perennials of medium to low grazing value, which are less sensitive to disturbances and usually characterize vegetation in a transitional phase; GFG 3 = annual, disturbance-tolerant grasses of low grazing value, whose presence in numbers is indicative of disturbed or degraded rangeland conditions (for details refer to Table A1).

A disc pasture meter (DPM) reading was taken at 2-m intervals along the two transects to determine the aboveground grass phytomass production, and the readings were then converted into dry matter production per hectare (kg DM ha⁻¹) based on Zambatis et al. (2006). In addition, the number of established grass tufts were recorded in a total of 16 plots of 1-m² systematically arranged along the two transects.

All sampling took place in the main rainy season in March 2012 and 2013 following months with effective rainfall for grass growth (Fig. 1b), so most species were clearly present in both reproductive and vegetative stages. All grass assessments were conducted by the same observer to minimize any related bias.

3. Analyses

3.1. Vegetation structure

Overall differences in the woody- and grass layer among the four treatments were tested using one-way analysis of variance (ANOVA), with above-mentioned vegetation parameters as the response variables. For between-treatment comparisons, Tukey's pairwise post-hoc test was used as implemented in PAST v3 (Hammer et al., 2001). If necessary, data were log- or square-root

transformed in order to meet assumptions of ANOVA. In cases where variances could not be homogenized, the robust Welch ANOVA with Dunnett's T3 robust post-hoc test (Quinn and Keough, 2002) was applied using SPSS v16 (SPSS Inc. 2007). The community structure was visualized using rank-frequency diagrams.

3.2. Grass species composition

In order to determine whether the grass species composition differed in relation to the treatments, the following set of analyses were conducted based on a grass species-by-site matrix. First, a nonmetric multidimensional scaling (NMDS) was done on the Bray-Curtis similarity measure to visualize patterns of resemblance between the grass assemblages associated with the treatments. Second, a non-parametric MANOVA (Anderson, 2001) based on the Bray-Curtis measure was used to test for significant compositional differences between the treatments, followed by pairwise post-hoc NPMANOVAs with sequential Bonferroni-adjusted significance levels (Quinn and Keough, 2002). Third, a SIMPER routine was run (Clarke, 1993) to identify which grass species best discriminated between the treatments and to quantify their percentage contribution to significant dissimilarities based on the Bray-Curtis measure. For any calculations, the relative frequencies of grass species were used and square-root transformed to down-weight the influence of dominating species. Analyses were performed using PAST v3 (Hammer et al., 2001) and PRIMER v6 (Primer-E Ltd, 2012).

3.3. Relationships between grass species and vegetation structure

The response in grass species distribution to structural properties of the woody and grass layer were examined by direct multi-variate gradient analysis using CANOCO v4.5 (ter Braak and Šmilauer, 2002). Following Lepš and Šmilauer (2003), a grass species-by-site matrix (based on relative frequencies) was first subjected to Detrended Correspondence Analysis (DCA) in order to test whether grass species show a unimodal or linear response to environmental gradients. The largest length of gradient was shorter than 3.0, indicating a dominance of linear gradients (low beta diversity), and thus appropriateness of a linear ordination method. Accordingly, a Redundancy Analysis (RDA) was performed to test the independence of the variability in grass species data from the variability in seven predictor variables: grass tuft density (no. m^{-2}), woody phytomass (TE ha^{-1}), woody density (plants ha^{-1}) and height of upper (>2 m) and lower (<2 m) woody stratum, variation of canopy profile. Grass species found in only one study site were omitted. Species data were square-root transformed and the

species weighted by the inverse of their error variance to gain a better estimate of their correlation with the predictor variables (Lepš and Šmilauer, 2003). In order to identify the most discriminating combination of predictor variables of low cross-correlation, forward selection with 499 unrestricted permutations was applied. In result, grass tuft density and height and density of both woody strata qualified for the final model at $\alpha = 0.05$. Variance inflation factors were between 1.8 and 3.3 indicating an appropriate level of low collinearity (Zuur et al., 2010).

4. Results

4.1. Vegetation structure

Compared to RMM conditions, both NSC- and SC-sites had a significantly lower woody density and phytomass. The values were similar among the two treatments and comparable to conditions under PRM (Table 1), but the woody layer differed in demographic structure. In both post-control environments, the density of the lower woody stratum (<2 m) was higher than in PRM sites with significantly smaller plant individuals (Table 1), indicating more woody recruits and saplings. Accordingly, the height structure of the woody layer showed an increased proportion of small woodies (<0.5 m) and less plants of 1–2 m (Fig. 2). This structural alteration was most pronounced in NSC sites with the densest lower woody stratum (Table 1), highest proportion of recruits and lowest proportion of medium-sized woodies (Fig. 2). NSC sites also had the highest variation in the canopy profile, differing significantly from RMM and PRM (Table 1). Some large trees remained after NSC (Fig. 2), accounting for the high woody layer >2 m (Table 1). This was mostly attributable to mature *B. albitrunca* trees, which were most frequent in the post-NSC environment due to their low sensitivity to Tebuthiuron, followed by *S. mellifera* and *G. flava* in the regeneration layer (Fig. 3b). In contrast, *G. flava* dominated in SC sites followed by *V. erioloba* with switched frequency-ranks in comparison to PRM sites (Fig. 3c–d). Across treatments, there was a similar pattern of 1–2 dominant woody species, 1–2 species of intermediate abundance and many species of rare occurrence (Fig. 3a–d).

The NSC-, SC- and PRM treatments differed significantly from RMM in all assessed grass layer attributes. The dry matter production was 3–4 times higher than in RMM sites with the grass layer being much denser in terms of plant individuals per m^2 and basal cover (Table 1). While NSC resembled conditions found under PRM, the dry matter production of SC sites was significantly lower than in PRM sites (Table 1). Grass species showed a similar

Table 1

Differences in the structure of the woody and grass layer among treatments (NSC = non-selective bush control, PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control). Values (means \pm SE) with different superscripts in a row are significantly different at $P < 0.05$ (ANOVA and Tukey's pairwise post-hoc test or in case of unequal variances Welch ANOVA with Dunnett's T3 post-hoc test). LS and US refer to lower (<2 m) and upper (>2 m) woody stratum, TE refers to tree equivalents (1 TE = woody of 1.5 m).

Treatments (n = 5 each)	RMM	NSC	SC	PRM	P
Woody layer					
Density (plants ha^{-1})	1013.86 \pm 99.97 ^a	427.72 \pm 122.29 ^b	387.30 \pm 132.79 ^b	236.66 \pm 49.52 ^b	<0.01
Density-LS (plants ha^{-1})	733.01 \pm 117.13 ^a	392.01 \pm 121.32 ^{a,b}	331.36 \pm 136.49 ^{a,b}	157.30 \pm 44.11 ^b	<0.01
Density-US (plants ha^{-1})	280.87 \pm 35.83 ^a	35.71 \pm 2.26 ^b	55.97 \pm 12.98 ^{b,c}	79.38 \pm 9.98 ^c	<0.001
Phytomass (TE ha^{-1})	1145.52 \pm 34.33 ^a	213.68 \pm 28.22 ^b	289.66 \pm 44.85 ^b	296.25 \pm 50.74 ^b	<0.001
Height (m)	2.80 \pm 0.13 ^b	1.93 \pm 0.12 ^a	2.13 \pm 0.12 ^a	2.16 \pm 0.14 ^a	<0.01
Height-LS (m)	1.10 \pm 0.07 ^{a,c}	0.44 \pm 0.04 ^b	0.83 \pm 0.10 ^a	1.18 \pm 0.05 ^c	<0.001
Height-US (m)	3.78 \pm 0.19 ^{a,b}	4.26 \pm 0.15 ^a	3.49 \pm 0.31 ^{a,b}	3.11 \pm 0.23 ^b	<0.05
CV canopy profile (%)	59.89 \pm 2.26 ^a	105.70 \pm 1.04 ^b	78.25 \pm 7.12 ^{a,b}	57.05 \pm 4.71 ^a	<0.001
Grass Layer					
Dry matter (kg ha^{-1})	457.04 \pm 68.31 ^a	1719.58 \pm 107.51 ^{b,c}	1352.84 \pm 147.7 ^b	1994.72 \pm 82.32 ^c	<0.001
Tuft density (no. m^{-2})	3.39 \pm 0.48 ^a	10.00 \pm 1.25 ^b	11.19 \pm 2.00 ^b	12.03 \pm 2.13 ^b	<0.001
Point-tuft distance (cm)	19.02 \pm 0.91 ^a	10.38 \pm 0.73 ^b	10.00 \pm 0.79 ^b	9.02 \pm 0.74 ^b	<0.001

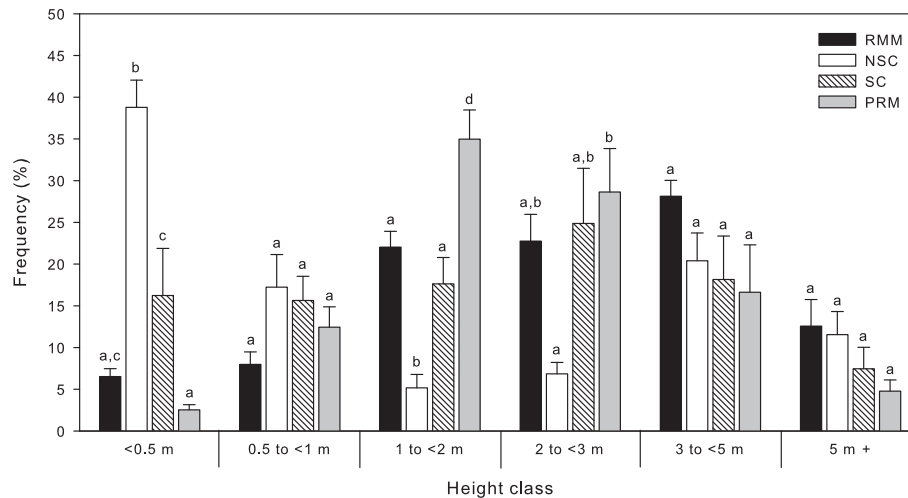


Fig. 2. Height class distribution of the woody savanna component across treatments with emphasis on relative differences (NSC = non-selective bush control, PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control). Per height class, different letters above error bars (\pm SE; $n = 5$) indicate significant differences between treatments at $P < 0.05$ (ANOVA and Tukey's pairwise *post-hoc* test).

abundance distribution in RMM- and NSC sites with most species of intermediate and rare occurrence (Fig. 3a–b), and in SC- and PRM sites with a single highly abundant species and only two species of intermediate abundance (Fig. 3c–d).

4.2. Grass composition

The grass species composition differed significantly among treatments (NPMANOVA: $F = 9.4$; $p < 0.001$). Grass assemblages showed distinct patterns with a clear sequence of increasing ecological distances in order of RMM > NSC > SC > PRM relative to RMM (Table 2; Fig. 4) and an overall Bray-Curtis dissimilarity of 46.6% (Table 2). All pair-wise dissimilarities were significant and related to dominance shifts of species rather than changes in local species pools (Table 2). Among the discriminating grass species, only 2–4 species already contributed about 50% to the dissimilarity among actions (Table 2). The species *Melinis repens*, *Schmidtia kalahariensis*, *S. pappophoroides* and *Urochloa brachyura* contributed most consistently to the compositional differences, as given by highest dissimilarity/SD ratios (Table 2). Among the most frequent species, *S. kalahariensis* in RMM sites was replaced by *Eragrostis lehmanniana* in NSC sites and by *S. pappophoroides* in SC- and PRM sites (Fig. 3a–c).

At the level of grass functional groups, RMM- and NSC sites were similar in the proportional composition with mostly GFG-2 and very few GFG-1 species (Fig. 5). In comparison, GFG-1 species constituted a significantly higher proportion in SC sites at the expense of GFG-2 species. By this, it resembled the proportional mix in PRM sites with the exception of GFG-3 species, which were only seldom observed under PRM (Fig. 5).

4.3. Direct species-environment relationships

The RDA revealed a significant explanatory effect ($P < 0.01$) of the five predictor variables on patterns in grass species composition (Fig. 6). The strong correlations of the predictor variables with the first two ordination axes ($R = 0.959$ and 0.880 , respectively) indicated density-related gradients in inter- and intra-life form competition, explaining 56.3% of the total variability in species data. At this, three competitive environments selecting for certain grass species were apparent: (1) open savanna with a dense grass layer of competitively strong GFG-1 species such as

S. pappophoroides and *Centropodia glauca* (corresponding to the PRM and SC treatment), (2) bush dominated savanna with a weakly developed grass layer (low basal cover), where the GFG-3 type grass *S. kalahariensis* was most abundant (corresponding to RMM treatment), and (3) open savanna with a relatively dense woody recruitment layer, which was positively correlated with particularly GFG-2 type grasses (corresponding to NSC treatment) (Fig. 6).

5. Discussion

5.1. Grass layer composition and productivity

Bush thickening-related compositional changes in grass species and the quantitative suppression of the grass layer significantly reduce the economic viability of savanna rangelands (Eldridge et al., 2011; Lukomska et al., 2014; Smit, 2005). Hence, controlling bush thickening in a context of livestock and game farming primarily aims at the recovery of high value fodder grasses that are in balance with the woody component. In this respect, the vegetation state associated with PRM qualified as a benchmark for ecological stable and productive savanna rangelands: First, the woody layer was open with only a minor proportion of woody recruits and a dominance of larger (mature) shrubs and trees. Second, the grass layer was relatively dense and consisted of predominantly perennial grasses of high grazing value that increase in abundance given a sustainable grazing management. Third, the grass dry matter production was highest among the assessed treatments. These results correspond to the recognition that best yields are generally gained with a well-structured, open woody layer that facilitates positive inter-life form interactions (Lukomska et al., 2014; Smit, 2004). Further, given the history of open savanna vegetation at PRM sites, it can be inferred from our results that the maintenance of a perennial grass layer can reduce the risk of bush thickening in the Molopo Bushveld savanna. Indeed, for a similar savanna environment it was shown that a weakening of grasses by grazing increases the success of recruitment and growth of *S. mellifera* (Ward and Esler, 2011), the major encroacher species in the present study. On sandy soils, below-ground rather than above-ground competition plays a role, where competitive grasses reduce the availability of limited water and nutrients (Graz, 2008; Kraaij and Ward, 2006) and hamper root growth of woody seedlings into the competition-free subsoil (Kambatuku et al., 2013).

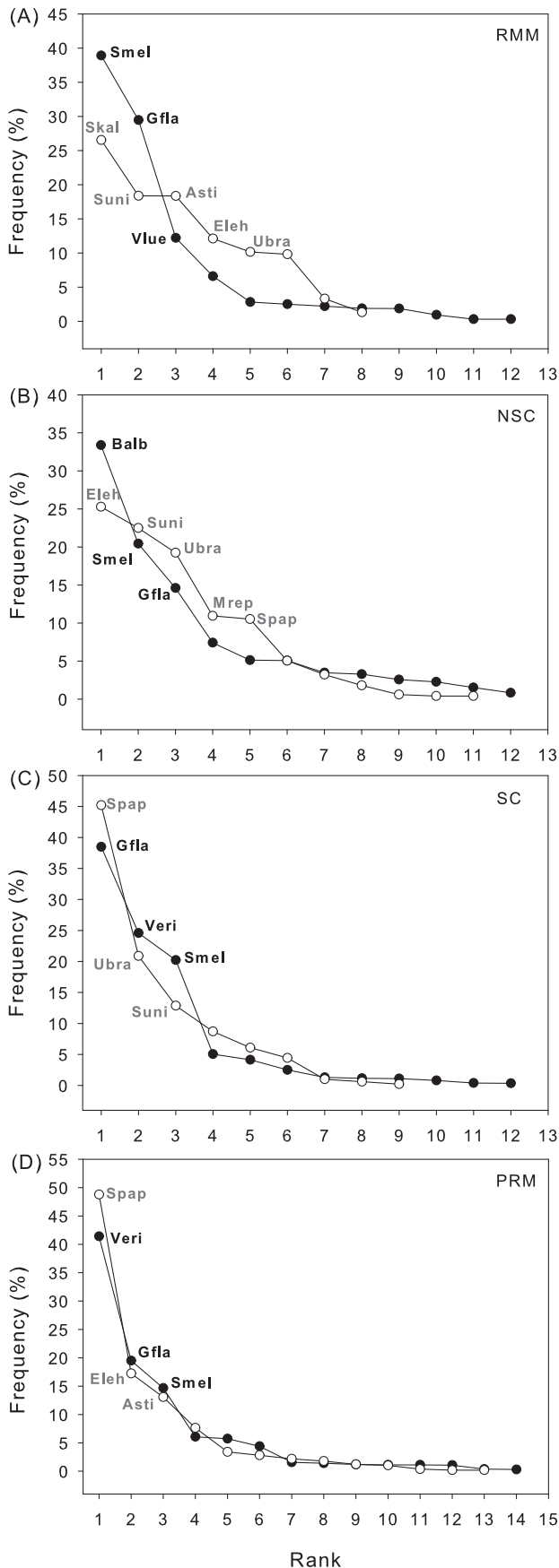


Fig. 3. Rank-frequency diagrams for species of the woody layer (filled circles) and grass layer (open circles) in each treatment (NSC = non-selective bush control,

Grass assemblages at the SC- and more recent NSC- sites differed in the dominance pattern of species and the proportional mix of grass functional groups. SC sites showed an overall lower ecological distance to the PRM sites, which was also reflected by the greater similarity in the density- and height structure of the woody layer. Granted that the bush-thickened state of RMM sites was close to the initial situation of the chemically treated sites, the SC treatment can be considered convincing in having the potential to create a competitive environment that facilitates the recovery of desirable grass species in the short term. In this respect, the present state of SC sites appeared fairly advanced, corresponding to what Joubert et al. (2008) describe as the “climax grassy state” in their state-and-transition model for bush-thickening prone Highland savannas of semi-arid Namibia. In contrast, the NSC treatment created an open environment, whose grass layer had a strong GFG-2 component. As such, the present state represented neither an early, post-disturbance “pioneer grassy state” nor an alternative “climax grassy state” (sensu Joubert et al., 2008), and rather appeared in a transitional stage. The direction of development (favorable or unfavorable), however, may largely depend on further management responses (see below).

The favorable transition from an early recovering grass layer to a well-developed grassy state dominated by GFG-1 type species may be a very slow process, particularly if grazing continues (Joubert et al., 2008). For southern African semi-arid savannas, information about recovery rates of grasses in post-control environments is scarce and inconsistent. For example, Smit and Rethman (1999) observed a predominance of annual “pioneer” grasses (corresponding to GFG 3) and a lack in recovery of perennial grasses three years after bush control. Among studies conducted in the Molopo savanna, Donaldson and Kelk (1970) found ineffective colonization of perennial “subclimax” and “climax” species even after eight years, including the GFG-1 and GFG-2 type grasses *S. pappophoroides* (there referred to as *S. bulbosa*) and *S. uniplumis*, respectively. Similar to the NSC sites, Moore et al. (1985) recorded a dominance of GFG-2 type “subclimax” grasses but also the presence of “climax” grasses already two years after chemical bush control. It is worth mentioning, however, that the potential for compositional changes in the grass layer varies with rainfall patterns since bush control took place (Smit et al., 1999; Smit and Rethman, 1999), as well as soil type and fertility (Smit, 2004). Furthermore, the density and structure of the woody layer before and after the control treatment is of great influence, as it directly impacts the water, light and nutrient regime of the environment (Graz, 2008; Scholes and Archer, 1997; Smit and Rethman, 1999, 2000). The level of bush density also determines which grass species are able to persist, and thus can effectively recover from soil seed banks in post-control environments (Donaldson and Kelk, 1970). Some of the grass species that were abundant in NSC- and SC sites also occurred in the RMM sites. This suggests that the competitive environment at around 1200 TE ha⁻¹ still provided niches for common open-matrix grass species, which could have been in favor of an accelerated post-control grass layer development.

The grass dry matter production in the chemically-treated sites was about 200% (SC) and 280% (NSC) higher than under bush-thickened conditions. This exemplifies the effect of grass-layer

PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control). Plotted are mean species frequencies against species ranks in descending order of abundance. Species names are given for the most common species (>10% frequency): Asti = *Aristida stipitata*, Balb = *Boscia albitrunca*, Eleh = *Eragrostis lehmanniana*, Gfla = *Grewia flava*, Mrep = *Melinis repens*, Skal = *Schmidtia kalahariensis*, Smel = *Senegalia mellifera*, Spap = *Schmidtia pappophoroides*, Suni = *Stipagrostis uniplumis*, Umos = *Urochloa brachyura*, Veri = *Vachellia erioloba*, Vlua = *Vachellia luederitzii*.

Table 2

Variation in composition of grass assemblages associated with the treatments based on Bray-Curtis dissimilarities. Differences were determined by non-parametric MANOVAs with sequential Bonferroni-adjusted significance levels of ecological distances. SIMPER statistics refer to the species contributing most to the overall average Bray-Curtis dissimilarity (BC dissimilarity (%)). 'Mean abundance' shows untransformed values compared as in first column (higher value in bold). 'Average dissimilarity' gives the average contribution of the species to the dissimilarity, and 'Dissimilarity/SD' its ratio with the standard deviation of these contributions. 'Contribution%' indicates the average percentage contribution for the species to the overall average Bray-Curtis dissimilarity. Shown are only species contributing >5% to dissimilarities. All dissimilarity calculations are based on square-root transformed species data. NSC = non-selective bush control, PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control.

	NPMANOVA		SIMPER	Species	Mean abundance	Average dissimilarity	Dissimilarity/SD	Contribution (%)	Cumulative (%)
	F	P							
RMM vs. PRM	17.7	<0.01	64.0	<i>Schmidtia pappophoroides</i>	0.0/ 48.8	15.1	3.1	23.6	23.6
				<i>Schmidtia kalahariensis</i>	26.5 /0.0	11.0	5.1	17.3	40.9
				<i>Urochloa brachyura</i>	10.2 /0.0	6.8	3.6	10.6	51.4
				<i>Melinis repens</i>	9.8 /0.4	6.1	2.5	9.5	61.0
				<i>Stipagrostis uniplumis</i>	18.4 /7.6	5.3	1.4	8.3	69.2
				<i>Aristida stipitata</i>	18.4 /13.1	3.3	1.5	5.2	74.4
NSC vs. RMM	5.0	<0.01	37.0	<i>Schmidtia kalahariensis</i>	5.1/ 26.5	8.4	2.1	22.6	22.6
				<i>Schmidtia pappophoroides</i>	10.5 /0.0	6.0	2.2	16.3	38.9
				<i>Aristida stipitata</i>	3.2/ 18.4	5.9	1.5	15.8	54.7
				<i>Urochloa brachyura</i>	19.2 /10.2	3.9	1.7	10.5	65.2
				<i>Eragrostis lehmanniana</i>	25.3 /12.1	3.7	1.0	9.9	75.1
				<i>Eragrostis trichophora</i>	1.8/ 3.3	2.5	1.5	6.8	81.8
NSC vs. PRM	9.2	<0.01	55.7	<i>Urochloa brachyura</i>	19.2 /0.0	9.0	2.1	16.2	16.2
				<i>Schmidtia pappophoroides</i>	10.5/ 48.8	9.0	1.7	16.1	32.3
				<i>Melinis repens</i>	10.9 /0.4	6.5	2.9	11.7	44.0
				<i>Stipagrostis uniplumis</i>	22.5 /7.6	6.1	1.4	10.9	54.9
				<i>Aristida stipitata</i>	3.2/ 13.1	5.0	1.6	9.0	63.9
				<i>Eragrostis lehmanniana</i>	25.3 /17.3	3.6	1.0	6.4	70.3
NSC vs. SC	3.7	<0.01	33.6	<i>Schmidtia pappophoroides</i>	10.5/ 45.2	8.2	2.1	24.4	24.4
				<i>Eragrostis lehmanniana</i>	25.3 /8.7	4.8	1.1	14.2	38.6
				<i>Aristida stipitata</i>	3.2/ 6.1	3.6	1.3	10.9	49.5
				<i>Urochloa brachyura</i>	19.2/ 20.9	3.5	1.4	10.5	59.9
				<i>Melinis repens</i>	10.9 /4.4	3.1	1.6	9.3	69.2
				<i>Stipagrostis uniplumis</i>	22.5 /12.9	3.0	1.4	8.8	78.0
SC vs. RMM	15.6	<0.01	45.3	<i>Schmidtia kalahariensis</i>	5.1 /1.0	2.9	0.9	8.6	86.6
				<i>Schmidtia pappophoroides</i>	45.2 /0.0	14.3	6.0	31.6	31.6
				<i>Schmidtia kalahariensis</i>	1.0/ 26.5	9.4	3.7	20.8	52.5
				<i>Aristida stipitata</i>	6.1/ 18.4	5.8	1.5	12.9	65.4
				<i>Urochloa brachyura</i>	20.9 /10.2	3.3	1.6	7.4	72.7
				<i>Melinis repens</i>	4.4/ 9.8	2.9	1.5	6.4	79.1
SC vs. PRM	6.3	<0.01	44.2	<i>Eragrostis trichophora</i>	0.6/ 3.3	2.8	1.1	6.1	85.1
				<i>Urochloa brachyura</i>	20.9 /0.0	10.4	4.2	23.5	23.5
				<i>Aristida stipitata</i>	6.1/ 13.1	5.0	1.5	11.3	34.7
				<i>Stipagrostis uniplumis</i>	12.9 /7.6	4.8	1.6	10.8	45.5
				<i>Melinis repens</i>	4.4 /0.4	3.9	1.8	8.9	54.3
				<i>Eragrostis lehmanniana</i>	8.7/ 17.2	3.9	1.5	8.8	63.1
				<i>Schmidtia pappophoroides</i>	45.2/ 48.8	3.6	1.5	8.2	71.4
				<i>Centropodia glauca</i>	0.0/ 2.2	2.6	1.2	5.9	77.3

release from competitive pressure by trees and shrubs, which usually scales up exponentially with the level of bush thinning (Richter et al., 2001; Scholes and Archer, 1997; Smit, 2005). Though the grass dry matter production in SC sites was slightly lower than in PRM sites, both control treatments proved to be an effective measure to restore highly productive rangelands. Following Tongway and Hindley (2004), the concomitant higher grass tuft density and basal cover than in RMM sites would suggest improved rangeland functional integrity in terms of water retention and infiltration. Indeed, the success of grass recovery in early post-control environments is directly linked to overall improving soil-water conditions (Graz, 2008; Smit, 2005; Smit and Rethman, 1999) and an increased water-use efficiency (Smit and Rethman, 2000). An additional facilitative effect could be attributed to more discarding wood and leaf matter after bush control, initially increasing the availability of nutrients in the soil (Hagos and Smit, 2005; Joubert et al., 2008; Scholes and Archer, 1997).

Overall, the results confirm the positive attitude of many Molopo land users towards the use of Tebuthiuron-based herbicides (Harmse, 2013). It should be noted, however, that from an economic point of view, the grass layer in NSC sites was less

profitable in species composition, so that the lower quality of forage certainly outbalanced the high productivity by negatively affecting the rangelands' grazing capacity. While the valuable forage grass *S. pappophoroides* dominated in SC sites by far, the high productivity of NSC sites was mainly due to the bigger-tufted GFG-2 type species *E. lehmanniana* and *S. uniplumis* and the GFG-3 type species *U. brachyura*. This concurs with observations made in experimental bush-thinning trials also conducted in the Molopo region by Donaldson and Kelk (1970), Moore et al. (1985) and Richter et al. (2001). All of them identified *E. lehmanniana* as being a major constituent of grass layer dynamics in post-control environments, which refers to the species' ability to multiply quickly in disturbed areas by a high seed set (as applying to *U. brachyura*) (van Oudtshoorn, 2012).

5.2. Woody layer and competitive relationships with grasses

The height and density of an upper and lower woody stratum were identified as significant explanatory factors for the variability in the distribution of grass species among sampling sites and treatments, respectively. This is consistent with the above-

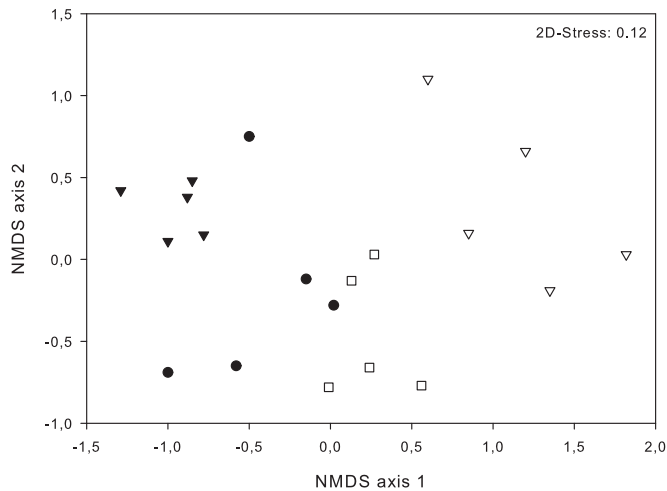


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of grass assemblages based on the Bray-Curtis similarity measure, showing the variation within and between treatments. Symbols represent the five sampling sites per treatment (filled triangles = rangeland mismanagement, filled circles = non-selective bush control, squares = selective bush control, open triangles = bush-thickening preventative range management).

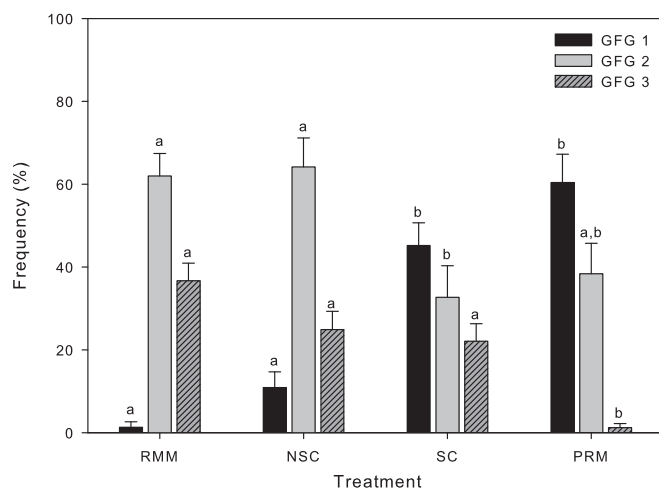


Fig. 5. Frequency distribution (mean \pm SE; $n = 5$) of grass functional groups (GFG) within and among treatments (NSC = non-selective bush control, PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control). Different superscripts per GFG indicate significant differences at $P < 0.01$ between treatments (ANOVA with Tukey's HSD *post-hoc* test or in case of unequal variances Welch-ANOVA with Dunnett's T3 *post-hoc* test). For description of GFGs see main text and Table A1.

mentioned variation in grass layer conditions resulting from differences in the structure of the woody layer and the related competitive environment. Looking at the density and height of the lower woody stratum, it is obvious that the recruitment layer in RMM-, SC- and PRM sites consisted mainly of saplings, whereas in NSC sites seedlings lower than 0.5 m dominated. Though it is difficult to deduce the age of recruits from size (Joubert et al., 2013), it seems likely that they emerged after bush control took place, particularly because of the low frequency of this size class in all other sites. The recruitment involved mainly the increaser species *S. mellifera*, *V. luederitzii* and/or *G. flava*. While little information is available for the other species, for *S. mellifera* it was shown that recruitment depends on frequent rain events (Kraaij and Ward, 2006), more specifically a sequence of at least two consecutive years of sufficient rainfall for seed production, germination and

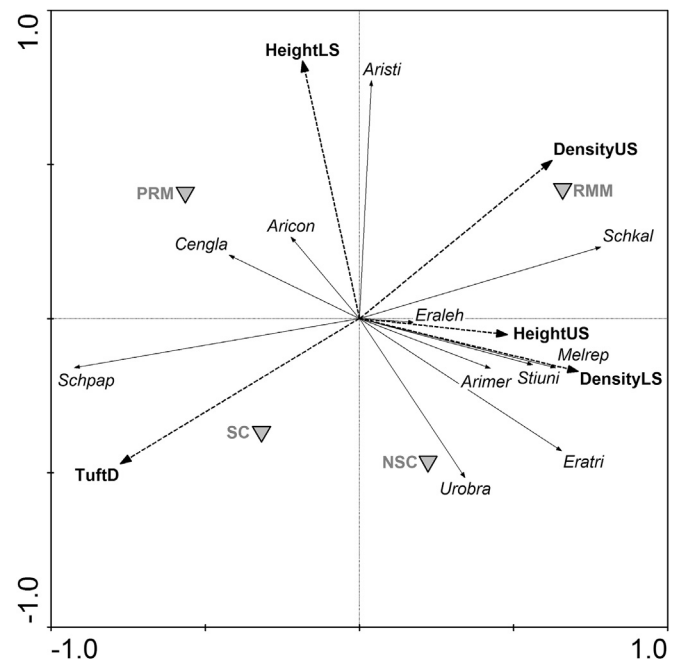


Fig. 6. Grass species-environment triplot from the redundancy analysis (RDA) with significant predictor variables qualified by forward selection (DensityLS = density of lower woody stratum (plants $\text{ha}^{-1} < 2$ m), DensityHS = density of upper woody stratum (plants $\text{ha}^{-1} > 2$ m), HeightLS = height lower woody stratum, HeightUS = height upper woody stratum, TuftD = density of grass tufts m^{-2}) and centroids for treatments plotted as supplementary variables (triangles: NSC = non-selective bush control, PRM = bush-thickening preventative range management, RMM = rangeland mismanagement, SC = selective bush control). Eigenvalues: first axis = 0.454, second axis = 0.109. Monte Carlo test of significance of all canonical axes: F -ratio = 4.978, $P = 0.002$. Grass species: Aricon = *Aristida congesta*; Arimer = *Aristida meridionalis*, Aristi = *Aristida stipitata*, Cengla = *Centropodia glauca*, Eraleh = *Eragrostis lehmanniana*, Eratri = *Eragrostis trichophora*, Melrep = *Melinis repens*, Schkal = *Schmidia kalahariensis*, Schpapp = *Schmidia pappophoroides*, Stiuini = *Stipagrostis uniplumis*, Urobra = *Urochloa brachyura*.

establishment (Joubert et al., 2013). In the study area, the last time such an event occurred was in the period 1999/2000 to 2001/02, whereas in the post-control seasons rainfall was generally below average with exceptions for the seasons 2004/05 and 2007/08 (Fig. 1a). However, provided within-season rainfall events were frequent, this might have been sufficient for the survival of germinated seedlings.

It can be assumed that the early disturbed environments at NSC sites have provided greater water availability for woody recruits, because of the incipiently low grass densities, and thus little inter-life form competition (Kraaij and Ward, 2006; Scholes and Archer, 1997; Skarpe, 1990). Likewise, there was a reduced intra-life form competition due to the intense thinning of larger woody. Such intra-specific effects between woody life history stages and size classes, respectively, are commonly reported (Joubert et al., 2013; Smit, 2004, 2014). Consequently, lower recruitment rates in SC sites were certainly facilitated by a better-structured woody layer and, at present condition, a high grass biomass and proportion of GFG-1 type grasses, likely able to negatively affect woody seedling establishment, as assumed for the PRM sites. The GFG-2 dominated grass layer of the NSC sites may not be able to outcompete the already established seedlings on the deep, sandy soils. Many seedlings of savanna tree species develop a taproot that can rapidly penetrate sandy soils given appropriate rainfall (Joubert et al., 2008; Wilson and Witkowski, 1998), making them less susceptible to below-ground competition for limiting resources (Donaldson, 1969; Kambatuku et al., 2013; Kraaij and Ward, 2006).

From the above mentioned it can be inferred that NSC sites were at an increased risk to re-thicken, meaning that the related vegetation state had a low threshold for a system switch back to a woody dominated state (Joubert et al., 2008; Smit, 2004). In other words, it is questionable whether grass layer dynamics in NSC sites were still progressive. Without active interventions, the system may rather last for some time in its current transitional state unless a disturbance event (e.g. heavy grazing or low-intensity fire) weakens the grass layer to the benefit of the woody recruitment layer. The transition towards bush dominance, however, would require recurrent adequate rainfall conditions, assuring the survival and growth of present woody recruits and promoting further recruitment events (Donaldson, 1969; Joubert et al., 2013; Kraaij and Ward, 2006; Smit, 2004). For a better understanding of post-control vegetation dynamics, more research is needed into the effects of grass competition on early life-history stages of woody species in this resource-limited, sandy Kalahari savanna, in particular under both varying conditions and compositions of the grass layer and related variation in the soil-water regime (Graz, 2008).

5.3. Concluding remarks and management implications

Land users in the Molopo generally recognize the need to also maintain a certain proportion of bush (about 25–30%, E. Graubner and C. Richter, pers. comm., 2014), which provides shelter and food for browsing stock and game over extended time periods (Harmse, 2013; Smit, 2014) and localized areas of improved soil fertility (Hagos and Smit, 2005). The SC treatment came closest to the dual goals forage production and woody patch conservation, whereas the non-selective application of the arboricide affected also valuable, non-target savanna shrubs and trees and reduced overall structural diversity. Species like *V. erioloba* represent key structural elements in southern Kalahari savannas if grown to maturity, whose presence contributes significantly to local biodiversity (Tews et al., 2004). We found at least the desirable *B. albitrunca* trees to be unaffected in NSC sites, supporting Moore et al. (1985) observation from the same area that this species is not sensitive to Tebuthiuron. Bezuidenhout et al. (2015) made a similar observation, but give cause for concern regarding potential delayed effects should Tebuthiuron accumulate at greater soil depths, which becomes eventually accessible for this slow-growing tree species.

The presence of many small woody recruits in NSC sites suggests that during the relatively short time period since application, the arboricide's active ingredient Tebuthiuron was either metabolized or leached out of shallow rooting zones due to the sandy textured soil with low adsorption ability (Bezuidenhout et al., 2015). At such a state, it is most critical for adaptive management interventions to counteract unfavorable transitions (Joubert et al., 2008, 2014). The situation in the NSC sites therefore confirms that intense thinning with chemicals may require more frequent and repeated follow-up and maintenance control (Smit, 2004). To maintain the competitive ability of the grasses and counteract vegetation retrogression, it would be further necessary to avoid temporarily intense utilization of the rangeland by grazing herbivores (Kambatuku et al., 2013; Tedder et al., 2014), particularly in wet years (Kraaij and Ward, 2006), and to adapt timing and duration of resting periods accordingly (Joubert et al., 2014). Additional options to keep woody recruitment under control would include managed fires following a sequence of good rainfall years or keeping herds of grazer and browser at an appropriate stocking rate and species-mix, which might conditionally be effective (Joubert et al., 2008, 2014; Smit, 2004; Smit et al., 1999). The decision about the implementation of a certain chemical control approach would therefore also mean to be aware of the involved costs and economic returns in the long

run (Donaldson, 1966; Lukomska et al., 2014; Moore et al., 1985).

An application of chemicals by airplane is usually necessary when the woody layer becomes too dense impeding free movement of workers (Smit et al., 1999), which becomes increasingly difficult from a phytomass of about 1500 TE ha⁻¹ onward. Above this threshold, airplane control starts to be more profitable compared to the labor intensive selective control by hand (C. Richter and J. Olivier, pers. comm., 2014). Moreover, using an airplane becomes more economical the larger the area to be treated, as less time and laborers are needed (Harmse, 2013; Smit et al., 1999). In the present study, however, the NSC treatment might not have been the optimal choice due to the supposed initial woody phytomass of about 1200 TE ha⁻¹, which still allows for a selective and ecologically advantageous application of the arboricide at an economically viable dosage.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2016.08.009>.

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