Some ecological side-effects of chemical and physical bush clearing in a southern African rangeland ecosystem

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Highlights

- Some ecological side-effects of bush thickening treatments were evaluated
- No effect on non-targeted tree species was found 24-36 months post treatment
- Both treatments were colonized by undesired sagebush *Pechuel-loeschea leubnitziae*
- Perennial grass species were particularly abundant in physically treated sites
- A side-effect of arborocide treatment: facilitating fast-growing, undesired species

Abstract

Bush thickening is a major concern to farmers of arid and semi-arid rangelands; reactive intervention remains the norm. Here we compared some of the short-term ecological implications of chemical and physical removal of the bush encroacher *Acacia mellifera* in the central Highland savanna of Namibia. We selected 21 invaded sites, 7 had been chemically cleared, 7 had been physically cleared and 7 had never been cleared. From each site, we recorded grass species composition, as well as the densities of *A. mellifera*, the undesired perennial shrub *Pechuel-loeschea leubnitziae* and a non-targeted tree *A. erioloba*, 24–30 months post-treatment. We fitted one-way ANOVA models to test for the effect of treatment on grass species richness and density of targeted and non-targeted tree species. A Canonical Correspondence Analysis was used to determine how treatment affected grass species composition. While both treatments reduced the density of the bush encroacher, *P. leubnitziae* effectively replaced *A. mellifera* in chemically treated sites, where die-back presumably happened faster and nutrient and water competition decreased more rapidly. In such sites, perennial grass species were effectively outcompeted by *P. leubnitiziae*.

Keywords

1. Introduction

Bush thickening forms a major agricultural concern in arid savanna ecosystems (de Klerk, 2004; Ward, 2005; Wiegand et al., 2006), where the associated suppression of palatable grasses, formation of impenetrable thickets and consequent reductions in carrying capacity have dire economic consequences (Bovey, 2001; de Klerk, 2004). Although a number of models have been proposed to explain the transformation from a grassy to a bushy state (e.g., Joubert et al., 2008; Wiegand et al., 2006) the ecological mechanisms causing bush thickening remain poorly understood (Smit, 2004; Ward, 2005). As a result, reactive intervention remains the norm (Joubert et al., 2008).

One of the main African bush encroachers is the woody shrub, *Acacia mellifera* (M.Vahl) Benth (synonym: *Senegalia mellifera* (Benth.) Seigler & Ebinger). This deciduous species has an extensive root system, concentrated in the top of the soil profile, and is considered a pioneer on shallow soil (Adams, 1967). Two of the most common methods to clear *A. mellifera* are chemical clearing through the application of arborocide, and physical clearing, mostly by manual axe hacking. The method of application is generally based on the size of the area that needs to be cleared, funding and availability of labour force (de Klerk, 2004). Furthermore, whereas manual hacking is labour intensive and slow, there are ecological concerns associated with the use of arborocides. These concerns are mostly related to their environmental persistence and effects on non-target species (Bovey, 2001; du Toit and Sekwadi, 2012; Emmerich, 1985).

The active ingredient present in many of the arborocides commonly used by Namibian rangeland owners is tebuthiuron (chemical formula: $C_9H_{16}N_4OS$). Tebuthiuron is a non-selective

photosynthesis inhibitor (Hatzios et al., 1980). It has a long half-life, especially in areas of low rainfall (Chang and Strizke, 1977), and residues have been detected in the soil more than a decade after application (Johnsen and Morton, 1991). Areas treated with tebuthiuron form bare patches, which may or may not be recolonised, depending on edaphic factors and local seed banks, and can be lethal to seedlings up to 8 years post-treatment (du Toit and Sekwadi, 2012). Research has been conducted on the efficacy of tebuthiuron on selected target species (Borrel et al., 2011), its environmental fate (Chang and Strizke, 1977; Johnsen and Morton, 1991), and its potential toxicity to cattle and other fauna (Morton and Hoffman, 1976; van Duyn et al., 1976). However, comparatively little is known about its effects on plant species composition, and more specifically grass species composition. In general, plant life forms and/or functional groups differ in their susceptibility to tebuthiuron, with grasses and deeply-rooted species generally being less susceptible than woody and shallowly-rooted species (Emmerich, 1985). However, the susceptibility of individual species is mostly unknown, making it difficult to predict which species will recolonize a bare patch (du Toit and Sekwadi, 2012).

Physical methods used for the control of woody plants generally range from manual hacking and chopping to using heavy machinery, such as tractors equipped with dozer blades (de Klerk, 2004). Because the use of heavy machinery is expensive, manual axe clearing or hacking is more common in Namibia (Namibia Agricultural Union, 2000). Trees can be manually removed either above-ground or also a few centimetres below-ground, with the intention of reducing the plant's resprouting capability. Whereas regrowth of *Acacia* stumps is almost certain with above-ground removal (Barnes, 2001), regrowth rarely occurs when tree stumps are also removed below-ground (de Klerk, 2004). Although physical clearing is preferable to chemical

clearing from an ecotoxicological perspective, there are also ecological consequences associated with physical clearing, especially when the topsoil is disturbed (Adams, 1967; de Klerk, 2004). Physical disturbance of the topsoil may alter habitat structure (Zou et al., 1989) and ultimately favour the re-establishment of the problem species (Zapke, 1986). In addition, exotic plant species are often favoured in areas of increased physical disturbance (Haussmann et al., 2013; Kalwij et al., 2008), such as those associated with physical clearing. Although manual clearing is undoubtedly less disruptive than mechanised clearing, it is labour-intensive and slow, especially when trees are also removed below-ground (de Klerk, 2004).

In this study we evaluate the short-term ecological effects (24–30 months post-treatment) of chemical and physical bush clearing in an arid savanna ecosystem. We do this by comparing grass species richness and composition of plots where *Acacia mellifera* had been cleared using tebuthiuron-containing arborocides with manually cleared plots, as well as uncleared, invaded control plots. We also compared the abundance of *A. mellifera* individuals between treatments, as well as the abundance of *Pechuel-loeschea leubnitziae* (Kuntze) O. Hoffm, an undesired perennial shrub species native to Namibia. Lastly, as a measure of undesired impacts on non-target tree species, we compared the abundance of the ecologically important, protected tree *A. erioloba* E.Mey. (synonym: *A. giraffae* Willd., *Vachellia erioloba* (E. Mey.) P.J.H. Hurter) between treatments.

2.   Materials and Methods

2.1.   Study area

The central Highland savanna of Namibia is situated in a semi-arid climatic region. The area receives on average approximately 360 mm rainfall annually, predominantly during summer. Days are usually warm (27 °C average annual maximum), while nights are cool to cold, with temperatures normally staying above freezing in winter (Namibia Meteorological Service, 2015a). The vegetation is characterised by woody species, of which *A. mellifera* is dominant. Soils in the area are typically shallow lithic leptosols (Joubert et al., 2008). Where grazing is heavy and fires are rare, *A. mellifera* forms dense impenetrable thickets, which slowly decreases the carrying capacity for livestock such as cattle and sheep (Joubert et al., 2008). In such areas, the cover of palatable, perennial grasses is low. As a result, both chemical and physical bush clearing methods are commonly applied in the region and the area thus forms an ideal setting to select independent treatment replicates across a large spatial extent.

2.2.   Study sites

A total of 21 invaded sites were identified on commercial cattle ranches within the central Highland savanna area of Namibia (Fig. 1). Seven sites had been chemically cleared of *A. mellifera* using tebuthiuron, another 7 had been cleared physically (through manual hacking) and the remaining 7 sites had never been cleared to the knowledge of the ranch owners. Chemical treatment consisted of applying granular arborocide directly to *A. mellifera* stems, following the concentrations recommended by the manufacturer. In physically treated sites, all *A. mellifera* individuals were removed by manually hacking out trees, including the underground part of the
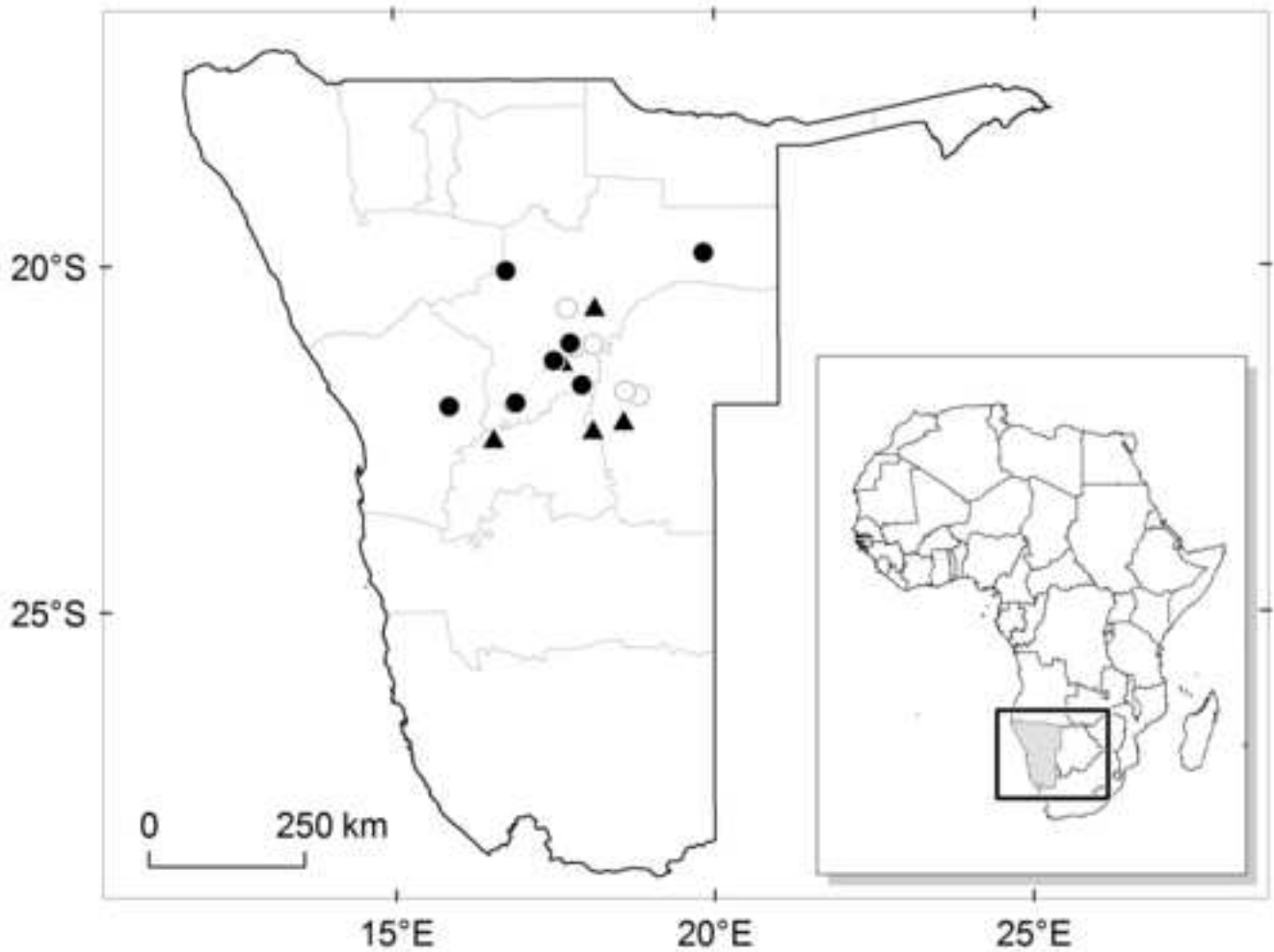
Fig. 1. Overview of the distribution of sites in Namibia and the respective treatments used to remove Acacia mellifera shrubs; triangles (▲) indicate arborocide treatment (N = 7), filled circles (●) physically cleared sites (N = 7), and open circles (○) untreated control sites (N = 7). Due to the scale of this map some site symbols overlap. For reference purposes we included the delineation of the administrative divisions of Namibia and its location in southern Africa (inset).

stump, or by manually pulling out in the case of small individuals. Both chemically and physically treated sites were treated 24–30 months prior to the study, during the active plant growth season (December to March). Although no formal pre-treatment vegetation data are available for the study sites, we have no reason to suspect that the vegetation differed systematically between treatment sites or between treatment and control sites. Furthermore, to validate this assumption, pre-treatment vegetation characteristics were compared between the three plot types using remote sensing data (see Environmental data).

2.3.   Vegetation sampling

In each site a 50×50-m plot was laid out in an area that was deemed representative of the surrounding vegetation. To quantify the effect of treatment on the target species, the number of *A. mellifera* trees was recorded from each of these plots. To estimate the treatments' impact on non-targeted tree species, we also recorded the number of *A. erioloba* individuals. Lastly, to determine if treatment affected other undesired species, we counted the number of *P. leubnitziae* shrubs. As it was impractical to record very small individuals from a 50×50-m plot, only individuals >0.50 m were recorded for all three tree/shrub species.

The dominant grass composition was sampled at a much finer spatial scale. Within each 50×50-m plot we laid out three 1×1-m squares in locations that were deemed representative for the entire plot. In each of these squares we recorded which grass species were present. The merger of these three lists indicated that the species-richness-area curve per location has flattened sufficiently to be considered as representative for the common, dominant grass species. Sampling took place during the dry season (June and July) of 2012. No rainfall occurred during

the sampling period that could have affected our response variables. Although sampling in the dry season is often challenging, in many plots grasses still had sufficient numbers of infloresences and other recognisable plant parts to allow for a reliable identification. For all species names we adoped the accepted taxonomical status as listed in The Plant List (Kalwij, 2012).

2.4.   Environmental data

At the approximate centre of each site, the geographic coordinates were recorded with a handheld GPS (Garmin GPSmap 62). These coordinates were used to derive a number of covariables. Euclidean distance to nearest waterbody and to nearest seasonal river bed were measured from topographical maps with scale of 1:50'000 (Chief Directorate of Surveys and Mapping, c1998). Elevation data were extracted from the Shuttle Radar Topography Mission (Jarvis et al., 2008). To confirm that pre-treatment plots were comparable in terms of vegetation density, we compared the MODIS 16-day Normalized Difference Vegetation Index (NDVI) at a 500-m spatial resolution of the pre-treatment situation as captured on 10 June 2009 (see https://lpdaac.usgs.gov/products/modis_products_table/mod13a1).

2.5.   Statistical analyses

To determine whether treatment and control plots had similar pre-treatment vegetation densities, we fitted a one-way ANOVA to the pre-treatment NDVI values. We then fitted one-way ANOVAs to test which response variables (grass species richness, number of *A. mellifera* trees, number of *A. erioloba* trees) were affected by treatment. To determine the direction of treatment effects we used Bonferroni post-hoc tests, as most variables were normally distributed.

Since no *P. leubnitziae* shrubs were found in the control sites, we used an independent *t*-test to test for differences between chemically and physically treated sites. We log-transformed the number of *P. leubnitziae* shrubs (ln + 0.5) to reduce variation.

We subsequently used multivariate analyses to determine how the different treatments and environmental variables affected the grass species. First, we used a Detrended Correspondence Analysis on the grass species data (in presence/absence format) to ensure that there was not one single environmental gradient or outlying cluster of sites. We then used a Canonical Correspondence Analysis on species presence data and variables that could potentially explain the overall variation in grass species composition (treatment, latitude, longitude, elevation, distance to nearest water body, distance to nearest seasonal river bed, *A. mellifera* abundance, *A. erioloba* abundance and *P. leubnitziae* abundance), with biplot scaling focused on inter-species distances, and using backward removal of non-significant environmental variables (Lepš and Šmilauer, 1999). The environmental variable treatment was analysed as a Boolean pseudovariable: herbicidal removal of *A. mellifera*, physical removal of *A. mellifera* or no removal as control. Each environmental variable's significance was estimated using a full model Monte Carlo permutation test with 999 iterations. Results were interpreted using a species-by-environmental-variables biplot in which the distance between nominal variable centroids and arrow length indicate the relative contribution of that particular variable to the overall model. All multivariate analyses were done in CANOCO 4.5 (Ter Braak and Smilauer, 2002).

3.   Results

The NDVI values did not differ significantly between the two treatments or between either of the two treatments and the control (ANOVA; $F_{2,18} = 0.093$, $p = 0.911$), supporting the assumption that all sites had similar vegetation densities prior to being treated (Munyati et al., 2013).

The one-way ANOVAs showed that 24–30 months after treatment both treatment categories displayed an equally significantly lower number of *A. mellifera* trees than in the control sites ($F_{2,18} = 12.628$, $p < 0.001$; Fig. 2A). We found no effect of treatment on the abundance of *A. erioloba* ($F_{2,18} = 0.359$, $p = 0.703$; Fig. 2B). No *P. leubnitziae* shrubs were found in the control sites, but chemically treated sites had a significantly higher abundance of *P. leubnitziae* shrubs than physically treated sites ($t = 3.112$, $p = 0.018$; Fig. 2C). Finally, grass species richness was affected by treatment ($F_{2,18} = 7.933$, $p = 0.003$), but only sites where *A. mellifera* was physically removed showed a significantly higher richness per plot (Fig. 2D). This increase in grass species richness for physically treated sites was due to an increase of perennial species, while there was no change in annual species richness (Figs 2E & F).

We found a total of 24 grass species in both treatment and control plots (Table 1). The most frequently occurring species in all three plot types was *Stipagrostis uniplumis*, occurring in 4 of the 7 arborocide treated sites, 5 of the 7 physically treated sites and all of the control sites. Other species frequently occurring in arborocide treated sites were *Eragrostis lehmanniana* (5/7 sites), *Aristida stipitata* (4/7 sites) and *Stipagrostis amabilis* (4/7 sites). Species occurring frequently in physically treated sites were *Enneapogon scoparius* (4/7 sites) and *Eragrostis*
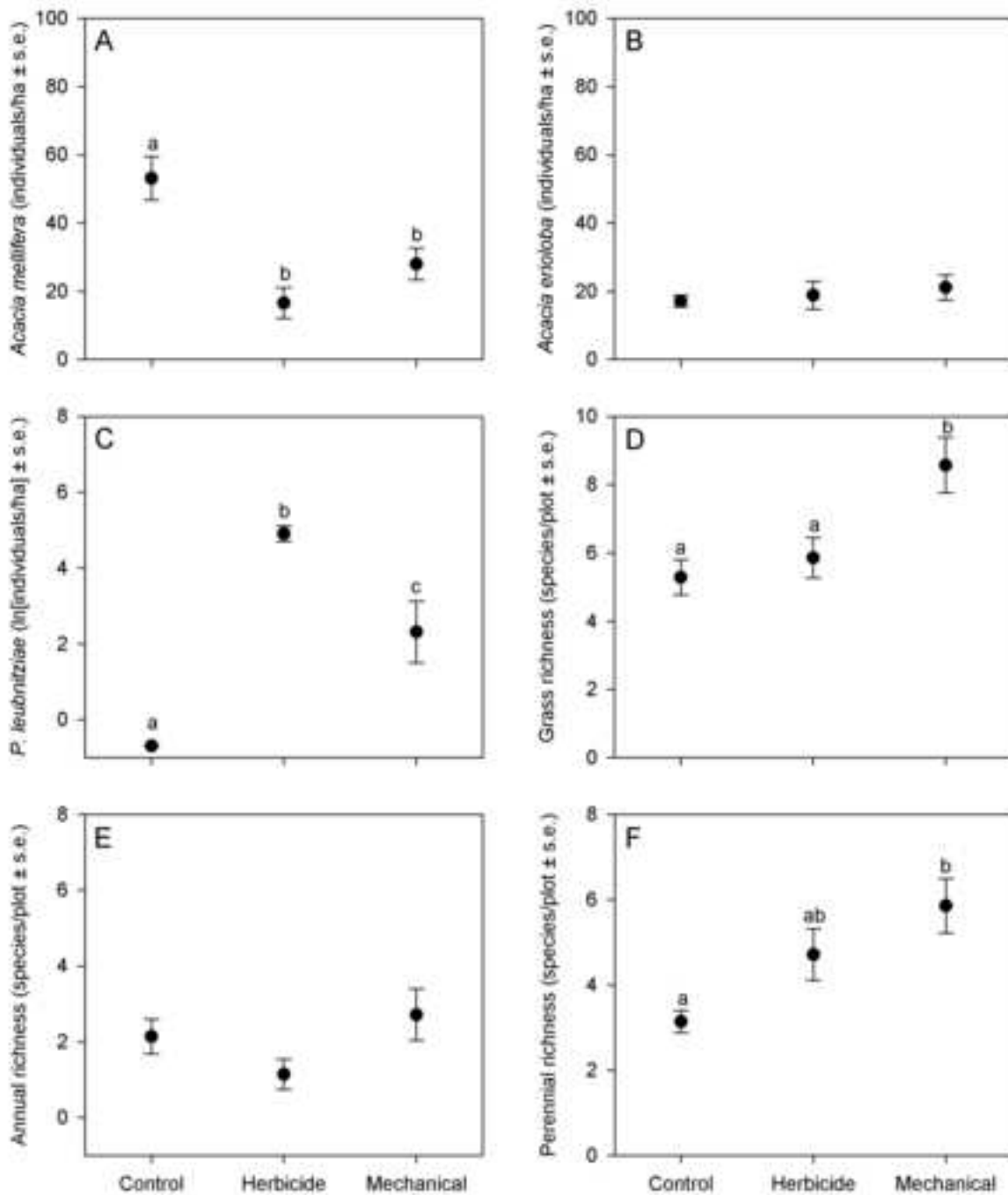
Fig. 2. Overview of the response of (A) Acacia mellifera, (B) A. erioloba, (C) Pechuel-loeschea leubnitziae (ln + 0.5 transformed), and (D) total, (E) annual and (F) perennial grass species richness to the various treatments. The response per treatment is indicated in absolute values (mean ± s.e.). All contrasts were tested with Bonferroni post-hoc tests. Significant differences between groups are indicted with lowercase letters.

Table 1. Observed grass species and the number of chemically-treated, physically-treated and control sites in which the respective grass species were found (maximum number of sites = 7). Life form indicates whether a species is predominantly annual (A) or perennial (P).

Grass species	Life form	Chemical	Physical	Control
Aristida adscensionis	A	1	3	4
Aristida congesta	P	3	2	0
Aristida meridionalis	P	0	3	2
Aristida stipitata	P	4	2	2
Chloris virgata	A	2	1	4
Enneapogon cenchroides	A	0	2	0
Enneapogon scoparius	P	1	4	1
Eragrostis jeffreysii	P	0	3	0
Eragrostis lehmanniana	P	5	1	0
Eragrostis porosa	A	0	4	4
Eragrostis rotifer	P	2	0	0
Eragrostis viscosa	A	3	4	0
Leptochloa fusca	P	0	2	2
Melinis repens	A	0	3	0
Microchloa caffra	P	3	3	0
Panicum maximum	P	2	1	0
Pogonarthria squarrosa	P	2	0	4
Schmidtia pappophoroides	P	2	3	3
Sporobolus panicoides	A	0	2	2
Stipagrostis amabilis	P	4	3	0
Stipagrostis brevifolia	P	0	2	0
Stipagrostis ciliata var. *capensis*	P	0	3	0
Stipagrostis uniplumis	P	4	5	7
Triraphis ramosissima	P	0	3	0
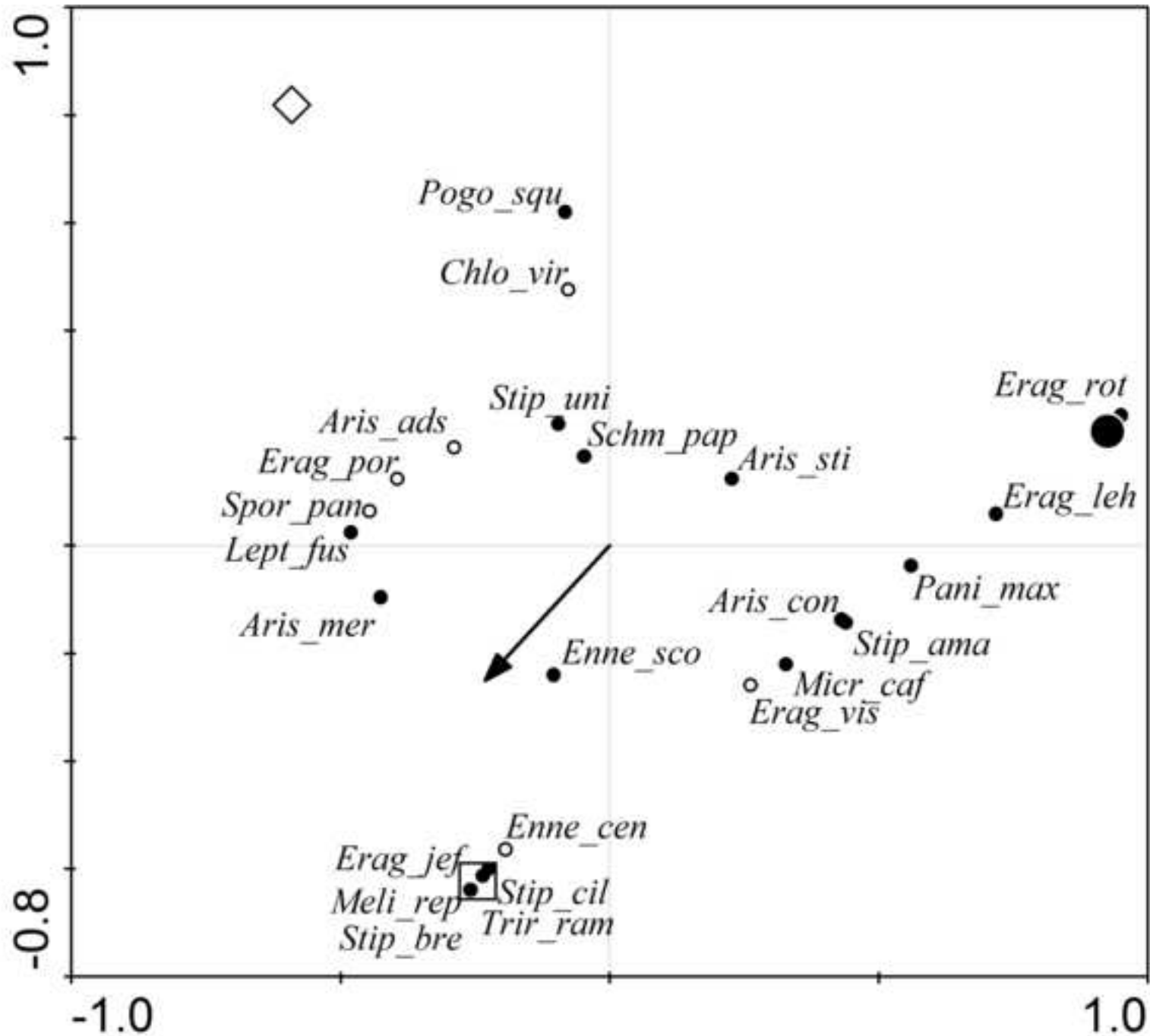
Fig. 3. Canonical correspondence analysis biplot of annual species (small ○), perennial species (small ●), and environmental variables against the first two canonical axes. Only variables that contributed significantly to overall species composition were included in the models namely, treatment (Acacia mellifera removed physically: □; A. mellifera removed with arborocide: ●; control sites: ◊) and latitude (arrow). A complete list of the species label acronyms can be found in Appendix A.

viscosa (4/7 sites), whereas frequently occurring species in control sites were *Aristida adscensionis* (4/7 sites), *Chloris virgata* (4/7 sites), *Eragrostis porosa* (4/7 sites) and *Pogonarthria squarrosa* (4/7 sites). Lastly, *E. porosa* occurred frequently (4/7 sites) in both physically cleared and control sites, but was absent from all of the arborocide treated sites.

The DCA analysis showed that species variation could not be explained by a single environmental variable, justifying the validity of the CCA analysis. The biplots showed that there was no correlation between species composition and the environmental covariables longitude, altitude, distance to nearest water body, distance to nearest seasonal river bed, *A. mellifera* abundance, *A. erioloba* abundance and *P. leubnitziae* abundance (Fig. 3).

Variation in grass species composition was thus primarily explained by treatment and to a lesser extent by latitude. None of the other covariables contributed significantly to the model (Appendix B). The CCA bi-plot also indicates that few species were exclusively associated with a particular treatment. Notable exceptions, however, were *Eragrostis rotifer* which was exclusively associated with arborocide treated sites, and *Eragrostis jeffreysii, Enneapogon cenchroides*, *Melinis repens*, *Stipagrostis ciliata* var. *capensis*, *Stipagrostis brevifolia* and *Triraphis ramosissima* which were exclusively associated with physically treated sites.

4.   Discussion

Our results confirmed that both chemical and physical clearing are effective at clearing *Acacia mellifera* shrubs, at least on a shorter term of 24–36 months post treatment (also see de Klerk, 2004 for a review of the efficacy of removal methods). In addition, abundances of the

ecologically threatened, non-target species, *A. erioloba*, were consistent between all three treatments, indicating that it was not affected by the chemical treatment of the target tree species. However, following the removal of *A. mellifera*, *Pechuel-loeschea leubnitziae*, an undesired woody species, established in both treatment sites, but especially the chemically treated sites. Notably, not a single individual of *P. leubnitziae* was observed in any of the control sites, indicating that a major ecological driver was affected by both treatments.

Competition plays an important role in determining tree composition in savanna ecosystems (Ben-Shahar, 1991; Smit, 2004). The removal of mature trees from savanna ecosystems leads to changes in intra- and inter-specific tree competition, often allowing new tree seedlings (of either the encroacher or other tree species) to establish (Smit, 2004; Teague and Smit, 1992). As a result, a transition in the dominant tree species can occur, depending on factors such as shade tolerance (Ben-Shahar, 1991) or herbivore population dynamics (Kalwij et al., 2010). Our results suggest that *P. leubnitziae* benefitted from the reduced competition, especially for water, following removal of *A. mellifera*. This is possibly because of a large *P. leubnitziae* seedbank. Once competition is reduced, these seeds are able to germinate and grow. Furthermore, *P. leubnitziae* is known to colonize bare patches in trampled and disturbed areas (Tedder et al., 2012), a characteristic which further benefitted *P. leubnitziae* in cleared areas. *A. mellifera*, on the other hand, requires exceptionally good rainfall in order to produce large crops of viable seed, while seeds may be absent, sterile or highly predated in years with low or moderate rainfall (Joubert et al. 2013; Bezuidenhout et al., 2015). This possibly explains why we do not see a recovery in *A. mellifera* numbers within the time frame of this study.

Although both physically and chemically treated sites showed an increase in *P. leubnitziae*, it was more successful at colonizing chemically treated sites than those treated physically. Following rainfall, tebuthiuron is carried to and absorbed by the tree roots, from where it works by inhibiting photosynthesis (Hatzios et al., 1980). The study area received above average rainfall during the summer of 2010/2011 (Namibia Meteorological Service, 2015b). Interestingly, this high rainfall did not result in an *en masse* sprouting of *A. mellifera* seedlings (Joubert et al., 2013). Instead, the high rainfall may have been conducive to the immediate die-back of *A. mellifera* and subsequent colonisation of *P. leubnitziae* following chemical treatment. In addition, *A. mellifera* is especially susceptible to tebuthiuron and requires a relatively low dosage compared to other species (de Klerk, 2004). Whereas chemical treatment is therefore quite effective at clearing *A. mellifera* immediately, physical treatment appears to result in a more gradual die-back of the underground root system, resulting in competition, presumably mostly for water, between *A. mellifera* and *P. leubnitziae*.

In addition to altered competition between woody species, tree thinning and clearing also leads to immediate changes in competition between woody and herbaceous species (Smit, 2004; Teague and Smit, 1992). Negasa et al. (2014) found that tree thinning of *A. mellifera* influenced grass species composition in Ethiopia, specifically by increasing perennial grasses. They ascribed this to reduced competition for water, nutrients and light. Similarly, Tedder et al. (2012) found an increase in perennial grass species in areas with a reduced cover of *P. leubnitziae*. Our results support these findings, with increased numbers of perennial species found in physically treated sites, where both *A. mellifera* and *P. leubnitziae* numbers were comparatively low. This suggests that, whereas perennial grass species were outcompeted by *A. mellifera* in the control

sites and by *P. leubnitziae* in the chemically treated sites, they were best able to establish in sites where competition between *A. mellifera* and *P. leubnitziae* kept both woody species in check. Competition between woody species therefore not only plays an important role in determining the dominant tree species in arid savannas (Ben-Shahar, 1991), but also in regulating grass species composition. Moreover, the earlier emergence of annual grasses can have a persisting competitive advantage over slower-growing perennials, especially in an ecosystem where water and other resources are scarce (Vaughn and Young, 2015). The dominance of annual grass species in arborocide treated sites is therefore likely to persist for some time to come.

The reduction in land productivity associated with bush thickening has severe economic consequences for both the livelihoods of thousands of households in communal areas, as well as commercial farmers in Namibia (de Klerk, 2004). The importance of combatting bush thickening is therefore apparent. However, the removal of large woody species can also lead to the rapid establishment of new woody seedlings (Kalwij et al., 2010; Smit, 2004). In this study, *P. leubnitziae* effectively replaced *A. mellifera* as a water and nutrient competitor in chemically treated sites, where die-back presumably happened faster and competition decreased more rapidly. Our results therefore demonstrate how the rapid removal of competition from one problem species can lead to replacement by another problem species (Caut et al., 2009). We thus concur with Smit (2004) that savanna restoration efforts should rather focus on restoring and maintaining large tree structure and competition between woody species, than on the rapid removal of encroaching species.

5. Conclusion

Both chemical treatment and manual axe hacking are effective measures of combatting *A. mellifera* thickening. In addition, neither method negatively impacted on the ecologically threatened, non-target species, *A. erioloba*. However, following *A. mellifera* removal, reduced competition, presumably mostly via increased water availability, led to the rapid establishment of *P. leubnitziae*, an unpalatable, competitive shrub species. This was especially evident in chemically treated sites, where *A. mellifera* clearing was presumably faster and *P. leubnitziae* was able to rapidly occupy the available niche. In such sites, perennial grass species were effectively outcompeted by *P. leubnitiziae*.

Acknowledgements

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Appendix A. Grass species list belonging the Canonical Correspondence Analysis biplot (Fig. 3), listing the label acronyms, the species name and the naming authority.

Abbreviation	Species name	Naming authority
Aris_ads	*Aristida adscensionis*	L.
Aris_con	*Aristida congesta*	Roem. & Schult.
Aris_mer	*Aristida meridionalis*	Henrard
Aris_sti	*Aristida stipitata*	Hack.
Chlo_vir	*Chloris virgata*	Sw.
Enne_cen	*Enneapogon cenchroides*	(Licht. ex Roem. & Schult.) C.E. Hubb.
Enne_sco	*Enneapogon scoparius*	Stapf
Erag_jef	*Eragrostis jeffreysii*	Hack.
Erag_leh	*Eragrostis lehmanniana*	Nees
Erag_por	*Eragrostis porosa*	Nees
Erag_rot	*Eragrostis rotifer*	Rendle
Erag_vis	*Eragrostis viscosa*	(Retz.) Trin.
Lept_fus	*Leptochloa fusca*	(L.) Kunth
Meli_rep	*Melinis repens*	(Willd.) Zizka
Micr_caf	*Microchloa caffra*	Nees
Pani_max	*Panicum maximum*	Jacq.
Pogo_squ	*Pogonarthria squarrosa*	(Roem. & Schult.) Pilg.
Schm_pap	*Schmidtia pappophoroides*	Steud. ex J.A. Schmidt
Spor_pan	*Sporobolus panicoides*	A. Rich.
Stip_ama	*Stipagrostis amabilis*	(Schweick.) De Winter
Stip_bre	*Stipagrostis brevifolia*	(Nees) De Winter
Stip_cil	*Stipagrostis ciliata* var. *capensis*	(Trin. & Rupr.) De Winter
Stip_uni	*Stipagrostis uniplumis*	(Licht. ex Roem. & Schult.) De Winter
Trir_ram	*Triraphis ramosissima*	Hack.

Appendix B. Overview of the Canonical Correspondence Analysis model and the explanatory

contribution (lambda) of each variable.

Variable	Lambda	F	p
Arborocide	0.31	2.52	0.001
Control	0.27	2.34	0.005
Latitude	0.19	1.69	0.038
Longitude	0.13	1.19	0.288
Altitude	0.11	0.96	0.502
Distance to nearest river	0.07	0.66	0.746
Distance to nearest water source	0.07	0.52	0.902