Short-term responses of herbaceous vegetation to bush clearing in semi-arid rangelands of South Africa

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Abstract

Bush thickening reduces herbaceous species diversity and forage production, leading to a decline in grazing capacity. Hence, altering the micro-climate and woody-grass competition in bush-encroached rangelands using bush clearing is instrumental for the restoration of herbaceous vegetation. The short-term recovery potential of herbaceous species composition, basal cover and biomass production was assessed following bush clearing at Makapaanstad, North West province, South Africa. The mean density was 6908 woody plants ha^{-1}, with *Vachellia tenuispina* encroaching at 6301 plants ha^{-1}. Paired observations were conducted in bush-cleared sites (where woody plants were cut using saws, with stumps treated with picloram at 1% concentration) and uncleared sites (where the woody cover was left intact). Forty-nine different herbaceous species were recorded, with grasses being more abundant in cleared (62%) than in uncleared sites (50%). Herbaceous species showed interspecific responses, with *Brachiaria eruciformis* and *Panicum coloratum* colonising in cleared sites, whereas the frequency of other species remained comparable between cleared and uncleared sites. Graminoids, largely bunch grasses, had a significantly greater basal cover in cleared (496 cm^2 m^{-2}) compared to uncleared (301 cm^2 m^{-2}) sites. Likewise, total biomass production was significantly ($p = 0.05$) higher in cleared (760 kg DM ha^{-1}) than in uncleared (636 kg DM ha^{-1}) sites. The principal component analysis (PCA) showed that most herbaceous species were associated with soils having high total nitrogen and nitrite. Seedlings of forbs ($r^2 = 0.81$), grasses ($r^2 = 0.97$) and succulents ($r^2 = 0.98$) were highly associated with nitrate-rich soils. Our results revealed that even at a short term, bush clearing is important for the restoration of herbaceous vegetation.

Keywords: Basal cover, Biomass production, Bush clearing, Species composition

Introduction

Semi-arid savannas of South Africa have high floristic diversity and are an important source of forage for herbivores (Osborne et al. 2018). Recently, bush thickening has increased vigorously, leading to the decline in rangeland grazing potential, owing to the reduction in forage production (Sebata 2017; Mndela et al. 2022). Bush thickening is defined according to Kellner et al. (2021) as an increase in cover and density of already established stands of woody plants. Bush thickening is caused by reduced fire frequencies and

overgrazing as well as increasing CO$_2$ concentrations (Ding and Eldridge 2019; Quirk et al. 2019; Kellner et al. 2021). Bush thickening does not only reduce biomass production, but also herbaceous species diversity (Liao et al. 2018). Thus, bush clearing is essential to restore the herbaceous cover and diversity to maximise forage resources in bush-encroached rangelands (Archer and Predick 2014).

However, the success of vegetation restoration depends largely on the bush clearing method applied, as different methods disturb soils to varying magnitudes (Mndela et al. 2020). The methods that use heavy machinery, e.g. bulldozing and mastication, may derail native vegetation restoration (Williams and Henderson 2002) and enhance regeneration

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of invasive species (Havrilla et al. 2017; Rubin and Roybal 2018). On the other hand, biological agents and chemical control are, in most cases, non-discriminant against non-target plants (DiTomaso et al. 2010). Thus, manual control of woody plants using chainsaws followed by chemical stump treatment is appropriate for opening a recruitment window for shade-intolerant herbaceous species (Frank et al. 2018).

In South Africa, a national programme called Working for Water (WfW) which controls woody invasion and encroachment was launched by the Department of Water Affairs and Forestry in 1995 (Fourie 2008). Bush-cleared areas by WfW are normally left to regenerate spontaneously, under the assumption that soil propagule bank will facilitate passive recovery of vegetation (Blanchard and Holmes 2008). However, in some rangelands, successful restoration may not be guaranteed because soil propagule bank or seeds dispersed from nearby areas may be dominated by undesirable species (Stephens et al. 2016). Moreover, the size of the soil seed bank might be too small to facilitate effective herbaceous vegetation restoration (Fourie 2008). Thus, early monitoring of the recovery potential of vegetation is crucial to establish the efficacy of passive restoration and decide if active restoration is necessary (Cuevas and Zalba 2010).

Herbaceous species composition, ground cover and biomass production are used as key indicators of vegetation recovery following bush clearing (Archer et al. 2011). These indicators are important as the modification of micro-climate and woody-grass competition through bush clearing is expected to improve these indicators (Stephens et al. 2016). However, according to Ruiz-Jaen and Aide (2005), assessing herbaceous restoration based only on vegetation indicators is not adequate. Thus, the whole vegetation recovery process and its potential drivers should be assessed holistically in order to inform appropriate future restoration applications (Ruwanza et al. 2013). Herbaceous species recruitment following bush clearing depends largely on the soils' capacity to meet species-specific recruitment and establishment requirements (Zuquim et al. 2019). However, despite the significance of soil properties in determining vegetation restoration success (Valladares et al. 2015), a knowledge gap still exists regarding the relationship between soil properties and vegetation. Understanding the relationship between soil properties and vegetation is significant not only for distinguishing plant communities, but also for designing management interventions for future restoration (Chen et al. 2020).
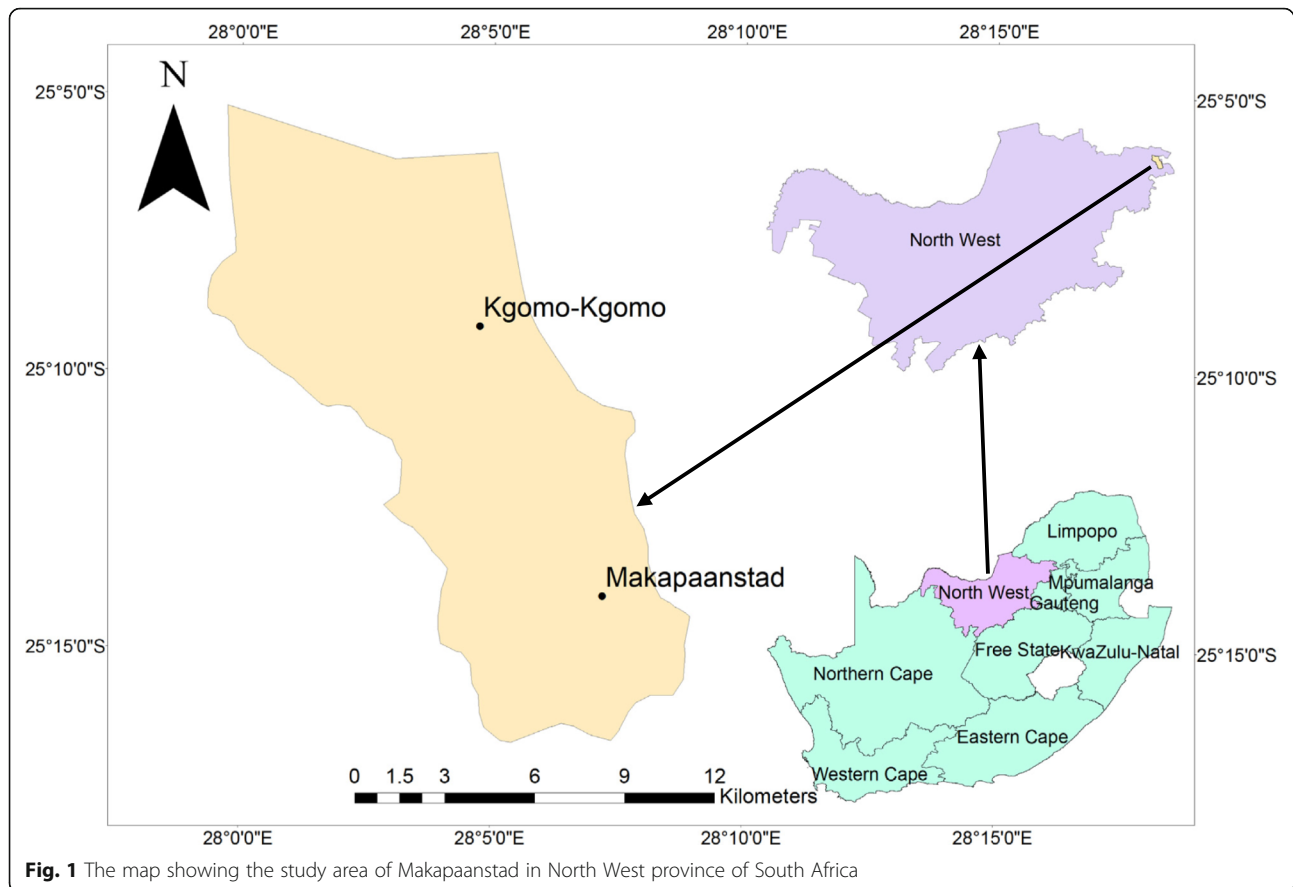
The objectives of the study were (1) to assess the short-term effects of bush clearing on herbaceous species composition, ground cover and biomass production and (2) to ascertain the relationship between various soil properties and herbaceous species communities. Our aim was to answer the following questions: (1) Does bush clearing result in changes in herbaceous species composition over a short term? (2) Do herbaceous basal cover and biomass production improve over a short term following bush clearing? and (3) How do herbaceous vegetation communities following bush clearing relate to soil properties?

Materials and methods

Description of the study area

The study was conducted at Radi communal rangeland at Makapaanstad (25° 14′ 36″ S and 28° 7′ 19″ E) in Bojanala District in North West province of South Africa (Fig. 1). The rangeland is used solely for grazing by cattle, sheep and goats owned by a group of Batswana pastoralists known as Barua Kgomo (translated as Makapaanstad cattle farmers). The Makapaanstad pastoralists are predominantly males, aged 51 years or older (Moerane 2013). Subsistence farming, largely livestock production, is the main production system from which pastoralists of Makapaanstad derive their livelihoods and economic returns (Moerane 2013). Continuous grazing is the main grazing system applied by Makapaanstad pastoralists. During informal interviews, pastoralists indicated that when forage is depleted in winter, they supplement their livestock with hay purchased from local hay markets. The herd size ranges from two to 63 cattle per pastoralist, with a mean of 12 cattle per pastoralist (Moerane 2013). The altitude of the rangeland ranges from 900 to 1200 m a.s.l. The annual rainfall in 2016 and 2017 was 563 and 622 mm year^{-1}, respectively. The maximum monthly average temperatures in summer range from 27 to 34 °C and 20 to 23 °C in winter, and the respective minimum temperatures range from 15 to 16 °C in summer and 3 to 6 °C in winter (DIGES 2012). The vegetation type of the rangeland is Springbokvlakte Thornveld found in the Central Mixed bushveld bioregion (Mucina et al. 2006). The vegetation type comprises open to dense low thorn savanna, dominated by *Acacia* species recently divided into two genera, namely Vachellia and Senegalia. The common woody species include *Vachellia karoo*, *Vachellia tortilis*, *Vachellia nilotica*, *Senegalia mellifera*, *Vachellia luederitzii* and *Ziziphus mucronata* (Mucina et al. 2006). *Vachellia tenuispina* forms a homogenous shrub layer, making up 92% of woody vegetation (Mndela et al. 2019). The herbaceous layer is dominated by the following grasses: *Ischaemum afrum*, *Dichanthium annulatum*, *Aristida bipartita* and *Brachiaria eruciformis* (Mucina et al. 2006). Parts of the rangeland are former cultivated land which were encroached by woody plants following the abandonment of cultivation (Appendix: Fig. 6). Woody cover increased from 33 to 42% from 1984 to 1996; thereafter, it increased to 56% in 2007 before bush clearing by WfW in 2013 (Appendix: Fig. 6). In 2016, the mean woody plant density was 6908 plants ha^{-1}, with *Vachellia tenuispina* encroaching at 6301 plants ha^{-1}.

Fig. 1 The map showing the study area of Makapaanstad in North West province of South Africa

Black vertic A clays (turf soils) also referred to globally as vertisols, with high cation exchange capacity and calcium carbonate content, dominate the rangeland. Turf soils have poor drainage with high swelling, shrinking, and cracking potential due to high smectitie clay minerals that facilitate self-mulching (Fey 2010).

Pre-treatment vegetation survey

The pre-treatment assessment of both herbaceous and woody vegetation was conducted during the flowering stage and peak production in February 2016. Three blocks (50 × 50 m) with similar woody vegetation structures, located in the same soil type and topography, were identified using fine resolution aerial maps (http://earthexplorer.usgs.gov). The coordinates of the blocks were recorded in the aerial maps and used to locate and peg the survey blocks. In each block, eight 25–m^2 plots were marked, with four plots marked parallel to each other. These two parallel lines of plots were 20 m apart, with the plots in each line interspaced by 5 m. Three 1.3 × 1.3 m quadrats were placed in the two opposite corners and centre of each 25-m^2 plot, totalling 72 quadrats (three quadrats × eight plots × three blocks).

Herbaceous species were identified by species, and their minimum and maximum tuft diameters were measured using a ruler in each quadrat. Herbaceous plants were

identified as seedlings when they are at a two-leaf stage. Seedlings were recorded according to plant functional groups as forbs, grass and succulent seedlings. For creeping species, directions of extraviginal stems (rhizomes and stolons) within the quadrat were tracked and diameters measured at every shoot emergence along the stem. In this scenario, a shoot emerging ≥ 10 cm away from the preceding shoot was treated as an individual plant (Davies et al. 2012). Thereafter, herbaceous vegetation was clipped at a stubble height of 5 cm in the whole 25-m^2 plots using sheep shears. During clipping, fresh biomass of grasses was sorted by species and placed into brown paper bags. Biomass of forbs and legumes was bulked according to plant functional groups. Fresh biomass was oven-dried at 75 °C until constant weight and weighed to determine the dry matter production. Biomass production was also separated into plant functional groups (grasses, forbs and legumes).

Post-treatment vegetation survey

All woody plants in the half of each block (25 × 50 m) were mechanically cleared and removed in April 2016, and the adjacent plots of the same size were left uncleared. Woody plants were cut at 6 cm above the soil surface using saws and loppers, with the stumps treated with picloram 4-amino-

3,5,6-trichloro-2-pyridinecarboxylic acid (240 g/Lt active ingredients). The picloram was mixed at a recommended concentration of 1% with a Browser for stump treatment and water for resprout control. The stump treatment was conducted within 10 min of woody plant sawing, whereas resprout control was conducted during the rainy season using knapsack sprayers. Post-treatment survey of vegetation was conducted during peak production in February 2017. In each microsite replicate, four 25-m^2 plots were marked, and the quadrats were nested in a similar way as the pre-treatment. Plant identification, measurement of tuft diameters and harvesting of biomass were conducted using the same method as for the pre-treatment. During plant identification, plants were recorded as seedlings or mature plants. The plants were regarded as seedlings if they were at or before reaching the two-leaf stage.

Species composition was determined by species identification, thereafter expressed as frequencies. Herbaceous species were further categorised according to Tainton (1999) using the ecological status (decreasers, increaser I and II species and invaders) and lifeforms (annual and perennial). The decreaser species are defined as the herbaceous species that dominate in well-managed or moderately grazed rangelands. Increaser I species are defined as the species that dominate in underutilised rangelands, whereas increaser II species are those that dominate in disturbed or overgrazed rangelands. The dominant grass species (six bunch grasses and three creeping species) were selected to assess the effect of bush clearing on their basal cover. The selected bunch grasses were *Eragrostis lehmanniana, Aristida bipartita, Brachiaria eruciformis, Digitaria eriantha, Aristida congesta* subsp. *barbicollis* and *Tragus berteronianus*, and the creeping species were *Cynodon dactylon, Bothriochloa insculpta* and *Panicum coloratum*. Species nomenclature by Van Oudtshoorn (1999) for grasses, Smith et al. (2017) for succulents and Van der Walt (2009) for forbs, sedges and legumes were used for plant identification.

To avoid confounding effects of chemical sprays on herbaceous responses following bush clearing, we conducted resprout control after sampling.

Soil chemical analysis and physical measurements

Soil samples were collected to a depth of 200 mm in the centre and two corners of each 25-m^2 plot in the cleared and uncleared sites. Soil samples for each plot were composited ($n = 12$ samples per microsite type), sieved and crushed to a fine form. The samples were analysed for pH, exchangeable cations [calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+) and sodium (Na^+)], total carbon (TC), total nitrogen (TN), nitrite (NO_2^-), nitrate (NO_3^-), chloride (Cl^- phosphate ($PO_4^3^-$), sulphate (SO_4^-) and soil fractions (clay, sand and silt). Soluble anions (NO_3^-, Cl^-, PO_4^{3-}, SO_4^- and NO_2^-) were analysed using the saturated water paste extract (SWPE) method in a 1:5 soil:water slurry, whereas pH (H_2O) was

determined using a pH metre. The basic cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) were analysed according Reeuwijk (2002) using the ammonium acetate method. The total carbon (TC) and total nitrogen (TN) were analysed using LECO CR-412 Carbon Analyzer (McDonald et al. 2006) and Kjeldahl method (AOAC 1990), respectively. The hydrometer method was used to determine clay, silt and sand fractions (Beretta et al. 2014). A double-ring infiltrometre was used to determine the infiltration rate, in which the infiltrometre was hammered to a depth of 10 cm in each 25-m^2 plot. Ten litres of water was poured in- and outside the inner ring and measured infiltrated water at 5-min intervals for 45 min per infiltrometre. Soil compaction was measured using a dynamic cone penetrometre by taking two penetrations on the bopposite corners of each 25-m^2 plot.

Statistical analysis

A univariate analysis was conducted to test the normality and equality of variances using the Shapiro-Wilk and Levene's tests. Biomass production and basal cover were transformed using $\log_e (x + 1)$ and $\log_{10} (x + 1)$ transformations, respectively. The mixed-effect model using Proc Mixed statement of SAS 9.4 was employed to assess the fixed effects of treatments (cleared and uncleared sites) and random effects of a block on biomass production and basal cover. The plots were nested within the blocks. A *t*-test was used to separate the means of paired treatments (cleared and uncleared sites) at a 95% confidence level. After data analysis, the means were back-transformed to the original mean values. Because pre-treatment data was collected during a severe drought in early 2016, there was no basis to use this data as a baseline because the herbaceous cover was heavily depleted relative to 2017 when rainfall was reliable.

A principal component analysis (PCA) was conducted to determine the relationships between soil properties and herbaceous species using a randomisation test with 999 randomisations and 200 runs. Because the species composition and soil properties of the cleared and uncleared sites did not differ considerably, a PCA biplot of the relationship of species and soil properties of cleared sites was created using Euclidean distance. The ordination was executed using PC-ORD for Windows 98 version 6.0, MjM software (McCune and Mefford 2011).

Results

Herbaceous species composition

Species frequency (%) in the cleared and uncleared sites in 2017 at Makapaanstad is shown in Table 1. In total, 49 species distributed across 16 families, dominantly Poaceae, Fabaceae and Amaranthaceae, were recorded, with forbs having higher species richness ($n = 22$ species) followed by grasses ($n = 16$ species). Cleared sites had higher species richness ($n = 44$ species) than uncleared sites ($n = 40$ species). Grasses were more frequent in cleared sites (62%) compared to

Table 1 Herbaceous species frequencies (%) in cleared and uncleared sites

Species	Family	Ecological status	Life form[†]	Cleared	Uncleared
Grasses					
Aristida bipartita (Nees.) Trin & Rupr.	Poaceae	Increaser II	P	7.3	4.5
Aristida congesta subsp. *barbicollis* Roen. & Schult.	Poaceae	Increaser II	WP	2.2	0.8
Bothriochloa insculpta (Hochst.) ex A. Rich.	Poaceae	Increaser II	WP	2.1	3.0
Brachiaria eruciformis (Sibth. & Sm.) Griseb.	Poaceae	Increaser II	A	9.9	3.2
Chloris virgata Sw.	Poaceae	Increaser II	A	1.0	0.0
Cynodon dactylon (L.) Pers.	Poaceae	Increaser II	P	5.8	5.4
Digitaria eriantha (Stent.) Steud.	Poaceae	Decreaser	P	5.6	7.8
Eragrostis lehmanniana (Nees.)	Poaceae	Increaser II	P	14.5	16.0
Fingarhuthia africana Lehm.	Poaceae	Increaser II	P	0.1	0.0
Heteropogon contortus (L.) Roen & Schult.	Poaceae	Increaser II	P	0.3	0.0
Ischaemum afrum (JF Gmel.) Dandy	Poaceae	Increaser I	P	1.2	2.9
Panicum coloratum L.	Poaceae	Decreaser	P	6.2	0.7
Setaria sphacelata (Schumach.) Stapf & C.E. Hub	Poaceae	Decreaser	P	0.7	0.0
Sporobolus ioclados (Trin.) Nees.	Poaceae	Increaser II	WP	0.0	0.6
Sporobolus ludwigii Hochst.	Poaceae	Increaser II	P	0.0	2.6
Sorghum versicolor Andersson.	Poaceae	Increaser II	P	0.2	0.0
Tragus berteronianus (Schult.)	Poaceae	Increaser II	A	4.0	1.5
Urochloa mosambicensis (Hack.) Dandy.	Poaceae	Increaser II	A	0.9	0.5
Total				**62.0**	**49.6**
Forbs					
Achyranthes aspera (L.) Griseb.	Amaranthaceae	Invader	P	0.0	0.0
Amaranthus hybridus (L.) Timeroy.	Amaranthaceae	Invader	P	0.8	0.7
Blepharis integrifolia (L.f.) Schinz.	Acanthaceae	Increaser II	P	8.6	18.0
Chochorous asplenifolius (Burch.)	Tiliaceae	Invader	P	5.6	5.2
Commelina benghalensis L.	Commelinaceae	Invader	P	0.2	1.4
Corbichonia decumbens (Forssk.) Exell.	Molluginaceae	Increaser II	A	5.5	8.8
Crabbea acaulis N.E.Br.	Amaranthaceae	Invader	P	0.4	0.2
Crabbea angustifolia (Nees.) Nees.	Amaranthaceae	Invader	P	1.4	0.1
Embrosia artemisiifolia L.	Asteraceae	Invader	P	0.4	0.3
Gomphrena celosoides Mart.	Amaranthaceae	Invader	P	0.0	0.0
Hibiscus trionum L.	Loranthaceae	Increaser II	A	2.4	0.8
Ipomoea sinensis (Desr.) Choisy.	Convolvulaceae	Invader	P	0.1	0.0
Jamesbrittennia aurantiaca Burch	Scrophulariaceae	Invader	P	0.2	0.1
Justicia flava (Vahl.) Vahl.	Acanthaceae	Increaser II	P	1.9	7.7
Kohautia virgata (Willd.) Bremek	Acanthaceae	Increaser II	P	1.4	1.9
Kyphocarpa angustifolia (Moq.) Lopr.	Amaranthaceae	Invader	A	0.7	0.2
Schkuhria pinnata (L.) Kuntze ex Thell.	Asteraceae	Invader	P	1.5	0.2
Nidorella resedifolia DC.	Acanthaceae	Increaser II	A	0.7	1.0
Spermacoce sinensis (Klotzsch.) Hiern.	Rubiaceae	Increaser II	A	2.0	0.2
Phyllanthus maderaspatensis L.	Phylanthaceae	Invader	A	1.5	1.0
Phyllanthus uniraria	Phylanthaceae	Invader	A	0.7	0.5
Tribulus terrestris (L.) Oliv.	Zygophyllaceae	Invader	A	0.1	0.1
Total				**36.1**	**48.4**
Legumes					
Crotalaria heidmannii Schinz.	Fabaceae	Invader	P	0.3	0.1
Senna italica Mill.	Fabaceae	Increaser II	P	0.1	0.1
Sesbania bispinosa (Willd.) Pers.	Fabaceae	Increaser II	B	0.2	0.1

Table 1 Herbaceous species frequencies (%) in cleared and uncleared sites *(Continued)*

Species	Family	Ecological status	Life form[†]	Cleared	Uncleared
Rhyncosia minima (L.) Pers.	Fabaceae	Increaser II	P	0.5	0.5
Tephrosia purpurea (L.) Pers.	Fabaceae	Invader	P	0.3	0.4
Total				**1.4**	**1.2**
Succulents					
Kalanchoe brachyloba Welw. ex Britten	Crassulaceae	Invader	P	0.3	0.4
Portulaca quadrifida L.	Portulacaceae	Invader	A	0.1	0.0
Total				**0.4**	**0.4**
Others					
Cyperus rotundus L.	Cyperaceae	Invader	P	0.1	0.4
Rush spp.	Hyacinthaceae	–	–	0.0	0.0
Total				**0.1**	**0.4**

[†]Life form: *P* perennial, *A* annual, *B* biennial, *WP* weak perennial

uncleared sites (50%). The short-term responses of herbaceous species to bush clearing were inter-specific. The frequency of the most dominant grass species (*E. lehmanniana*) was comparable between the cleared and uncleared sites. The annual grasses (*Brachiaria eruciformis* and *Tragus berteronianus*) and a stoloniferous perennial (*Panicum coloratum*) increased more than twofold in cleared relative to uncleared sites. Likewise, threeawns (*Aristida bipartita* and *Aristida congesta* subsp. *barbicollis*) were marginally more abundant in cleared compared to uncleared sites. The highly palatable grass (*Digitaria eriantha*) and *Ischaemum afrum* were less abundant in cleared compared to uncleared sites. The abundance of forbs was either lower in cleared sites or comparable between the two treatments.

Basal cover
The treatment effects varied by plant functional group ($p = 0.02$) on the basal cover, with graminoids covering a larger area compared to non-graminoides in both treatments (Fig. 2). Basal cover of graminoids was significantly ($p < 0.05$) higher (496 cm^2 m^{-2}) in cleared compared to uncleared sites (301 cm^2 m^{-2}; Fig. 2). Bunch grasses (*E. lehmanniana, A. bipartita, D. eriantha* and *B. eruciformis*) had a relatively greater basal cover compared to the creeping species in cleared than in uncleared sites (Fig. 3). Specifically, each bunch grass covered more than a 2-fold larger area in cleared compared to uncleared sites. Using stoloniferous growth, *P. coloratum* covered more than double the area covered by each of the selected creepers, more significantly ($p < 0.05$) in cleared than in uncleared sites (Fig. 3).

Biomass production
The interaction between treatment and plant functional groups on biomass production was not significant ($p > 0.05$). Treatments had a significant effect ($p = 0.05$) on the total biomass production (TBP), with cleared sites having higher biomass (760.1 kg DM ha^{-1}) compared to uncleared sites (636.4 kg DM ha^{-1}). However, bush clearing had no net effect on grass biomass ($p > 0.05$). The grass biomass in cleared and uncleared sites was 550 and 561 kg DM ha^{-1}, respectively (Fig. 4). Bush clearing rather increased forb biomass 2-fold in cleared than uncleared sites (Fig. 4). Of all the grass species, *Eragrostis lehmanniana* contributed most to the TBP in cleared sites (Table 2). Similarly, *Panicum coloratum* and *A. congesta* subsp. *barabicollis* contributed more to the TBP in cleared than in uncleared sites. Conversely, *Ischaemum afrum* and *A. bipartita* contributed significantly ($p < 0.05$) more biomass to the TBP than other species in uncleared than in cleared sites (Table 2).

Soil properties and herbaceous communities
The PCA separated four distinct herbaceous vegetation communities (Fig. 5). The total variance explained by principal components on herbaceous communities was 68%, with axes 1 and 2 accounting for 36 and 32%, respectively. Community 1 was the most species-rich community, characterised by a mosaic of grasses ($n = 8$ species) and forbs ($n = 7$; Fig. 5). The species in this community, e.g. *B. eruciformis, T.*
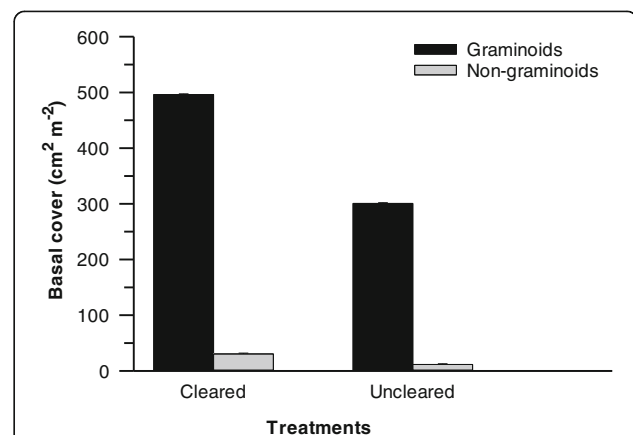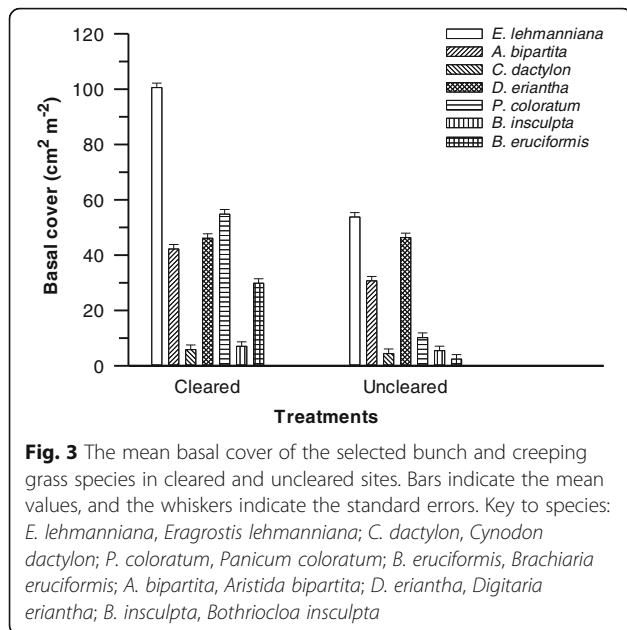
Fig. 2 The mean basal cover of graminoid and non-graminoid plants in cleared and uncleared sites. Bars indicate the mean values, and the whiskers indicate the standard errors

Fig. 3 The mean basal cover of the selected bunch and creeping grass species in cleared and uncleared sites. Bars indicate the mean values, and the whiskers indicate the standard errors. Key to species: *E. lehmanniana, Eragrostis lehmanniana; C. dactylon, Cynodon dactylon; P. coloratum, Panicum coloratum; B. eruciformis, Brachiaria eruciformis; A. bipartita, Aristida bipartita; D. eriantha, Digitaria eriantha; B. insculpta, Bothriocloa insculpta*

Table 2 Percent (%) contribution of herbaceous species to total biomass production in cleared and uncleared sites

Species	Palatability[†]	Cleared	Uncleared
Aristida bipartita	L	8.0	11.6
Aristida congesta subsp. *barbicollis*	L	11.4	2.0
Sporobolus ludwigii	L	0.0	4.3
Tragus berteronianus	L	1.5	0.0
Brachiaria eruciformis	M	4.0	5.2
Bothriochloa insculpta	M	1.8	3.2
Chloris virgata	M	2.9	0.0
Cynodon dactylon	M	5.7	7.4
Eragrostis lehmanniana	M	15.5	11.0
Fingerhuthia africana	M	0.0	0.8
Ischaemum afrum	M	5.8	20.1
Digitaria eriantha	H	8.5	8.9
Heteropogon contortus	H	0.3	0.0
Panicum colorotum	H	12.5	2.7
Setaria sphacelata	H	2.2	7.4
Sesbania bispinosa	H	0.5	0.0
Urochloa mosambicensis	H	2.3	5.7
Forbs	U	14.4	8.8
Indigofera species	U	0.6	0.4
Rhyncosia minima	U	1.3	0.4
Sena italica	U	0.7	0.0
Tephrosia purpurea	U	0.3	0.0

[†]*L* low palatability, *M* moderate palatability, *H* high palatability, *U* unpalatable

berteronianus and *P. coloratum,* were potential colonisers in cleared sites associated mostly with nitrite-rich soils (r = 0.6–0.94; Fig. 5, Table S1). Community 2 was the second largest vegetation community characterised by seedling recruitment of herbaceous plants. Seedling abundance of grasses (r = 0.97), forbs (r = 0.81) and succulents (r = 0.98) correlated mostly with NO_3^- content, whereas most of species (e.g. *D. eriantha, C. rotundus* and *G. celociodes*) in community 2 were associated with Na^+, SO_4^- and Mg^{2+} contents (Fig. 5, Table S1). The third largest community 3 was a forb community (n = 7 species), with only two grass species (*I. afrum* and *F. africana*), associated mostly with soils high in nitrogen (Fig. 5). Community 4 comprised three grasses (*E. lehmanniana, C. dactylon* and *Setaria sphacelata*), a legume and two forbs. The species in community 4 correlated positively with
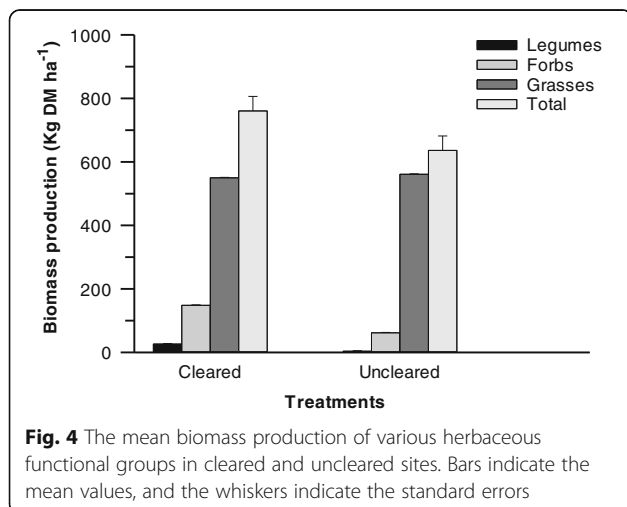

Fig. 4 The mean biomass production of various herbaceous functional groups in cleared and uncleared sites. Bars indicate the mean values, and the whiskers indicate the standard errors

silt content, infiltration, PO_4^{3-} and K^+ and negatively with soil compaction and sand content (Fig. 5).

Discussion

Species frequencies and composition over the short-term following bush clearing

The results of this study indicated that the regeneration following bush clearing was species-specific and that grasses increased to the dominant plant functional group in cleared sites (Table 1). However, the dominant grass (*E. lehmanniana*) was not altered by bush clearing, with its frequency being comparable between cleared and uncleared sites. This is not surprising given that *E. lehmanniana* is highly tolerant of the competition exerted by woody plants (Pease et al. 2006), and its seedlings tend to be protected from herbivory by woody plants (Ndlovu et al. 2011). These results concur with McClaran and Angell (2007) who found that the cover of *E. lehmanniana* remained comparable between mesquite (*Prosopis velutina*) cleared and uncleared sites.

The high recruitment of an annual grass (*B. eruciformis*) was due mainly to increased regeneration from the seeds in bare patches. *Brachiaria eruciformis* has high seed production, and its seeds germinate vigorously during early spring
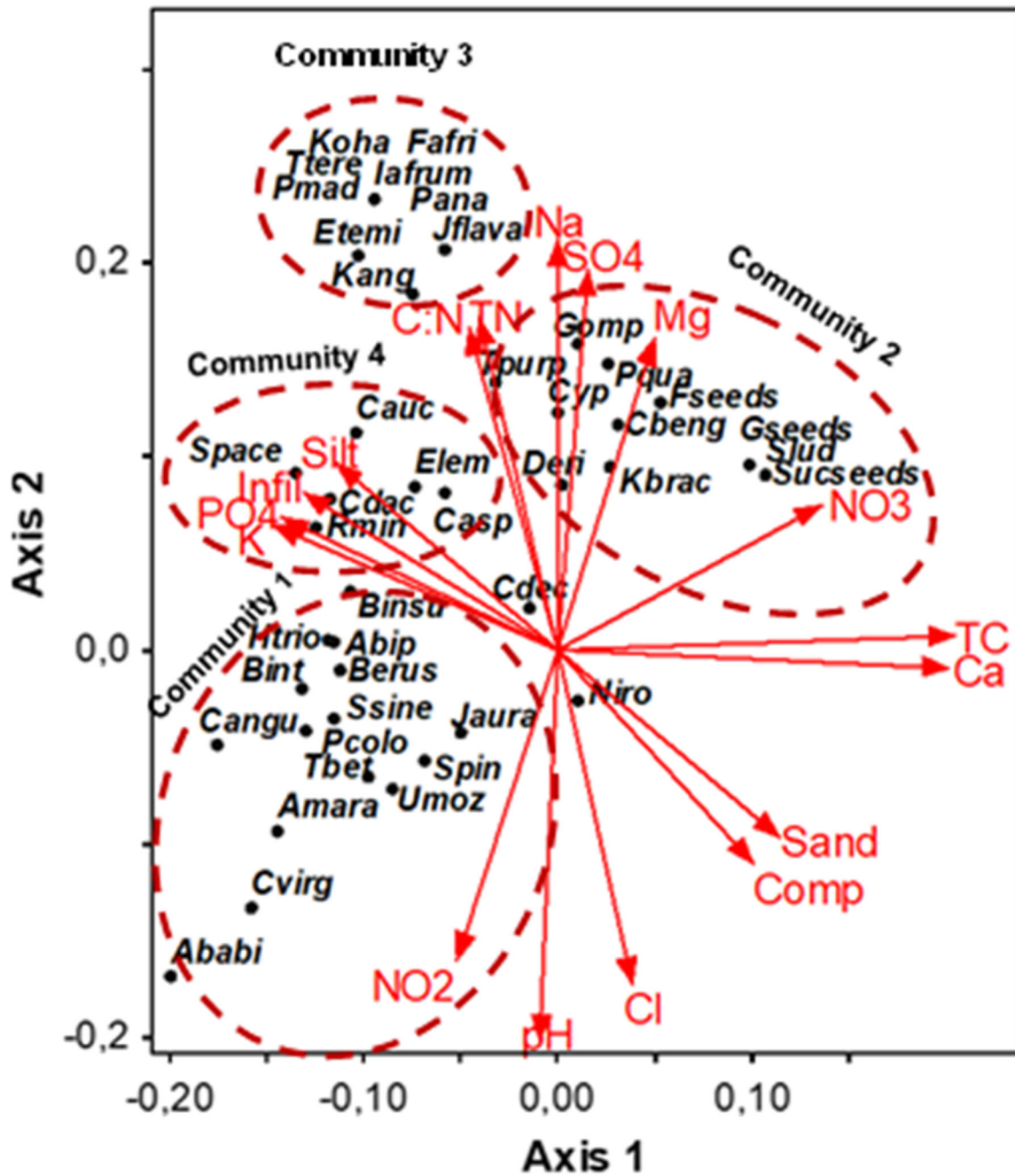
Fig. 5 Principal component analysis showing the relationships between soil properties and herbaceous species. Key to species: Ababi, *Aristida congesta* subsp. *barbicollis*; Abip, *Aristida bipartita;* Berus, *Brachiaria eruciformis*; Htrio, *Hibiscus trionum*; Tbet, *Tragus berteronianus*; Umoz, *Urochloa mosambicensis*; Cvirg, *Chloris virgata*; Cangu, *Crabbea angustifolia*; Pcolo, *Panicum coloratum*; Spin, *Schkuhria pinnata*; Space, *Setaria spacelata*; Sbisp, *Sesbania bispinosa*; Sperm, *Spermacoce sinensis*; Fafri, *Fingerhuthia africana*; Hcont, *Heteropogon contortus*; Sital, *Senna italica*; Pmad, *Phylanthus maderaspatensis*; Panau, *Phylanthus uniraria*; Amara, *Amaranthus hybridus*; Ttere, *Tribulus terestris*; Binsu, *Bothriochloa insculpta*; Niro, *Nidorella resedifolia*; Etemi, *Embrosia artemisifolia*; Bint, *Blepharis intergrifolia*; Koha, *Kohausia virgata*; Jflava, *Justicia flava*; Cdac, *Cynodon dactylon*; Rmin, *Rhyncosia minima*; Cdec, *Corbichonia decumbens*; Iafrum, *Ischaemum afrum*; Casp, *Chochorous asplenifolius*; Deri, *Digitaria eriantha*; Elem, *Eragrostis lehmanniana*; Cbeng, *Commelina benghalensis*; Slud, *Sporobolus ludwigii*; Cyp, *Cyperus rotundus*; Kbrac, *Kalanchoe brachyloba*; Tpurp, *Tephrosia purpurea*; Cauc, *Crabbea acaulis*; Kangu, *Kypocarpa angustifolia*; Pquad, *Portulaca quadrifida*; Jaura, *Jamesbrittenia aurantiaca*; Ssine, *Ipomoea sinensis*; Gomp, *Gomphrena celocioides*; Fseeds, forb seedlings; Gseeds, grass seedlings; Sseeds, succulent seedlings. Key to soil properties: Comp, compaction; Infil, infiltration

rains when temperatures and light are maximal (McGillion and Storrie [2006]). Thus, according to Mndela et al. ([2019]), high seedling recruitment, short growing cycle (4–6 weeks) and early response to change in micro-climate in cleared sites are the main underlying drivers of higher colonisation by *Brachiaria eruciformis* in cleared sites. Another potential coloniser (*P. coloratum*) did not emerge in the soil seed bank study conducted by Mndela et al. ([2019]) at Radi. Thus, high colonisation of *P. coloratum* in cleared sites was largely a function of clonal regeneration, largely by stolons. In contrast, Mndela et al. ([2019]) found a substantial decline in the seed bank densities of *B. eruciformis*, *T. berteronianus* and threeawns during the rainy season in cleared sites. Mndela et al. ([2019]) deduced that a decline in the seed bank densities and increase in above ground recruitment demonstrated that regeneration of these species was a function of the soil seed bank.

High recruitment, especially of fast-growing annuals in cleared sites, is driven mainly by an increase in light, soil nutrients and moisture availability (Stephens et al. [2016]). This view holds for this study because for both cleared and uncleared sites, regeneration during the wet season depended on similar pre-treatment seed bank density. This signifies that herbaceous recruitment in cleared sites was due largely to high resource availability rather than differences in the seed bank densities between sites. The low frequency of forbs in the cleared sites suggested that although the richness of undesirable forbs (e.g. *Blepharis intergrifolia* and *Corbiconia decumbens*) was higher (Table [1]), they do not pose a serious threat to grass recovery in cleared sites. This is likely due to the higher competitive effect of grasses for resources over forbs (Smit [2005]; Xu et al. [2012]), as grasses tended to grow taller and shade forbs in cleared sites.

Effect of bush clearing on herbaceous basal cover

The basal cover of graminoids, particularly bunch grasses, was higher than that of non-graminoids because most of the forbs recorded in this study had small erect stems that do not spread clonally, nor do they exhibit basal tillering. The results are in accordance with Bates et al. ([2000]) who recorded a large basal cover in *Juniper* cleared relative to uncleared sites, with perennial bunch grasses covering a large area. Similarly, Ndlovu et al. ([2016]) recorded a higher basal cover in *Prosopis* cleared sites compared to uncleared sites. The observed increase in basal cover in this study was attributed to basal tillering of bunch grasses because the frequency of these species remained similar between cleared and uncleared sites. On the other hand, annual bunch grass (*B. eruciformis*) colonised vigorously from the seed bank in bare patches, thereby covering bare patches in cleared sites.

The results obtained in this study suggest that increase in tuft diameters of perennial bunch grasses compensated for the lack of plant colonisation, whereas regeneration depended largely on the soil seed bank for annuals following bush clearing. Thus, any disturbance, e.g. grazing, burning and trampling, that would deteriorate the vigour of perennial bunch grasses and or impair the seedling recruitment of annuals should be avoided following bush clearing. In contrast to the results of this study, Pierson et al. ([2015]) found minimal responses of herbaceous cover one season after bush clearing. The differences can be attributable to the differences in the type of cleared woody species, site-specific conditions and methods applied. The mastication as applied in the latter study was more destructive than the use of saws applied in the former. Moreover, this study assessed herbaceous responses to clearing of leguminous species (Wickens et al. [1995]), whereas Pierson et al. ([2015]) studied herbaceous recovery following the clearing of non-leguminous species.

The species exhibiting prostrate growth, e.g. the creepers studied here, are, according to Scasta et al. ([2015]), vulnerable to competition for light where they coexist with tall bunch grasses as the latter intercept light more efficiently than the former. Thus, a low basal cover of creepers could be ascribed to restricted clonal growth and spread due to limited space and access to resources. Except for limited clonal spread, creeping species were generally less abundant than bunch grasses (Table [1]), with *P. coloratum* being the only stoloniferous species that responded positively to bush clearing. A generally low basal cover in uncleared sites is driven mainly by shade and competition for soil water and nutrients imposed by woody plants (Stephens et al. [2016]). Thus, reducing this competition through bush clearing opened a window for regeneration, which increased the abundance of annual species and tufts of most perennial species.

Effect of bush clearing on biomass production

The results revealed that despite an increase in total biomass production, over a short term, bush clearing was not beneficial for increasing grass biomass. Instead, bush clearing resulted in the increase in biomass production of unpalatable forbs, and this could reduce grazing capacity of cleared sites. Higher forb biomass could be attributed to higher leaf production because they remained less frequent in cleared relative to uncleared sites (Table [1]). In contrast, a marginally low biomass production of grasses in cleared sites relative to uncleared sites was due to the colonisation of small-leafed annual species, e.g. *B. eruciformis* and *T. berteronianus*, in cleared sites. Moreover, at the time of vegetation sampling, some leaves of these annual species were already lost due to their short growing cycle that causes early senescence. Due to the short-term nature of this study, no conclusions could be drawn regarding the long-term vegetation change following clearing. However, given that rainfall was above average and soil seed bank of grasses was high in 2017 (Mndela et al. [2019]), it is highly likely that biomass production of grasses increased post-2017 in cleared sites. Hence, long-term prohibition of herbivory is needed to allow plant recruitment and establishment following bush clearing.

However, not only do the growing conditions determine the responses of herbaceous vegetation to bush clearing but also the type, canopy size, age and densities of cleared woody species play a central role (Scholes and Archer 1997). For example, in this study, *I. afrum* and *A. bipartita* produced more biomass in uncleared sites where probably N-fixation by *V. tenuispina* benefitted the understory species. The coexistence of *I. afrum and V. tenuispina* was also reported by La Grande (2010), suggesting a close relationship between these species. Moreover, because most of *V. tenuispina* shrubs are short (< 1.5 m), competition with understory grasses for light should be minimal. Effects of bush clearing on herbaceous vegetation may be strong in scenarios where cleared encroachers were tall with large dense canopies (Scholes and Archer 1997).

Effects of soil properties on herbaceous communities

The ordination results showed that the largest vegetation community (community 1) was strongly associated with NO_2^- content (Fig. 5). The correlation between herbaceous species in community 1 and NO_2^- was moderate ($r = 0.45$) to high ($r > 0.70$; Table S1), underpinning that dependence on NO_2^- varied by species, as the NO_2^- requirements and tolerance differ by species. The species in this community did not correlate with many other soil properties measured in this study. This suggests that the occurrence of this community might also be explained by other environmental factors not considered here. More interestingly, vegetation community 2 was associated with seedling regeneration of forbs, grasses and succulents. These seedlings were correlated with NO_3^-, suggesting that this nitrogenous compound facilitates seedling recruitment either through breaking seed dormancy or as a nutrient or both.

The soil NO_3^- stimulate the breaking of seed dormancy through reducing abscisic acid, a hormone that promotes seed dormancy (Bethke et al. 2006; McIntyre et al. 1996). NO_3^- not only acts as a nutrient, but also as a signal during germination (Duermeyer et al. 2018) and is more active in seeds exposed to light (Vanderlook et al. 2008). It is therefore not surprising to see higher recruitment of annual grass species in cleared sites where light is probably higher than in uncleared sites. Our results further indicated that soil N was the key nutrient maintaining this forb dominated community (community 3). This was expected given that the species in this community colonised mostly in *Vachellia tenuispina* clumps, where N content is expected to be high due to N fixation and deposition of N-rich litter.

The correlation between species in community 4 with infiltration rate and silt content indicated that this vegetation type occurs mostly in moist soils. The negative correlation of the species in this cluster with soil compaction was not surprising because compaction reduces not only the infiltration, but also rooting depth thereby limiting nutrient and water uptake (Nawaz et al. 2013). Moreover, the cohesive strength of compacted soils impairs germination and seedling emergence (Nawaz et al. 2013); hence, compacted soils tend to lack vegetation cover due to poor plant adaptation.

The role pastoralists can play in bush control and post-clearing vegetation recovery

.09pt?>Our results indicated that basal cover and biomass production increase over a short term following bush clearing. This indicates a necessity for a temporary exclusion of grazing in bush cleared sites to allow the successional recovery of herbaceous vegetation. In the interim, Barua Kgomo pastoralists can utilise the green and lush grassland areas along the river to ease grazing pressure in bush cleared areas (Appendix: Fig. 6). In this instance, pastoralists through herding may redirect their cattle herds to areas along the river and kraal them during the night. This herd management strategy may assist in increasing the seed production and vigour of grasses, thereby improving grass cover in bush cleared sites. It is, however, reported that re-encroachment may occur within 5 years following bush clearing (Archer and Predick 2014). Thus, pastoralists' involvement in post-clearing management and monitoring of bush cleared rangelands may play a significant role in ensuring improved and sustained rangeland production following bush clearing. Amongst other strategies, pastoralists need to increase goat herd sizes to manage resprouting and seedling recruitment of woody plants through browsing (Maguraushe 2015). Increasing goat herds is not only the strategy to manage bush thickening, but also for diversifying livestock products to sustain pastoralists' livelihoods (Behnke 2021).

Conclusion

This study revealed that herbaceous responses to bush clearing are interspecific, as some grass species regenerated in cleared sites, whereas the frequencies of others remained comparable between cleared and uncleared sites. More interestingly, forbs were less abundant in cleared sites highlighting that by increasing grass cover, bush clearing reduces the likelihood of forb invasion. Moreover, an increase in ground cover and biomass production following bush clearing showed that even in a short term, bush clearing is a reliable management tool for the restoration of herbaceous vegetation.
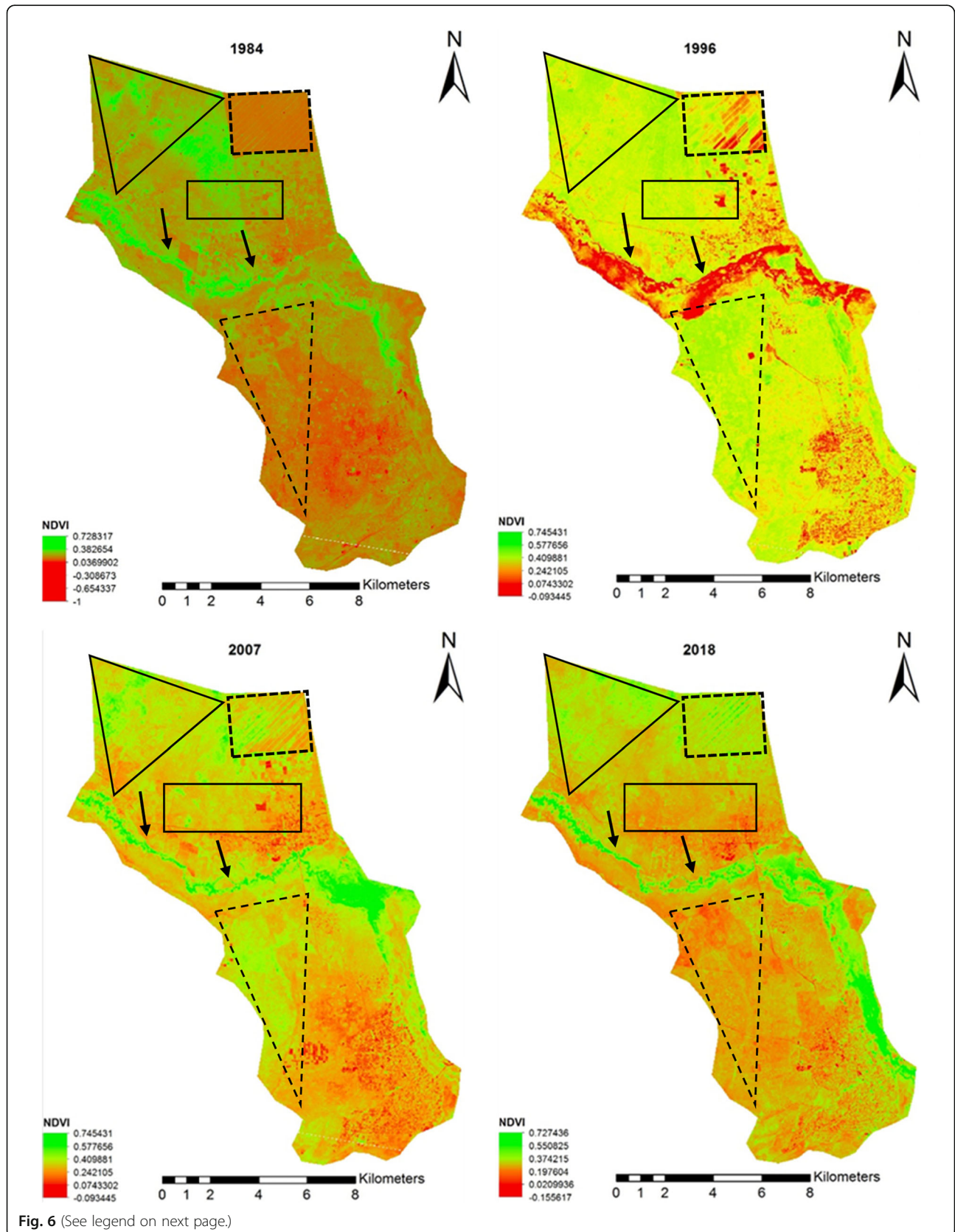
Appendix

Fig. 6 (See legend on next page.)

(See figure on previous page.)
Fig. 6 The NDVI maps indicating vegetation cover change from 1984 to 2018 at Makapaanstad. NDVI > 0.4 = woody cover, NDVI > 0.3–0.4 = humid grasslands and NDVI ≥ 0.2–0.3 = arid grasslands. NDVI < 0.2 are bare areas and water cover. Dotted square indicates an increase in woody cover in abandoned croplands, and dotted triangle indicates an increase in woody cover of grazing land. In 2018, woody cover declined in the dotted triangle and the rectangle where bush clearing was conducted by the Working for Water programme. The arrows indicate the areas along a stream. The red area with negative NDVI in 1996 indicates water overflowing from the stream

Additional file 1: Table S1. Pearson's correlation between herbaceous species and soil properties at Makapaanstad rangeland.

Availability of data and materials
The data used in this study will be made available upon request and discussions with the corresponding author.

Declarations

Ethics approval and consent to participate
Not applicable

Consent for publication
Not applicable

Competing interests
The authors declare that they have no competing interests.

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References
AOAC. 1990. *Association of official analytical chemists*. 13th ed. Washington, DC: Official methods of analysis.

Archer, S., K.W. Davies, T.E. Fulbright, K.C. McDaniel, B.P. Wilcox, and K. Predick. 2011. *Brush management as a rangeland conservation strategy: A critical evaluation. Conservation benefits of rangeland practices*, 105–170. Washington, DC: US Department of Agriculture Natural Resources Conservation Service.

Archer, S., and K.I. Predick. 2014. An ecosystem services perspective on brush management: research priorities for competing land-use objectives. *Journal of Ecology* 102 (6): 1394–1407. https://doi.org/10.1111/1365-2745.12314.

Bates, J.D., R.E. Miller, and T. Svejcar. 2000. Understory dynamics in cut and uncut western *Juniper* woodlands. *Journal of Range Management* 53 (1): 119–126. https://doi.org/10.2307/4003402.

Behnke, R.H. 2021. Grazing into the Anthropocene or back to the future? *Frontiers in Sustainable Systems* 5: 638806. https://doi.org/10.3389/fsufs.2021.638806.

Beretta, A.N., A.V. Silbermann, L. Paladino, D. Torres, D. Basahun, R. Musseli, and A. Garcia-lamohte. 2014. Soil texture analysis using a hydrometer, modification of the Bouyoucos method. *Ciencia Investigación Agraria* 41: 263–271.

Bethke, P.C., I.G.L. Libourel, and R.L. Jones. 2006. Nitric oxide reduces seed dormancy in Arabidopsis. *Journal of Experimental Botany* 57 (3): 517–526. https://doi.org/10.1093/jxb/erj060.

Blanchard, R., and P.M. Holmes. 2008. Riparian vegetation recovery after invasive alien tree clearance in the Fynbos biome. *South African Journal of Botany* 74 (3): 421–431. https://doi.org/10.1016/j.sajb.2008.01.178.

Chen, C., X. Fang, W. Xiang, P. Lei, S. Ouyang, and Y. Kuzyakov. 2020. Soil-plant co-stimulation during forest vegetation restoration in a subtropical area of southern China. *Forest Ecosystems* 32 (1): 2–17. https://doi.org/10.1186/s40663-020-00242-3.

Cuevas, Y.A., and S.M. Zalba. 2010. Recovery of native grasslands after removing invasive pines. *Restoration Ecology* 18 (5): 711–719. https://doi.org/10.1111/j.1526-100X.2008.00506.x.

Davies, K.W., J.D. Bates, and A.M. Nafus. 2012. Comparing burned and mowed treatments in mountain Big Sagebrush Steppe. *Environmental Management* 50 (3): 451–461. https://doi.org/10.1007/s00267-012-9898-2.

Ding, J., and D.J. Eldridge. 2019. Contrasting global effects of woody plant removal on ecosystem structure, function and composition. *Perspectives in Plant Ecology, Evolution and Systematics* 39: 125460. https://doi.org/10.1016/j.ppees.2019.125460.

DiTomaso, J.M., R.A. Masters, and V.F. Peterson. 2010. Rangeland invasive plant management. *Rangelands* 32 (1): 43–47. https://doi.org/10.2111/RANGELANDS-D-09-00007.1.

Duermeyer, L., E. Khodapanahi, D. Yan, A. Krapp, S.J. Rothstein, and E. Nambara. 2018. Regulation of seed dormancy and germination by nitrate. *Seed Science Research* 28 (3): 150–157. https://doi.org/10.1017/S096025851800020X.

Dynamic Integrated Geo-environmental Services (DIGES). 2012. *Proposed construction of 100 MW solar power plant on portion 6 and 7 of farm Bezuiidenhoutskraal 96 JR within Moretele Local Municipality of Bojanala Platinum District Municipality, Makapaanstad, North West Province, South Africa*. Draft scoping report.

Fey, M. 2010. *Soils of South Africa*. 1st ed. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511782183.

Fourie, S. 2008. Composition of the soil seed bank in alien-invaded grassy fynbos, potential for recovery after clearing. *South African Journal of Botany* 74 (3): 445–453. https://doi.org/10.1016/j.sajb.2008.01.172.

Frank, G.S., M.R. Saunders, and M.A. Jenkins. 2018. Short-term vegetation responses to invasive shrub control techniques for Amur Honeysuckle (*Lonicera maackii* [Rupr.] Herder). *Forests* 9. https://doi.org/10.3390/f9100607.

Havrilla, C.A., A.M. Faist, and N.N. Barger. 2017. Understory plant community responses to fuel-reduction treatments and seeding in an upland Pinyon-juniper woodland. *Rangeland Ecology and Management* 70 (5): 609–620. https://doi.org/10.1016/j.rama.2017.04.002.

Kellner, K., R.T. Mangani, T.J.K. Sebitloane, J.G. Chirima, N. Meyer, H.C. Coetzee, P. W. Malan, and J. Koch. 2021. Restoration after bush control in selected rangeland areas of semi-arid savannas in South Africa. *Bothalia* 51 (1): 1–13. https://doi.org/10.38201/btha.abc.v51.i1.7.

La Grande, M. 2010. *Vegetation classification of the proposed Heritage Park, North-West Province, South Africa. Master's Thesis*. Potchefstroom: North-West University.

Liao, C., P.E. Clark, and S.D. DeGloria. 2018. Bush encroachment dynamics and rangeland management implications in southern Ethiopia. *Ecology and Evolution* 8 (23): 11694–11703. https://doi.org/10.1002/ece3.4621.

Maguraushe, W. 2015. *The potential utilization of Acacia karroo in improving communal goat nutrition in the False Thornveld of the Eastern Cape Province, South Africa. MSc thesis*. Alice: University of Fort Hare.

McClaran, M.P., and D.L. Angell. 2007. Mesquite and grass relationships at two spatial resolutions. *Plant Ecology* 191 (1): 119–126. https://doi.org/10.1007/s11258-006-9220-6.

McCune, B., and M.J. Mefford. 2011. *PC-ORD. Multivariate analysis of ecological data. Version 6*. Oregon: MjM Software.

McDonald, S.J., D.S. Frank, J.A. Ramirez, B. Wang, and J.M. Brooks. 2006. *Ancillary methods of the National Status and Trends Program: 2000–2006 update*, 17. Silver Springs: NOAA Technical Memorandums NOS NCCOS 28.

McGillion, T., and A. Storrie, eds. 2006. *Integrated weed management in Australian cropping systems – A training resource for farm advisors*. Adelaide: CRC for Australian Weed Management.

McIntyre, G.I., A.J. Cessna, and A.I. Hsiao. 1996. Seed dormancy in *Avena fatua*: Interacting effects of nitrate, water and seed coat injury. *Physiologia Plantarum* 97 (2): 291–302. https://doi.org/10.1034/j.1399-3054.1996.970212.x.

Mndela, M., I.C. Madakadze, F. Nherera-Chokuda, and S. Dube. 2019. Dynamics of the soil seed bank over the short-term after bush clearing in a semi-arid shrubland in Springbokvlakte Thornveld of South Africa. *South African Journal of Botany* 125: 298–309. https://doi.org/10.1016/j.sajb.2019.07.033.

Mndela, M., I.C. Madakadze, F. Nherera-Chokuda, and S. Dube. 2020. Is the soil seed bank a reliable source for passive restoration of bush-cleared semi-arid rangelands of South Africa? *Ecological Processes* 9. https://doi.org/10.1186/s13717-019-0204-6.

Mndela, M., I.C. Madakadze, T.J. Tjelele, M. Mangwane, F. Nherera-Chokuda, S. Dube, A. Ramoelo, and N.L. Letsoalo. 2022. Responses of grass productivity traits to bush clearing in North-West Province in South Africa. The Rangeland Journal. https://doi.org/10.1071/RJ21053.

Moerane, R. 2013. *The impact of training using a structured primary animal health care model on the skills of rural small-scale farmers. Master's Thesis*. Pretoria: University of Pretoria.

Mucina, L., M.C. Rutherford, A.R. Palmer, S.J. Milton, L. Scott, J.W. Lloyd, B. van der Merwe, D.B. Hoare, H. Bezuidenhout, J.H.J. Vlok, D.I.W. Euston-Brown, L.W. Powrie, and A.P. Dold. 2006. Nama-Karoo Biome. In *The vegetation of South Africa, Lesotho and Swaziland*, ed. L. Mucina and M.C. Rutherford, 324–347. Pretoria: SANBI.

Nawaz, M.F., G. Bourrie, and F. Trolard. 2013. Soil compaction impact and modelling. A review. *Agronomy for Sustainable Development* 33 (2): 291–309. https://doi.org/10.1007/s13593-011-0071-8.

Ndlovu, T., S.J. Milton, and K.J. Esler. 2011. Impact of *Prosopis* (Mesquite) invasion and clearing on the grazing capacity of semiarid Nama Karoo rangeland, South Africa. *African Journal of Range and Forage Science* 28 (3): 129–137. https://doi.org/10.2989/10220119.2011.642095.

Ndlovu, T., S.J. Milton, and K.J. Esler. 2016. Effect of *Prosopis* (Mesquite) invasion and clearing on vegetation cover in semi-arid Nama Karoo rangeland, South Africa. *African Journal of Range and Forage Science* 33 (2): 101–110. https://doi.org/10.2989/10220119.2016.1184181.

Osborne, C.P., T. Charles-Dominique, N. Stevens, W.J. Bond, G. Midgley, and C.E.R. Lehmann. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist* 220 (1): 10–24. https://doi.org/10.1111/nph.15236.

Pease, S., P.F. Ffolliott, G.J. Gottfried, DeBano, and F. Leonard. 2006. *Mesquite removal and mulching impacts on herbage production on a semidesert grass-shrub rangeland. Res. Pap. RMRS-RP-59*, 5. Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Pierson, F.B., C.J. Williams, P.R. Kormos, O.Z. Al-Hamdan, S.P. Hardegree, and P.E. Clark. 2015. Short-term impacts of tree removal on runoff and erosion from pinyon- and juniper-dominated sagebrush hillslopes. *Rangeland Ecology and Management* 68 (5): 408–422. https://doi.org/10.1016/j.rama.2015.07.004.

Quirk, J., C. Bellasio, D.A. Johnson, and D.J. Beerling. 2019. Response of photosynthesis, growth and water relations of a savannah-adapted tree and grass grown across high to low CO_2. *Annals of Botany* 124 (1): 77–89. https://doi.org/10.1093/aob/mcz048.

Reeuwijk, L.P. 2002. *Procedures for Soil Analysis*. 6th ed. Wageningen: International Soil and Reference Information Centre, Food and Agriculture Organisation.

Rubin, R.L., and C.M. Roybal. 2018. Plant community responses to mastication and mulching of one-seed juniper (*Juniperus monosperma*). *Rangeland Ecology and Management* 71 (6): 753–756. https://doi.org/10.1016/j.rama.2018.04.008.

Ruiz-Jaen, M.C., and T.M. Aide. 2005. Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. *Forest Ecology and Management*. 218: 158–173.

Ruwanza, S., M. Gaertner, K.J. Esler, and D.M. Richardson. 2013. The effectiveness of active and passive restoration on recovery of indigenous vegetation in riparian zones in the Western Cape, South Africa: A preliminary assessment. *South African Journal of Botany* 88: 132–141. https://doi.org/10.1016/j.sajb.2013.06.022.

Scasta, J.D., D.M. Engle, S.D. Fuhlendorf, D.D. Redfearn, and T.G. Bidwell. 2015. Meta-analysis of exotic forages as invasive plants in complex multi-functioning landscapes. *Invasive Plant Science and Management* 8 (3): 292–306. https://doi.org/10.1614/IPSM-D-14-00076.1.

Scholes, R.J., and S.R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28 (1): 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517.

Sebata, A. 2017. *Ecology of woody plants in African savanna ecosystems*. Intechopen. Available from http://dx.doi.org/10.5772/intechopen.69865. Accessed 11 Nov 2018.

Smit, G.N. 2005. Tree thinning as an option to increase herbaceous yield of an encroached semi-arid savanna in South Africa. *BMC Ecology* 5: 1–15.

Smith, G.F., N.R. Crouch, and E. Figuereido. 2017. *Field guide to succulents in Southern Africa*. 1st ed, 427–429. Cape Town: Struik Nature.

Stephens, G.J., D.B. Johnston, J.L. Jonas, and M.W. Paschke. 2016. Understory responses of mechanical treatment of pinyon-juniper in North-western Colorado. *Rangeland Ecology and Management* 69 (5): 351–359. https://doi.org/10.1016/j.rama.2016.06.003.

Tainton, N.M. 1999. *Veld management in South Africa*. Pietermaritzburg: University of Natal Press.

Valladares, F., C.C. Bastias, O. Godoy, and A. Escudero. 2015. Species coexistence in a changing world. *Frontiers in Plant Science* 6: 866. https://doi.org/10.3389/fpls.2015.00866.

Van der Walt, R. 2009. *Wildflowers of the Limpopo Valley including Mapungubwe National Park*. 1st ed, 11–335. Musina: Buisness Print.

Van Oudtshoorn, F. 1999. *Guide to grasses of Southern Africa*. Pretoria: Briza Publications.

Vanderlook, F., D. Van de Moer, and J.A. Van Assche. 2008. Environmental signals for seed germination reflect habitat adaptations in four temperate Caryophyllaceae. *Functional Ecology* 22 (3): 470–478. https://doi.org/10.1111/j.1365-2435.2008.01385.x.

Wickens, G.E., Sief, A.G. El Din, G. Sita, and I. Nahal. 1995. *Role of Acacia species in the rural economy of dry Africa and the Near East. FAO conservation guide. No, 27*. Rome: FAO.

Williams, W.D. and Henderson, K. 2002. *Tree and brush control - for - county road right-of-way*. Final Report. Project No. TR-462.

Xu, Z., S. Wan, X.H. Ren, M. Li, W. Cheng, and Y. Jiang. 2012. Effects of water and nitrogen on species turnover in temperate grasslands in northern China. *PLoS ONE* 7 (6). https://doi.org/10.1371/Journal.pone.0039762.

Zuquim, G., F.R.C. Costa, H. Tuomisto, G.M. Moulatlet, and F.O.G. Figueiredo. 2019. The importance of soils in predicting the future of plant habitat suitability in a tropical forest. *Plant Soil* 450 (1-2): 151–170. https://doi.org/10.1007/s11104-018-03915-9.

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