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Responses of grass productivity traits to bush clearing in semi-arid rangelands in North-West Province of South Africa

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ABSTRACT

Woody plant encroachment threatens herbaceous plant productivity in many rangelands globally. We evaluated the impact of bush clearing on grass tiller, leaf and biomass production, and tuft sizes in the Kgomo-kgomo and Makapaanstad rangelands in North-West Province, South Africa. In each rangeland, the number of tillers and leaves, tuft sizes and biomass of eight dominant grass species were recorded in bush-cleared and uncleared treatments. The treatment and species interacted significantly ($P < 0.001$) for tiller and leaf production and tuft sizes. Bush clearing increased tiller production of bunch grasses but not stoloniferous grasses. At Kgomo-kgomo, bunch grasses (*Panicum maximum* (Jacq.) and *Urochloa mosambicensis* (Hack.) Dandy] had three to six times more tillers and leaves per plant in the cleared than uncleared treatment. At Makapaanstad, only annual bunch grasses [*Brachiaria eruciformis* (Sibth. & Sm.) Griseb and *Tragus berteronianus* (Schult.)] attained twice as many tillers and leaves per plant in the cleared compared to uncleared treatment. Biomass was 1776 ± 159 and $696 \pm 159\ g\ m^{-2}$ in cleared and uncleared treatments respectively at Kgomo-kgomo and 1358 ± 258 and $1089 \pm 258\ g\ m^{-2}$ at Makapaanstad. The tufts of bunch grasses were nearly twice as large in the cleared compared with the uncleared treatment at Kgomo-kgomo, whereas only stoloniferous grass tufts increased at Makapaanstad. Overall, bush clearing improved grass productivity and performance, but the responses varied by species.

Keywords: biomass production, bunch and stoloniferous grasses, bush clearing, leaves, South Africa, tillers, tuft sizes, woody plant encroachment.

Introduction

Herbaceous cover and productivity of South African semi-arid rangelands are threatened by rapid and extensive woody-plant encroachment (WPE), with WPE affecting almost 7.3 million hectares (Warren *et al.* 2018). Effects of WPE on grass productivity are most notable when woody cover and density exceed 40% and 2400 trees ha^{-1} respectively, in southern Africa (Roques *et al.* 2001). Tree-grass competition for light, soil water and nutrients favours woody plants over grasses, which reduces grass productivity (Simmons *et al.* 2008; Hare *et al.* 2020) and causes a decline in livestock carrying capacity (Hare *et al.* 2020).

Grasses employ differential evolutionary and life-history strategies to cope with WPE (Solofondranohatra *et al.* 2018; Holub *et al.* 2019; Woon *et al.* 2021). Clonal grasses may persist in bush-encroached rangelands through vegetative reproduction (O'Connor *et al.* 2020). These grasses exhibit a network of ramets that emerge on stolons or rhizomes and radiate from the main genet to acquire limited resources (Ye *et al.* 2014; Saixiyala *et al.* 2017). Conversely, high woody cover induces premature senescence (Bassett *et al.* 2011) and reduces tiller and leaf production (Volder *et al.* 2013), reducing grass productivity because of shade-induced reduction in bunch grass meristematic activity (Gomes *et al.* 2020).

Bush clearing is crucial to modify microclimate and increase soil water and nutrient availability for shade-intolerant bunch grasses (Stephens *et al.* 2016) and for increasing forage production (Hare et al. 2021). Reduction in woody cover and density facilitates tillering from dormant grass buds (O'Connor et al. 2020). Pierson et al. (1990) found higher tiller and leaf turnover, which translated to higher biomass production under unshaded than a shaded environment. However, most shading studies are conducted in glasshouses and do not mimic field conditions. Hence, a knowledge gap exists regarding how bush clearing alters grass productivity at a tiller and leaf level.

Although a national initiative, Working for Water, directed to control woody plant encroachment and invasion, was launched in 1995 by the Department of Water Affairs and Forestry (Van Wilgen et al. 2020), this programme does not monitor grass performance, such as tillering, leaf production and plant vigour, in response to bush clearing. Thus, this current study intended to address the following questions in semi-arid rangelands: (1) how does bush clearing affect grass tiller, leaf and biomass production, and tuft sizes; and (2) does grass leaf production depend on tillering following bush clearing?

Materials and methods

Site description

The study was conducted at the Makapaanstad and Kgomo-kgomo communal rangelands in the Bojanala District Municipality of the North-West Province in South Africa (Fig. 1). Collectively, these rangelands cover 16 400 ha at 900–1200 m above sea level (Mucina et al. 2006). The average annual rainfall is 459 mm annum^{-1} (Moerane 2013). The highest rainfall occurs from mid-summer to mid-autumn (December to March) in the study areas (Supplementary Fig. S1). Maximum monthly average temperatures range from 27°C to 34°C in summer and from 20°C to 23°C in winter, and respective minimums range from 15°C to 16°C in summer and from 3°C to 6°C in winter (DIGES 2012). The main soil types are vertisols at Makapaanstad and red-yellow apedal sandy soils at Kgomo-kgomo (Mucina et al. 2006). Vertisols (vertic clays) have a very loose structure (tending to crack when dry and shrink when wet), a high calcium carbonate content and a high cation exchange capacity, whereas red-yellow apedal soils are well drained sandy soils with a high base status (Fey 2010). These rangelands occur in the Central Mixed Bushveld bioregion in Springbokvlakte thornveld (Mucina et al. 2006). The tree layer is dominated by leguminous shrubs, predominantly a mixture of *Dichrostachys cinerea* (L.) Wight & Arn and *Vachellia tortilis* (Willd.) Hayne at Kgomo-kgomo (Mndela et al. 2019) and a homogenous layer of *Vachellia tenuispina* (I. Verd.) Kyal & Boatwr at Makapaanstad (Mndela et al. 2020). The Kgomo-kgomo and Makapaanstad rangelands are encroached at woody plant densities of 4850 and 6900 trees ha^{-1} respectively (Mndela et al. 2019, 2020). The woody canopy cover is 76% and 82% at Kgomo-kgomo and Makapaanstad rangelands respectively. These rangelands received bush clearing from 2012 to 2017 (Fig. 1c, d), but, for the purpose of this study, we established new experimental plots. Both rangelands are continuously grazed throughout the year by cattle, sheep and goats. However, the experimental plots were fenced immediately after bush clearing in April 2016 to prohibit grazing throughout the study period.

Experimental layout and sampling

Pre-treatment layout and species selection

In each rangeland, three blocks of similar woody vegetation type, soil type, and topography were randomly selected using aerial photographs in January 2016. In each block, an area of 0.25 ha was demarcated in which eight 5 × 5 m plots were permanently marked. The eight plots were divided into two rows, 30 m apart, with plots in each row interspaced by 5 m. Three 1.3 × 1.3 m quadrats were sampled in two opposite corners and at the centre of each plot, giving a total of 144 quadrats (3 quadrats × 8 plots × 3 blocks × 2 rangelands).

Herbaceous species were identified in the quadrats to determine species composition and calculate relative abundance (RA) for selection of the eight most dominant grass species in each rangeland. Relative abundance was calculated (Zakaria et al. 2009) as:

$$\mathrm{RA}\ (\%) = \frac{n}{N} \times 100 \tag{1}$$

where n = total number of individuals of a species and N = total number of individuals of all species.

The selected grass species were monitored for the responses to bush clearing (Table 1). Of the eight selected species per rangeland, at least four were bunch grasses (Van Oudtshoorn 1999), and the others were stoloniferous. The species were subjectively classified according to the dominant growth habit on the basis of visual judgement during vegetation survey. Thus, although *Digitaria eriantha* (Stent.) Steud and *Panicum coloratum* L. are tufted, they relied more on clonal growth through spreading stolons, and so were classified as stoloniferous grasses. The selected species in each rangeland comprised two annuals and six perennials (Table 1). After vegetation assessment, the plots were mowed to 5 cm to avoid the carryover effects of residual biomass.

Post-treatment design and sampling

In April 2016, after a pre-treatment vegetation survey, half of each of the 0.25 ha blocks was cleared, and the adjacent half left uncleared, resulting in three replicates of cleared

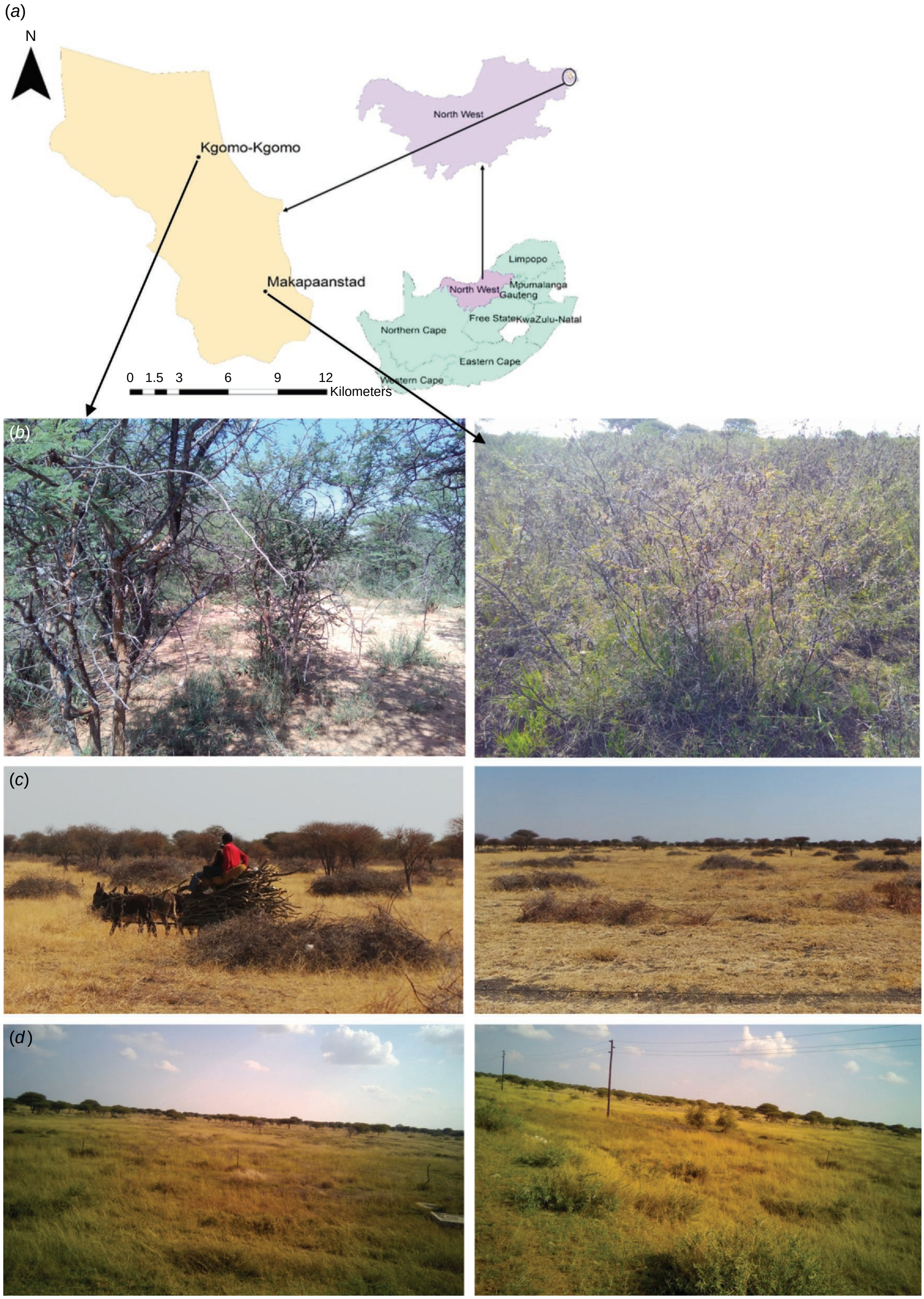

Fig. 1. (*a*) Location of the Kgomo-kgomo and Makapaanstad rangelands in North-West Province of South Africa and photographs (*b*) before bush control and (*c*, *d*) after bush control.

Table 1. Description of selected grass species in cleared and uncleared treatments at Kgomo-kgomo (KGO) and Makapaanstad (MKD).

Species	Description		Rangeland	
	Growth form	Life span	KGO	MKD
Eragrostis pseudoschlerantha (Chiov.)	Stoloniferous	Perennial	✓	
Cynodon dactylon (L.) Pers.	Stoloniferous	Perennial	✓	✓
Digitaria eriantha (Stent.) Steud.	Stoloniferous	Perennial	✓	✓
Bothriochloa insculpta (Hochst.) ex A. Rich.	Stoloniferous	Perennial		✓
Panicum coloratum L.	Stoloniferous	Perennial		✓
Panicum maximum (Jacq.)	Bunch grass	Perennial	✓	
Aristida barbicollis (Roen & Schult.)	Bunch grass	Perennial	✓	
Schmidtia pappophoroides (Steudel.)	Bunch grass	Perennial	✓	
Eragrostis lehmanniana (Nees.)	Bunch grass	Perennial		✓
Aristida bipartita (Nees.) Trin & Rupr.	Bunch grass	Perennial		✓
Tragus berteronianus (Schult.)	Bunch grass	Annual	✓	✓
Urochloa mosambicensis (Hack.) Dandy.	Bunch grass	Annual	✓	
Brachiaria eruciformis (Sibth. & Sm.) Griseb.	Bunch grass	Annual		✓

A tick ✓ indicates a species that was studied in each rangeland.

and uncleared treatments. In each replicate per treatment, four 5×5 m plots were marked. The three 1.3×1.3 m quadrats were sampled in each plot as for the pre-treatment sampling. The experiment was a completely randomised block design.

Tillers and leaves of the eight selected grass species were counted for individuals encountered in the quadrats during peak production in February 2017. The longest and the shortest tuft/crown diameters were measured and averaged to estimate a representative diameter. For stoloniferous grasses, the tiller and leaf counts, and tuft measurements, were conducted in every group of shoots emerging from each ramet attachment to the ground. The directions of the ramets were tracked from the genet within the quadrat and each measurement was conducted from those ramets assigned to the main genet by dividing the diameters of all ramet attachments with the number of attachments from which measurements were taken. Thereafter, grasses were clipped at 5 cm above the ground level and biomass was then sorted by species, oven-dried at 75°C to a constant weight and dry matter per sample determined.

Bush clearing method

Woody plants in the cleared treatment were cut 9 cm above the soil surface by using chainsaws and loppers and removed. Stumps were treated with Browser® herbicide, containing picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) as the active ingredient (240 g L^{-1}). The chemical was mixed with crop oil for cut stump treatment and water for resprout control at the recommended concentration of 1%. A minor woody plant resprouting occurred during the rainy season. Resprouts were sprayed using the herbicide after vegetation sampling at the end of February 2017 to avoid chemical interference with herbaceous vegetation.

Statistical analysis

The analysis was conducted in SAS 9.4 (SAS Institute Inc., Cary, NC, USA, 2009). The univariate analysis was performed using Kolmogorov–Smirnov and Levene's tests to assess data normality and homoscedasticity respectively (Pearce and Derrick 2019). Tiller and leaf numbers were transformed using square root ($\sqrt{x}$), whereas $\log_{10}(x + 1)$ transformation was applied for tuft size. Thereafter, two-way ANOVAs were generated using mixed models, with paired treatments ($n = 2$) and grass species ($n = 8$) and their interactions included as fixed factors, whereas a block ($n = 3$) was used as a random factor. The plots were nested within the blocks. The model was expressed as follows:

$$Y_{ijk} = \mu + \beta_h + S_i + M_j + SM_{ij} + \varepsilon_{hijk} \quad (2)$$

where, Y = dependent variables (numbers of tillers and leaves, biomass and tuft size), μ = overall mean, β = effect of the hth block, S_i = fixed effect of the ith species, M_j = fixed effect of the Jth treatment (bush-cleared and uncleared), SM_{ij} = effect of the species by treatment interaction and ε_{ijk} = experimental error associated with block, species and treatment.

Although the rangelands ($n = 2$) experience similar climatic conditions, there was no basis to compare them because of differences in soil and vegetation types. The means were separated using a paired Student's t-test, with significant differences noted at $\alpha = 0.05$. The means and standard errors were back-transformed to the original scale after analysis. We further conducted linear regression analysis to ascertain the bivariate relationships of tiller and leaf production for each grass species by using JMP software (SAS Institute 2015). We used root mean-square error (RMSE) and coefficient of determination (r^2) to measure the precision with which tiller production predicted leaf production.

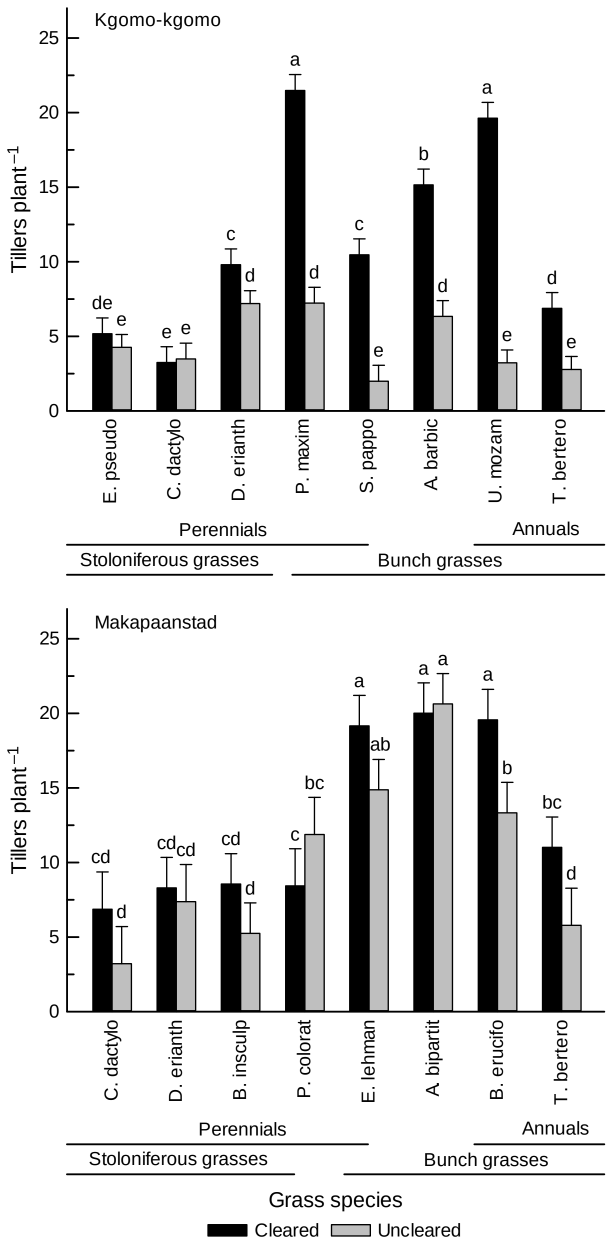

Fig. 2. Mean number of tillers of the eight selected grass species in cleared and uncleared treatments at Kgomo-kgomo and Makapaanstad rangelands. Bars indicate means and error bars indicate standard errors. Species sharing the same letter (e.g. 'c') are not significantly different ($P > 0.05$) from each other. Key to species: E. pseudo, *Eragrostis pseudoschlerantha;* C. dactylo, *Cynodon dactylon*; D. erianth, *Digitaria eriantha*; U. mozam, *Urochloa mosambicensis*; P. maxim, *Panicum maximum*; T. bertero, *Tragus berteronianus*; A. barbic, *Aristida barbicollis*, S. papoph, *Schmidtia papophoroides*; E. lehman, *Eragrostis lehmaniana*; A. bipartit, *Aristida bipartita*; B. insculp, *Bothriochloa insculpta*; P. colorat, *Panicum coloratum*; B. erucifo, *Brachiaria eruciformis*. The species underlined by the same line belong to the same category (growth habit or lifespan).

Results

Tiller production

At Kgomo-kgomo, treatment and grass species interacted significantly ($F_{7,40} = 21.23$, $P < 0.001$) on tiller number

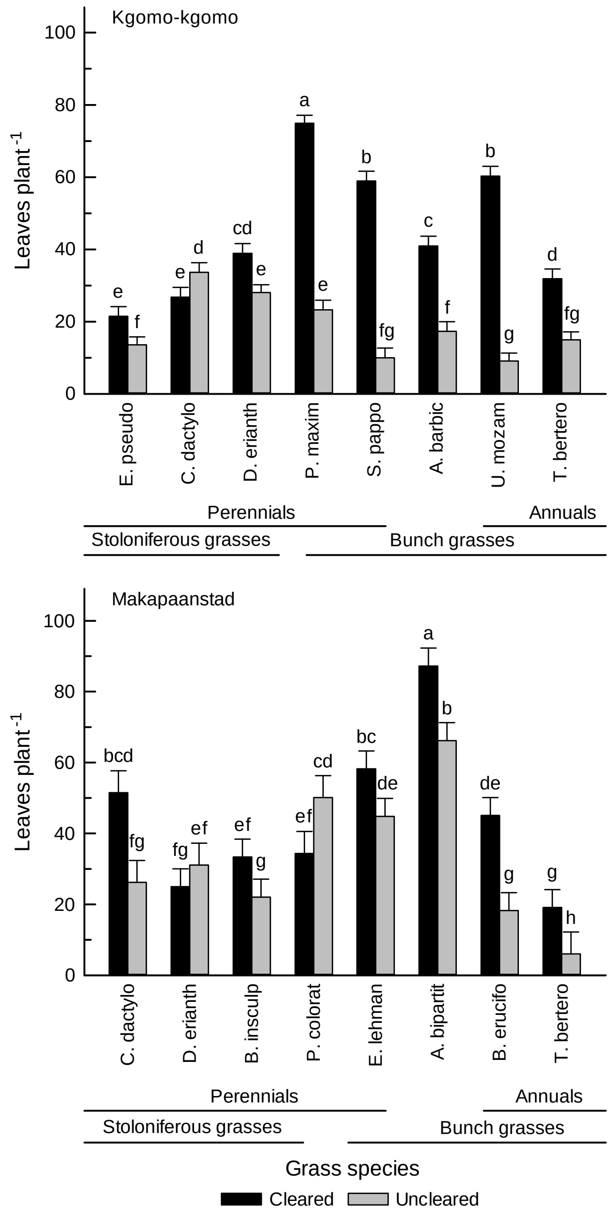

Fig. 3. Mean number of leaves of the eight selected grass species in cleared and uncleared treatments at Kgomo-kgomo and Makapaanstad rangelands. Bars represent means and error bars indicate standard errors. Species sharing the same letter (e.g. 'c') are not significantly different ($P > 0.05$) from each other. The species underlined by the same line belong to the same category (growth habit or life span). The species names are as explained in Fig. 2.

per plant of grass species. The number of tillers of *P. maximum* (t = 10.14, P < 0.001), *U. mosambicensis* (t = 12.77, P < 0.001) and *S. pappophoroides* (t = 6.03, P < 0.001) were three- to six-fold higher in the cleared than uncleared treatment and *T. berteronianus* (t = 3.18, P = 0.005) and *A. barbicollis* (t = 6.27, P < 0.001) had twice as many tillers in the cleared treatment (Fig. 2). Bush clearing increased tiller numbers of *D. eriantha*, but had no significant effects (P = 0.370) on other stoloniferous species (*E. pseudoschlerantha* and *C. dactylon*; Fig. 2).

Treatment and species also interacted significantly ($F_{7,40}$ = 2.81, P = 0.026) on grass tiller production at Makapaanstad. Bush clearing significantly altered tiller production of annual bunch grasses [*B. eruciformis* (t = 2.04, P = 0.04) and *T. berteronianus* (t = 3.15, P = 0.004) Fig. 2]. The number of tillers of *B. eruciformis* and *T. berteronianus* were 1.5–1.9-fold higher in cleared compared to uncleared treatment. There was no treatment effect on other species (P = 0.076; Fig. 2).

Leaf production

The treatment and grass species interacted significantly ($F_{7,40}$ = 28.51, P < 0.001) on leaf numbers of grasses at Kgomo-kgomo. The bunch grasses (*Panicum maximum*, *S. pappophoroides* and *U. mosambicensis*) had significantly (P < 0.001) more leaves in cleared than uncleared treatment. Among stoloniferous grasses, *E. pseudoschlerantha* (t = 2.78, P = 0.011) and *D. eriantha* (t = 2.84, P = 0.011) responded positively to clearing, whereas *C. dactylon* responded negatively (Fig. 3). *Tragus berteronianus* (t = 5.15, P < 0.001) and *A. barbicollis* (t = 5.95, P < 0.001) had double the number of leaves in cleared compared with uncleared treatment (Fig. 3). The treatment by species interaction on leaf production was also significant at Makapaanstad ($F_{7,40}$ = 5.68, P < 0.001). *Aristida bipartita* had significantly (t = 2.44, P = 0.022) more leaves in cleared than uncleared treatment (Fig. 3). The stoloniferous grasses (*C. dactylon* and *B. insculpta*) had 1.5–1.9-fold more leaves and annual bunch grasses (*T. berteronianus* and *B. eruciformis*) had two to three times more leaves in cleared than uncleared treatment (Fig. 3).

Biomass

Treatment by species interaction was not significant (P = 0.180), but treatment (P = 0.014) and species had a significant (P < 0.001) effect on biomass at Kgomo-kgomo. The cleared treatment had twice the biomass of the uncleared treatment (Fig. 4). *Panicum maximum* had a significantly higher biomass on both an area and per plant basis than did other grass species (Fig. 5). *Cynodon dactylon* and

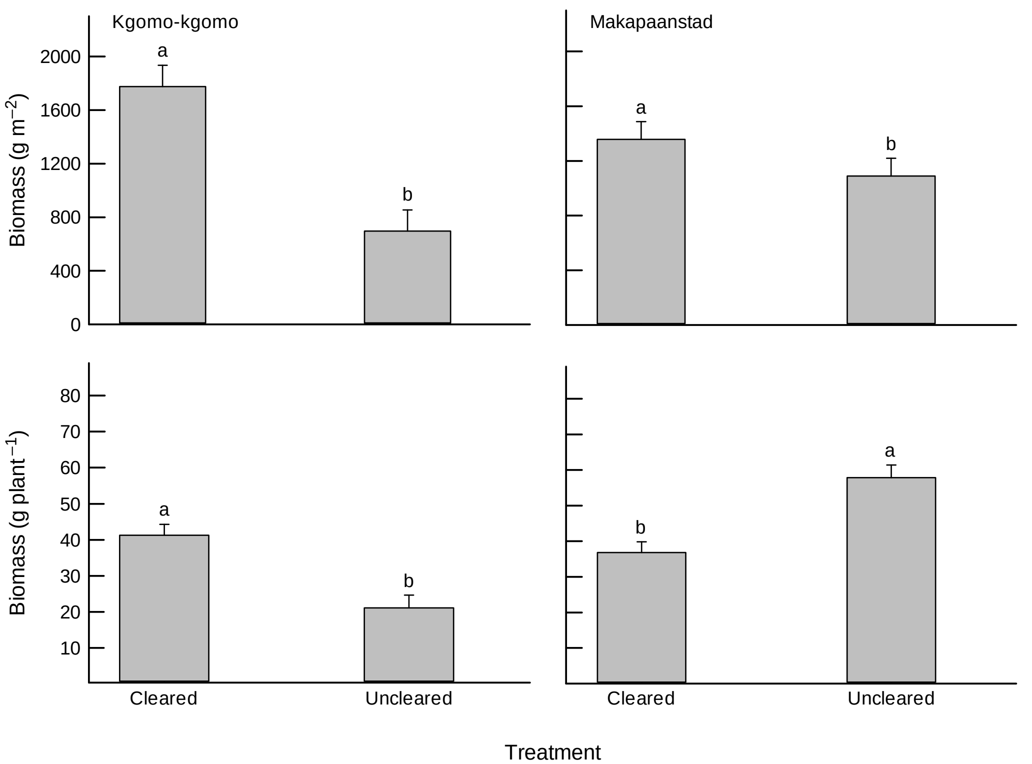

Fig. 4. Total biomass of the eight selected grass species in cleared and uncleared treatments at Kgomo-kgomo and Makapaanstad. Bars represent means and error bars indicate standard errors. Bars with different letters (e.g. 'a' and 'b') in each figure are significantly different (P < 0.05) from each other.

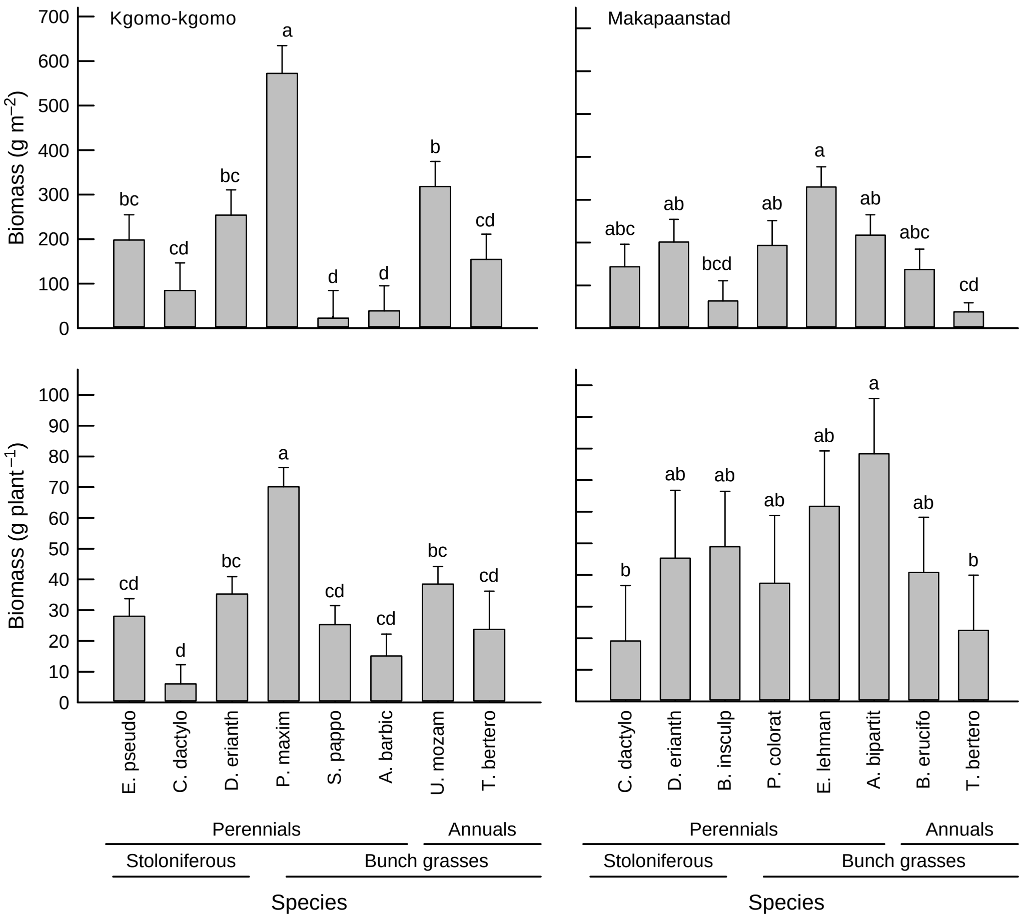

Fig. 5. Mean biomass production of the eight selected grass species at Kgomo-kgomo and Makapaanstad rangelands. Bars represent means and error bars indicate standard errors. Species sharing the same letter (e.g. 'c') are not significantly different ($P > 0.05$) from each other. The species underlined by the same line belong to the same category (growth habit or life span). The species names are as explained in Fig. 2.

A. barbicollis had the lowest biomass on both per plant and an area basis compared with the other species (Fig. 5). *Eragrostis pseudoschlerantha*, *D. eriantha* and *U. mosambicensis* had a comparable biomass on both per plant and an area basis (Figs 4, 5). On per plant basis, *Schmidtia pappophoroides* had the lowest biomass; however, on per area basis, its biomass was comparable to other species except for *P. maximum* and *U. mosambicensis* (Fig. 5).

Likewise, treatment and species had no significant ($P = 0.235$) interaction at Makapaanstad. However, the treatment ($P = 0.011$) and species ($P < 0.0001$) independently had a significant effect on biomass, with cleared treatment having a higher biomass than uncleared treatment on per area basis (Fig. 4). In contrast, when biomass per plant was averaged across species, cleared treatment had a lower biomass than did uncleared treatment (Fig. 4). On an area basis, *E. lehmanniana* generally produced more biomass than did other species (Fig. 5), whereas on per plant basis, *A. bipartita* attained a higher biomass (Fig. 5). However, these differences were not always significant.

Relationships between tiller and leaf production

At both Kgomo-kgomo and Makapaanstad, there were significant positive relationships ($P < 0.001$) between tiller and leaf production (Figs 6, 7). The relationships were strongest in cleared relative to uncleared treatment in both sites for stoloniferous grasses (Figs 6, 7), with their slopes (2–6 leaves tiller^{-1}) being steeper than for bunch grasses (1–3 leaves tiller^{-1}; Table 2). Leaf production was predicted from tillers with better accuracy for stoloniferous grasses than for bunch grasses in cleared treatment (Table 2). Except for *A. bipartita* and *T. berteronianus* at Makapaanstad, leaves of bunch grasses were better predicted from tillers (Table 2) and correlated more strongly in uncleared than cleared treatment in both rangelands (Figs 6, 7).

Tuft size

There was a significant treatment by species interaction on tuft size of grass species at Kgomo-kgomo ($F_{7,42} = 1.45$, $P < 0.01$). Tufts of *U. mosambicensis* ($t = 3.27$, $P = 0.003$),

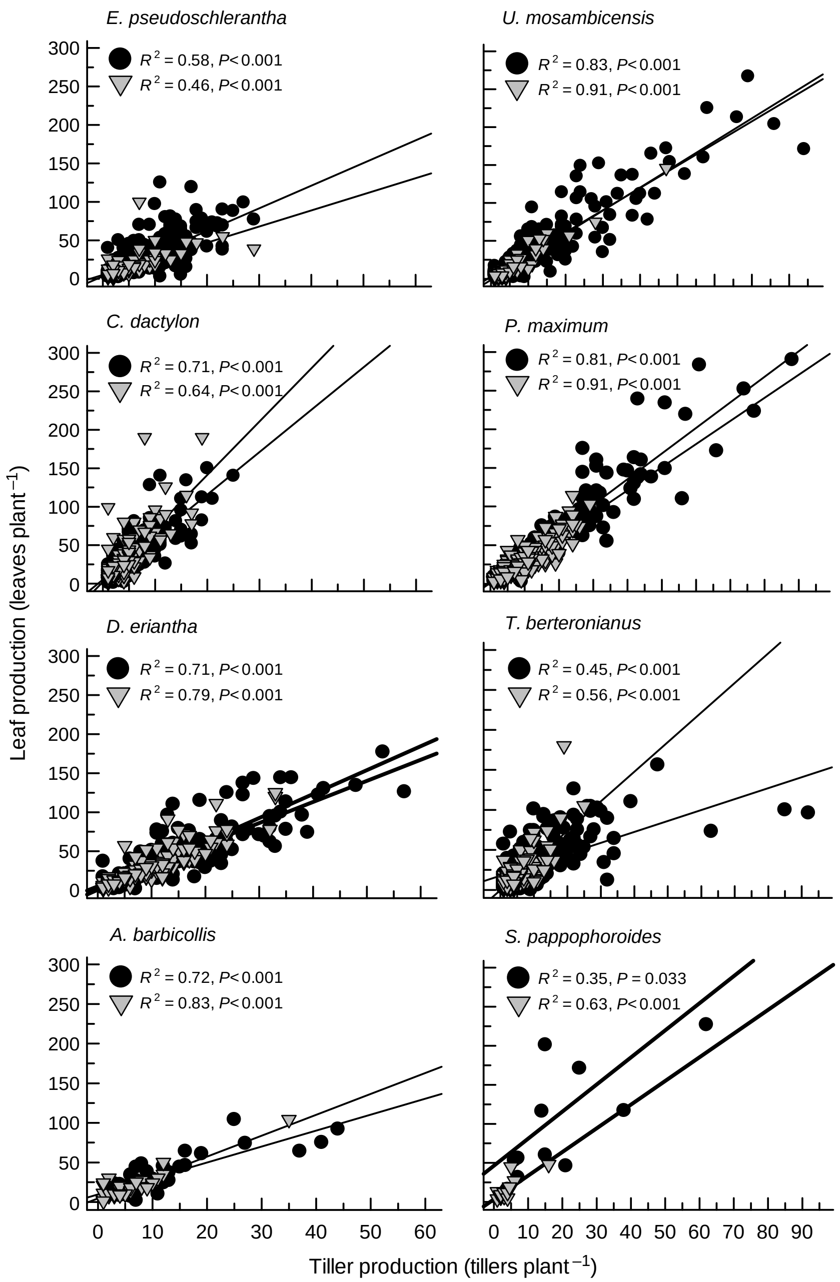

Fig. 6. The relationships between tiller and leaf production of various selected grass species in cleared (●) and uncleared (▼) treatments at Kgomo-kgomo. *E. pseudoschlerantha*, *C. dactylon* and *D. eriantha* arestoloniferous grasses and the rest from *A. barbicollis* to *S. pappsphoroides* are bunch grasses.

P. maximum ($t = 2.83$, $P = 0.009$) and *T. berteronianus* were two-fold larger in cleared than uncleared treatments (Fig. 8). At Makapaanstad, there was also a significant treatment by species interaction on tuft sizes ($F_{7,42} = 3.81$, $P = 0.005$). Bush clearing significantly ($P = 0.003$) increased only the tuft sizes of stoloniferous species (Fig. 8). However, *P. coloratum* tufts were significantly ($P = 0.039$) smaller in the cleared than in uncleared treatment (Fig. 8). Conversely, *D. eriantha* ($t = 2.33$, $P = 0.028$) and *C. dactylon* ($t = 3.83$, $P < 0.001$) respectively had two- and six-fold larger tufts in the cleared treatment (Fig. 8).

Discussion

The impact of bush clearing on tiller production varies by grass species

The effects of clearing on tiller production were species-dependent, depending largely on growth habits at Kgomo-kgomo and the lifespan of selected grass species at Makapaanstad. Bunch grasses responded most positively to treatment, most likely because stoloniferous grasses acquire, through clonal ramets, resources in fertile islands under tree canopies and between trees (Saixiyala *et al.* 2017). This result

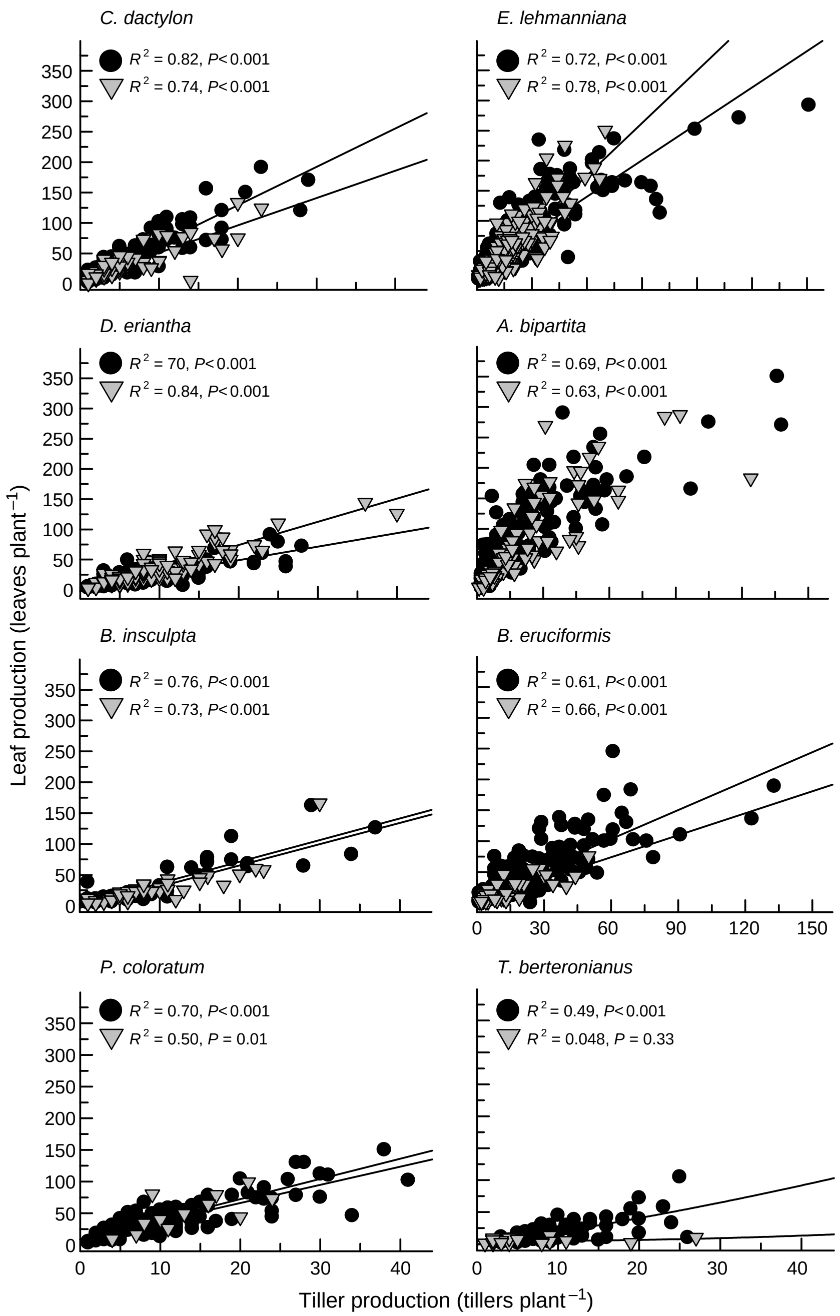

Fig. 7. The relationships between tiller and leaf production of selected grass species in cleared (●) and uncleared (▼) treatments at Makapaanstad. Species in the left column (from *C. dactylon* to *P. coloratum*) are stoloniferous grasses and those in the right column (from *E. lehmanniana* to *T. berteronianus*) are bunch grasses.

is consistent with Lett and Knapp (2003) who recorded low tiller densities of a rhizomatous grass following shrub control. Conversely, greater bunch grass tillering in the cleared treatment confirmed that bush encroachment can suppress grass productivity. Similarly, Pierce *et al.* (2019) recorded more axillary tillers in the grass growing in bush-cleared than uncleared shrublands.

At Kgomo-kgomo, clearing altered tiller production of shade-intolerant species and of *P. maximum* and *S. pappophoroides* (Fig. 2), the shade-tolerant perennial grasses (Van Oudtshoorn 1999), suggesting that tillering in uncleared treatments is largely governed by below-ground competition. In support, Simmons *et al.* (2008) reported that below-ground competition between *Prosopis glandulosa* and *Nassella leucotricha* was a more important determinant of grass tillering than was light. However, this did not seem to be true for *E. lehmanniana* and *A. bipartita* at Makapaanstad because they did not show a positive response to clearing.

Eragrostis lehmanniana and *A. bipartita* proliferated in dense swards in the clumps of encroaching shrubs. This could indicate a facilitative relationship between the encroacher shrub and these grass species, perhaps through soil fertility amelioration and protection from grazers (Pierce *et al.* 2019). Only annual-grass tiller production

Table 2. The results of the regression analysis indicating relationships between tiller and leaf production of selected grasses in cleared and uncleared treatments at Kgomo-kgomo and Makapaanstad.

	Cleared treatments					Uncleared treatments				
Species	***n***	**Intercept**	**Slope**	***F*-value**	**RMSE**	***n***	**Intercept**	**Slope**	***F*-value**	**RMSE**
Kgomo-kgomo										
E. pseudoschlerantha	448	3.17	2.95	612.74	12.20	90	5.04	2.09	76.84	10.84
C. dactylon	270	5.10	5.53	673.63	14.23	198	2.27	6.95	343.93	17.57
D. eriantha	205	6.41	2.58	446.66	18.18	162	0.70	3.06	606.75	10.66
U. mosambicensis	281	2.75	2.93	1391.97	16.64	160	−1.15	3.03	1553.31	5.02
P. maximum	135	3.59	3.34	625.76	26.24	310	1.27	2.99	1333.76	8.03
T. berteronianus	240	17.76	1.37	195.54	21.08	250	−0.40	3.70	324.37	11.81
A. barbicollis	40	9.52	2.02	103.62	12.99	28	4.51	2.64	136.24	7.94
S. pappophoroides	11	46.42	3.47	5.95	81.42	14	4.07	2.99	24.12	8.22
Total	1630					1212				
Makapaanstad										
E. lehmanniana	278	19.21	2.02	703.67	28.83	277	1.19	2.90	913.27	19.27
A. bipartita	141	36.84	2.50	318.98	40.76	75	23.88	2.52	128.26	43.37
C. dactylon	110	2.75	6.31	506.96	17.13	89	6.17	4.50	256.98	12.62
D. eriantha	108	4.17	2.25	249.30	9.26	137	−2.70	3.84	765.37	11.38
B. insculpta	40	1.28	3.50	128.93	18.47	48	−3.38	3.43	130.58	12.82
P. coloratum	118	8.58	2.88	277.68	15.63	12	8.54	3.19	10.16	20.73
B. eruciformis	189	9.85	1.56	298.44	25.04	43	2.73	1.19	81.68	10.44
T. berteronianus	75	−2.62	2.15	73.03	12.49	20	4.20	0.12	1.01	3.50
Total	1059					701				

RMSE, root mean square error.

(*B. eruciformis* and *T. berteronianus*) was responsive to clearing at Makapaanstad. However, tuft sizes were comparable between treatments, indicating a partial reliance on aerial tillering.

The impact of bush clearing on leaf production varies by grass species

Leaf production responses were governed by interactions between treatment and species. Stoloniferous-grass leaf production, e.g. *C. dactylon*, responded positively to clearing regardless of limited tillering. Results suggest that leaf production of stoloniferous grasses, to some degree, is a function of a higher leaf production per tiller. The emergence of spaced clustered shoots having more phytomers along the stolons is common in stoloniferous grasses (da Silva *et al.* 2015). Furthermore, our data indicated that stoloniferous grasses produced three to six leaves tiller^{-1} (Table 2), suggesting that these species invested more in higher leaf production per tiller. This is a common strategy in grasses, especially where competition among plants is high (Irving 2015). Unlike bunch grasses, stoloniferous species do not exhibit self-shading because of the lateral spread of ramets (Solofondranohatra *et al.* 2018). As expected, bunch grasses produced numerous leaves in the cleared relative to the uncleared treatment. This highlights that grasses employ differential response strategies to clearing.

Leaf production of grasses depends largely on tillering

Leaf production was positively related to tiller production in both cleared and uncleared treatments (Figs 6, 7). Bunch grasses produced more leaves in the cleared treatment, which led to dense and compact swards. Hence, leaves at the bottom of these grass swards were shaded, with some senesced leaves, which presumably increased prediction error (RMSE) for bunch grasses (see Table 2). Similarly, young tillers of bunch grasses may suffer similar effects of shading (Irving 2015) and intra-tiller competition within the sward (Tomlinson and O'Connor 2004; Gomes 2020). Thus, if leaf mortality surpasses leaf emergence, the linear correlation between tillering and leaf production is likely to be weakened for bunch grasses. Hence, well timed lenient

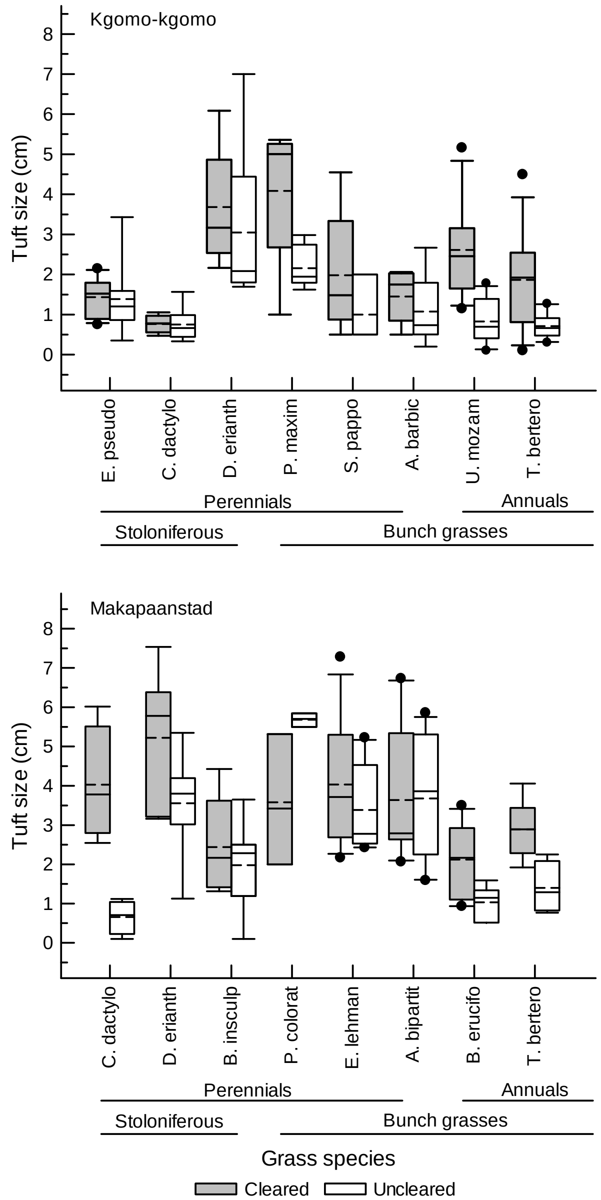

Fig. 8. Mean tuft sizes of various selected grass species in cleared and uncleared treatments at Kgomo-kgomo and Makapaanstad rangelands. The dotted line inside the box = mean, undotted line inside the box = median, upper whisker = maximum value, lower whisker = minimum value, dots outside the box = outliers, upper edge of a box = 95th quartile and lower edge of a box = 5th quartile. The species names are as explained in Fig. 2.

defoliation to ensure access to light for all vegetative sward components may be necessary (Pereira *et al.* 2017).

Conversely, with space stoloniferous grasses spread effectively through clonal ramets to access limited resources (Saixiyala *et al.* 2017). Thus, as indicated by steeper slopes (Table 2), stoloniferous grasses produced more leaves per tiller than did bunch grasses that relied largely on more tillers–more leaves relationships. The production strategy of stoloniferous grasses is more important for grazers because it ensures higher leaf than stem material. The higher leafiness of grasses not only serves as an indicator of productivity, but also of forage quality and palatability (O'Sullivan 2009). For bunch grasses, a good fit between tillers and leaves was obtained in uncleared treatments at Kgomo-kgomo. At low light levels, characteristic of the uncleared treatment, grasses tend to have a low leaf area that reduces self-shading and intra-tiller competition (Irving 2015).

Impact of bush clearing on grass biomass

Clearing increased grass biomass. Hare *et al.* (2021) reported similar results in Ethiopian rangelands, as did Smit (2005) in South Africa. Increased biomass is associated with a change in microclimate and increased resource availability, including soil nutrients and water, in cleared rangelands (Ding and Eldridge 2019). The higher biomass in the cleared treatment could be attributed to increased tiller and leaf production of grasses, largely bunch grasses. However, lack of interaction between treatment and species indicated that responses to clearing were not dependent on species type. Highly productive species (*P. maximum*) produced more biomass independent of the treatment (Fig. 5), despite a higher leaf and tiller production in the cleared than the uncleared treatment. This could perhaps be ascribed to higher plant densities of this species in the uncleared treatment, which is likely to have negated the positive effects of clearing on tiller and leaf production. At Makapaanstad, *E. lehmanniana* attained higher biomass on per area basis, whereas *A. bipartita* had a greater biomass per plant (Fig. 5). Tiller production of *A. bipartita* did not increase and leaf numbers increased, highlighting that biomass per plant was a function of a higher leaf production. The erect growth of bunch grasses promotes tillering from basal and axillary buds, which, subsequently, increases biomass production (Pereira *et al.* 2017). Even when space is limited for lateral tillering, stem elongation of bunch grasses allows a higher light interception, leading to a higher performance than for stoloniferous grasses (Scasta *et al.* 2015). This is mainly facilitated by partitioning of more photoassimilates to shoots in bunch grasses (Gomes *et al.* 2020).

Impact of bush clearing on tuft sizes of grasses

Grass tuft responses were explained largely by treatment and species interaction. At Kgomo-kgomo for example, the high tiller-producing grasses, *P. maximum* and *U. mosambicensis*, had larger tufts in cleared treatments, suggesting that an increase in basal tillering increased the tuft size, which may help rehabilitate bare areas (Pierce *et al.* 2019). Angassa (2002) reported similar findings. However, there were no differences in tuft sizes of *T. berteronianus* and *A. barbicollis* between treatments, despite higher tiller production in the cleared treatment, perhaps a consequence of both aerial and basal tillering, becaus the former does not contribute to an increase in tuft width. This implies that *T. berteronianus* and *A. barbicollis* are not reliable for increasing ground cover via vegetative growth of tufts, suggesting that land managers would need alternative restoration options, such as, for example, seeding with local adaptable species. Only the stoloniferous grasses increased in tuft sizes at Makapaanstad, despite their tillers being similar between cleared and uncleared treatments. Stolons radiate to long distances, with each stolon having multiple attachments on the ground from which shoots emerge (Da Silva *et al.* 2015). Thus, assigning all measurements taken from multiple ramet attachments to the main genet could explain why stoloniferous grasses had larger tufts. It is possible that some ramet attachments occurred in resource-rich patches, which is likely to have increased individual basal tiller sizes instead of tiller numbers.

Conclusions

Species' response to clearing in terms of tiller production varied with the species type, with clearing altering the tiller production of bunch but not stoloniferous grasses. However, leaf production of stoloniferous grasses increased despite tiller production not increasing in the cleared treatment. The increase in per plant biomass, more so for bunch grasses, signifies that bush clearing is important for increasing forage production in bush-encroached rangelands, through enhancement of plant performance, including increased tiller and leaf production. Thus, management following clearing should be directed towards promoting tillering, especially that leaf production increases linearly with tiller production.

Supplementary material

Supplementary material is available online.

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Data availability. The data used in this study will be made available on request and discussion with the corresponding author.

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