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Do soil nutrients mediate competition between grasses and *Acacia* saplings?

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Abstract

The structure and composition of savanna vegetation is influenced by resource availability and disturbance. Grasses, a major component of savanna systems, influence the tree-grass balance by competing with trees for light, water and soil nutrients as well as providing fuel for fires. Overgrazing, and the ensuing decreased grass competition and fire effects resulting from diminished grass vigor and cover, are thought to be major drivers of bush encroachment. To investigate impacts of competition from grass on saplings of *Acacia karroo* Hayne. and *Acacia nilotica* (L.) Willd. ex. Del. under high and low soil fertility, six grass species, *Aristida junciformis* (Trin & Rupr.), *Eragrostis capensis* (Thunb.) Trin., *Hyparrhenia hirta* Stapf., *Panicum maximum* Jacq., *Sporobolus africanus* (Poir.) Robyns & Tournay and *Themeda triandra* Forssk., were planted in pots with a tree sapling as the central test species. The major competitive effects experienced by tree saplings were dependent on nutrient level and the identity of the competing grass species ($P < 0.001$). Aboveground *A. karroo* was more strongly affected by grass competition under high nutrient conditions, whereas an increase in nutrient level had little effect on the competition between *A. nilotica* and the grasses ($P < 0.001$). *Acacia karroo* was also strongly affected by grass competition belowground; however, the opposite trend was observed for *A. nilotica* ($P < 0.001$). *Eragrostis capensis* was one of the most competitive grass species, reducing sapling aboveground biomass by 85% and 65% under high and low nutrient conditions, respectively, and sapling belowground biomass by 71% on average. Increasing nutrient availability resulted in an increase in competition exerted on *A. karroo* by all grasses but little to no change for *A. nilotica*. Changes in savanna composition and structure are thus likely to be influenced by grass species composition and soil nutrient status.

Introduction

The structure and composition of savanna systems is controlled by numerous interacting factors. Fire (Gibson and Hulbert 1987; Fynn *et al.* 2005), herbivory (Morris *et al.* 1992; Turner *et al.* 1993; Fuhlendorf and Smeins 1997; Kirkman 2002a,b) and soil fertility (Gibson and Hulbert 1987; Fynn and O'Connor 2005) all have a major effect on grass composition and productivity, which in turn is expected to affect tree growth rates and seedling

emergence (Chirara 2001; Riginos 2009). The level of influence that these factors have on the growth and survival of individual trees is largely dependent on tree size, with small trees generally being more susceptible than larger trees (Sankaran *et al.* 2004; Riginos 2009). Grasses compete directly with trees for light, water and nutrients, and indirectly by providing fuel, which affects the frequency and intensity of fires (Scholes and Archer 1997). Competition for aboveground resources, such as light, is generally asymmetric with large plants having a

disproportionately large competitive effect (Weiner and Damgaard 2006), while competition for belowground resources, such as water and nutrients, tends to be more symmetric (Messier *et al.* 2009). Chirara (2001) observed that high levels of shading from the grass sward decreased overall sapling biomass while concurrently altering sapling biomass allocation in favor of larger leaves and decreased root biomass. This not only resulted in smaller saplings but also decreased sapling competitive ability belowground (Chirara 2001). In a water limited environment those species with shallow root systems, such as grasses, are able to monopolize rainwater and shallow groundwater, while those with deeper root systems such as trees, are able to use deep groundwater resources, as predicted by Walter's two-layer hypothesis (Walter 1971).

In addition to competition for water and light, trees compete with grasses for nutrients. In both pot and field trials, additional nutrients resulted in increased grass growth suppressing both *Acacia mellifera* seed germination and seedling survival (Kraaij and Ward 2006). This suppressive effect is also observed in larger trees, with trees as tall as 4 m showing significant increases in both height and stem diameter with the removal of the surrounding grass (Riginos 2009). Similar trends were observed by Stuart-Hill and Tainton (1989) who found that browse production increased up to 166% with the removal of the surrounding grass. As many savanna tree species are members of the legume family and have the ability to fix atmospheric nitrogen it is expected that grasses may benefit more from additional nutrients than leguminous trees would. This corresponds with the findings of Kraaij and Ward (2006), while Mopipi (2005) suggests that soil moisture, rather than nutrients, may be a limiting factor during the sapling stage as trees interact within the same soil layer as the grass and thus will compete directly for moisture resources. While these studies confirm that grasses exert a competitive effect on trees it is not known if this effect is consistent for all grass species or varies according to size, structure, ecological status and other factors affecting grass vigor and potential competitive effect. These factors may have important implications for grassland management to achieve and/or maintain certain sward species composition.

Overgrazing and selective grazing may result in replacement of palatable perennial grasses with unpalatable perennial and annual grasses (Morris *et al.* 1992; Anderson and Briske 1995; Ash *et al.* 2011), which may also be less competitive than the grasses that they replaced (Fynn *et al.* 2011). Overgrazing and the ensuing decreased grass competition, resulting from diminished grass vigor and cover, as well as conversion of grassland from climax grass domination to domination by less competitive perennial and annual grasses (Morris *et al.* 1992; Anderson and Briske 1995; Ash *et al.* 2011), are likely to be

major drivers of bush encroachment. Accordingly grass-tree competition has become an important area of research focus (Scholes and Archer 1997).

Approximately half the *Acacia* species in South Africa (Smit 1999) are listed by the Conservation of Agricultural Resources Act, No.43 of 1983, as declared indicators of bush encroachment. Both *Acacia nilotica* (L.) Willd. ex. Del. and *Acacia karroo* Hayne. are included on this list and are regarded as species with high potential to rapidly increase in density (Smit 1999). *Acacia karroo* grows in a wide variety of habitats from river banks to bushveld, dry thornveld, grassland and coastal dunes (Davidson and Jeppe 1981). It occurs on most soil types but is usually associated with high fertility clay and loam soils (Smit 1999). Additional nitrogen does not appear to increase the growth rate of *A. karroo*, indicating that it is a good competitor for nutrients and uses nitrogen effectively (Boyes *et al.* 2010). *Acacia nilotica* is fairly shade tolerant, although stem length increases at a greater rate under low light conditions and thus may exhibit some level of shade avoidance (Gunton *et al.* 2010; Tsvuura *et al.* 2010). *Acacia nilotica* is a fairly common species in the thornveld, woodland and dry river valleys of southern Africa (Ross 1971; Davidson and Jeppe 1981; Acocks 1988). It is generally found on heavy soils with high clay content, although it may also occur on sodic soils. Along the coastline it has shown preference for sandy and alluvial soils (Smit 1999). The species grows best in direct sunlight, although some shading during the seedling stage may improve survival (Chaudhry *et al.* 2004). As both these species are considered to have invasive potential it is important to understand their behavior under different nutrient conditions and grass competition.

In this study we aimed to determine the following: (i) The effect of soil nutrient level on above- and belowground biomass accumulation *A. karroo* and *A. nilotica* saplings, (ii) The effect of competing grass species on the above- and belowground biomass of *A. karroo* and *A. nilotica* saplings; and (iii) The effect of the interaction between nutrient level and competing grass species on tree sapling biomass.

Our hypotheses were that: (i) *A. karroo* would perform better than *A. nilotica* in high nutrient treatments and *vice versa* in low nutrient treatments; (ii) Grass species would differ in their competitive ability in high and low nutrient treatments.

Materials and methods

Study site and experiment

The experiment was run from October 2005 to April 2006 at the University of KwaZulu-Natal's (UKZN)

Arboretum in Pietermaritzburg, KwaZulu-Natal (KZN), South Africa. The region experiences hot summers and mild winters with a mean monthly maximum of 26.4°C in February and minimum of 8.8°C in July. The experimental design was similar to the target technique described by McPhee and Aarsen (2001). Combinations of grass and tree species were planted in pots made from 50-cm lengths of PVC piping with a diameter of 15 cm (8839 cm³). The base of each of these tubes was covered with a square of 80% shade cloth secured with wire and the tubes were then filled with coarse, nutrient-poor sand. A sapling of either *Acacia karroo* Hayne. or *A. nilotica* (L.) Willd. ex. Del. (established in the UKZN greenhouses from seed collected locally) was planted as the central test species (phytometer) and four grass seedlings (established in the UKZN greenhouses from seed collected locally) of a single species were planted around it. The grass species used were *Themeda triandra* Forssk., *Eragrostis capensis* Trin., *Hyparrhenia hirta* Stapf, *Aristida junciformis* Trin. & Rupr., *Sporobolus africanus* (Poir.) Robyns & Tournay and *Panicum maximum* Jacq. These six grass species were selected because they are dominant at different soil depths and respond differently under different levels of grazing pressure (Tainton *et al.* 1976; van Oudtshoorn 2002). In addition, they vary in structure, with differing leaf heights and tillering ability, varying from short plants with small leaves, which form dense tufts (e.g., *Eragrostis capensis*) to tall plants with relatively few tillers but large leaves (e.g., *Hyparrhenia hirta*) (Tainton *et al.* 1976; van Oudtshoorn 2002; Fynn *et al.* 2009). Characteristics of these species are described in Table 1. Tree saplings and grasses were also planted alone to provide a control measure of growth without competition. Tree saplings were 80–150 mm tall at the time of planting, while grass seedlings were 40–65 mm tall. Each of the combinations of tree and grass species was subjected to both high and low soil nutrient additions. The high fertility treatment was watered with 300 mL of 80% Hoagland's nutrient solution ($n = 172$, $P = 25$, $K = 188 \text{ mg L}^{-1}$) (Hoagland and Arnon 1950 in Cabrera *et al.* 1995) every 4 days while the low fertility treatment was given no additional nutrients. The pots were irrigated with municipal water daily to ensure that water did not limit sapling growth. The experiment was a full factorial design, including all possible combinations of tree species (2), grass species (6) and nutrient level (2), and pots were laid out in a completely randomized arrangement with six replications of each treatment combination. Plants were harvested after 26 weeks of growth by soaking the pots in water for several minutes to loosen the sand and then removing the plants with the root material attached. Any remaining sand was washed off the roots and the tree roots were separated from the grass root mass. The above- and belowground material for both

trees and grasses was separated and dried for 48 h at 60°C before weighing to determine the final dry biomass.

Data analysis

Relative interaction indices (RII) were calculated for both aboveground and belowground biomass of each species within each combination and treatment in order to determine the level of competition exerted on each species within each treatment (Armas *et al.* 2004). RII is a ratio representing the net loss or gain of a measurable trait, generally biomass, as a result of inter-specific interaction relative to the value of that trait when this inter-specific interaction is absent. The values of this ratio range from -1 to 1, with negative values indicating competition, zero indicating symmetry and positive values indicating facilitation. RII is calculated as follows:

$$\text{RII} = (B_W - B_O) / (B_W + B_O)$$

where B_W is the biomass of plants growing with inter-specific interaction and B_O is the biomass of plants growing without inter-specific interaction (Armas *et al.* 2004).

As the data were normally distributed, a three-way ANOVA was used to assess the effects of tree species, grass species, nutrient level and their interaction, on RII based on: (i) aboveground (leaf and stem) biomass; and (ii) belowground (root) biomass. Plants that died were indicated as missing data in the ANOVA thus altering the degrees of freedom. When the ANOVA (F -test) revealed significant differences, a Tukey's test was used to separate means ($\alpha = 0.05$).

Results

Tree species, competing grass species and nutrient level had a significant effect on both above- and belowground tree biomass ($P < 0.05$) (Table 2). In addition, there was a strong tree species by nutrient level interaction both above- and belowground and a strong grass species by nutrient level interaction aboveground (Table 2).

Nutrient level had little effect on the growth of *A. nilotica*, resulting in a similar mean aboveground and belowground biomass under both high and low nutrient conditions (Table 3). In addition, nutrient availability had little effect on the magnitude of either the above- or belowground competition experienced by *A. nilotica*, with competing grasses reducing sapling aboveground biomass by 68% and 79%, and belowground biomass by 40% and 48%, under high and low nutrient conditions, respectively (Table 3, Figure 1). By contrast, under high nutrients *A. karroo* saplings had substantially greater biomass (Table 3) and experienced greater competition from the surrounding grasses (above and belowground) (Figure 1).

Table 1 Characteristics of competing grass species (van Oudtshoorn 2002)

Species		Tillers	Height (mm)	Leaf blade length (mm)	Leaf blade width (mm)	Soil	Grazing value†	Successional stage
<i>Panicum maximum</i>	Perennial	Few	600–2000	60–400	4–20	Fertile	High	Sub-climax to Climax
<i>Themeda triandra</i>	Perennial	Average	300–1500	150–300	1–8	All but prefers clay	High	Climax
<i>Hyparrhenia hirta</i>	Perennial	Few	300–1500	20–150	1–4	Well drained	Average	Sub-climax to Climax
<i>Eragrostis capensis</i>	Perennial	Many	200–900	70–350	2–5	Sand, loam or clay	Average	Sub-climax
<i>Aristida junciformis</i>	Perennial	Many	200–750	Up to 300	Up to 3	All soil types	Low	Climax
<i>Sporobolus africanus</i>	Perennial	Average	280–1500	200–400	1–4	All, prefers disturbed places	Low	Sub-climax

†The quantity and quality of material produced for grazing.

Table 2 Analysis of variance of the relative interaction index (RII) for aboveground biomass and belowground biomass

Source of variation	df	Aboveground		Belowground	
		F-ratio	P-value	F-ratio	P-value
Tree (T)	1	7.870	0.006	6.930	0.010
Grass (G)	5	5.020	< 0.001	4.100	0.002
Nutrient level (N)	1	93.990	< 0.001	26.170	< 0.001
T × G	5	1.030	0.402	0.810	0.548
T × N	1	51.990	< 0.001	42.180	< 0.001
G × N	5	2.800	0.020	1.610	0.163
T × G × N	5	0.470	0.798	1.420	0.224
Residual	108				
Total	131				

df, degrees of freedom. Significant effects ($P < 0.05$) in bold.

Plants that died were indicated as missing data in the ANOVA thus altering the degrees of freedom.

Under high nutrient conditions competing grasses reduced sapling aboveground biomass by 83% and belowground biomass by 79%, respectively, while under low nutrients, aboveground biomass remained unchanged and belowground biomass was reduced by only 28% (Table 3). Overall *A. karroo* was most strongly affected by grass competition under high nutrient conditions, while increased nutrient levels had little effect on the competition experienced by *A. nilotica* (Figure 1).

Additional nutrients significantly increased ($P < 0.05$) the magnitude of the aboveground competitive effect of all grass species except for *Aristida junciformis* and *Eragrostis capensis* (Figure 2). *Eragrostis capensis* exerted significantly more aboveground competition than *A. junciformis* under high nutrient conditions (Figure 2), reducing sapling aboveground biomass by 85% as opposed

to 37% (Table 3), and *P. maximum* and *S. africanus* under low nutrient conditions (Figure 2), reducing sapling aboveground biomass by 65% as opposed to 49% and 43%, respectively, (Table 3). Interestingly, under high nutrient conditions the aboveground biomass of *E. capensis* and *T. triandra* increased by 10% and 28%, respectively, when growing with a tree sapling compared to the grasses growing alone. Conversely, when growing with a sapling under low nutrient conditions *H. hirta* aboveground biomass increased by 9% (Table 4). Belowground, *E. capensis* was significantly more competitive than *P. maximum* and *T. triandra* (Figure 2), reducing sapling belowground biomass by 71% as opposed to 54% and 39%, respectively (Table 3).

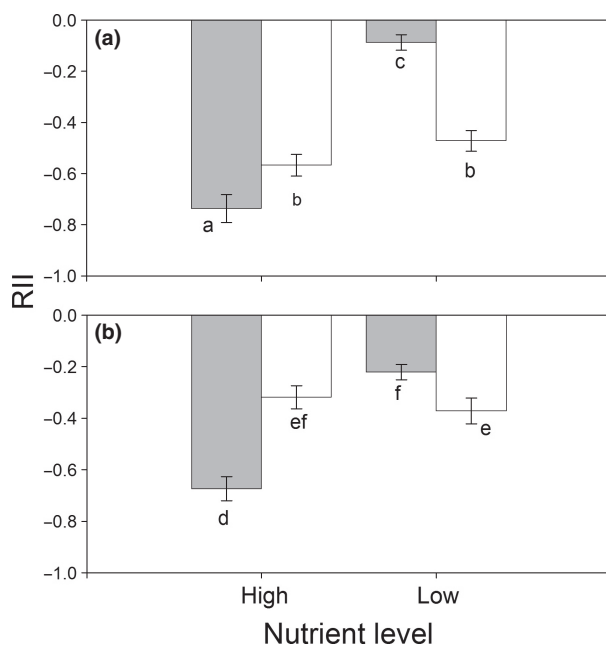
Discussion

The addition of a nutrient mixture substantially increased not only the biomass of *A. karroo* growing alone but also the competitive effect exerted by the surrounding grasses on this species, while having no effect on the biomass of or the competitive response of *A. nilotica*. This considerable effect of increased nutrient availability explains why *A. karroo* tends to occur in productive riverine habitats where light is often limited, and where it is advantageous to efficiently use available nutrients in order to grow quickly and avoid shading (Gunton *et al.* 2010). By contrast, *A. nilotica* grew better under low nutrients as the species favors unproductive, shallow soils where nutrients are limited, resulting in a slower growth rate and less efficient utilization of available nutrients (Venter and Venter 2002).

Our hypothesis that the six competing grass species would differ in their competitive ability in high and low nutrient treatments was supported. *Aristida junciformis*

Table 3 Mean aboveground and belowground dry biomass (g, \pm SE) of *Acacia karroo* and *Acacia nilotica* under high and low nutrient conditions growing alone and with *Aristida junciformis*, *Eragrostis capensis*, *Hyparrhenia hirta*, *Panicum maximum*, *Sporobolus africanus* and *Themeda triandra*

Item	<i>Acacia karroo</i>			<i>Acacia nilotica</i>		
	High nutrients	Low nutrients	Mean	High nutrients	Low nutrients	Mean
Aboveground biomass						
Control	12.6 \pm 4.17	1.1 \pm 0.36	6.9 \pm 2.64	4.4 \pm 2.36	5.2 \pm 0.94	3.5 \pm 1.24
<i>Panicum maximum</i>	2.0 \pm 0.17	1.3 \pm 1.29	1.7 \pm 0.35	1.9 \pm 0.23	1.8 \pm 0.60	1.8 \pm 0.34
<i>Themeda triandra</i>	2.0 \pm 0.48	1.5 \pm 0.36	1.8 \pm 0.32	1.1 \pm 0.04	1.0 \pm 0.04	1.0 \pm 0.06
<i>Hyparrhenia hirta</i>	2.3 \pm 0.31	1.0 \pm 0.26	1.6 \pm 0.29	0.7 \pm 0.44	0.7 \pm 0.40	0.7 \pm 0.09
<i>Eragrostis capensis</i>	0.8 \pm 0.12	0.6 \pm 0.12	0.7 \pm 0.09	1.0 \pm 0.20	0.6 \pm 0.12	0.8 \pm 0.12
<i>Aristida junciformis</i>	3.2 \pm 0.52	1.1 \pm 0.50	2.2 \pm 0.46	3.1 \pm 1.86	0.9 \pm 0.20	1.8 \pm 0.74
<i>Sporobolus africanus</i>	2.2 \pm 1.29	1.3 \pm 0.28	1.7 \pm 0.64	0.8 \pm 0.21	1.4 \pm 0.31	1.1 \pm 0.21
Belowground biomass						
Control	18.7 \pm 4.16	4.0 \pm 0.94	11.4 \pm 3.00	5.0 \pm 0.90	5.2 \pm 0.65	5.1 \pm 0.53
<i>Panicum maximum</i>	6.1 \pm 0.42	3.6 \pm 0.63	4.9 \pm 0.82	3.1 \pm 0.67	4.8 \pm 1.54	4.0 \pm 0.84
<i>Themeda triandra</i>	3.2 \pm 0.75	3.5 \pm 0.65	3.3 \pm 0.16	4.1 \pm 0.47	2.4 \pm 0.40	3.2 \pm 0.29
<i>Hyparrhenia hirta</i>	3.7 \pm 0.55	2.4 \pm 0.33	3.0 \pm 0.37	2.8 \pm 0.44	2.4 \pm 0.40	2.6 \pm 0.29
<i>Eragrostis capensis</i>	1.9 \pm 0.46	2.0 \pm 0.65	2.0 \pm 0.39	2.5 \pm 0.43	1.6 \pm 0.32	2.1 \pm 0.29
<i>Aristida junciformis</i>	4.8 \pm 0.70	2.6 \pm 0.65	3.7 \pm 0.57	4.4 \pm 2.51	2.4 \pm 0.50	3.2 \pm 0.95
<i>Sporobolus africanus</i>	3.7 \pm 1.56	3.2 \pm 0.65	3.4 \pm 0.81	1.1 \pm 0.13	2.6 \pm 0.61	1.9 \pm 0.40

**Figure 1** Mean (\pm SE) relative interaction index (RII) based on final biomass for *Acacia karroo* (grey) and *Acacia nilotica* (open) for (a) aboveground biomass ($F_{1,108} = 51.99$, $P < 0.001$) and (b) belowground biomass ($F_{1,109} = 42.18$, $P < 0.001$) for high and low nutrient levels, averaged across all competing grass species. Treatments with letters in common are not different ($P > 0.05$).

was the least competitive grass under increased nutrient conditions, while under low nutrient conditions *S. africanus* and *P. maximum* were also found to have a

low competitive effect on sapling biomass. *Eragrostis capensis* was one of the most competitive species, regardless of nutrient availability. In terms of belowground competition, *P. maximum* and *T. triandra*, were also found to be less competitive than *E. capensis*. While our experiment was not designed to specifically examine the relation between competitive effect and ecological status (i.e. purported grazing response), the competitive effect exhibited by the selected species suggest that competitiveness under a given nutrient regime does not appear to be consistently related to ecological status. However, a larger dataset would be required to examine this relationship further and to establish whether poor-condition grasslands exert less competition on trees than good quality swards.

Similar observations emphasizing the importance of nutrient availability in competitive interactions have been made by Fynn *et al.* (2011) who found that *E. capensis* was a strong competitor in a low nutrient situation and *P. maximum* a poor competitor, while *P. maximum* became more competitive under high nutrients (110% solution compared with our 80% solution). Similarly, Fynn and O'Connor (2005) observed that *P. maximum* can only invade fertile habitats with high levels of both nitrogen and phosphorus. During harvesting in the present experiment, *E. capensis* was observed to have fine, hair-like roots, while *P. maximum* was observed to have much thicker, more robust roots, which may affect the intensity of belowground competition for nutrients on nutrient limited soils as the greater surface area provided by the fine roots allows for increased nutrient uptake. In

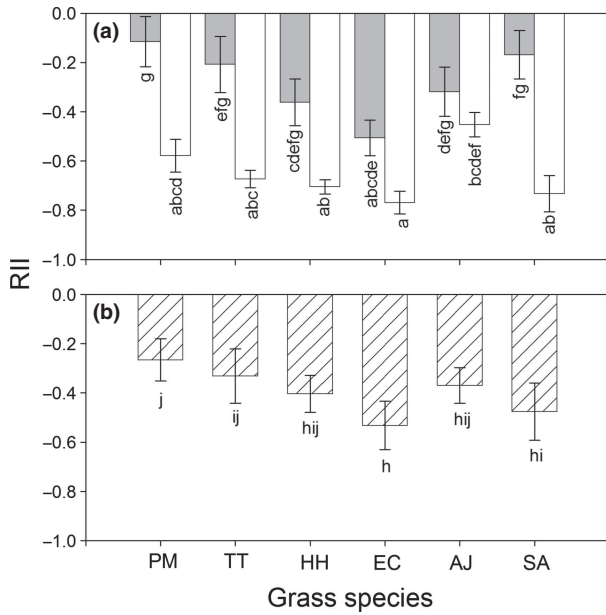


Figure 2 Mean (\pm SE) relative interaction index (RII) based on final dry biomass (a) for low (grey) and high (open) nutrient levels for aboveground ($F_{5,108} = 2.8, P = 0.020$) and (b) as a mean of high and low nutrient levels for belowground ($F_{5,109} = 4.10, P = 0.002$) dry biomass for both tree species together. Treatments with letters in common are not different ($P > 0.05$). Species are as follows: AJ, *Aristida junceiformis*; EC, *Eragrostis capensis*; HH, *Hyparrhenia hirta*; PM, *Panicum maximum*; SA, *Sporobolus africanus*; TT, *Themeda triandra*.

addition, *E. capensis* is a medium height species, ranging from 20 cm to 90 cm in height (van Oudtshoorn 2002; Fynn *et al.* 2009). The tillers of this species grow directly upright and form fairly dense shady tufts (May *et al.* 2009). This, coupled with the species tendency to increase aboveground biomass when experiencing competition, could account for the intense aboveground competition observed. Similar tendencies were observed by *T. triandra*, another medium height, leafy species.

These findings have implications for rangeland management in terms of the effect of grazing on grass composition, sward productivity and the ability of the grass sward to withstand woody plant invasion. It has been previously demonstrated that intensive grazing leads to both short-term changes in root biomass (Milchunas and Lauenroth 1989; Rodríguez *et al.* 1996) and long-term changes in sward species composition (O'Connor 1985 in O'Connor 1996). Similar examples of replacement of competitive by less competitive grasses exist in North America (Anderson and Briske 1995) suggesting that changes in composition to less productive or less competitive species under injudicious grazing management may be a fairly general occurrence. Thus, these compositional changes under grazing may facilitate tree seedling and sapling growth rates, allowing incur-

Table 4 Mean aboveground and belowground dry biomass ($g, \pm SE$) of the six competing grasses under high and low nutrient conditions growing alone and with *Acacia karroo* and *Acacia nilotica*

Item	Control			<i>Acacia karroo</i>			<i>Acacia nilotica</i>		
	High nutrients	Low nutrients	Mean	High nutrients	Low nutrients	Mean	High nutrients	Low nutrients	Mean
Aboveground biomass									
<i>Panicum maximum</i>	43.7 \pm 8.39	30.7 \pm 11.06	37.2 \pm 6.90	33.1 \pm 8.49	5.6 \pm 1.32	19.4 \pm 5.83	49.3 \pm 7.35	24.5 \pm 7.40	36.9 \pm 6.22
<i>Themeda triandra</i>	20.3 \pm 6.87	4.6 \pm 1.76	12.4 \pm 4.13	23.3 \pm 3.88	6.3 \pm 1.91	15.6 \pm 3.48	28.7 \pm 4.36	3.6 \pm 0.64	15.0 \pm 4.45
<i>Hyparrhenia hirta</i>	95.4 \pm 7.30	50.3 \pm 10.80	72.8 \pm 9.21	65.0 \pm 10.26	62.3 \pm 23.92	64.0 \pm 12.82	87.1 \pm 18.33	51.5 \pm 13.58	67.7 \pm 11.96
<i>Eragrostis capensis</i>	33.2 \pm 7.12	13.8 \pm 1.51	23.5 \pm 4.54	39.9 \pm 1.50	10.0 \pm 2.57	26.3 \pm 4.93	43.8 \pm 7.21	8.3 \pm 1.03	24.4 \pm 6.55
<i>Aristida junceiformis</i>	19.9 \pm 1.06	4.4 \pm 1.06	12.0 \pm 2.37	14.8 \pm 1.56	4.2 \pm 0.82	9.5 \pm 1.80	11.0 \pm 7.07	5.1 \pm 1.50	11.4 \pm 3.29
<i>Sporobolus africanus</i>	46.1 \pm 3.35	8.2 \pm 1.31	27.1 \pm 5.96	36.0 \pm 3.97	7.8 \pm 1.24	20.6 \pm 4.86	45.2 \pm 2.36	7.7 \pm 0.67	24.8 \pm 6.01
Belowground biomass									
<i>Panicum maximum</i>	84.4 \pm 5.08	44.0 \pm 3.16	27.0 \pm 5.03	59.3 \pm 10.16	11.1 \pm 1.22	15.8 \pm 5.79	97.1 \pm 15.38	36.4 \pm 3.93	29.9 \pm 9.30
<i>Themeda triandra</i>	7.8 \pm 2.07	5.7 \pm 1.90	6.7 \pm 1.38	11.9 \pm 5.65	7.1 \pm 2.09	9.7 \pm 3.20	20.1 \pm 6.28	4.9 \pm 1.71	11.8 \pm 3.89
<i>Hyparrhenia hirta</i>	19.0 \pm 2.35	8.8 \pm 1.21	13.9 \pm 1.99	19.6 \pm 6.52	11.0 \pm 2.30	14.9 \pm 3.32	19.0 \pm 4.26	11.7 \pm 1.29	15.3 \pm 2.49
<i>Eragrostis capensis</i>	16.3 \pm 5.36	17.8 \pm 2.85	17.0 \pm 2.90	18.2 \pm 4.04	13.0 \pm 1.67	15.8 \pm 2.39	23.0 \pm 5.41	14.8 \pm 2.71	18.5 \pm 3.00
<i>Aristida junceiformis</i>	29.5 \pm 4.20	6.0 \pm 1.39	17.1 \pm 3.96	12.0 \pm 2.43	5.5 \pm 1.01	8.8 \pm 1.59	7.6 \pm 3.11	4.8 \pm 0.95	8.7 \pm 2.23
<i>Sporobolus africanus</i>	39.5 \pm 7.00	6.2 \pm 1.0	22.9 \pm 6.09	35.5 \pm 7.04	8.2 \pm 1.03	26.6 \pm 5.43	50.0 \pm 13.64	7.1 \pm 1.20	26.6 \pm 8.93

sions of trees into grassland, as has been observed in intensely used and degraded regions of Swaziland, for example (Roques *et al.* 2001). Rainfall and topography may further exacerbate the problem of bush encroachment. Low rainfall will result in an associated decrease in grass biomass production while sloped areas, which are more prone to soil erosion, are also more likely to experience grazing-induced composition changes (Fynn and O'Connor 2000). At very low rainfall, however, trees are unable to attain high cover in grassland (Sankaran *et al.* 2004).

Conclusion

Although overgrazing is considered to reduce the competitive effects of the grass sward on woody species, thereby facilitating woody invasion of grassland, these effects were not consistently related to ecological status. Grass competitive resistance to woody invasion may rather depend on whether the compositional change was towards a fast, growing or slow-growing guild of grasses (e.g. Fynn *et al.* 2011). The effects of woody species invasion may be modified by soil fertility and woody species identity. *Acacia karroo* is more likely to invade degraded regions with nutrient rich soils as our results showed that it has a rapid growth rate under increased nutrient conditions and is able to grow more rapidly in combination with species characteristic of degraded grassland. A reduction of competition intensity allows *A. karroo* to make optimum use of the substantial supply of nutrients available and is therefore likely to invade grassland more easily. Conversely, *A. nilotica* is more likely to invade less fertile areas as it was more responsive than *A. karroo* in the low nutrient treatment, despite both these species being capable of producing nitrogen-fixing nodules (Cramer *et al.* 2007). It is therefore likely to invade regions on nutrient-poor or shallow unproductive soils than fertile productive habitats. As grass species identity and thus sward species composition plays an important role in impeding woody establishment and restricting sapling size, thus increasing their vulnerability to fire, further research is needed to determine grass traits that provide the most resistance to tree invasion.

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