



Competition between co-dominant plants of the Serengeti plains depends on competitor identity, water, and urine

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Abstract

Kyllinga nervosa (Steud.) and *Sporobolus kentrophyllus* (K. Schum.) are co-dominant plants of the Serengeti short-grass plains, Tanzania. The plains are characterized by seasonal and sporadic rainfall and currently support in excess of 1.5 million migratory ungulates. The interactive effect of simulated bovine urine and water availability were tested on the competitive interactions of these species in the laboratory.

Sporobolus kentrophyllus was a superior competitor to *K. nervosa* over the tested treatment levels with respect to growth and reproductive effort. *Sporobolus kentrophyllus* exhibited rapid growth in response to urine addition, leading to a significant species \times urine interaction while reduced growth by *K. nervosa* in response to low water availability explained the significant species \times water interaction and is likely explained by *K. nervosa*'s shallow root system. *Kyllinga nervosa*, however, appears to be more tolerant of low nitrogen conditions based on its similar growth with and without the urine treatment. The effect of intraspecific competition on total biomass was similar for *S. kentrophyllus* and *K. nervosa*. Competition resulted in increased size differences (asymmetry) for *K. nervosa* and for the interspecific competition treatments compared to the size differences observed for plants grown individually (in absence of competition).

Total reproductive biomass was reduced most by competition with *S. kentrophyllus*, irrespective of target species. The water treatment did not influence reproduction while the urine treatment significantly increased reproductive biomass and interacted with target species, competitor species, and yielded a three-way urine \times target \times competitor species interaction.

Results suggest that codominance of these two species in the Serengeti is regulated by water availability, nitrogen input from grazers, and local neighbor identity.

Introduction

Membership in a community, or the lack thereof, is regulated by many factors (Harper 1977; Hutchinson 1959; MacArthur and Wilson 1967). Our assessment of the importance of many of these factors is complicated by their ability to potentially interact. The Serengeti plant community is a well studied system that is susceptible to multiple interacting factors, including drought, urine deposition, grazing, and physical disturbance by hundreds of thousands of migrating ungulates (McNaughton 1983). This paper discusses a

laboratory experiment investigating how water availability and simulated bovine urine deposition interact to influence competition between two dominant plants of the Serengeti short-grass plains.

Plants in general and, in particular, those of grasslands, respond to urea–nitrogen addition by increasing growth and tissue nitrogen concentration (Day and Detling 1990; Jobin and Keough 1979; Thomas et al. 1986). Day and Detling (1990), for instance, found that patches with urine addition had stimulated plant growth, were grazed more heavily, provided more forage to ungulates, and had greater plant leaf nitro-

gen concentrations than control patches. They also suggested that plant competition was increased by ungulate urine deposition due to changes in plant nutrient status and growth, but that this was not explicitly tested (Day and Detling 1990). In the Serengeti, recent evidence of nutrient cycling 'hot spots' suggests a similar positive feedback in operation, controlled by resident herbivores (McNaughton et al. 1997).

Grazing and nitrogen addition have been shown to interactively influence competition between *Digitaria macroblephara* and *Sporobolus ioclados* in the Serengeti (Banyikwa 1988). Banyikwa (1988) found that productivity was reduced most by simulated grazing and that plants that received simulated defoliation were less responsive to nutrient addition than ungrazed plants. This study also found that grazing decreased the intensity of competition between these species by 17% relative to ungrazed competition treatments.

The response of plants to fertilization is coupled to water availability, a factor that is limiting in the Serengeti (McNaughton 1983) and, specifically, for the dryland sedge *Kyllinga nervosa* (McNaughton et al. 1983; Coughenour et al. 1985a). The interaction between fertilization and water stress may decrease leaf water potential (increase water stress) and ultimately, plant growth (Schulze and Hall 1982; Williams 1992). Serengeti plants that receive urine in the absence of sufficient water, however, may not respond or may even die (Banyikwa, personal communication). The interactive effects of water and urine application, therefore, and the differences in response among species, is likely to be an important determinant of plant species composition.

Methods

Two dominant species (the grass, *Sporobolus kentrophyllus*, and the dryland sedge, *Kyllinga nervosa*) of the Serengeti short-grass plains, Tanzania, were tested for the interactive effects of intra- and interspecific competition, water availability, and the addition of simulated bovine urine. The Serengeti ecosystem (1°15' S to 3°30' S and 34° to 37° E) occupies a region of approximately 25000 km². These two co-dominant species of the short-grass plains region are perennial and highly resistant to heavy grazing (McNaughton 1983). *Kyllinga nervosa*, in particular, has been shown to maximize net above-ground biomass production when clipped daily to a height of 4 cm (McNaughton 1979). *Sporobolus kentrophyllus* is a

fast growing plant that is readily propagated through the production of abundant stolons.

Plants were collected in 1977 and maintained through clonal propagation in a greenhouse in Syracuse NY, USA (43°02' N, 76°08' W). These two species differ greatly in their morphology and reproductive ecology. *Sporobolus kentrophyllus* is a stoloniferous grass while *K. nervosa* has a bunch-form, does not produce stolons and readily flowers (Hartvigsen 1995). Both species have the C4 photosynthetic pathway (McNaughton 1983). Reference to reproductive biomass for these two species, therefore, is represented by stolons in *S. kentrophyllus* and inflorescences in *K. nervosa*.

Prior to the initiation of the experiment plants were propagated in the greenhouse at Syracuse University. Individual plants for this experiment were divided from larger individuals. Each individual was clipped to 5 cm and weighed before planting in the experimental pots.

Individual plants of the target species (*S. kentrophyllus* and *K. nervosa*) were tested against three levels of competitor (none or single individuals of either *S. kentrophyllus* or *K. nervosa*), two levels of water (25 ml and 50 ml day⁻¹), and two levels of simulated bovine urine (present and absent) (Day and Detling 1990, following Stillwell 1983). Therefore, pots contained either one or two plants each. Plants were grown in 50 cm tall, 10.2 cm diameter, 4.2 L cylindrical pots filled with calcined clay. All treatments had three replicates each. Watering rates were similar to either mean daily field rainfall or twice this value, or equivalent to 3.1 and 6.2 mm rain day⁻¹ for a simulated 56-day growing season, or about 175 mm and 350 mm total simulated rainfall over the duration of the experiment, respectively. Sinclair (1979) reported an average of 500 mm of rainfall during the November–May wet season for the area where these plants were collected, though rainfall through this period is highly variable. Therefore, the low watering rate approximated average conditions while the higher level approximated a wet year. Accounting for the likely differences between evapotranspiration rates and water availability in the calcined clay medium, however, remains problematic. Water run-through did not occur.

115 ml simulated bovine was applied to half the treatment pots once after a two-week acclimation period, which delivered 40 g N m⁻² (Day and Detling 1990). An equal amount of H₂O was applied to control pots. In addition, all pots received a com-

plete Hoagland's nutrient solution, which included 0.66 g N m^{-2} in 25 ml H_2O , weekly. Baseline total nitrogen added in nutrient solution, therefore, was about 5.25 g N m^{-2} over eight weeks.

Plants were clipped at weeks 0, 2, 4, and 6 to a height of 5 cm, simulating biweekly herbivory. Plants in the short grass plains rarely escape herbivory and generally are grazed to less than 5 cm in height throughout the growing season (McNaughton 1984). Banyikwa (1988) showed that simulated grazing in the laboratory does affect plant competitive interactions but, since plants in the short-grass plains do not avoid grazing, competitive interactions under conditions that appear to be more variable in the field, were investigated.

The 50 cm tall pots were used to allow ample room for root exploration for nutrients and water. Day length was set at 12 h with temperatures ranging between 14°C at night and 30°C at mid-day using a sigmoidal curve for hourly temperature and light changes in a growth chamber (Convicon E15, Controlled Environments Ltd., Winnipeg, Manitoba) at Syracuse University, Syracuse, NY. Mean mid-day photosynthetically active radiation (PAR) for six evenly distributed locations within the chamber was $650 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Due to spatial variance of light within the chamber, pots were randomly moved each week. Plants were harvested eight weeks after urine application, divided into reproductive structures (stolons for *Sporobolus kentrophyllus* and inflorescences for *Kyllinga nervosa*), leaves, stems, crowns, and roots. Comparisons are discussed only for reproductive allocation and whole plant biomass. Plants were dried at 60°C for 48 h, and weighed to 0.1 mg. Clipped tissues were separated into leaf and reproductive structures and added to harvested material.

Pre-dawn leaf water potentials were measured prior to the final harvest using a pressure bomb. Water potentials were tested for only one, randomly chosen plant from each of the intraspecific competition pots; otherwise, all remaining plants were tested and used in the analysis.

To determine whether treatment effects were present at the beginning of the experiment plants were weighed before planting. Analysis of variance of fresh biomass at the beginning of the experiment revealed no significant treatment effects, both across and within treatments.

Analyses

Analyses were done using plant biomass at the end of the experiment combined with all removed tissues collected during the experiment. Competitive outcome was based on three measures of plant performance. The natural logarithm of absolute biomass in response to the four factors—target species, competitor, water, and simulated bovine urine using analysis of variance (ANOVA) were tested first. The occurrence of competition would be supported by a significant 'competitor' main effect, as well as its interaction with any other factor. Total plant biomass per pot was also tested with five treatment levels: *K. nervosa* and *S. kentrophyllus* grown alone, each in intraspecific competition, and the single interspecific competition mixture. Since *S. kentrophyllus* always produced more reproductive biomass (i.e., stolons in contrast to inflorescences of *K. nervosa*), only mean differences were considered when reproductive biomass was associated with competitor identity or water or urine treatments.

Two indices were also used to determine relative plant performance. These are response to competition (*RC*) and asymmetry (*A*). *RC* is the proportionate reduction in total, accumulated biomass for plants grown in competition, relative to how well they performed when grown alone. *RC* is calculated as $RC_i = 1 - B_{ij}/B_i$ where RC_i is response to competition for species *i*, B_{ij} is the biomass of *i* when competing with *j*, and B_i is the biomass of *i* when grown alone. This index generally ranges between 0 and 1, with higher values indicating a greater reduction in biomass when competing as compared to when grown alone. Negative values indicate facilitation. Although extreme negative values can occur in such indices, suggesting caution when interpreting such an index (Markham and Chanway 1996), this was not observed. *RC* was tested for four target species treatment levels (*K. nervosa* and *S. kentrophyllus* grown in intraspecific and interspecific competition tests), and both water and urine treatments.

Plant size asymmetry (*A*) was used to evaluate changes between competitors when grown alone in controls and when grown in competition. This index differs from *RC* by estimating the relative effect of competition between competitors, irrespective of the absolute effect of competition. Asymmetry is calculated as $A_{\text{trmt}} = 1 - B_{\text{small}}/B_{\text{big}}$ for the four treatment (trmt) levels: plants grown alone (A_{alone}), in monoculture (A_{Kyllinga} and $A_{\text{Sporobolus}}$, or in mixtures (A_{mixed}) for each of the four nutrient and water levels tested.

A_{alone} represents interspecific asymmetry for plants grown alone. For example, A_{alone} for low water and no urine represents the difference in biomass between *K. nervosa* and *S. kentrophyllus* grown alone under those treatment levels. B_{small} and B_{big} represent the biomass of the smaller and bigger plants in the pairwise test, respectively. There is no accounting for switches in the identity of the larger individual so A ranges between 0 and 1. The null hypothesis for A between plants grown alone is that $A = 0$ (i.e., no size difference exists between plants). The null hypothesis for competing plants, therefore, is $A_{\text{trmt}} = A_{\text{alone}}$. Thus, A tests whether size differs between individual plants in response to competition, accounting for differences that occur independent of direct interaction. RC and A data both had normal distributions with similar variances and were, therefore, tested using ANOVA.

ANOVA was performed on the natural logarithm of the absolute value of pre-dawn leaf water potentials. Scheffe's multiple comparison test was used to test differences between means.

Results

The response of plant biomass to competition

Sporobolus kentrophyllus had significantly greater biomass than *K. nervosa* at the end of the experiment (Figure 1, Table 1). *Sporobolus kentrophyllus* also had the greatest negative affect on biomass as competitor, resulting in a significant target species \times competitor species interaction ($F = 11.9$; $df = 2, 48$; $P < 0.001$; Figure 1; Table 1). Little difference was found between the analyses performed on biomass of plants harvested and total plant biomass, including clipped tissue biomass (Table 1). This suggests that plant biomass lost to herbivores does not significantly alter the effect of tested factors on plant biomass accumulation. This, of course, does not account for differences that might occur in above-ground competition in the absence of grazing among different genotypes, where within-species differences in height have been shown to differ significantly for *S. kentrophyllus* (Hartvigsen and McNaughton 1995). The biomass of plants prior to planting was not different (see Methods section) and, therefore, fails to explain these results.

Kyllinga nervosa and *S. kentrophyllus* differed in their response to the water and urine addition. *Kyllinga nervosa* responded to the high water treatment with

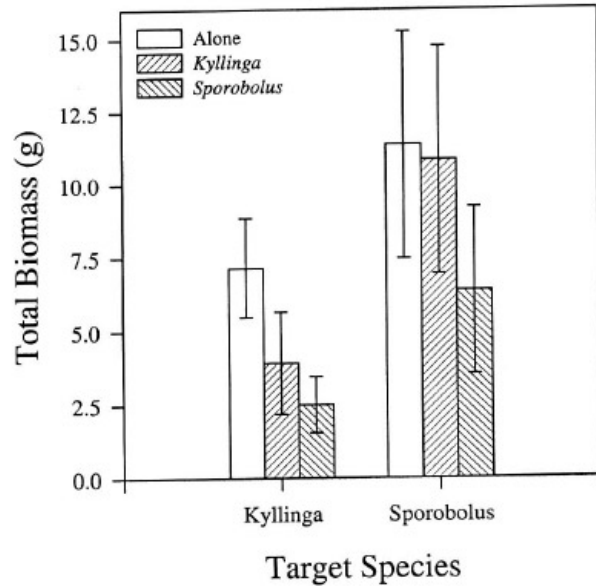


Figure 1. Mean total biomass plant⁻¹. Bars represent competitor identity or that plants were grown individually ('alone'). Target species \times competitor: $F = 11.9$; $df = 1, 48$; $P < 0.001$. Error bars are ± 1 sd.

increased growth but *S. kentrophyllus* did not, resulting in a significant target species \times water interaction ($F = 5.09$; $df = 1, 48$; $P = 0.029$; Table 1). *Sporobolus kentrophyllus* responded positively to the urine treatment but *K. nervosa* did not, resulting in a significant target species \times urine interaction ($F = 31.02$; $df = 1, 48$; $P < 0.001$; Table 1).

The comparison of total plant biomass per pot yielded a significant treatment effect for target species, with *S. kentrophyllus* pots having significantly greater biomass than pots with either *K. nervosa* alone or *K. nervosa* in intraspecific competition ($F = 8.30$; $df = 4, 55$; $P < 0.001$).

Leaf water potential

Plants had significantly higher leaf water potential (decreased water stress) at the higher (50 ml day⁻¹ watering rate ($F = 50.3$; $df = 1, 48$; $P < 0.001$; Figure 2; Table 1). In addition, the main effect of urine addition decreased leaf water potential (increased water stress) ($F = 7.50$; $df = 1, 48$; $P = 0.009$; Table 1). The level of water stress between these two species differed between the combined water and urine treatments resulting in a highly significant three-way interaction for target species, water, and urine ($F = 37.5$; $df = 1, 48$; $P < 0.001$; Figure 2). Specifically, on the low water treatment *K. nervosa* did

Table 1. Percent explained variance in analysis of variance for the natural logarithm of total plant biomass including clipped material (TB), total biomass of harvested plants (HB), pre-dawn leaf water potential (Ψ), reproductive biomass (RB), normalized reproductive biomass (NRB), number of reproductive structures (NRS), and normalized number of reproductive structures (NNRS).

Source	df	TB	HB	Ψ	RB	NRB	NRS	NNRS
SP	1	35.03***	23.31***	3.78*	27.1011*	21.66***	2.68***	36.89***
Comp	2	29.35***	35.04***	2.75	13.11***	12.54***	41.66***	16.67***
Water	1	6.37***	1.89*	42.78***	0.48	1.14	4.88***	1.04
Urine	1	5.56***	3.32**	8.40***	17.35***	9.45***	14.22***	1.96*
SP * Comp	2	4.50***	5.25***	0.54	3.44**	0.00	3.72***	11.17***
SP * Water	1	1.00*	0.11	0.14	0.00	1.14	0.54	0.48
SP * Urine	1	4.62***	6.32***	1.47	12.48***	6.68**	1.49*	0.04
Comp * Water	2	0.52	1.24	2.49	0.13	3.42	0.26	1.22
Comp * Urine	2	0.76	0.55	1.48	7.10***	5.37*	7.26***	3.27*
Water * Urine	1	0.23	0.96	0.43	0.63	0.00	1.89**	0.28
SP * Comp * Water	2	0.82	1.27	0.49	0.21	1.14	0.48	1.81
SP * Comp * Urine	2	0.70	0.21	0.3	2.19*	0.16	0.95	2.45
SP * Water * Urine	1	0.07	0.05	5.43***	0.04	0.00	0.03	0.43
Comp * Water * Urine	2	0.20	0.93	0.46	0.58	2.28	0.77	0.24
SP * Comp * Water * Urine	2	0.49	1.01	0.64	0.35	0.65	0.01	0.49
Error	48	9.79	14.79	19.35	14.80	34.36	9.16	21.57

* = $P \leq 0.05$ ** = $P \leq 0.01$ *** = $P \leq 0.001$

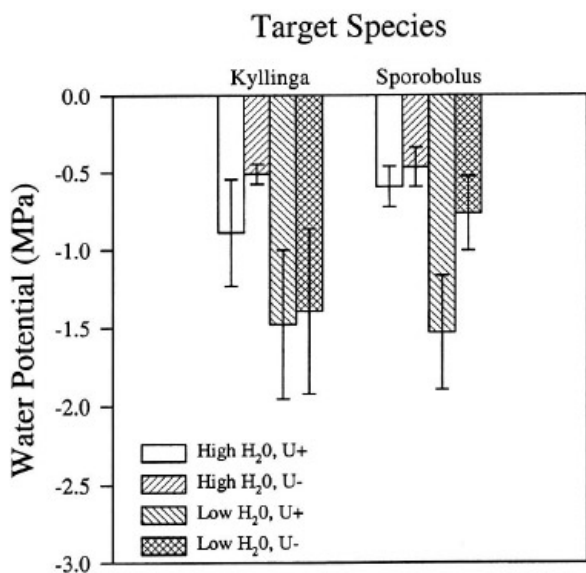


Figure 2. Mean pre-dawn leaf water potential plant⁻¹, measured just prior to harvest at week 8. Target species \times water \times urine: $F = 8.95$; $df = 1, 46$; $P = 0.004$. Error bars are ± 1 sd.

not exhibit increased water stress in response to urine addition while *S. kentrophyllus* became significantly more water stressed with urine addition (Figure 2).

Response to competition and size asymmetry

The response to competition index (RC) indicated that intraspecific competition had similar relative effects for both *S. kentrophyllus* and *K. nervosa* ($RC > 0$; Figure 3; Table 2). *Sporobolus kentrophyllus* growth was not altered when grown with *K. nervosa* while the greatest observed response to competition was by *K. nervosa* when grown with *S. kentrophyllus* (Figure 3). RC was higher on low water treatments than on high water treatments, indicating increased competition with increased water stress ($F = 9.90$; $df = 1, 32$; $P = 0.004$). Therefore, RC indicates that these species competed more intensely under low water availability than under high water availability while urine had no significant effect on competition (Table 2).

Plant size asymmetries (A) were significantly greater than zero for all four treatments tested (zero would indicate no difference in final plant biomass) (treatment main effect: $F = 18.3$; $df = 3, 32$; $P < 0.001$; Figure 4; Table 2). Using A for plants grown alone as the null model (no difference in size between *K. nervosa* and *S. kentrophyllus* grown individually), A was found to be significantly greater for both the *K. nervosa* intraspecific treatment and the *K. nervosa*-*S. kentrophyllus* interspecific treatment (Figure 4), with

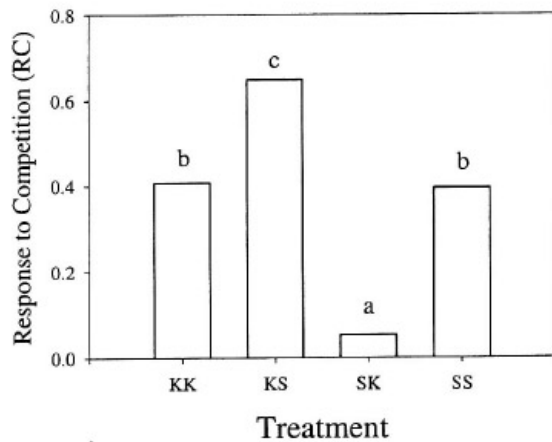


Figure 3. Response to competition (RC). Bars with similar letters are not statistically different. Treatment symbol are paired competition treatments with the first letter representing the genus of the target species, the latter letter representing the competitor species. $RC = 0.0$ means no proportional decrease in plant size in competition relative to when grown alone. Treatment main effect: $F = 41.8$; $df = 3, 48$; $P < 0.001$.

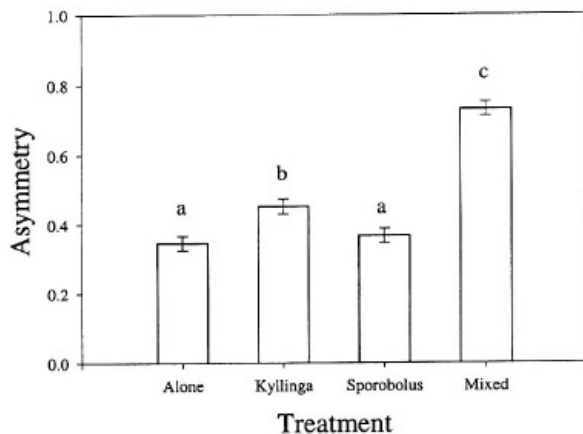


Figure 4. Mean asymmetry (A) for plants grown alone, compared across species, and in monocultures (*Kyllinga* or *Sporobolus*) or in interspecific mixtures. Similar letters represent no statistical difference. Treatment main effect: $F = 18.3$, $df = 3, 32$; $P < 0.001$. Error bars are ± 1 sd.

A being greatest for the interspecific treatment. Overall, the application of urine increased size asymmetry from a mean of 0.39 to 0.56 while additional water significantly reduced asymmetry from a mean of 0.52 with low water to 0.43 with high water, resulting in a significant treatment \times water \times urine interaction ($F = 5.04$; $df = 3, 32$; $P = 0.006$).

Table 2. Analysis of variance for response to competition (RC) and asymmetry (A). Values presented are percent variance explained in the ANOVA model. TRMT represents the four species treatment levels with both species grown in intra- and interspecific competition.

Source	df	RC	A
TRMT	3	64.82***	40.23***
Water	1	5.04**	3.84*
Urine	1	0.54	12.14***
TRMT * Water	3	3.87	3.67
TRMT * Urine	3	2.64	3.28
Water * Urine	1	0.42	2.39
TRMT * Water * Urine	3	1.68	11.07**
Error	32	21.00	23.40

* = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.

Reproductive effort

Sporobolus kentrophyllus, the stoloniferous species, produced significantly more reproductive biomass than *K. nervosa* as well as allocated more when normalized on total plant biomass (Table 1). *Sporobolus kentrophyllus* also significantly reduced *K. nervosa* reproductive biomass (Figure 5; Table 1). Urine increased both absolute and relative reproductive biomass and the relative number of reproductive structures. This increase, however, was observed most in *S. kentrophyllus* with little relative increase observed in *K. nervosa*, leading to a significant species \times urine interaction ($F = 5.58$; $df = 2, 48$; $P = 0.007$; Figure 5, Table 1). A significant target species \times competitor interaction was observed for absolute reproductive biomass that was not observed for relative reproductive biomass (compare RB to NRB, Table 1).

Sporobolus kentrophyllus also produced fewer stolon nodes than *K. nervosa* inflorescences and this was conserved when normalized on biomass (Figure 6; Table 1). Urine addition increased the absolute and normalized numbers of reproductive structures in both species. The significant increase in absolute numbers of reproductive structures was explained by increased plant size for the interactive factors of target species \times water and target species \times urine, being absent when the data were normalized on biomass (compare NRS to NNRS, Table 1).

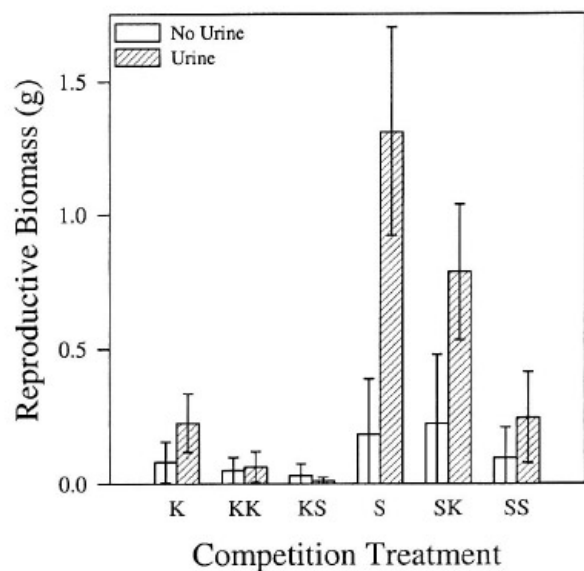


Figure 5. Mean total reproductive biomass plant⁻¹. Competition treatments are *K. nervosa* (K) and *S. kentrophyllus* (S), with the first letter of paired letters (e.g., KK) representing the genus of the target species (e.g., KS is *K. nervosa* grown with *S. kentrophyllus*). Single letters represent plants grown alone. Error bars are ± 1 sd.

Discussion

Total biomass

Sporobolus kentrophyllus and *Kyllinga nervosa* are codominant species of the Serengeti short-grass plains (McNaughton 1983). The results presented here from a short-term, two-month experiment suggest that *S. kentrophyllus* is a superior competitor to *K. nervosa* over most treatment levels tested with respect to biomass accumulation and reproductive effort. Water and urine differentially altered plant performance for these species in the laboratory and are, therefore, candidates for influencing competitive ability in the Serengeti.

Sporobolus kentrophyllus biomass was lowest under intraspecific competition. This suggests that increases in abundance may reduce individual-level productivity. *Kyllinga nervosa* biomass, however, was reduced most by competition with *S. kentrophyllus* suggesting that this species is competitively inferior. In an analysis of field competition experiments, published from 1979–1988, Goldberg and Barton (1992) found that, of the four studies that met their criteria, only one study by Berendse (1983) demonstrated that intraspecific competition was greater than interspecific competition. Berendse (1983) found that the two competing species had significantly different root-

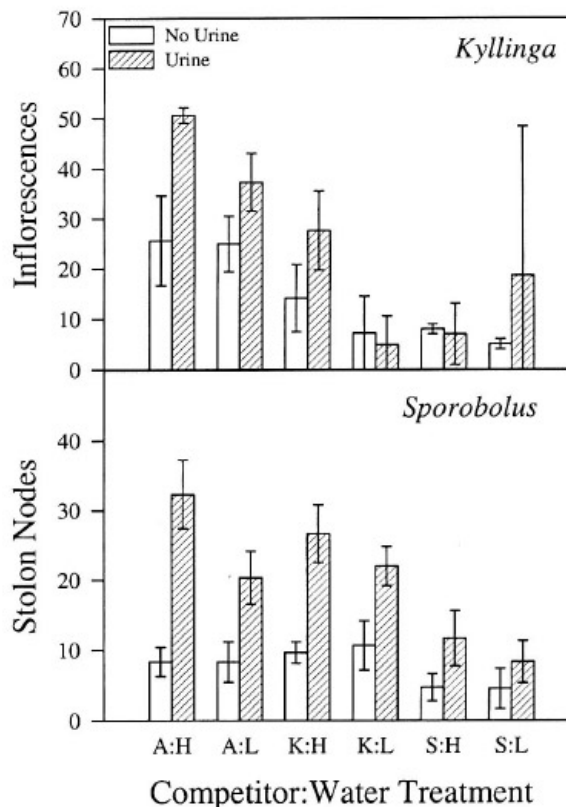


Figure 6. The mean number of reproductive structures produced plant⁻¹. The two graphs are for individuals of the two target species. Abscissa treatments are competitor (A, alone; K, *Kyllinga*; S, *Sporobolus*) and water (H, high; L, low). Error bars are ± 1 sd.

ing depths and were, therefore, apparently able to divide belowground resources and reduce interspecific competition.

The two significant interactions of target species by water and target species by urine suggest a mechanism that allows these species to coexist. *Sporobolus kentrophyllus* biomass accumulation was insensitive to water stress detected in the analysis of pre-dawn leaf water potential. This may be explained from the fact that roots of this species reached the bottom of the 50 cm deep pots while *K. nervosa* roots were limited to the top 20 cm of the medium, similar to the differential rooting depths found by Berendse (1983), mentioned above, resulting in the target species \times water interaction. The importance of this difference in morphology in the field is unknown and complicated by the relatively impenetrable calcium carbonate hardpan horizon at about 10 cm in the Serengeti plains where these species coexist (de Wit 1978). *Kyllinga nervosa* was unaffected by urine addition while *S. kentrophyllus* increased growth, resulting in the target

species \times urine interaction. *Kyllinga nervosa*'s failure to respond to urine addition suggests that it may function as a stress tolerator (*sensu* Grime 1977). Pre-dawn leaf water potential corroborates this interaction, revealing a highly significant interaction between target species, water, and urine. The most plausible explanation of this finding is that *K. nervosa* was able to continue growth despite the low nitrogen availability in absence of urine addition. An alternative explanation, however, is that *K. nervosa* became water stressed and was unable to respond to urine addition.

Total pot biomass was significantly greater when *S. kentrophyllus* was present, irrespective of the presence or identity of competitors. This result suggests that *K. nervosa* abundance is negatively associated with community biomass. Previous work, however, has shown that *K. nervosa* is highly tolerant of grazing with maximum productivity occurring with daily clipping to 4 cm in height (McNaughton 1979). These results suggest that *Kyllinga nervosa* may occupy a separate niche that interferes little if at all with *S. kentrophyllus*. In a separate study, Banyikwa (1988) found that grazing reduced the effect of competition between the short-grass species *Sporobolus ioclados* and *Digitaria macroblephara* by 17%. *Kyllinga nervosa*'s resilience to the intense grazing in the Serengeti may enable it to maintain its codominance. These results also suggest that productivity in the Serengeti would be indirectly maximized by an overdispersed distribution of *K. nervosa*, where it has little competitive effect on *S. kentrophyllus*. This effect could be tested empirically to determine whether *K. nervosa* functions as an 'ecological spacer' by reducing intraspecific competition among individual *S. kentrophyllus* plants and increasing community biomass.

RC vs A in measuring competitive interactions

Grace (1995) argued that relative measures of competition are better estimators of competition than absolute changes in biomass. RC, the proportional change in plant biomass resulting from competition, was, however, the most statistically conservative of the three measures of competition, detecting only differences between species and the main effect of water treatment. A, an estimate of the relative differences between competing plants (Weiner 1990), may be more important biologically and was more sensitive to detecting competition between these species for water and urine (a greater number of significant effects). Therefore, for these plants, competition is more likely

to be detected when relative size difference is assessed (A) than when change in biomass is compared between plants grown alone and with a neighbor (RC). In addition, use of RC should proceed with caution because of the potential for data to be highly skewed (see Markham et al. 1996), although the data presented here were normally distributed. Likewise, the use of A also is problematic because it does not differentiate the identity of competitors but simply evaluates size differences between competitors.

Asymmetry was highest in interspecific (mixed) associations and lowest when plants were not competing (i.e., individually-grown plants were most similar in size) and when *S. kentrophyllus* was grown in intraspecific competition. These results suggest that, although *S. kentrophyllus* exhibits relatively strong intraspecific competition by reducing biomass, the relative size differences among individuals are not effected. The previously demonstrated morphological variability among genotypes of *S. kentrophyllus* (Hartvigsen et al. 1995) raises an interesting question as to how individual genotypes might interact in the field.

Interspecific competition, based on A, was most intense in the presence of urine (high nitrogen), consistent with plant strategy theory (Grime 1977; Campbell and Grime 1992), which suggests that the intensity of competition increases with increasing resource availability and inconsistent with Tilman's findings (Tilman 1990; Tilman and Wedin 1991) that competition is unrelated to resource availability. Competition, however, was greater on low water availability treatments which is inconsistent with plant strategy theory. The significant interaction of water and urine on competitive interactions between these species in the laboratory suggests these factors may be important in the field.

Reproductive biomass

Sporobolus kentrophyllus had higher absolute reproductive biomass than *K. nervosa* and allocated more biomass to reproduction relative to total biomass (normalized reproductive biomass, NRB in Table 1). *Kyllinga nervosa* reproductive biomass was significantly reduced during competition with *S. kentrophyllus*. The significant target species by water and target species by urine interactions observed for total biomass were observed for absolute reproductive biomass but not for relative reproductive biomass. This indicates that, although reproductive biomass was dif-

ferentially affected by water and urine, the response is explained entirely by changes in plant size and not by actual changes in allocation (Gedroc et al. 1996).

Sporobolus kentrophyllus responded to urine addition with increased reproductive biomass, resulting in the species \times urine interaction. An important difference between species, however, was the number of reproductive structures produced. The production of nodes by *S. kentrophyllus* was related to the increased reproductive biomass. Ruess and McNaughton (1984) found urea addition increased the number of *K. nervosa* inflorescences produced over plants given an equal level of N as NH_4NO_3 . Similarly, McNaughton et al. (1983) found that water availability was coupled to increased numbers of inflorescences but inorganic N had no effect on inflorescence production. The biological significance of inflorescence production in *K. nervosa* is untested but may indicate a strategy favoring recombination and dispersal over the more prevalent clonal spread observed in *S. kentrophyllus*.

Leaf water potential depended on species, water, and urine

Water stress levels between species, indicated by leaf water potential, interactively depended on water and urine treatments. The largest variance component of this analysis was due to the main effect of water, followed by urine and the three-way interaction of species, water, and urine. *Kyllinga nervosa* had a similar level of water stress between no urine and urine treatments, suggesting the lack of change in biomass to urine found in this species was not due to water stress. *Sporobolus kentrophyllus*, however, exhibited increased water stress in response to urine application on low water treatments. The differential response of *K. nervosa* and *S. kentrophyllus* to water was likely due to the different rooting depths, although differences in such unmeasured factors as transpiration rates and leaf area might explain these differences. *Kyllinga nervosa* biomass was lower in response to low water treatments.

As discussed above the calcium carbonate hardpan horizon at about 10 cm in this part of the Serengeti (de Wit 1978) may interfere with percolation. Urine, therefore, is likely to be converted into NH_4 and/or NO_3 and made available to both species within this limited soil depth. Water also is likely to be limiting to *S. kentrophyllus* and *K. nervosa*. *Sporobolus kentrophyllus*, however, may be able to seek water laterally or, perhaps, penetrate the hardpan. In addition, the

negative effects of *K. nervosa* root morphological limitation may be moderated by the presence of hydraulic movement caused by night time wicking of water by *S. kentrophyllus* (Dawson 1993).

Conclusion

The relative success of *K. nervosa* and *S. kentrophyllus* appears to be regulated by differential responses of these species to intra- and interspecific competition, and water and urine availability. *Kyllinga nervosa*'s positive response to water addition may lead to an increase in the biomass of this species, and perhaps ultimately the number of individuals, during relatively wet years compared with *S. kentrophyllus*. This is consistent with the observation that *K. nervosa* did not send roots below 20 cm in depth. These results also suggest that *Kyllinga nervosa* should be sensitive to periods of low rainfall. *Sporobolus kentrophyllus* rapidly elongated roots in the 50 cm pots and was, therefore, relatively insensitive to the two tested watering rates, a response that may occur through lateral root growth in the field. *Sporobolus kentrophyllus*, and not *K. nervosa*, was strongly responsive to urine addition and is likely to benefit opportunistically from urine application in the field, growing rapidly and colonizing microsites vegetatively. Coexistence, the finding in this experiment that neither species was competitively excluded, may occur in the field due to a balance between differential reproductive effort and the different responses of these species to competitor identity, water availability, and the presence of urine. The combination of spatial heterogeneity of urine deposition and fluctuating levels of rainfall in the Serengeti, therefore, may interactively affect the abundance of *K. nervosa* and *S. kentrophyllus*.

Limitations in *S. kentrophyllus*'s ability to displace *K. nervosa* require explanation. First, *S. kentrophyllus* showed strong intraspecific biomass limitation and no response to interspecific competition with *K. nervosa*, suggesting that intraspecific competition may be greater than interspecific competition in the field for this species. This could be a factor allowing *K. nervosa* to coexist with *S. kentrophyllus* in the field (*sensu* Vance 1985; Volterra 1926). Second, results from this and another longer-term experiment of the *S. kentrophyllus*-*K. nervosa* interaction suggest that *K. nervosa* is more tolerant of drought and nitrogen limitation, allowing *K. nervosa* to persist in the short-grass plains irrespective of the negative effect of *S.*

kentrophyllus on *K. nervosa* biomass accumulation (Hartvigsen 1995). Third, the large, deep pots used in this experiment may have allowed these species to effectively occupy separate niches by dividing below-ground nitrogen between these two species. *Kyllinga nervosa* has been found to have higher uptake rates of nitrogen in the form of urea over NH_4NO_3 (Ruess et al. 1984) while *S. kentrophyllus* preferentially uptake nitrogen in the form of NH_4 over NO_3 (Ruess 1988). Levels of these various forms of nitrogen may have been spatially and/or temporally distributed in the 50 cm deep pots used in this experiment, although longer-term (five months) coexistence was observed for these species in a separate experiment that used 15 cm deep arenas (Hartvigsen 1995), suggesting that persistence here was not due to the short length of this experiment. Finally, it is possible, as these results suggest, that competitor identity, water, and urine interact in the field and allow these two species to coexist.

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