SEASON- AND HERBIVORE-DEPENDENT COMPETITION AND FACILITATION IN A SEMIARID SAVANNA

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Abstract. Empirical and theoretical evidence suggests that facilitation between plants, when it occurs, is more likely during periods of abiotic stress, while competition predominates under more moderate conditions. Therefore, one might expect the relative importance of competition vs. facilitation to vary seasonally in ecosystems characterized by pronounced dry (abiotically stressful) and wet (benign) seasons. Herbivory also varies seasonally and can affect the net outcome of plant–plant interactions, but the interactive effects of seasonality and herbivory on the competition–facilitation balance are not known. I experimentally manipulated neighboring plants and herbivory during wet and dry periods for two species of grass: *Cynodon plectostachyus* and *Pennisetum stramineum*, in the semiarid Laikipia District of Kenya. These experiments indicate that *Pennisetum* was competitively dominant during the wet season and that it responded negatively to grazing, especially during the dry season. *Cynodon* showed more complex season- and herbivore-dependent responses. *Cynodon* experienced facilitation that was simultaneously dependent on presence of herbivores and on dry season. During the wet season *Cynodon* experienced net competition. These results illustrate how herbivory and seasonality can interact in complex ways to shift species–species competition–facilitation balance. Additionally, because *Cynodon* and *Pennisetum* are key players in a local successional process, these results indicate that herbivory can affect the direction and pace of succession.

Key words: Acacia drepanolobium savanna; associational resistance; Cynodon plectostachyus; *facilitation; grasslands; herbivory; indirect effects; Kenya;* Pennisetum stramineum; *succession.*

Introduction

Plant communities are shaped by complex interactions among multiple biotic and abiotic factors. Although competition has been emphasized as the primary biotic driver of plant interactions (Connell 1983, Schoener 1983, Goldberg and Barton 1992), a more recent profusion of evidence indicates that net plant–plant interactions often are the result of both competitive and facilitative interactions (Callaway 1995, Holmgren et al. 1997, Kikvidze et al. 2006, Graff et al. 2007). Theoretical and empirical evidence suggests that facilitative (positive) relationships are more common in stressful or disturbed environments where the facilitator ameliorates abiotic stress (Pugnaire and Luque 2001, Callaway et al. 2002) or consumer stress (Holmes and Jepson-Innes 1989, Bertness and Callaway 1994, Gómez et al. 2001). Not surprisingly, a preponderance of examples of facilitation in plants, both direct (Callaway 1992, Maestre et al. 2003) and indirect (McNaughton 1978, Holmes and Jepson-Innes 1989, Gómez et al. 2001, Rebollo et al. 2002) are found in arid and semiarid systems that undergo extremes in both abiotic stress (e.g., drought) and consumer stress (e.g., herbivory).

Surprisingly few studies, however, have examined interactions between these two stresses.

Based on the abiotic stress hypothesis, the net direction of plant–plant interactions in water-limited environments would be expected to vary seasonally, according to water availability. In fact, several studies have found that the competition–facilitation balance varies according to annual water availability (Greenlee and Callaway 1996, Pugnaire and Lazaro 2000, Tielborger and Kadmon 2000; but see Casper 1996) and can even shift within a single year or season (Holzapfel and Mahall 1999, Kikvidze et al. 2006).

Herbivory also affects the net direction of plant–plant interactions by mediating both positive and negative interactions (Gurevitch et al. 2000, Hambäck and Beckerman 2003, Callaway et al. 2005, Brooker et al. 2006, Graff et al. 2007). If a plant species is selectively grazed, its fitness may be decreased, thereby altering competitive dynamics within the plant community (Gurevitch et al. 2000, van der Wal et al. 2000, Fowler 2002). On the other hand, positive plant–plant relationships are mediated by herbivore foraging behavior when one plant species benefits by growing in close proximity to another (better-defended) species (e.g., Rebollo et al. 2002).

The behavior of herbivores and their effects on the plant community often vary seasonally. Mammalian herbivores, driven by metabolic requirements, often

become more selective in order to attain high-quality forage during dry times (Demment and Van Soest 1985, Belovsky 1997). Additionally, defoliation may be more intense or spatially concentrated as quantity and availability of forage becomes limited during dry times (Scoones 1995, Illius and O'Connor 1999, 2000, Fynn and O'Connor 2000, Rousset and Lepart 2002). Conversely, defoliation may be less intense or more spatially diffuse during wet times when green forage is abundant (Scoones 1995, Illius and O'Connor 2000).

Different combinations of herbivory and rainfall intensities have contrasting effects on community patterns and processes (Proulx and Mazumder 1998, Fynn and O'Connor 2000, Osem et al. 2002, Augustine and McNaughton 2006). Understanding how herbivory interacts with seasonal dynamics has direct implications for our understanding of the mechanics of competition–facilitation processes as drivers of short-term community change (e.g., Callaway et al. 2005). Additionally, short-term processes can influence the longer-term trajectory of the ecosystem (Hobbs 1996, Goldberg et al. 1999, Rousset and Lepart 2002, Gratton and Denno 2003, Gómez 2005). Short-term competition–facilitation processes in particular can be key components of long-term successional change (Connell and Slatyer 1977, Olff et al. 1999, Baumeister and Callaway 2006, Zanini et al. 2006, Dickie et al. 2007).

I experimentally examined the roles of season and herbivory in the competition–facilitation balance between two grass species, Cynodon plectostachyus and Pennisetum stramineum, in a semiarid ecosystem. I manipulated neighboring plant composition and density, as well as herbivore access, in both wet and dry periods. These two grass species co-occur in large patches that undergo successional development from Cynodon dominance to Pennisetum dominance. I asked the following questions: (1) Does facilitation occur between Pennisetum and Cynodon? (2) If facilitation does occur, is it stronger in the dry season? (3) Is facilitation mediated by herbivory? (4) Do the effects of season and herbivory interact? and (5) How do short-term dynamics compare to the known long-term trajectory of the system?

METHODS

Study site

This research was conducted on the Mpala Research Centre and Farm and adjacent Segera and Jessel Ranches (36°52′ E, 0°17′ N), which cover more than 50 000 ha of semiarid savanna in Laikipia, Kenya. Annual rainfall is variable, but averages approximately 500–600 mm. The mean rainfall pattern is weakly trimodal, with the highest peak in mean rainfall occurring March–May (mean in April, 1998–2005, 120 mm) and two lesser peaks in July and November (means 84 mm and 107 mm, respectively). The longest and most pronounced dry season is typically from December through March.

My study area is located in Acacia drepanolobium savanna and is underlain with "black cotton" soils, poorly drained vertisols with high clay content (Ahn and Geiger 1987). In this system, 97% of the tree canopy cover is Acacia drepanolobium, and 90% of herbaceous cover is composed of six species: Pennisetum mezianum, P. stramineum, Themeda triandra, Lintonia nutans, Aerva lanata, and Brachiaria lachnantha (Young et al. 1998). Resident large mammals include elephants (Loxodonta africana), zebras (Equus burchelli), Grant's gazelles (Gazella grantii), hartebeests (Alcelaphus buselaphus), steinbucks (Raphicerus campestris), elands (Taurotragus oryx), buffaloes (Syncerus caffer), giraffes (Giraffa camelopardalis), spotted hyaenas (Crocuta crocuta), lions (Panthera leo), and leopards (Panthera pardus). This area is actively managed for cattle, with stocking rates of 0.5–0.7 livestock units/ha.

Historical and current cattle management has created a landscape mosaic of nutrient-rich, treeless "glades" scattered throughout the background of A. drepanolobium savanna. Once abandoned, temporary cattle corrals develop into these glades that are preferred by both livestock and wildlife. Vegetation in younger glades is dominated by the stoloniferous grass, Cynodon plectostachyus, while older glade vegetation is characterized by a near monoculture of an ascending bunchgrass, Pennisetum stramineum (K. Veblen, unpublished data). Glades of intermediate age are in transition and contain areas codominated by these two grass species.

Experimental design and data collection

I investigated competition and facilitation dynamics between Pennisetum stramineum and Cynodon plectostachyus in glades using a 2 × 2 × 2 factorial design. For each of these two species, I crossed species removal treatments (interspecific neighbors present vs. interspecific neighbors removed) with grazing treatments (grazers allowed vs. grazers excluded). Experimental plots were randomly located within glade areas codominated by Pennisetum and Cynodon (plots were considered "codominated" so long as neither species exhibited >80% cover).

Six neighbor/grazing treatment combinations were replicated within each of 12 randomly chosen glades (with treatments established in five glades in August 2004, and seven in August 2005) for a total of 72 experimental plots. Three of the six treatments were grazed, and the remaining three were ungrazed. Crossed with each grazing treatment were the following three species removal treatments: Pennisetum removal, Cynodon removal, and control (neither Cynodon nor Pennisetum removed). Each of the seven glades in 2005 included two additional treatments that were added to tease apart inter- vs. intraspecific neighbor effects: one grazed and one ungrazed density-reduced control plot. All 86 plots were 1 × 1 m.

Grazed plots were left open to grazing, and ungrazed plots were covered with $1 \times 1 \times 1$ m chicken-wire mesh cages that prevented grazing by larger vertebrate herbivores. The lower halves of the cages were covered with 30 cm tall hardware cloth to also exclude the dominant herbivorous rodent, *Saccostomus mearnsi*. In all plots, I identified all individual plants to species. In species removal plots, all individuals of target species were removed. In density-reduced control plots, I haphazardly removed individuals of both grass species until the overall cover was half of its starting density (with density first assessed visually and then confirmed by counting pin frame pin hits; see below). In all 86 plots, all forbs, which comprised an average of 2.9% of total cover, and all nontarget grass species, which comprised an average 2.8% of total cover, were removed. All removed plants were clipped to remove aboveground biomass and later were individually treated by sponge with Roundup (glyphosate) herbicide after rainfall and any new growth.

Prior to manipulation, within each 1×1 m plot, I quantified plant cover with five evenly spaced 10-point pin frames. I repeated baseline pin frame counts in "removal" plots immediately after neighbor removal treatments were complete. I assessed the effects of experimental treatments on *Cynodon* and *Pennisetum* by repeating pin frame measurements in all plots at the end of the three-month-long dry season in the March following plot setup (28 mm rainfall in January–March 2005 and 24 mm in January–March 2006). I repeated measurements three months later in June at the end of a heavy rainfall period (227 mm rainfall in April–June 2005, and 153 mm in April–June 2006). Plots set up in 2004 were assessed only during the 2005 dry and wet seasons. For pin frame cover estimates, I counted the total number of times that each species touched each pin. As a result, the pin frame count for any given species often far exceeded 10. Although I hereafter refer to pin frame measurements as "cover," total number of pin hits is positively correlated with biomass of each species (*Cynodon*, $R^2 = 0.89$, K. Veblen, *unpublished data*; *Pennisetum*, $R^2 = 0.65$, I. Kimathi, *unpublished data*).

Data analyses

I calculated mean *Cynodon* and *Pennisetum* cover values for each 1×1 m plot in each sampling period. I quantified how *Cynodon* and *Pennisetum* cover changed over time (in response to grazing, neighbor and season effects) by calculating a relative growth index. The relative growth index was calculated as ln([cover t_2]/[cover t_1]). I calculated relative growth during the dry season ($t_1 = $ post-manipulation baseline cover, $t_2 = $ March cover) and wet season ($t_1 = $ March cover, $t_2 = $ June cover) for each species/neighbor/grazing combination. Relative growth values are symmetrical around zero, with positive numbers indicating increases in cover and negative numbers indicating decreases in cover.

I calculated an additional index, relative interaction intensity (RII), to depict positive vs. negative effects of interspecific neighbor presence on cover of each species. The RII provides a measure of the relative difference in cover of a target species in plots with neighbors vs. plots without neighbors. I calculated the mean ($\pm$SE) relative interaction intensities (RII) between *Cynodon* and *Pennisetum* for all four season/grazing combinations (wet grazed, wet ungrazed, dry grazed, and dry ungrazed). RII was calculated with the following equation: $\text{RII} = (B_w - B_0)/(B_w + B_0)$ where B_w is the cover of target species growing with neighbors (i.e., control plot) and B_0 is the cover of target species growing without neighbors (i.e., removal plot) (Armas et al. 2004). RII values fall between -1 and $+1$, with negative values indicating competitive neighbor effects and positive values indicating facilitative neighbor effects.

I used a general linear mixed model (GLMM) to conduct a repeated-measures analysis of covariance (ANCOVA) testing treatment and time (i.e., season) effects on *Cynodon* and *Pennisetum* relative growth. For each grass species, grazing treatment (presence/absence), neighbor treatment (presence/absence), season (dry/wet), and interactions among the three were fixed factors. I used maximum-likelihood methodology, as well as Sattherthwaite's approximation of degrees of freedom (PROC MIXED, version 9.1; SAS Institute, Cary North Carolina, USA). Block (i.e., glade) was treated as the experimental unit and was designated as a random effect. Pre-manipulation baseline cover of target species was treated as the covariate. I made pairwise comparisons for grazing, competition, and grazing $\times$ competition within each season using unprotected LSD t tests, applying Bonferroni corrections to significance values ($P = 0.025$, 0.025, and 0.0125, respectively). For relative growth analyses, the two years' worth of data were pooled because species responses were qualitatively identical in the two years and preliminary models indicated that the effect of year was negligible. For density-reduction plots, relative growth and statistical calculations were performed as above, replacing "control" plots with "density-reduced control plots." Although mean RII values are presented to indicate the direction and magnitude of neighbor effects, I did not conduct statistical analyses of RII values, which are simply a composite representation of data already analyzed in relative growth analyses.

RESULTS

The two grass species differed in their responses to experimental grazing and neighbor treatments over the two seasons. *Pennisetum* showed negative responses to grazing, especially during the dry season, and a highly positive response to rainfall. *Cynodon* also experienced strong competitive suppression under several treatment combinations. However, *Cynodon* showed a net facilita-

TABLE 1. Effects of grazing (presence/absence), competitors (presence/absence), and season (dry/wet) on relative growth of the grasses *Cynodon plectostachyus* and *Pennisetum stramineum* in 1×1 m plots in the semiarid Laikipia District of Kenya.

	Cynodon plectostachyus			*Pennisetum stramineum*		
Factor	df	F	P	df	F	P
Grazing presence/absence	1, 22.0	23.34	<0.0001	1, 20.8	30.65	<0.0001
Competitor presence/absence	1, 23.4	6.57	0.017	1, 43.0	3.26	0.078
Grazing × competitor	1, 21.8	3.53	0.074	1, 44.0	0.16	0.69
Season	1, 21.8	0.59	0.45	1, 21.8	3.29	0.083
Season × grazing	1, 22.0	34.67	<0.0001	1, 20.8	5.05	0.034
Season × competitor	1, 21.8	27.21	<0.0001	1, 43.0	0.85	0.36
Season × grazing × competitor	1, 21.8	4.74	0.04	1, 43.0	2.35	0.13
Baseline covariate	1, 67.7	3.52	0.065	1, 82.9	8.79	0.0039

Notes: Each species was analyzed as a general linear mixed model (GLMM) repeated-measures ANCOVA. Grazing, competitors, season, and interactions among the three were fixed effects. The experimental unit, block, was a random effect, and baseline plant cover of the target species was treated as the covariate.

tion response to neighboring *Pennisetum* plants in the presence of herbivores in the dry season.

Pennisetum performance

The presence of herbivores significantly decreased cover of *Pennisetum*, and this effect was especially pronounced during the dry season (Table 1, Fig. 1c, d). *Pennisetum* cover was 44% lower in plots open to grazing. Although grazing decreased *Pennisetum* cover during the wet season (Fig. 1d), grazing led to net loss of *Pennisetum* cover only during the dry season (Fig. 1c). Though less influential than grazing and nonsignificant, interspecific competitors also decreased *Pennisetum* (Fig.

1c, Table 1), with *Cynodon* removal increasing *Pennisetum* cover by an average of 16%. Although the season × grazing × competitor interaction was not significant, (Table 1), the negative neighbor effects of *Cynodon* appear most pronounced in ungrazed plots during the dry season, (Fig. 1c). There was no evidence of facilitation of *Pennisetum* by *Cynodon* under any grazing × season combination (Fig. 1c, d, Table 1).

Despite the negative effects of grazing and neighbors on *Pennisetum* performance, wet-season *Pennisetum* growth was so pronounced that net increases in cover occurred in all plots, even those with both competition and grazing. *Pennisetum* cover was 33% higher in the wet
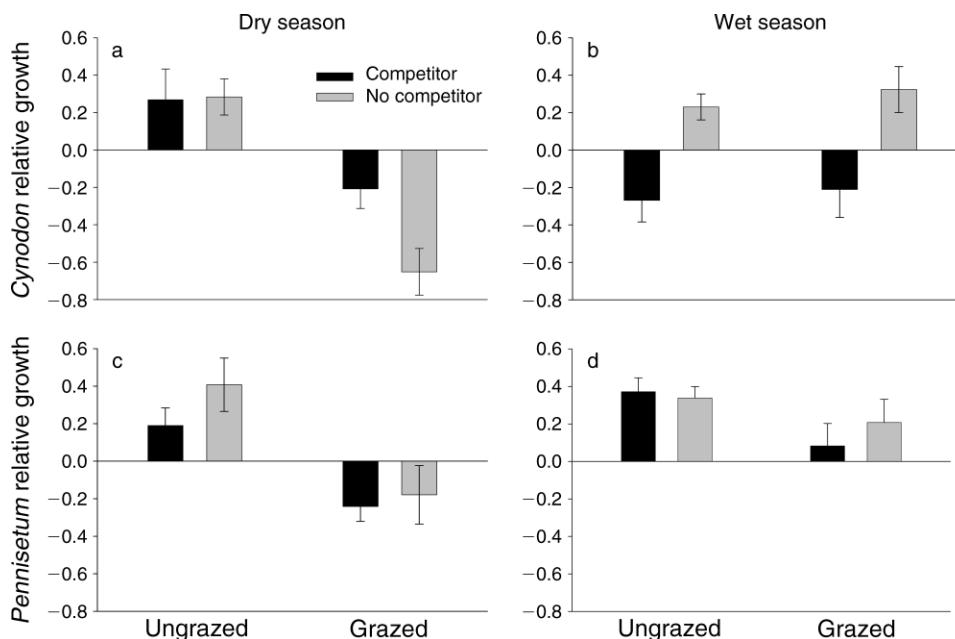

FIG. 1. Effects of interspecific competitors (presence/absence) and grazing (presence/absence) on relative growth (mean ± SE) of the grasses (a, b) *Cynodon plectostachyus* and (c, d) *Pennisetum stramineum* in 1×1 m plots during dry and wet seasons in the semiarid Laikipia District of Kenya. Relative growth was calculated as $\ln([\text{cover } t_2]/[\text{cover } t_1])$; where, in March, t_1 = post-removal baseline cover and t_2 = March cover and, in June, t_1 = March cover and t_2 = June cover.
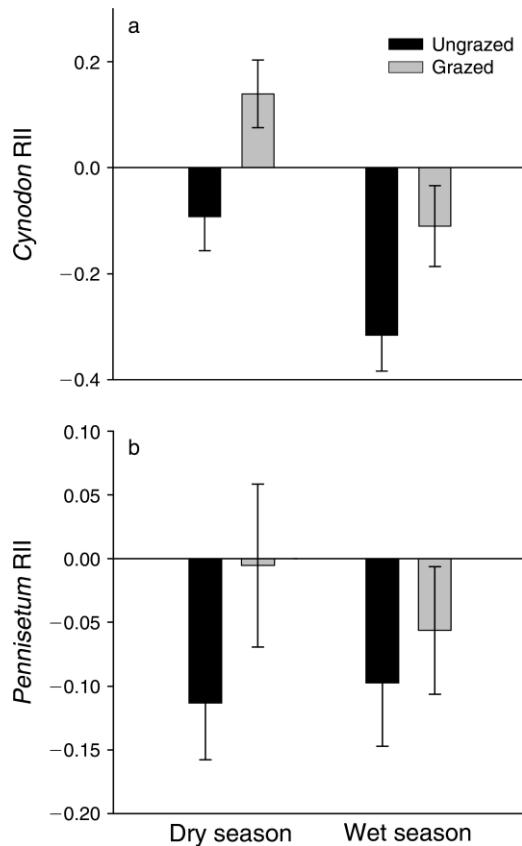
Fig. 2. Effects of season (dry/wet) and grazing (presence/absence) on relative interaction intensity (RII; mean ± SE) between *Cynodon plectostachyus* and *Pennisetum stramineum* in 1 × 1 m plots. RII ranges from −1 to 1, with positive numbers indicating a positive (facilitative) effect of interspecific neighbors and negative numbers indicating a negative (competitive) effect of neighbors. The effects of *Pennisetum* on *Cynodon* are indicated in panel (a) and the reverse in panel (b). Note different scales of *y*-axes.

season than in the dry season. During the wet season, *Pennisetum* was competitively dominant over *Cynodon*; *Pennisetum* cover increased (relative growth > 0) in control plots (both with and without grazing), while *Cynodon* decreased (relative growth < 0) (Fig. 1b, d).

Cynodon performance

Cynodon had a much more complex response to experimental treatments across sampling periods. During the dry season, grazing significantly reduced *Cynodon* cover ($t = -2.96$, df = 39.9, $P = 0.005$; Fig. 1a, Table 1). This effect was amplified by the removal of *Pennisetum*, demonstrating a facilitative effect (RII > 0) on *Cynodon* cover (Fig. 2a). *Cynodon* relative growth was significantly higher in the presence of its interspecific neighbor, but only in the presence of grazing (grazed, competitor presence/absence, $t = 3.19$, df = 42.3, $P = 0.0027$; ungrazed, competitor presence/absence, $t = 0.74$, df = 57.8, $P = 0.33$; Table 1, Fig. 1a). However, this was not true during the wet season when *Pennisetum* had a strongly negative (competitive) effect on *Cynodon* cover ($t = -4.49$, df = 33.3, $P < 0.0001$; Table 1, Fig. 2a). Wet season grazing did not significantly reduce *Cynodon* cover overall ($t = 1.33$, df = 39.9, $P = 0.19$; Table 1, Fig. 1b), and in contrast to the dry season, *Cynodon* cover increased when subjected to both neighbor removal and grazing ($t = -4.41$, df = 42.3, $P < 0.0001$; Table 1, Fig. 1b). Net facilitation did not occur during the wet season.

Density-reduction plots

The facilitative relationship between *Cynodon* and *Pennisetum* appears to be both unidirectional and species specific. A dry-season comparison of *Pennisetum* removal plots (leaving ~50% *Cynodon* cover) with density-reduced control plots (leaving ~25% *Pennisetum* and ~25% *Cynodon*) shows that, at a constant plant cover (~50%), *Cynodon* is facilitated only by *Pennisetum* (grazed, competitor presence/absence, $t = 3.76$, df = 29.7, $P = 0.0007$; ungrazed, competitor presence/absence, $t = 0.82$, df = 33.1, $P = 0.42$; Table 2, Fig. 3). This suggests

TABLE 2. Effects of grazing (presence/absence), competitors (presence/absence), and season (dry/wet) on relative growth of *Cynodon plectostachyus* and *Pennisetum stramineum* in density-reduced 1 × 1 m plots.

Factor	*Cynodon plectostachyus*			*Pennisetum stramineum*		
	df	F	P	df	F	P
Grazing presence/absence	1, 23.1	24.09	<0.0001	1, 18.1	28.08	<0.0001
Competitor presence/absence	1, 22.8	0.82	0.37	1, 13.7	0.50	0.49
Grazing × competitor	1, 20.8	1.32	0.26	1, 9.48	0.27	0.62
Season	1, 24.7	1.09	0.31	1, 22.2	4.64	0.042
Season × grazing	1, 22.4	22.11	0.0001	1, 17.8	6.58	0.02
Season × competitor	1, 17.9	8.03	0.011	1, 13.6	2.60	0.13
Season × grazing × competitor	1, 18.7	8.90	0.0078	1, 9.38	0.41	0.54
Baseline covariate	1, 58.0	1.22	0.27	1, 42.6	8.39	0.0059

Notes: In plots where competitors were present, overall density of both species was reduced to ~50% to match overall density of competitor absence plots. Each species was analyzed with a general linear mixed model (GLMM) repeated-measures ANCOVA. Grazing, competitors, season, and interactions among the three were fixed effects. Block was a random effect, and baseline plant cover of the target species was treated as the covariate.

that facilitation is due neither (1) to less cover (regardless of species identity) or (2) to presence of conspecifics.

Cynodon and *Pennisetum* performed as well or better in density-reduced plots than in neighbor removal plots in all season–grazing combinations except (1) *Cynodon*, grazed during dry season (discussed above) and (2) *Pennisetum*, ungrazed during wet season (data not presented). Overall, both species appeared to respond to a general reduction in competition (and increase in bare ground), irrespective of species identity. Additionally, *Pennisetum* appeared to respond (nonsignificantly) to higher inter- than intraspecific competition when ungrazed during the wet season.

Discussion

For a robust understanding of ecological interactions, ecologists must address context dependency and study how biotic and abiotic factors vary over time to influence species' interactions (Agrawal et al. 2007). Semiarid grazing ecosystems present an ideal opportunity to investigate how herbivory (biotic) effects and wet/dry (abiotic) cycles interact to influence plant–plant facilitation. This study provides experimental evidence that plant–plant interactions are highly contextual. Specifically, I have shown that facilitation (1) occurs only in the dry season, (2) occurs only in the presence of herbivores, (3) is asymmetric (*Cynodon* is facilitated by *Pennisetum*, but not vice versa), and (4) is species specific (*Cynodon* benefits from the presence of *Pennisetum*, but not from the presence of conspecifics). In addition to revealing contextual facilitation of *Cynodon*, the design also revealed more general patterns of competitive (negative) interactions between the two species.

Competitive dynamics

Both species showed strong responses to the wet season. *Pennisetum* responded to increased rainfall with clear competitive dominance and net growth, and *Cynodon* was strongly negatively affected by *Pennisetum* neighbors. These results are consistent with plant competition models indicating more intense competition at higher productivity (Grime 1973, 1977, Tilman 1985, 1988), including during pulses of productivity in dry environments (Goldberg and Novoplansky 1997).

The sensitivity of *Pennisetum*, the competitive dominant, to grazing may help explain two aspects of my experimental results. First, it may partially explain why there were no clear competitive effects of *Cynodon* neighbors on *Pennisetum*; the strong sensitivity of *Pennisetum* to grazing would have swamped any sensitivity to competition. Second, the strong suppression of *Pennisetum* by grazing in the wet season may have ameliorated the effects of grazing on *Cynodon*; this would have contributed to the appearance of *Cynodon* as grazing tolerant under competition in the wet season (Fig. 1b). Similarly, any negative effects of grazing on *Cynodon* also would have muted its competitive ability, thereby benefiting *Pennisetum*. In a Texas rangeland,
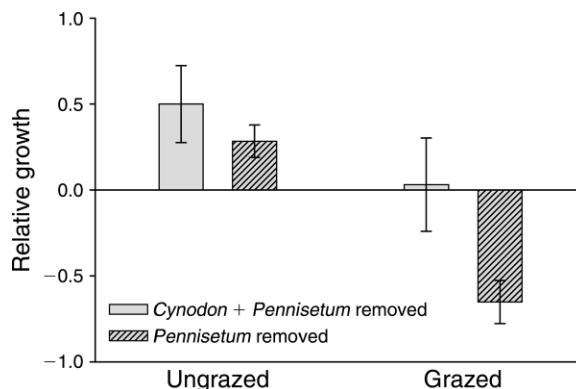

FIG. 3. Effects of grazing (presence/absence) and competitor removal (inter- and intraspecific vs. only interspecific) on relative growth (mean ± SE) of *Cynodon plectostachyus* during the dry season in 1×1 m plots. In *Pennisetum* removal plots, all *Pennisetum* plants were removed. In *Cynodon* + *Pennisetum* removal plots, half of each species was removed. Overall density of plants was held constant across all plots.

Fowler (2002) found that cattle grazing reduced plant–plant competition and attributed it to competitor damage, and a meta-analysis by Gurevitch et al. (2000) found evidence for a general pattern of predation (including herbivory) muting competition.

Dry-season facilitation

Regardless of any herbivory tolerance, *Cynodon* was buffered against the intense herbivory of the dry season through a facilitative relationship with its *Pennisetum* competitors. In addition to being unidirectional and species specific (Figs. 1 and 4), facilitation was limited to the dry season only and occurred only in the presence of herbivores. This net facilitative effect was a product of increased strength of facilitation, but also may have been due to the decreased strength of competition during the dry season.

The predominance of facilitation during the dry season, but not the wet season, is consistent with the abiotic stress hypothesis and with studies showing that facilitation generally strengthens under drier conditions (Greenlee and Callaway 1996, Holzapfel and Mahall 1999, Pugnaire and Lazaro 2000, Tielborger and Kadmon 2000, Kikvidze et al. 2006). Facilitation in these cases is typically attributed to the positive effects of shading and its associated benefits (particularly reduction in transpiration rates) outweighing any negative (competitive) effects. My results also are consistent with recent suggestions that herbivory is the major driver of facilitation in water-limited environments (Baraza et al. 2006, Graff et al. 2007). In these systems, where water is a primary limiting resource (Noy-Meir 1973, Casper and Jackson 1997) dry conditions may amplify the negative (competitive) effects of neighbors for water and outweigh any positive neighbor effects (Tielborger and Kadmon 2000, Maestre et al. 2005). Instead, neighbors may mitigate another major

stress: consumer (grazing) stress. My results demonstrate that neither abiotic stress alone, nor herbivory alone account for facilitation, but that facilitation is driven by an interaction between the two.

The contingency of facilitation upon both grazing and times of abiotic stress likely relates to grazing intensity. There is growing evidence pointing to the intensity (not simply presence or absence) of grazing as an important driver of facilitation (Rebollo et al. 2002, Graff et al. 2007), and the prevalence of facilitation is predicted to increase with increasing grazing stress (Bertness and Callaway 1994; but see Brooker et al. 2006, Smit et al. 2007). There are two major reasons to believe higher grazing intensity may have coincided with the dry season in my study: (1) dry seasons in general are associated with increases in grazing pressure on limited forage and/or with higher herbivore selectivity (Demment and Van Soest 1985, Scoones 1995, Belovsky 1997, Illius and O'Connor 1999, 2000, Fynn and O'Connor 2000, Rousset and Lepart 2002); and (2) in this particular study system, glade areas are subject to especially high herbivore use during dry periods (K. Veblen, *unpublished data*).

Associational resistance

Facilitation of *Cynodon* appears to be a case of "associational resistance" in which some plants gain an advantage by "hiding" among others of higher or lower palatability (Root 1973, Attsat and O'Dowd 1976, Hjältén et al. 1993, Callaway and Aschehoug 2000, Milchunas and Noy-Meir 2002, Bossuyt et al. 2005). Most examples of associational resistance relate to insect herbivores (e.g., Holmes and Jepson-Innes 1989, Hambäck et al. 2000). There are few explicit mammalian herbivore examples (Milchunas and Noy-Meir 2002, Hambäck and Beckerman 2003), which more commonly fall into the category of shared mechanical defenses, such as spines (e.g., Callaway et al. 2000 and references therein). *Cynodon* is considered the most palatable common grass in this ecosystem (T. Young, *personal communication*; K. Veblen, *Interviews with resident ranchers and herders*) and appears to gain associational resistance by growing within less palatable *Pennisetum* stands. Aside from palatability, *Pennisetum* may further deter grazing in the dry season because its stalks and remaining shoots are thick and sharp after being grazed (K. Veblen, *personal observation*).

A major assumption of associational resistance is that herbivores are deterred by the less palatable neighbor species. The neighbor species must be of sufficiently low relative palatability. The grazer must then be sufficiently selective in the quality of food it seeks out because an extremely unselective grazer is more likely to graze all plants, regardless of palatability or quality (McNaughton 1978). A potential mechanism of associational resistance is that the grazer makes foraging decisions at the stand level (Hjältén et al. 1993), whereby the grazer decides to pass over a whole stand due to the unpalatability of only some plants within that stand.

Because herbivores must optimize nutritional advantage (Arnold 1987, Milchunas and Noy-Meir 2002), herbivores may pass over a stand that includes less palatable *Pennisetum* if the costs of seeking out *Cynodon* outweigh nutritional benefits. Furthermore, *Cynodon*, which is characterized by long, thick, erect stolons that are difficult to visually distinguish from *Pennisetum* (K. Veblen, *personal observation*), may gain protection by being harder to detect when growing with *Pennisetum*.

Long-term vegetation dynamics

Short-term species interactions have the potential to profoundly affect longer-term dynamics (Goldberg and Novoplansky 1997, Olff et al. 1999, Rousset and Lepart 2000, Armas and Pugnaire 2005). In this system, short-term competition–facilitation dynamics between *Cynodon* and *Pennisetum* may affect long-term glade successional patterns. Glade vegetation is initially colonized by *Cynodon* before gradual invasion and dominance by *Pennisetum* (K. Veblen, *unpublished data*). This means that the wet season competitive dominance by *Pennisetum* may prevail over the long term, which suggests that increased frequency or duration of wet periods could speed the succession process. Conversely, my results illustrate that dry-season plant–plant interactions (such as the observed facilitation of *Cynodon* by *Pennisetum*) oppose the direction of succession, which may effectively retard or decrease the rate of glade succession.

Herbivory, including its intensity and interaction with wet/dry cycles, also is likely to mediate these successional processes. In savanna ecosystems, where the duration and intensity of herbivory and rainfall vary tremendously over time and space, herbivores—and their interactions with wet/dry cycles—have the potential to be major drivers of long-term ecosystem change. We know that herbivores can influence succession (e.g., Dormann et al. 2000, Fagan and Bishop 2000, Bokdam 2001, Skarpe 2001, Seabloom and Richards 2003), that intensity of herbivory matters (e.g., Rebollo et al. 2002, Brooker et al. 2006, Graff et al. 2007), and that different guilds of herbivores have different and sometimes interactive effects on the plant community (McNaughton 1978, Young et al. 2005). But we must explicitly test how herbivory interacts with temporal and spatial variation in plant community dynamics in order to elucidate and make meaningful predictions about the relationships between short-term and long-term dynamics in savanna ecosystems.

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