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**Season- and herbivore-dependent competition and facilitation
in a semi-arid savanna**

Kari E. Veblen

Dept of Plant Sciences and Graduate Group in Ecology

University of California

Davis, CA 95616

keveblen@ucdavis.edu

11 Abstract

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

29

30 Key words

31 *Acacia drepanolobium* savanna; associational resistance; *Cynodon plectostachyus*; grasslands;
32 facilitation; indirect effects; herbivory; *Pennisetum stramineum*; succession

33

34 **Introduction**

35 Plant communities are shaped by complex interactions among multiple biotic and abiotic
36 factors. Although competition has been emphasized as the primary biotic driver of plant
37 interactions (Connell 1983, Schoener 1983, Goldberg and Barton 1992), a more recent profusion
38 of evidence indicates that net plant-plant interactions often are the result of both competitive and
39 facilitative interactions (Callaway 1995, Holmgren et al. 1997, Kikvidze et al. 2006, Graff et al.
40 2007). Theoretical and empirical evidence suggests that facilitative (positive) relationships are
41 more common in stressful or disturbed environments where the facilitator ameliorates abiotic
42 stress (Pugnaire and Luque 2001, Callaway et al. 2002) or consumer stress (Holmes and Jepson-
43 Innes 1989, Bertness and Callaway 1994, Gómez et al. 2001). Not surprisingly, a preponderance
44 of examples of facilitation in plants, both direct (Callaway 1992, Maestre et al. 2003) and
45 indirect (McNaughton 1978, Holmes and Jepson-Innes 1989, Gómez et al. 2001, Rebollo et al.
46 2002) are found in arid and semi-arid systems that undergo extremes in both abiotic stress (e.g.,
47 drought) and consumer stress (e.g., herbivory). Surprisingly few studies, however, have
48 examined interactions between these two stresses.

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

55 Herbivory also affects the net direction of plant-plant interactions by mediating both
56 positive and negative interactions (Gurevitch et al. 2000, Hambäck and Beckerman 2003,

57 Callaway et al. 2005, Brooker et al. 2006, Graff et al. 2007). If a plant species is selectively
58 grazed, its fitness may be decreased, thereby altering competitive dynamics within the plant
59 community (Gurevitch et al. 2000, van der Wal et al. 2000, Fowler 2002). On the other hand,
60 positive plant-plant relationships are mediated by herbivore foraging behavior when one plant
61 species benefits by growing in close proximity to another (better-defended) species (e.g., Rebollo
62 et al. 2002).

63 The behavior of herbivores and their effects on the plant community often vary
64 seasonally. Mammalian herbivores, driven by metabolic requirements, often become more
65 selective in order to attain high quality forage during dry times (Demment and Van Soest 1985,
66 Belovsky 1997). Additionally, defoliation may be more intense or spatially concentrated as
67 quantity and availability of forage becomes limited during dry times (Scoones 1995, Ilius and
68 O'Connor 1999, Fynn and O'Connor 2000, Ilius and O'Connor 2000, Rousset and Lepar 2002).
69 Conversely, defoliation may be less intense or more spatially diffuse during wet times when
70 green forage is abundant (Scoones 1995, Ilius and O'Connor 2000).

71 Different combinations of herbivory and rainfall intensities have contrasting effects on
72 community patterns and processes (Proulx and Mazumder 1998, Fynn and O'Connor 2000,
73 Osem et al. 2002, Augustine and McNaughton 2006). Understanding how herbivory interacts
74 with seasonal dynamics has direct implications for our understanding of the mechanics of
75 competition-facilitation processes as drivers of short-term community change (e.g., Callaway et
76 al. 2005). Additionally, short-term processes can influence the longer-term trajectory of the
77 ecosystem (Hobbs 1996, Goldberg et al. 1999, Rousset and Lepar 2002, Gratton and Denno
78 2003, Gómez 2005). Short-term competition-facilitation processes in particular can be key
79 components of long-term successional change (Connell and Slatyer 1977, Olff et al. 1999,

80 Baumeister and Callaway 2006, Zanini et al. 2006, Dickie et al. 2007).

81 I experimentally examined the roles of season and herbivory in the competition-
82 facilitation balance between two grass species, *Cynodon plectostachyus* and *Pennisetum*
83 *stramineum*, in a semi-arid ecosystem. I manipulated neighboring plant composition and density,
84 as well as herbivore access, in both wet and dry periods. These two grass species co-occur in
85 large patches that undergo successional development from *Cynodon* dominance to *Pennisetum*
86 dominance. I asked the following questions: a) Does facilitation occur between *Pennisetum* and
87 *Cynodon*? b) If facilitation does occur, is it stronger in the dry season? c) Is facilitation
88 mediated by herbivory? d) Do the effects of season and herbivory interact? and e) How do short-
89 term dynamics compare to the known long-term trajectory of the system?

90

91 **Methods**

92 *Study site*

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

100 My study area is located in *Acacia drepanolobium* savanna and is underlain with “black
101 cotton” soils, poorly drained vertisols with high clay content (Ahn and Geiger 1987). In this
102 system, 97% of the tree canopy cover is *Acacia drepanolobium*, and 90% of herbaceous cover is

103 comprised of six species: *Pennisetum mezianum*, *P. stramineum*, *Themeda triandra*, *Lintonia*
104 *nutans*, *Aerva lanata* and *Brachiaria lachnantha* (Young et al. 1998). Resident large mammals
105 include: elephants (*Loxodonta africana*), zebras (*Equus burchellii*), Grant's gazelles (*Gazella*
106 *grantii*), hartebeests (*Alcelaphus buselaphus*), steinbucks (*Raphicerus campestris*), elands
107 (*Taurotragus oryx*), buffaloes (*Syncerus caffer*), giraffes (*Giraffa camelopardalis*), spotted
108 hyaenas (*Crocuta crocuta*), lions (*Panthera leo*), and leopards (*Panthera pardus*). This area is
109 actively managed for cattle, with stocking rates of 0.5-0.7 livestock units/ha.

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

117

118 *Experimental design and data collection*

119 I investigated competition and facilitation dynamics between *Pennisetum stramineum* and
120 *Cynodon plectostachyus* in glades using a 2 x 2 x 2 factorial design. For each of these two
121 species, I crossed species removal treatments (interspecific neighbors present vs. interspecific
122 neighbors removed) with grazing treatments (grazers allowed vs. grazers excluded).
123 Experimental plots were randomly located within glade areas co-dominated by *Pennisetum* and
124 *Cynodon* (plots were considered 'co-dominated' so long as neither species exhibited >80%
125 cover; measurements described below).

126 Six neighbor/grazing treatment combinations were replicated within each of twelve
127 randomly chosen glades (with treatments established in five glades in August 2004, and seven in
128 August 2005) for a total of 72 experimental plots. Three of the six treatments were grazed, and
129 the remaining three were ungrazed. Crossed with each grazing treatment were the following
130 three species removal treatments: *Pennisetum* removal, *Cynodon* removal, and control (neither
131 *Cynodon* nor *Pennisetum* removed). Each of the seven glades in 2005 included two additional
132 treatments that were added to tease apart inter- vs. intraspecific neighbor effects: one grazed and
133 one ungrazed density-reduced control plot. All 86 plots were 1x1m.

134 Grazed plots were left open to grazing, and ungrazed plots were covered with 1x1x1m
135 chicken wire mesh cages that prevented grazing by larger vertebrate herbivores. The lower
136 halves of the cages were covered with 30 cm tall hardware cloth to also exclude the dominant
137 herbivorous rodent, *Saccostomus mearnsi*. In all plots, I identified all individual plants to
138 species. In species removal plots, all individuals of target species were removed. In density-
139 reduced control plots, I haphazardly removed individuals of both grass species until the overall
140 cover was half of its starting density (with density first assessed visually and then confirmed by
141 counting pin frame pin hits; see below). In all 86 plots, all forbs, which comprised an average of
142 2.9% of total cover, and all non-target grass species, which comprised an average 2.8% of total
143 cover, were removed. All removed plants were clipped to remove above-ground biomass and
144 later were individually treated by sponge with Roundup® (glyphosate) herbicide after rainfall
145 and any new growth.

146 Prior to manipulation, within each 1x1m plot, I quantified plant cover with five evenly
147 spaced ten-point pin frames. I repeated baseline pin frame counts in 'removal' plots immediately
148 after neighbor removal treatments were complete. I assessed the effects of experimental

149 treatments on *Cynodon* and *Pennisetum* by repeating pinframe measurements in all plots at the
150 end of the three-month-long dry season in the March following plot set-up (28 mm rainfall in
151 January-March 2005 and 24mm in January-March 2006). I repeated measurements three months
152 later in June at the end of a heavy rainfall period (227 mm rainfall in April-June 2005, and 153
153 mm in April-June 2006). Plots set up in 2004 were assessed only during the 2005 dry and wet
154 seasons. For pin frame cover estimates, I counted the total number of times that each species
155 touched each pin. As a result, the pin frame count for any given species often far exceeded ten.
156 Although I hereafter refer to pin frame measurements as “cover,” total number of pin hits is
157 positively correlated with biomass of each species (*Cynodon* $R^2=0.89$, K. Veblen unpublished
158 data; *Pennisetum* $R^2=0.65$, I. Kimathi unpublished data).

159

160 *Data analyses*

161 I calculated mean *Cynodon* and *Pennisetum* cover values for each 1x1m plot in each
162 sampling period. I quantified how *Cynodon* and *Pennisetum* cover changed over time (in
163 response to grazing, neighbor and season effects) by calculating a relative growth index.
164 Relative growth was calculated as $\text{Ln}((\text{cover } t_2)/(\text{cover } t_1))$. I calculated relative growth during
165 the dry season (t_1 =post-manipulation baseline cover, t_2 =March cover) and wet season (t_1 =March
166 cover, t_2 =June cover) for each species/neighbor/grazing combination. Relative growth values are
167 symmetrical around zero, with positive numbers indicating increases in cover and negative
168 numbers indicating decreases in cover.

169 I calculated an additional index, relative interaction intensity (RII), to depict positive
170 versus negative effects of heterospecific neighbor presence on cover of each species. The RII
171 provides a measure of the relative difference in cover of a target species in plots with neighbors

172 versus plots without neighbors. I calculated the mean (\pm 1 SE) relative interaction intensities
173 (RII) between *Cynodon* and *Pennisetum* for all four season/grazing combinations (wet grazed,
174 wet ungrazed, dry grazed and dry ungrazed). RII was calculated with the following equation:
175 $RII = (B_w - B_o) / (B_w + B_o)$ where B_w = cover of target species growing with neighbor (i.e., control
176 plot) and B_o = cover of target species growing without neighbors (i.e., removal plot) (Armas et al.
177 2004). RII values fall between -1 and +1, with negative values indicating competitive neighbor
178 effects and positive values indicating facilitative neighbor effects.

179 I used a general linear mixed model (GLMM) to conduct a repeated measures analysis of
180 covariance (ANCOVA) testing treatment and time (i.e., season) effects on *Cynodon* and
181 *Pennisetum* relative growth. For each grass species, grazing treatment (presence/absence),
182 neighbor treatment (presence/absence), season (dry/wet), and interactions among the three were
183 fixed factors. I used maximum-likelihood methodology, as well as Satterthwaite's
184 approximation of degrees of freedom (PROC MIXED, version 9.1, SAS Institute 2002). Block
185 (i.e., glade) was treated as the experimental unit and was designated as a random effect. Pre-
186 manipulation baseline cover of target species was treated as the covariate. I made pairwise
187 comparisons for grazing, competition and grazing*competition within each season using
188 unprotected LSD t-tests, applying Bonferonni corrections to significance values ($p=0.025$, 0.025 ,
189 and 0.0125 , respectively). For relative growth analyses, the two years' worth of data were
190 pooled because species responses were qualitatively identical in the two years and preliminary
191 models indicated that the effect of year was negligible. For density reduction plots, relative
192 growth and statistical calculations were performed as above, replacing 'control' plots with
193 'density-reduced control plots. Although mean RII values are presented to indicate the direction

194 and magnitude of neighbor effects, I did not conduct statistical analyses of RII values which are
195 simply a composite representation of data already analyzed in relative growth analyses.

196

197 **Results**

198 The two grass species differed in their responses to experimental grazing and neighbor
199 treatments over the two seasons. *Pennisetum* showed negative responses to grazing, especially
200 during the dry season, and a highly positive response to rainfall. *Cynodon* also experienced
201 strong competitive suppression under several treatment combinations. However, *Cynodon*
202 showed a net facilitation response to neighboring *Pennisetum* plants in the presence of
203 herbivores in the dry season.

204

205 *Pennisetum* performance

206 The presence of herbivores significantly decreased cover of *Pennisetum*, and this effect
207 was especially pronounced during the dry season (Table 1; Fig. 1c,d). *Pennisetum* cover was
208 44% lower in plots open to grazing. Although grazing decreased *Pennisetum* cover during the
209 wet season (Fig. 1d), grazing led to net loss of *Pennisetum* cover only during the dry season (Fig.
210 1c). Though less influential than grazing and non-significant, interspecific competitors also
211 decreased *Pennisetum* (Fig. 1c; Table 1), with *Cynodon* removal increasing *Pennisetum* cover by
212 an average of 16%. Although the season*herbivory*competitor interaction was not significant,
213 (Table 1), the negative neighbor effects of *Cynodon* appear most pronounced in ungrazed plots
214 during the dry season, (Fig. 1c). There was no evidence of facilitation of *Pennisetum* by
215 *Cynodon* under any grazing by season combination (Fig. 1c,d; Table 1).

216 Despite the negative effects of grazing and neighbors on *Pennisetum* performance, wet
217 season *Pennisetum* growth was so pronounced that net increases in cover occurred in all plots,
218 even those with both competition and grazing. *Pennisetum* cover was 33% higher in the wet
219 season than in the dry season. During the wet season *Pennisetum* was competitively dominant
220 over *Cynodon*; *Pennisetum* cover increased (relative growth >0) in control plots (both with and
221 without grazing), while *Cynodon* decreased (relative growth <0) (Fig. 1b,d).

222

223 *Cynodon* performance

224 *Cynodon* had a much more complex response to experimental treatments across sampling
225 periods. During the dry season, grazing significantly reduced *Cynodon* cover ($t=-2.96$, $df=39.9$,
226 $p=0.005$; Fig. 1a; Table 1). This effect was amplified by the removal of *Pennisetum*,
227 demonstrating a facilitative effect ($RII>0$) on *Cynodon* cover (Fig. 2a). *Cynodon* relative growth
228 was significantly higher in the presence of its interspecific neighbor, but only in the presence of
229 grazing (grazed, competitor pres/abs: $t=3.19$, $df=42.3$, $p=0.0027$; ungrazed, competitor pres/abs:
230 $t=0.74$, $df=57.8$, $p=0.33$; Table 1; Fig. 1a). However, this was not true during the wet season
231 when *Pennisetum* had a strongly negative (competitive) effect on *Cynodon* cover ($t=-4.49$
232 $df=33.3$ $p<0.0001$; Table 1; Fig. 2a). Wet season grazing did not significantly reduce *Cynodon*
233 cover overall ($t=1.33$, $df=39.9$, $p=0.19$; Table 1; Fig. 1b), and in contrast to the dry season,
234 *Cynodon* cover increased when subjected to both neighbor removal and grazing ($t=-4.41$,
235 $df=42.3$, $p<0.0001$; Table 1; Fig. 1b). Net facilitation did not occur during the wet season.

236

237 Density reduction plots

238 The facilitative relationship between *Cynodon* and *Pennisetum* appears to be both
239 unidirectional and species-specific. A dry season comparison of *Pennisetum* removal plots
240 (leaving ~50% *Cynodon* cover) with density-reduced control plots (leaving ~25% *Pennisetum*
241 and ~25% *Cynodon*) shows that, at a constant plant cover (~50%), *Cynodon* is facilitated only by
242 *Pennisetum* (grazed, competitor pres/abs: $t=3.76$, $df=29.7$, $p=0.0007$; ungrazed, competitor
243 pres/abs: $t=0.82$, $df=33.1$, $p=0.42$; Table 2; Fig. 3). This suggests that facilitation is due neither
244 a) to less cover (regardless of species identity) or b) to presence of conspecifics.

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

252

253 **Discussion**

254 For a robust understanding of ecological interactions, ecologists must address context-
255 dependency and study how biotic and abiotic factors vary over time to influence species'
256 interactions (Agrawal et al. 2007). Semi-arid grazing ecosystems present an ideal opportunity to
257 investigate how herbivory (biotic) effects and wet/dry (abiotic) cycles interact to influence plant-
258 plant facilitation. This study provides experimental evidence that plant-plant interactions are
259 highly contextual. Specifically, I have shown that facilitation 1) occurs only in the dry season, 2)
260 occurs only in the presence of herbivores, 3) is asymmetric (*Cynodon* is facilitated by

261 *Pennisetum*, but not vice-versa), and 4) is species-specific (*Cynodon* benefits from the presence
262 of *Pennisetum*, but not from the presence of con-specifics). In addition to revealing contextual
263 facilitation of *Cynodon*, the design also revealed more general patterns of competitive (negative)
264 interactions between the two species.

265

266 Competitive dynamics

267 Both species showed strong responses to the wet season. *Pennisetum* responded to
268 increased rainfall with clear competitive dominance and net growth, and *Cynodon* was strongly
269 negatively affected by *Pennisetum* neighbors. These results are consistent with plant
270 competition models indicating more intense competition at higher productivity (Grime 1973,
271 1977, Tilman 1985, 1988), including during pulses of productivity in dry environments
272 (Goldberg and Novoplansky 1997).

273 The sensitivity of *Pennisetum*, the competitive dominant, to grazing may help explain
274 two aspects of my experimental results. First, it may partially explain why there were no clear
275 competitive effects of *Cynodon* neighbors on *Pennisetum*; the strong sensitivity of *Pennisetum* to
276 grazing would have swamped any sensitivity to competition. Second, the strong suppression of
277 *Pennisetum* by grazing in the wet season may have ameliorated the effects of grazing on
278 *Cynodon*; this would have contributed to the appearance of *Cynodon* as grazing tolerant under
279 competition in the wet season (Figure 1b). Similarly, any negative effects of grazing on
280 *Cynodon* also would have muted its competitive ability, thereby benefiting *Pennisetum*. In a
281 Texas rangeland Fowler (2002) found that cattle grazing reduced plant-plant competition and
282 attributed it to competitor damage, and a meta-analysis by Gurevitch et al. (2000) found evidence
283 for a general pattern for predation (including herbivory) muting competition.

284

285 Dry season facilitation

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

292 The predominance of facilitation during the dry season, but not the wet season, is
293 consistent with the abiotic stress hypothesis and with studies showing that facilitation generally
294 strengthens under drier conditions (Greenlee and Callaway 1996, Holzapfel and Mahall 1999,
295 Pugnaire and Lazaro 2000, Tielborger and Kadmon 2000, Kikvidze et al. 2006). Facilitation in
296 these cases is typically attributed to the positive effects of shading and its associated benefits
297 (particularly reduction in transpiration rates) outweighing any negative (competitive) effects.
298 My results also are consistent with recent suggestions that herbivory is the major driver of
299 facilitation in water-limited environments (Baraza et al. 2006, Graff et al. 2007). In these
300 systems, where water is a primary limiting resource (Noy-Meir 1973, Casper and Jackson 1997)
301 dry conditions may amplify the negative (competitive) effects of neighbors for water and
302 outweigh any positive neighbor effects (Tielborger and Kadmon 2000, Maestre et al. 2005).
303 Instead, neighbors may mitigate another major stress: consumer (grazing) stress. My results
304 demonstrate that neither abiotic stress alone, nor herbivory alone account for facilitation, but that
305 facilitation is driven by an interaction between the two.

306 The contingency of facilitation upon both grazing and times of abiotic stress likely relates
307 to grazing intensity. There is growing evidence pointing to the intensity (not simply presence or
308 absence) of grazing as an important driver of facilitation (Rebollo et al. 2002, Graff et al. 2007),
309 and the prevalence of facilitation is predicted to increase with increasing grazing stress (Bertness
310 and Callaway 1994, but see Brooker et al. 2006, Smit et al. 2007). There are two major reasons
311 to believe higher grazing intensity may have coincided with the dry season in my study: 1) dry
312 seasons in general are associated with increases in grazing pressure on limited forage and/or with
313 higher herbivore selectivity (Demment and Van Soest 1985, Scoones 1995, Belovsky 1997, Illius
314 and O'Connor 1999, Fynn and O'Connor 2000, Illius and O'Connor 2000, Rousset and Lepar
315 2002); and 2) in this particular study system, glade areas are subject to especially high herbivore
316 use during dry periods (K.Veblen, unpublished data).

317

318 Associational resistance

319 Facilitation of *Cynodon* appears to be a case of “associational resistance” in which some
320 plants gain an advantage by “hiding” among others of higher or lower palatability (Root 1973,
321 Attsat and O'Dowd 1976, Hjältén et al. 1993, Callaway and Aschehoug 2000, Milchunas and
322 Noy-Meir 2002, Bossuyt et al. 2005). Most examples of associational resistance relate to insect
323 herbivores (e.g., Holmes and Jepson-Innes 1989, Hambäck et al. 2000). There are few explicit
324 mammalian herbivore examples (Milchunas and Noy-Meir 2002, Hambäck and Beckerman
325 2003), which more commonly fall into the category of shared mechanical defenses, such as
326 spines (e.g., Callaway et al. 2000 and references therein). *Cynodon* is considered the most
327 palatable common grass in this ecosystem (T. Young, personal communication; K. Veblen,
328 interviews with resident ranchers and herders) and appears to gain associational resistance by

329 growing within less palatable *Pennisetum* stands. Aside from palatability, *Pennisetum* may
330 further deter grazing in the dry season because its stalks and remaining shoots are thick and sharp
331 after being grazed (K. Veblen, personal observation).

332 A major assumption of associational resistance is that herbivores are deterred by the less
333 palatable neighbor species. The neighbor species must be of sufficiently low relative
334 palatability. The grazer must then be sufficiently selective in the quality of food it seeks out
335 because an extremely unselective grazer is more likely to graze all plants, regardless of
336 palatability or quality (McNaughton 1978). A potential mechanism of associational resistance is
337 that the grazer makes foraging decisions at the stand level (Hjältén et al. 1993), whereby the
338 grazer decides to pass over a whole stand due to the unpalatability of only some plants within
339 that stand. Because herbivores must optimize nutritional advantage (Arnold 1987, Milchunas
340 and Noy-Meir 2002), herbivores may pass over a stand that includes less palatable *Pennisetum* if
341 the costs of seeking out *Cynodon* outweigh nutritional benefits. Furthermore, *Cynodon*, which is
342 characterized by long, thick, erect stolons that are difficult to visually distinguish from
343 *Pennisetum* (K. Veblen, personal observation), may gain protection by being harder to detect
344 when growing with *Pennisetum*.

345

346 Long-term vegetation dynamics

347 Short-term species interactions have the potential to profoundly affect longer-term
348 dynamics (Goldberg and Novoplansky 1997, Olff et al. 1999, Rousset and Lepart 2000, Armas
349 and Pugnaire 2005). In this system, short-term competition-facilitation dynamics between
350 *Cynodon* and *Pennisetum* may affect long-term glade successional patterns. Glade vegetation is
351 initially colonized by *Cynodon* before gradual invasion and dominance by *Pennisetum* (K.

352 Veblen, unpublished data). This means that the wet season competitive dominance by
353 *Pennisetum* may prevail over the long-term, which suggests that increased frequency or duration
354 of wet periods could speed the succession process. Conversely, my results illustrate that dry
355 season plant-plant interactions (such as the observed facilitation of *Cynodon* by *Pennisetum*)
356 oppose the direction of succession, which may effectively retard or decrease the rate of glade
357 succession.

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

370

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380

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555 Table 1. Effects of grazing (presence/absence), competitors (presence/absence) and season (dry/wet)
 556 on relative growth of *Cynodon plectostachyus* and *Pennisetum stramineum* in 1x1m plots.

557

Factor	<i>Cynodon plectostachyus</i>			<i>Pennisetum stramineum</i>		
	df	F	p	df	F	p
Grazing pres/abs	1, 22.0	23.34	<.0001	1, 20.8	30.65	<.0001
Competitor pres/abs	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	<.0001	1, 20.8	5.05	0.034
Season*Competitor	1, 21.8	27.21	<.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

558

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

563 Table 2. Effects of grazing (presence/absence), competitors (presence/absence) and season (dry/wet)
 564 on relative growth of *Cynodon plectostachyus* and *Pennisetum stramineum* in density-reduced 1x1m
 565 plots. In plots where competitors were present, overall density of both species was reduced to ~50%
 566 to match overall density of competitor absence plots.

567

Density-reduced

Factor	<i>Cynodon plectostachyus</i>			<i>Pennisetum stramineum</i>		
	df	F	p	df	F	p
Grazing pres/abs	1, 23.1	24.09	<.0001	1, 18.1	28.08	<.0001
Competitor pres/abs	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

568

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

572

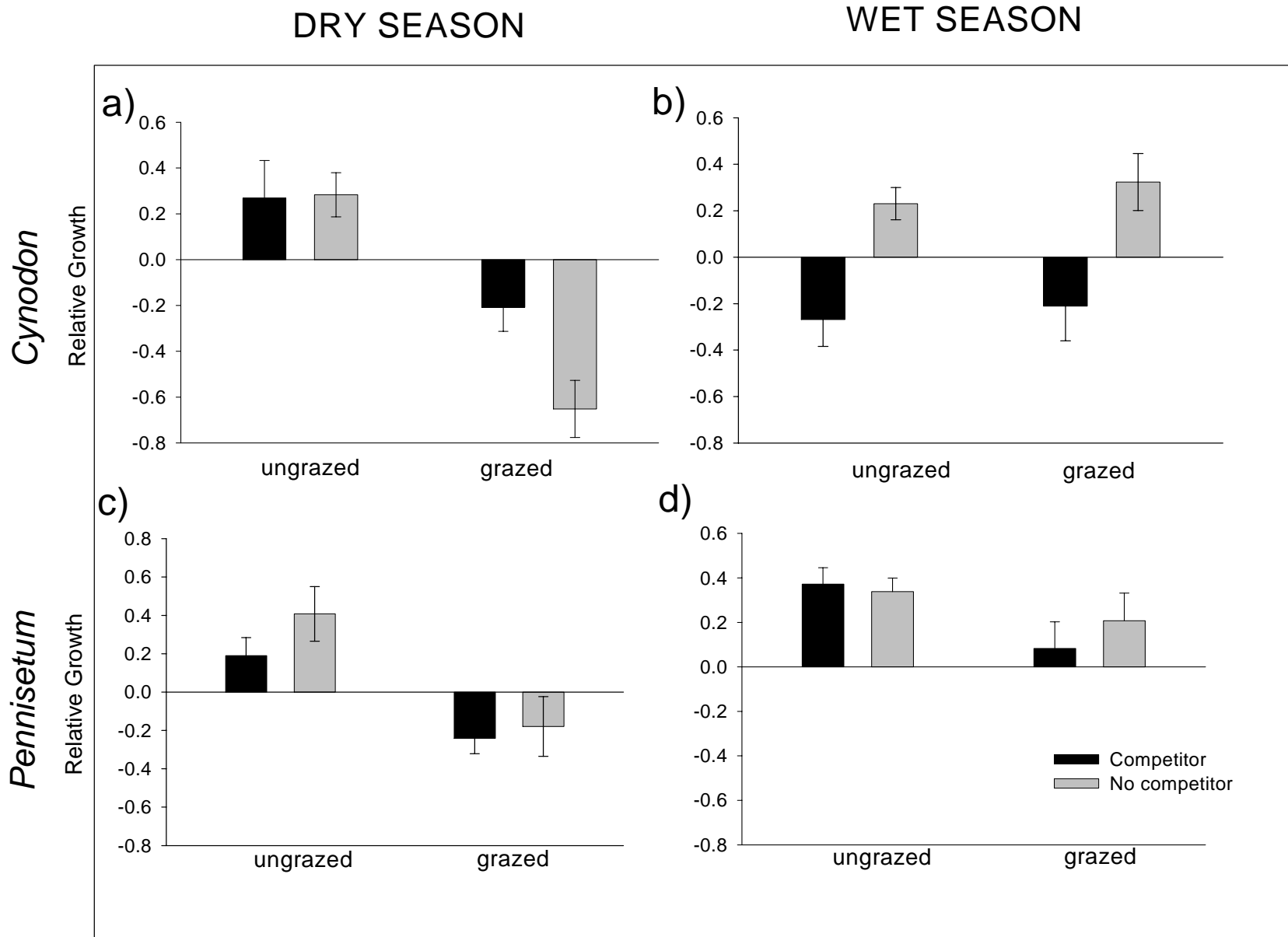
573 **Figure legends**

574 Figure 1. Effects of interspecific competitors (presence/absence) and grazing (presence/absence)
575 on mean (\pm 1SE) relative growth of *Cynodon plectostachyus* (a, b) and *Pennisetum stramineum*
576 (c,d) in 1x1m. plots during dry and wet seasons. Relative growth calculated as $\text{Ln}[(\text{cover}$
577 $t_2)/(\text{cover } t_1)]$.

578
579 Figure 2. Effects of season (dry/wet) and grazing (presence/absence) on mean (\pm 1SE) relative
580 interaction intensity (RII) between *Cynodon plectostachyus* and *Pennisetum stramineum* in 1x1m
581 plots. RII ranges from -1 to 1, with positive numbers indicating a positive (facilitative) effect of
582 interspecific neighbors and negative numbers indicating a negative (competitive) effect of neighbors.
583 The effects of *Pennisetum* on *Cynodon* are indicated in a), and the reverse in b). Note different scales
584 of y axes.

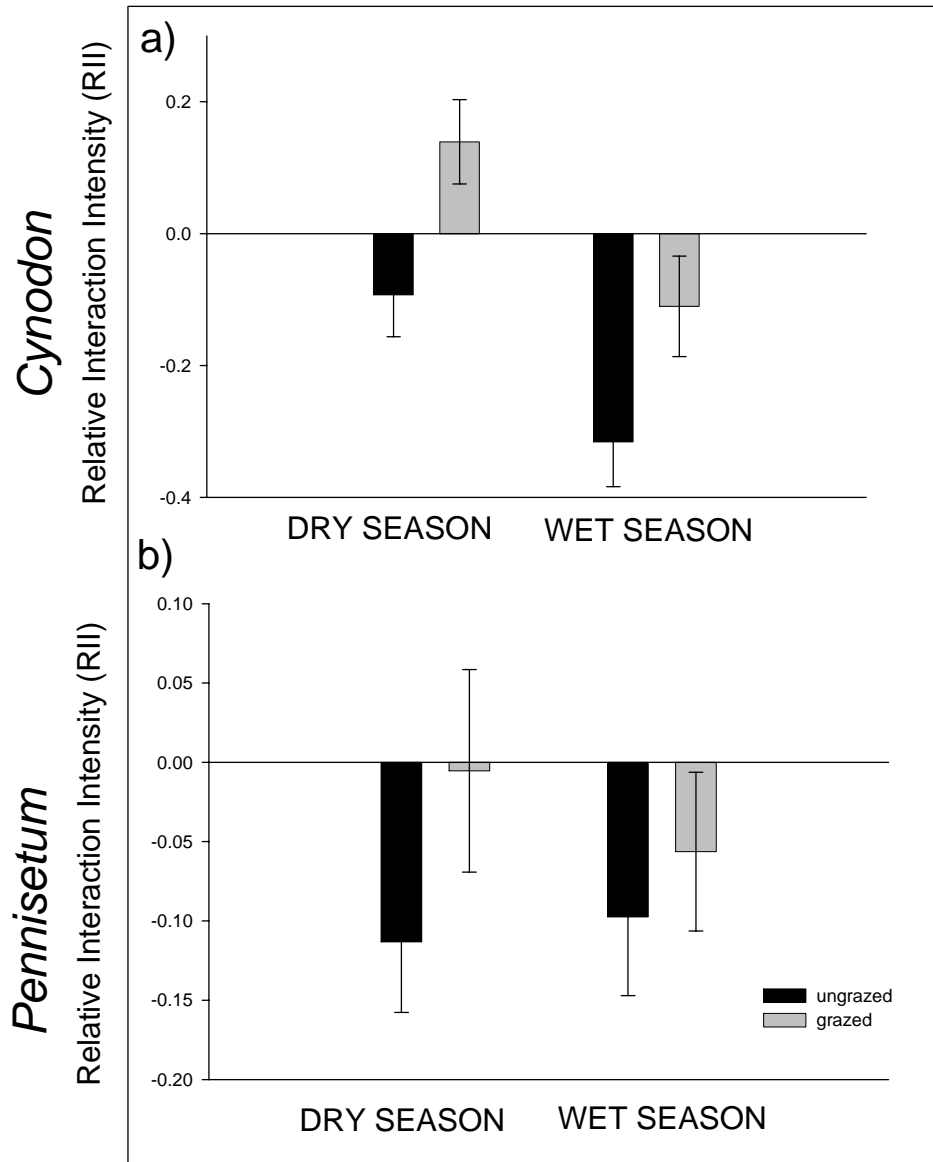
585
586 Figure 3. Effects of grazing (presence vs. absence) and competitor removal (inter- and intra-specific
587 vs. only interspecific) on mean (\pm 1SE) relative growth of *Cynodon plectostachyus* during the dry
588 season in 1x1m plots. In *Pennisetum* removal plots, all *Pennisetum* plants were removed. In
589 *Cynodon+Pennisetum* removal plots, half of each species was removed. Overall density of plants was
590 held constant across all plots.

591 **Figure 1.**



593
594

Figure 2.



595
596

597 **Figure 3.**

