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Season- and herbivore-dependent competition and facilitation

3
in a semi-arid savanna

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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**

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, Illius and

68   O'Connor 1999, Fynn and O'Connor 2000, Ilius and O'Connor 2000, Rousset and Lepart 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 Lepart 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 compestris*), 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 Ln ((cover t_2)/(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 (+/- 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 Sattherthwaite'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, Ilius and O'Connor 2000, Rousset and Lepart

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   <u>Long-term vegetation dynamics</u>

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

371   **Acknowledgments**

380

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554   subtropical old field. Plant Ecology **185**:179-190.

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	*Cynodon plectostachyus*			*Pennisetum stramineum*		
	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					
	Cynodon plectostachyus			***Pennisetum stramineum***		
Factor	**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

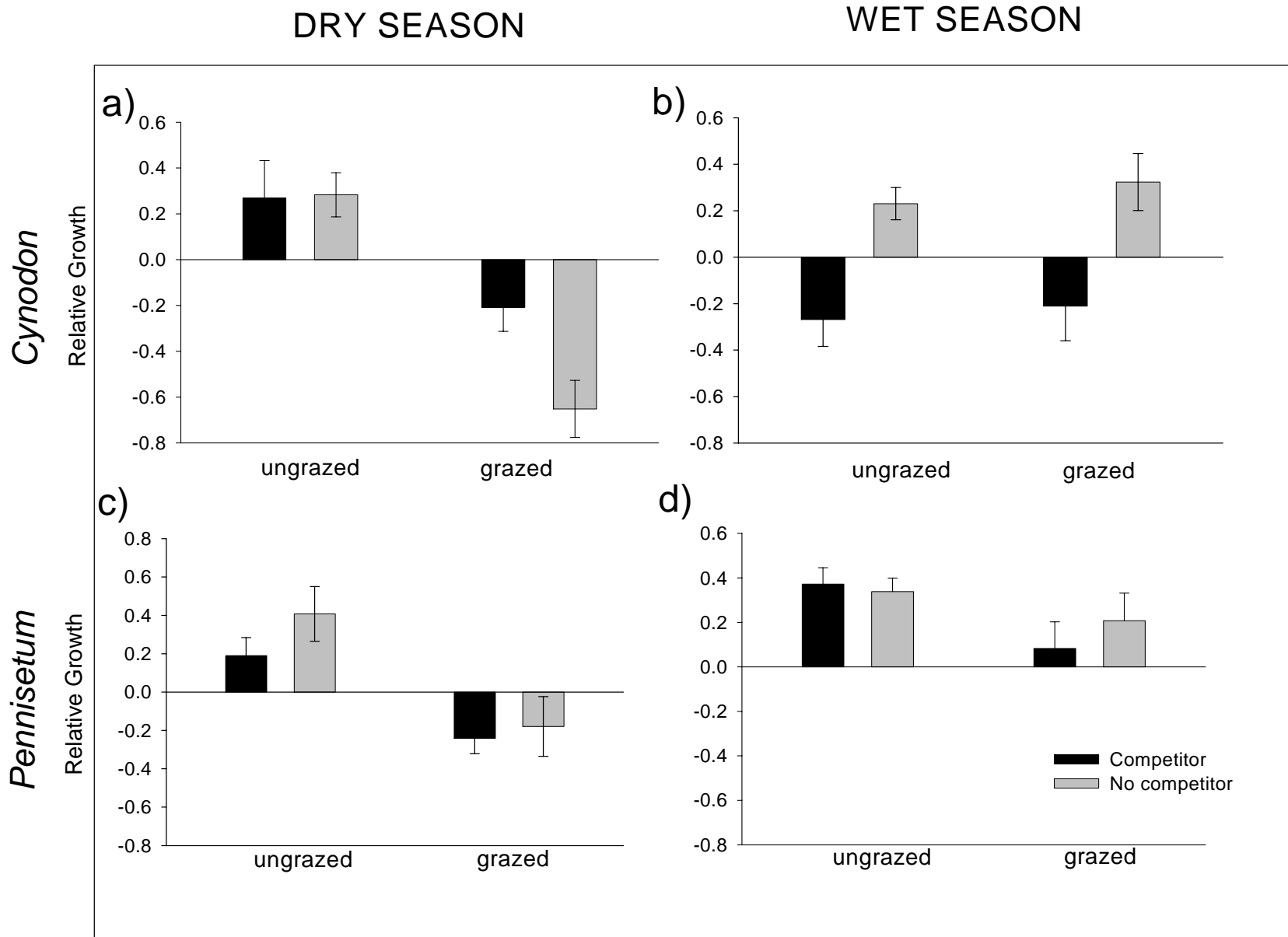571   was a random effect, and baseline plant cover of the target species was treated as the covariate.

572

573 **Figure legends**

574 Figure 1. Effects of interspecific competitors (presence/absence) and grazing (presence/absence)

575 on mean (+/-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 Ln [(cover

577 t2)/(cover t1)].

578

579 Figure 2. Effects of season (dry/wet) and grazing (presence/absence) on mean (+/-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
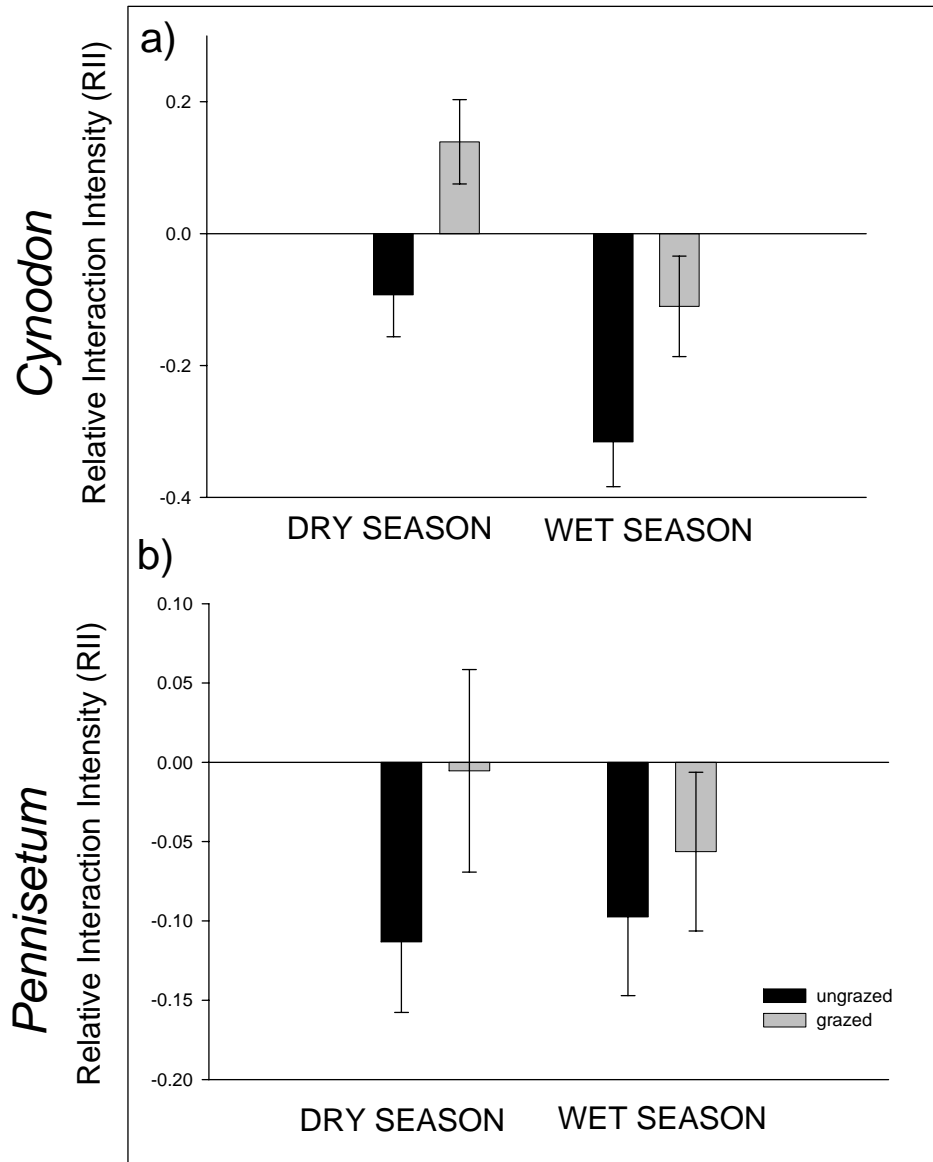
584 of y axes.

585

586 Figure 3. Effects of grazing (presence vs. absence) and competitor removal (inter- and intra-specific

587 vs. only interspecific) on mean (+/-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.**

DRY SEASON   WET SEASON

592

593 **Figure 2.**
594

595
596

597 **Figure 3.**

Cynodon, dry season