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Kari E. Veblen, *Utah State University*
T. P. Young



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**Contrasting effects of cattle and wildlife on the vegetation development of a savanna
landscape mosaic**

Kari E. Veblen^{1*}

Truman P. Young¹

¹Graduate Group in Ecology and Department of Plant Sciences, University of California, Davis,
CA 95616, USA and Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya

*Correspondence author. E-mail: keveblen@gmail.com

Running head: Cattle vs. wildlife effects on a savanna mosaic

21 **Summary**

- 22 1. Through their effects on plant communities, herbivores can exert strong direct and
23 indirect effects on savanna ecosystems and have the potential to create and maintain
24 savanna landscape heterogeneity. Throughout much of sub-Saharan Africa, periodic
25 creation and abandonment of livestock corrals leads to landscape mosaics of long-term
26 ecosystem hotspots that attract both cattle and large ungulate wildlife.
- 27 2. The development and maintenance of vegetation in these types of hotspots may be
28 controlled in part by herbivory. Cattle and wildlife may have different, potentially
29 contrasting effects on plant succession and plant–plant interactions. We ask how cattle
30 and wild herbivores affect the maintenance and vegetation development of corral-derived
31 landscape heterogeneity (0.25-1.0 ha treeless ‘glades’) in Laikipia, Kenya, through their
32 effects on long-term successional and short-term plant–plant dynamics.
- 33 3. We used the Kenya Long-term Exclosure Experiment (KLEE) to exclude from glades
34 different combinations of cattle, large ungulate wildlife (i.e. zebras, gazelles and other
35 antelopes), and mega-herbivore wildlife (i.e. giraffes and elephants). We first assessed
36 long-term changes in cover of the dominant grass species, *Cynodon plectostachyus* and
37 *Pennisetum stramineum* (the early- and late-dominant species, respectively). We then
38 used a neighbour-removal experiment to test the effects of different herbivores on
39 competition and facilitation between the two glade grass species.
- 40 4. In the long-term experiment, we found that large ungulate wildlife reinforce landscape
41 heterogeneity over time by helping maintain glades in their early *C. plectostachyus*-
42 dominated form. Cattle and mega-herbivore wildlife, on the other hand, appeared to
43 reduce the positive effects through forage preference for *C. plectostachyus*.

- 44 5. In the neighbour removal experiment, we found that each grass species benefited from
45 facilitation when it was the preferred forage for the dominant grazer. Facilitation of *C.*
46 *plectostachyus* was strongest when cattle co-occurred with wildlife, whereas facilitation
47 of *P. stramineum* was strongest when cattle were absent.
- 48 6. *Synthesis.* Our results demonstrate that different combinations of cattle and wildlife have
49 different effects, largely via contrasting forage preferences, on the persistence of
50 landscape heterogeneity in this savanna landscape. More generally, we provide evidence
51 for contrasting effects of cattle and wildlife on short-term plant interactions (facilitation)
52 and successional processes within the herbaceous plant community.

53

54 **Key-words**

55 cattle-wildlife interactions, ecological legacies, facilitation, foraging behaviour, landscape
56 heterogeneity, pastoralism, plant–herbivore interactions, rangeland, succession

57 **Introduction**

58 Herbivores can exert strong direct and indirect effects on savanna ecosystems through
59 their interactions with plant communities (Hobbs 1996; Anderson *et al.* 2007). In African
60 savannas, where large ungulates dominate the landscape, both wild and domestic herbivores can
61 dramatically alter herbaceous and woody plant communities, acting as ‘architects’ of the savanna
62 (de Knegt *et al.* 2008). The effects of herbivory, in turn, have the potential to affect multiple
63 ecosystem properties such as nutrient availability (Anderson *et al.* 2007), arthropod abundance
64 (Pringle *et al.* 2007), rodent populations (Keesing 1998; McCauley *et al.* 2006; Yarnell *et al.*
65 2007) or behaviour of other guilds of large herbivores (Young *et al.* 2005; Odadi *et al.* 2007,
66 2009).

67 Through their effects on plants, herbivores can create and maintain patterns of savanna
68 landscape heterogeneity (Adler *et al.* 2001; DuToit *et al.* 2003; Scholes & Walker 2004; de
69 Knegt *et al.* 2008), patterns typically defined, in part, by vegetation type or structure. One
70 pervasive form of large-scale heterogeneity throughout savannas in much of sub-Saharan African
71 is derived from former livestock corrals. Corral sites develop into long-term (decades to
72 centuries), nutrient-rich patches identifiable by their distinctive plant communities (Stelfox 1986;
73 Blackmore *et al.* 1990; Reid & Ellis 1995; Young *et al.* 1995; Muchiru *et al.* 2009, K. Veblen
74 unpublished data). In many savannas, these landscape features take the form of treeless ‘glades’
75 and can occur at densities of 2 km⁻² (Young *et al.* 1995, K. Veblen unpublished data) and cover
76 up to 17% of some landscapes (Blackmore *et al.* 1990). These glades are embedded in a wooded
77 savanna background (or patches of trees against open background), and with their highly
78 palatable vegetation they serve as foci of ungulate wildlife activity (Young *et al.* 1995;
79 Augustine 2003; Muchiru *et al.* 2008, K. Veblen unpublished data). The herbivores attracted to

80 these glades in turn have the potential to influence dynamics among plant species and maintain
81 vegetation in a nutritious short-grass state (*sensu* McNaughton 1984), producing a long-term
82 human “footprint” on the landscape. Yet, despite the ecological importance and ubiquity of
83 glade-like features in herbivore-dominated savannas, there has been very little experimental
84 investigation of how herbivores influence glade vegetation development.

85 One pathway for herbivores to influence plant community dynamics is through mediation
86 of positive and negative plant–plant interactions. Herbivore damage to plants can alter
87 competitive interactions (Gurevitch *et al.* 2000), and in other cases herbivore avoidance of well-
88 defended or unpalatable species may benefit more palatable plant neighbours (Bertness &
89 Callaway 1994; Rebollo *et al.* 2002). In an East African glade mosaic, for example, herbivore
90 avoidance of one glade-dominant grass species (*Pennisetum stramineum*) appears to benefit
91 another, more palatable, co-dominant grass species (*Cynodon plectostachyus*) (Veblen 2008b). In
92 that case, the balance of positive effects accrued during the dry season and negative effects
93 accrued during the wet season determined the net outcome of short-term plant interactions. Over
94 time, these interactions have the potential to influence longer-term processes such as succession
95 (Connell & Slatyer 1977) and landscape mosaic development (Veblen 2008a).

96 The role of herbivores in successional processes can be highly variable and context-
97 dependent (Davidson 1993; Hobbs 1996). In some cases, herbivores increase the rate of
98 succession, while in other cases herbivores decrease the rate of succession or appear not to affect
99 it at all (Connell & Slatyer 1977; Belsky 1986; Brown & Ewel 1987; Davidson 1993; Howe &
100 Lane 2004). This is at least partly due to differences in the ecology of different herbivore
101 species, particularly foraging habits and preferences that may have contrasting effects on the
102 growth and dominance of different plant species (Brown & Stuth 1993; Augustine &

103 McNaughton 1998; Seabloom & Richards 2003). In our study system, glades undergo
104 conversion from dominance by one grass species, *Cynodon plectostachyus*, to another
105 *Pennisetum stramineum*.(Veblen 2008a). In this case, preferential grazing of *C. plectostachyus*
106 may promote the conversion of glade vegetation, or conversely, grazing on *P. stramineum* may
107 hinder its ability to invade *C. plectostachyus*-dominated vegetation.

108 The possibility of interactions among multiple herbivore guilds adds another layer of
109 complexity to relationships between herbivores and plant communities. Wildlife grazing can
110 reduce cover of some plant species, resulting in measurable changes in cattle foraging behaviour
111 and preferences (Odadi *et al.* 2007). Similarly, mega-herbivores (i.e. elephants) can indirectly
112 benefit meso-herbivore wildlife via their effects on the plant community and other herbivores; in
113 one case, by suppressing cattle grazing, mega-herbivores increased grass availability for other
114 wildlife (Young *et al.* 2005). Plant community responses may be direct consequences of the net
115 effects of these types of indirect interactions among herbivores and will likely vary according to
116 the particular complement of herbivores.

117 Despite the potential for interactions among different herbivore guilds, there have been
118 few controlled replicated studies that experimentally examine separate and combined effects of
119 wild and domestic large herbivores on the ecosystems they share (Young *et al.* 1998). Moreover,
120 although large herbivores dominate many African savanna landscapes, there have been no
121 controlled studies of the potentially contrasting effects of cattle and wildlife on plant dynamics
122 and vegetation change associated with large-scale savanna landscape heterogeneity. Although we
123 have some experimental information about how large herbivores in general (i.e. mixed foraging
124 by cattle and wildlife) affect the small-scale competitive balance between the two main grass
125 species in a glade mosaic (Veblen 2008b), we have virtually no information about how the

126 different guilds each contribute to these relationships, or how these translate to landscape-scale
127 succession. Here we ask how cattle and wildlife (separately and in combination) affect the
128 maintenance and successional development of this form of landscape heterogeneity—the treeless
129 glades (0.25-1.0 ha) that are scattered across a wooded savanna landscape in Laikipia, Kenya.
130 We ask two specific questions: 1) How do cattle versus wildlife affect long-term patterns of
131 glade vegetation development? 2) How do cattle versus wildlife affect short-term plant–plant
132 dynamics in herbaceous glade vegetation?

133

134 **Materials and methods**

135 *Study site*

136 This research was conducted in an *Acacia drepanolobium* savanna in the semi-arid
137 Laikipia District of Kenya. The study area is located on the Mpala Research Centre property
138 (36°52'E, 0°17'N) where the average annual rainfall is 500 - 600 mm (mid-range for savanna
139 ecosystems). The mean rainfall pattern is weakly trimodal, with the highest peak in mean
140 rainfall occurring in March-May (mean in April, 1998-2005: 120 mm) and the longest, most
141 pronounced dry season typically from December to March (mean Jan-Feb, 1998-2005; 35 mm).
142 The study area is underlain with 'black cotton' soils, poorly drained vertisols with high (>50%)
143 clay content (Ahn & Geiger 1987). These black cotton savannas are widespread in Africa,
144 covering hundreds of thousands of km². Ninety-seven percent of the tree canopy cover is *Acacia*
145 *drepanolobium* Sjost., and 90% of herbaceous cover is comprised of five grass species:
146 *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans*
147 Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf. (Young *et al.* 1998). The area is actively
148 managed for cattle, with mean stocking densities of 0.5-0.7 cattle ha⁻¹. This stocking density

149 allows for the coexistence of a rich fauna of wildlife species such as: elephant (*Loxodonta*
150 *africana* Blumenbach), giraffe (*Giraffa camelopardalis* L.), eland (*Taurotragus oryx* Pallas),
151 oryx (*Oryx gazella beisa* L.), hartebeest (*Alcelaphus buselaphus* Pallas) Grant's gazelle (*Gazella*
152 *grantii* Brooke), zebra (*Equus burchelli* Gray), steinbuck (*Raphicerus campestris* Thunberg),
153 spotted hyaena (*Crocuta crocuta* Erxleben), and lion (*Panthera leo* L.).

154 Historical and contemporary cattle management has created a landscape mosaic of
155 nutrient-rich, treeless glades (0.25-1.0 ha) scattered throughout the *A. drepanolobium* savanna
156 (~2 trees km⁻²). Once abandoned, temporary cattle corrals ('bomas') develop into nutrient-rich
157 glades that are preferred by both livestock and wildlife (K. Veblen unpublished data, see also
158 Augustine 2004). After abandonment, a ring of dense, often taller, trees develops at the boma
159 margin and demarcates the abrupt boundary between woodland and the original boma,
160 coincident with an abrupt change in the understorey. Within months of abandonment the
161 stoloniferous mat-forming grass, *Cynodon plectostachyus* K. Schum, colonizes the dung layer,
162 covering the entire boma area in as little as two to three years (K. Veblen, unpublished data).
163 Vegetation in younger glades is dominated by this stoloniferous grass (>75% cover), while the
164 vegetation of older glades is dominated (>65% cover) by an ascending bunchgrass, *Pennisetum*
165 *stramineum* (Veblen 2008a). Immediately outside the glade boundary, the *C. plectostachyus* and
166 *P. stramineum* communities abruptly give way to a vegetation composition and density
167 resembling background non-glade vegetation, where *C. plectostachyus* is essentially absent (<1%
168 cover) and *P. stramineum* no longer dominates (20-40% cover).

169

170 ***Large herbivore exclosures***

171 To examine the separate and combined effects of cattle and wildlife on glade

172 development, we used the Kenya Long-term Exclusion Experiment (KLEE). Established in
173 1995, KLEE is a series of 4-ha plots that uses semi-permeable barriers to allow access by
174 different combinations of cattle ('C'), large ungulate wildlife >15kg ('W') and mega-herbivore
175 wildlife ('M') (i.e. elephants and giraffes). Each of the following six treatments is replicated
176 across three blocks: C, W, WC, MW, MWC and O. The capital letters indicate which herbivore
177 guilds are allowed access (e.g. 'O' allows no herbivores >15 kg, 'W' allows wildlife >15kg, but
178 no cattle or mega-herbivores, and 'MWC' allows mega-herbivores, wildlife and cattle). Six
179 glades were included within the study design which, when divided by fences, created 18 glade
180 portions. This included several glade sections adjacent to KLEE plots maintained in herbivore
181 treatments. All glade-herbivore treatments except MW were initially replicated three times, and
182 a third MW replicate was added in 2004.

183

184 ***Response of glade vegetation to long-term herbivore exclusion***

185 In August 2003, for each of the eighteen glade portions (hereafter referred to as
186 'glades') assigned to these six herbivore treatments, we sampled herbaceous vegetation along a
187 transect that ran from glade centre to 60 m beyond the glade edge (Fig. 1). Each transect was
188 oriented to bisect the angle created by the boundaries of herbivore treatments. Tree presence
189 around the glade perimeter coincided with the boundary of *C. plectostachyus*-*P. stramineum*
190 understory dominance and demarcated glade edge (and distance of zero). We sampled every 5
191 m between glade centre and 15 m outside the glade (+15 m), and at +30 m and +60 m, for a total
192 of 229 sample locations (mean of 13 per glade, depending on glade size). For statistical analysis,
193 at each glade, samples were averaged into three distance categories: 1) inside (from the glade
194 centre to -10 m), 2) glade edge (-5 m, 0, +5 m and +10 m) and 3) outside, (+15, +30 and +60 m).

195 At each sampling point, we used a ten-point pin frame to measure aerial plant cover (first hit of
196 each species, i.e. maximum of ten hits per species per pin frame), and we recorded the presence
197 of each species rooted within a 1-m² quadrat. In 2006 we added a second year of data collection
198 for vegetation inside glades (but not on edges or outside). We sampled all eighteen glade ×
199 treatment combinations (the original seventeen plus the recently added MW treatment), placing
200 6-18 pin frames per glade (mean=12) in a grid that covered the entire glade. The grid was
201 spaced at 5 m, and all points were at least 5 m from glade edge. We averaged pin hits across
202 frames within each glade to give a single cover value for each species in a given glade.

203

204 ***Plant neighbour experimental manipulation***

205 In August 2005, we used a neighbour removal experiment within the KLEE experiment
206 to investigate competition and facilitation between the two dominant herbaceous glade species,
207 *P. stramineum* and *C. plectostachyus*, in the context of different herbivore treatments. We
208 located areas where the two grass species co-occurred in two enclosure types: those that included
209 wildlife but not cattle (W and MW, n=4) and those that included wildlife plus cattle (WC and
210 MWC, n=4). Within these areas (in which neither species exhibited >90% cover), we randomly
211 assigned one of three treatments to three randomly located 1 × 1m plots: *C. plectostachyus*
212 removal, *P. stramineum* removal, and control (no plants removed). This resulted in a 2 × 2
213 factorial design for each of the two grass species with species removal treatments (heterospecific
214 neighbours present vs. heterospecific neighbours removed) crossed with grazing treatments
215 (wildlife only vs. wildlife plus cattle). Because removing the target species also reduced overall
216 plant density, we randomly located a fourth 1 × 1m plot in each glade, in which we reduced
217 overall plant density (of both species) by one-half. This density-reduced plot was treated as the

218 control (heterospecific neighbours present) in an additional 2×2 analysis of neighbour effect
219 and grazing treatment on each species. Neither C nor O plots contained enough co-dominated
220 areas to be included in the experiment; *C. plectostachyus* in these plots rarely occurred in
221 mixture with *P. stramineum* and instead primarily occurred in a few monoculture patches. All
222 removed plants were clipped to remove above-ground biomass and after rainfall and any new
223 growth were individually treated by sponge with Roundup® (glyphosate herbicide).

224 We measured total plant cover in each 1×1 m plot using five evenly spaced pin frames
225 (n=50 pins per plot). We counted the total number of times that each species touched each pin;
226 total number of pin hits is positively correlated with total biomass of each species (*C.*
227 *plectostachyus* $r=0.89$; *P. stramineum* $r=0.68$, K.Veblen, unpublished data). At the time of plot
228 set-up in August 2005, we quantified plant cover within each 1×1 m plot prior to manipulation
229 and then repeated baseline pin frame counts in ‘removal’ plots immediately after neighbour
230 removal treatments were complete. Seven months later (in March 2006), at the end of the three-
231 month-long dry season (24 mm rainfall in January-March 2006), we assessed the effects of
232 experimental treatments on *C. plectostachyus* and *P. stramineum* by repeating pin frame
233 measurements in all plots. We repeated measurements an additional four months later, in July
234 2006, at the end of a three-month period of heavy rainfall (153 mm in April-June 2006) and an
235 additional one year later in July 2007 (230 mm in April-June 2007). In 2007, the majority of the
236 rainfall fell in June, the month prior to sampling.

237

238 *Statistical analyses*

239 For all statistical analyses, we used generalized linear mixed models (GLMMs); we used
240 maximum-likelihood methodology and Satterthwaite’s approximation of degrees of freedom

241 (PROC MIXED, version 9.1, SAS Institute 2002). Variance-weighting was used when variances
242 were not homogenous, and values were log-transformed when necessary. We used Tukey's
243 HSD analyses for *post hoc* comparisons.

244

245 *Response of glade vegetation to long-term herbivore exclusion*

246 We used split-plot designs to test the effects of different herbivore treatments on
247 herbaceous vegetation. For the 2003 data on species richness (based on presence/absence) and
248 species diversity (H' calculated from pin hit data) each model included the following fixed
249 effects: main plot effect of herbivore treatment (O, C, W, WC, MW, MWC), subplot effect of
250 distance (inside, edge, outside of glade) and the herbivore \times distance interaction. Block, glade
251 nested within block, and their interactions were random effects.

252 To analyse 2003 *C. plectostachyus* and *P. stramineum* cover in a single model, a second
253 (fixed) subplot effect of species (*C. plectostachyus* vs. *P. stramineum*) was added to the model
254 described above, resulting in the following: main plot effect of herbivore treatment (O, C, W,
255 WC, MW, MWC), subplot effect of distance (inside, edge, outside of glade), subplot effect of
256 species (*C. plectostachyus* vs. *P. stramineum*), and all possible interactions. Block, glade nested
257 within block, and their interactions were treated as random effects. This model was used twice,
258 to separately test absolute and relative *C. plectostachyus* – *P. stramineum* cover. The same
259 statistical model was then used to analyse 2003 absolute grass and forb cover, replacing the
260 'species' subplot effect with 'vegetation type' (grass vs. forb).

261 The 2006 vegetation data (collected only from inside glades) were combined with the
262 2003 'inside glade' vegetation data, and the statistical model included the following fixed
263 effects: main plot effect of herbivore treatment, two subplot effects of species (*C. plectostachyus*

264 vs. *P. stramineum*) and year (2003/2006), and all interactions. Glade nested within block and its
265 interactions were treated as random effects. This model was used twice, to separately test
266 absolute and relative *C. plectostachyus* – *P. stramineum* cover.

267

268 *Plant neighbour experimental manipulation*

269 We calculated mean *C. plectostachyus* and *P. stramineum* cover values for each 1 × 1m
270 plot in each sampling period. We quantified how *C. plectostachyus* and *P. stramineum* cover
271 changed over time (in response to grazing, neighbour and season effects) by calculating a
272 relative growth index. Relative growth was calculated as $\ln((\text{cover } t_2)/(\text{cover } t_1))$. We
273 calculated relative growth during the dry season (t_1 =post-manipulation baseline cover, t_2 =March
274 cover) and wet season (t_1 =March cover, t_2 =July cover) for each species×neighbor×grazing
275 combination. Relative growth values are symmetrical around zero, with positive numbers
276 indicating increases in cover and negative numbers indicating decreases in cover. We analysed
277 the data using split-plot models. Herbivore treatment (wildlife vs. cattle plus wildlife) was
278 treated as the main plot effect, with season (dry vs. wet) and species removal (neighbour
279 removed vs. control) as subplot effects. These effects and their interactions were fixed. Random
280 effects were block and glade (nested within block), and their interactions. We used the SLICE
281 function in PROC MIXED for contrast tests of *a priori* hypotheses about the effects of neighbour
282 presence within each season×cattle presence combination. To analyse density-reduced plots, we
283 used the same split-plot model, replacing control plots with density-reduced control plots.

284

285 **Results**

286 *Response of glade vegetation to long-term herbivore exclusion*

287 Herbivore treatments significantly affected *C. plectostachyus* and *P. stramineum* cover
288 inside glades. Analysis of 2003 and 2006 data showed no significant year effect, but indicated
289 that relative cover of *C. plectostachyus* was significantly higher in W treatments than in all other
290 herbivore treatments (Figure 2a, Table 1). Conversely, relative *P. stramineum* cover was
291 significantly lower in W than in all other treatments except MW (Fig. 2b). Analyses of absolute
292 cover showed similar patterns, although Tukey *post hoc* tests distinguished fewer significant
293 differences in *P. stramineum* cover among herbivore treatments (Fig. 2c,d, Table 1).

294 Although neither total grass nor forb cover in 2003 varied significantly across herbivore
295 treatments or distances from glades (overall, grass: $100.0 \pm 2.8\%$; forbs: $16.0 \pm 2.2\%$), species
296 composition differed significantly between inside and outside glades. Absolute cover of *C.*
297 *plectostachyus* was 12 times higher in glades than outside ($20.5 \pm 5.7\%$ vs. $1.7 \pm 1.6\%$), and *P.*
298 *stramineum* cover was almost two times higher inside glades than outside ($86.4 \pm 4.2\%$ vs. 49.1
299 $\pm 3.3\%$). Inside glades, cover of *P. stramineum* ($74.1 \pm 3.1\%$) was significantly higher than *C.*
300 *plectostachyus* cover ($14.7 \pm 3.1\%$) (significant species \times distance interactions for both absolute
301 and relative cover, Tukey $\alpha < 0.05$, Table 1). Patterns of cover for the two species differed at
302 glade edges; *P. stramineum* cover at glade edges was similar to cover inside glades, whereas *C.*
303 *plectostachyus* cover at glade edges was more similar to cover outside of glades (significant
304 species \times distance interactions for both absolute and relative cover, Tukey $\alpha < 0.05$, Table 1).
305 *Pennisetum stramineum* edge patterns were driven largely by lower *P. stramineum* cover outside
306 of glades in MWC and C plots (significant species \times distance \times treatment interaction, Tukey $\alpha <$
307 0.05 , Table 1).

308

309 ***Plant neighbour experimental manipulation***

310 Neighbour removal plots indicate that both *C. plectostachyus* and *P. stramineum*
311 responded strongly to sampling period in three ways (Fig. 3). First, both species experienced
312 greater growth in July after the rainy seasons than in March after the dry season (season effect:
313 *C. plectostachyus* $F_{2,34} = 12.07$, $p = 0.0001$; *P. stramineum* $F_{2, 7.06} = 18.74$, $p = 0.0015$). Second,
314 both species responded negatively to cattle presence in the dry season but not during the wet
315 seasons (season×cattle presence interaction: *C. plectostachyus* $F_{2,34} = 6.54$, $p = 0.004$; *P.*
316 *stramineum* $F_{2,30.5} = 3.99$, $p = 0.03$; Tukey $p < 0.05$). Third, both species benefited from the
317 presence of heterospecific neighbours in the dry season (March 06, Fig. 3a,d), but in the wettest
318 season (July 07, Fig. 3c,f) heterospecific neighbour effects were competitive (season×neighbour
319 presence interaction: *C. plectostachyus* $F_{2,34} = 12.76$, $p < 0.0001$; *P. stramineum* $F_{2,24.6} = 5.44$, p
320 $= 0.01$).

321 Although both grass species benefited from heterospecific neighbours during the dry
322 season, the presence of cattle had contrasting effects on *C. plectostachyus* vs. *P. stramineum*
323 during this time (Fig. 3). For *C. plectostachyus*, positive (facilitative) effects of heterospecific
324 neighbours (i.e. *P. stramineum*) were significant only when cattle were present (cattle present:
325 $F_{1,34} = 10.97$, $p = 0.002$; cattle absent: $F_{1,34} = 2.34$, $p = 0.14$; Figure 3a). In contrast, for *P.*
326 *stramineum*, positive heterospecific neighbour effects were significant only when cattle were
327 absent (cattle present $F_{1,24.6} = 0.42$, $p = 0.53$; cattle absent $F_{1,24.6} = 4.17$, $p = 0.05$; Fig. 3d). That is,
328 during the dry season, *C. plectostachyus* was facilitated by heterospecific (*P. stramineum*)
329 neighbours when cattle were present, whereas *P. stramineum* was facilitated by heterospecific
330 (*C. plectostachyus*) neighbours when cattle were absent.

331 For both species, comparing neighbour removal plots against density-reduced control
332 plots produced results similar to those discussed above, suggesting that experimental effects

333 reflect species-specific removals rather than reduction in overall plant densities (of both con- and
334 heterospecifics). Facilitation occurred during the dry season for both species, while competition
335 was more important during wet seasons (season×neighbour presence interaction: *C.*
336 *plectostachyus* $F_{2,23,2} = 13.71$, $p = 0.0001$; season×neighbour presence×cattle presence interaction
337 *P. stramineum* $F_{2,26,7} = 3.83$, $p = 0.04$). For *C. plectostachyus*, dry season facilitation was
338 strongest in the presence of cattle (cattle present $F_{1,23,2} = 5.82$, $p = 0.02$; cattle absent $F_{1,23,2} =$
339 3.176 , $p = 0.09$) and for *P. stramineum* strongest in the absence of cattle (cattle absent $F_{1,26,7} =$
340 0.01 , $p = 0.92$; without cattle $F_{1,26,7} = 3.99$, $p = 0.06$). During the wet season, density-reduced
341 plots released both species from intra-specific competition. This reduction in intra-specific
342 competition offset some of the negative effects of interspecific competition seen in control plots
343 (e.g. more than doubling the increase in *P. stramineum* cover during July 2007; Table 2).

344

345 **Discussion**

346 We have previously shown that the treeless glades in this landscape are ecosystem hot
347 spots created by cattle management and that large herbivores in general (cattle and wildlife
348 grouped together) influence small-scale species interactions in these glades (Veblen 2008a).
349 Here we provide experimental evidence within a single system that different large herbivore
350 guilds (cattle and large ungulate wildlife) have differing effects on the herbaceous vegetation
351 associated with these important landscape features that play out at the scale of entire glades.
352 Evidence from several ecosystems suggests that both cattle and wildlife can be key players in the
353 maintenance of landscape heterogeneity through their effects on plant communities
354 (McNaughton 1984; Adler *et al.* 2001; Tobler *et al.* 2003; Augustine & McNaughton 2004;

355 Waldram *et al.* 2008), Rarely, however, are the effects of cattle and large ungulate wildlife
356 studied together.

357

358 ***Response of glade vegetation to long-term herbivore exclusion***

359 Wildlife appear to reinforce landscape heterogeneity by helping maintain glades in their
360 *C. plectostachyus*-dominated form. Glades undergo successional development in which they are
361 first dominated by *C. plectostachyus* and eventually invaded by *P. stramineum*). While previous
362 work indicates that the net effects of cattle and wildlife combined are to retard this invasion
363 (Veblen 2008a), the data we present here suggest that wildlife are primarily responsible for
364 retarding invasion and maintaining the *C. plectostachyus* component of glade plant communities.
365 Cattle and mega-herbivore wildlife, on the other hand, may moderate the positive effects of
366 wildlife on *C. plectostachyus* cover.

367 In glades, wildlife grazing and forage preferences appear to target *P. stramineum*,
368 releasing *C. plectostachyus* from competition. In plant communities, preferential foraging can
369 lead to suppression of preferred species (reviewed in Augustine & McNaughton 1998) and
370 consequent release of their competitors (Weltzin *et al.* 1997; Cadenasso *et al.* 2002; Aptroot *et*
371 *al.* 2007). In this study system, *P. stramineum* is heavily grazed by zebras, the dominant wildlife
372 species (Young *et al.* 1995). Because *P. stramineum* is a strong competitor in glades, its removal
373 or damage releases *C. plectostachyus* from competitive suppression, especially during the wet
374 season (Veblen 2008). This appears to result in greater *C. plectostachyus* cover in plots where
375 wildlife alone are present (Figure 2a). Furthermore, wildlife effects on *P. stramineum* may be
376 especially pronounced in ‘W’ (wildlife only) plots because zebra numbers increase when cattle
377 are removed (Young *et al.* 2005).

378 Cattle and mega-herbivores (i.e. elephants), by foraging on *C. plectostachyus*, may
379 moderate the effects of wildlife on glade vegetation. *C. plectostachyus* is highly palatable to
380 cattle (Pratt & Gwynne 1977, pers. comm. with local herders); in our short-term neighbour
381 removal experiment, dry season *C. plectostachyus* patches were grazed more intensely when
382 cattle were present (Fig. 3). Similarly, elephants uproot and forage on *C. plectostachyus* in glades
383 (K.E.V., pers. obs.), and *C. plectostachyus* can be an important component of elephant diets,
384 constituting up to one-third of the grass portion (Field 1971; Kabigumila 1993).

385 Through their forage preferences, cattle, wildlife and mega-herbivores have potentially
386 opposing effects on the long-term successional development of glade vegetation. By suppressing
387 the invading grass, *P. stramineum*, wildlife help maintain glades in an earlier successional state,
388 effectively lengthening this particularly desirable (palatable and high quality vegetation) stage in
389 the lifespan of glades. Cattle and mega-herbivores, on the other hand, by selectively foraging on
390 *C. plectostachyus*, may reinforce the successional trajectory of glade development toward *P.*
391 *stramineum* invasion. In savannas elsewhere, browsing on seedlings of woody species prevents
392 woody invasion of herbaceous communities (e.g., Scholes & Archer 1997). Similarly, herbivory,
393 particularly by cattle, often is implicated in accelerating invasion processes in rangelands; again
394 most examples involve woody plant encroachment following suppression of palatable
395 herbaceous communities (Vanvegtten 1984; e.g., Roques *et al.* 2001; Tobler *et al.* 2003). Ours
396 appears to be among the first examples of large herbivores affecting an invasion trajectory within
397 the herbaceous (grass) layer.

398

399 *Season and herbivore effects on plant–plant dynamics*

400 In the dry season, facilitation of *P. stramineum* by *C. plectostachyus* occurred when
401 wildlife, but not cattle, were present. Although previous research on dry season facilitation in
402 this system found no evidence for facilitation of *P. stramineum* (Veblen 2008b), that work took
403 place in the presence of a mixed herbivore assemblage that included both cattle and wildlife. The
404 present experimental design, however, allowed us to isolate the effects of wildlife, and we found
405 evidence for facilitation of *P. stramineum* in the presence of wildlife (without cattle).

406 Facilitation of *P. stramineum* by *C. plectostachyus* in wildlife ('W') plots likely reflect
407 the foraging patterns of zebras, the dominant wildlife species (discussed above). As hindgut
408 fermenters, zebras thrive on the greater-bulk and lower-quality forage provided by *P.*
409 *stramineum* and may therefore avoid mixed *C. plectostachyus*–*P. stramineum* stands. Protection
410 of *P. stramineum* via its association with a less palatable (to zebras) species, appears to be an
411 example of 'associational resistance' (whereby the facilitated species is obscured or hidden by
412 less palatable species) (Barbosa *et al.* 2009).

413 The absence of facilitation of *P. stramineum* in the presence of cattle and wildlife
414 together ('WC' plots) may indicate that *C. plectostachyus* no longer offers associational
415 resistance beyond a certain grazing threshold. Grazing pressure in plots where both wildlife and
416 cattle are present is likely higher than in plots where only wildlife are present, and facilitative
417 relationships may break down under higher levels of grazing pressure. The absence of facilitation
418 also may be driven by cattle foraging. In seeking out highly palatable *C. plectostachyus* (see
419 above), cattle may incidentally graze *P. stramineum*, a case of 'associational susceptibility'
420 (whereby a plant is more vulnerable because of its association with a more palatable species)
421 (Barbosa *et al.* 2009).

422 In contrast, facilitation of *C. plectostachyus* by *P. stramineum* was strongest in the
423 presence of cattle. These results are consistent with previous evidence for dry season facilitation
424 of *C. plectostachyus* in the presence of a mixed (cattle and wildlife) herbivore assemblage
425 (Veblen 2008b), and they are also consistent with cattle forage preference for high-quality *C.*
426 *plectostachyus* forage and associational resistance provided by less palatable *P. stramineum*.
427 Although cattle treatments produced clear experimental effects, our experimental design did not
428 allow us to determine whether treatment effects were due to the addition of cattle specifically, or
429 due to the addition of overall grazing pressure (regardless of herbivore identity). Thus,
430 experimental addition of more wildlife (instead of cattle) may have produced the same observed
431 pattern. In either case, our results show that facilitation of early successional *C. plectostachyus*
432 was strongest when cattle co-occurred with wildlife, whereas facilitation of late-successional *P.*
433 *stramineum* was strongest in the presence of wildlife alone.

434 Although facilitation predominated during the dry season, net competitive interactions
435 became more dominant as conditions became wetter and both species experienced net growth.
436 These results are consistent with previous work in the system (Veblen 2008) and broader patterns
437 of decreasing facilitation with increasing precipitation (Greenlee & Callaway 1996; Pugnaire &
438 Lazaro 2000).

439

440 ***Conclusions***

441 Through their effects on successional change and plant–plant dynamics, different
442 combinations of cattle and wildlife have contrasting effects on the development and persistence
443 of one important type of savanna landscape heterogeneity. Our first (large-scale) experiment
444 showed that, over the long-term (8+ years), wildlife presence contributed to the persistence of

445 younger glade vegetation, whereas cattle appeared to favour invasion by a later-successional
446 species. The forage preferences implicated in the aforementioned patterns are consistent with the
447 results of our second (neighbour removal) experiment; each species benefited from facilitation
448 when it was the preferred forage for the dominant grazer. That is, *C. plectostachyus* was
449 facilitated when cattle were present, and *P. stramineum* was facilitated when only wildlife were
450 present. In both cases, our results are consistent with patterns of greater facilitation with higher
451 grazing pressure (Bertness & Callaway 1994; Graff *et al.* 2007) and appear to be attributable to
452 associational resistance.

453 Our results suggest that, because wildlife presence favours *C. plectostachyus*, heavier or
454 more frequent wildlife grazing could lengthen the lifespan, or at least the most desirable seral
455 stage, of glades. The vegetation communities and herbivory associated with glades in other
456 ecosystems provide potential support for this idea. In a nearby ecosystem, wildlife numbers are
457 greater, and glades appear to be more heavily grazed than in our study system. Glades in that
458 study system also persist in a *C. plectostachyus*-dominated state for much longer (Young *et al.*
459 1995), suggesting that wildlife—through their effects on plant succession—may have a
460 measurable impact on glade lifetimes.

461

462

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473

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601

602

603

604 **Table 1.** Analysis of variance of relative and absolute cover of two grass species, *Cynodon*
 605 *plectostachyus* and *Pennisetum stramineum*, associated with glades

	Factor	Relative Cover			Absolute Cover		
		d.f.	F	P	d.f.	F	p
2003 & 2006	sp	1, 4.56	99.18	0.0003	1, 6.07	102.94	<.0001
	trt	5, 24.5	0.18	0.97	5, 33.3	0.45	0.81
	sp×trt	5, 24.5	7.12	0.0003	5, 33.3	7.13	0.0001
	yr	1, 37	0.48	0.49	1, 38	0.97	0.33
	sp×yr	1, 37	0.07	0.79	1, 38	0	0.98
	trt×yr	5, 37	0.06	0.99	5, 38	0.06	0.99
	sp×trt×yr	5, 37	0.42	0.83	5, 38	0.23	0.95
2003	sp	1, 55.2	407.46	<.0001	1, 36.3	425.22	<.0001
	trt	5, 63.9	2.08	0.08	5, 63.2	1.97	0.09
	sp×trt	5, 63.9	3.02	0.016	5, 63.2	3.84	0.004
	dist	2, 61.1	20.33	<.0001	2, 59.3	23.36	<.0001
	sp×dist	2, 61.1	6.58	0.003	2, 59.3	6.23	0.004
	trt×dist	10, 61.1	1.13	0.36	10, 59.3	1.61	0.13
	sp×trt×dist	10, 61.1	2.35	0.02	10, 59.3	2.85	0.006

606

607 Notes: sp=species (*C. plectostachyus* vs. *P. stramineum*), trt=treatment (O, W, C, WC, MW,

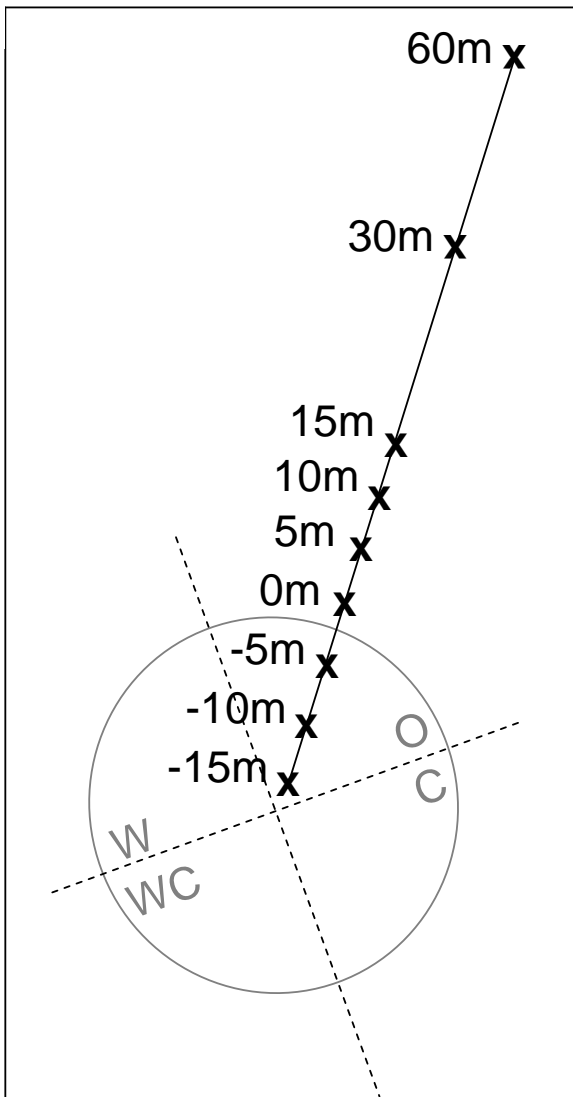
608 MWC), yr=year (2003 vs. 2006), dist=distance (inside, edge, outside of glades)

609 **Table 2.** Mean (± 1 SE) growth indices for *Cynodon plectostachyus* and *Pennisetum stramineum*
 610 growing in mixture in 1 \times 1m plots during three sampling periods (March 2006, July 2006, 2007)
 611 at two densities (full, density-reduced). Negative numbers indicate decreases in cover, and
 612 positive numbers indicate increases in cover measured by pin hits.

613

	<i>C. plectostachyus</i>		<i>P. stramineum</i>	
	Full density	Density-reduced	Full density	Density-reduced
March 2006				
(dry season)	-0.24 \pm 0.05	-0.23 \pm 0.11	-0.35 \pm 0.13	-0.47 \pm 0.17
July 2006				
(wet season)	0.10 \pm 0.20	0.02 \pm 0.16	-0.02 \pm 0.11	0.02 \pm 0.17
July 2007				
(wet season)	-0.28 \pm 0.33	0.27 \pm 0.20	0.35 \pm 0.22	0.90 \pm 0.16

614



616

617

618 **Fig. 1.**

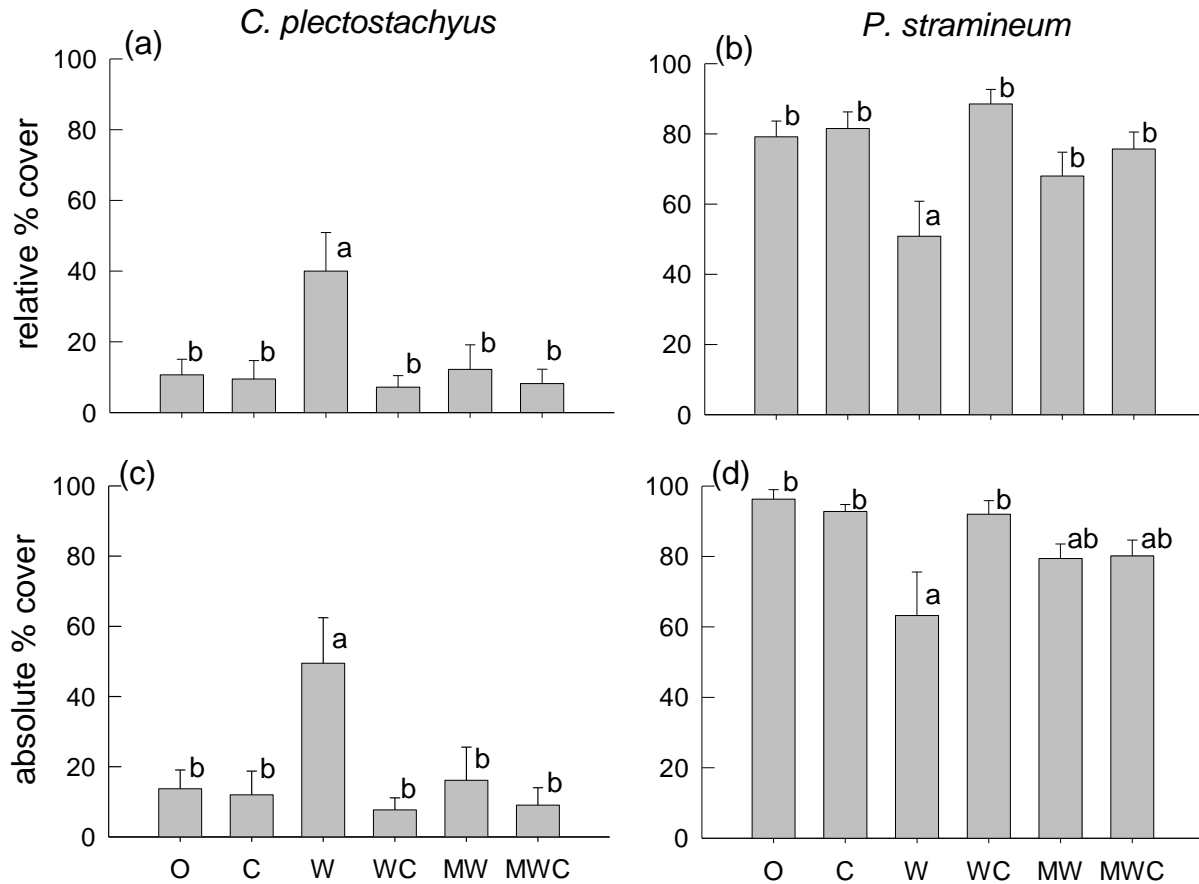
619 Glade sampling transects. Sampling occurred at 5-m intervals (marked 'x') along transects

620 bisecting each glade portion. Dotted line indicates treatment boundaries, and capital letters

621 indicate different herbivore treatments ('W'= large ungulate wildlife, 'C'= cattle, 'WC'= large

622 ungulate wildlife and cattle, and 'O'= neither large ungulate wildlife nor cattle).

623

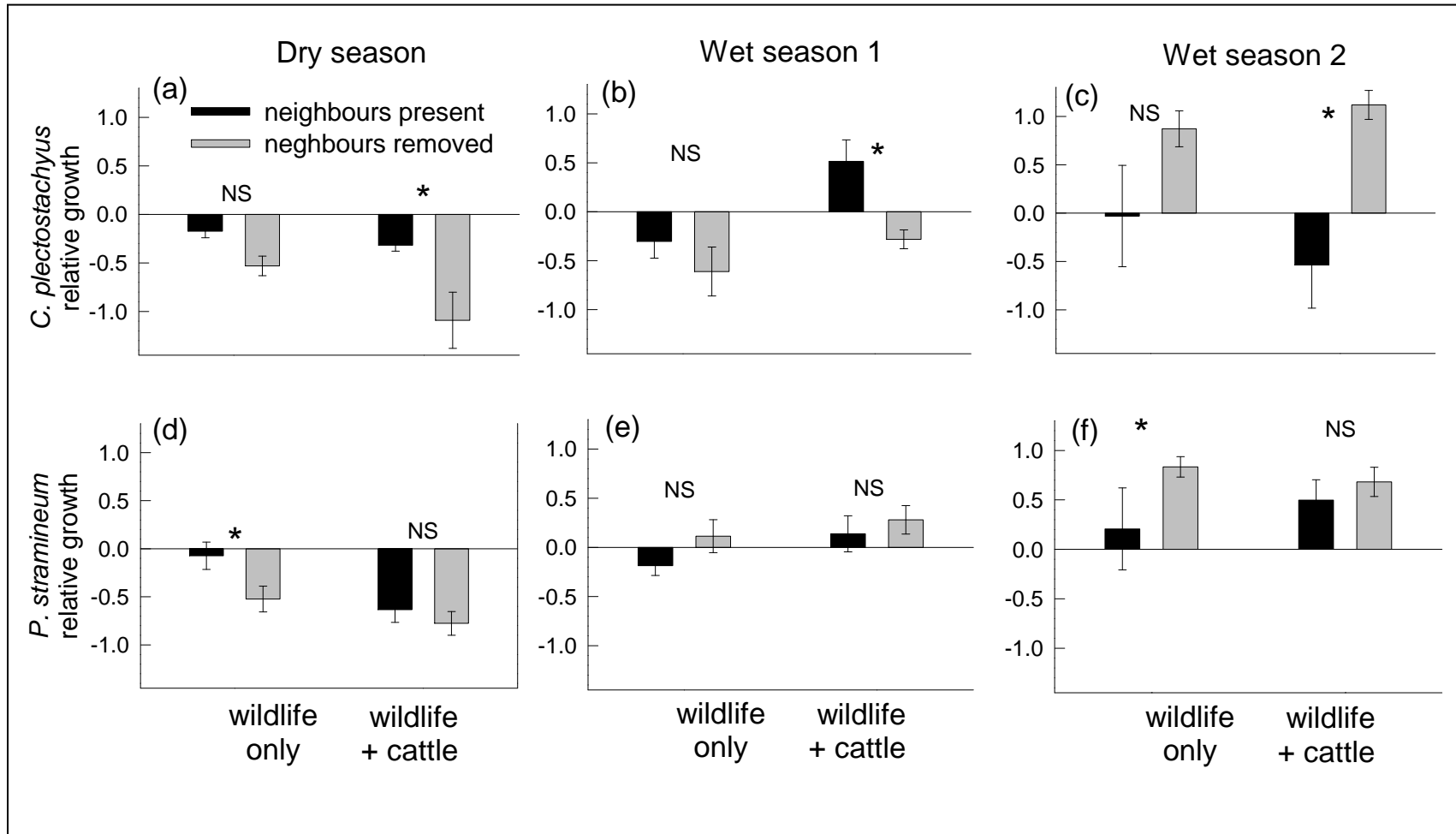


624

625 **Fig. 2.**

626 Mean (+1 SE) relative (a, b) and absolute cover (c,d) of two grass species, *Cynodon*
 627 *plectostachyus* and *Pennisetum stramineum*, inside treeless glades in six herbivore treatments
 628 allowing different combinations of cattle ('C'), wildlife (>15kg, 'W'), and mega-herbivore
 629 wildlife (elephants and giraffes, 'M'). Capital letters indicate which herbivore guilds are present
 630 in each treatment; 'O' plots indicate absence of all three types of herbivores. Cover values are
 631 means of multiple pin frame measurements per glade in August 2003 and 2006. Mixed-model
 632 analyses showed no significant sampling period effects. Species×treatment interactions were

633 significant for relative cover ($F_{5,24.5}=7.12$, $p=0.0003$) and absolute cover ($F_{5,33.3}= 7.13$, $p=0.0001$.
634 Shared letters within each species indicate no significant differences according to Tukey's HSD
635 ($\alpha= 0.05$).



638 **Fig. 3.**

639 Effects of interspecific competitors (presence vs. absence) and herbivory (wildlife vs. wildlife+cattle) on mean ($\pm 1SE$) relative growth
640 of (a-c) *Cynodon plectostachyus* and (d-f) *Pennisetum stramineum* in $1 \times 1m$ plots during three sampling periods (March dry season
641 2006 vs. July wet season 2006 vs. July wet season 2007). Relative growth is calculated as $\ln [(cover\ t2)/(cover\ t1)]$. 'NS' indicates no
642 significant differences and '*' indicates significant differences according to planned contrast tests of neighbour effects at the $p = .05$
643 level.

644