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

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Summary

1. Through their effects on plant communities, herbivores can exert strong direct and indirect effects on savanna ecosystems and have the potential to create and maintain savanna landscape heterogeneity. Throughout much of sub-Saharan Africa, periodic creation and abandonment of livestock corrals leads to landscape mosaics of long-term ecosystem hotspots that attract both cattle and large ungulate wildlife.

2. The development and maintenance of vegetation in these types of hotspots may be controlled in part by herbivory. Cattle and wildlife may have different, potentially contrasting effects on plant succession and plant–plant interactions. We ask how cattle and wild herbivores affect the maintenance and vegetation development of corral-derived landscape heterogeneity (0.25–1.0 ha treeless 'glades') in Laikipia, Kenya, through their effects on long-term successional and short-term plant–plant dynamics.

3. We used the Kenya Long-term Exclosure Experiment to exclude from glades different combinations of cattle, large ungulate wildlife (i.e. zebras, gazelles and other antelopes), and mega-herbivore wildlife (i.e. giraffes and elephants). We first assessed long-term changes in cover of the dominant grass species, *Cynodon plectostachyus* and *Pennisetum stramineum* (the early- and late-dominant species, respectively). We then used a neighbour removal experiment to test the effects of different herbivores on competition and facilitation between the two glade grass species.

4. In the long-term experiment, we found that large ungulate wildlife reinforced landscape heterogeneity over time by helping maintain glades in their early *C. plectostachyus*-dominated form. Cattle and mega-herbivore wildlife, on the other hand, appeared to reduce the positive effects through forage preference for *C. plectostachyus*.

5. In the neighbour removal experiment, we found that each grass species benefited from facilitation when it was the preferred forage for the dominant grazer. Facilitation of *C. plectostachyus* by *P. stramineum* was strongest when cattle co-occurred with wildlife, whereas facilitation of *P. stramineum* by *C. plectostachyus* was strongest when cattle were absent.

6. *Synthesis.* Our results demonstrate that different combinations of cattle and wildlife have different effects, largely via contrasting forage preferences, on the persistence of landscape heterogeneity in this savanna landscape. More generally, we provide evidence for contrasting effects of cattle and wildlife on short-term plant interactions (facilitation) and successional processes within the herbaceous plant community.

Key-words: cattle–wildlife interactions, ecological legacies, facilitation, foraging behaviour, landscape heterogeneity, pastoralism, plant–herbivore interactions, rangeland, succession

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Introduction

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

Through their effects on plants, herbivores can create and maintain patterns of savanna landscape heterogeneity (Adler, Raff & Lauenroth 2001; DuToit, Rogers & Biggs 2003; Scholes & Walker 2004; de Knegt *et al.* 2008), patterns typically defined, in part, by vegetation type or structure. One pervasive form of large-scale heterogeneity throughout savannas in much of sub-Saharan African is derived from former livestock corrals. Corral sites develop into long term (decades to centuries), nutrient-rich patches identifiable by their distinctive plant communities (Stelfox 1986; Blackmore, Mentis & Scholes 1990; Reid & Ellis 1995; Young, Patridge & Macrae 1995; Veblen, 2008a; Muchiru, Western & Reid 2009). In many savannas, these landscape features take the form of treeless 'glades' and can occur at densities of 2 km² (Young, Patridge & Macrae 1995; K. Veblen, unpubl. data) and cover up to 17% of some landscapes (Blackmore, Mentis & Scholes 1990). These glades are embedded in a wooded savanna background (or patches of trees against open background), and with their highly palatable vegetation they serve as foci of ungulate wildlife activity (Young, Patridge & Macrae 1995; Augustine 2003; Muchiru, Western & Reid 2008; Veblen, 2008a). The herbivores attracted to these glades in turn have the potential to influence dynamics among plant species and maintain vegetation in a nutritious short-grass state (*sensu* McNaughton 1984), producing a long-term human 'footprint' on the landscape. Yet, despite the ecological importance and ubiquity of glade-like features in herbivore-dominated savannas, there has been very little experimental investigation of how herbivores influence glade vegetation development.

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

The role of herbivores in successional processes can be highly variable and context dependent (Davidson 1993; Hobbs 1996). In some cases, herbivores increase the rate of succession, while in other cases herbivores decrease the rate of succession or appear not to affect it (Connell & Slatyer 1977; Belsky 1986; Brown & Ewel 1987; Davidson 1993; Howe & Lane 2004). This is at least partly due to differences in the ecology of different herbivore species, particularly foraging habits and preferences that may have contrasting effects on the growth and dominance of different plant species (Brown & Stuth 1993; Augustine & McNaughton 1998; Seabloom & Richards 2003). In our study system, glades undergo conversion from dominance by one grass species, *C. plectostachyus*, to another *P. stramineum* (Veblen 2008a). In this case, preferential grazing of *C. plectostachyus* may promote the conversion of glade vegetation, or conversely, grazing on *P. stramineum* may hinder its ability to invade *C. plectostachyus*-dominated vegetation.

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

Despite the potential for interactions among different herbivore guilds, there have been few controlled replicated studies that experimentally examine separate and combined effects of wild and domestic large herbivores on the ecosystems they share (Young *et al.* 1998). Moreover, although large herbivores dominate many African savanna landscapes, there have been no controlled studies of the potentially contrasting effects of cattle and wildlife on plant dynamics and vegetation change associated with large-scale savanna landscape heterogeneity. Although we have some experimental information about how large herbivores in general (i.e. mixed foraging by cattle and wildlife) affect the small-scale competitive balance between the two main grass species in a glade mosaic (Veblen 2008b), we have virtually no information about how the different guilds each contribute to these relationships, or how these translate to landscape-scale succession. Here we ask how cattle and wildlife (separately and in combination) affect the maintenance and successional development of this form of landscape heterogeneity – the treeless glades (0.25–1.0 ha) that are scattered across a wooded savanna landscape in Laikipia, Kenya. We ask two specific questions: (i) How do cattle vs. wildlife affect long-term patterns of glade vegetation development? (ii) How

do cattle vs. wildlife affect short-term plant–plant dynamics in herbaceous glade vegetation?

Materials and methods

STUDY SITE

This research was conducted in an *Acacia drepanolobium* savanna in the semi-arid Laikipia District of Kenya. The study area is located on the Mpala Research Centre property (36°52′ E, 0°17′ N) where the mean annual rainfall is 500–600 mm (mid-range for savanna ecosystems). The mean rainfall pattern is weakly trimodal, with the highest peak occurring in March–May (mean in April, 1998–2005: 120 mm) and the longest, most pronounced dry season typically from December to March (mean Jan–Feb, 1998–2005; 35 mm). The study area is underlain with 'black cotton' soils, poorly drained vertisols with high ($> 50\%$) clay content (Ahn & Geiger 1987). These black cotton savannas are widespread in Africa, covering hundreds of thousands of km^2. Ninety-seven per cent of the tree canopy cover is *Acacia drepanolobium* Sjost., and 90% of herbaceous cover is comprised of five grass species: *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf. and *Brachiaria lachnantha* (Hochst.) Stapf. (Young *et al.* 1998). The area is actively managed for cattle, with mean stocking densities of 0.5–0.7 cattle per hectare. This stocking density allows for the coexistence of a rich fauna of wildlife species such as: elephant (*Loxodonta africana* Blumenbach), giraffe (*Giraffa camelopardalis* L.), eland (*Taurotragus oryx* Pallas), oryx (*Oryx gazella beisa* L.), hartebeest (*Alcelaphus buselaphus* Pallas) Grant's gazelle (*Gazella grantii* Brooke), zebra (*Equus burchelli* Gray), steinbuck (*Raphicerus campestris* Thunberg), spotted hyaena (*Crocuta crocuta* Erxleben), and lion (*Panthera leo* L.).

Historical and contemporary cattle management has created a landscape mosaic of nutrient-rich, treeless glades (0.25–1.0 ha) scattered throughout the *A. drepanolobium* savanna (*c.* 2 trees km^{-2}). Once abandoned, temporary cattle corrals ('bomas') develop into nutrient-rich glades that are preferred by both livestock and wildlife (Veblen, 2008a, see also Augustine 2004). After abandonment, a ring of dense, often taller, trees develops at the boma margin and demarcates the abrupt boundary between woodland and the original boma, coincident with an abrupt change in the understorey. Within months of abandonment the stoloniferous mat-forming grass, *C. plectostachyus* K. Schum, colonizes the dung layer, covering the entire boma area in as little as 2–3 years (K. Veblen, un-publ. data). Vegetation in younger glades is dominated by this stoloniferous grass ($> 75\%$ cover), while the vegetation of older glades is dominated ($> 65\%$ cover) by an ascending bunchgrass, *P. stramineum* (Veblen 2008a). Immediately outside the glade boundary, the *C. plectostachyus* and *P. stramineum* communities abruptly give way to a vegetation composition and density resembling background non-glade vegetation, where *C. plectostachyus* is essentially absent ($< 1\%$ cover) and *P. stramineum* no longer dominates (20–40% cover).

LARGE HERBIVORE EXCLOSURES

To examine the separate and combined effects of cattle and wildlife on glade development, we used the Kenya Long-term Exclosure Experiment (KLEE). Established in 1995, KLEE is a series of 4-ha plots that uses semi-permeable barriers to allow access by different combinations of cattle ('C'), large ungulate wildlife > 15 kg ('W') and mega-herbivore wildlife ('M') (i.e. elephants and giraffes). Each

of the following six treatments is replicated across three blocks: C, W, WC, MW, MWC and O. The capital letters indicate which herbivore guilds are allowed access (e.g. 'O' allows no herbivores > 15 kg, 'W' allows wildlife > 15 kg, but no cattle or mega-herbivores, and 'MWC' allows mega-herbivores, wildlife and cattle). Six glades were included within the study design which, when divided by fences, created 18 glade portions. This included several glade sections adjacent to KLEE plots maintained in herbivore treatments. All glade–herbivore treatments except MW were initially replicated three times, and a third MW replicate was added in 2004.

RESPONSE OF GLADE VEGETATION TO LONG-TERM HERBIVORE EXCLUSION

In August 2003, for each of the 17 glade portions (hereafter referred to as 'glades') assigned to these six herbivore treatments, we sampled herbaceous vegetation along a transect that ran from glade centre to 60 m beyond the glade edge (Fig. 1). Each transect was oriented to bisect the angle created by the boundaries of herbivore treatments. Tree presence around the glade perimeter coincided with the boundary of *C. plectostachyus–P. stramineum* understorey dominance and demarcated glade edge (and distance of zero). We sampled every 5 m between glade centre and 15 m outside the glade ($+ 15$ m), and at $+ 30$ m and $+ 60$ m, for a total of 229 sample locations (mean of 13 per glade, depending on glade size). For statistical analysis, at each glade, samples were averaged
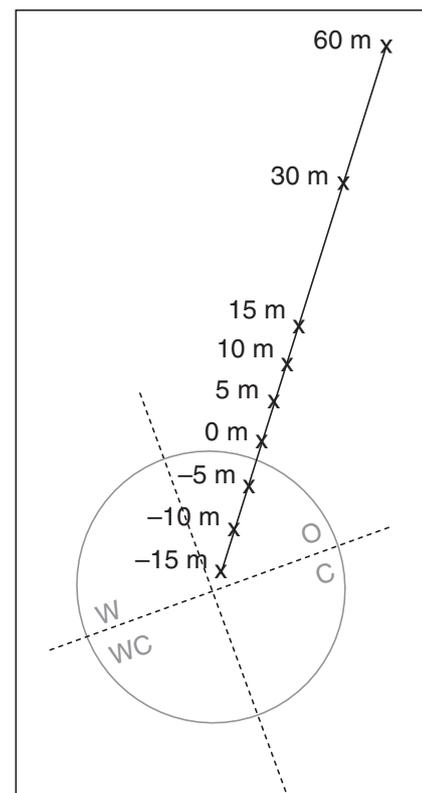

Fig. 1. Glade sampling transects. Sampling occurred at 5-m intervals (marked 'x') along transects bisecting each glade portion. Dotted line indicates treatment boundaries, and capital letters indicate different herbivore treatments ('W' = large ungulate wildlife, 'C' = cattle, 'WC' = large ungulate wildlife and cattle, and 'O' = neither large ungulate wildlife nor cattle).

into three distance categories: (i) inside (from the glade centre to −10 m), (ii) glade edge (−5 m, 0, +5 m and +10 m) and (iii) outside, (+15, +30 and +60 m). At each sampling point, we used a 10-point pin frame to measure aerial plant cover (first hit of each species, i.e. maximum of 10 hits per species per pin frame), and we recorded the presence of each species rooted within a 1-m^2 quadrat. In 2006, we added a second year of data collection for vegetation inside glades (but not on edges or outside). We sampled all 18 glade × treatment combinations (the original 17 plus the recently added MW treatment), placing 6–18 pin frames per glade (mean = 12) in a grid that covered the entire glade. The grid was spaced at 5 m, and all points were at least 5 m from glade edge. We averaged pin hits across frames within each glade to give a single cover value for each species in a given glade.

PLANT NEIGHBOUR EXPERIMENTAL MANIPULATION

In August 2005, we used a neighbour removal experiment within the KLEE experiment to investigate competition and facilitation between the two dominant herbaceous glade species, *P. stramineum* and *C. plectostachyus*, in the context of different herbivore treatments. We located areas where the two grass species co-occurred in two exclosure types: those that included wildlife but not cattle (W and MW, *n* = 4) and those that included wildlife plus cattle (WC and MWC, *n* = 4). Within these areas (in which neither species exhibited > 90% cover), we randomly assigned one of three treatments to three randomly located 1 × 1 m plots: *C. plectostachyus* removal, *P. stramineum* removal, and control (no plants removed). This resulted in a 2 × 2 factorial design for each of the two grass species with species removal treatments (heterospecific neighbours present vs. heterospecific neighbours removed) crossed with grazing treatments (wildlife only vs. wildlife plus cattle). Because removing the target species also reduced overall plant density, we randomly located a fourth 1 × 1 m plot in each glade, in which we reduced overall plant density (of both species) by one-half. This density-reduced plot was treated as the control (heterospecific neighbours present) in an additional 2 × 2 analysis of neighbour effect and grazing treatment on each species. Neither C nor O plots contained enough co-dominated areas to be included in the experiment; *C. plectostachyus* in these plots rarely occurred in mixture with *P. stramineum* and instead primarily occurred in a few monoculture patches. All removed plants were clipped to remove above-ground biomass and after rainfall any new growth was individually treated by sponge with Roundup® (glyphosate herbicide).

We measured total plant cover in each 1 × 1 m plot using five evenly spaced pin frames (*n* = 50 pins per plot). We counted the total number of times that each species touched each pin; total number of pin hits is positively correlated with total biomass of each species (*C. plectostachyus r* = 0.89; *P. stramineum r* = 0.68, K. Veblen, unpubl. data). At the time of plot set-up in August 2005, we quantified plant cover within each 1 × 1 m plot prior to manipulation and then repeated baseline pin frame counts in 'removal' plots immediately after neighbour removal treatments were complete. Seven months later (in March 2006), at the end of the 3-month-long dry season (24 mm rainfall in January–March 2006), we assessed the effects of experimental treatments on *C. plectostachyus* and *P. stramineum* by repeating pin frame measurements in all plots. We repeated measurements an additional 4 months later, in July 2006, at the end of a 3-month period of heavy rainfall (153 mm in April–June 2006) and an additional 1 year later in July 2007 (230 mm in April–June 2007). In 2007, the majority of the rainfall fell in June, the month prior to sampling.

STATISTICAL ANALYSES

For all statistical analyses, we used generalized linear mixed models; we used maximum-likelihood methodology and Satterthwaite's approximation of degrees of freedom (PROC MIXED, version 9.1; SAS Institute 2002). Variance weighting was used when variances were not homogenous, and values were log-transformed when necessary. We used Tukey's HSD analyses for *post hoc* comparisons.

Response of glade vegetation to long-term herbivore exclusion

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

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

The 2006 vegetation data (collected only from inside glades) were combined with the 2003 'inside glade' vegetation data, and the statistical model included the following fixed effects: main plot effect of herbivore treatment, two subplot effects of species (*C. plectostachyus* vs. *P. stramineum*) and year (2003/2006), and all interactions. Glade nested within block and its interactions were treated as random effects. This model was used twice, to separately test absolute and relative *C. plectostachyus* – *P. stramineum* cover.

Plant neighbour experimental manipulation

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

plots, we used the same split-plot model, replacing control plots with density-reduced control plots.

Results

RESPONSE OF GLADE VEGETATION TO LONG-TERM HERBIVORE EXCLUSION

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

Although neither total grass nor forb cover in 2003 varied significantly across herbivore treatments or distances from glades (overall, grass: $100.0 \pm 2.8\%$; forbs: $16.0 \pm 2.2\%$), species composition differed significantly between inside and outside glades. Absolute cover of *C. plectostachyus* was 12 times higher in glades than outside ($20.5 \pm 5.7\%$ vs. $1.7 \pm 1.6\%$), and *P. stramineum* cover was almost two times higher inside glades than outside ($86.4 \pm 4.2\%$ vs. $49.1 \pm 3.3\%$). Inside glades, cover of *P. stramineum* ($74.1 \pm 3.1\%$) was significantly higher than *C. plectostachyus* cover ($14.7 \pm 3.1\%$) (significant species × distance interactions for both absolute and relative

cover, Tukey $\alpha < 0.05$, Table 1). Patterns of cover for the two species differed at glade edges; *P. stramineum* cover at glade edges was similar to cover inside glades, whereas *C. plectostachyus* cover at glade edges was more similar to cover outside of glades (significant species × distance interactions for both absolute and relative cover, Tukey $\alpha < 0.05$, Table 1). *Pennisetum stramineum* edge patterns were driven largely by lower *P. stramineum* cover outside of glades in MWC and C plots (significant species × distance × treatment interaction, Tukey $\alpha < 0.05$, Table 1).

PLANT NEIGHBOUR EXPERIMENTAL MANIPULATION

Neighbour removal plots indicate that both *C. plectostachyus* and *P. stramineum* responded strongly to sampling period in three ways (Fig. 3). First, both species experienced greater growth in July after the rainy seasons than in March after the dry season (season effect: *C. plectostachyus* $F_{2,34} = 12.07$, $P = 0.0001$; *P. stramineum* $F_{2,7.06} = 18.74$, $P = 0.0015$). Secondly, both species responded negatively to cattle presence in the dry season but not during the wet seasons (season × cattle presence interaction: *C. plectostachyus* $F_{2,34} = 6.54$, $P = 0.004$; *P. stramineum* $F_{2,30.5} = 3.99$, $P = 0.03$; Tukey $P < 0.05$). Thirdly, both species benefited from the presence of heterospecific neighbours in the dry season (March 2006, Fig. 3a,d), but in the wettest season (July 2007, Fig. 3c,f) heterospecific neighbour effects were competitive (season × neighbour presence interaction: *C. plectostachyus* $F_{2,34} = 12.76$, $P < 0.0001$; *P. stramineum* $F_{2,24.6} = 5.44$, $P = 0.01$).

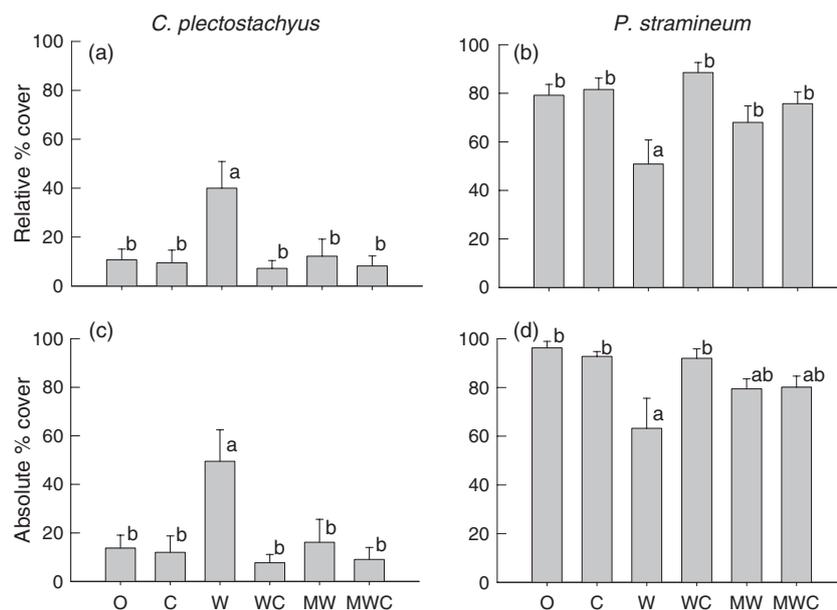**Fig. 2.** Mean ($+1$ SE) relative (a, b) and absolute cover (c, d) of two grass species, *Cynodon plectostachyus* and *Pennisetum stramineum*, inside treeless glades in six herbivore treatments allowing different combinations of cattle ('C'), wildlife (> 15 kg, 'W'), and mega-herbivore wildlife (elephants and giraffes, 'M'). Capital letters indicate which herbivore guilds are present in each treatment; 'O' plots indicate absence of all three types of herbivores. Cover values are means of multiple pin frame measurements per glade in August 2003 and 2006. Mixed-model analyses showed no significant sampling period effects. Species × treatment interactions were significant for relative cover ($F_{5,24.5} = 7.12$, $P = 0.0003$) and absolute cover ($F_{5,33.3} = 7.13$, $P = 0.0001$). Shared letters within each species indicate no significant differences according to Tukey's HSD ($\alpha = 0.05$).

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

	Relative cover			Absolute cover		
Factor	d.f.	*F*	*P*	d.f.	*F*	*P*
2003 and 2006						
sp	1, 4.56	99.18	0.0003	1, 6.07	102.94	< 0.0001
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	< 0.0001	1, 36.3	425.22	< 0.0001
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	< 0.0001	2, 59.3	23.36	< 0.0001
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

sp, species (*C. plectostachyus* vs. *P. stramineum*); trt, treatment (O, W, C, WC, MW, MWC); yr, year (2003 vs. 2006); dist, distance (inside, edge, outside of glades).
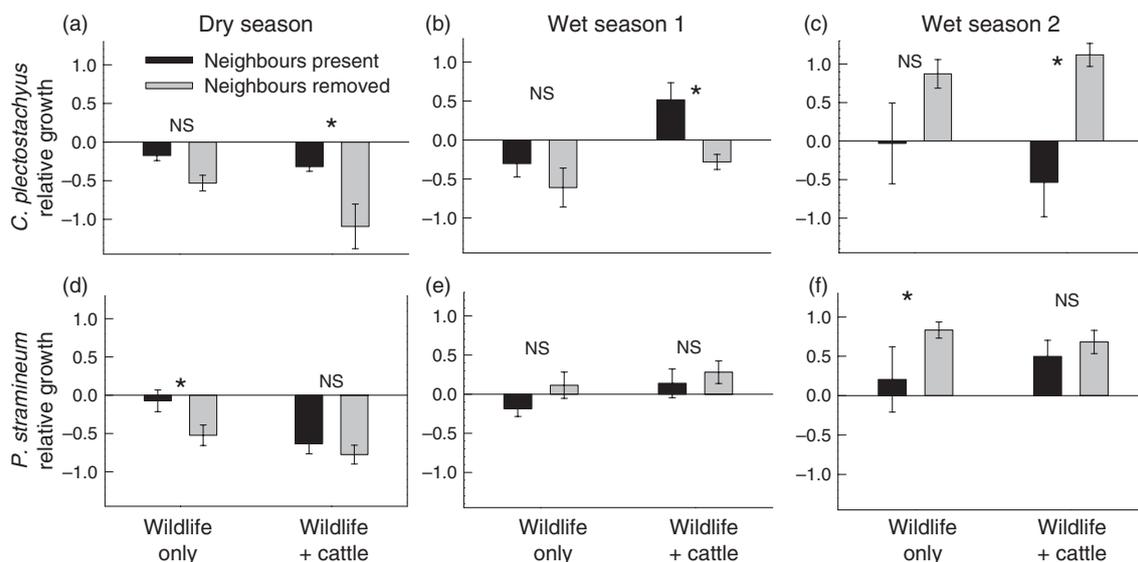

Fig. 3. Effects of interspecific competitors (presence vs. absence) and herbivory (wildlife vs. wildlife + cattle) on mean (±1 SE) relative growth of (a–c) *Cynodon plectostachyus* and (d–f) *Pennisetum stramineum* in 1 × 1 m plots during three sampling periods (March dry season 2006 vs. July wet season 2006 vs. July wet season 2007). Relative growth is calculated as ln [(cover *t*2)/(cover *t*1)]. 'NS' indicates no significant differences and '*' indicates significant differences according to planned contrast tests of neighbour effects at the *P* = 0.05 level.

Although both grass species benefited from heterospecific neighbours during the dry season, the presence of cattle had contrasting effects on *C. plectostachyus* vs. *P. stramineum* during this time (Fig. 3). For *C. plectostachyus*, positive (facilitative) effects of heterospecific neighbours (i.e. *P. stramineum*) were significant only when cattle were present (cattle present: $F_{1,34} = 10.97$, $P = 0.002$; cattle absent: $F_{1,34} = 2.34$, $P = 0.14$; Fig. 3a). In contrast, for *P. stramineum*, positive heterospecific neighbour effects were significant only when cattle were 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, during the dry season, *C. plectostachyus* was facilitated by heterospecific (*P. stramineum*) neighbours when cattle were present, whereas *P. stramineum* was facilitated by heterospecific (*C. plectostachyus*) neighbours when cattle were absent.

For both species, comparing neighbour removal plots against density-reduced control plots produced results similar to those discussed above, suggesting that experimental effects reflect species-specific removals rather than reduction in overall plant densities (of both con- and heterospecifics).

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

	C. plectostachyus		*P. stramineum*	
	Full density	Density reduced	Full density	Density reduced
March 2006 (dry season)	−0.24 ± 0.05	−0.23 ± 0.11	−0.35 ± 0.13	−0.47 ± 0.17
July 2006 (wet season)	0.10 ± 0.20	0.02 ± 0.16	−0.02 ± 0.11	0.02 ± 0.17
July 2007 (wet season)	−0.28 ± 0.33	0.27 ± 0.20	0.35 ± 0.22	0.90 ± 0.16

Facilitation occurred during the dry season for both species, while competition was more important during wet seasons (season × neighbour presence interaction: *C. plectostachyus* $F_{2,23.2} = 13.71$, $P = 0.0001$; season × neighbour presence × cattle presence interaction *P. stramineum* $F_{2,26.7} = 3.83$, $P = 0.04$). For *C. plectostachyus*, dry season facilitation was strongest in the presence of cattle (cattle present $F_{1,23.2} = 5.82$, $P = 0.02$; cattle absent $F_{1,23.2} = 3.176$, $P = 0.09$) and for *P. stramineum* strongest in the absence of cattle (cattle present $F_{1,26.7} = 0.01$, $P = 0.92$; absent cattle $F_{1,26.7} = 3.99$, $P = 0.06$). During the wet season, density-reduced plots released both species from intra-specific competition. This reduction in intra-specific competition offset some of the negative effects of interspecific competition seen in control plots (e.g. more than doubling the increase in *P. stramineum* cover during July 2007; Table 2).

Discussion

We have previously shown that the treeless glades in this landscape are ecosystem hot spots created by cattle management and that large herbivores in general (cattle and wildlife grouped together) influence small-scale species interactions in these glades (Veblen 2008a). Here we provide experimental evidence within a single system that different large herbivore guilds (cattle and large ungulate wildlife) have differing effects on the herbaceous vegetation associated with these important landscape features that play out at the scale of entire glades. Evidence from several ecosystems suggests that both cattle and wildlife can be key players in the maintenance of landscape heterogeneity through their effects on plant communities (McNaughton 1984; Adler, Raff & Lauenroth 2001; Tobler, Cochard & Edwards 2003; Augustine & McNaughton 2004; Waldram, Bond & Stock 2008), Rarely, however, are the effects of cattle and large ungulate wildlife studied together.

RESPONSE OF GLADE VEGETATION TO LONG-TERM HERBIVORE EXCLUSION

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

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

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

Through their forage preferences, cattle, wildlife and mega-herbivores have potentially opposing effects on the long-term successional development of glade vegetation. By suppressing the invading grass, *P. stramineum*, wildlife help maintain glades in an earlier successional state, effectively lengthening this particularly desirable (palatable and high quality vegetation) stage in the lifespan of glades. Cattle and mega-herbivores, on the other hand, by selectively foraging on *C. plectostachyus*, may reinforce the successional trajectory of glade development toward *P. stramineum* invasion. In savannas elsewhere, browsing on seedlings of woody species prevents woody invasion of herbaceous communities (e.g. Scholes & Archer 1997). Similarly, herbivory, particularly by cattle, often is implicated

in accelerating invasion processes in rangelands; again most examples involve woody plant encroachment following suppression of palatable herbaceous communities (Vanvegten 1984; e.g. Roques, O'Connor & Watkinson 2001; Tobler, Cochard & Edwards 2003). Ours appears to be among the first examples of large herbivores affecting an invasion trajectory within the herbaceous (grass) layer.

SEASON AND HERBIVORE EFFECTS ON PLANT–PLANT DYNAMICS

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

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

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

In contrast, facilitation of *C. plectostachyus* by *P. stramineum* was strongest in the presence of cattle. These results are consistent with previous evidence for dry season facilitation of *C. plectostachyus* in the presence of a mixed (cattle and wildlife) herbivore assemblage (Veblen 2008b), and they are also consistent with cattle forage preference for high quality *C. plectostachyus* forage and associational resistance provided by less palatable *P. stramineum*. Although cattle treatments produced clear experimental effects, our experimental design did not allow us to determine whether treatment effects were due to the addition of cattle specifically, or due to the addition of overall grazing pressure (regardless of herbivore identity). Thus, experimental addition of more wildlife (instead of cattle) may have produced the same

observed pattern. In either case, our results show that facilitation of early successional *C. plectostachyus* was strongest when cattle co-occurred with wildlife, whereas facilitation of late-successional *P. stramineum* was strongest in the presence of wildlife alone.

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

Conclusions

Through their effects on successional change and plant–plant dynamics, different combinations of cattle and wildlife have contrasting effects on the development and persistence of one important type of savanna landscape heterogeneity. Our first (large-scale) experiment showed that, over the long term (8 + years), wildlife presence contributed to the persistence of younger glade vegetation, whereas cattle appeared to favour invasion by a later-successional species. The forage preferences implicated in the aforementioned patterns are consistent with the results of our second (neighbour removal) experiment; each species benefited from facilitation when it was the preferred forage for the dominant grazer. That is, *C. plectostachyus* was facilitated when cattle were present, and *P. stramineum* was facilitated when only wildlife were present. In both cases, our results are consistent with patterns of greater facilitation with higher grazing pressure (Bertness & Callaway 1994; Graff, Auguiar & Chaneton 2007) and appear to be attributable to associational resistance.

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

Acknowledgements

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