

Grasses and browsers reinforce landscape heterogeneity by excluding trees from ecosystem hotspots

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Abstract Spatial heterogeneity in woody cover affects biodiversity and ecosystem function, and may be particularly influential in savanna ecosystems. Browsing and interactions with herbaceous plants can create and maintain heterogeneity in woody cover, but the relative importance of these drivers remains unclear, especially when considered across multiple edaphic contexts. In African savannas, abandoned temporary livestock corrals (bomas) develop into long-term, nutrient-rich ecosystem hotspots with unique vegetation. In central Kenya, abandoned corral sites persist for decades as treeless ‘glades’ in a wooded matrix. Though glades are treeless, areas between adjacent glades have higher tree densities than the background savanna or areas near isolated glades. The mechanisms maintaining these distinctive woody cover patterns remain unclear. We asked whether browsing or interactions with herbaceous plants help to maintain landscape heterogeneity by differentially impacting young trees in different locations. We planted the mono-dominant tree species (*Acacia drepanolobium*) in four locations: inside glades, far from glades, at edges of isolated glades and at edges between adjacent glades. Within each location, we assessed the separate and

combined effects of herbivore exclusion (caging) and herbaceous plant removal (clearing) on tree survival and growth. Both caging and clearing improved tree survival and growth inside glades. When herbaceous plants were removed, trees inside glades grew more than trees in other locations, suggesting that glade soils were favorable for tree growth. Different types of glade edges (isolated vs. non-isolated) did not have significantly different impacts on tree performance. This represents one of the first field-based experiments testing the separate and interactive effects of browsing, grass competition and edaphic context on savanna tree performance. Our findings suggest that, by excluding trees from otherwise favorable sites, both herbaceous plants and herbivores help to maintain functionally important landscape heterogeneity in African savannas.

Keywords Boma · Grazing lawn · Tree–grass interactions · Spatial heterogeneity · Edge interactions

Introduction

Understanding heterogeneity in vegetation structure has been a central goal of ecology, particularly in savanna ecosystems where mechanisms of tree–grass coexistence have long been debated (Walter 1971; Walker et al. 1981; Scholes and Archer 1997; Jeltsch et al. 2000; Sankaran et al. 2004). Patterns of woody cover in savannas can be driven by a multitude of factors including rainfall, nutrients, herbivory, fire, interactions with grasses or other woody plants, and interactions among these factors (Dublin et al. 1990; Scholes and Archer 1997; Jeltsch et al. 2000; van Langevelde et al. 2003; Sankaran et al. 2005; Riginos and Grace 2008; van der Waal et al. 2011). Heterogeneity in woody cover is important because it alters and possibly

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enhances biodiversity and ecosystem function (Young et al. 1995; Rietkerk et al. 2004; Riginos and Grace 2008; Lundholm 2009; Gregory et al. 2010).

In African savannas, heterogeneity in woody cover is often associated with heterogeneity in soil quality. Woody cover can be affected by regional-scale nutrient gradients as well as nutrient-rich micro-sites (e.g., termite mounds) (Sankaran et al. 2005; Fox-Dobbs et al. 2010; Levick et al. 2010). Intermediate in scale are nutrient-rich sites derived from traditional livestock corrals (bomas) (Western and Dunne 1979; Blackmore et al. 1990; Lamprey and Reid 2004). Throughout African savannas, former corral sites develop into long-term, nutrient-rich patches with unique vegetation (Blackmore et al. 1990; Reid and Ellis 1995; Young et al. 1995; Augustine 2003; Muchiru et al. 2009; van der Waal et al. 2011), distinctive plant community dynamics (Veblen 2008, 2011; Veblen and Young 2010) and broad-ranging ecological impacts (Augustine 2004; Gregory et al. 2010).

In wooded savannas, corral sites can persist as grass-dominated ‘glades,’ easily recognizable for decades to centuries as large treeless patches (50–100 m in diameter) embedded in a wooded matrix (Young et al. 1995; Muchiru et al. 2009; Veblen and Young 2010). Though glade interiors are treeless, areas between nearby glades (<150 m apart) have higher densities of trees than either the background savanna or areas near isolated glades (Porensky 2011). It is not clear how these distinctive patterns of woody cover associated with glade interiors (no trees) and adjacent glade edges (many trees) are maintained over the long-term. Inside nutrient-rich glades, at glade edges, and in the background savanna, we assessed the relative importance of two mechanisms that may drive heterogeneity in woody cover: herbivory and interactions with herbaceous plants.

Herbivory has major impacts on woody cover in savanna ecosystems (Pellew 1983; Augustine and McNaughton 2004; Goheen et al. 2010) and could play a particularly important role in determining woody cover patterns associated with glades, where use by mid-sized, mixed-feeder herbivores is elevated (Young et al. 1995; van der Waal et al. 2011). Herbivore preference may lead to elevated browsing pressure and reduced tree survival or growth within glades, particularly for young trees (seedlings and saplings) (Goheen et al. 2004; Midgley et al. 2010). Thus, initial anthropogenic disturbance may generate herbivore-mediated feedbacks that help maintain glades in a treeless state over the long term.

Very high densities of trees between nearby glades may also be caused by a combination of anthropogenic legacies and herbivore-mediated feedbacks. During active corral use, intensive livestock activity and human presence between nearby corrals may initiate a burst of tree establishment by reducing grass cover, deterring browsers and

increasing nutrient levels, especially if low grass cover causes reduced fire intensity or frequency (e.g., Tobler et al. 2003; van Langevelde et al. 2003; Augustine and McNaughton 2004; Muchiru et al. 2009; Davies et al. 2010; Goheen et al. 2010). Over the long term, herbivore behaviors may reinforce high tree densities between glades. The mid-sized wildlife species most likely to browse on tree seedlings tend to avoid heavily-treed areas (Riginos and Grace 2008). Reduced browsing pressure in heavily-treed areas between nearby glades could further increase tree density.

Herbaceous plants (hereafter ‘grasses’) can also exert controls over young trees (Riginos and Young 2007). Grasses often compete intensely with young trees (e.g., van der Waal et al. 2009; Cramer et al. 2010). Glades in our study site typically have very high grass cover (Veblen 2008; Porensky 2011), creating an environment in which grass competition may be severe enough to kill young trees (e.g., van der Waal et al. 2011). Areas between nearby glades have unusually low cover of dense glade grasses, which may release young trees from competition and help explain increased tree densities between nearby glades (Porensky 2011). At low-moderate densities (e.g., between nearby glades), grasses may even facilitate young trees by concealing them from herbivores (Western and Maitumo 2004; Riginos and Young 2007). Differences in grass cover can also impact tree density via interactions with fire (van Langevelde et al. 2003; Davies et al. 2010), although fire has been suppressed at our study site for decades.

This work goes beyond previous studies by experimentally testing the separate and combined effects of both herbivory and grasses on the survival and growth of young trees planted in the field in different edaphic contexts. Specifically, we determined the relative importance of herbivores and grasses as drivers of (1) extremely low densities of trees inside glades and (2) high densities of trees between nearby glades.

Materials and methods

Study site

This research took place in central Kenya on Mpala Conservancy (36°52'E, 0°17'N) and neighboring Jessel Ranch. These properties are managed for livestock production as well as biodiversity conservation, and host a full complement of wildlife species including native ungulates and their predators (see Young et al. 1998). Soils are ‘black cotton’ vertisols characterized by high clay content and poor drainage (Deckers et al. 2001). Mean annual rainfall is 500–600 mm. Topography is relatively uniform, and vegetation is dominated by a single tree species (*Acacia*

drepanolobium, comprising 97% of total woody cover) and five grass species (Young et al. 1998). The study area includes dozens of glades that are irregularly distributed throughout the landscape, creating variability in inter-glade distance (Fig. 1). Fire has not been an active part of this ecosystem since the 1960s, although small portions of the study site have been experimentally burned in recent years (R.L. Sensenig, personal communication).

Seed collection and germination

Between September 2008 and January 2009, we collected seeds from 33 adult *A. drepanolobium* trees located throughout the study site. Source trees were all greater than 3 m tall and occupied by the same symbiotic *Acacia* ant species (*Crematogaster mimosae*). Source trees were separated from each other by at least 60 m. In total, we collected 1,518 seeds, or 46 ± 3 (1SE) seeds per source tree. We randomly assigned half the seeds from each source tree to a ‘sapling’ treatment and the other half to a ‘seedling’ treatment.

Germination and initial tree growth took place in a tree nursery operated by Kiwi Consultants in Nanyuki, Kenya,

40 km from the study site. Seeds assigned to the sapling treatment were germinated in February 2009, and seeds assigned to the seedling treatment were germinated in June 2009. All trees were grown in potting soil and fertilized once during initial growth. Trees were kept outdoors under shade cloth for the first 2–3 months of growth and then moved into full sun. On 15 August 2009, we clipped the top 3 cm of each sapling to simulate natural browsing and induce allocation to defense structures (cf. Young et al. 2003). In October 2009, we retrieved 484 saplings and 245 seedlings from the nursery. Most saplings had well-developed woody stem tissue, while seedlings were just beginning to form woody tissue. Trees were individually tagged. For each tree, we measured stem length (length of the longest stem, measured while straightening the stem as much as possible), diameter at 3 cm height (hereafter ‘basal diameter’), and number of branches.

Experimental design and data collection

We split the study area into five blocks based on property ownership and geographic position (Fig. 1). Within each block, we randomly chose a relatively isolated glade (>250 m from any other glade), a non-isolated glade (<150 m from a second glade), and a ‘no glade’ area (>300 m from any glade). We planted trees in four 11×11 m plots in each block: within the isolated glade, 25 m outside the edge of the isolated glade, 25 m outside the edge of the non-isolated glade, and at a random location within the ‘no-glade’ area (Fig. 1). The 25-m edge distance was chosen to match the observed location of peak tree densities between nearby glades (Porensky 2011). Glade edges were defined as in previous work (Porensky 2011). We used aerial photographs from 1961 to ensure that all glades were >45 years old. Plots inside glades were all located in areas dominated by the grass *Pennisetum stramineum* to reduce variability caused by differences in glade vegetation (Veblen 2008).

Within each plot, we created two replicates of a 2×2 factorial design that included mammalian herbivore exclusion (caging) and herbaceous vegetation removal (clearing). The four treatments included caged, cleared, caged + cleared, and control (no caging or clearing). We randomly assigned treatments to eight 1.5×1.5 m ‘sites’ within each 11×11 m plot (Fig. 1). Sites were arranged in a grid and separated from one another by 1.5 m. Sites assigned to caged and caged + cleared treatments were covered by a $1 \times 1 \times 1$ m chicken-wire cage. To reduce rodent incursions, we covered the bottom half-meter of each cage with ≤ 1.3 -cm mesh. At sites assigned to cleared and caged + cleared treatments, we clipped all non-woody plants (almost entirely grasses) at ground level. At intervals throughout the experiment (0.5, 1.5, 3 and 6 months after

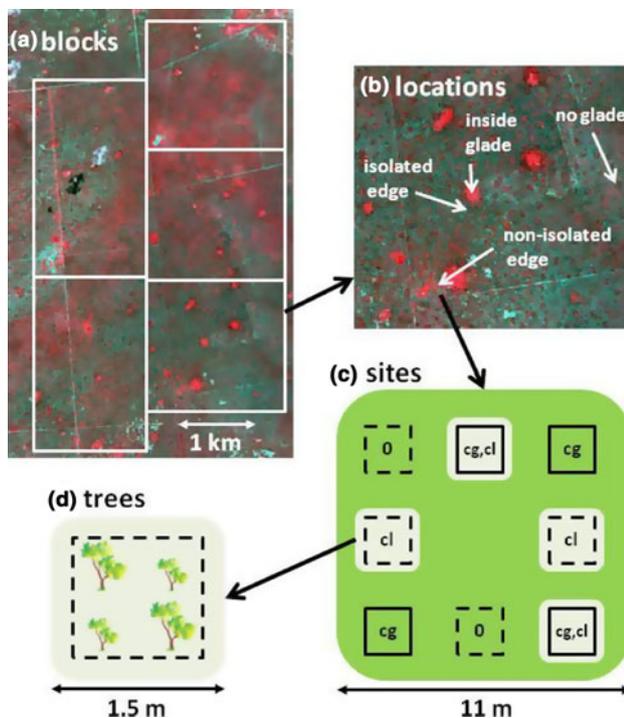


Fig. 1 The experimental design. **a** The study area was divided into five blocks. Glades are visible as round spots in this Quickbird image (DigitalGlobe 2003). **b** Each block contained four locations: far from glade, inside glade, isolated glade edge and non-isolated glade edge. **c** Within each location, two replicates of four treatments were randomly assigned to eight sites. Treatments included control (0), caging (cg), clearing (cl), and both caging and clearing (cg, cl). **d** Saplings and seedlings were randomly assigned to each site

planting), grass regrowth was sprayed with herbicide. Although the goal of caging was to protect trees from browsing, the cages also eliminated herbivory on herbaceous vegetation. In order to separate the direct effects of reduced browsing (the factor of interest) from indirect effects of reduced grazing inside cages (e.g., shading of trees by tall grasses), caged herbaceous plants were occasionally clipped so that average vegetation height inside cages matched that of surrounding, uncaged vegetation.

Within each 1.5×1.5 m site, we planted two randomly chosen saplings and either one or two randomly chosen seedlings (for a total of 16 saplings and 12 seedlings per plot, Fig. 1). Due to unexpectedly high mortality at the nursery, we were unable to plant two seedlings at every site, but within each plot we planted three seedlings per treatment. For each plot, we randomly chose which of the two sites assigned to a given treatment would receive two seedlings and which would receive one seedling. The orientation of seedlings and saplings within each site was also assigned randomly. Within each site, trees were planted ~ 70 cm apart (the maximum amount of separation possible given the size of the cages). Trees were planted in mid-October 2009, just before a short rainy season. At the time of planting, we watered each seedling or sapling with 1 L. We did not add any more water after planting. In total, we planted 320 saplings and 240 seedlings.

Trees were monitored in late August 2010. For each individually tagged tree, we recorded survival, stem length, basal diameter and number of branches (measured as described above). Of the 457 surviving trees, 6 were excluded from basal diameter analysis because the main stem had died or been severely browsed or broken.

Statistical analysis

The experiment had a blocked split-split-plot design with location as the main plot effect, treatment (caging and/or clearing) as the subplot effect, and tree age class as the sub-subplot effect. To evaluate factors responsible for reduced tree density inside glades, we compared three locations: far from glade, isolated glade edge and inside glade. To evaluate factors responsible for increased tree density between nearby glades, we compared isolated glade edges to non-isolated glade edges.

We analyzed tree survival using a generalized linear mixed model with a binary conditional probability distribution and residual pseudo-likelihood estimation. For trees that survived, we analyzed three different growth responses (stem length growth, basal diameter growth and branch production) using linear mixed models with restricted maximum-likelihood estimation. We analyzed each growth response separately because we expected stem length, basal

diameter and branch production to be differently affected by our treatments. In all cases, we used Satterthwaite's approximation of degrees of freedom and a 'variance components' covariance structure. For all models, fixed predictors included location, treatment, tree age class and all two-way interactions. If interactions were significant, we analyzed simple effects (e.g., differences among treatments within each location and differences among locations within each treatment). Random factors included block, location \times block and site nested within location \times block. We used transformations or variance-weighting when necessary in order to meet the assumptions of the models. We used Tukey's HSD method ($\alpha = 0.05$) for post hoc mean comparisons. All analyses were conducted in SAS 9.2 (SAS Institute, Cary, NC, USA).

Results

Baseline tree sizes

For seedlings, baseline stem length (measured just prior to planting) was 15.6 ± 0.4 (1SE) cm and baseline basal diameter was 2.2 ± 0.04 mm. For saplings, baseline stem length was 25.0 ± 0.5 cm and baseline basal diameter was 3.4 ± 0.06 mm. For both size classes, baseline branch number was 1.1 ± 0.02 branches.

Part I: inside and outside of isolated glades

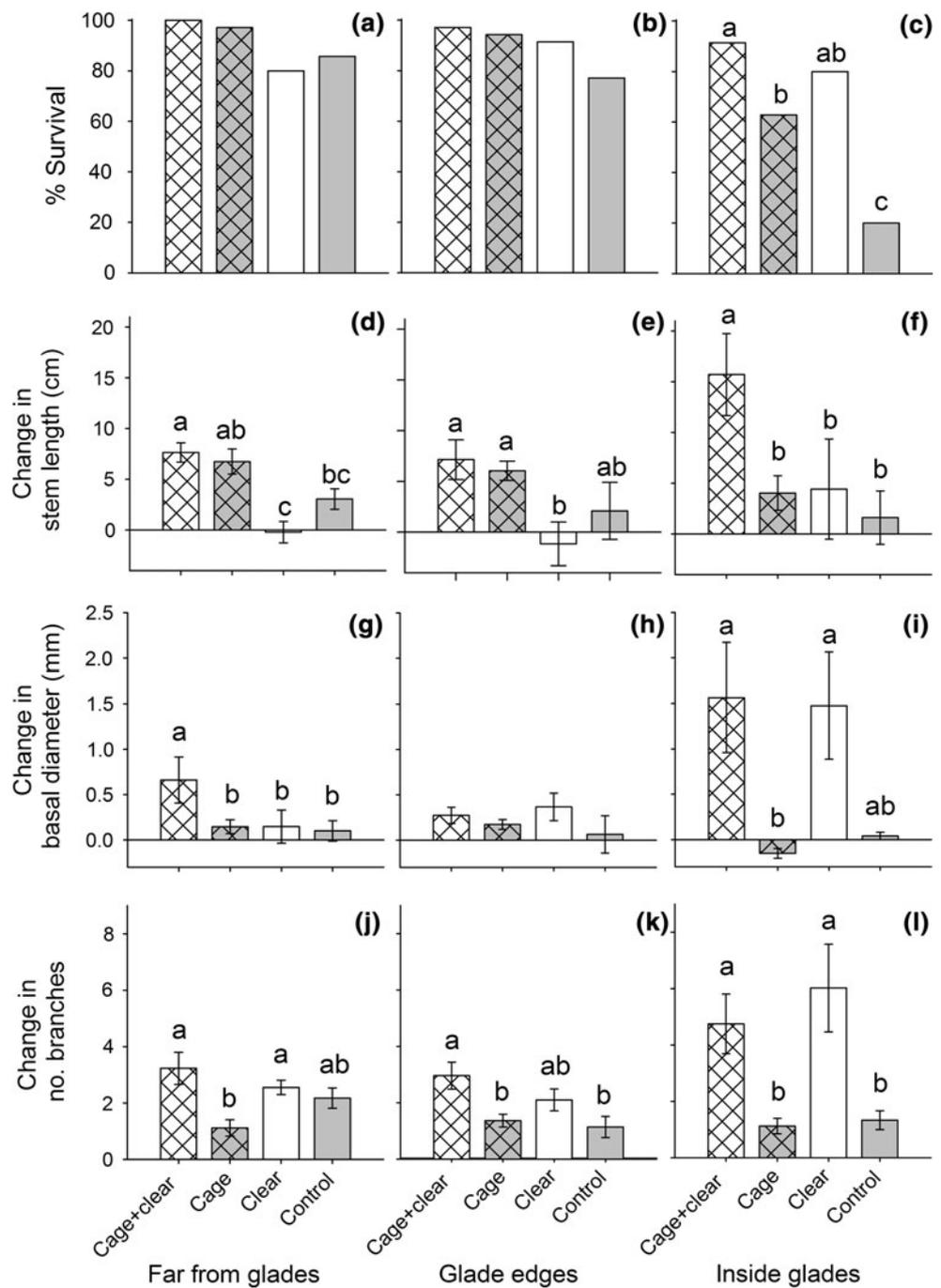
Survival

Saplings had significantly higher survival than seedlings (85 vs. 77%, $F_{1,402} = 3.55$, $P = 0.04$). Interactions involving age class were not significant, but the interaction between location (far from glade, glade edge, or inside glade) and treatment (caging and/or clearing) significantly affected survival ($F_{6,402} = 3.06$, $P = 0.006$).

Simple effects analysis revealed that caging and clearing did not significantly impact survival far from glades ($F_{3,136} = 2.55$, $P = 0.06$) or at glade edges ($F_{3,38.9} = 2.10$, $P = 0.12$), but strongly affected survival inside glades ($F_{3,136} = 11.16$, $P < 0.0001$). Inside glades, trees in the control treatment had less than one-third the survival of trees in any other treatment (Fig. 2a–c; Table 1).

Tree survival did not differ significantly across locations within the cleared ($F_{2,7.18} = 0.84$, $P = 0.5$) or caged + cleared ($F_{2,36.26} = 1.06$, $P = 0.4$) treatments. However, survival did differ by location within the caged ($F_{2,27.11} = 4.65$, $P = 0.02$) and control ($F_{2,6.61} = 9.17$, $P = 0.01$) treatments. Survival far from glades was 55% higher than survival inside glades for the cage treatment and over 300% higher for the control treatment (Fig. 2a–c; Table 1).

Fig. 2 Survival (a–c) and growth (d–l) of trees planted a, d, g, j far from glades, b, e, h, k at glade edges, and c, f, i, l inside glades. For growth responses, means \pm SE were calculated across blocks ($n = 5$) after averaging over all seven trees present within each block \times location \times treatment combination. Within each panel, treatments with shared letters are not significantly different (Tukey’s HSD method, $\alpha = 0.05$)



Stem length growth

Seedling stem lengths grew significantly more than those of saplings (8.6 ± 0.8 vs. 3.4 ± 0.6 cm; $F_{1,272} = 31.95$, $P < 0.0001$). Interactions involving age class were not significant. The interaction between location and treatment significantly affected stem length growth ($F_{6,104} = 3.28$, $P = 0.005$).

Treatment significantly affected stem length growth at all three locations (far from glades $F_{3,120} = 10.73$,

$P < 0.0001$; glade edge $F_{3,31.3} = 9.18$, $P = 0.0002$; inside glades $F_{3,24.5} = 7.51$, $P = 0.001$). Far from glades and at glade edges, caged + cleared trees grew about 8 cm more than cleared trees, while caged and control trees had intermediate growth (Fig. 2d–f; Table 1). Inside glades, growth of caged + cleared trees was over three times that of trees in other treatments (Fig. 2d–f; Table 1).

Stem length growth did not differ significantly across locations within any treatments (cage $F_{2,82.9} = 0.33$,

Table 1 Survival and growth of *A. drepanolobium* trees planted far from glades, at isolated glade edges and inside glades

| Treatment | Location | Survival | Stem length growth (cm) | Basal diameter growth (mm) | No. of new branches |
|--------------|----------------|----------|-------------------------|----------------------------|---------------------|
| Cage + Clear | Far from glade | 100 | 7.6 ± 0.9 | 0.7 ± 0.3 | 3.2 ± 0.6 |
| | Glade edge | 97 | 7.1 ± 1.9 | 0.3 ± 0.1 | 3.0 ± 0.5 |
| | Inside glade | 91 | 15.7 ± 4.0 | 1.6 ± 0.6 | 4.7 ± 1.1 |
| Cage | Far from glade | 97 a | 6.8 ± 1.2 | 0.1 ± 0.1 ab | 1.1 ± 0.3 |
| | Glade edge | 94 ab | 6.0 ± 0.9 | 0.2 ± 0.1 a | 1.4 ± 0.2 |
| | Inside glade | 63 b | 4.0 ± 1.7 | −0.2 ± 0.1 b | 1.1 ± 0.3 |
| Clear | Far from glade | 80 | −0.2 ± 1.0 | 0.1 ± 0.2 b | 2.6 ± 0.3 ab |
| | Glade edge | 91 | −1.2 ± 2.1 | 0.4 ± 0.2 ab | 2.1 ± 0.4 b |
| | Inside glade | 80 | 4.4 ± 4.9 | 1.5 ± 0.6 a | 6.0 ± 1.6 a |
| Control | Far from glade | 86 a | 3.1 ± 1.0 | 0.1 ± 0.1 | 2.2 ± 0.4 |
| | Glade edge | 77 a | 2.1 ± 2.8 | 0.1 ± 0.2 | 1.1 ± 0.4 |
| | Inside glade | 20 b | 1.6 ± 2.6 | 0.04 ± 0.04 | 1.3 ± 0.3 |

For growth responses, mean ± SE were calculated across blocks ($n = 5$) after averaging over all seven trees present within each block × location × treatment combination. Within each combination of treatment and response variable, locations with shared letters are not significantly different (Tukey's HSD method, $\alpha = 0.05$)

$P = 0.7$; caged + cleared $F_{2,7.16} = 4.07$, $P = 0.07$; clear $F_{2,7.39} = 1.49$, $P = 0.3$; control $F_{2,5.86} = 0.01$, $P = 0.99$; Fig. 2d–f; Table 1).

Basal diameter growth

Seedling basal diameters increased significantly more than those of saplings (0.8 ± 0.1 vs. 0.2 ± 0.1 mm; $F_{1,269} = 46.15$, $P < 0.0001$). Interactions involving age class were not significant, but growth was significantly affected by the interaction between location and treatment ($F_{6,116} = 6.56$, $P < 0.0001$).

Treatment significantly affected basal diameter growth far from glades ($F_{3,119} = 4.04$, $P = 0.009$) and inside glades ($F_{3,28.5} = 6.61$, $P = 0.002$). Far from glades, growth of caged + cleared trees was over 4.5 times that of trees in other treatments (Fig. 2g–i; Table 1). Inside glades, cleared and caged + cleared trees grew significantly more than caged trees, while control trees had intermediate growth (Fig. 2g–i; Table 1). Treatment did not significantly affect basal diameter growth at glade edges ($F_{3,118} = 1.87$, $P = 0.1$).

Within the cage treatment, basal diameter growth differed significantly among locations ($F_{2,84.5} = 3.45$, $P = 0.04$). Caged trees inside glades grew significantly less than caged trees in glade edges, while caged trees far from glades had intermediate growth (Fig. 2g–i; Table 1). Locations also differed significantly within the cleared treatment ($F_{2,9.65} = 4.01$, $P = 0.05$). Cleared trees inside glades grew over 10 times as much as cleared trees far from glades, while cleared trees at glade edges had intermediate growth (Fig. 2g–i; Table 1). Basal diameter growth did not differ significantly across locations within the caged + cleared ($F_{2,7.16} = 3.97$, $P = 0.07$) or control ($F_{2,9.66} = 0.02$, $P = 0.98$) treatments.

Branch production

Saplings produced significantly more new branches than seedlings (2.9 ± 0.2 vs. 2.3 ± 0.2 new branches; $F_{1,257} = 13.14$, $P = 0.0003$). Interactions involving age class were not significant. Branch production was significantly affected by the interaction between location and treatment ($F_{6,86.4} = 3.29$, $P = 0.006$).

Treatment significantly affected branch production in all locations (far from glades $F_{3,120} = 9.02$, $P < 0.0001$; glade edges $F_{3,31} = 7.04$, $P = 0.001$; inside glades $F_{3,26.9} = 14.58$, $P < 0.0001$). Far from glades and at glade edges, caged + cleared trees produced over twice as many branches as caged trees, while cleared and control trees produced an intermediate number of branches (Fig. 2j–l; Table 1). Inside glades, cleared and caged + cleared trees produced more than three times as many branches as caged and control trees (Fig. 2j–l; Table 1).

Branch production was not significantly affected by location in the cage ($F_{2,24.9} = 0.40$, $P = 0.7$), caged + cleared ($F_{2,11.7} = 1.82$, $P = 0.2$) or control ($F_{2,7.62} = 1.47$, $P = 0.3$) treatments. In the cleared treatment, location had significant effects on branch production ($F_{2,8.36} = 6.62$, $P = 0.02$). Cleared trees inside glades produced almost three times as many branches as cleared trees at glade edges, and cleared trees far from glades produced an intermediate number of branches (Fig. 2j–l; Table 1).

Part II: isolated versus non-isolated glade edges

Survival

When we compared isolated and non-isolated edges, tree survival was only affected by treatment ($F_{3,85.28} = 5.68$, $P = 0.001$). Caged and caged + cleared trees had about

30% higher survival than control trees, and cleared trees had intermediate survival (Fig. 3a). Edge type, tree age class, and interactions had no significant impact on survival.

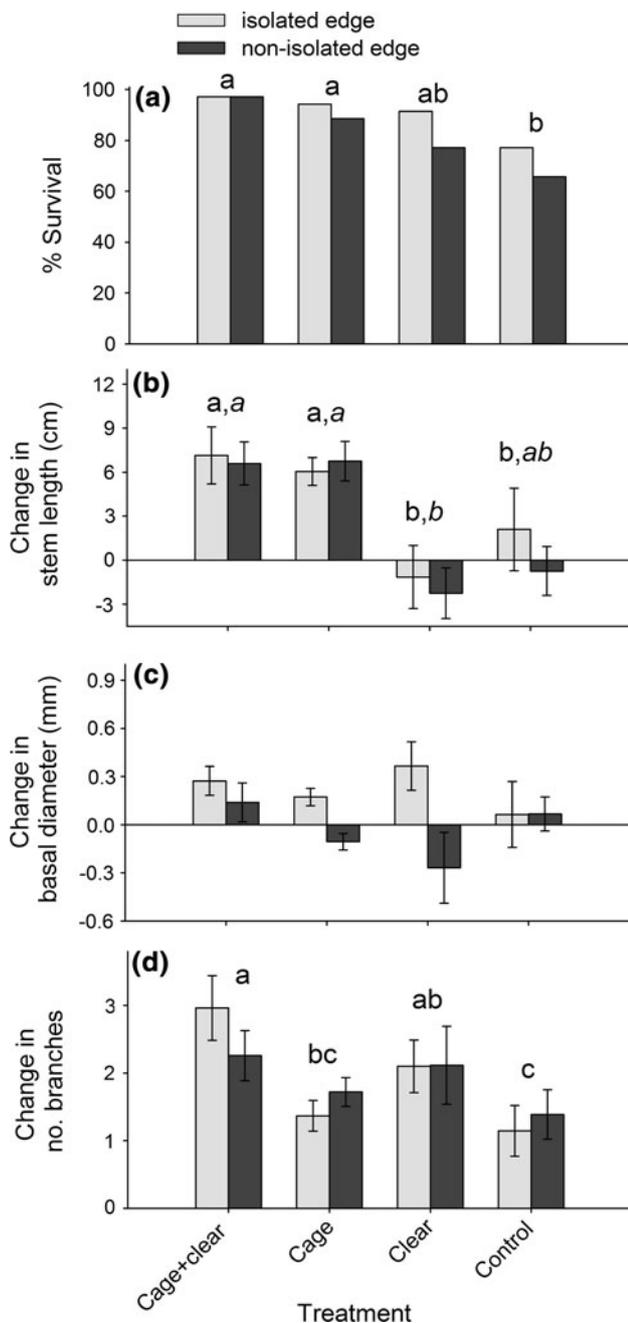


Fig. 3 Survival (a) and growth (b–d) of trees planted in isolated and non-isolated glade edges. For growth responses, bars are mean \pm SE calculated across blocks ($n = 5$) after averaging over all seven trees present within each block \times location \times treatment combination. Within each panel, across both edge types, treatments with shared letters are not significantly different (Tukey’s HSD method, $\alpha = 0.05$). For stem length growth, non-italicized letters indicate significance groups for saplings, while italicized letters indicate significance groups for seedlings (tree age \times treatment $F_{3,182} = 2.72$, $P = 0.046$)

Stem length growth

Stem growth was not significantly affected by edge type, but was affected by the interaction between treatment and tree age class ($F_{3,182} = 2.72$, $P = 0.046$). Treatments had significant effects on stem length growth for both saplings ($F_{3,55.3} = 16.54$, $P < 0.0001$) and seedlings ($F_{3,57.3} = 6.94$, $P = 0.0005$). Saplings that were caged or caged + cleared grew significantly more than control or cleared trees (Fig. 3b). Seedling results were similar except that growth in the control treatment was intermediate between the cleared treatment and the other treatments (Fig. 3b). In three out of four treatments, seedlings grew significantly more than saplings (caged: 8.5 ± 1.0 vs. 4.9 ± 1.1 cm, $F_{1,55.1} = 5.64$, $P = 0.02$; cleared: 1.3 ± 1.2 vs. -2.9 ± 1.2 cm, $F_{1,51} = 6.91$, $P = 0.01$; control: 5.5 ± 1.5 vs. -0.8 ± 1.5 cm; $F_{1,35.4} = 9.88$, $P = 0.003$). In the caged + cleared treatment, stem length growth did not differ significantly between tree age classes (6.7 ± 1.2 cm for seedlings vs. 7.1 ± 1.1 cm for saplings; $F_{1,49.1} = 0.04$, $P = 0.8$).

Basal diameter growth

Across edge types, basal diameters of seedlings grew significantly more than those of saplings (0.4 ± 0.05 vs. -0.1 ± 0.05 mm; $F_{1,217} = 49.61$, $P < 0.0001$). Edge type, treatment and all interactions had no significant impact on growth, though we observed a trend towards more growth in isolated than non-isolated edges ($F_{1,8.37} = 4.35$, $P = 0.07$; Fig. 3c).

Branch production

Branch production in glade edges was affected by tree age class and treatment. Saplings produced about 30% more branches than seedlings (2.2 ± 0.1 vs. 1.6 ± 0.2 new branches; $F_{1,179} = 13.57$, $P = 0.0003$). Caged + cleared trees produced significantly more branches than caged and control trees, and cleared trees produced significantly more branches than control trees ($F_{3,63.5} = 8.11$, $P < 0.0001$; Fig. 3d). Edge type and all interactions did not significantly affect branch production.

Discussion

Previous studies have identified herbivores, grass competition and soil nutrients—along with other factors such as fire and rainfall regime—as important drivers of woody vegetation cover and density in savanna landscapes (Knoop and Walker 1985; Augustine and McNaughton 2004; Sankaran et al. 2005; Goheen et al. 2007, 2010; Bond 2008;

Riginos 2009; Cramer et al. 2010; van der Waal et al. 2011). To our knowledge, our study is the first to experimentally test the separate and combined impacts of browsing, competition with herbaceous plants, and edaphic context on tree survival and growth in a field setting. We examined these factors in the absence of fire, which is not a major factor at our study site, although fire is a critical driver of tree cover in many savannas (Sankaran et al. 2005; Bond 2008). The lack of fire in our system provides an opportunity to distinguish direct impacts of grasses and browsing from more indirect, fire-mediated impacts on tree cover (e.g., Roques et al. 2001; van Langevelde et al. 2003; Staver et al. 2009).

Impacts of grasses and browsing

Our results provide field-based evidence that the influence of grass and browsers on woody cover depends strongly on edaphic context. Both browsing and grass competition reduced *A. drepanolobium* survival, but only inside nutrient-rich glades. Grass removal improved survival inside glades more than herbivore exclusion, and the combination of grass removal and herbivore exclusion led to the highest survival rates. Outside glades, however, browsing and grasses had no significant impacts on survival. These results differ from those of van der Waal et al. (2011), who planted young trees in field plots in South Africa and found that fertilization, but neither herbivory nor the interaction of fertilizer and herbivory, reduced tree survival.

Grass competition emerged as the major factor limiting basal diameter growth and branch production inside glades, and to a lesser degree, it also limited growth outside glades. These results support previous studies in our system (Riginos and Young 2007; Riginos 2009) and other savannas (Knoop and Walker 1985; van der Waal et al. 2009; Cramer et al. 2010; Ward and Esler 2011) which found that grass competition can significantly restrict tree growth and recruitment. In a pot experiment, van der Waal et al. (2011) went a step further by showing that competition between grasses and trees was more intense when plants were grown in glade-derived, nutrient-rich soil. Our results support these findings, in that growth reductions due to grass competition were greater inside than outside glades.

In contrast to basal diameter and branch production results, which suggested that grass removal overwhelmingly benefits trees, stem length growth results revealed a trade-off between the benefits (release from competition) and costs (e.g., increased visibility to herbivores; Riginos and Young 2007) of grass removal. Inside glades, cleared and control trees had similar stem length growth, and this growth was significantly less than that of caged + cleared trees. This result suggests that the benefits of grass removal were offset by negative impacts of increased visibility.

Outside glades, the negative impacts of grass removal were even more prominent. Caged and cleared + caged trees had significantly higher stem length growth than cleared trees, while control trees had intermediate growth. Thus, outside glades, the negative impacts of increased apparency seemed to significantly outweigh any benefits of release from competition. By continually reducing tree height, browsers can have large impacts on three-dimensional landscape structure in this ecosystem (see also Levick et al. 2009). Continual browsing is also likely to keep small trees in the grass layer, making them more susceptible to damage and mortality during fire (Okello et al. 2008; Staver et al. 2009; Midgley et al. 2010).

As mentioned previously, glades are only one of several major sources of edaphic variation in savanna ecosystems. Our work and that of van der Waal et al. (2011) suggest that, at intermediate spatial scales, edaphic context can modify the importance of grass competition and browsing as drivers of tree survival and growth. Findings from both studies support the hypothesis that tree establishment is more limited by grass competition in nutrient-rich patches. The two studies differ in their conclusions about the role of browsing and its interactions with nutrient context. These findings add to the existing body of work on how edaphic context influences savanna tree cover (e.g., Eckhardt et al. 2000; Dickie et al. 2007; Levick et al. 2010), and suggest that future research is necessary in other landscapes and at multiple scales.

Tree age

We found significant and consistent differences in survival and growth between seedlings and saplings. Saplings had higher survival and branch production, but seedlings had higher stem length growth and basal diameter growth. These results parallel those of previous studies on other plant species (Horvitz and Schemske 2002; Hodar et al. 2008). Although some studies (e.g., Hodar et al. 2008) identified interactions between age and experimental treatments, we found that seedlings and saplings generally displayed similar responses across herbivore, grass competition, and planting location treatments.

To establish inside glades, trees must disperse into glades as seeds, avoid seed death (via predation, pathogens, or desiccation), germinate, emerge, and survive seedling and sapling growth stages. In this study, we focused on the latter two stages, but processes during other life stages may also limit tree establishment inside glades. Predation by rodents may be important for seeds and young seedlings (Goheen et al. 2004, 2010; Walters et al. 2005), especially given high rodent densities inside glades (Veblen, unpublished data). In this study, rodents likely contributed to seedling mortality in uncaged treatments, especially in the control treatment where grasses provided protective cover

from predation (Peles and Barrett 1996). Rodents are unlikely to have caused mortality of saplings, and this may have contributed to the higher survival rates of saplings compared to seedlings.

Isolated versus non-isolated glade edges

Tree survival and growth did not differ significantly between isolated and non-isolated glade edges, suggesting that high densities of trees between nearby glades are not maintained via reduced impacts of grass or herbivores on trees at the seedling or sapling stages. However, reduced grass competition and herbivory may help maintain high tree densities between glades by impacting other tree life stages. For example, reduced wildlife use of areas between nearby glades (Porensky 2011) may cause increased *A. drepanolobium* seed production (Goheen et al. 2007), which may then result in higher tree recruitment. Alternatively, high tree densities may be a legacy of past events. Livestock and human impacts create a region of intensive use (i.e., low grass cover, high livestock use and low wildlife use) around active corrals, and impacts are especially pronounced between active corrals and nearby glades (unpublished data; see also Muchiru et al. 2009). The combination of low browser density, low grass cover and ample fertilization in areas between active corrals and nearby glades may initiate a burst of tree establishment, especially if low grass cover causes reduced fire intensity or frequency (e.g., Tobler et al. 2003; van Langevelde et al. 2003; Augustine and McNaughton 2004; Goheen et al. 2007, 2010). Increased tree establishment during boma use could have long-term consequences for local tree densities.

Landscape heterogeneity

At our study site, grasses and browsers may be able to maintain the conversion of wooded savanna to treeless grassland even in the absence of fire, but only in edaphically distinct landscape patches. Grasses and browsing, separately and especially in combination, reduced the survival and growth of *A. drepanolobium* seedlings and saplings inside glades, but not outside glades. When grasses were removed (in cleared and caged + cleared treatments), survival rates inside glades were high and statistically indistinguishable from survival rates outside glades. Moreover, when grasses were removed, trees inside glades had higher basal diameter growth and produced more branches than trees planted in other locations. Thus, in the absence of grass competition, *A. drepanolobium* actually grows better in glade-like conditions. Herbivores consume trees (a top-down mechanism), while grasses reduce the availability of resources required by trees (a bottom-up mechanism). In our system, both mechanisms

appear to increase landscape heterogeneity by helping to maintain glades in a treeless state.

Implications for management

In general, spatial heterogeneity tends to be good for biodiversity (e.g., Lundholm 2009; Tamme et al. 2010), and heterogeneity created via glades is no exception (e.g., Young et al. 1995; Augustine 2004; Gregory et al. 2010; van der Waal et al. 2011). Glade treelessness is initiated by anthropogenic activities and attracts herbivores (especially mid-sized species such as Grant's gazelles and oryx), probably by allowing for improved predator detection (Riginos and Grace 2008). Grazers attracted to glades could potentially promote tree establishment by reducing grass competition and fire frequency or intensity (Roques et al. 2001; van Langevelde et al. 2003; Riginos and Young 2007). However, the mixed-feeder herbivores most attracted to glades probably contribute to the maintenance of these treeless sites both directly, by browsing on *A. drepanolobium* seedlings, and indirectly, by increasing grass productivity through fertilization (Odadi 2010; Augustine et al. 2011; van der Waal et al. 2011). Thus, our results suggest that loss of either livestock (which initiate glade formation) or wildlife (which help to maintain glades) from this savanna ecosystem could lead to homogenization of the landscape, with negative consequences for biodiversity. Many livestock–wildlife interactions have negative impacts on human livelihoods or conservation objectives (e.g., Young et al. 2005; Laporte et al. 2010). When managed sustainably, glades appear to represent an example of positive synergy between livestock production and biodiversity conservation.

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