

Browsing wildlife and heavy grazing indirectly facilitate sapling recruitment in an East African savanna

ERIC M. LaMALFA ,^{1,2} CORINNA RIGINOS ,^{2,3} AND KARI E. VEBLEN ,^{1,2,4}

¹*Department of Wildland Resources & Ecology Center, Utah State University, Logan, Utah 84321 USA*

²*Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya*

³*The Nature Conservancy, 258 Main Street, Suite 200, Lander, Wyoming 82520 USA*

Citation: LaMalfa, E. M., C. Riginos, and K. E. Veben. 2021. Browsing wildlife and heavy grazing indirectly facilitate sapling recruitment in an East African savanna. *Ecological Applications* 00(00):e02399. 10.1002/eap.2399

Abstract. Management of tree cover, either to curb bush encroachment or to mitigate losses of woody cover to over-browsing, is a major concern in savanna ecosystems. Once established, trees are often “trapped” as saplings, since interactions among disturbance, plant competition, and precipitation delay sapling recruitment into adult size classes. Saplings can be directly suppressed by wildlife browsing and competition from adjacent plants, and indirectly facilitated by grazers, such as cattle, which feed on neighboring grasses. Yet few experimental studies have simultaneously quantified the effects of cattle and wildlife on sapling growth, particularly over long time scales. We used a series of replicated 4-ha herbivore-manipulation plots to investigate the net effects of wildlife and moderate cattle grazing on *Acacia drepanolobium* sapling growth over 10 years that encompassed extended wet and dry periods. We also simulated more intense cattle grazing using grass removal treatments (0.5-m radius around saplings), and we quantified the role of intraspecific tree competition using neighborhood tree surveys (trees within a 3-m radius). Wildlife, which included elephants, had a positive effect on sapling growth. Wildlife also reduced neighbor tree density during the 10-yr study, which likely caused the positive effect of wildlife on saplings. Although moderate cattle grazing did not affect sapling growth, grass removal treatments simulating heavy grazing increased sapling growth. Both grass removal and neighbor tree effects on saplings were strongest during above-average rainfall years following drought. This highlights that livestock-driven reductions in grass cover and catastrophic wildlife damage to trees during droughts present a need, or an opportunity, for targeted management of sapling growth and woody plant cover during ensuing wet periods.

Key words: *browse trap; bush encroachment; density dependence; Kenya Long-term Exclosure Experiment; native invasion; self-thinning; tree-grass interactions.*

INTRODUCTION

In savanna systems, recruitment of new trees from seeds to reproducing adult trees is a dynamic process that, if accelerated, can rapidly increase tree cover and therefore affect provision of forage for livestock and wildlife (Scholes and Archer 1997), energy balance (Giambelluca et al. 2009), carbon flux (Blaser et al. 2014), nutrient cycling (Hibbard et al. 2001), the hydrologic cycle (Huxman et al. 2005), and soil fertility (Eldridge et al. 2011). Savanna trees experience a major bottleneck during seedling recruitment, a time period encompassing germination, emergence, and seedling establishment (Midgley and Bond 2001, Maclean et al. 2011, Wahungu et al. 2011, Morrison et al. 2019). Seedling recruitment is subject to a multitude of inter-related

filters, such as granivory and herbivory (Andersen and Lonsdale 1990, Shaw et al. 2002, Goheen et al. 2004, 2010, Vaz Ferreira et al. 2011, Costa et al. 2017), nutrient and moisture limitation (Paul et al. 2005, Kraaij and Ward 2006, Cramer et al. 2012), and grass competition (Grellier et al. 2012, Morrison et al. 2019). Once established, trees are often then “trapped” as saplings whereby interactions among disturbance, precipitation, and plant competition delay their recruitment to the next size class, which we define here as the transition from the short statured sapling to adult height class (typically between 1 and 3 m; Higgins et al. 2000, Bond 2008, Hoffmann et al. 2009, Werner and Prior 2013, Holdo et al. 2014). Mortality of large adult trees additionally limits tree populations (Ruess and Halter 1990, Baxter and Getz 2005, Holdo 2006a, Morrison et al. 2016). But saplings have garnered increased attention as a key functional stage comprising not only newly established plants, but older plants that are kept short due to repeated burning or browsing. When released from disturbance en masse,

Manuscript received 9 June 2020; revised 7 October 2020; accepted 3 March 2021. Corresponding Editor: Elisabeth Huber-Sannwald.

⁴E-mail: kari.veblen@usu.edu

transitions of these plants into adult height classes constitute major tree recruitment events (Grady and Hoffmann 2012, Sankaran et al. 2013, Staver and Bond 2014).

Determining how biotic and abiotic factors affect sapling-to-adult recruitment, and ultimately changes in tree cover (Bond and Midgley 2001, O'Connor et al. 2014), is critical for conserving and managing savanna systems (Archer and Predick 2014, Nackley et al. 2017). In some situations, managers aim to combat increases in woody cover. In these cases, “bush encroachment” is undesirable because over-abundance of woody species reduces grass production, thereby limiting availability of forage for grazing livestock and wildlife (Roques et al. 2001, Tobler et al. 2003, O'Connor et al. 2007). In other situations, managers seek to avoid loss of woody cover to heavy browsing; in African savannas, this is due primarily to elephants (Western and Maitumo 2004, O'Connor et al. 2007, Riginos et al. 2015). In these cases, loss of large trees, and failure to replace those trees, alters habitat structure and reduces forage for other browsing herbivores (Birkett 2002, Birkett and Stevens-Wood 2005). Despite their importance for management of tree cover, sapling-to-adult recruitment dynamics remain poorly understood in semiarid savanna systems.

Several potentially interactive factors affect this demographic transition. These include, but are not limited to, competition with neighboring plants (Riginos and Young 2007, Riginos 2009), inappropriate management of cattle grazing (Schlesinger et al. 1990, Seymour 2008, Angassa and Oba 2010), reductions in keystone browsing wildlife species (Hatton and Smart 1984, Van Auken 2000, Sankaran et al. 2008, Daskin et al. 2016, Stevens et al. 2017), and amount and timing of precipitation (Sankaran et al. 2005, Angassa and Oba 2010, Naito and Cairns 2011, Case and Staver 2018). Although fire also has important impacts on sapling-to-tree recruitment, here we focus on the interrelated variables of precipitation, grazing, browsing, and tree–grass and tree–tree competition in systems with suppressed historical fire regimes.

Neighboring plants, including both grasses and larger trees, compete with saplings for moisture (Scholes and Archer 1997, Riginos 2009, Holdo and Brocato 2015) and water availability ultimately constrains maximum tree cover in savanna systems (Sankaran et al. 2005). Sapling recruitment is infrequent (Bond and Midgley 2001, Staver and Bond 2014) and tends to occur during above-average precipitation periods (Seymour 2008, Case and Staver 2018) or following high intensity precipitation events that recharge deep soil layers (Berry and Kulmatiski 2017). Likewise, extended dry periods are associated with high sapling mortality (Fensham et al. 2017) and height class retrogression (i.e., shrinkage) caused by desiccation or “top-kill” of apical stem tissue (Chapin et al. 1990, Belsky et al. 1993). This suggests saplings can be subject to interference competition from

shallow-rooted grasses when water is limited (Holdo and Brocato 2015). Negative effects of neighbor tree density on sapling growth and survival (Veenendaal et al. 1996, Vadigi and Ward 2012, Dohn et al. 2017) could also be exacerbated during dry periods (Riginos and Young 2007). There is a need for long-term longitudinal studies where recruitment of individual saplings to adult trees is measured as the net result of growth and retrogression of aboveground structural tissues during wet and dry periods, respectively.

In ungulate-rich African savannas, large browsing herbivores directly limit sapling growth. Browsing ungulates consume woody sapling tissue, thereby preventing or delaying sapling transitions to larger tree size classes (Sankaran et al. 2013, Staver and Bond 2014). Elephants browse on trees ranging from sapling size to larger trees with high canopies (Woolery and Jacobs 2011). Once trees are >2 m, elephants are a primary driver of mortality via toppling behavior (Baxter and Getz 2005, Morrison et al. 2016). High densities of elephants can lead to loss of tree cover (Western and Maitumo 2004), threatening forage provisioning for other browsing herbivores such as giraffes and black rhinos (Birkett 2002, Birkett and Stevens-Wood 2005). For saplings, however, elephants could also have indirect positive effects through at least two paths. First, elephants can reduce the competitive effects of large trees by toppling, injuring (i.e., bark stripping), and browsing (O'Connor et al. 2007), thereby releasing smaller saplings from tree–tree competition (Riginos and Young 2007, Calabrese et al. 2010). Second, large trees that are toppled by elephants often survive and resprout (Midgley et al. 2005), and the resulting “resprouts” (i.e., trees that have retrogressed in height) have high relative growth rates (Holdo 2006b) or may exhibit compensatory growth responses to browsing (*sensu* Fornara and Du Toit 2007, Riginos and Young 2007).

Grazing herbivores do not directly affect trees via tissue removal but can indirectly facilitate sapling growth by reducing grass competition and increasing resources available to trees (Scholes and Archer 1997, Riginos and Young 2007, Seymour 2008, Palmer and Brody 2013, O'Connor et al. 2014). When combined with infrequent high precipitation periods, grass reduction can allow cohorts of saplings to recruit into the adult tree stage (Seymour 2008). Conversely, grazing could indirectly reduce sapling growth by removing grass cover that would otherwise ameliorate abiotic stress (Palmer et al. 2017) or reduce detection by browsing ungulates that consume sapling tissue (Western and Maitumo 2004, Riginos and Young 2007, Porensky and Veblen 2012).

To investigate the separate and combined effects of co-occurring domestic cattle and wild herbivores on long-term sapling growth in semiarid savannas, we conducted an herbivory manipulation experiment with nested grass removal treatments during a 10-yr study period marked by periods of above- and below-average precipitation. The initial results of the study,

reported two years following grass removal treatments by Riginos and Young (2007), showed that, during a below-average rainfall period (1) grass removal increased the frequency of wildlife browse damage but this was offset by increased sapling stem growth, and (2) the net effect of wildlife was positive, attributed to either or both compensatory growth or low neighbor tree density. After monitoring annual precipitation and changes in sapling height and diameter for an additional eight years, as well as cumulative changes in neighbor tree density, we asked (1) what are the net effects of wildlife vs. cattle on sapling recruitment to the next size class (i.e., taller than the grass layer) through multi-year wet vs. dry periods and (2) how do effects of neighbor trees and grasses, both of which can mediate indirect effects of herbivores on sapling recruitment, change over multi-year wet vs. dry periods? Here we provide experimental evidence for indirect pathways of cattle and wildlife effects on saplings, new results that could only be revealed by the 10-yr study period that included extended wet and dry periods.

METHODS

Study site and species

The Mpala Ranch and Conservancy, Laikipia, Kenya, is a semiarid tropical savanna site with variable interannual rainfall (30 yr mean ~580 mm/yr, range 364–1,010 mm/yr). Our study site is located within a mono-dominant stand of *Acacia (Vachellia) drepanolobium*, a tree species that accounts for 97% of woody cover. Mono-dominant stands of *A. drepanolobium* are widespread throughout East Africa and frequently occur in “black cotton” vertisol soils. *Acacia drepanolobium* has been identified as one of East Africa’s most pervasive rangeland invaders (Angassa and Oba 2010), but on lands managed for wildlife conservation, declines in tree cover due to high elephant activity are a significant concern (Birkett 2002, Birkett and Stevens-Wood 2005, Riginos et al. 2015).

Acacia drepanolobium is consumed by a wide variety of insect and mammalian browsers (Maclean et al. 2011), whereas an extensive diet study found no evidence that cattle consume the plant at any demographic stage (Odadi et al. 2007). *Acacia drepanolobium* is a myrmecophyte with each tree typically occupied by one of four defensive symbiotic ant species: *Crematogaster mimosae*, *Crematogaster nigriceps*, *Crematogaster sjostedti*, or *Tetraponera penzigi* (Young et al. 1997b, Palmer et al. 2000). Ants vary in their ability to protect trees against herbivory, and within an individual tree, ant species turnover occurs frequently (Palmer et al. 2010). The most aggressively protective ant mutualists (*C. mimosae* and *C. nigriceps*) can deter most ungulate browsing, but this comes at a high energetic cost to the trees, as they

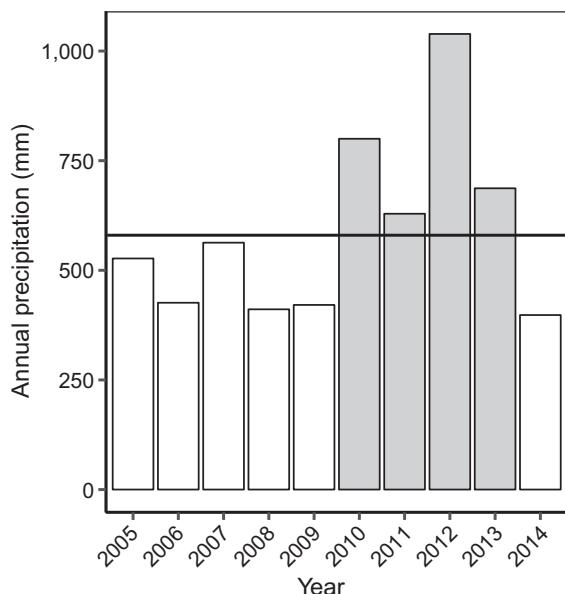


FIG. 1. Annual precipitation at the Kenya Long-term Exclosure Experiment (KLEE). Vertical bars represent annual precipitation for the 12 months preceding sapling measurements (i.e., July–June). The 10-yr study period had distinct below-average (2005–2009, white bars) and above-average rainfall periods (2010–2013, gray bars). The horizontal black line represents the running 30-yr average annual precipitation (580 mm/yr).

provide carbon-rich extra-floral nectar to the ants (Palmer and Brody 2013).

Precipitation

The 10-yr study period was marked by two distinct multi-year periods, one with below-average (“dry period”) and the other with above-average (“wet period”) annual precipitation. To define annual rainfall for each tree survey, we used the 12-month precipitation total preceding each tree survey ($July_{n-1}$ – $June_n$). At the beginning of the experiment, a 5-yr dry period (2004–2009) occurred during which annual precipitation was less than the 30-yr running average (580 mm/yr). The wet period began in the sixth year of the experiment (2009–2010) and lasted 4 yr (Fig. 1, 2010–2013). The last year of the study (2013–2014) was a below-average precipitation year.

Experimental design

We investigated several different pathways of cattle and wildlife effects on *A. drepanolobium* sapling growth during dry and wet periods. For 10 yr, we monitored annual changes in height and diameter for saplings growing under four long-term herbivory regimes (no large herbivores, cattle only, wild herbivores only, and cattle + wild herbivores). We investigated the effects of

grass and neighboring trees on sapling growth by, respectively, applying a nested grass removal treatment to half of the saplings and monitoring changes in neighborhood tree density.

Herbivore treatments

We conducted the study within the Kenya Long-term Exclusion Experiment (KLEE; Young et al. 1997a). Each of six herbivore treatments is replicated in three blocks, and each plot is 4 ha in size. For the present study, we used four KLEE herbivore treatments in a 2×2 factorial design to test the effects of both cattle and wildlife on sapling growth: no large herbivores, O; cattle only, C; wildlife only, MW; and cattle + wildlife, MWC (where MW refers to presence of both megaherbivores [M] and mesoherbivore wildlife [W]). The O treatment is fenced to prevent wild ungulates >15 kg from accessing the plots. Small herbivores <15 kg, can access plots by slipping between the electrified wires. These include steinbuck (*Raphicerus campestris*), rodents (mostly *Saccostomus mearnsi*), and insects. The C plots are fenced in the same way as O plots to exclude wildlife, but cattle are herded into selected plots during controlled grazing treatment applications. The MW plots are unfenced to allow access by all wildlife species, including a mix of grazers (plains zebras [*Equus burchelli*], hartebeest [*Alcelaphus buselaphus*], Cape buffalo [*Synacerus caffer*], and oryx [*Oryx gazella*)], as well as browsers and mixed feeders (Grant's gazelles [*Gazella granti*], giraffes [*Giraffa camelopardalis*], eland [*Taurotragus oryx*], and elephants [*Loxodonta africana*]). The MWC plots are unfenced but cattle are periodically herded into them, as in C plots. In all cattle-accessible plots (i.e., C and MWC), staff use a small herd of cattle to graze four to six times per year at a moderate utilization rate (Odadi et al. 2007), mimicking ranch-wide cattle management practices. For wildlife abundance estimates in KLEE see Veblen et al. (2016).

Sapling selection

We consider saplings to be established individuals (i.e., several years old), but otherwise of unknown age, that are of a height such that most of their woody biomass exists within the grass canopy. Based on our definition and our observation that seedling recruitment events are rare, some saplings may be relatively old due to being unable to escape the sapling phase and/or having reverted to a smaller height class as adults because of a top-killing disturbance (i.e., "gullivers" *sensu* Bond and van Wilgen 1996). When taller than the height of the grass layer, trees may become more susceptible to browsers or less susceptible to fire (Higgins et al. 2000, Riginos and Young 2007, Hoffmann et al. 2009, Staver et al. 2009, Sankaran et al. 2013, Werner and Prior 2013), or begin to escape aboveground competition from grass (Werner et al. 2006, Riginos 2009, February et al. 2013).

We defined saplings operationally as those <0.7 m in height (short enough to have their canopies contained within the grass layer at our study site). All saplings of this size were mapped and inventoried in one 50×200 m transect in each of the 12 treatment plots in 2004. We then used stratified random sampling to select 28 saplings per plot ($n = 336$ saplings). Initial sapling height in 2004 did not differ by herbivore treatment (Riginos and Young 2007). We excluded saplings occupied by the ant *C. sjostedti* (Cs) due to low natural abundance. Selection was then stratified among saplings with four other levels of ant occupancy: *C. nigriceps* (Cn), *C. mimosae* (Cm), *T. penzigi* (Tp), and unoccupied (na). Within each plot, six saplings were selected from each of three ant-occupied categories (Cm = 6, Cn = 6, Tp = 6), and 10 saplings were selected that were not occupied by ants (na = 10). A greater number of unoccupied saplings were included with the expectation that mortality and/or ant colonization would reduce the number of unoccupied saplings over the course of the long-term study (Riginos and Young 2007).

Grass removal treatment

Half of the saplings in each ant-occupancy by herbivore plot combination were randomly assigned to the grass-removal sub-plots. After wrapping selected saplings in protective plastic, glyphosate herbicide was applied to adjacent herbaceous plants growing within a 0.5-m radius (Riginos and Young 2007). All grass-removal and herbivore treatments were maintained from 2004 to 2014 with subsequent herbicide applications occurring as needed. Grass-removal simulates on a small scale (0.5 m) the bare ground conditions characteristic of heavily grazed rangelands common throughout Laikipia (Kimiti et al. 2017). In comparison, the KLEE "C" treatment (i.e., the plot-level herbivore treatment described above) is a direct application of moderate livestock grazing, reducing total cover by approximately 18% relative to total herbivore exclusion plots (Porensky et al. 2013).

Neighbor tree survey

Tree density in our study system varies due to two main influences. First, higher clay soils are associated with lower tree densities, and the KLEE plots overlie a natural north-south gradient in soil texture (Riginos and Grace 2008). Second, the KLEE treatments themselves are associated with differences in tree density, with 30% lower plot-wide average tree densities in plots accessible to mega-herbivores, attributed to the effects of elephants (Kimuyu et al. 2014, 2017). In addition to these plot-scale sources of variation, tree density varies at smaller scales within plots, likely due to more localized variation in soils or biotic dynamics.

Because we were interested in the potential competitive effects of neighbor trees on sapling growth, we

counted the number of neighbor trees adjacent to each sapling (trees within a 3 m radius and >50 cm height). At the beginning of the experiment (2004), neighbor trees ranged in size from 1 to 4 m in height. We resurveyed neighbor trees in 2017 to estimate changes in neighbor trees that occurred over the study period, but we were only able to do this for the subset of live and dead saplings that could be positively identified with tags intact (260 of 336 saplings; 77%). These neighbor tree surveys were done to characterize the immediate competitive neighborhood that saplings experienced, but it is important to also consider that they were nested within larger patterns of plot-scale variation in tree densities due to soils and herbivory.

Sapling measurements

Annual measurements of saplings took place following the long rainy season (July of each year, 2004–2014). We measured height and basal diameter (for multi-stemmed individuals, we summed stem diameters originating from the root collar), and identified ant species occupant (Cm, Cn, Cs, Tp, or unoccupied).

Data analysis

Sapling height and diameter were analyzed using two separate generalized linear mixed models (GLMMs). We parameterized height and diameter GLMMs using variables selected in the original analysis by Riginos and Young (2007). These variables included factorial combinations of cattle and wildlife herbivores (four levels: O, C, MW, and MWC), nested grass-removal treatment (two levels: grass control or grass removed), and the 2004 neighbor tree count (continuous covariate). In addition to the original variables, we added parameters to account for the main effects of year (11 levels, 2004–2014) and all possible two-way interactions with year. The random effects structure included intercepts for block, plot, sub-plot, and sapling (ID). We fit the model using a first-order autoregressive AR(1) covariance structure that allowed residuals to vary by year (R nlme package). The models were fit using Restricted Maximum Likelihood (REML) estimation and type III analysis of deviance tests. In all analyses, we log-transformed the covariate (neighbor tree count + 1) and log-transformed height and diameter response variables to better meet normality, homogeneity of variance, and linearity assumptions. We excluded 20 out of 336 saplings (6%) from the analysis that were burned during experimental fires conducted within the KLEE plots in 2013 (Kimuyu et al. 2014), and 1 out of 336 saplings (<0.01%) that occurred on a termite mound, where it is known that sapling growth rates are higher (Fox-Dobbs et al. 2010).

We also investigated the indirect effects of herbivores on saplings, specifically the association between large mammalian herbivores and neighbor tree density. The effects of cattle and wildlife on neighborhood tree count

were analyzed using a GLMM. The response variable, ending neighbor tree count (2017), was modeled as a function of initial neighbor tree count (2004), cattle (present vs. absent), and wildlife (present vs. absent), and all possible two-way interactions. The random effects structure included intercepts for block and plot. Neighbor tree counts (i.e., initial 2004 and ending 2017) were square-root-transformed to improve normality and homogeneity of variance. The model was fit using restricted maximum likelihood (REML) estimation and type III analysis of deviance tests.

Sapling mortality and sapling size class transitions were compared at the end of the study (2014) using a series of Pearson's χ^2 tests. First, sapling mortality (number live vs. number dead) was compared between two levels of grass removal and then among four levels of herbivory. Second, we assessed sapling size class transitions by comparing the number of saplings that grew taller than the grass layer (number of saplings ≥ 70 cm vs. number of saplings <70 cm) among the following treatments: (1) between the two levels of grass removal, (2) between two levels of cattle, (3) between two levels of wildlife, (4) between ant-occupied (Cm, Cn, Cs, Tp) vs. unoccupied (na) saplings, and (5) among four species of ant mutualists.

RESULTS

Sapling height

The effect of herbivore treatment on sapling height was not statistically significant (herbivores $P = 0.106$; herbivores \times year $P = 0.119$; Appendix S1: Table S1), but there was a consistent trend for saplings in the wildlife-present plots to be taller than saplings in the wildlife-absent plots (Fig. 2a). Grass removal was associated with a large initial reduction in sapling height followed by slight height increases in each of the three following dry years and even greater increases during the following wet years (year \times grass removal $P < 0.001$; Fig. 2b, Appendix S1: Table S1). Control saplings (i.e., those with an intact grass understory) steadily declined in height throughout the dry period and then increased during the wet period (Fig. 2b). The net effect of grass removal was generally negative during the dry period and positive during the wet period (Fig. 2c), with the greatest height increases associated with grass-removal occurring during the wet period.

Neighbor trees generally had a negative effect on sapling height, and the largest annual height increases occurred among saplings that had no neighbor trees, particularly during the wet period (year \times neighbor $P < 0.001$, Fig. 2d, Appendix S1: Table S1). During the dry period, saplings with fewer neighbors grew taller, while saplings with many neighbors were reduced in height. During the wet period, all saplings increased in height, but the magnitude of this increase was reduced with more neighbor trees (Fig. 2d). Across all saplings, the average number of neighbor trees declined

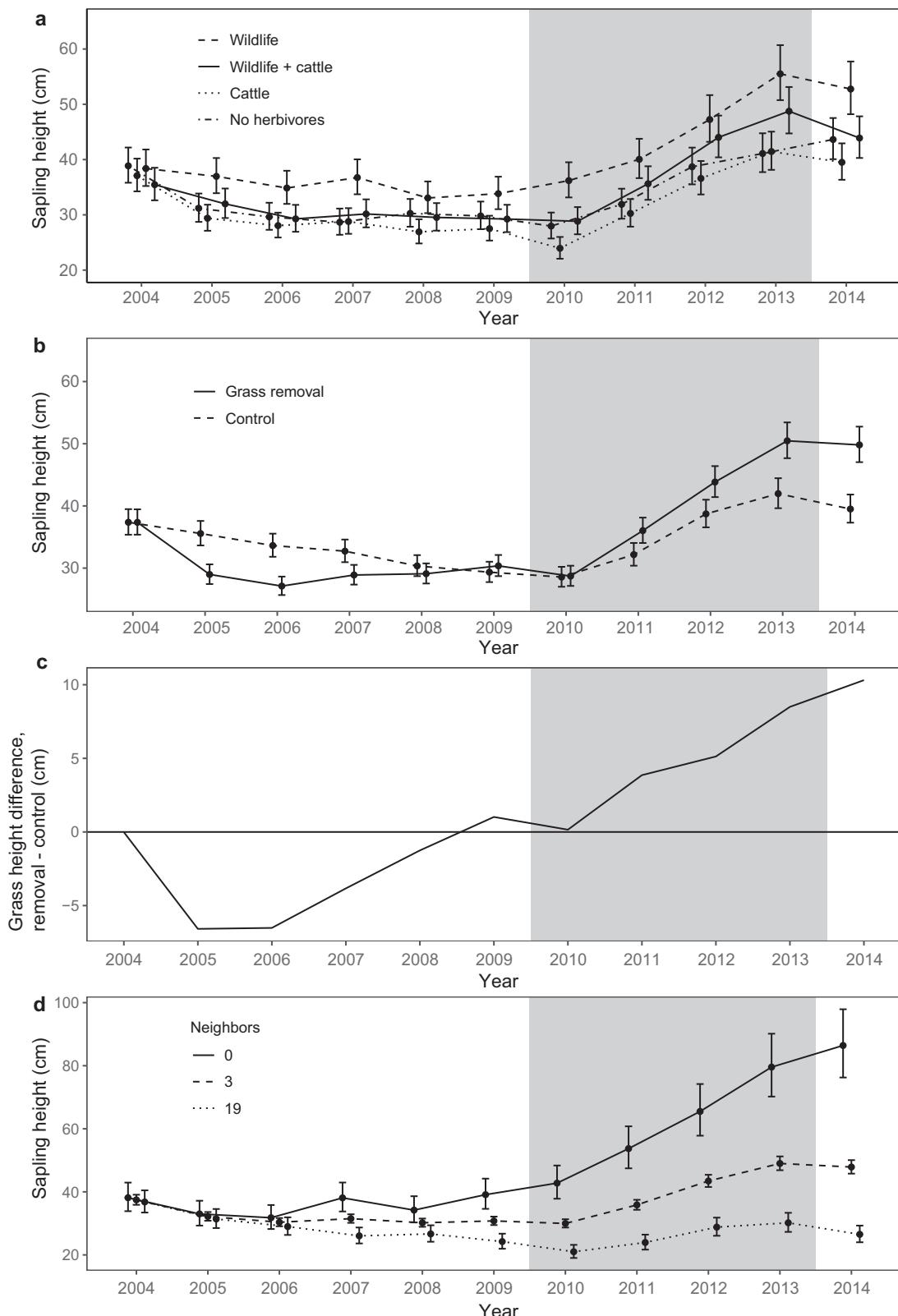


FIG. 2. (a) Fitted model for annual heights of saplings at four levels of herbivory: wildlife only, wildlife plus cattle, cattle only, and no large herbivores. (b) Fitted model for annual height of saplings exposed to grass removal and control (i.e., with intact grass understory) treatments. (c) Height difference between grass removal and control saplings. (d) Fitted model for the (continuous) covariate, 2004 neighborhood tree count, where neighbor trees were ≥ 50 cm height and within a 3-m radius; model was fit at three specified levels (0, 3, 19) to illustrate the significant year \times neighbors interaction. In all cases, mean estimates and standard error bars are back-transformed to the original scale. Estimates for herbivory, grass removal, and neighborhood tree count each are averaged over levels of the other two variables. Gray shading represents above-average rainfall period (2010–2013). Symbols are jittered along the horizontal axis to eliminate overlap.

significantly between 2004 and 2017, but only in plots where wildlife were present (i.e., MW and MWC plots) and the initial 2004 neighbor tree density was high (neighbors \times wildlife $P < 0.001$, Fig. 3, Appendix S1: Table S2).

Sapling diameter

Herbivore treatment effects on sapling diameter showed a similar, but stronger, pattern as herbivore effects on sapling height. Wildlife presence was associated with significantly increased sapling diameter,

especially during the wet period and near the end of the study (herbivores $P < 0.001$, Fig. 4a, Appendix S1: Table S3). Sapling diameter also responded positively to grass removal (Fig. 4b) and negatively to neighbor trees (Fig. 4c). The positive effects of grass removal on sapling diameter began almost immediately and increased throughout both dry and wet periods (year \times grass removal interaction $P < 0.001$, Appendix S1: Table S3, Fig. 4b). Diameter of control saplings with grass-present showed little to no increase over the study (Fig. 4b). Similar to sapling height patterns, the most negative effects of

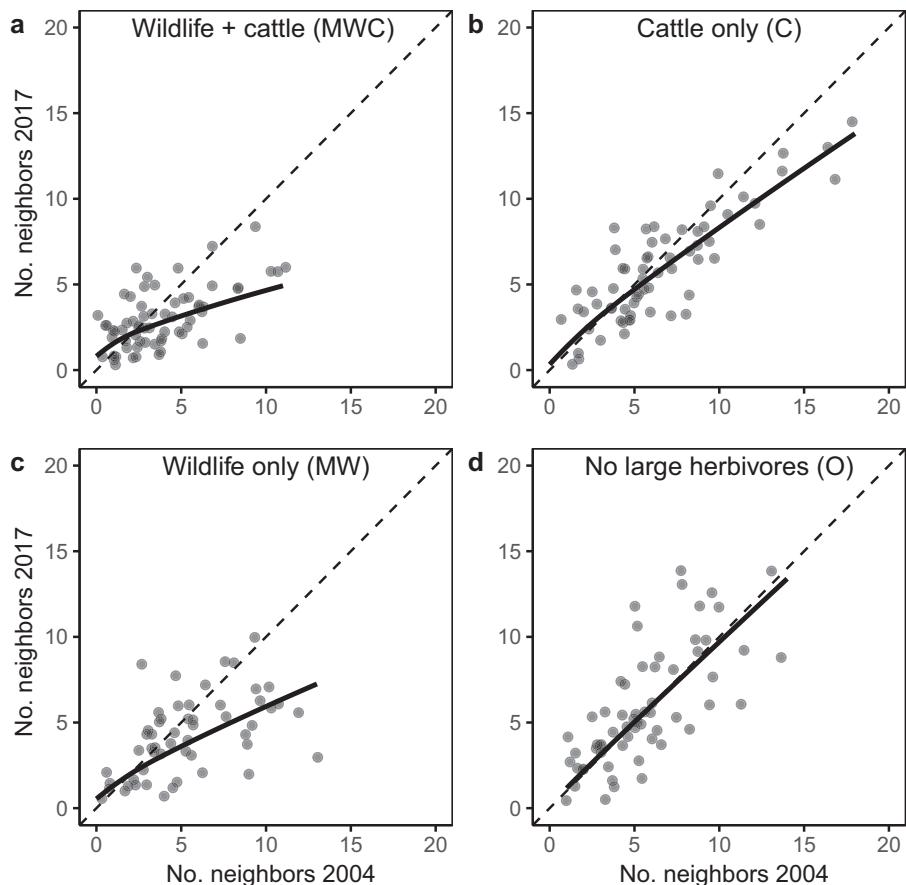


FIG. 3. The relationship between neighbor tree count at the beginning of the study (2004) and at the end of the study (2017) in four herbivore treatments. Panels show factorial combinations of cattle (absent, “O” vs. present, “C”) and wildlife (absent, “O” vs. present, “MW”). Solid line represents fitted model for number of neighbor trees in 2004 back-transformed to the original scale. Dashed line represents one to one line (hypothetical, no change in neighbor tree count from 2004 to 2017). Points are jittered and transparent to allow for visualization of overlapping neighborhood count values.

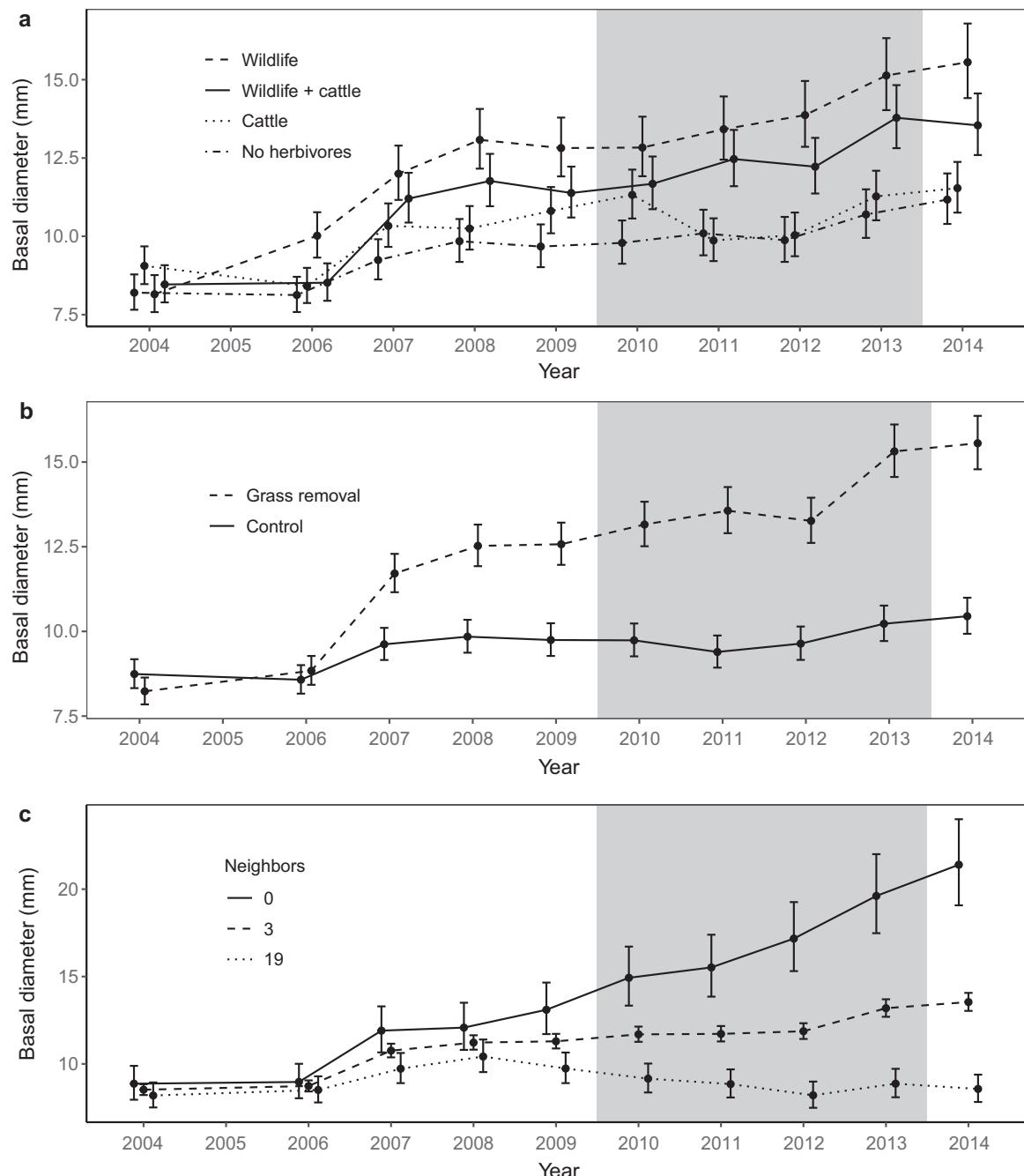


FIG. 4. Fitted models of annual diameter of saplings at (a) four levels of herbivory (wildlife only, wildlife plus cattle, cattle only, and no large herbivores), (b) in grass removal and control (i.e., with intact grass understory) treatments, and (c) fitted model for the (continuous) covariate, 2004 neighborhood tree count, where neighbor trees were ≥ 50 cm height and within a 3-m radius; model was fit at three specified levels (0, 3, 19) to illustrate the significant year \times neighbors interaction. In all cases, mean estimates and standard error bars are back-transformed to the original scale. Estimates for herbivory, grass removal, and neighborhood tree count each are averaged over levels of the other two variables. Gray shading represents above-average rainfall period (2010–2013). Symbols are jittered along the horizontal axis to eliminate overlap.

neighbor trees on diameter occurred during the wet period (year \times neighbor interaction $P < 0.001$, Appendix S1: Table S3, Fig. 4c). Ultimately, diameter

doubled for saplings with no neighbors, while the diameter remained unchanged for saplings with the greatest number of neighbor trees.

Size class transitions

Most saplings (87%) survived over the 10-yr study period. Sapling mortality ranged from 10% to 15% for all treatments and did not differ significantly among herbivore treatments (Pearson's $\chi^2_{(3)} = 1.358$, $P = 0.71$) or grass treatments (Pearson's $\chi^2_{(1)} = 0.804$, $P = 0.37$). However, there were significant differences among treatments in the number of individuals that transitioned out of the sapling stage (<0.7 m) to a taller size class (≥ 0.7 m) during the course of the study (Fig. 5). A total of 84 of 262 surviving saplings (32%) grew taller than the grass layer, and most had low neighbor tree density (Fig. 6). Transition rates were higher in the grass-removal (40%) than in the grass-present (24%) treatment (Pearson's $\chi^2_{(1)} = 7.263$, $P < 0.01$; Fig. 5a). Transition rates also were higher in plots where wildlife were present (MW and MWC, 42%) compared to wildlife absent (O and C, 23%) plots (Pearson's $\chi^2_{(1)} = 10.841$, $P < 0.01$; Fig. 5b). We did not find significant differences in sapling transition rates between cattle-present (C and MWC, 31%) and cattle-absent (O and MW, 33%) treatments (Pearson's $\chi^2_{(1)} = 0.035$, $P > 0.85$). Sapling transition rates were much higher in saplings occupied by ants of any species (Cm, Cn, Cs, or Tp; 55%) compared to unoccupied saplings (no-ants; 2%) (Pearson's $\chi^2_{(1)} = 79.911$, $P < 0.001$; Fig. 5c). Most saplings that transitioned (76%) were occupied by either *C. mimosa* or *C. nigriceps* ant species, which occupied the majority of all saplings by 2014 (Appendix S2: Fig. S1b). However, transition rates were not significantly different among saplings occupied by different ant species in 2014 (Cm (57%), Cn (59%), Cs (64%) Tp (39%); Pearson's $\chi^2_{(3)} = 3.503$, $P < 0.32$), Fig. 6c; Appendix S2: Fig. S1b).

DISCUSSION

In savanna ecosystems, rapid growth at the sapling stage (Higgins et al. 2000, Hoffmann et al. 2009, Werner and Prior 2013, Holdo et al. 2014) can increase tree cover and lead to undesirable woody encroachment (Bond and Midgley 2001, O'Connor et al. 2014). Conversely, in areas where loss of tree cover to overbrowsing is a management concern, suppression of sapling-to-tree recruitment can hamper the desired recovery of tree cover. We present experimental evidence that wildlife are drivers of sapling growth, particularly when coupled with high precipitation "triggering events" (*sensu* Kraaij and Ward 2006), and largely through indirect effects on neighboring tree density. Our results also suggest that sapling growth is increased by another indirect plant–herbivore mechanism: reduced grass competition associated with intensely grazed conditions.

Tree–grass interactions

Grasses have been shown to suppress sapling growth in a variety of savanna and woodland systems on annual time scales (Riginos 2009, Ward and Esler 2011,

February et al. 2013), and here we found that grasses had a net negative effect on sapling height and diameter over the course of a decade. Grasses can outcompete saplings for belowground resources such as soil moisture or nutrients (Anderson et al. 2010, Cramer et al. 2012, February et al. 2013). Tree seedlings also can be competitively suppressed by grasses that shade them (Morrison et al. 2019), and it is possible that our saplings, which were shorter than the grass layer, were subject to light limitation.

We also found evidence for positive effects of grasses on sapling growth. During the first several drought years, when saplings would have been limited in their capacity to respond positively to release from grass competition, we found that saplings in grass removal treatments decreased, rather than increased, in height. One possible explanation is that grass removal left saplings more vulnerable to drought stress, for example if grasses reduce evaporative water loss from the soil (Palmer et al. 2017), or if saplings growing in more direct sunlight experience higher transpiration (Vadigi and Ward 2014). More drought-stressed plants may have been smaller due to death of aboveground plant tissue or physiologically driven increases to root:shoot ratios (Xi et al. 2018). Another possible explanation for shorter saplings in grass-removal treatments, supported by evidence from the first two years of this study (Riginos and Young 2007), is that grass removal reduced sapling heights by increasing appärencey, and therefore vulnerability to browsing herbivores. Further experimental manipulations would be necessary to distinguish between the relative effects of drought stress vs. sapling appärencey on the reductions in sapling height in grass removal treatments.

The cycles of sapling height growth during wet periods and retrogression during dry periods could explain why trees persist in the sapling state for many years. We found overall low rates of sapling-to-tree demographic transitions, even after 10 yr, especially when grass was not removed. This suggests that some "saplings" are potentially several decades old and persist in a "sapling bank" for many years. Our results illustrate the potential for grasses and drought to act synergistically with fire or browse "traps" (*sensu* Higgins et al. 2000, Grady and Hoffmann 2012, Sankaran et al. 2013, Staver and Bond 2014) to maintain sapling banks.

Tree–tree interactions

While tree–grass competition has been the focus of much savanna literature, less attention has been put on intraspecific tree competition (but see Kambatuku et al. 2011). Here we found evidence consistent with competitive effects of large conspecific neighbor trees on sapling size that were strongest during wet periods. Saplings growing in the absence of immediate neighbors more than doubled in both height (>40 cm/10 yr) and diameter (>10 mm/10 yr), and most saplings that transitioned out of the grass layer (≥ 70 cm) during the

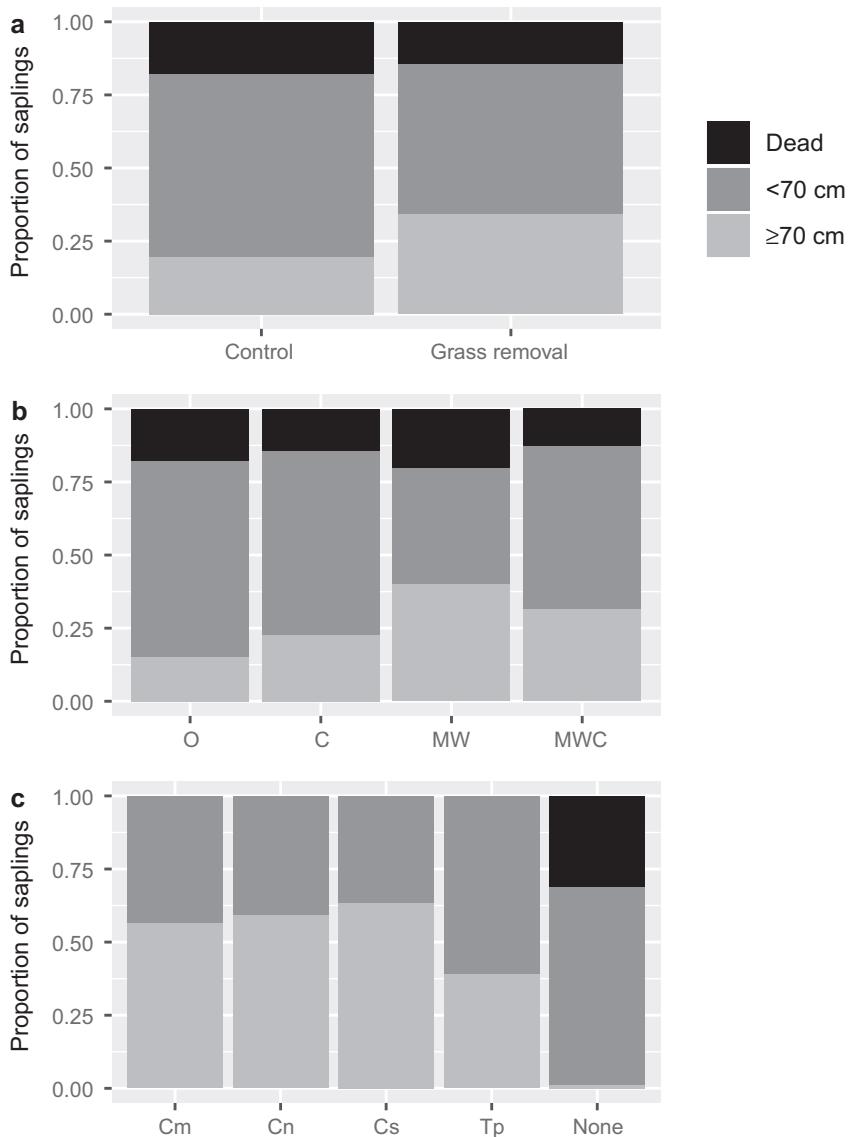


FIG. 5. Counts of surviving saplings (all initially < 70 cm) that grew to ≥ 70 cm in height and those that remained < 70 cm by the end of the study period in 2014. Saplings (a) with grass removed vs. control, (b) in different herbivore treatments (O, all large herbivores excluded; C, cattle present; MW, wildlife present; MWC, wildlife and cattle present), and (c) with different ant occupants as of 2014: *C. mimosae* (Cm), *C. nigriceps* (Cn), *C. sjostedti* (Cs), *T. penzigi* (Tp), and unoccupied (none).

study had low neighbor tree density (Fig. 6). Saplings with high neighbor tree density, on the other hand, increased in height during the wet period, but these increases did not fully compensate for the height reductions that had occurred during the dry period. The net result may be that height losses during dry periods prevent recruitment of saplings into larger size classes in areas where tree densities are already high. Because these saplings continued to grow in diameter and presumably also increase their belowground resources, they may be poised to recruit more rapidly

during more favorable conditions in the future. However, we did not specifically test for competition, nor did we measure other variables, such as fine-scale variation in soil texture or nutrients, that may also be important determinants of tree growth and sapling-to-adult recruitment rates. The overall patterns of our results nonetheless reveal that managers should anticipate that reductions of mature tree densities may be offset by increased recruitment from sapling to adult size classes unless saplings are themselves being heavily browsed or limited by other factors.

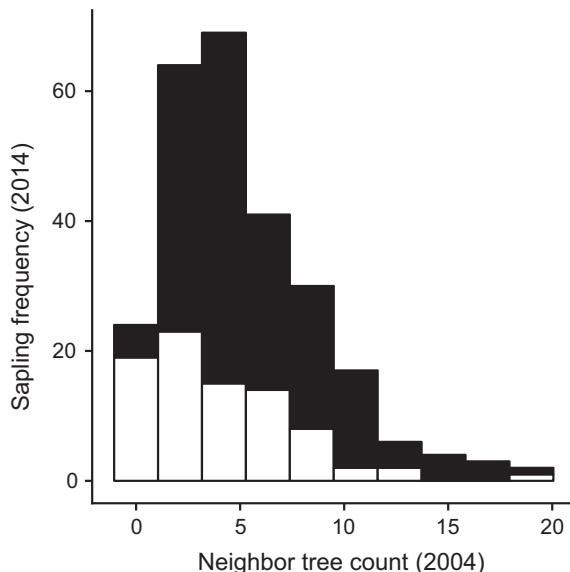


FIG. 6. Histogram of sapling recruitment to the taller size classes in 2014 binned by the number of neighbor trees in 2004. Saplings that transitioned out of the grass layer by 2014 (achieved a height ≥ 70 cm after 10 yr) are shown with white bars, and saplings that did not transition out of the grass layer (height < 70 cm after 10 yr) are shown with black bars.

Herbivore effects

Herbivory is widely recognized as a key determinant of African savanna vegetation composition and structure (Scholes and Archer 1997, Augustine and McNaughton 1998, Bond 2008), and sustainable management of livestock is a significant challenge in most savanna rangelands (du Toit and Cumming 1999). Because cattle remove more grass biomass than do grazing wildlife in the KLEE experiment (Charles et al. 2017), we expected to find that our moderate cattle grazing treatment would increase annual sapling growth and demographic transition rates by reducing the competitive effects of grass. However, we did not detect significant effects of our moderate cattle grazing treatment. In contrast, our grass-removal treatment (0.5-m bare-ground radius treatment), which simulates (albeit at an artificially small scale) heavily grazed conditions common to *A. drepanolobium* rangelands (Angassa et al. 2012, Kimiti et al. 2017), indicated that increasing bare ground has a positive effect on sapling growth. This key result suggests that surpassing a livestock grazing threshold (i.e., utilization rates that reduce plant basal cover and increase the proportion of bare ground) will accelerate sapling recruitment and increase the upper limit of tree density in this system. It is unclear, however, whether bare ground would improve sapling growth on other soil types that, unlike the vertisols at our study site, are more sensitive to physical crusting, surface water flow, and erosion.

We also found that wildlife presence was associated with both increases in sapling growth and decreases in

neighbor tree density between 2004 and 2017. Our interpretation of these results is that wildlife had an indirect positive effect on sapling growth by reducing tree density. In KLEE, plot-wide average tree density is lower in plots accessible to mega-herbivores compared to those that exclude megaherbivores (Kimuyu et al. 2014, 2017). Neighborhood density of larger trees around our study saplings was already lower in wildlife-accessible plots at the beginning of our experiment in 2004 and additionally decreased between 2004 and 2017 in these plots. This is most likely due to elephant activity. Although both elephants and giraffes browse trees >2 m, and smaller browsers hedge or prune shorter trees (Augustine and McNaughton 2004, Fornara and Du Toit 2007), only elephants topple whole trees (Birkett and Stevens-Wood 2005, Midgley et al. 2005), and elephant populations increased in the region during the course of this study (Ihwagi et al. 2015). Elephants also appear to do more tree damage in areas with higher density of *A. drepanolobium* (Riginos and Grace 2008). All of these lines of evidence suggest that elephants were a primary cause of reduced neighbor tree density. We suggest that this, in turn, increased sapling growth, leading to the overall positive effect of wildlife presence on saplings via reduced intraspecific competition with large trees.

Spatial patterning of woody plants in savannas is suggestive of the importance of tree-tree competition (e.g., Riginos et al. 2005, Moustakas et al. 2008, Kambatuku et al. 2011) and Dohn et al. (2017) provides empirical evidence that tree growth rates are affected by competition with neighboring trees, likely for water, in semiarid systems (Calabrese et al. 2010, Dohn et al. 2017). However, we cannot rule out the possibility that the positive effects of wildlife on sapling growth were, in part, due to over-compensatory growth in response to browsing (Riginos and Young 2007). However, the fact that sapling growth was strongly related to neighboring tree density indicates that over-compensation alone does not explain our results. That wildlife presence had a weaker positive effect on sapling height than diameter also indicates that any height gains were at least partially offset by wildlife browsing.

An alternative mechanistic explanation for the positive effect of wildlife on sapling growth is that grazing wildlife were attracted to graze more in areas of low tree density and thereby reduced grass competition with trees. Grazing wildlife are known to prefer areas with fewer trees in this system (Riginos and Grace 2008, Riginos 2015), and we know that grass has strong net negative effects on sapling growth (see *Tree–grass interactions*). However, two lines of evidence contraindicate this hypothesis. First, total grass cover and tree density do not covary in this system (Riginos and Grace 2008), although we acknowledge that this could be due to both higher grass production and consumption in places with fewer trees, resulting in no net cover difference. Second and more importantly, we found no significant effects of moderate cattle grazing treatments on

sapling growth, so we would not expect wildlife, which remove considerably less grass biomass than cattle (Charles et al. 2017), to affect sapling growth via grazing. It is possible that, at the scale of individual saplings, localized grazing by wildlife could reduce grass competition in ways not reflected by plot-wide average effects of wildlife vs. cattle on grass consumption. However, given the strong relationship between individual sapling growth and the number of larger trees in its vicinity, we believe that the most plausible and/or influential mechanism for the positive effect of wildlife on saplings is that wildlife, mostly elephants, reducing neighborhood tree-tree competition.

The positive effects of wildlife on sapling growth did not translate into increases in sapling survival, which was overall relatively high, but presence of wildlife did increase the proportion of saplings that transitioned out of the grass layer (≥ 70 cm). This suggests that wildlife, particularly elephants, can have complex effects on tree demography. On the one hand, elephants can reduce the density of large trees, leading to declines in tree cover. On the other hand, this decline in large trees can accelerate the rate at which saplings transition to the larger tree size class. Depending on the intensity of elephant damage to trees and browse pressure (from elephants or other herbivores) on saplings, as well as other factors such as precipitation, the net effect of wildlife may be to stabilize or reduce tree cover.

Ant mutualism defense

Occupation by any species of ant mutualist was strongly and positively associated with sapling transitions to larger size classes. Although transition rates did not differ significantly across ant species, the majority (76%) of saplings that grew taller than the grass layer by 2014 were occupied by the two most protective ant species, *C. mimosae* or *C. nigriceps*, both of which depend on extrafloral nectar (Rudolph and Palmer 2013). The proportion of saplings occupied by one of these species, *C. mimosae*, also increased in plots where grass had been removed (Appendix S2: Fig. S1) and where neighbor tree density declined (Appendix S2: Fig. S2). Together these results are consistent with previous studies reporting that nectar-dependent ants are more likely to colonize (Palmer et al. 2002) and less likely to abandon (Palmer et al. 2000) saplings with high growth rates, particularly when reduced tree-tree competition increases the number of nectaries available to ants (Palmer et al. 2017). One notable difference is that Palmer et al. (2017) found that grass presence (rather than absence) improved saplings' capacity to offer rewards to the defensive ant *C. mimosae* likely by reducing evaporative water loss from the soil. We speculate that grass effects may become more negative during extended dry periods (which were not included in Palmer et al. 2017). Overall, further experimentation is required to determine whether (1) saplings were taller because they were

defended by ants or (2) taller saplings were more likely to be colonized by defensive ants.

CONCLUSIONS

In savannas around the world, management of woody cover is an important concern. In some African savanna systems managed for conservation of browsing wildlife, mitigating declines in woody cover is the primary concern. In most other savannas, including parts of Africa, increases in tree cover are widespread and of greatest concern (Scholes and Archer 1997, Bond 2008, O'Connor et al. 2014, Stevens et al. 2017). Understanding the mechanisms of changes in tree cover and the opportunities to leverage those mechanisms to meet management goals are important to savanna management.

Results from the first two years of the current study showed that grass removal treatments, which partially simulate heavy grazing by livestock, increase sapling growth during below-average rainfall (Riginos and Young 2007). By following saplings over 10 yr and extended dry and wet periods, we found that grass-removal effects became even stronger during above-average rainfall years, leading to increased sapling recruitment to the next demographic stage. It may follow that the effects of grass competition observed on larger trees during dry periods (Riginos 2009) are also greater during wet periods. Regardless of initial tree cover or tree size, we found that increasing the proportion of bare ground, a common consequence of intense grazing, can be expected to increase tree growth rates and the maximum tree density constrained by edaphic site conditions (*sensu* Sankaran et al. 2005). This supports mechanistically the widespread observation that heavy livestock grazing leads to woody encroachment.

In African savannas where the wild ungulate community includes many species of browsers, several studies have reported evidence of rapid woody encroachment following abrupt declines in these wild herbivores (Hutton and Smart 1984, Prins and Vanderjeugd 1993, Daskin et al. 2016). Persistent saplings released from abiotic or biotic stress are known to contribute substantially to woody encroachment (Bond and Midgley 2001, O'Connor et al. 2014). The loss of direct browsing pressure on saplings may contribute to rapid sapling growth and recruitment to larger size classes. Our findings, however, suggest an additional mechanism: that tree-tree competition is low in the first years following wildlife declines, enabling rapid sapling growth.

Management implications

Our results highlight key time periods that should be targeted by managers wishing to maintain, increase, or reduce woody cover. During extended droughts, savannas are at greatest risk of heavy grazing and loss of herbaceous plant cover. Our data and others' (Rietkerk et al. 2004, Case et al. 2019) indicate that, for some

species, optimal conditions for sapling recruitment into taller size classes occur during average or above-average rainfall periods that follow long drought periods and when bare ground is at its peak. If livestock managers could minimize the creation of bare ground during drought by moderating stocking rates, the intensity of sapling recruitment in the ensuing wet periods may also be moderated. Likewise, managers could anticipate a greater need for woody control efforts during these post-drought periods. In situations where more trees are desired, post-drought periods may be opportunities to capitalize on rapid sapling growth, which could be accelerated by temporarily protecting them from herbivores. Overall, our results provided a more nuanced and mechanistic understanding of how large herbivores affect tree cover and add to the growing body of evidence that management of wildlife populations in conjunction with moderate livestock stocking rates can be used to purposefully manipulate woody cover in savannas.

ACKNOWLEDGMENTS

We would like to thank Susan Durham, Andrew Tredennick, and Kyle Nehring for comments on analysis and presentation of results, as well as Kendall Becker, Ryan Choi, and Kate M. Lillie for valuable comments on the overall manuscript. The comments of the subject matter editor and anonymous reviewers also substantially improved the manuscript. Thanks to Frederick Erii, John Lochukuya, Patrick Etelej, Jackson Ekadeli, Mathew Nermon, and Steven Ekuam for invaluable assistance in the field. Other staff at the Mpala Research Centre provided logistical support and access to field sites. The enclosure plots were built and maintained by grants from the James Smithson Fund of the Smithsonian Institution (to A. P. Smith), The National Geographic Society (grants 4691-91 and 9106-12 to T. P. Young), and the National Science Foundation (LTREB BSR 97-07477, 03-16402, 08-16453, 12-56004, and 12-56034 to T. P. Young, K. E. Veblen, and C. Riginos). Additional funding was provided by Utah State University (USU) Ecology Center, the S. J. Quinney Foundation, USU School of Graduate Studies, USU College of Natural Resources, and USU Department of Wildland Resources (to E. LaMalfa).

LITERATURE CITED

- Andersen, A. N., and W. M. Lonsdale. 1990. Herbivory by insects in Australian tropical savannas: A review. *Journal of Biogeography* 17:433–444.
- Anderson, T. M., J. G. C. Hopcraft, S. Eby, M. Ritchie, J. B. Grace, and H. Olff. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology* 91:1519–1529.
- Angassa, A., and G. Oba. 2010. Effects of grazing pressure, age of enclosures and seasonality on bush cover dynamics and vegetation composition in southern Ethiopia. *Journal of Arid Environments* 74:111–120.
- Angassa, A., G. Oba, and A. Tolera. 2012. Bush encroachment control demonstrations and management implications on herbaceous species in savannas of southern Ethiopia. *Tropical and Subtropical Agroecosystems* 15:173–185.
- Archer, S. R., and K. I. Predick. 2014. An ecosystem services perspective on brush management: Research priorities for competing land-use objectives. *Journal of Ecology* 102:1394–1407.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165–1183.
- Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41:45–58.
- Baxter, P. W. J., and W. M. Getz. 2005. A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecological Applications* 15:1331–1341.
- Belsky, A. J., W. P. Carson, C. L. Jensen, and G. A. Fox. 1993. Overcompensation by plants: Herbivore optimization or red herring? *Evolutionary Ecology* 7:109–121.
- Berry, R. S., and A. Kulmatiski. 2017. A savanna response to precipitation intensity. *PLoS ONE* 12:e0175402.
- Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology* 40:276–282.
- Birkett, A., and B. Stevens-Wood. 2005. Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *African Journal of Ecology* 43:123–130.
- Blaser, W. J., G. K. Shanungu, P. J. Edwards, and H. O. Venterink. 2014. Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. *Ecology and Evolution* 4:1423–1438.
- Bond, W. J. 2008. What limits trees in C₄ grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39:641–659.
- Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16:45–51.
- Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Population and community biology series 14. Chapman and Hall, New York, New York, USA.
- Calabrese, J. M., F. Vazquez, C. Lopez, M. San Miguel, and V. Grimm. 2010. The independent and interactive effects of tree-tree establishment competition and fire on savanna structure and dynamics. *American Naturalist* 175:E44–E65.
- Case, M. F., and A. C. Staver. 2018. Soil texture mediates tree responses to rainfall intensity in African savannas. *New Phytologist* 219:1363–1372.
- Case, M. F., C. Wigley-Coetsee, N. Nzima, P. F. Scogings, and A. C. Staver. 2019. Severe drought limits trees in a semi-arid savanna. *Ecology* 100:e02842.
- Chapin, F. S., E. D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21:423–447.
- Charles, G. K., L. M. Porensky, C. Riginos, K. E. Veblen, and T. P. Young. 2017. Herbivore effects on productivity vary by guild: cattle increase mean productivity while wildlife reduce variability. *Ecological Applications* 27:143–155.
- Costa, A. N., H. L. Vasconcelos, and E. M. Bruna. 2017. Biotic drivers of seedling establishment in Neotropical savannas: selective granivory and seedling herbivory by leaf-cutter ants as an ecological filter. *Journal of Ecology* 105:132–141.
- Cramer, M. D., J. L. Wakeling, and W. J. Bond. 2012. Below-ground competitive suppression of seedling growth by grass in an African savanna. *Plant Ecology* 213:1655–1666.
- Daskin, J. H., M. Stalmans, and R. M. Pringle. 2016. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology* 104:79–89.
- Dohn, J., D. J. Augustine, N. P. Hanan, J. Ratnam, and M. San-karan. 2017. Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna. *Ecology* 98:478–488.

- du Toit, J. T., and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8:1643–1661.
- Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14:709–722.
- February, E. C., S. I. Higgins, W. J. Bond, and L. Swemmer. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology* 94:1155–1164.
- Fensham, R. J., M. E. Freeman, B. Laffineur, H. Macdermott, L. D. Prior, and P. A. Werner. 2017. Variable rainfall has a greater effect than fire on the demography of the dominant tree in a semi-arid Eucalyptus savanna. *Austral Ecology* 42:772–782.
- Fornara, D. A., and J. T. Du Toit. 2007. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88:200–209.
- Fox-Dobbs, K., D. F. Doak, A. K. Brody, and T. M. Palmer. 2010. Termites create spatial structure and govern ecosystem function by affecting N₂ fixation in an East African savanna. *Ecology* 91:1296–1307.
- Giambellucca, T. W., F. G. Scholz, S. J. Bucci, F. C. Meinzer, G. Goldstein, W. A. Hoffmann, A. C. Franco, and M. P. Buchert. 2009. Evapotranspiration and energy balance of Brazilian savannas with contrasting tree density. *Agricultural and Forest Meteorology* 149:1365–1376.
- Goheen, J. R., F. Keesing, B. F. Allan, D. L. Ogada, and R. S. Ostfeld. 2004. Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology* 85:1555–1561.
- Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology* 79:372–382.
- Grady, J. M., and W. A. Hoffmann. 2012. Caught in a fire trap: Recurring fire creates stable size equilibria in woody resprouters. *Ecology* 93:2052–2060.
- Grellier, S., S. Barot, J.-L. Janeau, and D. Ward. 2012. Grass competition is more important than seed ingestion by livestock for Acacia recruitment in South Africa. *Plant Ecology* 213:899–908.
- Hatton, J. C., and N. O. E. Smart. 1984. The effect of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park, Uganda. *African Journal of Ecology* 22:23–30.
- Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82:1999–2011.
- Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213–229.
- Hoffmann, W. A., R. Adasme, M. Haridasan, M. T. de Carvalho, E. L. Geiger, M. A. B. Pereira, S. G. Gotsch, and A. C. Franco. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90:1326–1337.
- Holdo, R. M. 2006a. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science* 17:509–518.
- Holdo, R. M. 2006b. Tree growth in an African woodland savanna affected by disturbance. *Journal of Vegetation Science* 17:369–378.
- Holdo, R. M., T. M. Anderson, and T. Morrison. 2014. Precipitation, fire and demographic bottleneck dynamics in Serengeti tree populations. *Landscape Ecology* 29:1613–1623.
- Holdo, R. M., and E. R. Brocato. 2015. Tree-grass competition varies across select savanna tree species: a potential role for rooting depth. *Plant Ecology* 216:577–588.
- Huxman, T. E., B. P. Wilcox, D. D. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319.
- Ihwagi, F. W., T. Wang, G. Wittemyer, A. K. Skidmore, A. G. Toxopeus, S. Ngene, J. King, J. Worden, P. Omondi, and I. Douglas-Hamilton. 2015. Using poaching levels and elephant distribution to assess the conservation efficacy of private, communal and government land in northern Kenya. *PLoS ONE* 10:e0139079.
- Kambatuku, J. R., M. D. Cramer, and D. Ward. 2011. Intraspecific competition between shrubs in a semi-arid savanna. *Plant Ecology* 212:701–713.
- Kimiti, D. W., A. M. C. Hodge, J. E. Herrick, A. W. Beh, and L. E. Abbott. 2017. Rehabilitation of community-owned, mixed-use rangelands: lessons from the Ewaso ecosystem in Kenya. *Plant Ecology* 218:23–37.
- Kimuyu, D. M., R. L. Sensenig, C. Riginos, K. E. Veblen, and T. P. Young. 2014. Native and domestic browsers and grazers reduce fuels, fire temperatures, and Acacia ant mortality in an African savanna. *Ecological Applications* 24:741–749.
- Kimuyu, D. M., K. E. Veblen, C. Riginos, R. M. Chira, J. M. Githaiga, and T. P. Young. 2017. Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores. *Ecological Applications* 27:786–798.
- Kraaij, T., and D. Ward. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology* 186:235–246.
- Maclean, J. E., J. R. Goheen, D. F. Doak, T. M. Palmer, and T. P. Young. 2011. Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. *Ecology* 92:1626–1636.
- Midgley, J. J., D. Balfour, and G. I. Kerley. 2005. Why do elephants damage savanna trees? *South African Journal of Science* 101:213–215.
- Midgley, J. J., and W. J. Bond. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology* 17:871–886.
- Morrison, T. A., R. M. Holdo, and T. M. Anderson. 2016. Elephant damage, not fire or rainfall, explains mortality of overstorey trees in Serengeti. *Journal of Ecology* 104:409–418.
- Morrison, T. A., R. M. Holdo, D. M. Rugemalila, M. Nzunda, and T. M. Anderson. 2019. Grass competition overwhelms effects of herbivores and precipitation on early tree establishment in Serengeti. *Journal of Ecology* 107:216–228.
- Moustakas, A., K. Wiegand, S. Getzin, D. Ward, K. M. Meyer, M. Guenther, and K.-H. Mueller. 2008. Spacing patterns of an Acacia tree in the Kalahari over a 61-year period: How clumped becomes regular and vice versa. *Acta Oecologica* 33:355–364.
- Nackley, L. L., A. G. West, A. L. Skowno, and W. J. Bond. 2017. The nebulous ecology of native invasions. *Trends in Ecology and Evolution* 32:814–824.
- Naito, A. T., and D. M. Cairns. 2011. Patterns and processes of global shrub expansion. *Progress in Physical Geography* 35:423–442.
- O'Connor, T. G., P. S. Goodman, and B. Clegg. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation* 136:329–345.

- O'Connor, T. G., J. R. Puttik, and M. T. Hoffman. 2014. Bush encroachment in southern Africa: Changes and causes. African Journal of Range and Forage Science 31:67–88.
- Odadi, W. O., T. P. Young, and J. B. Okeyo-Owuor. 2007. Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. *Rangeland Ecology & Management* 60:179–185.
- Palmer, T. M., and A. K. Brody. 2013. Enough is enough: the effects of symbiotic ant abundance on herbivory, growth, and reproduction in an African acacia. *Ecology* 94:683–691.
- Palmer, T. M., D. F. Doak, M. L. Stanton, J. L. Bronstein, E. T. Kiers, T. P. Young, J. R. Goheen, and R. M. Pringle. 2010. Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *Proceedings of the National Academy of Sciences USA* 107:17234–17239.
- Palmer, T. M., C. Riginos, R. E. Damiani, N. Morgan, J. S. Lemboi, J. Lengingiro, J. C. Ruiz-Guajardo, and R. M. Pringle. 2017. Influence of neighboring plants on the dynamics of an ant-acacia protection mutualism. *Ecology* 98:3034–3043.
- Palmer, T. M., T. P. Young, and M. L. Stanton. 2002. Burning bridges: priority effects and the persistence of a competitively subordinate acacia-ant in Laikipia, Kenya. *Oecologia* 133:372–379.
- Palmer, T. M., T. P. Young, M. L. Stanton, and E. Wenk. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* 123:425–435.
- Paul, E. L., F. D. B. Willem, M. A. H. Ignas, and H. T. P. Herbert. 2005. Germination strategy of the East African Savanna Tree *Acacia tortilis*. *Journal of Tropical Ecology* 21:509–517.
- Porensky, L. M., and K. E. Veblen. 2012. Grasses and browsers reinforce landscape heterogeneity by excluding trees from ecosystem hotspots. *Oecologia* 168:749–759.
- Porensky, L. M., S. E. Wittman, C. Riginos, and T. P. Young. 2013. Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. *Oecologia* 173:591–602.
- Prins, H. H. T., and H. P. Vanderjeugd. 1993. Herbivore population crashes and woodland structure in East-Africa. *Journal of Ecology* 81:305–314.
- Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926–1929.
- Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* 90:335–340.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* 84:124–133.
- Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology* 89:2228–2238.
- Riginos, C., M. A. Karande, D. I. Rubenstein, and T. M. Palmer. 2015. Disruption of a protective ant-plant mutualism by an invasive ant increases elephant damage to savanna trees. *Ecology* 96:654–661.
- Riginos, C., S. J. Milton, and T. Wiegand. 2005. Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland. *Journal of Vegetation Science* 16:331–340.
- Riginos, C., and T. P. Young. 2007. Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. *Oecologia* 153:985–995.
- Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38:268–280.
- Rudolph, K. P., and T. M. Palmer. 2013. Carbohydrate as fuel for foraging, resource defense and colony growth—a long-term experiment with the plant-ant *Crematogaster nigriceps*. *Biotropica* 45:620–627.
- Ruess, R. W., and F. L. Halter. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *African Journal of Ecology* 28:259–275.
- Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. *Nature* 438:846–849.
- Sankaran, M., D. J. Augustine, and J. Ratnam. 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology* 101:1389–1399.
- Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17:236–245.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043–1048.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- Seymour, C. L. 2008. Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology* 197:131–138.
- Shaw, M. T., F. Keesing, and R. S. Ostfeld. 2002. Herbivory on *Acacia* seedlings in an East African savanna. *Oikos* 98:385–392.
- Staver, A. C., and W. J. Bond. 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology* 102:595–602.
- Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19:1909–1919.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy, and G. Durigan. 2017. Savanna woody encroachment is widespread across three continents. *Global Change Biology* 23:235–244.
- Tobler, M. W., R. Cochard, and P. J. Edwards. 2003. The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology* 40:430–444.
- Vadigi, S., and D. Ward. 2012. Fire and nutrient gradient effects on the sapling ecology of four *Acacia* species in the presence of grass competition. *Plant Ecology* 213:1793–1802.
- Vadigi, S., and D. Ward. 2014. Herbivory effects on saplings are influenced by nutrients and grass competition in a humid South African savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 16:11–20.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.
- Vaz Ferreira, A., E. M. Bruna, and H. L. Vasconcelos. 2011. Seed predators limit plant recruitment in Neotropical savannas. *Oikos* 120:1013–1022.
- Veblen, K. E., L. M. Porensky, C. Riginos, and T. P. Young. 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. *Ecological Applications* 26:1610–1623.
- Veblen, K. E., C. Riginos, and E. LaMalfa. 2021. Browsing wildlife and heavy grazing indirectly facilitate sapling recruitment in an East African savanna. Figshare, data set. <https://doi.org/10.6084/m9.figshare.14210648.v2>
- Veenendaal, E. M., M. D. Swaine, V. K. Agyeman, D. Blay, I. K. Abebrese, and C. E. Mullins. 1996. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* 84:83–90.

- Wahungu, G. M., L. K. Mureu, D. M. Kimuyu, A. Birkett, P. G. Macharia, and J. Burton. 2011. Survival, recruitment and dynamics of *Acacia drepanolobium* Sjøstedt seedlings at Olpejeta Conservancy, Kenya, between 1999 and 2009. African Journal of Ecology 49:227–233.
- Ward, D., and K. J. Esler. 2011. What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment? Plant Ecology 212:245–250.
- Werner, P. A., I. D. Cowie, and J. S. Cusack. 2006. Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia: an experimental field study in Kakadu National Park. Australian Journal of Botany 54:283–296.
- Werner, P. A., and L. D. Prior. 2013. Demography and growth of subadult savanna trees: interactions of life history, size, fire season, and grassy understory. Ecological Monographs 83:67–93.
- Western, D., and D. Maitumo. 2004. Woodland loss and restoration in a savanna park: a 20-year experiment. African Journal of Ecology 42:111–121.
- Woolery, P. O., and D. F. Jacobs. 2011. Photosynthetic assimilation and carbohydrate allocation of *Quercus rubra* seedlings in response to simulated herbivory. Annals of Forest Science 68:617–624.
- Xi, N., C. Chu, and J. M. G. Bloor. 2018. Plant drought resistance is mediated by soil microbial community structure and soil-plant feedbacks in a savanna tree species. Environmental and Experimental Botany 155:695–701.
- Young, T. P., B. D. Okello, D. Kinyua, and T. M. Palmer. 1997a. KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range & Forage Science 14:94–102.
- Young, T. P., C. H. Stubblefield, and L. A. Isbell. 1997b. Ants on swollen thorn acacias: species coexistence in a simple system. Oecologia 109:98–107.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2399/full>

OPEN RESEARCH

Associated data (Veblen et al. 2021) are available on Figshare: <https://doi.org/10.6084/m9.figshare.14210648>.