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FIRE - HERBIVORY INTERACTIONS IN AN EAST AFRICAN SAVANNA:
EFFECTS ON *ACACIA DREPANOLOBIUM* TREES

by

Eric M. LaMalfa

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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ABSTRACT

Fire – Herbivory Interactions in an East African Savanna: Effects on *Acacia*
Drepanolobium Trees and the Demographic Bottleneck

by

Eric M. LaMalfa, Doctor of Philosophy

Utah State University, 2019

Major Professor: Dr. Kari E. Veblen
Department: Wildland Resources

Anthropogenic activities have disrupted natural disturbance regimes globally, leading to widespread changes in plant community structure. Altering the type, frequency, or severity of disturbance favors plant functional groups (i.e., grasses, shrubs, trees) whose traits are more suited to the new regime. Extreme modifications to structure, such as increasing the proportion of woody species, can ultimately compromise soil, water, forage, habitat, and other ecosystem services. Understanding the mechanisms that underlie these vegetation changes is critical for managing ecosystem function.

In semi-arid rangelands, vegetation structure is often dynamic due to multiple types of interacting disturbance. Savannas are characterized by the codominance of grasses and trees, but the proportion of tree cover responds dynamically to changes in fire, and herbivory. Because both these factors primarily damage low plant tissues within the grass layer they cause a demographic bottleneck, which delays transitions from the

ontogenic sapling stage (<1 m) to taller tree stage (>1 m). In this dissertation, I investigated several fire × herbivory interactions to gain a mechanistic understanding of recruitment processes, which ultimately affect savanna structure. I used the Kenya Long-term Exclosure Experiment (KLEE) to investigate how fire and different combinations of cattle, meso-wildlife (mammalian herbivores 15–1000 kg), and megaherbivores (elephant and giraffe) affect saplings.

First, I found evidence that tree recruitment in *A. drepanolobium* savanna is limited by both meso-wildlife and elephant browsing. Second, in the absence of fire, the primary effects of cattle and wildlife on sapling growth occurred indirectly via tree-grass and tree-tree interactions, respectively. I found that overgrazing had the potential to increase sapling recruitment by reducing interspecific tree-grass competition. The highest sapling growth, however, occurred where large neighbor trees were absent, a condition maintained primarily by elephants browsing and damaging large neighbor trees. Finally, I found that saplings conditioned by wildlife “browsing legacies” had high tolerance to combined fire and wildlife browsing. These results highlight the importance of several mechanisms which increase saplings persistence despite frequent tissue removal. In summary, the sequence and type of interacting disturbances affects sapling recruitment. My results highlight the importance of using long-term herbivory studies to investigate sapling recruitment, which is a key demographic transition that often limits savanna tree cover.

PUBLIC ABSTRACT

Fire – Herbivory Interactions in an East African Savanna: Effects on *Acacia drepanolobium* Trees and the Demographic Bottleneck

Eric M. LaMalfa

Globally, changes in plant community structure have occurred in ecosystems where humans have altered natural disturbance regimes. Many plants have adaptive life histories and morphological traits that have coevolved with fire and herbivory, which allows them to thrive despite repeated tissue losses. Therefore, altering the type, frequency, or severity of disturbance affects individual plant growth and competition among species. When these changes benefit or disadvantage different plant functional groups (i.e., grasses, shrubs, trees) it alters ecosystem structure and function. Understanding and predicting these vegetation changes, is critical for conservation and management of biodiversity, wildlife habitat, livestock forage, and water.

Savannas are characterized by the codominance of grasses and trees, but the proportion of tree cover responds dynamically to changes in precipitation, fire, and herbivory. These factors often cause a ‘demographic bottleneck,’ which delays transitions from sapling size (<1 m) to adult size trees (>1 m). In this dissertation, I investigated several fire × herbivory interactions to gain a mechanistic understanding of sapling recruitment processes that ultimately affect savanna structure.

I made use of a long-term experiment that used semi-permeable fencing to manipulate presence and absence of different types of herbivores, to explore how fire and different combinations of domestic cattle, meso-wildlife, and megaherbivores (elephant

and giraffe) affect sapling recruitment. First, I found clear evidence that a wide range of tree height classes resprout after being top-killed by fire, but they were all subsequently kept short by meso-wildlife browsing. Elephants played a key role in suppressing the largest resprouts after fire possibly because fire had reduced the presence of ant mutualists that defend the trees. Second, I found that in the absence of fire, cattle and wildlife indirectly affected saplings by altering competition with neighboring vegetation. Saplings competed with grass and trees during above-average rainfall years. Bare ground—a condition often caused by overgrazing—was positively associated with sapling growth. The highest sapling growth, however, occurred where large neighbor trees were absent, a condition maintained primarily by elephants browsing and damaging large neighbor trees. Finally, I found that saplings conditioned by pre-fire wildlife “browsing legacies” had high tolerance to combined fire and wildlife browsing. These results help explain how saplings tolerate repeated tissue loss to disturbance. Understanding how interactions between fire and herbivory affect sapling recruitment will help managers effectively use natural disturbance processes to manage savanna structure and function.

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Eric M. LaMalfa

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CHAPTER 1

INTRODUCTION

Savannas occur globally across broad environmental gradients and are characterized by their dynamic woody structure that ranges from treeless to closed tree canopy. Tree cover influences important ecosystem processes such as provision of forage (Scholes & Archer, 1997), energy balance (Giambelluca et al., 2009), carbon flux (Blaser et al., 2014), and nutrient cycling (Hibbard et al., 2001). As such, changes in land management practices that alter vegetation cover directly influence global carbon uptake (Cox et al., 2000). Determining what mechanistic processes control changes in tree cover has posed a classic theoretical dilemma—dubbed the savanna problem—for ecologists. Two common disturbances, fire and ungulate herbivory, are known to affect tree demographic transitions from sapling to adult stage, but mechanistic interactions between fire and herbivory become complex when considering the diversity of wild and domestic ungulate herbivores, plant-plant interactions, and variable rainfall characteristic of semi-arid African savannas.

Ecologists have investigated grass-tree coexistence in savannas from various perspectives examining species and community level interactions at many scales, with most empirical studies focusing on tradeoffs in the performance of grasses versus trees. Several authors have reviewed the large body of tree-grass coexistence literature in attempts to comprehensively understand the mechanisms that determine the proportion of tree cover in savannas (Scholes & Archer, 1997; House et al., 2003; Sankaran et al., 2004; Bond, 2008). A global analysis of savanna distribution recently found that the

relationships among woody vegetation, fire, and climate vary across continents (Lehmann et al., 2014). This suggests that a single model may not adequately represent savanna woody biomass because of differences in evolutionary history (Lehmann et al., 2014), and highlights the need to understand the community level processes that occur as a result of fire and herbivory interactions.

Savanna ecologists recognize five key determinants of savanna vegetation structure and function: precipitation, soils, nutrients, fire, and herbivory (Bond, 2008). Precipitation and soil properties related to water (i.e., texture and depth) largely determine the amount of water available to plants in a given system. A large body of work has focused on how niche differentiation between deep rooted trees and shallow rooted grasses promotes coexistence by stabilizing maximum potential tree cover in equilibrium with available resources (Holdo, 2013; Mazzacavallo & Kulmatiski, 2015). However, observed tree cover in savannas is often less than would be predicted based on mean annual precipitation (Sankaran et al., 2008), suggesting that other non-equilibrium disturbance processes such as fire and herbivory maintain savanna structure and function (Scholes & Archer, 1997). Fire and browsing can severely damage short-statured trees but these negative effects generally decrease with increasing tree height. For this reason, tree cover is frequently limited by delayed transitions from sapling size (<1 m) to larger reproductive tree size classes (Gignoux et al., 1997; Higgins et al., 2000; Hoffmann et al., 2009; Werner & Prior, 2013), a phenomenon referred to as the “demographic bottleneck” (Higgins et al., 2000). If fire and browsing frequency are reduced, sapling recruitment rates increase, ultimately causing an increase in large tree density (Bond & Midgley, 2001; O'Connor et al., 2014). Interactions between fire and herbivory that reduce sapling

growth and survival should, in theory, maintain or reduce savanna tree cover.

Fire and herbivory can each independently affect tree cover by delaying demographic height transitions from sapling (<1 m) to adult tree stages (>1 m). For example, frequent fires can create a “fire trap” whereby short saplings are repeatedly top-killed and then resprout from surviving belowground tissues (Hoffmann et al., 2009; Grady & Hoffmann, 2012). Saplings may escape the cycle during long fire-free intervals by growing to large fire-resistant sizes (Bond & Midgley, 2001; Freeman et al., 2017), or by growing rapidly during short fire-free intervals (Wakeling et al., 2011). Similarly, herbivore browsing alone can limit tree demographic transitions by directly removing biomass and altering height (Augustine & McNaughton, 2004; Sankaran et al., 2013). Fire and browsing disturbances differ in the proportion of tissue they damage, the frequency of tissue removal, and the seasonality of disturbance (Bellingham & Sparrow, 2000; Archibald & Hempson, 2016). Grazers, such as cattle, can have an indirect positive effect on tree growth rates by reducing interspecific grass competition (Riginos & Young, 2007; Riginos, 2009).

The interaction of fire and ungulate herbivory can occur in many ways but empirical tests of these interactions are rare in the literature (Foster et al., 2016). Fire can alter the quantity, composition, and palatability of resprouting forage resulting in increased ungulate utilization levels (Sensenig et al., 2010; Augustine & Derner, 2014). Conversely, ungulate herbivory can modify vegetation community composition and biomass, both of which affect fire behavior (van Langevelde et al., 2003; Holdo et al., 2013). Interactions between grazing (grass eating) herbivores and fire are well documented. Cattle grazing reduces fine fuels (i.e., grass biomass) which alters fire

behavior (Higgins et al., 2000; Kirkpatrick et al., 2011). Recently-burned areas are visited more frequently by both cattle (Fuhlendorf & Engle, 2004; Augustine & Derner, 2014) and bison (Vinton et al., 1993).

Much less is known about how interactions between fire and browsing (i.e., woody plant eating) ungulates impact sapling recruitment. Empirical studies that explicitly test for interactive effects of fire and browsing are rare in the literature (Staver et al., 2009; Foster et al., 2016). Theory suggests that browsing should delay the onset of ‘escape height’ (i.e., the minimum height for a meristems to survive surface fire) and that, conversely, fires should increase the palatability of resprouting woody plants due to reductions in plant defense (Dublin et al., 1990; Scholes & Archer, 1997). In a recent study by Staver et al. (2009), model projections based on empirical data found that fire alone did not affect large tree density. Instead, the combination of both wild ungulates (including both grazers and browsers) and fire were required in order to suppress large tree density. This resulted from population projections that accounted for both decreased tree growth in years following fire and decreased growth in non-fire years when wildlife browsers remove tree tissue. It remains unclear if the net interactive effects of fire and herbivory on tree growth depends on the type of ungulate herbivores (e.g., domestic cattle, wild grazers, browsers and mixed-feeders) present following fire.

RESEARCH SUMMARY

My dissertation examines how fire, rainfall, and factorial combinations of domestic livestock (i.e., cattle), meso-wildlife (mammalian herbivores 15–1000 kg), and megaherbivores (elephants and giraffes), affect demographic transitions of saplings (<1

m) into larger tree size classes. Using an experimental approach, I investigated sapling recruitment in the whistling thorn (*Acacia drepanolobium*), a widespread, often monodominant tree species in East Africa. I asked three questions: 1) how factorial combinations of cattle, meso-wildlife and megaherbivores affect the post-fire resprout response, 2) how the indirect effects of wildlife and cattle affect sapling recruitment during high and low rainfall periods, and 3) how the frequency of tissue removal that occurs during sapling development (i.e., browsing legacy) affects post-fire resprout size.

Study site

The Mpala Ranch and Conservancy is located in Laikipia, Kenya. It hosts the Kenya Long-term Exclosure Experiment (KLEE). Since 1995, KLEE has manipulated the presence and absence of different combinations of large herbivores (Young & Okello, 1998). Semi-permeable fencing is used to control access by cattle, meso-wildlife, and megaherbivores, in large 4-ha plots. The treatments are replicated in three blocks (North, Central, and South) for a total of 18 plots. Within this larger experimental design, I applied prescribed fire and caging treatments to investigate my study questions.

Summary: Ungulate effects on post-fire resprouting

The first data chapter of my dissertation compares the post-fire resprout size among saplings exposed to different levels of herbivory. Large ungulate herbivores prefer to forage in burned areas, but it is unknown how the net effects of herbivore community composition affect post-fire tree resprout responses. Using the KLEE plots, I compared post-fire tree height and stem length among six herbivore treatments that included factorial combinations of cattle, meso-wildlife, and megaherbivores. Controlled burns

were conducted within the KLEE exclosures in 2013 (Kimuyu et al., 2014). I investigated the relationship between pre-fire and post-fire tree size among six herbivore treatments.

I hypothesized that one year following top-kill by fire tree resprout size depends on the herbivore community composition. Specifically, I expected cattle to have positive, meso-wildlife to have net negative, and megaherbivore (primarily elephant) to have the most negative effects on tree resprout size. I expected that factorial combinations of cattle and wildlife would result in additive responses, such that the presence of cattle would consistently offset the negative relationship between wildlife presence and resprout size, owing to the different indirect positive (i.e., grazers reduce grass competition with trees) and direct negative (i.e., browsers remove tree biomass) mechanisms hypothesized to affect tree size. I expected that despite differences in height caused by browsing, compensatory growth would result in equal stem lengths across herbivore treatments.

I found that saplings attained the greatest post-fire height in the absence of all ungulate herbivores. Contrary to my expectations, cattle had a small negative rather than positive effect on resprout height but only in the absence of all wildlife. Meso-wildlife treatments significantly reduced resprout height relative to no-herbivory or cattle-only treatments. When megaherbivores were combined with meso-wildlife resprout height was further diminished.

Contrary to my prediction, we found no evidence of compensatory branch growth in response to browsing when considering all trees top-killed by fire. However, saplings (<1 m) exposed to megaherbivores had larger stem lengths than those in other herbivore treatments. This led to the question of my third data chapter, which postulated that saplings (<1 m) exposed to wildlife prior to fire have “browsing legacy” effects that

increase post-fire resprouting.

My results also provide empirical evidence that tree growth following top-kill by fire is diminished in the presence of a mixed diet meso-wildlife community and even more so by the presence of megaherbivores (i.e., elephants) that directly limit tree height by consuming the biomass of resprouting trees top-killed by fire. This supports the conclusion of Staver et al. (2009), who suggested that fire and browsing interactions over many fire cycles, reduce tree cover by limiting escape from the fire trap and browse trap cycles.

Summary: Indirect effects of ungulates on sapling recruitment

For the second data chapter of my dissertation, I used a long-term dataset to investigate sapling recruitment dynamics in semi-arid savanna. Long-term studies of sapling recruitment are rare but necessary in these systems because growth rates are highly variable and dependent on rainfall.

In African savannas, multiple lines of evidence suggest that supplanting wildlife with domestic livestock has resulted in bush encroachment (i.e., increasing tree cover or density), but no single study previously quantified the effects of cattle and wildlife on sapling growth during long multi-year wet and dry periods. Previous studies reported that grass removal increases tree growth during below-average rainfall (Riginos & Young, 2007).

The KLEE experimental plots were used to investigate the net effects of wildlife and cattle on *Acacia drepanolobium* saplings over 10 years. Grass removal treatments (0.5-m radius glyphosate application) were used to simulate the indirect effects of

overgrazing by cattle. Neighborhood tree surveys (trees within a 3-m radius and >1 m height) were used as a proxy for intraspecific competition from mature trees. I also used before (pre-treatment) and after (end of study) tree surveys to estimate indirect effects of wildlife (i.e., elephant toppling of neighbor trees >1 m) on sapling growth.

The early (2 years) results of the study reported that grass removal increases tree growth during below-average rainfall (Riginos & Young, 2007). I found that, after 10 years, grass-removal effects became even stronger during above-average rainfall years leading to increased sapling recruitment (i.e., escape from the grass layer). This is consistent with anecdotal observations of rapid bush encroachment occurring over short time scales in overgrazed areas. My results also suggest there may be a lag between changes in herbivory regime and tree encroachment. Overgrazing often occurs during dry periods (i.e., multi-year drought conditions) and increases the proportion of bare ground. Therefore, optimal conditions for sapling recruitment could occur during above-average rainfall periods that follow long drought periods.

I also found that the direct effects of wildlife browsing were small compared to the indirect effects of wildlife via intraspecific neighbor tree competition. The highest sapling growth occurred where neighbor trees were absent, a condition maintained primarily by elephant browsing. High sapling growth coincided with reductions in large neighbor tree density caused by wildlife. This suggests that increases in tree cover may occur during above-average rainfall periods where wildlife populations have recently declined, or where chronic overgrazing has preceded high rainfall. These effects may be greatest where wildlife is reduced and there are high densities of cattle (i.e., overgrazing). Conversely, conservation of wild ungulate browsers in conjunction with sustainable

livestock grazing could reduce tree cover in semi-arid savannas.

Summary: Browsing legacy effects on post-fire resprouting

The third data chapter of my dissertation was motivated by an unexpected result in preliminary analyses of chapter two data. Despite varying levels of wildlife browsing in the KLEE plots, total-stem responses of saplings (<1 m) were similar across all six post-fire herbivore treatments. Many “resprouter” species in savannas have relatively large root biomass (Jackson et al., 1996; Hoffmann et al., 2004) and mobilize non-structural carbon to replace tissues removed by fire or herbivory (Schutz et al., 2009; Poorter et al., 2010). Moderate frequency of defoliation can increase carbohydrate allocation to belowground storage vessels at the expense of aboveground re-growth (Vanderheyden & Stock, 1995; Wiley et al., 2013), leading to more available belowground carbon storage per unit of aboveground biomass. I hypothesized that 1) with increasing levels of pre-fire wildlife browsing (browsing ‘legacy’) would increase post-fire resprout potential, but that 2) concomitant levels of post-fire browsing would counteract these potential increases by removing biomass, resulting in no net differences in post-fire tree sizes among browsing levels.

To test for browsing legacy effects I experimentally separated the effects of pre-fire browsing vs. post-fire browsing on tree resprout size for sapling size class trees. I used a burn bin to top-kill saplings in each of the six KLEE herbivore treatment levels. Half of the saplings were subsequently caged to prevent post-fire browsing while the other half were left exposed to browsing. My first prediction was that for saplings (~1 m height), potential post-fire resprout size (i.e., caged) would increase with increasing

levels of “legacy” browsing intensity. My second prediction was that for 1-m saplings, there would be no differences in net post-fire resprout size (i.e., uncaged) among browsing regimes, because browsing would counteract any increases in resprouting potential associated with pre-fire browsing legacy.

Saplings that experienced a long-term browsing legacy (i.e., wildlife-present plots) indeed had larger relative growth responses (height, main-stem length and total-stem length) following fire. Saplings conditioned by pre-fire wildlife browsing legacies maintained post-fire biomass equal to unbrowsed saplings despite compound fire and browsing tissue losses. These results demonstrate that a low-severity, high-frequency disturbance legacy (i.e., wildlife browsing) can increase tolerance to high-severity, low-frequency disturbances such as fire.

Conclusions

My dissertation work has provided evidence for several mechanisms that influence sapling recruitment in semi-arid savanna systems: positive feedbacks between fire and browsing, indirect positive effects of wildlife on sapling growth that occurs via reduction in large neighbor trees, indirect positive effects of overgrazing on saplings via increasing bare ground, and browsing legacy effects which increase sapling tolerance to compound fire and herbivory disturbances.

These findings provide evidence of mechanisms that influence dynamic changes in savanna tree cover. Although sapling growth and retrogression generally correspond to annual precipitation cycles (Nackley et al., 2017; Skowno et al., 2017), the processes driving sapling recruitment are complex. While some obvious processes such as fire top-

kill and browsing have direct negative effects on saplings, I have shown that indirect effects such as those of herbivory on plant-plant interactions only play out over longer time scales and only become most apparent during high precipitation periods.

Additionally I show that underlying these exogenous factors that influence sapling growth are legacy effects that can alter post-fire resprouting. This work highlights that the recruitment of individual saplings is generally a slow (>10 year) process which can be modified by the legacies of past herbivory and fire regimes, and by indirect and precipitation- dependent community interactions.

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CHAPTER 2

TREE RESPROUT DYNAMICS FOLLOWING FIRE DEPEND ON HERBIVORY BY
WILD UNGULATE HERBIVORES¹

Abstract

1. Savanna tree cover is dynamic due to disturbances such as fire and herbivory. Frequent fires can limit a key demographic transition from sapling to adult height classes in savanna trees. Saplings may be caught in a ‘fire trap’, wherein individuals repeatedly resprout following fire top-kill events. Saplings only rarely escape the cycle by attaining a fire-resistant height (e.g. taller than the minimum scorch height) during fire-free intervals.

2. Large mammalian herbivores also may trap trees in shorter size classes. Browsing herbivores directly limit sapling height, while grazing herbivores such as cattle facilitate sapling growth indirectly via grass removal. Experimental studies investigating how meso-wildlife, megaherbivores, and domestic livestock affect height of resprouts following fire are rare, but necessary for fully understanding how herbivory may reinforce (or counteract) the fire trap. In our study system, interactive fire-herbivore effects on transitions from sapling (<1 m) to adult tree (>1 m) height classes may be further influenced by plant defenses, such as symbiotic ants.

3. We used the Kenya Long-term Exclosure Experiment (KLEE) to investigate how post-fire resprout size of a widespread monodominant East African tree, *Acacia*

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drepanolobium was influenced by 1) herbivory by different combinations of cattle, meso-wildlife (15–1000 kg), and megaherbivores (>1000 kg) and 2) the presence of acacia-ant mutualists that confer tree defenses. We sampled height, stem length, and ant occupant of resprouts exposed to different herbivore combinations before and after controlled burns.

4. Resprout height of saplings that were short prior to fire (<1 m) was reduced primarily by meso-wildlife. Negative effects of elephants on post-fire resprout height increased with pre-fire tree size, suggesting that resprouts of the tallest trees (with the greatest potential to escape the fire trap cycle) were preferentially browsed and reduced in height by elephants. There were no significant cattle effects.

5. *Synthesis.* We provide experimental evidence for two potential pathways through which large herbivores exert control over sapling escape from the fire trap: 1) post-fire meso-wildlife browsing of short (<1 m) resprouts and 2) elephant browsing of the largest size class of resprouts, which would otherwise be most likely to escape the fire trap.

INTRODUCTION

Tree cover and density are fundamental properties of savannas that affect many ecosystem processes and services, and understanding which factors influence savanna tree cover has long been a focus of ecology (Scholes & Archer 1997; House et al., 2003; Sankaran et al., 2004; Bond, 2008; Lehmann et al., 2014). In these systems, fire has been identified as a key determinant of tree cover, primarily via its influence on demographic transitions between tree life stages (Higgins et al., 2000; Langevelde et al., 2003; Staver et al., 2009; Wakeling et al., 2011; Grady & Hoffmann 2012). Frequent fires prolong the critical transition from sapling to adult size classes via a “fire trap” cycle whereby

individuals that resprout after fire fail to reach a fire resistant height (generally, taller than the flame scorch height) before being top-killed by a subsequent fire (Gignoux et al., 1997; Higgins et al., 2000; Hoffmann et al., 2009; Staver et al., 2009; VanderWeide and Hartnett, 2011; Werner & Prior, 2013; Mondal & Sukumar, 2015). Here we use “sapling recruitment” to mean the transition from sapling (<1 m) to a tree (>1 m) height class (i.e., taller than the grass layer). The term “resprout” is used to describe trees in all pre-fire size classes that were top-killed and thereby retrogressed back to the sapling stage (<1 m). Escape from the fire trap is influenced by factors such as fire behavior (Werner and Prior 2013), edaphic conditions (Bond and Midgley 2001, Grady and Hoffmann 2012, Schafer and Just 2014), and tree species traits (Bond et al. 2012, Dantas and Pausas 2013). Recently, several authors have suggested that large browsing herbivores also play an important role in delaying or preventing tree escape from the fire trap by consuming plant tissues that would otherwise attain a fire resistant height (Sankaran et al. 2013, Staver and Bond 2014). However, there has been little experimental investigation of how different types of herbivores influence escape from the fire trap (but see Staver et al. 2009).

Negative effects of elephants on tree cover may be amplified by fire (Okello et al. 2008, Pellegrini et al. 2017). For example, elephant damage prior to fire reduces post-fire tree survival and recovery (Shannon et al. 2011, Vanak et al. 2012), and large trees weakened by fire damage experience increased rates of elephant toppling (Asner and Levick 2012, Levick et al. 2015, Pringle et al. 2015). Elephants also can limit sapling recruitment by trampling (Cumming & Cumming, 2003) and/or directly consuming

tissues <1 m (Legendijk et al., 2011), effects that could be magnified in burned areas (Dublin, 1986) but remain untested.

The impacts of meso-wildlife (15-1000kg) on tree cover, too, may be amplified following fire. Many wildlife species preferentially forage in burned sites (Sensenig et al., 2010), and post-fire wildlife browsing can reduce tree and shrub cover (Andruk et al., 2014; Silva et al., 2015; Rhodes et al., 2017). Meso-herbivore browsers directly suppress tree height and biomass (Augustine & McNaughton, 2004; Sankaran et al., 2013; Staver & Bond, 2014), and decrease height:stem diameter ratios (Moncrieff et al., 2011), which could delay demographic transitions out of the short, multi-stemmed, and fire-vulnerable ‘sapling’ size class, into single-stem, high canopy and fire resistant heights (Okello et al., 2001). Grazing herbivores – either wild or domestic – on the other hand, can indirectly facilitate woody sapling growth by reducing grass competition and increasing available resources (Scholes & Archer, 1997; Riginos & Young, 2007; Palmer & Brody, 2013).

Theoretical models have examined how different types of herbivores (e.g. grazing vs. browsing) could interact with fire to produce long term changes in tree cover (Higgins et al., 2000; van Langevelde et al., 2003; Baxter & Getz, 2005; Holdo, 2006; Holdo et al., 2009; De Michele et al., 2011; Holdo et al., 2013). However, absent from these models are the processes by which different types of herbivores influence the development of fire resistance traits such as “escape” height (Osborne et al., 2018). To our knowledge, there are no experimental studies quantifying the potentially interactive effects of megaherbivores, meso-wildlife, and cattle on post-fire resprout height or potential for escape from the fire trap.

An added layer of complexity in understanding post-fire tree responses to herbivory is the potential for plant defenses to influence herbivory. Investments in plant defense have been shown to decrease in some acacia species when resprouting after fire (Vadigi & Ward, 2012). In our study system the dominant tree, *Acacia drepanolobium*, has evolved an ant mutualism to defend against browsing ungulates (Palmer & Brody, 2013). Because *A. drepanolobium* ant occupancy is closely correlated with growth and browse damage for individual saplings (Riginos & Young, 2007), the post-fire resprouting phase, when ant colonies are reduced or absent, may render trees even more vulnerable to browsing. We hypothesized that since fire reduces ant mutualism defense in *A. drepanolobium* (Kimuyu et al., 2014; Sensenig et al., 2017), it should therefore increase vulnerability of resprouts to browsing and ultimately delay the transition to fire resistant height classes.

Here we used the Kenya Long-term Exclosure Experiment (KLEE) (Young et al., 1997a) to investigate how fire, herbivory regime, and ant defenses affect post-fire resprout size of a widespread monodominant East African tree, *A. drepanolobium*. We predicted that 1) post-fire resprout height would be increased by cattle and reduced by meso-wildlife and megaherbivores, and 2) presence of ant mutualists would increase height (and therefore fire resistance) of resprouting trees.

METHODS

Study site

This research was carried out at the Mpala Ranch and Conservancy (0°17'N, 36°52'E; 1800m asl) in an *A. drepanolobium* (“whistling thorn”) wooded savanna in the

Laikipia District, Kenya. Mean annual rainfall is 580 mm/year and occurs in a weakly tri-modal pattern with major peaks in April–May and November, a minor peak in July. The study site is situated on a flat plateau underlain with deep clay-rich vertisol (‘black cotton’) soils. *Acacia drepanolobium* occurs as a mono-dominant shrub or dwarf tree on vertisol sites throughout East Africa (Ross, 1979; Deckers et al., 2001). This species is highly adapted to fire with relatively thick bark (Midgley et al., 2016) and strong post-fire resprouting (Okello et al., 2008). It is the most widespread myrmecophyte tree in East Africa (Ross, 1979), producing domatia (swollen thorns) and extrafloral nectaries that provide food rewards to ants (Young et al., 1997b). These ant species include *Crematogaster mimosae* (Cm), *Crematogaster nigriceps* (Cn), *Crematogaster sjostedti* (Cs), and *Tetraponera penzigi* (Tp), which provide varying levels of protection against browsing insects and mammalian herbivores including elephants (Young et al., 1997b; Palmer et al., 2010).

The Mpala Ranch and Conservancy is managed for both wildlife conservation and livestock production. Cattle are stocked at low to moderate densities (0.10 - 0.15 cattle ha⁻¹), although they outnumber native ungulates (Veblen et al., 2016). The meso-wildlife community includes grazers (e.g. plains zebras [*Equus burchelli*], Grevy's zebra [*Equus grevyi*], hartebeest [*Alcelaphus buselaphus*], Cape buffalo [*Syncerus caffer*], and oryx [*Oryx gazella*]), as well as browsers and mixed feeders (e.g. Grant's gazelles [*Gazella granti*] and eland [*Taurotragus oryx*]). The two megaherbivores in the system are browsing giraffes (*Giraffa camelopardalis*, which do not feed on saplings) and mixed feeding elephants (*Loxodonta africana*). For herbivore abundances in KLEE see Veblen

et al. (2016). Prior to our (and other) experimental burn treatments (described below), fire had not been an active part of the study site since the 1970s (Sensenig et al., 2017).

Experimental design

We monitored the size-dependent response of trees top-killed by prescribed fire and subsequently exposed to herbivory by different combinations of cattle, meso-wildlife (15–1000 kg), and megaherbivores (elephants). We accounted for the natural presence (or absence) of ant-mutualists to determine whether plant defenses mediated the effects of specific herbivore groups on post-fire resprout height.

The Kenya Long-term Exclosure Experiment (KLEE) was established in 1995 (Young et al., 1997a). Semi-permeable fencing is used to control access by meso-wildlife (large mammals 15–1000 kg, “W”) and megaherbivores (elephants and giraffes, “M”), and herding is used to control access by livestock (cattle, “C”). Each of three blocks (North, Central, and South) contains six 200 x 200 m (4 ha) herbivory treatment plots (total of 18 plots). Naming conventions for the six plot types — MWC, MW, WC, W, C, and O — denote which herbivores are present within a given treatment, e.g. MWC = all large herbivore groups present and O = no large herbivores present (Appendix A).

Steenbok (*Raphicerus campestris*), small (12kg) ungulate browsers, are present within all plots, as are rodents mostly *Saccostomus mearnsi* (Keesing, 1998). Cattle are herded into C, WC and MWC plots typically 6-8 times per year to maintain a grass utilization rate comparable to the surrounding rangeland. The timing and number of grazing days largely depends on forage production (i.e., seasonal precipitation). The KLEE grazing regime is

representative of stocking densities and grazing frequency used on large cattle ranches in Laikipia (Odadi et al., 2007).

One 30 x 30 m (0.09 ha) subplot within each of the 18 KLEE plots was burned during a three-day period in February 2013 (see Kimuyu et al., 2014 for details). Prior to burning each subplot, all *A. drepanolobium* trees were labeled with aluminum tags, and measurements of height, stem diameter, and ant occupancy were recorded. After 18 months we re-measured all trees that had been top-killed by the fire treatments and were resprouting from live belowground tissues in 3-6 belt transects (30 x 5 m) per plot (n=755 resprouting trees). We recorded ant species occupancy, tree resprout height (max height of live tissue) and total stem length (sum length of all live stems and branches; sensu Okello et al., 2001; Riginos & Young, 2007).

Data analysis

For tree resprout height and total stem length, we tested factorial combinations of cattle (two levels: present “C” vs. absent “O”) and wildlife (three levels: all wildlife absent “O”, only meso-wildlife present “W”, or both meso-wildlife and megaherbivores present “MW”), as well as effects of pre-fire tree height and post-fire ant species occupancy (four levels: none, Cn, Cm, Cs). We excluded from analysis data for resprouts occupied post-fire by the ant mutualist *Tetraponera penzigi* due to low abundance following the fire: Tp occupied only 17 out of 755 top-killed trees (2.3%). This low post-fire abundance is consistent with previous reports of *Tetraponera* mortality during fire (Kimuyu et al., 2014) and low post-fire *Tetraponera* recruitment (Sensenig et al., 2017).

Data were analyzed in a blocked split-split plot design with herbivore treatment plots as the whole plot units nested within blocks. The six herbivore treatments comprised fixed effects factors which were randomly assigned to whole plots. Trees within a plot were clustered as “tree-sets”, such that each tree-set was associated with one level of ant occupancy (none, Cs, Cn, or Cm). These tree-sets served as the split plot units; ant occupancy was the split-plot fixed effects factor assigned to these tree-sets. Individual trees within sets were the split-split units, with pre-fire tree size measured on each tree as a fixed effects continuous covariate.

We used generalized linear mixed models to do separate analyses of resprout height and total stem length response. For each model, fixed factors included wildlife (O, W, MW), cattle (O, C), ant occupancy (none, Cs, Cn, Cm), and pre-fire tree size. Because fire resistance in *A. drepanolobium* is primarily a function of height (Okello et al., 2008), we used pre-fire height (which was highly correlated with pre-fire stem diameter, $r = 0.8$) as a covariate to account for size-dependent response. The random effects structure included intercepts for block, plot (nested in block), and tree-set (nested in block and plot). For each response variable, we fit three candidate models to test hypothesized interactions among wildlife, cattle, ant, and pre-fire tree size. These included a global model examining all possible interactions (4-way interaction), a reduced 3-way interaction model including wildlife*ant*pre-fire height, and our *a priori* hypothesis model including 2-way interactions among cattle*wildlife, ant*wildlife, ant*pre-fire height and wildlife*pre-fire height. We retained cattle*wildlife and ant*wildlife interaction terms in all models to test *a priori* hypotheses. We fit candidate models using maximum likelihood (ML) estimation and used the small-sample-size corrected version

of Akaike Information Criterion (AICc) to select among the candidate models (Arnold, 2010). The selected models were fit using Restricted Maximum Likelihood (REML) estimation and type III F tests using the Kenward-Roger method to obtain approximate denominator degrees of freedom.

Pairwise mean comparisons of resprout height or total stem length among combinations of cattle, wildlife, and ant levels were evaluated as needed using the Tukey method to control family-wise Type I error rate. We evaluated the estimated marginal means (i.e., *ls means*) of resprout height and stem length at the pre-fire tree height of 1 meter. For visualization of interactions involving trees over a range of pre-fire heights, we estimated marginal means at several values of pre-fire height (20, 100, 200, 300, and 400 cm). For the resprout height model, we constructed *post hoc* pairwise tests to compare the effect of pre-fire height among the three wildlife treatment levels. We considered differences among factors to be significant at the $p < 0.05$ level. In all analyses, we log transformed post-fire height and post-fire stem length to better meet normality, homogeneity of variance, and linearity assumptions. The pre-fire height covariate was log-transformed and centered on its overall mean value to improve interpretability of the main effects.

In order to qualitatively compare herbivory effects on growth of burned vs. unburned trees, we conducted similar analyses on unburned trees (Appendix B).

RESULTS

Post-fire tree height

We monitored the response of 738 top-killed trees whose pre-fire heights ranged from 4 cm to 512 cm (mean = 81 cm, median = 50 cm). Live resprouting stem tissues originated from the base of charred tree skeletons/stumps near the soil surface (we found no epicormic resprouting). The height of the resprouts 18 months post-fire ranged from 4 cm to 103 cm (mean = 26 cm, median = 24 cm).

Height of resprouts eighteen months post-fire was negatively affected by all combinations of herbivore treatments that included wildlife (“W”, “WC”, “MW”, “MWC”) relative to the no-herbivore (“O”) treatment (Fig. 2.1, Table 2.1). Height reductions in cattle only treatment (“C”) were not significantly different from no-herbivore or any treatment that included wildlife (Fig. 2.1), but cattle were significant overall (Table 2.1). At a pre-fire height of 100 cm (the height at which we chose to make means comparisons), the addition of megaherbivores did not appear to reduce resprout height more than the effects of wildlife alone. However, when evaluated across all pre-fire tree heights, resprout height was positively related to pre-fire height (Fig. 2.2) – a relationship that differed significantly among wildlife treatment levels (log(pre-fire height) * wildlife interaction; $F_{(2, 712.2)} = 5.53$ $p = 0.004$; Fig. 2.2, Table 2.1). In particular, megaherbivore presence diminished the positive effect of pre-fire size compared to no-wildlife and meso-wildlife treatments (O vs MW slope contrast; $p = 0.001$, and W vs MW slope contrast; $p = 0.008$, Fig. 2.2). The negative effects of megaherbivores (i.e., the difference between MW and O) became more pronounced as pre-fire tree size increased.

Although we did not perform a true statistical test of the fire*wildlife interaction a supplemental analysis of unburned trees suggests effects of wildlife browsing were less pronounced in the absence of fire (Appendix B).

Resprout height eighteen months post-fire was positively associated with presence of defensive ants, regardless of ant species. After controlling for other variables estimated marginal means for ant-occupied trees were 6-9 cm (24-37%) taller than unoccupied trees at pre-fire height = 100cm (Fig. 2.3). Ant occupancy status and relative proportion of trees in each ant level changed between pre- and post-fire sampling periods (Table 2.2). The proportion of unoccupied trees increased (+24%) as did the proportion of trees occupied by the ant Cm (+42%). The proportion of trees occupied by the remaining ant species decreased after fire: *Tetraponera* (-86%), Cs (-20%) and Cn (-10%) (Table 2.2).

Post-fire stem length

Resprout stem length was positively associated with pre-fire tree height and ant occupancy (Table 2.3, Fig. 2.4), although there were no significant differences in predicted stem length among ant species (means and confidence limits estimated at pre-fire tree height = 100cm and back transformed: none= 213 cm [+14, -14], Cs= 377 cm [+34, -31], Cn = 351 cm [+39, -34], and Cm = 343 cm [+25, -23]). We did not find evidence that herbivore treatment significantly affected post-fire stem length (Table 2.3).

DISCUSSION

Several authors have suggested that, together, fire and herbivory decrease sapling recruitment rates, thereby decreasing savanna tree cover and density (Dublin et al., 1990, Scholes & Archer, 1997; Staver et al., 2009; Morrison et al., 2016). Using experimental

fires within a long-term herbivore exclusion experiment, we performed the first empirical test of how factorial combinations of cattle, meso-wildlife, and megaherbivores affect resprout size following fire. We found clear evidence that a wide range of tree height classes re-sprout after being top-killed by fire and are subsequently kept short primarily by large mammalian herbivores. We also found evidence that, by suppressing the height of the largest re-sprouts, elephants prolong susceptibility to future fire top-kill events, which could prevent saplings from escaping from the ‘fire trap’. An important element of our experimental design is that trees were subject to a given herbivore treatment both before (i.e., KLEE herbivory treatments initiated 18 years prior to burn treatments, see Methods) and after fire. As such, rather than isolate post-fire effects of any given herbivore type, our study provides important information on how long-term herbivore regimes influence resprout responses following fire (and indicates that herbivore effects on growth differ between burned and unburned trees; see Appendix B).

Herbivory effects on post-fire resprout height

We found that meso-wildlife, regardless of presence of megaherbivores, showed the strongest negative effects on saplings that were small (1 m) before top-kill. This is likely because resprouting tissues are most accessible to meso-herbivores. Meso-wildlife driven reductions in sapling height are consistent with previous work demonstrating that meso-wildlife browsers limit tree height both in the absence of fire (Augustine & McNaughton, 2004; Moncrieff et al., 2011; Sankaran et al., 2013; Moncrieff et al., 2014) and during resprouting following fire (Andruk et al., 2014; Silva et al., 2015; Rhodes et

al., 2017). We found the effects of meso-herbivores were greater in magnitude on burned than unburned trees (Appendix B).

Our work goes a step further than previous work and provides quantitative evidence that, following fire, heights of the largest resprouting stems (>1 m pre-fire height) are reduced by elephants. We found that elephant presence diminished the positive effect of pre-fire tree height on post-fire resprout height (*sensu* Grady and Hoffmann 2012; Schafer & Just, 2014), and the suppressive effects of elephant presence strengthened as pre-fire tree size increased. These results are consistent with evidence from our study system that elephant presence (Odadi et al., 2017) and density of elephant-damaged trees (Pringle et al., 2015) are greater in burned than unburned areas. Others have found that, elsewhere, elephant tree damage frequency increases with tree diameter (Holdo, 2006) and diverse herbivore assemblages that include megaherbivores such as elephants drive long-term declines in semi-arid savanna tree density (Staver et al. 2009; Pellegrini et al., 2017). Here we have provided quantitative evidence that elephants limit the height of the largest (most capable of rapid growth following fire) resprouts, which are those otherwise most likely to escape the fire trap cycle (Wakeling et al., 2011).

The presence of ant mutualists was associated with increased resprout height. Following fire, individuals that were occupied by ant mutualists of any species were taller than unoccupied resprouts, consistent with results of previous studies reporting ant presence confers defense against browsing (Palmer & Brody, 2007). An alternative interpretation of these latter results, however, is that ants preferentially colonized the tallest or healthiest resprouts post-fire (*sensu* Palmer et al., 2000) which offer greater

nectar rewards and more domatia. Indeed, for a given pre-fire tree size, ant-occupied resprouts had higher post-fire stem length (biomass) than unoccupied resprouts, suggestive of greater ‘health’ (Fig. 2.4). Only future studies of ant colonization dynamics can elucidate the level of herbivore defense conferred by ants following fire. The present study cannot rule out the possibility that other factors such as plot size or proximity to unburned ant colonies drove changes in ant occupancy.

Cattle presence did not increase resprout heights (e.g. via reduction of grass competition) as we had expected (Fig. 2.1, Table 2.1). Reduced abundance of ant-occupied resprouts following fire (Table 2) as well as decreased worker ant density (Sensenig et al., 2017) may have left resprouting plant tissues vulnerable to consumption by cattle. Similarly, new resprouting tissues may have been more vulnerable to cattle due to the absence of physical defenses (i.e., new unlignified spines), compounded by the low concentrations of polyphenolics and tannins in young *A. drepanolobium* leaves (Rubanza et al., 2005), though an extensive diet study (in unburned habitat) found no evidence that cattle consume *A. drepanolobium* (Odadi et al., 2007). We suggest several other potential reasons that cattle did not increase tree height as we had expected, and may instead have reduce it: 1) by reducing grass cover, cattle may have increased the apparency of resprouts to wild ungulate browsers (Riginos & Young 2007), in particular steenbok, which are small browsers that have access to all KLEE plots; 2) grass reduction by cattle may have indirectly increased stress from the physical environment, for example by increasing evaporative demand (Maestre et al., 2003; Palmer et al., 2017); or 3) cattle may have trampled resprouting tree tissues (Cumming & Cumming 2003).

Herbivory effects on post-fire biomass

Resprout size often scales with pre-disturbance tree size (Young & Francombe 1991; Grady & Hoffmann 2012; Schafer & Just 2014) due to factors such as root carbohydrate reserves (Schutz et al., 2009) or root depth and surface area (Nolan et al., 2014). Accordingly, we found that total stem length of resprouts, a proxy for above-ground biomass, was strongly associated with pre-fire height. We expected to find negative effects of wildlife on total stem length due to post-fire browsing, but did not find significant differences in total stem length among herbivory treatments, perhaps because heavily browsed trees can exhibit compensatory growth (Gadd et al., 2001; Fornara & du Toit 2007; Riginos & Young, 2007). It is possible that “legacy effects” of pre-fire herbivory (Johnstone et al., 2016) in KLEE plots have influenced our post-fire herbivory results; greater pre-fire browsing intensity may confer greater potential for compensatory growth following top-kill by fire (LaMalfa unpublished data).

We also expected stem length and heights of resprouting trees to respond to herbivory in similar ways, but found two primary differences. First, post-fire browsing by wildlife decreased resprout height but had no significant effect on stem length. This could have occurred because the vertical height lost to browsing takes longer to replace due to delayed activation of a new apical meristem (Moncrieff et al., 2014), whereas unbrowsed lateral branches continue to elongate horizontally. Second, cattle had no measurable effects on total stem length but appeared to decrease resprout height following fire. We had expected that, by removing grass, cattle would increase resource availability and thereby increase tree biomass. However, we did not find evidence that grass removal by cattle increased tree biomass or offset any negative effects of cattle on height.

CONCLUSIONS

In the last century changes in savanna vegetation structure and function have occurred as cattle have increasingly replaced native herbivores (du Toit & Cumming, 1999) and altered fire regimes (Roques et al., 2001). Understanding how different types of large herbivores affect post-fire resprout size is important for predicting vegetation response to fire regimes across differing large herbivore assemblages (Bond, 2008; Staver et al., 2011; Dantas & Pausas, 2013; Lehmann et al., 2014). Our results support the assertions of other authors that over long time scales and many fire cycles, the presence of wild browsing ungulates, both meso-wildlife and elephants, combined with fire creates a positive feedback that reduces or maintains low sapling recruitment (Dublin et al., 1990; Staver et al., 2009; Staver & Bond, 2014). Our study uniquely parsed out how different herbivore regimes affect post-fire resprout size. We also found evidence that reductions in post-fire ant-plant defense mediate browser-driven reductions of *A. drepanolobium* height, and we provide quantitative evidence that elephants exert important controls over tree demography by targeting the largest resprouts most likely to escape the fire trap.

AUTHORS' CONTRIBUTIONS

RLS, DMK, TPY, CR, and KEV, designed and implemented the KLEE experimental burns treatments. EML, TPY, and KEV conceived the ideas and designed methodology; EML and DMK collected the data; EL analyzed the data and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA ACCESSABILITY

Data and figures archived at figshare <https://doi.org/10.6084/m9.figshare.c.3143716.v1>

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TABLES AND FIGURES

TABLE 2.1 Type – III ANOVA table for the resprout height model.

	F	Df	Df _{K-R}	p
				<
(Intercept)	2315.3	1	2.2	0.001
wildlife	6.8	2	13.8	0.009
cattle	6.9	1	9.9	0.025
				<
ant	24.1	3	58.2	0.001
				<
log(pre-fire height)	45.9	1	689.2	0.001
wildlife:cattle	1.4	2	9.8	0.287
ant:log(pre-fire height)	1.5	3	685.0	0.222
wildlife:log(pre-fire height)	5.5	2	712.2	0.004
wildlife:ant	1.6	6	48.0	0.166

TABLE 2.2 Total numbers and relative proportions of top-killed trees occupied by different symbiotic ant species pre-fire and 1.5 years post-fire, and % change pre- to post-fire, across all herbivore treatments combined. Total numbers of trees by herbivore treatments (right) where O=no herbivores, C= cattle only, W=meso-wildlife only, WC=meso-wildlife + cattle, MW=megaherbivores + meso-wildlife, and MWC megaherbivores + meso-wildlife + cattle. Fire resistant trees (i.e., those not top-killed by experimental fires) were excluded from the analysis.

Ant occupancy	ID	pre-fire		post-fire		% change	Post-fire, Ant-Herbivory Combination					
		Total # trees	Relative proportion	Total # trees	Relative Proportion	relative change pre- to post-fire	O	C	W	WC	MW	MWC
no - ants	O	328	0.43	406	0.54	0.24	62	55	96	43	90	60
<i>Crematogaster sjostedti</i>	Cs	106	0.14	85	0.11	-0.20	16	12	11	11	13	22
<i>Crematogaster nigriceps</i>	Cn	80	0.11	72	0.10	-0.10	5	10	23	12	14	8
<i>Crematogaster mimosa</i>	Cm	123	0.16	175	0.23	0.42	23	24	29	31	24	44
<i>Tetraponera penzigi</i>	Tp	118	0.16	17	0.02	-0.86	2	3	3	4	4	1

TABLE 2.3 Type – III ANOVA table for the resprout stem length model.

	F	<i>Df</i>	<i>Df</i> _{K-R}	<i>p</i>
(Intercept)	9673.6	1	3.4	<0.001
wildlife	0.3	2	15.7	0.779
cattle	0.6	1	9.8	0.451
ant	34.2	3	63.7	<0.001
log(pre-fire height)	139.4	1	699.8	<0.001
wildlife:cattle	0.5	2	9.7	0.615
ant:log(pre-fire height)	2.4	3	691.5	0.066
wildlife:log(pre-fire height)	0.7	2	715.0	0.501
wildlife:ant	1.0	6	51.9	0.428

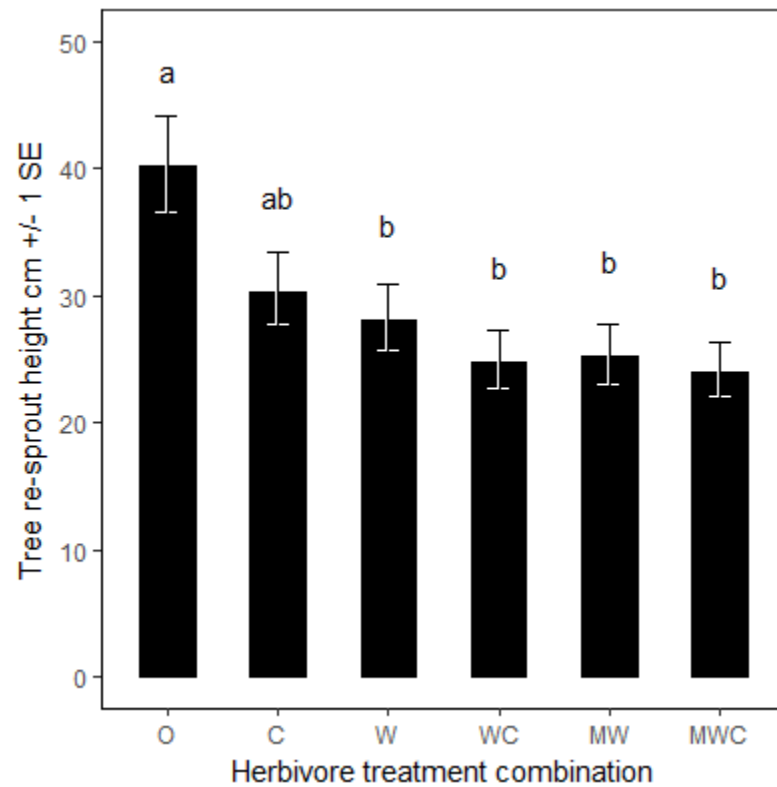


FIGURE 2.1 Post-fire resprout height of trees in different herbivory treatments. Estimated means at pre-fire height = 100 cm and averaged across levels of post-fire ant occupancy. C = cattle allowed, W = meso-wildlife allowed, M = megaherbivores allowed, and O = all large herbivores excluded. Bars not sharing letters indicate significant differences for Tukey HSD comparisons ($p < 0.05$ with Kenward-Roger degrees of freedom). Values are back transformed to the original height scale.

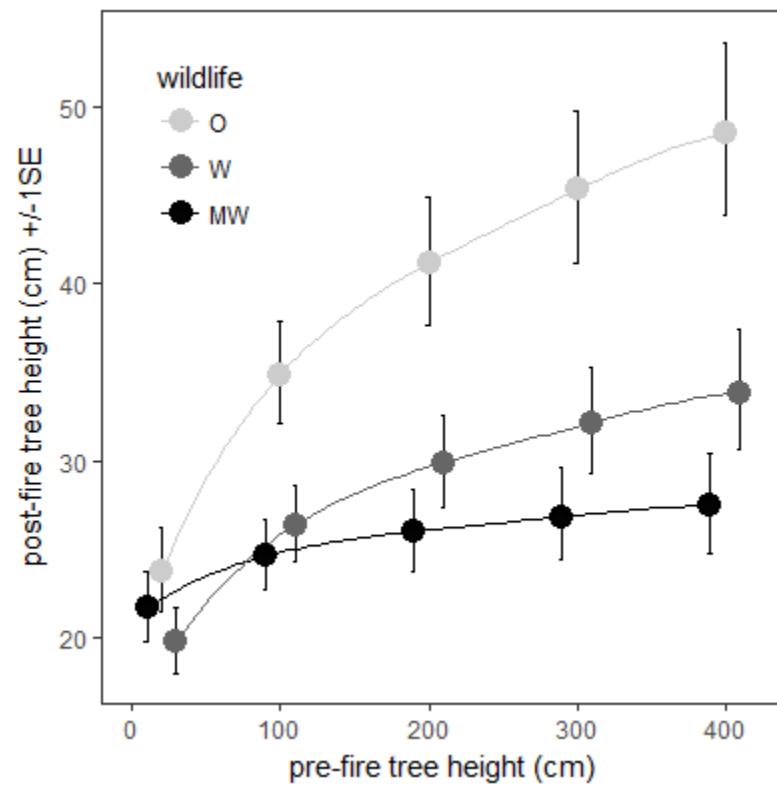


FIGURE 2.2 Fitted model height of trees exposed to three levels of wildlife herbivory: O=all wild herbivores excluded; W=meso-wildlife allowed; MW=meso-wildlife and megaherbivores (i.e., elephants) allowed. The $\log(\text{pre-fire-height}) \times \text{wildlife}$ slope coefficients were 0.17, 0.16 and 0.09, respectively for O, W, and MW treatments. Standard error bars displayed at pre-fire height = 20, 100, 200, 300, and 400 cm. Values back transformed to the original scale. Symbols are jittered along the horizontal axis to eliminate overlap.

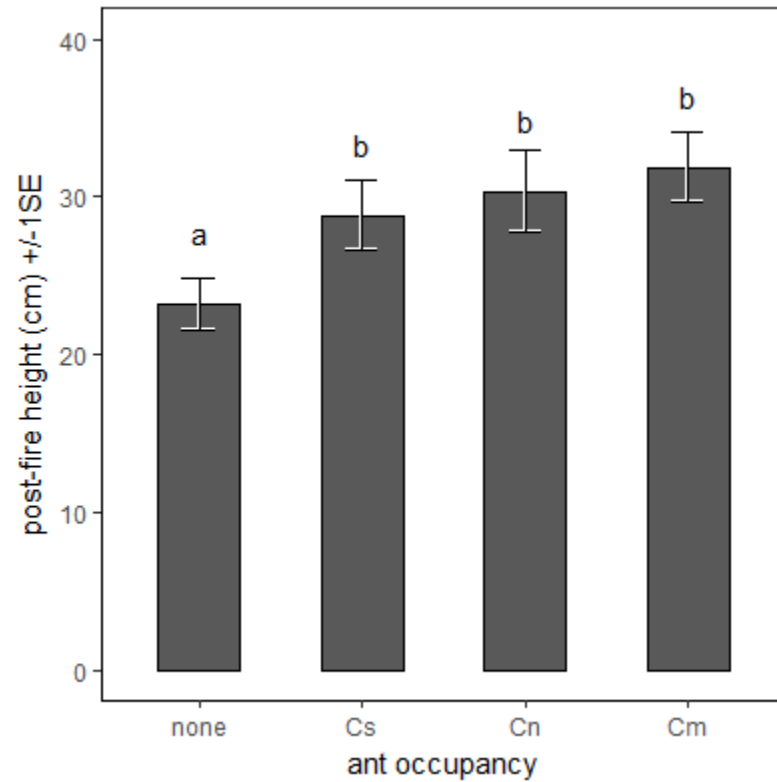


FIGURE 2.3 Post-fire resprout height among trees with different post-fire ant occupancy in order of increasing level of plant defense (0 = no ants, Cs = *Crematogaster sjostedti*, Cn = *Crematogaster nigriceps*, Cm = *Crematogaster mimosa*). Estimated means at pre-fire height = 100 cm and averaged across levels of cattle and wildlife. Bars not sharing letters indicate significant differences for Tukey HSD comparisons ($p < 0.05$ with Kenward-Roger degrees of freedom). Values are back transformed to the original height scale.

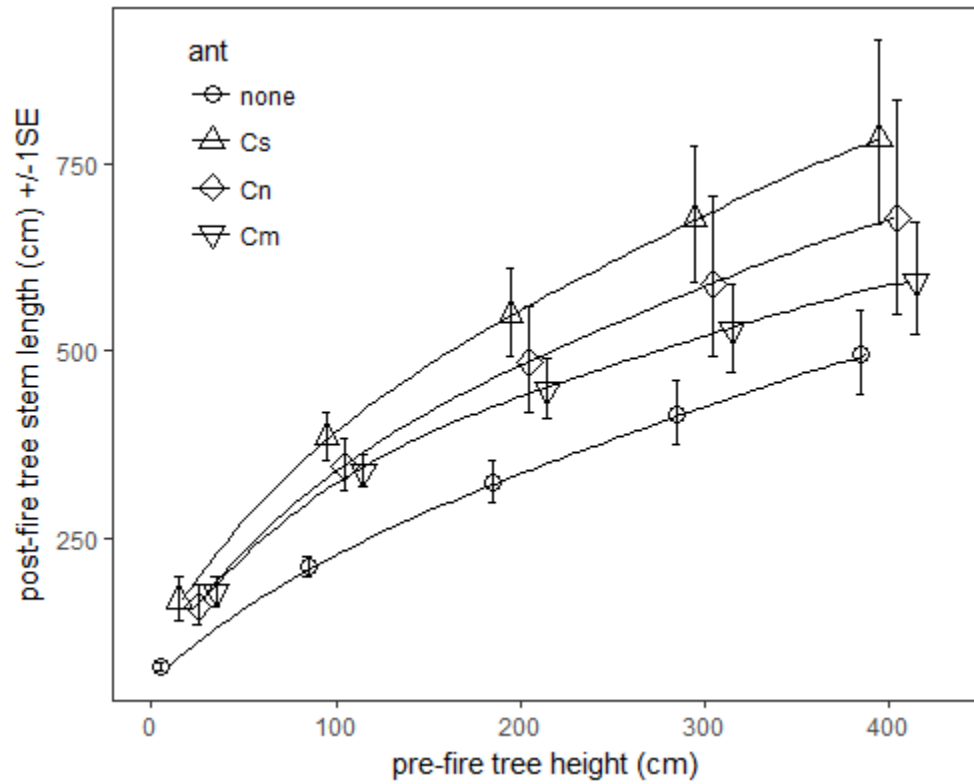


FIGURE 2.4. The effects of ant and pre-fire height on total stem length. Standard errors are estimated at pre-fire height = 20, 100, 200, 300, and 400 cm. Four levels of ant occupancy: none, *Crematogaster sjostedti* (Cs), *Crematogaster nigriceps* (Cn), and *Crematogaster mimosae* (Cm). Values back transformed to the original scale. Symbols are jittered along the horizontal axis to eliminate overlap.

CHAPTER 3

CATTLE AND WILDLIFE INDIRECTLY FACILITATE SAPLING RECRUITMENT IN AN EAST AFRICAN SAVANNA²

Summary

- 1) Savanna tree cover is limited by a recruitment bottleneck at the sapling stage. Saplings are subject to direct limiting effects of wildlife browsing and competition from adjacent grasses and trees. Saplings also can be indirectly affected by grazing herbivores, such as cattle, which feed on neighboring grasses, and precipitation can influence this relationship. Yet, few experimental studies have simultaneously quantified the effects of cattle and wildlife on sapling growth, particularly over longer time scales that encompass extended wet and dry periods. Moreover, no studies have considered an alternative pathway for indirect herbivore effects on saplings: wildlife-driven reductions of competing large neighbor trees.
- 2) We used a series of replicated 4-ha herbivore manipulation plots to investigate the net effects of wildlife and cattle on *Acacia drepanolobium* saplings over 10 years. We tested the indirect effects of cattle and wildlife on sapling growth via grass removal treatments (0.5-m radius) and neighborhood tree surveys (trees within a 3-m radius and >1 m height), respectively.
- 3) Wildlife had an indirect positive effect on saplings by reducing neighbor tree density (i.e., intraspecific competition) during the 10-year study. Saplings

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growing in the absence of neighbor trees more than doubled in both height (>40 cm 10 years^{-1}) and diameter (>10 mm 10 years^{-1}), and sapling growth decreased with increasing neighbor density. Grass removal treatments at the individual sapling scale increased sapling height (10 cm 10 years^{-1}) and diameter (5 mm 10 years^{-1}). Both grass removal and neighbor tree effects were strongest during above-average rainfall years.

- 4) In a semi-arid savanna with high variation in annual precipitation, we found that the primary effects of cattle and wildlife on sapling growth occurred indirectly via tree-grass and tree-tree interactions, respectively. Our grass removal treatments indicate that overgrazing—which increases bare ground—has the potential to increase sapling recruitment during years with above average precipitation. Rapid sapling recruitment associated with reductions in wildlife—particularly elephants—is in part due to high sapling growth rates when neighbor tree density (i.e., intraspecific competition) is low in combination with above average rainfall. Our results highlight the importance of using long-term herbivory studies to investigate sapling recruitment, which is a key demographic process controlling savanna tree cover.

Introduction

Sapling recruitment is a dynamic process in savanna systems that, if accelerated, can rapidly increase tree cover and therefore ultimately affects provision of forage for livestock and wildlife (Scholes & 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). In savannas worldwide, saplings experience a “demographic bottleneck” whereby interactions among disturbance, precipitation, and competition delay transition from the short statured (<1m) sapling to the adult (>1 m) stage (Higgins, Bond & Trollope, 2000; Hoffmann et al., 2009; Werner & Prior, 2013; Holdo, Anderson & Morrison, 2014). Determining how biotic and abiotic factors affect sapling recruitment—and ultimately woody encroachment (Bond & Midgley, 2001; O'Connor, Puttick & Hoffman, 2014) and tree cover change—is critical for conserving and managing savanna systems (Archer & Predick, 2014; Nackley et al., 2017). Yet, recruitment dynamics remain poorly understood in semi-arid systems, where several potentially interactive factors affect sapling recruitment, including overgrazing by cattle (Schlesinger et al., 1990; Riginos & Young, 2007; Seymour, 2008; Riginos, 2009; Angassa & Oba, 2010), reductions in keystone wildlife species (Hatton & Smart, 1984; Van Auken, 2000; Sankaran, Ratnam & Hanan, 2008; Daskin, Stalmans & Pringle, 2016; Stevens et al., 2017), and amount and timing of precipitation (Sankaran et al., 2005; Angassa & Oba, 2010; Naito & Cairns, 2011; Case & Staver, 2018).

Competition from neighboring grasses and trees limits the growth of saplings, and in semi-arid systems these effects are mediated via precipitation. Water is a limiting resource that constrains maximum tree cover in semi-arid savannas (Sankaran et al., 2005). Sapling recruitment is infrequent in these systems (Bond & Midgley, 2001; Staver & Bond, 2014), with the greatest recruitment occurring during above-average precipitation periods (Seymour, 2008). Tree growth responds positively to deep soil water associated with high intensity precipitation events (Berry & Kulmatiski, 2017),

longer wet seasons (Case & Staver, 2018), or increased annual precipitation (Sankaran, Ratnam & Hanan, 2008). Most sapling mortality occurs in dry periods (Fensham et al., 2017). During drought, saplings may retrogress in size due to desiccation or “top-kill” of apical stem tissue (Chapin, Schulze & Mooney, 1990; Belsky et al., 1993). Additionally, saplings can be subject to interference competition from shallow-rooted grasses when water is limited (Holdo & Brocato, 2015). Negative effects of neighbor tree density on sapling growth and survival (Veenendaal et al., 1996; Vadigi & Ward, 2012; Dohn et al., 2017) could be exacerbated by low precipitation (Riginos & Young, 2007). High rainfall variability and drought cycles in semi-arid tropical systems (Bartzke et al., 2018) result in variable sapling growth rates. This highlights the need for long-term longitudinal studies in semi-arid systems where recruitment of individual saplings is the net result of growth and shrinkage (i.e., retrogression) of aboveground structural tissues during wet and dry periods respectively.

In ungulate-rich African savannas, large mammalian herbivores can directly affect sapling growth, but these effects vary according to species-specific diets and plant responses to herbivory (Augustine & McNaughton, 1998). Browsing ungulates consume woody sapling tissues, thereby preventing or delaying sapling (<1 m) transitions to larger tree size classes (>1 m) (Sankaran, Augustine & Ratnam, 2013; Staver & Bond, 2014). Elephants browse from saplings <1 m to tree branches high in the canopy (Woolery & Jacobs, 2011), and once trees are >2 m, are a primary driver of mortality via toppling behavior (Baxter & Getz, 2005; Morrison, Holdo & Anderson, 2016). Cattle and wild mammalian grazers such as Cape buffalo and zebra, primarily consume grasses and forbs

(Kimuyu et al., 2017) and do not consume woody sapling tissues (Odadi, Young & Okeyo-Owuor, 2007).

Large mammalian herbivores can also have indirect effects on sapling recruitment. Grazing herbivores (e.g., cattle, Cape buffalo, zebra) can indirectly facilitate woody sapling growth by reducing grass competition and increasing water available to trees (Scholes & Archer, 1997; Riginos & Young, 2007; Seymour, 2008; Palmer & Brody, 2013; O'Connor, Puttick & Hoffman, 2014) and, when combined with infrequent high precipitation periods, may allow for cohorts of saplings to recruit into the adult tree stage (Seymour, 2008). Conversely, grazing can also indirectly reduce sapling growth by removing grass cover that would otherwise ameliorate abiotic stress (Riginos, 2009; Palmer et al., 2017) or reduce detection by browsing ungulates (Riginos & Young, 2007; Moser & Greet, 2018). Sapling apparency can increase as a result of abiotic (e.g. drought) or biotic (e.g. grazing) factors that reduce the height of herbaceous layer and increase sapling detection.

The most conspicuous pathway for indirect positive effects of browsing ungulates involves elephants, which can mediate tree-tree interactions in several ways. First, elephants can reduce the density of large trees by toppling, injuring (i.e., bark stripping), and browsing (O'Connor, Goodman & Clegg, 2007), which releases smaller saplings (<1 m) from intraspecific (i.e., asymmetrical) tree-tree competition (Riginos & Young, 2007; Calabrese et al., 2010). Second, large trees that are toppled by elephants often resprout (Midgley, Balfour & Kerley, 2005) and have high relative growth rate (Holdo, 2006) or exhibit compensatory growth responses to browsing (Fornara & du Toit, 2007; Riginos &

Young, 2007). Finally, tree branches and litter that result from elephant toppling can create refuges for saplings that physically inhibit browsing (Coverdale et al., 2016).

To investigate the effects of cattle, wildlife, and precipitation on long-term sapling growth in semi-arid savanna, we conducted an herbivory manipulation experiment with nested grass removal treatments during a 10-year study period marked by periods of above- and below-average precipitation. The initial results of the study were reported 2 years following grass removal treatments by Riginos & Young (2007). They found 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, 2) the net effect of wildlife was positive (possibly due to compensatory growth or low neighbor tree density). After monitoring annual precipitation, height, and diameter for an additional 8 years, we asked: 1) Do neighbor trees and grasses directly limit sapling recruitment (i.e., escape out of the grass layer), 2) Do cattle and wildlife indirectly affect saplings via their effects on neighbor grass and trees, respectively, and 3) Which of these mechanisms described affect sapling size during multi-year wet vs. dry periods?

Methods

STUDY SITE AND SPECIES

The Mpala Ranch and Conservancy, Laikipia, Kenya, is a semi-arid tropical savanna site with variable inter-annual rainfall (30 years: mean $\sim 580 \text{ mm yr}^{-1}$, range 364 - 1010 mm yr^{-1}). Our study site is within a mono-dominant stand of *A. drepanolobium*. Seven grass species and six forb species account for more than 95% of the herbaceous

cover (Young et al., 1997). *Acacia drepanolobium* accounts for 97% of woody cover at the study site. 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 & Oba, 2010). *Acacia drepanolobium* is consumed by a wide variety of insect and mammalian herbivores (Maclean et al., 2011), but an extensive diet study found no evidence that cattle consume the plant at any demographic stage (Odadi, Young & Okeyo-Owuor, 2007).

Acacia drepanolobium are a myrmecophyte typically occupied by one of four symbiotic ant species: *Crematogaster mimosae*, *Crematogaster nigriceps*, *Crematogaster sjostedti*, or *Tetraponera penzigi* (Young, Stubblefield & Isbell, 1997; Palmer et al., 2000). A large number of small saplings (<1 m) are not occupied by ants (Palmer and Young unpublished data). 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 aggressive ant mutualists (*C. mimosae* and *C. nigriceps*) can deter most ungulate browsing, but this comes at an energetic cost to the trees, as they provide carbon-rich extra-floral nectar to the ants (Palmer & Brody, 2013). Interspecific interactions between grasses and saplings can affect nectar production, sapling defense, and sapling growth (Palmer et al., 2017), but it is not clear how different ant species affect sapling recruitment, or alternatively, if various ant species preferentially occupy saplings with high growth rate.

PRECIPITATION

The 10-year study period was marked by two distinct multi-year periods of below-average (“dry period”) and above-average (“wet period”) annual precipitation. To define annual rainfall for each annual July tree survey, we used the 12-month precipitation total preceding each summer tree survey ($\text{July}_n - \text{June}_{n+1}$). The dry period began in the first year of the study (2004-2005), and precipitation was then less than the 30-year running average (580 mm year^{-1}) for five consecutive years (2005-2009). The wet period began in the sixth year of the experiment (2009-2010) and lasted four consecutive years (Fig. 3.1, 2010-2013). The last year of the study (2013-2014) was also a below-average precipitation year.

EXPERIMENTAL DESIGN

We investigated the direct, indirect, and net effects of cattle and wildlife on *A. drepanolobium* sapling growth during dry- and wet periods. For 10 years, we monitored annual changes in height and diameter for saplings growing under four long-term herbivory regimes (wild herbivores, cattle, cattle + wild herbivores, and no large herbivores). We investigated the effects of neighboring trees and grass (plant-plant interactions) on sapling growth by applying nested grass removal treatments and monitoring changes in neighborhood tree density.

Herbivore treatments

We conducted the study within the Kenya Long-term Exclusion Experiment (KLEE) (Young et al., 1997). 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 x 2 factorial design to compare the effects of both cattle and wildlife on sapling growth: no large herbivores “O”, cattle only “C”, wildlife only “MW”, and cattle + wildlife “MWC”). The O treatment is fenced to prevent wild ungulates >15 kg from accessing the plots. Small wild 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 [*Syncerus 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 4 to 6 times per year at a moderate utilization rate (Odadi, Young & Okeyo-Owuor, 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 short, persistent (sensu Bond & Midgley, 2001), individuals of unknown age, that occur within the grass layer. All saplings <0.7 m in height (short enough to have their canopies contained within the grass layer) were mapped and inventoried in one 50 x 200 m transect in each of the twelve treatment plots

in 2004. We then used stratified random sampling to select 28 saplings per plot ($n = 336$ saplings). 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 ten 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 & Young, 2007).

Grass removal treatment

Half of the saplings in each ant-occupancy by herbivore plot combination were randomly assigned to the grass-removal treatment. After wrapping selected saplings in protective plastic, glyphosate herbicide was applied to adjacent herbaceous plants growing within a 0.5-m radius (Riginos & 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 overgrazed rangelands common throughout Laikipia (Kimiti et al., 2017). In comparison, the KLEE “C” treatment (i.e., 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

At the beginning of the experiment (2004), we counted the number of neighbor trees adjacent to each sapling (trees within a 3-m radius and >1 m height: Dohn et al., 2017). We resurveyed neighbor trees a in 2017 to estimate change in neighbor tree count that occurred during the 10-year 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 n=336 saplings; 77%).

Sapling measurements

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

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 & Young (2007). These variables included factorial combinations of cattle and wildlife (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 2-way interactions with year. The random effects structure included intercepts

for block, herbivory, grass removal, 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%) because it 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 wildlife 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 2-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 was compared between two levels of grass removal and then among four levels of herbivory. We also compared the number of sapling "escapes" from the grass layer (saplings >70 cm

vs. <70 cm) among treatments. Sapling escape rates were compared: 1) between the two levels of grass removal, 2) between two levels of cattle, 3) between two levels of wildlife, 4) between all ant-occupied (Cm, Cn, Cs, Tp) vs. unoccupied (na) saplings, and 5) among four species of ant mutualists.

Results

SAPLING HEIGHT

Although herbivore treatment did not appear to directly affect sapling height (herbivory Wald χ^2 (3) = 6.12, $p=0.106$; herbivory * year Wald χ^2 (30) = 39.33, $p=0.119$; Table 1), grass neighbors, tree neighbors, and precipitation did affect sapling height. 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 (year * grass removal Wald χ^2 (10) = 53.9, $p<0.001$; Fig. 3.2a, Table 1). Control saplings (i.e., those with intact grass understory) steadily declined in height throughout the dry period and then increased during the wet period (Fig. 3.2a). The largest height increases associated with grass-removal occurred during the wet period. The net effect of grass removal was generally negative during the dry period and positive during the wet period (Fig. 3.2b).

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 (neighbor * year Wald χ^2 (10) = 47, $p<0.001$, Fig. 3.3, Table 2). During the dry period, saplings without neighbors grew taller, while saplings with neighbors were reduced in height (Fig. 3.3). During the wet period, all saplings increased in height, but the magnitude of this increase was reduced by neighbor trees (Fig. 3.3).

Analysis of plot-wide patterns in neighborhood trees indicated that number of neighbor trees declined 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 ($\sqrt{\text{neighbors}} * \text{wildlife}$ Wald $\chi^2(1) = 15.035$, $p < 0.001$, Fig. 3.4, Table 3).

SAPLING DIAMETER

In contrast to its effects on sapling height, herbivore treatment did affect sapling diameter. Wildlife presence was associated with increased sapling diameter, especially during the wet period and near the end of the study (Wald $\chi^2(27) = 54$, $p < 0.001$, Fig. 3.5, Table 2). Sapling diameter also responded positively to grass removal (Fig. 3.6) and negatively to neighbor trees (Fig. 3.7); though, unlike sapling height responses, these changes did not always clearly correspond to wet- and dry periods. The positive effects of grass removal on sapling diameter began almost immediately and increased throughout the dry- and wet periods (grass removal * year interaction Wald $\chi^2(9) = 62$, $p < 0.001$, Fig. 3.6). Diameter of control saplings with grass-present showed little to no increase over the study (Fig. 3.6). Similar to sapling height patterns, neighbor trees had a negative effect on sapling diameter, and the largest diameter changes occurred during the wet period ($\log(\text{neighbors} + 1) * \text{year}$ interaction Wald $\chi^2(9) = 28$, $p < 0.001$, Fig. 3.7). Ultimately, sapling diameter doubled in 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. Sapling mortality ranged from 10-15% 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 differences among treatments in the number of individuals that transitioned out of the persistent sapling stage ($<0.7\text{m}$) to a larger size class over the course of the study (Fig. 3.8 and 3.9). A total of 84 of 262 surviving saplings (32%) “escaped” from the grass layer (i.e., attained height $>0.7\text{ m}$; functionally reached the next demographic stage). Escape rates were higher in the grass-removal (40%) than in the grass-present (24%) treatment (Pearson's $\chi^2 (1) = 7.263$, $p\text{-value} < 0.01$). Sapling escape rates were also higher in plots where wildlife were present (MW and MWC, 42%) compared to wildlife absent (O and C, 23%) plots (Pearson's $\chi^2 (1) = 10.841$, $p < 0.01$). Most saplings that escaped (76%) were occupied by either *C. mimosae* or *C. nigriceps* ant species, which occupied the majority of all saplings by 2014 (Appendix A). Sapling escape rates were higher in all ant-occupied saplings (Cm, Cn, Cs, or Tp; 55%) compared to unoccupied saplings (no-ants; 2%) (Pearson's $\chi^2 (1) = 79.911$, $p\text{-value} < 0.001$). Escape rates were not significantly different among saplings occupied by different ant species in 2014 (Cm (57%), Cn (59%), Cs (64%) Tp (39%): Pearson's $\chi^2 (3) = 3.503$, $p\text{-value} < 0.32$), Fig. 3.8; Appendix A). We did not find significant differences in sapling escape rates between cattle-present (C and MWC, 31%) and cattle-absent (O and MW, 33%) treatments (Pearson's $\chi^2 (1) = 0.035$, $p\text{-value} > 0.85$).

Discussion

We found evidence that wildlife browsing reduced neighbor tree density, which had an indirect positive effect on sapling diameter and height growth. In savanna ecosystems, rapid growth at the sapling stage (Higgins, Bond & Trollope, 2000;

Hoffmann et al., 2009; Werner & Prior, 2013; Holdo, Anderson & Morrison, 2014) can lead to woody encroachment (Bond & Midgley, 2001; O'Connor, Puttick & Hoffman, 2014). In the absence of tree neighbors, height remained constant during the dry period and then nearly doubled during the wet period (~40 cm, 2010-2013; Fig. 3.3). Although we did not detect an effect of moderate cattle grazing, the grass-removal treatment—representative of extreme grazing utilization rates—had a positive effect on saplings. This indicates that increasing the proportion of bare ground caused by overgrazing could release saplings from interspecific competition with grass. Consistent with the early results of the same experiment (Riginos & Young, 2007), we found that grass temporarily benefited saplings, likely by reducing apparency to browsers during the onset of the dry period. Analysis of the 10-year time period, however, revealed that grass had an overwhelmingly net negative effect on sapling growth that was strongest during the wet period.

INTERSPECIFIC (TREE-GRASS) INTERACTIONS

Grass-removal had a net positive effect on sapling height and diameter over the course of the 10-year study. Sapling apparency remained high in grass-removal treatments for the duration of the 10-year experiment but fluctuated in response to precipitation in grass-present treatment (personal obs). During the first dry year (2005), the grass-removal treatment had a negative effect on sapling height compared to the control (i.e., grass-present) treatment. The grass-removal treatment likely caused an abrupt increase in sapling apparency by reducing grass height (Riginos & Young, 2007). In the following dry period heights of saplings in the control plot that were protected by

grass steadily declined until they matched the height of saplings exposed to herbivory in grass removal plots (Fig. 3.2a). Because meso-wildlife increase use of dense *A. drepanolobium* habitat during dry conditions due to forage scarcity at the landscape level (Riginos, 2015), we suspect that forage scarcity (i.e., reduced grass height caused by grazers) led to increased apparency of grass-present saplings by the end of the dry period. Although grass benefited saplings by reducing apparency to browsers during the dry period, the net effects of grass-presence (i.e., including interspecific competition) reduced sapling growth over the long-term because of reduced growth during the wet periods.

Two of our results suggest that browsing rather than abiotic (drought) stress reduced sapling height during the dry period. First, during the dry period, diameter increased while height simultaneously decreased in grass-removal saplings (i.e., saplings subject to greater apparency and vulnerability to browsing). Second, sapling diameters (but not height) also increased in the presence of wildlife during the dry period, indicating that plants were actively growing despite height reductions due to browsing. Both results are consistent with previous studies which have found that, positive sapling diameter growth despite height reductions caused by browsing or clipping (Moncrieff, Chamaille-Jammes & Bond, 2014; Vadigi & Ward, 2014).

INTRASPECIFIC (TREE-TREE) INTERACTIONS

Neighbor tree density had a negative effect on sapling height and diameter growth that was most pronounced during the wet period. Saplings growing in the absence of immediate neighbors more than doubled in both height (>40 cm 10 years $^{-1}$) and diameter (>10 mm 10 years $^{-1}$). Although saplings with high neighbor tree density increased in

height during the wet period, these increases did not offset the height loss that occurred during the dry period. High neighbor tree density suppressed diameter growth during both dry- and wet periods. Our neighbor tree results are consistent with studies that have found spatial aggregation of savanna trees (Pillay & Ward, 2012; Axelsson & Hanan, 2017) and density-dependent tree growth rates (Pillay & Ward, 2014; Dohn et al., 2017), indicative of intraspecific competition for water in semi-arid savannas. Most saplings that escaped the grass layer (>70 cm) during the study had low neighbor tree density.

HERBIVORY

Herbivory is widely recognized as a key determinant of African savanna vegetation composition and structure (Scholes & Archer, 1997; Augustine & McNaughton, 1998; Bond, 2008a). We expected to find that our moderate cattle grazing treatment would increase annual sapling growth and 10-year escape rates by reducing the competitive effects of grass (see above). However, we did not detect significant differences between plots exposed to moderate cattle grazing and the “no large herbivore” treatment plots. Our grass-removal treatment (0.5-m bare ground radius treatment), however, is a conservative estimate of “overgrazed” expansive bare ground conditions common to East Africa rangelands where *A. drepanolobium* occurs (Angassa, Oba & Tolera, 2012; Kimiti et al., 2017). The results of our grass removal treatment indicate that increasing bare ground—a condition often caused by overgrazing—has a positive effect on sapling growth in semi-arid systems.

Wildlife presence was associated with increased sapling diameter and decreased neighbor tree density from 2004 to 2017. Together these results suggest that wildlife had

an indirect positive effect on sapling growth by reducing intraspecific competition with large neighbor trees (Calabrese et al., 2010). Neighbor trees ranged in size from 1 to 4 m in height. The negative effects of wildlife on neighbor trees also increased with initial (2004) tree density (Table 3), and elephants likely were the primary cause of reduced neighbor tree density over the 10-year period. Unlike meso-wildlife that avoid dense tree cover due to predation risk, elephants prefer to browse areas of dense *A. drepanolobium* thickets (Riginos & Grace, 2008). Although both elephants and giraffe browse trees >2 m, only elephants topple the largest trees (Midgley, Balfour & Kerley, 2005). The positive effects of wildlife on saplings could, in part, have resulted from compensatory growth response to browsing (Riginos & Young, 2007) caused by previous elephant damage (Holdo, 2006). One explanation for the positive association between wildlife presence and sapling diameter growth may be largely an indirect effect of elephants reducing neighbor tree density (i.e., intraspecific competition for water).

Sapling survival was not influenced by wildlife, but presence of wildlife did increase the proportion of saplings that “escaped” from the grass layer (>70 cm). Elephant populations increased in Laikipia County from 2002 to 2012 (Ihwagi et al., 2015) during the same period when neighbor tree density declined in wildlife plots. This suggests that wildlife, especially elephants, shift the size class distribution to favor small trees and saplings that have high relative growth rates.

ANT MUTUALISM DEFENCE

Ant mutualism defense was positively associated with sapling recruitment. Across all plots, 76% of the saplings that “escaped” the grass layer by 2014 were occupied by *C.*

mimosae or *C. nigriceps*. These are the two most aggressive ant species, both of which depend on extrafloral nectar (Rudolph & Palmer, 2013). Our results are consistent with previous studies reporting that nectar-dependent ants are more likely to colonize (Palmer, Young & Stanton, 2002) and less likely to abandon (Palmer et al., 2000) saplings with high growth rates.

The nectar-feeding ant *C. mimosae* increased in plots where neighbor tree density declined (i.e., wildlife accessible plots), suggesting that relaxation of intraspecific tree-tree competition increased ant mutualism defense (Appendix A). Relaxation of neighbor tree competition for water, would have increased the number of active extra floral nectaries (Palmer et al., 2017) and amount of nectar produced (Rudolph & Palmer, 2013).

In a similar way, grass removal was also associated with increased abundance of *C. mimosae* suggesting that relaxation of interspecific tree-grass competition also increased ant mutualism defense. We found that the proportion of grass-removal saplings occupied by *C. mimosae* increased from 2004 to 2014 (Appendix A), which may be, in part, why the net effect of grass removal was positive over the 10-year period. But these results are not consistent with Palmer et al. (2017), who, in the same system, found that presence of grass neighbors increased soil moisture, nectary production, and survival of transplanted *C. mimosae* colonies. The study by Palmer et al. (2017) was conducted during the wet period (2013: 821 mm over the 40-weeks), hence, the discrepancy in our results could mean that the effects of grass neighbors on *C. mimosae* depend on precipitation. We speculate that the effects of grass presence on *C. mimosae* may become negative during dry periods due to reductions in grass height (i.e., reduced shading).

Future studies are needed to determine how the interaction between grass neighbours and precipitation affects ant occupancy dynamics in *A. drepanobuim* saplings.

Conclusions

Increases in savanna tree cover are globally widespread (Scholes & Archer, 1997; Bond, 2008b; O'Connor, Puttick & Hoffman, 2014; Stevens et al., 2017). Multiple lines of evidence indicate that supplanting wildlife with cattle has resulted in bush encroachment, but no single study has previously quantified the effects of cattle and wildlife on saplings over a time period encompassing extended wet and dry periods. During dry periods, grass removal increases growth of *A. drepanolobium* saplings (Riginos & Young, 2007). Here, by following saplings over ten years which encompassed both dry and wet periods, we found that grass-removal effects became even stronger during above-average rainfall years leading to increased sapling recruitment (i.e., escape from the grass layer). This suggests that the effects of grass competition observed on larger demographic tree stages (>1 m) during dry periods (Riginos 2009) also may be even greater during wet periods.

There will be a delay between changes to herbivory regimes and changes in tree cover. In pastoral areas, forage scarcity during drought conditions can lead to overgrazing and increase the proportion of bare ground. But that increased bare ground likely will not affect sapling growth until the drought ends and an above-average rainfall period occurs (Rietkerk et al., 2004). This mechanism is consistent with spatial patterns of bush encroachment (Nackley et al., 2017; Skowno et al., 2017) occurring over short time scales in overgrazed areas.

We posit that rapid (~20 year) tree encroachment following large wild herbivore declines is related to enhanced sapling escape rates where intraspecific competition from neighbor trees is low. Several studies have reported evidence of rapid woody encroachment following abrupt declines in large mammalian herbivores (Hatton & Smart, 1984; Prins & Vanderjeugd, 1993; Daskin, Stalmans & Pringle, 2016). We observed high sapling growth rates were associated with reduced neighbor tree densities, and presence of wildlife. Elephants reduced the number of neighbor trees >1 m primarily by size retrogression (toppling and stem breakage) rather than outright killing neighbor trees. Elephants therefore appear to help maintain a population of small saplings (coppicing from large trees) with high relative growth rates. If released from browsing these ‘persistent’ saplings contribute substantially to woody encroachment (Bond & Midgley, 2001; O'Connor, Puttick & Hoffman, 2014). Removal of wildlife should therefore result in rapid rates of sapling recruitment—bush encroachment—that approaches a maximum density constrained by edaphic site conditions (*sensu* Sankaran et al., 2005).

Human and livestock populations are projected to increase in sub-Saharan Africa and if unmanaged these changes will lead to increased tree cover and density. Our results suggest that accelerated sapling recruitment rates associated with overgrazing during drought followed by high rainfall could be exacerbated in areas with recent declines in wild browsing ungulate populations. Alternatively, management of wildlife populations in conjunction with moderate cattle stocking rates could be used to curtail increases in tree cover. Finally, our work identifies the need to further evaluate bush management as an ecosystem service conferred by megaherbivores.

Authors' contributions

CR designed and implemented the sapling experimental treatments. CR, KEV, and EML conceived the ideas and designed methodology; CR and EML collected the data; EML analyzed the data and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

Data Accessibility

Data and figures archived at figshare <https://doi.org/10.6084/m9.figshare.c.3143716.v1>

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Tables and Figures

Table 3.1. Analysis of Deviance (Type – III Wald Chi-square) height model.

	Chisq	Df	Pr(>Chisq)
(Intercept)	1511.13	1	<0.001
year	99.47	10	<0.001
log(neighbors +1)	10.29	1	0.001
herbivory	6.12	3	0.106
grass removal	0.03	1	0.872
year*log(neighbors +1)	46.98	10	0.000
year*herbivory	39.33	30	0.119
year*grass removal	53.89	10	<0.001

Table 3.2. Analysis of Deviance (Type – III Wald Chi-square) basal diameter model

	Chisq	Df	Pr(>Chisq)
(Intercept)	828.95	1	<0.001
year	80.13	9	<0.001
log(neighbors +1)	7.74	1	0.005
herbivory	11.48	3	0.009
grass removal	18.42	1	<0.001
year*log(neighbors +1)	28.59	9	0.001
year*herbivory	54.04	27	0.002
year*grass removal	62.21	9	<0.001

Table 3.3. Analysis of Deviance (Type – III Wald Chi-square) neighbor tree count model.

	Chisq	Df	Pr(>Chisq)
(Intercept)	26.03	1	<0.001
sqrt(neighbors)	28.87	1	<0.001
wildlife	2.85	1	0.091
cattle	1.15	1	0.284
sqrt(neighbors)*wildlife	15.04	1	<0.001
sqrt(neighbors)*cattle	3.17	1	0.075

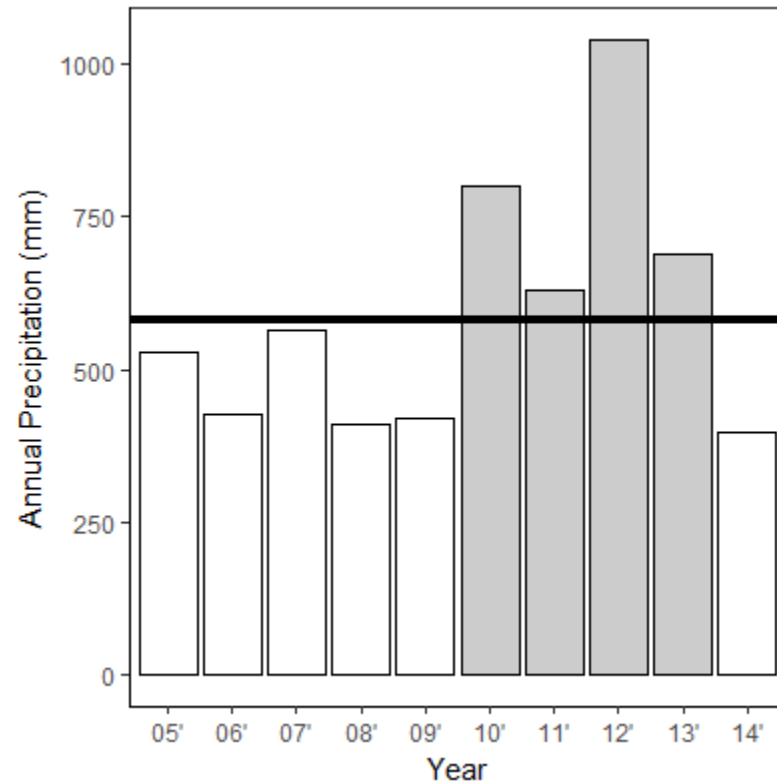


Fig. 3.1. Annual precipitation at the Kenya Long-term Exclosure Experiment (KLEE). Vertical bars represent annual precipitation for the twelve months preceding sapling measurements (i.e., July – June). The 10-year study period had distinct below-average (2005-2009, white bars) and above-average rainfall periods (2010-2013, grey bars). The horizontal black line represents the running 30-year average annual precipitation (580 mm yr⁻¹).

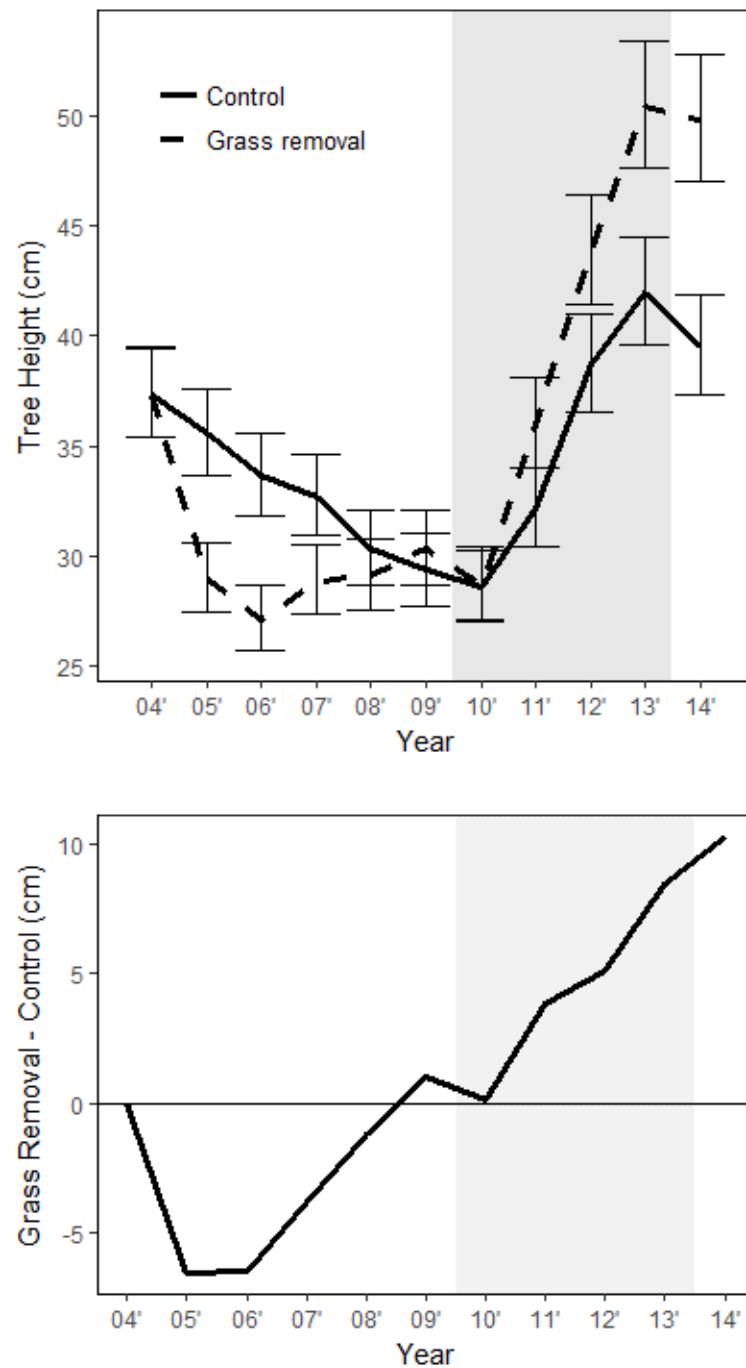


Fig. 3.2. a) Fitted model for annual height of saplings exposed to grass removal treatment (dashed line) and control treatment (solid line). Estimates are averaged over all levels of herbivory and number of neighboring trees. Mean estimates and standard error bars are back transformed to the original scale. b) Height difference between mean grass removal and mean non-removal saplings. Grey shading represents above-average rainfall period (2010-2013).

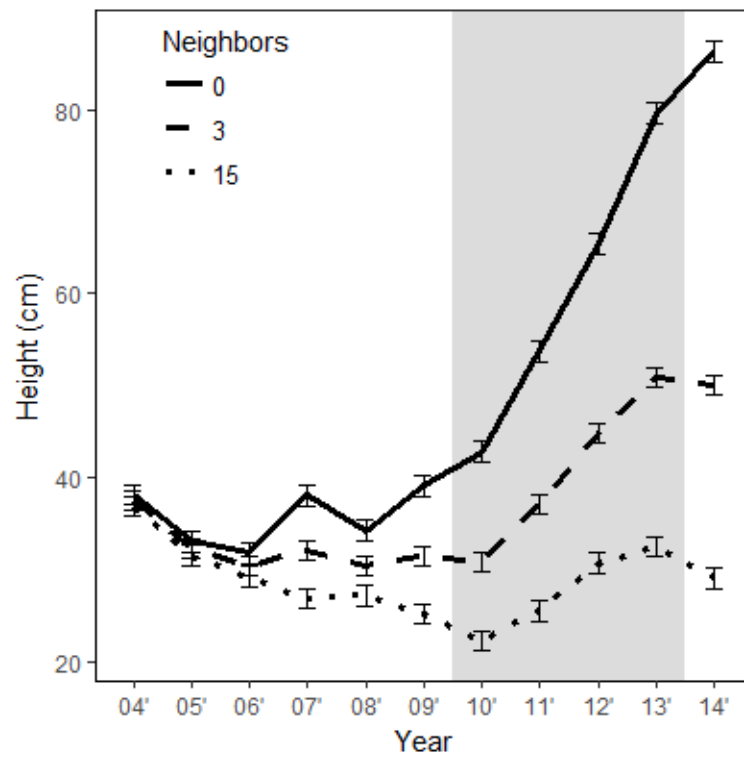


Fig. 3.3. Fitted model of annual height of saplings at three levels of the continuous covariate neighborhood tree count: 0, 3 and 15. Neighbor trees were >50 cm height, and within 3-m radius. Estimates are averaged over herbivory and grass removal treatments. Mean estimates and standard error bars are back transformed to the original scale. Grey shading represents above-average rainfall period (2010-2013).

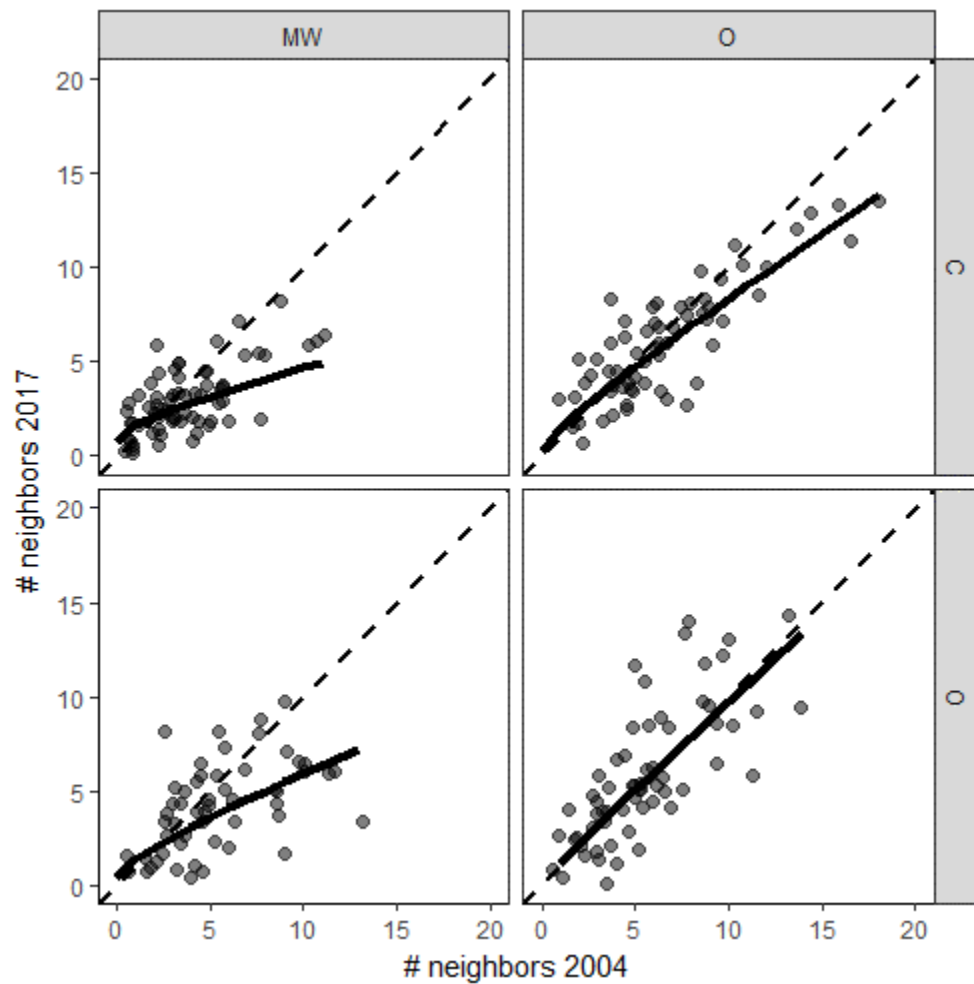


Fig. 3.4. The relationship between neighbor tree count at the beginning of the study (2004) and at the end of the study (2017) in four herbivore treatments. Panels show factorial combinations of cattle (absent = 'O' vs present = 'C') and wildlife (absent = 'O' vs. present = 'MW'). Solid line – Fitted 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 2004-2017). Points are jittered and transparent to allow for visualization of overlapping neighborhood count values.

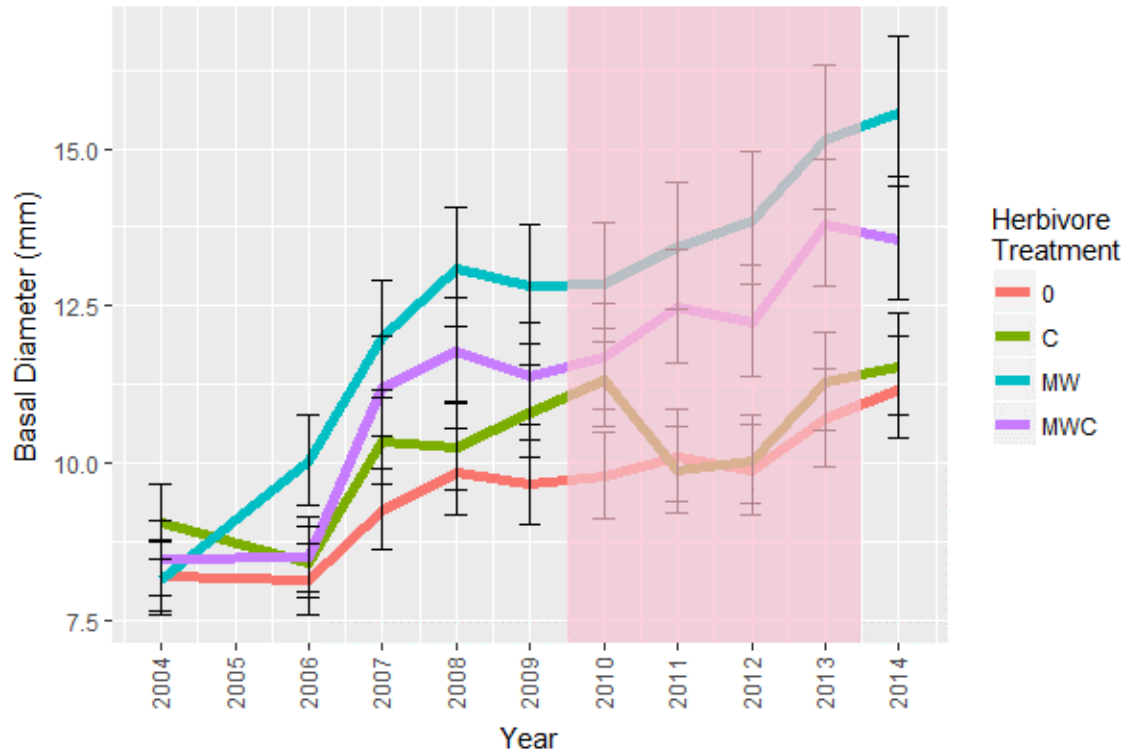


Fig. 3.5. Fitted model of annual diameter of saplings at four levels of herbivory: 0 = all large herbivores excluded; C = cattle present; MW = wildlife present; MWC = wildlife and cattle present. Estimates are averaged over neighbor tree count and grass removal treatments. Mean estimates and standard error bars are back transformed to the original scale. Grey shading represents above-average rainfall period (2010-2013).

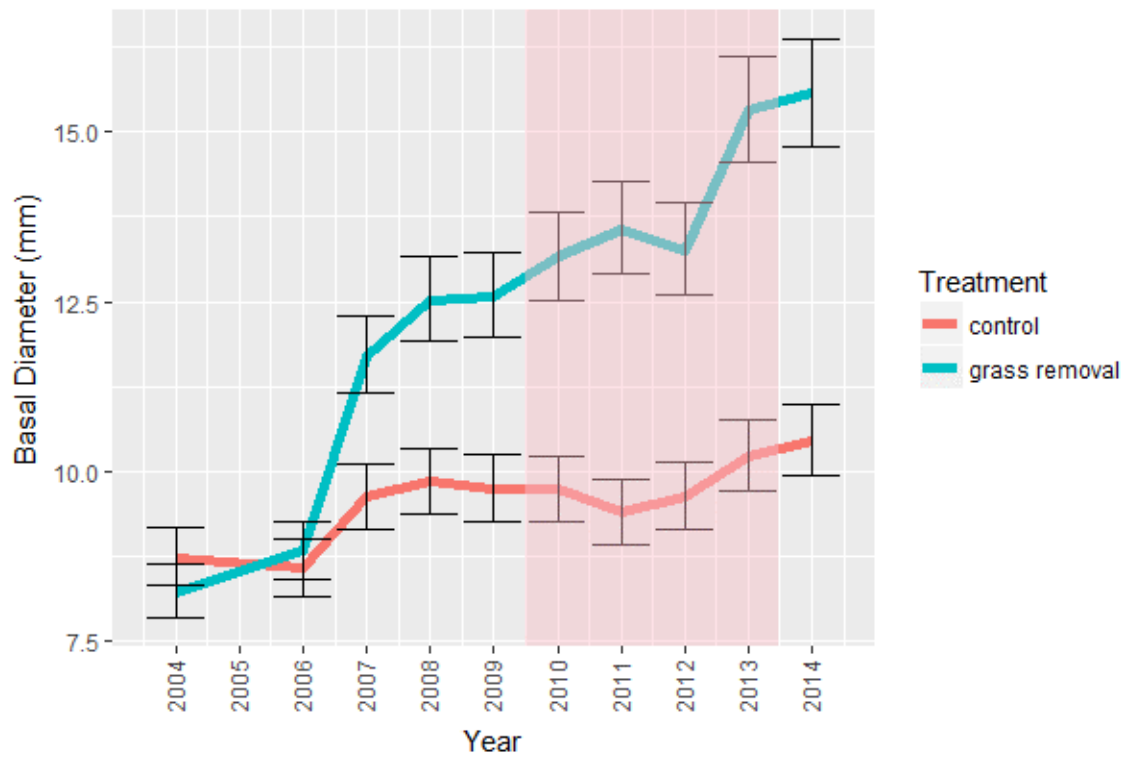


Fig. 3.6. Fitted model of annual basal diameter of saplings exposed to grass removal treatment (red line) and control saplings (green line). Estimates are averaged over herbivory and neighbor tree count. Mean estimates and standard error bars are back transformed to the original scale.

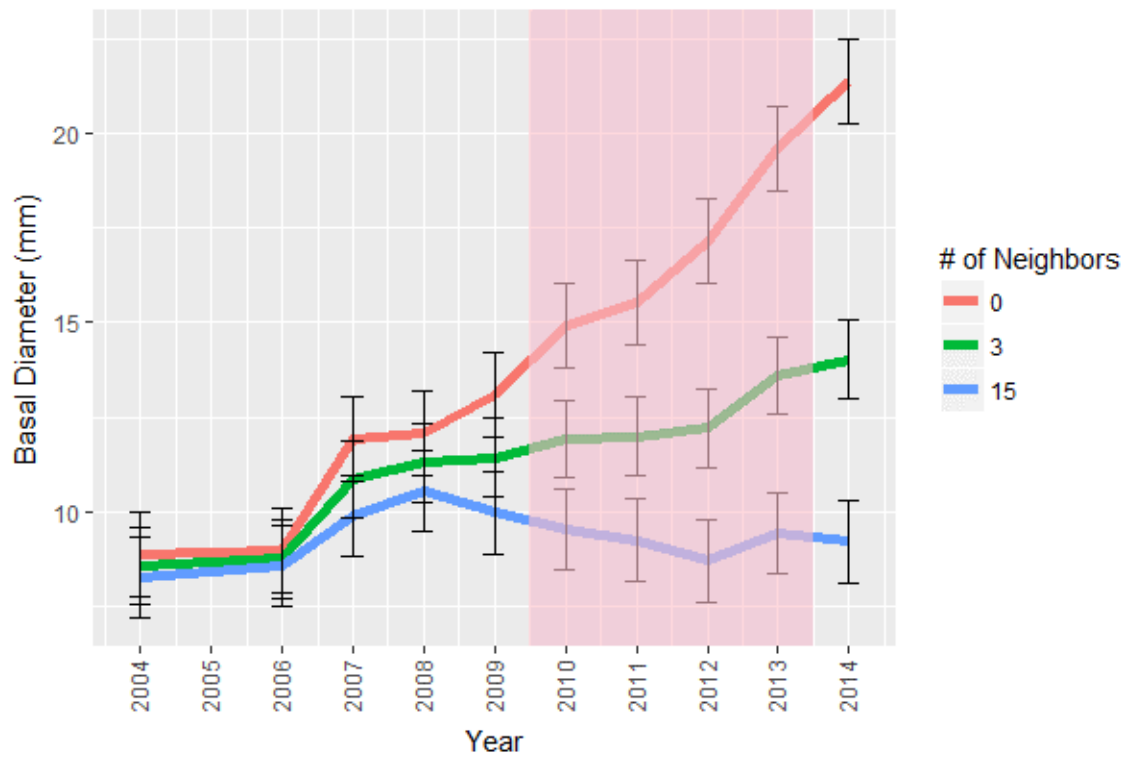


Fig. 3.7. Fitted model of annual basal diameter of saplings at three specified levels of the covariate neighborhood tree count [0 (red), 3 (green), 15 (blue). Neighbor trees were >50 cm height, and within 3-m radius. Estimates are averaged over herbivory and grass removal treatments. Mean estimates and standard error bars are back transformed to the original scale. Pink shading represents above-average rainfall period (2010-2013).

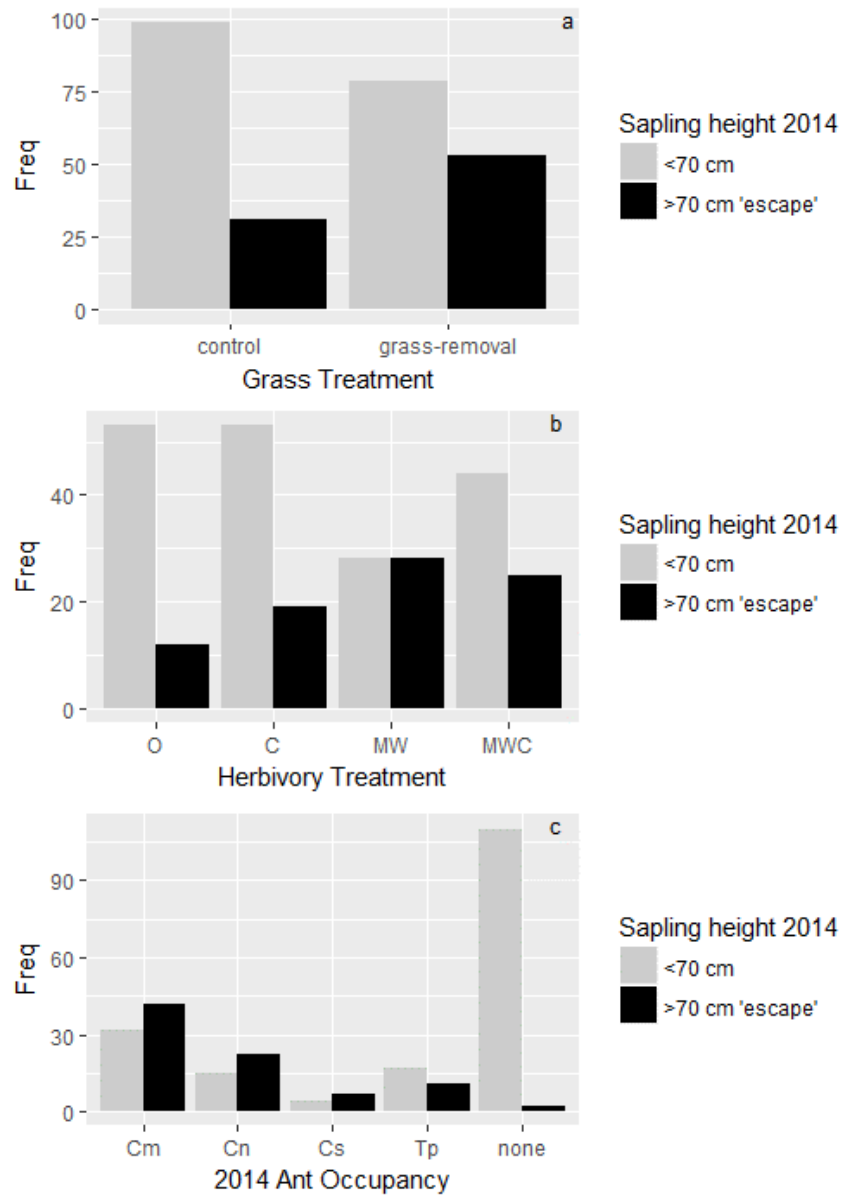


Fig. 3.8. Counts of surviving saplings that grew to >70 cm in height and those that remained <70 cm by the end of the study period in 2014. Saplings a) with grass-removed vs. control, b) in different herbivore treatments: O = all large herbivores excluded; C = cattle present; MW = wildlife present; MWC = wildlife and cattle present, and c) with different ant occupants as of 2014: *Tetraponera penzigi* (Tp), *Crematogaster nigriceps* (Cn), *Crematogaster mimosa* (Cm), *Crematogaster sjostedti* (Cs), and *unoccupied* (none). The initial height of all saplings was <0.7 m.

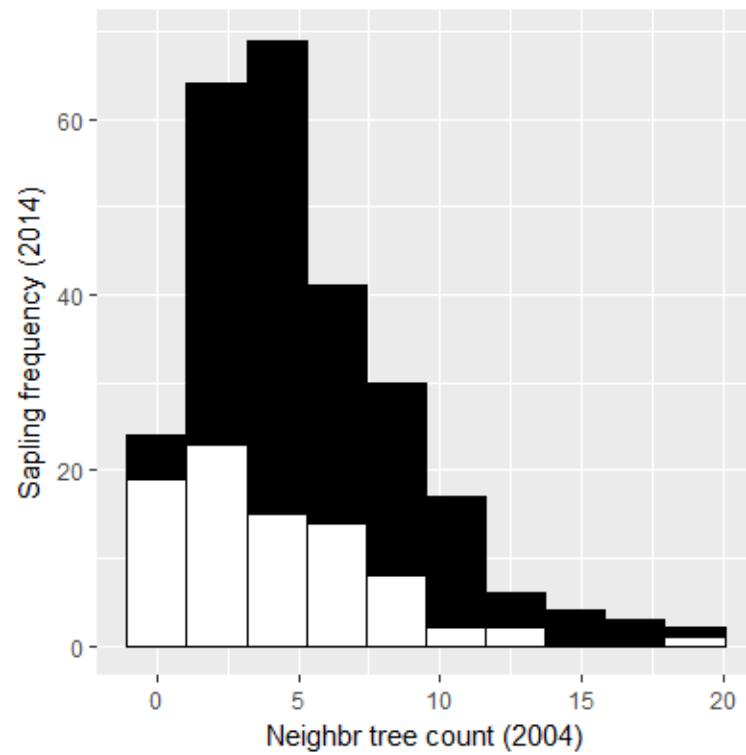


Fig. 3.9. Histogram of saplings escapes in 2014 by the number of neighbor trees in 2004. Saplings that escaped the grass layer by 2014 (white bars: >70 cm) vs. saplings that did not escape the grass layer (black: <70 cm).

CHAPTER 4

PRE-FIRE BROWSING LEGACY INCREASES POST-FIRE RESPROUT
POTENTIAL IN SAVANNA SAPLINGS³

Abstract

Savanna saplings can be “trapped” in a short (< 1 m) demographic stage due to fire and browsing pressures which both repeatedly remove aboveground tissues. Sapling growth response following one disturbance can be affected by tissue damage associated with a prior disturbance. Compounded disturbances, for example, fire followed by herbivory, may exhaust plant reserves. Alternatively, depending on the sequence and severity of disturbances, one type of disturbance may instead condition saplings to better tolerate the next disturbance. We predicted that persistent saplings (< 1 m) conditioned by 20-years of large mammalian herbivore browsing would exhibit positive growth response following top-kill by fire in an East African savanna. We investigated post-fire size responses of a widespread monodominant East African tree, *Acacia drepanolobium*, under six different herbivory “legacies” using the Kenya Long Term Exclosure Experiment (KLEE). The herbivore treatments included factorial combinations of cattle, meso-wildlife (large ungulates, 15–1000 kg), and megaherbivores (elephants and giraffes). After 20 years of controlled herbivory treatments, we used controlled burns (to achieve top-kill) and cages (to isolate and manipulate post-fire herbivory) to apply two treatments: burned-caged and burned-uncaged. Two years post-burn, we assessed sapling

³ Collaborator Kari E. Veblen

height, main-stem length, total-stem length, basal diameter, and survival of burned saplings. Compared to caged saplings that had been protected from browsing for 20 years, caged saplings with a browsing legacy grew larger (height, main-stem length and total-stem length) post-fire. Additionally, saplings conditioned by 20-year browsing legacies maintained post-fire biomass equal to unbrowsed saplings, despite continuous browse pressure. For uncaged saplings exposed to 20 years of browsing, the positive effects of pre-fire browsing were offset by post-fire wildlife browsing. Post-fire sapling survival was high ($> 92\%$) and not significantly different among treatments. Wildlife browsing legacy increased post-fire resprout size. Using a novel approach we demonstrate that a low-severity, high-frequency browsing legacy (i.e., wildlife damage to sapling tissues) can increase tolerance to high-severity, low-frequency disturbances such as fire, that top-kill all aboveground sapling tissue. We found that pre-fire browsing legacy effects increased the post-fire resiliency of savanna saplings (< 1 meter class).

Introduction

Ecological legacies are physical or biological components of a pre-disturbance environment that ‘carry over’ to affect ecosystem resilience and resistance post-disturbance (Fountain et al. 1999). Plant propagules are one type of material legacy, which transfers biological components of the pre-disturbance community into the future (Monger et al. 2015, Johnstone et al. 2016). In terrestrial systems, the flora that persist after a fire might arise from material legacies that include resprouting propagules and on-site seed banks (Donato et al. 2009, Pausas and Keeley 2014). Legacy effects can arise from anthropogenic land-uses such as rangeland cultivation (Monaco et al. 2018) or

pastoral cattle production (Veblen and Young 2010, Marshall et al. 2018), or from physical processes such as drought, erosion and fire. Cattle grazing legacies are known to affect herbaceous plant propagules (O'Connor and Pickett 1992, Keeley et al. 2003, Benson et al. 2004), but how browsing legacies affect resprouting woody plant propagules remains largely unexplored.

In frequently-disturbed systems, such as savannas, resprouting is a key life history trait that allows plants to persist despite frequent aboveground tissue loss (Bellingham and Sparrow 2000, Bond and Midgley 2001, Midgley et al. 2010). Species adapted to tissue loss caused by fire or herbivory often exhibit compensatory growth whereby aboveground biomass is maintained by high growth rates that replace lost tissue (Gold and Caldwell 1989, Belsky et al. 1993, Stowe et al. 2000). Ungulate herbivores can increase compensatory growth by urine and dung deposition which increase nutrient mineralization rates (Rexroad et al. 2007, Schrama et al. 2013). Herbivory also stimulates mobilization of non-structural carbon stores to replace lost structural tissues (Vanderheyden and Stock 1995). Over time, repeated herbivory alters non-structural carbon allocation within the plant canopy and roots (Palacio et al. 2008) and plant architecture (Moncrieff et al. 2014). Once aboveground tissues are replaced, growth allocation to belowground storage vessels replaces “borrowed carbon,” which may come at the expense of additional aboveground tissue growth (Vanderheyden and Stock 1995, Wiley et al. 2013).

Fire also removes aboveground plant tissues in savannas, but, compared to ungulate browsing, fire is generally less frequent and more severe. The amount of tissue damage inflicted by a single fire depends on the fire behavior, plant species traits, and

plant size. Saplings in the < 1 meter height class are usually “top-killed” when all aboveground meristematic tissue is damaged by heat. Following top-kill, resprouters activate belowground buds (Clarke et al. 2013) and mobilize belowground non-structural carbon (Schutz et al. 2009) to replace aboveground tissue. The pre-fire size of a plant generally correlates with post-fire resprout size (Grady and Hoffmann 2012, Schafer and Just 2014a), but is also limited by post-fire competition (Collins et al. 2018) and the availability of light (Cruz et al. 2003, Casals and Rios 2018), water (Schafer et al. 2014), nutrients (Vadigi and Ward 2012). Survival of resprouting plants decreases with increasing fire severity (Bennett et al. 2016, Casals and Rios 2018) and frequency (Fairman et al. 2017) and also is reduced by fires that occur during the active growing season (Robertson and Hmielowski 2014).

Compound disturbances can affect tree resprout size (Simler et al. 2018) but the direction of these effects depends on the order, timing, and characteristics of successive disturbances and species traits (Foster et al. 2016, Johnstone et al. 2016). Savanna saplings are recognized for their ability to persist despite repeated browsing and fire, but how they do this is poorly understood (Midgley et al. 2010). Sequential browsing followed by fire could result in a positive post-fire resprout response that ultimately increases persistence. For instance, chronic tissue removal by browsing ungulates can condition plants to exhibit compensatory growth (Fornara and du Toit 2007), because of increased non-structural carbon storage in stem and root tissues (Palacio et al. 2008). We suspected saplings with a 20-year browsing legacy would have higher belowground:aboveground biomass that would therefore increase post-fire resprout size.

We used a novel approach to investigate the effects of pre-fire browsing legacy on

post-fire resprout response in savanna saplings. We expected that saplings with a 20-year browsing legacy, would have greater post-fire resprout size than saplings protected from pre-fire browsing for 20 years. We asked two specific questions: 1) Does pre-fire wildlife presence have a positive effect on post-fire resprout size? 2) Are the negative effects of continuous (pre-and post-fire) wildlife browsing and fire on sapling size additive?

Methods

Study site and species

The Mpala Ranch and Conservancy is located in the Laikipia District, Kenya (0°17'N, 36°52'E; 1800 m asl). The research site is a semi-arid (580 mm year⁻¹) tropical savanna where fire has been excluded since the 1970s (Kimuyu et al. 2014). The overstory vegetation is a monodominant stand of *Acacia drepanolobium* (whistling thorn tree) underlain with deep clay-rich vertisol ('black cotton') soils. *Acacia drepanolobium* is highly adapted to fire with relatively thick bark (Midgley et al. 2016) and robust post-fire resprouting (Okello et al. 2008). Trees produce swollen thorn domatia and extrafloral nectaries that are used by ant mutualist partners (Young et al. 1997b). Ant colony density and mutualism defense against ungulate herbivores are reduced by fire (Sensenig et al. 2017). The number of domatia can be used as an unbiased estimate of total-stem length in unburned *A. drepanolobium* saplings (Riginos and Young 2007).

The Mpala Ranch and Conservancy is managed for both wildlife conservation and livestock production. Cattle (*Bos taurus*) are stocked at low to moderate density (0.10-0.15 cattle ha⁻¹) and they outnumber native ungulates (Veblen et al. 2016). The meso-wildlife community includes grazers (e.g., plains zebras [*Equus burchelli*], Grevy's zebra

[*Equus grevyi*], hartebeest [*Alcelaphus buselaphus*], Cape buffalo [*Syncerus caffer*], and oryx [*Oryx gazella*]), as well as browsers and mixed-feeders (e.g., steenbok [*Raphicerus campestris*], Grant's gazelles [*Gazella granti*] and eland [*Taurotragus oryx*]). The two megaherbivores are browsing giraffes (*Giraffa camelopardalis*) and mixed-feeding elephants (*Loxodonta africana*). For all herbivore abundances see Veblen et al. (2016).

Experimental design

We investigated browsing legacy in the Kenya Long-term Exclosure Experiment (KLEE), where the presence of different ungulate herbivores was experimentally controlled for 20 years preceding our study. KLEE is a set of 4-ha plots that were installed at Mpala ranch in 1995 (Young et al. 1997a). Naming conventions for the six herbivory treatment levels — MWC, MW, WC, W, C, and O — denote which ungulate herbivores are present within a given treatment where M = megaherbivores, W = meso-wildlife, C = cattle, and O = no ungulate herbivores (e.g., MWC = all herbivore groups present). The six herbivory treatment combinations are replicated in three blocks (North, Central, and South) for a total of 18 plots. Two different types of semi-permeable electric fences control access by meso-wildlife (large mammals 15–1000 kg) and megaherbivores (elephants and giraffes). Steenbok are small (12 kg) ungulate browsers present within all plots. Cattle grazing treatments occur 6 to 8 times per year by herding cattle into selected plots for several hours. This “moderate” grazing treatment is representative of cattle stocking densities and grazing frequency used on large private ranches in Laikipia county (Odadi et al. 2007).

We manipulated saplings in each of the KLEE plots to investigate how saplings conditioned by different 20-year herbivore treatments would respond after fire. Two treatments were randomly applied to individual saplings growing within each KLEE plot: burned-caged and burned-uncaged. After burning, saplings selected for the burned-caged treatment (three per plot) were protected from post-fire browsing using a 1-m³ steel frame cage covered in hexagonal mesh chicken wire (3-cm openings). This burned-caged treatment excluded post-fire browsing by large ungulate herbivores. Burned-uncaged were left open to herbivory.

Because resprout size often scales with pre-fire size (Grady and Hoffmann 2012, Schafer and Just 2014b) we selected saplings that fell within a small < 1 m size class. Based on a July 2015 sapling survey in which we measured sapling height, main-stem length, total-stem length (all branches and stems), and main-stem diameter, we restricted eligible saplings to 0.6 to 1 m height, 0.6 to 1.7 m main-stem length, >300 cm of total-stem length, and 15 to 30 mm main-stem diameter (Figs. 4.1a-d)

In each of the 18 KLEE plots, we randomly selected six similarly-sized saplings that met the criteria above for experimental treatments. All saplings (n = 108) were tagged and four additional variables were measured. In January 2016 (Figs. 4.1e-h): 1) we counted the number of swollen thorn domatia, previously documented to scale with total-stem length (Riginos and Young 2007); 2) we measured grass height in a 1-m² area beneath each sapling, and 3) clipped and measured air dry weight of this grass, as indices of grass fuel; and 4) we calculated the Neighborhood Basal Area (NBA) as basal area (cm²) of all trees occurring within 3 m of each sapling, to account for intraspecific competition.

We applied burn and cage treatments to saplings in February 2016, prior to the long rainy season. Individual saplings were burned by centering a “burn bin” (open top steel drum, 0.56 m circular diameter \times 1 m height) over the stem before ignition (Luna et al. 2014, Gonzalez et al. 2015). We controlled for fire severity by clipping the (variable amount of) understory grass biomass in a 1-m² quadrat beneath each sapling and replacing understories of all saplings with 250 g of cured grass fuel prior to ignition (Ellair and Platt 2013). In February 2018, two years following the experimental burns, we measured mortality, height, main-stem length, total-stem length, and main-stem diameter of all experimental saplings.

Data Analysis

Post-fire sapling responses.—We calculated relative response for each of four variables (i.e., height, main-stem length, total-stem length and main-stem diameter) using the formula:

$$\text{Relative response } (y) = \frac{F_y - B_y}{B_y}$$

where F_y is the final y measurement two years after burning and B_y is the baseline y measurement prior to burning. We then used an Information Theoretic (IT) approach to model the relative response variable. The IT method accounts for model selection uncertainty, and, unlike classical null hypothesis testing, can be used to compare among competing hypotheses that are not nested models (Burnham et al. 2011). For each of the four response variables we constructed a set of 22 linear mixed models (LMMs). Each model in the set predicted the post-fire response using different combinations of the following fixed factors: 1) cattle—to test for reduced interspecific grass-competition (2

levels: present vs. absent), 2) Neighbor Basal Area (i.e., NBA) —to test for intraspecific competition (continuous covariate), 3) cage—to test for post-fire browsing (2 levels: uncaged vs. caged), 4) wildlife – to test for legacy browsing effects (parameterized both as a 3-level factor [O, W, and MW] to distinguish between the effects of megaherbivores vs. meso-wildlife and as a 2-level factor [O vs. W/MW] to test for effects of browsing wildlife regardless of size, 5) cage*neighbor interaction—to test for intraspecific competition dependent upon post-fire browsing levels, and 6) cage*wildlife—to test our *a priori* browsing legacy hypothesis, in which we expected that the size of burned-caged saplings would increase with increasing levels of pre-fire browsing. The random effects structure for all 22 models included intercepts for block, plot (nested in block), and cage (nested in block and plot). We excluded the small number of saplings (7% of the 108 saplings) that died following the burn treatments from analysis.

To test our *a priori* browsing legacy hypothesis, twelve models included a cage*wildlife interaction. The remaining ten models omitted the cage*wildlife interaction and were used to test alternative hypotheses about the effects of various combinations of cattle, neighbor, and/or cage (Table 4.1). Each of the 22 candidate models was fitted separately for each of the four response variables (i.e., height, main-stem length, total-stem length and diameter) using maximum likelihood (ML) estimation. We used the small-sample-size corrected version of Akaike Information Criterion (AICc) to select among the candidate models (Arnold 2010). A best model selected for each response was the model with the lowest number of parameters (K), selected from the top set of models with AICc within 2 units of the model with the smallest AICc ($\Delta\text{AICc} < 2$) (Pan and Mitchell Dayton 2005, Arnold 2010, Burnham et al. 2011). The selected model was then

refit using Restricted Maximum Likelihood (REML) estimation and evaluated using type III F tests with Kenward-Roger approximate denominator degrees of freedom. We compared interaction means using Tukey adjusted pairwise comparisons. In all models, we square-root transformed and centered the variable Neighbor Basal Area (NBA) to better meet normality, homogeneity of variance, and linearity assumptions. We used R statistical software version 3.5.0 for all analyses (Bates et al. 2015).

Post-fire survival.—Differences in mortality of burned saplings were assessed using two separate Pearson's χ^2 tests. We compared mortality between different cage treatments (2 levels: burned-uncaged vs. burned-caged) and between wildlife treatments (2 levels: wildlife-present vs. wildlife-absent).

Results

Cage \times Wildlife interaction

The best models for height, main-stem length, and total-stem length included a cage*2-level wildlife interaction (Tables, 4.2-4.4), indicating that pre-fire wildlife presence vs. absence affected post-fire resprouting. For all response variables, saplings with 20-year browsing legacy exhibited more resprout growth associated with pre-fire exposure to herbivory in two main ways. First, caged saplings lost less size in wildlife-present compared to wildlife-absent treatments (Figs. 4.2a-c). In other words, pre-fire browsing increased the post-fire resprout size, but only when saplings were protected from post-fire browsing. Second, despite being exposed to large mammal herbivory post-fire, saplings in the wildlife-accessible plots were of similar size to those in herbivore-exclusion plots that had been protected from browsing (Fig. 4.2).

Our results also indicate herbivore and caging treatments successfully manipulated browsing activity. In wildlife-absent plots, there were no significant differences between caged and uncaged saplings in height, main-stem length or total-stem length (Fig. 4.2), whereas in wildlife-present plots, sapling height and main-stem length were significantly greater for caged than uncaged saplings (and total-stem length showed non-significant trends in the same direction) (Fig. 4.2).

Neighbor basal area

The best model for post-fire main-stem length included Neighbor Basal Area (NBA; Table 4.4). Plants with more conspecific competitors (greater NBA) had lower main-stem lengths (Fig. 4.2d).

Post-fire diameter

We found no significant evidence that post-fire relative main-stem diameter was affected by treatments or the covariate NBA (Table 4.5). The post-fire main-stem diameter was highly variable (range 3-22 mm), as was the count of basal stems resprouting from belowground root collar (1-16 stems per sapling). Post-fire main-stem mean length was correlated with post-fire mean diameter (Pearson's $r(98) = 0.75$, $p < 0.001$). Mean values of all responses variables (i.e., height, main-stem length, total-stem length and main-stem diameter) followed similar patterns to the 'relative responses' but were not significant for post-fire total-stem length and diameter (Appendix C2).

Survival

Most burned saplings (100 of 108) survived 2 years post-fire, and there were no

significant differences in survival between wildlife-present and wildlife-absent treatments (Pearson's $\chi^2(1) < 0.001$, $p > 0.99$), or between caged and uncaged treatments (Pearson's $\chi^2(1) = 1.22$, $p = 0.27$).

Discussion

Legacy effects can influence plant community composition and structure following disturbance in several ways (Taylor et al. 2012, Johnstone et al. 2016). Browsing and fire each can delay sapling recruitment by repeatedly removing above-ground tissues (Staver et al. 2009, Sankaran et al. 2013, Staver and Bond 2014) and how legacy effects manifest in systems with compound disturbances is poorly understood. The effects of browsing legacies on post-fire resprouting, prior to this study, had not been empirically tested (Midgley et al. 2010, Foster et al. 2016). We found evidence of a positive browsing legacy effect that increased the resprout size of saplings recovering from fire (i.e., a less negative response), but this was only evident when saplings were protected from post-fire browsing. The browsing legacy effect was offset when saplings were continuously browsed (i.e., uncaged) post-fire. Consistent with these results, saplings that were protected (caged) from herbivory after fire but were not conditioned by pre-fire browsing legacy, were no larger than browsing legacy-conditioned saplings. This suggests that saplings in the <1 meter size class with a browsing legacy have high post-fire resilience (i.e., ability to replace lost tissues) following fire that is equal to unbrowsed saplings. Resprouting is a common trait shared by plants adapted to different types of exogenous tissue loss (Bellingham and Sparrow 2000, Fornara and du Toit 2007, Clarke et al. 2013). In theory resprouters optimize growth allocation to increase fitness following

tissue loss (Poorter et al. 2012) which should manifest as a material legacy effect.

Consistent with these predictions, we found that browsing legacy increased post-fire resprout size, suggesting that saplings adapted to chronic fire and browsing defoliation were able to survive compounded fire and browsing defoliation pressures.

Browsing legacy effect

Saplings exposed to wildlife before fire were less negatively affected by the fire (when caged). One potential explanation for this is that saplings with a browsing legacy have more belowground resources available per unit of above-ground size (Moreira et al. 2012, Schafer et al. 2014). There are two ways that browsing legacy could have increased belowground resources. First, browsing could increase allocation to belowground storage, even among saplings of the same age (Chapin et al. 1990, Bellingham and Sparrow 2000, Palacio et al. 2008, Palacio et al. 2011, Poorter et al. 2012, Ward 2016). Over time, this may lead to more available belowground carbon storage per unit of aboveground biomass. This effect of a “browsing legacy” may be why individual savanna saplings exposed to chronic browsing can sustain compensatory growth for decades (Riginos and Young 2007, Fornara and du Toit 2008) but experience delayed recruitment to larger size classes.

Second, although we controlled for pre-fire sapling size aboveground, we cannot assume that saplings were the same age or overall size (Harper 1977) among different KLEE treatments; browsed individuals may simply have been older and larger belowground, either in the form of accumulated greater belowground resources or a more developed root system more able to garner current resources (Schafer et al. 2014). We

expect that both these processes could be operating in the KLEE plots, but that the latter is the pre-dominant driver. Determining the exact causes of browsing legacy effect, specifically changes in growth allocation, warrants future investigation (Poorter et al. 2012), which would involve a long term study with individuals of known age or examination of roots/underground dynamics.

Post-fire compensatory growth

That post-fire saplings browsed by wildlife were not smaller (aboveground) than saplings that had never been browsed by wildlife suggests the “browsing legacy effect” compensated for the negative effects of post-fire browsing. This may mean that the negative effects of compound fire and post-fire browsing reported to cause tree mortality in other studies (Clarke and Knox 2002, Schutz et al. 2011, Ascoli et al. 2013) are in part due to the sequence and severity of different tissue removing events (e.g. a severe fire top-kill event followed by frequent browsing). The browsing legacy effects we observed may be specific to short saplings, which can recover their pre-fire size more quickly than large trees (Grady and Hoffmann 2012) and are also more susceptible to repeated fire and browsing compared to taller trees (Staver et al. 2009, Staver et al. 2012, Osborne et al. 2018). That saplings in wildlife-absent plots did not have a size advantage, suggests that a belowground growth surplus associated with browsing legacy allowed browsed saplings to compensate for continuous tissue losses following fire. Saplings caught in fire or browse traps may be essentially “hiding” their true size (age) belowground where resources are safe from tissue loss and can be used to replace damaged aboveground tissues. These growth patterns are consistent with what has previously been described as

“compensatory growth” in this study system (Young and Okello 1998, Riginos and Young 2007) and elsewhere in other heavily browsed African savannas (McNaughton 1983, Fornara and du Toit 2008). This interpretation suggests that compensatory growth response (high growth rate), induced by chronic pre-fire wildlife browsing, can persist following fire.

Browser identity

The addition of megaherbivores (i.e., elephant) was negligible with respect to browsing legacy effects. We found that wildlife presence vs. absence, was the best predictor of browsing legacy effect. This was surprising because megaherbivores such as elephants have a larger, more-severe, bite size in comparison to meso-wildlife. We had predicted that browsing legacy would increase with the addition of megaherbivores. Although we cannot rule out the possibility that megaherbivore and meso-wildlife effects would have been distinguishable with higher statistical power, we interpret our results to mean that sapling utilization (i.e., amount of biomass removed) is not different among plots with different ungulate browser species. Indeed, a recent study in the KLEE plots found 20% lower meso-wildlife dung density in plots that allow megaherbivores, suggesting that megaherbivores compete for browse with other species such as eland (Kimuyu et al. 2017) and that the net amount of browsing may be similar regardless of browser community composition

Intraspecific competition

Acacia drepanolobium saplings used in this study occurred in mono-dominant stands comprised of conspecific neighbors. Intraspecific competition with neighboring *A.*

drepanolobium trees, likely for water, may have reduced main-stem lengths of burned saplings (Fig. 4.2d). Water limits the growth of saplings (Riginos and Young 2007) and large trees (Riginos 2009), and the upper boundary for maximum tree cover in semi-arid savanna (Sankaran et al. 2005). Competition for other resources such as light is unlikely in semi-arid savannas (Ludwig et al. 2004), and plants grown in low-light environments generally have longer stems but no change in stem mass (Poorter et al. 2012). Here, we found height and total-stem length were not affected by small differences in neighbor density suggesting that light was not a limiting resource.

Our results are consistent with previous research that found that reduction in intraspecific competition following severe compound disturbances can increase growth in surviving resprouts (Simler et al. 2018). However, the negative effect of neighbor tree density on main-stem length may be artificially high in our study because of the small footprint of the experimental burn bin. Whereas we would expect plant competition to be reduced following large and severe fires that top-kill neighbors (Zimmermann et al. 2015), our burn bin treatments did not affect surrounding vegetation (i.e., grass and trees) outside the 0.5-m² circular burn footprint. For this reason, the effects of neighbor basal area on resprout growth that we observed may be less important in more severe or larger fires.

Conclusions

Browsing legacies may arise from an adaptive plant response to tissue loss, or altered belowground:aboveground biomass that simply masks advanced belowground size of browsed individuals. We found that, although browsing (and repeated fire) can

create “traps” for entire populations of saplings, the survivors in these traps are only deceptively “small” and vulnerable, when in fact they are, resilient, and persistent in the face of severe disturbances. We found that frequent, low-severity disturbance (i.e., browsing legacy) in *A. drepanolobium* appeared to ‘condition’ saplings that were able to replace lost tissues more rapidly than other unbrowsed but equal size saplings. This is contradictory to observations that, high-frequency disturbance by fire (Grady and Hoffmann 2012) or post-fire browsing (Schutz et al. 2011) can potentially exhaust nonstructural carbon reserves and cause mortality. Our results, similar to those of Fulbright et al. (2011) suggest that the sequence of past fire and herbivory disturbances can affect the magnitude of future resprout size responses. When reductions in the frequency or severity of tissue removal occur within an individual plant’s lifetime, the legacy of prior tissue loss can affect growth rate.

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Tables and Figures

Table 4.1. Definitions of 22 linear mixed models (LMMs) representing different hypotheses and fitted to post-fire relative responses of sapling height, main-stem length, total-stem length, and diameter. Models included different combinations of the following fixed-effects factors, as indicated by “+” in the corresponding columns: *cattle* (2 levels; present vs. absent), *neighbor* (continuous covariate; NBA), *cage* (2 levels; uncaged, caged), *cage*neighbor* interaction, *wild 3-level* (3 levels; O, W, MW), *cage*wild 3-level* interaction, *wild 2-level* (2 levels; O, [W or MW]), and *cage*wild 2-level* interaction. The *wild 3-level* factor levels: no wildlife (O), meso-wildlife (W), and meso-wildlife + megaherbivores (MW). The *wild 2-level* factor (models H10-H15: shaded) also included wildlife-absent (no-wildlife [O]) and wildlife-present (W and MW treatments combined into a single factor level). Each model also contained 4 random effects parameters (not shown). *K* is the total number of fixed plus random parameters.

Model	Intercept	cattle	neighbor	cage	cage:neighbor	wild 2-level	cage:wild 2-level	wild 3-level	cage:wild 3-level	K
H0	+									5
H1	+	+								6
H2	+		+							6
H3	+	+	+							7
H4	+		+	+						7
H5	+		+	+		+				8
H6	+	+		+						7
H7	+	+	+	+						8
H8	+	+	+	+			+			9
H9	+			+						6
H10	+		+	+		+	+			9
H11	+		+	+		+	+			10
H12	+	+		+		+	+			9
H13	+	+	+	+		+	+			10
H14	+	+	+	+		+	+			11
H15	+			+		+	+			8
H16	+		+	+				+	+	11
H17	+		+	+			+		+	12
H18	+	+		+				+	+	11
H19	+	+	+	+				+	+	12
H20	+	+	+	+			+		+	13
H21	+			+				+	+	10

Table 4.2. Results for 22 models fitted to relative height. The selected model is highlighted in grey. Selection criteria were lowest number of Δ parameters (K) in the top group of models Δ AICc <2 (all models above the black line). For each model integers and + signs indicate which parameters were included. The number of parameters (K) includes four random effects parameters (not shown in columns).

Model	Intercept	cattle	neighbor	cage	cage:neighbor	wild 2-level	cage: wild 2-level	wild 3-level	cage:wild 3-level	K	logLik	AICc	Δ AICc
H14	-0.503	+	-0.019	+	+	+	+			11	27.21	-29.43	0.00
H13	-0.503	+	-0.011	+		+	+			10	25.85	-29.22	0.20
H11	-0.531		-0.017	+	+	+	+			10	25.79	-29.1	0.32
H10	-0.531		-0.009	+		+	+			9	24.47	-28.94	0.49
H15	-0.531			+		+	+			8	23.01	-28.44	0.98
H12	-0.509	+		+		+	+			9	23.85	-27.71	1.72
H7	-0.534	+	-0.014	+						8	21.06	-24.54	4.88
H20	-0.569	+	-0.019	+	+			+	+	13	27.28	-24.32	5.11
H19	-0.563	+	-0.011	+				+	+	12	25.87	-24.16	5.26
H17	-0.602		-0.018	+	+			+	+	12	25.84	-24.1	5.32
H16	-0.596		-0.009	+				+	+	11	24.49	-23.97	5.45
H4	-0.570		-0.012	+						7	19.39	-23.57	5.85
H21	-0.590			+				+	+	10	23.02	-23.56	5.86
H8	-0.534	+	-0.019	+	+					9	21.56	-23.12	6.30
H18	-0.564	+		+				+	+	11	23.86	-22.71	6.71
H5	-0.571		-0.017	+	+					8	19.85	-22.12	7.31
H9	-0.569			+						6	16.98	-21.06	8.36
H6	-0.542	+		+						7	17.91	-20.6	8.83
H3	-0.460	+	-0.012							7	15.10	-14.98	14.44
H2	-0.496		-0.010							6	13.89	-14.87	14.56
H0	-0.496									5	12.35	-14.06	15.37
H1	-0.467	+								6	13.03	-13.17	16.26

Table 4.3. Results for 22 models fitted to relative main-stem length. The selected model is highlighted in grey. Selection criteria were lowest number of parameters (K) in the top group of models $\Delta AICc < 2$ (all models above the black line). For each model integers and + signs indicate which parameters were included. The number of parameters (K) includes four random effects parameters (not shown in columns).

Model	Intercept	cattle	neighbor	cage	cage:neighbor	wild 2-level	cage:wild 2-level	wild 3-level	cage:wild 3-level	K	logLik	AICc	$\Delta AICc$
H10	-0.435		-0.012	+		+	+			9	17.77	-15.55	0.00
H11	-0.435		-0.007	+	+	+	+			10	18.27	-14.06	1.49
H13	-0.421	+	-0.013	+		+	+			10	18.06	-13.65	1.90
H15	-0.435			+		+	+			8	15.33	-13.08	2.47
H14	-0.421	+	-0.008	+	+	+	+			11	18.55	-12.11	3.44
H12	-0.429	+		+		+	+			9	15.39	-10.77	4.77
H16	-0.430		-0.012	+				+	+	11	17.85	-10.69	4.86
H17	-0.426		-0.007	+	+			+	+	12	18.38	-9.17	6.37
H4	-0.437		-0.015	+						7	12.17	-9.12	6.43
H5	-0.436		-0.007	+	+					8	13.30	-9.01	6.54
H19	-0.414	+	-0.013	+				+	+	12	18.14	-8.69	6.86
H21	-0.421			+				+	+	10	15.44	-8.41	7.14
H7	-0.417	+	-0.016	+						8	12.52	-7.46	8.08
H8	-0.416	+	-0.007	+	+					9	13.65	-7.29	8.26
H20	-0.410	+	-0.007	+	+			+	+	13	18.67	-7.11	8.44
H18	-0.414	+		+				+	+	11	15.50	-6.00	9.55
H9	-0.435			+						6	8.79	-4.68	10.87
H6	-0.425	+		+						7	8.87	-2.52	13.03
H2	-0.355		-0.014							6	7.56	-2.23	13.32
H3	-0.334	+	-0.015							7	7.83	-0.43	15.11
H0	-0.354									5	4.84	0.96	16.51
H1	-0.343	+								6	4.91	3.09	18.64

Table 4.4. Results for 22 models fitted to relative total-stem length. The selected model is highlighted in grey. Selection criteria were lowest number of parameters (K) in the top group of models $\Delta AICc < 2$ (all models above the black line). For each model integers and + signs indicate which parameters were included. The number of parameters (K) includes four random effects parameters (not shown in columns).

Model	Intercept	cattle	neighbor	cage	cage:neighbor	wild 2-level	cage:wild 2-level	wild 3-level	cage:wild 3-level	K	logLik	AICc	$\Delta AICc$
H15	-0.568			+		+	+			8	-38.94	95.47	0.00
H10	-0.569		-0.006	+		+	+			9	-38.78	97.56	2.09
H0	-0.473									5	-43.57	97.78	2.31
H12	-0.569	+		+		+	+			9	-38.94	97.89	2.42
H21	-0.506			+				+	+	10	-38.13	98.73	3.26
H9	-0.516			+						6	-42.98	98.86	3.39
H2	-0.474		-0.011							6	-43.07	99.04	3.57
H13	-0.567	+	-0.006	+		+	+			10	-38.78	100.03	4.56
H11	-0.569		-0.005	+	+	+	+			10	-38.78	100.03	4.56
H1	-0.473	+								6	-43.57	100.04	4.57
H4	-0.518		-0.011	+						7	-42.42	100.06	4.59
H16	-0.510		-0.005	+				+	+	11	-37.99	100.97	5.50
H6	-0.516	+		+						7	-42.98	101.17	5.70
H18	-0.508	+		+				+	+	11	-38.13	101.25	5.78
H3	-0.467	+	-0.011							7	-43.05	101.31	5.84
H5	-0.517		-0.005	+	+					8	-42.29	102.16	6.69
H7	-0.510	+	-0.011	+						8	-42.40	102.39	6.92
H14	-0.567	+	-0.005	+	+	+	+			11	-38.78	102.56	7.09
H19	-0.509	+	-0.006	+				+	+	12	-37.98	103.56	8.09
H17	-0.510		-0.006	+	+			+	+	12	-37.99	103.56	8.09
H8	-0.510	+	-0.006	+	+					9	-42.27	104.54	9.07
H20	-0.509	+	-0.006	+	+			+	+	13	-37.98	106.20	10.73

Table 4.5. Results for 22 models fitted to relative diameter. The selected model is highlighted in grey. Selection criteria were lowest number of parameters (K) in the top group of models $\Delta AICc < 2$ (all models above the black line). For each model integers and + signs indicate which parameters were included. The number of parameters (K) includes four random effects parameters (not shown in columns).

Model	Intercept	cattle	neighbor	cage	cage:neighbor	wild 2-level	cage:wild 2-level	wild 3-level	cage:wild 3-level	K	logLik	AICc	$\Delta AICc$
H7	-0.597	+	-0.007	+						8	36.73	-55.87	0.00
H6	-0.600	+		+						7	35.45	-55.68	0.19
H9	-0.631			+						6	34.20	-55.5	0.37
H1	-0.568	+								6	34.14	-55.38	0.48
H0	-0.599									5	32.98	-55.32	0.55
H3	-0.564	+	-0.007							7	35.26	-55.29	0.57
H12	-0.558	+		+		+	+			9	37.53	-55.07	0.80
H15	-0.582			+		+	+			8	36.30	-55.02	0.85
H4	-0.631		-0.006	+						7	35.00	-54.78	1.09
H13	-0.554	+	-0.006	+		+	+			10	38.51	-54.54	1.33
H2	-0.599		-0.006							6	33.68	-54.46	1.41
H8	-0.597	+	-0.012	+	+					9	37.20	-54.4	1.47
H10	-0.583		-0.005	+		+	+			9	36.86	-53.73	2.14
H14	-0.554	+	-0.012	+	+	+	+			11	39.24	-53.47	2.39
H5	-0.632		-0.010	+	+					8	35.50	-53.41	2.46
H11	-0.583		-0.010	+	+	+	+			10	37.61	-52.74	3.13
H21	-0.665			+				+	+	10	36.35	-50.23	5.64
H18	-0.635	+		+				+	+	11	37.59	-50.18	5.69
H19	-0.635	+	-0.007	+				+	+	12	38.62	-49.65	6.22
H16	-0.669		-0.005	+				+	+	11	36.95	-48.9	6.97
H20	-0.639	+	-0.012	+	+			+	+	13	39.39	-48.54	7.33
H17	-0.673		-0.011	+	+			+	+	12	37.73	-47.88	7.99

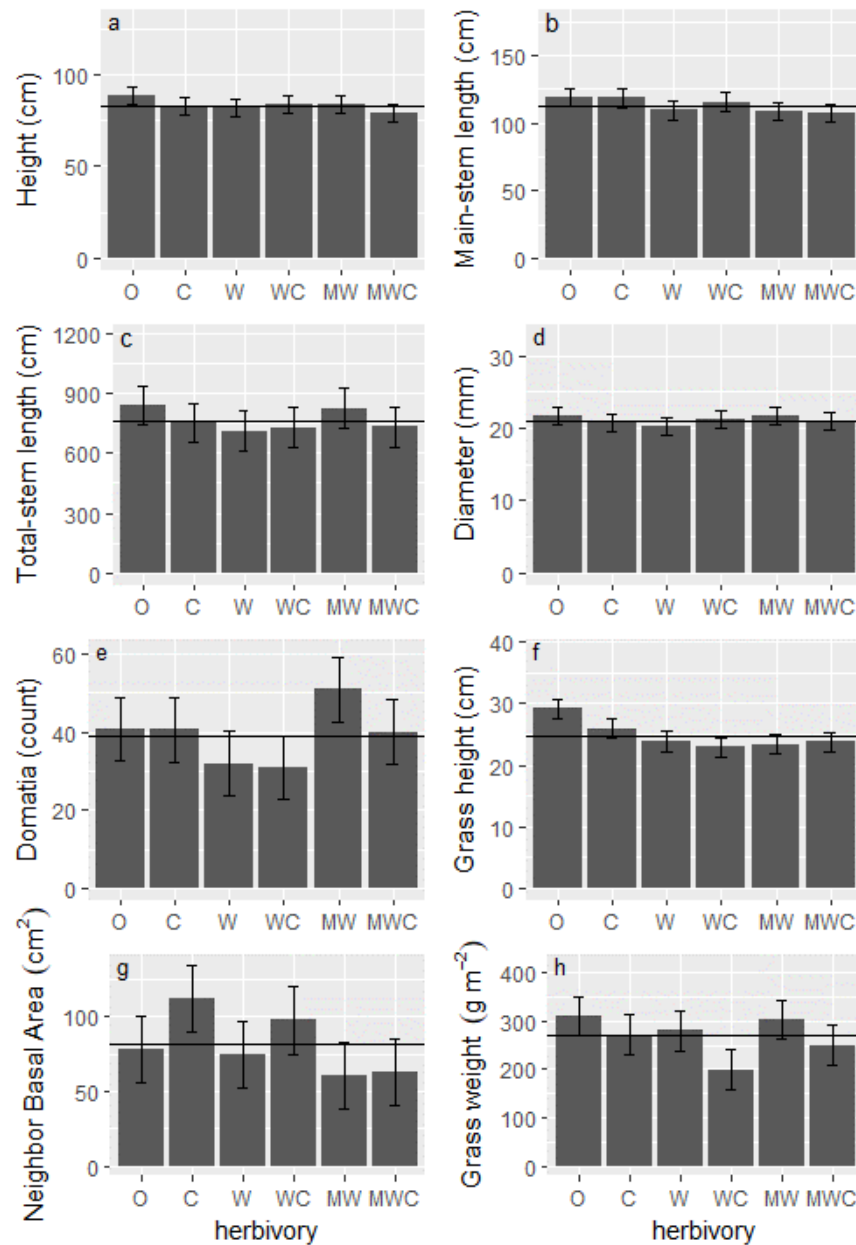


Figure 4.1. Baseline sapling measurements (mean \pm 1SD) for all experimental units (n=216) in each the 6 KLEE herbivore treatment types: O = all large herbivores excluded; C = cattle present; W = meso-wildlife present, WC = meso-wildlife + cattle present, MW = meso-wildlife + megaherbivores present; MWC = meso-wildlife + megaherbivores and cattle present. Horizontal black line - mean value for all selected saplings (n=216). (a) Sapling height. (b) Sapling main-stem length. (c) Sapling total-stem length. (d) Sapling diameter (largest stem). (e) Count of swollen thorn domatia per sapling. (f) Grass height beneath saplings. (g) Neighborhood basal area for all neighboring trees within a 3-m radius of each selected sapling. (h) The oven dry weight of grass biomass clipped in 1-m² quadrat below each sapling prior to burn bin treatment.

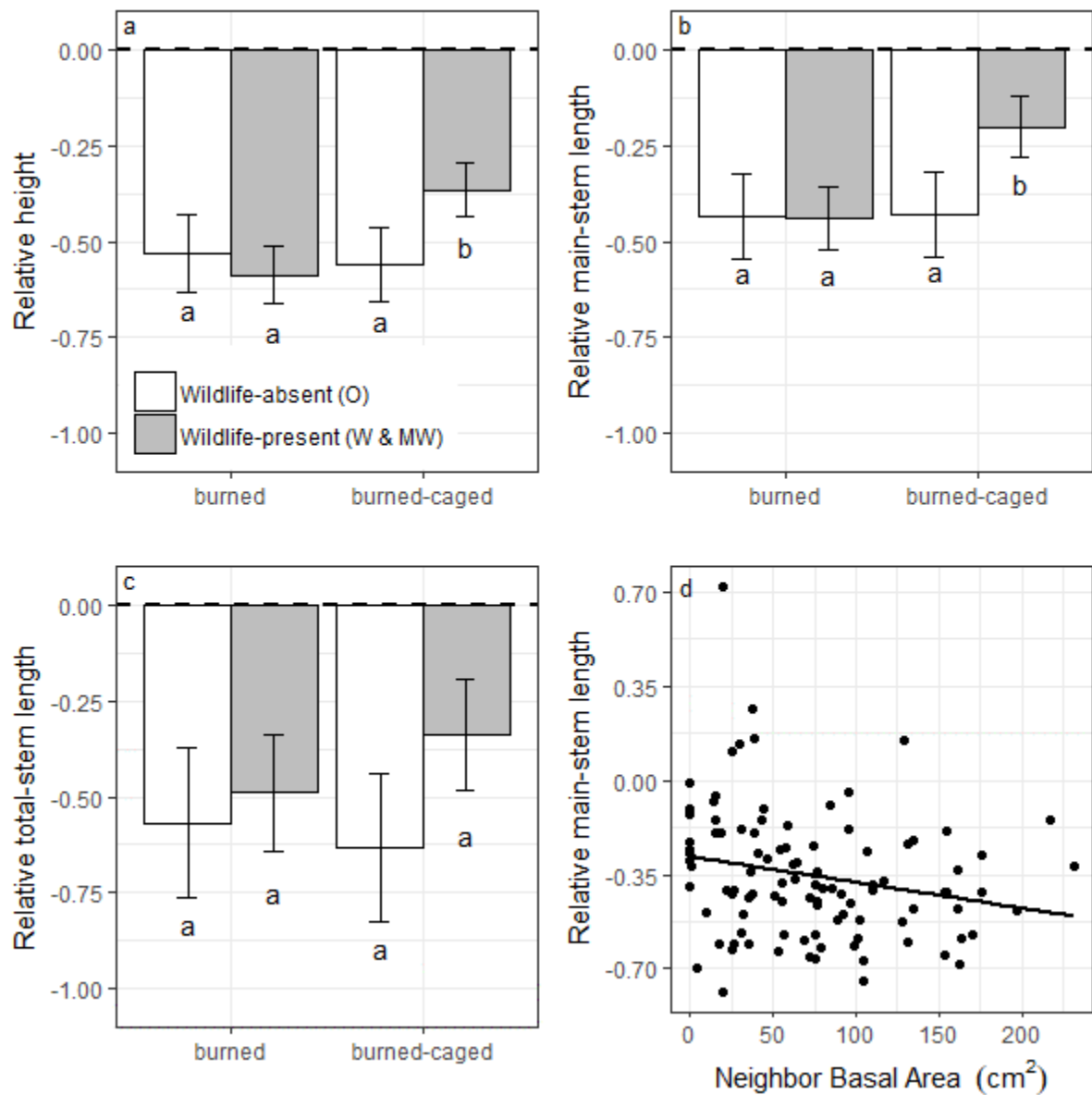


Figure 4.2. Predicted means for saplings responses 2.5 years post-fire. Caged treatment prevented post-fire wildlife browsing. Wildlife-absent (white bars) saplings were protected from wildlife browsing for 20-years pre-fire. Wildlife-present (grey bars) saplings were exposed to wildlife browsing for 20-years pre-fire (i.e., pre-fire browsing legacy). (a) Relative height response. (b) Relative main-stem length, estimated at the average value of Neighbor Basal Area (NBA). (c) Relative total-stem length. (d) Relationship between relative main-stem length of burned saplings and NBA, averaged across 2-level-wildlife and caged treatments. Letters indicate Tukey adjusted pairwise comparisons ($\alpha = 0.05$).

CHAPTER 5

CONCLUSION

Fire and herbivory are fundamental disturbance processes in savanna systems that shape woody vegetation structure (Bond, 2008; Scholes & Archer, 1997). Precipitation and soil properties (e.g., depth and texture) constrain the upper boundary for tree cover in African savannas (Sankaran et al., 2005), but anthropogenic management of cattle, wildlife, and fire ultimately determine tree cover within edaphic boundaries (Archer & Predick, 2014). My research focused on sapling recruitment, a key demographic process in savannas that ultimately affects tree cover change (Bond & Midgley, 2001; Higgins, Bond & Trollope, 2000). I used experimental manipulations to test several interactions between fire, herbivory, and precipitation. My results build on the emerging consensus that the effects of fire herbivory interactions on tree cover are not generalizable. Rather the effects of these disturbances on tree cover depend on community context (Staver, Archibald & Levin, 2011), ecological legacies (Monger et al., 2015), plant functional traits (Osborne et al., 2018), and evolutionary history (Lehmann et al., 2014). In this work, I have provided evidence of several mechanisms that influence sapling recruitment in mono-dominant *A. drepanolobium* savannas.

Post-fire herbivory

In chapter two, I found that the post-fire resprout height of saplings was reduced primarily by meso-wildlife and that the negative effects of elephants increased with pre-fire tree size. Short trees may be caught in a fire trap (Higgins, Bond & Trollope, 2000) or browse trap (Staver & Bond, 2014). My work builds on these concepts by

demonstrating that elephant \times fire interactions that suppress sapling recruitment (Dublin, Sinclair & McGlade, 1990).

Herbivore mediated plant-plant interactions

In chapter three, I used the KLEE herbivory manipulation plots to investigate the net effects of wildlife and cattle on *A. drepanolobium* saplings over a 10-year period. Wildlife presence had an indirect positive effect on saplings by reducing neighbor tree density (i.e., intraspecific competition). Saplings growing in the absence of neighbors more than doubled in both height and diameter, and sapling growth decreased with increasing neighbor density. Grass removal treatments, simulating overgrazed conditions, also increased sapling height and diameter.

Many investigators have associated changes in tree cover with overgrazing by cattle (Angassa & Oba, 2010; Riginos, 2009; Riginos & Young, 2007; Seymour, 2008) and reductions in keystone wildlife species (Daskin, Stalmans & Pringle, 2016; Hatton & Smart, 1984; Sankaran, Ratnam & Hanan, 2008; Stevens et al., 2017). My results build on this previous research by providing empirical evidence that the primary effects of cattle and wildlife on sapling growth occur indirectly via tree-grass and tree-tree interactions, respectively. These results have important implications for the management of African savannas. Rapid sapling recruitment associated with reductions in wildlife—particularly elephants—is in part due to high sapling growth when neighbor tree density (i.e., intraspecific competition) is low and rainfall is high. I also found that overgrazing has the potential to increase sapling recruitment by reducing interspecific tree-grass competition during high precipitation periods.

Browsing legacy effects

In chapter four, I used a novel approach to investigate browsing legacy effects on sapling resprout size. After 20-years of exposure to wildlife browsing treatments, I used burn bins and cages to top-kill saplings and manipulate post-fire herbivory. Two years post-fire, saplings that had experienced a long-term browsing legacy had larger relative growth responses. For uncaged saplings, the positive effects of browsing legacy were offset by post-fire wildlife browsing, but sapling survival was high (> 92%) and not significantly different among herbivory levels or caged treatments.

This suggests that frequent, low-severity disturbance (i.e., browsing legacy) in *A. drepanolobium* ‘conditioned’ saplings to persist following high-severity disturbances such as fire. Extremely high-frequency disturbance by fire (Grady & Hoffmann, 2012) or post-fire browsing (Schutz, Bond & Cramer, 2011) can potentially exhaust nonstructural carbon reserves and cause mortality. Legacy effects of fire and herbivory have been shown to reduce survival and height of large savanna trees (Levick, Baldeck & Asner, 2015; Mayr et al., 2018). My results highlight that for the sapling stage browsing legacy effects can confer positive resprout growth post-fire.

Synthesis

A central question in ecology is identifying which biological mechanisms affect community responses to changing disturbance regimes (e.g., reintroduction of fire, fire exclusion, and changes in herbivore community/density). In this work, I have provided evidence of several mechanisms that influence sapling recruitment in semi-arid savanna systems: positive feedbacks between fire and browsing, indirect positive effects of

wildlife on sapling growth that occurs via reduction in large neighbor trees, and browsing legacy effects which increase tolerance to compound fire and herbivory disturbances. Further investigation of these mechanisms in other communities and ecosystems will yield broader understanding how fire and browsing interactions affect vegetation structure and ecosystem function.

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APPENDICES

APPENDIX A

CHAPTER 2 SUPPLEMENTAL FIGURE

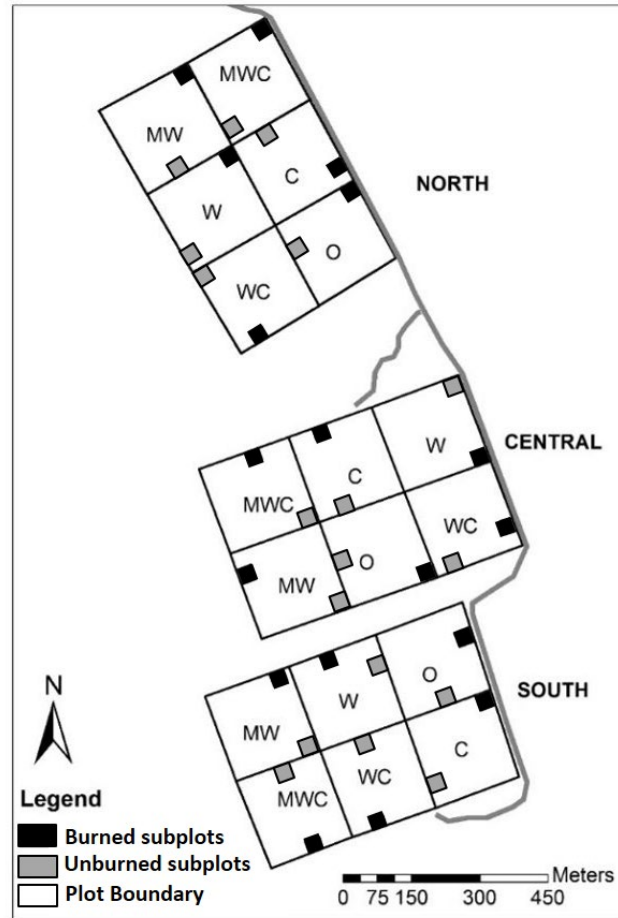


Figure A1. The KLEE study design includes three blocks (North, Central, and South) adapted from (Kimuyu et al. 2014). Letters denote which herbivores are present within six factorial herbivore combinations including: no-access by cattle or wildlife “O”, cattle only “C”, meso-wildlife only “W”, meso-wildlife + cattle “WC”, megaherbivores + meso-wildlife “MW”, and megaherbivores + meso-wildlife + cattle “MWC”. One 30 x 30 m (.09 ha) subplot was burned within each of the 18 KLEE plots. One 30 x 30 m (.09 ha) subplot was left unburned within each of the 18 KLEE plots, but W and WC plots were not used in the analysis (see Appendix B). Dung pellet data collected in treatment and control plots indicate that fences are >90% effective at creating the desired treatments (Young and Okello 1998, Young et al. 2005, Kimuyu et al. 2016) and that wildlife use of the unfenced plots (MWC) is similar to the adjacent matrix (Veblen et al. 2016).

APPENDIX B

CHAPTER 2 SUPPLEMENTAL ANALYSIS

Heights of unburned trees were recorded in a 30 x 30 m unburned subplot within 12 of the 18 KLEE plots. These included four of the six KLEE herbivore treatments (O, C, MW, MWC, but not W or WC). Data were first collected at the start of the growing season following the burn treatment (June 2013), and data were subsequently collected 14 months later, at the same time that burned trees were resampled (August 2014). We used a generalized linear mixed model to test response of tree height to KLEE herbivore treatments: Fixed factors included wildlife (O, MW), cattle (O, C), ant occupancy (none, Cs, Cn, Cm), and initial tree size. The random effects structure included intercepts for block, plot (nested in block), and tree-set (nested in block and plot). We used Restricted Maximum Likelihood (REML) estimation and type III F tests using the Kenward-Roger method to obtain approximate denominator degrees of freedom. Pairwise mean comparisons of tree height among combinations of cattle, wildlife, and ant levels were evaluated using the Tukey method to control family-wise Type I error rate. We excluded from analysis data for trees occupied by the ant mutualist *Tetraponera penzigi* at the final survey. In contrast to our analysis of burned trees, in the current analysis unburned tree height data were not centered and did not require transformation to meet model assumptions.

Post-fire height of unburned trees was positively related to initial 2013 height (Fig. B1), a relationship that differed significantly among wildlife treatment levels (2013 height * wildlife interaction; $F_{(1, 796.2)} = 12.5$ $p = 0.001$, Fig. B2, Table B1; note that

model estimates for unburned trees not occupied by ants are uncertain because only 18 out of 260 unburned unoccupied trees were >1 m in height). A qualitative comparison of burned vs. unburned tree analyses suggests that a) the magnitude of wildlife effects on unburned trees was small compared to the effects of wildlife on burned trees and b) in the absence of fire, herbivore presence is positively associated with tree height (Fig. B2), whereas wildlife have a negative effect on tree height following fire (main text Fig. 2.2). These observations are consistent with previous work that has reported positive effects of wildlife on *A. drepanolobium* sapling growth in the absence of fire (Riginos and Young 2007) and increased meso-wildlife browsing post-fire (Sensenig et al. 2010).

Table B1. Type – III ANOVA table for unburned tree height model.

	F	Df	Df _{K-R}	p
(Intercept)	51058.4	1	3.9	<0.001
wildlife	9.4	1	10.1	0.012
cattle	0.2	1	5.4	0.674
ant	32.6	4	84.4	<0.001
2013 height	1887.3	1	855.5	<0.001
wildlife:cattle	1.2	1	5.5	0.324
ant:2013 height	15.1	4	855.4	<0.001
wildlife:2013 height	12.5	1	796.2	<0.001
wildlife:ant	0.5	4	52.8	0.719

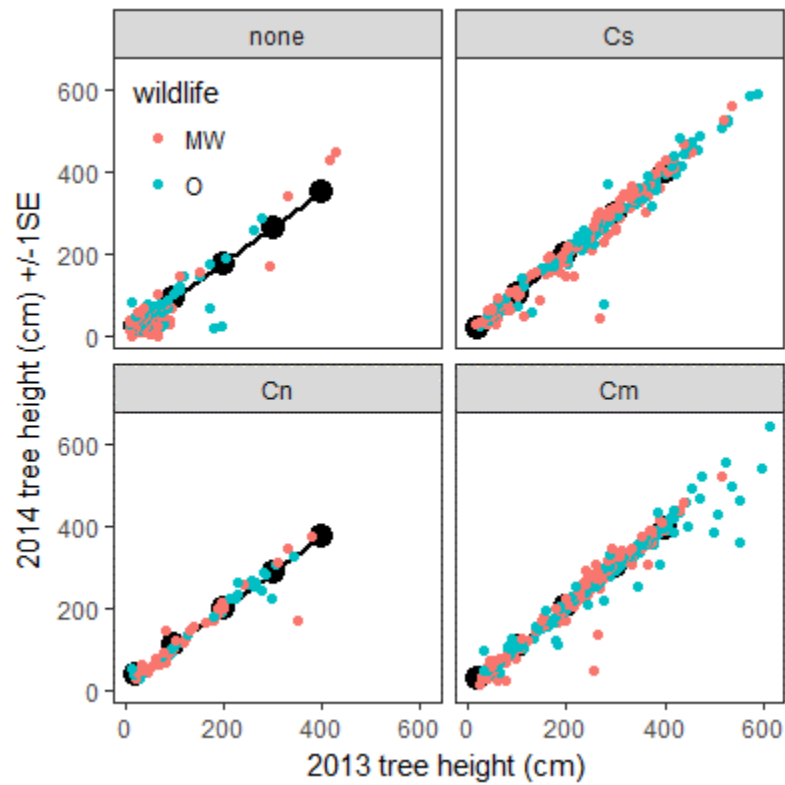


Figure B1. Fitted model height of unburned trees exposed to two levels of wildlife herbivory: O=all wild herbivores excluded; MW=meso-wildlife and megaherbivores. Predicted values are represented by black line and dots. Observed tree height is represented by small red (“MW”) and blue (“O”) dots. Panels show results for each ant occupancy level in order of increasing plant defense (none, Cs = *Crematogaster sjostedti*, Cn = *Crematogaster nigriceps*, Cm = *Crematogaster mimosa*).

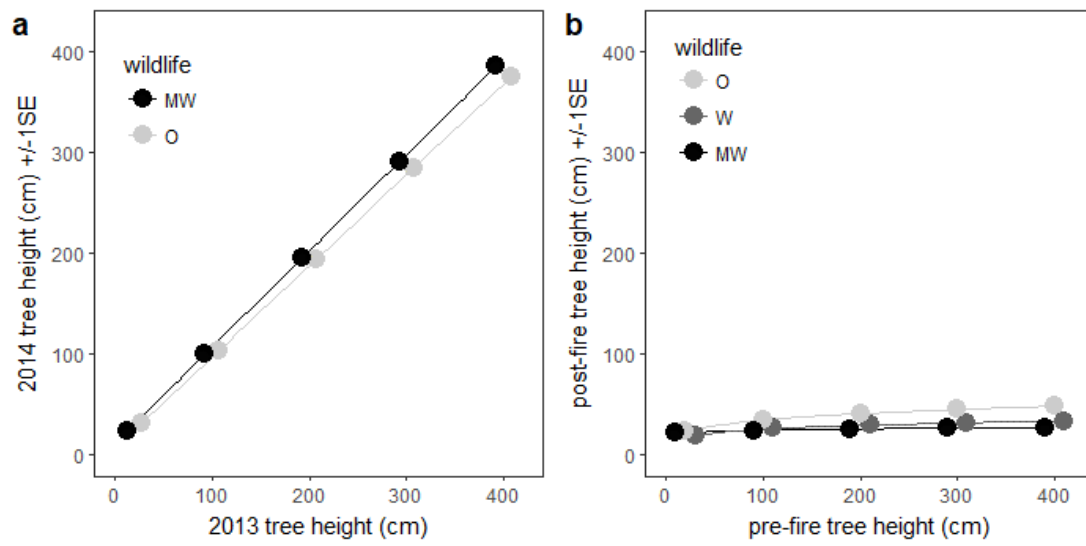


Figure B2. Fitted models for the height of a) unburned trees measured June 2013 and August 2014 and b) trees that were top-killed by burn treatments measured February 2013 (pre-fire) and August 2014 (post-fire). Burned trees were exposed to three levels of wildlife herbivory: O=all wild herbivores excluded; W=meso-wildlife allowed; MW=meso-wildlife and megaherbivores (i.e., elephants) allowed. No unburned data were available for the “W” treatment. Standard error bars displayed at pre-fire height = 20, 100, 200, 300, and 400 cm, but are small and not visible due to scale. Values back transformed to the original scale. Symbols are jittered along the horizontal axis to eliminate overlap. The burned tree height model (b) is the same as was presented in Figure 2 of the manuscript but it has been scaled for qualitative comparison to the unburned tree height model (a).

APPENDIX C

CHAPTER 3 SUPPLEMENTAL FIGURES

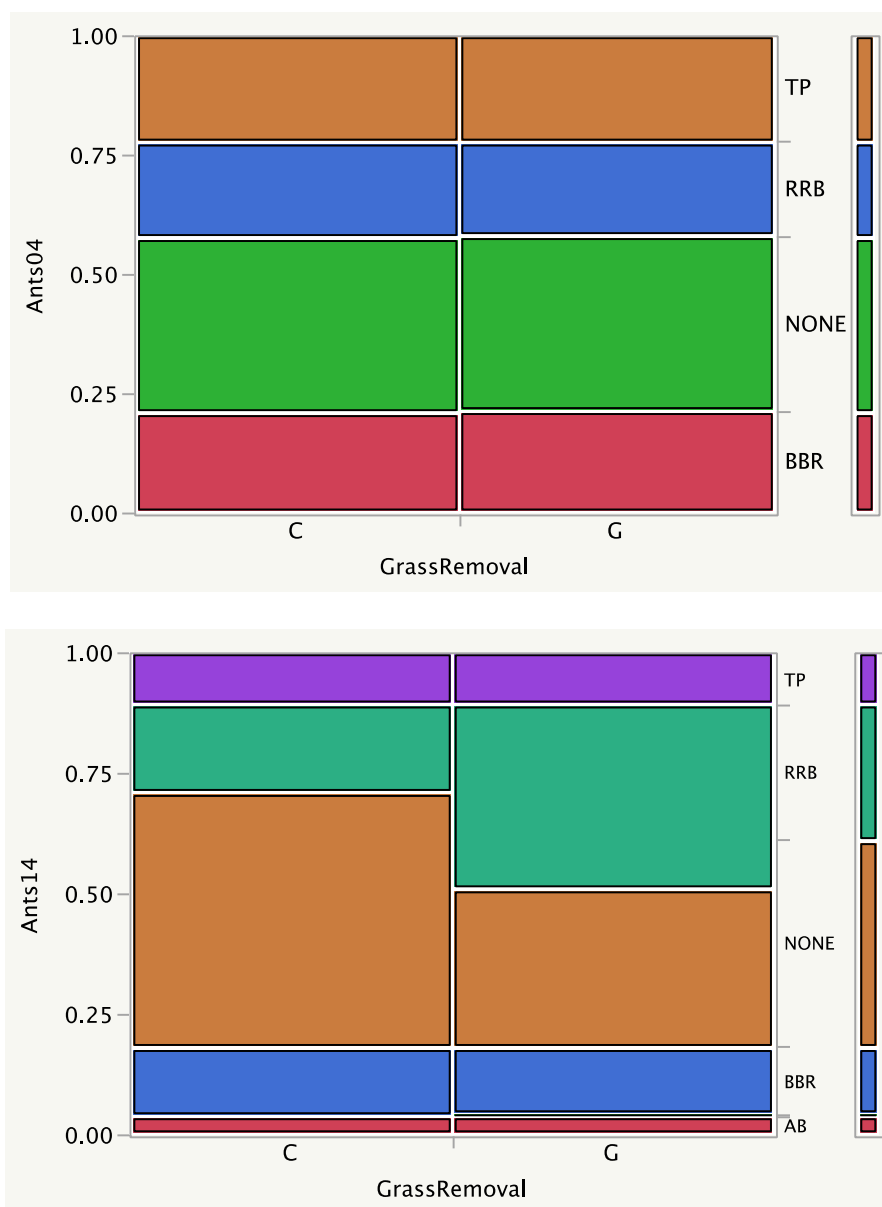


Fig. C1. Ant occupancy as a proportion of all saplings within each grass removal treatment level. At the beginning of the experiment in 2004 (top panel), ant occupancy was balanced across treatment levels as part of the experimental design. By the end of the experiment in 2014 (bottom panel), there were more unoccupied saplings in grass-control treatment and more *Cm* (*Crematogaster mimosae*) saplings in grass-removal treatment. Note that the colors and order of ant occupancy levels is not the same on both graphs.

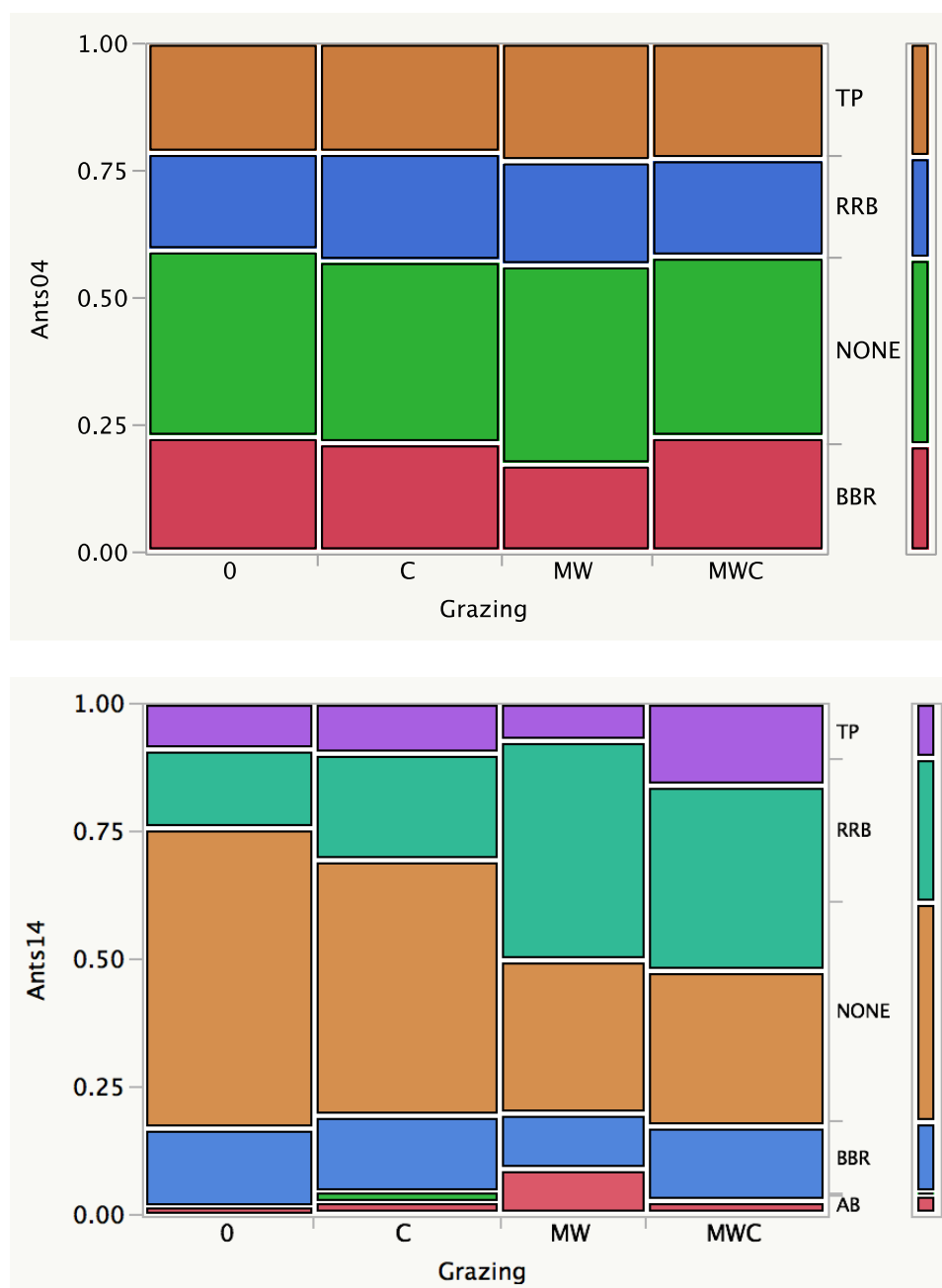


Fig. C2. Ant occupancy as a proportion of all saplings within each herbivory treatment level. At the beginning of the experiment 2004 (top panel), ant occupancy was balanced across treatment levels as part of the experimental design. By the end of the experiment 2014 (bottom panel), there were more vacant (no-ant) saplings in O and C and more Cm (*Crematogaster mimosae*) saplings in MW and MWC. Note that the colors and order of ant occupancy levels is not the same on both graphs.

APPENDIX D

CHAPTER 4 SUPPLEMENTAL FIGURES

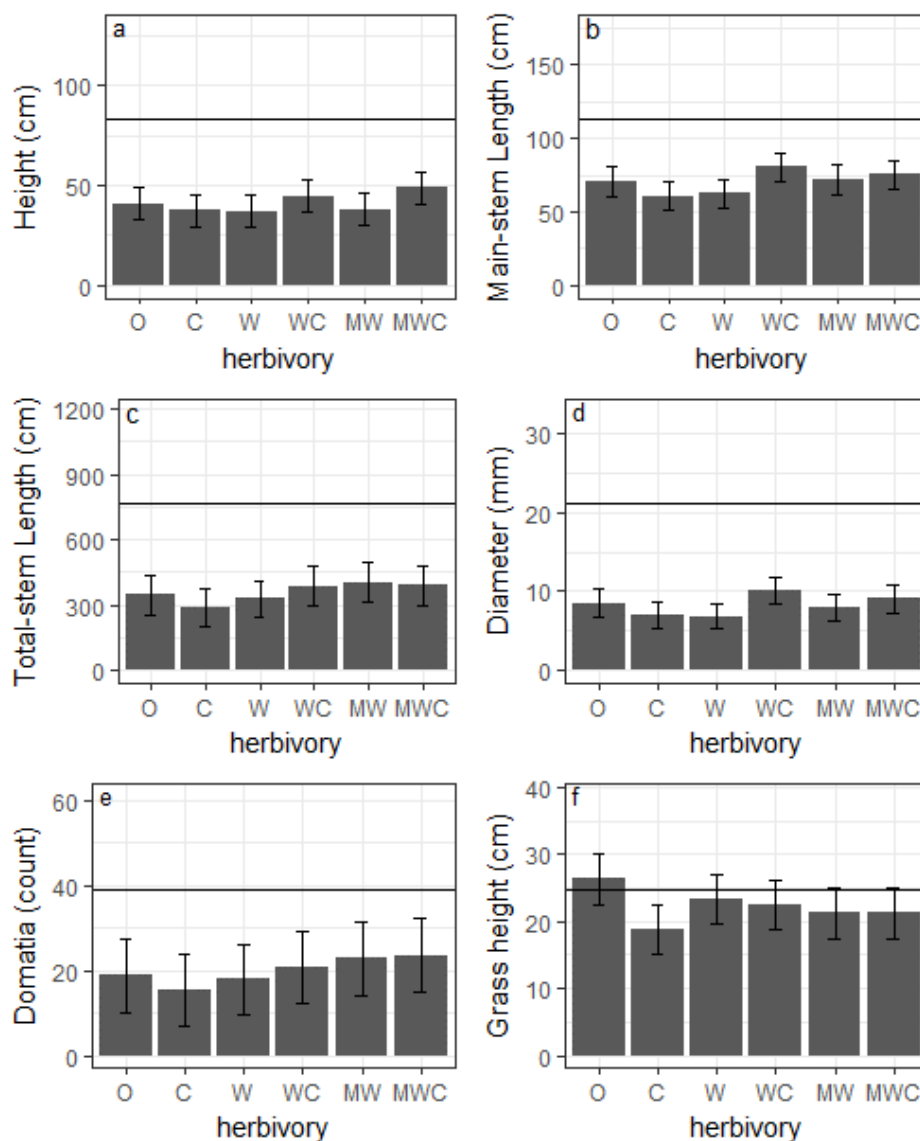


Fig. D1. Burned sapling mean estimates (\pm 1SD) two years post-fire. All surviving saplings ($n=102$) in each of the six KLEE herbivore treatment types: O = all large herbivores excluded; C = cattle present; W = meso-wildlife present, WC = meso-wildlife + cattle present, MW = meso-wildlife + megaherbivores present; MWC = meso-wildlife + megaherbivores and cattle present. Horizontal black line = mean pre-fire value for all selected saplings ($n=216$). (a) Sapling height. (b) Sapling main-stem length. (c) Sapling total-stem length. (d) Sapling diameter (largest stem). (e) Count of swollen thorn domatia per sapling. (f) Grass height beneath saplings.

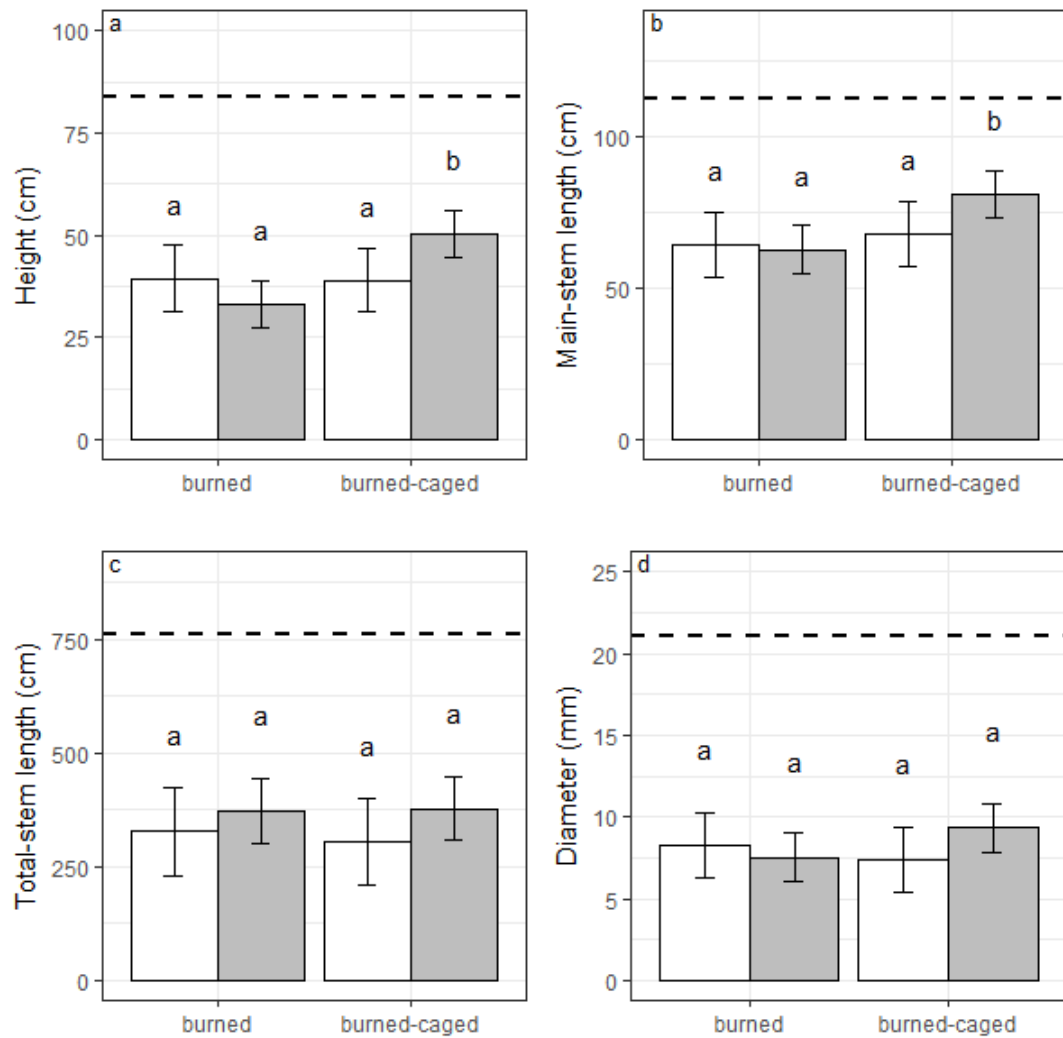


Fig. D2. Predicted mean post-fire sapling responses: (a) height, (b) main-stem length, (c) total-stem length, and (d) diameter (linear mixed model H10: using transformed values). Dashed lines = mean pre-fire mean value for each response variable. Bar color indicates 2-level-wildlife factor levels: grey - wildlife-present (W or MW), white - wildlife-absent (O). All models include the cage*wildlife (i.e., browsing legacy) interaction and three random intercepts for, block, plot (nested in block), and cage (nested in block and plot). The main-stem length model also includes the main effect of $\sqrt{\text{neighbor basal area} + 1}$. Letters indicate Tukey adjusted pairwise comparisons ($\alpha = 0.05$).

APPENDIX E

CHAPTER 2 JOURNAL OF ECOLOGY LICENCE AGREEMENT

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elamalfa@aggiemail.usu.edu**EDUCATION**

Ph.D. in Ecology, Utah State University, 2018. Fire-Herbivory Interactions in an East African Savanna: Effects on *Acacia drepanolobium* Trees. Advisor Dr. Kari E. Veblen**M.S. in Ecology**, Utah State University, 2007. Comparison of Water Dynamics in Aspen and Conifer: Implications for Ecology and Water Yield Augmentation. Advisor Dr. Ron Ryel**B.S. in Range Science**, *cum laude*, Utah State University, 2004**PROFESSIONAL EXPERIENCE**

- 2013-present Quinney Doctoral Research Fellow**
Utah State University, Advisor: Dr. Kari Veblen
- 2012-2013 Planning Coordinator (NEPA)**
US Bureau of Land Management, West Desert District, UT
- 2008-2012 Prescribed Fire and Fuels Management Specialist**
US Forest Service, Uinta Wasatch Cache National Forest, UT
- 2005 & 2008 East Africa Fire and Natural Resource Consultant**
Utah State University, Ethiopia
- 2007 Senior Range Technician**
US Bureau of Land Management, UT
- 2003 Invasive Plant Survey Technician**
Utah State University Extension, UT
- 2002 Fire Effects Monitor**, Tehabi Internship USU
US Bureau of Land Management, NV
- 1999-2001 Forest Field Technician**
US Forest Service, CO & UT
- 2000 River Guide/Music Therapy Internship**
501c non-profit, S.P.L.O.R.E., UT
- 1998-2000 Range Ecology Lab Technician**

Utah State University, UT

TEACHING

* IDEA student course evaluations collected in 2018 by the USU office of Analysis, Assessment and Accreditation (5-point scale). See supplemental materials for details.

- 2018*** **Instructor** - Vegetation and Habitat Management – Forest (WILD 3850, *broadcast and face to face instruction*), Utah State University. University. IDEA scores, Excellent Teacher (3.9), Summary Evaluation (4.0), and Comparison Category (Similar 40%)
- 2018** **Instructor** - Firefighter training, Mpala Research Centre, Kenya
- 2017-2018*** **Designer/ Instructor** - Fire Ecology and Management (WILD 6900, *online*), Utah State University. New course developed for the Masters of Natural Resources program. IDEA scores, Excellent Teacher (4.5), Summary Evaluation (4.6), and Comparison Category (Higher 30%)
- 2017-2018*** **Designer/ Instructor** - Fire Ecology and Management (WILD 4250, *online*), Utah State University. Course cross listing of WILD 6900 (see above) for undergraduate students. IDEA scores, Excellent Teacher (4.6), Summary Evaluation (4.6), and Comparison Category (Higher 30%)
- 2013** **Instructor** - Wildland Fire Behavior Calculations (S-390), Utah Valley University
- 2010** **Instructor** - Introduction to Fire Effects (RX-310), US Forest Service
- 2005** **Designer/ Instructor** - Prescribed Fire in Range Management, USAID, Yabelo, Ethiopia
- 2005** **TA**- Introduction to Natural Resources (WILD 2200), Utah State University
- 2004** **TA** - Wildland Flora of Utah (WILD 3200), Utah State University

Training manual

LaMalfa, E.M., and D.L. Coppock (eds. and compilers). 2005. Use of Prescribed Fire in Rangeland Management. Training manual for a short-course held 20-26 February at the Southern Rangelands Development Unit (SORDU). Yabelo, Ethiopia. 241 pp.

Guest Lectures & Panels

- 2018** Ecology Field Day, Daraja Girls Academy, Mpala Research Centre, Kenya

2018 Kenya	Ecology, Swedish University of Ag. Sci., Mpala Research Centre,
2017 Kenya	Academic Safari, Turkana Basin Institute, Mpala Research Centre,
2015-2018 USU	Human Dimensions of Natural Resource Management (ENVS 4000),
2014	Anthropology, Turkana Basin Institute, Mpala research Centre, Kenya
2005	Wildland Fauna (WILD 3400), Utah State University

PUBLICATIONS

Peer-reviewed manuscripts in preparation

LaMalfa, E.M., C. Riginos, and K.E. Veblen. Pre-fire browsing legacy confers post-fire compensatory growth response in savanna saplings (in preparation for *Ecology*).

LaMalfa, E.M., and K.E. Veblen. Cattle and wildlife indirectly facilitate sapling recruitment in an East African savanna. (in preparation for *Journal of Applied Ecology*).

Peer-reviewed Journal Articles

LaMalfa, E.M., R.L. Sensenig, D.M. Kimuyu, T.P. Young, C. Riginos, and K.E. Veblen. 2019. Tree resprout dynamics following fire depend on herbivory by wild and domestic ungulate herbivores. (Accepted Article published online on 7 April, 2019 *Journal of Ecology*).

LaMalfa, E.M., and R. Ryel. 2008. Water dynamics in aspen and conifer; implications for water yield augmentation and ecology. *Ecological Applications* 11:569–581.

St. Clair, S.B., K. Mock, **E.M. LaMalfa**, R.B. Campbell, G. Schier, and R. Ryel. 2008. Genetic contributions to phenotypic variation in physiology, growth and vigor of western aspen (*Populus tremuloides*) clones. *Forest Science* 56(2):222–230.

Conference Proceedings Papers

LaMalfa, E.M., A.J. Leffler, and R. Ryel. 2007. Differential snowpack accumulation and soil water dynamics in aspen and conifer communities: Implications for water yield. Proceedings of the 2006 Western Snow Conference. Available at: <https://westernsnowconference.org/sites/westernsnowconference.org/PDFs/2007LaMalfa.pdf>

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Outreach Publications

LaMalfa, E.M. 2018. Moto kichakani: Fire in the bush. Mpala Memos. April issue. Available at: http://www.mpala.org/Moto_Kichakani.php

Veblen, K.E., B.A. Newingham, J. Bates, **E.M. LaMalfa**, and J. Gicklhorn. 2015. Post-fire grazing management in the Great Basin. Great Basin Factsheet Series. Number 7. (peer-reviewed). Available at: <http://www.sagegrouseinitiative.com/post-fire-grazing-management-in-the-great-basin/>

Campbell, J., R. Tonioli, A. McAdams, S. Holdsambeck, T. Ledger, C. Ourada, **E.M. LaMalfa**. 2009. USFS region 4 wildfire season review (USDA). Fire cost, ecological outcomes, safety and risk management, & policy.

LaMalfa, E.M. 2008. Guideline on the application of prescribed fire in the Borana Rangelands of Ethiopia. USAID, CARE PLI project, PARIMA.

LaMalfa, E.M. 2008. Guideline on monitoring the effects of prescribed fire in the Borana Rangelands of Ethiopia. USAID, CARE PLI project, PARIMA.

LaMalfa, E.M., and D.L. Coppock (eds.). 2008. Proceedings of the PARIMA 2008 annual meeting. OARI Pastoral and Dry Land Agricultural Research Center. Yabello, Ethiopia.

LaMalfa, E.M. 2007. Wildfires can destroy greater sage grouse habitat. Snapshots. Bureau of Land Management newsletter. September Issue. *Also published in.* The Communicator. A Quarterly Issue of Utah's Community Based Conservation Program. Utah State University. Fall Issue.

LaMalfa, E.M., and D.L. Coppock. 2005. Rebuilding the capacity to burn: Community development and rangeland productivity. Pages 8-11 in Ruminations - Newsletter of the Global Livestock Collaborative Research Support Program. University of California at Davis. Spring Issue.

Dewey S., K. Andersen, M. Ballard, J. Simonson, R. Richards, and **E.M. LaMalfa**. 2003. Invasive non-native plant inventory; conducted in portions of Arches, Canyonlands, Hovenweep, Natural Bridges, Black Canyon of the Gunnison, and Zion National Parks within the Northern Colorado Plateau Network of the National Park Service. Utah State University Extension. 61 pp.

PRESENTATIONS & POSTERS

LaMalfa, E.M., and K.E. Veblen. 2018. Does compensatory growth persist following top-kill by fire? Effects of herbivore browsing legacy on post-fire tree size. Contributed talk at the Ecological Society of America annual meeting, New Orleans, LA.

LaMalfa, E.M., C. Riginos, and K.E. Veblen. 2017. Acacia sapling escape following a decade of grass removal and herbivory manipulations in an East African savanna. Poster presentation at the Ecological Society of America annual meeting, Portland, OR.

LaMalfa, E.M., D.M. Kimuyu, R.L. Sensenig, C. Riginos, T.P. Young, and K.E. Veblen. 2016. Elephants and wildlife browsers limit tree resprout responses following experimental fires. Poster presentation at the Ecological Society of America annual meeting, Fort Lauderdale, FL.

LaMalfa, E.M., D.M. Kimuyu, R.L. Sensenig, C. Riginos, T.P. Young, and K.E. Veblen. 2016. Fire and herbivore interactions limit tree demographic transitions East African savannas: how do juveniles persist? Oral presentation at the USU Student Research Symposium, Logan, UT.

LaMalfa, E.M., D.M. Kimuyu, R.L. Sensenig, C. Riginos, T.P. Young, and K.E. Veblen. 2016. Herbivory affects post-fire tree resprout size: implications for demographic transitions. Oral Presentation at USU Wildland Resources Department Pre-Project Symposium, Logan, UT.

LaMalfa, E.M., D.M. Kimuyu, R.L. Sensenig, C. Riginos, T.P. Young, and K.E. Veblen. 2015. Unraveling fire and herbivore interactions to manage tree cover in an African savanna. Oral presentation at the Restoring the West Conference. Logan, UT.
Tredennick, A.T., P.B. Adler, C.L. Aldridge, C.G. Homer, D.T. Iles, A.R. Kleinhesselink, **E.M. LaMalfa**, and R. Mann. 2015. Pixel-based modeling of plant population dynamics at meso-scales: A test case with sagebrush (*Artemisia*) species. Contributed talk at the Society for Range Management, Sacramento, CA.

LaMalfa, E.M., D.M. Kimuyu, R.L. Sensenig, C. Riginos, T.P. Young, and K.E. Veblen. 2014. Effects of fire and herbivory on tree size transitions in *Acacia drepanolobium*. Oral presentation at the Utah Section of the Society for Range Management. Logan, UT.

LaMalfa, E., G. Gebru, T. Sexton, D. Amosha, S. Moats, R. Morrow, F. Taffa, L. Gizachew, D. Dallas, and D.L. Coppock. 2007. Re-introduction of managed fire in the pastoral production systems of the southern Ethiopian rangelands. Poster presentation at the Human Dimensions of Wildland Fire Conference, Fort Collins, CO

LaMalfa, E.M., and R. Ryel. 2007. Differential snowpack accumulation and water dynamics in aspen and conifer communities: Implications for water yield and function. Poster presentation at the Ecological Society of America, San Jose, CA

LaMalfa, E.M., and R. Ryel. 2007. Differential snowpack accumulation and water dynamics in aspen and conifer communities: Implications for water yield and function. Poster presentation at the Western Snow Conference, Hilo, HI.

LaMalfa, E.M., and R. Ryel. 2007. Differential snowpack accumulation and water dynamics in aspen and conifer communities: implications for water yield and function. Contributed talk at the Society for Range Management, Reno, NV.

LaMalfa, E.M., and R. Ryel. 2006. Comparison of water dynamics in aspen and conifer: Implications for ecology and water yield augmentation. Oral presentation at the Utah Section, Society for Range Management, Logan, UT.

LaMalfa, E.M., and R. Ryel. 2006. Differences in water balance transfer mechanisms between aspen and conifer communities: The fate of spring snow melt in a Northern Rocky Mountain watershed. Poster presentation at the Ecological Society of America, Memphis, TN.

LaMalfa, E.M., and R. Ryel. 2006. Differences in water balance transfer mechanisms between aspen and conifer communities: The fate of spring snow melt in a Northern Rocky Mountain watershed. Poster presentation at the Western Snow Conference, Las Cruces, NM.

LaMalfa, E.M., and R. Ryel. 2006. Differences in water balance transfer mechanisms between aspen and conifer communities: The fate of spring snow melt in a Northern Rocky Mountain watershed. Poster presentation at the Spring Runoff Conference, Logan, UT.

LaMalfa, E.M., and R. Ryel. 2006. Differences in water balance transfer mechanisms between aspen and conifer communities: The fate of spring snow melt in a Northern Rocky Mountain watershed. Poster presentation at the Restoring the West Conference, Logan, UT.

LaMalfa, E.M., and S. Dewey. 2004. The effects of herbicides and herbivory on root development of salt cedar (*Tamarix ramosissima*). Contributed talk at the Society for Range Management, Salt Lake City, UT.

LaMalfa, E.M., and S. Dewey. 2004. The effects of herbicides and herbivory on root development of salt cedar (*Tamarix ramosissima*). Poster presentation at the Western Weed Society of America, Denver, CO.

LaMalfa, E.M., and S. Dewey. 2003. The effects of herbicides and herbivory on root development of salt cedar (*Tamarix ramosissima*). Poster presentation at the Tamarix Symposium, Grand Junction, CO.

GRANTS and AWARDS

2017-2018	National Geographic Society, “Savanna synergies: complex interactions between fire and wild and domestic herbivores” (\$24,400 to T.P. Young, PI; co-investigators: Veblen, Kimuyu, and Odadi)
2018	BLM momentum of appreciation: One Millionth Acre of Fuels Treatment
2017	USU Ecology Center Graduate Research Award, “Effects of herbivore browsing legacy on post-fire juvenile tree resprout size” (\$4,000)
2013-2017	USU Quinney Doctoral Fellowship (\$60,000)
2012	BLM Superior Performance Award (\$1,100)
2011	US Forest Service Certificate of Merit (\$25)
2010	US Forest Service Certificate of Merit (\$500)
2009	US Forest Service Certificate of Appreciation (\$300)
2009	US Forest Service Certificate of Merit (\$750)
2006	Western Snow Conference Dr. J.E. Church Memorial Award (\$100)
2006	USU Spring Runoff Conference 2 nd Prize: Poster Presentation (\$150)
2004	Kiwanis International Outstanding Student Award (\$25)
2003-2004	USU Poe Brothers Scholarship (\$400)
2003-2004	USU George A. Judah Memorial Scholarship (\$400)
2003	USU Undergraduate Research and Creative Opportunities grant (\$500)
2003	USU College of Natural Resources Tuition Waiver (~\$1000)
2003	Society for Range Management Scholarship (\$400)
2002-2003	USU Joseph Barry Bass Memorial Scholarship (\$400)
2002-2003	USU Arthur Dwight Smith Scholarship (\$400)
2002	USU Partial Tuition Waiver (\$500)
2002	BLM “PAW” Peer Award (\$50)
2001-2002	USU Dwight D. Smith Scholarship (\$400)
2000-2001	USU Poe Brothers Scholarship (\$400)

Travel Grants

2018	USU Dept. of Wildland Resources travel funds (\$300)
2018	USU Quinney College of Natural Resources travel funds (\$400)
2018	USU Ecology Center travel grant (\$400, \$300)
2017	USU Dept. of Wildland Resources travel funds (\$300)
2017	USU Quinney College of Natural Resources travel funds (\$300)
2017	USU RGS Graduate student travel grant (\$300)
2017	USU Ecology Center travel grant (\$300)
2016	USU Dept. of Wildland Resources travel funds (\$300)
2016	USU Quinney College of Natural Resources travel funds (\$300)
2016	USU RGS Graduate student travel grant (\$300)
2016	USU Ecology Center travel grant (\$600)

Service Activities

- 2018** Session Facilitator, Dept. of Wildland Resources Graduate Student
symposium
- 2015-2017** Ecology Center Seminar Selection Committee
- 2014-2017** Ecology Center Seminar Speaker Host
- 2016** Session Facilitator, Ecological Society of America, FL
- 2015** Restoring the West conference planning committee, USU, UT
- 2015** Reviewer *African Journal of Ecology*

Outreach Activities

- 2018** Lewa Wildlife Conservancy Rangeland Assessment, Kenya
- 2018** The Nature Conservancy (TNC) Wildfire Training Exchange (TREN), NM
- 2017** Hells Hollow Prescribed Fire Staff Ride, Uintah Wasatch Cache USFS, UT

Professional Development

2018	Empowering Teaching Excellence (ETE) conference, USU, UT
2018	Inclusive and Accurate Approaches for Teaching Sex and Gender in Biology Workshop, Ecological Society of America, LA
2016	ETE E-Learning Workshop, Utah State University, UT
2014	Climate Change Vulnerability Assessment Workshop, USU, UT

Fire Qualifications, National Wildfire Coordination Group (NWCG)

Type 3 Incident Management Team – Planning Chief
 Type 4 Incident Commander – ICT4
 Type II Burn boss – RXB2
 Engine Boss – ENGB
 Crew Boss – CRWB
 Firing Boss – FIRB
 Firefighter Type 1 – FFT1
 Helicopter Crewmember – HECM
 Resource Advisor – READ
 Remote Automated Weather System Operator – RAWS