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Fire and Herbivory Interactively Suppress the Survival and Growth of Trees in an African Semiarid Savanna

Mary W. Ngugi ^{1,*}, Duncan M. Kimuyu ^{2,3}, Ryan L. Sensenig ⁴, Wilfred O. Odadi ^{3,5}, Samuel K. Kiboi ¹ , Joyce K. Omari ¹ and Truman P. Young ^{3,6,*}

¹ Department of Biology, University of Nairobi, Nairobi P.O. Box 30197-00100, Kenya

² Department of Natural Resources Management, Karatina University, Karatina P.O. Box 1957-10101, Kenya

³ Mpala Research Centre, Nanyuki P.O. Box 555-10400, Kenya

⁴ Department of Biology, Goshen College, Goshen, IN 46526, USA

⁵ Department of Natural Resources Management, Egerton University, Njoro P.O. Box 536-20115, Kenya

⁶ Department of Plant Sciences, University of California, Davis, CA 95616, USA

* Correspondence: waithirangugi@students.uonbi.ac.ke (M.W.N.); tpyoung@ucdavis.edu (T.P.Y.)

Abstract: There has been a long-standing interest in understanding how interactions between fire and herbivory influence woody vegetation dynamics in savanna ecosystems. However, controlled, replicated experiments examining how different fire regimes interact with different herbivore groups are rare. We tested the effects of single and repeated burns, crossed with six replicated herbivore treatments, on the mortality and growth of woody vegetation in the Kenya Long-term Exclosure Experiment plots located in a semi-arid savanna system in central Kenya. Burned plots experienced higher tree mortality overall, but differences between burns and non-burns were only significant in plots excluding all wild herbivores and in plots accessible to megaherbivores. Cattle ameliorated the negative effects of repeat burns on tree mortality, perhaps by suppressing fuel load accumulation. Across all herbivore treatments, trees experienced a significant reduction in height within the first two years after fire (top-kill), which was followed by a gradual recovery. Saplings and coppices subjected to repeated burns regrew faster than those that were burned once, except in the presence of megaherbivores. This study highlights strong context-dependent interactions between fire and different herbivore groups, and extends previous approaches to understanding fire–herbivory interactions, which have tended to lump the effects of different herbivore groups, or study them separately.

Keywords: *Acacia drepanolobium*; elephants; vegetation dynamics; Laikipia Kenya; tree mortality



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1. Introduction

Vegetation in savanna ecosystems is highly dynamic, often alternating between woody-dominated phases and grass-dominated phases in space and time [1]. Fire and herbivory are among the major top-down drivers of woody vegetation dynamics in many savanna ecosystems [2–5], and their effects have ramifications for biodiversity and ecosystem functions [6–8]. While the effects of fire and herbivory have often been studied independently, it is increasingly apparent that these two drivers interact through complex feedbacks and their combined effects are often not simply additive [1,3,9,10]. However, experiments that independently manipulate both fire and different herbivore groups are rare.

Understanding the interactive roles of fire and herbivory is particularly important in African savannas, where fire has a long history [11] and a rich fauna of large mammalian herbivores in large densities still exists [12]. Fire may suppress the density of woody vegetation through direct mortality [13,14], but also indirectly through attracting herbivores to burned areas [15]. However, different herbivore groups respond differently to fire-induced habitat heterogeneity and also interact differently with different vegetation components. For example, small-sized herbivores tend to be more selective in diet and may prefer burned areas with high-quality forage, while large-bodied herbivores may be more tolerant of

low-quality forage outside burns [16–18]. Meanwhile, grazers indirectly influence woody cover by reducing herbaceous fuel loads [16] or suppressing tree grass competition [18], while browsers exert a direct effect by browsing and toppling trees [19–21].

The impacts of fire and herbivores are expected to vary with tree height. Generally, short trees tend to be more vulnerable to savanna fires than taller ones because most savanna fires are fueled by herbaceous biomass and thus tend to be hotter nearer to the ground [16]. Frequent fires may delay the transition of saplings (i.e., trees < 100 cm tall) to mature individuals [17] and retrogress adult trees to the sapling stage via top-kill, producing a ‘fire trap’. On the other hand, the effects of different herbivore groups may vary disproportionately with the height of trees. For example, large herbivores—elephants and giraffes—target taller trees while shorter trees are more vulnerable to small to medium browsers such as steinbuck and Grant’s gazelle [20,22,23]. Intensive browsing may suppress growth, thus retaining trees within the reach of herbivores, a phenomenon that has been described as a ‘browsing trap’ [7,8,17]. However, considering the large diversity of herbivores and the vertical stratification in their browsing impact, we have less evidence for the prevalence of a browsing trap, which suggests experiments that control browsers of varying body size are required in demonstrating a browsing trap [8].

To understand how fire and herbivory interactively suppress the survival and growth of trees, we conducted a series of controlled burns in the Kenya Long-term Exclusion Experiment (KLEE), which uses fenced plots to exclude six different combinations of herbivores. The KLEE plots are located in a nutrient-rich ‘black cotton’ soil (vertisols) semi-arid savanna ecosystem at Mpala Research Center in central Kenya. The dominant tree species at the study site is *Acacia drepanolobium*, which constitutes >95% of woody vegetation, and the biotic community is representative of those on similar ecosystems throughout East Africa. Our study aimed at examining the extent to which different herbivore groups (herbivore treatments) may interact with fire to influence growth and mortality of trees. We hypothesized that (i) differences in tree mortality between burned and unburned plots would vary among herbivore treatments because the different herbivore groups interact with fire differently, (ii) because herbivores preferentially browse on trees in burned areas, there would be a greater reduction in height of trees in burned plots that are accessible to herbivores than plots without herbivores and (iii) Trees subjected to repeated burns and herbivory would generally have lower growth rate than trees in plots burned once and protected from herbivores because both fire and herbivory additively suppress tree growth.

2. Materials and Methods

2.1. Study Site

The study was carried out at the Mpala Research Centre in Laikipia, Kenya, at the Kenya Long-term Exclusion Experiment (KLEE). The study area lies just north of the equator (0°17' N, 37°52' E), at an altitude of 1800 m a.s.l., on the leeward side of Mt. Kenya. The vegetation is semi-arid savanna, with a mean annual rainfall of ~600 mm in a weakly trimodal pattern, with a distinct dry season from December to March. Study plots are located within the homogeneous heavy clay black cotton soil (vertisols), which is dominated by *Acacia drepanolobium* trees constituting over 95% of the woody vegetation [21]. *Acacia drepanolobium* grows up to a height of 7 m and taller trees survive most of the low intensity ground fires that characterize semi-arid savannas [19]. Additionally, *A. drepanolobium* defense strategies against herbivory, in addition to protective spines, are ant symbionts hosted by the tree that protect it from herbivores by swarming and biting herbivores. Previous work has demonstrated that this myrmecophyte tree may be highly vulnerable to post-fire browsing because fire may result in the loss of the defensive ants [24]. Less common woody species in this system include *Acacia mellifera*, *Balanites aegyptiaca*, *Boscia angustifolia*, *Rhus natalensis*, and *Croton dichogamus*. The herbaceous layer may reach 100% cover, and is dominated by five grass species: *Pennisetum stramineum*, *P. mezianum*, *Themeda triandra*, *Brachiaria lachnantha*, and *Lintonia nutans* [25], and a rich forb community [26]. The

native large mammalian herbivores in this system include two megaherbivores, elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*), and mesoherbivores, plains zebras (*Equus burchelli*), elands (*Taurotragus oryx*), Grant's gazelles (*Gazella granti*), oryx (*Oryx beisa*), buffaloes (*Syncerus caffer*), hartebeests (*Alcelaphus buselaphus*), warthogs (*Phacochoerus africanus*), and steinbucks (*Raphicerus campestris*) and bush duiker (*Sylvicapra grimmia*).

2.2. Experimental Design

2.2.1. Enclosure Plots

KLEE consists of 18 herbivore enclosure plots, each measuring 200 m × 200 m (4 ha), established in 1995 (Figure 1). KLEE uses a series of semi-permeable barriers to exclude different combinations of herbivores. There are six different herbivore treatments; (i) open plots that are accessible to all combinations of wild herbivores and cattle (MWC), (ii) open plots that are accessible to all combinations of wild herbivores but exclude cattle (MW), (iii) plots that are fenced off to exclude only megaherbivores (elephants and giraffe) but allow access by cattle and wild mesoherbivores 15–1000 kg (WC), (iv) plots that are fenced off and only allow wild mesoherbivores (W), (v) plots that are fenced off and allows access by cattle only (C), and (vi) plots that are fenced and do not allow access by any of the above herbivore groups (O). The type of fencing used does not effectively exclude steinbucks, duikers, and smaller herbivores [21].

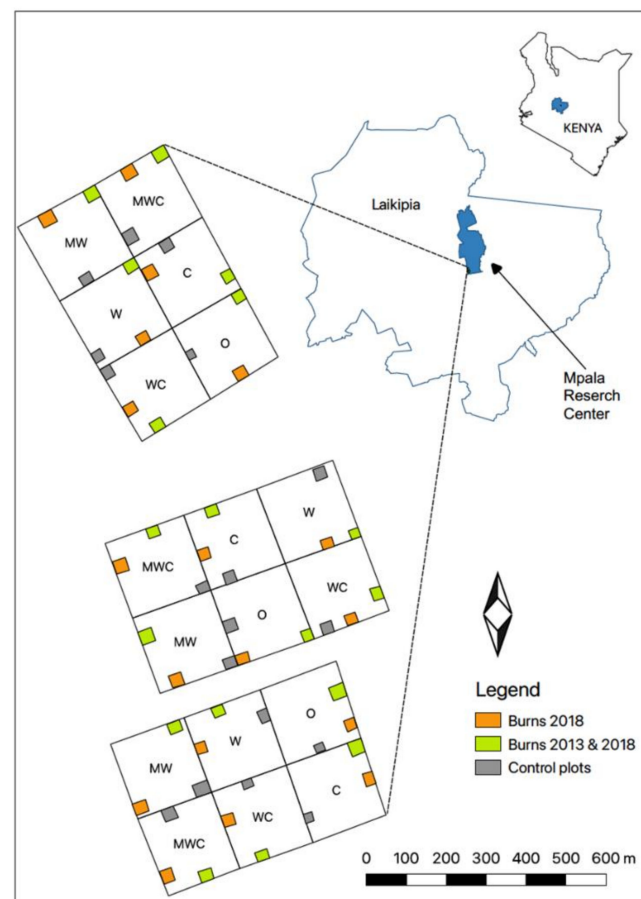


Figure 1. Layout of KLEE plots showing the locations of the burned and the control subplots. “Burns 2018” indicates subplots that were burned in 2018. “Burns 2013 & 2018” indicates subplots that were burned in 2013 and reburned in 2018. Letters denote the herbivore groups that are allowed in a particular plot; M = megaherbivores, W = wild mesoherbivores, C = cattle, O = completely fenced plots that exclude all herbivores larger than steinbucks (~15 kg).

For cattle treatment plots (C, WC, and MWC), herders graze a herd of 100–120 cattle for a three-day series, 3–4 times annually, for two hours each day. Depending on forage availability, grazing time and days may defer but the amount of time spent across all cattle plots is equal and return interval is approximately 16 weeks. This grazing pattern imitates grazing management practices in Mpala Ranch and adjacent grazing areas [27]. Apart from controlled burns, which were implemented for the first time in 2013, fire has been absent at the study plots since their inception in 1995 (and for decades before).

2.2.2. Fire Treatments

Within each of the 18 KLEE herbivore plots, one subplot measuring 30 m × 30 m was burnt in February/March 2013 [16]. A corresponding control subplot (also measuring 30 m × 30 m) was located at least 100 m away from each burned subplot. In February 2018, we reburned the subplots that had been initially burned in 2013, and additionally burned 18 (30 m × 30 m) new subplots (Figure 1). Before burning, all trees within each subplot were mapped and individually tagged using a numbered aluminum tag. We attempted to minimize variability across the subplots by selecting areas that were similar with respect to the density and size structure of *Acacia drepanolobium* trees and avoiding areas with known sources of heterogeneity, such as termite mounds. To control the spread of fire beyond the designated subplots, we created fire breaks by clearing grass in a 1–2 m wide swath around each burn, wet-lining, and back-burning the downwind side of the burn before lighting head fires. We monitored fire temperatures using ceramic tiles painted with Tempilaq (LA-CO industries, Elk Grove Village, IL, USA) paints. For details on the burning protocol, see [16].

All the burns were conducted towards the end of the dry season when all herbaceous biomass was dry. In 2013, we completed all 18 burns within three consecutive days, while it took five days to complete the 36 burns in 2018. Each day, burning started at 08:00 a.m. and ended by 13:00 p.m. Air temperatures during the burns ranged from 15 to 31 °C, increasing during the course of each day. Winds ranged from 1.5 to 18.7 km/h, increasing during the course of each day. Relative humidity ranged from 80% to 23%, declining during the course of each day [16,28]. For logistical and safety reasons, we tended to burn plots with higher fuel loads earlier in the day (during more moderate wind, temperature, and humidity conditions). Thus, our estimates for fire intensity and severity in these plots were rather conservative.

2.3. Data Collection

Before burning in 2013 and 2018, we measured the height (to the nearest cm) of the tallest live tissue of all individual trees (including saplings) within each of the 18 or 36 (30 m × 30 m) subplots and the corresponding control subplots. After burning in 2013, we measured the tree height in the burned and unburned subplots in July every year for four years (i.e., 2013–2017). We then resurveyed these subplots in October to December 2021, three years after reburning in 2018. The new burns that were implemented in 2018 were only surveyed once in October to December 2021, three years after burning. During each of the surveys, we recorded all of the dead trees. Trees were considered to be dead if they lacked any live tissue, and (because of top-kill) this was confirmed during subsequent surveys.

Additionally, during January to February 2022, we collected additional data on all saplings/coppices (trees that were <100 cm tall) in each subplot. For each sapling/coppice, we measured the height, the length of the longest canopy axis, and the length of its perpendicular axis to the nearest cm. From these measurements, we estimated canopy volume (index of growth) as $\pi \times$ average length of the longest axis and its perpendicular axis \times canopy height (~tree height in these saplings) for all individual trees.

2.4. Statistical Analysis

Our approach to the analysis of tree mortality data involved (i) comparing subplots burned for the first time in 2013 with those burned for the first time in 2018, and (ii)

comparing subplots that were burned for the first time in 2018 and those that were reburned in 2018. For both cases, we used data collected for up to three years after fire (2013 to 2016 and 2018 to 2021). For changes in tree height, we analyzed the yearly data collected from 2013 to 2017. For saplings/coppices, we analyzed the canopy volume data collected in all of the burned subplots to test for differences in single and repeat burns across all herbivore combinations.

We calculated mortality rate (m) per year for each plot as $m = (\ln n_0 - \ln S_t)/t$; where t is the time interval between the first and the last sampling periods (here 3 years; 2013–2016 and 2018–2021), n_0 is the population size prior to burning, and S_t is the number of survivors three years after burning [29]. The values for mortality obtained using the above equation were in an open unit scale (0–1), where it is possible to obtain values equal to 0 and 1. We converted them to a bounded scale of (0–1) (where all values are between 0 and 1) by applying the following transformation $y' = [y(N - 1) + s]/N$, where s is a constant between 0 and 1, serving as a prior from the Bayesian standpoint (here $s = 0.0001$) and N is the sample size [30]. This transformation was necessary for the application of beta regression models.

We analyzed mortality data using generalized (beta regression) models mixed models (GLMMs) in the R package *glmmTMB* [31], testing the interactive effect of herbivore treatment (six herbivore treatments; O, C, W, WC, MW, and MWC) and fire treatment (burned versus unburned), and the interactive effect of herbivore treatment and frequency of fire (burned once versus burned twice). Both GLMM's included year of burn as a random effect.

Furthermore, we used a linear mixed model (LMM) in the “*lme4*” R package [32] to test for yearly tree height differences in burns across herbivore treatments. For this analysis, we selected only trees that were taller than 100 cm prior to burning. Lastly, we used LMM to test the interactive effect of initial tree height, herbivore treatment, and fire frequency on the canopy volume (growth index) of saplings. For the LMM's, we specified individual tree IDs nested within herbivore treatment plots nested within replicate blocks as the random effects. For both GLMMs and LMMs, we constructed analysis of deviance tables with Type II Wald χ^2 tests using the function ANOVA in the package *car* [33]. We accepted statistical significance at $p < 0.05$. We used the “*emmeans*” function in the R package *emmeans* [34] to separate means for statistically significant main effects or interactions. All of the analyses were performed in R version 4.0.2 [35].

3. Results

3.1. Fire Temperatures

Fires were generally hotter in the O and C plots than in all of the herbivore treatments. Additionally, plots burned for the second time (repeat burns) were on average cooler than plots burned for the first time in both 2013 and 2018 (Table 1).

Table 1. Mean fire temperature in each herbivore treatment for the three sets of burns (plots burned for the first time in 2013, plots burned for the first time in 2018, and plots reburned in 2018).

Herbivore Treatment	2013		2018	
	First	First	First	Reburns
C	180	211	211	166
O	168	212	212	211
W	191	182	182	164
MW	178	157	157	170
WC	158	147	147	109
MWC	154	140	140	136
Mean temperature	172 ± 5.7 (SE)	175 ± 13.0 (SE)	175 ± 13.0 (SE)	159 ± 14.1 (SE)

3.2. Effect of Herbivory Regime and Fire Treatment on Tree Mortality

We sampled a total of 9854 trees, 4184 of which were located in the 2013 burns, 2707 in the 2018 burns, and 2963 in the unburned control plots. Ten percent (10%) of the tagged trees died during the entire survey period (from 2013 to 2021).

When considering only the subplots burned for the first time (in 2013 and 2018), we found that the mortality rate was influenced by the interaction among the herbivore treatment and fire treatment ($\chi^2 = 33.48, p < 0.001$; Table 2, Figure 2). The post hoc analysis revealed that mortality was significantly higher (all $p < 0.007$) in the burned than unburned (control) subplots in all of the herbivore treatments, except for the ($p > 0.310$) plots accessible to wild mesoherbivores alone (W) and those accessible to both the wild mesoherbivores and cattle (WC).

Table 2. Analysis of deviance table (Type II Wald Chi-square tests) of generalized linear mixed models (GLMMs) testing the effects of various fixed effects on tree mortality, tree height, and canopy volume of sapling.

Response Variable	Fixed Effects	Type II Wald χ^2	<i>p</i> Value
Mortality	Herbivore	20.88	0.001
	Fire	22.02	<0.001
	Herbivore \times Fire	33.48	<0.001
Mortality	Frequency	7.60	0.006
	Herbivore	18.82	0.002
	Frequency \times Herbivore	20.29	0.001
Tree height in 2017	Herbivore	12.96	0.024
	Survey period	457.99	<0.001
Canopy volume	Original height	231.57	<0.001
	Frequency	56.36	<0.001
	Herbivore	9.70	0.084
	Frequency \times Herbivore	14.15	0.015

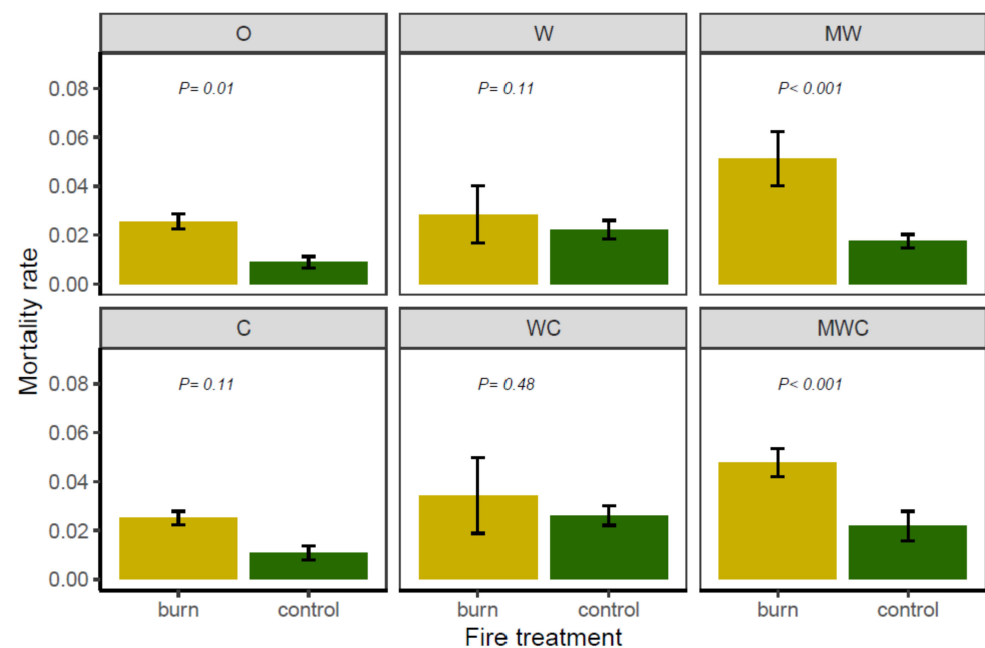


Figure 2. Interactive effects of the fire and herbivore treatments on tree mortality comparing plots burned for the first time in 2013 and in 2018. *p* values on top of the bars are obtained from all pairwise comparisons using *emmeans* in the R package *emmeans* [34].

3.3. Effect of Herbivory Regime and Fire Frequency on Tree Mortality

The tree mortality rate was influenced by the interaction between herbivore treatment and fire frequency ($\chi^2 = 20.29$, $p = 0.001$; Table 2 and Figure 3). We found a lower tree mortality rate in the subplots burned for the second time compared with in the subplots burned for the first time, in the herbivory treatments accessible to cattle (C, WC, and MWC; $p < 0.044$), but not in any other herbivory treatment (all $p > 0.14$) (Figure 3).

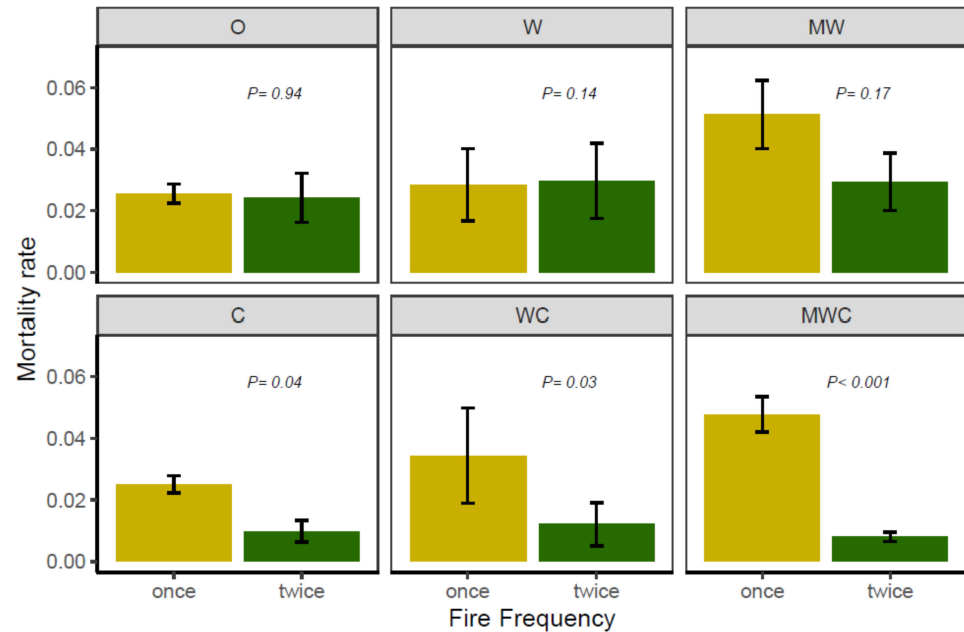


Figure 3. Effects of herbivores and fire frequency on tree mortality. *p* values on top of the bars are obtained from all pairwise comparisons using *emmeans* in the R package *emmeans* [34].

3.4. Effect of Fire on Tree Heights

For a subset of trees that were at least 100 cm tall before the first burn, the height of the surviving trees varied significantly over the six sampling periods ($\chi^2 = 457.99$, $p < 0.001$ Table 2, Figure 4); pre-burn > 2013 and 2014 > 2015, 2016 and 2017. These variations in height were relatively consistent for all herbivore treatments (no significant interaction between herbivory and survey period ($\chi^2 = 2.59$, $p = 0.09$)).

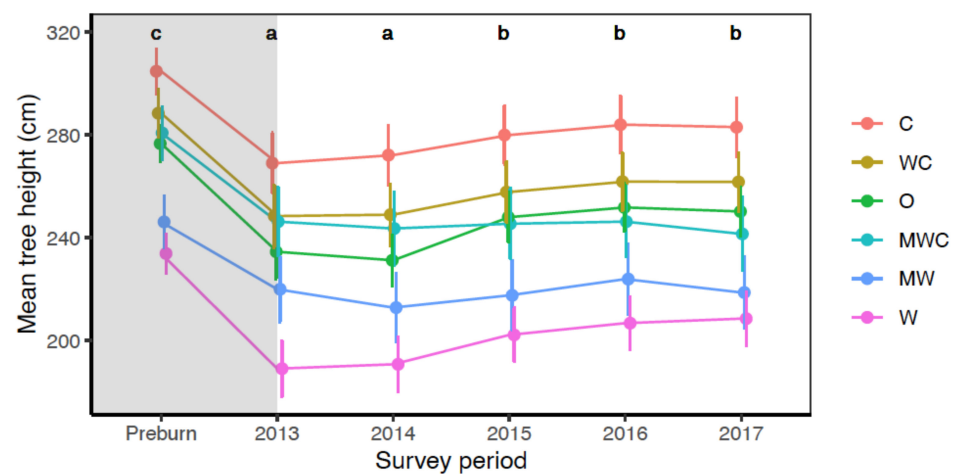


Figure 4. Yearly changes in mean tree height across the six herbivore treatments. Letters inside the graph denote significant yearly differences in mean heights. Sampling periods where the average tree height differs significantly from the subsequent years are annotated with different letters.

3.5. Sapling Canopy Volume

We sampled a subset data of 1423 saplings trees that were below 100 cm tall before the 2018 burns. There was a significant interaction between fire frequency and herbivore treatment ($\chi^2 = 14.15$, $p = 0.015$; Table 2, Figure 5), with all the plots that were burned twice showing a greater canopy volume than those burned once in all of the herbivore treatments (all $p < 0.021$), except for those accessible to megaherbivores and wild mesoherbivores (MW) and MWC (both $p > 0.14$).

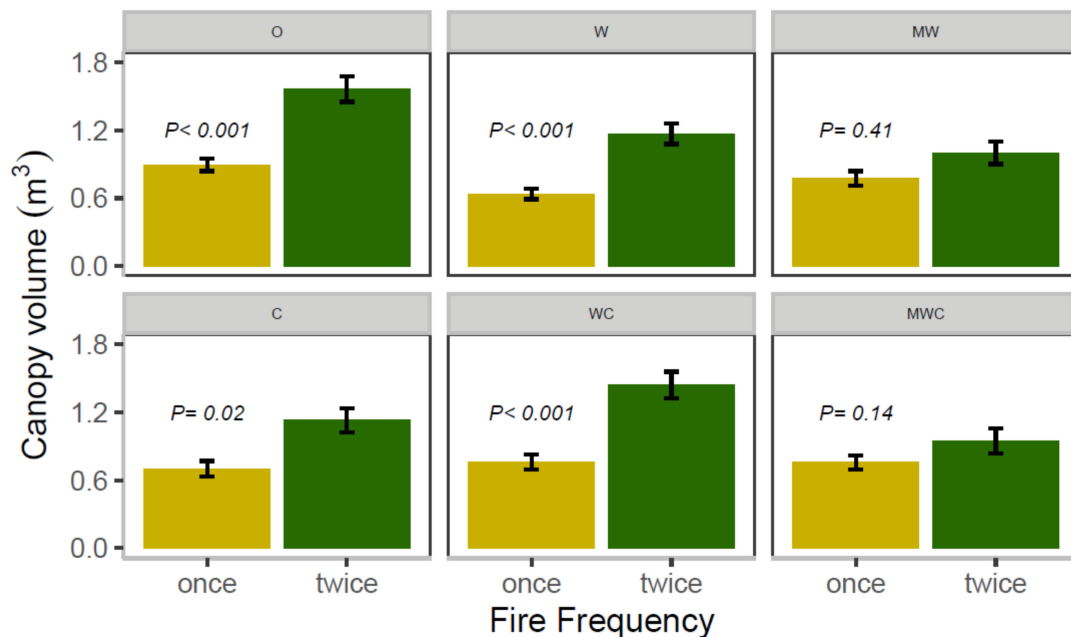


Figure 5. Differences in sapling/coppice growth (canopy volume) between plots burned once (2018) and plots burned twice (2013 and 2018). p values on top of the bars are obtained from all pairwise comparisons using *emmeans* in the R package *emmeans* [34].

4. Discussion

This study demonstrates strong interactive effects of fire and herbivory on the growth and survival of trees. Both fire and megaherbivore presence increased tree mortality, but these two drivers interacted in complex ways. Trees that survived previous burning were less vulnerable to subsequent fires. For tall trees (>100 cm) that survived fire, there was an overall reduction in tree height (via top-kill—complete death of the aerial biomass, regardless of whether the plant recovered by resprouting). However, saplings/coppices (<100 cm) in previously burned subplots grew faster than those that had not been previously exposed to fire, contrasting with our hypothesis.

Consistent with our hypotheses that fire effects on tree mortality would vary depending on herbivore combination, we recorded higher mortality in burns compared with unburned areas in herbivore plots, excluding all large wild herbivores (O and C), and also in megaherbivore plots (MW and MWC). However, such differences were not evident in W and WC plots, where megaherbivores were excluded. The high mortality in burned O and C subplots is likely as a result of the direct effect of fire. Pre-burn herbaceous biomass tended to be higher in these two herbivore treatments than in all of the other herbivore treatments, and fire temperatures were also the highest [16,28], despite the fact that the two plots were usually burned during weather conditions that should have resulted in the coolest burns (see methods). Why would there be higher mortality in burned MW and MWC plots that experienced the coolest temperatures [28], and not in W and WC that experienced moderate temperatures? We suggest two possibly interacting explanations. First, it is likely that even low intensity fires in these plots cause a significant disruption in ant-acacia mutualism, thus increasing the vulnerability of trees to severe damage by

megaherbivores (especially elephants). These results are consistent with previous studies in this system that have demonstrated that fire causes shifts in plant–ant occupancy, thus increasing susceptibility to elephant damage [36]. Secondly, megaherbivores (elephants) may have been attracted to the burns by other factors, such as high-quality regrowth, resulting in heavy browsing damage. Fires are known to stimulate high quality herbaceous regrowth and tree resprouts [37] because after fire, nutrients in soils are readily obtainable, stimulating nutritious growth which may attract different herbivores, including elephants [15].

Our work goes further to provide evidence that in single versus repeated burns, the presence of cattle appeared to ameliorate the effects of subsequent fires on trees in previously burned subplots. For all cattle plots (C, WC, and MWC), we found lower tree mortality rates in repeat burns than single burns. We attribute this to a reduction in post-fire biomass accumulation; where cattle maintain lower herbaceous vegetation cover in previously burned areas, thus reducing severity of subsequent fires. We have previously demonstrated in this system that cattle may affect fire spread by creating bare patches that do not carry fire [25]. In our experimental set up, cattle grazing intensity was controlled by herders in a way to simulate episodic grazing consistent with cattle herding practices in the region [27]. It is possible that even such similarly-timed grazing events are enough to retard biomass accumulation in previously burned areas, because cattle feed more intensely in burned subplots [38]. For herbivore treatments of WC and MWC, episodic grazing by cattle may maintain forage at a higher quality, thus attracting other wild herbivores, which may additionally retard biomass accumulation [38]. Taken together, these findings suggest that cumulative mortality resulting from frequent fires may be less pronounced in intensively grazed areas than in areas experiencing lower grazing pressure.

For all tall trees (here individuals >100 cm) that survived the fire, there was a net reduction in height within the first two years after fire. Subsequently, there was a gradual gain in average height, but the trees had not regained the original height by the end of five-year survey period. These patterns were consistent for all herbivore treatments, including those that excluded the major browsers. We attribute this reduction in height to top-kill of a proportion of these trees, mainly from intense fires in O and C plots and from post-fire browsing in the other herbivore treatments. Our results render partial support to our prediction that fire may interact with herbivores to suppress tree growth (in this case an increase in height), and are consistent with studies elsewhere [39,40].

Furthermore, post-fire regrowth (measured as increase in canopy volume) of top-killed saplings was generally higher in repeat burns than in single burns, although these differences were not significant in the presence of megaherbivores (MW and MWC). We attribute the higher resprout vigor in repeat burns to the fact that trees may have suffered less tissue damage in repeat burns than in single burns, therefore retaining more above ground tissue after fire. Our fire temperature data show that the repeat burns were generally cooler than single burns (Table 1). Earlier studies have also demonstrated that repeat burns tend to be more heterogeneous, leaving behind more unburned patches [25] than the single burns. Secondly, it is possible that the higher regrowth rates in repeat burns is a product of the initial tree height. Previous work has shown that pre-disturbance tree size is a strong predictor of resprout size [17,41–43], because bigger trees have more root carbohydrate reserves [44] or root depth and surface area [45]. As there is a higher probability of having more coppicing trees that were initially tall in repeat burns than in single burns, it is reasonable to expect more compensatory growth on average in repeat burns than in single burns. Consistent with a previous study in this system [17], megaherbivores (especially elephant) appear to suppress the growth of saplings/coppices, thus masking the effects of fire frequency. Similar patterns have been reported on bigger trees, where elephants remove more canopy volume from trees in previously burned areas [46,47].

5. Conclusions

In a world where herbivores and fire regimes are rapidly changing (due to loss of some herbivore groups and an increase in others, as well as changes in fire prescriptions), being able to predict the impact on vegetation within this dynamic has never been more important. This study highlights the complexities of the interactions between fire and herbivores and their implications on the survival and growth of woody vegetation in semiarid savannas. We provide evidence that cattle and wild mesoherbivores may reduce the susceptibility of trees to the direct effect of fire, while megaherbivores amplify the effects of fire by increasing tree mortality and suppressing the regrowth of saplings and coppicing trees. The study highlights strong context-dependent interactions of fire and different herbivore groups, and extends previous approaches to understanding fire herbivory interactions, which have tended to lump the effects of different herbivore groups, or study them separately. These findings represent some of the only experimental evidence that different herbivore groups interact differently with fire to produce different outcomes for tree mortality and growth in savanna ecosystems.

Author Contributions: T.P.Y., D.M.K. and R.L.S. designed and implemented the KLEE experimental burns treatments. M.W.N., D.M.K. and T.P.Y. conceived the ideas and designed methodology; M.W.N. and D.M.K. conducted field work and analyzed the data. M.W.N. and D.M.K. drafted the manuscript. T.P.Y., W.O.O., R.L.S., S.K.K. and J.K.O. contributed to the revising of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Sankaran, M.; Hanan, N.P.; Scholes, R.J.; Ratnam, J.; Augustine, D.J.; Cade, B.S.; Gignoux, J.; Higgins, S.I.; Le Roux, X.; Ludwig, F. Determinants of woody cover in African savannas. *Nature* **2005**, *438*, 846–849. [[CrossRef](#)]
2. Archibald, S.; Hempson, G.P. Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philos. Trans. R. Soc. B Biol. Sci.* **2016**, *371*, 20150309. [[CrossRef](#)] [[PubMed](#)]
3. Bond, W.J.; Keeley, J.E. Fire as a global ‘herbivore’: The ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **2005**, *20*, 387–394. [[CrossRef](#)] [[PubMed](#)]
4. Keeley, J.; Pausas, J.; Rundel, P.; Bond, W.; Bradstock, R. Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* **2011**, *16*, 406–411. [[CrossRef](#)] [[PubMed](#)]
5. Sankaran, M.; Ratnam, J.; Hanan, N. Woody cover in African savannas: The role of resources, fire and herbivory. *Glob. Ecol. Biogeogr.* **2008**, *17*, 236–245. [[CrossRef](#)]
6. Higgins, S.I.; Bond, W.J.; Trollope, W.S.W. Fire, Resprouting and Variability: A Recipe for Grass-Tree Coexistence in Savanna. *J. Ecol.* **2000**, *88*, 213–229. [[CrossRef](#)]
7. Sankaran, M.; Augustine, D.J.; Ratnam, J. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *J. Ecol.* **2013**, *101*, 1389–1399. [[CrossRef](#)]
8. Staver, A.C.; Bond, W.J. Is there a ‘browse trap’? Dynamics of herbivore impacts on trees and grasses in an African savanna. *J. Ecol.* **2014**, *102*, 595–602. [[CrossRef](#)]

9. Bond, W.J.; Woodward, F.I.; Midgley, G.F. The global distribution of ecosystems in a world without fire. *New Phytol.* **2005**, *165*, 525–538. [[CrossRef](#)]
10. Van Langevelde, F.; Van De Vijver, C.A.D.M.; Kumar, L.; Van De Koppel, J.; De Ridder, N.; Van Andel, J.; Skidmore, A.K.; Hearne, J.W.; Stroosnijder, L.; Bond, W.J.; et al. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **2003**, *84*, 337–350. [[CrossRef](#)]
11. Bond, W.J.; Archibald, S. Confronting complexity: Fire policy choices in South African savanna parks. *Int. J. Wildland Fire* **2003**, *12*, 381. [[CrossRef](#)]
12. Reid, R. *Savannas of Our Birth: People, Wildlife, and Change in East Africa*; University of California Press: Berkeley, CA, USA, 2012; ISBN 978-0-520-95407-6.
13. Reinhardt, E.D.; Dickinson, M.B. First-Order Fire Effects Models for Land Management: Overview and Issues. *Fire Ecol.* **2010**, *6*, 131–142. [[CrossRef](#)]
14. Ryan, K.; Elliot, W.J. Chapter 9: Fire effects and soil erosion models. In *Wildland Fire in Ecosystems: Effects of Fire on Soils and Water*; U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Washington, DC, USA, 2005.
15. Sensenig, R.L.; Demment, M.W.; Laca, E.A. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology* **2010**, *91*, 2898–2907. [[CrossRef](#)] [[PubMed](#)]
16. Kimuyu, D.M.; Sensenig, R.L.; Riginos, C.; Veblen, K.E.; Young, T.P. Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna. *Ecol. Appl.* **2014**, *24*, 741–749. [[CrossRef](#)]
17. LaMalfa, E.M.; Kimuyu, D.M.; Sensenig, R.L.; Young, T.P.; Riginos, C.; Veblen, K.E. Tree sprout dynamics following fire depend on herbivory by wild ungulate herbivores. *J. Ecol.* **2019**, *107*, 2493–2502. [[CrossRef](#)]
18. Sankaran, M.; Ratnam, J.; Hanan, N.P. Tree-grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecol. Lett.* **2004**, *7*, 480–490. [[CrossRef](#)]
19. Midgley, J.J.; Sawe, T.; Abanyam, P.; Hintsa, K.; Gacheru, P. Spinescent East African savannah acacias also have thick bark, suggesting they evolved under both an intense fire and herbivory regime. *Afr. J. Ecol.* **2016**, *54*, 118–120. [[CrossRef](#)]
20. Young, T.; Isbell, L. Sex Differences in Giraffe Feeding Ecology: Energetic and Social Constraints. *Ethology* **1991**, *87*, 79–89. [[CrossRef](#)]
21. Young, T.P.; Okello, B.D.; Kinyua, D.; Palmer, T.M. KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr. J. Range Forage Sci.* **1997**, *14*, 94–102. [[CrossRef](#)]
22. Du Toit, J.T.; Olff, H. Generalities in grazing and browsing ecology: Using across-guild comparisons to control contingencies. *Oecologia* **2014**, *174*, 1075–1083. [[CrossRef](#)]
23. Moncrieff, G.R.; Chamaille-Jammes, S.; Higgins, S.I.; O'Hara, R.B.; Bond, W.J. Tree allometries reflect a lifetime of herbivory in an African savanna. *Ecology* **2011**, *92*, 2310–2315. [[CrossRef](#)] [[PubMed](#)]
24. Sensenig, R.L.; Kimuyu, D.K.; Ruiz Guajardo, J.C.; Veblen, K.E.; Riginos, C.; Young, T.P. Fire disturbance disrupts an acacia ant–plant mutualism in favor of a subordinate ant species. *Ecology* **2017**, *98*, 1455–1464. [[CrossRef](#)] [[PubMed](#)]
25. Werner, C.M.; Kimuyu, D.; Veblen, K.E.; Sensenig, R.L.; LaMalfa, E.; Young, T.P. Synergistic effects of long-term herbivory and previous fire on fine-scale heterogeneity of prescribed grassland burns. *Ecology* **2021**, *102*, e03270. [[CrossRef](#)] [[PubMed](#)]
26. Porensky, L.M.; Wittman, S.E.; Riginos, C.; Young, T.P. Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. *Oecologia* **2013**, *173*, 591–602. [[CrossRef](#)] [[PubMed](#)]
27. Kimuyu, D.M.; Veblen, K.E.; Riginos, C.; Chira, R.M.; Githaiga, J.M.; Young, T.P. Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores. *Ecol. Appl.* **2017**, *27*, 786–798. [[CrossRef](#)]
28. Young, T.P.; Kimuyu, D.N.; LaMalfa, E.M.; Werner, C.M.; Jones, C.; Masudi, P.; Ang'ila, R.; Sensenig, R.L. Effects of large mammalian herbivory, previous fire, and year of burn on fire behavior in an African savanna. *Ecosphere* **2022**, *13*, e3980. [[CrossRef](#)]
29. Condit, R.; Ashton, P.S.; Manokaran, N.; LaFrankie, J.V.; Hubbell, S.P.; Foster, R.B. Dynamics of the forest communities at Pasoh and Barro Colorado: Comparing two 50-ha plots. *Phil. Trans. R. Soc. Lond. B* **1999**, *354*, 1739–1748. [[CrossRef](#)]
30. Smithson, M.; Verkuilen, J. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychol. Methods* **2006**, *11*, 54–71. [[CrossRef](#)]
31. Brooks, M.E.; Kristensen, K.; van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Skaug, H.J.; Mächler, M.; Bolker, B.M. Modeling zero-inflated count data with glmmTMB. *BioRxiv* **2017**, 132753. [[CrossRef](#)]
32. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Soft.* **2015**, *67*, 1–48. [[CrossRef](#)]
33. Fox, J.S.; Weisberg, S. *An R Companion to Applied Regression*; The R Journal: Indianapolis, IN, USA, 2019.
34. Russel, L.; Buerkner, P.; Herve, M.; Love, J.; Riebl, H.; Singmann, H. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. CRAN. 2020. Available online: <https://cran.r-project.org/web/packages/emmeans/index.ht> (accessed on 26 June 2020).
35. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018. Available online: <https://www.r-project.org/> (accessed on 17 August 2018).
36. Pringle, R.M.; Kimuyu, D.M.; Sensenig, R.L.; Palmer, T.M.; Riginos, C.; Veblen, K.E.; Young, T.P. Synergistic effects of fire and elephants on arboreal animals in an African savanna. *J. Anim. Ecol.* **2015**, *84*, 1637–1645. [[CrossRef](#)] [[PubMed](#)]
37. Archibald, S. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *J. Wildl. Manag.* **2008**, *72*, 492–501. [[CrossRef](#)]
38. Odadi, W.O.; Kimuyu, D.M.; Sensenig, R.L.; Veblen, K.E.; Riginos, C.; Young, T.P. Fire-induced negative nutritional outcomes for cattle when sharing habitat with native ungulates in an African savanna. *J. Appl. Ecol.* **2017**, *54*, 935–944. [[CrossRef](#)]

39. Pellegrini, A.F.A.; Pringle, R.M.; Govender, N.; Hedin, L.O. Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. *J. Ecol.* **2017**, *105*, 111–121. [[CrossRef](#)]
40. Staver, A.C.; Bond, W.J.; Stock, W.D.; van Rensburg, S.J.; Waldram, M.S. Browsing and Fire Interact to Suppress Tree Density in an African Savanna. *Ecol. Appl.* **2009**, *19*, 1909–1919. [[CrossRef](#)]
41. Young, T.P.; Francombe, C. Growth and yield estimates in natural stands of leleshwa (*Tarconanthus camphoratus*). *For. Ecol. Manag.* **1991**, *41*, 309–321. [[CrossRef](#)]
42. Grady, J.M.; Hoffmann, W.A. Caught in a fire trap: Recurring fire creates stable size equilibria in woody resprouters. *Ecology* **2012**, *93*, 2052–2060. [[CrossRef](#)]
43. Schafer, J.L.; Just, M.G. Size Dependency of Post-Disturbance Recovery of Multi-Stemmed Resprouting Trees. *PLoS ONE* **2014**, *9*, e105600. [[CrossRef](#)]
44. Schutz, A.E.N.; Bond, W.J.; Cramer, M.D. Juggling carbon: Allocation patterns of a dominant tree in a fire-prone savanna. *Oecologia* **2009**, *160*, 235–246. [[CrossRef](#)]
45. Nolan, R.H.; Mitchell, P.J.; Bradstock, R.A.; Lane, P.N.J. Structural adjustments in resprouting trees drive differences in post-fire transpiration. *Tree Physiol.* **2014**, *34*, 123–136. [[CrossRef](#)]
46. Shannon, G.; Thaker, M.; Vanak, A.T.; Page, B.R.; Grant, R.; Slotow, R. Relative Impacts of Elephant and Fire on Large Trees in a Savanna Ecosystem. *Ecosystems* **2011**, *14*, 1372–1381. [[CrossRef](#)]
47. Vanak, A.T.; Shannon, G.; Thaker, M.; Page, B.; Grant, R.; Slotow, R. Biocomplexity in large tree mortality: Interactions between elephant, fire and landscape in an African savanna. *Ecography* **2012**, *35*, 315–321. [[CrossRef](#)]