ARTICLE

Effects of large mammalian herbivory, previous fire, and year of burn on fire behavior in an African savanna

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Abstract

Fire, herbivores, and climatic factors are all major drivers of savanna and grassland dynamics, and they interact in complex ways, which are still in the process of being explored. In particular, herbivores can reduce fire intensity by removal of biomass, and this could be reinforced by herbivores' attraction to recently burned sites, although grassland resilience may limit the temporal depth of such effects. Fire temperature is the most common fire metric reported for grassland fire, but additional aspects of fire behavior can also be measured. Using a set of controlled, replicated experiments, we examined the effects of year of burn, herbivory by livestock and wildlife, previous burn, and weather history on fire behavior in an African savanna. Multiple measures of fire behavior (minimum fire temperature, flame front speed, fire residence time, maximum flame height, and flame length) in 36 controlled burns were positively intercorrelated. Burns conducted in 2018 were significantly cooler, especially at heights >0.5 m above the ground, than those in 2013, a wetter year with more grass fuel. Grass fuel loads and fire temperatures were reduced by the presence of livestock and wildlife. Our sampling methods did not for the most part reveal expected differences in fire temperatures or other behaviors between the reburned plots and those burned for the first time in 2018, with or without herbivores, suggesting strong postfire resilience in this semi-arid savanna rangeland.

KEYWORDS
fire behavior, fire intensity, flame height, Kenya, Kenya Long-term Exclosure Experiment, pyric herbivory

INTRODUCTION

Fire, herbivores, and climatic factors are considered the major drivers of savanna and grassland dynamics, and all three interact in complex ways (Anderson, 2006; Bond et al., 2005; Bond & Keeley, 2005; Sankaran et al., 2005; van Langevelde et al., 2003). Grassland fire and its impacts are sensitive to seasonal (Sparks et al., 2002) and interannual weather patterns (Launchbaugh et al., 2008; Probert et al., 2019), as is herbivory (Davies et al., 2016). Interactions between fire and herbivory, or "pyric herbivory" (Bowman et al., 2016; Fuhlendorf et al., 2009), can influence subsequent fuel loads and fire frequency and behavior (see below).

Many of the Earth's grasslands are fire-dependent, with ancient histories of anthropogenic and natural fire. Similarly, herbivory by large mammals has long helped maintain grasslands and savannas (Bond & Keeley, 2005; Veldman et al., 2015; Voysey et al., 2021). The management and, in many cases, the restoration of regimes of fire and herbivory by large herbivores in these ecosystems are considered central to their health and maintenance (Buisson et al., 2019; Buisson et al., 2021).

Fire temperatures are the most reported grassland fire trait, but other fire metrics are also of interest (Engle et al., 1989; Scott & Burgan, 2005), including fire spread speed and residence time, and flame height and flame breadth. These measures are related but different aspects of fire behavior (Keeley, 2009; Rossi et al., 2018), with potentially different impacts in different vegetation contexts. For example, the survival of trees and their arboreal residents (Kimuyu et al., 2014; Sensenig et al., 2017) could be more dependent on the interaction between temperature and residence time rather than temperature alone, and different flame heights could produce different effects on grasses versus trees.

Herbivores are often drawn to burned areas (Allred et al., 2011; Archibald et al., 2005; Klop et al., 2007; Sensenig et al., 2010; Vinton et al., 1993), to feed on nutritious flushes of fresh regrowth (Foster et al., 2015), as well as on the newly established more palatable species (Greene et al., 2012), but perhaps also for increased antipredator visibility (Eby et al., 2014). Conversely, herbivory by large mammals can decrease fuel loads (Foster et al., 2020; Porensky et al., 2018) and fire intensity (Hobbs et al., 1991, Kimuyu et al., 2014, reviewed in Johnson et al., 2018 and Foster et al., 2020), even to the extent of suppressing fire completely (Johansson et al., 2020; Kimuyu et al., 2014; Liedloff et al., 2001). This effect is strong enough that the use of livestock has been proposed as a tool to mitigate fire risk (Bailey et al., 2019; Nader et al., 2007).

Complex feedback is also possible between fire and herbivores. In particular, the combination of fire and subsequent herbivory can exceed the effect of either and can be more than their sum of their individual effects. For example, the effects of fire and herbivory on woody vegetation can be synergistic (LaMalfa et al., 2019; Midgley et al., 2010; Pringle et al., 2015; Shannon et al., 2011). These effects may fade with time as the vegetation recovers, although positive feedback loops may also create long-term "grazing lawns" of reduced grassland biomass (Donaldson et al., 2018). Yet, these interactions are still rarely explored (Davies et al., 2017), and a few studies have manipulated both fire and herbivory in replicated crossed experimental designs (but see Collins & Smith, 2006, Koerner & Collins, 2013, Smith et al., 2016, Sonnier et al., 2020).

Postfire herbivory can also decrease fuel loads more than fire or herbivory alone (Blackhall et al., 2017; Donaldson et al., 2018; Kirkpatrick et al., 2011; Sonnier et al., 2020). In our ecosystem, controlled burns produce fresh regrowth that is attractive to herbivores, sensitive to burn size (Sensenig et al., 2010). Werner et al. (2021) documented that the subplots in our experimental system previously burned that was accessible to both cattle and wildlife had significantly more unburnt patches in a subsequent fire (2018) than other subplots. This synergistic effect of previous fire and herbivory on the fuel loads in turn has been hypothesized in other ecosystems to influence future fire behaviors (Donaldson et al., 2018; Starns et al., 2019; van Langevelde et al., 2003), although these patterns have rarely been formally experimentally tested. Clarifying the interacting impacts of weather patterns, herbivory, and fire history on savanna fire behavior will improve our understanding of the ecology, management, and restoration of these fire-dependent ecosystems.

In a seminatural rangeland in Kenya, we used two sets of controlled burns (18 burns in 2013 that were also reburned in 2018, and new burns in 2018) within the Kenya Long-term Exclosure Experiment (KLEE) (Young et al., 1997), to test the following predictions:

1. Different measures of fire behavior will be positively correlated.
2. Fuel loads and fire temperatures will be lower in 2018 (a drier prefire period) than in 2013 (a wetter prefire period).
3. Both herbivory by cattle and herbivory by wildlife will reduce fuel loads and fire temperatures.
4. There will be a significant interaction between previous fire and herbivory: Reburned plots will be particularly cooler in those plots accessible to herbivores.

METHODS

Study site and herbivore experiment

This research was carried out at the Mpala Research Centre and Conservancy on the Laikipia Plateau, Kenya

(36°52′E, 0°17′N; 1800 m above sea level). The *Acacia drepanolobium* wooded savanna is underlain with high-clay "black cotton" soils (vertisols) and is representative of similar ecosystems that occur extensively throughout eastern and southern Africa. Mean annual rainfall is 600 mm, in a weakly trimodal pattern with a distinct dry season in December–March.

Five grass species make up 85% of the more or less continuous herbaceous cover (Porensky et al., 2013): *Brachiaria lachnantha* [Hochst.] Stapf, *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., and *Lintonia nutans* Stapf. The Mpala Research Centre and Conservancy is managed for both wildlife conservation and livestock production (mainly cattle). This range-land is seminatural (i.e., not disced, seeded, or irrigated). Although there has been little or no recent history of fire in this ecosystem (since the 1960s), historically it was subject to considerable burning by traditional cultures and early commercial ranching management (Heady, 1960; Sensenig et al., 2010).

In the KLEE, we have been manipulating the presence and absence of three guilds of large herbivores since 1995: livestock (C: cattle), wildlife (W: large mammals 15–1000 kg; "meso-herbivores"), and megaherbivores (M: elephants and giraffes). KLEE consists of a series of 18 plots that use a combination of electric wildlife fencing, megaherbivore fencing, and visual livestock barriers to exclude different combinations of herbivores. There are six different treatments, each replicated three times. The six treatments are as follows: (1) open plots that are accessible to all combinations of wild ungulates and cattle (MWC), (2) open plots that are accessible to all combinations of wild ungulates but exclude cattle (MW), (3) plots that are fenced off to exclude only megaherbivores (elephants and giraffe) but allow access by cattle and wild meso-herbivores (WC), (4) similarly fenced plots from which cattle are also excluded (W), (5) plots that have wildlife fencing and allow access by cattle only (C), and (6) plots that have wildlife fencing and do not allow access by any large herbivores (O) (see Figure 1). Dung counts and camera traps confirm that our barriers are 95%–99% effective in excluding targeted herbivores (for more details of the KLEE design, see Young et al., 1997).

Controlled burns

From 28 February to 2 March 2013, we burned one representative 30 × 30-m subplot in each of the eighteen 4-ha KLEE plots (see Kimuyu et al., 2014 for details). On 19–23 February 2018, we reburned these subplots and burned an additional subplot in each KLEE plot (36 burns total; Figure 1).
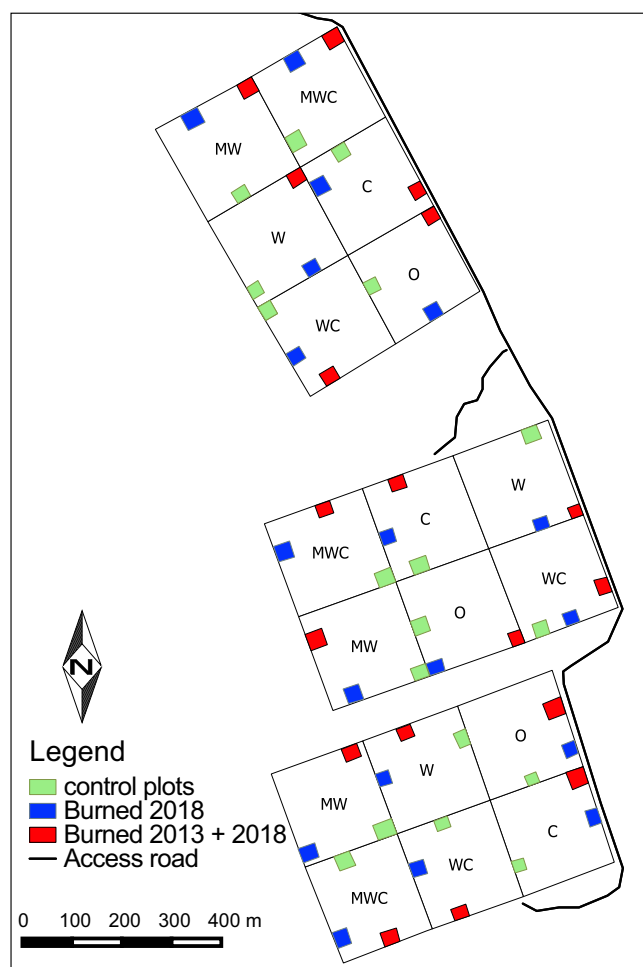
FIGURE 1 The Kenya Long-term Exclosure Experiment (KLEE) experimental design, showing the locations of the subplots burned in 2013 (and reburned in 2018) and the subplots burned for the first time in 2018. For an explanation of the KLEE treatments, see text

We refrained from grazing cattle in their designated KLEE plots for the 5 months prior to the burns to help ensure sufficient fuel loads. The 2013 burns were preceded by wetter than average rainfall (806 mm over the preceding 12 months) than the 2018 burns (446 mm). Before the burns, we assessed aerial cover in all 36 subplots designated for burning. Fifteen 10-pin point frames were regularly placed in each subplot, and the number of pins hit by each plant species was recorded. To facilitate comparison with the 2013 burns, we also clipped all aboveground material in three 1 × 1-m quadrats in each of the 18 subplots designated to be burned for the first time in 2018.

A 1-m firebreak had its vegetation cut to a height of 5–10 cm around each of the subplots designated for a controlled burn. For some subplots, an access road or cleared fence-line provided a functional firebreak along one side. We carried out all of the burns between 8:00 AM and

1:00 PM each day, recording air temperature, relative humidity, wind speed, and wind direction before each burn. Firebreaks were wet-lined and burn boundaries then "black-lined" with backfires to create 5–10 m of additional firebreak along downwind edges and 2–5-m breaks along the flanks. The interiors of all plots were then burned using a strip head fire. Due to discontinuous fuel loads in some subplots, we spotlit head fires for the larger (>5 m^2) unburned grass patches not burned by the original head fire, to ensure that the burn occurred throughout across the subplot.

Fire behavior

To estimate fire temperatures in 2018, we used ceramic tiles painted with an array of six different temperature-sensitive paints (Tempilstik), designed to melt at 79, 107, 149, 204, 260, and 316°C. Similar to the 2013 burns, a painted tile was placed at each of three replicates of five microsites in each of the 36 subplots designated for controlled burns in 2018 (540 total tiles). These microsites were as follows: (1) ground level among grasses away from a tree canopy, (2) attached with wire to a piece of rebar at 0.5 m above the ground at the same grass location, (3) ground level below an *A. drepanolobium* tree, (4) attached by wire to the same tree 1 m above the ground, and (5) attached by wire to the same tree 2 m above the ground. After the burns, these tiles were collected and scored for which paints had melted (minimum fire temperature).

Flame speed, maximum flame height, flame depth, and flame length were estimated through analysis of videos of the 36 controlled burns. A line of 2-m-tall Robel poles, painted with 10-cm bands of alternating colors, was placed at intervals of 5 m across the center diameter of each subplot. Fire residence time and flame front speed (Stephens et al., 2008) were estimated by measuring the time the flame front took to pass a pole (residence time) and to travel a known distance (flame front speed), through the placement of the Robel poles, occasionally adjusted for flame angle. The length of the same flame varied over time; flame height reported here is the maximum height the flame reached as it passed any nonobstructed Robel pole. Flame depth (Simard et al., 1989) was estimated as the time for the fire to pass through a fixed object (residence time) multiplied by the calculated fire speed (Albini, 1976).

Statistical analyses

Values within each subplot were averaged, and these means were used in all analyses, with the three blocks as replicates. First, we produced a correlation matrix of the six metrics of fire behavior: mean minimum fire temperature (across all microsites), maximum flame height, flame depth, flame length, and fire residence time. We carried out a series of ANOVAs testing the effects on fire temperatures at the five microsites of year of burn (2013 vs. 2018), burned for the first time versus reburned, KLEE treatment (six levels), and their interactions, with the three blocks as replicates, using JMP version 9.0.

Because Werner et al. (2021) found that plots accessible to both wildlife and cattle (WC and MWC) had significantly greater unburnt patches than other plots (O, C, W, and MW), we did a separate series of ANOVAs for each of the five microsites, testing the effects of previous burn and the presence of both wildlife and cattle and their interaction on mean minimum fire temperature and other fire metrics.

In one of the previously burned subplots (S-WC, with an oryx midden), the fire was so patchy that video analysis could not be done, but the absence of this single plot did not significantly affect interaction terms. We tested this by reanalyzing the results after adding fire behavior values of zero for this plot, which did not decrease the p values for the interaction terms nearly enough to be significant (all $p > 0.60$).

RESULTS

Fire behavior and abiotic conditions

Air temperatures increased (range: 17–31°C), and relative humidities decreased (range: 23%–67%) throughout the mornings of the five burn days, and wind speeds were variable (range: 1.5–18.7 km/h), but none of these factors were significantly correlated with any of the measures of fire behavior across the 36 burns in 2018, in part because herbivore effects were so strong.

Across microsites, all measures of fire behavior were significantly positively intercorrelated: minimum fire temperature, flame front speed, fire residence time, maximum flame height, flame depth, and flame. Thirteen of the 15 correlations were statistically significant, including all correlations with mean minimum fire temperature (Table 1). Mean minimum fire temperatures for each of the five microsites were strongly positively correlated with overall mean minimum temperature (all $r^2 > 0.50$ and all $p < 0.0001$). All metrics responded similarly to the effects of herbivore exclusion and past fire. Hereafter, we will report mainly mean minimum fire temperatures.

Height, cover, and year effects

For both 2013 and 2018 burns, mean minimum fire temperature declined with distance from the ground (Figure 2).

TABLE 1 Correlation matrix for six metrics of fire behavior, across 35 controlled burns carried out in 2018

Metric	Maximum flame height	Flame depth	Flame length	Fire spread speed	Residence time
Mean fire temperature	0.765 (<0.0001)	0.552 (0.0006)	0.741 (<0.0001)	0.505 (0.002)	0.369 (0.030)
Maximum flame height		0.602 (<0.0001)	0.936 (<0.0001)	0.657 (<0.0001)	0.280 (0.11)
Flame depth			0.676 (<0.0001)	0.740 (<0.0001)	0.805 (<0.0001)
Flame length				0.689 (<0.0001)	0.381 (0.024)
Fire spread speed					0.224 (0.20)

Note: One subplot (in treatment WC in the south block) was too patchy to make reliable video measurements (see text). These correlations included both reburned plots and those burned for the first time in 2018. Numbers in parentheses are *p* values. All *p* values except four of the five with residence time are still significant after Bonferroni corrections.
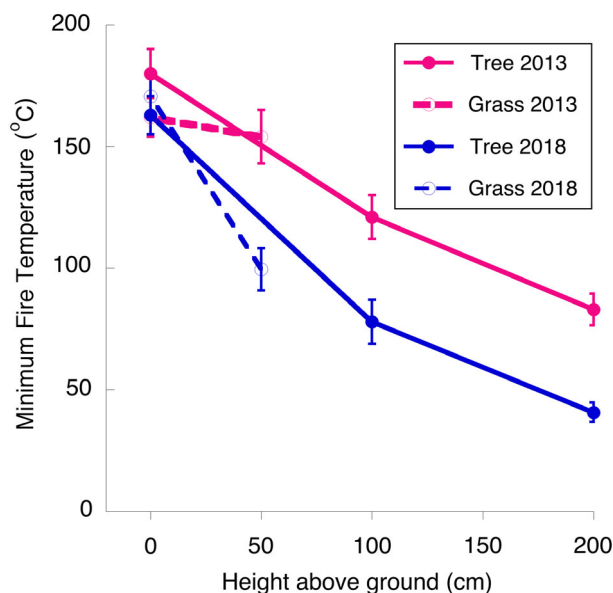
FIGURE 2 Mean minimum fire temperatures for the 2013 burns (in red) and the 2018 burns (in green), for five microsites within each subplot (see text for details). The 2018 means include both reburned plots and those burned for the first time in 2018. Error bars are one standard error. All differences between burn years were significant (all $p < 0.005$), except at ground level

As in 2013 (see Kimuyu et al., 2014), mean minimum fire temperatures in 2018 were strongly positively correlated with preburn vegetation cover (measured in mid-2017), similarly for both subplots burned for the first time ($r^2 = 0.48$, $p = 0.0014$) and previously burned subplots ($r^2 = 0.49$, $p = 0.0013$). These mid-2017 cover measures were strongly correlated with the biomass from clips (from the subplots first burned in 2018) in the week before the burns ($r^2 = 0.56$, $p = 0.0004$).

Year effects

The 2018 mean minimum fire temperatures were significantly cooler ($p = 0.015$) than those in 2013, likely because of lower rainfall in the preceding months (3 months: 5 vs. 60 mm; 12 months: 446 vs. 806 mm), and subsequent lower fuel loads (276 vs. 489 g/m²; $p = 0.001$). Fire temperatures in 2018 were particularly cooler than those in 2013 at heights above ground level (Figure 3).

Herbivore effects

Fire temperatures were significantly reduced by cattle ($p < 0.001$) and by wildlife ($p < 0.001$), but were simply additively (interaction $p = 0.93$), likely due to lower grass fuel loads ($p < 0.001$; Figure 4). Megaherbivores did not add to the wildlife effect overall, in part because they reduced the negative impacts of cattle in plots that they shared (compare MWC to WC, see Young et al., 2021).

Interactions with previous burns and herbivores

Werner et al. (2021) found a positive synergy between previous burn and access to both cattle and wildlife in creating fire heterogeneity (bare patches). This combination also had the lowest temperatures (and all other metrics of fire behavior) in our analysis, but the three-way interactions were not significant for any fire metrics (all $p > 0.60$). In particular, although all microsites burned cooler in plots accessible to both cattle and wildlife (all $p < 0.015$), this was not more pronounced in reburned plots than in plots burned for the first time in any microsite (WC × year of first burn interaction, all $p > 0.60$). This result did not support our prediction of a herbivory × previous fire interaction.

More generally, 2018 burn temperatures were similar in plots that had been previously burned and in plots burned for the first time at all microsites (all $p > 0.6$) with the exception of the (grass) ground layer not under trees, which were hotter in plots burned for the first time (187 vs. 154°C; $p = 0.06$).
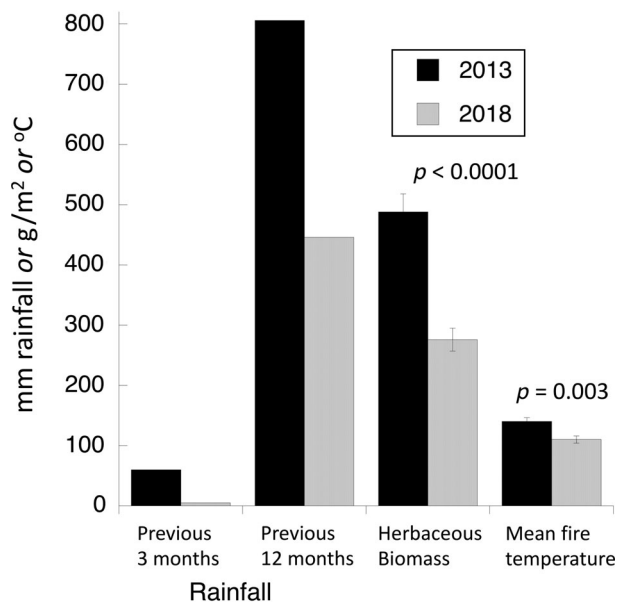
FIGURE 3 Rainfall 3 and 12 months before the burns, mean aboveground preburn herbaceous biomass (in grams per square meter), and mean minimum fire temperature (in degree Celsius) for the 2013 controlled burns and the 2018 controlled burned in previously unburned subplots, across all microsites. Error bars are 1 SD
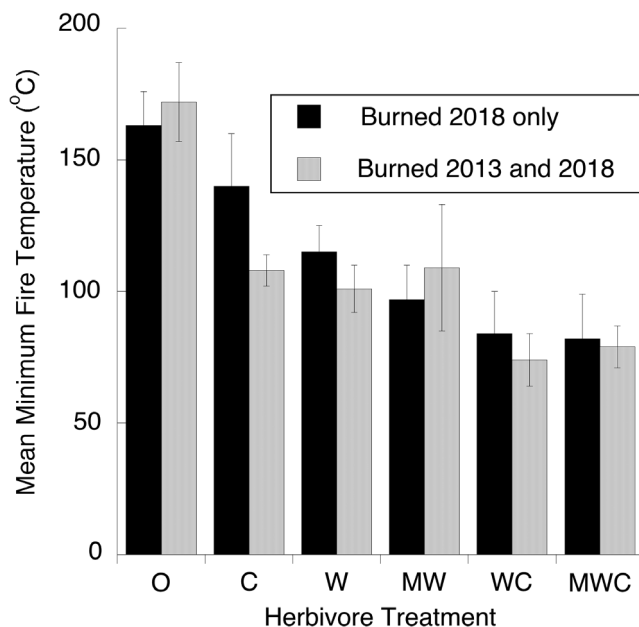
FIGURE 4 Mean minimum 2018 fire temperatures for each of the Kenya Long-term Exclosure Experiment (KLEE) herbivore treatments, for both the subplots burned for the first time in 2018, and those burned in 2018 that had been previously burned in 2013. Letters indicate which large mammalian herbivores are allowed into each KLEE treatment: C, cattle; M, megaherbivores (elephants and giraffes); O, not large herbivores allowed; W, meso-wildlife 20–1000 kg. Error bars are 1 SD

DISCUSSION

Weather prior to and during fire can be a central driver of fire behavior (Hart & Preston, 2020; McGranahan & Wonkka, 2021; N'Dri et al., 2018). Variation in extreme weather conditions has been reported to be associated with variation in grassland fire behavior, even swamping the effects of (natural) variation in herbivory (Launchbaugh et al., 2008). In our study under moderate variation in weather conditions, however, the effects of controlled exclusion of herbivores were strong enough to swamp moderate variation in weather traits (wind speed, temperature, and humidity). Similarly, Fontaine et al. (2012) found that fuels were a better predictor of fire than weather in West African grasslands.

Several of our results were similar to those reported from the 2013 controlled burns in KLEE (Kimuyu et al., 2014): fire temperatures declining sharply with height above the ground (Figure 2), fire temperatures positively correlated with fuel loads, and both fuels and fire temperatures being reduced by cattle and wildlife herbivory. We here extend those results in several ways.

First, we assessed multiple metrics of fire behavior: minimum fire temperature, speed of the flame front, fire residence time, maximum flame height, and flame breadth. It is perhaps not surprising that all of these (some mathematically related) were positively correlated, mostly significantly (see also Fontaine et al., 2012). However, one might expect that fire duration could be negatively correlated with flame front speed. Indeed, this was one of the least strong positive correlations (Table 1), but even here, the overall intensity of the fires appears to trump this trade-off. It is reassuring that our estimates of fire temperature using painted tiles appear to be appropriate surrogates for more complex fire metrics. We also suspect that use of ceramic tiles (micro heat sinks) minimizes registering flash temperatures and may at least partially integrate fire residence times.

Second, mean minimum fire temperatures were significantly lower in the 2018 burns than in the 2013 burns (Figures 2 and 3). Both sets of burns were carried out at the end of the local main dry season (December to mid-March), but the preceding months before each burn differed considerably in total rainfall at the study site. Fire ecologists have long understood that fire risks and behaviors differ considerably between seasons and between years (Johnson & Balice, 2006; Jolly et al., 2015; Platt et al., 2015; Saha et al., 2019), and our results are an experimental version of such year effects. Given the sensitivity of symbiotic ant colonies on *A. drepanolobium* trees within this same range of temperatures (see figure 5 in Kimuyu et al., 2014; Sensenig et al., 2017), these year effects are likely to have major cascading community consequences after fire (see also Werner et al., 2021).

Third, we were able to explore the effects of previous burning on fire behavior by simultaneously burning subplots that had been burned in 2013 to subplots that had not previously been burned. We had noticed in the years after the 2013 burn that certain KLEE treatments, especially some of those exposed to both cattle and wildlife, seem to be much more close-cropped. Werner et al. (2021) found, just before the 2018 burns, that these plots did have significantly larger patches of bare ground, with possible consequences for the sapling survival of *A. drepanolobium*. We were therefore surprised when our analyses failed to find either a general difference in fire behavior, between the reburned subplots and those burned for the first time, or more particularly, and greater reduction in fire intensity in reburned plots that were accessible to both cattle and wildlife (all metrics, all interaction *p* values >0.80).

It appears that this savanna ecosystem was strongly resilient to the effects of burns of this scale 5 years previously, even in the presence of herbivores attracted to these burns, at least with regard to the fire behaviors that we report here. Modeling of fire–herbivory interactions in a different grassland ecosystem suggested that herbivory reduced fire behavior more than previous fire alone, but these differences declined with time, and disappeared for some fire metrics within 3–4 years (Starns et al., 2019). In a separate set of burn experiments in this ecosystem (Sensenig et al., 2010), both 1-ha continuous and patchy (30 × 30 m) burns were no longer attractive to herbivores 6–7 years after fire (Kimuyu et al., 2017). Intermediate-size burns 9- and 81-ha patchy were the most attractive, while large-size 81-ha continuous burns were less attractive. It appears that in our study also, the small burns (30 × 30 m) could not attract enough herbivores to keep reinforcing the primary effects of fire. An isolated exception was in S-WC and S-MWC, where an oryx had established dung middens in the subplots burned in 2013.

This black cotton wooded grassland is fairly fertile and productive (Charles et al., 2017), with moderate rainfall. Perhaps drier or less fertile ecosystems would experience slower or less recovery from fire. The rest from grazing in the months prior to the 2018 burns may also have buffered these effects. There are indications that this ecosystem has in its past experienced more frequent fire, and demonstrates plant adaptations to fire similar to those in other fire-prone ecosystems (Keeley et al., 2011; Pausas & Keeley, 2017), including the resprouting of woody species (LaMalfa et al., 2019; Okello et al., 2001) and vigorous tillering of palatable grasses (Sensenig et al., 2010; T. P. Young, personal observation), and so perhaps this resilience is not surprising. It remains to be seen how general this resilience is of other grass-dominated ecosystems.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.17048330.v1.

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