UNIVERSITY OF NAIROBI

EFFECTS OF POST-FIRE BROWSING ON MORTALITY AND GROWTH OF

Vachellia drepanolobium **TREES IN SEMI-ARID SAVANNA ECOSYSTEM AT**

MPALA RESEARCH CENTRE IN LAIKIPIA, KENYA

BY

NGUGI MARY WAITHIRA

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DECLARATION

I Mary Waithira Ngugi declare that this thesis is my original work and has not been submitted to any other institution for the award of a degree. Any works cited herein have been referenced with the University of Nairobi guidance.

Signature: _____ Date: 28th July 2023

I56/38344/2020

Supervisors

This thesis has been submitted with our approval and permission as university supervisors and we confirm that the work has not been presented elsewhere for an academic award.

Dr. Samuel Kiboi

Faculty of Science and Technology
University of Nairobi

Signature: _____ Date: 31st July 2023

Dr. Joyce Omari

Faculty of Science and Technology
University of Nairobi

Signature: _____ Date: 31st July 2023

Dr. Duncan Kimuyu

School of Natural Resources and Environmental Studies
Karatina University

Signature: _____ Date: 31st July 2023

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF APPENDICES

1. **KLEE Research Grant**

2. **Sample Datasheet used in Data Collection**

LIST OF ACRONYMS AND ABBREVIATIONS

a.s.l- above the sea level

ANOVA- Analysis of Variance

C- Plots accessible to Cattle only

GLMM- Generalized Linear Mixed Models

KLEE- Kenya Long-term Exclosure Experiments

LMM- Linear Mixed Model

MRC- Mpala Research Centre

MW- Plots accessed by mega and wild meso-herbivore

MWC- Plots allowing all herbivores (mega-herbivores, wild meso-herbivore and cattle)

O- Plots excluding all herbivores

W- Plots accessible to wild- meso-herbivores

WC- Plots accessible to all meso-herbivores (wildlife and cattle)

ABSTRACT

Fire and herbivory have been identified as the key top-down drivers of vegetation in savannas ecosystems. There has been a long-standing interest in understanding how interactions between fire and herbivory influence woody vegetation dynamics in savanna. Effects of both fire and herbivory on woody vegetation are quite diverse, including direct mortality, reducing on growth and limited rates, as well as reproductive success. While there is extensive studies on how both fire and herbivory may affect trees in virtually all height classes, vulnerability of trees to ground fires is remarkably higher for coppices and saplings, which are within the height where temperatures from grassy fires are the highest and also because they have less below ground storage, their interaction and implications on tree cover are poorly understood, yet most management decisions in savanna ecosystem revolve around fire and herbivory prescription. This study represents results from controlled, replicated experiments examining how different fire regimes interact with different herbivore groups are rare. This study investigated the effects of single and repeated burns, crossed with six replicated herbivore treatments on mortality and growth of *Vachellia drepanolobium* at Mpala Research Centre (MRC) within the Kenya Long-term Exclosure Experiment (KLEE) plots located in a semi-arid savanna system in Laikipia Kenya. The study examined mortality rates of *Vachellia drepanolobium* coppices and saplings in a controlled burned area, tested the influence of tree height on survival and compared growth rates of coppices and saplings in burned and unburned plots that are either protected or exposed to different herbivores combinations. Data was collected by locating individual trees that were previously marked with an aluminum tag before burning to assess mortality, examine regrowth rates, located survivors were measured, survival class size determined and canopy volume as an index of growth. Data was analyzed using generalized linear mixed models (GLMMs) to assess mortality rate and

influence of tree height on survival while linear mixed models (LMMs) were used to test for growth rate using function ANOVA. 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 megaherbivore. Additionally, mortality was lower in subplots burned for the second time than in subplots burned once but in herbivore treatment accessible by cattle (C, WC, MWC). Cattle ameliorated the negative effects of repeat burns on tree mortality, perhaps by suppressing fuel load accumulation. Across all herbivore treatments taller trees (>100cm) demonstrated a higher survival probability than shorter individuals (<100cm). Yearly height variations showed trees experienced a significant reduction in height within the first two years after fire (top-kill), which was followed by a gradual recovery across all herbivore regimes. Saplings and coppices (here trees <100cm) subjected to repeated burns regrew faster than those that were burned once, except in presence of megaherbivores. Findings from this study provide evidence that fire and herbivory interactively influence woody vegetation dynamics. Specifically, 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 effects of different herbivore groups, or study them separately. Therefore, this study provides significant theoretical and conservation implications.

CHAPTER ONE

1.0   INTRODUCTION

1.1 Background information

Savanna ecosystems are widespread, covering approximately 65% and 80% of land mass in Africa and East Africa, respectively (Augustine and Mcnaughton, 2004). Vegetation cover in savanna ecosystems is highly dynamic, frequently oscillating between woody and grass dominated phases in space and time (Sankaran et al., 2005). These systems receive an annual precipitation ranging between 100-650mm. Savannas support diverse and abundant wildlife, especially large mammalian herbivores (du Toit and Cumming, 1999; Reid, 2012) and recently supported about 50% of livestock population (Georgiadis et al., 2007). These systems are also prone to frequent fires, and fire is believed to have played a major role in their evolution and emergence (Riginos et al., 2012) and large mammalian herbivores still exists in large densities. In Kenya, savannas in Laikipia is the second largest after the Mara-Serengeti ecosystem hosting the most richest biodiversity hotspots and they also support large populations of livestock (Georgiadis et al., 2007). This system has a variety of soil types, but black cotton soil in Laikipia covers approximately 48% and 10% at Mpala Research Centre (Pringle et al., 2016) and are dominated (most common) by *Vachellia drepanolobium* tree species covering over 95% of the woody vegetation (Young et al., 1997) and the biotic community is demonstrative of those in close resemblance ecosystems all over Eastern Africa.

Fire and herbivory are among the main top-down drivers of woody vegetation dynamics in many savanna ecosystems (Archibald and Hempson, 2016; Bond and Keeley, 2005; Keeley et al., 2011; Sankaran et al., 2008), and their effects have ramifications for biodiversity and ecosystem functions (Higgins et al., 2000; Sankaran et al., 2013; Staver and Bond, 2014). While the effects

of fire and herbivory have often been studied independently, it is increasingly apparent that these two drivers interact through complex feedback and their combined effects are often not simply additive (Bond et al., 2005; Bond & Keeley, 2005; Sankaran et al., 2005; Van Langevelde et al., 2003). However, experiments that independently manipulate both fire and different herbivore groups are rare.

Understanding the interactive effects of fire and herbivory is particularly important in African savannas, where fire has a long history (Bond and Archibald, 2003) and rich fauna of large mammalian herbivores in large densities still exists (Reid, 2012). Fire may suppress the density of woody vegetation through direct mortality (Reinhardt and Dickinson, 2010; Ryan and Elliot, 2005), but also indirectly through attracting herbivores to burned areas (Sensenig et al., 2010). 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 (Wilsey, 1996; Sensenig, Demment and Laca, 2010; du Toit and Olff, 2014). Meanwhile, grazers indirectly influence woody cover by reducing herbaceous fuel loads (Kimuyu et al., 2014) or suppressing tree grass competition (Sankaran et al., 2004) while browsers exert a direct effect by browsing and toppling trees (Asner and Levick, 2012; Levick et al., 2015; Pringle et al., 2015).

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 (Kimuyu et al., 2014). Frequent fires may delay the transition of saplings (here trees <100cm tall) to mature individuals (LaMalfa et al., 2019) and retrogress adult trees to the sapling stage via top-kill (hereafter

referred to coppices), 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 particularly elephants and giraffes target taller trees while shorter trees are more vulnerable to small to medium browsers like Grant's gazelle (*Gazella granti*) and steinbuck (*Raphicerus campestris)* (du Toit and Olff, 2014; Moncrieff et al., 2011; Young and Isbell, 1991). Intensive browsing may suppress growth, thus retaining trees within the reach of herbivores, a phenomenon that has been described as a 'browsing trap' (LaMalfa et al., 2019; Sankaran et al., 2013; Staver and Bond, 2014). However, considering the large diversity of herbivores and the vertical stratification in their browsing impact, these studies 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 (Staver and Bond, 2014).

To understand how fire and herbivory interactively increase mortality and suppress the growth of trees, this study conducted a series of controlled burns in the Kenya Long-term Exclosure Experiment (KLEE), which uses semipermeable fences to exclude six different combinations of herbivores. The KLEE experimental plots are located in a nutrient-rich 'black cotton' soil (vertisols) semi-arid savanna ecosystem at Mpala Research Center (MRC) in Laikipia County, Kenya. The dominant (most common) tree species at the study site is *Vachellia drepanolobium*, which constitutes >95% of woody vegetation. Other trees species found in the area include *Senegalia mellifera, Balanites aegyptica*, *Boscia anguistifolia*, *Rhus natalensis,* and *Vachellia nilotica*. This study reports on the interactive effects of different herbivore regimes and fire treatments influence on the mortality and growth of trees.

1.2 Statement of the problem

Previous studies have focused on independent roles of fire and herbivory on woody species cover, it is recently emerging that these two drivers interact in complex ways, some of which may be more than additive (Kimuyu et al., 2014; Sankaran et al., 2008; Sankaran et al., 2005). The research study aimed at investigating the degree to which browsing megaherbivores and mesoherbivores may limit the growth of *Vachellia drepanolobium* tree saplings and coppices after fire damage. While the effects of both fire and herbivory are well studied, relatively few studies have examined the interactive roles of these two drivers in maintaining trees within the vulnerable height class. Yet, there is increasing evidence that both fire and herbivory interact in ways that may be synergistic.

1.3 Justification

In the past century, savanna ecosystems have gone through significant transformations such as increased livestock grazing replacing wildlife and changes in fire regimes as a management strategy. These transformations have resulted in changes in vegetation dynamics. Understanding how interaction between fire and herbivory influence *Vachelia drepanolobium* tree in savanna ecosystems is therefore critical to their management. This study is a critical step in comprehending the techniques that underpin fire-browser effects, hence vegetation dynamics.

1.4 Objectives of the study

1.4.1 General objective

The primary aim of this study was to investigate the effects of post-fire browsing on mortality and growth of *Vachellia drepanolobium* in a semi-arid savanna ecosystem at Mpala Research Centre in Laikipia County, Kenya.

1.4.2 Specific objectives

The specific objectives included;

1. To examine mortality rates of *Vachellia drepanolobium* tree in burned and unburned (control) subplots with different herbivore combinations of megaherbivores, mesoherbivores and cattle

2. To establish the influence of tree height on probability of *Vachellia drepanolobium* surviving fire.

3. To compare growth rate of *Vachellia drepanolobium* adult trees (tree >100cm), and coppices and saplings (trees < 100cm) between subplots burned once and subplots burned twice across the different herbivore treatments of megaherbivore, mesoherbivores and cattle.

1.5 Research hypotheses

1. Differences in tree mortality between burned and unburned subplots does not vary among different herbivore plots.

2. Post-fire survival of *Vachellia drepanolobium* is not influenced by initial tree height.

3. There is no difference in growth rate between trees in subplots burned once and subplots burned twice across all the herbivore treatments.

1.6 Scope and limitation of the study

The study area was located within a site characterized by a homogenous black-cotton (vertisols) soil. This soil type constitutes a significant proportion of savanna ecosystems inclusive of Laikipia. Biodiversity, landscape and soil structure of black-cotton soils contrast with other soil types e.g.,

red soils. This requires precaution in extrapolating results from this study to other systems with different soil types.

Additionally, the experimental plots include manipulation of herbivores (both wild and domestic – cattle) and different fire frequency. This manipulation is meant to mimic land use and management practices by different communities and ranches in most savanna ecosystems. However, the controlled experimental plots cannot fully simulate these practices.

CHAPTER TWO

2.0   LITERATURE REVIEW

African savannas supports diverse groups of herbivores especially the large mammalian herbivores that is elephants and giraffes and often attributed to high heterogeneity in vegetation (Barraquand and Benhamou, 2008; Christensen, 1997; du Toit, 2003; Wiens, 2002, 1997). Additionally, savanna ecosystems are susceptible to frequent fires, while fire is thought to have played a key role in their development and inception (Riginos et al., 2012). Recently these systems have supported a blooming pastoral livelihood that integrates local management practices such as traditional livestock husbandry and episodic burning (Kimuyu et al., 2014). These integrations have influenced the distribution of herbivores within the ecosystem. In African savannas, these changes have influence concerns on the interactive effects of fire and herbivory on woody vegetation. Such concerns have resulted into diverse management approaches such as exclusion of different herbivore groups and different fire frequencies (Riginos et al., 2012). For example, most of the conservancies and ranches are wildlife conservation and livestock production. Additionally, there is eradication of some herbivore groups such as megaherbivores particularly elephants and giraffes and increase in others predominantly livestock and changes in fire as a management tool (Ogutu et al., 2011).

Fire as one of the primary drivers of vegetation heterogeneity (Bond, 2008; Holdo et al., 2009; Kimuyu et al., 2017; Sankaran et al., 2005; Sensenig et al., 2010, 2017). By influencing the quality and quantity of different vegetation elements, fire may in turn influence distribution and movement patterns of herbivores. Understanding factors that influence woody vegetation have been an interesting goal for savanna ecologist (Bond, 2008; House et al., 2003; Lehmann et al., 2014; Sankaran et al., 2004; Scholes and Archer, 1997). While the independent roles of fire and herbivory

on woody species cover have been extensively studied, the interactive effects of these divers on vegetation cover in savanna ecosystem remains poorly understood. Yet it is increasingly evident that these two drivers interact in synergetic ways. Long-term field experiments simulating these management tools could provide practical evidence to inform fire and herbivory prescriptions.

In the savanna ecosystem, fire is among the major ecological determinant that has been applied deliberately for millions of years (Archibald et al., 2005). Traditionally, fire was used as a management tool and it relates to influences landscape heterogeneity through forage quality and quantity (Archibald et al., 2005; Sensenig et al., 2010) and influences woody vegetation structure and composition dynamics such as *Vachellia drepanolobium* (Sensenig et al., 2010). Previous studies suggest that absence of fire could easily switch mesic savanna to woody dominated vegetation (Bond, 2008; Higgins et al., 2007; Holdo et al., 2009; Sankaran et al., 2005). To achieve conservation of biodiversity and sustainable ecology systems, functions, temporal and spatial heterogeneity must be maintained (Wiens, 1997).

Prescribed burning is an ecological and management tool that has been employed in the savanna ecosystem to create and maintain landscape heterogeneity and increase biodiversity composition and structure (Parr and Brockett, 1999; Sensenig et al., 2010). Fire is known to improve the forage quality by removals of herbaceous vegetation and stimulating fresh nutritious growth through changes in vegetation life cycles (Eby et al., 2014; Grady and Hoffmann, 2012; Higgins et al., 2000; Laclau et al., 2002; Staver et al., 2009; Van Langevelde et al., 2003; Wakeling et al., 2011). The new growth attracts diverse numbers of herbivores in burned areas because of high macronutrients concentration such as potassium, nitrogen, phosphorus and magnesium (Sensenig et al., 2010; Wilsey, 1996), resulting to an indirect effect of fire. The implication of fire on woody plants such as *Vachellia drepanolobium* is dependent on individual tree class size (Hanan et al.,

2008; Midgley et al., 2010). Fire suppress growth and increase mortality of *Vachellia drepanolobium* saplings and retrogress mature trees with frequent fires having collective impacts (Midgley et al., 2010) delaying the transition process of saplings to adult trees. The effect of burns on trees cover like *Vachellia drepanolobium* may persist for a long which is dependent on the post-fire herbivory response (Kimuyu et al., 2017). Understanding post-fire herbivory response of *Vachellia drepanolobium* to different fire frequencies can provide importance insights in the managements of savannas.

Herbivores differ in how they utilize landscape influencing diverse interactive outcomes such as an increase in grass biomass and production (Riginos et al., 2009). While megaherbivores particularly elephants reduce tree cover and density in the African savanna (Holdo, 2007; Holdo et al., 2009; Sankaran et al., 2008) through retrogressing adult individuals by knocking them down, stripping their bark and trampling and browsing on saplings (Midgley et al., 2010). This reduces vegetation density through direct mortality increasing predator visibility (Eby et al., 2014; Midgley et al., 2006; Prior et al., 2004). Herbivore utilizations play an important role in ecological structuring and community composition. For instance, in savannah ecosystems, medium to small sized herbivores suppress the height of seedlings and coppices of woody vegetation such as *Vachellia drepanolobium* (Augustine and Mcnaughton, 2004) directly through browsing and trampling. This limits the ability *Vachellia drepanolobium* saplings to grow past a vulnerable height, a phenomenon described as a browsing trap (LaMalfa et al., 2019). For individuals past the sapling stage, the survival rate is higher with an exception of other factors such as fire and drought (Midgley et al., 2010). Most trees recover from heavy browsing by compensation (Midgley et al., 2010) producing dominant apical-meristems that influence horizontal growth for saplings (Midgley et al., 2010) while limiting vertical growth (Augustine and Mcnaughton, 2004; Staver et

al., 2009) leading to prolonged transition (Staver et al., 2009) where saplings and coppices are top-killed by herbivores. Browsing on *Vachellia drepanolobium* adult trees changes the structure (Staver et al., 2009; Staver and Bond, 2014) through height reversals back to saplings where herbivore forage on plant tissues that would otherwise grow past the vulnerable height .

Previous studies have proposed that megaherbivore (here elephants and giraffes) and mesoherbivores (here any herbivore larger than a steinbuck (~15kg) are important in preventing and/or delaying the effects of fire on woody vegetation such as *Vachellia drepanolobium* through foraging hence reducing biomass/ fuel load accumulation (Sankaran et al., 2013; Staver and Bond, 2014), though these theory have not been proven experimentally. Adequate studies have examined the impacts of herbivory on vegetation recruitment rates (Goheen et al., 2010). In the long-term effectiveness and functioning of savanna are critical and for this reason, there has been a rising interest in the causes of their mortality (Asner and Levick, 2012).

Generally, herbivores are known to be attracted to previously burned areas which may support the immediate effects of fire through retaining a dwarf height of herbaceous vegetation and influencing *Vachellia drepanolobium* tree cover (Archibald et al., 2005; Sensenig et al., 2010). Additionally, undesirable effects of herbivores on woody vegetation are escalated by fire (Okello et al., 2008; Pellegrini et al., 2017). Understanding how long post-fire herbivory response may persist is important and remains poorly addressed.

2.1 Interaction of fire and herbivores

In African savannas, fire has a long history (Bond and Archibald, 2003) and rich fauna of large mammalian herbivores in large densities still exist (Reid, 2012). Fire and herbivory interact in ways that may influence biodiversity positively or negatively (Van Langevelde et al., 2003). For instance, fuel load availability influence fire intensity and severity (Stephens et al., 2009) although

other aspects such as moisture content, burning season, wind speed and direction, topography and fuel composition also play an important role (Kimuyu et al., 2014). Through the removal of aboveground biomass, herbivores reduce fuel loads altering fire intensity and severity.

Additionally, different herbivore groups interact differently with vegetation components depending on their body size, nutritional requirement and grazing history (Sensenig et al., 2010). 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 (du Toit & Olff, 2014; Sensenig et al., 2010; Wilsey, 1996). Meanwhile, grazers indirectly influence woody cover by reducing herbaceous fuel loads (Kimuyu et al., 2014) or suppressing tree grass competition (Sankaran et al., 2004) while browsers exert direct effects by browsing and toppling trees (Asner and Levick, 2012; Levick et al., 2015; Pringle et al., 2015). Therefore, different species may impact fire differently.

The contribution of each of these two drivers may vary from one region to another, depending on the underlying climatic and edaphic factors (Sankaran et al., 2004). For example, fire is an important regulator of woody species cover in mesic savannas, where annual productivity is high and there is adequate fuel load accumulation (Kimuyu et al., 2017). In drier savannas, the role of herbivores may be more pronounced than the role of fire because hardly enough fuel loads accumulate to support frequent high intensity fires. Similarly, nutrient levels in soils after fire are higher which may influence plant growth that are nutritious attracting more herbivores in burnt areas in comparison to unburned areas species may impact fire differently. In moderate rainfall and nutrient rich black cotton soils in Laikipia, the effects of either fire or herbivores are hard enough to suppress the dominant *Vachellia drepanolobium* trees. However, combination of both fire and herbivory produce dramatic decline in density of *Vachellia drepanolobium* trees in the

region (Kimuyu et al., 2014). Tree height may mediate the out-turns of both fire and herbivores on trees. Generally, shorter trees are more vulnerable to browsing by many of the medium to large herbivores, as well as to frequent but less severe ground fires that characterize most of the savanna ecosystem. Indeed, in areas where herbivory pressure or fire frequency is high enough, trees may be prevented from growing past this vulnerable height class, a phenomenon that has been described as 'herbivory trap' and 'fire trap' respectively (LaMalfa et al., 2019)

Understanding interaction between fire and herbivory and how they influence tree cover is particularly important and have not been broadly addresses in savanna ecosystem. Most of the existing information is from studies on other ecosystems such as the European temperate ecosystem (Amsten et al., 2021), and studies that do not regulate and supervise grazers in pre-burn areas (Kerby et al., 2007) and those that lack replicates (Leonard et al., 2010). In order to understand long-term effects of post-fire browsing on mortality and growth of *Vachellia drepanolobium,* this study used replicated experiment manipulating six different herbivore groups and two different fire frequencies which is important to a better understanding hence bridging the existing knowledge gap.

CHAPTER THREE

STUDY AREA, MATERIALS AND METHODS

3.0   STUDY AREA

This research study was carried out at Mpala Research Center in Laikipia, Kenya (see Figure 1), on the Kenya Long-term Exclosure Experiment Plots (hereafter referred to as KLEE plots). The study area lies north of the equator, at an altitude of 1800m a.s.l, on the leeward side of Mount Kenya.
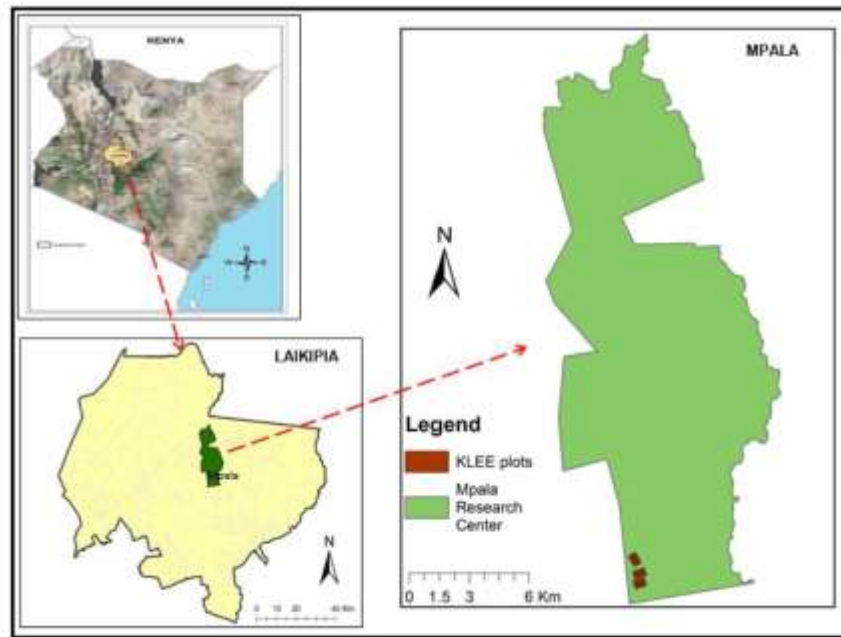
Figure 1: Study area within Mpala research center (MRC) in Laikipia county of central Kenya.

The area can be classified as semi-arid savanna, with a trimodal annual rainfall of 550 – 600mm and one definite dry season from December to March. The study plots are located within the homogeneous heavy clay black cotton soil (vertisol) (Plate 1), which is dominated by *Vachellia drepanolobium* trees constituting over 95% of the tree cover (Young et al., 1997).

Plate 1*: Black cotton soil showing heavy cracking during the dry season*

Vachellia drepanolobium trees grow up to a height of 7m with an average canopy cover of 15-20% (Werner et al., 2021). The tree species have a relatively thick bark allowing them to effectively survive most of the low-intensity ground fires that characterize semi-arid savannas (J. Midgley *et al.*, 2016). *Vachellia drepanolobium* produces swollen thorns that host exclusive mutualistic ant colonies of *Crematogaster mimosae*, *Crematogaster nigriceps*, *Crematogaster sjostedti*, and *Tetraponera penzigi* (Ross, 1979), *(*Plate 2*)*. The *V. drepanolobium* tree species secretes nectar through extrafloral nectarines to nourish the symbiotic ant species (Young et al., 1997). In return, the ants defend the tree from browsers (Palmer et al., 2010; Young et al., 1997).

Plate 2: *Vachellia drepanolobium* tree species

3.1 Major plants and common animal species

Woody vegetation cover in black cotton soil is dominated by *Vachellia drepanolobium* trees. Other tree species in this area comprise *Senegalia mellifera, Balanites aegyptica*, *Boscia anguistifolia*, *Rhus natalensis,* and *Vachellia nilotica*. Herbaceous layer is predominated by five grass species *Pennisetum stramineum*, *P. mezianum*, *Themeda triandra*, *Brachiaria lachnantha* and *Lintonia nutans* accounting for 85% of grass species (Werner et al., 2021), and common forbs species include *Aspilia pleuriseta*, *Commelina* spp, *Helichrysum glumaceum* and *Aerva lanata*. These grass and forbs species form 95% of the non-woody plants (Porensky et al., 2013). Common mammalian herbivores in this region include megaherbivores i.e., elephant (*Loxodonta africana*)

and giraffe (*Giraffa camelopardalis*), mesoherbivores i.e., hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), Grevy's zebra (*Equus grevyi*), African buffalo (*Syncerus caffer*), plains zebra (*Equus burchelli*), eland (*Taurotragus oryx*), warthog (*Phacochoerus africanus*), steinbuck (*Raphicerus campestris)*, Grant's gazelle (*Gazella granti*) and cattle (*Bos indicus*).

3.2 KLEE Experimental design

3.2.1 Herbivore treatment

KLEE plots were established in 1995 and they consist of a series of 18 herbivore exclosure plots with six herbivore treatments that were replicated thrice. Each herbivore plot measuring 200m x 200m (4ha) in three blocks (North, Central, and South) fenced off to exclude different combinations of herbivores using two types of semi-permeable barriers and controlled cattle grazing. The six different herbivore treatments include:

 i) open plots that allow access by all combinations of herbivores (megaherbivore that is elephants and giraffe, wild mesoherbivores and cattle (MWC)

 ii) open plots that allow access by all combinations of megaherbivores and wild mesoherbivores but exclude cattle (MW)

 iii) plots that are fenced off to exclude only megaherbivores but allow access for wild mesoherbivores and cattle (WC)

 iv) plots that are fenced off to exclude megaherbivores and cattle and only allow access for wild mesoherbivores (W)

 v) plots that are fenced off completely and only allow access for cattle (C)

 vi) plots that are fenced off completely and do not allow access for any of the above medium to large mammalian herbivore groups (O) (see Figure 2).
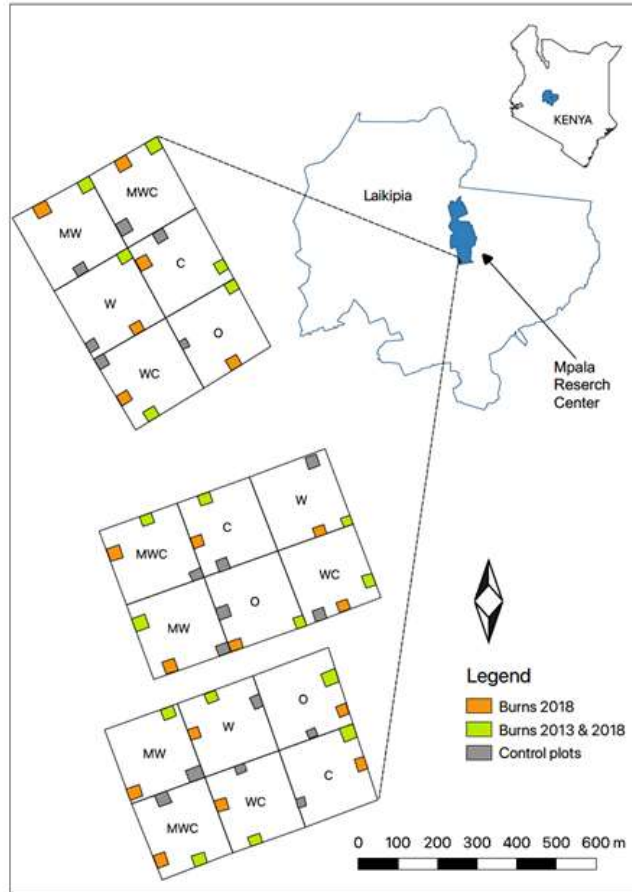
Figure 2: *Layout of KLEE plots showing the location of all the burned and unburned subplots. "Burns 2018" indicates subplots that were burned in 2018. "Burns 2013 & 2018" indicates subplots that were burned in 2013 and reburned in 2018. Letters denote the herbivore groups that were allowed access to a particular plot; M = megaherbivores, W = wild mesoherbivores, C = cattle, and O = completely fenced plots that exclude all herbivore larger than steinbuck (~15kg).*

Semi permeable fences controlling the access of wild herbivores included;

i. Megaherbivore fence (excluding only megaherbivores – Elephants and Giraffes) consist of two electrified wires with dingle dangle strands hanging approximately 1.8 m high to allow all medium to small herbivores to pass underneath while preventing access of megaherbivores *(*see Plate 3*)*

ii.   Fence with 12 stranded of electrified wires at intervals of 17-18cm and stretching up to 2

meters high to exclude all herbivores *(*see Plate 4*)*. This type of fencing used does not

effectively exclude steinbucks, duikers and other smaller herbivores (Young et al., 1997).

Plate 3*:* Two strands and dingle dangles, that allows wild and domestic meso-herbivores (15~

1000kg) to pass underneath while excluding megaherbivores

Plate 4: A twelve-stranded fence that excludes all herbivores except less than a steinbuck (~15kg)

For cattle treatment plots (C, WC and MWC), plots were monitored through controlled grazing where herders graze a herd of about 100-120 cattle for a three-day series, 3-4 times annually, for several hours each day. Depending on forage availability, grazing time and days may differ but the amount of time spent within all cattle plots is equal and the return interval is approximately 16 weeks. This grazing simulates modern livestock management practices in Mpala Ranch, adjacent communal and private areas and other savannah regions at large (Kimuyu et al., 2014). Apart from the 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).

3.2.2 Fire treatment

The first set of burns in each of the 18 KLEE herbivore plots were established in 2013 (Kimuyu et al., 2014). Within each of the 18 KLEE herbivore plots, one subplot measuring 30m x 30m was

burnt in February/March 2013 (Kimuyu et al., 2014) (a total of 18 burned subplots in 2013). A corresponding control 18 subplots (also measuring 30m x 30m) was located at least 100m away from each burned subplot. In February 2018, the subplots that had been initially burned in 2013 were reburned, and additionally 18 new subplots (30m x 30m) were burned (Figure 2) bringing the total burned and unburned plots to 54. All the selected burned and control (unburned) subplots were located in areas with similar tree density and size structure of *Vachellia drepanolobium*, avoiding areas with known source of heterogeneity, such as termite mounds in order to minimize variability across the subplots. Before burning, all trees within each subplot were mapped and individually tagged using a numbered aluminum tag.

To control the spread of fire beyond the designated subplots, fire breaks were created 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. Fire temperatures were monitored using painted ceramic tiles with Tempilaq (LA-CO industries, Elk Grove Village, Illinois, USA) paints. For details on burning protocol see Kimuyu et al., (2014).

Plate 5: Example of a burn in the KLEE plots

3.3 Data collection

a.   Examining mortality rates

Before burning in 2013 and 2018, height was measured (to the nearest cm) of the tallest live tissue

of all individual trees (including saplings) within each of the 36 (30 m × 30 m) subplots and the

corresponding 18 control subplots. After burning in 2013, tree height in the burned and unburned

subplots was measured in July every year for four years (i.e., 2013–2017). Tress was resurveyed

in all the subplots in October to January 2021, three years after reburning in 2018. The new burns

that were implemented in 2018 were only surveyed once in October to January 2021, three years

after burning. During each of the surveys, all of the dead trees were recorded. Trees were

considered to be dead if they lacked any live tissue and (because of top-kill) which was confirmed

during the subsequent surveys.

b.   Establishing the influence of initial tree height on survival

To quantify the effects of tree height on survival, all trees tagged and surveyed before burning were resurveyed in 2021 to confirm whether they were still alive or dead. Dead individuals here were defined by saplings and coppices that were dry and brittle stem, a brownish color under the bark and no leaves or signs of living buds and where there was no signs of the sapling and coppice at all. Trees were scored 0 if dead and 1 if alive.

c.   Growth rate estimation

To estimate tree growth rate across plots, two datasets were used. First, the height of individual trees at least 100cm before the first burns in 2013, was recorded, height was measured (to the nearest cm) of the tallest live tissue of all individual trees (excluding saplings) and subsequently monitored on a yearly basis to examine the variations in height.

In 2022, data on a subset of all the saplings and coppices of trees that were <100 cm in all 36 burnt plots and 18 control plots were collected in February to March. Additionally, measurements of canopy spread, (the length of the longest canopy axis and the length of a perpendicular axis) were recorded. The canopy volume was estimated as an index of growth.

3.4 Data analysis

Mortality rate (*m*) of *Vachellia drepanolobium* trees in each subplot was calculated as follows:

$$m = (\ln n_0 - \ln S_t)/t$$

   Where:

   m is the mortality rate of *Vachellia drepanolobium* trees in each subplot

   t is the time interval between the two sampling periods (here 3 years).

n_0 is the population size during the first survey.

S_t the number of survivors at the time of the second survey (Condit et al., 1999).

The values for mortality rate obtained using the above equation were in open unit scale (0,1). The values were converted to a bounded scale [0, 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 Bayesian standpoint (here s= 0.0001),

N is the sample size (Kimuyu et al., 2017; Smithson & Verkuilen, 2006)

Mortality data was analyzed using generalized linear mixed models (GLMMs) in the R package *glmmTMB* (Brooks et al., 2017) to test 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 effects of herbivore treatment and frequency of fire (burned once versus burned twice). Both GLMM's included the year of burn as a random effect, survival rate was treated as the response variable while plots and fire treatment were treated as the fixed effects.

Generalized linear mixed model (GLMM) in the "*glmmTMB*" R package (Brooks et al., 2017) was used to test the effects of initial tree height on survival across the six-herbivore treatment. Here data analyzed was for the pre-burn only (in 2013 and 2018) where probability of survival in 2021 was depended on initial tree height. This included initial height as the fixed variable and replicated blocks, herbivore treatment plots, and fire treatment subplots as random effects, with subplots nested within plots and plots nested within blocks to address the non-independence of repeated measures within the same subplot.

Further, to examine growth rate, linear mixed model (LMM) using function *lmer* in the "*lme4*" R package (Bates et al., 2015) was used to test for yearly tree height differences in burns across all the herbivore treatment. For this analysis only trees that were initially taller than 100cm prior to burning were selected. The analysis included herbivore treatment and the year that each survey was conducted as the fixed effects and selected unique tree identities as random effects, with tree identities nested within replicated blocks nested within herbivore treatment plots to account for repeated measurements on the same individual over time. Lastly, linear mixed model (LMM) was used to test the interactive effect of initial tree height, herbivore treatment and fire frequency on canopy volume (growth index) of saplings (tree<100 cm). The analysis treated canopy volume as the response variable and as an index of growth, which was dependent on mean growth in height and canopy diameter. Canopy volume was calculated by:

$$Canopy\ spread\ =\ (longest\ axis\ +\ length\ of\ perpendicular\ axis)\ /\ 2$$

$$Canopy\ volume\ =\ \pi\ \times\ canopy\ spread\ \times\ height$$

To test statistical significance of GLMM and LMM models, Type II Chi-square deviance tables were generated using function ANOVA in the package car (Fox and Weisberg, 2019). Type II P-values are calculated using the sums of squares for each main effect conditional on the other main effect. This is the recommended approach for testing significance of GLMM and LMM (Fox and Weisberg, 2019). Statistical significance at $P < 0.05$ was accepted. The "*emmeans*" function in the R package emmeans (Russel et al., 2020) were used to separate means for statistically significant main effects or interactions. All analyses were performed in R programming version 4.0.2 R Code (Team, 2020).

CHAPTER FOUR

4.0   RESULTS

4.1 Rainfall data

Average annual rainfall at Mpala Research Centre (the south most extent where the study area was located) for the period between 2013 and 2022 was 565 ± 80 mm (range: 299 - 877mm). 2019 was the wettest year, while 2022 was the driest year (Figure 3) and April and May were the wettest months (Figure 4).
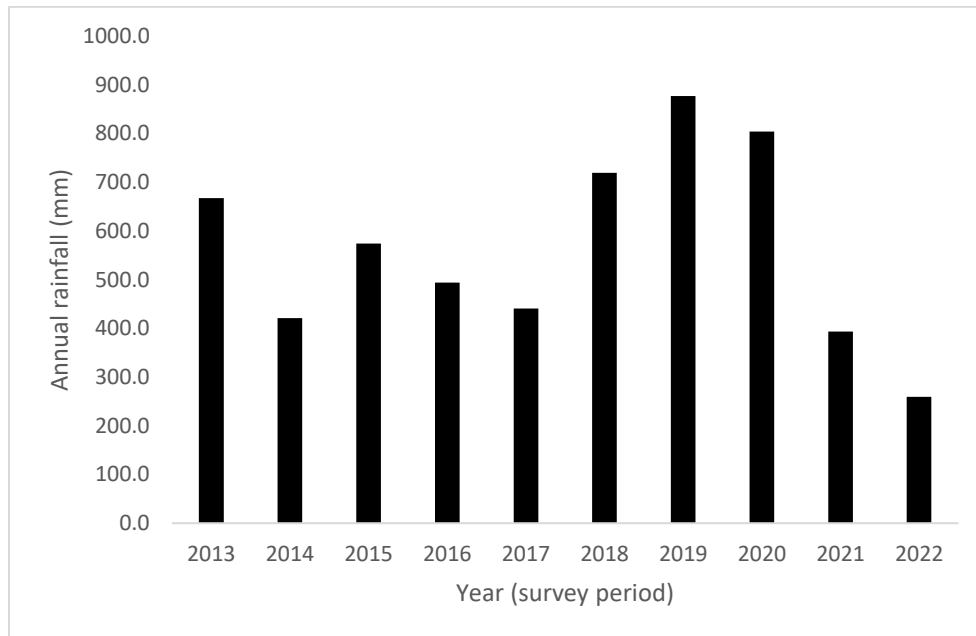
Figure 3: *Total annual rainfall received at Mpala Research Centre between 2013 and 2022 (data source: Metrological database at Mpala Research Centre)*
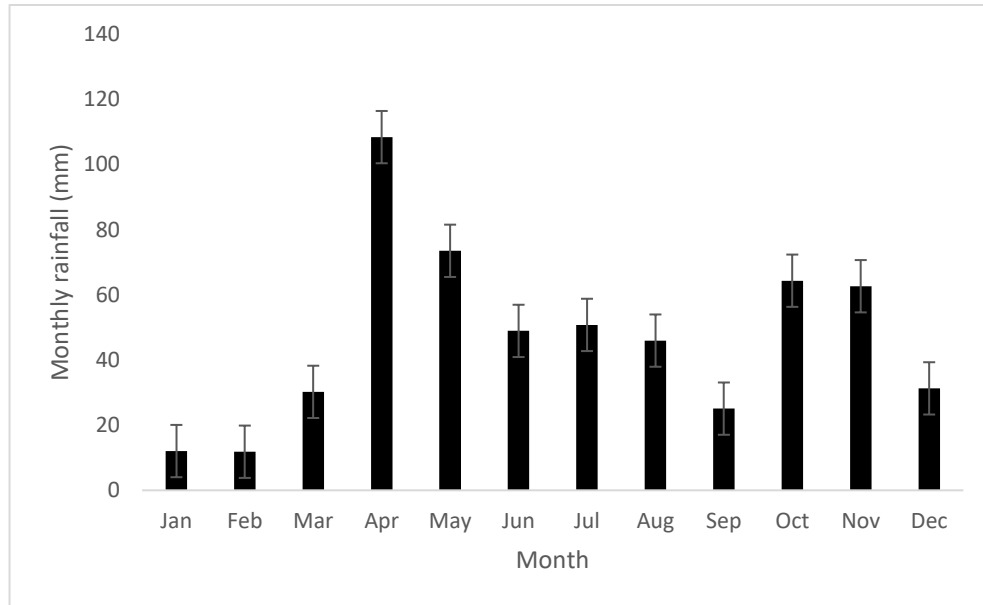
Figure 4: Average monthly rainfall received at Mpala Research Centre between 2013 and 2022 (data source: metrological database at Mpala Research Centre)

4.2 Research findings

A total of 9,854 *Vachellia drepanolobium* trees were sampled, 4,184 were located in the 2013 burns, 2,707 in the 2018 burns, and 2,963 in the unburned control plots. Ten percent (10%) of the originally tagged trees died during the entire survey period between 2013 to 2021.

4.2.1 Effects of herbivory and fire on tree mortality

Here, two different analyses were carried out. The First analysis tested the effects of herbivory regime and fire treatment on tree mortality. This analysis considered subplots burned for the first time (in 2013 and 2018) only and it found that mortality was influenced by the interaction among herbivore treatment and fire treatment ($\chi^2 = 33.48$, $Df = 5$, $P < 0.001$; Table 1, Figure 5). Post hoc analysis revealed that mortality was significantly higher (all $P < 0.05$) in burned than the respective unburned (control) subplots across all the herbivore treatments, except plots accessible to wild

mesoherbivores only (W) and those accessible to both wild mesoherbivores and cattle (WC), (P > 0.05) (see Figure 3).

Table 1: Analysis of deviance table (Type II Wald Chi-Square tests) of Generalized Linear Mixed models (GLMM's) testing the interactive effects of herbivory regime and fire treatment on tree mortality (*P <0.001*)

Response variable	Fixed effects	Wald χ^2	Df	P value
Mortality	Herbivore	20.88	5	0.001
	Fire	22.02	1	0.000
	Herbivore x Fire	33.48	5	0.000
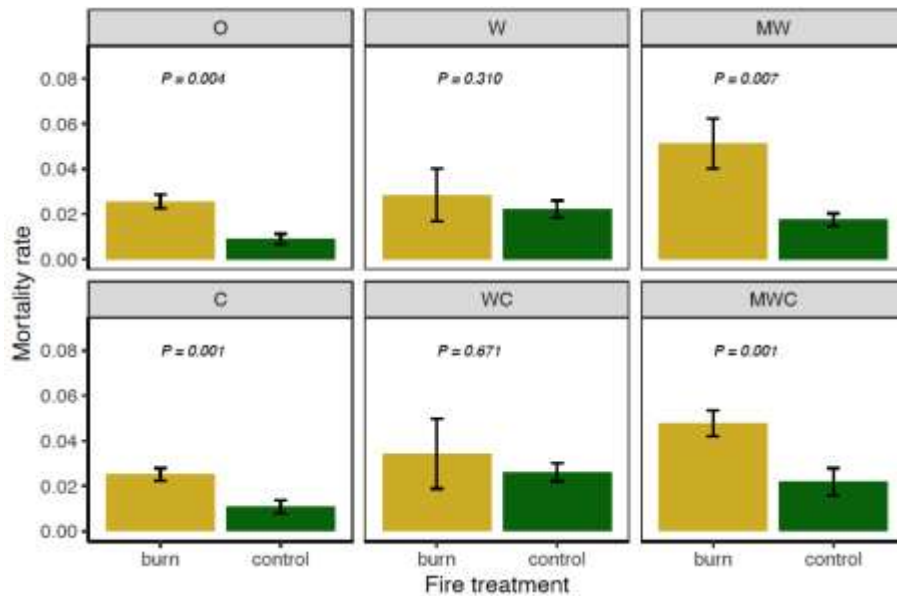
Figure 5: *Effects of fire and herbivore treatment on tree mortality comparing plots burned for the first time (2013 and 2018) and unburned control plots. Error bars represent standard error. P values on top of the bars are obtained from all pairwise comparisons using emmeans package in R (Russel et al., 2020). Letters denote the herbivore groups that were allowed access to a particular plot M = megaherbivores, W = wild mesoherbivores, C = cattle, and O = completely fenced plots that exclude all herbivore larger than steinbuck (~15kg).*

The second analysis tested the effects of herbivory regime and fire frequency on tree mortality. The results revealed that tree mortality was influenced by an interaction between herbivore treatment and fire frequency ($\chi^2 = 20.29$, $Df = 5$, $P = 0.001$; Table 2, Figure 6). Tree mortality rate was lower in subplots burned for the second time than in subplots burned for the first time but in herbivore treatment accessible to cattle (C, WC, and MWC; $P < 0.05$) but not in any other herbivore treatment (all $P > 0.05$; Figure 8).

Table 2: Analysis of deviance table (Type II Wald Chi-Square tests) of Generalized Linear Mixed models (GLMM's) testing the interactive effects herbivory regime and fire frequency on tree mortality ($P = 0.001$).

Response variable	Fixed effects	Wald χ^2	Df	P value
Mortality	Fire Frequency	7.60	1	0.006
	Herbivore	18.82	5	0.002
	Frequency x Herbivore	20.29	5	0.001
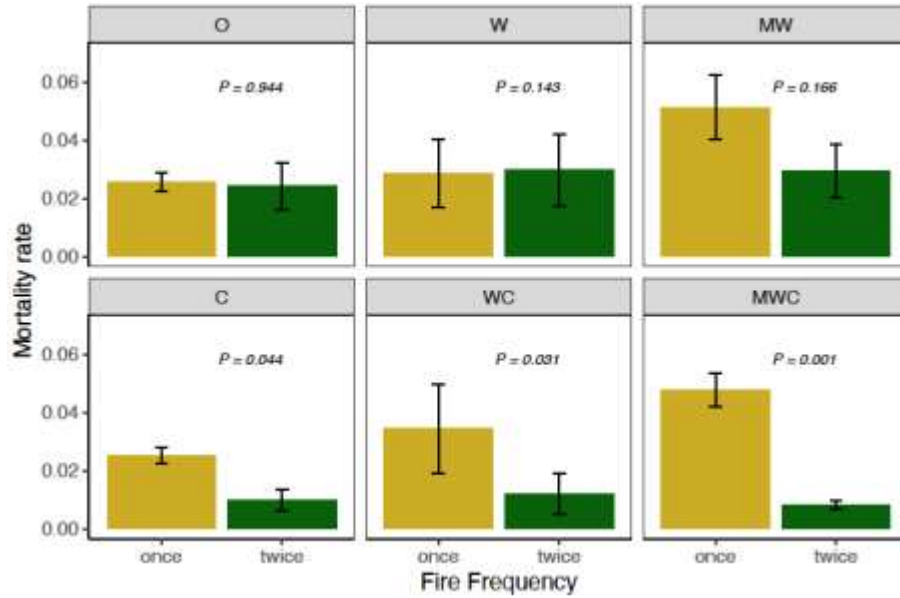
Figure 6: Effects of herbivores and fire frequency on tree mortality in single (once) and repeated (twice) burns. Error bars represent standard error. P values on top of the bars were obtained from all pairwise caparisons using emmeans package in R (Russel et al., 2020). Letters denote the herbivore groups that were allowed access to a particular plot M = megaherbivores, W = wild mesoherbivores, C = cattle, and O = completely fenced plots that exclude all herbivore larger than steinbuck (~15kg).

4.2.2 Effect of initial tree height on survival

This study found that survival probability was influenced by initial tree height ($\chi^2 = 56.024$, *Df = 5, P < 0.001*; Table 3, Figure 7). Although, survivorship was above average across all tree heights, taller trees (>100cm) showed higher survival probability than shorter tree (<100cm). The tree survival curve revealed an increase in survival probability with increase in tree height.

Table 3: Analysis of deviance table (Type II Wald Chi-Square tests) of Generalized Linear Mixed model (GLMM) testing the effects initial height on tree survival.*)*

Response variable	Fixed effects	Wald χ^2	Df	P value
Survival	Initial tree height	56.024	1	0.000
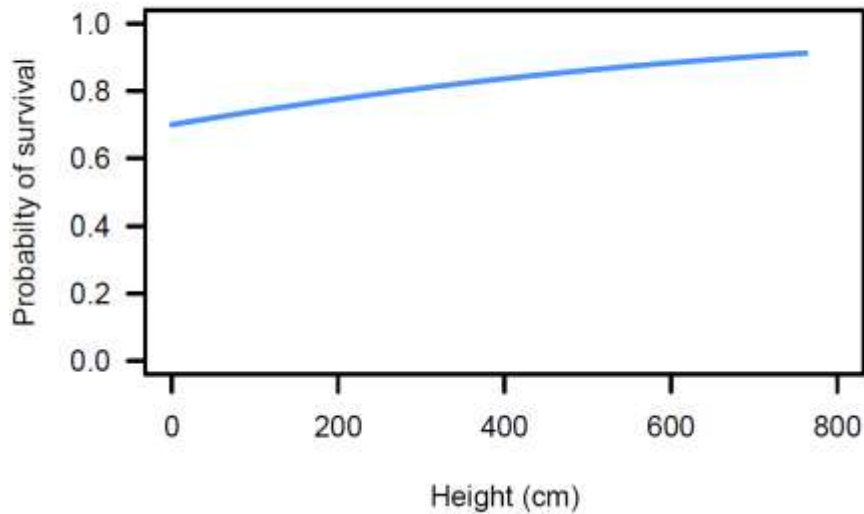
Figure 7: Influence of tree height on probability of survival of Vachellia drepanolobium trees

4.2.3 Effects of fire and herbivory on growth rate

Here, two different analyses were carried out to quantify growth rate. The first analysis tested the effects of fire on tree height. The analysis considered a subset data of trees that were at least 100cm tall before the first burn. The height of the surviving tree varied significantly over the six sampling periods ($\chi^2 = 457.99$, $Df = 6$, $P < 0.05$; Table 4, Figure 8); pre-burn > 2013 & 2014 > 2015, 2016 & 2017. These variations in height were relatively consistent for all herbivore treatments (there was no significant interaction between herbivory and survey period: ($\chi^2 = 2.59$, $Df = 5$, $P = 0.09$).

Table 4: Analysis of deviance table (Type II Wald Chi-Square tests) of Linear Mixed Models (LMM's) testing the effects of fire on tree height in different herbivore combination ($P < 0.001$)

Response variable	Fixed effects	Wald χ^2	Df	P value
Tree height in 2017	Herbivore	13.37	5	0.02
	Survey period	583.25	6	0.000
	Herbivore x Survey period	2.59	6	0.09
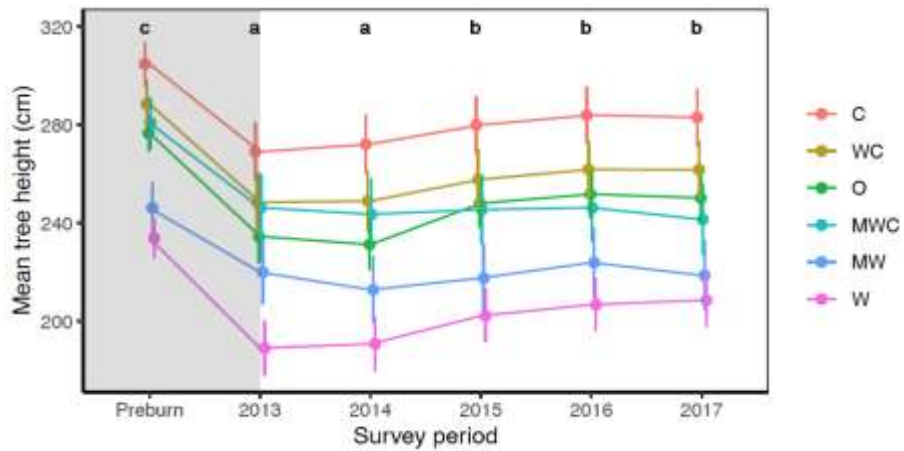
Figure 8: Yearly changes in mean tree height across the six herbivore treatments. Letters inside the graph denote significant yearly differences in mean heights. Different letters denote significant differences in tree height across the sampling periods. Letters on the legend denote the herbivore groups that were allowed access to a particular plot M = megaherbivores, W = wild mesoherbivores, C = cattle, and O = completely fenced plots that exclude all herbivore larger than steinbuck (~15kg).

Further, this study tested the effects of initial height, herbivore treatment and fire frequency on canopy growth. Here, a subset data of 1423 sapling and coppicing of *Vachellia drepanolobium* trees that were below 100cm before 2018 burns were sampled. There was a significant interaction between fire frequency and herbivore treatment ($\chi^2 = 14.15$, $Df = 5$, $P = 0.015$; Table 5, Figure 9), with all the plots that were burned twice showing greater canopy volume than those burned once in all herbivore treatments (all; $P < 0.021$), except those accessible to megaherbivores and wild mesoherbivores MW and MWC (both $P > 0.05$).

Table 5: Analysis of deviance table (Type II Wald Chi-Square tests) of Linear Mixed Models (LMM's) testing the effects initial height, herbivore treatment and fire frequency on canopy volume of sapling

Response variable	Fixed effects	Wald χ^2	Df	P value
Canopy volume	Original height	231.57	1	0.000
	Frequency	56.36	1	0.000
	Herbivore	9.70	5	0.084
	Frequency x Herbivore	14.15	5	0.015
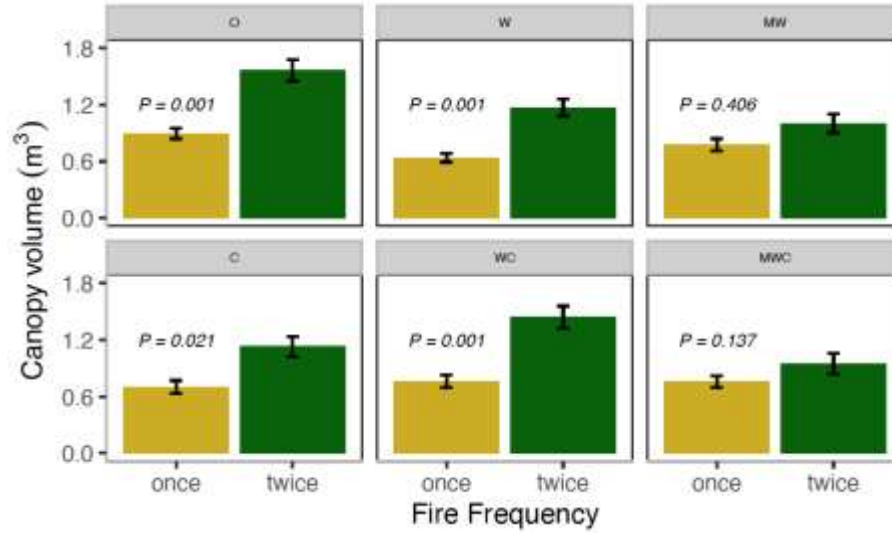
Figure 9: *Differences in sapling/coppice growth (canopy volume) between plots burned once (2018) and plots burned twice (2013 and 2018). Error bars represent standard error. P values on top of the bars are obtained from all pairwise caparisons using emmeans package in R (Russel et al., 2020). Letters denote the herbivore groups that were allowed access to a particular plot M = megaherbivores, W = wild mesoherbivores, C = cattle, and O = completely fenced plots that exclude all herbivore larger than steinbuck (~15kg).*

CHAPTER FIVE

5.0   DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

5.1 Discussion

Results from this study demonstrate strong interactive effects of fire and herbivory on the survival and growth of *Vachellia drepanolobium* tree. Both fire and megaherbivore presence increased tree mortality, but these two drivers interacted in complex ways. Trees that survived previously burned subplots 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 recovers 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.

5.1.1 Mortality rate influenced by fire and herbivore treatment

Consistent with the hypotheses that fire effects on tree mortality varies depending on herbivore combination, this study recorded higher mortality in burned than 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 direct effect of fire. Pre-burn herbaceous biomass and fire temperatures tended to be higher in these two herbivore treatments than in the other herbivore treatments (Kimuyu et al., 2014; T. P. Young et al., 2022) despite the fact that the two plots were usually burned during weather conditions that should have resulted in the coolest burns. But why would there be higher mortality in burned MW and MWC plots, which experienced the coolest temperatures (T. P. Young et al., 2022) and not in W and WC

which experienced intermediate temperatures? This study suggests two possibly interacting explanations. First, it is likely that even low intensity fires in these plots causes significant disruption in ant-acacia mutualism, thus increasing the vulnerability of trees to severe damage by megaherbivore (especially elephants). These results are consistent with previous studies in this system that demonstrated fire causes shifts in plant-ant occupancy, thus increasing susceptibility to elephant damage (Pringle et al., 2015). Secondly, megaherbivores (elephants) may have been attracted to the burns by other factors, such as high-quality regrowth, resulting into heavy browsing damage. Fires are known to stimulate high quality herbaceous regrowth and tree resprouts (Archibald, 2008), which may attract different herbivores including elephants (Sensenig et al., 2010).

This study goes further to provide evidence that in single versus repeated burns, 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), this study found lower tree mortality rates in repeat burns than single burns. This was attributed to reduction of post-fire biomass accumulation; where cattle maintain lower herbaceous vegetation cover in previously burned areas thus reducing severity of subsequent fires. Evidence previously demonstrated in this system suggest that cattle may affect fire spread by creating bare patches that do not carry a fire (Werner et al., 2021). This study site experimental set up, cattle grazing intensity is controlled by herders in a way to simulate episodic grazing consistent with cattle herding practices in the region (Kimuyu et al., 2017). 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 (Odadi et al., 2017). For herbivore treatments WC and MWC, episodic grazing by cattle may maintain forage at higher quality thus attracting other wild herbivores which may additionally retard biomass accumulation

(Odadi et al., 2017). Taken together, these findings suggest that cumulative mortality resulting from frequent fires may be less pronounced in intensively grazed areas than areas experiencing lower grazing pressure.

5.1.2 Influence of tree height on survival rate

Evidence from this study demonstrated that sapling height (<100 cm) is negatively correlated with survival of *Vachellia drepanolobium* tree species. Height is a significant predictor of survival because fires are mostly grass fires and don't get as high thus higher survival of tall trees. These findings suggests that, interaction between tree height and survival, showed that survivorship was dependent on tree height with probability of survival increasing with increase in height, although shorter trees are generally more vulnerable to fire and herbivory than taller individuals. There are several possible explanations for this increase in survival for taller trees. First, it is possible that fire delayed effects on mortality of sapling *Vachellia drepanolobium* trees. Secondly, it is also possible that fire increases susceptibility of sapling trees to herbivores. Third possibility is that factors such as increased quality forage in burned areas attracts herbivores that preferentially browse on sapling trees. Previous studies have shown that elephants preferentially browse on *Vachellia drepanolobium* trees following fire (Goheen et al., 2010) thus attraction other herbivore which may limit survival of sapling trees. This is consistent with previous study in this system demonstrating taller trees have the ability to survive fire even after pre-fire browsing history (LaMalfa et al., 2019), and fully supports predictions that herbivore preferentially browse on sapling/coppices in burnt areas limiting their ability to grow.

Hence this is attributable to why saplings individuals remain at a static height delaying transition to mature tree and at its worse leading to mortality a long-term effect termed as 'fire trap' and 'browse trap' (LaMalfa et al., 2019).

5.1.3 Growth rate

For all tall trees (here individuals >100 cm) that survived 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 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. These findings were attributed 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. Results from this study render partial support to the hypothesis that fire may interact with herbivore to suppress tree growth (in this case increase in height), and are consistent with studies elsewhere (Pellegrini et al., 2017; Staver et al., 2009).

In addition, for saplings (here individuals <100 cm), 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 presence of megaherbivores (MW and MWC). This study attributed the higher resprout vigor in repeat burn 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. This agrees with previous studies in the system, which have demonstrated that the repeat burns were generally cooler (T. P. Young et al., 2022) and more heterogeneous, leaving behind more unburned patches (Werner et al., 2021) than the single burns. Secondly, it is possible that the higher regrowth rates in repeat burns is an artifact of the initial tree height. Previous work has shown that pre-disturbance tree size is a strong predictor of resprout magnitude (Grady and Hoffmann, 2012; LaMalfa et al., 2019; Schafer and Just, 2014; Young and Francombe, 1991) because bigger trees have more root carbohydrate reserves (Schutz et al., 2009) or the depth of the root and surface area (Nolan et al., 2014). Since there is 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 (LaMalfa et al., 2019), megaherbivores (especially elephant) appear to suppress 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 (Shannon et al., 2011; Vanak et al., 2012).

5.2 Conclusion

In a world where herbivores and fire regimes are rapidly changing (due to loss of some herbivore groups and increase in others and 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 important complexities of interaction between fire and herbivores and their implications on the survival and growth of woody vegetation in semiarid savannas.

The research findings presented in this study provide evidence relating to the impact of different herbivore groups on fire which is consistent with the hypothesis that effects of fire on tree mortality vary depending on herbivore combinations of megaherbivore, mesoherbivores and cattle. For example, cattle and wild meso-herbivores may reduce susceptibility of trees to direct effect of fire by suppressing biomass accumulation hence reducing fire intensity and severity while megaherbivores amplify the effects of fire by increasing tree mortality. This study suggest that loss of some herbivore groups would result to increased fuel loads and fire temperatures resulting to increased tree mortality. Replacement of native herbivores and increase in cattle would only compensate partly by reducing herbaceous fuel load accumulation but not woody fuels released by wild herbivores. Secondly, height is a significant predictor of survival. Evidence from this study is consistent with the hypothesis that initial height influence survival. Generally shorter trees are

susceptible to fire and herbivory may persist over a long-time limiting their transition to adult trees and at its worse resulting to mortality, a long-term effect a phenomenon referred to as 'fire trap' and 'browse trap'. Thirdly, megaherbivores amplify the effects of fire by suppressing regrowth of saplings and coppicing trees. Results from this study render partial support to the hypotheses that frequent fires and herbivores would interact to suppress tree growth. Hence, findings from this study could inform fire and herbivore prescriptions to decrease mortality and increase growth rate of *Vachellia drepanolobium* tree and to increase or decrease fire severity and intensity depending on the target management goal depending on the spatial scale and time.

Taken together 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 effects of different herbivore groups, or study them separately. These results represent some of the unique experimental evidence that different herbivore groups interact differently with fire to produce different outcomes for tree mortality and growth in savanna ecosystems.

5.3 Recommendations

An interesting direction for further research on interaction of fire and herbivory would be inclusion of other wildlife groups not considered in this study. For instance, goats could change the outcome of interactive effects of fire and herbivory by influencings browsing impact on *Vachellia drepanolobium.* Additionally, inclusion of other drivers such as soil type and rainfall. For example, the experimental plots in this study were located in black cotton 'vertisols' soils which represent a large proportion of semi-arid savanna ecosystem, inclusion of other soil types could generate a more understanding of some of these complex interactions as well as how precipitation would influence these interactions. Another interesting direction could be understanding tree responses

to annual fire and subsequent herbivory such plant stability, adaptation and resilience to fire and herbivores. Such information is critical in managing fire and herbivory prescriptions to attain management objectives in savanna ecosystems. Some of the results presented in this study are part of a continuous long-term monitoring research that will further highlight more information on interactive effects of different herbivore regime and annual fires in the savanna ecosystems.

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APPENDICES

Appendix : 1.1   KLEE Research Grant

Appendix : 2.1   Sample of datasheet used in data collection