EFFECTS OF DOMESTIC AND WILD HERBIVORES ON VEGETATION QUALITY, COVER, SPECIES TURNOVER AND DIVERSITY RESPONSE TO FIRE IN AN EAST AFRICAN SAVANNA

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR DEGREE OF MASTER OF SCIENCE IN ANIMAL NUTRITION AND FEED SCIENCE OF THE UNIVERSITY OF NAIROBI

SHERRIL PHYLLIS MASUDI
BVM-UNIVERSITY OF NAIROBI

2021

DECLARATION

This thesis is my original work and has not been presented for a degree in any other university.

Investigator

Dr. Sherril P. Masudi (Reg. No. J57/8584/2017)

Signature: ____ ________ Date: _______29th November, 2021_______

Supervisors

This thesis has been submitted with our approval as University supervisors and we confirm that it is the work of Dr. Sherril Phyllis Masudi and has not been presented elsewhere for any academic award.

Prof. Charles Gachuiri [PhD-University of California, Davis]

Sign:_ 29th November, 2021

Department of Animal Production,
The University of Nairobi.

Dr. Wilfred Odadi [PhD- Egerton University]

Sign:___ 29th November, 2021

Department of Natural Resources
Egerton University

Dr. Duncan Kimuyu [PhD-University of Nairobi]

Sign:_ 29th November, 2021

Department of Natural Resources

Karatina University

DEDICATION

This thesis is dedicated to my family whom I consider a pillar in my education, my husband Dr. Jones Mutua and my daughter Amani Mutua.

ACKNOWLEDGEMENTS

My acknowledgement goes to Prof. Charles Gachuiri, Dr. Wilfred Odadi, Dr. Duncan Kimuyu and Prof. Margaret Wanyoike for their support during my MSc work as project supervisors. I am grateful to the Mpala Research Centre fraternity for their hospitality during this study period and to the Kenya Long-term Exclosure Experiment (KLEE) research assistants for assistance with fieldwork.

Special gratitude to Truman Young for granting me permission to conduct this study in the KLEE plots. I am indebted to the University of Nairobi's Department of Animal Production for access to laboratory facilities. My sincere gratitude goes to Mr. Benjamin Kyalo for assistance with laboratory analyses. I am grateful to the Animal Nutrition Laboratory staff; Purity Gakii, Samuel Githua and Nathan Misigo for their technical assistance.

My special gratitude goes to my family; Dad (Yusuf Masudi), Mums (Josephine Masudi and Monica Masudi), Molly, Daddy, Daisy, Sadam, Kezia, Ben, Ken, Bahati, Talia, Butch and Blessing for their prayers and for always giving me a reason to work harder. Special thanks also to my husband Dr. Jones Mutua for being an inspiration and for the moral support he accorded me during my MSc. program.

I would also like to extend my gratitude to the University of Nairobi Scholarship Fund for offering me a scholarship to help me pursue my education. Special thanks to the National Geographic Society for awarding me a grant (Grant #EC-44772R-18) that ensured successful running and completion of this project. Finally, I thank the almighty God for this far, He is Ebenezer.

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LIST OF ABBREVIATIONS

DM	Dry Matter
KLEE	Kenya Long Term Exclosure Experiments
CP	Crude Protein
CF	Crude Fiber
IVDMD	*In Vitro* Dry Matter Digestibility
AOAC	Association of Official Analytical Chemists
NGOs	Non-governmental Organizations

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ABSTRACT

The primary effects of fire on forage attributes such as quality, vegetation community structure (species diversity, turnover and vegetation cover) have been shown to be short lived, diminishing within a few months after fire for forage quality or a few years for cover and composition. There is evidence that herbivores that are attracted to and feed on previously burned areas are able to maintain such pastures in a highly post fire nutritious state for longer thus prolonging effects of fire on the pastures. However, these herbivore effects may differ amongst different herbivore guilds thus there is need for experimental designs that are able to tease out such differences. In this study, therefore, we investigated the separate and interactive effects of cattle and wild herbivores on post-fire herbaceous vegetation nutrient quality, cover and species composition, and how these effects change with time after burning. The study was conducted at the Kenya Long-term Exclosure Experiment (KLEE) site that was established in the year 1995 and is located at Mpala Research Center in Laikipia County, Kenya. The KLEE plots were ideal for this study due to various reasons: First, the plots are designed in a way that the effect of different herbivore species and or groups can be clearly determined; secondly, the study plots are inhabited by a diverse group of herbivores in a way that simulates various savanna ecosystems in Africa; and lastly, the site also boasts of diverse vegetations which are a forage resource to these herbivores. The KLEE setup consisted of six herbivore treatment plots that: 1) exclude all large herbivores(O); 2) allow only cattle grazing (C); 3) allow herbivory by wild mesoherbivores (W); 4) allow combined herbivory by cattle and wild mesoherbivores (WC); 5) allow wild mesoherbivores and megaherbivores (elephants and giraffes) (MW); and 6) allow access to all herbivores (MWC). Each herbivore treatment plot was established in a 4-ha plot and the plots replicated three times in a randomized block design creating a North, Central and South Blocks. Within each plot, controlled burning was applied to a 30m by 30m sub-plot in 2013 and a separate similar-sized sub-plot in February 2018. A similar-sized sub-plot in the unburned matrix, located at least 50 m away from the burned sub-plot was delineated to serve as a control sub-plot. Leaf samples of two main grasses, *Brachiaria lacnantha* and *Themeda triandra* were obtained from each of the sub-plots burned in 2018 and each corresponding control (unburned) subplot at one, four, seven and fifteen months after burning giving a total of 288 grass samples (72 samples per sampling season). The samples were separately analyzed for forage nutritional quality (crude protein [CP], crude fiber [CF], in vitro dry matter digestibility [IVDMD], Potassium [K], Phosphorus [P] and Sodium [Na] contents). These two grass species were selected as they are among the most common grass species at the study site. Vegetation cover, species turnover and diversity were also estimated from pin hit data obtained from vegetation surveys carried out in the sub-plots burned in 2013 and corresponding controls every July since 2013 to 2017. Linear mixed models and GLMM were used to test for the effects of herbivore treatment, fire, grass species and time after burning and their interactions on the measured vegetation attribute. Herbivory did not have significant effect on how forage quality and herbaceous vegetation species diversity responded to controlled burning regardless of the amount of time after fire and the herbivore guild grazing on the pastures. Herbivory however caused a 20%-29% reduction in vegetation cover in the burns of plots O, W, MW, WC and MWC burns compared to controls. Species turnover rate in W, MW, WC, and MWC burns were higher than non-burn controls by 12%-20%. These changes in vegetation cover and species turnover rates however were not demonstrated in plots C and MWC. Therefore, both wild and domestic herbivores have similar effect on post-fire forage quality and species diversity. However, wild herbivores, separately or while foraging with cattle improve species turnover (except when megaherbivores forages with both cattle and the mesoherbivores) while reducing post-fire vegetation cover. The current land uses that simulates the experimental plots thus still remains feasible with regards to vegetation quantity and species diversity. However, more research should be conducted to establish ways of preserving post-fire vegetation cover especially under herbivory by wild herbivores.

CHAPTER ONE: INTRODUCTION

Tropical savanna ecosystems are among the most widespread ecosystems in Africa, comprising approximately 50% of the landmass (Lehmann *et al.*, 2014), and extends from western Africa through central, eastern and southern Africa. Savannas cover about 75% of total land area in East Africa (Reid *et al.*, 2005). In Kenya, savanna ecosystems cover approximately 80% of the land surface area (Stephenes *et al.*, 1990), and extend from the border of Tanzania in the south to the borders of Ethiopia and South Sudan in the north, Somalia in the east and Uganda in the northwestern region. These ecosystems are vital areas for livestock rearing and biodiversity conservation, and also supports human livelihoods (Ottichilo *et al.* 2000, O'Connor, 2005, Kgosikoma *et al.*, 2013, Searchinger *et al.*, 2015). In these systems, fire plays an important ecological role, and has for long been used by humans in livelihoods activities such as hunting, clearing of land for cultivation and improving habitats for wild and domestic herbivores (Mbow *et al.*, 2002, Laris *et al.*, 2002, Sheuyange *et al.*, 2002).

Fire rejuvenates pastures by removing old less nutritious growth, thus stimulating new growth (Van de Vijver *et al.* 1999; Laclau *et al.* 2002; Eby *et al.* 2014), accelerating nutrient recycling by releasing nutrients trapped in litter and old growth (Bodi *et al.*, 2014, Pereira *et al.*, 2015), or altering herbaceous species composition (Bond and Keeley, 2005, Barlow and Peres, 2008, Christin *et al.*, 2008, Edwards *et al.*, 2010, Scheiter, 2012). In similar ways, herbivores may improve pasture quality through increased net primary productivity (Towne *et al.*, 2005, Porenski *et al.*, 2013, Charles *et al.*, 2017), by redistributing nutrients through dung, urine, and carcasses (Bakker *et al.*, 2003, Barthelemy, 2016) and preventing accumulation of old less nutritious growth (Falk *et al.*, 2015). However, both fire and herbivores may also have negative implications for pastures. For example, intensive grazing in burned areas by the herbivores may promote dominance of unpalatable species as a result of selective feeding (El-Keblawy *et al.*, 2009, Al-Rowaily *et al.*, 2015).

Although many studies have examined both independent and interactive effects of fire and herbivory (Fuhlendorf 2009, Allred *et al.*, 2011, Masunga *et al.*, 2013, Eby *et al.*, 2014) on vegetation quality and composition, hardly any study has compared the effects of the different herbivore guilds on herbaceous vegetation responses to controlled burning. Previously burned areas are known to attract many groups of both wild and domestic herbivores, mainly because of improved forage quality but also because of low perceived predation risk emanating from increased visibility and predator detection (Sensenig et al., 2010; Allred *et al.*, 2011, Eby *et al.*, 2014). By preferentially grazing in previously burned areas, herbivores may reinforce the initial impacts of fire, thus maintaining forage in burns at elevated nutrient levels. On the other hand, preferential grazing in previously burned areas may alter herbaceous vegetation species composition and dynamics in subsequent seasons after fire. These responses would be expected to vary based herbivore exclusion for up to 22 years and across different herbivore guilds because of inherent differences in diet selectivity and forage consumption rates (Wang *et al.*, 2011, Müller *et al.*, 2013, Redjadj *et al.*, 2014).

1.1 Statement of Problem

Fire and herbivory have been major forces of determinants in African Savannas for millions of years. Understanding how fire and herbivory interact to shape community structure and composition is fundamental to effective management of savanna landscapes. Fire can influence the distribution of both wild and domestic herbivores, which preferentially forage in recently burned areas. However, there has been little scientific research on whether or not domestic and or wild herbivores have dissimilar effects on how herbaceous vegetation responds to controlled burning. This is an important question because domestic and wild herbivores may differ in their feeding behavior, and can thus influence post-fire vegetation changes differently. Therefore, generalizations based on all herbivores in a system may be misleading. This study examined the extent to which various herbivore guilds, separately and interactively influenced the trajectories in herbaceous vegetation nutrient quality, herbaceous vegetation cover, species diversity and turnover following controlled burning. Such information is required for better management of savanna ecosystems.

1.2 Justification

This study provides information on the separate and combined effects of domestic and wild herbivores on savanna vegetation responses to controlled burning. African savannas provide ecosystem goods and services that are essential for the achievement of food security and livelihoods. Kenyan savannas support over 60% of Kenya's livestock population (GoK, 2008) and wild animals through provision of feed and habitat to these animals. As such, it ensures a continuous flow of meat and milk to the population in addition to improving daily incomes through tourism. The findings of this study are relevant to sustainable management of these multi-use savanna landscapes hence facilitating steps towards achieving food security and poverty reduction in Kenya. Specifically, these findings are beneficial to various stakeholders including ranchers whose ranches doubles as tourism sites and pastoralists whose livelihoods depend on the livestock they keep. Conservationists, national and the local governments will be able to use these findings in developing prescriptions for sustainable management of these savanna landscapes.

1.3 Broad objective

The overall objective of this study was to examine the effects of domestic and or wild herbivores on herbaceous vegetation responses to controlled burning in a multiuse African savanna rangeland for better management of the ecosystem. The specific objectives were to:

1.3.1: Specific objectives

i. Assess the effects of herbivory by the herbivores present at the study site on herbaceous vegetation cover, nutritional quality, species diversity and turnover response to controlled burning
ii. Demonstrate difference and or similarities in how the attributes in (i) responds to fire following separate and or combined herbivory by cattle and wild herbivores on fire effects on the herbaceous vegetation attributes above (i)
iii. Examine whether experimental exclusion of megaherbivores (elephants and giraffes) alters the effects above (i & ii)
iv. Evaluate the effects of time after burning on the above effects (i-iii).

1.4 Research questions

i) Do the effects of controlled burning on herbaceous vegetation cover, nutritional quality, species diversity and turnover differ between areas accessed by cattle and wild ungulates and areas from which these ungulates have been experimentally excluded since the year 1995?
ii) Do cattle and wild herbivores have similar or dissimilar herbivory effects on how the attributes in (i) responds to controlled fire, and how do the separate effects of these herbivore guilds compare to their combined effects?
iii) Does experimental exclusion of megaherbivores alter the responses above (i & ii)?

iv) How do the effects above (i-iii) vary with increasing time since burning?

CHAPTER TWO: LITERATURE REVIEW

2.1 Characteristics and distribution of Tropical Savanna

Tropical savanna ecosystems are found at the boundary between tropical rain forest and the semi-desert vegetation and are characterized by a continuous layer of grass, and sparsely distributed woody vegetation (Langevelde *et al.*, 2003). Rainfall in this ecosystem is widely varied, averaging between 300mm-1500mm annually with distinct wet and dry seasons (Riggio *et al.*, 2013). Globally, tropical savannas cover more than 25% of the total land surface area (Asner *et al.*, 2004, Bond, 2005). Savannas cover a significant proportion of land mass in Africa, Asia, Australia and South America. In Africa, savannas cover approximately 50% of the land area (Lehmann *et al.*, 2014).

Herbaceous vegetation in tropical savannas is dominated by C4 grasses (Ratnam *et al.*, 2011, Lehmann, 2011). The dominance of the C4 grasses is attributed to a number of factors including their ability to effectively utilize the less available nutrients and water (Ehleringer *et al.,* 1997, Knapp and Medina, 1990), as well as adaptability to fire (Scheiter, 2012, Barlow and Peres, 2008), historical decline in levels of carbon dioxide (Ehleringer *et al.,* 1997) and increased rainfall seasonality (Osborne, 2008). While grasses dominate savannas, decline in grass cover due to encroachment of trees and shrubs have been reported in many landscapes (Wigley *et al.*, 2009, Angassa and Oba, 2010).

Based on nutrient content of savanna vegetation, tropical savannas can be grouped into nutrient rich (eutrophic) or nutrient poor (dystrophic) savannas (House *et al.*, 2003, Sankaran and Anderson, 2009). The savannas in the wetter parts of Africa tend to be dystrophic while the eutrophic savannas are found on relatively drier and fertile regions of Africa (Scholes and Walker, 1993). In the arid North African savanna extending to the west of Africa, the vegetation is mainly eutrophic and is dominated by shrubs of *Acacia laeta* and *Acacia tortilis,* and *Balanites aegyptiaca* trees while the grass cover is dominated by annual *Cenchrus biflorus*, *Schoenefeldia gracilis* and *Aristida sti-poides* (Sankaran and Ratnam, 2013). In South African savanna ecosystems with annual rainfall at 200-500mm on average, the vegetation is predominated by succulent stemmed plants e.g. *Aloe dichotoma*, *Euphorbia guerichiana*, and *Moringa ovalifolia* (Sankaran and Ratnam, 2013). This transits into open grassland towards the south of this region with *Parkinsonia africana*, *Acacia newbrownii*, with a dominance of *Boscia species* shrubs . The savanna of East African is dominated by the nutrient poor or dystrophic forages and this has been attributed to the relatively higher annual rainfall (average 600-800mm) it gets unlike similar ecosystems in the North and the West of Africa (Sankaran and Ratnam, 2013). Some of the grasses that dominate the East African savanna include *Themeda triandra*, *Panicum coloratum*, *Aristida adscencionis,* and *Andropogon* and *Eragrostis* species (Sankaran and Ratnam, 2013). At the study ecosystem, grass cover comprises mainly; *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Bracharia lachnantha* (Kimuyu *et al.*, 2016).

2.2. Characteristics of selected East African savanna grasses

2.2.1 *Themeda triandra*

This is a perennial grass which can grow up to 1.5m tall with slender and straight stem which has many branches. The leaves are up to 50cm long and 3mm wide, grey to green in colour but turns to an orange- brown colour in summer (Quattrocchi, 2006). It's a dominant grass species in the Eastern Africa Savanna (Snyman *et al.*, 2013) where it is commonly referred to as red oat grass while in Australia, it is known as kangaroo grass (Fig. 1; (a) and (b). Its growth is usually enhanced by fire (Bennett *et al.*, 2002, Snyman, 2013) hence dominate fire prone areas. Continuous grazing may however impact negatively on its survival as noted by Novellie and Kraaij (2010).

Figure 1**:** Red Oat grass ***(****Themeda Triandra)* stand (a) and seedheads (b). Photo (a) courtesy John Tann and (b) courtesy Peripitus as reviewed from www.feedipedia.org

Themeda triandra is palatable especially when young and in the 1960's, it was perceived by most farmers as a good source of nutrients for beef herds (Marshall and Bredon, 1967). However, in a recent study among the Borana in Ethiopia where farmers ranked grasses in order of preference for grazing, *T. triandra* was excluded from the top five preferred grasses species (Keba *et al.*, 2013). Keba *et al.*, (2013) reported CP levels of between 5.4%-7.3%, ADF values ranging between 44.1%-48.2% levels and NDF values of the order 72.2%-75.3% in *T. triandra* depending on geographical location. Its palatability decreases with increasing maturity (Macandza *et al.*, 2004, Keba *et al.*, 2013). Animals may select against *T. triandra* due to the high stem to leaf ratio, which increases with maturity, coupled with its low protein contents. For instance, buffaloes have been reported to select against *T. triandra* (Macandza et al., 2004) towards the end of dry season. The reason for this is because that at the end of the dry season, most grass species are in the mature state hence is less palatable, less digestible and some are of a low nutritional quality.

2.2.2 *Brachiaria* species

Brachiaria species belongs to the genus *Brachiaria* which forms a vital component of the savanna vegetation acting as an important nutrient source to the various herbivores in this ecosystem (Kelemu *et al.*, 2011). There are about a hundred species of *Brachiaria*, some growing in the savanna while others are cultivated as pastures (Rao and Ghimire, 2016). Their inherent ability to withstand drought and less fertile soil make them an important pasture component in the arid and semi-arid regions of East Africa. Some of the documented species in East African include; *Brachiaria brizantha, B. ruziziensis, B. serrifolia, B. mutica, B. dictyoneura, B. nigropedata, B. solute, B. humidicola, B. radicans, B. serrate, B. jubata, B. leucocrantha, B. platynota* and *B. bavonei* (Keller-Grein *et al.*, 1996).

Brachiaria grasses are indigenous to Africa where they are a natural component of savanna pastures (Boonman, 1993). There is virtually no data on *B. lacnantha* however, a number of important features are documented in the current study. Other species like *B. mulato* are currently grown extensively for cattle feed due to its high crude protein content coupled with reduced stem to leaf ratio (Maass *et al.*, 2015). *B. brizantha* has been reported as a good forage (Musimba *et al.*, 2016, Wassie *et al.*, 2018) with CP ranging between 6.72%-16.33%, 59.9%-76.1%NDF and ADF levels ranging between 41.8%-57.4% (Wassie *et al.*, 2018).

2.2.3 *Pennisetum* Species

These are loosely tufted perennial or annual grasses commonly found growing in the black earth soils and can be up to 90cm high. This genus comprises about 80-140 species (Chemisquy *et al.*, 2010) and in Kenya, among the common ones are Napier grass (*P. purpureum*), Kikuyu grass (*P. clandestinum*), pearl millet (*P. glaucum*), among others. Grasses in this genus are also among the most common C4 grasses found within Laikipia's rangelands (Butynski and de Jong, 2014). *Penisetum mezianum* and *P. stramenium* are the most common at the study site. *Penisetum stramenium* is generally less palatable and mostly dominates rangelands that are in a state of deterioration (Shibia, 2011). *P.stramenium* has up to 10% CP levels, 36.8% CF content and 71.9% NDF content (FAO, 2014) and is more tolerant to high defoliation intensity by intense grazing and also trampling effect thus can do well even in intensely grazed areas (Oba *et al.*, 2000). The CP contents of *P. mezianum* can range from 5.8%-7.4% and NDF at 72.1%-73.6% (Keba *et al.*, 2013).

2.2.4: *Lintonia* species

This is a perennial grass that can grow up to 90cm tall and is common in the savannas of East Africa (Watson, 1992). This genus consists of two species; *L. nutans* and *L. brizoides* of which *L. nutans* is common at the study site (Young, 1998).

2.3 Livestock-wildlife herbivory interactions in tropical savannas

Herbivores can be classified as either grazers, browsers or combined feeders based on the plant types they prefer to feed on (Gordon, 2003). This feed preference is often determined by the anatomy and the physiology of an individual animal's digestive tract. This therefore allows for different herbivore guilds to occupy different nutritional niches. Among these herbivory guilds, interactions during access to feed may be experienced which could either be a facilitation or a competitive interaction (Augustine and Springer, 2013).

Domestic and wild herbivores coexist in most of savanna ecosystem of Africa. However, this coexistence is at a constant threat of competition due to inadequate feed resources in these ecosystems especially forbs (Odadi *et al.*, 2007). Despite being grazers, cattle at times forage for forbs and legumes and this is influenced by season and location. As such, cattle can pose competition to the browsers and the mixed grazers (Fulbright and Ortega, 2006). Odadi *et al.* (2013) reported that this interaction (competition for forbs) can greatly reduce in cases where cattle are given protein supplements as supplementation allows cattle to replace the intake of forbs with increased intake of the low-quality grasses. Supplementation may therefore enable a facilitative relationship between domestic and wild herbivores. Based on seasonality, it has been reported that wildlife causes a reduction in cattle feed intake due to competition as a result of reduced feed availability (Odadi *et al.*, 2011). However, wild herbivores and cattle facilitate each other during the wet season when forage resources are abundant and also under regimes where cattle are fed on supplements (Stears and Shrader, 2020, Odadi *et al.* 2011, Kimuyu *et al.*, 2016, Odadi *et al.*, 2013). Specifically, wild herbivores facilitate cattle diets during wet seasons by encouraging new growth and maintaining pastures in short defoliated nutrient rich status. On the other hand, cattle diet supplementation improves wild herbivore diets by reducing non-grass foraging by cattle making the forbs and legumes available for the wild herbivores (Odadi *et al.*, 2013).

2.4 Effects of herbivores on pasture attributes

Herbivores impact directly on pasture nutrient quality, quantity and composition through consumption of the herbaceous vegetation (Morrison *et al.*, 2016, Liu *et al.*, 2015, Rueda *et al.*, 2013, Kgosikoma *et al.*, 2013). The magnitude of such impact depends on the ecosystem, grazing intensity and herbivore traits such as body size, herbivore combinations and plant traits before herbivory (Liu *et al.*, 2015, Rueda *et al.*, 2013, Veblen and Young, 2010, Nolan *et al.*, 2001). Elephants have been shown to reduce woody vegetation cover by suppressing recruitment of trees or breaking mature trees (Morrison *et al.*, 2016, Asner & Levick 2012, Qolli, 2011). By breaking trees, elephants may impact directly on pastures through reduction in tree density which eventually reduces resource competition among plants allowing increased forage growth in addition to eliminating canopy cover that prevent sunlight from reaching understory vegetation like grasses.

In cases of overstocking, either by domestic or wild animals, ecosystem degradation characterized by pasture depletion and emergence of unpalatable plants and woody plant encroachment may occur. Kgosikoma *et al.*, (2013) in reported that increased cattle stocking rate has been reported to cause pasture exhaustion and depletion. This may lead to reduction in pasture species turnover, richness and diversity. In other studies, uninterrupted selective grazing was noted to cause a decline in the density of *T. triandra* (Snyman *et al.*, 2013). In addition to pasture depletion, overgrazing also causes changes in pasture composition and this can affect livestock production sustainability within an ecosystem (Sankaran *et al.*, 2005).

Moderate grazing however has been reported to reverse the effects of higher intensity grazing (Porenski *et al.*, 2016) and can lead to an increase in species richness and diversity (Wang and Tang, 2018, Milchunas *et al* 1988) and in some cases, cause a long-term stability of the savanna ecosystem (Riginos *et al.*,2018, Milchunas *et al* 1988). Effect of herbivory on pastures also differs based on the types of herbivores that are included in a pasture. For instance, it has been reported that combined sheep and cattle grazing cause a significant increase in vegetation diversity in highly diverse pastures compared to when cattle or sheep, are grazed alone (Liu *et al.*, 2015). The authors also reported that cattle or combined cattle and sheep grazing may lead to an increase in pasture diversity in grasslands with reduced species richness but also cause a reduction in pasture quantity.

Generally, herbivores tend to avoid less nutritious pasture species (Van Beest *et al.*, 2010). Such selective grazing may suppress the palatable species, resulting in an overall reduction in pasture richness and diversity. Pastures also become dominated by the non-palatable species that are less preferred hence no space for recruitment of new growth eventually reducing species turnover rate. Veblen and Young (2010) reported that cattle, giraffes and elephants, through preferential consumption of *Cyanodon plectostachyus* led to a reduction in the cover of this forage species in glades. This was unlike in exclosures accessible only to the medium-sized herbivores in which the forage *C. plectostachyus* was maintained in its previous state through herbivory.

Higher forage CP contents in grazed than non-grazed pastures have also been reported in other studies (Ainalis *et al.*, 2006, Aremu *et al.*, 2007, Anderson *et al.*, 2007, Mikola *et al.*, 2009, van der Waal *et al.*, 2011, Aremu *et al.*, 2016). This effect is attributable to enhanced nutrient cycling (Falk *et al.*, 2015, Novellie and Gaylard, 2013, Archibald 2008, Aremu *et al.*, 2007) in grazed than non-grazed plots. Grazing also can increase forage and soil K, Ca, Mg and P (van der Waal *et al.*, 2011) and these become available to the animals feeding on the forages. Henkin *et al.*, (2011) demonstrated that pasture CP, digestibility, NDF and ADF increases with increasing grazing intensity as grazers are able to maintain younger herbage and new regrowth at higher nutritive status during the growing season. Another study however reported a reduction in CP and an increase in ADF and NDF with no significant difference in digestibility in grazed pastures compared to non-grazed pastures (Bell *et al.*, 2020). In absence of herbivory or under low grazing intensities, increase in vegetation biomass has negative impacts on overall pasture heterogeneity (Jacobs & Naiman, (2008) as there is no opening up of microsites for new growth.

2.5 Occurrence and ecological effects of fires in the savanna ecosystem

Fire, an abiotic component of an ecosystem, is either of natural origin as seen with lightning strikes or can be human induced (Trollope and Trollope, 2010). African Savanna has high occurrence of fires that has been attributed to its distinct climatic conditions (dry season and wet season), lightning and the available vegetation and fuel loads which are highly flammable especially during the dry seasons (Trollope, 2011, van Wilgen, 2009). This has led to the establishment of open canopies due to reduction in tree densities and also establishment of the fire adapted C4 grasses (Beckage *et al.*, 2009).

Fire has been used by pastoralists as a means of pasture management and to improve pasture quality for their livestock in Africa (Klop, 2009, Trollope, 2011, Odadi *et al.*, 2017). In a study in South Eastern Montana, it was noted that through burning, the nutritional quality of Purple threeawn (*Aristida purpurea* Nutt.), which usually is not preferred by herbivore (due to low forage quality), was significantly improved (Dufek *et al.*, 2014). Burning increase forage CP and digestibility while decreasing forage CF (Gul *et al.*, 2014, MacGranaham *et al.*, 2014), increases forage digestibility (Klop, 2009). This increase in forage quality after burning have been attributed to the elimination of dead and mature pasture components hence creating space for new growth with high leaf to stem ratio (Van de Vijver *et al.*, 1999). These however are inconsistent with findings by Anderson *et al.*, (2007) who reported lower CP levels in grasses from burns compared to those from non-burns. This finding by Anderson *et al.*, (2007) was attributed to fire ability to encourage low quality fire adapted grasses but suppressing higher quality forages and show the need of avoiding frequent fires that can lead to undesirable vegetation shifts.

Bebawi and Campbell (2002) reported that through burning, smoke and the elevated temperatures caused the seeds of Bellyache bush (*Jatropha gossypiifolia*) to undergo scarification hence promoting seed germination and seedling growth. Also, through burning of above ground organic matter, nutrients are retained in the soil in form of ash and these acts as reservoirs for plant nutrients requirement (Bodi *et al.*, 2014, Pereira *et al.*, 2015). Such nutrients like Phosphorus, Sulfur and Nitrogen are then absorbed by plants and become available to the animals that consume such plants. Burning thus is beneficial to pasture since despite the elimination of the organic matter, it still makes available the inorganic matter rich ash from the burned dead or moribund forages to the new post fire regrowth. As a result, wild herbivores tend to be attracted to these burnt pastures because of their enhanced nutritional value (Klop, 2009, Eby *et al.*, 2014). This therefore impacts on the distribution of herbivores (Kimuyu *et al.*, 2016) and eventually affect pastures utilization by the animals.

2.6 Fire and Herbivory Interactions.

There is evidence of footprints of an interactive effect between fire and herbivory in the world's ecosystem (Bond *et al.*, 2005). This evidence has been used to explain in part the creation and maintenance of grasslands and savannas (Milchunas *et al.*, 1988; van Langevelde *et al.*, 2003; Anderson 2006). These interactions change in space and time hence their effect may not be constant (Fuhlendorf and Engle, 2004). The interactive effect has at times been termed as pyric herbivory which refers to spatial and temporal interactions between grazing and fire that enhance changing patterns of disturbance across ecosystems (Fuhlendorf *et al.*, 2009).

Both domestic and wild herbivores, are particularly significant in the savanna because of their cohabitation in this ecosystem. These are either grazers or browsers and their interactive effect, by themselves and with fire, on the savanna has been reported to be more pronounced than their individual effects especially in the fire dependent landscapes (Fuhlendorf *et al.*, 2009, Allred *et al.*, 2011). It has been reported in some studies that allowing herbivores to graze or browse on vegetation can cause a reduction in fuel loads within the savanna grassland (Kimuyu *et al.*, 2014), a negative impact of herbivory on the effect of fire.

Because burning increases pasture nutrient quality thus attracting more herbivores, fire can indirectly cause a decrease in species richness overtime through herbivory (Dorrough and Moxham, 2012, Archibald *et al.*, 2005). As herbivores consume this post burn regrowth, they can cause a reduction in plant abundance (Scholes and Archer, 1997, Riginos and Young, 2007) in burnt areas and also reduce biodiversity. Reduction in diversity may be due to grazers tending to select more nutritious pasture species against species with low nutrient contents (Dorrough and Moxham, 2012). With increased selectivity over time, the pasture becomes dominated with the grazing tolerant or less nutritive and less palatable species as the more nutritious are depleted (Jacobs & Naiman, 2008, Archibald *et al.*, 2005)

There is evidence from other studies showing that periodic drought seasons with moderate cattle grazing, spaces are created on which rare plant species germinate (Porenski *et al.*, 2013). With time, pasture species diversity and abundance are increased. Fuhlendorf and Engle, (2001) reported that combination of controlled burning and herbivory by indigenous grazers led to the creation of a heterogenous vegetation structure in the European grasslands even before the European settlement. Thereafter, it was also noted that species richness for both plants and animals is enhanced with reintroduction of grazers in a way to simulate the interactions between grazers and fire during the pre-settlement period (Hayes and Holl 2003; Fuhlendorf *et al.*, 2006; Engle *et al.*, 2008; Burns *et al.*, 2009).

The interactions between herbivory and fire also influences pasture nutritive value and quality. In a study by Masunga *et al.*, (2013) an increase in nitrogen content of pastures in fire treated and grazed plots compared to fire-alone treated plots was reported. As herbivores graze on previously burned pastures, they are able to reinstate the initial effects of fire on pasture quality. This is explained by their ability to maintain pasture plants in a relatively short and highly nutritious state and also via nutrient recycling through dung and urine (Archibald 2008, Novellie and Gaylard 2013). Continuous defoliation also helps in enhancing forage nutritive value as has been demonstrated in other forages (Ren *et al.*, 2016, Bai *et al.*, 2012).

2.7 Research gaps

The primary effects of fire on forage attributes such as quality and quantity have been shown to be short lived, diminishing within a few months after fire for forage quality (Nghalipo *et al.*, 2019, Eby et al. 2014, McGranahan *et al.*, 2014) or few years for vegetation quantity, cover and composition (Klanderud *et al.*, 2010, Adedoja *et al.*, 2019). There is evidence from previous research showing that the herbivores that are attracted to and feed on the previously burned areas are able to maintain such pastures in the status they were just after the burning thus prolonging effects of fire on the pastures. This can be attributed to the maintenance of such pastures in short-cropped highly nutritious condition, and also through nutrient cycling from dung, carcasses and urine (Archibald 2008, Aremu *et al.*, 2007, Novellie and Gaylard 2013, Falk *et al.*, 2015).

There is little information as to whether domestic and wild herbivore guilds have different effects on post-fire forage nutrient value, vegetation cover, species turnover and diversity. This aspect forms an interesting question since herbivores differ in their feeding behaviour, and can thus influence post-fire vegetation differently. It has been noted that different herbivores may have different effects on forages (Charles *et al.*, 2017, Towne *et al.*, 2005, Carpio *et al.*, 2015, Coughenour, 1991, Kgosikoma *et al.*, 2013, Snyman *et al.*, 2013, Liu et al., 2015). Hence, generalizations based on all herbivores in a system may be misleading. The focus of the current study therefore was to compare differences in nutrient parameters and vegetation cover and composition dynamics of burned plots that have been subjected to herbivory by different herbivore guilds, so as to establish trajectories on how these different herbivore groups that inhabit the savanna may influence vegetation response to fire. This information is vital for sustainable management of these multi-use savanna landscapes hence facilitating steps towards achieving food security and poverty reduction in Kenya.

CHAPTER THREE: MATERIALS AND METHODS

3.1 Study Area

3.1.1 Location and size

This study was conducted at the Kenya Long-term Exclosure Experiment (KLEE) site located at the Mpala Research Centre and Conservancy in Laikipia County, Kenya (Fig. 2). Laikipia County and is an intermediate zone between the dry and the wet areas of Eastern and Central Kenya respectively. It covers an area of 9,462 km^2. Mpala Research Centre and Conservancy is located in Central Laikipia and covers approximately 192 km^2 on latitude of 0^o $17^'$ N, 37^o 52' E and 1810 m altitude above sea level. The study site satisfied the requirements needed to achieve the objectives its design into exclosures allows for the effects of the different herbivore species and groups to be teases apart. In addition, the study site also offer habitation to a diverse group of herbivores, domestic and wild and is thus a representation of other savanna ecosystems.

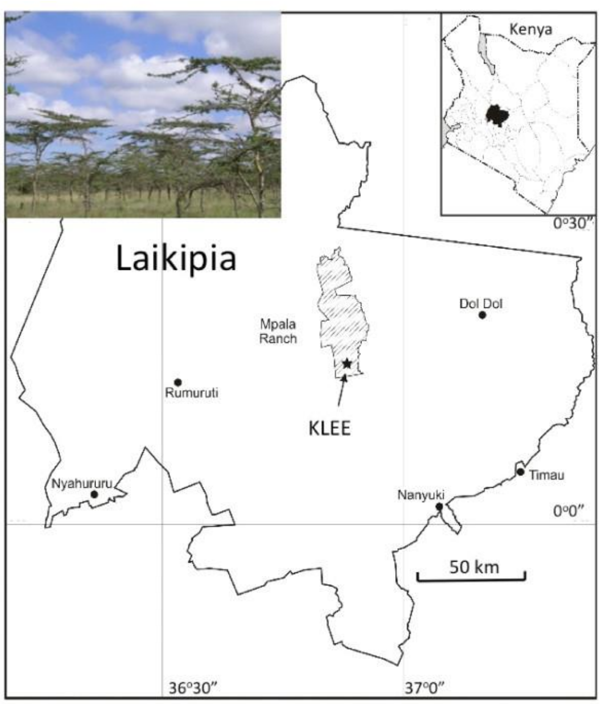


Figure 2: Map showing the locations of Laikipia County, Mpala Research Centre, and the Kenya Long-term Exclosure Experiment (KLEE) where this study was conducted. The inset photo shows vegetation structure at the study site. Photo Credit: Kari Veblen

3.1.2 Climate attributes of the study area and study site

Laikipia County is majorly made of plateaus and has an altitude ranging from 2000m to 2250m and 2500m at the Aberdare and Mount Kenya slopes respectively. The county lies between latitudes 0°17′S and 0°45′N and longitudes 36°15′E and 37°20′E. Annual rainfall in Laikipia ranges between 700mm at the southern parts to 3000mm in the North. The rainfall trend is mainly determined by the north, south and east trade winds, westerly winds and the inter-tropical convergence zone. Rainfall in Laikipia County averages 400-750mm with the long rains occurring from April to May, short rains in August and November and a dry season from January to March (Atsiaya *et al.*, 2019). Annual rainfall at the KLEE study site averages 500-600mm of rainfall annually (Kimuyu *et al.*, 2014). The rainfall pattern is slightly trimodal being higher in April, August and November with a dry season commencing in December and ending in March. The average temperature at the study site ranges between 12^{o}C and 35^{o}C.

3.1.3 Soils and vegetation

Laikipia County primarily comprises semi-arid savanna rangelands, with a few isolated pockets of dry forests and woodland. The soil in Laikipia is mainly black cotton which comprises *c*. 50% clay and *c*. 24% sand and red soil comprising *c*. 74% sand and *c*. 15% clay (Young *et al.*, 1998, Augustine 2003). Primarily, the Laikipia ecosystem is dominated by grasslands, bush and woodlands in addition to dry forests and these are spread all over the county depending on the prevailing environmental conditions. At the dry forest, *Juniperus procera, Olea europaea, Afrocarpus gracilior, Euclea divinorum, Acokanthera schimperi* and *Croton maegalocarpus* are the main vegetation (Butynski and de Jong, 2014). The central part of Laikipia where our study site is located is mainly covered by bush and woodlands with *Acacia drepanolobium* being the main woody vegetation at the black cotton soil (Young *et al.*, 1997, Riginos *et al.*, 2009). It has a continuously spreading grasscover comprising mainly of *Pennisetum stramineum*, *Pennisetum mezianum*, *Brachiaria lachnantha, Themeda triandra,* and *Setaria sphacelata*. At the red soil however, grass cover is discontinuous mainly dominated by *Digitaria milanjiana*, *Cynodon dactylon, P. stramineum,* and *Chloris roxburghiana* while the dominant woody vegetation is *Acacia mellifera, Acacia etbaica,* and *Acacia brevispica.* At the KLEE plots, above ground woody vegetation is dominated by *Acacia drepanolobium* while there are five main grasses; *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Bracharia lachnantha* (Kimuyu *et al.*, 2016).

3.1.4 Land use activities at the study area

Because of the prevailing vegetation, edaphic and climatic conditions, Laikipia County largely supports livestock rearing and is generally less suitable for crop cultivation (LWF, 2013). Livestock rearing is mainly conducted in ranches that are either privately owned, government, community or company owned and these ranches covers over 50% of the total land area. Livestock keeping thus is a source of livelihood to about 80% of the population (CAS, 2013). In addition to being a home for domestic animals, the county also provides habitat to approximately 65% of wildlife in Kenya (Frank *et al.*, 2005) and is thus important for wildlife conservation and wildlife-based tourism.

3.1.5 Faunal life of Laikipia savannas

The savanna rangelands of Laikipia host a high diversity of animals and have been reported to have some of the highest population densities of domestic and wild animals in Kenya (GoK, 2018, Georgiadis, 2011). The main wild ungulate species in this county include: elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), Burchell's zebras (*Equus quagga burchellii*), rhinoceros (*Diceros bicornis*), Grants gazelles (*Nanger granti*), Thompson's gazelles (*Eudorcas thomsonii*), impalas (*Aepyceros melampus*), buffaloes (*Syncerus caffer*), elands (*Taurotragus oryx*) and grevy zebras (*Equus grevyi*) among others. Most of these species occurred at the study site. Livestock production is widely practiced in most parts of the county is a source of livelihood to about 80% of the population (CAS, 2013). Among the dominant domestic ungulate species are cattle, sheep and goats and the populations of these ungulates have been estimated at 266,200 cattle, 344,200 sheep, and 322,000 goats (GoK, 2018). Mpala Research Centre and Conservancy has a livestock ranch with cattle, sheep and camels as the main livestock species. Only cattle are the domestic livestock that have access to the study site.

3.2 Study design

3.2.1 Herbivory treatments plots design

The study used the Kenya Long-term Exclosure Experiment (KLEE) study plots established in 1995. The KLEE consists of a series of 4-ha (200 m x 200 m) plots designed to hold different combinations of cattle and wild ungulates (See Young *et al.*, 1998) including: livestock (mainly cattle, C), wild mesoherbivores (large mammals 15–1000 kg, W), and wild mega-herbivores (over 1000kg; elephants and giraffes, M).

Overall, KLEE comprises six herbivore treatment plots, with each treatment replicated three times, resulting in a randomized block design consisting of three blocks (North, Central and South) thus 18 herbivore treatment plots (Figure 3). The six KLEE herbivore treatments are:

i. Full fencing (with twelve evenly spaced wire strands) to exclude all herbivores (O).

ii. Full fencing with a gate that remains closed and is opened to allow cattle grazing within the exclosure (C) as further explained in section 3.2.3.

iii. Single strand electric fence high enough and with wire strands hanging about 1.5m tall to exclude megaherbivores (elephants and giraffes) but accessible to other herbivores (WC).

iv. Single strand electric fence excluding megaherbivores and cattle but allowing mesoherbivores (W)

v. Treatment excluding cattle but allowing megaherbivores and mesoherbivores (MW)

vi. Treatment is accessible to cattle, megaherbivores and mesoherbivores (MWC)

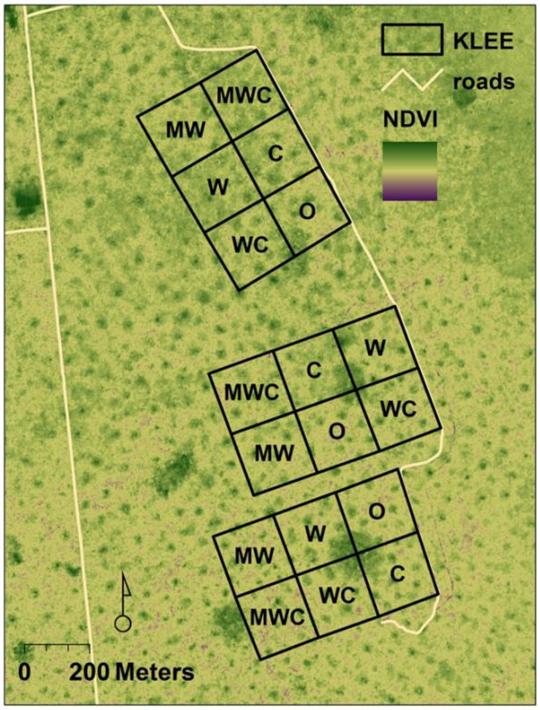


Figure 3: Outline of the Kenya Long-term Exclosure Experiment (KLEE) study plots showing herbivory treatments and experimental blocks.

Full descriptions of herbivory treatments are provided in subsection 3.2.1. Source: KLEE**.**

3.2.2 Burning treatments sub-plots design

In each of the 18 herbivore treatment plots (Fig. 3), a 30m by 30m subplot was subjected to controlled burning in February-March 2013 (Fig. 4). Further, additional new 18 separate subplots of similar dimension were subjected to controlled burning in February 2018. In addition to the burned subplots, a 30m by 30m unburned sub-plot in the unburned matrix in each herbivore treatment plot was demarcated for use as a control sub-plot based on the vegetation and landscape similarity with the sub-plots intended for burning. The 30m by 30m area covered 2.25% of each herbivore treatment plots thus leaving the remaining spaces unburned to be used for other research purposes. These burned subplots and the respective controls were demarcated within each plot using the following criteria: (1) subplots were demarcated along the plot border to make it accessible to the burning crew members and the equipment in addition to fire-fighting equipment, (2) landscape features heterogeneity (e.g., presence termite mounds and old livestock bomas/kraal) were avoided, and (3) similarity based on the density and size structure of the trees especially *Acacia drepanolobium* trees (.1 m tall) and understory composition (see Young et al. 1998, Kimuyu *et al.*, (2013). Burning was carried out in February-March as this period marks the end of the dry season and is a month away from the beginning of the early rainy season in April (Kimuyu *et al.*, 2014) thus the rains could facilitate post fire vegetation recovery. For more details on how the controlled burning was conducted, see Kimuyu *et al.*, (2014)

Figure 4: Controlled burning at the Kenya Long-term Exclosure Experiment (KLEE) in 2013. Photo Courtesy Matthew Snider

3.2.3 Cattle and wildlife use of study plots

Cattle accessed the C, WC and MWC treatment plots at given planned timing yearly depending on forage availability. During every cattle run, 100-120 animals were herded in each of these plots for a maximum of three consecutive days. Every grazing took two hours per day with grazing in the burns being restricted to 2-3 minutes (Odadi *et al.*, 2017). Cattle runs were conducted at the plots for a maximum of four times a year and these runs are dependent on forage availability (Odadi *et al.*, 2017). This regime was designed to reflect the grazing practices used in the study region (Veblen *et al.* 2016). Wild herbivores grazed and or browsed at the experimental plots accessible to them *ad lib* and throughout the year and this simulated the naturally uncontrolled nature by which these wild herbivores accessed the savanna grazing lawns.

3.2.4 Rainfall pattern and periods of cattle runs during the study period

The average monthly rainfall during one of the study periods (February 2018 to May 2019) was 530mm (Standard deviation = 54.5); with three rainfall peaks in April 2018, October 2018, and April 2019 and two distinct dry periods between July to September 2018 and January to March 2019 (Fig. 5). For 2018 burns, cattle were grazed in the plots three times during the study period (Fig. 5). For the 2013 burns, first cattle run post fire in plots accessible to cattle conducted only for a two hours duration, the second one carried out 49days later and this marked last cattle run before the first vegetation survey that was conducted after over 30days later and the other cattle runs in the succeeding years after 2013 were conducted about 4 times every year.

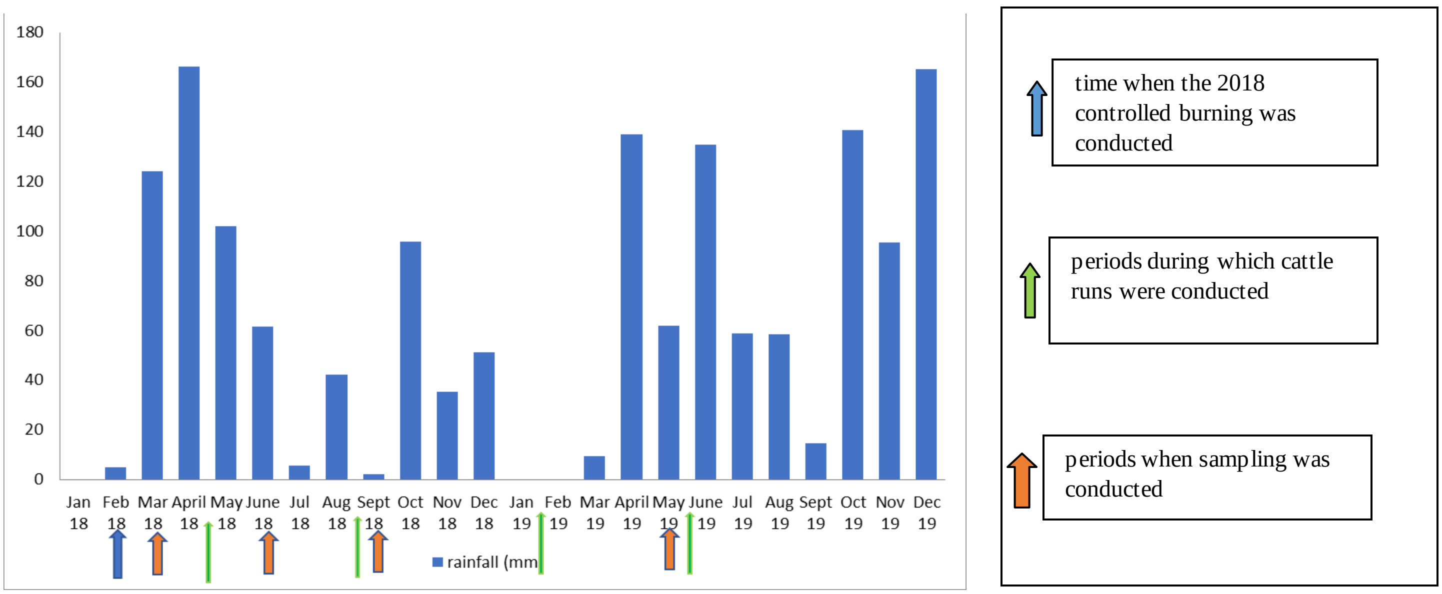


Figure 5: Average monthly rainfall in the years 2018/2019 at the study plots and the different times during which cattle runs and sampling were conducted.

3.4 Leaf sampling, nutritional quality determination and vegetation survey protocols

Forage nutritional quality attributes measured were crude protein, crude fiber, digestible dry matter and mineral (Na, P, K) contents. These measurements were performed during four sampling periods (Figure 5) based on the rainfall patterns and which targeted three wet seasons and one dry season; March 2018 (1 month after burning), June 2018 (4 months after burning), September 2018 (7 months after burning) and May 2019 (15 months after burning. March 2018, June 2018 and May 2019 were all wet, whereas September 2018 was relatively dry. To estimate each of these attributes, leaf samples of the two main grass species (*T. triandra* and *B. lachnantha*) were collected through hand plucking from each of the sub-plots burned in 2018 and corresponding control sub-plots (Figure 6 (a) & (b)). These two grasses were selected on the basis that they are among the most dominant grass species at the study site as demonstrated by vegetation surveys that had been done at the study sites (KLEE unpublished data) For each sub-plot, leaves from at least six individual plants of each of the two sampled forage species were clipped within 5m x 5m quadrats located at the sub-plot corners and center. For each grass species, leaves from all the five quadrats were composited per sub-plot per sampling period.

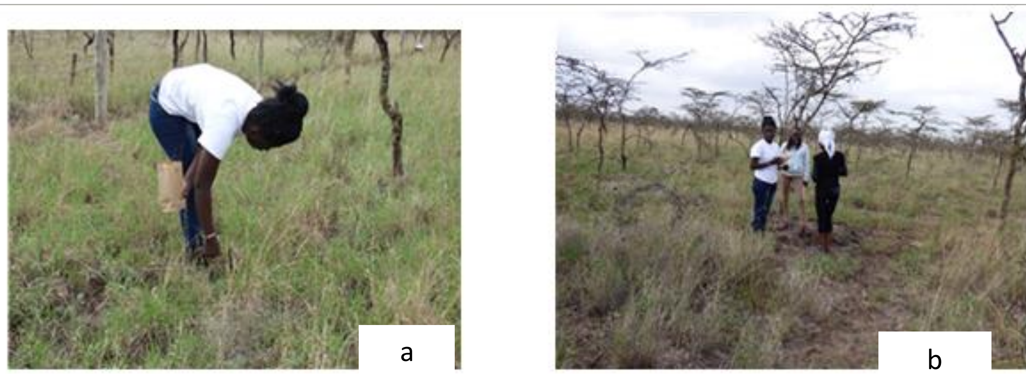


Figure 6: Researchers collecting forage samples in (a) previously burned plot and (b) control plot. Photo Credit: Phyllis

Leaf samples were transported to the Animal Nutrition Laboratory at the University of Nairobi for chemical analyses. At the laboratory where they were in an oven at 60^0C before milling into fine particle in readiness for chemical analysis. Forage crude protein content was obtained through determination of forage nitrogen levels using the Micro-Kjeldahl technique (AOAC, 1990). Crude protein content was then calculated by multiplying nitrogen content by 6.25. In addition, forage crude fiber content was determined as per the AOAC (1990) guidelines. Forage digestibility was assessed using the Tilley and Terry method of *in vitro* digestibility (Tilley and Terry, 1963). Rumen fluid was obtained from a rumen fistulated four-year old Boran bull weighing approximately 800 kg and housed at the University of Nairobi's large animal unit compound. Forage mineral (Na, P and K) contents were analyzed according to the procedures outlined by AOAC (1990). Specifically, Flame Emission Spectrophotometry was used to quantify the levels of Na and K, while Ultraviolet Spectrophotometry was used to estimate forage P content.

Post-fire data on herbage cover, species turnover and diversity were obtained from vegetation surveys carried out in sub-plots burned in 2013 and corresponding controls every July during the period 2013-2017. These data were collected using the pin frame method (Bonham, 2013), with sampling being conducted along three 25cm long transects located at 5m intervals across each subplot. Along each 25cm transect, three pin frame sampling stations were created giving a total of nine stations per sub-plot (three sampling stations in each of the three 25cm long transects per sub-plot). At each sampling station, ten pins were perpendicularly dropped and the number of first hits (the first contact a lowered pin made with an herbaceous species) recorded by species. The pin hits data were used to calculate vegetation cover, species turnover, richness and diversity.

Vegetation cover, species diversity, and species turnover were calculated for each of the five surveys conducted during 2013- 2017 using the formulae below. The total number of pins per subplot was used as an index of herbaceous vegetation cover. Species diversity was calculated using Shannon Wiener Index (1948). Species turnover was estimated as the ratio of total number of species gained and those lost during the study period to the number of species observed over time.

Vegetation cover index = Total pin hits on vegetation

Vegetation species diversity (H′) = $-\sum (ni/N \times \log(ni/N))$

where ni is the number of individuals of amount (biomass) of each of the i species and N is the total number of individuals (or biomass) for the site.

$$\textbf{Total turnover} = \frac{\text{Species gained} + \text{Species lost}}{\text{Total species observed in both timepoints}}$$

3.5 Data Analysis

Data analysis was performed using the *R* software (R Core Team, 2020). Linear mixed models (LMMs) with the *lmer* function in the package *LmerTest* (Kuznetsova *et al.*, 2017) were used to test the effects of herbivore treatment, fire, grass species and time since burning and their interactions on each of the measured herbage quality attributes (CP, CF, IVDMD, K, Na and P). For forage quality attributes, data were square-root, cube-root or log transformed to meet model assumptions. Linear mixed models were also used to test for the effects of fire, herbivore treatment and time since burning and their interactions on vegetation species diversity and turnover rate. Additionally, generalized linear mixed models (GLMMs) in the package *glmmTMB* (Mollie *et al.*, 2017) was used to test for the effects of fire, herbivore treatment and time since burning and their interactions on total vegetation cover using the generalized Poisson error distribution with log link. Analysis of variance (ANOVA) tables were constructed using Satterthwaite's method for denominator degrees-of-freedom using the ANOVA function in the *LmerTest* package for LMMs. For GLMMs, analysis of deviance tables with Type II Wald χ^2 tests were constructed using the function ANOVA in the package *car* (Fox and Weisberg, 2011). These ANOVA tables generated the *P*-values, *F*-values and the χ^2 test values. For all the attributes, blocks, herbivory plots nested within blocks and fire treatment subplots nested within herbivory plots were included as the random effects. Statistical significance was accepted at $P < 0.05$. When appropriate, means were separated for significant interactions or multi-level main effects using *multicomp* package (Torsten *et al.*, 2008). All data are presented as untransformed means ± standard errors (SE)

CHAPTER FOUR: RESULTS

4.1: Forage quality response to fire in different herbivore plots

The effects of fire, herbivory, type of grass and time since burning on various forage quality attributes (crude protein, crude fiber, in vitro dry matter digestibility, potassium, phosphorus and sodium levels) and their interactions are presented in Tables 1-6. Four-way interaction among fire, herbivory, time since burning and grass species was not significant for all measured forage quality attributes (all $F < 1.6$, $P > 0.05$).

Table 1: Crude protein (CP) contents (means ± SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments.

			Mean CP (% DM basis) in the herbivore treatment plots					
Time after fire	Species	Fire treatment	C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	22.9±0.4	23.5±0.6	24.5±1.2	21.9±0.9	23.3±1.4	22.2±1.0
		Control	8.6±1.0	10.2±1.1	11.2±1.0	5.8±2.4	9.5±0.6	11.4±0.6
	T. triandra	Burn	20.1±0.2	19.8±0.2	19.0±0.6	16.9±2.7	19.8±1.1	19.4±0.9
		Control	8.5±0.3	9.5±0.4	8.7±0.5	7.4±0.9	7.21±1.0	8.2±1.3
4 Months	*B. lacnantha*	Burn	13.8±1.0	10.4±0.6	13.4±1.8	10.2±0.7	10.1±0.7	11.9±0.5
		Control	9.5±1.3	9.8±1.4	10.7±10.7	8.1±0.4	9.0±1.5	12.0±1.2
	T. triandra	Burn	10.2±0.9	11.6±2.2	9.9±0.2	8.5±0.8	10.6±0.4	13.0±1.2
		Control	9.7±0.6	5.0±0.9	8.8±0.5	7.9±0.9	7.8±0.8	8.7±0.7
7 Months	*B. lacnantha*	Burn	5.1±0.3	6.0±0.2	5.7±0.3	4.1±0.5	5.0±1.0	5.5±0.3
		Control	6.4±0.4	5.2±0.1	5.2±0.4	5.2±0.1	5.6±0.3	5.4±0.2
	T. triandra	Burn	5.1±0.3	5.2±0.6	5.1±0.5	4.1±0.0	4.9±0.5	4.1±0.3
		Control	4.2±0.4	3.5±0.2	6.0±1.3	3.4±0.9	4.4+0.5	4.7±0.3
15 Months	*B. lacnantha*	Burn	16.2±1.5	13.6±1.4	14.3±0.4	12.5±0.5	16.3+1.6	14.6±0.4
		Control	14.9±1.3	13.7±1.1	12.2±0.2	12.9±0.5	14.3+2.4	14.3±2.0
	T. triandra	Burn	15.0±0.4	11.9±1.6	13.1±0.6	11.1±1.4	12.0+1.0	13.2±0.4
		Control	12.8±0.9	10.8±0.8	10.1±2.8	11.2±0.3	13.5+1.0	12.7±1.2[1]

[1]Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were: fire x time (F = 123.8, P < 0.01) and main effect of herbivore (F = 7.8, P = 0.003). Full statistical model is presented in Appendix 4

Table 2: Crude fiber (CF) contents (means ± SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

Time after fire	Species	Fire treatment	Mean CF (% DM basis) in the herbivore treatment plots					
			C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	28.1±0.9	28.0±0.5	29.1±2.7	28.6±1.2	28.2±0.2	28.6±2.0
		Control	34.1±1.6	32.3±1.7	33.1±0.8	34.3±1.2	35.1±1.4	33.3±1.1
	T. triandra	Burn	30.3±1.3	30.2±1.1	29.4±1.1	30.1±1.1	31.1±0.6	29.9±1.5
		Control	33.2±3.7	34.8±0.9	34.8±1.0	37.6±0.7	34.4±1.7	36.4±1.7
4 Months	*B. lacnantha*	Burn	39.1±2.3	38.2±0.4	35.7±1.9	37.1±2.3	36.0±1.0	38.8±0.6
		Control	39.2±1.2	40.7±0.9	36.7±0.4	39.9±0.9	37.7±0.2	39.7±1.2
	T. triandra	Burn	37.5±1.5	38.1±0.3	36.2±0.3	40.3±1.0	36.7±1.3	37.0±0.7
		Control	38.0±1.6	39.0±0.4	36.8±0.8	39.9±1.5	40.0±1.4	40.0±1.0
7 Months	*B. lacnantha*	Burn	37.5±1.3	39.1±1.3	37.1±0.4	39.4±0.8	37.5±2.8	36.4±0.5
		Control	37.4±0.8	39.2±0.5	37.5±0.9	38.4±0.6	39.9±0.4	38.0±0.7
	T. triandra	Burn	38.7±0.9	38.5±1.1	37.5±0.9	38.9±0.7	37.7±1.6	36.6±0.8
		Control	40.0±0.4	38.4±0.4	37.7±1.0	39.3±0.6	37.8±0.7	41.0±2.7
15 Months	*B. lacnantha*	Burn	35.1±0.3	34.2±0.5	34.4±0.6	34.8±0.3	35.1±0.3	33.5±0.6
		Control	33.8±0.9	34.4±0.7	34.7±0.4	35.3±0.2	34.7±0.5	33.4±1.5
	T. triandra	Burn	33.5±0.8	32.4±1.5	34.3±1.3	34.5±0.8	35.2±0.5	35.1±0.3
		Control	35.9±1.4	33.1±0.8	36.9±2.6	34.5±0.3	35.5±0.6	34.0±1.8[2]

[2] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were: fire x time (F = 123.8, P < 0.01) and main effect of herbivore (F = 7.8, P = 0.003). Full statistical model is presented in Appendix 5

Table 3: *In vitro* Dry Matter Digestibility (IVDMD) levels (means ± SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

			Mean IVDMD (%) in the herbivore treatment plots					
Time after fire	Species	Fire treatment	C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	63.6±1.8	67.7±0.7	60.7±2.4	72.1±5.9	63.6±1.6	67.0±4.3
		Control	47.0±5.0	43.4±4.7	47.3±5.3	41.0±1.0	42.1±1.6	49.5±5.3
	T. triandra	Burn	62.6±6.0	66.6±0.7	65.7±4.7	64.8±2.3	64.3±3.0	68.3±0.5
		Control	42.9±4.1	40.8±2.3	44.2±5.1	37.3±5.4	38.3±0.6	48.0±1.2
4 Months	*B. lacnantha*	Burn	42.9±4.6	45.7±0.9	36.7±2.6	42.9±2.1	32.1±4.0	33.5±4.4
		Control	28.8±4.6	41.2±3.8	34.6±2.9	36.8±0.4	37.5±3.8	36.5±0.8
	T. triandra	Burn	35.6±4.9	38.2±2.9	36.9±6.2	36.4±2.2	31.7±5.8	25.3±0.6
		Control	28.5±5.6	31.6±4.7	33.0±2.0	27.6±2.8	26.4±1.3	31.7±3.8
7 Months	*B. lacnantha*	Burn	43.4±2.4	47.2±2.3	47.6±5.1	40.1±0.6	46.7±3.6	36.7±3.1
		Control	38.5±3.1	45.6±2.4	46.1±2.6	37.9±7.0	40.3±1.2	41.1±4.0
	T. triandra	Burn	36.5±2.6	37.1±1.7	33.7±1.3	37.4±2.6	35.8±3.2	44.3±2.4
		Control	35.6±2.2	35.2±2.1	40.2±5.0	35.8±1.7	34.3±0.2	43.1±4.2
15 Months	*B. lacnantha*	Burn	51.3±2.0	47.1±3.6	45.7±1.3	47.7±4.6	48.0±1.8	50.7±1.9
		Control	47.5±3.7	44.8±2.7	50.0±5.2	49.6±4.0	41.3±5.2	49.7±2.0
	T. triandra	Burn	49.0±0.3	49.0±1.6	45.5±2.5	45.1±1.8	47.6±3.0	40.7±0.9
		Control	43.9±3.4	46.2±2.5	37.9±1.1	40.3±3.3	40.6±4.0	46.9±3.4[3]

[3] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were: fire x time (F = 36.96, $P < 0.001$) and main effect of grass (F = 29.01, $P < 0.001$). Full statistical model is presented in Appendix 6.

Table 4: Potassium (K) contents (means ±SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

			Mean K content (g/kg) in the herbivore treatment plots					
Time after fire	Species	Fire treatment	C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	3.00±0.17	2.83±0.34	3.06±0.09	3.8±0.8	2.67±0.13	3.02±0.28
		Control	0.83±0.11	1.20±0.14	1.17±0.11	0.80±0.05	0.87±0.12	1.21±0.09
	T. triandra	Burn	1.45±0.19	1.67±0.07	1.50±0.13	1.37±0.13	1.44±0.04	1.65±0.09
		Control	0.62±0.09	0.59±0.05	1.36±0.7	0.43±0.07	0.43±0.04	0.41±0.04
4 Months	*B. lacnantha*	Burn	1.77±0.12	2.23±0.04	1.46±0.29	1.71±0.14	1.41±0.14	1.14±0.66
		Control	1.41±0.28	1.80±0.39	1.14±0.35	1.54±0.14	1.19±0.29	1.67±0.06
	T. triandra	Burn	0.85±0.15	0.65±0.05	0.93±0.12	1.01±0.14	0.84±0.09	1.48±0.42
		Control	0.74±0.06	0.83±0.07	1.03±0.30	0.92±0.07	1.15±0.21	1.08±0.35
7 Months	*B. lacnantha*	Burn	0.51±0.07	0.58±0.06	0.42±0.02	0.46±0.07	0.55±0.03	0.32±0.07
		Control	0.31±0.05	0.52±0.05	0.40±0.11	0.45±0.08	0.51±0.01	0.37±0.11
	T. triandra	Burn	0.24±0.04	0.19±0.03	0.32±0.16	0.18±0.04	0.21±0.02	0.27±0.10
		Control	0.17±0.02	0.15±0.01	0.31±0.13	0.16±0.02	0.17±0.02	0.18±0.02
15 Months	*B. lacnantha*	Burn	2.89±0.54	1.92±0.19	2.17±0.22	1.78±0.16	2.16±0.35	2.31±0.25
		Control	2.64±0.12	1.54±0.14	1.80±0.27	1.91±0.11	1.50±0.23	1.73±0.17
	T. triandra	Burn	2.02±0.22	1.03±0.14	1.04±0.03	0.87±0.10	1.03±0.05	0.99±0.03
		Control	1.16±0.18	0.91±0.07	0.89±0.05	1.05±0.06	1.87±1.03	0.87±0.04[4]

[4] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were: fire x time x grass (F = 7.7, P < 0.01) and herbivore x time (F = 2.8, P < 0.01). Full statistical model is presented in Appendix 9.

Table 5: Sodium (Na) contents (means± SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

Mean Na content (g/kg) in the herbivore treatment plots								
Time	Species	Fire treatment	C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	0.07±0.01	0.22±0.10	0.08±0.02	0.12±0.04	0.07±0.01	0.07±0.00
		Control	0.06±0.00	0.05±0.00	0.12±0.04	0.05±0.01	0.07±0.01	0.07±0.02
	T. triandra	Burn	0.07±0.00	0.09±0.02	0.06±0.01	0.07±0.01	0.07±0.01	0.07±0.01
		Control	0.09±0.02	0.05±0.00	0.05±0.00	0.06±0.02	0.07±0.01	0.06±0.01
4 Months	*B. lacnantha*	Burn	0.09±0.01	0.06±0.01	0.07±0.02	0.07±0.01	0.09±0.01	0.56±0.5
		Control	0.09±0.02	0.06±0.01	0.07±0.02	0.11±0.03	0.06±0.02	0.07±0.02
	T. triandra	Burn	0.07±0.00	0.07±0.01	0.07±0.02	0.07±0.01	0.08±0.02	0.07±0.02
		Control	0.08±0.02	0.08±0.04	0.07±0.01	0.05±0.001	0.05±0.01	0.08±0.01
7 Months	*B. lacnantha*	Burn	0.04±0.02	0.06±0.02	0.04±0.00	0.04±0.01	0.04±0.01	0.04±0.02
		Control	0.04±0.01	0.05±0.02	0.02±0.00	0.03±0.02	0.03±0.02	0.04±0.01
	T. triandra	Burn	0.02±0.01	0.02±0.01	0.02±0.00	0.02±0.01	0.02±0.00	0.02±0.00
		Control	0.02±0.00	0.02±0.00	0.03±0.01	0.03±0.01	0.03±0.01	0.04±0.01
15 Months	*B. lacnantha*	Burn	0.34±0.06	0.46±0.02	0.26±0.02	0.46±0.02	0.43±0.06	0.43±0.04
		Control	0.35±0.06	0.42±0.02	0.40±0.04	0.38±0.07	0.39±0.04	0.40±0.08
	T. triandra	Burn	0.41±0.03	0.33±0.05	0.31±0.03	0.30±0.01	0.34±0.08	0.25±0.00
		Control	0.26±0.01	0.31±0.07	0.43±0.04	0.31±0.04	0.83±0.56	0.34±0.07[5]

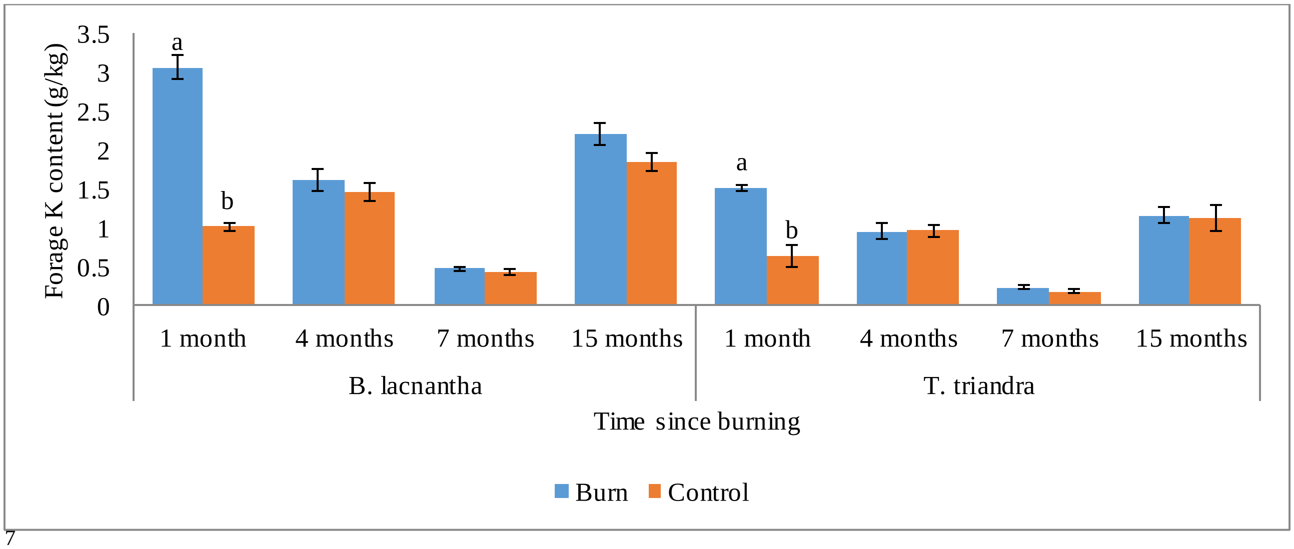
[5] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were the main effect of time since burning (F = 417.35, P < 0.01) and grass (F = 18.09, P < 0.01). Full statistical model is presented in Appendix 8.

Table 6: Phosphorus (P) contents (means ±SE) of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

Time after fire	Species	Fire treatment	Mean P content (g/kg) in the herbivore treatment plots					
			C	MW	MWC	O	W	WC
1 Month	*B. lacnantha*	Burn	0.28±0.02	0.3±0.04	0.34±0.03	0.29±0.05	0.25±0.02	0.28±0.03
		Control	0.09±0.02	0.12±0.01	0.27±0.09	0.11±0.02	0.11±0.02	0.13±0.00
	T. triandra	Burn	0.33±0.12	0.30±0.06	0.26±0.03	0.22±0.03	0.26±0.04	0.25±0.02
		Control	0.08±0.03	0.10±0.01	0.12±0.01	0.08±0.01	0.11±0.02	0.08±0.01
4 Months	*B. lacnantha*	Burn	0.15±0.01	0.14±0.02	0.12±0.04	0.10±0.01	0.11±0.02	0.12±0.02
		Control	0.12±0.01	0.11±0.01	0.07±0.02	0.11±0.02	0.08±0.01	0.11±0.01
	T. triandra	Burn	0.09±0.01	0.07±0.01	0.11±0.01	0.08±0.02	0.09±0.01	0.13±0.02
		Control	0.09±0.01	0.09±0.01	0.10±0.01	0.08±0.01	0.08±0.00	0.09±0.01
7 Months	*B. lacnantha*	Burn	0.06±0.01	0.06±0.00	0.07±0.01	0.04±0.01	0.06±0.01	0.07±0.01
		Control	0.05±0.00	0.07±0.01	0.05±0.01	0.06±0.01	0.05±0.00	0.06±0.00
	T. triandra	Burn	0.04±0.00	0.04±0.01	0.04±0.00	0.04±0.01	0.04±0.00	0.04±0.01
		Control	0.03±0.00	0.04±0.01	0.06±0.01	0.04±0.01	0.04±0.01	0.05±0.01
15 Months	*B. lacnantha*	Burn	0.43±0.01	0.56±0.02	0.47±0.04	0.49±0.01	0.43±0.03	0.44±0.02
		Control	0.40±0.01	0.43±0.03	0.44±0.03	0.45±0.06	0.5±0.01	0.47±0.01
	T. triandra	Burn	0.41±0.04	0.42±0.04	0.42±0.02	0.34±0.03	0.39±0.06	0.39±0.06
		Control	0.39±0.04	0.50±0.05	0.46±0.06	0.41±0.04	0.42±0.03	0.41±0.04[6]

[6]Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Significant effects were: fire x time (F = 54.75, P = < 0.001) and main effect of grass (F = 44.38, P < 0.001). Full statistical model is presented in Appendix 7.

Likewise, all three-way interactions involving fire, herbivory, grass species and time since burning were not significant for all forage quality attributes (all $F < 2.6$, $P > 0.05$) except forage K content which was influenced by an interaction among fire, grass species and time since burning ($F = 7.7$, $P < 0.01$) ;(Fig. 7). For both *T. triandra* and *B. lachnantha*, leaf K content was significantly higher in burns than non-burns (controls) during one month after fire but not during any of the subsequent sampling periods. Furthermore, for burns (but not non-burns), leaf K content was significantly higher in *B. lacnantha* than *T. triandra* during one, four- and fifteen-months post-fire but not during seven months post fire.



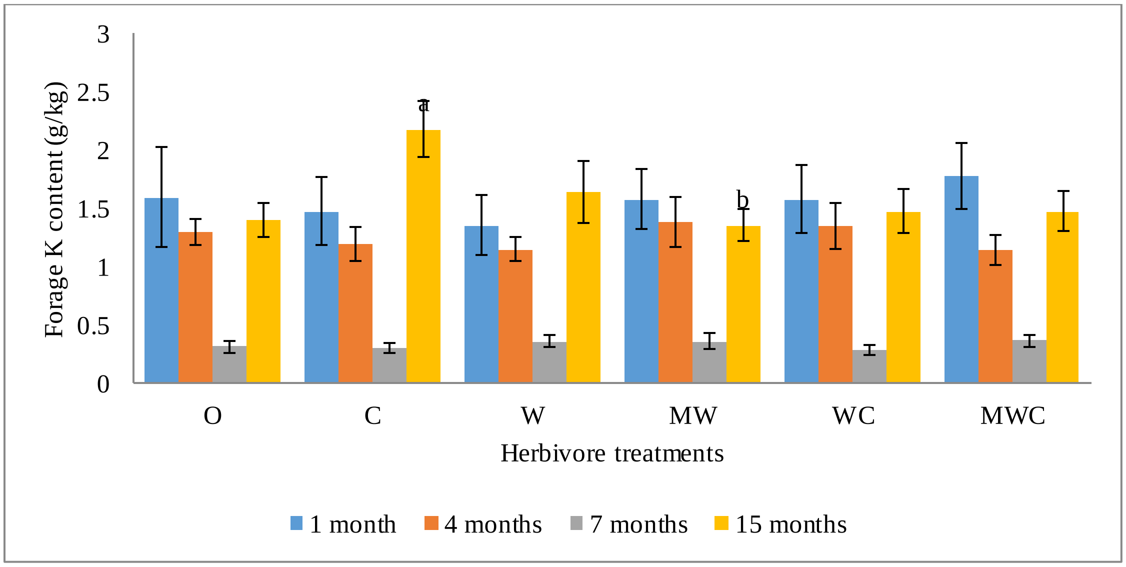
[7]

Figure 7: Potassium (K) contents of the grasses *Brachiaria lachnantha* and *Themeda triandra* in burned and unburned (control) areas at different time periods since burning.

Forage K content was additionally influenced by herbivory x time interaction ($F > 2.8$, $P < 0.01$); (Fig. 8). The overall trend showed a decrease in K levels in forages from one-month sampling up to the seventh-month sampling which was the least (except MWC where there was no significant difference between seventh-month sampling and fourth-month sampling) and an increase at the fifteenth month in all herbivore treatments. There was no significant difference between herbivore treatment O and each of the other herbivore treatments during all the study periods.

[7] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

Moreover, there were no herbivore treatment differences in forage K levels for all post-fire time periods, except for fifteenth-month sampling when this attribute was significantly higher in C than MW.



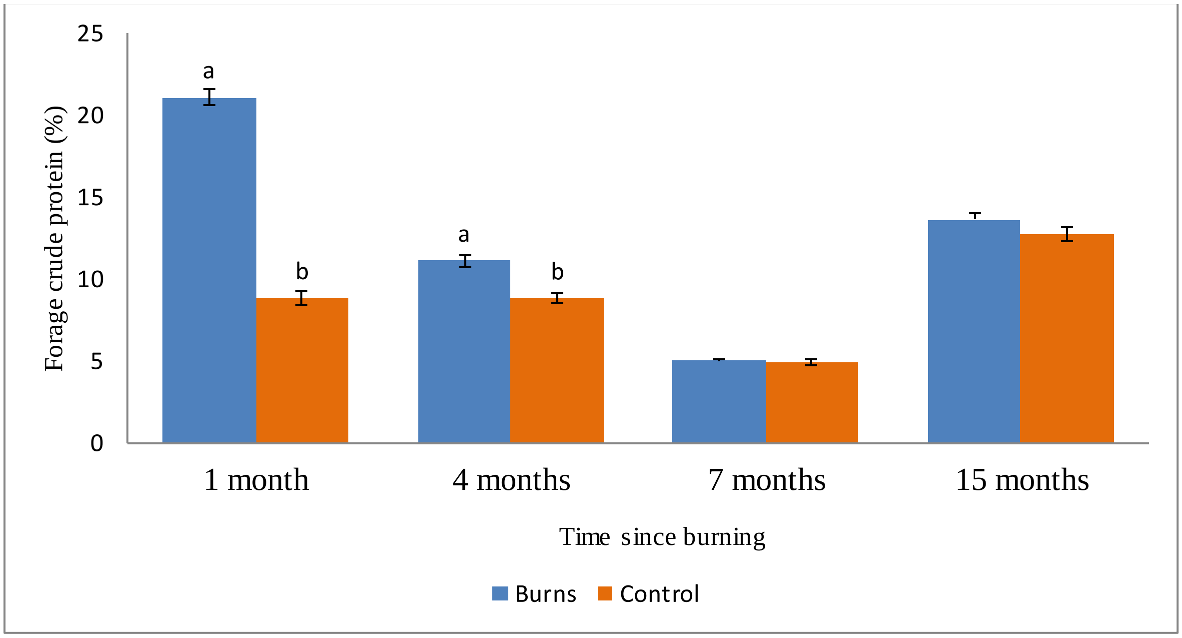
[8]

Figure 8: Potassium (K) content of forage within different herbivore treatment plots during different sampling periods

Forage crude protein (CP), crude fiber (CF), *in vitro* digestible dry matter digestibility (IVDMD) and phosphorus contents were all influenced by a two-way interaction between fire and time since burning (all $F > 20.0$, $P < 0.01$); (Fig. 9-12). Specifically, forage CP was significantly higher in burns than non-burns during both one month and four months after fire but not during any other period post-fire (Fig. 9). Conversely, forage CF was significantly lower in burns than non-burns during one-month post-fire, but not during any other period (Fig. 10). Forage IVDMD was higher in the burns than the non-burn controls at one- and four-months after fire but not later on (Fig. 11). In addition, forage phosphorus content was significantly higher in burns than non-

Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

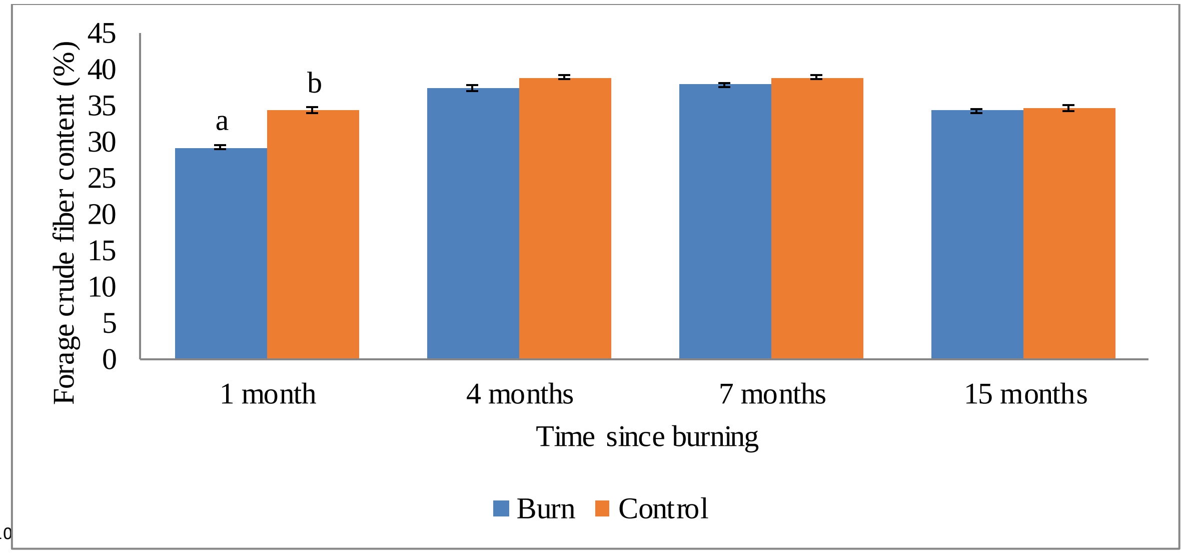
burns during one-month post-fire but not during each of the subsequent post-fire time periods (Fig. 12).



[9]

Figure 9: Forage crude protein (CP) content across fire treatments during different post-burning.

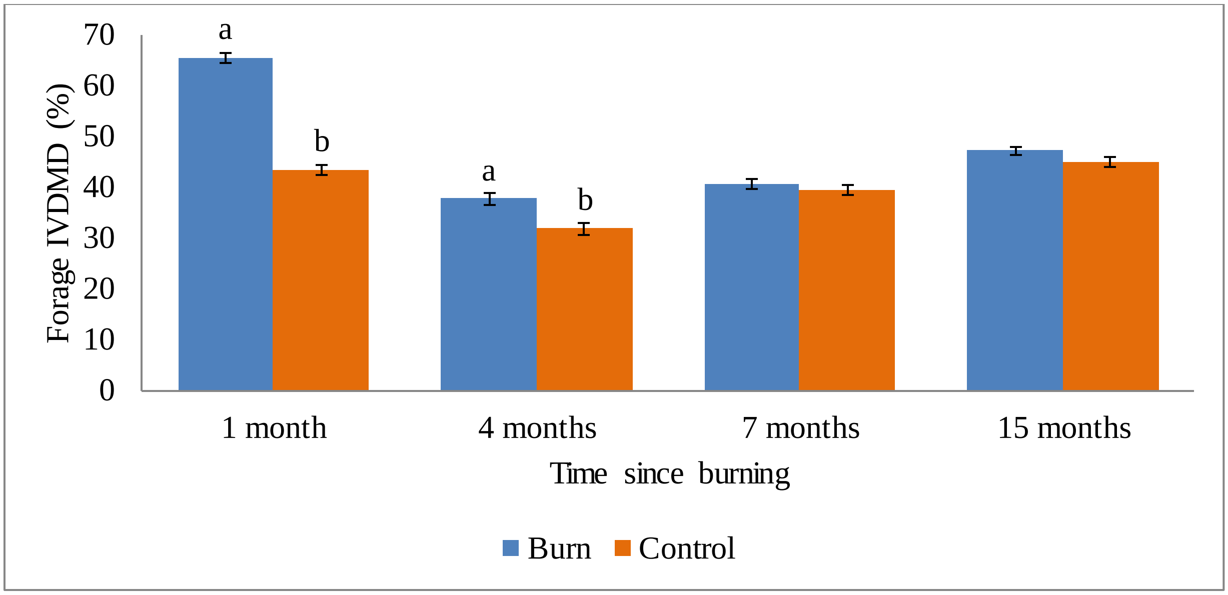
[9] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.



[10]

Figure 10: Forage crude fiber (CF) content across burns and non-burns during different time periods since burning.

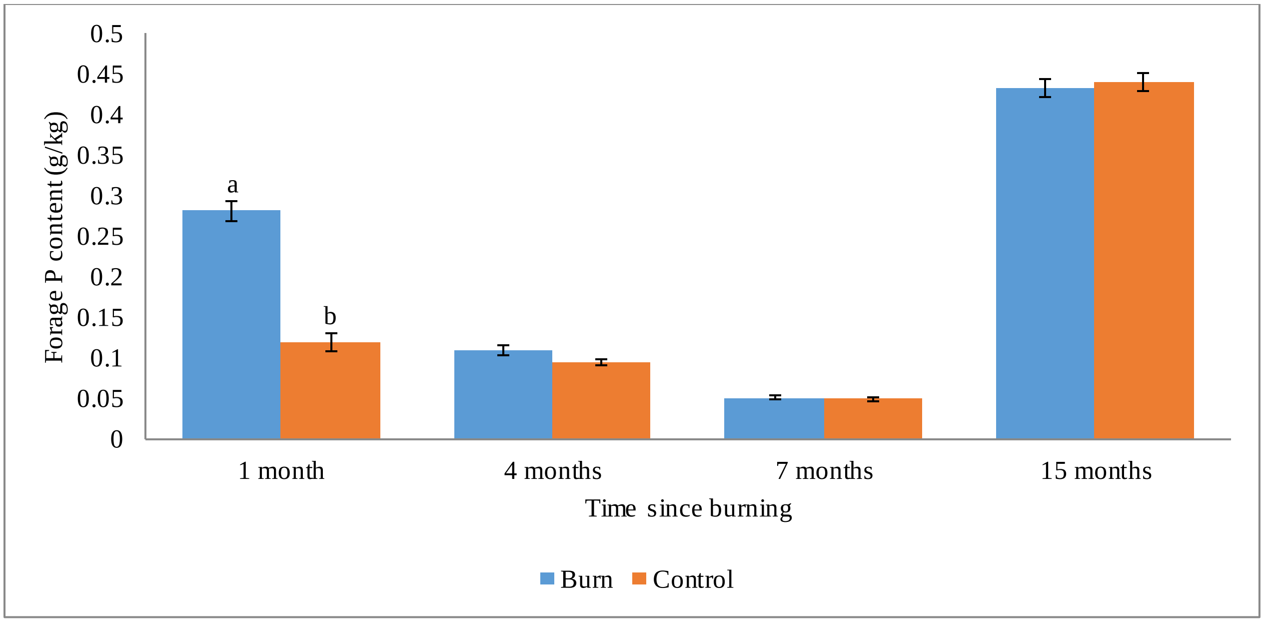
[10] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.



[11]

Figure 11: In vitro dry matter digestibility (IVDMD) levels of forages within the burned and the unburned controls over time since burning.

[11] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

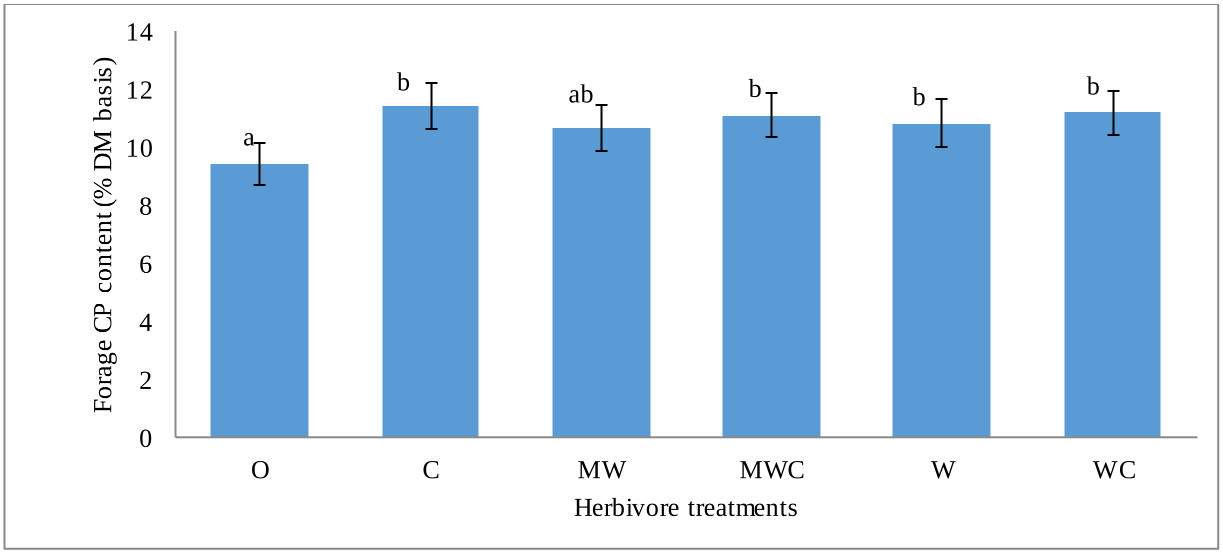


12

Figure 12: Phosphorus levels of forages within the burned and the unburned controls over time since burning.

The main effect of herbivory significantly influenced forage CP content (F = 7.89, P =0.003); (Fig. 13). Specifically, CP was significantly lower in the non-grazed treatment (O) than in each of the grazed treatments except in MW. However, there was no significant difference in mean forage CP content among herbivory treatments accessible to large herbivores.

[12] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.



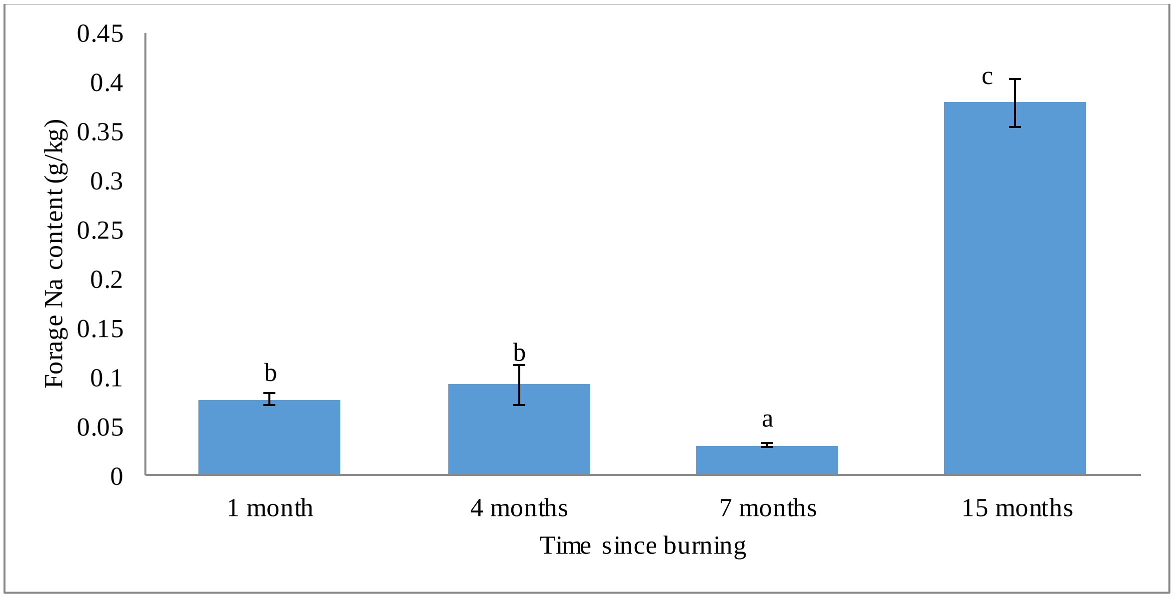
[13]

Figure 13: Crude protein (CP) of forages within the different herbivore treatment plots.

Based on the effect of grass species on forage quality attributes measured, *Themeda triandra* was significantly more fibrous (36.03% DM +0.29) than *B. lachnantha* (35.53%DM +0.32); (*P*=0.03, *F*=4.8**)**. In addition, *T. triandra* was less digestible (*P*< 0.001, *F*= 29.01) than *B. lachnantha* (42.08+0.95 % vs. 45.64+ 0.0.90%), and contained lower (*P*<0.001, *F*=44.38) phosphorus levels than *B. lacnantha* (0.183+0.013g P/kg vs. 0.21+0.014g P/kg) *Brachiaria lacnantha* had higher (*P* < 0.01, *F* > 48.83) CP (11.58+0.48% vs. 9.98+0.40% DM) and Na (0.16+0.0.02g Na/kg vs. 0.13+0.02g Na/kg) levels than *T. triandra*.

[13] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

Main effect of time affected Sodium levels significantly. Forage Na content was significantly higher during 15 months than any other time period post-fire, and significantly lower during 7 months than each of the earlier time periods post-fire, irrespective of herbivore and fire treatments (Fig. 14).



[14]

Figure 14: Sodium (Na) levels of forages during different times since burning.

[14] Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

4.2: Differences in herbaceous vegetation structure and species composition

The effects of fire, herbivory, and time (years) since burning, and their interactions on the measured herbaceous vegetation structure and species composition attributes (cover, diversity and turnover) are presented in Tables 7-9. Three-way interaction among fire, herbivory and time since burning effect was not significant for vegetation cover (χ^2>29.0, P=0.07), species diversity and turnover rate (all $F < 1.5$, $P > 0.1$).

Table 7: Total herbaceous vegetation cover index (means ± SE) in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

		Mean herbaceous species cover index (pin hit count) in the herbivory treatment plots					
Year	**Fire treatment**	**O**	**C**	**W**	**MW**	**WC**	**MWC**
2013	Burn	77.3±6.1	95.3± 2.9	68.3± 3.3	80.33± 19.9	58.0± 5.2	78.0±7.1
	Control	148.0±9.1	112.3± 7.75	131.7± 4.7	155.3±19.8	114.0±1.0	117.3± 11.5
2014	Burn	113.7± 6.0	86.3± 6.6	78.7± 11.2	62.0± 8.1	47.7± 13.3	57.3± 19.8
	Control	122.7± 7.4	106.3± 13.3	126.3± 5.8	124.3± 2.8	91.0± 9.0	93.3± 10.7
2015	Burn	162.3± 16.2	135.3± 18.0	122.7± 9.2	143.7± 11.6	92± 17.2	119.0± 6.7
	Control	153.3±4.1	129.7± 11.2	151.33± 5.8	147.0± 3.8	125.0± 2	129.0± 9.1
2016	Burn	141.7±15.6	159.3± 3.2	140.7± 9.8	143.7± 5.5	114.0± 3.6	135± 10.4
	Control	137.0± 5.0	123.3± 7.0	138.3± 12.4	126.7± 15.2	118.0± 3.6	134.3± 16.2
2017	Burn	113.3± 5.9	90.7± 7.2	49.0± 3.5	66.3± 7.0	39.3± 6.2	47± 15.8
	Control	123.0± 18.7	68.7± 12.4	70.3± 19.2	72.3± 6.8	40.0± 8.7	55.0± 6.1 [15]

[15]Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Full statistical model is presented in Appendix 11. Significant effects were: fire x time and herbivore x fire (both; $\chi^2>77$, $P<0.001$)

Table 8: Herbaceous species diversity (means ± SE) in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

		Mean herbaceous species diversity in the herbivory treatment plots					
year	**Fire treatment**	O	C	W	MW	WC	MWC
2013	Burn	4.6±0.1	4.3±1.1	5.2±0.9	5.5±1.4	4.7±0.2	6.3±1.0
	Control	5.6±0.8	5.8±0.8	6.6±0.5	6.1±0.4	6.2±0.9	5.4±0.6
2014	Burn	4.1±0.4	3.8±0.3	4.2±0.9	4.1±0.5	3.7±0.5	4.3±0.5
	Control	4.6±0.5	4.6±0.2	5.4±0.2	5.4±0.7	4.5±0.7	5.4±0.3
2015	Burn	5.7±0.3	4.8±0.3	5.8±0.5	7.3±0.9	7.3±2.0	7.3±1.0
	Control	5.5±0.8	4.5±0.8	7.9±1.8	6.3±0.3	6.8±1.0	8.7±0.6
2016	Burn	4.3±1.1	4.6±0.1	4.7±0.4	5.2±0.6	5.9±0.6	5.8±0.7
	Control	4.1±0.6	4.7±05	6.5±0.2	5.5±1.4	5.0±0.9	5.7±0.4
2017	Burn	2.9±0.0	3.6±0.0.6	4.0±0.6	4.2±0.0.1	5.4±1.1	4.9±0.8
	Control	3.8±0.7	3.4±0.2	4.3±0.2	3.5±0.4	3.7±0.3	5.2±0.8[16]

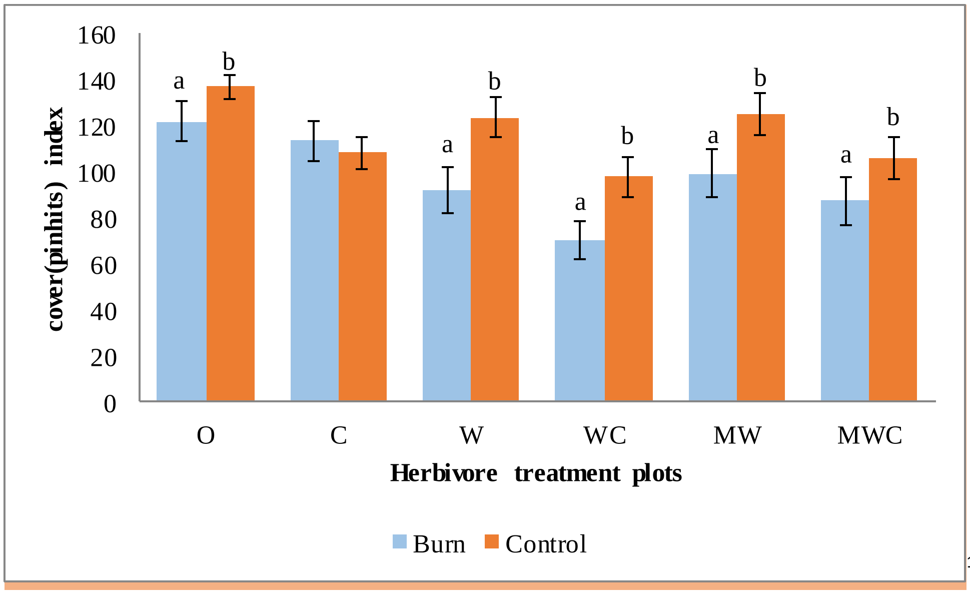
[16]Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Full statistical model is presented in Appendix 12. Significant effects were: herbivore and year (both; $P < 0.01$, $F < 28.5$)

Table 9: Herbaceous species turnover (means ± SE) in burned and unburned (control) areas within different herbivory treatments at different time periods since burning.

year	Fire treatment	Mean herbaceous species turnover (%) in the herbivory treatment plots					
		O	C	W	MW	WC	MWC
2013	Burn	0.59±0.03	0.52±0.05	0.53±0.06	0.61±0.04	0.58±0.01	0.55±0.05
	Control	0.46±0.06	0.51±0.08	0.42±0.09	0.44±0.07	0.40±0.01	0.53±0.02
2014	Burn	0.44± 0.07	0.44± 0.07	0.60±0.07	0.62±0.08	0.57±0.09	0.54± 0.00
	Control	0.45± 0.04	0.45± 0.04	0.38±0.08	0.45±0.06	0.53±0.05	0.42± 0.08
2015	Burn	0.44±0.05	0.63±0.03	0.64±0.03	0.74±0.02	0.69±0.04	0.60±0.03
	Control	0.53±0.09	0.46±0.04	0.57±0.03	0.48±0.10	0.63±0.05	0.62±0.01
2016	Burn	0.49±0.10	0.52±0.14	0.55±0.06	0.52±0.02	0.57±0.09	0.51±0.08
	Control	0.51±0.12	0.57±0.03	0.47±0.03	0.57±0.01	0.59±0.10	0.59±0.03
2017	Burn	0.52±0.10	0.50±0.11	0.60±0.01	0.48±0.05	0.61±0.10	0.53±0.06
	Control	0.72±0.05	0.66±0.05	0.52±0.08	0.48±0.04	0.52±0.02	0.46±0.04[17]

[17] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Full statistical model is presented in Appendix 13. Significant effects were: fire x time (F =3.5, P =0.01) and herbivore x fire (F = 3.2, P = 0.01).

Fire effects was however significantly affected by the two-way interactions of herbivory by fire (χ^2 =18.84, P<0.001); (Figure 15). Post hoc analysis revealed that vegetation cover was lower in burns than non-burns for herbivore treatment plots accessed by mesoherbivores exclusively (W); mesoherbivores and megaherbivores only (MW); mesoherbivores and cattle only (WC); 4) mesoherbivores, megaherbivores and cattle (MWC); and 5) plots from which all herbivores were excluded (O). However, there was no significant difference between burns and non-burns in plot accessible to cattle (C)

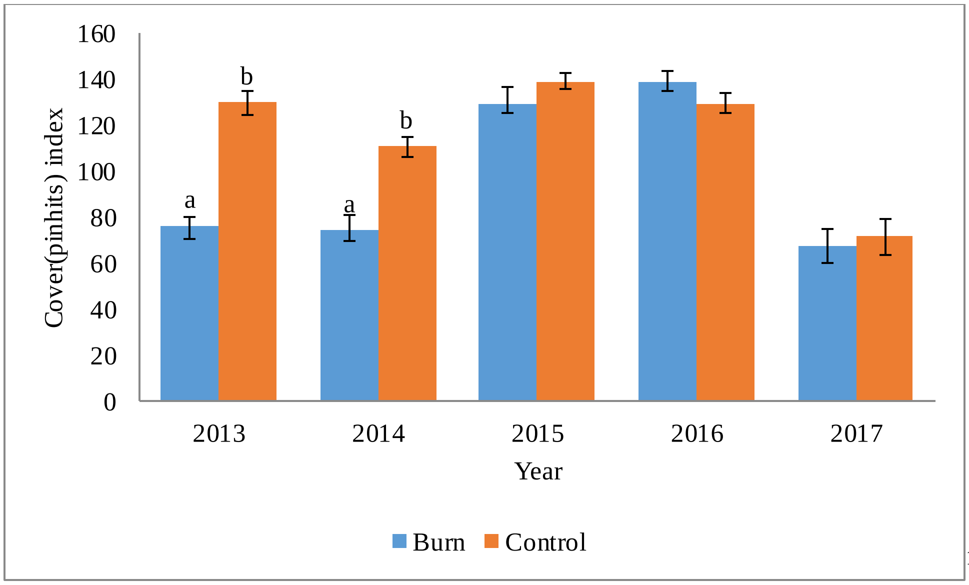


[18]

Figure 15: Herbaceous cover in burned and unburned (control) areas within different herbivore treatments

Effects of fire on herbaceous vegetation cover varied significantly over time (fire x time interaction: χ^2 =123.88, P <0.001). In the first two years after fire (2013 and 2014), burns had significantly lower herbaceous vegetation cover than the respective controls but these effects diminished in the subsequent years (Fig. 16)

[18] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Error bars represent standard errors. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

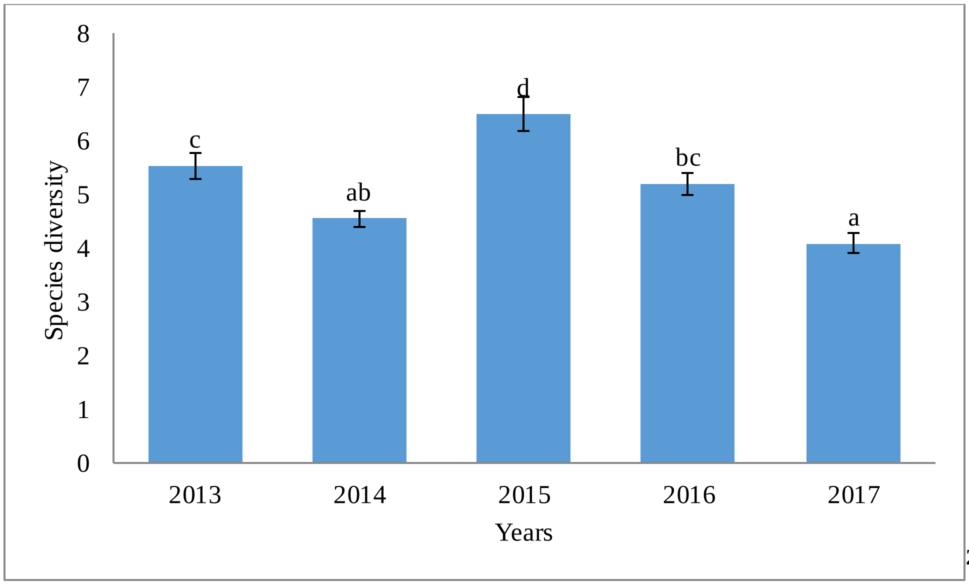


[19]

Figure 16: Herbaceous cover in burned and unburned (control) areas across different times post fire.

On the other hand, herbaceous vegetation species diversity was not influenced by two-way interactions of fire x herbivory (P =0.1, F = 1.8) and fire x time since burning (P =0.1, F = 1.9). However, the main effects of time since burning ((P <0.01, F =28.3) and herbivory (P <0.01, F =8.7) significantly influenced species diversity. Herbaceous vegetation species diversity was significantly higher in year 2015 and lower in 2014 and 2017 than 2013 and 2016 (Fig. 17). Species diversity was significantly higher in herbivore treatments W, WC, MW and MWC than C and O (Fig. 18).

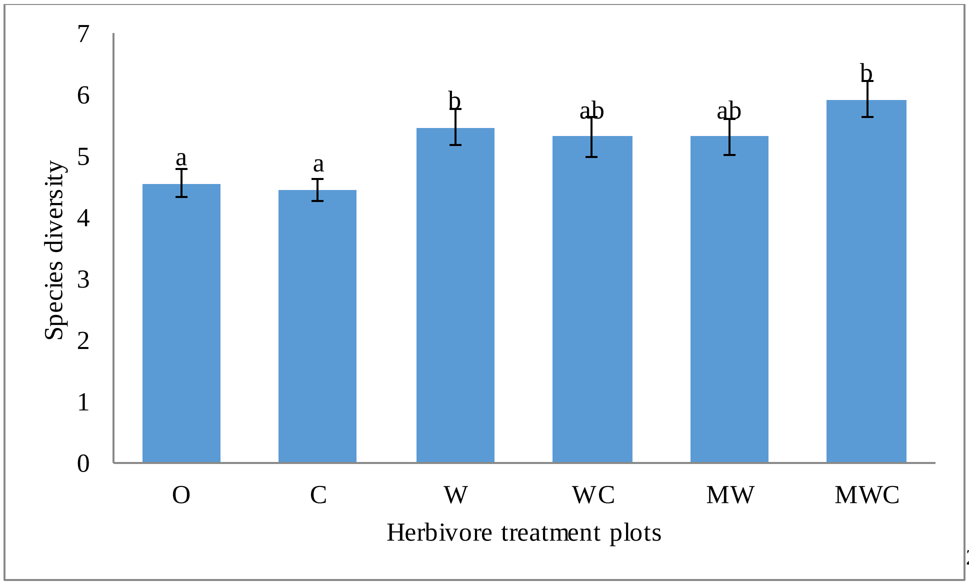
[19] Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters shows that the means are significantly different.



[20]

Figure 17: Herbaceous species diversity at different times after fire during the survey period.

[20] Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while bars with different letters show that the means are significantly different.

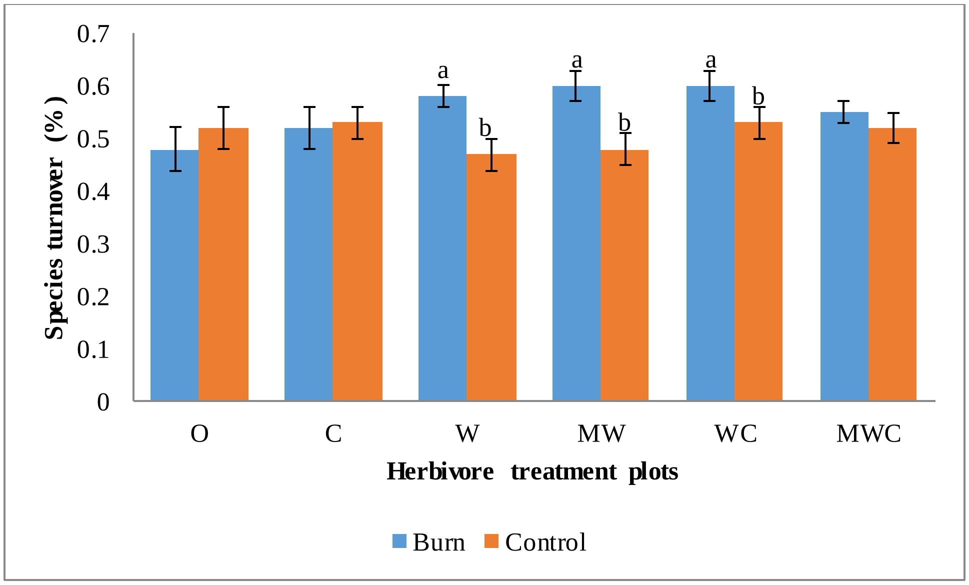


[21]

Figure 18: Herbaceous species diversity in the different herbivore treatments at different times post fire within the burned and unburned (control) areas.

Herbaceous vegetation species turnover was significantly affected by fire x herbivory (*P*=0.01, *F*=3.2) and fire x time (*P*=0.01, *F*=3.4) since burning interactions (both *P*=0.01, *F* > 3.0); (Fig. 19) There was no significant difference in vegetation species turnover between burns and the non-burn in herbivore treatments O, C and MWC. However, herbivory caused an increase in post fire herbaceous species turnover in the herbivore treatments (W, WC, and MW); (Fig. 19). Additionally, Vegetation species turnover was higher in burns than non-burns for at least three years after fire but not during the later time periods (Fig. 20).

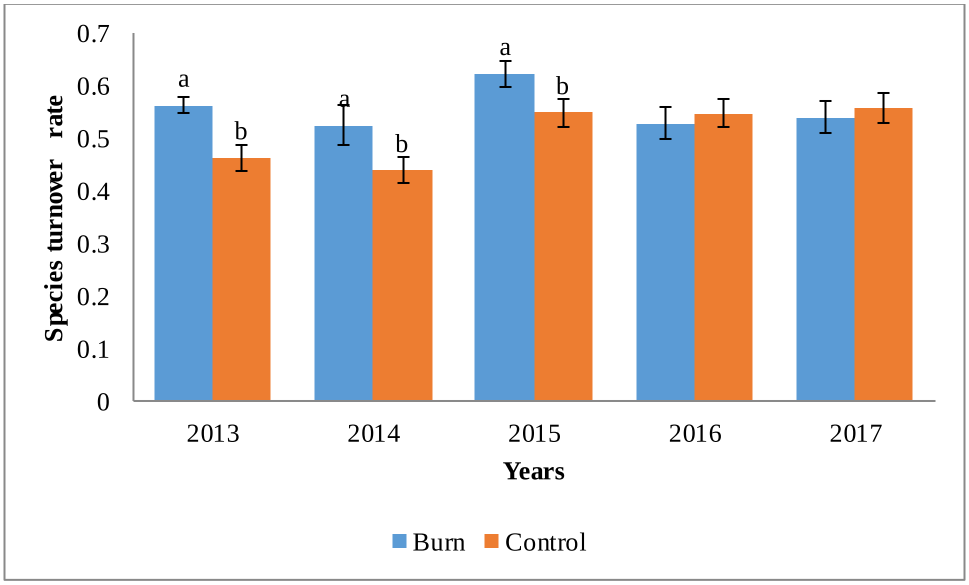
[21] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.



[22]

Figure 19: Herbaceous species turnover in burned and unburned (control) areas within the different herbivore treatments.

[22] Abbreviations C refers to plots accessed by cattle, W refers to plots accessible to mesoherbivores, WC refers to plots accessed by cattle and the mesoherbivores, MW refers to plots accessible to megaherbivores and mesoherbivores, MWC refers to plots accessible to cattle, mesoherbivores and the megaherbivores; O refers to plots inaccessible to all herbivores. Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.



[23]

Figure 20: Herbaceous species turnover in burned and unburned (control) areas across different times post fire.

[23] Error bars represent standard errors. Bars sharing a common letter show that the means are not significantly different while those with different letters show that the means are significantly different.

CHAPTER FIVE: DISCUSSION

We had postulated that herbivores that are attracted to and graze in burned areas are able to maintain forage quality in a highly nutritious state following fire for longer periods. On the contrary, this was not evident from the study findings as there was no significant interactive effect of fire, herbivore and time since burning on forage CP, CF, IVDMD, K, P and Na contents. The effect of fire on the measured forage quality attributes was similar in all herbivory treatments regardless of time period post-burning. However, interaction between fire and time since burning had significant effects on all quality attributes except for forage Na. In addition, the main effect of herbivory significantly affected forage CP but not any other attribute while the grasses differed significantly based on their nutrient content during the study period. Herbivores influenced herbaceous vegetation cover and species turnover rate response to controlled burning, but not species diversity. The main effect of herbivory however had significant effect on vegetation species diversity irrespective of burning or lack of fire. There was no significant effect of herbivory x fire x time since burning interaction on each of the measured herbaceous vegetation structure and species composition attributes. However, fire by time since burning interaction had significant effect on vegetation cover and species turnover.

5.1: Effects of fire, herbivory and time since burning on forage quality

Lack of significant effect of herbivores on vegetation CP, CF, IVDMD, K, Na and P response to controlled burning is inconsistent with our prediction that herbivores that are highly attracted to burns are able to maintain the post fire pastures in an elevated nutrient status for longer through nutrient cycling and also by maintaining forages in short and nutritious state through defoliation. These findings also contradict the study by Masunga *et al.* (2013) who reported higher levels of N in fire treated grazed plots compared to fire treated non-grazed plots. The lack of significant effect of herbivory on the effects of fire on forage quality even with increasing time since burning can be explained by a number of factors. First, the relatively high amounts of rainfall that immediately followed burning (Fig 5) may have dampened the effects of grazing herbivores. High precipitation has been reported to suppress herbivore use and effect on herbaceous vegetation in this ecosystem while low precipitation does the opposite (Young *et al.*, 2013, Pringle *et al.*, 2007).

Secondly, the findings were due to suppressed wild herbivore visitation and use of the plots in the immediate periods post fire. This reduced visitation could have been due to herbivores avoiding the black cotton soils due to its characteristic stressful shrink-and-swell nature during seasons of higher precipitation (Young *et al.*, 2013). Also, herbivores avoid the black cotton soil during rainy season possibly due to increase in the abundance of less palatable, poor quality forages (Goheen and Palmer, 2010). This increase in less palatable species is as a result of increase forage moisture contents in addition to increased vegetative growth that fastens forage maturity. Coupled with the fact that cattle runs were conducted during the late growing season after fire effect had diminished (Fig. 5), all these factors presumably caused a marked reduction of herbivore population at the plots in the immediate periods after fire.

Therefore, herbivore effect following fire could have been too minimal to sustain pastures in their high-quality post burn state for longer periods even after fire effect diminished. These reasons also explain why there was no significant difference on forage quality response to fire between the different herbivore treatments accessible to domestic and wild herbivores, combined or separately, and why exclusion of megaherbivores from an area did not have an effect on how the other herbivores influenced forage quality response to fire. The lack of significant effect of herbivory on post fire forage quality shows that post fire pasture quality in the studied ecosystem may not be altered by grazing or browsing.

The main effect of herbivores increased forage CP levels in grazed than non-grazed plots except for MW (Fig 13). Consistent with this study, higher forage CP contents in grazed than non-grazed pastures have also been reported in other studies (Ainalis *et al.*, 2006, Aremu *et al.*, 2007, Anderson *et al.*, 2007, Mikola *et al.*, 2009, van der Waal *et al.*, 2011, Aremu *et al.*, 2016). This effect is attributable to enhanced nutrient cycling (Falk *et al.*, 2015, Novellie and Gaylard, 2013, Archibald 2008, Aremu *et al.*, 2007) in grazed plots. As herbivores graze, they deposit their excreta into the soil thus increasing soil N content. This N is absorbed by the pastures hence increasing the plant N levels. Also, plots accessible to grazers are expected to have higher CP content in forages as defoliation especially during the growing season helps maintain pastures in younger, shorter and more nutritious status (Ren *et al.*, 2016, Bai *et al.*, 2012, Falk *et al.*, 2015).

The lack of forage CP enhancement by grazing in MW plots compared to non-grazed plots was presumably because of the effect of megaherbivores. For instance, megaherbivores such as elephants cause damage to trees (Pringle *et al.*, 2008) yet these trees such as *Acacia. drepanolobium* which are leguminous have been reported to improve grass quality through enhanced nitrogen fixation into the soil (Treydte *et al.*, 2007, Ludwig *et al.*, 2008, Riginos *et al.*, 2009). Findings by a recent study at the KLEE plots though noted contradicting evidence and reported that megahebivores are capable of increasing soil and grass N (Sitters *et al.*, 2020). This study by Sitters *et al.*, (2020) however investigated the impact of megaherbivores inclusion on pastures accessible to cattle. In this current study, the negative impact of megaherbivores on forage CP was however not experienced in MWC, possibly due to enhanced grazing intensity as a result of access of this plot by all herbivores eventually causing more defoliation, trampling and also enhanced nutrient cycling. Therefore, the current study provides an additional new finding that megaherbivores also have negative effect on forage CP in areas that they access together with the mesoherbivores but these effects can be reversed through inclusion of cattle to graze together with these wild herbivores as in MWC plot.

Fire effect on forage quality was noted to last for at least four months; by the seventh month post-fire and after, there was no difference in pastures from burns or non-burn controls. The improvement in forage quality in the early growth season can be attributed to forage age and stage of maturity in addition to fire effect. For instance, elevated concentration of K in the forages for at least one-month post-fire (Fig. 8) could be due to the reduction in competition for these minerals by the plant due to decreased above ground biomass as a result of fire (Van de Vijver *et al.*, 1999). The higher K levels in burns than non-burns for at least one-month post-fire falls within the range of timelines reported by Hanselka (1989) of up to 3-4 months increase in forage K in a fire treated grass and Van de Vijver *et al.*, (1999) who reported higher K levels in burns than controls for up to three months post fire.

This study demonstrated that irrespective of the presence or absence of large herbivores, and irrespective of large herbivore guild, the effects of controlled fire on forage CP content are transient, lasting only up to four months post-fire (Fig. 9). This can be attributed to the fact that forage in burns was just sprouting immediately after burning as this had coincided with the early growing season. The transience of fire effects on forage CP content in this current study provides additional new evidence that forage CP can remain higher fifty days longer than the duration reported by Sensenig *et al.*, (2010) who reported up to seventy days but not later than 150days increase in forage CP post-fire. The observed lower forage fiber content in burned than unburned areas during one-month post-fire and higher IVDMD for up to four months after fire (Fig. 10 and 11) can be attributed to the role of fire in removing old, dead, more fibrous and less digestible forage components thus creating space for less fibrous and more digestible new growth (Eby *et al.*, 2014). While fire effect on forage fiber content lasted only for one month in this study, longer-term effects of fire on forage fibrousness has been reported for up to one year (Gullap *et al.* 2018). This discrepancy could be due to the variation in sampling method by Gullap *et al.*, (2018) compared to this study.

While the current study sampled leaves of two main grass species, Gullap *et al.*, (2018) sampled a variety of pasture components thus may have included even legumes. Legumes have been reported to have lower levels of CF even at the same age of maturity as grasses (Stallcup, 1958, Ball *et al.*, 2001, Amiri *et al.*, 2012), and higher cell content (Dewhurst *et al.*, 2009). Therefore, legumes can potentially dilute the cell wall contents of higher crude fiber level forages such as grasses and lower fiber levels eventually increasing overall pasture quality (Olivo *et al.*, 2009, Tambara *et al.*, 2017). Therefore, lowered CF in grasses following fire can only last for up to four months before returning to pre-burn state. However, the overall fire effect on the CF of all pasture components may last longer due to the diluting effect of some species such as legumes.

Elevated levels of phosphorus in burns unlike in the non-burn control also lasted for one-month post-fire (Fig 12). This effect is likely due to phosphorus retention in the soil in form of ash after burning (Bodi et al., 2014, Pereira et *al.*, 2015), which then become available to forage plants in burned areas. Increase in forage P one-month post-fire but not later has also been reported elsewhere and attributed to the rejuvenation of the regrowth rather than mineralization of the new growth due to ash (Van de Vijver *et al.*, 1999). Unlike in studies that have reported that rangeland forages are limiting in phosphorus (Tefera, 2010, Ndebele *et al.*, 2005, Nsinamwa *et al.*, 2005;), this study showed that, irrespective of burning, forage phosphorus levels in the system studied were adequate for cattle requirement recommended at 0.02-0.06g/kg (Engle *et al.*, 2016) for all the sampling periods except at seven months post-fire which was relatively dry.

Consistent with this study, interspecific differences in nutrient quality among forage plants have also been reported in other studies. For example, Osier and Lindroth (2001) reported that there exists genetic variation in plants that influence nutrient concentrations. This has also been reported in other studies (Herencia *et al.*, 2007, Lovkova *et al.*, 2008, White and Brown, 2010, Fageria *et al.*, 2011). The fact that *Brachiaria lacnantha* was less fibrous, had higher CP, K, Na and was more digestible than *Themeda triandra* was possibly due to *B. lacnantha* having elevated levels of nutrients as a result of its physical characteristics such as large roots that allow it to mobilize and store more nutrients (Arango *et al.*, 2014, Moreta *et al.*, 2014). In the neighboring Ethiopian savanna, *T. triandra* has also been reported to be of relatively low nutritional quality and less preferred by livestock based on ranking by pastoralists (Keba *et al.*, 2013). *Brachiaria lacnantha* is therefore nutritionally a better forage species as it has higher nutrient content, is more digestible and less fibrous compared to *T. trinadra*.

Therefore, herbivores do not influence grass CP, CF, IVDMD, K, P and Na levels response to controlled burning regardless of the herbivore type, presence or absence of megaherbivores and the amount of time that has passed after fire.

5.2: Effects of fire, herbivory and time since burning on herbaceous vegetation cover, species turnover and diversity

Fire effects coupled with attractiveness of burns to herbivores (Sensenig *et al.*, 2010; Allred *et al.*, 2011; Eby *et al.*, 2014), can cause increase in forage consumption in burns leading to reduced herbage cover (Whisenant, 2004). Therefore, in the present study, it was expected that fire-driven reduction in herbage cover would be more pronounced in plots accessible to large herbivores (i.e., treatments W, MW, C, WC and MWC) than in plots from which large herbivores were excluded (O). Inconsistent with this expectation, fire significantly altered herbage cover in treatment O (Fig. 15) with burns showing lower vegetation cover than the non-burns. This was unexpected since due to the absence of herbivory in this plot, vegetation cover was expected to be restored to the pre-burn levels. The significant difference between burns and the non-burn controls in plot O is attributable to the higher fire intensity in the burns in this plot due to the higher fuel load content than the grazed plots due to the absence of herbivory (Savadogo *et al.*, 2007, Dayamba *et al.*, 2010, Kimuyu *et al.*, 2014). High fire intensities caused marked damage to vegetation and could have led to plant mortality and also delayed post-fire regeneration as has been noted in other studies (Moreno and Oechel, 1991, Savadogo *et al.*, 2007, Dayamba *et al.*, 2010, Basset *et al.*, 2017). Therefore, fires in areas with higher fuel loads will markedly reduce vegetation cover even in the absence of herbivores.

Fire decreased herbage cover in all grazed plots (W, WC, MW and MWC) but not in C (Fig. 16). The lack of significant fire effect on vegetation cover in treatments C was unexpected because the C plot was grazed and reduction in vegetation cover was expected. Similarity in vegetation cover in burns and controls in plot C is presumably due to the cattle grazing pattern in the periods following fire. First cattle run after fire was conducted only for two hours, the second one carried out 49days later. This was the last cattle run before the first vegetation survey conducted after over 30days later. These timings, episodic grazing and the periodical temporary release of plot C from grazing within the period from March to June (a period usually marked with increase in precipitation at the study area) could have led to an increase in vegetation growth in the burns. This eventually led to the restoration of vegetation cover back to pre-burns state. Temporary release from herbivory has also been reported to increase vegetation cover (Jacobo *et al.*, 2006, Ash *et al.*, 2011, Boughton *et al.*, 2016) more especially during rainy seasons as rains have been widely document to increase vegetation cover by enhancing growth (He, 2014, Patton *et al.*, 2007, Fynn and O'connor, 2000, Hoof *et al.*, 2018).

While cattle were noted to cause no significant difference in post fire forage cover between burns and controls, wildlife (W and MW) caused a reduction in post fire vegetation cover in burns but not in the non-burns. The reason behind the contrasting findings in C plots and the wildlife (W, MW) plots could have been due to the frequency at which these herbivore guilds accessed their respective plots for grazing. Wild herbivores grazed the plots accessible to them *ad lib* but cattle could only access the plots only during the runs. The grazing pattern in the C plot enabled restoration of vegetation cover of burns in C plots back to pre-burn state due to temporary lack of grazing. Continuous access to burns in W and MW plots caused a significant reduction in vegetation cover in burns compared to the controls. This continuous access of burns by the wild herbivores also maintained lower vegetation cover in burns than the non-burn control sub-plot of WC regardless of the temporary release from grazing by cattle. Exclusion of megaherbivores from an area they utilize together with the mesoherbivores in the absence or in the presence of cattle however did not change how vegetation cover responded to controlled fire. Therefore, herbivores reduce vegetation cover after fire irrespective of megaherbivore presence or absence. However, in areas where cattle grazing is episodic, vegetation cover restoration to pre-burn levels soon after fire should be expected.

Species turnover was higher in burns than controls for herbivory treatments W, MW and WC, but not for C, MWC and O (Fig. 19). Evidence from this current study indicates that fire effect on herbaceous vegetation species turnover is influenced by herbivory and that different herbivore guilds may have varying effects on how vegetation species turnover responds to fire. Lack of significant effect of grazing on species turnover in burns of treatment C and MWC was unexpected whereas findings in W, MW and WC were consistent with our expectations that grazing improves how herbaceous vegetation species turnover rate respond to fire. Grazing has also been reported by other studies to have a positive effect on vegetation species turnover (Bakker *et al.*, 2003, Rutherford and Powrie, 2013, Schimtz and Isselstein, 2020) through removal of forages and creation of patches through which new plants establishes and colonize pastures.

The similarity in species turnover rate that was demonstrated between burns and the non-burn sub-plots of treatment C is presumably due to temporary release of this plot from grazing coupled with light grazing after fire, and during periods that preceded the first vegetation survey. The observed grazing pattern in C plot gave the burns a sufficient time to recover from fire and the initial grazing effect. Presumably this led to vegetation species turnover returning to the pre-burn state by the time the first vegetation survey was conducted. The restoration of vegetation species turnover rate to pre-burn state in treatment C burns could have been as a result of an increase in herbaceous vegetation biomass. Increase in vegetation biomass can cause a reduction and stagnation of vegetation species turnover and heterogeneity due to establishment of dominance by some vegetation species (Jacobs & Naiman, 2008). Cattle effect however was not eminent in treatment WC. The constant presence of and grazing by the wild mesoherbivores in WC allowed constant removal of forages and at the same time creating microsites for new growth. The observed lack of significant effect of grazing in MWC burns is presumably due to higher grazing pressure in treatment MWC leading to a more uniform grazing in both burns and non-burn controls of MWC. Uniform grazing in both burns and the non-burns in MWC evened out any difference in species turnover between burns and the non-burns. Another study in the savanna of South Africa demonstrated that higher grazing pressures may have a negligible or no impact on herbaceous species turnover rate (Rutherford and Powrie, 2013).

Excluding megaherbivores from grazing with the mesoherbivores and cattle led to an improved species turnover in burns than non-burns possibly due to a reduction in the grazing pressure. However, absence of megaherbivores in areas they graze on together with the mesoherbivores did not have an effect on species turnover in burns despite the expected reduction in grazing pressure. The mechanism behind the observation in MW compared to W was however not clear from this study. Therefore, herbaceous species turnover rate following fire treatment can only be enhanced if burns are continuously grazed on and probably only under feasible stocking rates as overstocking as may impact negatively on species turnover rates in burns.

The observed lack of significant effect of grazing on how herbaceous vegetation species diversity responded to fire contradicts the expectation that grazing in burns can help improve species diversity by suppressing dominance and opening microsites for new growth (Olff & Ritchie, 1998, Riginos *et al.*, 2018). The lack of significant difference between burns and the non-burns following herbivory is however consistent with other study findings. For instance, van Coller *et al.*, (2015) and Ruthven *et al.*, (2000) reported that interactively, fire and herbivore do not have significant effect on vegetation species diversity. Burned pastures are attractive to herbivores due to their enhanced forage quality and reduced predation risk (Kimuyu *et al.*, 2017, Riginos & Grace, 2008). These attributes can increase consumption and trampling of the post fire regrowth leading to the establishment of more grazing tolerant species at the expense of species that are intolerant to enhanced grazing intensity (Jacobs & Naiman, 2008, Archibald *et al.*, 2005).

Alternatively, this lack of change in species diversity could have been as a result of dominance by less preferred, low or unpalatable vegetation species following selective grazing since most of these herbivores are selective grazers (Al-Rowaily *et al.*, 2015, Ferreira *et al.*, 2013, Treydte *et al.*, 2013, Savadogo *et al.*, 2008, El-Keblawy *et al.*, 2009). It has been demonstrated that dominance by a single or few species have a suppressive effect on overall species diversity (van Coller *et al.*, 2013). However, the above explanations may not suffice for treatment C since its burns and the whole plot experienced limited and episodic grazing during periods following fire. Therefore, the observed lack of significant difference in vegetation species diversity between burns and the non-burns in plot C was not due to enhanced grazing, but rather due to insufficient grazing. Lack of adequate grazing in the C plot led to an increase in vegetation biomass that has negative impacts on overall pasture heterogeneity (Jacobs & Naiman, (2008) as there is no opening up of microsites for new growth.

Based on the main effects of herbivory, herbaceous vegetation species diversity was greater in treatments W and MWC (but not C, WC and MW) than in treatment O (Figure 18). Consistent with our findings, other studies have reported that grazing may bear positive and sometimes no effects on vegetation species diversity (Rutherford and Powrie, 2013, Shackleton, 2000, Anderson and Hoffman, 2007, Mwendera *et al.*, 1997) depending on grazing animal type, grazing intensities, land use and ecosystem type. The observed higher diversity in W and MWC was expected and is due to the ability of these herbivores to open up areas through which new plant species can grow as they graze (Porenski *et al.*, 2013, Riginos *et al.*, 2018).

Lack of significant difference in herbaceous species diversity between treatment MW, WC or C and O was however unexpected. Finding in treatment C is presumably as a result of the temporary release of this plot from grazing since cattle runs are conducted at intervals hence giving cattle accessed pastures a resting period. During such periods of rest, there is neither trampling nor defoliation and this encourages pasture growth leading to emergence of overgrown mature pastures. Intake of these overgrown mature pastures is less (Tarazona *et al.*, 2012, Jalali *et al.*, 2012) and this reduction in consumption can cause the rise of dominance and emergence of a more homogenous pasture. This establishment of dominance is however absent in MWC probably due to the presence of the wild herbivores that are always continually grazing in these herbivore treatment plots thus compensating for cattle absence.

This compensatory effect of wild herbivores however was not observed in WC and this shows that probably, it is mainly driven by the megaherbivores. Megaherbivores have been reported to reverse negative effects cattle may have on pastures and soil through increase in nutrient cycling via excreta deposition (Sitters *et al.*, 2020). Elsewhere, increase in dung deposition has been reported to improve vegetation diversity (Olff and Ritchie, 1998, Dai, 2000, Gillet *et al.*, 2010, Barthelemy *et al.*, 2015) by increasing seed density in seed banks, altering seed distribution and facilitating seed growth. Therefore, absence of megaherbivore in pastures accessed by cattle and mesoherbivores could be the reason behind the lack of significant effect of herbivores on species diversity in WC. On the other hand, absence of cattle in pastures accessed by the mesoherbivores led to higher pasture species diversity regardless of megaherbivore exclusion probably due to the lack of the suppressive effects that cattle have been reported to have on these mesoherbivores (Young *et al.*, 2005; Kimuyu *et al.*, 2017). The mechanism behind lack of significant effect of herbivory on herbaceous species diversity in treatment MW was however not clear in this study since it is expected that the presence of the megaherbivores in the treatment should create a more diverse vegetation community.

The effects of herbivores on how the measured herbaceous vegetation cover, species turnover and diversity responded to controlled fire were not influenced by time since burning. It had been expected that herbivore effects on the measured vegetation attributes would decrease and even diminish with increasing time after burning. The reduction in herbivore effect is as a result of the burns becoming less attractive to herbivores due to decreasing forage quality. The reduction in herbivore visitation and use of burns could have been so marked in this current study leading to restoration of measured attributes to the pre-burn state. Also due to reduction in forage quality, herbivore may tend to graze selectively preferring high quality species (WallisDeVries *et al.*, 1999, Ferreira *et al.*, 2013, Treydte *et al.*, 2013) leading to the establishment of and dominance by less palatable and less preferred species. Such dominance does not give space for new growth and eventually, herbaceous cover, species turnover and diversity in the burns become similar to those of the non-burns.

Although the interaction between fire and herbivory was not influenced by time since fire, there was a significant effect of fire by time since burning interaction on vegetation cover and turnover rates (Fig. 16 and 20). Overall, fire effect on forage cover changed as time elapse since burning (Fig. 16). Specifically, burns had significantly lower vegetation cover than non-burns during the first three years post-fire, but not in any of the later years. Reduction in forage cover immediately after burning is due to the effects of fire on the above ground biomass in addition to the effects of herbivores that are attracted to the burns due to the improved forage quality in burns (Sensenig *et al.*, 2010; Allred *et al.*, 2011; Eby *et al.*, 2014). With increasing time post-fire, however, forage quality begins to decline, as was found in this study, leading to reduced grazing pressure in burns and restoration of herbage cover to pre-burn levels (Allred *et al.* 2011, Whisenant, 2004, Sensenig *et al.*, 2010; Kimuyu *et al.*, 2017). This finding was consistent with a study by Basset *et al.*, (2017) that reported up to at least two years reduction in canopy cover after fire. The demonstrated time also is within the timelines suggested in other studies of up to three years for post fire vegetation cover to return to pre-burn state (Jandt *et al.*, 2012, Yeung and Li, 2018).

Species turnover rate was higher in burns than controls during the first three years post fire but not during the later times (Fig. 20) possibly due to the effects of herbivores that were attracted to the burns. As these herbivores feed on post fire regrowth, they open up spaces through which new plant are established (Porenski *et al.*, 2013). This could explain the observed increase in species turnover in burns than controls during the first three years but not later year as herbivore use of burns reduces with increasing time after fire and since fire and herbivory interact to increase species diversity, a reduction in the strength of this interaction as time after fire increases can lead to the observed lack of significant difference between the burns and the non-burns

CHAPTER SIX: CONCLUSION AND RECOMMENDATIONS

6.1 Conclusions

i. Herbivory did not influence the effects of fire on the measured forage quality attributes but some herbivores influenced vegetation cover and species turnover.

ii. Grazing by wild herbivores only or in combination with cattle reduced post-fire vegetation cover and improved species turnover but not grazing by cattle only

iii. Experimental exclusion of megaherbivores did not have an effect on vegetation quality, cover and species diversity but in the absence of megaherbivores, cattle and mesoherbivores significantly reduced post fire species turnover

iv. Herbivore effects on the measured vegetation attributes were not influenced by time after fire

6.2 Recommendations

i Herbivores do not sustain post fire rise in forage quality thus when fire is used to enhance pasture quality, it should be periodically applied to eliminate dead, mature and moribund pastures and encourage new growth.

ii Just like it was observed in plots grazed by wild herbivores, cattle should also continuously graze on burns to improve post-burn species turnover

iii Alternatively, wild herbivores can be allowed to graze on such pastures during periods of cattle absence so as to prevent such pastures from getting overgrown and mature due to lack of defoliation and trampling.

iv More research however should focus on how stocking rates can influence the effect of fire-driven herbivory on vegetation metrics measured since most of the observed responses have presumably been attributed to the varying stocking rates at the study site yet stocking rate was not among the explanatory variables measured.

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APPENDICES

Appendix 1.1: KLEE Research Grants

This research was carried out under Government of Kenya research clearance permit No. NCST/RCD/12B/012/42. The KLEE exclosure plots were built and maintained and the fire treatments funded by grants from the James Smithson Fund of the Smithsonian Institution (to A.P. Smith), The National Geographic Society (Grants 4691-91, 9106-12, and 9986-16), The National Science Foundation (LTREB BSR 97-07477, 03-16402, 08-16453, and 12-56034) and the African Elephant Program of the U.S. Fish and Wildlife Service (98210-0-G563) (to T.P. Young, C. Riginos, and K.E. Veblen), and Goshen College (to R.L. Sensenig).

Appendix 1.2: ANOVA Tables

Anova components analysis for Pasture CP

	numDF	denDF	F-value	p-value
(Intercept)	1	168	21210.218	<.0001
HERBIVORY	5	10	7.889	0.0030
FIRE	1	12	254.162	<.0001
TIME	3	168	429.671	<.0001
GRASS	1	168	48.833	<.0001
HERBIVORY:FIRE	5	12	0.239	0.9377
HERBIVORY:TIME	15	168	1.412	0.1467
FIRE:TIME	3	168	123.830	<.0001
HERBIVORY:GRASS	5	168	0.303	0.9107
FIRE:GRASS	1	168	0.005	0.9418
TIME:GRASS	3	168	0.715	0.5444
HERBIVORY:FIRE:TIME	15	168	0.996	0.4622
HERBIVORY:FIRE:GRASS	5	168	0.856	0.5124
HERBIVORY:TIME:GRASS	15	168	0.615	0.8603
FIRE:TIME:GRASS	3	168	1.757	0.1573
HERBIVORY:FIRE:TIME:GRASS	15	168	1.565	0.0884

Anova components analysis for Pasture CF

	numDF	denDF	F-value	p-value
(Intercept)	1	168	49719.96	<.0001
HERBIVORY	5	10	0.96	0.4878
FIRE	1	12	61.17	<.0001
TIME	3	168	164.44	<.0001
GRASS	1	168	4.80	0.0298
HERBIVORY:FIRE	5	12	0.35	0.8754
HERBIVORY:TIME	15	168	1.25	0.2410
FIRE:TIME	3	168	20.57	<.0001
HERBIVORY:GRASS	5	168	0.61	0.6926
FIRE:GRASS	1	168	0.02	0.8776
TIME:GRASS	3	168	2.90	0.0367
HERBIVORY:FIRE:TIME	15	168	0.57	0.8928
HERBIVORY:FIRE:GRASS	5	168	0.49	0.7806
HERBIVORY:TIME:GRASS	15	168	1.00	0.4585
FIRE:TIME:GRASS	3	168	0.45	0.7189
HERBIVORY:FIRE:TIME:GRASS	15	168	0.99	0.4694

Anova components analysis for Pasture IVDMD

	numDF	denDF	F-value	p-value
(Intercept)	1	168	40140.18	<.0001
HERBIVORY	5	10	1.43	0.2945
FIRE	1	12	111.34	<.0001
TIME	3	168	139.02	<.0001
GRASS	1	168	29.01	<.0001
HERBIVORY:FIRE	5	12	1.38	0.2972
HERBIVORY:TIME	15	168	1.40	0.1537
FIRE:TIME	3	168	36.96	<.0001
HERBIVORY:GRASS	5	168	2.09	0.0690
FIRE:GRASS	1	168	0.55	0.4592
TIME:GRASS	3	168	1.23	0.3010
HERBIVORY:FIRE:TIME	15	168	1.01	0.4475

HERBIVORY:FIRE:GRASS	5	168	0.31	0.9065
HERBIVORY:TIME:GRASS	15	168	1.69	0.0563
FIRE:TIME:GRASS	3	168	0.60	0.6147
HERBIVORY:FIRE:TIME:GRASS	15	168	0.77	0.7122

Anova components analysis for Pasture P

	numDF	denDF	F-value	p-value
(Intercept)	1	168	2999.6349	<.0001
HERBIVORY	5	10	1.7122	0.2193
FIRE	1	12	73.8888	<.0001
TIME	3	168	926.4382	<.0001
GRASS	1	168	44.3844	<.0001
HERBIVORY:FIRE	5	12	1.1659	0.3804
HERBIVORY:TIME	15	168	1.5951	0.0796
FIRE:TIME	3	168	54.7486	<.0001
HERBIVORY:GRASS	5	168	0.9393	0.4570
FIRE:GRASS	1	168	0.7855	0.3767
TIME:GRASS	3	168	1.5664	0.1994
HERBIVORY:FIRE:TIME	15	168	1.0918	0.3674
HERBIVORY:FIRE:GRASS	5	168	0.4592	0.8061
HERBIVORY:TIME:GRASS	15	168	1.6838	0.0583
FIRE:TIME:GRASS	3	168	2.5260	0.0593
HERBIVORY:FIRE:TIME:GRASS	15	168	0.8780	0.5898

Anova components analysis for Pasture Na

	numDF	denDF	F-value	p-value
(Intercept)	1	168	7320.418	<.0001
HERBIVORY	5	10	0.671	0.6546
FIRE	1	12	2.089	0.1739
TIME	3	168	417.349	<.0001
GRASS	1	168	18.085	<.0001
HERBIVORY:FIRE	5	12	1.496	0.2624

HERBIVORY:TIME	15	168	0.703	0.7788
FIRE:TIME	3	168	2.073	0.1057
HERBIVORY:GRASS	5	168	0.811	0.5436
FIRE:GRASS	1	168	3.845	0.0515
TIME:GRASS	3	168	2.001	0.1157
HERBIVORY:FIRE:TIME	15	168	1.280	0.2197
HERBIVORY:FIRE:GRASS	5	168	0.658	0.6561
HERBIVORY:TIME:GRASS	15	168	0.770	0.7092
FIRE:TIME:GRASS	3	168	0.436	0.7275
HERBIVORY:FIRE:TIME:GRASS	15	168	1.253	0.2374

Anova components analysis for Pasture K

	numDF	denDF	F-value	p-value
(Intercept)	1	168	1085.0352	<.0001
HERBIVORY	5	10	0.7204	0.6230
FIRE	1	12	89.5230	<.0001
TIME	3	168	155.5265	<.0001
GRASS	1	168	200.3289	<.0001
HERBIVORY:FIRE	5	12	0.7719	0.5879
HERBIVORY:TIME	15	168	2.8087	0.0006
FIRE:TIME	3	168	52.1104	<.0001
HERBIVORY:GRASS	5	168	1.7594	0.1239
FIRE:GRASS	1	168	19.0328	<.0001
TIME:GRASS	3	168	12.1735	<.0001
HERBIVORY:FIRE:TIME	15	168	0.8808	0.5866
HERBIVORY:FIRE:GRASS	5	168	1.2591	0.2840
HERBIVORY:TIME:GRASS	15	168	1.5115	0.1058
FIRE:TIME:GRASS	3	168	7.7077	0.0001
HERBIVORY:FIRE:TIME:GRASS	15	168	1.4626	0.1244

Anova component for herbaceous vegetation cover

Analysis of Deviance Table (Type II Wald chisquare tests)

	Chisq	Df	Pr(>Chisq)	
FTREAT	19.791	1	8.638e-06	***
HTREAT	78.325	5	1.880e-15	***
TIME	349.086	4	< 2.2e-16	***
FTREAT:HTREAT	20.845	5	0.0008664	***
FTREAT:TIME	149.496	4	< 2.2e-16	***
HTREAT:TIME	88.056	20	1.618e-10	***
FTREAT:HTREAT:TIME	29.961	20	0.0704943	.

: Anova component for herbaceous vegetation species diversity

Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
treatment	7.386	7.3855	1	177	6.7271	0.01029	*
herbivores	47.835	9.5671	5	177	8.7142	2.09e-07	***
year	124.147	31.0367	4	177	28.2698	< 2.2e-16	***
treatment:herbivores	9.966	1.9933	5	177	1.8156	0.11200	
treatment:year	8.520	2.1300	4	177	1.9401	0.10579	
herbivores:year	23.106	1.1553	20	177	1.0523	0.40439	
treatment:herbivores:year	21.092	1.0546	20	177	0.9606	0.51218	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

: Anova component for herbaceous vegetation species turnover

Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
treatment	0.089742	0.089742	1	180	10.1888	0.001668	**
herbivores	0.071183	0.014237	5	180	1.6163	0.157843	
year	0.219937	0.054984	4	180	6.2426	0.000100	***
treatment:herbivores	0.143083	0.028617	5	180	3.2490	0.007815	**
treatment:year	0.122581	0.030645	4	180	3.4793	0.009157	**

```
herbivores:year           0.289059 0.014453    20   180  1.6409 0.047539 *
treatment:herbivores:year 0.222458 0.011123    20   180  1.2628 0.209498
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```