EFFECTS OF DOMESTIC AND WILD HERBIVORE UTILISATION ON HERBACEOUS LAYER ABOVEGROUND PRIMARY PRODUCTION IN CENTRAL KENYA SAVANNA

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DECLARATION

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

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DEDICATION

This work is dedicated to the memory of Jonathan Burchell and Ian Ross who cherished and appreciated the complexity and functions of Laikipia savanna We met during the time of my research and maintained close friendship until the time of the fateful plane crash May their genuine friendship, understanding, simplicity and love for natural savannas live in many hearts forever

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ABSTRACT

This study investigated the separate and combined influences of livestock and wild herbivores on herbaceous layer primary production in central Kenya rangelands. The treatments included cattle (C), wild herbivores (with- [MW] and without- [W] mega herbivores), combined cattle and wild herbivores (with- [MWC] and without- [WC] mega herbivores) and control (O), which excluded all large herbivores. Each treatment occupying four-hectare pasture plot was replicated in three blocks and has been operational since 1995. Standing biomass, primary productivity, aboveground litter and herbage utilisation in each treatment pasture were measured six times between August 2002-May 2003 using movable cage method.

The results show that standing biomass was higher in the growing (wet) than in dry season and differed significantly ($p<0.05$) among the treatments. For the two seasons, treatment W had the highest biomass, while treatments C and WC had the lowest. In the wet season, treatments W and MW had significantly higher ($p<0.05$) biomass than the other treatments, while in the dry season, treatments C and WC had significantly lower biomass than the other four treatments. Treatment MWC that combined mega herbivores, other large wild herbivores and cattle sustained intermediate standing biomass. In the wet season, the highest and lowest net primary productivity averaged 2.7 ± 0.8 gm^{-2} and 1.3 ± 0.8 gm^{-2} per day in W and MW treatments respectively. Net primary productivity declined with increased amount of aboveground litter and stronger correlation was observed in O ($R^2=0.71$, $p<0.01$), but significantly explained 47% of the variations observed in standing biomass in pastures utilised by large herbivores.

The proportion of standing biomass contributed by perennial grasses was maximum in grazed treatments while that of forbs peaked in O. *Pennisetum mezianum* and *Themeda triandra* had lowest proportions in O and highest in the grazed treatments. Aboveground litter was higher in the dry than in the wet season in all treatments, but highest in O in both seasons. In the growing season, as high as 75% and as low as 25% of the season's aboveground net primary production was utilised in MW and W respectively, while in the dry season utilisation of primary production continued at a daily rate of 1.7 gm^{-2} and 1.3 gm^{-2} respectively in these treatments. The tussock utilisation was greatest in all treatments that accommodated cattle and most minimum in W.

Different groups of large herbivores exhibit different levels of utilisation that differently affects herbaceous layer standing biomass, aboveground litter and proportions of forage classes. Seasonally, cattle alone have relatively greater reductive capacity on herbaceous layer standing biomass than either wild herbivores alone or combinations of cattle and wild herbivores. Long term exclusion of large herbivores and fire from grazed pastures encourages accumulation of litter which negatively correlate with net primary productivity, such exclusions result in declined vigour of some perennial graminoid plants species such as *Pennisetum stramineum* and *Themeda triandra* but increases domination of dicotyledonous forbs. Combination of cattle and wild herbivores appear to be superior management approach in unprotected grazing lands as it maintained intermediate standing biomass and productivity hence providing a viable management option in conflict prone savanna grasslands.

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ACRONYMS AND ABBREVIATIONS

ASALs	Arid and Semi Arid Lands
C	Cattle
MW	Mega herbivores and other large wild mammalian herbivores
MWC	Mega herbivores, other large wild mammalian herbivores and cattle
O	Total large herbivore exclusion
W	Other large wild mammalian herbivores
WC	Other large wild mammalian herbivores and cattle

CHAPTER ONE

1.0 Introduction

Rangelands cover approximately 51% (6.7 billion ha) of earth's land surface and support different vegetation types such as deserts, chaparrals, grasslands, steppes, and woodlands (Heady and Child, 1994). As sub-sets of rangelands, arid and semi-arid lands (ASALs) cover approximately 12.4 million square kilometres in Africa, or about 50% of the tropical zone (Darkoh, 1992). In Kenya, ASALs constitute four-fifths of the country's total land surface, host over 25% of the total human population, slightly more than half of the livestock population (Kariuki *et al.* 1996), and are home to the majority of large mammal wildlife species.

ASALs have been and continue to be used by domestic and wild herbivores, either separately or jointly. Domestic stock, which comprises cattle, sheep, goats, donkeys and camels, continues to increase rapidly as human population increases (Gichohi *et al.* 1996). Though the effects of livestock on savanna habitats are often profound depending on numbers of animals involved, intensity of vegetation off-take, movement patterns, urination and defecation (Gichohi *et al.* 1996), their coexistence with wild herbivores has been proposed to be more feasible under ranching and pastoral managements, than with cultivation agriculture (Pratt and Gwynne, 1977; Swift *et al.* 1996; Bourn and Blench, 1999). This is because there exist large complementarities in feeding among large herbivores; between grazers and browsers, and course feeders and fine feeders. Cattle commonly convert long grass to short grass, which is subsequently used by other stock such as sheep, goats and juvenile stock (Gichohi *et al.* 1996).

Wildlife populations of the African savannas remained relatively intact during the Pleistocene period when most similar large mammals became extinct on other continents. Nonetheless, other pressures have recently come to bear on these populations, reducing them to small remnants of more impressive herds that existed several decades ago The moist savanna ecosystems, which constitute areas of higher agricultural potential, have been settled and the dry semi-arid zones where much of wildlife now occurs are currently under similar threats Habitat fragmentation and changes induced by the (removal of) traditional human activities also continue to affect the savanna's wildlife populations (Gichohi *et al* 1996) It is therefore becoming more important to understand the coexistence of wildlife with enterprises that are favoured by humans One such enterprise is cattle production Cattle production is a major domestic livestock enterprise in Kenya and elsewhere in the world, with various ecological, cultural, traditional and commercial purposes that could combine better with wildlife management. It is known that species of livestock, the intensity of grazing, climate and edaphic factors influence plant species composition, below and aboveground biomass and productivity of pasture of the common grazing lands (Woldu and Saleem, 2000). Generally, grazing directly affects vegetation by reducing its height, phytomass, density and botanical composition in any particular area (Whyte and Cain, 1981). But little is known of the effects of separate and combined cattle and wild herbivores on production of the vegetation resource Therefore, a study investigating existance of complementary and supplementary effects of groups of herbivores could be beneficial for sustainable management of rangelands

Vegetation productivity (the rate of biomass accumulation in plant tissues) and utilisation of accumulated biomass by herbivores are two critical factors determining the type and number of animals that can occupy an area within an ecosystem at any particular time. These also determine the vegetation structure and floristic composition They provide important parameters to range or wildlife managers, and scientists with interest in forage quality, production and use. Proper use of primary production ensures quality secondary ecosystem productivity and influences production goals, management strategies and kinds of land use in an area.

1.1 Justification

Wildlife management and conservation is facing crisis. Protected areas alone set out for conservation cannot guard against large-scale species extinction, ecological disruption and biological impoverishment within the next fifty years (Western, 1998). This is because vital parts of these conservation units are external to the protected area boundaries, which cannot be brought to new protection without problems. This is presenting concerns regarding wildlife and livestock compatibility. In Kenya, all wildlife cannot fit in the 10% protected land set apart for conservation, consequently wildlife often occur in unprotected properties where they inevitably interact with livestock. Proposals regarding profitability of wildlife management in unprotected areas have been presented by a number of authors including Hopcraft (1990) and Kreuter and Workman (1994).

Recent research suggest that wildlife possess the capability of providing additional revenue on rangelands, either due to its tourism attraction or game ranching potentials. On the other hand, cattle and other domestic livestock have traditionally been considered economically viable by herders and ranchers. This suggests that a mixed strategy of wildlife and livestock with suitable management may be economically optimal and could facilitate maintenance of desirable degree of biodiversity (Hopcraft, 1990, Farnsworth *et al.* 2002) even in unprotected areas. Despite this potential, little is known of the distinctive effects imparted by separate and combined livestock and wildlife on common rangeland natural resources. This gap reveals the need for comprehensive understanding of the multi-consumer effects on the resource that supports wildlife and livestock. Equally, for better management strategies of the savanna herbaceous layer, more information is required on separate and combined effects of livestock and wild-herbivores

The findings of this study will be invaluable to conservation scientists, grassland managers and conservation agents who are concerned with the equilibrium, productivity and interactions of plants and animal species in these ecosystems. The information is further useful for the long-term sustainable conservation of biodiversity that the future well being of the tourism and livestock industries securely depends on in Kenya and elsewhere in the African continent

1.2 Study objectives

The overall objective of this study was to evaluate separate and combined effects after eight years of range utilisation by cattle and large wild herbivores on herbaceous layer production, litter accumulation and relative proportions of grasses and forbs

The specific objectives of this study were to determine

1 Effects of long-term rangeland utilisation by cattle (C), large wild herbivores (with [MW] and without [W] mega herbivores) and combinations of cattle and wild herbivores (with [MWC] and without [WC] mega herbivores) on seasonal herbaceous layer standing biomass, primary productivity and litter accumulation
2 Effects of cattle (C), large wild herbivores (W and MW) and their combinations (WC and MWC) on relative proportions of grasses and forbs in standing biomass.
3. Levels of herbaceous layer tussock and biomass utilisation by cattle (C), large wild herbivores (W and MW) and their combinations (WC and MWC)

1.3 Hypothesis

The essential hypotheses are that

i. Long-term rangeland utilisations by cattle, large wild herbivores or combined cattle and wild herbivores have no measurable effects on seasonal standing biomass and litter amounts in pastures

ii. Proportions of grasses and forbs in pasture are independent of whether long-term pasture utilisation is by cattle, wild herbivores or joint wild herbivores and cattle

iii Levels of tussock and herbage utilisation are independent of groups of large herbivores present in the pastures

CHAPTER TWO

2.0 Literature Review

2.1 Net primary production

Net primary production (NPP) is the total amount of organic matter assimilated by plants less that lost due to respiration (Lieth and Whittaker, 1975, Begon *et al.* 1990, Roberts *et al.* 1993; Gichohi *et al.* 1996, Molles, 1999). It includes both below (roots, rhizomes, corms, tubers and bulbs) and aboveground (stems, branches, leaves, flowers and fruits) phytomass and has been estimated at ecosystem level in a number of studies. Root biomass alone has been reported to account for 50-80% of annual primary production (Chapin III *et al.* 1987). A number of studies (Strugnell and Pigot 1978, Owaga 1980, Macharia 1981, Clary and Jameson 1981, Sala *et al.* 1981, Deshmukh and Baig 1983, Deshmukh 1986; Kinyamario 1987; Cox and Waithaka 1989; Kinyamario and Macharia 1992, Okello 1996) have estimated aboveground component of NPP while Ekaya *et al.* (2001) estimated total net primary production in ungrazed arid and semi arid lands (ASALs) in Kenya. Other studies Bouton *et al.* (1988) have studied biomass dynamics in protected and semi-protected areas in Kenya while Harcombe *et al.* (1993) studied aboveground net primary productivity in Texas prairies of U.S.A.

The aboveground net primary production (ANPP) is a fraction of net primary production (NPP), either biomass or total energy that is incorporated into the aerial parts (leaf, stem, seed and associated shoot organs) of the plant community. It is the most important parameter of most in an ecosystem where large vertebrates are the principal herbivores (Milner and Hughes, 1970)

ANPP has been measured in different sites of the world by different authorities using different methods. Sala *et al.* (1981) estimated ANPP in Argentina grasslands by assessing differences in soi successive harvests measured within the calendar year in ungrazed area where livestock had been excluded for four years. McNaughton (1979a, 1979b, 1985) using movable cages in Serengeti grasslands and Mordelet and Menaut (1995) in humid savanna of West Africa estimated ANPP by summing only positive biomass increments, but with caution for possible ANPP overestimation (Sala *et al.* 1988; McNaughton *et al.* 1996). In North American grasslands, ANPP has been measured in grazed and ungrazed sites (Sims *et al.* 1978; Sims and Singh 1978a, 1978b), and on shallow, rocky, deep, non rocky (upland and lowland) soils on both burned and unburned watersheds of the prairies of U.S.A. (Abrams *et al.* 1986). Elsewhere in Venezuela ANPP has been estimated in burned, unburned and in irrigated sites (San Jose and Medina 1976).

Effects of rainfall amount, rainfall distribution and grazing intensity have also been examined on the net primary production in dry tropical savanna (Pandey and Singh, 1992). Light and moderate grazing have been reported to stimulate increases in aboveground net primary production. Significant reductions in below ground net primary production with profound effects being noted at higher grazing intensities have also been reported (Pandey and Singh 1992). Similarly, higher aboveground biomass has been observed in ungrazed than in grazed grasslands (Sims *et al.* 1978), but seasonal live biomass has been observed to be similar in grazed and ungrazed sites (Sims and Singh 1978a). Significant differences have been observed in aboveground primary productivity and reported to be higher in ungrazed than in grazed grasslands (Sims and Singh, 1978b). Live biomass on the other hand has been shown to be greater in burned than in unburned sites and the proportions of forbs and woody plants reported to be 200-300% higher in the former than in the latter when burned annually (Abrams *et al.* 1986). In East African ecosystems, aboveground primary production has been reported to be higher under tree canopies than in the open grasslands (Belsky *et al.* 1989, Kinyua 1996; Okello 1996). However, contradicting results documenting high production in the open (out side canopy) have been found elsewhere in humid savanna of West Africa (Mordelet and Menaut, 1995)

Functional groups contributing to total aboveground net primary production or standing biomass have also attracted considerable investigation in different parts of the world. In coastal plain pineland of Florida, Ball *et al.* (1981) found grasses to be the most productive functional group recording highest (2190 kg/ha) plant biomass. In the same site forbs production was 334 kg/ha, while sedges production declined from 117 kg/ha in the second year to less than 0.42 kg/ha in the tenth year when disturbance was excluded from the site. Litter accounted for greatest amount of biomass-it increased from 3605 kg/ha in the second year to over 8000 kg/ha in the fifth year on the sites excluding grazing or burning. In Texas prairies, Harcombe *et al.* (1993) reported high live grass biomass, forbs and sedges in unburned relative to burned areas and found grasses to comprise 70-80% of the total peak biomass. In East African ecosystems, Bouton *et al.* (1988) reported that dead standing biomass and litter components had higher biomass proportion than live components and always comprised 50% during the long rains and 94% during the dry seasons in Nairobi National Park. They further reported that more than 90% of the herb layer biomass were contributed by grasses, when forbs and sedges accounting for less than 10%. In the same park, Kinyamario and Macharia (1992) reported *Themeda triandra* as the most productive grass species contributing 42% of the total standing biomass, P *mezianum* 28%, dicots 17% and other grasses combined contributed only 13%.

Resource partitioning and herbivores coexistence

Generally, aboveground net primary production is food for grazers like zebras (*Equus burchelli* and *Equus grevyi*), hartebeests (*Alcelaphus buselaphus*) and wildebeests (*Connochaetes taurinus*), browsers like giraffes (*Giraffa camelopardalis*), dik-diks (*Madoqua saltiana*, *Rhynchotragus kirkii* and R. *guentheri*) and black rhinoceroses (*Diceros bicornis* and

Ceratotherium simum) or mixed feeders like Grant's gazelles (*Gazella granti*), oryx (*Oryx gazella*) and elephants (*Loxodonta africana*). Virtually all grasslands are grazed by more than one species of herbivore and a large number of these consumers depend on grass resource for food (Farnsworth *et al.* 2002). They consume a good proportion of annual net primary production. For instance, McNaughton (1985) reported that between 15-90% of annual net primary production is consumed by large herbivores. Components of aboveground primary production that drop on the ground form litter and humus- food for microfauna such as termites and decomposers (detritivores).

Most field studies on sympatric ungulates have concentrated on assessing the degree of niche separation and identification of the most relevant differences in resource use among the studied species. On the other hand, theoretical studies suggest that species with completely overlapping niches cannot coexist, because if they do, all but one of them are eventually doomed to extinction (Farnsworth *et al.* 2002). The diversity and abundance of herbivores in East African savanna can be explained, to a large extent, by resource partitioning, high primary production and evolutionary history (Voetin and Prins, 1999). The patterns of resource partitioning have been well described for different assemblages of herbivore species and such information may be used to explain how species coexist despite extensive ecological overlap. However, for purposes of managing multipurpose rangelands, resource partitioning and use as exhibited by domestic and wild herbivores would be more informative. Voetin and Prins (1999) demonstrated that resource use by cattle overlapped with that of zebra and wildebeest in the wet season, while that of wildebeest and zebra did not overlap except when resources were in high supply. Different species or groups of wild herbivores appear to have exhibited coexistence with each other for millennia, such that overlaps at the time of resource abundance are considered non-competitive. Groups of wild herbivores and herds of cattle may coexist especially in unprotected areas because of differences in feeding habits, (Werger, 1977), but more data are needed in this area for better understanding of their separate and combined effects on resources that support their coexistence

2.2 Effects of grazing on vegetation biomass

Resource competition, herbivory and predation all have roles in ecosystem productivity Herbivory (grazing) on plants and competition among plants independently reduce biomass and flowering of target plants (Rene Van der Wal *et al* 2000) When plants are protected from herbivory for a long period, competition among them is increased, however, their persistence in the short term is determined by grazing

Herbivores affect plants directly when they remove biomass (Pratt and Gwynne 1977; Painter and Detling 1981, Whyte and Cain 1981, Rene Van Der Wal 2000) and have myriad indirect effects on plants They modify resource availability; enhance light penetration through the canopy (Rene Van Der Wal 2000) as they graze differentially on neighbouring plants (Belsky 1986, 1987; Belsky *et al* 1993; Rene Van Der Wal 2000). This suggests that short-term exclusion of direct herbivore attack on plants always leads to increased plant biomass. On the other hand, total exclusion of herbivores can result in reduced incremental biomass of older plants (Rene Van Der Wal, 2000) This shows that grazing and long-term competition among plants (herbivore exclusion) negatively affects total plant biomass in an ecosystem

In most cases, herbivory removes less than 10% of the annual aboveground net primary production, but sometimes up to 50% (Painter and Detling, 1981), 85% standing crop (McNaughton 1976), 15-90% (McNaughton, 1985) or more of the annual aboveground production in the grasslands may be used up by herbivores. In such cases, the effect of short period herbivore exclusion may result in rapid increase of cover and biomass yield of formerly grazed plants

In the short run, grazing exclusion can significantly influence species composition and growth forms of plants According to Sala *et al.* (1986) this results in higher basal area cover in ungrazed sites than in grazed grassland communities, but the former maintains lower floral diversity than in the latter Under grazed unlike ungrazed conditions biomass may be negatively correlated to species diversity (Rusch and Oesterheld, 1997) Hence herbivory may reduce the effects of competitive exclusion of plant species from an ecosystem

Sala *et al* (1986) suggested that periodic disturbance on sites such as those caused by herbivory allows for coexistence of higher diversity of vegetation species This implies that quality of vegetation in grazed conditions is likely to be higher than in ungrazed conditions since most plants are constantly in a growing and greening up mode, subject to favourable environmental conditions It is apparent that grazed systems are ecologically distinct from ungrazed ones, but for the purposes of prudent management, it is to the benefit of managers to ascertain effects when different kinds or groups of herbivores utilise rangelands

2.3 Interactive relationships among herbivores

Interactions between livestock and wildlife in African ecosystems are often thought to be negative (Young *et al.* 1998) due to limited resources that are common and needed by both However, among the herbivores, one consumer may increase accessibility to food for another when a common resource is partitioned (Farnsworth *et al.* 2002) Among the wild ungulates, inter-species interactions can be competitive, synergistic or complementary (Kinyua and Njoka 2001). In Serengeti (like in other East African ecosystems) considerable overlap on resource use has been observed and reported, thus ecological separation is largely due to differences in herbivore feeding behaviour. For instance, grazing succession begins with larger species such as buffaloes (*Syncerus caffer*) and zebras (*Equus burchelli*) followed by topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*), and then Thomson's gazelles (*Gazella thomsoni*) (Maddock, 1979). This is probably so because most of the time larger herbivore species are bulk feeders hence prepare the pastures for fine feeders. Among the domestic stock, presence of one species may increase the performance of another, for example cattle increased the performance of sheep (Morris *et al*. 1999). Kinyua and Njoka (2001) presented logistic interaction models for Grant's gazelle (*Gazella granti*), Thomson gazelle (*Gazella thomsoni*), giraffe (*Giraffa camelopardalis*), zebra (*Equus burchelli*), Oryx (*Oryx gazella*), Kongoni (*Alcelaphus buselaphus*) and impala (*Aepyceros melampus*).

Plate 1. Complementary interaction between browser giraffes (*Giraffa camelopardalis*, a strict browser) and zebras (*Equus burchelli* a grazer) observed in Mpala Ranch Laikipia

Plate 2. Competitive interaction between zebras (*Equus burchelli*) and warthogs (*Phacochoerus aethiopicus*), both grazers in a Laikipia glade

These models explored competitive (Plate 2), complementary (Plate 1) and synergistic relationships among these herbivores. Competitive relationships were found between Thomson gazelles and zebras and between oryx and Grant's gazelles. Complementary interactions were found between Thomson gazelle and cattle, Grant's gazelle with giraffes and impalas, and zebra and oryx. Other complementary relationships were found among Oryx, hartebeest (kongoni) and wildebeest and finally between the hartebeest and Grant's gazelle. In general these models suggest that, mixed feeders such as Grant's gazelle, impala and oryx remained complementary to obligate browsers such as giraffes or grazers such as zebras (see Plate 1).

The models indicate the complexity that exists among wild ungulates. They also show that greater diversity of ungulates in grazed systems may be to the advantage of ecosystem utilisation. These results form the basis for coexistence of domestic and wild herbivores as the complementary and supplementary effects may be exploited to counter competitive effects

2.4 Effects of herbivores on plants: their role in compensatory growth

Herbivores are an integral component of grasslands and their effects at the ecosystem level may include nutrient transformation and translocation, nutrient flow rates, and nutrient availability due to plant responses to grazing and nitrogen. Grazing can influence soil nitrogen mineralisation, facilitate rapid substrate decomposition and increase rate of nitrogen recycling as a result of dung and urine deposition (Shariff *et al.* 1994). Cattle have in the past attracted a number of research discussions and investigations of its effects on rangeland resources. At the ecosystem level, cattle increase nutrient flow, forage quality (Phillips *et al.* 1999) reduce branch length, aboveground biomass and height of individual plant species (Maschinski, 2001). Improper cattle management can accelerate stream bank erosion; increase site disturbance (Kauffman *et al.* 1983a) and retard community succession (Kauffman *et al.* 1983b).

A number of field experimental results (McNaughton 1979a; 1983; Cargill and Jefferies 1984; Georgiadis *et al.* 1989; Hik and Jefferies 1990) and model simulations (Hilbert *et al.* 1981; Dyer *et al.* 1986; de Mozancourt *et al.* 1998; Leriche *et al.* 2001) suggest that net primary production (NPP) could be maintained (compensatory) or stimulated (over-compensatory) in response to herbivory or clipping to mimic herbivory. But Belsky (1986, 1987) and Belsky *et al.* (1993) have raised serious concerns on the ecological significance and general application of these results with significant questions about the experimental designs, methodologies in data collection, and semantics. Perhaps due to conflicting results, Crawley (1987) maintained indecision in his conclusion by upholding that both McNaughton and Belsky are right since the bottom line of this debate is yet to be unveiled.

Plate 2. Competitive interaction between zebras (*Equus burchelli*) and warthogs (*Phacochoerus aethiopicus*), both grazers in a Laikipia glade

These models explored competitive (Plate 2), complementary (Plate 1) and synergistic relationships among these herbivores. Competitive relationships were found between Thomson gazelles and zebras; and between oryx and Grant's gazelles. Complementary interactions were found between Thomson gazelle and cattle; Grant's gazelle with giraffes and impalas; and zebra and oryx. Other complementary relationships were found among Oryx, hartebeest (kongoni) and wildebeest and finally between the hartebeest and Grant's gazelle. In general these models suggest that, mixed feeders such as Grant's gazelle, impala and oryx remained complementary to obligate browsers such as giraffes or grazers such as zebras (see Plate 1).

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Grazing affects the form and stature of plants. In general, the pattern of response by plants to herbivory depends on the vegetation type, prevailing environmental conditions, temporal and spatial scales of grazing (Brown and Allen 1989; Holland *et al* 1992; Biondini *et al.* 1998). Belsky (1992) found higher cover values among short-statured grass species in grazed blocks while tall grass species dominated ungrazed blocks. An exception was *Themeda triandra*, which had almost disappeared from the ungrazed block. The effect of grazing on plants largely depends on the space and time scales considered. In the short term (within a growing season), response of net primary production (NPP) to grazing is determined by complex interactions among various factors such as light availability, water stress, nutrient recycling, biomass allocation to shoots and roots, and photosynthetic rates of specific plants (Lenche *et al.* 2001). Herbivory effects on available phytomass and primary productivity per unit area determine its impacts in the long-term scales on the entire range (Weber and Jeltsch, 2000). Quantification of these effects needs to consider what is consumed and to what extent. Previous tests of the overcompensation hypothesis for aboveground or total NPP have found significant overcompensation (McNaughton 1979b; Cargill and Jefferies 1984; Georgiadis *et al.* 1989), compensation (Beaulieu *et al.* 1996) or under compensation (Rusch and Oesterheld 1997; Maschinski 2001)

In simulated resource availability, Leriche *et al* (2001) reported weak over-compensatory growth under herbivory within restricted conditions of resource availability. On the other hand, Biondini *et al.* (1998) found no consistent effects of eight-year cattle grazing on aboveground net primary production. In a short period of observation, Maschinski (2001) and Puettmann and Saunders (2001) reported that plants do not fully compensate for lost biomass lost due to grazing within one growing season. However, different levels of herbivory manifest stimulation on vertical height growth, diameter growth and total biomass of the plant (Puettmann and

Saunders, 2001). On the other hand, cattle and wild ungulates affect plant height, total branch length, mean plant biomass and cause plant mortality on rare willows (Maschinski, 2001). The magnitude of the impact however, varies with types, numbers and kinds of herbivores present, the amount of time plants are exposed to herbivory, and the amount of recovery time

The foregoing literature review provides general information on interactions between herbivores and vegetation. It is apparent that the livestock - wild herbivores - vegetation interactions are complex and present challenges to grassland management and operations. Aboveground primary production is continually being removed by herbivores as plant grows, but effects of such removal need better understanding in order to generate even more appropriate grassland management programmes. Upon this premise, this study was undertaken

CHAPTER THREE

3.0 Materials and Methods

3.1 Site description

The study was conducted at the Mpala Research Centre (MRC) located 40 kilometres northwest of Nanyuki town in Laikipia district, Rift Valley province, Kenya. The centre is situated on longitude 36º 54' 0"E and latitude 0º 17' 24"N (Figures 3.1 and 3.2) in the Ewaso Nyiro North ecosystem at 1800m above sea level.

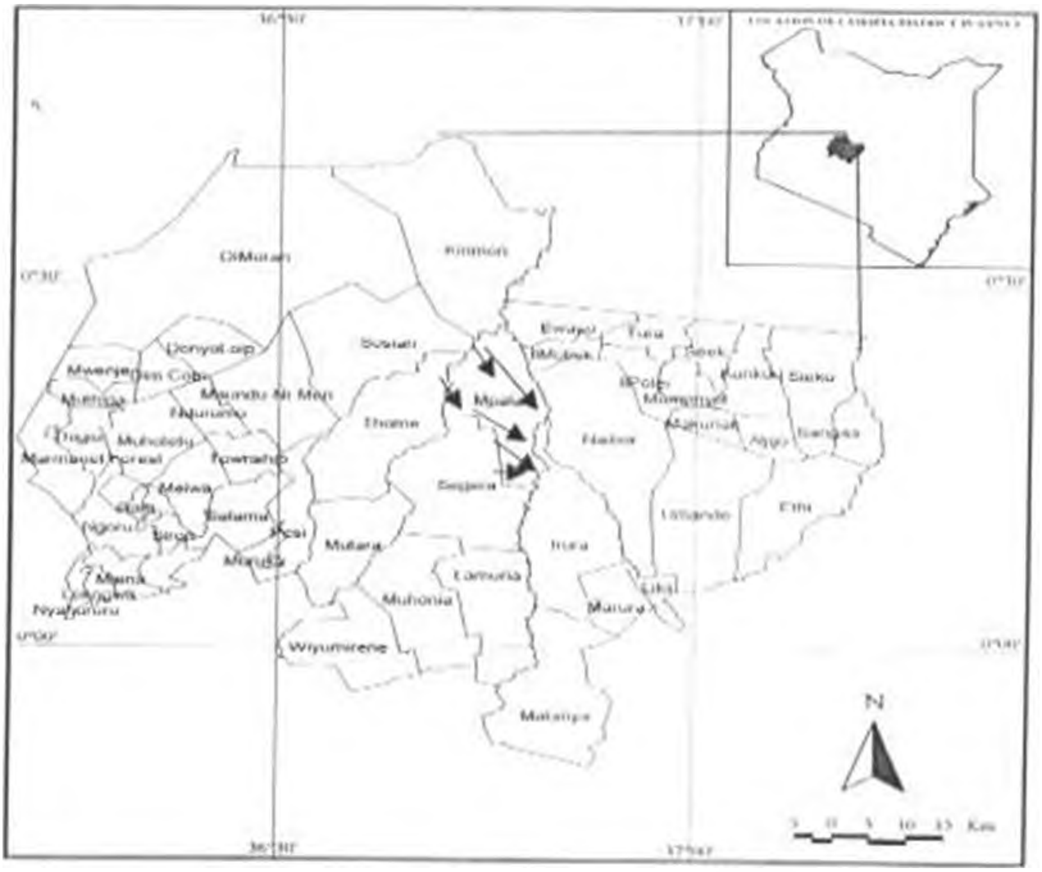


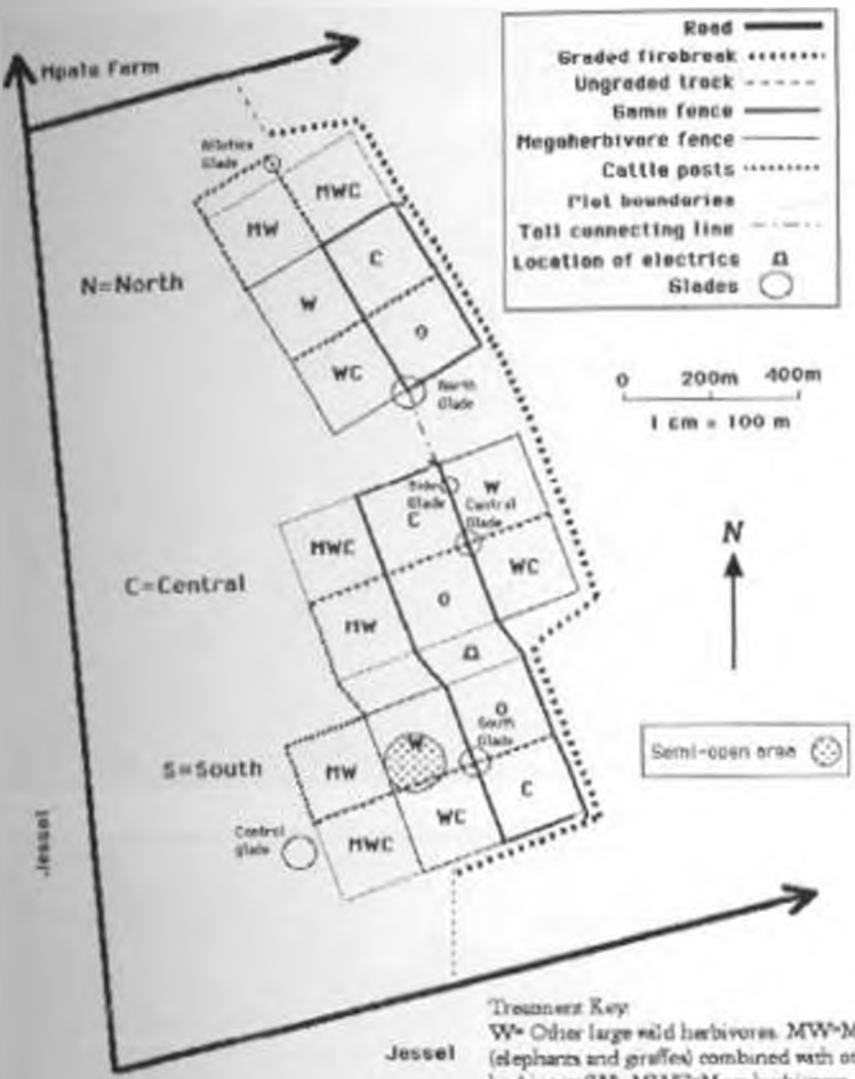
Figure 3.1 Geographic Location of Mpala conservancy in Laikipia District

Figure 3.2 Map of Mpala Research Centre Showing Study Sites (Courtesy of T.P. Young)

Low and variable rainfall averaging 500mm in the North and 650mm in the South characterizes the area. The rainfall has a weakly trimodal distribution with peaks in April, July and November (Young *et al.* 1998). The rainfall is usually low between December and February. Maximum temperatures range from 25°C to 30°C, while minimums range from 12°C to 17°C (Young *et al.* 1998). The soils are deep clay black cotton soils (vertisols), which cover about 43% of Laikipia district (Young *et al.* 1998). These soils are low in vegetation diversity, high in large herbivore diversity and support some of the most productive rangelands in East Africa (Young *et al.* 1998). Other soil types as reviewed in Young *et al.* (1995) include well drained, moderately deep to very deep, dark reddish brown, friable, gravely, sandy clay loam to clay loam. The overstorey vegetation is dominated by *Acacia drepanolobium* Harms. Other woody species include *Cadaba farinosa* Forssk, *Balanites aegyptiaca* (L.) Del., *Rhus natalensis* Krauss, and *Acacia mellifera* (Vahl) Benth. Dominant grasses are *Lintonia nutans* Stapf., *Brachiaria lachnantha* (Hochst.) Stapf., *Themeda triandra* Forssk., *Pennisetum mezianum* Leeke, and *P* *stramineum* Peter. The dominant forbs include *Aerva lanata* (L.) Juss and *Commelina* spp (Young *et al* 1998)

3.2 Experimental layout and treatments

In September 1995, the Kenya Long-term Exclosures Experiment (KLEE) project started long-term herbivore exclosure pastures at the Mpala Research Centre. The experiment was organized in a stratified block design with six treatments: cattle (C), wild herbivores-with [MW] and without [W] mega herbivores, combined cattle and wild herbivores- with [MWC] and without [WC] mega herbivores and, ungrazed control (O), which excluded all large herbivores in the pastures. Each treatment was replicated three times along North-South gradient for a total of eighteen pastures of 4 hectares each (Figure 3.3 below). Mega-herbivores (M) in this study refer to elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). Wild herbivores (W) refer to large mammalian wild herbivores smaller than the mega herbivores that included zebras (*Equus burchelli* and *Equus grevyi*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), Beisa oryx (*Oryx gazella*), hartebeest (*Alcelaphus bucelaphus*) and Grant's gazelle (*Gazella granti*). The experiment used wildlife and mega herbivores fence while cattle barriers in pastures dedicated for wild herbivores alone were visual (Young *et al* (1998). The study evaluated treatment effects after eight years in a black-cotton-soil savanna ecosystem. The treatments represented diverse land use and management strategies practiced in most arid and semi arid lands in Kenya and elsewhere in African continent.



Treatment Key:
W= Other large wild herbivores. MW=Mega herbivores (elephants and giraffes) combined with other large wild herbivores(W). MWC=Mega herbivores, combined with other large wild herbivores and cattle. WC= Other large wild herbivores combined with cattle. C= cattle. O=total Large herbivores excluded

Figure 3.3 Design of the experimental layout

Plate 3. Cattle treatment in the exclosures twenty-one days into the growing (wet) season

Plate 4. Yearlings leaving electrified cattle exclosure through a gate

3.3 Determination of aboveground standing biomass, productivity and herbage utilisation

During the study period (August 2002-May 2003), six cattle 'runs' each having an average of 120 heads of cattle, utilised MWC, WC and C treatment pastures; as has been the case for most of the time since September 1995. In each 'run' a herd of cattle (plates 3 and 4) grazed for an average of two hours to provide moderate utilisation levels equivalent to those being practiced in the entire Mpala ranch. Sampling (clipping) dates were synchronized such that cattle 'runs' always preceded clipping activities to provide closest utilisation estimates.

Aboveground net primary production, productivity and litter amounts were estimated using movable cage (exclosure) method in each of the eighteen 4 ha KLEE pasture plots (illustrated in Plates 5 and 6). The cages whose metal-bar frames were covered with chicken wire of 2.5cm mesh internally measured 1meter by 1meter by 1meter. These cages were set randomly in treatment pastures as recommended by Klingman *et al.* (1943) and moved in pasture plots as described by McNaughton *et al.* (1996) and daily productivity calculated by method used by Williamson *et al.* (1989)

Sampling was done in wet and dry seasons. A total of six sampling dates (sessions) were undertaken at bimonthly intervals. Four dates were in the wet and two in the dry season (Table 3.1) because herbaceous layer changes in the wet season are more dynamic hence more sampling frequency. At each sampling date, five 1m^2 cage plots and un-caged counterparts were selected randomly in each of the 4 ha treatment pasture. Ideally total number of samples would be 540 cages, but due to randomisation some cages sampled the glade areas, which have different vegetation and productivity characteristics, and as such they were excluded from the analysis. This resulted to a final study sample of 495 cages (Table 3.1). All the herbage biomass in each of these plots was clipped to the ground level and mulch (litter) removed.

Differences obtained by subtracting herbage biomass in grazed (uncaged) from those in caged plot herbage biomass provided amounts utilised by large herbivores over the period of observation (Klingman *et al* 1943; McNaughton *et al* 1996)

Table 3.1 Study samples size

Treatment	Dry season # of 1 M^2	Wet season # of 1 M^2	Total # of (1 M^2)
Wild herbivores	29	57	86
Mega-herbivores & Wild herbivores	30	52	82
Mega-herbivores Wild herbivores and Cattle	30	54	84
Wild herbivores and cattle	29	58	87
Cattle	29	52	81
Herbivore exclusion	30	45	75
Totals	177	318	495

Plate 5. Scientist relocating cage position within a pasture treatment

Increments in production (productivity) were estimated in the wet (growing) season by comparing caged herbage (Plate 6) with herbage initially observed in reference 1 m^2 plot (McNaughton *et al.* 1996). Differences from all five sampling points per treatment pasture were included irrespective of whether negative or positive (McNaughton *et al* 1996) and mean of these represented productivity for the sampling date. Mean productivity from various sampling dates were summed together to form aboveground net primary production (ANPP) over the effective study period. The mean ANPP for the treatment was calculated by considering ANPP from different blocks namely North, Central and South (Figure 3.3) in which the treatment was represented. Mean daily aboveground net primary productivity (mass area^{-1} time^{-1}) for each treatment was calculated by dividing ANPP (change in biomass) by the number of days in the effective study period (Williamson *et al.* 1989). Effective study period in the growing season refers to the mean total number of days in which movable cages remained in the field. Seasonal standing biomass was estimated by the average dry plant material biomass harvested inside the cage in different sampling dates within the season.

Plate 6. Movable cage on a sampling site

The standing biomass captured both primer and regrowth biomass, and excluded large herbivores from grazing during the period when cage was in place. The proportion of perennial grasses, forbs and individual grasses was calculated from their relative contribution to the total standing biomass in the caged plot.

Each grass species present in the plot was clipped and packaged in specific paper bag. Paper bag details included individual grass species, herbivore treatment, sampling station location or co-ordinates, plot status (either reference, caged or grazed) and date. The other harvested functional groups were placed into specific paper bag (e.g. all forbs or all collected litter were put into own separate paper bags at the time of harvesting). These were dried to a constant weight at internal (within the bag) temperatures ranging between 50°C to 80°C and external (outside the bag) temperatures ranging from 125°C to 135°C in a forced draught oven for 24 hours before weighing (8 hours drying per day for three consecutive days). The temperatures were measured using the thermometers, which were placed, inside the paper bag together with [illegible] material and in the inter-bags space but within the forced draught oven.

3.3.1 Herbivore dung piles

Data on freshly deposited dung piles were collected from two 200mx4m transects totalling 1600m² per herbivore treatment. Transects stretched to a full treatment length on a North-South gradient. They were 100m apart but approximately 50m from eastern and western sides (ends) of the treatment plots. The freshly deposited dung piles on these transects were recorded by herbivore species. This provided indications for kinds, or groups of herbivores present and utilising the pastures plots as treatment. According to Rene Van der Wal *et al* (2000) utilisation (consumption) can be estimated using dung counts.

3.3.2 Tussock utilisation

To determine herbivore preference and grazing intensities on individual grass species in different herbivore treatments, grass tussocks were surveyed. A total of 240 1m ^{2} quadrats were assessed (40 plots per treatment). Sixteen plots were sampled from each treatment in the northern and southern block and eight other plots were from the central block. This was done once to further provide evidence for large herbivore utilisation. The characteristics recorded included total tussocks per quadrat, total grazed tussocks and grass species heights (stubble and ungrazed). The individual grass species heights were summed and averaged to provide herbaceous layer height in different treatments. Relative proportions (%) of tussocks utilised provided herbivore preferences to grass species while mean stubble height of grass species determined grazing intensity.

3.4 Data analysis

Data on seasonal primary production, aboveground Litter and herbage utilisation were first summarised before subjecting normally distributed data sets to analysis of variance. Results were considered significantly different when $P<0.05$. Significant mean differences were separated using Tukey Honest Significant Differences (HSD) at $P<0.05$. Data on productivity, standing biomass, litter, utilisation, tussocks and stubble biomass were subjected to correlation and regression analysis.

CHAPTER FOUR

4.0 Results and Discussion

4.1 Seasonal aboveground standing biomass

Table 4.1 represents mean aboveground standing biomass for all treatments during both seasons. Only treatments WC and W were significantly different in terms of standing biomass between wet and dry season. For the two seasons, treatment W had relatively higher biomass, while treatments C and WC had lower. In the wet season, treatments W and MW had significantly higher ($p<0.05$) biomass than the other treatments, while in the dry season, treatments C and WC had significantly lower biomass than the other four treatments.

Table 4.1 Mean seasonal standing biomass (gm^{-1}) by treatments

Treatment	Wet season	Dry season
C	324.9 ± 18.9^{a1}	291.9 ± 20.1^{a1}
WC	342.9 ± 15.8^{a1}	283.4 ± 16.9^{a2}
MWC	348.8 ± 16.1^{a1}	314.0 ± 17.9^{b1}
W	441.1 ± 16.8^{b1}	377.8 ± 23.1^{b2}
MW	375.0 ± 16.4^{b1}	358.4 ± 22.7^{b1}
O	366.6 ± 18.5^{a1}	323.0 ± 20.7^{b1}

Treatment means with different superscript letters in the same column and different superscripted numbers in the same row show significant differences.

Results of this study show that pastures utilised by cattle alone have relatively lower herbaceous layer standing biomass, while those utilised by wild herbivores without the mega herbivores have higher irrespective of the season. The intermediate standing biomass obtained in this study in pastures utilised by both cattle and wild herbivores suggest that the two can coexist in a common range at the current level of stocking. This coexistence hinges on the supplementary or complementary effects of different herbivore species on each other's niche (Kinyua and Njoka, 2001). Therefore, with respect to herbaceous layer resources, it seems that in pastures already occupied by cattle, introduction of other mammalian wild herbivores might have a complementary effect. This could provide a viable solution to the crisis facing conservation in the unprotected lands. The standing biomass in pastures utilised by both cattle and wild herbivores could be due to the fact that wild herbivore species are at minimum impact density to avoid direct competition with domestic animals or that the level of cattle grazing and impacts of rotational grazing within the seasons could also have affected the interactive effects observed with wild herbivores. Other explanation to this could on the basis of grazing succession patterns. At the end of a wet season, Maddock (1979) observed that Thomson's gazelle occupied parts of plains previously used by zebras and wildebeests. McNaughton (1976) reported grazing succession of zebra followed by wildebeest and then by Thomson's gazelle. In the present study, it is thought that after cattle have utilised pastures, wild herbivores of equivalent or higher body mass such as elephants and giraffes, utilised those pastures relatively much less, but spent more time in adjacent pastures dedicated to wild herbivores alone. This could be due to the large herbivore's tendency to utilise certain herbage heights (Farnsworth *et al.* 2002) and may probably be suggesting that cattle may not facilitate for herbaceous layer utilisation for mega wild herbivores, even though they may do so for wild herbivores with body mass less than their own.

Evidence based on relative number of fresh dung piles of different herbivores within the various treatment pastures, reveal that elephant activity in MW treatment was twice as much as in MWC and zebras activity was also relatively higher in treatments that excluded cattle (Table 4.2)

Table 4.2 Relative herbivore activity within treatments based on fresh dung deposits

Treat.	Cattle	Cattle/ Buffalo	Buffalo	Elephants	Giraffes	Eland	Grant's gazelle	Zebra	Oryx	Hartebeest	Steenbok	Max diversity
C	85 3	-	-	-	-	-	-	-	-	-	14 7	2
WC		81 2	-	-	-	1 8	6 5	5 9	1 8	1 2	1 8	0
MWC		72 2	-	4 3	-	0 6	6 8	9 3	0 6	3 1	3 1	7
W			6 6	-	-	3 3	22 0	27 5	5 5	6 6	28 6	6
MW			7 6	8 6	2 9	13 3	9.5	43 8	2 9	4 8	6.7	7

Relative activity is presented as % of specific herbivore dung piles per total fresh piles sampled

Grants gazelle and steenbok activity was relatively higher in W than in any other treatment. Cattle and buffaloes dung could not be distinguished especially in WC and MWC treatment hence were referenced together. Giraffe appeared to avoid pastures with cattle presence

(MWC) despite the fact that the former is obligate browser and the latter almost obligate grazer In general most large mammalian wild herbivores reduced their presence in pastures with cattle presence, this could have contributed to intermediate herbaceous layer standing biomass observed in pastures combining cattle and wild herbivores. Hence large and extensive pastures need to be planned in such a way that they accommodate areas for wild herbivores alone in addition to combinations of domestic and wild herbivores

The essential null hypothesis was that long-term rangeland utilisations by cattle, large wild herbivores or combined cattle and wild herbivores had no measurable effects on seasonal herbaceous layer standing biomass and litter amounts in pastures In the light of results and the foregoing discussion, this study fails to accept this hypothesis and infer that separate and combined cattle and wild herbivores utilisation have effects on seasonal standing biomass

4.2 Herbaceous layer aboveground net primary productivity (ANPP) (gm^{-2})

Figure 4 1 presents mean aboveground net primary production by treatments measured in the growing season These represented mean daily aboveground net primary productivity of 2 5±0 2 gm^{-2}, 1.9±0.4 gm^{-2}, 2.0±0.4, 2.7±0.8 gm^{-2}, 1.3± 0 8 gm^{-2} and 1.9±0.1 gm^{-2} per day in treatments C, WC, MWC, W, MW and O respectively Results show that all grazed treatments except MW exhibited higher mean ANPP than the control (O) (Figure 4 2a).

Treatments C and W had the highest ANPP, and MW had the lowest As shown in the (Figure 4 1), standing biomass in treatment utilised by cattle alone was minimum relative to other treatments (Table 4 1), however productivity was high This could be attributed to the fact that plants are incapable of compensating for all their grazed biomass within a growing season (Maschinski, 2001, Puettmann and Saunders, 2001) Also the fact that cattle grazing results in lower stubble height (Maschinski, 2001) means low available standing biomass.

Results of this study are consistent with experimental studies in Canada (Cargill and Jeffries, 1984; Hik and Jeffries, 1990) and in East Africa region (McNaughton, 1979a, 1979b, 1985), which have shown evidence that herbivory could maintain (compensate) or increase (over-compensate) aboveground net primary production above the controls (Figure 4.2a). Although the increased plant growth and reproduction that occasionally follow grazing can be interpreted in terms of overcompensation, Belsky *et al.* (1993) argues that a simpler explanation is that they demonstrate vigorous regrowth by damaged plants and that regrowth is a generalized response by plants to all types of damage not just an adaptation to herbivory.

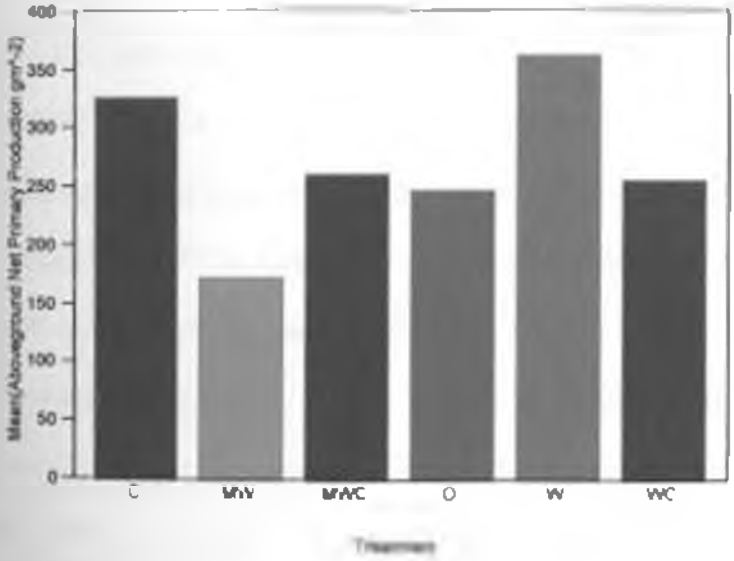
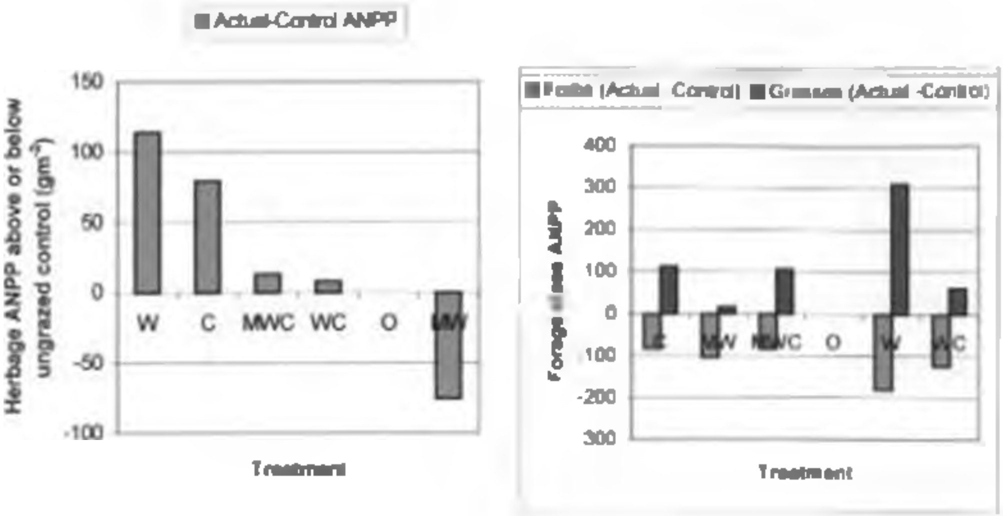


Figure 4.1 Mean aboveground net primary production measured over a period of 133 days in the growing period



a. b.

Figure 4.2 ANPP in grazed treatments after subtracting ANPP in the ungrazed control (O) for total herbage ANPP (a) and forage class ANPP (b)

Compensatory growth data has been subjected to theoretical mathematical models and has been shown to be plausible when herbivore utilisation affects the rate of recycling limiting nutrient (Dyer *et al.* 1986), relative growth rate of plants during certain period of growth (Hilbert *et al.* 1981), cause loss of limiting nutrient (de Mozacourt *et al.* 1998) or restricts the availability of resources required by growing plants (Leriche *et al.* 2001). However, work done by Rusch and Osterheld (1997) in Argentina reported under-compensation. From the results of the present study, it can be inferred that there is under-compensation in MW and over-compensation in treatments W, C, MWC and WC. Treatments W and C can further be inferred to have strongly overcompensated ANPP while MWC and WC weakly over-compensated. W strongly overcompensated ANPP with highest standing biomass in grazed pastures and it represented the grazing intensity at which overcompensation was maximised. Treatment C strongly overcompensated with least standing biomass. Treatments MWC and WC weakly overcompensated while maintaining intermediate amounts of standing biomass. Conversely, MW strongly under-compensated while maintaining second highest standing biomass.

Most pasture treatments utilised by different kinds or groups of large mammalian herbivores maintained herbage ANPP above the ungrazed control (Figure 4.2a). This is probably due to the rankness of herbaceous plants and increased litter accumulation in the control treatment. Hilbert *et al.* (1981) concluded that there exist complex relationship between relative growth rates and production following grazing by different herbivores. This complex relationship could be a reason for the herbaceous layer productivity patterns observed in the present study. Treatments with high standing biomass such as MW gave lowest ANPP, those with lowest standing biomass such as C having high ANPP, and yet others such as W sustaining both highest standing biomass and ANPP. A number of mechanisms may account for increase in primary productivity following grazing. These include increased photosynthetic rates in tissues remaining after grazing (Painter and Detling, 1981), high proportion of stored carbohydrate being mobilized to the grazed parts for production of new leaf area, increased tillering (Hilbert *et al.* 1981) or opening up of the canopies and increasing light penetration, conservation of soil moisture by reduced transpirational leaf area and other indirect mechanisms (McNaughton 1979a).

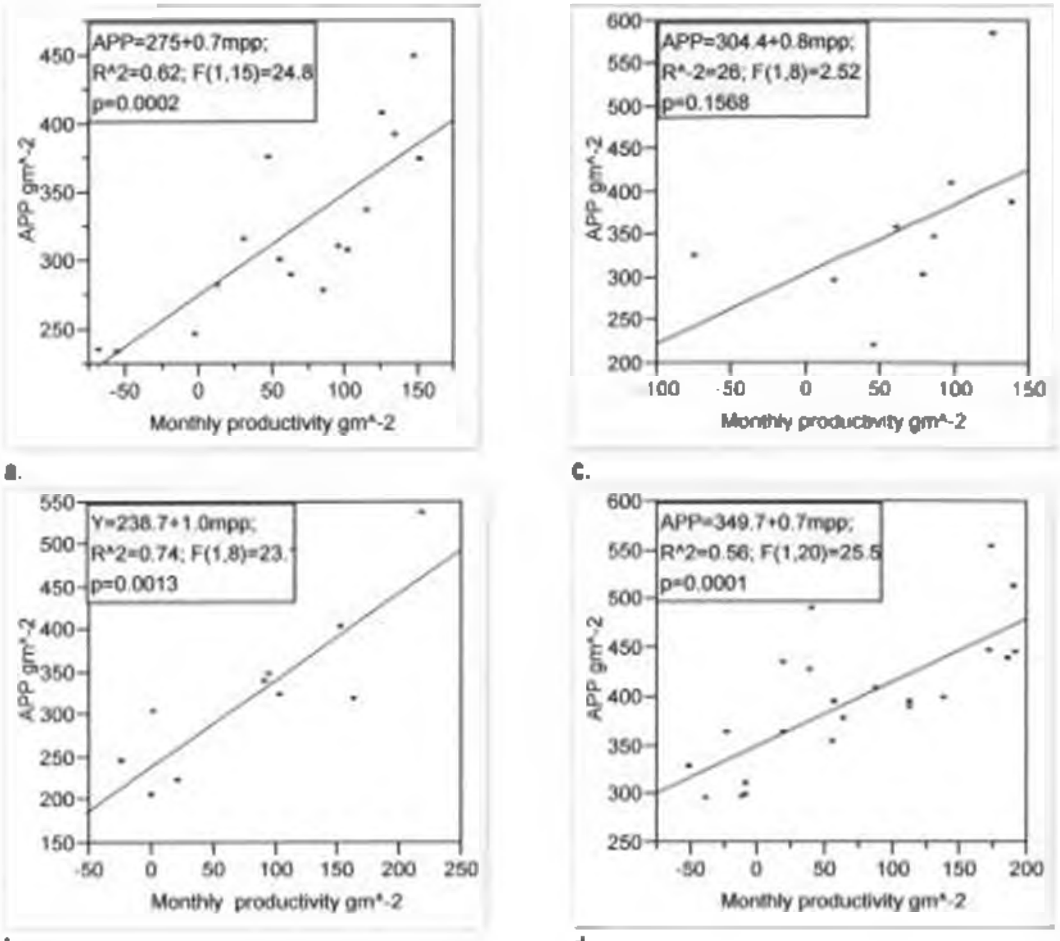
Different forage classes, grasses, forbs, and individual forage plant species respond differently to grazing thus they make different contributions to total herbage ANPP. In the present study grasses overcompensated ANPP in all grazed treatments while forbs under-compensated (Figure 4.2b). Belsky (1986, 1987) and Belsky *et al.* (1993) question the validity of the over-compensatory theory and casts doubts as to whether compensatory gain is of any relevance to grassland managers. Current results further casts doubts whether it is ecologically proper to partition ANPP according to respective forage functional groups present in pastures when comparing long term grazed and ungrazed pastures. However, regardless of what one calls increased plant growth following grazing, management decisions should be based on standing biomass, which is the component that is usually available to grazing animals. It is also appropriate to understand the age of the sward before grazing since age of the residual leaf area has an influence on the photosynthetic efficiency and hence the regrowth rate

Presence of mega herbivores resulted in decline in herbaceous layer aboveground productivity especially in pastures separately utilised by wild herbivores. The highest productivity was recorded in W treatment that excluded mega herbivores, while the least was observed in MW, where mega herbivores were present. Although pastures utilised by cattle alone consistently exhibited the least standing biomass, they maintained high productivity rates (ANPP), suggesting that they could reduce the negative effects of mega herbivores on herbaceous layer productivity thus MW had significantly lower productivity than MWC. Though information on the direct effects of trampling on herbaceous layer productivity is scanty (Rusch and Osterheld (1997), the strong negative effects of mega herbivores on the herbaceous layer productivity observed in this study could be attributed to complete physical destruction of herbaceous layer plants through hoof action resulting in bare ground pockets as is clearly visible in Plate 7. These effects are probably reduced by cattle, which often visit MWC in both dry and wet seasons hence increasing herbaceous layer productivity. The hoof actions of cattle result in pitting-like effects on bare compacted ground, this probably may have favourable conditions for herbaceous plant species seed recruitment, growth and productivity and hence recovery from trampling effects.

Plate 7. Elephant track made in the wet season is persisting as bare ground in the dry season in MW treatment southern block

4.2.1 Relationships between standing biomass and monthly herbaceous layer productivity

For all grazed treatments, monthly herbaceous layer productivity significantly ($F_{(1, 43)}=38.3$, $p=0.0001$) accounted for 47% of the variations observed in standing biomass in the growing season. Figure 4.3a-d presents linear regression analysis of standing biomass as a function of herbaceous layer monthly productivity. These regression results reveal that there was high correlation between standing biomass and herbaceous layer monthly productivity in grazed than in the ungrazed pastures. In all treatments, initial standing biomass at the beginning of the growing season is marked by the Y-intercept. The monthly productivity explained 74%, 62%, 56% and 26% of the variations observed in the standing biomass in pastures utilised by cattle, combined cattle and wild herbivores, wild herbivores and ungrazed control respectively



a.

c.

b.

d

Figure 4.3a-d Relationships between standing biomass (APP) and monthly productivity in pastures utilised by a) Cattle and wild herbivores b) cattle c) ungrazed d) Wild herbivores

These regression results demonstrate that in pastures dominated by perennial grasses, the lower the standing biomass at the beginning of the growing season, the higher the impact of the herbaceous layer productivity on the end of season production. From these regression results, it is suggested that herbaceous layer productivity builds up standing biomass faster in pastures dominated by perennial grasses where standing biomass at the beginning of the growing season ranges 150 - 200 gm^{-2}. Heitschmidt *et al* (1982) noted that reduction of standing crop biomass accelerates vegetation growth and increases aboveground production under moist environmental conditions. Gutman *et al* (1999) concluded that with grazing deferment during the growing season, herbage production could be maintained at normal levels even under heavy grazing pressure during the subsequent grazing season. This implies that under favourable soil moisture conditions, forage plants are capable of maintaining production even after a substantial proportion of their phytomass has been removed. While the preceding discussion underscores the importance of herbage productivity in the growing season, the data of this study showed that the amount of biomass consumed by large herbivores in the growing season provide weaker explanation to the variations observed in standing biomass (13% ($F_{(1,58)}$ =9.1, p=0.0038). This shows that during the growing period, the negative effects of herbivory on standing biomass are ameliorated by plant productivity

4.3 Relative proportions of forbs and grasses in standing biomass by treatments

Table 4.3 presents the relative proportions of grasses, forbs and other herbaceous layer plant species categories in each treatment. Perennial grasses comprised the most important forage class in grazed pastures while forbs importance increased in ungrazed pastures. The relative proportions of forbs increased to 25.6% and 28.2% (Table 4.3) in the wet and in the dry season, respectively over the eight years of large herbivores exclusion (1995-2002). The proportions of key perennial grasses remained lower in ungrazed pastures than those recorded in the grazed treatment. This suggests that forbs probably out compete grasses in pastures devoid of large herbivores. Although large herbivores reduce phytomass of grass plants through consumption, their dung and urine deposits influence nutrient transformation, translocation, flow rates and nutrient availability due to feedbacks, thereby prompting positive plant responses to grazing and nitrogen additions. Large herbivores may also influence nitrogen mineralisation, facilitate rapid substrate decomposition and increase the rate of nitrogen recycling (Shariff *et al.* 1994). On the other hand, these herbivores may also mechanically disperse seeds and reduce the sizes of competing plants (Belsky, 1986). Grasses appear to be the primary beneficiaries of a number of these aspects as their productivity is promoted under grazing conditions. Consequently, the proportions of the dominant perennial grasses remained higher in all grazed treatments than in the ungrazed (Table 4.3). On the other hand, forbs are suppressed by grazing. Combined use by cattle and wild herbivores further appear to suppress forbs (Table 4.3). In all the treatments, annual grasses and sedges contributed higher biomass during the wet than the dry season. The proportion of sedges was least in the control treatment than in any of the grazed treatments. This is consistent with the results of Ball *et al.* (1981) who observed their value to have reduced to less than 0.42 kg/ha in the tenth year in ungrazed-unburned pastures. In most savanna ecosystems, grasses have been reported to be the most productive herbaceous layer functional group (Ball *et al.* 1981, Bouton *et al.* 1988, Harcombe *et al.* 1993) while forbs and sedges have been found to contribute only slightly to the herbage structure and function (Ball *et al.* 1981, Harcombe *et al.* 1993).

Table 4.3 Mean percent (±se) seasonal proportions of grasses, forbs and other herbaceous layer plant species classes in each treatment

Treatment	Dominant perennial grasses*		Forbs		Other perennial grasses**		Annual grasses		Sedge	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
C	76.8±3.7	83.9±2.3	16.4±3.8	13.5±2.3	3.8±2.1	2.0±1.6	1.3±0.4	0.1±0.1	1.7±1.1	0.4±0.1
WC	84.7±2.1	82.0±1.1	8.7±1.3	7.6±1.0	3.8±1.6	7.9±4.0	2.2±0.5	2.1±2.1	0.8±2	0.4±0.3
MWC	85.5±1.0	85.7±1.0	8.5±1.0	8.3±1.0	3.1±0.8	5.4±1.6	1.5±0.4	0.4±0.2	1.4±0.5	0.3±0.1
W	81.8±2.3	83.6±1.8	12.6±2.2	10.9±1.5	3.9±1.1	5.0±2.8	0.6±0.2	0.2±0.1	1.1±0.7	0.3±0.1
MW	83.5±1.2	85.4±1.6	9.8±1.2	10.7±1.5	5.8±1.9	3.6±1.2	0.6±0.2	0.1±0.1	0.4±0.2	0.2±0.0
O	68.2±4.1	68.7±3.8	25.6±4.1	28.2±3.6	5.1±2.0	2.5±0.9	0.7±0.3	0.4±0.3	0.3±0.1	0.2±0.1

* Five dominant perennial grasses combined

** Other six minor perennial grasses combined

The effects of mega herbivores such as elephants on vegetation have mainly been associated with the overstorey plant species, – specifically trees and shrubs (Dublin 1995, Sinclair 1995), but marginally with herbaceous layer species. Comparing the proportions of forbs in W and MW, it is apparent that presence of mega herbivores (elephants and giraffes) in pastures utilised by wild herbivores alone over a period of eight years suppressed the proportion of forbs (Table 4.3). In both wet and dry season, treatments utilised by combined wild herbivores and cattle (WC and MWC) registered slightly higher proportions of dominant perennial grasses than those found in treatments separately utilised by either cattle or wild herbivores. This trend, however, was not observed in forbs (Table 4.3).

4.3.1 Effects of large herbivores on the dynamics of key grass species

Extending the herbivore optimisation hypothesis to individual grass species, Hendrix and Trapp (1989) reported failure of compensatory responses to offset reductions in maternal fitness of the damaged plants of the species *Pastinaca sativa*. Hik and Jefferies (1990) reported higher ANPP and biomass in the grazed than the ungrazed swards of *Puccinellia phryganodes*. In the present study, a total of eleven perennial grasses, several annual grasses and sedges were identified on the study site.

Table 4.4 Relative seasonal proportions (%±se) of key perennial grasses in standing biomass in different treatments

Treatment	*Pennisetum stramineum*		*Brachiaria lachnantha*		*Pennisetum mezianum*		*Themeda Triandra*		*Lintonia nutans*	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
C	22.0±6.1	38.5±9.2	19.1±4.4	20.6±4.9	18.2±3.6	14.5±4.7	13.5±3.8	7.6±3.0	3.0±1.1	5.7±1.4
WC	30.2±4.0	31.7±5.2	20.4±3.8	14.9±3.0	11.6±3.3	17.0±3.3	10.4±2.3	12.0±3.4	6.3±2.0	5.6±1.5
MWC	31.0±6.6	33.0±4.6	16.6±4.8	17.7±3.2	21.6±5.3	15.3±3.4	11.6±3.1	14.8±2.6	4.5±1.1	4.9±0.6
W	25.6±5.6	29.6±5.1	27.9±4.6	19.8±4.6	13.0±3.1	12.0±2.7	11.2±3.4	17.9±4.7	3.6±1.1	4.3±1.1
MW	21.7±5.1	17.5±4.3	28.6±4.3	27.0±3.9	17.2±4.0	20.3±3.8	13.5±4.0	12.9±3.2	4.5±1.1	6.7±1.5
O	23.5±5.3	22.0±4.4	22.0±5.5	21.5±4.7	11.6±4.8	11.8±3.4	7.5±4.9	9.2±4.0	3.0±1.6	4.1±1.1

The perennial grasses included *Pennisetum stramineum*, *Brachiaria lachnantha*, *Pennisetum mezianum*, *Themeda triandra*, *Lintonia nutans*, *Bothriochloa insculpta*, *Eragrostis tenuifolia*, *Digitaria milanjiana*, *Setaria spp.* and *Cynodon spp.* The annual grass species were *Microchloa kunthii*, *Brachiaria eruciformis*, *Aristida kinensis*, and *Dinebra retroflexa*. Five of the perennial grasses (*Pennisetum stramineum*, *Brachiaria lachnantha*, *Pennisetum mezianum*, *Themeda triandra* and *Lintonia nutans*) contributed more 70% of the seasonal standing biomass in all the pastures. *Pennisetum stramineum* was the most dominant during both seasons in C, WC, MWC and O treatments, while *Brachiaria lachnantha* was the most dominant in W and MW. *Pennisetum mezianum* maintained third rank in most treatments (Table 4.4) while *Themeda triandra* was fourth in most treatment except in treatment W during the dry season where it occupied the third rank to *Brachiaria lachnantha* in the sub-dominant. The proportions of *Themeda triandra* and *Pennisetum mezianum* greatly declined to miniscule proportions in the ungrazed pastures implying that they succumbed to competition from forbs. This also suggests that exclusion of large herbivores and hence the nutrients they add on pastures have direct contribution to the reduced vitality of these perennial grasses. Comparisons of grazed treatments and ungrazed treatment show that proportions of *Pennisetum stramineum* were relatively higher in all grazed treatments except in C and MW in the wet season. *Brachiaria lachnantha* was relatively higher in grazed treatments except in C, WC and MWC in wet season.

Comparisons of W and MW revealed that presence of mega herbivores reduced proportions of *Pennisetum stramineum*, but increased those of *Pennisetum mezianum* and *Lintonia nutans* in both wet and dry seasons (Table 4.4). The Table 4.5 presents monthly standing biomass dynamics for forbs, dominant perennial grasses and other herbaceous plant categories in each treatment while figures 4.4 and 4.5 present monthly herbage standing biomass recorded between August 2002 and April 2003.

As the second hypothesis of this study states, proportions of grasses and forbs in pasture are independent of whether long-term pasture utilisation is by cattle, wild herbivores or joint wild herbivores and cattle. However, as indicated by the results and the foregoing discussion, this study fails to accept the hypothesis and infer that presence of wild herbivores or cattle in pastures either separately or in combination affects the proportions of grasses and forbs. This is an indication that the relative proportions of functional forage classes (grasses, forbs) or even of the individual plant species largely depend on the kinds of herbivores accessing the pastures over a period of time. This is in agreement with suggestions from several previous studies that herbivores may act as ecosystem regulators by modifying productivity and community structure (Chew, 1974).

Table 4.5 Monthly mean standing biomass (gm^{-2}) for forbs, individual dominant perennial grass species, annual grasses and sedges by treatments

	Aug-Sept 02	Sept-Oct 02	Nov-Dec 02	Dec 02 Jan 03	Feb-Mar 03	Apr-May 03
C						
Forbs	40.90	27.48	51.61	50.44	35.13	69.18
Pennisetum stramineum	140.31	48.49	113.05	161.85	138.62	128.11
Brachiaria lachnantha	106.43	87.28	83.02	99.55	80.58	175.48
Pennisetum mezianum	88.38	65.87	39.86	40.60	35.38	90.37
Themeda triandra	21.90	52.58	40.01	49.61	28.63	74.93
Lintonia nutans	14.03	14.14	13.22	48.65	21.82	25.61
Other Perennial grasses	11.70	10.35	18.30	2.30	23.55	9.70
Annual grasses	0.30	0.20	6.00	0.95	0.10	3.85
Sedges	0.82	0.70	1.17	1.69	1.17	6.13
WC						
Forbs	25.48	20.58	28.31	38.98	15.97	33.98
Pennisetum stramineum	138.03	167.67	168.67	215.24	97.60	138.63
Brachiaria lachnantha	68.35	28.58	122.22	83.92	49.75	107.29
Pennisetum mezianum	61.39	52.18	37.43	41.13	105.03	53.12
Themeda triandra	47.09	21.37	49.49	98.28	53.60	69.07
Lintonia nutans	15.97	19.55	27.73	28.52	20.95	28.28
Other Perennial grasses	6.60	21.20	9.70	28.05	4.60	6.60
Annual grasses	0.70	0.00	2.60	0.20	0.00	8.91
Sedges	1.57	0.10	1.70	1.23	0.80	6.01
MWI						
Forbs	38.46	20.21	35.97	32.41	20.61	24.23
Pennisetum stramineum	100.83	129.73	168.95	221.59	108.03	138.60
Brachiaria lachnantha	83.38	75.04	58.38	67.08	79.75	112.93
Pennisetum mezianum	36.02	57.95	106.62	45.41	71.68	128.78
Themeda triandra	87.89	43.27	62.99	50.32	54.98	70.18
Lintonia nutans	16.66	18.40	18.16	19.41	14.78	23.75
Other Perennial grasses	5.58	30.60	0.00	11.55	69.40	0.00
Annual grasses	0.20	1.30	0.00	1.15	0.00	5.07
Sedges	0.78	0.50	1.18	0.98	0.63	6.73
W						
Forbs	33.12	50.17	39.86	46.96	50.03	68.29
Pennisetum stramineum	165.52	123.77	200.45	152.58	161.99	117.28
Brachiaria lachnantha	103.34	74.54	205.01	172.21	45.93	268.75
Pennisetum mezianum	63.70	75.04	70.19	71.83	69.98	67.47
Themeda triandra	128.59	69.31	43.79	118.99	84.12	96.77
Lintonia nutans	16.66	14.88	9.17	20.42	28.95	35.84
Other Perennial grasses	21.70	18.30	11.31	13.06	19.23	20.98
Annual grasses	2.15	0.00	0.00	1.04	0.40	3.10
Sedges	0.23	0.43	1.20	1.07	0.60	10.99
MW						
Forbs	40.01	28.17	43.07	40.04	25.37	38.84
Pennisetum stramineum	116.65	48.60	109.09	87.94	46.89	178.40
Brachiaria lachnantha	91.97	124.75	127.98	133.93	105.71	182.38
Pennisetum mezianum	103.59	62.48	98.71	72.43	94.27	63.58
Themeda triandra	46.75	65.72	85.18	42.28	99.78	28.69
Lintonia nutans	25.19	18.30	19.18	30.18	26.22	28.13
Other Perennial grasses	0.00	17.03	31.50	0.00	39.70	1.80
Annual grasses	3.70	0.85	0.70	1.15	19.20	3.70
Sedges	0.35	0.60	1.35	0.75	0.98	5.02
D						
Forbs	70.52	71.91	112.21	144.76	94.93	78.18
Pennisetum stramineum	82.79	90.90	129.98	141.78	94.63	130.31
Brachiaria lachnantha	79.48	97.75	73.83	123.11	122.18	187.45
Pennisetum mezianum	65.33	55.10	30.82	59.66	28.01	101.84
Themeda triandra	33.70	81.81	15.33	55.49	68.63	31.07
Lintonia nutans	14.01	9.02	14.52	24.27	21.97	38.38
Other perennial grasses	22.90	16.00	0.00	10.60	0.00	14.80
Annual grasses	0.10	0.00	0.00	0.50	0.00	4.88
Sedges	0.40	0.50	0.00	0.78	0.60	1.38

Figure 4.4 Rainfall and herbage aboveground standing biomass in separate cattle and wild herbivore treatments

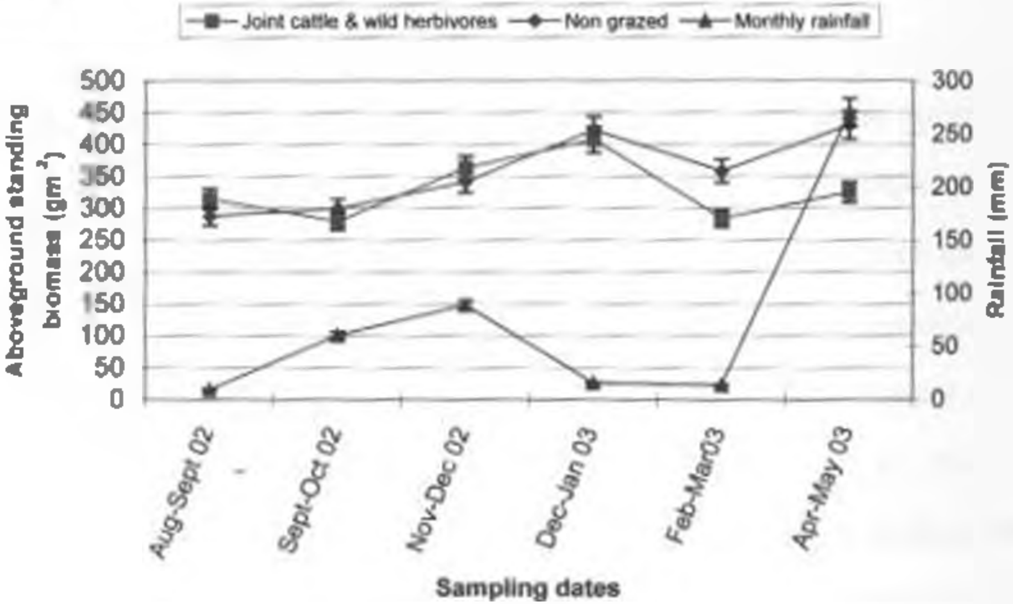
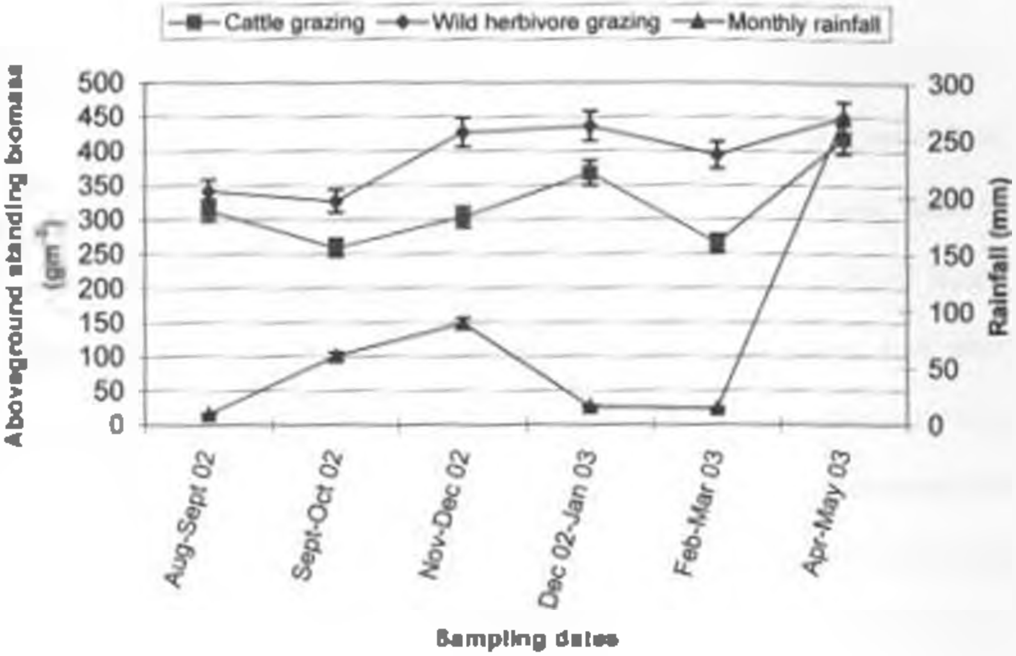


Figure 4.5 Rainfall and aboveground standing biomass in joint cattle and wild herbivores treatment and in non-grazed treatment


Cattle grazing
Wild herbivore grazing
Monthly rainfall
Aboveground standing biomass (gm^{-2})
500
450
400
350
300
250
200
150
100
50
0
Rainfall (mm)
300
250
200
150
100
50
0
Aug-Sept 02
Sept-Oct 02
Nov-Dec 02
Dec 02-Jan 03
Feb-Mar 03
Apr-May 03
Sampling dates

4.4 Aboveground litter

Table 4.6 presents mean seasonal aboveground amounts of litter in each treatment. Average amounts of litter were observed to be consistently high in the dry than in wet season in all treatments. This observation concurs with that of Boulon *et al.* (1988) where peak values of litter were reported in the dry season. Ekaya and Kinyamario (2001) observed lowest aboveground litter amounts to occur during rainfall peaks. In the present study, there were significant differences (P<0.05) between the wet and dry season aboveground litter amounts in treatments C, W, MW and O (Table 4.6). In both wet and dry season, mean aboveground litter in C, WC, MWC and MW treatments were similar but differed significantly (P<0.05) with W and O treatments. The control treatment (O) maintained higher litter amounts in both seasons than all the other grazed treatments. This is probably due to accumulated moribund aboveground herbaceous layer components and low decomposition rates.

Ball *et al.* (1981) reported more than two fold increase in litter between the second and eighth year on ungrazed unburned sites. Green and Kauffman (1995) reported that aboveground litter in ungrazed sites was twice as much as in grazed sites. The high aboveground litter in ungrazed ecosystems can be largely attributed to low organic matter decomposition rates. Heitschmidt *et al.* (1982) reported relatively slower rate of disappearance of standing dead biomass in ungrazed pastures. Litter accumulation is generally associated with low soil temperature, improved soil moisture regimes, and subdued light availability for seedlings and individual plant species. Litter accumulation may also result in nutrients immobilised in litter pool (Green and Kauffman, 1995).

Decomposition rate is influenced by moisture, temperature and chemical composition of the litter (Mullos, 1999). Shariff *et al.* (1994) reported higher decomposition rates in moderately grazed than in long term ungrazed pastures of North Dakota. These reports imply that the rate of aboveground organic matter decomposition in the present study could have been higher in the wet season in grazed than in the ungrazed pastures. This could have contributed to lower litter amounts observed in the wet than in the dry season in all treatments in the study.

Table 4.6 Seasonal mean aboveground litter contents (± se) by treatments

Treatment	Wet season gm^{-2}	Dry Season gm^{-2}
C	66.9±5.8^{a2}	98.4±8.7^{a1}
WC	68.1±5.5^{a1}	73.9±8.7^{a1}
MWC	61.3±5.9^{a1}	77.2±8.0^{a1}
W	79.7±5.6^{a2}	134.2±8.7^{b1}
MW	52.8±5.7^{a1}	90.7±8.7^{a1}
O	95.1±5.8^{b2}	120.9±8.5^{b1}

Treatment means with different superscript letters in the same column and different superscript numbers in the same row show significant differences

Beyon *et al.* 1990 profiled wet and dry season patterns of dung decomposition in grazed pastures. They noted that during the rains, the area becomes alive with dung beetles a few minutes after elephant dung is deposited on the ground. In the dry season, dung deposited had only few colonies and activities of the beetle declined as the dung dried out. Thus, generally, decomposition is presumed to be higher in grazed than in ungrazed pastures and in wet than in dry season. This suggests that both transient and resident herbivores suppress accumulation of aboveground litter. During wet season, grazed pastures grow very rapidly resulting in build up of standing biomass but simultaneously, aboveground litter declines rapidly from the pastures. In the dry season, standing biomass decline as aboveground litter increases.

4.4.1 Relationships between aboveground litter and productivity

The linear regression analysis between aboveground primary productivity and aboveground litter accumulation revealed negative relationships in all treatments. The data showed that strong negative relationships existed between herbaceous layer productivity and litter amounts in O (r^2=-0.71, P=0.0044 - Figure 4.6a). This suggests that pastures with high litter accumulation are likely to exhibit lower rates of herbaceous layer productivity hence litter accumulation affects the rates of herbaceous layer productivity.

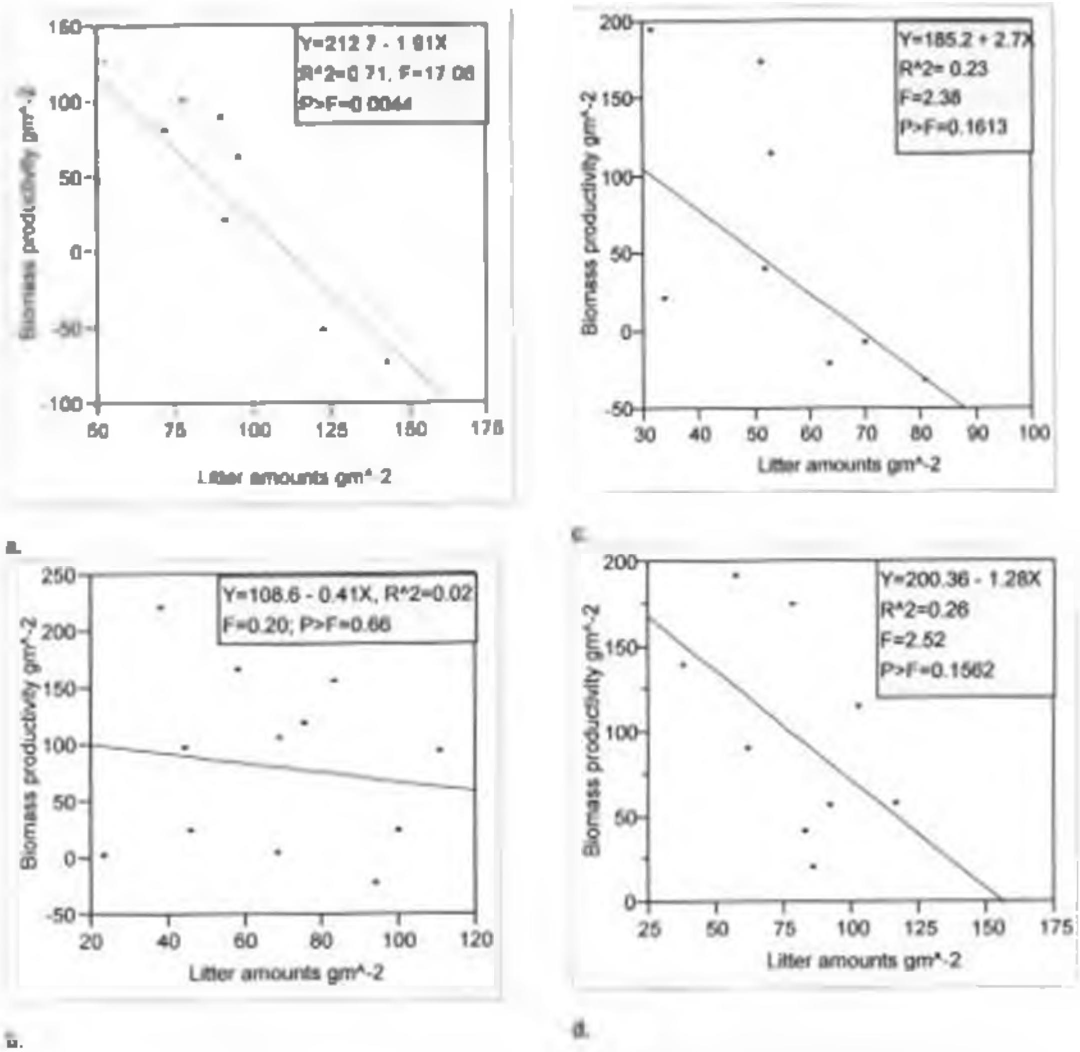


Figure 4.6 a-d Effects of aboveground litter on herbaceous layer primary productivity in unutilised pastures (control) (a), and pastures utilised by cattle (b), wild herbivores with mega herbivores (c) and wild herbivores without mega herbivores (d)

4.5 Utilisation by large herbivores

Table 4.7 Mean daily herbage biomass utilisation (±se gm^{-2} day^{-1}) by large herbivores in different treatments and season

Treatment	Wet season	Dry season
C	1.32±0.59	1.66±0.47
WC	0.81±0.43	1.32±0.07
MWC	0.77±0.33	1.51±0.15
W	0.64±0.26	1.28±0.41
MW	0.97±0.62	1.70±0.04

Table 4.7 presents mean daily herbage utilisation by large herbivores in different treatments. Utilisation by large herbivores was lower in the wet than in the dry season in all treatments. Treatments C and MW had the highest daily herbage biomass utilisation in the wet and dry

season respectively while W had the lowest in both seasons. On the overall, approximately 53%, 42%, 39%, 24% and 75% of wet season's net primary production was utilised by large herbivores in C, WC, MWC, W and MW treatments respectively. Painter and Detling (1981) reviewed that herbivory removes 10-50% of annual ANPP, however, some studies conducted in the East African region reported that 15-90% of annual ANPP (McNaughton, 1985) or 85% standing crop (McNaughton 1976) could be used up by large herbivores. Wilms *et al.* (1996) reported a loss of more than 50% of available herbage to non-livestock species, decomposition or to litter pool.

4.5.1 Tussock utilisation

Herbage biomass utilised by large herbivores negatively correlated with stubble biomass ($F_{(1,10)}=10.78$, $p=0.0082$, $R^2=0.52$) and positively correlated to the number of tussocks utilised ($F_{(1,10)}=6.69$, $p=0.0271$, $R^2=0.40$). The stubble biomass negatively correlated with the proportions of tussocks utilised by large herbivores per unit area (Figure 4.7). These results suggest that, to a large extent, the number of tussocks utilised by herbivores could be used to estimate the amount of herbage removed by large herbivores.

Table 4.8 presents the total and grazed number of tussocks, mean tussock height and tussock stubble height in different treatments. Mean total number of tussocks per unit area (tussock density) was highest in MWC treatment (21.4±1.0) and lowest in W treatment (15.5±0.8). Mean number of tussocks utilised were highest in WC (15.8±1.0) and lowest in W treatment (4.2±0.4). Treatment MWC had the lowest mean stubble height while the highest was in W treatment.

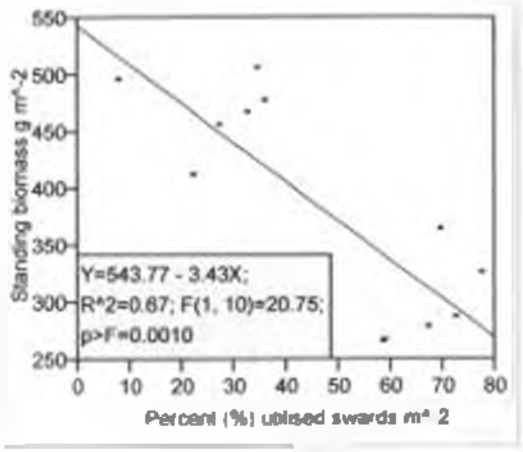


Figure 4.7 Relationship between proportions of tussocks utilised by large herbivores and standing biomass in grazed pastures

Table 4.8 Mean total number of grazed tussocks (m^{-2}), mean tussock height and mean tussock stubble height in different treatments

Treatments	Total number of tussocks m^{-2}	Number of grazed tussocks m^{-2}	% tussock utilisation	Total tussock height (cm)	Stubble height (cm)
C	18.7 (1.1)	13.9 (1.1)	74.3 (5.9)	53.0 (2.0)	13.8 (1.0)
WC	20.9 (1.1)	15.8 (1.0)	75.6 (5.0)	63.4 (2.9)	15.3 (1.1)
MWC	21.4 (1.0)	15.0 (1.1)	70.1 (4.9)	50.2(2.3)	10.5(0.8)
W	15.5 (0.8)	4.2 (0.4)	27.1 (3.9)	64.4(1.6)	18.7(1.1)
MW	16.7 (0.8)	7.0 (0.7)	41.9 (4.5)	65.3(1.6)	15.1(0.9)
O	18.0 (1.1)			67.7 (2.5)	

Numbers in parentheses are standard errors of the mean

4.5.2 Preference of dominant species

Table 4.9 presents relative proportions (%) of tussocks of key perennial grasses utilised. *Pennisetum stramineum* was most preferred in both C (22%) and WC (23%), *Themeda triandra* preference ranked second in these treatments. In MWC treatment, *Lintonia nutans* was the most preferred (16%) while *Pennisetum stramineum* ranked second, others included *Brachiaria lachnantha* and *Themeda triandria*, which showed similar preference (Table 4.8). In W the most preferred grass species *Pennisetum stramineum* (7.1%) followed by *Themeda triandra* (6.5%). *Pennisetum mezianum* and *Lintonia nutans* had equal preference in this treatment. In MW *Brachiaria lachnantha* (11%) was the highly preferred dominant grass followed by *Themeda triandria* (10%). The preference of grass species differed with groups of herbivores utilising the pastures. However, in general *Pennisetum stramineum* received relatively higher preference in most treatments except in MWC and MW where *Lintonia nutans* and *Brachiaria lachnantha* were respectively relatively more preferred

Table 4.9 Relative proportions (%) of tussocks of key perennial grasses utilised in each treatment

Treatment	*Pennisetum stramineum* %	*Brachiaria lachnantha* %	*Pennisetum mezianum* %	*Themeda triandra* %	*Lintonia nutans* %
C	21.9	12.8	10.2	20.3	8.0
WC	23.4	15.3	10.5	15.79	10.0
MWC	15.4	14.95	9.3	14.95	18.18
W	7.1	4.3	4.5	6.45	4.5
MW	6.6	11.4	8.4	9.6	5.99

%=mean number of grazed tussocks per total tussocks m^{-2}x100

4.5.3 Grazing intensity on dominant species

Table 4.10 The mean ungrazed heights and respective stubble heights (cm) of key perennial grasses in each treatment

Treatment	*Pennisetum stramineum*		*Brachiaria lachnantha*		*Pennisetum mezianum*		*Themeda triandra*		*Lintonia nutans*	
	Unhgt	Stubble	unhgt	Stubble	unhgt	Stubble	unhgt	Stubble	unhgt	Stubble
C	46.0	21.1	43.7	10.5	31.7	21.0	46.3	7.6	35.6	8.4
WC	51.3	23.5	50.0	9.7	42.4	17.1	46.9	10.1	44.9	9.6
MWC	45.3	19.6	38.9	9.0	41.2	11.7	37.6	6.7	39.8	8.5
W	50.1	23.1	53.2	16.6	32.9	25.3	46.2	13.4	47.1	17.9
MW	45.3	23.2	53.6	14.4	45.7	17.2	59.9	12.1	62.1	12.1

Unhgt= mean ungrazed height and Stubble=mean stubble height as indicator of grazing intensity.

Table 4.10 presents mean ungrazed and stubble heights for key perennial grasses in different treatments. From their mean stubble heights, *Themeda triandra*, *Brachiaria lachnantha* and *Lintonia nutans* received heaviest grazing intensity in all treatments than *Pennisetum stramineum* and *Pennisetum mezianum* in all the herbivore treatments. This could be due to their general vertical stem characteristics, which are relatively softer and occur in clumps. This enables herbivores to remove more per bite and hence, a lowest net stubble height. On the other hand, in the case of *Pennisetum stramineum* and *P. mezianum*, the stems are much tougher and mostly occur singly aboveground. Therefore, herbivores only utilize the upper leafy and soft stem parts leaving the rest of the stems as stubble. These species traits together with herbivore muzzle sizes, can to some extent explain salient differences in intensity of utilisation among grass species

4.6 Management Implications

The data indicated that utilisation of pastures by both cattle and wild herbivores maintain intermediate herbaceous layer productivity and standing biomass" This provides a better direction for ecosystem management in the future than extreme productivity observed in pastures separately utilised by wild herbivores or cattle This allows for diversity of native and domestic biodiversity coexistence at the crucial time when native biodiversity are threatened with habitat loss in the unprotected savanna ecosystems

Large and extensive pastures need to be planned in such a way that some sectors are made available for separate wild herbivore utilisation while others for joint utilisation with domestic livestock but none should totally exclude large herbivores. In this study, seasonal herbaceous layer standing biomass and productivity were not highest in herbivore exclusion pastures The only parameters that had the highest values in such pastures were litter amounts and forbs proportions The patterns revealed by proportions of key perennial grasses imply that grasses need to be monitored periodically in grasslands inhabited by a diversity of large herbivores, so that detection of over utilisation of particular types of grasses can proactively stimulate management responses This can also prompt timely decision for responses that facilitate application of rest, burning and reseeding management practices

In making management decisions, these results indicate that protected areas should be maintained in their contemporary form as in their current state they could maintain higher aboveground production. But if need be, there is no evidence that controlled cattle utilisation could damage their herbaceous layer resources However, unprotected areas need to be encouraged to accommodate wild herbivores, this is because joint utilisation of pasture is more beneficial to production of herbaceous layer vegetation resources

Pastures destined for utilisation by cattle alone should be encouraged only under very restricted and well defined management plan. This should be so as long as the management seasonally monitors proportions of forbs and grasses in such pastures. In areas where cattle are the dominant grazer, it would be practical to accommodate wild herbivores while allowing for long term monitoring of the system and documenting the dynamics of the herb layer productivity and cover. This kind of monitoring may also provide necessary information on how protected areas may be managed for posterity.

CHAPTER FIVE

5.0 Conclusions and Recommendations

5.1 Conclusions

1. The results disapprove the study hypothesis that large herbivores do not have measurable effects on seasonal herbaceous layer standing biomass. The evidence shows that separately, mega herbivores (mostly elephants) and cattle had greater effects than other large mammalian wild herbivores in reducing the potential amounts of herbaceous layer standing biomass in grazed ecosystems. Utilisation of pastures by other large mammalian wild herbivores in absence of cattle and mega herbivores resulted in highest standing biomass and productivity in the growing season. Joint grazing by wild herbivores and cattle did not reduce herbage-standing biomass as was done by cattle alone grazing. Long term exclusion of large herbivores from formerly grazed lands reduced herbaceous layer productive capacity due to change in functional groups and litter accumulation
2. Large herbivore grazing influenced proportions of biomass contributed by functional groups to the total standing biomass. Presence of large herbivores tended to favour higher grass proportions than forbs as their absence reverse this trend. Cattle presence promoted relatively higher grass proportions than wild herbivores did when mega herbivores were present. Long term exclusion of large herbivores promoted increased domination of dicotyledonous species and negatively affected the standing biomass and productivity of monocotyledonous species. Pastures exclosed from large herbivore utilisation for eight years changed such that proportions of dicotyledonous plants increased in herbaceous layer standing biomass
3. Biomass consumed by large herbivores did not show strong correlation with stubble biomass during the growing period. However, in the dry season there was strong

negative relationship between the proportions of tussocks utilised per unit area and the stubble biomass and or herbaceous layer biomass consumed by large herbivores.

5.2 Recommendations

Introduction

The short duration cattle grazing as applied in this study provided very moderate yet uniform utilisation that is very distinct from those of pastoral areas whose ecological status are much different. However, short duration cattle grazing in the present study may be similar to those of most commercial ranches hosting both wild herbivores and cattle. The recommendations of this study are therefore, more applicable under moderate grazing management by cattle and very light by large mammalian wild herbivores. Further research is necessary for more explicit grazing management.

1. As a management strategy, grazed lands should not be left ungrazed for longer periods (more than eight years) if the management intends to improve herbaceous layer productivity. Short-term rest should be appropriate but rotation between wild herbivores and cattle combinations would be preferred in a patch-designed pasture with sectors accommodating both joint and wild herbivore alone pastures.
2. Management in unprotected areas with cattle should consider tolerating large wild herbivores or consider their gradual introduction in their management plan. This is because other than wild herbivores helping to reduce the adverse effects measurable on herbage production due to moderate cattle grazing, they will also open up other avenues for operators' diversification of enterprises -ecotourism, game cropping, and beauty in general.
3. There is need for a more detailed investigation in the Kenya Long-term Exclosure Experiment (KLEE) plots for a detailed analysis of the low productivity in MW treatment

captured by the movable cage method in this study. The study showed that MW had the second highest seasonal standing biomass

4. Further work needs to be carried out for better understanding of litter disappearance in these experimental plots. The scientists and managers need to understand the effects of litter disappearance under long-term grazing and long-term herbivore exclusion. There is also need to know the sequential effect of time and long-term seasonality of excluding large herbivores on herbaceous layer production

5. This experimental study, which involved wild herbivores and one type of domestic livestock, has provided interesting results regarding separate and combined effects of these herbivores on herbaceous layer resources. However, more studies are required to analyse these effects in protected areas; national parks with and without mega herbivores, semi protected areas-national reserves with domestic livestock (with and without mega herbivores), wildlife corridors with domestic stock (with and without mega herbivores), commercial ranches with situations similar to treatments in the present study in varied soil types. It would also be of ecological use if KLEE would consider integration of other domestic stock interactions with wild herbivores

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