RESPONSES OF HUMID SAVANNA VEGETATION TO THE INTERACTION OF LIVESTOCK GRAZING AND RAINFALL VARIABILITY IN LAMBWE VALLEY, KENYA

BY

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DECLARATION

This dissertation is my original work and has not been previously presented for a degree in any other university. All sources of information have been specifically acknowledged by means of references. No part of this thesis may be reproduced without prior permission of the author and/ or Maseno University.

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I devote this work to my parents Mr. Reuben Otieno and Mrs. Ruth Atieno and to my son Ryan. You are my pillars of strength and hope.

ABSTRACT

Tsetse fly control in Lambwe valley has made the region habitable and opened it up for human settlement. The region has, therefore, experienced a steady increase in human population growth. Since most of the households in Lambwe keep livestock as a source of livelihood, the increased human population has consequently resulted in increased livestock numbers and grazing pressure. At the same time, the region is experiencing changes in rainfall patterns which are projected through increased rainfall during wet seasons and prolonged dry periods. Increased livestock grazing and changing rainfall regimes in Lambwe valley Homabay County, Kenya is threatening the existence of plant life forms in Lambwe, but has rarely been studied. The increased grazing and rainfall variability are occurring simultaneously and their implication on the savanna vegetation is not known. Holistic studies that monitor vegetation responses in this valuable ecosystem, are limited. This study analysed the responses of the herbaceous and tree layers to livestock grazing and rainfall variability. The objectives of the study were; i. To determine the interactive effect of livestock grazing and rainfall variability on CO_2 exchange, species diversity, composition and palatability of the herbaceous vegetation, ii. To determine the effect of livestock grazing and rainfall variability on CO_2 exchange of the tree canopy, iii. To compare productivity responses of tree and herbaceous vegetation under livestock grazing and rainfall variability. Within the herbaceous layer, rain-out shelters were erected above canopy of herbaceous vegetation that was either grazed by livestock or fenced to exclude livestock. The shelters, each measuring 9 m by 6 m were replicated three times on both the grazed and fenced plots. On each of the plots, ambient rainfall was reduced or increased by 50 % using transparent plastic sheets. Within the tree vegetation, three replicates of grazed and fenced plots, each measuring 70 m by 50 m were demarcated for measurements. There was no rainfall manipulation on the tree plots. Measurements included microclimate, soil moisture content, soil bulk density, CO_2 fluxes, biomass, species diversity and palatability in the herbaceous layer and sap flow measurements in the trees. Herbaceous Gross Primary Productivity (GPP) was calculated from Net Ecosystem Exchange (NEE) and Ecosystem Respiration (R_{eco}) measured directly with the chambers. Daily GPP for both trees and herbaceous layer was determined using PIXGRO model. Livestock grazing significantly ($P \leq 0.05$) reduced herbaceous CO_2 exchange but had no influence on tree productivity. The interaction of grazing and rainfall reduction significantly ($P \leq 0.05$) reduced GPP, NEE and R_{eco} by 22.5 %, 33% and 39% respectively. The interaction of grazing and rainfall increment significantly increased GPP and NEE by 47 % and 54.8 % respectively, but had no influence on R_{eco}. The interaction of grazing and rainfall reduction significantly ($P \leq 0.05$) reduced herbaceous diversity whereas the interaction of grazing and rainfall increment had no significant ($P > 0.05$) impact on herbaceous diversity. Rainfall manipulation had no significant ($P > 0.05$) impact on dominance of herbaceous vegetation in either fenced or grazed plots. Herbaceous daily maximum GPP exhibited higher seasonal fluctuations than the tree layer. The overall mean maximum daily ecosystem productivity for the study site was 10.73 ± 1.7 g C m $^{-2}$ d^{-1} and 13.75 ± 1.62 g Cm^{-2} d^{-1} in the grazed and fenced plots respectively. The herbaceous vegetation, which was the dominant vegetation life form in the valley, contributed about 60 % to the overall mean maximum daily ecosystem productivity. The CO_2 fluxes, diversity and composition of the herbaceous layer in the grazed savanna responded disproportionately to the rainfall manipulation, suggesting that grazing and rainfall are not the sole factors driving herbaceous CO_2 exchange in this ecosystem. The differential response of trees and herbaceous GPP to livestock grazing was linked to the variations in rooting patterns of the two vegetation types. The significant contribution of the herbaceous layer to the overall ecosystem productivity was connected to higher herbaceous vegetation cover of about 80 %. The results of this study have a significant implication for the theoretical understanding of the tree-herbaceous responses to livestock grazing and rainfall variability. Further, this study provides empirical data that can be used for refining and parameterizing vegetation models that predict future savanna ecosystem responses to livestock grazing and rainfall variability.

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LIST OF ABBREVIATIONS

AWS	Automatic Weather Station
DBH	Diameter at Breast Height
E_c	Canopy transpiration
EU	European Union
FAO	Food and Agriculture Organization
G_c	Canopy conductance
HSD	Tukey's Honestly Significant Difference
IPCC	Intergovernmental Panel on Climate Change
IRGA	Infra red Gas Analyzer
LSD	Least Significant Difference
NEE	Net Ecosystem CO_2 Exchange
NEP	Net Ecosystem Production
NPP	Net Primary Productivity
NYS	National Youth Service
PAR	Photosynthetic Active Radiation
PIXGRO	Process-based canopy sub model
PPFD	Photosynthetic Photon flux Density
PROXEL	PROcess pixel net ecosystem exchange model
R_{eco}	Ecosystem Respiration
SFD	Sap flux density
SOC	Soil Organic Carbon
SOM	Soil Organic Matter
SWC	Soil Water Content
VPD	Vapor Pressure Deficit

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CHAPTER ONE

INTRODUCTION

1.1 Background of the Study

Savanna is an ecosystem characterized by scattered trees and continuous layer of herbaceous vegetation (Sankaran *et al*., 2004). It supports diverse animal and plant populations and provides valuable ecosystem goods and services such as rich biodiversity, food, fodder, fiber, water storage and towers, carbon sequestration among others (Bombelli *et al*., 2009; Sankaran and Ratnam, 2013). Savanna occupies approximately 65 % of Africa, 60 % of Australia and 45 % of South America, areas characterized by wet and dry seasons (Anderson *et al*., 1999; Wang *et al*., 2010). Some areas of savannas are conserved as forests and national parks to protect them from illegal land and resource use (Sankaran, 2019). Based on the mean annual rainfall, savannas can be grouped into arid and humid, with a rainfall threshold between arid and humid savannas lying between < 600 and > 820 mm/year respectively (Higgins *et al*., 2010).

Worldwide, savannas are undergoing changes in their structure and function, most of which are attributed to changing climate and land-uses (Baudena *et al*., 2015; Hill and Southworth, 2016). Altered rainfall patterns, characterized by longer periods of drought and short episodes of intense rainfall, have been observed (IPCC, 2007b; Franz *et al*., 2010). As a result, the dry seasons are getting longer and the wet seasons are short but more intense (IPCC, 2007a; Berry and Kulmatiski 2017). The strong influence of water availability on savanna vegetation structure implies that the changes in rainfall significantly impact vegetation dynamics (Räsänen *et al*., 2020). Evidence shows that altered rainfall patterns affect plant physiological processes such as photosynthesis, which in turn feedback on to ecosystem productivity and stability (Sankaran *et al*., 2004; Kramer *et al*., 2020). For instance, a reduction in vegetation cover and productivity along an aridity gradient in South African savanna was linked to the observed drying trend of about 8mm/year since 1970 (Woodward and Lomas, 2004).

In addition to changing rainfall regimes, savannas are undergoing significant changes in land use, characterized by declining areas occupied by vegetation, an increase in livestock grazing fields, replacement of wild free ranging mega herbivores and an increasing area under crop cultivation (Kgosikoma *et al*., 2015; Warth, *et al*., 2020). Such changes are altering savanna ecology, its structure and functions i.e. biodiversity, species composition, hydrological balance, carbon balance, and other ecosystem values (Ganjurjav *et al*., 2015; Warth *et al*., 2020). These stressors are increasing, yet it is not clear how savanna ecosystems are responding to the ongoing environmental shifts. Given that rainfall and livestock are the dominant drivers of change in the African savanna, characterization of the mechanisms that underlie plant responses to increased livestock grazing and declining soil moisture are key to understanding how the ecosystem is responding to the ongoing environmental change.

A distinct ecological feature of savanna is the co-existence of trees and herbaceous vegetation (Scholes and Archer, 1997, D'Onofrio *et al*., 2019). This co-dominance of the distinct plant functional groups has been explained by both competitive and facilitative mechanisms (Sankaran *et al*., 2004; February and Higgins, 2010). The competitive-based model explores niche separation as a mechanism of co-existence, and proposes differences in resource acquisition between trees and herbaceous vegetation, based on variation in the depth of root distribution (Sankaran *et al*., 2004; Baudena *et al*., 2010). According to this model, trees acquire below ground resources, including water predominantly through their deep roots and remain physiologically active during dry seasons (Sankaran et al., 2004). They, therefore, exhibit uninterrupted growth and C assimilation during conditions of water deficit. The facilitative model, on the other hand, postulates the beneficial environmental modification by neighboring organisms (Ward *et al*., 2013). According to this theory, the herbaceous vegetation benefits from soil moisture brought to the upper surface, within reach of their roots, through hydraulic lifting by adjacent trees (Ludwig *et al*., 2003; Yu and D'Odorico 2015). In such suits of interactions, the vegetation mixture is assumed to co-exist in a state of equilibrium, with each functional group contributing to the overall ecosystem structure and function (Scholes and Archer 1997). However, the structuring and metastable persistence of the trees-herb mixtures may be disrupted by an increase in livestock grazing and changing rainfall pattern (Mojeremane and Harvie, 2015; Sankaran, 2019).

Changes in soil moisture, resulting from altered rainfall patterns modify tree water access and impact productivity. During dry seasons, tree productivity is not only affected by CO_2 exchange but also through structural and physiological adjustments that alter the ability of trees to access and utilize soil moisture (Plaut *et al*., 2013; Brunner *et al*., 2015). Physiological changes such as leaf drop or hydraulic isolation via mortality of fine roots may promote immediate drought survival but limit the ability of trees to respond to soil moisture availability during wet season (Plaut *et al*., 2013; Brunner *et al*., 2015). Moreover, the reduction in stomata conductance in response to lower moisture levels not only lowers water transport but possess risks of carbon starvation and lower productivity in trees (Case *et al*., 2019). The physiological alterations may, therefore, promote tree survival during drought but limit their productivity and other ecosystem values.

Livestock grazing influences soil water infiltration with resulting implication on vegetation production. At high grazing intensities and on slopes, trampling by grazers may result in increased surface runoff and reduced soil water infiltration thus reducing the water reaching the root zones of trees (DeLonge and Basche, 2018). Such conditions induce tree water stress and lower productivity. Livestock grazing may increase the availability of soil water for trees by reducing competition for moisture among the herbaceous layer, as suggested by models of savanna tree-grass co-existence (Sankaran *et al*., 2004; Baudena *et al*., 2010). Empirical studies have revealed positive (Leriche *et al*., 2003; Ritchie, 2020), neutral (Southers *et al*., 2019) or negative effects (K' Otuto *et al*., 2012) of livestock grazing on herbaceous diversity and assimilation rates. Livestock grazing affects productivity by lowering soil water content (SWC), soil organic matter input and photosynthesis (Leriche *et al*., 2003; Ren *et al*., 2017). Livestock grazing, at higher intensities is thought to decrease herbaceous productivity and carbon exchange by direct removal of the herbaceous biomass and reduction in potential carbon fixation in the photosynthetic tissues (Ren *et al*., 2017). The dominance of grazing-intolerant species is significantly reduced under increased livestock grazing in savannas (Schietz and Rubenstein, 2016). Moreover, shifts in plant composition from perennials to annuals have been observed in intensely grazed savannas (Kioko *et al*., 2012; Ondier *et al*., 2019b). Moderate grazing, however, increases herbaceous productivity through increased assimilation of the freshly sprouted shoots (K'Otuto *et al*., 2012). Suppression of herbaceous dominance and an overall increase in species diversity has been documented under moderate grazing (Ondier *et al*., 2019b).

Humid savannas receive relatively higher rainfall amounts that translate to active vegetation growth throughout the year (Grace *et al*., 2006). Because of this, they have become hotspots for land use changes associated with livestock production (Ciais *et al*., 2009; Otieno *et al*., 2009).

The Kenyan savanna in Lambwe valley is humid, with a mean annual rainfall of between 1200-1600 mm. It has relatively fertile soils that support vegetation growth. Therefore, it has experienced significant land use changes associated with increased livestock grazing and crop production (Muriuki *et al*., 2005; K'Otuto *et al*., 2012; Ondier *et al*., 2019ab). The ecosystem has witnessed changes in the rainfall patterns characterized by shorter but more intense rainy seasons, while the dry seasons have become longer (K'Otuto *et al*., 2012; Otieno *et al*., 2015). Changes in mean annual rainfall amounts have been recorded for Lambwe valley. In 2008 and 2009, the mean annual rainfall reported for Lambwe was 820 mm and 1100 mm respectively (K'Otuto *et al*., 2012). The reported annual rainfall amounts were however, lower than the 15 year average (1997-2012) of 1346 mm recorded for same region (K'Otuto *et al*., 2012). These changes in rainfall patterns and amounts are modifying soil moisture content, with implication on vegetation structure and functions. Studies have shown that in the event of drought, trees have a competitive advantage over the herbaceous vegetation owing to their deep rooting system that reaches the aquifers (Sankaran, 2019). Such observations are of ecological interests since they relate to vegetation functions, albeit the current poor state of knowledge regarding the response mechanisms of trees and herbaceous vegetation to the environmental change in the savanna in Lambwe.

Previous studies in Lambwe valley (Otieno *et al*., 2009; Nyongesa, 2010; K'Otuto *et al*., 2012; K'Otuto, 2014) reported responses of the herbaceous vegetation to changing rainfall regime and livestock grazing as independent factors, however, the ongoing transition in land uses and rainfall are occurring simultaneously. Livestock grazing and rainfall variability are concurrently impacting the herbaceous layer, and modifying productivity, diversity, palatability, and carbon exchange in ways that are not yet clearly understood. Since the impact of livestock grazing and rainfall on herbaceous layer may be antagonistic, they must be studied concurrently to draw conclusions on their interactive influence on the herbaceous layer. A recent 10 month study of the ecosystem in Lambwe by Okach *et al*., (2019) reported that livestock grazing lowered herbaceous net ecosystem CO_2 exchange (NEE) more during wet months than dry months. The study did not however explicitly explain the implications of the rainfall variability and livestock grazing on herbaceous CO_2 exchange diversity and palatability. Moreover, the 10 month study duration was inadequate for drawing scientific conclusions on the ecosystem's response to livestock grazing and rainfall variability. There is recognized need for multiyear experiments because many of the grazing-rainfall experiments that have been performed in Lambwe and other savannas to date have been limited to a single growing season (Beier *et al*., 2012; Hoover *et al*., 2014; Okach *et al*., 2019; Ondier *et al*., 2019a). Again for this ecosystem, little scientific investigation on the responses of trees to grazing and rainfall variability has been conducted. The only scientific investigation involving tree layer was by Otieno *et al*., (2015). It investigated the general productivity patterns of trees and herbaceous vegetation, but was limited to a single growing season and did not include grazing as a factor that may influence productivity. A comparison of productivity responses of tree and herbaceous to the witnessed environmental alteration (increased livestock grazing and rainfall variability) for Lambwe valley is lacking yet such a study would inform key management decision on sustainability of the vegetation life forms (trees and herbaceous vegetation) of the savanna. For the first time, this study reports on an integrated response of the vegetation to changes in rainfall and grazing by livestock. For a period of two years, this study used continuously measured tree sap flow data to derive tree productivity under rainfall variability and livestock grazing. During the same period, herbaceous diversity and palatability was determined and productivity derived from chamber measurements and plant biomass.

1.2 Statement of the Problem

For the past 40 years, human population in Lambwe valley has been on a steady increase and in the last two years, a 7 % population growth rate was reported in the area (Valeska *et al.*, 2017; Kenya Population Cencus, 1979 and 2019). The increasing trend in human population growth in Lambwe has been linked to tsetse fly control which has made the valley habitable for human and livestock (Muriuki *et al*., 2005; Valeska *et al*., 2017). Most of the households in Lambwe valley keep livestock (cows, goats and sheep) as a source of livelihood, and hence with the expanding human population, livestock numbers have increased, creating demand for more grazing land. As a result, large tracts of the natural savanna have been converted into grazing grounds, putting more pressure on the vegetation. Moreover, rainfall patterns have been changing in Lambwe. Longer periods of droughts and short wet seasons, with intense rainfall, have been observed in the region. The changing rainfall patterns and increased grazing pressure have led to decline in vegetation composition and ecosystem productivity in Lambwe valley (Njoka *et al*., 2003). Moreover, the increase in livestock grazing and rainfall variability are concurrently impacting the savanna in Lambwe valley but the responses of trees and herbaceous vegetation to the changing environmental variables is not known. The responses of herbaceous productivity, species composition and diversity to the interactive impact of livestock grazing and rainfall variability are not known. The influence of increased livestock grazing and rainfall variability on tree productivity is not known. This study hypothesised that the balanced co-existence between trees and the herbaceous vegetation in this savanna may be altered as a result of the witnessed environmental change scenario.

1.3 Justification

The tree and herbaceous vegetation of the savanna in Lambwe valley are key in provision of valuable ecosystem services such as carbon sequestration, fodder, and genetic sources among others. The environmental modification resulting from increased grazing pressure and rainfall variability might be threatening the existence of the important vegetation life forms in Lambwe. It is, therefore, imperative to investigate the responses of the vegetation to the current environmental change processes with an aim of mitigating the adverse impacts of the change processes, and maintain valuable ecosystem service delivery.

1.4 Main Objective

To identify and quantify the interactive effects of livestock grazing and rainfall variability on the savanna vegetation in Lambwe valley.

1.4.1 Specific Objectives

i. To determine the interactive effect of livestock grazing and rainfall variability on CO_2 exchange, species diversity, composition and palatability of the herbaceous vegetation.

ii. To determine the effect of livestock grazing and rainfall variability on CO_2 exchange of the tree canopy.

iii. To compare productivity responses of tree and herbaceous vegetation under livestock grazing and rainfall variability.

1.5 Hypotheses

i. The interactive effect of livestock grazing and rainfall variability have no impact on CO_2 exchange, diversity, species composition and palatability of the herbaceous layer.

ii. Livestock grazing and rainfall variability have no effect on CO_2 exchange of the tree canopy.

iii. Productivity responses of tree and herbaceous vegetation do not vary under livestock grazing and rainfall variability.

CHAPTER TWO

LITERATURE REVIEW

2.1 Influence of Livestock Grazing and Rainfall Variability on Soil Moisture

Soil moisture is an important component of the hydrological cycle of savanna and other terrestrial ecosystems (Berry and Kulmatiski, 2017; Geiβler *et al*., 2019), and play a critical role in predicting and understanding various hydrological processes, including precipitation pattern, soil water infiltration and runoff generation (Berry and Kulmatiski, 2017). Rainfall variability changes the water supplied to plants by soil and the moisture gradient between land surface and atmosphere, which control the water exchange between the land surface and atmosphere (Räsänen *et al*., 2020). Reduction in mean annual rainfall in most savannas, a consequence of climate change (IPCC 2007a), is likely reducing soil moisture with implications on the ecosystems structure and functions. The situation could be further aggravated by the introduction of livestock grazing which together modify the ecosystem soil moisture in ways that are not clearly understood. Grazing animals can alter savanna soil moisture by compacting the top soil, indicated by increased bulk density and decreasing macro-porosity, resulting in accelerated runoffs (Ondier *et al*., 2019a; Muhonji et al., 2020). The increased bulk density decreases infiltration capacity of the soil and consequently, reduces in soil moisture content. This is especially so if the stocking rate and intensity of grazing is high. However, the effects of moderate or light continuous grazing are significantly less deleterious on soil moisture and frequently not significantly different from each other (Weber and Gokhale, 2011).

Researchers have also found that rainfall characteristics such as amount, frequency and intensity affect the temporal and spatial heterogeneity of soil water content in savannas and other water limited ecosystems (Reynolds *et al*., 2004; Knapp *et al*., 2008; Berry and Kulmatiski, 2017). The amount of water infiltrating the soil surface as a result of rainfall has a direct effect on the recharge of both soil and ground water (Geiβler *et al*., 2019). It is therefore an important factor in determining the soil moisture levels. There are other factors that affect infiltration and consequently soil moisture, including rainfall regime, soil texture, soil structure, vegetation and so on (Geiβler *et al*., 2019). Moreover, the effects of these factors are often interdependent. High rainfall intensity impact can seal the soil, significantly reducing the rate of infiltration and hence soil water content (Geiβler *et al*., 2019). Schoonover and Crim (2015) reported that intensive rainfall can destroy or deform the arrangement of soil particles and that the detached particles can clog soil pores, again reducing infiltration and consequently soil moisture.

2.2 CO_2 Exchange in the Savanna

In the context of climate change, the role of savannas in the C cycle is of great importance. This is because savannas are widely distributed and vast in nature, and may, therefore, significantly influence sequestration or emission of carbon dioxide as the main greenhouse gas (Ciais *et al*., 2011; Räsänen *et al*., 2017). Atmospheric CO_2 is taken up and incorporated into the ecosystem through photosynthesis or gross primary production (GPP). The C integrated into the ecosystem is later lost via respiration, (autotrophic respiration), decomposition of litter and soil organic matter (SOM) (heterotrophic respiration), burning and other forms of export (Räsänen *et al*., 2017). The sum of autotrophic and heterotrophic respiration is referred to as ecosystem respiration (R_{eco}) while the difference between GPP and R_{eco} is the net ecosystem CO_2 exchange (NEE) (Räsänen *et al*., 2017; Ondier *et al*., 2019a). The balance between C gains and losses constitute the net ecosystem production (NEP) that is the net accumulation/ loss of C by the ecosystem and account for the terrestrial C stock. Current estimates of terrestrial carbon stock are between 2 and 4 $PgCy^{-1}$ globally (FAO 2004), 30% of which are in savannas (Ciais *et al*., 2011).

Even though there has been a deliberate attempts to estimate carbon stocks for savannas (Ciais *et al*., 2011), the African savannas are underrepresented (Djagbletey *et al*., 2018). Moreover, the parameters used to model African savanna carbon stock and carbon exchange are from outside Africa and are hence unrepresentative (Sankaran, 2019). There is therefore need to carry out longtime experiments on the African savanna carbon exchange to provide representative data that can model the carbon balance of the savannas.

2.3 Influence of Livestock Grazing on Savanna CO_2 Exchange

Intensive livestock grazing witnessed in savannas is capable of altering the ecosystems' C integration and exchange (Njoka *et al*., 2003; Muriuki *et al*., 2005; Otieno *et al*., 2011; K'Otuto *et al*., 2012; Ondier et al., 2019a and b). Previous studies have revealed mixed results of livestock grazing effects on savanna ecosystem CO_2 exchange and productivity, with studies showing positive (Leriche *et al*., 2003; Asha *et al*., 2011), neutral (Peng *et al*., 2013) or negative effects (K' Otuto *et al*., 2012). Livestock grazing affects ecosystem GPP by lowering soil water content (SWC), soil organic matter input and photosynthesis (Leriche *et al*., 2003). Grazing by livestock, especially at higher intensities are thought to decrease herbaceous productivity and ecosystem CO_2 exchange by direct removal of the herbaceous biomass and hence reduction in potential CO_2 fixation in the photosynthetic tissues. Grazers, especially at high livestock intensities may over-defoliate and trample on the vegetation and lower its potential for CO_2 uptake through physical injury of the canopy vegetation or indirectly through drought stress (Koerner and Collins, 2014). Grazing may alter species composition of the herbaceous layer from palatable to unpalatable plants (Kgosikoma *et al*., 2013). Depending on the CO_2 exchange differences among the species, alteration in species composition may finally change the ecosystem capacity for C uptake (Asha *et al.*, 2011). In response to grazing, non-adopted (grazing intolerant) plants deposit and store chemicals on their leaves to discourage grazing, thus, altering litter quality. Changes in litter quality in response to grazing are increased C: N ratio, high molecular weight carbohydrates-cellulose and lignin which are often resistant to decomposition (Kooch *et al*., 2020). Such changes in litter quality decreases decomposition rates and heterotrophic respiration and consequently decreased ecosystem respiration. Nevertheless, African savannas have evolved with grazing and their structure and function may be effectively adjusted to grazing (McNaughton, 1985, 1986). Actually, grazing at low livestock densities has been revealed to stimulate tillering of grasses and other herbaceous vegetation (Leriche *et al*., 2003). The young sprouting shoots from the tillers increases generation of fresh actively photosynthesizing biomass (Leriche *et al*., 2003) which enhances CO_2 uptake and integration by the herbaceous layer (K'Otuto *et al*., 2012).

Grazing, therefore, affects savanna productivity and C exchange in a complex manner depending on grazing intensity, species composition and litter quality. Savannas are also quite diverse and may therefore respond differently to grazing depending on the location, intensity of grazing, species composition and other factors impacting it. It is therefore imperative to investigate influence of grazing on savanna C exchange and productivity at local scale. Data from such studies can therefore be used to redefine ecological models used to quantify African savanna C balance because the current models used are from outside Africa and are therefore unrepresentative.

The savanna located in Lambwe valley in Kenya has experienced increased cattle grazing over the years (Ondier et al., 2019a). At the same time, rainfall patterns have been changing, characterised by a few episodes of intense rainfall followed by prolonged drought. The consequences of the changes on the ecosystem carbon fluxes are varied, ranging from increased GPP following increases in rainfall amounts (Otieno et al., 2009) and reduction in carbon fluxes as a result of grazing activities (K'Otuto et al., 2012). However, livestock grazing and rainfall variability are concurrently impacting the ecosystem, and modifying its productivity and carbon exchange in ways that are not yet clearly understood. Since the impact of livestock grazing and rainfall may be antagonistic, additive or synergistic, they must be studied concurrently to draw conclusions on their interactive influence on the ecosystem productivity and CO_2 exchange, under varying environmental change scenarios.

2.4 Influence of Livestock Grazing on Herbaceous Biomass Production

Most savannas in Africa are abundantly inhabited by active mix of wild and domesticated herbivores (Ondier et al., 2019a). Herbaceous productivity is key in providing forage for animals and contribute significantly to global carbon sequestration and stocks and local nutrient cycling (Leriche *et al*., 2003). Despite benefiting from available forage, herbivores have both positive and negative impacts on herbaceous production (McNaughton 1985). Positive impacts include stimulation of growth after grazing (compensatory growth) (McNaughton *et al*., 1986), nutrient cycling (Augustine and McNaughton 2006) and enhancing species diversity (McNaughton 1985). Grazing may also negatively influence herbaceous production through reduction of photosynthetic area, loss of nutrients for growth stored in shoots or removal of apical meristems that produces new shoots (Ondier et al., 2019a). Herbivore grazing may also reduce survival fitness of plants due to injury on the stolons or rhizomes and physical damage by trampling (K'Otuto *et al*., 2012). Grazing affects plant tussocks, leading to a decline in tussock vigor and an increase in plant mortality (Kikoti and Mlingo, 2015). Moreover, overgrazing may promote bush encroachment and favour growth of less productive annual grasses and forbs over perennial grasses (Kikoti and Mlingo, 2015).

The effects of herbivores on herbaceous plant production are much debated in literature and remain unresolved. There are no unifying hypotheses about herbivores impacts in African savannas, though several contradicting alternative hypotheses have been developed. The equilibrium hypotheses (DeAngelis and Waterhouse 1987) postulates density-dependent relationship between herbivores and vegetation production, where plant production increases with grazing intensity and reaches a maximum at a moderate rate of herbivory. One possible explanation for the beneficial effect of herbivores on plant production is that they recycle a limiting nutrient and hence promote plant growth (Yuan *et al*., 2020). More precisely, some authors have suggested that a beneficial effect of herbivory through recycling of limiting nutrient comes from increased turnover rates (Carvalho *et al*., 2010; Wang *et al*., 2016).

Alternatively, the disequilibrium hypothesis (Ellis and Swift 1988) posits that herbivores have no effect on vegetation production in a climatically determined ecosystems such as savannas, experiencing an approximately 30% variation in rainfall. Arguably, frequent droughts maintain herbivore densities at low levels beyond which density they can exert significant top-down control on plant production (Vetter 2005). This study explores the effect of grazing on herbaceous layer production with an aim of unraveling biomass development changes when subjected or protected from livestock grazing. Such studies are necessary for scientific management and rational use of savanna.

2.5 Influence of Grazing and Rainfall Variability on Composition and Diversity Herbaceous Vegetation

Savanna vegetation, particularly in Africa, is largely exploited through livestock grazing (Scholes and Archer, 1997). The repercussion of this practice is evident on the herbaceous composition and diversity (Mhinyane *et al*., 2008). Most grasses in savanna ecosystems are fairly tolerant to grazing, but prolonged intense grazing eventually leads to shifts in species composition and reduction in biomass especially when soil nutrients are depleted (van Auken, 2009). Overgrazing leads to shifts in species composition and diversity by depressing the vigor and presence of dominant species, which then enable colonization of less competitive, but grazing tolerant species (Schieltz and Rubenstein, 2016). Livestock also selectively graze palatable herbaceous plants and bushes resulting in decline in species richness (Schieltz and Rubenstein, 2016).

Most Savannahs in East Africa have evolved in conjunction with wild grazing herbivores (Kioko *et al*., 2012), which normally occur at ecologically sustainable levels (Kioko *et al*., 2012; Mureithi *et al*., 2014). However, the introduction and expansion of livestock in the savannahs has poses major challenges, given that the ecosystems are subjected to increased grazing pressure. This potentially alters vegetation structure and function. In a study on a savanna in the Southern Kenya, it was revealed that continuous grazing had negative effects on aboveground biomass production and plant functional properties (Kioko *et al*., 2012). Studies by Ondier *et al*., (2019b) revealed that herbaceous diversity loss in grazed savannahs is experienced mostly in low productive savannahs with mean annual rainfall of less than 600mm.

In addition to grazing, savannahs experience changes in rainfall patterns where both shorter periods of intense rainfall and longer periods of drought have been recorded (Kioko *et al*., 2012;

K'Otuto *et al*., 2012). The results of these have varying consequences on the herbaceous structure (Zerbo *et al*., 2016). Increases in rainfall intensities often result in accelerated runoffs and soil erosion, and destroy shallow-rooted plants (Baudena *et al*., 2015; Zerbo et al., 2016). On the other hand, reduced rainfall may limit plant physiological functions such as photosynthetic CO_2 uptake and fixation, plant growth, and species survival. Drought inhibits seed germination, causes plant mortality and alters community structure (Wang *et al*., 2010; Western *et al*., 2015; Harrison and La Forgia, 2019). Depending on the time-span, drought may cause dominant deep-rooted vegetation in the herbaceous layer to replace shallow rooted vegetation (Hoover *et al*., 2014). Cumulatively, these factors alter herbaceous plant communities, reducing plant cover, and potentially lowering the survival chances of intolerant species (Ji and Peters, 2003). In some instances, such outcomes are short-term, with recovery occurring during subsequent favorable years. In other cases, however, changes in rainfall intensity may stimulate irreversible shifts in species composition in the herbaceous community (van der Plas *et al*., 2013).

The ecosystem in Lambwe valley in southwestern Kenya is predominantly savannah. It has experienced significant climate and land use modification due to changing rainfall patterns and increased livestock grazing intensities (Njoka *et al*., 2003; Muriuki *et al*., 2005). The rainy periods have become shorter but more intense, while the dry seasons have become longer, with extended droughts (Njoka *et al*., 2003; K'Otuto *et al*., 2012). These changes are likely altering composition and richness of the herbaceous layer community in ways that are not yet fully understood. Because both livestock grazing and rainfall variability are acting simultaneously on the vegetation. The effect of the interacting environmental variable on the composition and diversity of the herbaceous vegetation in Lambwe is not known.

2.6 Influence of Livestock Grazing and Changing Rainfall Variability on Savanna Tree Productivity

Climate has rapidly changed and modified savanna rainfall patterns into short episodes of intense rainfall followed by longer periods of drought (Sankaran, 2019). These climate trends have had varying implications on savanna tree carbon exchange and overall productivity. At the same time, increase in livestock grazing, owing to the expanding livestock population has been witnessed in savannas and with varying impact on tree productivity (Goheen *et al*., 2010; Otieno *et al*., 2015). Savanna trees exchange significant amounts of carbon dioxide (CO_2) with the atmosphere and, thus, form a crucial component of the global carbon cycle. However, the impacts of rainfall variability and livestock grazing could impact the tree carbon exchange, with resulting feedback to future climates.

Droughts, resulting from the changing rainfall regimes witnessed in savannas has been reported to cause widespread losses in tree productivity and episodes of tree die off (Sankaran, 2019; Bond *et al.,* 2020). Drought modifies both rates of carbon uptake by photosynthesis, and, thus gross primary productivity (GPP), and release by respiration and the coupling between them (Sankaran, 2019; Deng et al., 2020). Structural changes in the tree response to drought may cause reduction in GPP. These changes include reduction in leaf area due to early senescence, and leaf shed or arrest of leaf expansion as observed in some savannas (Nguyen *et al.,* 2019), and the alteration of leaf angle distribution within canopy (Sastry et al., 2018). Stomata closure during drought reduces photosynthesis and hence, productivity, potentially starving the trees if carbon reserves are exhausted (Schwarz *et al*., 2020). Two contrasting strategies for water use by savanna trees has been hypothesised, although in reality these likely represent point of a continuum: isohydric species decrease stomatal conductance to prevent leaf water potential from reducing below critical level, while anisohdric species are able to exert a little more or no stomatal control in response to drought. Because stomatal closure also reduces CO_2 diffusion into the leaf (Schwarz *et al*., 2020), isohydric species experience longer term reduction in GPP than anisohydric species.

Drought induced loss in tree productivity in savannas can be spatially variable across landscape in ways that are not just related to patchiness in rainfall, but also topography and local edaphic features (Andrew *et al*., 2016). Topography and edaphic features drive drainage and infiltration influencing both surface soil water availability and water table depth and in turn, rooting depth (Mutuku *et al*., 2019). Such variability across land scape (e.g. between upslope and foot slope locations in savanna landscapes; Scholes and Walker, 1993) can lead to differences in the extent of water stress and in turn productivity losses and mortality experienced by different individuals during drought. Patchiness in mortality can also result from underlying differences in tree densities across landscape, with higher density sites typically suffering greater productivity losses and mortality, potentially a result of more intense competition from limited water in those sites during drought (Andrew *et al*., 2016).

Increase in rainfall has been shown to increase tree GPP in savannas because water is a limiting resource for tree growth, up to a point (Berry and Kulmatiski, 2017). However, once rainfall exceeds tree demand (i.e. when rainfall exceeds hydrological losses via evapotranspiration and runoffs), the influence of further increase in rainfall on GPP is likely indirect, due to decline in nutrient cycling and progressive anoxic conditions (Thomas *et al*., 2016). Livestock grazing on the other hand influences soil water infiltration with resulting implication on vegetation production. At high grazing intensities and on slopes, trampling by grazers may result in increased surface runoff and reduced soil water infiltration thus reducing the water reaching the root zones of trees (DeLonge and Basche, 2018). Such conditions induce tree water stress and lower productivity. Alternatively, grazing may increase the availability of soil water for trees by reducing competition for moisture among the herbaceous layer, as suggested by models of savanna tree-grass co-existence (Sankaran *et al*., 2004; Baudena *et al*., 2010).

A recent study on a humid savanna in Lambwe valley revealed a significant decline in herbaceous productivity during dry periods (K'Otuto *et al*., 2012). For this ecosystem, information regarding tree responses is lacking. It is not clear how the tree layer would respond to the increased livestock grazing and rainfall variability that is currently witnessed in Lambwe valley.

2.7 Tree-herb Interactions in Savannas

There are many examples where plants coexist using the same space and resources without outcompeting the other. Trees and herbaceous vegetation in savanna are such an example. This coexistence may be possible due to multiple mechanisms that operate in addition to competition, like resource partitioning, facilitation or differences in phenology (Callaway, 2007; Sankaran, 2019). For example, how key resources like water and nutrients are used by plants, do they use the same resource or have complementary patterns in the way use these key resources? Therefore, resource-use patterns are an important aspect that will influence interactions among plants.

Much of the tree-herb interactions have been evaluated largely with measurements of aboveground productivity and foliar nutrient contents (Casper *et al*., 2003; Ludwig *et al*., 2004a, 2004b). A few studies have used root trenching experiments and variation in stable isotopes to test root competition between trees and herbaceous vegetation; however, with ambiguous results suggesting both the absence (Knoop and Walker 1985; Belsky 1994) and presence (Belsky 1994, Scholes and Archer 1997, Ludwig *et al*., 2004a, 2004b) of competitive effects of trees on herbaceous layer. Additionally, it has been shown that herbaceous vegetation also negatively influence tree growth (Riginos 2009, February *et al*., 2013). Again many questions have been formulated on the basis of competition as the overriding interaction in trees and herbaceous vegetation in savannas and much less attention has been given to measuring tree-herb interactions or on the underlying operating mechanisms.

The view on the interactions of tree-herb vegetation in savannas has been that of intense competition for water and nutrients influencing aboveground productivity of the two vegetation types (Sankaran *et al*., 2004; February *et al*., 2013). Therefore, the concept of competition based on the Gaussian principle of niche differentiation formulates the fundamental basis of all hypotheses (Schoener 1974). Moreover, a lot of the research in savanna ecology is inclined towards the subject ‘‘Savanna-stability’’ (Sankaran *et al*., 2005; Staver *et al*., 2011a, 2011b). Savanna stability refers to a state of equilibrium in the ration of trees to herbaceous vegetation in savannas. Nonetheless, periodic changes occur but not in the magnitude to warrant irreversible changes in the landscape (Scheffer *et al*., 2001). Savanna instability is witnessed when abrupt biome shifts like desertification or conversions to woodlands occur resulting in environmental degradation (Bestelmeyer *et al*., 2015). The causes cited for savanna instability range from the effects of climate change, human-interference (e.g. through livestock grazing) resulting in increased or decreased tree densities that could either potentially competitively exclude grasses from savannas or lead to desertification (Sankaran *et al*., 2005, Buitenwerf *et al*., 2011).

These biome shifts, also termed “regime shifts” are potentially economically undesirable changes to human kind (Folke *et al*., 2004, Kinzig *et al*., 2006). Consequently, much of the recent research is focused on landscape analysis, metadata analysis or modelling studies with much of the emphasis on the drivers that influence tree densities in savannas (Hirota *et al*., 2011, Dohn *et al*., 2013). Several authors have proposed many hypotheses to explain tree-herb interactions in savannas. The most common and most debated concept invoked for tree-herb co-existence is the “Spatial-niche-separation” hypothesis based on the differences in rooting patterns of trees and herbaceous vegetation (Sankaran *et al*., 2004, Scheiter and Higgins 2007). This hypothesis has both support (Belsky 1994, Scholes and Archer 1997, Ludwig *et al*., 2004b) and arguments against it (Belsky 1994, Scholes and Archer 1997; Ludwig *et al*., 2004a). Furthermore, studies seem to indicate a climatic influence in the way this hypothesis is manifest suggesting that niche separation might operate in drier areas but not in areas with a higher moisture content (Ward *et al*., 2013).

The “Pulse Reserve Hypothesis” proposes that the responses of different plant functional types to short but biologically relevant rainfall events (pulses) are different, for example, fast growth in herbaceous layer and slow growth in trees (Ogle and Reynolds 2004, Reynolds *et al*., 2004). Sankaran *et al*., (2004) reviewed the existing hypotheses that explain tree-herb interactions based on largely two aspects: the role of competition in tree-herb interactions and on demographic bottlenecks in the savanna tree ontogeny that potentially influence the densities of trees in savannas. The premise for the “demographic bottleneck” hypothesis is that a tree faces adverse conditions at different ontological stages of its life history, which may limit its growth and survival (e.g., competition with herbaceous vegetation during the seedling stage, herbivory and fire). Sankaran *et al*., (2004) propose an integration of the “demographic bottleneck” and “pulse reserve” hypotheses to explain tree-herb interactions in savannas.

Since savannas have evolved with grazing by mega-herbivores, it is assumed that the grazing activity contributes to the stable coexistence of tree-herb layer. However, with the introduction of livestock grazing together with the changing rainfall patterns witnessed in the savannas, the stable coexistence of tree-herb layer might be impacted. There is therefore need to investigate the influence of the changing environmental factors on the co-existence of the two vegetation functions with an aim of sustainably managing the ecosystem in Lambwe.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Site

The study was conducted in Ruma (00°35'S, 34°12'E), located within the Lambwe valley in Homa Bay County, Suba District, western Kenya from 2014 to 2015. The elevation of the area is around 1,300 meters above sea level. The site was located on a north-facing slope at the foothills of the Gwasi massif, on land belonging to the Kenya National Youth (NYS). The climate is warm and humid, with a mean (2003-2013) annual air temperature of 22 °C (Otieno *et al*., 2015). In addition to the expansive savanna, with semi-natural vegetation, other land cover types include a conserved area within the Ruma National Park, human settlements, open livestock (cows, sheep, and goats) grazing fields, and seasonally cultivated crop fields (Maitima *et al*., 2010).The animal stocking rate is at 7.4 animal units ha^{-1}. The mean annual rainfall (1993-2013) is 1100 mm, with a weak bimodal distribution pattern between April-June and September-November. January-March is usually the driest and hottest period of the year. Soils are shallow, stony, red-brown clay loams. The higher elevations support ferruginous tropical soils and holomorphic soils on rocks that are rich in ferromagnesian minerals. Mixed soil formations of red-brown friable clays, grey mottled clays, and gray compacted loamy sands predominate. Towards the valley bottom, the soils are largely black clays, i.e., “black cotton” (Arnhold *et al*., 2015). Soils here have a high mineral content and tend to be alkaline (Allsop and Baldry, 1972; Arnhold *et al*., 2015). The hills are covered with scattered trees, whose density and diversity decreases downslope where the herbaceous vegetation dominates (Arnhold *et al*., 2015). Measurements were conducted on a 150-ha area of mainly rolling grassland, with tracts of open woodland and thickets dominated by *Acacia ancistroclada*, *Bridelia scleroneura*, *Combretum molle,* and *Rhus netalensis* (Table 2) and a wide diversity of herbaceous vegetation, dominated by the grasses *Bracharia decumbens* and *Hyparrhenia filipendula* (Table 1). The area has a slight slope (3°). Tree vegetation cover at the measurement site was about 20% while the herbaceous vegetation accounted for the 80 % of vegetation cover.

3.1.1 Experimental Layout

The experiment was set up on a savanna landscape, dominated by herbaceous vegetation and a few scattered trees. Split-factorial design, with three replicates of grazed and fenced areas as main treatments, and rainfall manipulation splits that included ambient rainfall (100 % rainfall), fifty percent more rainfall (150 % rainfall), and fifty percent less rainfall (50 % rainfall) were set up within herbaceous layer. The split-plots were entrenched within the main plots that were respectively grazed by livestock or fenced (2 m high perimeter fence since 2011) to exclude livestock. The grazed plots were open savanna subjected to all year-round livestock grazing since 2005. At any grazing event, animals stayed on the site for not more than one hour. Manipulation of the ambient rainfall was achieved by the construction of rain-out shelters above the herbaceous vegetation canopy according to the original design of February *et al*., (2013). To exclude rainfall, bisections of the rain exclusion split plots were covered with transparent plastic sheets, regularly spaced and inclined at 2° downslopes to re-direct 50% of the excluded rainfall to the split plots designated for more rainfall (150% rainfall). Tests using portable soil moisture sensors revealed homogeneity in soil moisture distribution within the plots designated for more rainfall. Control plots received ambient rainfall. Each rainfall manipulation shelter measured 6 m by 3 m and were embedded on either grazed or fenced land use plots each measuring 70 m by 100 m. Trenches, 50 cm deep and 30 cm wide, were dug (dug once during plots preparation stage and 3 months before onset of measurements) around the plots and plastic vertically aligned on the walls of the trenches to prevent surface runoff and lateral movement from the surrounding soil. Rain-out sheets were replaced every six months. On the hill slope dominated by trees, grazed and ungrazed/fenced plots measuring 70 m by 50 m were randomly established and each replicated three times. Fenced plots (since 2006) were set up by erecting 2 m high perimeter fence to exclude livestock whereas grazed plots were open savannas subjected to livestock grazing. The plots were established 100 m apart. In the fenced plots, three individuals of each of the dominant trees of *Acacia ancistroclada* and *Comberatum molle* were utilized for estimation of sap flow, while in the grazed plots, three individuals of each of the dominant *Acacia ancistroclada, Bridelia scleroneura* and *Comberatum molle* were measured for sap flow, from which CO_2 assimilation by trees was derived. The tree layer was not subjected to rainfall manipulation due to lack of strong metallic frames for construction of rainout shelters above tree canopy.

3.2 Measurements

3.2.1 Microclimate

During the experimental period, weather parameters were continuously monitored using an automatic weather station (AWS-GP1, Delta-T Devices, Cambridge, UK) installed in 2008 within the study site in an open area to avoid interference from trees. Parameters that were continuously monitored included rainfall, air temperature and humidity. Measurements were taken every 5 minutes, and data averaged and logged half-hourly. Data was downloaded monthly and arranged into means.

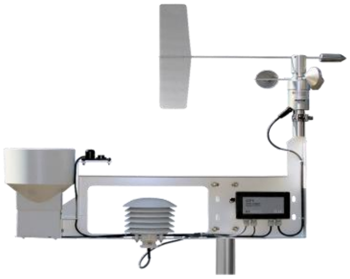

Plate 1: An image of AWS-GP1 Weather station installed within the study site. The WS includes high grade sensors to measure rain, solar radiation, wind speed, wind direction, relative humidity and air temperature.

3.2.2 Soil water content

Within the herbaceous vegetation study plots, volumetric water content (SWC) was determined monthly for a period of 2 years (January 2014-December 2015). Soil volumetric water content was measured using TOMST automatic sensors with data loggers (TMS Data loggers, C, Zech republic, EU). Three logger sensors were installed horizontally at 30 cm soil depth in each plot and set to log every 30 minutes.

Under the trees, continuous SWC in the upper 30-cm soil layer was monitored between January 2014 to December 2015 using Theta probes (type ML 2X, Delta-T Devices, Cambridge, Uk). Data was collected every 30 min, averaged, and logged hourly using a delta logger (DL 2e-Delta-T Devices, Cambridge, UK). Data was downloaded monthly and arranged into means.

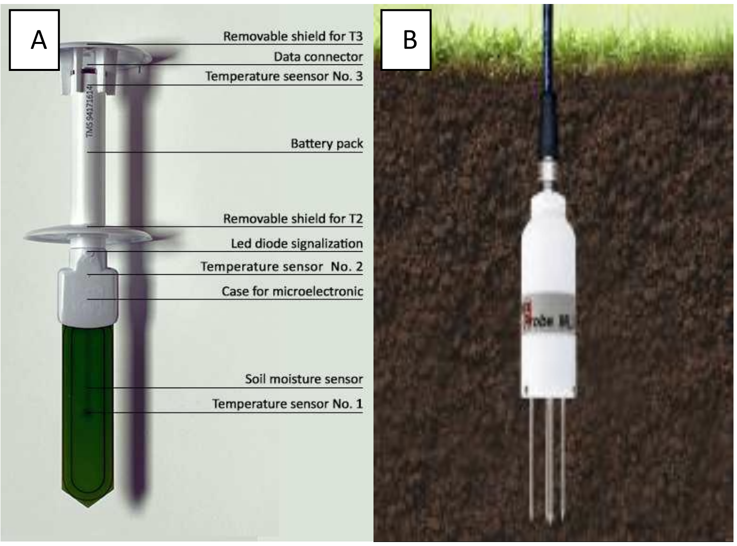

Plate 2: Images of TMS data logger (A) and theta probe sensor (B) used to measure SWC within the experimental sites.

3.2.3 CO_2 Exchange in the herbaceous layer

On any measurement day, net ecosystem CO_2 exchange (NEE) and ecosystem respiration (R_{eco}) was sequentially recorded in a systematic rotation over all replicate plots. Net ecosystem CO_2 exchange and R_{eco} was measured using a portable, temperature controlled 40 cm × 40 cm ×54 cm transparent (light, NEE) and opaque (R_{eco}) closed chamber system (Li *et al*., 2008; Droesler, 2005). The light chamber was constructed from a 3 mm thick Plexi glass XT type 200070, with >95% light transmittance. The dark chamber was made of opaque PVC and further covered with a reflective layer of aluminium. To ensure close air circulation, frames with 39.5 cm × 39.5 cm base and 10 cm height, and externally fitted with a 3 cm wide platform (3 cm from the top) was inserted to a minimum of 4 cm into the soil at least 3 days before the beginning of the measurements. Extension bases were used to adjust chamber height to the canopy height whenever necessary. Chambers were sealed to the plastic frames with a flexible rubber gasket and the chamber firmly secured using elastic straps fastened onto the ground from two sides.

Tests indicate that leakages don’t occur, however, this was examined regularly in the case of systematic field measurements and each set of data was scrutinized for abnormalities.

The chamber temperature was maintained within 2^0 C of the ambient using frozen cool packs and air inside the chamber mixed using three fans. Air temperature within and outside the chamber was continuously monitored and recorded during the CO_2 flux measurements to check against wide variations. Sudden rise in pressure inside the chamber was avoided by opening a 12 mm diameter vent at the top of the chambers during their replacement, and closing the vent soon after the chamber was secured onto the frames before the onset of CO_2 flux measurement. Chamber CO_2 concentration was read from portable infrared gas analyser (IRGA, LI-820, LI-COR, USA) connected to the chamber via flexible 0.32 cm diameter inflow and outflow tubes (Droesler, 2005). A battery driven pump was used to maintain a constant air flow rate through the IRGA-chamber system (IRGA, LI-820, LI-COR, USA). Photosynthetic photon flux density (PPFD) was measured using a PAR sensor (LI-190, LI-COR, USA) installed inside the chamber. Once a steady state had been maintained, CO_2 concentration (ppm) was recorded every 15 sec for a period of 2.5 hrs before shifting to the next frame. Soil temperatures within the frames were recorded at 10 cm depth, at the start and end of the CO_2 concentration measurements, from digital thermometers (Eintichthermometer, Conrad, Hirschau, Germany). Changes in CO_2 concentration within the chamber headspace were calculated by linear regression of linear portion of the plot of CO_2 against time for the duration of the measurement. CO_2 fluxes were calculated according to Risch and Frank (2010).

$$CO_2 \text{ flux} = \frac{\partial CO2}{\partial t} * \frac{PV}{ART} \qquad \text{eq. 1}$$

Where $\frac{\partial CO2}{\partial t}$ = rate of exchange in CO_2 concentration with time; V= volume of headspace within the chamber; P= atmospheric pressure; A= ground area covered by chamber; R= gas constant; T= air temperature (K).

A functional relationship between PPFD and NEE, also known as "light response curve" described by a rectangular hyperbola (Gilmanov *et al.*, 2007) (Eq. 2) was employed to parameterise NEE response to light using Sigma-Plot 8.0. (http:www.sigmaplot.com/products/sigmaplot/sigmaplot-details.php)NEE = - $\frac{\alpha\beta Q}{\alpha Q+\beta}+\gamma O$.eq. 2

Where Q is PPFD (µmol $m^{-2}s^{-1}$), NEE (µmol CO_2 $m^{-2}s^{-1}$), α is an approximation of the canopy light utilization efficiency (µmol CO_2 $m^{-2}s^{-1}$), β is the maximum CO_2 uptake rate of the canopy (µmol CO_2 $m^{-2}s^{-1}$) and γO is an estimate of the average ecosystem respiration ($R_{eco,}$ µmol CO_2 m^{-2} s^{-1}) occurring during the observed period.

3.2.4 Gross Primary Production of Herbaceous Layer

Gross primary production (GPP) was estimated via the general equation (Gilmanov *et al.*, 2007):

$GPP = \mathrm{Re}co + NEE$ ……………………………………………………………………….eq. 3

Where R_{eco} = ecosystem respiration (µmol CO_2 $m^{-2}s^{-1}$)

3.2.5 Determination of Herbaceous Biomass, Species Diversity, Composition and Dominance

At the end of CO_2 flux measurements all plant biomass within the 40 cm by 40 cm frames were harvested monthly during the entire two-year study period. The harvested biomass was separated into live and dead biomass. Green standing plant material constituted live biomass, whereas brown standing and non-standing (on the ground / litter) plant material constituted dead biomass. The aboveground samples were oven-dried at 80 °C for 48 h, before determining their dry weight. Species composition within the herbaceous layer was assessed towards the end of the rainy season (June and November) in 2014 and repeated at the same period in 2015. The sampling time coincided with the flowering period of most herbaceous species, making their identification easier. Plant species composition was estimated by randomly establishing 3 separate 40 cm by 40 cm quadrats in each of the treatment plots. All the standing plant materials in the quadrats were identified at Maseno University herbarium using taxonomic keys (Agnew and Agnew, 1994) and recorded. Individual species were further classified in terms of life-forms (i.e. annuals and perennials) and their palatability was determined by checking and identifying from the literature (Boonman, 1993; Muyekho *et al*., 2004). Point frame method (Bonham, 1989), with pinholes 10 cm apart was used to determine species ground cover within plots. Relative abundance of species was calculated from the total counts of individuals forming the ground cover as;

Relative abundance (%) = No. of hits of species z/Total No. of hits of all species * 100……………………………………………………………………………………..eq. 4

(Bonham, 1989).

Species dominance (d) was calculated using Berger-Parker index as follows:

$$d = \frac{N\max}{N} \quad \text{……………………………………………………………………..……eq. 5}$$

Where Nmax = number of individuals in the most abundant species and N is the total number of individuals in the sample. The herbaceous species were classed as dominant (≥ 15%) and less dominant (< 15%) (Tefera *et al*., 2010) based on their mean percentage cover. Species richness (Dmg) was calculated according to (Magurran, 2004) as; Dmg = S-1/lnN…………………..eq.6

Where S is Total No. of plant species, ln= natural log and N= total number of individuals

Herbaceous diversity was determined using species richness (R) and Simpson's index (D) of diversity. Species richness was defined as the total number of species present in a particular sampling plot, (Waite, 2000). Simpson's index of diversity was calculated as follows:

$(D') = 1 - D$ ……………………………………………………………………..…eq. 7

Where *(D')* is diversity and *D*= $\sum (Pi)^2$ and *Pi* = *ni/N*. *ni* is the number of individuals of species in *i* and *N* is the total number of individuals in the sample. Simpson's index of diversity has a range of 0-1 where 1 represents maximum diversity.

3.2.6 Sap Flow Measurements in Trees

Sap flux density SFD (g m^{-2} s^{-1}) was measured in 3 individuals of each of the three dominant tree species (80% of crown cover), *A. ancistroclada*, *B. scleroneura* and *C. molle*, using custom-made, heat dissipation probes constructed following Granier's (1987) original design. Each sensor consisted of a pair of 2-mm-diameter probes vertically aligned ca. 10 cm apart. Each probe contained an in-built 0.2-mm-diameter copper-constantan thermocouple. The two thermocouples were joined at the constantan leads, so that the voltage measured across copper leads provide the temperature difference between the heated upper probe and the lower reference. Heating across the entire length of the 20 mm upper probe was achieved with a constant current of 120 mA supplied to a constantan heating wire, resulting in a heating power of 200 mW (Granier, 1987).

Sensors were placed in the outer 20 mm of the sap wood (annulus, 1, 0-20 mm radial sapwood depth). In cases where the tree trunk had large radius with sapwood radius greater than 20 mm, a second sensor was placed 10-15 cm circumferentially, away from the first sensor pair, on the same side of the stem to avoid azimuth differences. Temperature differences were measured every 5 minutes and 30 minutes mean value logged (DL2e with LAC-1 in single ended mode, Delta-T Devices, England). Sap flux density (SFD, g m^{-2} s^{-1}) for each sensor was calculated from ΔT in accordance with Granier (1987) assuming zero SFD (i.e. ΔT_{max}) at night and VPD near zero:

$$SFD = 119K^{1.231} \qquad \text{eq. 8}$$

Where,

$$K = \frac{\Delta T_{\max} - \Delta T}{\Delta T} \qquad \text{eq.9}$$

Tree water use (TWU, Kg h^{-1}) was obtained by multiplying SFD by sap wood cross-sectional area (SA, m^2): $TWU = \sum_{i=1}^{n} (SFDi * SAi)$ ……………………………………………………...eq. 10

Where SFDi is flux density of the annulus i (g m^{-2} s^{-1}) and SA_i is sap wood areas of the annulus i(m^2). This took into account the second annulus ring, in case a second sensor was installed into the tree. For example, i=1 will be annulus in 0-20 mm sap wood depth, i=2 will be annulus ring 20-40 mm sap wood depth.

In order to calculate canopy transpiration, the trees were grouped according to their diameter at breast height (DBH, about 1.3 m height above the ground surface) classes of 5-10, 11-20, 21-30, 31-40, 41-50, 51-60, and 61-70 cm. Canopy transpiration (Ec) was calculated for each diameter class by combining mean SFD for each DBH class and total S_A in each DBH class per unit ground areas (G_A) (Ewers *et al*., 2002).

$$Ec\frac{1}{4}SFD^{*}S_A = G_A \text{ ....} \quad \text{eq. 11}$$

Canopy conductance (G_c, mm s^{-1}) was determined from E_c as

$$G_c = k\frac{Ec}{VPD} \text{ where } k = G_vT_k \text{ ....} \quad \text{eq. 12}$$

Where G_v is the universal gas constant =0.462 m^{-3} kPa $Kg^{-1}k^{-1}$ and T_k is the air temp in Kelvin (K)

3.2.7 Estimation of Daily GPP using PIXGRO Model

3.2.7.1 Model Characteristics

For the purposes of comparing tree and herbaceous layer, daily gross primary production (GPP) for the trees and the herbaceous vegetation were estimated using the PIXGRO model (Adiku *et al*., 2006). The model PIXGRO consists of two coupled modules, the canopy flux module $PROXEL_{NEE}$ (PROcess pixel net ecosystem exchange model) and vegetation structure module CGRO. The module $PROXEL_{NEE}$ captures canopy processes such as GPP, R_{eco}, NEE and transpiration. The simulation of GPP is implemented in module $PROXEL_{NEE}$ using algorithms of Farquhar and Caemmerer (1982), modified by Harley and Tenhunen (1991). CGRO simulates growth and development processes e.g. leaf area index (LAI). This module was developed for C3 plants. The C4 plants, however, are known to have less photorespiration compared to the C3 due to the CO_2 concentration mechanism of the C4 cycle (Edwards and Walker, 1983; Taiz and Zeiger, 1991). In order to simulate GPP for C_4 grasses, leaf internal CO_2 concentration was set to

3000μmol mol^{-1} (Ruidisch *et al*., 2015), thus estimating gas exchange under conditions of CO_2 saturation as is the case with C_4 plants.

The simulated LAI from CGRO is passed to the $PROXEL_{NEE}$ canopy process module and the computed fixed C fluxes are returned to CGRO, which then simulates growth. Dry matter accumulation rate is simulated from the hourly GPP ($molCO_2$ m^{-2} h^{-1}) after conversion to gross carbohydrate production rate, P_g (gCH_2O m^{-2} h^{-1}) and the latter reduced by plant respiration losses (Adiku *et al*., 2006). The canopy was treated as a single layer.

3.2.7.2 Model Calibration and Parameter Setting

The PIXGRO model for trees was calibrated using tree canopy transpiration (Ec. Eq. 11) and canopy conductance (Gc. Eq. 12) data derived from sap flow measurements between January 2014 and December 2015. For comparison, similar simulation was performed for the herbaceous vegetation for the same period over which sap flow measurements were conducted. The herbaceous vegetation model was calibrated using GPP and NEE data derived from chamber measurements.

3.2.8 Analysis of Plant Root Distribution

Plant root distribution was analyzed according to Arnhold *et al*., (2015). Soil profiles (~0.5 x 1 m) down to a depth of consolidated rock material were dug within the open locations, outside tree canopies, dominated by herbaceous vegetation, and also at locations under the tree canopies. Three soil profiles were dug in each of the two locations (within tree canopies and open locations dominated by herbaceous vegetation). Each profile was divided into individual soil horizons (FAO, 2006) in order to obtain depth distribution of sampled roots. Plant roots within the soil horizons were picked (using forceps and blunt knife), washed in running water and their diameters measured using a micrometer screw gauge. Coarse (>2 mm diameter) and fine (<2 mm diameter) root densities for each horizon were determined by counting all roots found in each horizon and dividing the number by the area of the profile wall covered by the associated horizon.

3.3 Data Analysis

Statistical analysis was performed using SAS software version 9.1, California, USA. The effect of livestock grazing, rainfall manipulation and their interaction on herbaceous biomass GPP, NEE, R_{eco} , species diversity, palatability, and soil bulk density were tested using factorial ANOVA (fully crossed) and their means (±SD) calculated. Post hoc test for multiple comparison of the means (±SD) was done using Tukey LSD ($P \leq 0.05$). Linear regression analysis was used to investigate the relationship between CO_2 exchange and SWC within grazed and fenced plots. For comparison of herbaceous and tree productivity, a factorial ANOVA was performed on mean daily GPP of both trees and herbaceous vegetation and comparison made using t-test at 5% significance level.

CHAPTER FOUR

RESULTS

4.1 Microclimate of the Study Region

Rainfall was bimodal, occurring from April to June and September to December (Figure 4.1). The total rainfall amounts in 2014 and 2015 were 1148.4 mm and 1169.5 mm, respectively. Air temperature increased during the dry period and decreased during the wet months.

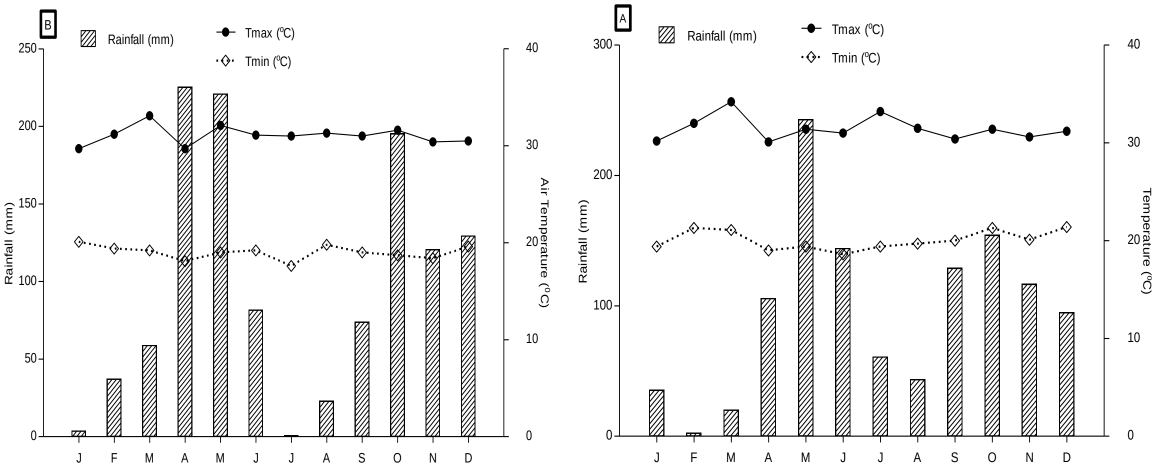

Figure 4.1: Monthly rainfall amounts (mm) and average maximum and minimum air temperatures, T_{air} (^{0}C) recorded in the study site in (A) 2014 and (B) 2015, when measurements were conducted.

4.2 Pattern of Soil Water Content within Grazed and Fenced Plots

In all the plots, soil water content followed seasonality in rainfall pattern, increasing during wet season and decreasing during dry seasons (Figure 4.2). April- June and September-December were wet periods while January-March and July and August were dry periods. Grazed plots recorded significantly ($P < 0.05$) lower SWC than grazed plots.

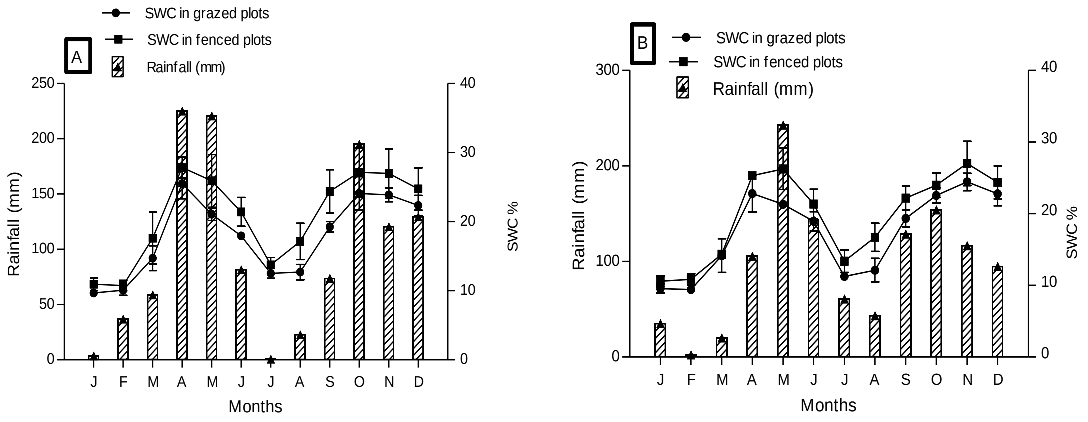

Figure 4.2: Mean soil water content (%) within grazed and fenced plots measured in (A) 2014 and (B) 2015 respectively. Bars are means with ± SD.

4.4 Root Distribution Patterns and Soil Characteristics within Herbaceous Layer and under Tree Canopies

The depth of soil on which our plots were established ranged between 50 and 70 cm below which there were strong presence of course rock fragments (Figure 4.3a and b) Root distribution patterns were different between the two locations (open spaces and between trees). In the open locations, the densities of coarse and fine roots were highest at around 20 cm depth, but declined sharply between 30 and 60 cm depths. Some of the coarse roots found here belonged to the trees, while majority of the fine roots were grass roots. Under the tree canopies, there was a strong increase in coarse root density in the deeper soils > 40 cm depth, all of which belonged to the trees. Fine root density within the top 60 cm soil profile under the tree canopies was low and declined between 10 and 50 cm depths. There was a mix of both trees and herbaceous roots. The soil textural composition was 50 % - 80% clay, 10 % - 40 % silt and 5 % - 10 % sand, with no differences between the open locations, outside tree canopies, and under the tree canopies. In both locations, soil bulk density ranged from 0.8 to 1.0 g cm^{-3}, while soil hydraulic conductivity ranged from 20 to 70 mm h^{-1}. Differences between locations under the tree canopies and open locations were not significant. Under the tree canopies and in the open locations, soil hydraulic conductivity dropped sharply within the shallow 30 cm soil profile, while plant available water capacity was stable between 0.17 and 0.19 m^3 m^{-3}. Differences in bulk densities and hydraulic properties between the two locations were also not significant. The distribution patterns and quantities of soil C and N within the upper 60 cm of the soil profiles below and outside the tree canopies were similar, with values ranging from 0.3 % and 4 % within the top 10 cm soil profile and around 0.1 % and 1.5 % in the 40 cm depth for N and C respectively (Figure 4.3c, d).

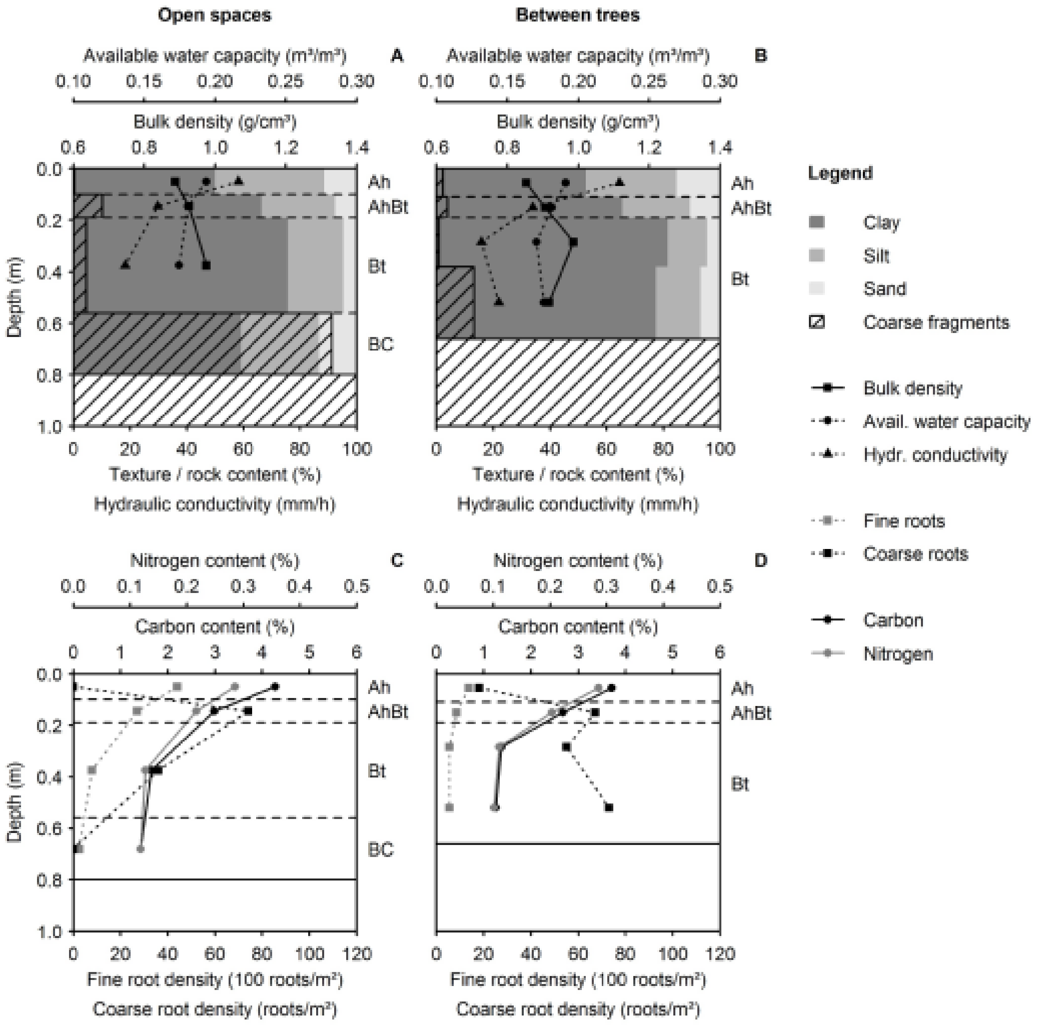

Figure 4.3: Root distribution in the (a and c) locations outside the tree canopies dominated by herbaceous vegetation and (b and d) locations under the tree canopies, and soil characteristic including (upper panel) soil texture, soil structure and hydraulic parameters, (lower panel) soil nitrogen and carbon contents.

4.5. Herbaceous composition, life forms and palatability within grazed and fenced plots

List of herbaceous species and their percentage composition within grazed and fenced plots are shown in Table 4.1. A total of 29 species and 25 species were recorded in the grazed and fenced plots respectively. Fenced plots were dominated by *Hyparrhenia filipendula (52%)* and *Brachiaria decumbens (25%)*. The dominant vegetation in the grazed plots was *Bothriochloa insculpta (28%)* and *Paspalum dilatatum* (19%). There was a mix of both palatable and unpalatable vegetation within grazed and fenced plots. Both plots were dominated by perennial vegetation and a few annual species.

Table 4.1: The composition, life forms, and palatability of the herbaceous plants in Lambwe between 2014 and 2015

Grazed				**Fenced**			
Plant species	**Life form**	**Palatability**	**% composition**	**Plant species**	**Life form**	**Palatability**	**% composition**
Bothriochloa insculpta (A. Rich) A. Camus	Perennial	Palatable	27.8	*Hyparrhenia filipendula* (Hochst) Stapf.	*perennial*	*palatable*	51.97
Paspalum dilatatum Poir	Perennial	*Palatable*	18.72	*Brachiaria decumbens* Stapf	*perennial*	*palatable*	24.92
Hyparrhenia fillipendula (Hochst) Stapf.	Perennial	*Palatable*	11.83	*Aspilia pluriseta* Schweinf	*perennial*	*Unpalatable*	3.11
Sporobolus agrostoides Chiov.	Perennial	*Unpalatable*	9.09	*Triumphetta rhomboidea* Jacq.	*perennial*	*palatable*	2.42
Vernonia glabra (Steetz) Vatke	Perennial	*Unpalatable*	5.41	*Justicia striata* Vahl	*Annual*	*Unpalatable*	2.35
Justicia striata Vahl	Annual.	*Unpalatable*	3.92	*Vernonia glabra* (Steetz) Vatke	*perennial*	*Unpalatable*	1.73
Brachiaria decumbens Stapf	Perennial	*Palatable*	2.67	*Ipomoea tenuirostris* Steud ex Choisy	*perennial*	*palatable*	1.59
Aspilia pluriseta Schweinf	Perennial	*Unpalatable*	2.35	*Desmodium gangeticum* (L.) D.C.	*perennial*	*palatable*	1.45
Ipomoea tenuirostris Steud ex Choisy	Perennial	*Palatable*	1.88	*Barleria acanthoides* Vahl.	*perennial*	*palatable*	1.25
Digitaria sanguinalis (L) Scop	Annual	*Palatable*	1.73	*Cajanus cajan* L. Millsp	*perennial*	*palatable*	1.11
Cynodon dactylon (L) Pers	Perennial	*Palatable*	1.73	*Rhynchosia minima* (L.) DC.	*perennial*	*palatable*	1.04
Barleria acanthoides Vahl.	Perennial	*Palatable*	1.34	*Themeda triandra* Forssk	*perennial*	*palatable*	0.97
Triumphetta rhomboidea Jacq.	Perennial	*Palatable*	1.26	*Hypoestes aristata* Soland ex Roem & Schalt	*perennial*	*palatable*	0.76
Indigofera arrecta Hochst ex. A. Roch.	Perennial	*Palatable*	1.18	*Urena lobata* L.	*Annual*	*palatable*	0.63
Urena lobata (L).	Annual	*Palatable*	1.1	*Hoslundia opposita* Vahl.	*perennial*	*Unpalatable*	0.56
Hypoestes aristata Soland ex Roem & Schalt	Perennial	*Palatable*	1.1	*Cynodon dactylon* (L) Pers	*perennial*	*palatable*	0.56
Sida acuta Burm. F	Perennial	*Unpalatable*	1.1	*Paspalum dilatatum* Poir	*perennial*	*palatable*	0.49
Waltheria indica Bak.	Perennial	*Unpalatable*	0.94	*Hypoestes forskaolii* (Vahl) R.Br.	*Annual*	*Unpalatable*	0.49
Striga asiatica (L) Kuntze	Annual	*Unpalatable*	0.71	*Leonotis nepetifolia* (L) R.Br.	*Annual*	*palatable*	0.42
Euphorbia hirta Linn.	Annual	*Unpalatable*	0.71	*Digitaria sanguinalis* (L) Scop	*Annual*	*palatable*	0.42
Rhynchosia minima (L.) DC.	Perennial	*Palatable*	0.47	*Indigofera arrecta* Hochst ex. A. Roch.	*perennial*	*palatable*	0.42
Cajanus cajan L. Millsp	Perennial	*Palatable*	0.47	*Ocimum kilimandscharicum* Guerke	*perennial*	*palatable*	0.42
Hoslundia opposita Vahl.	Perennial	*Unpalatable*	0.47	*Bothriochloa insculpta* (A. Rich) A. Camus	*perennial*	*palatable*	0.35
Sonchus schweinfurthii Oliv.	Perennial	*Palatable*	0.47	*Panicum maximum* Jacq.	*perennial*	*palatable*	0.35
Sphaeranthus suaveolens (Forsk) DC	Perennial	*Palatable*	0.47	*Lantana trifolia* L.	*Annual*	*Unpalatable*	0.35
Solanum incanum Linn	*Perennial*	*Unpalatable*	0.47				
Desmodium gangeticum (L.) D.C.	*Perennial*	*Palatable*	0.24				
Hypoestes forskaolii (Vahl) R.Br.	Annual.	*Unpalatable*	0.24				
Indigofera brevicalyx Bak.	Perennial	*Unpalatable*	0.24				

4.6 Characteristics of the Studied Trees

Table 4.2 shows studied tree species within grazed and fenced plots. Individual trees were organized according to Diameter at breast height (DBH) classes. Grazed plots were dominated by *Acacia ancistroclada*, *Bridelia scleroneura*, *Comberatum molle* and *Rhus natalensis* while the dominant trees in the fenced plots were *Acacia ancistroclada*, *Comberatum molle*, and *Rhus natalensis*

Table 4.2: Characteristics of studied tree species within grazed and fenced plots during the study period (January 2014-December 2015).

	Tree species	no. of individuals measured for sap flow	no. of erect stems with DBH ranges (cm) n						
Grazed			5-10	11-20	21-30	31-40	41-50	51-60	61-70
	Acacia ancistroclada	4			5				
	Bridelia scleroneura	3	14	94	12				
	Comberatum molle	5	13	20					
	Rhus natalensis		5	12					
	Celtis Africana		5						
	Psedium guajava		2						
	Piliostigma thonningii		3	5	1				
Fenced	*Comberatum molle*	4	8	8	2				
	Acacia ancistroclada	4	3	6	1	1			1
	Rhus natalensis		5	1	1				
	Psedium guajava		3						
	Celtis africana		3						
	Balanites aegyptiaca						1		
	Albizia coriaria				1				
	Piliostigma thonningii		1	4	1	1			

4.7 Impact of Livestock Grazing and Rainfall Manipulation on Herbaceous Characteristics

All the sites were dominated by perennial herbaceous species with few annuals. Percentage cover of perennials differed significantly ($P \leq 0.05$) between grazed (90.72 %± 1.95) and fenced plots (96.67 %± 1.92). There was a significant difference ($P \leq 0.05$) in the percentage cover of annuals within grazed (9.27 %± 1.95) and fenced plots (3.33 %± 1.92). The coverage of palatable herbaceous species was higher in both grazed (87.89 %± 2.87) and fenced plots (96.72 ± 3.82%), but the differences was not significant ($P = 0.057$). Rainfall manipulation had no significant ($P > 0.05$) influence on herbaceous life forms (perennials and annuals) and palatability within grazed and fenced plots.

Table 4.3: Mean (±SE) percentage of life forms (perennials and annuals) and palatability of the herbaceous layer in Lambwe at grazing and rainfall treatments. Values across plots not sharing the same letters are significantly different from each other (Tukey-LSD, $P \leq 0.05$).

Plant attributes	Grazed			Fenced			LDS
	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)	
Perennials (%)	91.5 ±2.4^{a}	92.2 ±2.8^{a}	88.5 ±3.8^{a}	98.5 ±1.5^{b}	96.8 ±4.7^{b}	94.7 ±2.0^{b}	3.10
Annuals (%)	8.5 ±2.4^{a}	7.8 ±2.7^{a}	11.5 ±3.8^{b}	1.5 ±1.5^{c}	3.2 ±4.7^{c}	5.3 ±2.0^{c}	3.27
Palatable (%)	86.5 ±11.2^{a}	91.2 ±2.9^{a}	86.0 ±1.6^{a}	96.8 ±3.4^{b}	97.7 ±2.3^{b}	95.67 ±0.5^{b}	5.22

4.8 Interaction of Livestock Grazing and Rainfall Manipulation on Soil Bulk Density within Herbaceous Layer

Either ambient rainfall or increment of rainfall to 150 % had no significant ($P > 0.05$) impact on soil bulk density across studied plots. In comparison to fenced plots, grazed plots recorded significantly higher bulk densities ($F= 70.02$, $P \leq 0.05$). Grazed and fenced plots recorded mean soil bulk densities of 1.26±0.14 and 1.03 ±0.07 g cm^{-3} respectively. The interaction of grazing and rainfall reduction led to a significant ($P \leq 0.05$) increase in soil bulk density (Figure 4.4).

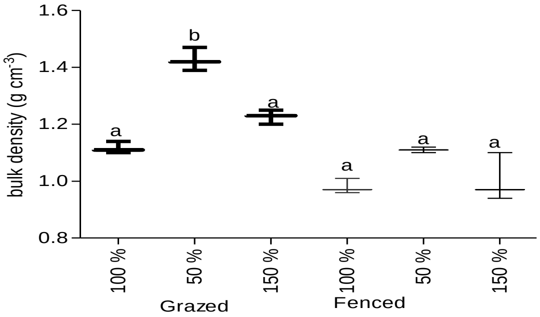

Figure 4.4: Mean soil bulk density (g cm^{-3}) within herbaceous study plots. Different in letters indicate significant differences ($P \leq 0.05$) in treatments across plots

4.9 Interaction of Livestock Grazing and Rainfall Manipulation on Herbaceous Biomass

Rainfall manipulation significantly ($P \leq 0.05$) affected biomass across grazed and fenced plots. Significant reduction in aboveground biomass (green and dead) was observed in the rainfall reduction plots. Within the fenced plots, the reduction and increment in ambient rainfall led to respective decrease and increase in green and dead biomass. There were significant differences ($P < 0.0001$, $F = 322.7$) in total aboveground biomass between the plots (Table 4.4). The highest total aboveground biomass (1198.2 ± 78.4 g m^{-2}) was recorded in the fenced plots while the lowest biomass (473.7 ± 23.8 g m^{-2}) was recorded in the grazed plots. The highest standing (green) biomass recorded during the growing period (703.4 ± 50.7 g m^{-2}) was in the fenced plots. A significantly higher (494.8 ± 27.7 g m^{-2}) amount of dead biomass accumulated in the fenced plot compared to the grazed plot. The interaction of grazing and rainfall reduction led to a significant ($P \leq 0.05$) decrease in both green and dead biomass. The interaction of grazing and rainfall increment led to a significant ($P \leq 0.05$) increase in both green and dead biomass.

Table 4.4: Aboveground plant biomass measured across the studied plots. Values are means ± SE. Values not sharing the same letters indicate significant difference across plots (Tukey LSD, $P \leq 0.05$).

Plant Biomass	Grazed				Fenced				LSD
	Ambient rainfall (100 %)	Reduced rainfall (50 %)	Increased rainfall (150 %)	Means biomass	Ambient rainfall (100 %)	Reduced rainfall (50 %)	Increased rainfall (150 %)	Mean biomass	
Aboveground Green (g m^{-2})	373.7 ± 51.9^{d}	210.0 ±21^{e}	378.0 ± 21^{d}	320.6 ± 31.3	749. 19 ± 9.9^{b}	561. 7 ± 10.7^{c}	799.3 ± 9.9^{a}	703.4 ± 50.7	5.38
Aboveground Dead (g m^{-2})	196.4 ± 15.2^{e}	75.2 ± 6.1^{f}	217.6 ± 1.2^{d}	163.1 ± 7.5	521.1 ± 1.6^{b}	353.2 ± 2.5^{c}	610.1 ± 5.9^{a}	494.8 ± 27.7	90.3

4.10 Herbaceous CO$_2$ Exchange within Grazed and Fenced Plots

The difference in GPP$_{max}$ between grazed (14.33 ± 3.5 μ mol m^{-2} s^{-1}) and fenced plots (17.79 ± 3.12 14.33 ± 3.5 μ mol m^{-2} s^{-1}) were statistically different ($P \leq 0.05$). In both grazed and fenced plots, GPP and R$_{eco}$ increased and reduced during the wet and dry periods respectively. In most instances, GPP and R$_{eco}$ in the grazed plots were significantly ($P \leq 0.05$) lower compared to the fenced plots. For grazed and fenced plots, NEE increased (more negative) between April and June and September and December coinciding with periods of high SWC. The dry periods between January and March were marked with lower NEE in both plots.

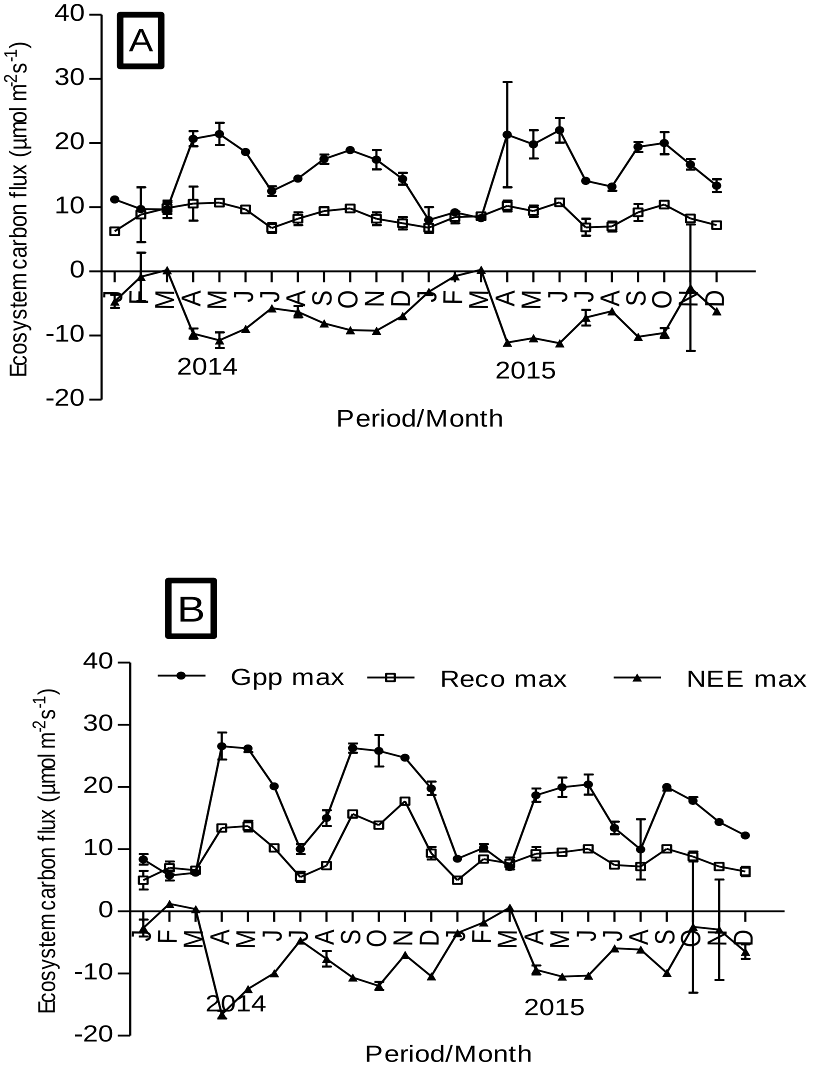

Figure 4.5: Seasonal trends of maximum net ecosystem CO_2 exchange (NEE max), ecosystem respiration (R_{eco} max) and gross primary productivity (GPP max) in (A) grazed and (B) fenced plots between 2014 and 2015. Values are means (±SD). Negative NEE values represent ecosystem CO_2 uptake while positive value represent CO_2 release into the atmosphere.

4.11. Interaction of Livestock Grazing and Rainfall on Herbaceous CO_2 Flux

The interaction of grazing and rainfall reduction significantly ($P \leq 0.05$) lowered GPP, NEE and R_{eco} by 22.5 %, 33 % and 39 % respectively. The interaction of grazing and rainfall increment significantly ($P \leq 0.05$) increased GPP and NEE, by 47 %, 54.8 % but had no significant influence on R_{eco}hn.

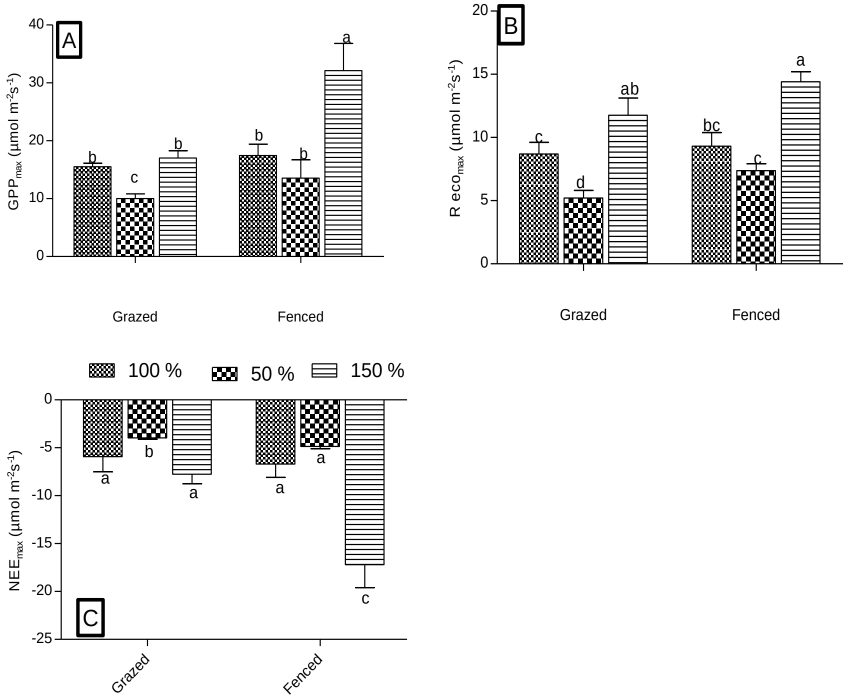

Figure 4.6: GPP (a), R_{eco} (b) and NEE (c) in grazed and fenced plots at ambient rainfall (100 %), fifty percent rainfall reduction (50 %) and fifty percent rainfall increment (150 %) for the entire study period. Different letters indicate significant differences ($P \leq 0.05$) in treatments across plots. Bars are means ± SD.

4.12 Influence of Grazing, Rainfall Manipulation and their Interaction on Herbaceous Diversity and Dominance

Herbaceous diversity was high within the plots (Simpson's index 0.63-0.87; Figure 4.7A). The herbaceous diversity in grazed plots was 19.6 % higher than fenced plots ($P \leq 0.05$; Figure 4.7 A). The reduction of rainfall by 50 % led to a significant ($P \leq 0.05$) decline in diversity within grazed plots but had no significant ($P > 0.05$) impact on diversity within fenced plots. Rainfall increment to 150 % had no significant ($P > 0.05$) impact on diversity in both grazed and fenced plots (Figure 4.7B). Vegetation dominance in fenced plots was 38.9 % higher than grazed plots ($P \leq 0.05$; 8C).

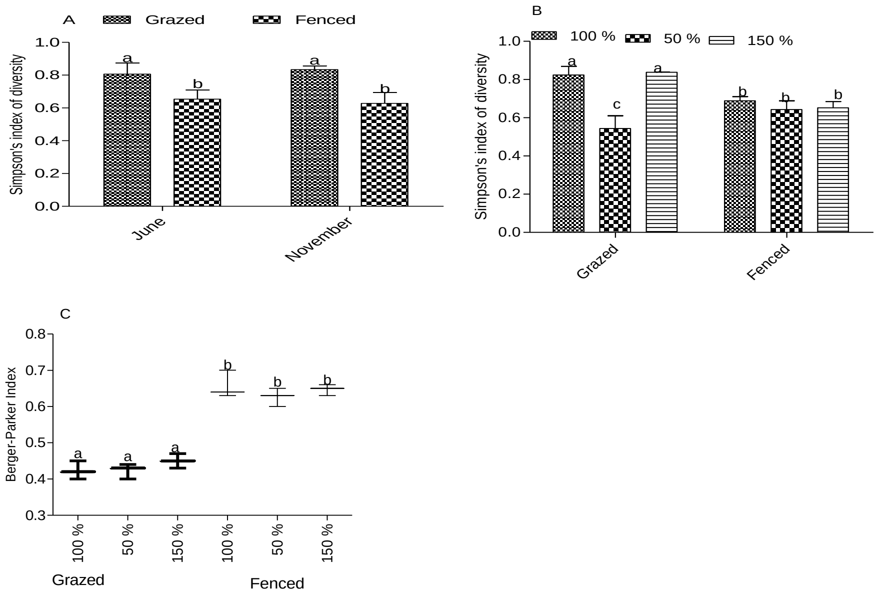

Figure 4.7: Herbaceous plant diversity within grazed and fenced plots (A). Interaction of grazing and rainfall manipulation on herbaceous plant diversity (B) and herbaceous dominance within study plots. Bars are means (±SD). Bars across plots not sharing the same letters are significantly different from each other (Tukey-LSD, $P \leq 0.05$).

4.13 Modeled Daily Herbaceous and Tree Canopy GPP

Simulated daily GPP for the herbaceous and tree canopies between January 2014 and December 2015 is shown in Figure 4.8. The mean daily GPP for tree canopies were not significantly ($P = 0.071$, $F= 3.67$) different between grazed (4.31 ± 0.49 g C m $^{-2}$ d) and fenced plots (4.78 ± 0.51 g C m $^{-2}$ d). The average daily herbaceous GPP in the grazed (6.42 ± 1.21 g C m $^{-2}$ d) and fenced plots (8.97 ± 1.11 g C m $^{-2}$ d) were significantly ($P < 0.0001$, $F = 68.16$) different. On average, the total ecosystem GPP day (sum of herbaceous and tree vegetation) in the grazed and fenced plots were 10.73 ± 1.7 g C m^{-2} d^{-1} and 13.75 ± 1.62 g C m^{-2} d^{-1} respectively. The contribution of herbaceous vegetation to the total ecosystem GPP$_{day}$ was 59.9 % and 65.3 % in the grazed and fenced plots respectively. The contribution of the tree layer to the total ecosystem GPP was 40.1 % and 34.7 % in the grazed and fenced plots respectively. Seasonal fluctuations in tree GPP was less variable over the course of the study in comparison to the herbaceous GPP. There were slight decreases in tree GPP at the onset of dry seasons, especially in January. The daily herbaceous canopy GPP exhibited a double peak pattern that coincided with wet seasons between April-May and September-November. During wet season, herbaceous canopy GPP rates were two fold higher than in the tree vegetation. During the dry seasons, however, the herbaceous vegetation daily GPP dropped significantly compared to trees.

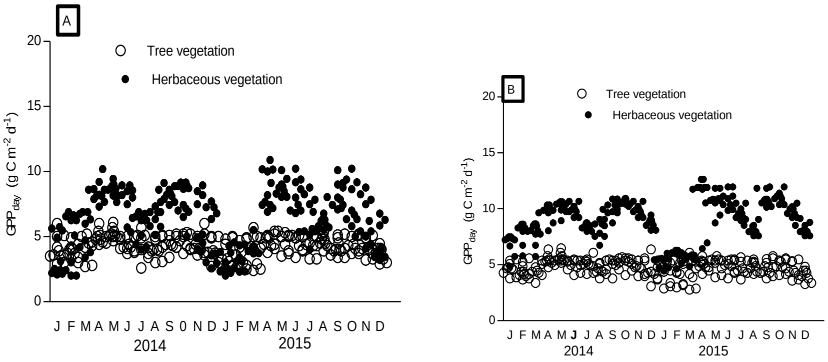

Figure 4.8: Modeled daily gross primary production (GPP) of the herbaceous and tree canopies between January 2014 and December 2015 within Grazed (A) and Fenced (B) plots.

4.14 Tree Canopy Conductance and Canopy transpiration within Grazed and Fenced Plots

Tree canopy transpiration (Ec) was linearly and positively correlated with VPD in both grazed ($r^2 = 0.64$) and fenced plots ($r^2 = 0.74$) (Figure 4.9 a and b) whereas canopy conductance was linearly and negatively correlated with VPD in both grazed ($r^2 = 0.78$) and fenced plots ($r^2 = 0.63$) (Figure 4.9 c and d).

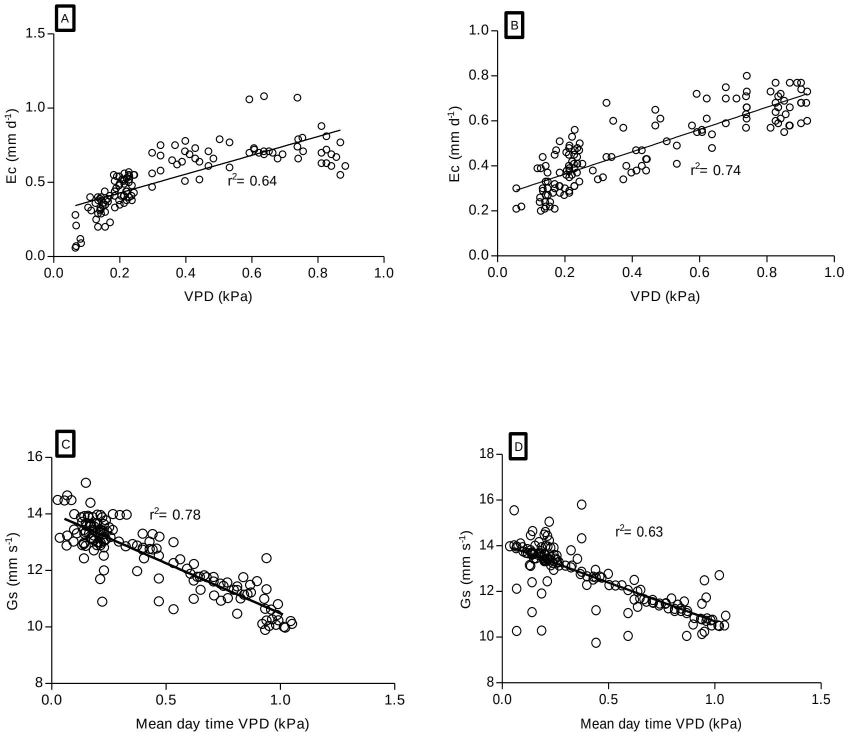

Figure 4.9: Response of tree canopy transpiration (Ec) within grazed (A) and fenced (B) plots and canopy conductance (Gc) within grazed (C) and fenced (D) plots to changes in water deficit during the day.

CHAPTER FIVE

DISCUSSION

5.1 Influence of Livestock Grazing and Rainfall Variability on Herbaceous CO_2 Exchange

This study results showed a significant ($P \leq 0.05$) decrease in herbaceous GPP, R_{eco}, and NEE as a result of livestock grazing (Figure 4.5 and 4.6). Liu *et al*., (2016) reported a similar decline in CO_2 assimilation and release in a Chinese rangeland. The reduction in CO_2 uptake reported in this study is a result of reduced photosynthetically-active biomass (Table 4.4) due to harvesting by the feeding livestock. Studies conducted in African grazed savannas and semiarid grasslands have shown strong relationships between GPP, NEE, and the aboveground green biomass (Sjögersten *et al*., 2008; K'Otuto *et al.,* 2012; Nakano and Shinoda, 2015). Through the reduced photosynthetic surface area, there is reduced carbon assimilation and consequent translocation to the roots resulting in lower microbial activity and hence reduced R_{eco} (Ondier *et al*., 2019a; Tessema *et al*., 2020). The results of this study are in agreement with reports from other African savannas (Ciais *et al*., 2011; Tagesson *et al*., 2015; Räsänen *et al*., 2017). A study by Susiluoto *et al*., (2008), which used similar methodology as this study in monitoring CO_2 exchange in a Finnish National Park, revealed that grazing had no influence (neutral impact) on ecosystem CO_2 exchange. The findings were explained by the fact that grazing increased vegetation heterogeneity resulting in varying carbon fluxes among the different plant functional groups. Other studies, however, revealed that urine and faecal matter from grazers contribute to higher ecosystem CO_2 exchange because the faecal matter stimulate plant growth, microbial activity and increase the labile carbon and nitrogen (Jiang *et al*., 2012; Ritchie, 2020). Moreover, grazing can increase ecosystem photosynthesis and respiration by stimulating development of new leaves with higher photosynthetic capacity (K'Otuto *et al*., 2012).

The response of ecosystem CO2 exchange to grazing is ecosystem-dependant and a function of other interacting environmental variables such as availability of soil moisture and herbaceous species composition. The interaction of livestock grazing and rainfall reduction led to a significant ($P \leq 0.05$) decrease in herbaceous GPP, NEE and R_{eco}, by 22.5 %, 33% and 39% respectively. The results are linked to the imposition of drought by grazing which exposes the soil to water loss and rainfall reduction that further amplifies drought conditions. Plant response to drought conditions is through restriction of stomatal conductance, resulting in reduced CO_2 exchange (Cardoso *et al*., 2015; Tessema *et al*., 2020). These results were not unexpected since water is a major factor influencing ecosystem CO_2 fluxes in savannas and other grasslands (Polley *et al*., 2010; Otieno *et al*., 2015). The interactive influence of grazing and rainfall increment resulted in a significant increase in GPP and NEE, this further confirms the significant role of water in driving carbon exchange in this grazed ecosystem, however, the interaction of grazing and rainfall increment had no significant influence on R_{eco}. Since R_{eco} is linearly dependant on soil temperature (Räsänen *et al*., 2017), it is possible that the increase in water moderated soil temperature resulting in neutral influence R_{eco}. Therefore, CO_2 exchange within the grazed plots do not always respond directly or proportionately to rainfall variation (increase or decrease); either because of nonlinearity in soil moisture recharge in response to rainfall manipulation; or because of the variation in environmental factors such as temperature, which modify CO_2 response to soil moisture availability.

5.2 Influence of Livestock Grazing on Herbaceous Diversity

Higher species diversity in the grazed plots (Figure 4.7A and B) is a result of reduced vegetation dominance (Figure 4.7C). Decreased dominance of vegetation can be linked to improved availability of resources, such as light, nutrients, and water. With the enriched resources, diversity is often improved through the proliferation of less common species, colonisation of new species and/or a decrease in local species extinctions (Olff and Ritchie, 1998). By feeding and trampling on dominant vegetation, grazers alter the competitive interactions within the herbaceous layer by reducing the vigour and presence of dominant plants, consequently enabling the establishment of less competitive species, which in the long run increases diversity (Pekin *et al*., 2014). During grazing, cattle may introduce new plant propagules in the environment through their droppings; these propagules later grow into new vegetation and improve diversity within the savanna (Fynn *et al*., 2016). Grazing disturbance of herbaceous canopies likely increase plant diversity by promoting colonization of ruderal species (Huston, 1979; Bakker *et al*., 2006). Grazing also promotes the growth of forb species leading to a relatively high species-rich community in semiarid savannas (Jacobs and Naiman, 2008). The findings of this study, which point to a positive relationship between livestock grazing and plant diversity is in agreement with other studies in savannas in Africa and other rangelands (Hanke *et al*., 2014; Hempson *et al*., 2017). The results of this study, however, contradict previous studies that examined less productive savannas with mean annual rainfall of less than 600 mm (Lechmere-Oertel et al., 2005; Rutherford and Powrie, 2013; Scott-Shaw and Morris, 2015). One possible interpretation of these contradictory results is that grazing has a positive influence on herbaceous diversity only in productive ecosystems with mean annual rainfalls of greater than 600 mm. For example, the Lambwe plots on which this study was conducted lie on a humid savanna, with a mean annual rainfall of about 1,100 mm (Figure 4.1). In unproductive ecosystems with limited soil resources, grazing reduces plant diversity by eliminating rare palatable species through direct feeding and by trampling on plants, which often do not recover from such impacts (Lezama *et al*., 2014).

In this experiment, fencing reduced animal disturbance and allowed a few species to develop large local populations with more biomass (Table 4.4 and Figure 4.7C), i.e., become dominant. The dominant vegetation in the fenced plots out-competed other less colonising species for canopy resources (i.e light) (Thirgood, 2009). A considerable number of species with lower competitive abilities reduce their densities or diminish within plant communities as competition for light resources and nutrients increases (Van der Plas *et al.*, 2013). This is in agreement with competitive exclusion theory which states that at high levels of biomass, dominant species tend to out-compete other species for resources (Grime, 1973; Jacobs and Naiman, 2008). Competitive exclusion leads to the dominance of a few species and causes an increase in spatial homogeneity and a decrease in species diversity. Additionally, higher levels of dead biomass accumulation in the fenced plots (Table 4.4) may be the reason for lower diversity within the plots. Accumulated litter may limit seedling emergence and growth with regard to forming a mechanical barrier, reducing the light radiation to the soil surface or possibly releasing toxic secondary metabolites that ultimately lower diversity (Zhu *et al.*, 2012; Xiong *et al.*, 2016). These results are in agreement with several studies in African savannas, which have found that exclusion of grazing has negative impacts on herbaceous plant diversity through the build-up of biomass and promotion of coloniser or competitive species (Jacobs and Naiman, 2008; Hanke *et al.*, 2014; Van Coller and Siebert, 2014).

5.3 Interactive Effect of Livestock Grazing and Variability on Herbaceous Species Diversity

Grazing and soil water are likely the key drivers of species change in grazed savannas and other similar ecosystems (Bat-Oyun *et al.*, 2016). In this study, the reduction of rainfall by fifty percent led to a decrease in species diversity in grazed plots (Fig 4.7.B). The results may be a consequence of direct and indirect effects of both the abiotic (rainfall manipulation, i.e. reducing ambient rainfall) and biotic (grazing) factors. As reduced rainfall treatment decreased rather than increased resources, a reduction in diversity could be expected which is consistent with observations in low productivity ecosystems (Yan *et al*., 2015). Grazing in water-limited environments tends to increase plant mortality and ultimately decrease species richness and diversity (Proulx and Mazumder, 1998; Fynn and O'Connor, 2000). Grazing reduces vegetative biomass and exposes soil to direct radiation and, therefore, warming which is further amplified by the reduction in rainfall. Such warming negatively impacts diversity either directly through species-specific physiological responses, such as heat stress (Klein *et al*., 2014), or through ecological factors such as altered species interactions (Farrer *et al*., 2014).

At lower soil moisture levels, stimulated by reducing ambient rainfall in grazed plots, biodiversity was predicted to decrease due to herbivore grazing and an increase in dominance by drought tolerant species; together, these two factors may reduce colonisation rates or enhance extinction of species which are less tolerant to grazing and low moisture levels (Olff and Ritchie, 1998; Bat-Oyan *et al*., 2016). Rainfall manipulation had no significant impact on herbaceous diversity within fenced plots (Fig. 4.8B). This response points to the fact that the altered ambient rainfall in our fenced plots did not significantly change soil moisture levels to the extent that it would elicit change in plant diversity. Fencing improves soil macro-aggregation, which prevents water loss and ensures adequate soil moisture supply irrespective of the rainfall treatment. One possible explanation of the results is that species in the fenced plots are inherently less sensitive to the rainfall manipulations as used in this study. The mechanisms of species change might, therefore, be largely site-specific.

5.4 Impacts of LIvestock Grazing and Rainfall Variability on Characteristics of Herbaceous Layer

The composition of herbaceous vegetation varied considerably within the study sites irrespective of rainfall treatment (Table 4.1 and 4.3), which characterises the heterogeneity of Lambwe valley (Allsopp and Baldry, 1972; Ondier et al., 2019b). Spatial variation in the composition of herbaceous species may be attributed to the ability of individual species to adapt to local and edaphic conditions (Augustin, 2003; Silva *et al*., 2013), which are different within the study sites (Otieno *et al*., 2011). It is possible that the lower vegetation dominance in the grazed plots (Fig. 8C) was as a result of reduced competition for light, allowing different species to flourish. Grazing at moderate intensities depresses the vigor and presence of dominant species, enabling colonisation by less competitive species with an overall increase in diversity (Kikoti and Mlingo, 2015). These results are similar to the findings of Zerbo *et al.*, (2016) that linked grazing to the reduction in vegetation dominance in West African savanna ecosystems. The results of this study reveal an abundance of palatable species (Table 4.1). Moreover, perennial species dominated all plots irrespective of the rainfall treatment (Table 4.3). The higher dominance of palatable species within the plots can be attributed to a decline in selective grazing which minimises overconsumption of palatable plants. Since the abundance of palatable species appears to be an indicator of moderate grazing (Ren *et al*., 2012), this study concludes that grazing within our plots is within a sustainable range that does not necessarily lead to ecosystem degradation. The interaction of livestock grazing and rainfall manipulation is complex and requires additional survey campaigns to create a complete picture of its implication on the savanna structure and composition.

5.5 Productivity Responses of Trees and Herbaceous Vegetation to Rainfall Variability and Livestock Grazing

On a ground area basis, the overall daily maximum ecosystem GPP for the study area was 10.75 ± 1.44 g C m $^{-2}$ d and 13.75 ± 2.73 g C m $^{-2}$ d in the grazed and fenced plots respectively. The contribution of herbaceous vegetation to the overall ecosystem GPP_{day} was about 60 % in both grazed and fenced plots (Fig 4.8a, b). For this ecosystem a study by Otieno *et al*. (2015) reported about 70% and 30% respective contribution of herbaceous and tree canopies to the total ecosystem GPP_{day} during the wet season. Even though the study by Otieno *et al*. (2015) did not reveal the overall daily productivity for this ecosystem, it reported a higher contribution of the herbaceous canopy to the total ecosystem productivity, which is also true for this study. A study by Lloyd *et al*., (2008) on the contribution of woody and herbaceous vegetation to tropical savanna ecosystem productivity revealed a 59 % contribution of herbaceous vegetation to the ecosystem productivity. Thus, the 60 % contribution of herbaceous vegetation to the ecosystem productivity, reported for this study is comparable. Trees and herbaceous canopy cover at the measurement site in Lambwe was about 20% and 80% respectively (Otieno *et al*., 2015). The differences in the canopy cover between the two plant functional groups (herbaceous and tree vegetation) accounted for their varying contribution to the total ecosystem GPP_{day}. A greater percentage of herbaceous productivity occurred in the wet season. The higher productivity in the wet season was driven by rainfall which is a major contributor to savanna productivity (Otieno *et al*., 2015). Unlike the tree layer, the herbaceous daily GPP_{day} was highly seasonal in all plots and was largely driven by the differences in wet to dry season (Figure 4.9). The fluctuation was explained by soil moisture in the top 30 cm soil profile (Figure 4.2), which was further explained by the root distribution data (Figure 4.3), which showed that most roots of the herbaceous layer are confined within the upper 30 cm soil layer. The herbaceous daily GPP did not fully drop in the dry season, an indication that despite periods without rainfall, soil moisture in this savanna remains above the threshold that can support high productivity in the herbaceous vegetation. It could be speculated that the dry season contribution of herbaceous daily GPP was most likely due to the utilisation of soil moisture brought to the surface through hydraulic lifting by adjacent trees. Another reason could be that the dominant species, taking advantage of the senescent grasses to gain biomass in the early dry season between January –February and July-August (Werner, 2012).

The lower variability in mean daily tree GPP in comparison to herbaceous daily GPP over the course of the study was related to the rooting patterns of the two vegetation types. The herbaceous roots were confined within the shallow 40 cm soil depth while those of trees were both located in the shallow 40 cm depth and beyond (> 40 cm depth). The presence of tree roots beyond 40 cm soil depth is an indication of continued/maintained access to soil moisture reserves in the deeper soil layers compared to the herbaceous vegetation, especially during drought. This confirms the sustained productivity of the tree layers during drought as compared to herbaceous vegetation. These findings are in agreement with a study by Beringer *et al*. (2007), which revealed that tree GPP has a modest inter annual variability, with dry season productivity maintained by available soil moisture sourced from deep soil layers (Paquette *et al*., 2015). Paquette *et al*. (2015) confirmed the existence of tree roots down beyond 0.4 m soil depth which is also true for this study (Figure 4.3). Despite the availability of deep roots that could extract deeper underground waters and sustain productivity during the dry seasons, there were slight linear decreases in tree GPP from the onset of dry seasons that could be attributable to either stomatal closure or reduced leaf canopy area (Zenes *et al*., 2020). For this study, trees closed their stomata leading to a reduction in Gs at higher VPD (Figure 4.9), and reduced their leaf canopy area through leaf shedding (personal observation). Given that a proportion of the studied tree species within our plots are semi deciduous, which drop foliage during dry seasons, the observed slight seasonal variability in tree GPP is likely as a result of the loss of photosynthetic leaf area. Other than loss of leaf area, savanna tree overall growth slows in dry season and prioritise starch storage (Rossatto *et al*., 2009; Wakeling *et al*., 2012). Hence, growth occurring during this period is likely redirected from biomass accumulation to starch reserves, to help replace damaged foliage after dry season (Beringer *et al*., 2007). *Acacia ancistroclada* and *Comberatum molle* also flower and fruit in the dry season, which would redirect carbon allocation from biomass accumulation to flowering and fruiting.

Livestock grazing significantly reduced herbaceous daily GPP by about 25 % but had insignificant influence on daily tree GPP (Figure 4.8). The observation on herbaceous GPP is explained by the reduction in herbaceous photosynthetic-active biomass due to feeding by grazing animals. This is especially true since studies have shown a strong relationship between GPP and the aboveground herbaceous biomass (Sjögersten *et al*., 2008; Liu *et al*., 2016). Through reduced photosynthetic surface, there is reduced carbon translocation to the roots resulting in lower microbial activity and hence reduced GPP (Zhou *et al*., 2008). This study finding on the impact of livestock grazing on herbaceous productivity are in agreement with reports from other savannas in Africa (Ciais *et al*., 2011; Tagesson *et al*., 2015; Rasanen *et al*., 2017). This study revealed a linear increase in daily Ec with increasing VPD that tended to saturate at VPD> 1kPa (Figure 4.9). This characteristic stringent stomatal regulation by the trees has a direct impact on productivity. Since VPD and stomata regulations have an influence on tree CO_2 uptake, and hence, productivity, the results of this study suggest that the trees were more affected by VPD than grazing. Similar to results of this study (Figure 4.8), evidence suggest that stomatal conductance declines under high VPD and transpiration increases in most species up to a given threshold, leading to a cascade of subsequent impacts including risk of carbon starvation, reduced GPP, and hydraulic failure. This kind of stomata regulation is displayed by isohydric tree species and has significant impact on tree survival under climate change scenario.

CHAPTER SIX

CONCLUSIONS, RECOMMENDATIONS AND SUGGESTIONS FOR FUTURE RESEARCH

6.1 Conclusions

Both independent and interactive effects of livestock grazing and rainfall manipulation alter herbaceous CO_2 exchange, herbaceous diversity and composition through their impact on biomass growth and development, soil bulk density, soil moisture and soil nutrient. The decline in herbaceous CO_2 exchange and productivity following reduction in rainfall within grazed plots was as a result of reduction of photosynthetic biomass through harvesting by feeding animals and drought imposed through rainfall reduction. The increase in GPP and NEE following the interaction of grazing and rainfall increment confirms the role of water in driving carbon exchange in this grazed savanna.

Livestock grazing enhanced species diversity in the herbaceous layer through reduction in species dominance. The interaction of grazing and rainfall reduction reduced species diversity, consequence of plant mortalities induced by direct feeding by grazing animals and induced drought (rainfall reduction). The insignificant impact of increased rainfall on species diversity within this grazed savanna points to the fact that rainfall reduction has more impact on diversity changes than rainfall increment. The mechanisms of species change is, therefore, site specific and vary significantly in water limited ecosystems than in ecosystems with adequate soil moisture supply.

The lower variability in mean daily tree GPP in comparison to herbaceous GPP over the course of the study period was linked to differences in rooting patterns of the two vegetation types. The presence of tree roots beyond 40 cm soil depth enabled continued access of soil water within the stable aquifers. The access to the belowground aquifers by tree roots ensured maintenance of productivity even during dry periods. The variability of herbaceous mean daily GPP over the course of the study period confirmed the role of seasonal soil moisture availability in driving productivity of the vegetation type. This is because soil moisture in the shallow 30 cm soil profile that is accessed by herbaceous vegetation is highly seasonal. This study made the first attempt to integrate productivity of herbaceous and tree vegetation under livestock grazing and rainfall variability. The herbaceous layer had a larger contribution to the overall ecosystem productivity in comparison to the tree layer. This was linked to differences in percentage vegetation cover between trees (20 %) and herbaceous (80 %) vegetation. The differences in productivity responses between trees and herbaceous vegetation to livestock grazing and seasonal soil moisture changes was linked to the differential rooting depth of the two vegetation types. The deep rooting system of the tree layer enabled access and extraction of deep stable waters for maintenance of productivity, including during drought periods. The results provide an empirical support for the occurrence of competitive advantage of trees over the herbaceous vegetation under increased grazing and may be used to parameterize future interactions of plants in the savanna.

6.2 Recommendations

Livestock grazing within the study plots is within sustainable range that does not necessarily lead to ecosystem degradation. The current animal stocking rate of 7.4 animal units hac^{-1} should therefore be maintained.

A rigorous study focusing on productivity responses of dominant herbaceous vegetation to the interaction of grazing and rainfall variability should be carried out to point out the responses of key species to the environmental alterations. It should include establishing an increased number of large enclosures and open grazed plots for increased data accuracy.

A meta-stable coexistence between trees and herbaceous vegetation has been confirmed in this ecosystem and has been attributed to the variations in rooting depth between the vegetation types. However, the seasonal variability of herbaceous productivity confirmed that soil moisture is a significant driver of herbaceous productivity in this ecosystem.

6.3 Suggestions for Future Research

Future research in this ecosystem should include grazing intensity as a factor that would influence biomass development, species change and productivity of the herbaceous layer.

Future research should investigate on hydraulic lift of savanna trees to determine the facilitative role of the dominant tree vegetation in the determination of herbaceous productivity under the environmental change scenario.

For accurate determination of ecosystem productivity, future research should employ, in addition to the manual chamber measurement, eddy covariance technique. The results from the two carbon measurement methods can be used for accurate partitioning of both tree and herbaceous productivity which could be more accurate than modelling.

REFERENCES

Adiku, S., Reischstein, M., Lohila, A., Dinh, N., Aurela, M., Laurila, T. and Tenhunen, J. (2006). PIXGRO: a model for simulating the ecosystem CO_2 exchange and growth of spring barley. *Ecology Models*, 190: 260-276.

Agnew, A. and Agnew, S. (1994). Upland Kenya Wild Flowers. A flora of Ferns and Herbaceous Flowering Plants of Upland Kenya. 2nd Edition, East African Natural History, Nairobi, Kenya.

Allsopp, R. and Baldry, T. (1972). A general description of the Lambwe Valley area of South Nyanza District, Kenya. *World Health Organisation Bulletin*, 47: 691-697.

Anderson, R.A., Fralish, J.S. and Baskin, J.M. (1999). Savannas barrens and rock outcrops plant communities of North America. *Cambridge University Press.*

Andrew, M., Ruthrof, K., Matusick, G. and Hardy, G. (2016). Spatial configuration of drought disturbance and forest gap creation across environmental gradient. *PLoS ONE*, 11: 321-341

Arnhold, S., Otieno, D., Onyango, J., Koeller, T., Huwe, B and Tenhunen, J (2015). Soil properties along a gradient from hillslopes to the savanna plains in the Lambwe Valley, Kenya. *Soil and Tillage Research*, 154: 75-83.

Asha, A., Corfield, J., Mclvor, J. and Ksiksi, T. (2011). Grazing management in tropical savannas: utilization and rest strategies to manipulate rangeland conditions. *Rangeland Ecology and Management*, 64: 223-239.

Augustine, D.J. and McNaughton, S.J. (2006). Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems*, 9: 1242-1256.

Augustine, J. (2003). Spatial heterogeneity of herbaceous layer of a semi-arid savanna ecosystem. *Plant Ecology*, 167: 319-332.

Bakker, E., Ritchie, M., Olff, H., Milchunas, D. and Knops, J. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, 9: 780-788.

Bat-Oyan, T., Shinoda, M., Cheng, Y. and Purevdorj, Y. (2016). Effect of grazing and precipitation variability on vegetation dynamics in a Mongolian dry steppe. *Journal of Plant Ecology*, 9: 508-519.

Baudena, M., D’ Andrea, F. and Provenzale, A. (2010). An idealised model for tree-grass coexistence in savannas: the role of life stage structure and fire disturbances. *Journal of Ecology*, 98: 74-80.

Baudena, M., Dekker, S., Bodegom, P., Cuesta, B., Higgins, S., Lehsten, V., Reick, C., Rietterk, M., Yin, Z., Zavala, M. and Brovkin, V. (2015). Forests, savannas, grasslands: bridging the knowledge gap between ecology and Dynamic Vegetation Models. *Biogeosciences*, 12: 1833-1848.

Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Korner, C., Hans de Boeck., Christensen, J., Leuzinger, S., Janssens, I. and Hansen, K. 2012. Precipitation manipulation experiments-challenges and recommendations for the future. *Ecology Letters*, 15: 899-911.

Belsky, A. and Canham, C. (1994). Forest gaps and isolated savanna trees. *BioScience*, 44: 77–84.

Beringer, J., Hutley, B., Tapper, J. and Cernusak, A. (2007). Savanna fires and their impacts on net ecosystem productivity in North America. *Global Change Biology*, 13: 990-1004.

Berry, R. and Kulmatiski, A. (2017). A savanna response to precipitation intensity. *PLoS ONE*, 12: 1-18

Bestelmeyer, T., Okin, G., Duniway,M., Archer, S.,Sayre,N., Williamson,J. and Herrick, J. (2015) Desertification, land use, and the transformation of global drylands. *Frontiers in Ecology and the Environment*, 13: 28–36.

Bombelli, M., Henry, S., Castsldi, S., Adu-Bredu, S., Arneth, A., Grandcourt, A., Grieco, E., Kutsch, W., Lehsten, V., Rasile, A., Reichstein, M., Tanley, K., Waber, U. and Valentine. R. (2009). An outlook on the sub-Saharan Africa carbon balance. Biogeosciences, 6: 2195-2205.

Bond, W., Toit, J. and Malherbe, J. (2020). Special issue: drought in South African savannas. *African Journal of Range and Forage Science*, 37: 1-4.

Bonham, C. (1989). Measurements for terrestrial vegetation. John Wiley and Sons, New York, USA.

Boonman, J. (1993). East Africa’s grasses and fodder: Their ecology and Husbandry. Kluwer Academic Publishers.

Brunner, I., Herzog, C., Dawes, M., Arend, M. and Sperisen, C. (2015). How tree roots respond to drought. Review. *Frontiers in Plant Science*. 6: 547-561.

Buitenwerf, R., Swemmer, A. and Peel, M. (2011). Long-term dynamics of herbaceous vegetation structure and composition in two African savanna reserves. *Journal of Applied Ecology*, 48: 238–246.

Callaway, M. (2007). Positive interactions and interdependence in plant communities.

Cardosso, J., Pinade, M., Jimenez, J., Vergara, M., and Rao, I. (2015). Catastrophic strategies to cope with drought conditions by two tropical forage C4 grasses. *AoB Plants*. 7: 1-15

Carvalho, P., Anghinoni, I., Moraes, A., Damacena de Souza, E., Fontaneli, R. and Bayer, C. (2010). Managing grazing animals to achieve nutrient cycling and soil improvement in a non till integrated systems. *Nutrient Cycling in Agroecosystems*, 88: 259-273.

Case, M., Wigley-Coetsee, C., Nzima, N., Scoging, P. and Staver, A. (2019). Severe drought limits trees in a semi-arid savanna. *Ecology*. 100: 284-298.

Casper, B., Schenk, H. and Jackson, R. (2003). Defining a plant’s belowground zone of influence. *Ecology*, 84: 2313–2321.

Ciais, P., Bombelli, A., William, M., Piao, S., Chave, C., Ryan, M., Henry, M., Brender, P. and Valentine, R. (2011). The carbon balance of Africa: synthesis of recent research studies. *Philosophical Transactions of the Royal Society of America*, 369: 2038-2057.

Ciais, P., Piao, S.L., Cadule, P., Friedlingstein, P. and Ch'din, A. (2009).Variability and recent trends in the African terrestrial carbon balance. *Biogeosciences*, 5: 3497-3532.

D Odorico, P., Caylor, K., Okin, G. and Scanlon. T. (2007). On soil moisture-vegetation feedbacks and their possible effects on dynamics of dryland ecosystems. *Journal of Geophysical Research*, 112: 219-231.

DeAngelis, D. and Waterhouse, J. (1987). Equilibrium and non-equilibrium concepts in ecology models. *Ecological Monographs*, 57: 1-21.

DeLonge, M. and Basche, A. (2018). Managing grazing land to improve soil and promote climate change adaptation and mitigation: A global sysnthesis. *Renewable Agriculture and Food Systems*, 33: 267-278.

Deng, H., Yin, Y. and Han, X. (2020). Vulnerability of vegetation activities to drought in central Asia. *Environmental Research Letters,* 15:1-13.

Djagbletey, E., Logah, V., Mensah, N. and Tuffor, H. (2018). Carbon stocks in the Guinea savanna of Ghana. Estimates from the protected areas. *Biotropica*, 0: 1-9.

Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor,K and Hanan, P. (2013). Tree effects on grass growth in savannas: Competition, facilitation and the stress gradient hypothesis. *Journal of Ecology*, 101:202–209.

Droesler, M. (2005). Trace gas exchange of bog ecosystems, Southern Germany. Lehrstuhl fur vegetationsokoloie. Doctoral Thesis. Technical University of Munich. http://www.wzw.tum.de/vegoek/publikat/dissdipl.html.

Edwards, E. and Walker, A. (1983). C3, C4: Mechanism and Cellular and Environmental Regulation of Photosynthesis. Blackwell Scientific Publications, Oxford.

Ellis, J. and Swift, D. (1988). Stability of African pastoral ecosytems: alternate paradigms and implications for development. *Journal of Range Managements*, 41: 450-459.

Engelbrechcht, B. and Kursar, T. (2003). Comparative drought resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, 136: 383-393.

Ewers, B., Mackay, D., Growes, S., Ahl DE., Burrows, S. and Samanta, S. (2002). Tree species effects on stand transpiration in northern Wisconsin. *Water Resource Research*, 38: 218-228

Farquhar, D. and Caemmerer, S. (1982). Modeling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PS, Osmond CB, Ziegler H(eds) *Physical Plant Ecology* II, 12/B. Springer, Berlin. Page 549-587.

Farrer, E., Ashton, J. and Suding, N. (2014). Separating direct and indirect effects of global change: a population dynamic modelling approach using readily available field data. *Global Change Biology,* 20: 1238-1250.

February, E and Higgins, S. (2010). The distribution of tree and grass roots in savannas in relations to soil nitrogen and water. *South African Journal of Botany*, 76: 517-523.

February, E., Higgins, S., Band, W. and Swemmer, L. (2013). Influence of completion and rainfall manipulation on the growth and responses of savanna trees and grasses. *Ecology*, 94: 1155-1164.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling. C. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, 35: 557–581.

Food and Agricultural Organisation of the United Nations (FAO), (2006). Guidelines for Soil Description, 4th Edition. United Nations, FAO, Rome.

Food and Agricultural Organisations of the United Nations, Rome, (2004). Assessing carbon stocks and modelling win-win scenarios of carbon sequestration through land use changes.

Franz, T., Caylor,K., Nordbotten, J., Rodriguez, I. and Celia, M. (2010). An ecohydrological approach to predicting woody species distribution patterns in dryland ecosystems. *Advances in Water Resources*, 33: 215-230.

Fynn, R., and O Connor, T. (2000). Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semiarid savanna, South Africa. *Journal of Applied Ecology*, 37: 491-507.

Fynn, S., Augustine, J., Peel, S. and Michael de Garine-Wichatitsky. (2016). Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife-livestock coexistence- A review. *Journal of Applied Ecology*, 53: 388-397.

Ganjurjav, H., Duan, M., Wan, Y., Zhang, W., Gao, Q., Li, Y., Juangcun, W., Danjiu, L. and Guo, H. (2015). Effects of grazing by large herbivores on plant diversity and productivity of a semi-arid alpine steppe on the Qinghai-Tibetan Plateau. *The Rangeland Journal*, 37: 389-401.

Geiβler, K., Heblack, J., Uugulus, S., Wanke, H. and Blaum, N. (2019). Partitioning of water between differently sized shrubs and potential ground water recharge in a semiarid savanna in Namibia. *Frontiers in Plant Science*, 10: 1411-1430.

Gilmanov, G., Soussana, J., Aires, L., Allard, V., Amman, C., Balzarolo, M., Barcza, Z., Bernhofer, C., Tuba, Z., Valentini, R., William, M. and Wolfahrt, G. (2007). Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agricultural Ecology and Environment*, 121: 93-120.

Goheen, J., Palmer, T., Keesing, F., Reginos, C. and Young, T. (2010). Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology*, 79: 372-382.

Grace, J., Jose, S., Meir, P., Miranda, H. and Montes, R.A. (2006). Productivity and carbon fluxes of tropical savanna. *Biogeography,* 33: 387-400.

Grainer, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology,* 3: 309-320.

Grime, J. (1973). Competitive exclusion in herbaceous vegetation. *Nature,* 242: 344-347.

Hanke, W., Bohner, J., Dreber, N., Jurgen, N., Schmiedel, U., Wesuls, D. and Dengler, J. (2014). The impact of livestock grazing on plant diversity: an analysis across dryland ecosystems and scales in South Africa. *Ecological Applications,* 24: 1188-1203.

Harley, P. and Tenhunen, J. (1991). Modeling the photosynthetic response of C_3 leaves to environmental factors. In: Boote, KJ, Loomis RS (eds) Modeling crop photosysnthesis-from biochemistry canopy. *Crop Science Society of America Anaheim*, Page 17-39.

Harrison, S., and La Forgia, M. (2019). Seedling traits predict drought-induced mortality linked to diversity loss. *PNAS*, 116: 5576-5581.

Hempson, G., Archibald, S. and Bond, W. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports,* 7: 1719-1927.

Higgins, S.I., Scheiter, S. and Sankaran, M. (2010). The stability of African savannas: insight from the direct estimation of the parameters of dynamic model. *Ecology*, 91: 1682-1692.

Hill, M. and Southworth, J. (2016). Anthropogenic change in savanna and associated forest biomes. *Journal of Land Use Science,* 11: 1-16.

Hirota, M., Holmgren, M., Van Nes, E and Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, 334:232–235.

Hoover, D., Knapp, K. and Smith, D. (2014). Resistance and resilience of grassland ecosystem to climate extremes. *Ecology*, 95: 2646-2656.

Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist*, 113: 81-101.

Intergovernmental Panel on Climate Change. (2007a.) Impacts, adaptations and vulnerability contributions of working group II to the fourth assessment report of the IPCC. Cambridge, Uk.

Intergovernmental Panel on Climate Change. (2007b). The physical basis contributions of working group1 to the fourth assessment report of the IPCC. Cambridge University Press, Cambridge, Uk.

Jacobs, S. and Neiman, R. (2008). Large African herbivores decrease herbaceous plant biomass while increasing plant species richness in a semiarid savannah toposequence. *Journal of Arid Environments*, 72:891-903.

Ji, L. and Peters, A. (2003). Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote sensing of environment*, 87: 1555-1570.

Jiang, Y., Tang, S., Wang, C., Zhou, P., Tenuta, M., Han, G. and Huang, D. (2012). Contribution of urine and dung patches for grazing sheep to methane and carbon dioxide fluxes in an inner Mongolian desert grassland. *Journal of Animal Science*, 25: 207-212.

K' Otuto, G., Otieno, D., Seo, B., Ogindo, H. and Onyango, J. (2012). Carbon dioxide exchange and biomass productivity of the herbaceous layer of a managed tropical savanna ecosystem in western Kenya. *Journal of Plant Ecology*, 6: 286-297.

K'Otuto, G. (2014). Effects of Agroecosytems on carbondioxide exchange and carbon storage in the herbaceous layer of a moist savanna ecosystem in Ruma, Lambwe valley, Kenya. Maseno University, Kenya. (PhD. Thesis). Maseno University, Kenya.

Kenya, Republic of Kenya (1981). Kenya Population Census, 1979, volume 1. Ministry of Economic Planning and Development. Central Bureau of Statistics. Government Printers, Nairobi, Kenya. Page 326.

Kenya, Republic of Kenya (2019). Kenya Population Census 2019 volume 1. Ministry of Economic Planning and Development. Central Bureau of statistics. Government Printers, Nairobi, Kenya. Page 28-37.

Kgosikoma, E., Mojeremane, E. and Harvie, B. (2013). Grazing management systems and their effects on savanna ecosystems dynamics. A review. *Journal of Ecological and Natural Environments,* 5: 88-94.

Kgosikoma, E., Mojeremane, W. and Harvie, B. (2015). The impact of livestock grazing management systems on soil and vegetation characteristics across savanna ecosystems in Botswana. *African Journal of Range and Forage Science,* 32: 271-278.

Kikoti, A. and Mlingo, C. (2015). Impact of livestock grazing on plant species composition in a montane forest of the northern slope of Mount Kilimanjaro, Tanzania. *International Journal of Biodiversity Science, Ecosystem Services and Management*, 11: 114-127.

Kinzig, A., Ryan, P., Etienne, M., Allison, H., Elmqvist, T. and Walker, B. (2006). Resilience and regime shifts: Assessing cascading effects. *Ecology and Society,* 11:20.

Kioko, J., Kiringe, J. and Seno, S. (2012). Impact of livestock grazing on savanna grassland in Kenya. *Journal of Arid Land*, 4: 29-35.

Klein, J., Harte, J. and Zhao, Q. (2014). Experimental warming causes large species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7: 1170-1179.

Knapp, K., Beier, D., Classen, T., Luo, Y., Reichstein, M., Smith, M., Smith, S., Bell, J., Fay, P., Heisler, J., Leavitt, S., Sherry, R., Smith, B. and Wang, E. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Biosciences*, 58: 811-821.

Knoop, W. and Walker, B. (1985). Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, 73: 235–253.

Koerner, S. and Collins, S. (2014). Interactive effect of grazing, drought and fire on grassland plant communities in North America and South Africa. *Ecology*, 95: 98-109.

Kooch, Y., Moghimian, N., Wirth, S. and Noghre, N. (2020). Effects of grazing management on leaf litter decomposition and soil microbial activities in northern Iranian rangeland. *Geoderm*a, 361:114100.

Kramer, R., Ishii, H., Carter, K., Miyazaki, Y., Cavaleri, M., Araki, M., Azuma, W., Inoue,Y. and Hara, C. (2020). Predicting effects of climate change on productivity and persistence of forest trees. *Ecological Research*, 35: 562-574.

Lechmer-Oertel, R., Kerley, G. and Cowling, R. (2005). Patterns and implications of transformation in semi-arid succulent thicket, South Africa. *Journal of Arid Environments*, 63: 459-474.

Leriche, H., Roux, X., Desnoyers, F., Benest, D., Simion, G. and Abbadie, L. (2003). Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications*, 13: 1346-1354.

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, J. and Paruelo, M. (2014). Variation of grazing induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science*, 25: 8-21.

Li, Y., Tenhunen, J., O wen, K., Schmitt, M., Bahn, M., Droesler, M., Otieno, D., Schmidt, M., Gruenwald, T., Hussein, M., Mirzae, H. and Bernhofer, C. (2008). Patterns of CO_2 exchange capacity of grassland ecosystems in the Alps. *Agricultural and Forest Meteorology*, 148: 51-68.

Liu, H., Zang, R. and Chen, H. (2016). Effect of grazing on photosynthetic features and soil respiration of rangelands in the Tianshan Mountains of North West China. *Scientific Reports*, 6: 387-398.

Lloyd, J., Bird, M., Vellen, L., Miranda, A., Veenendaal, E., Djagbletey, G., Miranda, H., Cook, H. and Farquhar, D. (2008). Contribution of wood and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Physiology*, 28: 451-468.

Ludwig, F., Dawson, T., Kroon, H., Berendse, F. and Prins, H. (2003). Hydraulic lifts in *Acacia tortilis* trees on an East African Savanna. *Oecologia*, 134: 293-300.

Ludwig, F., de Kroon, H, and Prins, H. (2004a). Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, 7:623–631.

Ludwig, F., de Kroon, H., Berendse, F. and Prins, H. (2004b). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170:93–105.

Magurran, A. (2004). Measuring biological diversity, 2nd edition. Blackwell Science Ltd, Oxford, UK.

Maitima, J., Olson, J., Mugatha, S., Mugisha, S. and Mutie, I. (2010). Land use changes, impacts and options for sustaining productivity and livelihoods in the basin of lake Victoria. *Journal of Sustainable Development in Africa*, 12: 3-15.

McNaughton, S.J. (1985). Ecology of a grazing ecosystem: The Serengeti. *Ecological Monograph*, 55: 260-294.

McNaughton, S.J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, 17: 39-65.

Mhinyane,W., Tacheba, G., Mangope, S. and Makore, J. (2008). Influence of stocking rate on herbage production, steers live mass gain and carcass price on semi-arid sweet bushveld in Southern Botswana. *African Journal of Agricultural Research*, 3: 84-90.

Mojeremane, O. and Harvie, B. (2015). The impact of livestock grazing management systems on soil and vegetation characteristics across savanna ecosystems in Botswana. *African Journal of Range and Forage Science*, 33: 271-278.

Muhonji, L., Ayisi, K., Mudongo, E., Paulus, T., Behn, K., Mokoka, M. and Linstadter, A. (2020). Disentangling drought and grazing effect on soil carbon stocks and CO_2 fluxes in a semi-arid African savanna. *Frontiers in Environmental Science*, 8: 590-610.

Mureithi, S., Verdoodt, A., Njoka, T., Gachene, K., Warinwa, F. and Ranst, E. (2014). Impact of community conservation management on herbaceous layer and soil nutrients in a Kenyan semi-arid savannah. *Land Degradation and Development*, 10: 1002-1015.

Muriuki, G., Njoka, T., Reid, R. and Nyariki, D. (2005). Tsetse control and landuse change in Lambwe valley, south western Kenya. *Agricultural Ecosystems and Environments*, 106: 99-107.

Mutuku, D., Kamiri, H., Ndafu, J., Kiama, S. and Mugo, M. (2019). Influence of vegetation cover and topography position on water infiltration, organic matter content and aggregate stability of grasslands soils in semiarid Kenya. *Advances in Agricultural Science*, 7: 1-7.

Muyekho, F., Barrion, A. and Khan, Z. (2004). A preemier on grass identification and their uses in Kenya. Development Communication Limited, Nairobi. Page 1-85.

Nakano, T. and Shinoda, M. (2015). Modeling gross primary production and ecosystem respiration in a semiarid grassland of Mongolia. *Soil Science and Plant Nutrition*, 61: 106-115.

Nguyen, T., Arndt, S. and Baker, P. (2019). Leaf Physiological Responses to Drought Stress and Community Assembly in an Asian Savanna. *Forests*, 10: 110-119.

Njoka, T., Muriuki, G., Reid, R. and Nyariki, D. (2003). The use of sociological methods to asses land use change: a case study of Lambwe valley, Kenya. *International Journal of Sociology*, 7: 181-185.

Nyongesa, M. (2010). Effects of ungulate herbivory and tree canopy on ecosystem processes in Ruma National Park, Kenya. (MSc. Thesis). Maseno University, Kenya.

Ogle, K., and Reynolds, J. (2004). Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, thresholds, and delays. *Oecologia*, 141: 282–294.

Okach, D., Ondier, J., Kumar, A., Rambold, G., Tenhunen, J., Huwe, B. and Otieno, D. (2019). Livestock grazing and rainfall manipulation alter the patterning of CO_2 fluxes and biomass development of the herbaceous community in a humid savanna. *Plant Ecology*, 220: 1085-1100.

Olff, H. and Ritchie, M. (1998). Effect of herbivores on grassland plant biodiversity. *Trends in Ecology and Evolution*, 13: 261-265.

Ondier, J., Okach, D., Onyango, J. and Otieno, D. (2019a). Influence of rainfall amount and livestock grazing on soil respiration in a moist Kenyan savanna. *African Journal of Ecology*, 58: 92-99.

Ondier, J., Okach, D., Onyango, J. and Otieno, D. (2019b). Interactive influence of rainfall manipulation and Livestock grazing on species diversity of the herbaceous layer community in a humid savannah in Kenya, *Plant Diversity*, 41: 198-205.

Otieno, D., K'Otuto, G., Jakli, B., Maina, J., Jung, E. and Onyango, J. (2011). Spatial heterogeneity in ecosystem structure and productivity in a moist Kenyan savanna. *Plant ecology*, 212: 769-789.

Otieno, D., Ondier, J., Arnhold, S., Okatch, D., Ruidsch, M., Lee, B., Kolb, A. and Onyango, J. (2015). Patterns of CO_2 exchange and productivity of the herbaceous vegetation and trees in a humid savannah in western Kenya. *Plant Ecology*, 10: 1215-1236.

Otieno, D., Wartinger, M., Nishiwaki, A., Hussain, M., Muhr, J., Borken, W. and Lischeid G. (2009). Responses of CO_2 exchange and primary production of the ecosystem components to environmental changes in a mountain peatland. *Ecosystems*, 12:590–603.

Paquette, A., Joly, S. and Messier, C. (2015). Explaining forest productivity using tree functional traits and phylogenetic information: two sides of the same coin over evolutionary scale. *Ecology and Evolution*, 5: 1774-1783.

Pekin, B., Wisdom, M., Endress, B., Neylor, B. and Parks, C. (2014). Ungulate browsing maintains shrub diversity in the absence of episodic disturbance in seasonally-arid conifer forest. *PloS ONE*, 9: 310-319.

Peng, H., Li, X., Li, G., Zhang, S., Li, L., Zhao, G., Jiang, Z. and Ma, Y. (2013). Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands China. *CATENA*, 109: 39-48.

Plaut, J., Wadsworth, W., Pangles, R., Yepez, E., McDowell, N. and Pockman, W. (2013). Reduced transpiration response to precipitation pulses precedes mortality in a pinon-juniper woodland subject to prolonged drought. *New Phytologist*, 200: 375-387.

Polley, W., Emmerich, W., Bradford, J., Slims, P., Johnson, D., Saliendra, N., Svejcar, T., Angell, R., Frank, A., Phillips, R., Snyder, Kan Morgan, J. (2010). Physiological and environmental regulation of inter-annual variability in co_2 exchange on rangelands in the Western United States. *Global Change Biology*, 16: 990-1002.

Proulx, M. and Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs nutrient rich ecosystems. *Ecology*, 79: 2581-2591.

Ren, H., Schonbach, P., Wan, H., Gierus, M. and Taube (2012). Effect of grazing intensity and environmental factors on species composition and diversity in Typical Steppe of Inner Mongolia, China. *PLoS ONE*, 7: 113-120.

Ren, H., Xu, Z., Isbell, F., Huang, J., Han, X., Wan, S., Chen, S., Wang, R., Zeng, D. and Jiang, Y. (2017). Exacerbated nitrogen limitation ends transient stimulation of grassland productivity by increased precipitation. *Ecological Monographs*, 87: 457-469.

Reynolds, J., Kemp, P., Ogle, K and Fernández, R. (2004). Modifying the “pulse reserve” paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141: 194-210.

Riginos, C. (2009). Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology*, 90: 335–340.

Risch, A. and Frank, D. (2010). Diurnal and Seasonal Patterns in Ecosystem CO_2 Fluxes and their controls in a temperate grassland. *Rangeland Ecology and Management*, 63: 61-71.

Ritchie, M. (2020). Grazing management, forage production and soil carbon dynamics. *Resources*, 9: 49-62.

Rossato, D., Hoffmann, W. and Franco, A. (2009). Differences in growth pattern between co-occurring forest and savanna trees affect the forest. *Functional Ecology*, 23: 689-698.

Rudisch, M., Nguyen, T., Li, Y., Geyer, R. and Tenhunen, J. (2015). Estimation of annual spatioal variations in forest production and crop yields at landscape in temperate climate regions. Special issue: longterm and interdisciplinary research on forest ecosystem functions: challenges at Takayama site since 1993. *Ecological Research*, 30: 279-292.

Rurtherford, C. and Powrie, W. (2013). Impacts of heavy grazing on plant species richness: A comparison across rangeland biomes of South Africa. *South African Journal of Botany*, 87: 146-156.

Räsänen, M., Aurela, M., Vakkari, V., Beukes, J., Tuovinen, J., VanZyl, P., Josipovic, M., Venter, A., Jaars, K., Siebert, S., Laurila, T., Rinne, J. and Laakso, L. (2017). Carbon balance of a grazed savanna grassland ecosystem in South Africa. *Biogeosciences*, 14: 1039-1054.

Räsänen, M., Aurela, M., Vakkari, V., Beukes, J., Tuovinen, J., VanZyl, P., Josipovic, M., Siebert, S., Laurila, T., Kalmala, M., Laakso, L., Rinne, J., Oren, R. and Katul, G. (2020). The effect of rainfall amount and timing on annual transpiration in grazed grassland. *Hydrology and Earth System Sciences*, 10: 540-651.

Sankaran, M. (2019). Drought and ecological future of tropical savanna vegetation. *Journal of Ecology*, 107: 1531-1549.

Sankaran, M. and Ratnam, J. (2013). African and Asian savannas. Encyclopaedia of Biodiversity, 1: 1-18.

Sankaran, M., Hanan, N., Scholes, R., Ratnam,J., Augustine,D., Cade, B., Gignoux, J., Higgins, S., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K., Coughenour, M., Diouf, A., Ekaya, W., Feral, C., February, E., Frost, P., Hiernaux, P., Hrabar, H., Metzger, K., Prins,H., Ringrose, S., Sea,W., Tews, J., Worden, J.and. Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, 438: 846–849.

Sankaran, M., Ratman, J. and Hannan, P. (2004). Tree-grass coexistence in savannas revisited-insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, 7:480-490.

Sastry, A., Guha, A. and Barua, D. (2018). Leaf thermotolerance in dry tropical forest tree species: relationships with leaf traits and effects of drought. *AoB PLANTS*, 10: 1-13.

Scheffer, M., Carpenter, S., Foley,J., Folke, C. and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413: 591–596.

Scheiter, S., and Higgins,S. (2007). Partitioning of root and shoot competition and the stability of savannas. *The American Naturalist*, 170: 587–601.

Schieltz, M. and Rubenstein, I. (2016). Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environmental Research Letters*, 11:1130- 1142.

Schoener, T. (1974). Resource partitioning in ecological communities. *Science*, 185:27–39.

Scholes, J. and Walker, H. (1993). An African savanna. Synthesis of the Nylsvley study. Cambridge University Press, United Kingdom.

Scholes, R. and Archer, S. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28: 517–544.

Schoonover, J. and Crim, J. (2015). An introduction to soil concepts and role of soils in watershed management. *Journal of Contemporary Water Research and Education*, 154: 21-47.

Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V. and Bauhas, J. (2020). Quantifying growth responses of trees to drought-a critique of commonly used resilience indices and recommendations for future studies. *Current Forestry Reports*, 6: 185-200.

Scott-Shaw and Morris, (2015). Grazing depletes forbs species diversity in mesic grasslands of KwaZulu-Natal, South Africa. *African Journal of Range Forage Science*, 32: 21-31.

Silva, K., Santos, J., Santos, D., Ferraz, E. and Aruaj, E. (2013). Spatial variation in structure and composition of the herbaceous community in a semiarid region of north-eastern Brazil. *Brazilian Journal of Biology*. 73: 135-148.

Sjögersten, S., Van der Wal, R. and Woodin, J. (2008). Habitat type determines herbivory controls over CO_2 fluxes in warmer arctic. *Ecology*, 89: 2103-2116.

Southers, S., Loeser, M., Crews, T. and Sisk, T. (2019). Complex response of vegetation to grazing suggest need for coordinated, landscape level approaches to grazing management. *Global Ecology and Conservation*, 20: 1-17.

Staver, A., Archibald, S. and Levin, S. (2011a). Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, 92: 1063–1072.

Staver, A., Archibald,S. and Levin,S. (2011b). The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334: 230–232.

Susiluoto, S., Rasilo, T., Pumpanen, J. and Berninger, F. (2008). Effect of grazing on the vegetation structure and carbondioxide exchange of a Fennoscandian Fell Ecosystem. *Arctic, Antarctic, and Alpine Research*, 40: 422-431.

Tagesson, T., Fensholt, R., Cropley, F., Guiro, I., Horion, S., Ehammer, A. and Ardo, J. (2015). Dynamics in carbon exchange fluxes for grazed semiarid savanna ecosystem in West Africa. *Agriculture, Ecosystems and Environment*, 205: 15-24.

Taiz, L. and Zeiger, E. (1991). Plant Physiology: Mineral nutrition. The Benjamin Cumming Publishing Company, Red Wood City, Pages 100-119.

Tefera, S., Dlamini, B. and Dlamini, A. (2010). Changes in soil characteristics and grass layer condition in relation to land management systems in the semi-arid savannas of the Swaziland. *Journal of Arid Environments*, 74: 675-684.

Tessema, B., Sommer, R., Piikki, K., Soderstrom, M., Namirembe, S., Tamene, L., Nyawira, S. and Paul, B. (2020). The potential for soil organic carbon sequestration in grasslands in East African countries: A review. *Grassland Science*, 66: 135-144.

Thirgood, S. (2009). Effect of fencing and grazing on a kobresia-dominated meadow in the Quinghai Plateau. *Plant and Soil*, 319: 115-126.

Thomas, B., Bahrangi, A. and Famiglietti, J. (2016). Precipitation intensity effects on ground water recharge in the southwestern United States. *Water*, 8: 90.

Van Auken, O. (2009). Causes and consequences of woody plant encroachment into wetern North American grassland. *Journal of Environmental Management*, 90: 2931-2942.

Van Coller. And Siebert, F. (2014). Herbaceous biomass-species diversity relationship in nutrient hotspots of a semi-arid African riparian ecosystem. *African Journal of Range and Forage Science*, 119: 1-11.

Van der Plas, A., Zeinstar, P., Veldhuis, M., Fokkema, R., Tielens, E., Howinson, R. and Olff, H. (2013). Response of savannah lawn and bunch grasses to water limitation. *Plant Ecology*, 214: 1157-1168.

Vetter, S. (2005). Rangelands at equilibrium and non-equilibriums: recent developments in the debate. *Journal of Arid Environments*, 62: 321-341.

Waite, S. (2000). Statistical Ecology in Practice; A guide to Analysing Environmental and Ecological Field Data. Prentice Hall, England.

Wakeling, J., Cramer, M. and Bond, W. (2012). The savanna-grassland treeline: why do savanna trees occur in upland grassland? *Journal of Ecology*, 100: 381-391.

Wang, W., Wang, J., Li, S., Wu, H. and Liu, T. (2010). The impact of sustained drought on vegetation ecosystem in South West China based on remote sensing. *Procedia Environmental Sciences*, 2: 1679-1691.

Wang, X., McCkonkey, B., VandenBygaart, A., Fan, J., Iwaasa, A. and Schellenberg, M. (2016). Grazing improves C and N cycling in Northern Great Plains: meta-analysis. *Scientific Reports*, 6: 33190.

Ward, D., Wiegand, K. and Getzin, S. (2013). Walter's two-layer hypothesis revisited. Back to the roots! *Oecologia*, 172: 617-630.

Warth, B., Marohn, C. and Ash, F. (2020). Modeling land use change effects on ecosystem functions in African savannas- A review. *Global Food Security*, 26: 316-327.

Weber, K. and Gokhale, B. (2011). Effect of grazing on soil water content in a semi-arid rangelands of southeast Idaho. *Journal of Arid Environments*, 75: 464-470.

Western, D., Mose, V., Worden, J. and Maitumo, D. (2015). Predicting extreme drought in savannah Africa: a comparison of proxy and direct measures in detecting biomass fluctuations, trends and their causes. *PLoS ONE*, 10: 1371-1384.

Woodward, I. and Lomas, M. (2004). Vegetation dynamics-simulating responses to climate change. *Biological Reviews*, 79: 643-670.

Wu, X., Tang, Y., Chen, Y., Wen, J., Xie, Y. and Lu, S. (2017). Sap flow characteristics and response to summer rainfall for *Pinus tabulaeformis* and *Hippophae rhamnoides* in the Loess hilly region of China. *Ecology and Evolution*, 8: 617-630.

Xiong, D., Shi, P., Zhang, X. and Zou, B. (2016). Effects of grazing exclusion on carbon sequestration and plant diversity in grassland of China. A meta-analysis. *Ecological Engineering*, 94: 647-655.

Yan, H., Liang, C., Li, Z., Liu, Z., Miao, B., He, C. and Sheng, L. (2015). Impact of precipitation patterns on Biomass and species richness of annuals in dry steppe. *PLoS ONE*, 10: 1-19.

Yu, K. and D'Odorio, P. (2015). Hydraulic lifts as a determinant of tree-grass coexistence on savanna. *New Phytologist*, 207: 1038-1051.

Yuan, J., Li, H. and Yuang, Y. (2020). The compensatory tillering in forage grass Hordeum brevisubulatum after simulated grazing of different severity. *Frontiers in Plant Science*, 11: 792-1011.

Zenes, N., Kerr, K., Trugman, A. and Anderegg, W. (2020). Competition and drought alter optimal stomatal strategy in tree seedlings. *Frontiers in Plant Science*. 11: 478-501.

Zerbo, I., Markus, B., Ouedraogo, O., Hahn, K. and Thiombiano, A. (2016). Effects of climate and landuse on herbaceous species richness and vegetation composition in West Africa Savanna Ecosystem. *Journal of Botany*, 10: 1155-1166.

Zhu, X., Jia, H., Jiang, P., Zhao, C., Hu, Y. and Cao, Y. (2012). Effects of enclosure on plant diversity and community characteristics of pasture of Middle Tianshan Mountain. *Pratacult Science*, 29: 989-992.

APPENDICES

Appendix 1. Interactive influence of rainfall manipulation and livestock grazing on species diversity of the herbaceous layer community in a humid savannah in Kenya

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Interactive influence of rainfall manipulation and livestock grazing on species diversity of the herbaceous layer community in a humid savannah in Kenya

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ABSTRACT

Changes in rainfall regime and grazing pressure affect vegetation composition and diversity with ecological implications for savannahs. The savannah in East Africa has experienced increased livestock grazing and rainfall variability but the impacts associated with those changes on the herbaceous layer have rarely been documented. We investigated the effect of livestock grazing, rainfall manipulation and their interaction on the composition and diversity of the herbaceous community in the savannah for two years in Lambwe, Kenya. Rainfall manipulation plots were set up for vegetation sampling; these plots received either 50% more or 50% less rainfall than control plots. Simpson's diversity and Berger–Parker indices were used to determine diversity changes and dominance respectively. The frequency of species was used to compute their abundance and their life forms as determined from the literature. Grazing significantly increased species diversity through suppression of dominant species. Rainfall manipulation had no significant impact on plant diversity in fenced plots, but rainfall reduction significantly reduced diversity in grazed plots. In contrast, rainfall manipulation had no impact on dominance in either fenced or grazed plots. The interaction of grazing and rainfall manipulation is complex and will require additional survey campaigns to create a complete picture of the implications for savannah structure and composition.

1. Introduction

Climate change and land use are modifying plant composition and vegetation cover within East African savannahs (Ssemmanda et al., 2014; Serdeczny et al., 2015). In recent decades, the savannahs have experienced a rise in human settlement. There has also been an increase in land use intensity, especially due to increasing livestock density. These changes are characterized by the conversion of natural ecosystems into agricultural use (Muriuki et al., 2005; K'Otuto et al., 2012; Musau et al., 2016). Climate variability manifested through changing rainfall patterns is ongoing in East African regions (Conway et al., 2005; Serdeczny et al., 2015), where both shorter periods of intense rainfall and longer periods of drought have been recorded (K'Otuto et al., 2012).

Changing rainfall patterns have varying consequences on herbaceous structure and composition (Lovette et al., 2005; Zerbo et al., 2016). Increases in rainfall intensities often result in accelerated runoffs and soil erosion, and destroy shallow-rooted plants (Baudena et al., 2015; Zerbo et al., 2016). On the other hand, reduced rainfall may limit plant physiological functions such as photosynthetic CO_2 uptake and fixation, plant growth, and species survival. Drought inhibits seed germination, causes plant mortality and alters community structure (Wang et al., 2010; Western et al., 2015). Depending on the time-span, drought may cause dominant deep-rooted vegetation in the herbaceous layer to replace shallow rooted vegetation (Hoover et al., 2014). Cumulatively, these factors alter herbaceous plant communities, reducing plant cover, and potentially lowering the survival chances of intolerant species (Ji and Peters, 2013). In some instances, such outcomes are short-

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term, with recovery occurring during subsequent favourable years. In other cases, however, changes in rainfall intensity may stimulate irreversible shifts in species composition in the herbaceous community (van der Plas et al., 2013).

Savannah in East Africa has evolved in conjunction with wild grazing herbivores, which normally occur at ecologically sustainable levels (Kioko and Seno, 2012; Mureithi et al., 2014). The introduction and expansion of livestock in the savannah, however, poses major challenges, given that the ecosystem is subjected to increased grazing pressure. This potentially alters vegetation structure and function. Overgrazing by livestock may notably reduce plant growth and vigor which in turn may lead to shifts in species composition (Schieltz and Rubenstein, 2016). There is also a reduction in class 1 (palatable species) category plants which are often consumed by livestock before seed dispersal (Rutherford et al., 2012; Koerner and Collins, 2014). Overgrazing also leads to a shift from communities of perennials to those predominately composed of annual vegetation, which exhibit superior growth and seed dispersal abilities, and, therefore, rapidly colonize open, grazed patches (Holmes and Rice, 1996; Bilota et al., 2007; Kioko et al., 2012). Moderate and light grazing, on the other hand, suppress dominant species and promote diversity, especially in productive ecosystems (Koerner and Collins, 2014). This may occur in the savannah in Lambwe, which is relatively productive (K'Otuto et al., 2012). At within patch-scale, grazing at moderate intensity can also promote plant diversity by reducing the intensity of competition for light (Bakker et al., 2003; Deng et al., 2014) and by opening colonizing windows due to gap creation. This enables the regeneration of gap opportunistic plant species (Kikoti et al., 2015).

The ecosystem in Lambwe valley in southwestern Kenya is predominantly savannah. It has experienced significant modification due to changing rainfall patterns and increased livestock grazing intensities (Njoka et al., 2003; Muriuki et al., 2005). The rainy periods have become shorter but more intense, while the dry seasons have become longer, with extended droughts (Njoka et al., 2003; K'Otuto et al., 2012). These changes are likely altering composition and richness of the herbaceous layer community. Because both livestock grazing and rainfall act simultaneously on the vegetation, this study sought to identify changes that occur in the herbaceous layer as a result of shifts in rainfall intensity and increased livestock grazing. We hypothesize that livestock grazing, changing rainfall regimes, and the interaction between these factors decrease the diversity and richness of the savannah herbaceous layer.

2. Materials and methods

2.1. Study site

This study was conducted in Ruma (00°35′S, 34°12′E), located within the Lambwe valley in Homa Bay County, Suba District, western Kenya from 2014 to 2015. The elevation of the area is around 1300 m above sea level. The site was located on a north-facing slope at the foothills of the Gwasi massif, on land belonging to the Kenya National Youth (NYS). The climate is warm and humid, with a mean (2003–2013) annual air temperature of 22 °C. In addition to the expansive savannah, with semi-natural vegetation, other land cover types include a conserved area within the Ruma National Park, human settlements, open cattle (cows, sheep, and goats) grazing fields, and seasonally cultivated crop fields (Maitima et al., 2010). The animal stocking rate is at 7.4 animal units ha^{-1}. The mean annual rainfall (1993–2013) is 1100 mm, with a weak bimodal distribution pattern between April–June and September–November. January–March is usually the driest and hottest period of the year. Soils are shallow, stony, red-brown clay loams. The higher elevations support ferruginous tropical soils and holomorphic soils on rocks that are rich in ferromagnesian minerals. Mixed soil formations of red-brown friable clays, grey mottled clays, and gray compacted loamy sands predominate. Towards the valley bottom, the soils are largely black clays, i.e., "black cotton" (Arnhold et al., 2015). Soils here have a high mineral content and tend to be alkaline (Allsop and Baldry, 1972). Measurements were conducted on a 150-ha area of mainly rolling grassland, with tracts of open woodland and thickets dominated by *Acacia*, *Combretum*, *Bridelia* and *Rhus* and a wide diversity of herbaceous vegetation, dominated by the grasses *Hyparrhenia filipendula* and *Bracharia decumbens*. The area has a slight slope (3°).

2.2. Microclimate

During the experimental period, weather parameters were continuously monitored using an automatic weather station (AWS-GP1, Delta-T Devices, Cambridge, UK) installed within the study site in an open area to avoid interference from trees. Parameters that were continuously monitored included rainfall and air temperature. Measurements were taken every 5 min, and data averaged and logged half-hourly for a period of 2 years.

2.3. Experimental design

The experiments were set in a split-plot design, with three replicates of grazed and fenced areas as main plots, and rainfall manipulation splits that included ambient rainfall (control), 50% more rainfall, and 50% less rainfall. The split-plots were nested within the land use plots that were respectively grazed by livestock or fenced (2 m high perimeter fence since 2011) to exclude livestock. The grazed plot was an open savannah subjected to year-round livestock grazing since 2005. The rain manipulations were achieved by the construction of rain-out shelters above the herbaceous vegetation canopy. To exclude rainfall, bisections of the rain exclusion split plots were covered with transparent plastic gutters and inclined at 2° downslopes to re-direct 50% of the excluded rainfall to the split plots designated for more rainfall. Control plots received ambient rainfall. Each rainfall manipulation shelter measured 6 m by 3 m and were embedded on land use plots each measuring 70 m by 100 m. The land use plots were either grazed or fenced. Trenches, 30 cm deep, were dug around the plots and plastic gutters vertically inserted into the trenches to prevent surface runoff and lateral movement from the surrounding soil. Rain-out gutters were replaced every six months.

2.4. Soil water content

In the herbaceous vegetation study plots, gravimetric soil water content (SWC) was determined monthly for a period of 2 years. Soil samples were taken using a 3-cm-diameter corer down to 30 cm. Each sample was immediately weighed before oven drying at 105 °C for 48 h and re-weighing. SWC was determined as the relative change in weight between fresh and dry soil samples (Brady and Weil, 2002).

2.5. Plant biomass determination

Plant biomass within the 40 cm by 40 cm frames was harvested monthly for the two-year study period. The harvested biomass was separated into live and dead biomass. Green standing plant material constituted live biomass, whereas brown standing and non-standing (on the ground/litter) plant material constituted dead biomass. The aboveground samples were oven-dried at 80 °C for 48 h, before determining their dry weight.

2.6. Vegetation composition and diversity

Species composition within the herbaceous layer was assessed towards the end of the rainy season (June and November) in 2014 and repeated at the same period in 2015. The sampling time coincided with the flowering period of most herbaceous species, making their identification easier. Plant species composition was estimated by randomly establishing 3 separate 40 cm by 40 cm quadrats in each of the treatment plots. All the standing plant materials in the quadrats were identified and recorded. Individual species were further classified in terms of life-forms (i.e. annuals and perennials) and their palatability was determined from the literature (Van Oudtshoorn, 2002; Muyekho et al., 2004). Species counts were then used to calculate percentage cover; herbaceous diversity was determined using species richness (R) and Simpson's index (D) of diversity. Species richness was defined as the total number of species present in a particular sampling plot, which could also be referred to as diversity (Waite, 2000). Simpson's index of diversity was calculated as follows:

(D') = 1-D, where $D = \sum (Pi)^2$ and $Pi = ni/N$. *ni* is the number of individuals of species in *i* and *N* is the total number of individuals in the sample. Simpson's index of diversity has a range of 0–1 where 1 represents maximum diversity.

2.7. Statistical analysis

All statistical analyses were performed using SAS software (version 9.1, California, USA). One way ANOVA was used to compare herbaceous vegetation variables (palatability and life form) within the research plots. Two-way ANOVA was used to test the effect of grazing and/fencing and rainfall manipulations on plant species diversity, composition, and dominance as measured by the Berger–Parker index. Tukey's t-test was used for mean comparison of the treatment plots. Data on biomass was compared using one-way ANOVA, with site as the fixed effect. Tukey-HSD post hoc tests for pairwise comparison of means was conducted with significance level of $P < 0.05$ (see Fig. 1).

3. Results

3.1. Monthly rainfall and soil water content

Rainfall was bimodal, occurring from April to June and September to December (Fig. 2). The total rainfall amounts in 2014 and 2015 were 1148.4 mm and 1169.5 mm, respectively. Gravimetric soil water content within the 0–30 cm soil profile followed the rainfall pattern, increasing during the wet months and declining during the dry months (Fig. 2).

3.2. Plant biomass determination

There were significant differences ($P < 0.0001$, $F = 322.7$) in total aboveground biomass between the plots (Table 1). The highest total aboveground biomass (1198.2 ± 78.4 g m^{-2}) was recorded in the fenced plot while the lowest biomass (473.7 ± 23.8 g m^{-2}) was recorded in the grazed plots. The highest standing (green) biomass recorded during the growing period (703.4 ± 50.7 g m^{-2}) was in the fenced plot. A significantly higher (494.8 ± 27.7 g m^{-2}) amount of dead biomass accumulated in the fenced plot compared to the grazed plot.

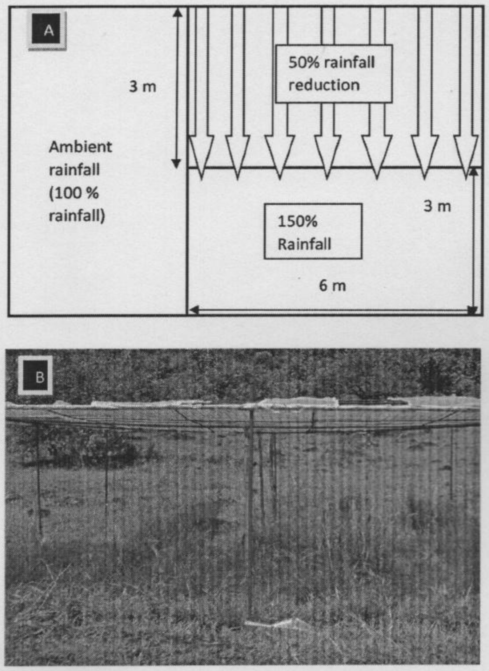

Fig. 1. (A) The layout of rainfall manipulation plots. Parallel arrows show transparent rainout gutters used to simulate rainfall reduction and direction to which excluded rainfall flows (rainfall increment plot/150% rainfall). (B) Photograph of rainfall manipulation plot with a slanting roof partially covered by transparent rainout gutters to exclude 50% of the rainfall and redirect it to the plot designated to receive more rainfall (i.e., 150% rainfall).

3.3. Plant diversity and dominance

Herbaceous diversity was high within the plots (Simpson's index 0.63–0.87; 3A and B). The herbaceous diversity in grazed plots was 19.6% higher than fenced plots ($p = 0.021$; 3A and B). When rainfall was reduced on grazed plots, herbaceous diversity decreased by 13.8% in comparison to ambient conditions ($p = 0.079$; 3C). The interaction between grazing and rainfall enhancement had no significant ($p = 0.075$) influence on diversity in comparison to ambient conditions. The interaction of grazing exclusion and rainfall treatments had no significant effects on diversity ($p = 0.077$; Fig. 3C). Vegetation dominance in fenced plots was 38.9% higher than grazed plots ($p < 0.0005$; 3 D). However, the interaction of grazing and rainfall manipulation did not have a significant effect on dominance.

3.4. Characteristics of herbaceous vegetation at grazed/ungrazed and rainfall treatment plots

All the sites were dominated by perennial herbaceous species with few annuals. Percentage cover of perennials differed significantly ($p < 0.05$) between grazed (90.72 ± 1.95%) and fenced plots (96.67 ± 1.92%). There was a significant difference ($p < 0.05$) in the

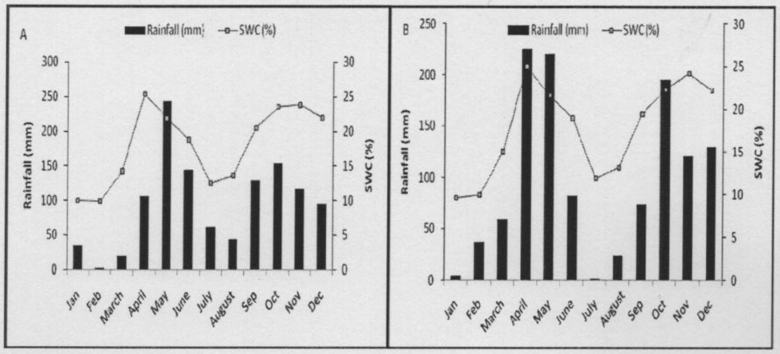

Fig. 2. Mean monthly rainfall amount (mm) and soil water content (%) within 0–30 cm soil profile recorded in 2014 (A) and 2015 (B) when measurements were conducted.

Table 1
Aboveground plant biomass measured across the studied plots. Values are means ± SE. Values not sharing the same letters indicate significant difference within plots (Tukey HSD, P < 0.05).

Plant Biomass	Grazed plot				Fenced plot			
	Ambient rainfall	Reduced rainfall	Increased rainfall	Means biomass	Ambient rainfall	Reduced rainfall	Increased rainfall	Mean biomass
Green ($g\ m^{-2}$)	373.7 ± 51.9^a	$210.0 \pm 2\ 1^b$	378.0 ± 21^a	320.6 ± 31.3^a	749.19 ± 9.9^a	561.7 ± 10.7^b	799.3 ± 9.9^c	703.4 ± 50.7^a
Dead ($g\ m^{-2}$)	196.4 ± 15.2^a	75.2 ± 6.1^b	217.6 ± 1.2^b	163.1 ± 7.5^b	521.1 ± 1.6^a	353.2 ± 2.5^b	610.1 ± 5.9^c	494.8 ± 27.7^b
Total ($g\ m^{-2}$)	570.1 ± 67.1^a	285.2 ± 27.1^b	595.6 ± 22.2^b	483.6 ± 38.8^c	1270.29 ± 11.5^a	914.9 ± 13.2^b	1409.4 ± 15.8^c	1198.2 ± 78.4^c

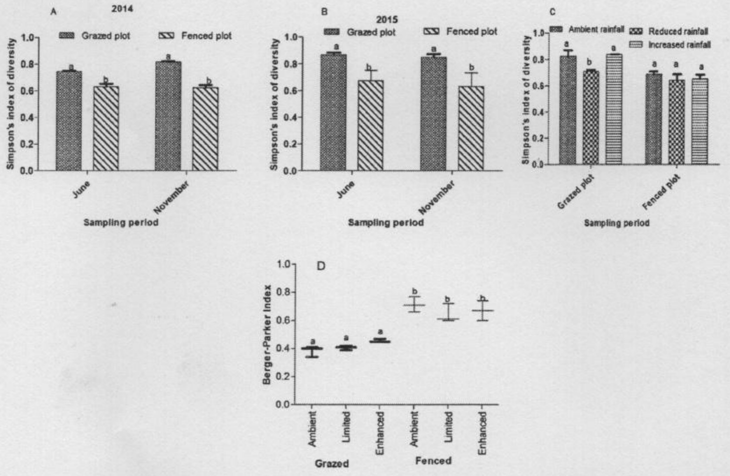

Fig. 3. (A and B) Herbaceous plant diversity within grazed and fenced plots in 2014 and 2015 respectively. Interaction of grazing and rainfall manipulation on herbaceous plant diversity (C) and dominance (D) for the entire study period. Bars are means (±SD). Bars within plots not sharing the same letters are significantly different from each other (Tukey-LSD, p < 0.05).

cover of annuals within grazed (9.23 ± 1.95%) and fenced plots (3.33 ± 1.92%). The coverage of palatable herbaceous species was higher in both grazed (87.89 ± 2.87%) and fenced plots (95.06 ± 3.82%), but the differences was not significant (p = 0.057).

3.5. Herbaceous plant species within grazed and fenced plots

List of herbaceous species and their percentage composition within grazed and fenced plots are shown in Table 2. A total of 29

Table 2
Mean (±SE) percentage of life forms (perennials and annuals) and palatability of the herbaceous layer in Lambwe at grazing and rainfall treatments. Values not sharing the same letters are significantly different from each other (Tukey-LSD, $p < 0.05$).

Plant attributes	Grazed plots			Fenced plots		
	Ambient rainfall	Reduced rainfall	Increased rainfall	Ambient rainfall	Reduced rainfall	Increased rainfall
Perennials (%)	91.5 ± 2.4^{a}	92.2 ± 2.8^{a}	88.5 ± 3.8^{b}	98.5 ± 1.5^{a}	96.8 ± 4.7^{a}	94.7 ± 2.0^{b}
Annuals (%)	8.5 ± 2.4^{a}	7.8 ± 2.7^{a}	11.5 ± 3.8^{b}	1.5 ± 1.5^{a}	3.2 ± 4.7^{a}	5.3 ± 2.0^{b}
Palatable (%)	86.5 ± 11.2^{a}	91.2 ± 2.9^{b}	86.0 ± 1.6^{a}	96.8 ± 3.4^{a}	97.7 ± 2.3^{a}	90.67 ± 0.5^{b}

and 25 species were recorded in the grazed and fenced plots respectively. Fenced plots were dominated by *H. filipendula (52%)* and *Brachiaria decumbens (25%)*. The dominant vegetation in the grazed plots was *Bothriochloa insculpta (28%)* (see Table 3).

4. Discussion

4.1. The response of plant species diversity to grazing

Higher species diversity in our grazed plots (Fig. 3A and B) is a result of reduced vegetation dominance (Fig. 3D). Decreased dominance of vegetation can be linked to improved availability of resources, such as light, nutrients, and water. With the enriched resources, diversity is often improved through the proliferation of less common species, colonisation of new species and/or a decrease in local species extinctions (Olff and Ritchie, 1998). By feeding and trampling on dominant vegetation, grazers alter the competitive interactions within the grass layer by reducing the vigor and presence of dominant plants, consequently enabling the establishment of less competitive species, which in the long run increases diversity (Pekin et al., 2014). During grazing, cattle introduce new plant propagules in the environment through their droppings; these propagules later grow into new vegetation and improve diversity within the savannah (Fynn et al., 2016). Grazing disturbance of herbaceous canopies likely increase plant diversity by promoting colonization of ruderal species (Huston, 1979; Bakker et al., 2006). Grazing also promotes the growth of forb species leading to a relatively high species-rich community in semiarid savannahs (Jacobs and Naiman, 2008). Our finding that there is a positive relationship between livestock grazing and plant diversity is in agreement with those of Hanke et al. (2014). Our results, however, contradict previous studies that examined less productive savannahs with mean annual precipitations less than 600 mm (Lechmere-Oertel et al., 2005; Rutherford and Powrie, 2012; Scott-Shaw and Morris, 2015). One possible interpretation of these contradictory results is that grazing has a positive influence on diversity only in productive ecosystems with mean annual rainfalls of greater than 600 mm. For example, the Lambwe savannah plots we studied lie on a humid savannah with a mean annual rainfall of about 1100 mm. In unproductive ecosystems with limited soil resources, grazing reduces plant diversity by eliminating rare palatable species and trampling on plants, which often do not recover from such impacts (Lezama et al., 2014).

In this experiment, fencing reduced grazing disturbance and allowed a few species to develop large local populations with more biomass (Table 1 and Fig. 3D), i.e., become dominant. The dominant vegetation in the fenced plots out-competed other less colonising species for canopy resources (i.e light) (Thirgood, 2009). A considerable number of species with lower competitive abilities reduce their density or diminish in plant communities because of competition for light resources and nutrients (Grime, 1998; Van der Wal et al., 2004). This is in agreement with competitive exclusion theory which states that at high levels of biomass, dominant species tend to outcompete other species for resources (Grime, 1973; Abrams, 1995 and Jacobs and Naiman, 2008). Competitive exclusion leads to the dominance of a few species and causes an increase in spatial homogeneity and a decrease in species diversity. Additionally, higher dead biomass accumulation in the fenced plots (Table 1) may be the reason for lower diversity in the plots. Accumulated litter may limit seedling emergence and growth with regard to forming a mechanical barrier, reducing the light radiation to the soil surface or possibly releasing toxic secondary metabolites that ultimately lower diversity (Zhu et al., 2012; Xiong et al., 2016). These results are in agreement with a number of field studies in African savannahs, which have found that exclusion of grazing has negative impacts on herbaceous plant diversity through the build-up in biomass and promotion of coloniser or competitive species (Jacobs and Naiman, 2008; Hanke et al., 2014; van Coller and Siebert, 2014).

4.2. Interaction of grazing and rainfall treatment on plant diversity

Grazing and water availability are likely the key drivers of species change in grazed savannahs and other similar ecosystems (Bat-Oyun et al., 2016). In this study, we expected that the interaction of grazing and reduced rainfall would decrease species diversity (Fig 3C). These results maybe a consequence of direct and indirect effects of both the abiotic (rainfall manipulation, i.e. reducing ambient rainfall) and biotic (grazing) factors. As reduced rainfall treatment decreased rather than increased resources, we could expect a reduction in diversity, consistent with observations in low productivity ecosystems (Ren et al., 2012). Grazing in water-limited environments tends to increase plant mortality and ultimately decrease species richness and diversity (Proulx and Mazumder, 1998; Fynn and O'Connor, 2000). Grazing reduces vegetative biomass and exposes soil to direct radiation and therefore warming which is further aggravated by the reduction in rainfall which would otherwise dampen the increased soil temperatures. Such warming negatively impacts diversity either directly through species-specific physiological responses, such as heat stress, or through ecological factors such as altered species interactions (Farrer et al., 2014). At lower soil moisture levels, stimulated by reducing ambient rainfall in grazed plots, biodiversity was predicted to decrease due to herbivore grazing and an increase in dominance by drought tolerant species; together, these two factors may reduce colonisation rates or enhance extinction of species which are less tolerant to grazing and low moisture levels (Olff and Ritchie, 1998; Bat-Oyan et al., 2016). The interaction between fencing that excluded grazing and either increased or decreased ambient rainfall did not have a significant effect on species diversity (Fig. 3C). This response points to the fact that the altered ambient rainfall in our fenced plots did not significantly change soil moisture levels to the extent that it would elicit change in plant diversity. Fencing improves soil macro-aggregation, which prevents water loss and ensures adequate soil moisture supply irrespective of the rainfall treatment. One possible explanation of our results is

Table 3
The composition, life forms, and palatability of the herbaceous plants in Lambwe between 2014 and 2015.

Grazed plots			
Plant species	Life form	Palatability	% composition
Bothriochloa insculpta (A. Rich) A. Camus	Perennial	Palatable	27.8
Paspalum dilatatum Poir	Perennial	Palatable	18.72
Hyparrhenia fillipendula (Hochst) Stapf.	Perennial	Palatable	11.83
Sporobolus agrostoides Chiov.	Perennial	Unpalatable	9.09
Vernonia glabra (Steetz) Vatke	Perennial	Unpalatable	5.41
Justicia striata Vahl	Annual	Unpalatable	3.92
Brachiaria decumbens Stapf	Perennial	Palatable	2.67
Aspilia pluriseta Schweinf	Perennial	Unpalatable	2.35
Ipomoea tenuirostris Steud ex Choisy	Perennial	Palatable	1.88
Digitaria sanguinalis (L) Scop	Annual	Palatable	1.73
Cynodon dactylon (L) Pers	Perennial	Palatable	1.73
Barleria acanthoides Vahl.	Perennial	Palatable	1.34
Triumphetta rhomboidea Jacq.	Perennial	Palatable	1.26
Indigofera arrecta Hochst ex. A. Roch.	Perennial	Palatable	1.18
Urena lobata L.	Annual	Palatable	1.1
Hypoestes aristata Soland ex Roem & Schalt	Perennial	Palatable	1.1
Sida acuta Burm. F	Perennial	Unpalatable	1.1
Waltheria indica Bak.	Perennial	Unpalatable	0.94
Striga asiatica (L) Kuntze	Annual	Unpalatable	0.71
Euphorbia hirta Linn.	Annual	Unpalatable	0.71
Rhynchosia minima (L.) DC.	Perennial	Palatable	0.47
Cajanus cajan L. Millsp	Perennial	Palatable	0.47
Hoslundia opposita Vahl.	Perennial	Unpalatable	0.47
Sonchus schweinfurthii Oliv.	Perennial	Palatable	0.47
Sphaeranthus suaveolens (Forsk) DC	Perennial	Palatable	0.47
Solanum incanum Linn.	Perennial	Unpalatable	0.47
Desmodium gangeticum (L.) D.C.	Perennial	Palatable	0.24
Hypoestes forskaolii (Vahl) R.Br.	Annual	Unpalatable	0.24
Indigofera brevicalyx Bak.	Perennial	Unpalatable	0.24
Fenced plots			
Hyparrhenia filipendula (Hochst) Stapf.	Perennial	Palatable	51.97
Brachiaria decumbens Stapf	Perennial	Palatable	24.92
Aspilia pluriseta Schweinf	Perennial	Unpalatable	3.11
Triumphetta rhomboidea Jacq.	Perennial	Palatable	2.42
Justicia striata Vahl	Annual	Unpalatable	2.35
Vernonia glabra (Steetz) Vatke	Perennial	Unpalatable	1.73
Ipomoea tenuirostris Steud ex Choisy	Perennial	Palatable	1.59
Desmodium gangeticum (L.) D.C.	Perennial	Palatable	1.45
Barleria acanthoides Vahl.	Perennial	Palatable	1.25
Cajanus cajan L. Millsp	Perennial	Palatable	1.11
Rhynchosia minima (L.) DC.	Perennial	Palatable	1.04
Themeda triandra Forssk	Perennial	Palatable	0.97
Hypoestes aristata Soland ex Roem & Schalt	Perennial	Palatable	0.76
Urena lobata L.	Annual	Palatable	0.63
Hoslundia opposita Vahl.	Perennial	Unpalatable	0.56
Cynodon dactylon (L) Pers	Perennial	Palatable	0.56
Paspalum dilatatum Poir	Perennial	Palatable	0.49
Hypoestes forskaolii (Vahl) R.Br.	Annual	Unpalatable	0.49
Leonotis nepetifolia (L) R.Br.	Annual	Palatable	0.42
Digitaria sanguinalis (L) Scop	Annual	Palatable	0.42
Indigofera arrecta Hochst ex. A. Roch.	Perennial	Palatable	0.42
Ocimum kilimandscharicum Guerke	Perennial	Palatable	0.42
Bothriochloa insculpta (A. Rich) A. Camus	Perennial	Palatable	0.35
Panicum maximum Jacq.	Perennial	Palatable	0.35
Lantana trifolia L.	Annual	Unpalatable	0.35

that species in our fenced plots are inherently less sensitive to the rainfall manipulations as used in this study. The mechanisms of species change might be largely site-specific. Furthermore, they may vary significantly in water-limited ecosystems similar to our grazed plots but dissimilar to our fenced plots.

4.3. Characteristics of herbaceous vegetation within grazed and rainfall treatment plots

The composition of herbaceous vegetation varied considerably within our study sites irrespective of rainfall treatment, which characterises the heterogeneity of Lambwe valley (Allsopp and Baldry, 1972). Spatial variation in the composition of herbaceous species may be attributed to the ability of individual species to adapt to local and edaphic conditions (Silva et al., 2013; Augustin, 2003), which are different within our sites (Otieno et al., 2011). It is possible that the lower vegetation dominance in the grazed plots (Fig. 3D) was as a result of reduced competition for light, allowing different species to flourish. Grazing at moderate intensities depresses the vigor and presence of dominant species, enabling colonisation by less competitive species with an overall increase in diversity (Kikoti and Mlingo, 2015). These results are similar to the findings of Zerbo et al. (2016) who linked grazing to the reduction in vegetation dominance in West African savannah ecosystems. Our results reveal an abundance of palatable species (Table 2). Moreover, perennial species dominated all plots irrespective of the rainfall treatment (Table 2). The higher dominance of palatable species within our plots can be attributed to a decline in selective grazing which minimises overconsumption of palatable plants. Since the abundance of palatable species appears to be an indicator of moderate grazing (Ren et al., 2012), we can conclude that grazing within our plots is within a sustainable range that does not necessarily lead to ecosystem degradation. The interaction of grazing and rainfall manipulation is complex and requires additional survey campaigns to create a complete picture of its implications on savannah structure and composition.

Conflict of interest

None declared.

Acknowledgment

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2019.04.005.

References

Abrams, A., 1995. Monotonic or unimodal diversity-productivity gradient: What does competition theory predict? Ecology 76 (7), 2019–2027.
Allsopp, R., Baldry, T., 1972. A general description of the Lambwe valley area of south Nyanza district, Kenya. World Health Organisat. Bull. 47, 691–697.
Arnhold, S., Otieno, D., Onyango, J., Koeller, T., Huwe, B., Tenhunen, J., 2015. Soil properties along a gradient from hillslopes to the savanna plains in the Lambwe Valley, Kenya. Soil Tillage Res. 154, 75–83.
Augustine, J., 2003. Spatial heterogeneity of herbaceous layer of a semi-arid savannah ecosystem. Plant Ecol. 167, 319–332.
Bakker, C., Blair, J., Knnap, A., 2003. Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grassland? Oecologia 137, 385–391.
Bakker, E., Ritchie, M., Olff, H., Milchunas, D., Knops, J., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecol. Lett. 9, 780–788.
Bat-Oyan, T., Shinoda, M., Cheng, Y., Purevdorj, Y., 2016. Effect of grazing and precipitation variability on vegetation dynamics in a Mongolian dry steppe. J. Plant Ecol. 9 (5), 508–519.
Baudena, M., Dekker, S., Bodegom, P., Cuesta, B., Higgins, S., Lehsten, V., Reick, C., Rietterk, M., Yin, Z., Zavala, M., Brovkin, V., 2015. Forests, savannas, grasslands: bridging the knowledge gap between ecology and Dynamic Vegetation Models. Biogeosciences 12, 1833–1848.
Bilota, G., Brazier, R., Haygarth, P., 2007. The impact of grazing animals on the quality of soils, vegetation, and surface waters in intensively managed grasslands. Adv. Agron. 94, 237–280.
Brady, N., Weil, R., 2002. The Nature and Properties of Soils, 13th Ed. Prentice-Hall Inc, New Jersey, USA, p. 960.
Conway, D., Allison, E., Felstead, R., Goulden, M., 2005. Rainfall variation in East Africa: implication for natural resources management and livelihood. Phil. Trans. 363, 49–54.
Deng, L., Sweeney, S., Shangguan, Z., 2014. Grassland responses to grazing disturbance: plant diversity changes with grazing intensity in a desert steppe. Grass Forage Sci. 69, 524–533.
Farret, E., Ashton, J., Suding, N., 2014. Separating direct and indirect effects of global change: a population dynamic modelling approach using readily available field data. Glob. Chang. Biol. 20, 1238–1250.
Fynn, R., O'Connor, T., 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semiarid savannah, South Africa. J. Appl. Ecol. 37, 491–507.
Fynn, S., Augustine, J., Peel, S., de Garine-Wichatitsky, Michael, 2016. Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife-livestock coexistence- A review. J. Appl. Ecol. 53, 388–397.
Grime, J., 1973. Control of species density in a herbaceous vegetation. J. Environ. Manag. 1, 151–167.
Grime, J., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.
Hanke, W., Bohner, J., Dreber, N., Jurgen, N., Schmiedel, U., Wesuls, D., Dengler, J., 2014. The impact of livestock grazing on plant diversity: an analysis across dryland ecosystems and scales in South Africa. Ecol. Appl. 24 (5), 1188–1203.
Holmes, T., Rice, K., 1996. Patterns of growth and soil-water utilization in some exotic and native perennial bunch grasses of California. Ann. Bot. 78, 233–243.
Hoover, D., Knapp, K., Smith, D., 2014. Resistance and resilience of grassland ecosystem to climate extremes. Ecology 95, 2646–2656.
Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.
Jacobs, S., Neiman, R., 2008. Large African herbivores decrease herbaceous plant biomass while increasing plant species richness in a semiarid savannah toposequence. J. Arid Environ. 72, 891–903.
Ji, L., Peters, A., 2013. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. Remote sensing environments. Elsevier 87 (1), 1555–1570.
K'Otuto, G., Otieno, D., Seo, B., Ogindo, H., Onyango, J., 2012. Carbon dioxide exchange and biomass productivity of the herbaceous layer of a managed tropical savanna ecosystem in western Kenya. J. Plant Ecol. 6 (4), 286–297.
Kikoti, A., Mlingo, C., 2015. Impact of livestock grazing on plant species composition in a montane forest of the northern slope of Mount Kilimanjaro, Tanzania. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 11, 114–127.
Kikoti, A., Mligo, C., Kilemo, B., 2015. The impact of grazing on plant natural regeneration in Northern Slopes of Mount Kilimanjaro, Tanzania. Open J. Ecol. 5, 266–273.
Kioko, J., Kiringe, J., Seno, S., 2012. Impact of livestock grazing on savanna grassland in Kenya. J. Arid Land 4 (1), 29–35.
Koerner, S., Collins, S., 2014. Interactive effects of grazing, drought and fire on grassland plant communities in North America and South Africa. Ecology 95, 98–109.
Lechmer-Oertel, R., Kerley, G., Cowling, R., 2005. Patterns and implications of transformation in semi-arid succulent thicket, South Africa. J. Arid Environ. 63, 459–474.
Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, J., Paruelo, M., 2014. Variation of grazing induced vegetation changes across a large-scale productivity gradient. J. Veg. Sci. 25, 8–21.
Lovette, J., Midgley, P., Barnard, B., 2005. Climate change and ecology in Africa. Afr. J. Ecol. 43, 279–281.
Maitama, J., Oslon, J., Mugatha, S., Mugisha, S., Mutie, I., 2010. Land use changes, impacts and options for sustaining productivity and livelihoods in the basin of Lake Victoria. J. Sustain. Dev. Afr. 12, 189–206.
Mureithi, S., Verdoodt, A., Njoka, T., Gachene, K., Warinwa, F., Ranst, E., 2014. Impact of community conservation management on herbaceous layer and soil nutrients in a Kenyan semi-arid savannah. Land Degrad. Dev. 10, 1002–1015.
Muriuki, G., Njoka, T., Reid, R., Nyariki, D., 2005. Tsetse control and landuse change in Lambwe valley, south western Kenya. Agric. Ecosyst. Environ. 106, 99–107.
Musau, J., Patil, S., Sheffield, J., Marshall, M., 2016. Spatio-temporal vegetation dynamics and relationship with climate over East Africa. Hydrol. Earth Syst. 10, 502–519.
Muyekho, F., Barrison, A., Khan, Z., 2004. A Primer on Grass Identification and their uses in Kenya. Communication Limited, Nairobi, Kenya.
Njoka, T., Muriuki, G., Reid, R., Nyariki, D., 2003. The use of sociological methods to asses land use change: a case study of Lambwe valley, Kenya. Int. J. Sociol. 7 (3), 181–185.
Olff, H., Ritchie, M., 1998. Effect of herbivores on grassland plant biodiversity. Trends Ecol. Evol. 13, 261–265.
Otieno, D., K'Otuto, G., Jakli, B., Maina, J., Jung, E., Onyango, J., 2011. Spatial heterogeneity in ecosystem structure and productivity in a moist Kenyan savanna. Plant Ecol. 212, 769–789.
Pekin, B., Wisdom, M., Endress, B., Neylor, B., Parks, C., 2014. Ungulate browsing maintains shrub diversity in the absence of episodic disturbance in seasonally-arid conifer forest. PLoS One 9, e86288. https://doi.org/10.1371/journal.Prone.0086288.
Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs nutrient rich ecosystems. Ecology 79, 2581–2591.
Ren, H., Schonbach, P., Wan, H., Gierus, M., Taube, 2012. Effect of grazing intensity and environmental factors on species composition and diversity in Typical Steppe of Inner Mongolia, China. PLoS One 7 (12), E52180 doi:137/journal.pone.0052180.
Rutherford, M., Powrie, L., Husted, L., 2012. Herbivore-driven land degradation: consequences for plant diversity and soil in arid subtropical thicket in south eastern African savannah. Nat. Lett. 438, 846–849.
Schieltz, M., Rubenstein, I., 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? Environ. Res. Lett. 11, 113003.
Scott-Shaw, Morris, 2015. Grazing depletes forbs species diversity in mesic grasslands of KwaZulu-Natal, South Africa. Afr. J. Range Forage Sci. 32, 21–31.

Serdeczny, O., Adams, S., Baarsch, F., Coumou, D., Robinson, A., Hare, W., Schaeffer, M., Perrette, M., 2015. Climate change impact in Sub-Saharan Africa: from physical changes to their social repercussions. Region. Clim. Change 15, 8–21.

Silva, K., Santos, J., Santos, D., Ferraz, E., Aruaj, E., 2013. Spatial variation in structure and composition of the herbaceous community in a semiarid region of northeastern Brazil. Braz. J. Biol. 73, 135–148.

Ssemmanda, I., Gelorini, V., Verschuren, D., 2014. Sensitivity of East African savannah vegetation to historical moisture-balance variation. Clim. Past 10, 2067–2080.

Thirgood, S., 2009. Effect of fencing and grazing on a kobresia-dominated meadow in the Quinghai Plateau. Plant Soil 319 (1–2), 115–126.

Van Coller, Siebert, F., 2014. Herbaceous biomass-species diversity relationship in nutrient hotspots of a semi-arid African riparian ecosystem. Afr. J. Range Forage Sci. 119, 1–11.

Van der Plas, A., Zeinstar, P., Veldhuis, M., Fokkema, R., Tielens, E., Howinson, R., Olff, H., 2013. Response of savannah lawn and bunch grasses to water limitation. Plant Ecol. 214 (9), 1157–1168.

Van Oudtshoorn, F., 2002. Guide to Grasses of South Africa. BRIZA Publication, Pretoria, South Africa.

Waite, S., 2000. Statistical Ecology in Practice; A Guide to Analysing Environmental and Ecological Field Data. Prentice Hall, England.

Wang, W., Wang, J., Li, S., Wu, H., Liu, T., 2010. The impact of sustained drought on vegetation ecosystem in South West China based on remote sensing. Proc. Environ. Sci. 2, 1679–1691.

Western, D., Mose, V., Worden, J., Maitumo, D., 2015. Predicting extreme drought in savannah Africa: a comparison of proxy and direct measures in detecting biomass fluctuations, trends and their causes. PLoS One 10 (8), 1371–1384.

Xiong, D., Shi, P., Zhang, X., Zou, B., 2016. Effects of grazing exclusion on carbon sequestration and plant diversity in grassland of China. A meta-analysis. Ecol. Eng. 94, 647–655.

Zerbo, I., Markus, B., Ouedraogo, O., Hahn, K., Thiombiano, A., 2016. Effects of climate and landuse on herbaceous species richness and vegetation composition in West Africa Savanna Ecosystem. J. Bot. 10, 1155–1166.

Zhu, X., Jia, H., Jiang, P., Zhao, C., Hu, Y., Cao, Y., 2012. Effects of enclosure on plant diversity and community characteristics of pasture of Middle Tianshan Mountain. Pratacult. Sci. 29, 989–992.

Appendix 2. Ecosystem productivity and CO_2 exchange response to the interaction of livestock grazing and rainfall manipulation in a Kenyan savanna

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Ecosystem productivity and CO_2 exchange response to the interaction of livestock grazing and rainfall manipulation in a Kenyan savanna

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ABSTRACT

Savanna ecosystems in Kenya are experiencing altered rainfall amount and increased grazing pressure. These environmental alterations occur simultaneously and impact on productivity and CO_2 exchange of the savanna in unclear ways. Rainfall was manipulated and its interaction with livestock grazing on productivity and CO_2 exchange within the herbaceous vegetation investigated for two years. Rainfall manipulation plots which received ambient rainfall (100% rainfall), fifty percent more rainfall (150% rainfall) or fifty percent less rainfall (50% rainfall) were set up within grazed and fenced areas respectively. Measurement chambers were used to quantify monthly CO_2 exchange. Monthly biomass and soil water content (SWC), bulk density, plant and soil C/N were quantified. Grazing reduced CO_2 exchange through reduction in aboveground green biomass. The interaction of grazing and rainfall reduction lowered Gross Primary Productivity (GPP), Net Ecosystem Exchange (NEE) and Ecosystem Respiration (R_{eco}) through the imposition and amplification of drought by grazing and rainfall reduction respectively. The interaction of grazing and rainfall increment led to increased GPP and NEE, confirming the role of SWC in driving CO_2 exchange in the grazed savanna, however, R_{eco} was not significantly ($P > 0.05$) affected by the interaction of grazing and rainfall increment. This shows that the CO_2 exchange in this ecosystem do not always respond linearly to rainfall variation. These results demonstrate the importance of the interacting environmental variables in determination of carbon balance of savannas.

1. Introduction

In Africa, savanna ecosystems cover about half of the continent, with a significant contribution to the regional and global productivity (Grace et al., 2006; Ciais et al., 2011). Land use and climate are key in determining the savanna carbon balance and other ecosystem services (Bombelli et al., 2009; Dimobe et al., 2018). The ecosystems' carbon balance is vulnerable to climate change, and land use which modify CO_2 exchange and plant productivity in unpredictable ways (Bombelli et al., 2009; Räsâ;nen et al., 2016). Grazing, especially by wild herbivores have been part of African savannas for millions of years (Sankaran and Ratnam, 2013). However, with the increase in the human population and hence increased demand for animal production, most of the savannas have been subjected to livestock grazing, and the numbers of animals have increased over the years (Kgosikoma et al., 2013; Osborne et al., 2018). Grazing patterns in these savannas are controlled by rainfall amount and seasons where animals are divided over landscape to ensure reduced grazing pressure during dry periods (Kioko et al., 2012). However, regional climates have been changing and modifying the ecosystems' rainfall amount and patterns, including the tendency for reduced annual rainfall, short episodes of intense rainfall followed by longer duration of drought (K'Otuto et al., 2012; Synodinos et al., 2018; Zhang et al., 2019). Evaluating the consequences of the changing rainfall and increased livestock grazing on CO_2 exchange and productivity of the savannas could be a starting point in the understanding of the response of the ecosystems to land use and climate change.

Previous studies have revealed mixed results of livestock grazing effects on savanna ecosystem CO_2 exchange and productivity, with studies showing positive (Leriche et al., 2003), neutral (Peng et al., 2013) or negative effects (K' Otuto et al., 2012). Livestock grazing affects ecosystem Gross Primary Productivity (GPP) by lowering soil water content (SWC), soil organic matter input and photosynthesis (Leriche et al., 2003). Grazing by livestock, especially at higher intensities is thought to decrease herbaceous productivity and ecosystem CO_2 exchange by direct removal of the herbaceous biomass and hence reduction in potential CO_2 fixation in the photosynthetic tissues (Ren et al., 2017).

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Rainfall, on the other hand, affects soil moisture and has an impact on ecosystem productivity and carbon exchange (Bao et al., 2019) and therefore, changes in rainfall, such as those projected in savannas (Otieno et al., 2015; Synodinos et al., 2018), will, directly and indirectly, impact the ability of savannas to fix and store carbon (Meza et al., 2018). Previous studies reported positive relationships between increased rainfall and Gross Primary Productivity (GPP), Net Ecosystem Exchange (NEE), and Ecosystem Respiration (R_{eco}) (Scott et al., 2015; Ren et al., 2017) and linked the association to improved photosynthesis and soil nutrient availability (Jenerettem et al., 2009; Zhang et al., 2019). Other studies revealed that reduced rainfall can infer soil water stress which reduces GPP and NEE through the reduction in mesophyll and stomatal conductance (Konings et al., 2017), dormancy or death of microbial organisms (Ondier et al., 2019), and reduction in leaf area (Fisher et al., 2006).

The savanna located in Lambwe valley in Kenya has experienced increased cattle grazing over the past 40 years (Muriuki et al., 2005; K'Otuto et al., 2012). At the same time, rainfall has been changing, increasingly characterised by reduction in mean annual rainfall and increased inter annual rainfall variability. Previous studies in this region (Otieno et al., 2009; Nyongesa, 2010; K'Otuto et al., 2012; K'Otuto, 2014; Arnhold et al., 2015) reported responses of the ecosystem to changing rainfall regime and grazing as independent factors impacting the ecosystem, however, the ongoing transition in land uses and rainfall are occurring simultaneously. Livestock grazing and rainfall variability are concurrently impacting the ecosystem, and modifying its carbon exchange in ways that are not yet clearly understood. Since the impact of livestock grazing and rainfall may be antagonistic, they must be studied concurrently to draw conclusions on their interactive influence on the ecosystem's CO_2 exchange under the current environmental change scenarios. A recent 10 month study in this ecosystem by Okach et al. (2019) reported that livestock grazing lowered herbaceous NEE more during wet months than dry months. The study did not however explicitly explain the implications of the rainfall variability and grazing on herbaceous CO_2 exchange. Moreover, the 10 month study duration was inadequate for drawing scientific conclusions on the ecosystem's response to livestock grazing and rainfall variability. There is recognised need for multiyear experiments because many of the grazing-rainfall experiments that have been conducted in Lambwe and other savannas to date have been limited to a single growing season (Beier et al., 2012; Hoover et al., 2014; Okach et al., 2019; Ondier et al., 2019) This study, therefore, extends beyond the wet/dry season to conclusively understand the ecosystem's carbon flux response to the interaction of livestock grazing and rainfall variability in a span of 2 years.

The ambient rainfall was experimentally manipulated in an open savanna subjected to either livestock grazing or fencing (to keep away livestock), to examine the interactive influence of livestock grazing and rainfall on CO_2 exchange of the herbaceous vegetation. We hypothesised that the ecosystem carbon flux components have differential sensitivities to the interaction of livestock grazing and rainfall manipulation.

2. Materials and methods

2.1. Study site

The study was conducted in Ruma (00°35'S, 34°12'E), located within the Lambwe valley in Homa Bay County in western Kenya from January 2014 to December 2015. The elevation of the area is around 1300 m above sea level. The site was located on a north-facing slope at the foothills of the Gwasi massif, on land belonging to the Kenya National Youth (NYS). The climate is warm and humid, with a mean (2003–2013) annual air temperature of 22 °C. The mean annual rainfall (1993–2013) is 1100 mm, with a weak bimodal distribution pattern between April–June and September–November. January–March is usually the driest and hottest period of the year. In addition to the expansive savanna, with semi-natural vegetation, other land cover types include a conserved area under the Ruma National Park, human settlements, open cattle (cows, sheep, and goats) grazing fields, and seasonally cultivated crop fields (Maitima et al., 2010). The animal stocking rate is at 7.4 ha per animal head. Soils are shallow, stony, red-brown clay loams. The higher elevations support ferruginous tropical soils and holomorphic soils on rocks that are rich in ferromagnesian minerals. Mixed soil formations of red-brown friable clays, grey mottled clays, and grey compacted loamy sands predominate. Towards the valley bottom, the soils are largely black clays, i.e., "black cotton" (Arnhold et al., 2015). Soils here have a high mineral content and tend to be alkaline (Allsopp and Baldry, 1972). Measurements were conducted on a 150-ha area of mainly red-brown soils, rolling grassland with tracts of open woodland and thickets dominated by *Acacia ancistroclada*, *Combretum molle*, *Bridelia scleroneura* and *Rhus netalensis* and a wide diversity of herbaceous vegetation, dominated by the grasses *Hyparrhenia filipendula* and *Bracharia decumbens*. The area has a mean slope of 3°.

2.2. Microclimate

During the experimental period, weather parameters were continuously monitored using an automatic weather station (AWS-GP1, Delta-T Devices, Cambridge, UK) installed within the study site in an open area to avoid interference from trees. Parameters that were continuously monitored included rainfall and air temperature. Measurements were taken every 5 min, and data averaged and logged half-hourly for a period of 2 years.

2.3. Experimental design

The experiment was set in a split-factorial design, with three replicates of grazed and fenced areas as main treatments, and rainfall manipulation splits that included ambient rainfall (100% rainfall), fifty percent more rainfall (150% rainfall), and fifty percent less rainfall (50% rainfall). The split-plots were embedded within the main plots that were respectively grazed by livestock or fenced (2 m high perimeter fence since 2011) to exclude livestock. The grazed plots were open savanna subjected to all year-round livestock grazing since 2005. At any grazing event, animals stayed on the site for not more than one hour. Manipulation of the ambient rainfall was achieved by the construction of rain-out shelters above the herbaceous vegetation canopy according to the original design of February et al. (2013). To exclude rainfall, bisections of the rain exclusion split plots were covered with transparent plastic sheets (10 sheets as seen in Fig. 1), regularly spaced and inclined at 2° downslopes to re-direct 50% of the excluded rainfall to the split plots designated for

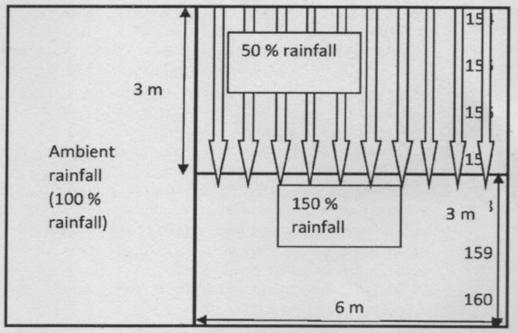

Fig. 1. A bird's eye view of an experimental plot. Open block arrows show transparent plastic sheets used to simulate reduced rainfall and direction of excluded rain water (to increased rainfall plot/150% rainfall).

more rainfall (Fig. 1). Tests using portable soil moisture sensors revealed homogeneity in soil moisture distribution within the plots designated for more rainfall. Control plots received ambient rainfall. Each rainfall manipulation shelter measured 6 m by 3 m and were embedded on either grazed or fenced land use plots each measuring 70 m by 100 m. Trenches, 50 cm deep and 30 cm wide, were dug (dug once during plots preparation stage and 3 months before onset of measurements) around the plots and plastic sheets buried into the trenches to prevent surface runoff and lateral movement from the surrounding soil. Rain-out gutters were replaced every six months (Fig. 1).

2.4. Soil water content and bulk density determination

A 3-cm diameter corer was used to obtain soil samples, down to 30 cm depth, for determination of gravimetric soil water content (SWC) and bulk density. At every sampling event, respective three samples were randomly obtained for determination of SWC and bulk density. Soil samples were immediately weighed to determine fresh weights. The samples were later oven dried at 105 °C for 48 h and re-weighed. Gravimetric soil water content was determined as relative change in weight between fresh and dry soil samples while bulk density was computed by dividing oven dry weight of the dried soil samples by the total volume of the sampled soils according to Brady and Weil (2002).

2.5. Ecosystem CO_2 exchange in the herbaceous layer

On each measurement day, net ecosystem CO_2 exchange (NEE) and ecosystem respiration (R_{eco}) were sequentially recorded in a systematic rotation over all replicate plots. Net ecosystem CO_2 exchange and R_{eco} were measured using a portable, temperature controlled 40 cm × 40 cm × 54 cm transparent (light, NEE) and opaque (R_{eco}) closed chamber system (Li et al., 2008; Droesler, 2005). Transparent chambers used for NEE were to allow light penetration so as not to halt photosynthesis while dark chambers were used to block photosynthesis. The light chamber was constructed from a 3 mm thick Plexiglass XT type 200070, with >95% light transmittance. During serial measurements, it took 3–5 min to alter one frame to another. The time lapse between NEE and R_{eco} measurements on every plot was between 20 and 30 min with NEE measurements taken upfront. The dark chamber was made of opaque PVC and further covered with a reflective layer of aluminium. To ensure close air circulation, frames with 39.5 cm × 39.5 cm base and 10 cm height, and externally fitted with a 3 cm wide platform (3 cm from the top) were inserted to a minimum of 4 cm into the soil at least 3 days before the beginning of the measurements. Extension bases were used to adjust chamber height to the canopy height whenever necessary. Chambers were sealed to the plastic frames with a flexible rubber gasket and the chamber firmly secured using elastic straps fastened onto the ground from two sides. Tests indicate that leakages did not occur, however, this was examined regularly in the case of systematic field measurements and each set of data was scrutinized for abnormalities.

The chamber temperature was maintained within 2 °C of the ambient using frozen cool packs and air inside the chamber mixed using three fans yielding a wind speed of 1.5 $m\ s^{-1}$. Air temperature within and outside the chamber was continuously monitored and recorded during the CO_2 exchange measurements to check against wide variations. Sudden rise in pressure inside the chamber was avoided by opening a 12 mm diameter vent at the top of the chambers during their replacement, and closing the vent soon after the chamber was secured onto the frames before the onset of CO_2 exchange measurement. Chamber CO_2 concentration was read from portable infrared gas analyser (IRGA, LI-820, LI-COR, USA) connected to the chamber via flexible 0.32 cm diameter inflow and outflow tubes (Droesler, 2005). A battery driven pump was used to maintain a constant air flow rate through the IRGA-chamber system. Photosynthetic photon flux density (PPFD) was measured using a PAR sensor (LI-190, LI-COR, USA) installed inside the chamber. Once a steady state had been maintained, CO_2 concentration (ppm) was recorded every 15 s for a period of 2.5 min before shifting to the next frame. Soil temperatures within the frames were recorded at 10 cm depth, at the start and end of the CO_2 concentration measurements, from digital thermometers (Eintichthermometer, Conrad, Hirschau, Germany). Changes in CO_2 concentration within the chamber headspace were calculated by linear regression of linear portion of the plot of CO_2 against time for the duration of the measurement. CO_2 exchange was calculated according to Davidson et al.

$$CO_2\ \text{exchange} = \frac{\partial CO2}{\partial t} * \frac{PV}{ART} \tag{1}$$

where $\frac{\partial CO2}{\partial t}$ = rate of exchange in CO_2 concentration with time; V = volume of headspace within the chamber; P = atmospheric pressure; A = ground area covered by chamber; R = gas constant; T = air temperature (K).

$$\text{NEE} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma O \tag{2}$$

where Q is PPFD ($\mu mol\ m^{-2}s^{-1}$), NEE ($\mu mol\ CO_2\ m^{-2}s^{-1}$), α is an approximation of the canopy light utilization efficiency ($\mu mol\ CO_2\ m^{-2}s^{-1}$), β is the maximum CO_2 uptake rate of the canopy ($\mu mol\ CO_2\ m^{-2}s^{-1}$) and γO is an estimate of the average ecosystem respiration (R_{eco}, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) occurring during the observed period.

2.6. Gross primary production

Gross primary production (GPP) was estimated via the general equation (Gilmanov et al., 2007):

$$\text{GPP} = R_{eco} + \text{NEE} \tag{3}$$

Where R_{eco} = ecosystem respiration ($\mu mol\ CO_2\ m^{-2}s^{-1}$).

Negative NEE value represent ecosystem CO_2 uptake while positive value represent CO_2 release to the atmosphere. All terminology and abbreviation used here were adopted from previous publication (K'Otuto et al., 2012).

2.7. Plant biomass determination

Monthly biomass harvested from the frames (for CO_2 exchange measurements) were separated into live and dead biomass. Green standing plant material constituted live biomass, whereas brown standing and non-standing (on the ground/litter) plant material constituted dead biomass. The aboveground samples were oven-dried at 80 °C for 48 h, before determining their dry weight (K'Otuto et al., 2012).

2.8. Soil and plant carbon (C) and nitrogen (N) determination

Part of the samples used for determination of soil moisture and plant biomass were used to analyze Plant and soil Carbon and Nitrogen. The samples were dried, homogenized in a ball mill, and re-dried in a desiccator to eliminate all the water. About 5 g of the dried soil and 1 g of plant samples were analyzed to determine their C and N concentrations (%) using elementary analysis according to Markert (1996). The analysis was done at the isotopic laboratory, University of Bayreuth, Germany.

2.9. Statistical analysis

Statistical analysis was carried out using SAS (version 9.1, USA). The interactive effect of grazing and rainfall manipulation on SWC, NEE, R_{eco}, GPP, bulk density, aboveground biomass, and C/N content were tested using factorial ANOVA (crossed) with grazing and rainfall manipulations as fixed effects. Post hoc test for multiple comparison of means (±SD) of the CO_2 exchange, aboveground biomass SWC, C/N content and bulk density was done by Tukey HSD with significance level set at $P \leq 0.05$.

Linear regression analysis was used to investigate the relationship between CO_2 exchange and SWC within grazed and fenced plots.

3. Results

3.1. Microclimate of the study region

The total rainfall amounts in 2014 and 2015 were 1148.4 mm and 1169.5 mm, respectively. Mean air temperature increased and decreased slightly during dry and wet months respectively. The mean diurnal air temperature of the area was 25.39 ± 3.4 °C. The highest and lowest mean maximum air temperatures were 33.65 ± 2.2 °C and 18.5 ± 1.7 °C in March and July respectively (Fig. 2).

3.1.1. Influence of livestock grazing and rainfall manipulation on soil water content

Livestock grazing significantly ($P < 0.05$) reduced soil water content by 19.25%. The interaction of grazing and rainfall reduction significantly ($P < 0.05$) reduced soil water content by 22.73%. The interaction of grazing and rainfall increment significantly ($P < 0.05$) increased soil water content by 23.78%. (Fig. 3).

3.1.2. Influence of livestock grazing and rainfall manipulation on herbaceous biomass

Rainfall manipulation significantly ($P < 0.05$) affected biomass across grazed and fenced plots. Significant reduction in aboveground biomass (green and dead) was observed in the rainfall reduction plots. Within the fenced plots, the reduction and increment in ambient rainfall led to respective decrease and increase in green and dead biomass. There were significant differences ($P < 0.05$) in total aboveground biomass between the plots (Table 1). The highest total aboveground biomass (1198.2 ± 78.4 g m^{-2}) was recorded in the fenced plots while the lowest biomass (473.7 ± 23.8 g m^{-2}) was recorded in the grazed plots. The highest standing (green) biomass recorded during the growing period (703.4 ± 50.7 g m^{-2}) was in the fenced plots. A significantly higher (494.8 ± 27.7 g m^{-2}) amount of dead biomass accumulated in the fenced plot compared to the grazed plot. The interaction of grazing and rainfall reduction led to a significant ($P < 0.05$) decrease in both green and dead biomass. The interaction of grazing and rainfall increment led to a significant ($P < 0.05$) increase in both green and dead biomass.

3.1.3. Influence of livestock grazing and rainfall manipulation on CO_2 exchange

Grazed plots recorded significantly ($P < 0.05$) lower CO_2 exchange than fenced plots across the three rainfall treatments. The interaction of grazing and rainfall reduction significantly ($P < 0.05$) lowered GPP, NEE and R_{eco} by 22.5%, 33% and 39% respectively. The interaction of grazing and rainfall increment significantly ($P < 0.05$) increased GPP and NEE, by 47%, 54.8% but had no significant influence on R_{eco}. There were no mean differences in GPP between ambient rainfall plots in grazed and fenced sites (Fig. 4).

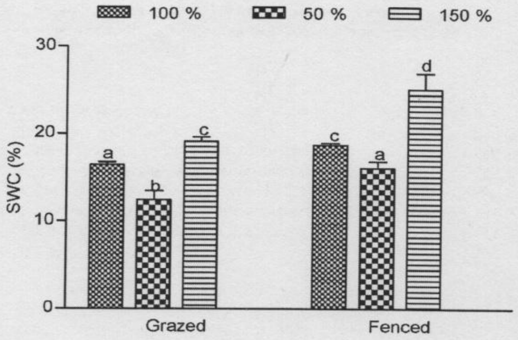

Fig. 3. Mean soil water content (%) in grazed and fenced plots at ambient rainfall (100%), fifty percent rainfall reduction (50%) and fifty percent rainfall increment (150%) for the entire study period. Different letters indicate significant differences ($p \leq 0.05$) in treatments across plots. Bars are means ± SD.

3.1.4. Relationship between CO_2 exchange and SWC

GPP, NEE, and R_{eco} were linearly and significantly correlated with SWC in all the plots (Fig. 5). The stronger relationships ($r^2 = 0.65$ for GPP, $r^2 = 0.66$ for NEE and $r^2 = 0.60$ for R_{eco}) occurred in the fenced site while weaker relationships ($r^2 = 0.56$, $r^2 = 0.41$, and $r^2 = 0.54$ for GPP, NEE, and R_{eco} respectively) occurred in the grazed sites.

3.1.5. Plant and soil C/N measured across the studied plots

Rainfall manipulation had no significant ($P > 0.05$) effect on soil carbon in all the plots. The interaction of grazing and rainfall reduction led to a significant ($P < 0.05$) decline in soil N whereas the interaction of grazing and rainfall increment led to significant ($P < 0.05$) increase in soil N. Interaction of grazing and rainfall reduction had no significant ($P > 0.05$) influence on shoot N whereas the interaction of grazing and rainfall increment significantly ($P < 0.05$) increased shoot N. Interaction of grazing and rainfall reduction significantly ($P < 0.05$) reduced shoot C:N ratio whereas the interaction of grazing and rainfall increment had no significant ($P > 0.05$) influence on shoot C:N ratios.

3.1.6. Influence of grazing and rainfall manipulation on soil bulk density

Either ambient rainfall or increment of rainfall to 150% had no significant ($P > 0.05$) impact on soil bulk density across studied plots. In

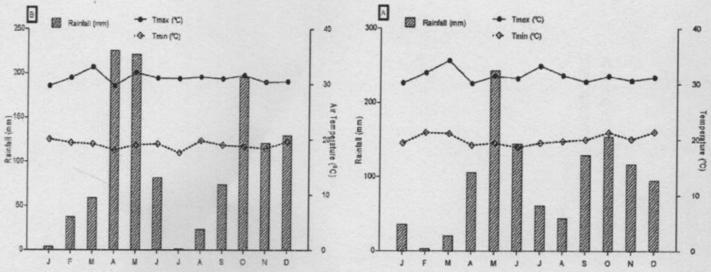

Fig. 2. Monthly rainfall amount (mm) and average maximum and minimum air temperature, T_{air} (°C) recorded in the study site in (A) 2014 and (B) 2015 when measurements were conducted.

Table 1
Aboveground plant biomass measured across the studied plots. Values are means ± SE. Values not sharing the same letters indicate significant difference across plots (Tukey HSD, $P < 0.05$).

Plant Biomass	Grazed				Fenced			
	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)	Means biomass	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)	Mean biomass
Aboveground Green ($g\ m^{-2}$)	373.7 ± 51.9^d	$210.0 \pm 2\ 1^e$	378.0 ± 21^d	320.6 ± 31.3	749.19 ± 9.9^b	561.7 ± 10.7^c	799.3 ± 9.9^a	703.4 ± 50.7
Aboveground Dead ($g\ m^{-2}$)	196.4 ± 15.2^e	75.2 ± 6.1^f	217.6 ± 1.2^d	163.1 ± 7.5	521.1 ± 1.6^b	353.2 ± 2.5^c	610.1 ± 5.9^a	494.8 ± 27.7

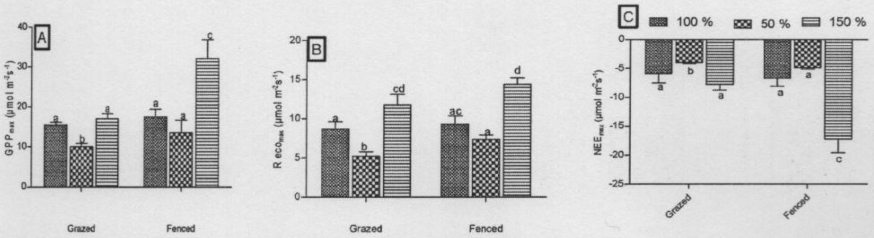

Fig. 4. GPP (a), R_{eco} (b) and NEE (c) in grazed and fenced plots at ambient rainfall (100%), fifty percent rainfall reduction (50%) and fifty percent rainfall increment (150%) for the entire study period. Different letters indicate significant differences ($P < 0.05$) in treatments across plots. Bars are means ± SD.

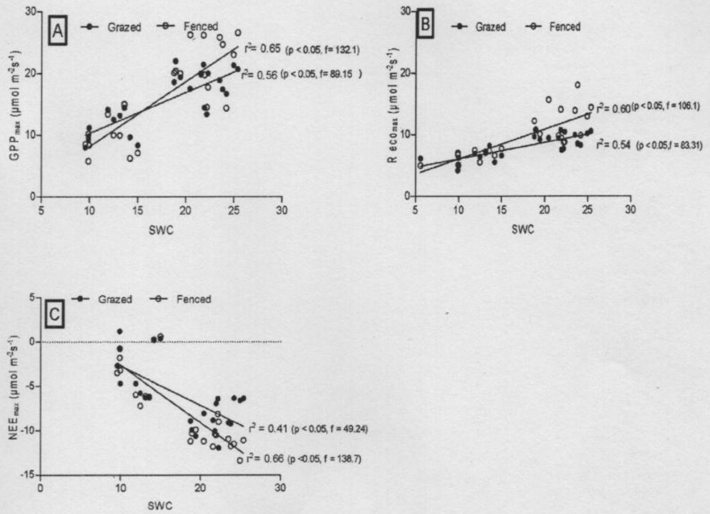

Fig. 5. Relationships between (A) GPP, (B) R_{eco}, (C) NEE and SWC within the 0–30 cm soil profile in the grazed and fenced plots, for the entire measurement period.

comparison to fenced plots, grazed plots recorded significantly higher bulk densities ($P < 0.05$). Grazed and fenced plots recorded mean soil bulk densities of 1.26 ± 0.14 and 1.03 ± 0.07 g cm^{-3} respectively. The interaction of grazing and rainfall reduction led to a significant ($P < 0.05$) increase in soil bulk density (Fig. 6).

4. Discussion

4.1. Influence of livestock grazing on aboveground biomass

The results of this study show a significant decline in total aboveground biomass as a result of livestock grazing (Table 1) which could be linked to harvesting by feeding animals (Ondier et al., 2019; Hao and He, 2019). The effects of grazing, including a reduction in leaf area and

Table 2
Plant and soil C/N measured in the studied plots. Values are means ± SD. Values not sharing the same letters indicate differences across plots (Tukey HSD, $P \leq 0.05$).

C/N concentrations In soil and aboveground tissue (%)	Grazed			Fenced		
	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)	Ambient rainfall (100%)	Reduced rainfall (50%)	Increased rainfall (150%)
Soil N	0.22 ± 0.03^{c}	0.086 ± 0.05^{d}	0.21 ± 0.01^{c}	0.5 ± 0.07^{b}	0.3 ± 0.01^{c}	0.9 ± 0.05^{a}
Soil C	2.27 ± 0.21^{a}	1.9 ± 0.09^{a}	2.1 ± 0.08^{a}	2.5 ± 0.31^{a}	2.1 ± 0.21^{a}	2.7 ± 0.41^{a}
Shoot N	1.6 ± 0.21^{abc}	0.9 ± 0.11^{d}	1.3 ± 0.04^{cd}	1.8 ± 0.40^{ab}	1.2 ± 0.8^{cd}	2.0 ± 0.06^{a}
Shoot C:N ratio	12.3 ± 3.1^{c}	7.2 ± 1.6^{d}	17.3 ± 4.9^{a}	16.6 ± 4.4^{ab}	13.3 ± 5.8^{c}	18.1 ± 2.7^{a}

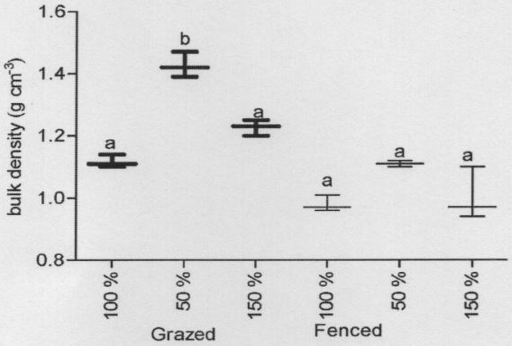

Fig. 6. Mean soil bulk density (g cm^{-3}) in grazed and fenced plots and at ambient rainfall, fifty percent rainfall reduction and fifty percent rainfall increment for the study period. Differences in letters indicate significant differences ($p < 0.05$) in treatments across plots.

increase in soil compaction (Fig. 6) often result in losses of soil organic matter including N (Table 2) which is needed for biomass development. Because soil organic matter improves soil physical structure and ecosystem services such as nutrient retention and water storage, its reduction could lead to reduced soil fertility and consequently reduced biomass (Toru and Kibret, 2019). Our results are in agreement with the findings of Yan et al. (2013) and Koerner and Collins (2014). However, studies by Frank et al. (2016) reported results contradictory to our study and linked grazing to increased soil nitrogen mineralisation, leaf nitrogen concentration and an overall increase in aboveground biomass.

4.2. Interaction of livestock grazing and rainfall manipulation on aboveground biomass

Soil moisture and grazing appear to interact to influence aboveground biomass development in African savannas (Sankaran and Ratnam, 2013). The reduction in green and dead biomass as a result of the interaction of grazing and rainfall reduction reported in our study could be expected (Table 1). As the reduced rainfall simulated drought, plant photosynthesis and GPP was likely curtailed, a conclusion supported by (K' Otuto et al., 2012; Quirk et al., 2019). Further, the reduction in total leaf area as a result of grazing reduced the photosynthetic capacity of the plants resulting in lower aboveground biomass. In most instances, grazed herbaceous vegetation recovers from the effect of animal grazing (Hempson et al., 2014). However, the recovery of such vegetation is dependent on factors such as the intensity and duration of grazing and the availability of soil moisture and nutrients (Leriche et al., 2003). In our grazed plots, however, grazing and reduction in rainfall induced both biotic and abiotic stresses to plants resulting in restricted growth and hence reduction in total aboveground biomass (Table 1). The reduction in soil moisture was further amplified by grazing which removed vegetation and exposed the soil to water loss through evaporation. Consequently, there could have been restricted nutrient uptake as water is the major medium for moving nutrients in plants (Ghosh et al., 2018). The resulting limitation in nutrients (Table 2) could have contributed to the reduction in aboveground biomass observed in our grazed plot under rainfall reduction. The increase in aboveground biomass resulting from the interaction of livestock grazing and rainfall increment was expected. As increase in soil moisture enhances mineralisation of soil nutrients (Kuzyakov and Cheng, 2001), there was increased nutrient availability to plant roots, resulting in increased biomass development (Oyun-Bat et al., 2016; Yao et al., 2019).

4.3. Influence of grazing on ecosystem CO_2 exchange

Our results revealed that livestock grazing significantly decreased ecosystem CO_2 exchange (Fig. 4). This could be true since grazing has been linked to reduced carbon assimilation and release (Liu et al., 2016). This can also be explained by the reduction in photosynthetically active biomass (Table 1) as a result of grazing and thereby less carbon uptake as studies have shown a strong relationship between GPP, NEE and the aboveground green biomass (Sjögersten et al., 2008; Liu et al., 2016). Through reduced photosynthetic surface, there is reduced carbon translocation to the roots resulting in lower microbial activity and hence reduced R_{eco} (Ondier et al., 2019). Our results are in agreement with reports from other savannas in Africa (Ciais et al., 2011; Tagesson et al., 2015). Studies conducted in grazed savannas and semiarid grasslands have shown strong relationships between GPP, NEE, and the aboveground green biomass (Sjögersten et al., 2008; K'Otuto et al., 2012; Nakano and Shinoda, 2015). Through the reduced photosynthetic surface area, there is reduced carbon assimilation and consequent translocation to the roots resulting in lower microbial activity and hence reduced R_{eco} (Ondier et al., 2019). A study by Susiluoto et al. (2008), which used similar methodology to ours in monitoring CO_2 exchange in a Finnish National Park, revealed that grazing had no influence (neutral impact) on ecosystem CO_2 exchange. The findings were explained by the fact that grazing increased vegetation heterogeneity resulting in varying carbon fluxes among the different plant functional groups. Our study however did not determine the link of grazing and vegetation heterogeneity. Other studies, however, revealed that urine and faecal matter from grazers contribute to higher ecosystem CO_2 exchange through stimulation of plant growth and rhizo-microbial activities (Jiang et al., 2012; Ritchie, 2020). Thus the responses of ecosystem CO_2 exchange to grazing maybe ecosystem-dependant and a function of other interacting environmental variables such as availability of soil moisture and plant species composition.

4.4. Interaction of livestock grazing and rainfall manipulation on herbaceous CO_2 exchange

The interaction of grazing and rainfall reduction led to a significant ($P < 0.05$) decrease in herbaceous GPP, R_{eco}, and NEE (Fig. 4abc). The decrease in CO_2 exchange is linked to the imposition of drought by grazing and rainfall reduction (Fig. 3). Plant response to drought conditions is through restriction of stomatal conductance, resulting in reduced CO_2 exchange (Tessema et al., 2020). Further, grazing and drought (through reduced rainfall) reduces photosynthetic biomass through direct harvesting and trampling by grazing animals and wilting due to the imposed drought (Tessema et al., 2020). Plant photosynthetic biomass has a direct link to CO_2 assimilation and release (K'Otuto et al., 2012; Ritchie, 2020), therefore, the reduction in biomass resulted in the observed reduction of GPP, NEE and R_{eco}. Liu et al. (2016) reported a similar decline in CO_2 assimilation and release in a Chinese rangeland and linked the result to drought that was imposed by the interaction of grazing and reduced rainfall. The interactive influence of grazing and rainfall increment resulted in a significant increase in GPP and NEE, but had no effect on R_{eco}. The increased GPP and dependant NEE further confirms the significant role of water in driving carbon exchange in this ecosystem (Fig. 5abc), however, being that R_{eco} is linearly dependant on soil temperature (Räsä;nen et al., 2016), it is possible that the increase in water moderated soil temperature resulting in neutral influence R_{eco}. Similar to findings of this study, GPP and NEE have been found to increase with increased rainfall in a grazed prairie ecosystem (Chemner and Welker, 2011). However, unlike our study that reported neutral influence of increased rainfall on R_{eco}, Zhang et al. (2010) reported increased R_{eco} with increasing rainfall whereas Li et al. (2019) reported decrease in R_{eco}, NEE and GPP with increased rainfall. Therefore, CO_2 exchange within the grazed ecosystems do not always respond directly or proportionately to rainfall variation (increase or decrease); either because of nonlinearity in soil moisture recharge in response to rainfall manipulation; or because of the variation in environmental factors such as temperature, which may modify CO_2 exchange.

5. Conclusion

Our results show that livestock grazing lowers productivity and CO_2 exchange through reduction in photosynthetic biomass and reduction in soil water content. The interaction of livestock grazing and rainfall reduction reduced CO_2 exchange through imposition and amplification of drought conditions. The increase in GPP and NEE as a result of the interaction of grazing and rainfall increment revealed the facilitative role of soil moisture in driving CO_2 exchange in this savanna, however the interaction of grazing and rainfall increment had no effect on R_{eco}, suggesting that herbaceous CO_2 exchange in the grazed savanna do not always respond directly or proportionately to the rainfall variation.

Abbreviations

Not applicable.

Ethical approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Authors' contributions

All authors contributed equally in the production of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

Non declared.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Allsopp, R., Baldry, T., 1972. A general description of the Lambwe Valley area of South Nyanza District, Kenya. World Health Organ. Bull. 47, 691–697.

Arnhold, S., Otieno, D., Onyango, J., Koeller, T., Huwe, B., Tenhunen, J., 2015. Soil properties along a gradient from hillslopes to the savanna plains in the Lambwe Valley, Kenya. Soil Tillage Res. 154, 75–83.

Bao, K., Tian, H., Su, M., Qui, L., Wei, X., Zhang, Y., Liu, J., Gao, H., Cheng, J., 2019. Stability of Ecosystem CO_2 Flux in response to changes in precipitation in a semiarid grassland. Sustainability 11 (9), 2597.

Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Korner, C., de Boeck, Hans, Christensen, J., Leuzinger, S., Janssens, I., Hansen, K., 2012. Precipitation manipulation experiments-challenges and recommendations for the future. Ecol. Lett. 15, 899–911.

Bombelli, M., Henry, S., Castsldi, S., Adu-Bredu, S., Arneth, A., Grandcourt, A., Grieco, E., Kutsch, W., Lehsten, V., Rasile, A., Reichstein, M., Tansley, K., Waber, U., Valentine, R., 2009. An outlook on the sub-saharan Africa carbon balance. Biogeosciences 6, 2195–2205.

Brady, N., Weil, R., 2002. The Nature and Properties of Soil, 13th ed. Pearson and Prentice Hall, Pearson Education Inc, Upper Saddle River, New Jersey.

Chemner, R., Welker, J., 2011. Influence of grazing and precipitation on ecosystem carbon cycling in a mixed-grass prairie. Pastoralism 1, 20.

Ciais, P., Bombelli, A., William, M., Piao, S., Chave, C., Ryan, M., Henry, M., Brender, P., Valentine, R., 2011. The carbon balance of Africa: synthesis of recent research studies. Philosophical Transactions of the Royal Society of America 369, 2038–2057.

Dimobe, K., Kouakou, J., Tondoh, J., Zoungrana, B., Forkuor, G., Ouedraogo, K., 2018. Predicting the potential impact of climate change on carbon stock in semi-arid West African savanna. Land 7, 124. https://doi.org/10.3390/land7040124.

Droesler, M., 2005. Trace gas exchange of bog ecosystems, Southern Germany. Lehrstuhl fur vegetationsokoloie. Doctoral Thesis. Technical University of Munich. http://www.wzw.tum.de/vegoek/publikat/dissdipl.html.

February, E., Higgins, S., Band, W., Swemmer, L., 2013. Influence of completion and rainfall manipulation on the growth and responses of savanna trees and grasses. Ecology 945, 1155–1164.

Fisher, R., Williams, M., Vale, DOR., Da Costa, A., Meir, P., 2006. Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. Plant Cell Environ. 29 (2), 151–165.

Frank, D., Wallen, R., White, P., 2016. Ungulate control of grassland production: grazing intensity and ungulate species composition in Yellowstone Park. Ecosphere 7 (11), e01603, 10/1002/ecs2.1603.

Ghosh, U., Chatterjee, A., Bremer, E., 2018. Determining the moisture and plant effect on nutrient release, and plant nutrient uptake using ion exchange resin membrane. Commun. Soil Sci. Plant Anal. https://doi.org/10.1080/00103624.2018.1432639.

Gilmanov, T., Soussana, J., Aires, L., Allard, V., Amman, C., Balzarolo, M., Bernhofer, C., Campbell, C., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, B., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Hazpra, L., Hensen, A., Ibrom, A., Jacobs, A., Jones, M., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Marcolla, B., Nagy, Z., Pilgaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M., Wohlfart, G., 2007. Partitioning European grassland net ecosystem CO2 exchange into grass primary productivity and ecosystem respiration using light response function analysis. Agric. Ecosyst. Environ. 121, 93–120.

Grace, J., Jose, S., Meir, P., Miranda, H., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savanna. Biogeography 33, 387–400.

Hao, Y., He, Z., 2019. Effect of grazing patterns on grassland biomass and soil environment in China. A meta-analysis. PloS One 14 (4), e0215223. https://doi.org/10.1371/journal.pone.0215223.

Hempson, G., Archibald, S., Bond, W., Ellis, R., Grant, C., Kruger, F., Kruger, L., Moxley, C., Owen-Smith, N., Peel, M., Smit, I., Vickers, K., 2014. Ecology of grazing lawns in Africa. Biol. Rev. 90 (3), 979–994.

Hoover, D., Knapp, K., Smith, D., 2014. Resistance and resilience of grassland ecosystem to climate extremes. Ecology 95, 2646–2656.

Jenerettem, G., Scott, R., Barron-Gafford, A., Huxman, T., 2009. Grass primary production variability associated with meteorology, physiology, leaf area, and water supply in contrasting woodland and grassland semiarid riparian ecosystems. Journal of Geographical Research: Biogeosciences 114, G04010. https://doi.org/10.1029/2009JG001074.

Jiang, Y., Tang, S., Wang, C., Zhou, P., Tenuta, M., Han, G., Huang, D., 2012. Contribution of urine and dung patches for grazing sheep to methane and carbon dioxide fluxes in an inner Mongolian desert grassland. Australus Journal of Animal Science 25, 207–212.

Konings, A., William, A., Gentine, P., 2017. Sensitivity of grassland productivity to aridity controlled stomatal and xylem regulation. Nat. Geosci. 104, 284–288.

K'Otuto, G., 2014. Effects of Agroecosytems on Carbon dioxide Exchange and Carbon Storage in the Herbaceous Layer of a Moist Savanna Ecosystem in Ruma, Lambwe Valley, Kenya. PhD. Thesis. Maseno University, Kenya (Maseno University, Kenya).

K'Otuto, G., Otieno, D., Seo, B., Ogindo, H., Onyango, J., 2012. Carbon dioxide exchange and biomass productivity of the herbaceous layer of a managed tropical savanna ecosystem in western Kenya. J. Plant Ecol. 6 (4), 286–297.

Kgosikoma, O., Mojeremane, W., Harvie, B., 2013. Grazing management systems and their effects on savanna ecosystem dynamics: a review. J. Ecol. Nat. Environ. 5 (6), 88–94.

Kioko, J., Kiringe, J., Seno, S., 2012. Impact of livestock grazing on a savanna in Kenya. Journal of Arid Land 4 (1), 29–35.

Koerner, S., Collins, S., 2014. Interactive effect of grazing, drought and fire on grassland plant communities in North America and South America. Ecology 95 (1), 98–109.

Kuzyakov, Y., Cheng, 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biol. Biochem. 33, 1915–1925.

Leriche, H., Roux, X., Desnoyers, F., Benest, D., Simion, G., Abbadie, L., 2003. Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. Ecol. Appl. 13 (5), 1346–1354.

Li, L., Zheng, Z., Biederman, J., Xu, C., Xu, Z., Che, R., Wang, Y., Cui, X., Hao, Y., 2019. Ecological responses to heavy rainfall depend on seasonal timing and multi-year reccurance. New Phytol. 223 (3), 647–660.

Li, Y., Tenhunen, J., Owen, K., Bahn, M., Droesler, M., Otieno, D., Schmidt, M., Gruenwald, T., Hussain, M., Mirzae, H., Bernhofer, C., 2008. Patterns in CO_2 exchange capacity of grassland ecosystems in the Alps. Agric. For. Meteorol. 148 (1), 51–68.

Liu, H., Zang, R., Chen, H., 2016. Effect of grazing on photosynthetic features and soil respiration of rangelands in the Tianshan Mountains of North West China. Sci. Rep. 6, 30087. https://doi.org/10.1038/srep30087.

Maitima, J., Mugatha, S., Mugisha, S., Mutie, I., 2010. Land use changes, impacts and options for sustaining productivity and livelihoods in the basin of Lake Victoria. J. Sustain. Dev. Afr. 12, 189–206.

Meza, F., Montes, C., Martinez, F., Ortiz, P., Kowalski, A., 2018. Soil water content effects on CO_2 exchange and actual evapotranspiration in a Mediterranean semiarid savanna of central Chile. Sci. Rep. 8, 8570.

Muriuki, G., Njoka, T., Reid, R., Nyariki, D., 2005. Tsetse control and landuse change in Lambwe valley, south western Kenya. Agric. Ecosyst. Environ. 106, 99–107.

Nakano, T., Shinoda, M., 2015. Modeling gross primary production and ecosystem respiration in a semiarid grassland of Mongolia. Soil Sci. Plant Nutr. 61, 106–115.

Nyongesa, M., 2010. Effects of Ungulate Herbivory and Tree Canopy on Ecosystem Processes in Ruma National Park, Kenya. MSc. Thesis. Maseno University, Kenya.

Okach, D., Ondier, J., Kumar, A., Rambold, G., Tenhunen, J., Huwe, B., Otieno, D., 2019. Livestock grazing and rainfall manipulation alter the patterning of CO_2 fluxes and biomass development of the herbaceous community in a humid savanna. Plant Ecol. 220, 1085–1100.

Ondier, J., Okach, D., Onyango, J., Otieno, D., 2019. Influence of rainfall amount and livestock grazing on soil respiration in a moist Kenyan savannah. Afr. J. Ecol. 58 (1), 92–99.

Osborne, C., Charles-Dominique, T., Stevens, N., Bond, W., Midgley, G., Lehmann, C., 2018. Human impacts in African savannas are mediated by plant functional traits. New Phytol. 220 (1), 10–24.

Otieno, D., Ondier, J., Arnhold, S., Okatch, D., Ruidsch, M., Lee, B., Kolb, A., Onyango, J., 2015. Patterns of CO_2 exchange and productivity of the herbaceous vegetation and trees in a humid savannah in western Kenya. Plant Ecol. 10, 1215–1236.

Otieno, D., Wartinger, M., Nishiwaki, A., Hussain, M., Muhr, J., Borken, W., Lischeid, G., 2009. Responses of CO_2 exchange and primary production of the ecosystem components to environmental changes in a mountain peatland. Ecosystems 12, 590–603.

Oyun-Bat, T., Shinoda, M., Cheng, Y., Purevdorj, Y., 2016. Effect of grazing and precipitation variability on vegetation dynamics in a Mongolian dry steppe. J. Plant Ecol. 9 (5), 508–519.

Peng, H., Li, X., Li, G., Zhang, S., Li, L., Zhao, G., Jiang, Z., Ma, Y., 2013. Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands China. Catena 109, 39–48.

Quirk, J., Bellasio, C., Johnson, D., Beerlin, D., 2019. Response of photosynthesis, growth and water relations of savannah-adapted tree and grass grown across high to low CO_2. Ann. Bot. 124, 77–89.

Ren, H., Xu, Z., Isbell, F., Huang, J., Han, X., Wan, S., Chen, S., Wang, R., Zeng, D., Jiang, Y., 2017. Exacerbated nitrogen limitation ends transient stimulation of grassland productivity by increased precipitation. Ecol. Monogr. 87, 457–469.

Ritchie, M., 2020. Grazing management, forage production and soil carbon dynamics. Resources. https://doi.org/10.3390/resources9040049.

Räsänen, M., Aurela, M., Vakkari, V., Beukes, J., Tuovinen, J., VanZyl, P., Josipovic, M., Venter, A., Jaars, K., Siebert, S., Laurila, T., Rinne, J., Laakso, L., 2016. Carbon balance of a grazed savanna grassland ecosystem in South Africa. Biogeosciences 14, 1039–1054.

Sankaran, M., Ratnam, J., 2013. African and Asian savannas. Encyclopaedia of Biodiversity 1, 58–74.

Scott, R., Biederman, J., Hamerlynck, E., Bavron-Gafford, G., 2015. The carbon balance pivot point of southwestern US semiarid ecosystems: insight from the 21st centuary drought. J. Geophys. Res.: Biogeosciences 120, 2612–2624.

Sjögersten, S., Van der Wal, R., Woodin, J., 2008. Habitat type determines herbivory controls over CO_2 fluxes in warmer arctic. Ecology 89 (8), 2103–2116.

Susiluoto, S., Rasilo, T., Pumpanen, J., Berninger, F., 2008. Effect of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian Fell Ecosystem. Arctic Antarct. Alpine Res. 40 (2), 422–431.

Synodino, D., Tiet, B., Lohmann, D., Jeltsch, F., 2018. The impact of inter-annual rainfall vaiability on African savannas changes with mean rainfall. J. Theor. Biol. 437, 92–100.

Tagesson, T., Fensholt, R., Cropley, F., Guiro, I., Horion, S., Ehammer, A., Ardo, J., 2015. Dynamics in carbon exchange fluxes for grazed semiarid savanna ecosystem in West Africa. Agric. Ecosyst. Environ. 205, 15–24.

Tessema, B., Sommer, R., Piikki, K., Soderstrom, M., Namirembe, S., Tamene, L., Nyawira, S., Paul, B., 2020. The potential for soil organic carbon sequestration in grasslands in East African countries: A review. Grassl. Sci. 663, 135–144.

Toru, T., Kibret, K., 2019. Carbon stock under major land use/land cover types of Hades sub-watershed, eastern Ethiopia. Carbon Bal. Manag. 14, 7. https://doi.org/10.1186/s13021-019-0122-z.

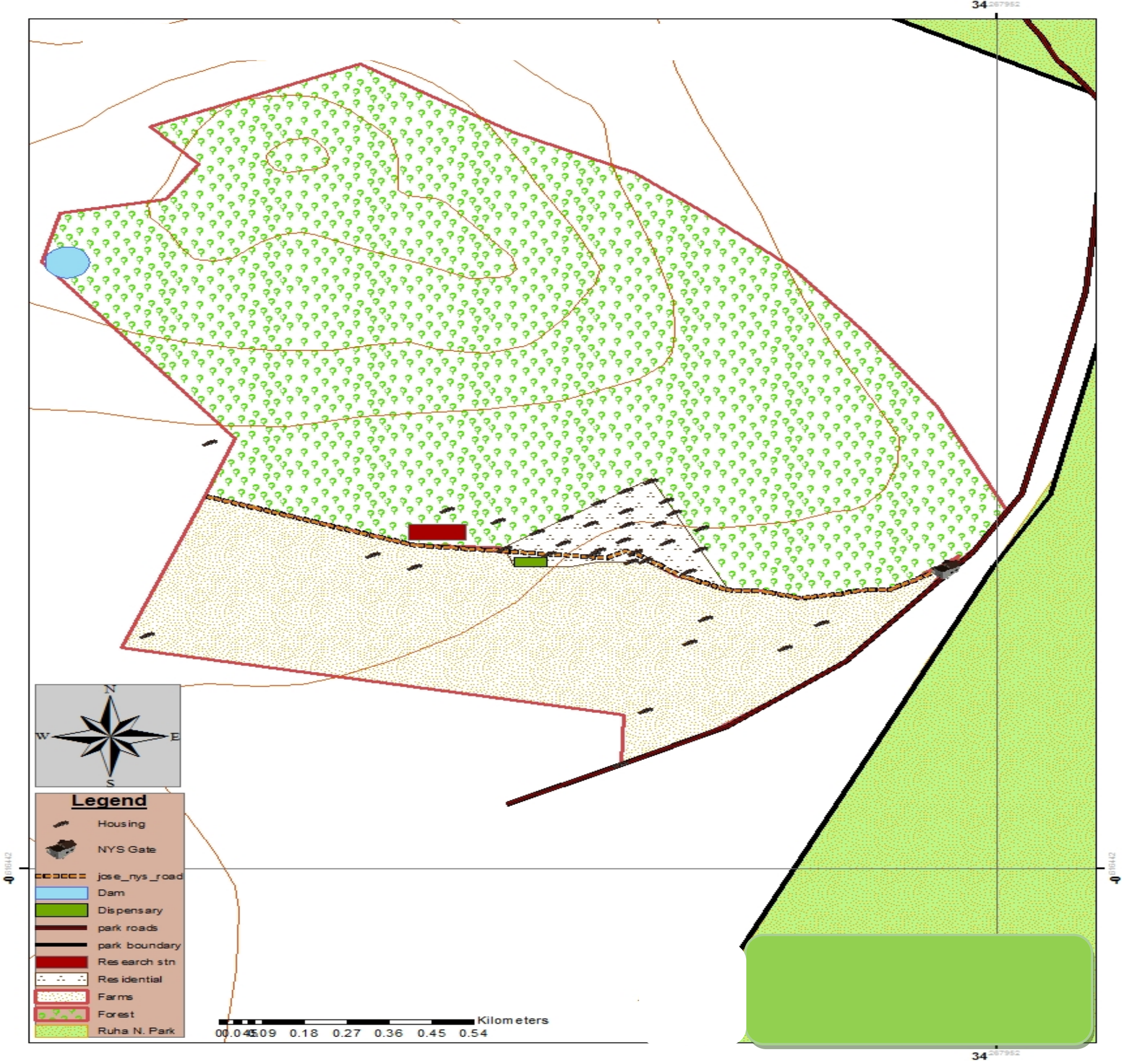
Yan, L., Zhou, G., Zhang, F., 2013. Effects of different grazing intensities on grassland production in China. A Meta-Analysis. PloS One 8 (12), e81466. https://doi.org/10.1371/journal.pone.0081466.

Yao, X., Wu, J., Gong, X., Lang, X., Wang, C., 2019. Grazing exclosure solely are not the best methods for sustaining alpine grasslands. Peer Journal 7, e6462. https://doi.org/10.7717/peerj.6462.

Zhang, H., Yu, H., Zhou, C., Zhou, H., Qian, X., 2019. Aboveground net primary productivity not CO_2 exchange remain stable under three timing of extreme drought in a semi-arid steppe. PloS One 14 (3), e0214418. https://doi.org/10.1371/journal.pone.0214418.

Zhang, L., Wylie, B., Lei, J., Gilmanov, T., Tieszen, L., 2010. Climate-driven interannual variability in net ecosystem exchange in the northern Great plains grasslands. Rangel. Ecol. Manag. 63, 40–50.

Appendix 3: A map showing the research site at Lambwe valley in Western Kenya



Appendix 4: ANOVA RESULTS

Table Analyzed GPP

Factorial ANOVA

Source of Variation	% of total variation	P value
Interaction	16.37	0.0014
Column Factor	53.03	< 0.0001
Row Factor	22.39	< 0.0001

Source of Variation	P value summary	Significant?
Interaction	**	Yes
Column Factor	***	Yes
Row Factor	***	Yes

Table Analyzed R_{eco}

Factorial ANOVA

Source of Variation	% of total variation	P value
Interaction	2.02	0.1802
Column Factor	83.25	< 0.0001
Row Factor	8.63	0.0014

Source of Variation	P value summary	Significant?
Interaction	ns	No
Column Factor	***	Yes
Row Factor	**	Yes

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	2	3.403	1.702	1.984
Column Factor	2	140.6	70.29	81.95
Row Factor	1	14.58	14.58	17.00
Residual	12	10.29	0.8578	

Table Analyzed NEE

Factorial ANOVA

Source of Variation	% of total variation	P value
Interaction	19.91	0.0002
Column Factor	57.43	< 0.0001
Row Factor	16.59	< 0.0001

Source of Variation	P value summary	Significant?
Interaction	***	Yes
Column Factor	***	Yes
Row Factor	***	Yes

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	2	73.95	36.97	19.69
Column Factor	2	213.4	106.7	56.82
Row Factor	1	61.64	61.64	32.84

Residual	12	22.53	1.877	

Table Analyzed Diversity (GvsF)

Two-way ANOVA

Source of Variation	% of total variation	P value
Interaction	1.62	0.2597
Column Factor	74.26	< 0.0001
Row Factor	0.00	0.9790

Source of Variation	P value summary	Significant?
Interaction	ns	No
Column Factor	***	Yes
Row Factor	ns	No

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	1	0.004199	0.004199	1.346
Column Factor	1	0.1921	0.1921	61.57
Row Factor	1	0.000002208	0.000002208	0.0007078
Residual	20	0.06240	0.003120	

Table Analyzed DIVERSITY (Gvs rainfall trs)

Factorial ANOVA Matching by cols

Source of Variation	% of total variation	P value
Interaction	32.44	0.0018
Time	11.53	0.0079
Column Factor	46.57	0.0009
Subjects (matching)	4.9370	0.4589

Source of Variation	P value summary	Significant?
Interaction	**	Yes
Time	**	Yes
Column Factor	***	Yes
Subjects (matching)	ns	No

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	2	0.06924	0.03462	21.52
Time	1	0.02461	0.02461	15.30
Column Factor	2	0.09941	0.04970	28.30
Subjects (matching)	6	0.01054	0.001756	1.092
Residual	6	0.009652	0.001609	

Table Analyzed Data 1

Two-way ANOVA (GPP-Tree vs Herb 2014)

Source of Variation	% of total variation	P value
Interaction	15.44	< 0.0001
Column Factor	28.96	< 0.0001
Row Factor	30.02	< 0.0001

Source of Variation	P value summary	Significant?

Interaction	***	Yes
Column Factor	***	Yes
Row Factor	***	Yes

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	23	283.3	12.32	11.33
Column Factor	1	531.3	531.3	488.8
Row Factor	23	550.7	23.95	22.03
Residual	432	469.5	1.087	

Two-way ANOVA(GPP-Tree vs Herb 2015)

Source of Variation	% of total variation	P value
Interaction	8.95	< 0.0001
Column Factor	68.62	< 0.0001
Row Factor	15.39	< 0.0001

Source of Variation	P value summary	Significant?
Interaction	***	Yes
Column Factor	***	Yes
Row Factor	***	Yes

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	23	275.3	11.97	23.90
Column Factor	1	2111	2111	4215
Row Factor	23	473.5	20.59	41.11
Residual	432	216.3	0.5008	

Table Analyzed Perennials

Factorial ANOVA

Source of Variation	% of total variation	P value
Interaction	2.91	< 0.0001
Column Factor	19.74	< 0.0001
Row Factor	77.34	< 0.0001

Source of Variation	P value summary	Significant?
Interaction	***	Yes
Column Factor	***	Yes
Row Factor	***	Yes

Source of Variation	Df	Sum-of-squares	Mean square	F
Interaction	2	3.847	1.923	2379000000000
Column Factor	2	26.06	13.03	16120000000000
Row Factor	1	102.1	102.1	126300000000000
Residual	6	0.000000000005	0.000000000001	

```
1 The GLM Procedure

 Dependent Variable: b_d   b/d

                                Sum of
        Source            DF       Squares     Mean Square    F Value    Pr > F
```

```
       Model                    5      0.40596111      0.08119222      45.39    <.0001

       Error                   12      0.02146667      0.00178889

       Corrected Total         17      0.42742778


                 R-Square     Coeff Var      Root MSE      b_d Mean

                 0.949777      3.697497      0.042295      1.143889


       Source                  DF     Type III SS     Mean Square    F Value    Pr > F

       land_use                 1      0.00000000       .              .       .
       ppt                      5      0.17702222      0.04425556      24.74    <.0001
```

```
1                               The GLM Procedure

 Dependent Variable: soilC   soilC

                                        Sum of
       Source                  DF         Squares     Mean Square    F Value    Pr > F

       Model                    5      1.29625000      0.25925000      Infty    <.0001

       Error                   12      0.00000000      0.00000000

       Corrected Total         17      1.29625000


                 R-Square     Coeff Var      Root MSE    soilC Mean

                 1.000000             0             0      2.261667


       Source                  DF     Type III SS     Mean Square    F Value    Pr > F

       land_use                 1      0.00000000       .              .       .
       ppt                      5      0.76580000      0.19145000      Infty    <.0001
```

```
1                               The GLM Procedure

 Dependent Variable: shoot_N   shoot N

                                        Sum of
       Source                  DF         Squares     Mean Square    F Value    Pr > F

       Model                    5      3.08500000      0.61700000      Infty    <.0001

       Error                   12      0.00000000      0.00000000

       Corrected Total         17      3.08500000


                R-Square     Coeff Var      Root MSE    shoot_N Mean

                1.000000             0             0        1.616667


       Source                  DF     Type III SS     Mean Square    F Value    Pr > F

       land_use                 1      0.00000000       .              .       .
       ppt                      5      0.88000000      0.22000000      Infty    <.0001
```

```
1                               The GLM Procedure
```

```
Dependent Variable: Soil_N   Soil N

                              Sum of
     Source              DF       Squares     Mean Square    F Value    Pr > F

     Model                5     1.29436000     0.25887200      Infty    <.0001

     Error               12     0.00000000     0.00000000

     Corrected Total           17     1.29436000


               R-Square     Coeff Var      Root MSE    Soil_N Mean

               1.000000            0            0      0.369333


     Source              DF     Type III SS     Mean Square    F Value    Pr > F

     land_use             1      0.00000000       .              .      .
     ppt                  5      0.59343200      0.14835800      Infty    <.0001
1                        The GLM Procedure

Dependent Variable: C_N_ratio   C:N ratio

                              Sum of
     Source              DF       Squares     Mean Square    F Value    Pr > F

     Model                5     251.9200000     50.3840000      Infty    <.0001

     Error               12      0.0000000       0.0000000

     Corrected Total           17     251.9200000


              R-Square     Coeff Var      Root MSE    C_N_ratio Mean

              1.000000            0            0         14.13333


     Source              DF     Type III SS     Mean Square    F Value    Pr > F

     land_use             1      0.0000000       .              .      .
     ppt                  5     189.2000000      47.3000000      Infty    <.0001
1                        The GLM Procedure

Dependent Variable: diversity   diversity

                              Sum of
     Source              DF       Squares     Mean Square    F Value    Pr > F

     Model                5     0.16515324     0.03303065      19.63    <.0001

     Error               12     0.02019028     0.00168252

     Corrected Total           17     0.18534353


              R-Square     Coeff Var      Root MSE    diversity Mean

              0.891066      5.828475      0.041019        0.703762


     Source              DF     Type III SS     Mean Square    F Value    Pr > F
```

```
      land_use                  1      0.00000000      .              .      .
      ppt                       5      0.13259057      0.03314764      19.70    <.0001
1                               The GLM Procedure

  Dependent Variable: dominance   dominance

                                      Sum of
      Source                   DF         Squares     Mean Square    F Value    Pr > F

      Model                     5      0.20337778      0.04067556      64.79    <.0001

      Error                    12      0.00753333      0.00062778

      Corrected Total          17      0.21091111


                R-Square     Coeff Var      Root MSE    dominance Mean

                0.964282      4.659079      0.025055          0.537778


      Source                   DF     Type III SS     Mean Square    F Value    Pr > F

      land_use                  1      0.00000000      .              .      .
      ppt                       5      0.00282222      0.00070556       1.12    0.3906
```