Effects of livestock grazing and rainfall variability on the structure and function of the herbaceous layer community of a humid savanna ecosystem in Lambwe Valley - Kenya.

DISSERTATION

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Submitted by

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TABLE OF CONTENT

Abstract

Savanna ecosystems have undergone structural and functional transformations in the last two centuries, following a shift in the grazing communities from predominantly migratory wild mega-herbivores, to sedentary domestic herbivore populations (livestock). The dominance of livestock and their sedentary grazing patterns have increased pressure on the herbaceous layer communities. Changes in rainfall regimes, characterized by shorter but more intense rainy seasons (flooding) and prolonged dry seasons (drought) have also occurred during the same period. This transformation threatens the sustainability of the herbaceous layer, but has rarely been studied.

Rapid increase in livestock populations in Lambwe Valley, a typical savanna in Western Kenya, has increased grazing pressure on the herbaceous vegetation during the last three decades. Extended dry periods and shorter, but more intense, rainy periods have also become common in the region. Phenotypic and structural alterations caused by the ongoing grazing pressure and increased rainfall variability are likely the visible ramification of the changing ecosystem processes, taking place at the background, and which have rarely been investigated. Lambwe valley is, therefore, a suitable study object for understanding how savanna ecosystems respond to the ongoing changes in grazing and rainfall variability. This study investigated how two levels of livestock grazing (grazed and ungrazed) and three levels of rainfall amounts (50%, 100%, and 150% of ambient) affected (i) soil properties; (ii) plant species diversity, and (iii) CO_2 fluxes in the herbaceous layer community during dry and wet periods. Study plots were abbreviated using first letters of the grazing levels (grazed - G or ungrazed - U) followed by the amounts of rainfall (50%, 100% and 150%) i.e. G50%.

Volumetric soil water content (VWC) increased along a rainfall gradient of 50–150% (RMSE = 3.55; $r^2 = 0.61$; $p < 0.05$), from an average amount of 17.5 ± 4.9% to 26.9 ± 4.9% in the G50% and U150% plots, respectively. This shows that rainfall was the main source of water at

the 20 cm soil depth during the measurement period. The grazed plots had higher soil bulk density of 3.2% and nitrogen (N) content of 7.8% compared to the ungrazed, however, VWC and soil carbon (C) content decreased by 19.64% and 11.45%, respectively in the grazed plots compared to the ungrazed. Reducing the ambient rainfall by 50% had a significant effect ($p < 0.05$) on the soil properties compared to a 50% increase (150%). VWC significantly correlated to soil bulk soil density ($r^2 > 0.62$; $p = 0.05$).

Livestock grazing increased species diversity (H), but decreased aboveground biomass (AGB). *Hyparrhenia fillipendulla* (Hochst) Stapf. and *Brachiaria decumbens* Stapf, dominated the ungrazed plots, making up > 70% of the relative abundance and a larger proportion of AGB. Mean H did not vary amongst G50%, G100%, and G150% plots. In the ungrazed plots, however, H was higher in the U100% than both U50% and U150% plots. The AGB and species abundance mediated (indirect-only mediation) the effect of VWC on H.

The highest mean net ecosystem exchange (NEE) of -8.80 ± 2.26 µmol m^{-2} s^{-1}, AGB of 1208.41 g m^{-2}, and total biomass of 1589.06 g m^{-2} were reported in the U150% plot during the wet months. VWC significantly correlated ($p < 0.05$) to the changes in NEE ($r^2 \geq 0.65$), ecosystem respiration (R_{eco}) ($r^2 \geq 0.52$), gross primary production (GPP) ($r^2 \geq 0.71$), and total biomass ($r^2 \geq 0.61$) across plots. CO_2 fluxes and the total biomass of the herbaceous layer community decreased due to: grazing by livestock; 50% reduction of ambient rainfall; and during the dry months, when VWC was lower. During the dry months, NEE in the G50% plot declined to 3.68 ± 0.81 µmol m^{-2} s^{-1}, from -3.06 ± 1.56 µmol m^{-2} s^{-1}, observed when soil moisture was high. The interaction among grazing, rainfall manipulation, and seasonality in rainfall significantly regulated AGB, total biomass, and root to shoot biomass ratio (R:S).

The total amount of rainfall received during the entire period of measurement directly affected soil moisture availability, however, variations in VWC among the plots resulted from the interaction of livestock grazing and rainfall manipulation. Grazing and reduction of ambient rainfall decreased the soil C content, species diversity, CO_2 uptake, and biomass production, particularly, during the dry months when the negative effects were more pronounced. By reducing biomass of the most dominant species, grazing increased species diversity. This study demonstrated that the Lambwe Valley ecosystem has adjusted to the current grazing levels and rainfall amounts. Future decrease or increase in current ambient rainfall or grazing exclusion will lower herbaceous species diversity, due to adaptation of the current vegetation types to grazing under ambient rainfall amount. Interaction between livestock grazing and variation in rainfall amount will inform sustainable management strategies to regulate the herbaceous diversity and productivity.

Zusammenfassung

Die Ökosysteme der Savannen haben in den letzten Jahrhunderten strukturelle und funktionelle Veränderungen durchlebt, anschließend folgte eine Verschiebung der Weidegemeinschaften von überwiegend wild umher wandernden Megaherbivoren zu Großteils domestizierten Herbivorenpopulationen (Nutztiere). In Folge dessen wurde der Druck auf die Krautschichtgemeinschaft durch die Dominanz der Nutztiere und ihre sesshaften Weidemuster erhöht. Ebenso sind Veränderungen der Niederschlagsbilanz, gekennzeichnet durch kürzere, aber intensivere Regenzeiten (Überschwemmungen) und längere Trockenzeiten (Dürren), im gleichen Zeitraum aufgetreten. Dieser Wandel bedroht die Zukunftsfähigkeit der Krautschicht, wurde bis dato jedoch selten untersucht. Der rasante Anstieg der Viehbestände im Lambwe Valley, einer typisch afrikanischen Savanne, hat in den letzten drei Jahrzehnten zunehmend den Weidedruck auf die Vegetation erhöht. Verlängerte Trockenzeiten und kurze, aber zugleich intensivere Regenzeiten sind in der Region üblich geworden. Phänotypische und strukturelle Veränderungen, durch den anhaltenden Weidedruck und die erhöhte Niederschlagsvariabilität, sind wahrscheinlich die sichtbaren Konsequenzen der sich verändernden Ökosystemprozesse, die im Hintergrund stattfinden und bisher selten untersucht wurden. Das Lambwe Valley ist daher ein geeignetes Untersuchungsobjekt, um zu verstehen, wie die Ökosysteme der Savannen auf die anhaltenden Veränderungen der Weide- und Niederschlagsvariabilität reagieren. Diese Studie untersuchte, wie sich zwei Arten der Beweidung (beweidet und unbeweidet) und drei verschiedene Niederschlagsmengen (50%, 100%, und 150% des Umgebungsniederschlages) auf (i) Bodenbeschaffenheit; (ii) Vielfalt der Pflanzenarten und, (iii) CO_2-Flüsse in der Krautschicht während Dürre- und Nassperioden auswirken. Die Untersuchungsflächen wurden mit dem ersten Buchstaben der Beweidungsart (beweidet - G oder unbeweidet - U) abgekürzt, gefolgt von den Niederschlagsmengen (50%, 100% und 150%), z.B. G50%.

Der volumetrische Bodenwassergehalt (VWG) stieg entlang eines Niederschlagsgradienten von 50-150% (RMSE = 3,55; $r^2 = 0,61$; $p < 0,05$), von einer durchschnittlichen Menge von 17,5 ± 4,9% auf 26,9 ± 4,9% in den G50%- bzw. U150%-Flächen. Dies zeigt, dass der Niederschlag während der Messperiode in 20 cm Bodentiefe die Hauptwasserquelle war. Die beweideten Flächen hatten eine höhere Bodendichte von 3,2% und einen Stickstoffgehalt von 7,8% im Vergleich zu den nicht beweideten Flächen, jedoch gingen der VWG und der Bodenkohlenstoffgehalt auf den beweideten Flächen im Vergleich zu den nicht beweideten Flächen um 19,64% bzw. 11,45% zurück. Die Reduktion des Umgebungsniederschlages von 50% hatte einen signifikanten Einfluss ($p < 0,05$) auf alle Bodenbeschaffenheiten im Vergleich zu einem 50%igem Anstieg (150%).

Der VWG korrelierte signifikant mit der Bodendichte ($r^2 > 0,62$; $p = 0,05$). Die Beweidung erhöhte die Artenvielfalt (H), verringerte jedoch die oberirdische Biomasse (AGB). *Hyparrhenia fillipendulla* (Hochst) Stapf. und *Brachiaria decumbens* Stapf, dominierten auf den unbeweideten Flächen und machten > 70% der relativen Häufigkeit und einen noch größeren Anteil der AGB aus. Der Mittelwert der Artenvielfalt (H) variierte nicht zwischen G50%, G100% und G150%. Allerdings wiesen die unbeweideten Flächen eine höhere Artenvielfalt (H) in U100% im Gegensatz zu U50% und U150% auf. Die AGB und der Artenreichtum vermitteln (nur unter indirektem Einfluss) den Effekt von VWG auf die Artenvielfalt (H). Der höchste mittlere Nettoökosystemaustausch (NEE) von –8,80 ± 2,26 µmol m^{-2} s^{-1}, eine AGB von 1208,41 g m^{-2} und eine Gesamtbiomasse von 1589,06 g m^{-2} wurden im U150%-Plot während der feuchten Monate gemessen. Das VWG korrelierte über alle Messflächen hinweg signifikant ($p < 0,05$) mit Veränderungen im NEE ($r^2 \geq 0,65$), in der Atmung des Ökosystems (R_{eco}) ($r^2 \geq 0,52$), in der Bruttoprimärproduktion (BPP) ($r^2 \geq 0,71$) und in der gesamten Biomasse ($r^2 \geq 0,61$). CO_2-Flüsse und die Gesamtbiomasse der Krautschicht nahmen bei Beweidung, sowie bei 50%iger Reduktion der

Umgebungsniederschläge und auch während den Trockenmonaten, als der VWG niedrig war, ab. Bei einer hohen Bodenfeuchte wurde beobachtet, dass während der Trockenmonate der NEE im G50%-Plot auf 3,68 ± 0,81 µmol m^{-2} s^{-1}, von –3,06 ± 1,56 µmol m^{-2} s^{-1} gesunken ist. Das Zusammenspiel von Beweidung, Niederschlagsmanipulation & Saisonalität der Niederschläge regulierte signifikant die AGB, die Gesamtbiomasse und das Biomassenverhältnis von Wurzel zu Spross (R:S). Die Gesamtniederschlagsmenge, die während des gesamten Messzeitraums dokumentiert wurde, wirkte sich direkt auf die Verfügbarkeit der Bodenfeuchte aus, jedoch ergaben sich die Schwankungen der VWG zwischen den Flächen aus dem Zusammenspiel von Beweidung und Niederschlagsmanipulation. Die Beweidung und Reduzierung der Umgebungsniederschläge reduzierten den Kohlenstoffgehalt des Bodens, die Artenvielfalt, die CO_2-Aufnahme und die Produktion von Biomasse, insbesondere in den trockenen Monaten, in denen die negativen Auswirkungen stärker ausgeprägt waren. Durch die Verringerung der Biomasse der dominierenden Arten erhöhte die Beweidung die Artenvielfalt. Diese Studie zeigte, dass sich das Ökosystem des Lambwe Valleys an die aktuellen Weide- und Niederschlagsmengen angepasst hat. Die zukünftige Ab- oder Zunahme der aktuellen Niederschlagsmengen oder der Ausschluss von Weidegang wird die Vielfalt der Krautarten aufgrund der Anpassung der aktuellen Vegetationstypen an die Beweidung unter der Menge des Umgebungsniederschlages verringern. Die Wechselwirkung zwischen der Beweidung durch das Vieh und der Variation der Niederschlagsmenge wird in nachhaltige Managementstrategien einfließen, um die Pflanzenvielfalt und Produktivität zu regulieren.

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List of figures

List of tables

List of abbreviations

Abbreviation/symbol	**Definition**	**Unit(s)**
AGB	Aboveground biomass	g/m^{-2}
a.s.l.	above sea level (altitude)	m
BES	British Ecological Society	
BGB	Belowground biomass	g/m^{-2}
C content	Amount of carbon present in the soil	%
C:N ratio	Ratio of soil carbon and nitrogen	
D_{mg}	Margalef's index of Richness	
GCM	Global Circulation Models	
GPP	Gross primary production	µmol m^{-2} s^{-1}
H	Shannon index of diversity	
IPCC	Intergovernmental Panel on Climate Change	
J	Pileou's index of evenness	
KNBS	Kenya National Bureau of statistics	
N content	Amount of nitrogen present in the soil	%
NEE	Net ecosystem exchange	µmol m^{-2} s^{-1}
PAR	Photosynthetic active radiation	µmol m^{-2} s^{-1}
PVC	polyvinyl chloride plastic	
R_{eco}	Canopy/ecosystem respiration	µmol m^{-2} s^{-1}
RMPs	Rainfall manipulation plot(s)	
RMSE	Root mean square error	
R:S ratio	Proportion of root to soot biomass allocation	
S	Number of species	
SID	Society for International Development	
SOC	Soil organic carbon	g/kg soil
Soil ρ (BD)	Soil bulk density	g cm^{-3}
SON	Soil organic nitrogen	g/kg soil
TLU	Tropical livestock Unit	number/ha^{-1}
VWC (θ_v)	Volumetric water content	%

Chapter one: Synopsis

1.1 General background

1.1.1 Distribution of the savanna ecosystems in Africa

Savanna ecosystems cover 20% of the earth's surface (Scholes and Walker, 1993) and accounts for 30% of the global net primary production (NPP) (Grace et al., 2006; Reynolds et al., 2005; Ritcher and Houghton, 2011). Approximately 40% of the African continent is savanna (Furley, 2006; Osborne et al., 2018; Scholes et al., 2002). Found between 10–30° latitudinal range, savanna ecosystems experience high radiation loads, characterized by high daily temperatures, and distinct seasonality in rainfall, which affect soil moisture availability. These properties play an important role in defining the ecosystem's structure and function (Scholes et al., 2002; William and Albertson, 2004).

Proximity of the savanna ecosystems to the equator determines whether they are humid or dry (Bond, 2008; Ford, 2009; Sankaran and Ratnam, 2013). Most of them are wetter at lower latitudes due to the prevailing equatorial climate (Ford, 2009; Nicholson, 2013; Sinclair and Fryxell, 1985). Towards the higher latitudes, however, the mean daily temperatures gradually increase, making the savanna over there drier. Exceptions occur, for example in the southern parts of Africa, where patches of humid savanna ecosystems are found in Lesotho, Malawi, South Africa and Zimbabwe (Ingvar, 1992), mostly due to the influence of relief. In the horn of Africa and Sahel regions, humid savanas are found in Chad, Ethiopia, Somalia, Sudan, and the northern parts of Kenya (Sinclair and Fryxell, 1985). In West Africa, a humid savanna ecosystem (Guinea savanna) extends from Senegal to Nigeria, and borders the Equitorial forest. Higher annual rainfall (> 650 mm) in most of the humid savanna increase the rate of nutrient leaching and lowers soil fertility, making these ecosystems dystrophic (Sankaran and Ratnam, 2013; Scholes and Walker, 1993).

Humid savanna ecosystems form dense vegetation cover constituting mainly grasses, forbs, shrubs, and trees (Scholes and Walker, 1993). Their structural composition regarding the dominant life forms, however, depends on vegetation's response to variations in temperature, soil fertility, and rainfall (Sankaran and Ratnam, 2013; Shorrocks, 2007). The different vegetation forms coexist due to an elaborate competition/facilitation mechanism that allows the maintenance of spatial structuring within the ecosystem (Sankaran et al., 2004; Scholes and Archer, 1997). Humid savanna ecosystems are more productive compared to their arid counterparts, however during the dry seasons, they lose a substantial amount of herbaceous biomass due to senescence imposed by severe water stress (Oesterheld et al., 1999). Thus, ecosystem processes such as CO_2 uptake, plant growth, and the general plant cell metabolism significantly decline during the dry season. The reduction in soil moisture particularly affects the herbaceous layer communities more, influencing plant species diversity and ecosystem productivity (Lloyd et al., 2008).

1.1.2 Influence of biotic and abiotic factors on savanna structure and functions

Interactions amongst biotic and abiotic factors govern the structural and functional attributes of savanna ecosystems globally (Bond et al., 2008; Lehmann et al., 2011; Sankaran and Anderson, 2009). Rainfall, temperature, hydrology, herbivory, fire incidences, soil properties, and human activities regulate the physiognomy of the savanna (Higgins et al., 2000; Sankaran and Ratnam, 2013; Scheiter et al., 2012). According to Sankaran and Anderson (2009), structural and functional shifts in the savanna depend on the direct and indirect effects of external (soil properties and climate) and internal (fire and herbivory) drivers on the vegetation and soil (Figure 1). An external driver constrains the effects of different drivers within an ecosystem, without being directly affected, while an internal driver modifies the structural and functional components of an ecosystem (Sankaran and Anderson, 2009). Structural differences across most savanna ecosystems, however, arise from dominant plant life forms, spatial patterns of trees, and soil characteristics (Sankaran and Ratnam, 2013; Scholes and Archer, 1997).

Combined biotic and abiotic factors influence most ecosystem functions through variations in soil physical and chemical properties (Zeppel et al., 2014). For instance, the combined influence of rainfall variability and grazing on soil moisture and nutrient availability effectively regulate primary productivity and species diversity (Anderson et al., 2007; Augustine, 2003; Dangal et al., 2016; Koerner and Collins, 2014; Scholes and Archer, 1997). Rainfall and nutrients potentially moderate the negative effects of fire and grazing on savanna ecosystems, therefore, regulating ecosystem functions and processes (Dangal et al., 2016; Koerner and Collins, 2014). Scheiter et al. (2015), explored the interaction between future climatic conditions and fire using dynamic vegetation models to predict C sequestration and grass productivity at a regional scale. They showed that C storage in the savanna depends on seasonality in rainfall.

Structural transformation of the savanna in the last centuries has significantly influenced key functionalities, thus affecting ecosystem services (Osborne et al., 2018). According to Brearley and Thomas (2015), expansion of agriculture and pastoralism in the sub-tropical savanna ecosystems have reduced soil organic matter, degraded the soils, and reduced soil microbial activities, thus, diminishing soil resource base. Degradation of savanna ecosystems also results from settlement due to the increasing human population; logging for fuel provision and construction materials; increased agriculture to boost food security; livestock keeping as a cultural practice, among other causes (Said et al., 2016; Sankaran and Ratnam, 2013; Scholes and Archer, 1997). Grazing, however, dominates these land uses due to the strong values attached to livestock ownership in the tropical regions, causing intense degradation of the savanna ecosystems (Kaur, 2006; Meitzer, 1995). This makes livestock grazing a key component for scrutiny, given its varied effects across ecosystems. Habitat destruction and soil degradation caused by grazing of livestock compromise the ecosystem's capacity to provide essential services (Kaur, 2006), including reduced primary productivity, decreased biodiversity, and increased CO_2 emission into the atmosphere (Grace et al., 2006; Malhi, 2017; Osborne et al., 2018; Searchinger et al., 2015). The impact of livestock grazing may however, be moderated by rainfall in ways that are not clearly understood. This makes rainfall an important parameter of study, to establish the extent to which it modifies the structure and functions of the herbaceous community in a grazed humid savanna ecosystem.

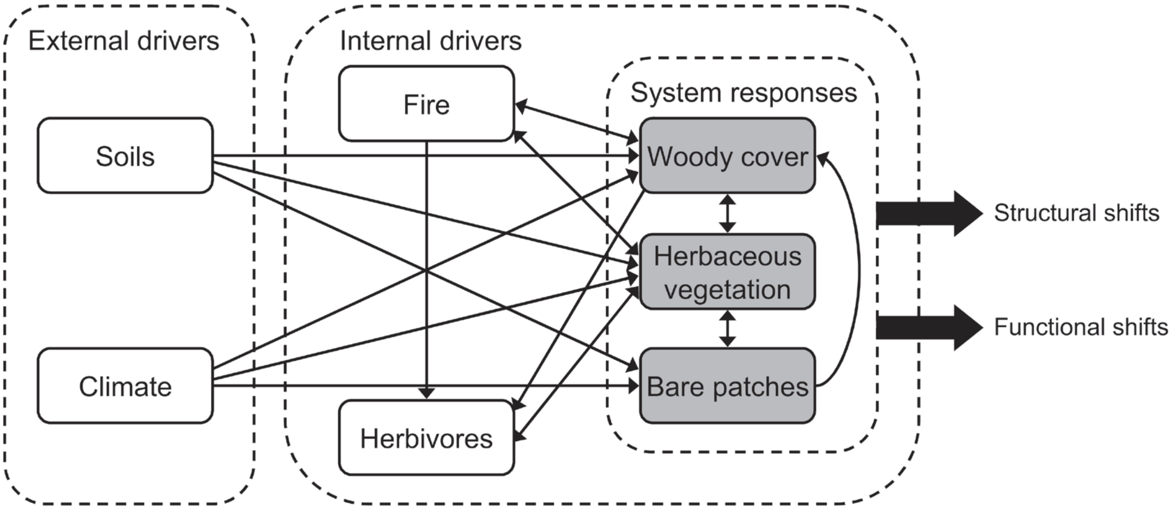

Figure 1: An illustration of the relationships amongst factors that govern structural and functional attributes of plant communities in a typical African savanna ecosystem. Unidirectional arrows (→) show causal relationships of variables on others, whereas, double headed arrows (↔) show correlational associations between variables. Adopted from Sankaran and Anderson, (2009).

1.1.3.1 Ecosystem response to grazing by herbivores

Savanna ecosystems have evolved with grazing as a modifier of their structural and functional properties (Asner et al., 2016; Schuman et al., 1999), through the action of herbivores on vegetation and soil (Augustine, 2004; Augustine and McNaughton, 2006; Harrison and Bardgett, 2004; Piñeiro et al., 2010). Increased human population, the rise in agriculture, animal husbandry, and indiscriminate hunting in the past 12,000 years, significantly reduced the population of wild mega-herbivores (> 1000 kg body weight) that previously dominated the savanna (Anderson et al., 2016; Bocherens, 2018; Malhi et al., 2016). Due to their free-range grazing patterns, the wild mega-herbivores facilitated species coexistence, seed dispersal, nutrient cycling, and promoted large-scale spatial heterogeneity in vegetation formations (Bernard et al., 2014; Malhi et al., 2016; Marshall et al., 2018). Currently, ecosystems hosting the remnants of wild mega-herbivores include some protected tropical areas in Africa and Asia (Bocherens, 2018; Malhi et al., 2016; Ripple et al., 2015), however, their population keeps dwindling due to over-exploitation for game meat and body parts (Ripple et al., 2015). Despite contributing 40–70% of the total mammalian biomass in savanna ecosystems, wild mega-herbivores currently constitute only a small fraction of the total herbivore population, rodents included (Anderson et al., 2016; Johnson, 2009). In contrast, the global population of livestock (ruminants) has steadily increased over the same time to a current estimation of 3.6 billion (Ripple et al., 2015), although they are still outnumbered by the mega-herbivores. The large population of livestock in the savanna, coupled with their sedentary grazing patterns have significantly reduced the available forage due to high stocking rates and degraded the soils through trampling, hence affecting the structure and function of these ecosystems (Anderson et al., 2016; Augustine and McNaughton, 2006; Marshall et al., 2018).

Numerous studies have focussed on the influence of wild herbivores on the savanna (Anderson et al., 2007; Augustine and McNaughton, 2004; Bardgett and Wardle, 2003; Charles et al., 2017; Koerner and Collins, 2014), but a few have addressed the impacts of grazing livestock on the ecosystem (K'Otuto et al., 2012; Owensby et al., 2006). For instance, trampling by livestock increases soil bulk density through compaction, decreases soil water infiltration and availability to the vegetation and soil microbes (Batey, 2009; Holdo and Mack, 2014; Tate et al., 2004). Livestock also add nutrients to the soil through dung and urine deposition (Bardgett and Wardle, 2003; Olff and Ritchie, 1998). They clip the vegetation, hence regulate the herbaceous biomass, CO_2 exchange (K'Otuto et al., 2012; Otieno et al., 2011) and species diversity (Augustine and McNaughton, 2006).

Past studies show that the effect of trampling by livestock on soil properties in the savanna ecosystems increases with grazing intensity (Arnhold et al., 2015; Brearley and Thomas, 2015; Holdo and Mack, 2014; Piñeiro et al., 2010). For instance, at higher grazing intensities, trampling alters processes that are sensitive to soil moisture variation such as nitrification, volatilization, leaching, and organic matter decomposition due to soil compaction (Adviento-Borbe et al., 2006; Drewry et al., 2000; Savadogo et al., 2007). Compaction further affects soil organic carbon (SOC) and nitrogen (SON) contents and alters soil nutrient availability (Piñeiro et al., 2010; Schuman et al., 1999). Higher grazing intensity either increases soil C due to enhanced fine root density (Reeder et al., 2004; Schuman et al., 1999) or decreases it when livestock compact soils, hindering root penetration during plant growth (Derner et al., 2006; Savadogo et al., 2007).

Grazing as a modifier of the structural components in savanna ecosystems is pivotal in influencing species diversity, seasonally and across precipitation gradients (Pandey and Singh, 1992). Livestock grazing opens the dense herbaceous canopies to allow species, out-performed by dominant ones, to access resources including water and sunlight (Owensby et al., 2006; Verblen and Young, 2010). This promotes co-existence amongst various species and enhances plant community diversity (Verblen and Young, 2010). Some studies, however, show that varying grazing intensities have differential effects on species diversity of the herbaceous layer communities (Adler et al., 2011; Graham and Duda, 2011). At lower grazing intensities, species diversity in the herbaceous communities increase (Koerner and Collins, 2014; Hanke et al., 2014) but declines as grazing intensifies (Anderson et al., 2007). Higher grazing intensity therefore threatens sustainable species diversity of the savanna by removing key species that drive richness (Frank, 2005). On the contrary, moderate grazing intensities increase plant diversity (Harisson and Bardgett, 2004; Kioko et al., 2012) by reducing competition amongst species through preferential feeding of the dominant species, thus promoting regeneration of less dominant plants (Olff and Ritchie, 1998). This creates spatial heterogeneity between grazing tolerant (increasers) and non-tolerant (decreasers) plant species (Walker et al., 1997) as a way of enhancing resource utilization, for their survival.

Grazing increases, decreases or has no effect on CO_2 exchange rates and biomass production of the herbaceous vegetation (Bremer et al., 1998; Frank, 2007; Owensby et al., 2006). This, however, depends on canopy structure, grazing intensity, history, and the herbivores involved (Marshall et al., 2018). Reduction of vegetation cover through grazing reduces net CO_2 assimilation (GPP) due to reduced CO_2 uptake and higher net ecosystem respiration - R_{eco} (Grace et al., 2006; Otieno et al., 2011; Wilsey et al., 2002). The ecosystem, in this case, potentially transforms into a net C source. On the contrary, low grazing intensity enhances CO_2 uptake when the younger and more active leaves in the herbaceous layer community replace the clipped ones (Owensby et al., 2006). Scanty information, however, still exists on the response of humid savanna ecosystems to livestock grazing. Studies on carbon sequestration in dry and humid savanna of East Africa established links between grazing and C budget and recommended proper management of grazed systems for sustainable primary productivity and carbon storage (Augustine and McNaughton, 2006; Kioko et al., 2012; K’Otuto et al., 2012; Otieno et al., 2011).

1.1.3.2 Ecosystem response to changes in rainfall amounts

Distinct seasonality in rainfall, common in savanna ecosystems (Kutsch et al., 2008; Osborne et al., 2018; Scholes et al., 2002; William and Albertson, 2004), essentially modify the vegetation structure and functions. Seasonality in rainfall influences CO_2 exchange rates (Ago et al., 2015; K'Otuto et al., 2014; Kutsch et al., 2008), species diversity, biomass production (Augustine, 2003; Austin and Sala, 2002; Frank, 2005), soil organic matter decomposition (Austin, 2002; Kutsch et al., 2008; Makhado and Scholes, 2011), plant phenology, and physiology (Merbold et al., 2009; William and Albertson, 2004; Zeppel et al., 2014). However, most arid and semi-arid savanna ecosystems experience prolonged drought interrupted by rainfall pulses (William et al., 2009). These ecosystems optimize their productivity using the available rainwater (William and Albertson, 2004). The episodic rainfall enhances microbial decomposition, community succession, germination, and growth of plants (Schwinning and Sala, 2004), that are sensitive to rewetting preceded by a long dry spell.

Prolonged drought imposes physiological stress on plants, hinders CO_2 uptake, reduces GPP and C storage in soil and plants, and increases C emission into the atmosphere (Grace et al., 2006; van der Molen et al., 2011). Consequently, most ecosystems transform into net C sources or weak sinks during dry seasons (Veenendaal et al., 2004). However, during the rainy seasons, increased soil moisture alleviates the adverse effects of drought on C balance by enhancing CO_2 uptake (Grace et al., 2006). This depends on habitat, microclimate, soil properties, and plant functional types (Sarmiento et al., 2004; Zeppel et al., 2014).

Huntington (2006), IPCC (2007) projected that the effects of extreme rainfall events (floods and drought) will adversely degrade vegetation and soil resources, by 2100, shifting the structural and functional patterns of savanna ecosystems. These reports recommended further research to evaluate the extent to which the fluctuation in rainfall intensities may affect sustainable productivity and the management of ecosystems. Consequently, studies that evaluate the impacts of extreme rainfall events and its variability in humid and dry ecosystems have increased in the last 2 decades (Smith, 2011; Zeppel et al., 2014). Global Circulation Models (GCM) predict a more spatially heterogeneous and less predictable change in precipitation both at local and regional scales (Christensen and Christensen, 2007; Huntington, 2006; IPCC, 2007; Wu et al., 2011). Despite the advantages of climatic modelling, challenges related to abstraction, timing of events, accuracy, and precision compromise the predictive ability of models on ecosystem functions and processes (Evans et al., 2012; Yates et al., 2018). Rainfall manipulation experiments are powerful tools for predicting and monitoring ecological changes resulting from rainfall variability in natural ecosystems (Beier et al., 2012; Fay et al., 2008; Smith et al., 2009). The ability of rainfall manipulation experiments to incorporate multiple parameters of a study, including confounding factors, enhance their predictability of ecological response to varying rainfall events (Beier et al., 2012). By simulating increases or decreases in rainfall from the ambient, manipulation experiments generate gradients in soil moisture, potentially altering ecosystem functions and processes (Beier et al., 2012; Knapp et al., 2008; Miranda et al., 2011; Wu et al., 2011; Zeppel et al., 2014). Rainfall manipulation experiments enhance the capacity to predict future patterns of CO_2 exchange rates, biomass development, species diversity, soil microbial activity, primary productivity, and soil properties (English et al., 2005; Knapp et al., 2008; Koerner and Collins, 2014; Miranda et al., 2011; Yahdjian and Sala, 2002). These studies show linear responses of the tested parameters to experimental rainfall regimes with nuances experienced at higher precipitation levels (Beier et al., 2012; Zeppel et al., 2014). Beier et al. (2012) underscore the importance of rainfall manipulation experiments in monitoring the responses of vegetation to the prevailing precipitation conditions and their resilience to disturbances. Despite the increased application of rainfall manipulation experiments globally, fewer studies exist on the African continent (February et al., 2013; Koerner and Collins, 2014), necessitating further research (Beier et al., 2012; Zeppel et al., 2014), especially in the savanna.

Case (2006) and Zeppel et al. (2014) projected that dry seasons in the tropical ecosystems will become drier, while wet seasons are likely to get wetter because of increased rainfall variability. In Eastern Africa (EA), climate prediction models (Coupled model Inter-comparison Project - CMIP3; Meteorological Research Institute-Global Climate Model - MRI-CGCM3) show a 5–10% decrease and 5–20% increase in rainfall during dry and wet seasons, respectively, by 2050 (Case, 2006; Conway, 2009; Hulme et al., 2001; IPCC, 2001; Taylor et al., 2012; Yang et al., 2015). Such changes will significantly affect the spatio-temporal distribution and availability of soil moisture and its effect on ecosystem processes (Conway et al., 2009; Funk et al., 2005). Studies on the possible impacts of such changes on the savanna, which covers approximately, 80% of the East African land mass, are scanty.

Tree-grass interaction is essential in determining the effect of rainfall on soil moisture availability in the herbaceous layer communities of most savanna ecosystems (Sankaran et al., 2004; Scholes and Archer, 1997). Numerous studies underscore the sensitivity of the herbaceous communities to variations in soil moisture availability (Berry and Kulmatisky, 2017; Bond et al., 2008; Otieno et al., 2015; Schwinning and Kelly, 2013; William et al., 2009). This, however, varies across ecosystems, depending on rainfall intensities (Berry and Kulmatisky, 2017). For instance, herbaceous vegetation in dry compared to humid savanna ecosystems rapidly respond to increases in soil moisture by enhancing their germination, growth and other phenological processes over a short time (Schwinning and Kelly, 2013). Extensive rooting system coupled with various morphological and physiological adaptations, additionally, enable plants in these ecosystems to survive extreme water stress resulting from prolonged dry seasons. However, most herbaceous plants in the arid savanna ecosystems are shallow rooted and so they resort to other mechanisms of surviving drought including stomatal closure. Water potential of plants within the herbaceous layer community increases above their wilting points during wet seasons, allowing the vegetation to sustain numerous physiological processes (Bond et al., 2008). During the dry seasons, however, water potential significantly declines, causing most plants to wilt. Through the hydraulic lift mechanism, the shallow-rooted herbaceous species escape the devastating effects of drought by accessing soil moisture availed from deeper soil layers by trees (Ludwig et al., 2003; Scott et al., 2008).

1.1.4 State of research in Lambwe Valley

Lambwe Valley in Western Kenya (00°35` 27.72`` S and 34°18` 81.64`` E) is a typical humid savanna, supporting a large population of humans and livestock. Prior to the 1960s, tsetse fly infestation drove humans and their livestock out of Lambwe valley, allowing rich biodiversity to flourish. The government control initiatives on the tsetse flies between 1950-60s opened the area for human resettlement (Wellde et al., 1989) leading to rapid population growth estimated at 88,454 people (KNBS and SID, 2013) from the census report of 2009. The rising human population in the last 6 decades has transformed the landscape, soil, and vegetation cover (Muriuki et al., 2005). Increased human activities particularly livestock grazing (cattle's and goats) have significantly reduced the vegetation cover by > 30% therefore threatening biodiversity and sustainability of ecosystem services.

The Lambwe Valley savanna currently faces a myriad of ecological challenges related to overstocking of livestock and agricultural extensification. These activities degrade habitats, threatening the sustainability of this ecosystem (Muriuki et al., 2005). Increased demand for land for agricultural food production and settlement for the ever-growing human population has led to the conversion of natural ecosystems to the current land uses. The small fragments of land remaining are overgrazed. Unpredictable rainfall leading to prolonged drought, short rainy seasons, severe run-offs, and floods, is likely to compromise primary production, plant physiology, phenology, and floral diversity in Lambwe Valley. This follows a prediction by Case (2006) that the changes in climatic patterns of East Africa will alter the ecological processes and functions from their current status by 2050. Combined with changes in rainfall and temperature, human activities, especially grazing pose serious challenges to the structure of savanna ecosystem. Maitima et al. (1998) recommended research to determine the extent to which human influence combined with climatic conditions affect various components of the Lambwe Valley ecosystem. Studies conducted in the last 10 years on the herbaceous layer community of the Lambwe Valley ecosystem show negative ecological impacts of grazing (Arnhold et al., 2015; K’Otuto et al., 2012, 2014; Otieno et al., 2010, 2011, 2015). The influence of grazing on the herbaceous species diversity is, however, less studied.

Arnhold et al. (2015) assessed the changes in soil properties in Lambwe Valley as influenced by land uses along an altitudinal gradient. They showed that crop cultivation and livestock grazing increased soil bulk density, reduced hydraulic conductivity, soil moisture available to plants, and soil C and N levels due to increased compaction. In their study, the hill slopes experienced lower compaction levels since they were less accessible to the livestock. Chapter two of the current study investigated how manipulated rainfall amounts (50%, 100%, and 150%) influenced changes in VWC in grazed and ungrazed plots. Variations in bulk density and quantities of C and N at the 20 cm soil depth in response to manipulated rainfall amounts and livestock grazing were also considered.

Previous studies in Lambwe Valley have attempted to explain the role played by rainfall and livestock grazing in determining ecosystem CO_2 exchange rates and primary productivity of the herbaceous layer community (K'Otuto et al., 2014; Otieno et al., 2011). These studies reported a stronger dependence of CO_2 exchange rates and biomass development on soil moisture availability. They further showed that grazing despite enhancing leaf-level CO_2 uptake capacity, reduced the overall ecosystem primary productivity through clipping of leaves by livestock (reduced total leaf surface area) (K'Otuto et al., 2012; Otieno et al., 2011). Information linking herbaceous species diversity to grazing and variation in soil moisture status is still lacking. The current study, analysed the herbaceous community structure to determine the extent to which grazing and rainfall influence species composition, evenness in their distribution, and their diversity (Chapter three).

Most studies in Lambwe Valley focused on the effects of ambient rainfall (100%) on biomass production and CO_2 exchange rates in the herbaceous layer community (K'Otuto et al., 2014; Otieno et al., 2011). Otieno et al. (2010), however, simulated 10% and 20% rainfall reduction to predict their effects on soil moisture, aboveground biomass and CO_2 exchange rates. The reduction of 20% ambient rainfall decreased biomass, net ecosystem exchange (NEE), and respiration (R_{eco}) by 38.5%, 32.6%, and 25.6%, respectively. The study, however, did not explore how rainfall addition above ambient may influence the patterning of CO_2 exchange rates and biomass. To address this concern, the current study manipulated ambient rainfall amounts (100%) by 50% reduction (50%) and 50% increase (150%), in grazed and ungrazed sites. The quantified parameters included various soil properties (Chapter two), herbaceous species diversity (Chapter three), biomass production, and CO_2 exchange rates in the herbaceous layer community (Chapter three).

The display of a typical savanna characteristics and its humid nature informed the choice of Lambwe Valley as a study area for this research. The geography of this ecosystem and its proximity to Lake Victoria contribute to its humidity. Patches of forests in a protected national park, within Lambwe Valley create a modified microclimate that additionally enhances the rainfall pattern. Rainfall availability and seasonal variation favoured the setting up of rainfall manipulation experiment within this region. Large population of humans (88,454) and an increasing number of livestock in Lambwe Valley provided a basis for investigating the effect of grazing as a common form of disturbance caused by humans.

1.1.5 Study hypotheses and objectives

The following hypotheses guided the study:

i. Soil physical and chemical properties dictate soil moisture availability and plant performance but not species diversity.
ii. Livestock grazing positively affects productivity through regulation of herbaceous community structure.
iii. Manipulated rainfall amounts have similar effects on herbaceous species diversity and productivity to natural rainfall.

Main objective of the study

This study aimed at determining the effects of livestock grazing and rainfall manipulation at 50% and 150% of ambient (100%) on soil properties, species diversity, biomass production and CO_2 exchange within the herbaceous layer community of humid savanna.

The specific objectives of the study were:

Objective 1

To determine the impact of soil physical and chemical properties on plant species diversity and productivity in the herbaceous layer community.

Objective 2

To quantify the impacts of livestock grazing on the structure and function of the herbaceous layer community.

Objective 3

To evaluate the spatio-temporal effects of rainfall variability on herbaceous species diversity and productivity.

1.2 List of manuscripts and their specific contribution of authors

This dissertation is submitted as a cumulative thesis of three articles published in different journals.

Manuscript 1

Authors: Okach DO, Ondier JO, Kumar A, Rambold G, Tenhunen J, Huwe B and Otieno D.

Title: Interactive influence of livestock grazing and manipulated rainfall on soil properties in a humid tropical savanna.

Status-DOI. DOI.org/10.1007/s11368–018–2117–X.

Journal: Journal of Soils and Sediments (2019)

Own contribution: concept and study design 80%, data acquisition 90%, analysis of samples 55%, data analyses and figure 85%, discussion of results 80%, manuscript writing 90%.

HB, OD, ODO and TJ conceived the idea and designed the experiment. ODO and OJO constructed the rainfall manipulation plots (RMPs) and maintained them. OJO installed (and maintained) the weather stations around the study sites whereas, ODO installed soil probes in the rainfall manipulation plots. ODO monitored, downloaded, and processed VWC data, alongside datasets pertaining to other soil properties. ODO wrote the manuscript with advice from OD. TJ, OD, HB, and KA reviewed the manuscript and recommended corrections. ODO did the statistical analysis of data, created tables and figures with the guidance of HB and RG.

ODO is the corresponding author.

Manuscript 2

Authors: Okach DO, Ondier JO, Rambold G, Tenhunen J, Huwe B, Eun-Young J, Otieno DO.

Title: Interaction of livestock grazing and rainfall manipulation enhances herbaceous species diversity and aboveground biomass in a humid savanna.

Status-DOI. DOI: 10.1007/s10265-019-01105-x.

Journal: Journal of Plant Research.

Own contribution: concept and study design 75%, data acquisition 80%, analysis of samples 85%, data analyses and figure 95%, discussion of results 85%, manuscript writing 80%.

HB, OD, ODO and TJ conceived the idea and designed the experiment. ODO laid out the plots for monitoring herbaceous species diversity within the RMPs with guidance from E-Y J. ODO and OJO routinely collected the respective data. ODO wrote the manuscript with the support of E-YJ and reviews from OD and RG. ODO did the statistical analysis of data and created figures and tables presented in the manuscript.

The corresponding author is ODO.

Manuscript 3

Authors: Okach DO, Ondier JO, Kumar A, Rambold G, Tenhunen J, Huwe B and Otieno D.

Title: Livestock grazing and rainfall manipulation alter the patterning of CO_2 fluxes and biomass development of the herbaceous community in a humid savanna.

Status-DOI. DOI.org/10.1007/s11258-019-00977-2

Journal: Plant Ecology.

Own contribution: concept and study design 65%, data acquisition 70%, analysis of samples 95%, data analyses and figure 95%, discussion of results 90%, manuscript writing 85%.

HB, OD, ODO, and TJ conceived the idea and designed the experiment. ODO and OJO set up the experiments in the field and collected the respective data, routinely. ODO processed and analysed the CO_2 flux data, with the support of OD. ODO compiled the manuscript and presented it to OD, TJ, and HB for review. ODO did the statistical analysis, assisted by KA. HB, OD, RG, and TJ provided editorial advice.

ODO is the corresponding author.

1.3 General materials and methods

1.3.1 Description of the study area

Lambwe Valley (00°35` 27.72`` S and 34°18` 81.64`` E) is a humid savanna ecosystem covering 324 km^2. A fenced National Park (Ruma) makes up 120 km^2 of the total area. The valley lies 10 km east of Lake Victoria and southeast of Homa Bay town in Kenya at an altitudinal range of 1190–1280 m ASL. The adjacent hills to the valley at different peaks (Figure 2b) include Usengere (2270 m), Gwasi (1945), Gembe (1898), Sumba (1838) and Ruri (1615–1700 m) among others (Allsopp and Baldry, 1972). Rainfall is bi-modal with the long rains occurring from April to June and short rains from October to December, with an annual range of 700–1100 mm. The changing climatic pattern resulting in prolonged dry periods and flooding has increased variability in rainfall (CV = 20.57%) in the last 15 years (Unpublished data from the Kenya Wildlife Services – Ruma National Park). The mean air temperature is 25° C. The dominant rock type at the valley floor is biotite and the soils are Vertisols (Allsopp and Baldry, 1972; Sombroek et al., 1982) made up of 50–81% clay, 14–46% silt and 4–15% sand (Arnhold et al., 2015).

The landscape is characterized by different plant life forms from the hill-tops to the valley floor (Figure 2c). Grass species, particularly *Bothriochloa insculpta* (Hochst. ex A. Rich) A. Camus, *Brachiaria decumbens* Stapf, *Cynodon dactylon* (L) Pers, *Hyparrhenia fillipendula* (Hochst) Stapf, *Paspalum dilatatum* Poir, and *Sporobolus agrostoides* Chiov. dominate the Valley floor. Forb Species such as *Justicia striata* Vahl, *Vernonia glabra* (Steetz) Vatke and *Ipomoea tenuirostris* Steud ex Choisy occur at the human-inhabited sections but also extended to higher elevations. The valley floor also comprises scattered tree species, mostly *Acacia*, however, at some point, they form patches of forests. The Olambwe river that crosses the valley (Figure 2b), forms a riverine vegetation pattern comprising various tree and shrub species. Dense thicket composed of *Bridelia scleroneura* Müll. Arg, *Combretum mole* R. Br. ex G. Don, *Euphorbia candelabrum* (A. Berger) N.E. Br, *Ficus* and *Rhus species* occupy the steep escarpments and hilly parts of Lambwe Valley.

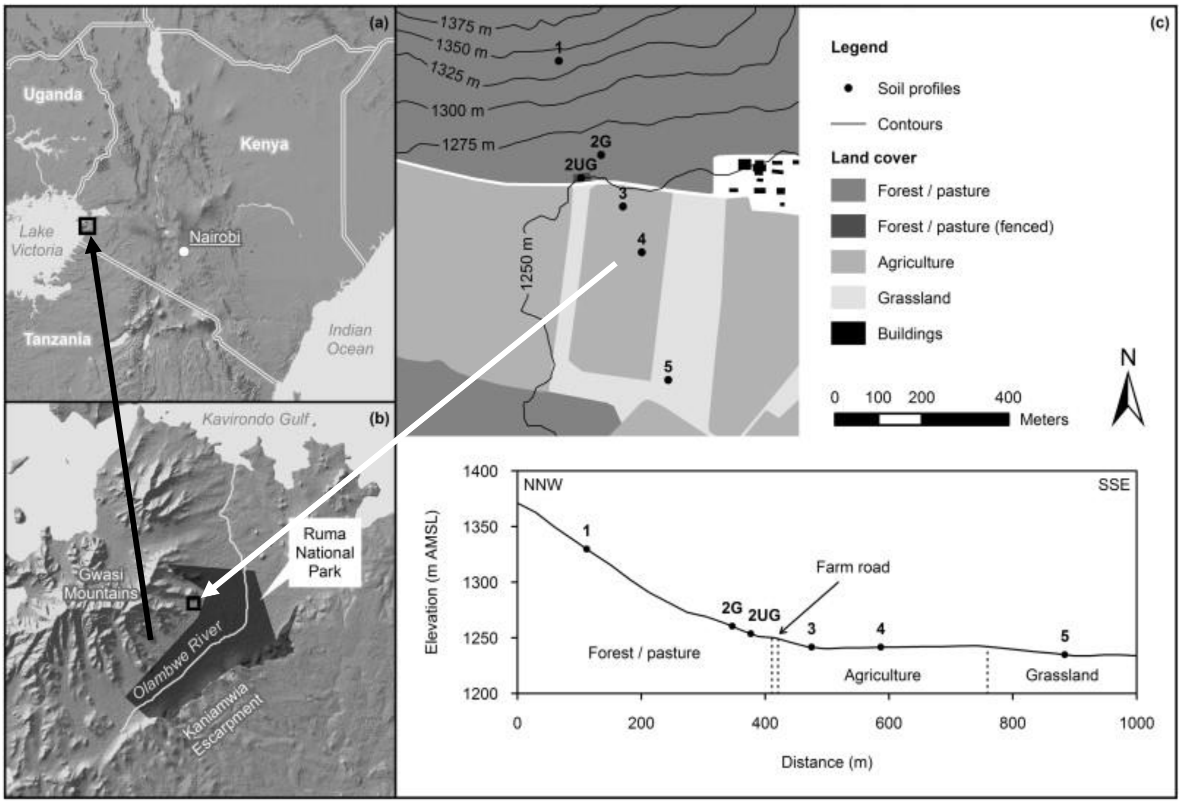

Figure 2: Map of Kenya showing the (a) position of Lambwe Valley (in the dark squared frame), the (b) neighbouring physical features. Images on the right side (c) illustrate the altitudinal gradient and vegetation cover of the areas surrounding the study sites. Images from Arnhold et al. (2015).

The study sites were located on selected open land belonging to the National Youth Service (NYS), neighbouring Ruma National Park. The selection and design of the plots were done in a manner that represented the valley bottom, where most of the human activities were concentrated. No plots were set up on the steep slopes (Figure 3c) given that livestock avoided them because of their bushy and rocky nature.

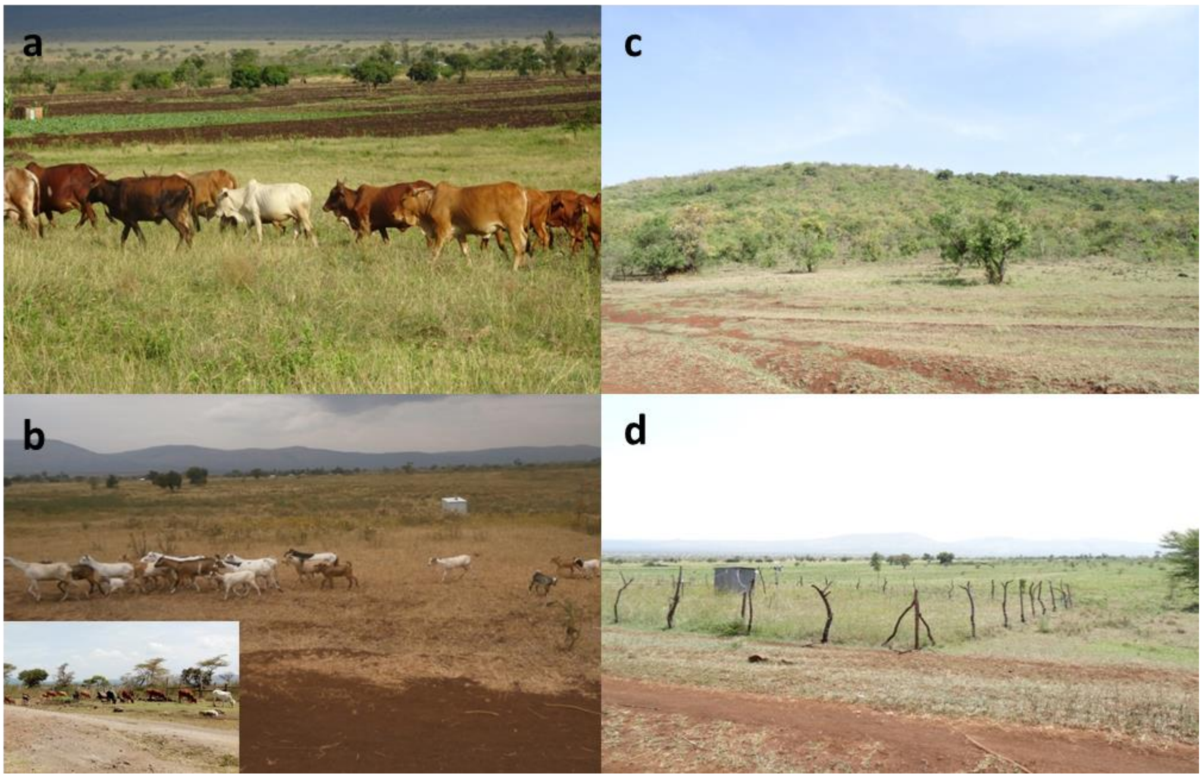

Figure 3: Images of land uses, mainly crop cultivation and grazing of cattle and goats in Lambwe Valley during wet (a) and dry (b) seasons. Image b (inset) shows cattle grazing along a fence surrounding the the Ruma National Park. Differences in vegetation cover (c) between frequently grazed areas and sloppy terrain (background) that is less accessible to livestock. A fenced plot intended to receive ambient rainfall (d): notice the taller vegetation compared to the surrounding grazed.

1.3.2 Experimental design

The study adopted a split plot factorial design (2 x 3) comprising 2 levels of livestock grazing: grazed (G) and ungrazed (U) and 3 levels of rainfall manipulation: 50%, 100%, and 150%. Ambient rainfall amount (100%) was reduced by 50% to simulate drought (50%) and increased by 50% to simulate rainfall abundance (150%). The set-up was replicated 3 times with 3 internal replications. The plots were abbreviated using the first letter of the grazing level (grazed - G or ungrazed - U) followed by rainfall amount (50%, 100% and 150%) i.e. G50%, U150%, among others. The rainfall manipulation plots (RMPs) were set up in 2015 on initially grazed areas that were fenced (2 m high) in 2013 to exclude goats and cattle (the common livestock). The grazed plots were fully accessible to livestock throughout the year. Measurements began on 15th September 2015 and ended on 2nd June 2016 although the RMPs were established 3 months before the actual data collection began. This duration allowed the area covered by the rainfall manipulation plots to adjust to the new conditions.

The 50% and 150% RMPs each measured 6 m length, 3 m wide and 2 m high and were constructed next to each other (Figure 5). The control plots, receiving 100%, ambient rainfall had no gutters constructed over them. The reduction in 50% of ambient rainfall was achieved using transparent plastic gutters (30 cm width) intermittently stretched to cover 50% of the total plot/ground surface. The gutters (10 strips per set up) were inclined at an angle of 14° to redirect the excluded rainwater (by gravity) onto the plots intended to receive 150% of the ambient rainfall. The even distribution of rainwater in the soil following 50% exclusion or addition of ambient rain was routinely tested using a portable soil moisture sensor, a day after a rainfall event. Trenches (50 cm deep and 30 cm wide), reinforced with plastic sheets buried in the soil, were dug between plots to exclude lateral water flow across plots following heavy rains. The sides of the RMPs were left open to reduce possible greenhouse effect resulting from the gutters. Possible modification of microclimate by the gutters was monitored using light and temperature sensors installed on the plots. Routine replacement of the gutters was done to minimize the shading effect caused by dust and other particles that would settle on them.

1.4 Measurements

1.4.1 Microclimate and Volumetric water content

Real-time data on rainfall, air temperature, humidity, and solar radiation were automatically logged every 30 minutes from different microclimate stations (AWS-WS-GP1, Delta-T Devices, Cambridge, UK). The stations were strategically installed 2 m above the ground at the study site. The data was collected from 15th September 2015 to 2nd June 2016. 5TE probes (Resolution: 0.0008 m^3/m^3 from 0–50% VWC) connected to EM50 data loggers (Decagon Devices Inc., Washington, USA) were used for measuring soil volumetric water content (VWC) at 20 cm soil depth in every plot. Three probes (6 cm prong length) were installed horizontally at 20 cm soil depth in each plot and set to log data every 30 minutes. Mean VWC of the grazed and ungrazed plots were averaged over different times (daily, monthly, and seasonally) and subsequently analysed. Dry days were determined by prolonged duration (at least 7 days) between rainfall events $\geq$ 1 mm, three days following the cessation of rainfall.

1.4.2 Bulk density, carbon, nitrogen contents and herbaceous belowground biomass

Soil bulk density, belowground biomass, C and N contents were sampled seasonally (in September 2015, January, March, and May 2016) using a soil corer (diameter 8 cm, height 10 cm) from every plot. Undisturbed soil cores were carefully extracted at the 10–20 cm soil depth, weighed, and their volumes recorded for subsequent calculation of bulk density. Soil bulk density was calculated by dividing the dry soil weight by the total volume of the soil sample.

Prior to C and N analyses, the soil samples were sieved, finely ground and oven-dried at 105 °C for 48 hours. Approximately 20 g of each dried soil sample was placed in a tared large tin capsule (PerkinElmer, N2411362) and precisely weighed using a PerkinElmer AD6 Auto balance and analysed using EA2400CHNS/O elemental analyser and EA2410 N nitrogen analysers for C and N, respectively.

The soil cores for belowground biomass were extracted and then washed over soil sieves (2 mm mesh sizes) to extract the roots. The roots were oven dried at a constant weight at 80°C for 48 hours to obtain the dry mass.

1.4.3 Assessment of herbaceous species richness, evenness, and diversity

The assessment of the herbaceous community dynamics was done seasonally (September 2015, January, March, and May 2016) in plots measuring 1 m x 1 m within the experimental set-up. Species composition data of March 2016 were however excluded from the study given that most species, especially the less dominant ones could not be identified, since plants either lost their shoots to grazing or withered beyond visual recognition. March is the driest month of the year. 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 count of individuals forming the ground cover as outlined in the formulae below:

$$\text{Relative abundance (\%)} = \frac{Number\ of\ hits\ of\ species\ x}{Total\ number\ of\ hits\ of\ all\ the\ species} \text{ x } 100$$

To assess the changes in richness, diversity, and evenness, Margalef richness (D_{mg}), Shannon's diversity (H) and Pielou's evenness (J) indices were used, respectively as detailed by Magurran (2004).

$$\text{Margalef index of species richness } (D_{mg}) = \frac{(S-1)}{InN}$$

$$\text{Shannon index of diversity } (H) = -\sum\left(\frac{ni}{N}\right) In\left(\frac{ni}{N}\right) = \sum pi\ In\ pi$$

$$\text{Pielou's evenness } (J) = \frac{H}{In\ S}$$

Where:

S - Total number of plant species.

N - Total number of individuals.

ln - Natural log.

ni - important value index of the i^{th} species.

All parameters above were computed from the relative abundance data.

1.4.4 Herbaceous aboveground biomass

Herbaceous aboveground biomass (AGB) was sampled in plots measuring 40 x 40 cm, adjacent to the plots intended for monitoring species diversity. Biomass sampling plots were demarcated using 4 wooden pegs fixed on the ground at 90° angle corners (Figure 18a). 4 biomass plots were installed in every rainfall manipulation unit, and each plot was labelled in accordance with the targeted season of sampling (S1 - September 2015; S2 - January 2016; S3 - March 2016; S4 - May 2016) to avoid repeated harvesting in the subsequent seasons. The estimation was done seasonally at the end of September 2015, January, March, and May 2016. Both destructive (direct measurement) and nondestructive (photographic imaging) (Ganguli et al., 2000; Limb et al., 2007; Tackenberg, 2007) methods were employed in the estimation of aboveground biomass. At the initial stages of the study, the two methods were used concurrently on the same stand for correlating the image output (pixels) to the exact biomass. Subsequently, photographic method was used.

Images for non-destructive biomass estimation were taken against a dark background (attached to a metre rule) using a high-resolution digital camera (20.4 mega pixels). The distance of the camera depended on the height of the targeted vegetation. Image analysis was done to account for the vertical distribution of the plant matter in terms of characterized pixels. All the images were saved as JPG files and were later analysed using Image Software J 1.46 Version (Casadesús and Villegas, 2016; Schneider et al., 2012).

Direct measurement involved clipping the standing plant material at the base of the stem and drying them to obtain biomass. This was done after photos of the vegetation stand were taken. Two most dominant species were sorted from the harvested samples and their masses established relative to the total aboveground biomass. All the samples were later oven dried at 80°C for 48 hours and later, the dry mass weighed.

1.4.5 NEE, R_{eco} and GPP

NEE, R_{eco}, and GPP were measured every month from September 2015 to May 2016. Considering the variations in the microclimate, CO_2 flux measurements were taken at 3 various times of the month (early, mid, and later days). Manually operated ecosystem chambers were used to estimate CO_2 fluxes within the herbaceous layer community, comprising mainly of C4 grasses and forbs. NEE was measured using a transparent gas chamber made of Plexiglas (3mm XT–20070), with a light transmission efficiency of 95% of the ambient light conditions. R_{eco} was measured with an opaque chamber made of PVC insulated with a reflective aluminium foil to maintain the internal chamber conditions. Both chambers had similar dimensions which included a base area of 40 cm^2 (reinforced with a rubber gasket) and a height of 54 cm. Every chamber was fitted with a digital thermometer (T–107 Campbell Scientific, USA) on the inner wall, 30 cm above the base. The thermometer was insulated with an aluminium foil. A second thermometer was installed on the outer wall of each chamber,, at the same height to compare the variation in temperature with the inner chamber. To aid in chamber ventilation and air mixing, 3 fans with 1.5 m s^{-1} flow speed were installed inside the chamber. A small opening on top of the chamber allowed for pressure balancing within the head space shortly before measurements were taken. Soil frames (38.5 cm^2), for mounting the chambers were permanently fixed 3 cm into the ground, 3 weeks before the first measurements were taken. This was intended to minimize gas leakage through the soil during the measurements period. The frames were uninterrupted during the subsequent campaigns, and were only removed at the end of the field work. During measurement of CO_2 fluxes, the chamber was mounted on the soil frame and tightened using elastic bands. Subsequently, a screw-top opening of the chamber was loosened for 30-45 seconds to ease pressure that accumulated within. A portable gas exchange analyser (LI-COR 820, USA) connected to the chamber using Bev-A-line tubes (1/4'' OD; 15 cm length), was used for detecting changes in CO_2 concentration. CO_2 fluxes were measured every hour from 07:00–18:00 hrs and daily averages calculated. The temperature within the chamber was maintained at 3 °C compared to the ambient, using frozen ice packs. Photosynthetic active radiation (PAR) reaching the vegetation within the transparent chamber was monitored using a quantum sensor (LI-190, LI-COR, USA), towering above the enclosed vegetation. Soil temperature at the specific time of measurement was extracted from the EM50 data loggers. Records for the CO_2 fluxes and PAR (in the case of NEE) were taken 30–60 seconds after placing the chamber on the soil frame and recorded every 15 seconds for 2 minutes and 15 seconds. CO_2 fluxes were obtained from the time-dependent changes in CO_2 concentration within the chambers ($r^2 > 0.95$) and the flux rate ($F\mathrm{CO}_2$) calculated using the equation below:

$$F\mathrm{CO}_2 = k\mathrm{CO}_2 \frac{273.15}{\mathrm{T}air} \frac{\mathrm{V}}{\mathrm{A}} \frac{dc}{dt}$$

where: $F\mathrm{CO}_2$ - CO_2 flux density (mg CO_2-C m^{-2} h^{-1}); $k\mathrm{CO}_2$ - gas-constant (conversion factor) at 273.15 $k = 0.536$ [µg C $µl^{-1}$]; T_{air} - air temperature in chamber (k); V - chamber volume (l); A - collar area (m^2); dc/dt - CO_2 concentration change in chamber (CO_2: ml l^{-1} h^{-1}).

We calculated R_{eco} based on regressions between respiration rates and air temperature (Lloyd & Taylor, 1994) as shown in the formula below:

$$R_{eco} = R_{ref}\, e^{E_o\left(\frac{1}{T_{ref}} - T_0\right) - \left(\frac{1}{T_{soil}} - T_0\right)}$$

where: R_{ref} is the respiration at the reference temperature (CO_2-C mg m^{-2} h^{-1}); E_o is the activation energy (K); T_{ref} is the reference temperature = 283.15 (K); T_0 is the temperature threshold of biological processes; T_{soil} is the soil temperature.

NEE was calculated according to Gilmanov et al. (2003) as summarized in the formula below:

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

Where: α is the initial slope of the light response curve and an approximation of light use efficiency (CO_2 m^{-2} s^{-1}/µmol m^{-2} s^{-1}); β is the maximum rate of carbon fixation at infinite PPFD (CO_2 m^{-2} s^{-1}); Q is the photosynthetic photon flux density (µmol m^{-2} s^{-1}); γ is the average daytime respiration.

Subsequently, GPP was calculated from the general equation below:

GPP = NEE - R_{eco}

The meteorological sign convention was used to characterize the CO_2 fluxes, where positive (R_{eco}) and negative fluxes (GPP and NEE) indicated the loss of CO_2 to the atmosphere and flow of CO_2 into the plant leaves, respectively (Skinner and Adler 2010).

1.5 General results and discussions

1.5.1 Soil properties and their influence on the herbaceous layer diversity and productivity

Results of bulk density (ρ), volumetric water content (VWC - θ_v), carbon (C), nitrogen (N) contents, and C:N ratio at the 20 cm soil depth are presented in Figures 6–10 and Table 1 (Chapter 2). Findings displayed on Figure 7 (Chapter 2) show that soil bulk density ranged from 1.12 ± 0.1 g m^{-3} to 1.24 ± 0.1 g m^{-3} in the grazed and 1.1 ± 0.05 g m^{-3} to 1.2 ± 0.1 g m^{-3} in the ungrazed plots. VWC in each plot during the entire measurement period ranged from 17.5 ± 4.9% in the G50% plot to 20.64 ± 4.67% in the G150% plot and between 19.15 ± 4.18% to 26.9 ± 4.9% in the U50% and U150% plots (Figure 8a). Noticeably, the plots with higher bulk density had lower VWC (Figure 8a; Chapter 2). Similarly, soil C:N ratio (Figure 10; Chapter 2), NEE, R_{eco}, GPP (Figure 22; Chapter 4), AGB and total biomass (Figure 23; Chapter 4) were lower in plots of higher bulk density. The relationship between bulk density and VWC was quantified by regression analysis to determine the extent of influence on soil moisture availability. The outcome revealed a significant correlation between bulk density and VWC across all the plots (Figure 9).

Figure 10 shows that the G50% and U50% plots, whose VWC were significantly reduced, had lower C content of 1.2 ± 0.3% and 2.1 ± 0.1% and N content of 0.15 ± 0.02% and 0.17 ± 0.02% respectively, compared to the other plots. Similar patterns were observed for species richness (Figure 14), CO_2 fluxes (Figure 22; Chapter 4) and biomass (Figure 23; Chapter 4). This was an indication that processes that promoted C and N input into the soil, namely photosynthesis and nitrification, were hindered. For instance, the lowest NEE of 3.68 ± 0.81 µmol m^{-2} s^{-1}, and GPP of -2.02 µmol m^{-2} s^{-1} reported in the G50% plot, during the dry months (Figure 22; Chapter 4) likely reduced soil C input and the amount of exudates required to support the microbial activities. The lower rates of carbon exchange shown by NEE and GPP following the significant reduction of VWC in the G50% plot implied that plant had lower CO_2 uptake rates, therefore lowering C assimilation, and biomass production. According to Kuzyakov et al. (2000) soil water stress lowers root exudation, limiting microbial activities in the soil, potentially slowing down the release of bound C and N contained in the detritus. This may partially explain the results of soil C and N reported in this study. For instance, K'Otuto et al. (2012), Otieno et al. (2010; 2011) attributed the lower C and N contents under reduced soil moisture conditions in Lambwe Valley to drought and significant loss of biomass resulting from grazing (Discussed in section 1.5.2.1). Contrary to the hypothesis, this study found out that the effect of bulk density on productivity of the herbaceous layer community in Lambwe Valley, despite being indirect, was achieved by regulating the soil moisture available for plant functional processes. Although, this study, did not correlate bulk density to CO_2 fluxes and biomass, past studies in the savanna ecosystems report significant decline in productivity in highly compacted soils (Cumming and Cumming, 2003; Holdo and Mack, 2014).

The structural equation modelling (SEM) used to predict the effect of VWC on AGB and species diversity parameters fitted well with the respective data sets ($x^2 = 2.98$; $p = 0.84$; RMSEA < 0.05) (Figure 16; Chapter 2). VWC increased D_{mg} and AGB, but had no direct effect on H and J. The response of H and J to variations in VWC were, however, mediated (indirect-only mediation) by changes in D_{mg} and AGB. These results relate to the results illustrated on Figure 25 (Chapter 4) which show that NEE, R_{eco}, GPP, and total biomass (productivity parameters) strongly depended on changes in soil VWC. Unlike the NEE, R_{eco}, GPP, and total biomass, which increased along a soil moisture gradient (Figure 25), the species diversity parameters were not correlated to soil VWC (Figure 16). This shows that, despite the strong influence of soil moisture, species diversity also depended on other factors that regulated the structure and function of the herbaceous layer community, including nutrient availability, grazing intensity, light limitation and productivity (Bakker et al., 2004; Coller et al., 2013; Koerner and Collins, 2014).

The structure of the herbaceous layer community of Lambwe Valley was also influenced by the correlations amongst D_{mg}, H, and J, signifying the key role played by species abundance and evenness. AGB reduced J and H (Figure 16; 17), contrary to other studies that reported a positive correlation between AGB and species diversity and linked the trends to facilitation and niche complementarity (Loreau et al., 2001; Schläpfer and Schmid, 1999). Overall, results summarized in Figure 16 and 17 (Chapter 2) of this study show that biomass production at a range of 400g m^{-2}–800 g m^{-2} promote higher herbaceous species diversity, implying that livestock grazing regulates the dominance of particular species that out-compete others for the available resources.

1.5.2 Effects of livestock grazing on soil properties, structure, and function of the herbaceous layer community

1.5.2.1 Soil properties

The results presented in Chapter 2 (Figures 6–10; Table 1) show a significant increase ($p < 0.05$) in bulk density and soil N content by 3.2% and 7.8%, respectively, in the grazed compared to the ungrazed plots (Figure 7). On the contrary, livestock grazing reduced the VWC and soil C content by 19.1% and 11.45%, respectively (Table 1). By increasing the soil bulk density, livestock grazing limited the rate of rainwater infiltration, lowering the VWC in the grazed plots. The current observations on soil C and N concentrations in the grazed plots are attributed to lower CO_2 flux into the soil, resulting from decreased NEE (Figure 22, Chapter 4), which is linked to reduced soil moisture input (Figure 25). In most savanna soils, C and N input largely result from biological sources, particularly detritus from previous seasons, and are regulated by variations in soil moisture (Savadogo et al., 2007). Grazing, plant community composition, microbial diversity, soil moisture and nutrient availability, additionally control the soil C and N contents, both at spatial and temporal scales (Derner et al., 2006; Pineiro et al., 2010). From the results presented in Figure 14 and Table 4 (Chapter 3), the grazed plots, besides showing higher N content than the ungrazed plots, also exhibited greater species diversity, indicating that livestock grazing enhanced herbaceous community composition by partly promoting soil nitrogen availability through dunging and urination. The significant decrease in C content in the grazed plots was attributed to lower standing biomass, especially AGB (Figure 23b; c), limiting soil C input. However, the lack of significant grazing effect on BGB (Table 5; Chapter 4) suggests that, other confounding factors that regulated C input in the soil, namely, soil respiration, temperature, soil structure, and topography (Pineiro et al., 2010) further contributed to the lower C content in the grazed plot.

1.5.2.2 Diversity of the herbaceous layer community

This study further explored the effects of livestock grazing on the herbaceous community in Chapter 3 to examine the extent to which species diversity correlated with the aboveground biomass (AGB). The findings summarized in Figures 14–17 and Table 3, show higher S, D_{mg}, H, and J by 35.89%, 45.06%, 47.62, and 32.09% respectively, in the grazed plots compared to the ungrazed plots, implying that livestock grazing significantly ($p < 0.05$) increased the herbaceous species diversity. These wider differences were mostly contributed by the larger effects of grazing on S, D_{mg}, H, and J within plots whose ambient rainfall were either reduced (50%) or increased (150%) (Figures 14a, b, c). Plots which received ambient rainfall in grazed and ungrazed sites (G100% and U100%) did not show significant differences in herbaceous species diversity. Specifically, there were no mean differences in any of the species diversity parameters between the G100% and U100% plots (Figures 14). This is unlike in Chapter 2 and

Chapter 3 where pronounced effects of grazing on most soil properties, CO_2 fluxes, and biomass occurred in the 100% and 150% rainfall plots.

Through clipping effect, grazing lowered the competitive ability of *Bothriochloa insculpta* and *Paspalum dilatatum* (co-dominant species) (Table 4) for resources, facilitating the emergence of otherwise subdued species. Species evenness, consequently, increased in the grazed sites due to enhanced co-existence among species. Other ecosystems have reported similar results (Koerner and Collins, 2014; Hanke et al., 2014). Besides clipping by livestock, the higher soil N as shown in Figure 10 (Chapter 2) possibly contributed to the increased species diversity in the grazed plots (Figure 14). The findings by Fornara and Tilman (2008) on the effects of grazing on species diversity confirm the results from the current study. They reported that the combined presence of C4 grasses and leguminous species increased the accumulation of soil C and N in both lower and higher diversity plant assemblages. Such patterns result from a balance between the ability of the legumes to fix N and the efficient use of N by the C4 plants to store C.

The current study, however, shows lower C content in the grazed plot, but higher N content compared to the ungrazed plots (Figure 10 a, b), suggesting that livestock contributed a significant amount of N in the soil. Table 4, additionally, shows higher abundance of grasses compared to forbs in both grazed and ungrazed plots. Common legumes including *Cajanus sp*, *Indigofera sp*, and *Rhynchosia sp* constituted less than 3% of the relative abundance. This implies that the extra N content in the grazed plots, compared to the ungrazed, potentially resulted from dunging and urination by livestock (Augustine and McNaughton, 2006; Piñeiro et al., 2010). Overall, these results demonstrated that livestock grazing promoted diversity of the herbaceous layer community, despite its negative effects on most soil properties (Chapter 2), CO_2 fluxes, and biomass development (Chapter 4).

1.5.2.3 CO_2 exchange rates and biomass production

Variations in CO_2 fluxes (NEE, GPP, and R_{eco}), and biomass production of the herbaceous layer community resulting from the influence of livestock grazing was examined in Chapter 4 and the findings presented in Figures 20–25 and Table 5. NEE, GPP, R_{eco} (Figure 22), AGB, and total biomass (Figure 23) decreased by 57.14%, 28.61, 37.62, 46.62% and 37.03% respectively due to grazing. This effect was attributed to the continuous clipping of the herbaceous vegetation by livestock. The lower AGB reported in the grazed plots (Figure 23a) indicates that a considerable amount of biomass was lost due to livestock grazing and lower moisture availability (addressed in section 1.5.1), lowering the CO_2 exchange rates. This is emphasized by results displayed in Chapter 3 which reveal that grass species constituted a larger proportion of the relative abundance (Table 4) and AGB (Figure 15 b). Consequently, clipping of the highly preferred dominant species including *Brachiaria decumbens* and *Hyparrhenia fillipendulla*, reduced AGB, significantly. Given the high photosynthetic efficiency and robust growth patterns exhibited by these two species (Coughenour et al., 1985; Gomez et al., 2012; Quattrocchi 2006), their depletion from the grazed plots significantly decreased the CO_2 exchange rates. Comparatively, the mean NEE of -3.43 ± 0.19 µmol m^{-2} s^{-1} and -6.01 ± 0.23 µmol m^{-2} s^{-1} reported in the G100% and U100% plots (ambient rainfall) respectively, for the entire measurement period, showed that grazing, by removing the dominant species (Table 3) reduced CO_2 uptake, by > 40%. GPP and AGB exhibited similar patterns. For instance, the 1034.89 g m^{-2} average AGB in the U100% plot almost doubled the amount of AGB in the G100% plot of 571.57 g m^{-2}, for the entire measurement period.

These results are supported by findings which attribute the reduction in productivity under grazed conditions to the removal of active photosynthetic tissues therefore lowering CO_2 uptake and other physiological processes (Bremer et al., 1998; Grace et al., 2006; K'Otuto et al., 2012; McNaughton et al., 1998). Others studies report that the effect of grazing on CO_2 uptake and biomass production varies with the intensity of grazing (and other forms of disturbance), plant life forms, soil moisture, and prevailing abiotic factors (Bardgett and Wardle, 2003; Grace et al., 2006; Otieno et al., 2011; Owensby et al., 2006). These factors partly explain our results. For instance, Figure (23 a) shows that AGB in the grazed plots did not reduce below 300 g m^{-2} due to the abundance of unpalatable forb species, *Vernonia glabra* (Steetz) Vatke (Forsk) DC (Table 4 in Chapter 3). The woody stem of this species contributed more to aboveground biomass after the depletion of grasses due to drought or clipping by livestock.

1.5.3 Spatio-temporal effects of rainfall variability on herbaceous layer diversity and productivity

The amount of rain received in the measurement plots designed for this study varied based on the manipulation experiments (50%, 100%, and 150%) and seasonality in rainfall (dry and wet seasons), primarily driving the variability in soil moisture (Chapter 2). The results in Figure (20 a) emphasize this by showing a significant correlation between VWC and the experimental amounts of rainfall ($r^2 = 0.61$; $p < 0.05$; RSME = 3.55), implying that rainfall was the main source of moisture at the study site. Through rainfall manipulation, VWC decreased by 17.6% and increased by 7.1%, with the 50% reduction and addition of ambient rainfall, respectively. The effect of rainfall manipulation was however pronounced in the ungrazed plot where the VWC in the U50% plot was 23.3% lower than U100%. This was compared to the 10.1% difference between G50% and G100% plots in the grazed site. Regarding the effect of seasonality in rainfall, VWC significantly decreased by > 20% during the dry periods, as reported in various figures (8b,c; 13b; 20b) in Chapters 2, 3, and 4. Overall, the VWC varied with changes in rainfall regime at both plot and seasonal scales.

Further results displayed in Tables 3 (Chapter 3) and 5 (Chapter 4) show that rainfall manipulation and seasonality in rainfall also influenced species diversity, CO_2 fluxes, and biomass. These ecosystem components were directly (Figure 16) or indirectly (Figure 25) affected by the variation in soil moisture. By significantly reducing VWC, both the experimental reduction (50%) in ambient rainfall and the dry periods lowered H, GPP, and total biomass (Figure 4). For instance, the lowest VWC reported in the G50% rainfall plot was 13.99 ± 3.15% during the dry months, leading to > 30% decrease in GPP (Figure 22; Chapter 4) and total biomass (Figure 23; Chapter 4) compared to the G100% plot. Similarly, H decreased in the G50% plot (Figure 14; Chapter 3). These significant reductions in diversity, net assimilation rates of carbon, and biomass development adversely affected the productivity potential of the herbaceous layer community, given their significant correlation with VWC (Discussed in section 1.5.1). The experimental reduction of 50% of ambient rainfall caused soil drought which lowered soil water potential, limiting plant functional process (William and Albertson, 2004), production and diversity (Koerner and Collins 2014). This situation worsened during the dry periods given the significant effect of seasonality of rainfall ($p < 0.05$) on the VWC and the structural components of the herbaceous layer community.

The results in Figure 15 show that species diversity declined with changes in rainfall from the ambient amount (100%). Specifically, higher D_{mg} and H were reported in the G100% and U100% plots compared to their respective rainfall manipulation plots (50% and 150%). This showed that an increase in rainfall above ambient amount potentially lowered the herbaceous diversity by reducing species composition and evenness. Similar findings have been reported in a savanna ecosystem, where an intermediate rainfall gradient promoted increased herbaceous species richness compared to lower and higher rainfall amounts (Anderson et al., 2007). Subsequent increase in rainfall on a higher gradient lowered species richness by promoting faster growth of highly competitive species capable of suppressing the less dominant species (Smith et al., 2016). This was demonstrated in the U150% plot, which, despite its lower diversity compared to the U100% (Figure 14), had higher (> 11%) AGB (Figure 15; 23a) and total biomass (Figure 23c). The overall net effect of 50% increase in ambient rainfall promoted CO_2 exchange rates, however, at the plot level, only GPP significantly increased during the wet months (Figure 22f). Soil bulk density (Figure 7), C and N contents (Figure 10), belowground biomass (Figure 23b), and R:S biomass ratio (Figure 24) did not change with the 50% increase in ambient rainfall, contrary to most of the results reported on species diversity parameters. These patterns were attributed to various interactive biotic and abiotic factors that regulate ecological processes and functions in soils whose moisture contents were experimentally manipulated (English et al., 20004; Miranda et al., 2011; Zeppel et al., 2014).

Together, these results suggest that rainfall manipulation and seasonality in rainfall determined soil moisture availability in the study plots. However, numerous factors including grazing, differential plant growth patterns, phenology, and physiology influenced the response of the herbaceous layer community to the changes in soil moisture regime (K'Otuto et al., 2014; Merbold et al., 2009; William and Albertson, 2004; Zeppel et al., 2014).

1.5.4 Interaction of livestock grazing and rainfall manipulation

The interaction of livestock grazing and rainfall manipulation influenced the patterns of VWC, soil C and N contents (Table 1; Chapter 2). Larger effects of grazing on VWC occurred at higher rainfall amounts (100% and150%), causing wider differences between the corresponding plots of grazed and ungrazed sites (Figure 8). This shows that the effects of livestock grazing on the soil structure intensified with increased rainfall, making the soil compact, hence reducing the infiltration of rainwater. Soil N displayed a similar pattern to that of VWC, however, higher N was observed in the G100% and G150% plots compared to the U100% and U150% plots, respectively (Figure 10b), due to grazing effect (explained in section 1.5.1). No mean differences in soil C were observed between similar rainfall treatment plots of grazed and ungrazed at 100% and 150% rainfall.

These changes in soil properties, especially N likely influenced the patterning of the species diversity parameters (Figure 14; Chapter 3), which increased in the grazed compared to the ungrzaed plots. Contrary to the soil properties, the effect of grazing on species diversity and related parameters was larger at the manipulated rainfall amounts (50% and 150%) compared to ambient (Figure 14; Table 3). This indicates that shifts in rainfall from the ambients conditions potentially reduce the herbaceous species diversity in ungrazed ecosystems. According to Anderson et al. (2007), higher herbaceous diversity at an intermediate rainfall gradient results from the trade-off between biotic and abiotic components of the ecosystem. For instance, the effect of livestock grazing and rainfall on biomass production regulates species diversity as shown by the results displayed on Figures 15 and 17 (Chapter2). These results show that higher AGB above 800 g m^{-2} lowers the herbaceous species diversity by imposing dominance of grass species that contribute a larger proportion of biomass (Figure 15).

Further findings in chapter 3 revealed that the interactive influence of grazing and rainfall manipulation only affected changes in AGB, BGB, root to shoot ratio, and the total biomass (Table 3). The patterning of biomass, especially AGB and total biomass conformed to that of VWC (Figure 8; 23). Considering the stronger correlation between biomass and VWC (Figure 25), the wider differences of AGB between the grazed and ungrazed plots at higher rainfall amount imply that increased VWC least likely compensated the removed biomass. This possibly resulted from slower regrowth of vegetation following clipping by livestock as reported in other ecosystems (Dangal et al., 2016).

1.6 General conclusion and recommendation

Independent and combined effects of livestock grazing, rainfall manipulation and seasonality in rainfall modified herbaceous species diversity, biomass development and CO_2 exchange rates through their effects on soil properties, light environment, biomass growth and plant physiology. Soil bulk density modified the variation in VWC resulting from rain input. The grazed plots were more compact, hindering infiltration of rainwater after rainfall events. All the studied variables, namely soil carbon input, herbaceous CO_2 uptake and biomass were sensitive to changes in soil moisture, declining at lower VWC. Ecological functions and processes, consequently, dependent on soil moisture, potentially declined as a result of drought imposed through rain exclusion or seasonal variations in rainfall. This study shows that, the grazed plots suffered from intense water stress during the dry periods, lowering soil C and N contents, decreasing belowground biomass, and reducing ecosystem CO_2 exchange rates.

Further results demonstrated that the impacts arising from lower rainfall input were more intense in the plots grazed by livestock. We postulate that the humid savanna of Lambwe Valley, and likely others with typical characteristics, may similarly respond to future changes in rainfall and livestock grazing. One key finding of this study was the facilitative effect of livestock grazing on herbaceous species diversity under the current rainfall levels (100% ambient rain), suggesting that the ecosystem has adjusted to the current environmental conditions. Any shift from the current conditions will likely impact negatively on species diversity, and in extension, the community structure as shown by the 50% reduction in ambient rainfall. At lower rainfall intensities, the herbaceous vegetation was characterized by declining rates of NEE, GPP and R_{eco}, as well as reduced biomass production when subjected to grazing. Although we did not vary the intensity of grazing, it is likely that at higher grazing pressures, the ecosystem suffers and the gains in species diversity observed here, may eventually be lost. These results demonstrated that this humid savanna, in its current form, is sustained by the balance between grazing intensity and rainfall amounts, both of which interact to determine the herbaceous species diversity and productivity. Similar findings have been reported for other savanna ecosystems in Africa (Koerner and Collins 2014).

Evaluation of the structural and functional components of the herbaceous layer community in response to the influence of livestock grazing and rainfall variability provided an insight into the patterning of diversity and productivity of the Lambwe Valley ecosystems. These findings are essential in informing sustainable management strategies to regulate C balance and productivity. This research, therefore, forms a base for future studies by adding knowledge on herbaceous community dynamics, their drivers, and moderators in Lambwe Valley. Despite the success of the rainfall manipulation experiments, set up during this study, there is a greater need to vary the rainfall regimes at smaller intervals of 5% from ambient to ± 50%. Through this, it will be easier to establish the nuances in structural and functional responses resulting from prevailing changes in rainfall. Modelling the effects of rainfall manipulation on a varying scale of grazing intensities (non-grazing to intensely grazed) will essentially generate an in-depth understanding of the extent to which the Lambwe Valley ecosystem is resilient to disturbances caused by livestock grazing. Additionally, manipulation of other abiotic factors including soil nutrients and temperature to simulate the anticipated variations resulting from climate change will project a feasible transformation of the herbaceous layer community.

1.7 References of the synopsis

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Chapter 2

Manuscript 1: Interactive influence of livestock grazing and manipulated rainfall on soil properties in a humid tropical savanna.

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Abstract

The effect of uncontrolled grazing and unpredictable rainfall pattern on future changes in soil properties and processes of savanna ecosystems is poorly understood. This study investigated how rainfall amount at a gradient of 50%, 100%, and 150% would influence soil bulk density (ρ), volumetric water content (θ_v), carbon (C) and nitrogen (N) contents in grazed (G) and ungrazed (U) areas. Rainfall was manipulated by 50% reduction (simulating drought – 50%) and 50% increase (simulating abundance – 150%) from the ambient (100%) in both G and U areas. Plots were named by combining the first letter of the area followed by rainfall amount i.e. G150%. Samples for soil ρ, C, and N analysis were extracted using soil corer (8 cm diameter and 10 cm height). Real-time θ_v was measured using 5TE soil probes (20 cm depth). The EA2400CHNS/O and EA2410 analyzers were used to estimate soil C and N contents respectively. The interaction between grazing and rainfall manipulation increased θ_v and C but decreased N with no effect on ρ and C:N ratio. Rainfall reduction (50%) strongly affected most soil properties compared to an increase (150%). The highest (1.241 ± 0.10 g cm^{-3}) and lowest (1.099 ± 0.05 g cm^{-3}) ρ were in the G50% and U150% plots respectively. Soil θ_v decreased by 34.0% (grazed) and 25.8% (ungrazed) due to drought after rainfall cessation. Soil ρ increased with grazing due to trampling effect therefore reducing infiltration of rainwater and soil moisture availability. Consequently, soil C content (11.45%) and C:N ratio (24.68%) decreased whereas N increased (7.8%) in the grazed plots due to reduced C input and decomposition rate. The combined effect of grazing and rainfall variability will likely increase soil θ_v thereby enhancing C and N input. Grazing during drought will induce water stress that will destabilize soil C and N contents therefore affecting other soil properties. Such changes are important in predicting the response of soil properties to extreme rainfall pattern and uncontrolled livestock grazing that currently characterize most savanna ecosystems.

Keywords Drought, trampling, defoliation, climate change, volumetric water content.

1 Introduction

Land use changes and varying climatic patterns are likely to influence soil properties of the savanna ecosystems and therefore their functionality (Brearley and Thomas, 2015; Holdo and Mack, 2014). This is supported by strong variability in rainfall pattern predicted to occur by 2100 in both dry and wet seasons of East Africa and other parts of the Sub-Saharan Africa (IPCC, 2007). Intensive livestock grazing, and unpredictable rainfall patterns associated with frequent droughts and flooding, potentially change soil properties and processes, with consequences on ecosystem functions (Derner et al., 2006; Knapp et al., 2002). For instance, heavy rains, severe drought, and livestock grazing in the savannas are detrimental to soil structure, since they facilitate degradation through erosion, and flooding (Tully et al., 2015). Grazing intensity varies with the type of herbivore, nature of the ecosystem and its management, quality of forage, and the plant life forms (Tobler et al., 2003). Mucina and Rutherford (2006) reported highly variable stocking density between lightly grazed (0.020–0.13 LSU ha^{-1}) and heavily grazed (0.042–0.68 LSU ha^{-1}) sites across six South African biomes. In a Kenyan savanna where sustainable grazing of wildlife and cattle is practiced, the stocking densities were 1.7 elephants km^{-2}, 12.2 cattle km^{-2}, 20.3 (impala km^{-2}) and 139 dik dik km^{-2} (Augustine and McNaughton, 2004). However, in the drier northern Kenya, higher cattle stocking density was pronounced due to pastoralism (Opiyo et al., 2015).

Tropical savanna ecosystems have evolved with grazing as a modifier of their structural and functional components (Schuman et al., 1999) through clipping of vegetation, trampling on soil, dunging, and urination (Piñeiro et al., 2010). Livestock trampling increases soil bulk density through compaction that decrease soil water infiltration and availability to the vegetation and soil microbes (Batey, 2009; Tate et al., 2004). Increased grazing intensities therefore alter processes that are sensitive to variation in soil moisture such as nitrification, volatilization, leaching, and organic matter decomposition (Adviento-Borbe et al., 2006;

Drewry et al., 2000; Savadogo et al., 2007). Furthermore, changes in soil properties due to compaction are likely to influence soil organic carbon (SOC) and nitrogen (SON) (Piñeiro et al., 2010; Schuman et al., 1999). Studies show that the effect of trampling by livestock on soil properties will be worsened if the current grazing intensity in most of the savanna ecosystems remain unmitigated (Arnhold et al., 2015; Brearley and Thomas, 2015; Holdo and Mack, 2014; Piñeiro et al., 2010). Increased grazing intensity is reported to either increase (Arnhold et al., 2015; Reeder et al., 2004; Schuman et al., 1999) or decrease soil C (Derner et al., 2006; Savadogo et al., 2007) due to enhanced fine root density and compaction that regulate root penetration respectively. Moderate or low grazing intensity over a lengthy period has however demonstrated increased organic matter input due to enhanced allocation of photosynthates to the roots as a way of tolerating the grazing pressure (McNaughton et al., 1998). The manner with which soil C influence soil N and C:N ratio is however dependent on the nature of the ecosystem, existence of other forms of disturbances and nutrient availability (Piñeiro et al., 2010). With increased population and agriculture in Lambwe Valley, the grazing field are lately shrinking leading to overgrazing of livestock. It was therefore important that we test how soil bulk density, moisture, C and N contents would respond to livestock grazing in this ecosystem. Soil properties such as pH, cation exchange capacity, hydraulic conductivity, nutrient availability, porosity, organic and inorganic matter contents are affected by changes in soil moisture (Adviento-Borbe et al., 2006; Drewry et al., 2000). The key question however is, how would subjecting soils to manipulated reduction and increase in ambient rainfall affect various properties? Experiments aimed at modelling soil eco-hydrological components across ecosystems have manipulated rainfall amount and tested its effect on soil properties (Beier et al., 2012; Knapp et al., 2008; Miranda et al., 2011). The African Savanna, particularly the East and Central parts have not been well represented, given that most experiments have focused South (February et al., 2013; Koerner and Collins, 2014) and tested the effect of rainfall manipulation on plant community composition. Majority of the previous studies in Lambwe Valley focused on the ambient rainfall amount (K'Otuto et al., 2012; Otieno et al., 2011), however Otieno et al. (2010) simulated 10% and 20% rainfall reduction to predict the likely effect of future pattern on soil properties and CO_2 exchange. Additionally, Arnhold et al. (2015) reported higher bulk density (ρ) (1.03–1.19 g cm^{-3}) in the upper sub-soil due to intensive livestock grazing that negatively affected hydraulic properties of the soil. Soil ρ was however lower in the top soil (0–15 cm) and deeper soil horizons (40–100 cm).

This study aimed to investigate the extent to which grazing and manipulated rainfall would affect various physico-chemical soil properties within the Lambwe Valley ecosystem. Two profiles (grazed and ungrazed) mapped by Arnhold et al. (2015) were subjected to rainfall treatment of 50%, 100% (ambient), and 150% to test how patterns in soil ρ, θ_v, N, C, and C:N ratio would shift. We hypothesized that: (i) the interaction of grazing and rainfall manipulation would negatively affect the changes in various soil properties; (ii) grazing would predominantly reduce soil ρ, θ_v, C content, N content, and C:N ratio however rainfall manipulation would trigger an increase along rainfall gradient of 50%, 100%, and 150%.

2 Materials and methods

2.1 Study area

The study was conducted in Lambwe Valley (00°35`27.72`` S and 34°18`81.64`` E), a humid savanna covering 324 km^2 and hosts Ruma National Park (120 km^2) at an altitude of 1200–1600 m a.s.l in Homa-Bay County, Kenya (Figure 1a, b). Rainfall is bimodal between April and June (long rains) and September and December (short rains) amounting to 900–1300 mm with mean air temperature of 25º C. The soils at the valley bottom are Vertisols (Allsopp and Baldry, 1972; Sombroek et al., 1982) exhibiting 50–81% clay, 14–46% silt, and 4–15% sand content (Arnhold et al., 2015) with biotite rock. *Hyparrhenia fillipendula* dominates the landscape however, there are open tracts of woodland and thicket of *Acacia* and other shrubs scattered. Tsetse fly infestation kept humans and livestock out of Lambwe valley between 1930’s to 1960's, therefore allowing rich biodiversity to flourish. Subsequent government control initiatives of the tsetse fly opened up the area for human re-settlement (Wellde et al., 1989) leading to rapid population growth currently estimated at 88,454 people (KNBS and SID 2013). Livestock grazing (cattle’s and goats) and other human activities such as logging, and agriculture have reduced vegetation cover (< 30%) especially in grasslands and degraded the ecosystem (Muriuki et al., 2005), therefore threatening biodiversity. Measurements were done in selected open areas neighboring Ruma National Park, on land belonging to the National Youth Service (NYS). Our sites represented the valley bottom where most of the human activities were concentrated.

2.2 Experimental design

The design was a split plot factorial setup with 2 levels of grazing, G and U and 3 levels of rainfall manipulation, 50%, 100%, and 150%. The plots were abbreviated using the first letter of the grazing level (G or U) followed by rainfall amount (50%, 100% and 150%) i.e. G50%, U150%, among others. The design was replicated 3 times and applied for 260 days beginning 15th September 2015 to 2nd June 2016, however the rainfall manipulation plots were ready 3 months before the first set of measurements were conducted. Initially grazed areas were fenced (2 m high) to exclude livestock (ungrazed) in 2013. The grazed plots were on the other hand accessible to livestock throughout the year. Livestock included 180 goats and 130 cattle randomly grazed on an area covering 133 acres throughout the year. To exclude and include the desired amount of ambient rainfall, rainfall manipulation plots - RMPs (6 m x 3 m wide and 2 m high) were constructed (Figure 4c, d, Figure 5).

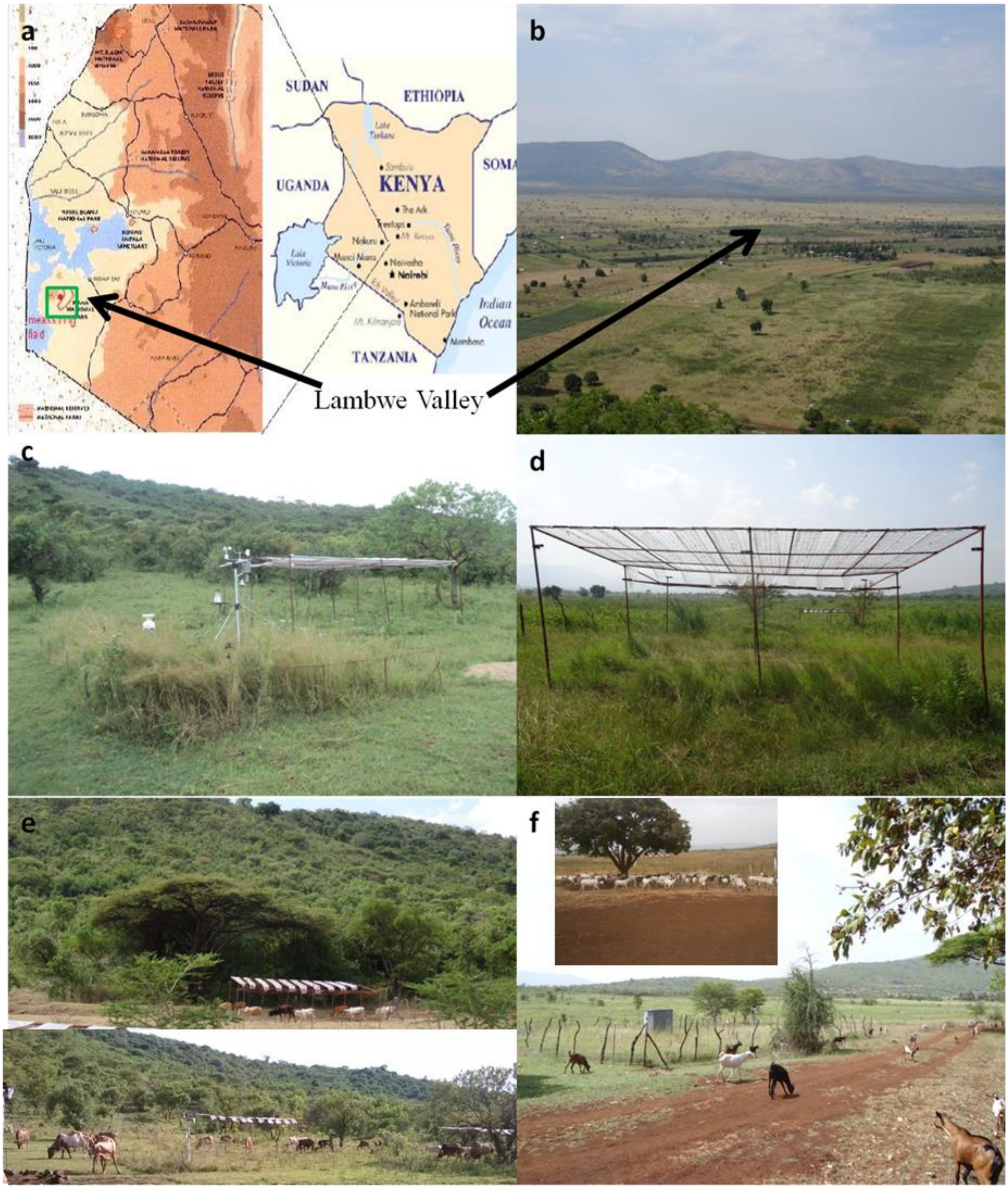

Figure 4: A map of Lambwe Valley (a) showing the location of the study area. A section of the valley (b) showing the protected national park (from the mid to the background) and the inhabited area separated by a fence. A weather station (c) installed in one of the control plots simulating lack of grazing (notice the shorter grasses in the surrounding grazed area). Rainfall manipulation plot (d) with a slanting roof (14°) partially covered with intermittently spread polythene sheets to exclude 50% rainfall and redirect it to the 150% rainfall plot. Cattle grazing through a rainfall manipulation plot (e) and goat grazing around a fenced plot during a dry season.

Rainfall reduction by 50% was achieved using rain exclusion gutters (inclined at 14° angle) from strips of transparent plastic sheets (30 cm width) intermittently stretched to cover 50% of the total plot/ground surface (10 strips were used). The excluded rainwater was redirected (by gravity) on to the 150% rain treatment plots, giving 150% of the ambient rainfall (Figure 5). A portable soil moisture sensor was used to randomly test the homogeneity in soil water distribution following rain addition (150%) within plots, a day after rainfall event. Trenches (50 cm deep and 30 cm wide), reinforced with plastic sheets buried in soil, were dug between plots to reduce lateral water flow across plots following heavy rains.

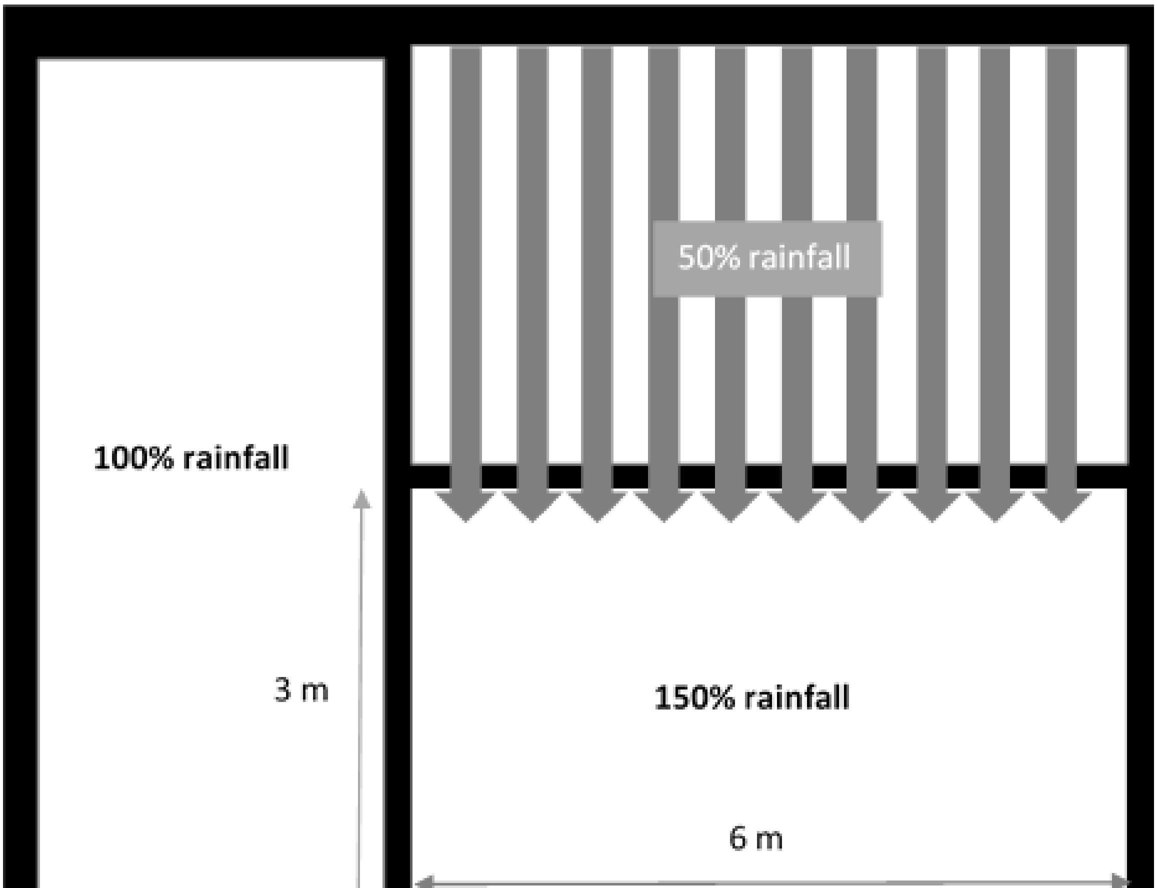

Figure 5: Layout of the rainfall manipulation plots separated by trenches (50 cm deep and 30cm wide - black band), shielded by polythene to prevent lateral flow of water. Gray parallel arrows represent the polythene strips used on the 50% rainfall plot to simulate rainfall reduction and the direction to which the excluded rainfall amount flows (150% rainfall plot).

The roofs of the control plots were uncovered to receive ambient rainfall (100%). The shelters had open sides to reduce the greenhouse effect from gutters. The influence of gutters on microclimate was monitored using parallel installation of light and temperature sensors under the RMPs. With this design, we were able to cover the open areas dominated by herbaceous species, which were accessible to livestock at the valley bottom (Figure 4e, f). The elevated areas surrounding the valley were ungrazed due to their steep gradient, rocky, and bushy nature making them inaccessible to livestock.

2.3 Microclimate and soil water content

Weather parameters (rainfall, air temperature, humidity, and solar radiation) were measured using three automatic microclimate stations (AWS-WS-GP1, Delta-T Devices, Cambridge, UK) installed 2 m above the ground, within the study site (Figure 4c). Data were logged every 30 minutes from 15th September 2015 to 2nd June 2016. Maximum and minimum amounts of rain were obtained from the rainfall events during the entire measurement period. Soil volumetric water content (θ_v) was measured using 5TE probes (Resolution: 0.0008 m^3/m^3 from 0–50% VWC) connected to EM50 data loggers (Decagon Devices Inc., Washington, USA). Three probes (6 cm prong length and 5 m cable length) were installed horizontally at 20 cm soil depth in each plot and set to log data every 30 minutes. Mean θ_v of different plots from grazed and ungrazed were calculated over different times (daily, dry days and wet days) from the automated data log. Dry days were determined by prolonged duration (at least 7 days) between rainfall events ≥ 1 mm, three days following cessation of rainfall.

2.4 Soil bulk density (ρ), C and N contents

Undisturbed soil cores for soil bulk density (ρ), C and N contents were extracted (once every month in September 2015, January 2016, and May 2016) using a corer (diameter 8 cm, height

10 cm) from 10–20 cm soil depth. The fresh soil samples were weighed and then oven-dried at 105 °C for 48 hours before determining the dry weight. Soil ρ was calculated by dividing the dry soil weight by the total volume of the soil sample.

Soil samples for C and N analyses were sieved, finely ground, and dried at 80° C for 48 hours prior to analysis. 20 g of each sample was placed in a tared large tin capsule (PerkinElmer, N2411362) and precisely weighed using a PerkinElmer AD6 Auto balance and analyzed using EA2400CHNS/O elemental analyzer and EA2410 N nitrogen analyzer for C and N, respectively.

2.5 Statistical analysis

The effects of grazing (G and U), rainfall manipulation (50%, 100% and 150%) and their interaction (grazing x rainfall manipulation) on ρ, θ_v, C, N, and C:N ratio ($p \leq 0.05$) were tested using factorial ANOVA (fully crossed). The θ_v dataset logged every 30 minutes in each plot for the entire duration of measurement were analyzed using repeated measure ANOVA and means (± SD) calculated in dry and wet days. Post-hoc test for multiple comparison of means (± SD) for θ_v, ρ, θ_v, C, N, and C:N ratio was done by Tukey HSD ($p \leq 0.05$). Linear regression analysis was used to investigate the relationship between θ_v and ρ. All these analyses were done using JMP (Version 13) statistical software by SAS Institute Inc (Cary, NC).

3 Results

3.1 Microclimate

The rainy and dry seasons were clearly distinct however, some rains, though short-lived, occurred during the dry season between February and April (Figure 6a). There were 89 rainy days characterized by several rainfall events amounting to 964.5 mm of rainfall during the entire period of measurement. Daily rainfall amount ranged from 0.2–58.6 mm with the maximum rainfall intensity of 44.6 mm/hr reported between April and May. Mean air temperature was 24.5 °C and 22.2 °C during the dry and wet seasons, respectively. The daily soil θ_v conformed to the rainfall pattern in both G (Figure 6b) and U (Figure 6c) plots.

Table 1: Full factorial repeated measures ANOVA. The F statistics and P values in parenthesis (the bold values show significance), show how grazing, rainfall manipulation (RM) (50%, 100% and 150%) and their interaction affect soil ρ, θv, N, C contents and C:N ratio.

Soil properties	**Variables**		
	Grazing	Rainfall Manipulation	Grazing x RMP interaction
Soil bulk density (*ρ*)	8.68 (**0.04**)	26.08 (<**0.05**)	0.36 (0.70)
Volumetric water content (θ_v)	382.71(<**0.05**)	199.01(<**0.05**)	37.58 (<**0.05**)
Soil nitrogen (N)	4.60(**0.037**)	22.31(<**0.05**)	8.14(<**0.05**)
Soil carbon (C)	4.58(**0.038**)	34.95(<**0.05**)	7.61(<**0.05**)
C:N ratio	12.53(<**0.05**)	5.31(<**0.05**)	2.22(0.12)

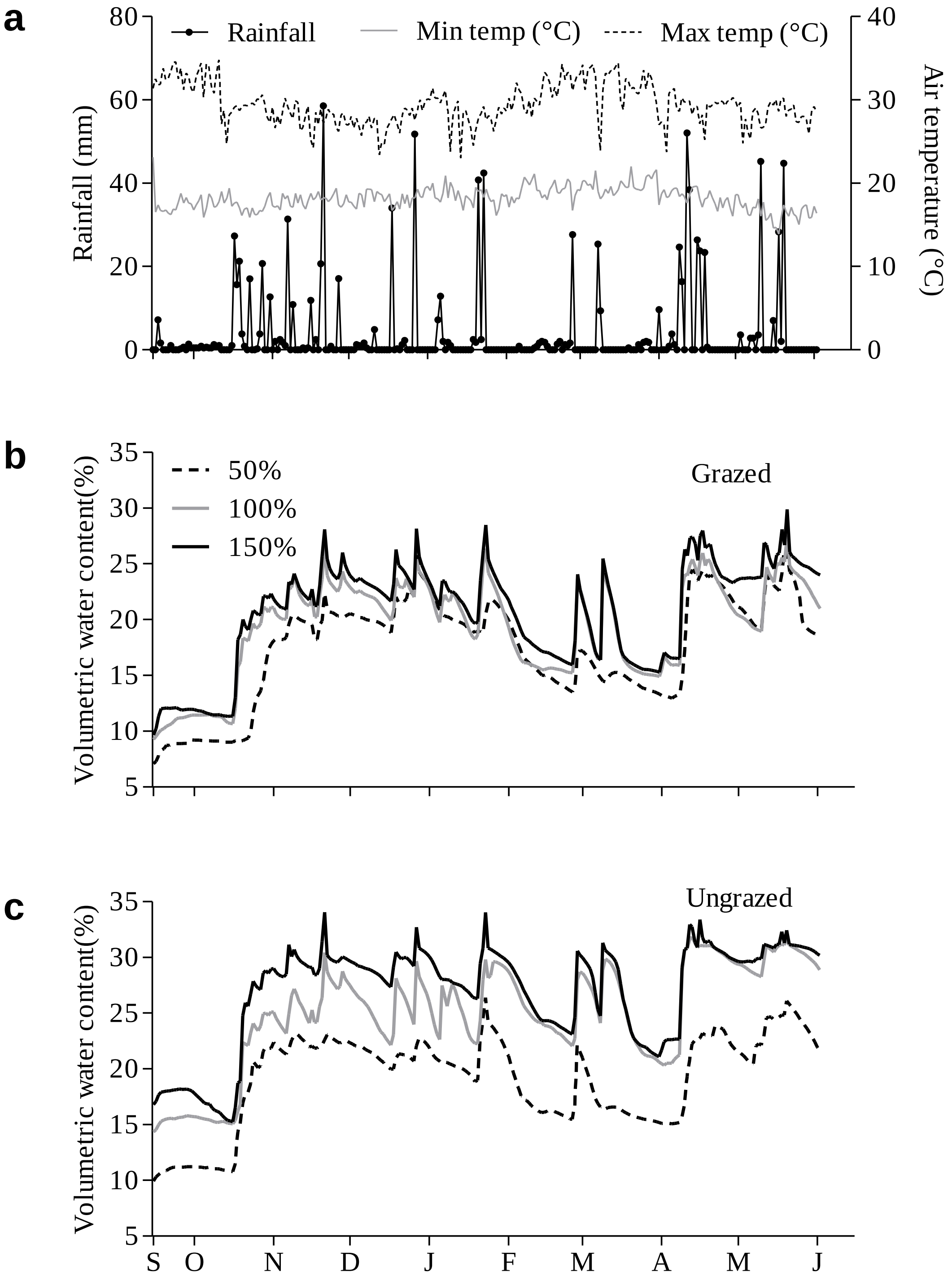

Figure 6: Pattern of rainfall and air temperature (**a**) measured between 15th September 2015 to 2nd June 2016 from the microclimate stations installed at the study site. Variation in soil volumetric water content (VWC) of (**b**) grazed (G50%, G100%, G150%) and (**c**) ungrazed (U50%, U100%, U150%) plots. Automated soil moisture sensors logged the VWC data every 30 seconds for the entire period of study. The 50%, 100% (ambient), and 150% show total rainfall amount allowed.

3.2 Soil bulk density (ρ)

Soil ρ significantly increased by 3.2% due to grazing (Table 1), however, no mean differences were observed between similar treatment plots of G and U (Figure 7). Soil ρ declined at a rainfall gradient of 50% to 150% due to rainfall manipulation (Table 1). Soil ρ did not change (Turkey HSD, $p < 0.05$) (Figure 7) with reduction in rainfall amount from 100% to 50% in the G plots ($p = 0.10$) and increase in rainfall from 100% to 150% in the U plots ($p = 0.52$). The U150% and G50% plots had the lowest and highest soil ρ of 1.10 ± 0.05 g cm^{-3} and 1.24 ± 0.10 g cm^{-3} respectively (Figure 7). There was no effect of the interaction between grazing and rainfall manipulation on soil ρ.

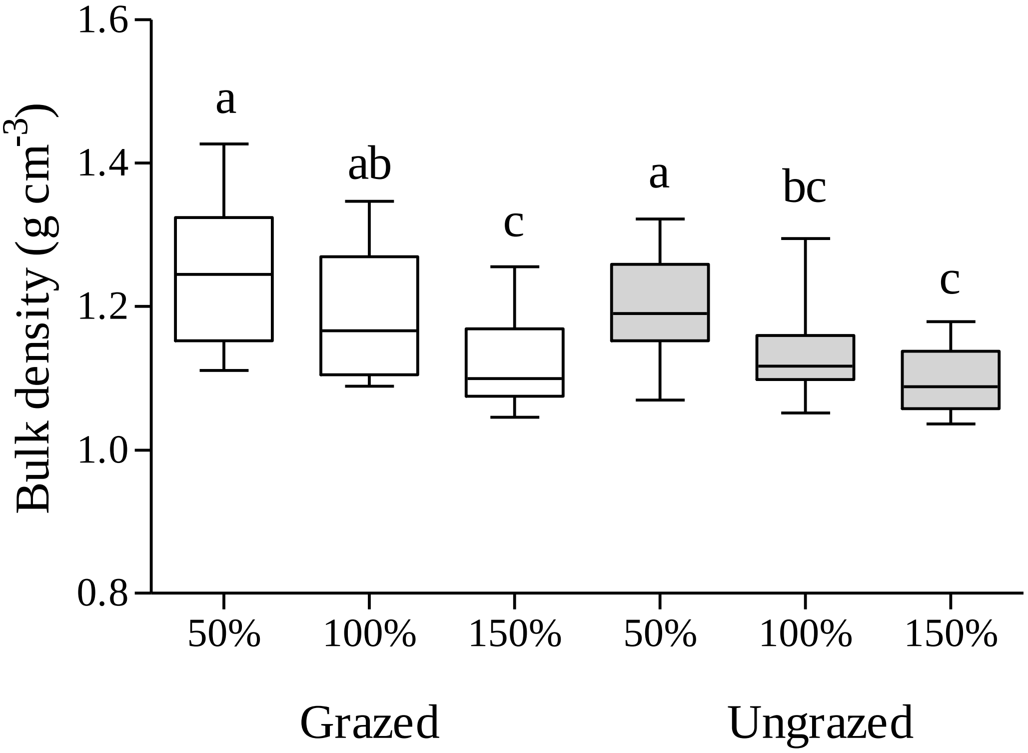

Figure 7: Soil bulk density (g cm^{-3}± SD) in grazed and ungrazed plots. The 50%, 100% (ambient), and 150% show reduction, ambient, and increase in rainfall amount, respectively. The letters indicate significant differences across the treatments (Tukey HSD $p < 0.05$). The levels not connected by same letter are significantly different.

3.3 Volumetric soil water content (θv)

Soil θ_v decreased (17.6%) and increased (7.1%) from ambient at 50% and 150% rainfall, respectively. These changes were pronounced in the U plots, with higher mean differences between the ambient and rainfall manipulation plots compared to those of the G (Figure 8a). For instance, the 50% plots recorded lower θ_v of 10.1% and 23.3% compared the 100% plots in the G and U sites respectively (Figure 8a). At 150% rainfall, the differences in θ_v compared to 100% rainfall were marginal, though significant in both the G (6.4%) and U (7.6%) (Figure 8a). Grazing lowered θ_v (Table 1) by 19.1% at the top 20 cm soil depth. The lowest and highest mean θ_v ranged from 17.5 ± 4.9% to 26.9 ± 4.9% in the G50% and U150%, respectively (Figure 8a). The response of θ_v to rain input ($f = 68.70$; $p < 0.05$) and the way soils dried after rainy event ($f = 19.07$; $P < 0.05$) was influenced by the interaction between grazing and rainfall manipulation. Changes in θ_v were more accurately predicted during the wet days (RMSE = 2.70; $r^2 = 0.61$; $p < 0.05$) as compared to the dry (RMSE = 3.89; $r^2 = 0.44$; $p < 0.05$) days. The θ_v declined by 34.0% in the G and 25.8% in the U during dry days (Figure 8b and c). With rainfall manipulation, θ_v of the 50% plots reduced by 33.2% as those of 100% and 150% plots dropped by 27.63% and 28.51% respectively under the dry conditions. Soil θ_v strongly depended on soil ρ and it sharply declined ($p < 0.0001$) with increases in the latter (Figure 9).

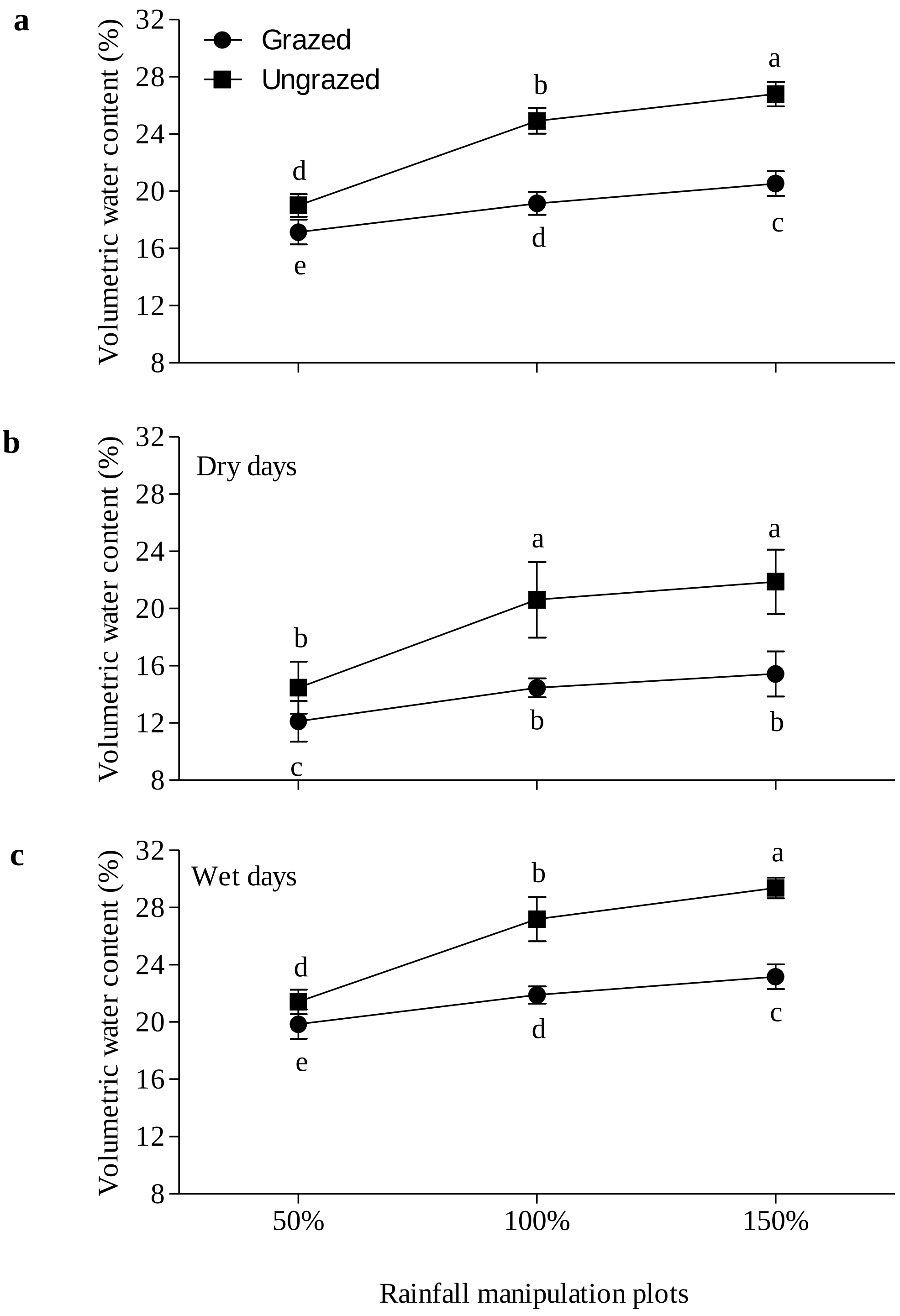

Figure 8: Variation in volumetric water content (θ_v) among rainfall manipulation plots at 50%, 100% and 150% rainfall amount during (**a**) the entire period (15th September 2015 to 2nd June 2016) of data collection, (**b**) dry, and (**c**) wet days in grazed and ungrazed sites. Different letters indicate significant differences ($p < 0.05$) among treatments.

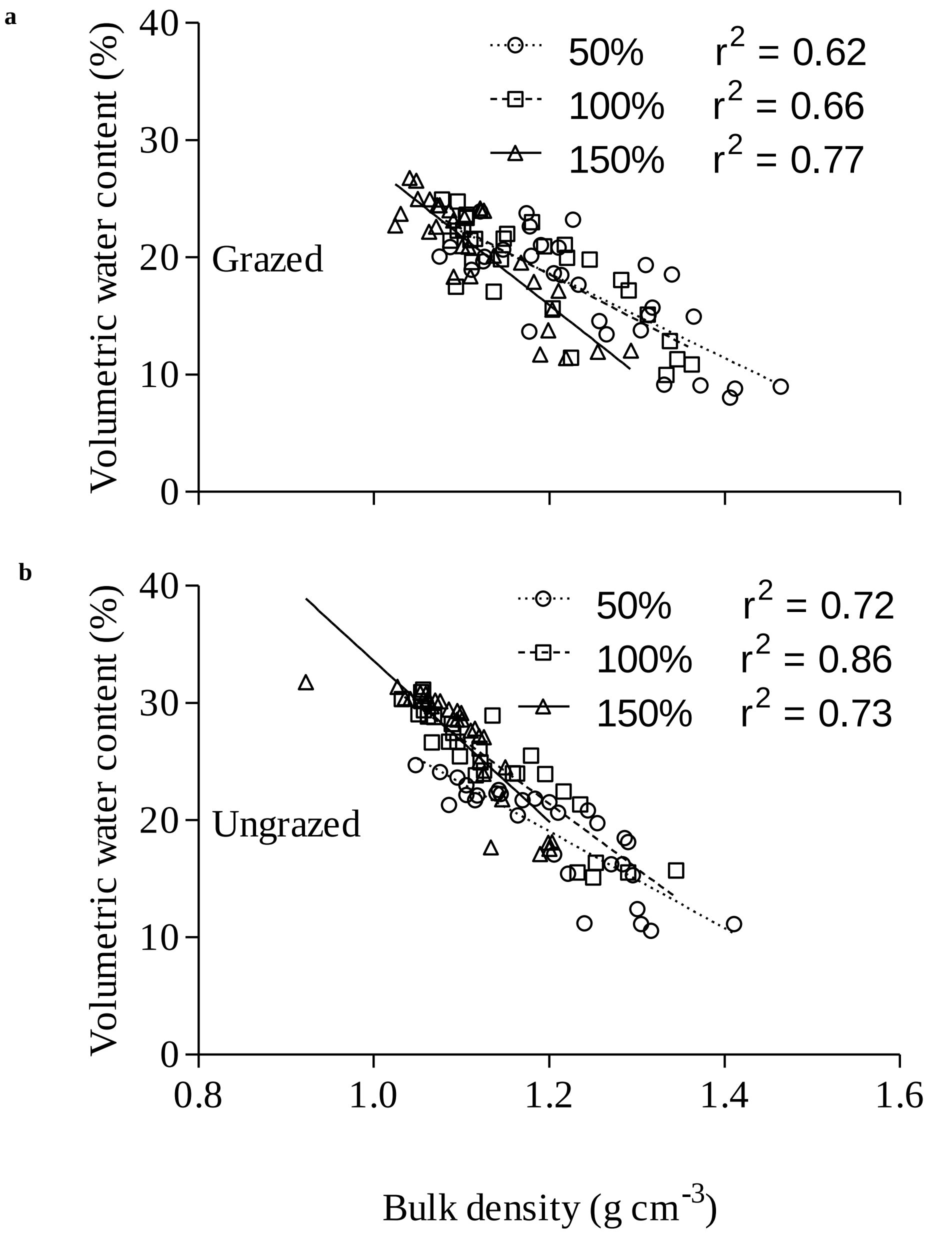

Figure 9: Relationship between changes in soil bulk density (ρ) and volumetric water content (θ_V) at the top 20 cm soil depth of (**a**) grazed and (**b**) ungrazed plots. The lines show significant ($p < 0.05$) regression fits for the plots.

3.4 Soil carbon and nitrogen dynamics

Rainfall manipulation significantly increased (Table 1) soil C, N, and their ratio (C:N) from 50% to 100% rainfall amount. Further rainfall addition (150%) however, had no effect. Soil C and C:N reduced by 11.5% and 24.7% respectively, whereas N increased by 7.8% due to grazing (Table 1). The interaction of grazing and rainfall manipulation affected changes in soil C and N contents but not C:N ratio (Table 1).

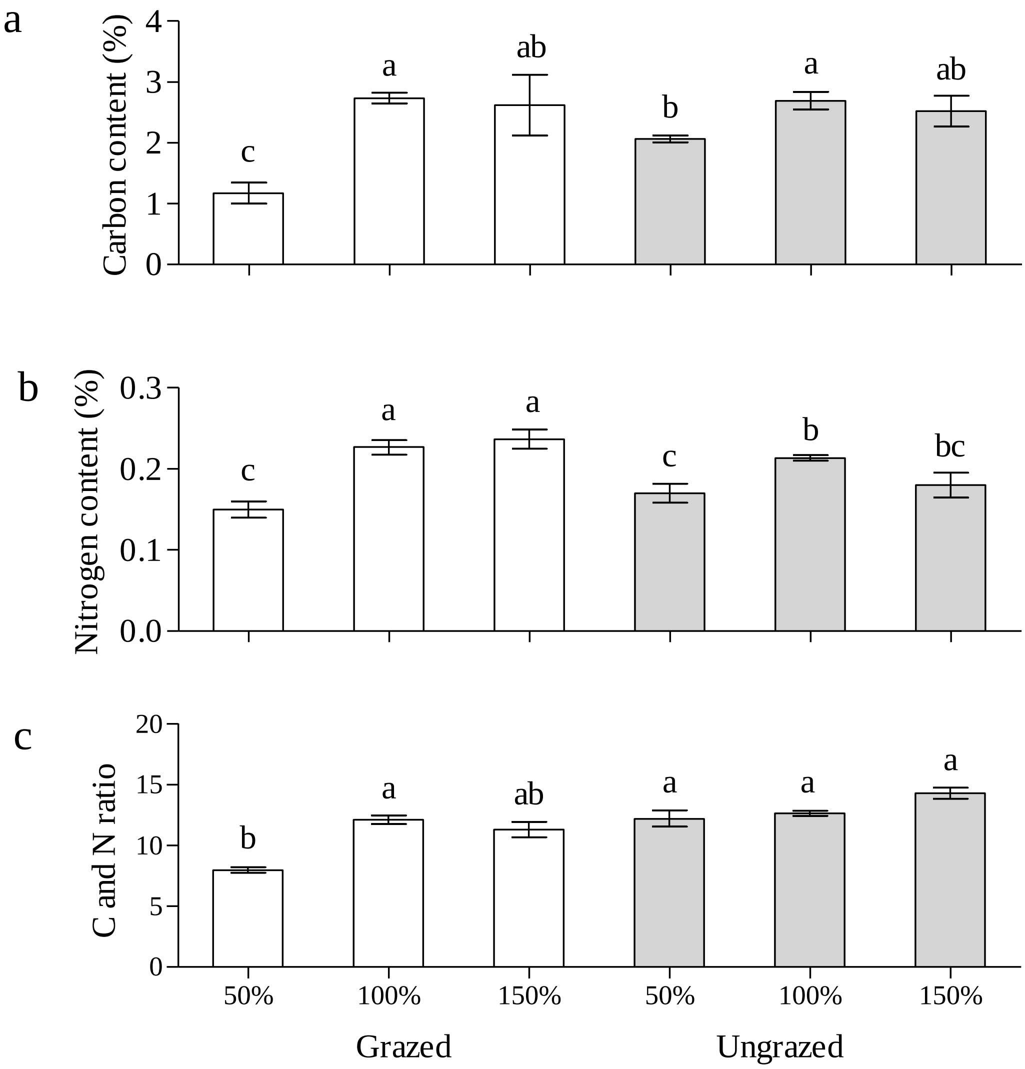

Figure 10: Mean (± SD) (**a**) soil carbon, (**b**) nitrogen contents, and (**c**) C:N ratio in grazed and ungrazed plots showing variation among 50%, 100% (ambient), and 150% rainfall amount. Different letters indicate significant differences ($p < 0.05$) among treatments.

The lowest soil C and N contents of 1.17 ± 0.30% and 0.15 ± 0.02%, respectively were observed in the G50% plot. Soil C and N declined with decreasing rainfall amounts in both the

G and U plots, however, the effect of increased rainfall manipulation was not pronounced (Figure 10). There were no mean differences in C between the 100% rainfall plots of G and U sites, similarly, to the 150% rainfall plots (Figure 10a). In the case of N, significant mean differences between similar treatment plots of G and U were only observed at 150% rainfall amount (Figure 10b). Mean (± SD) C:N ranged from 7.97 ± 0.41% (G50%) to 14.28 ± 0.82% (U150%) with no significant differences among plots except in G50% (Figure 10c).

4 Discussion

4.1 Soil bulk density (ρ)

The increase in soil ρ resulted from both grazing and rainfall reduction (50%) consequently, compacting the soils due to trampling of livestock. Rainfall manipulation influenced 5.21% increase and 4.3% decrease in soil ρ from ambient at 50% and 150% rainfall, respectively. Trampling facilitates the collapse of macropores and mesopores, eventually compressing soils and limiting their ability to hold water (Villamil et al., 2001). This was evident in our case where higher soil ρ was observed in the G plots, particularly G50% which had the lowest θ_v (Figure 7). Furthermore, increased soil ρ reduced θ_v (Figure 9) which could be attributed to lower porosity therefore limiting infiltration of rainwater into the soil. This might have resulted into accelerated surface run-off during heavy downpour in the G plots, making them drier. The 19.04% lower θ_v in the G plots compared to U could have hindered root penetration and development, growth rate of plants and reduced soil organic matter, as illustrated by the lower C content (Figure 10). In the U plots, the lower soil ρ could have resulted from high organic matter content (increases ability of soil to hold water), increased porosity; high soil silt and clay content; extensive shallow rooting system as reported elsewhere (Arnhold et al., 2015; Su et al., 2005; Yuan et al., 2012). The marginal difference in mean effect of soil ρ due to grazing resulted from the short fencing history of the U plots (Since February 2013), which were initially grazed. Arnhold et al. (2015) reported from a study conducted in the same area that bulk density and other soil properties indicated slight differences between open pasture and fenced area, demonstrating minor recovery effects after grazing exclusion of livestock. His study though, did not employ the rainfall manipulation design. Grazed sites with low stocking rates might not significantly affect soil bulk density due to variation in soil water, type, and texture (Drewry, 2000; Tobaoda et al., 2011). This partly explains our case given the expansive nature of the study area, which never restricted livestock to grazing at specific points thus reducing their impact, hence the minimal variation of soil ρ of G and U plots.

Mean soil ρ between the U100% and U150% plots did not vary (Figure 7) despite significant differences in their θ_v (Figure 8a, b & c), an indication that rainfall addition above ambient had marginal or no effect on soil porosity in the ungrazed site. Furthermore, the mean C content of the two plots were not different (Figure 10a), implying that soil organic matter, essential for changes in bulk density was not affected by rainfall addition. Similarly, no differences were observed in mean soil ρ between G50% and G100% plots (Figure 7), indicating that rainfall reduction below ambient was unable to further compress pore spaces in the grazed soil. According to Batey (2009) and Bilotta et al. (2007) trampling by livestock in drier soils reduced the risk of compaction, pugging, and poaching compared to wetter soils therefore reducing porosity and increasing bulk density. Furthermore, enhanced compaction by the extra soil present at the subsoil layer following rewetting and expansion of clay (Batey, 2009) partly explains the findings above (Figure 7). Arnhold et al. (2015), working in the same area, reported higher bulk density in the upper subsoil compared to the topsoil which was attributed to altered hydraulic conductivity. In our case, the G50% plot was mostly drier compared to the G100% because it was designed to receive less rainfall. Trampling in this plot, which was presumably of the same magnitude as the G100% plot was unable to further lower ρ at a depth of 10–20 cm where the samples were obtained.

4.2 Volumetric water content (θ_v)

The significant interaction of grazing and rainfall manipulation was characterized by the linear increase in θ_v along rainfall gradient in both G and U sites (Figure 8), contrary to our prediction. The effect of livestock grazing would significantly lower soil moisture. The larger mean effect size in θ_v at 100% and 150% rainfall indicated that higher rainfall amount influenced significant changes in θ_v compared to lower rainfall. For instance, the G50% and U50% plots that simulated drought had very low θ_v (Figure 8a, b & c) compared to their counterparts. K'Otuto et al. (2012), working in the same area revealed that the soil moisture of grazed and ungrazed plots did not vary during dry months, indicating that, intensified drought, enhanced soil moisture loss, regardless of the grazing status. Skinner et al. (2002) who revealed that the interaction of grazing and rainfall regulates soil moisture through evaporation and transpiration, support our findings. Livestock action on herbaceous vegetation increases the sensitivity of grasslands to rainfall hence moderating soil moisture. Low vegetation cover, due to clipping in the G plots could have facilitated further loss in θ_v due to increased evaporation, compared to the U plots that were densely vegetated. During drought, significant reduction in θ_v could have been facilitated by increased evaporation in the G plots as described by Polley et al. (2008) resulting from direct radiation and evapo-transpiration in the U plots due to high water uptake by the live standing plant mass (Bremer et al., 1998; Li et al., 2013).

The narrow rise in mean θ_v with rainfall addition (150%) could be explained by the nature of soils in Lambwe Valley (vertisols) which are poorly drained, (Allsopp and Baldry, 1972), crack during drought, and are prone to run-off during rain events, thus limit water infiltration. During heavy rains, the open cracks of vertisols resulting from drought are filled with finely aggregated topsoil which expand the soil matrix and disrupts the least stable large pores therefore reducing rainwater infiltration (Batey, 2009; Sullivan and Montgomery, 1998). Similar findings (Arnhold et al., 2015; Kurz et al., 2006; Moebius-Clune., et al., 2011; Nyberg et al., 2012) that support our results indicate that low infiltration rate increased surface run-off, and that high clay content hindered soils from taking up sufficient rainwater. The absence of livestock from the U plots was expected to improve the soil structure and allow seepage of water to saturation levels unlike in the G plots. Surprisingly, no persistent soil water saturation was observed in any of the U plots as θ_v stabilized few hours (5–18 hrs) after rainfall event. This indicated that infiltration of water could have been influenced by other factors affecting the soil structure apart from grazing.

Past studies from various ecosystems (Beier et al., 2012: Emmett et al., 2004; English et al., 2005; Huxman et al., 2005; Miranda et al., 2011) on the effect of manipulated rainfall amount (35% to 152% of ambient) on soil moisture and other properties revealed much sensitivity towards drought compared to increased rainfall. Such responses were attributed to variation in the sensible and latent heat fluxes (Bowen ratio) during drought and extremely wet season. According to Gu et al. (2006), higher Bowen ratio is critical in regulating soil moisture during drought compared to when the soils are wet. Consequently, the intensification of drought leads to greater loss in soil moisture compared to wet season when the Bowen ratio is less sensitive to variation in precipitation. This conforms to our findings that, 50% rainfall had more influence on changes in θ_v from ambient than 150% rainfall (Figure 8a, b, c). This resulted from increased evapotranspiration during drought that created water deficit in the soil, leading to rapid drop in θ_v. Furthermore, the findings by Otieno et al., 2010) revealed that reduction of ambient rainfall by 20% significantly lowered soil moisture in Lambwe Valley unlike 10% reduction. They however attributed such disparity to increased surface run-off during heavy downpour.

4.3 The effect of grazing and manipulated rainfall on C and N dynamics

Changes in soil C and N content were affected by the interaction of rainfall manipulation and grazing unlike C:N ratio. The responses were however only significant with manipulated rainfall reduction. This is contrary to the findings of Otieno et al. (2010), working in the same area, who reported that reduction of ambient rainfall by 10–20% did not influence soil C and N contents. We could attribute this to differential rainfall treatments applied in both studies. The lower C, N, and C:N ratio from the 50% rainfall plots (Figure 10a, b, c), could be due to induced water stress that slowed down plant growth, biomass build up, and litter accumulation. Drought reduces soil moisture, which affects nutrient and C availability via root exudation and turnover therefore killing soil microbes and causing a flush in C and N mineralization upon rewetting (Kuzyakov et al., 2000). This could have occurred in the plots with low θ_v between February and April, when the dry period was interrupted by rainy days (Figure 6a, b, c). Furthermore, a decline in C and N with limited θ_v might have resulted from low biological activities that influenced C and N input as reported elsewhere (Frank et al., 2015; Smith et al., 2009). The higher C:N ratio in the U150% plot, resulted from lower soil N (Figure 10b, c). Increased θ_v in the U150% during the wet season facilitated denitrification due to persistent heavy rains. Some studies in tropical savanna (Austin and Sala, 2002; Feral et al., 2003; Han et al., 2008; Moebius-Clune et al., 2011; Piñeiro et al., 2010; Wang et al., 2009) partly support our findings. They underscore the role of soil moisture in nutrient cycling through uptake by plants; mineralization; immobilization; nitrification, biomass build-up, decomposition, and denitrification. Water saturated soils are prone to N losses, due to reduced porosity hindering oxygen circulation and limiting its ability to combine with nitrogen to form nitrates (Fisher et al., 2007; Lata et al., 2004).

Our results on reduced C content due to livestock grazing is supported by two previous studies in Lambwe Valley (K'Otuto et al., 2012; Otieno et al., 2011) explaining that repeated biomass removal, lowered litter decomposition and subsequently C input in the soil. On the contrary, Arnhold et al. (2015) reported lower C content despite higher litter accumulation in plots where grazing was excluded in the same area. Increased N content from our G plots was however, only confirmed by Arnhold et al. (2015) since Otieno et al. (2011) reported a decrease in N content with grazing while K'Otuto et al. (2012) observed no significant variation between grazed and ungrazed plots. They attributed these dynamics to increased decomposition and microbial activity, due to favourable soil temperature. Moreover, high fine root density and increased belowground investment by plants to withstand grazing pressure (Piñeiro et al., 2010; Reeder and Schuman, 2002; Schuman et al., 1999) could help in corroborating our results on N content. Some studies support increased C and N contents with grazing exclusion due to increased litter accumulation and integration into the soil by microorganisms, leading to C and N build up (Han et al., 2008; Wu et al., 2010) whereas others contrast (McSherry and Ritchie, 2014; Piñeiro et al., 2010). Such dynamics of grazing on soil C and N depend on; soil moisture variation; plant species composition, grazing intensity, soil type, and properties (Arnhold et al., 2015; Derner and Schuman, 2007; Piñeiro et al., 2010).

5 Conclusion

The combined effect of grazing and rainfall variability will increase soil moisture in Lambwe Valley. Such changes in soil moisture regime will be regulated by bulk density that will increase with livestock grazing but decrease with increased rainfall amount therefore enhancing C and N input. Grazing during drought will induce soil and plant water stress that will destabilize soil C and N contents therefore likely to affect other soil properties and plant physiological processes. Increased rainfall beyond ambient is highly unlikely to affect most soil properties due to its minimal effect on soil moisture. Such changes are important in predicting how various soils properties will respond to extreme rainfall regimes that might have profound consequences on the ecosystem functions in Lambwe Valley.

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Chapter 3

Manuscript 2: Interaction of livestock grazing and rainfall manipulation enhances herbaceous species diversity and aboveground biomass in a humid savanna

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Abstract

The interaction of livestock grazing and rainfall variability may aid in predicting the patterns of herbaceous species diversity and biomass production. We manipulated the amount of ambient rainfall received in grazed and ungrazed savanna in Lambwe Valley-Kenya. The combined influence of livestock grazing and rainfall on soil moisture, herbaceous species diversity, and aboveground biomass patterns were assessed. We used the number of species (S), Margalef's richness index (D_{mg}), Shannon index of diversity (H), and Pileou's index of evenness (J) to analyse the herbaceous community structure. S, D_{mg}, H, and J were higher under grazing whereas volumetric soil water contents (VWC) and aboveground biomass (AGB) decreased with grazing. Decreasing (50%) or increasing (150%) the ambient rainfall by 50% lowered species richness and diversity. Seasonality in rainfall influenced the variation in VWC, S, Dmg, H, and AGB but not J ($p = 0.43$). Overall, D_{mg} declined with increasing VWC. However, the AGB and D_{mg} mediated the response of H and J to the changes in VWC. The highest H occurred at AGB range of 400–800 g m^{-2}. We attribute the lower diversity in the ungrazed plots to the dominance (relative abundance > 70%) of *Hyparrhenia fillipendulla* (Hochst) Stapf. and *Brachiaria decumbens* Stapf. Grazing exclusion, which controls AGB, hindered the coexistence among species due to the competitive advantage in resource utilization by the more dominant species. Our findings highlight the implication of livestock grazing and rainfall variability in maintaining higher diversity and aboveground biomass production in the herbaceous layer community for sustainable ecosystem management.

Keywords

Herbaceous layer community, plant biomass, rainfall variability, savanna ecosystem, species evenness.

Introduction

Grazing, fire, soil moisture, and nutrient availability are the major modifiers of the vegetation structure and function in the African savanna (Cumming 1982; Hulme et al., 2001). Extreme weather events due to climate change, expanding agriculture and settlement resulting from increased human population threaten the sustainability of these ecosystems. The areas affected most include the East African and Sudanian savanna ecosystems (Case, 2006; Davidson et al., 2003; Osborne et al., 2018), where pastoralism is common. Human and climatic dynamics negatively affect ecosystem services, by decreasing productivity and intensifying loss of biodiversity (Alley et al., 2003; Anderson et al., 2007). The extent to which such changes affect the herbaceous diversity and productivity in the East Africa savanna is still unclear.

Grazing modifies savanna ecosystems through the action of herbivores on vegetation and soil (Augustine and McNaughton, 2006; Harrison and Bardgett, 2004; Savadogo et al., 2008). Livestock grazing, for instance, adds nutrients to the soil through their dung and urine (Bardgett and Wardle, 2003; Olff and Ritchie, 1998), clip the vegetation, and compact the soils by trampling. Through selective removal of the herbaceous vegetation, livestock grazing influence biomass and species richness (Kioko et al., 2012). The response of the herbaceous species diversity to grazing, however, strongly depends on the grazing intensity (Adler et al., 2001; Graham and Duda, 2011). This results from the trade-off between the ability of plants to withstand grazing pressure, enhance their utilization of resources, and increase their growth patterns (Bakker et al., 2003). For instance, at lower grazing intensity, herbaceous diversity increases due to competitive exclusion which allows the less dominant plants to access vital resources (Borer et al., 2014; Koerner and Collins, 2014; Hanke et al., 2014). However, conflicting reports exist on the effects of intense grazing on the herbaceous communities (Cingolani et al., 2005). Overgrazing, therefore, decreases or has no effect on the herbaceous diversity (Anderson et al., 2007; Cingolani et al., 2005; Frank, 2005; Milchunas et al., 1988).

Such patterns result from increased functional redundancy of the grazing-tolerant species (Milchunas et al., 1988; Mouillot et al., 2013), modification of nutrient hotspots (Marshall et al., 2018; van der Waal et al., 2011), and the adaptability of ecosystems to long term grazing pressure (Cingolani et al., 2005; Marshall et al., 2018; Savadogo et al., 2008).

In East Africa, models predict a 5–10% decrease and 5–20% increase in rainfall in dry and wet seasons, respectively by 2050 (Conway, 2009; Hulme et al., 2001), which is likely to affect ecosystem structure and functions. Rainfall manipulation experiments at plot scale have been used to predict how changes in precipitation affect the natural ecosystems (Jones et al., 2016; Knapp et al., 2008; Nippert et al., 2006; Swemmer et al., 2007). Such studies assume that the influences of precipitation on the vegetation are primarily a function of soil moisture. However, temperature and light intensity also vary with rainfall events and are therefore significant in predicting precipitation patterns in the natural ecosystems (Zeppel et al., 2014). Despite the projected rainfall variability in East Africa (Case, 2006), the application of rainfall manipulation experiments to monitor the effects of extreme precipitation is still missing (Beier et al., 2012). There is no quantified effect of extreme rainfall events on the spatial and temporal heterogeneity of the herbaceous vegetation within these ecosystems. Such findings will provide insight on the potential impact of increased rainfall variability on the herbaceous diversity and biomass production.

Seasonality in rainfall in savanna ecosystems results in distinct dry and wet periods, dictating soil moisture availability, plant physiology, patterns of biomass development, and species richness (William and Albertson, 2004; Zeppel et al., 2014). Previous studies have assessed the response of photosynthesis, respiration, and phenology to seasonal variation in soil moisture across savanna ecosystems (K'Otuto et al., 2014; Merbold et al., 2009; William and Albertson, 2004). These studies underscore the importance of soil moisture availability on the functionality of grazed and non-grazed savanna ecosystems. However, the effect of soil moisture variation on the herbaceous species diversity of these ecosystems remains unclear, therefore, necessitating further investigations. Studies conducted under ambient rainfall across East Africa (Augustine, 2003; Harrison and Bardgett, 2004; Kioko et al., 2012) and in the Lambwe Valley ecosystem in Kenya (K'Otuto et al., 2012; Otieno et al., 2011) have reported variations in herbaceous biomass in response to seasonal changes in soil moisture. These studies concluded that changes in the herbaceous biomass were more affected by the seasonal and not annual rainfall totals.

Grazing intensity is rising in Lambwe Valley, but its effect on the ecosystem has not been fully explored. K'Otuto et al. (2012) and Otieno et al. (2010; 2011) examined the effects of cattle grazing on CO_2 exchange and biomass production in the herbaceous layer community of this ecosystem. These studies reported significant reduction in herbaceous productivity due to grazing. To the best of our knowledge, the interactive influence of livestock grazing and rainfall intensity on the structure and function of the herbaceous community in Lambwe Valley, remains unexplored. However, in other ecosystems, livestock grazing modified the effect of rainfall on soil moisture availability, nutrient distribution, and herbaceous species diversity (Dangal et al., 2016; Koerner and Collins, 2014; Porensky et al., 2013). The interaction of grazing and other climatic factors additionally facilitates such changes. We selected Lambwe Valley as a typical savanna to test the interactive influence of livestock grazing and rainfall variability on species diversity and aboveground biomass production. This ecosystem was suitable because of its humid nature characterized by higher rainfall variability and the large population of livestock that dominate the area. The current study assessed how grazing and manipulated rainfall affected the herbaceous species diversity and aboveground biomass production (AGB) in a typical savanna ecosystem in Lambwe Valley Kenya. We hypothesized that: (1) herbaceous diversity shifts seasonally with rainfall amount. The changes are, however modified by livestock grazing; (2) Higher AGB increases the herbaceous community diversity through enhanced soil moisture condition.

Materials and methods

Study area

The study was conducted in the Lambwe Valley ecosystem (0°30´ & 0°45´ south; 34°10´ & 34°20´ east), a humid savanna in Kenya covering 324 km^2 and hosts Ruma National Park (120 km^2). The Valley is located in Homa Bay County, 10 km east of Lake Victoria at an altitude of 1200-1600 m ASL. It is surrounded by Gembe and Gwasi Hills to the west, and Kanyamwa escarpment on the east. The annual rainfall is 700-1100 mm in two seasons: April to June and October to December, with mean air temperature of 25º C. The soils at the valley bottom are Vertisols with biotite rock (Allsopp and Baldry 1972). The landscape is dominated by *Hyparrhenia fillipendula*, with thickets of *Acacia* and other shrubs. Peasant farming and livestock keeping are the common economic activities in the area. Measurements were done in selected open areas neighboring Ruma National Park, on land belonging to the National Youth Service (NYS).

Experimental design

The design was a split plot factorial setup with 2 levels of grazing and 3 levels of rainfall manipulation. Grazing was categorized into grazed (G) and ungrazed (U) as the main sites (plots) split into 3 levels of rainfall achieved through manipulating ambient rainfall (100%), by reducing 50% (50%) and increasing 50% (150%) respectively (Figure 1a). Each set up, comprising the 50%, 100% and 150% rainfall plots were replicated three times in both grazed and ungrazed sites, giving a total of 6 rainfall manipulation plots (RMPs) used during dry and wet months. The grazed and ungrazed sites were separated by a farm road, however the closest RMPs in both sites were 30 m apart. The RMPs, constructed 10-20 m apart, within respective sites, allowed free movement of livestock (Figure 1b, c), and were ready 3 months before the measurement period (15th September 2015 to 2nd June 2016). We considered months with less than 60 mm of rainfall as dry and those with higher rainfall (>60 mm) as wet (Figure 1a, b) (Mc Knight et al. 2000). September 2015 marked the end of prolonged dry season (Figure 1a), whereas, January and May characterized the end of two rainy seasons, interrupted by short dry spell in February and March 2016 (Figure 1a b). The plots were abbreviated using the first letters of the grazing level (G or U) followed by rainfall amount (50%, 100% and 150%) i.e. G50%, U150%. In 2013, open fields regularly grazed by livestock (G) were fenced with a 2 m high-chain link to exclude livestock and create ungrazed site (U). Soil type, drainage, terrain, and vegetation distribution and structure were considered when fencing the ungrazed site to minimize the effects of confounding factors. Livestock included 180 goats and 130 cattle, randomly grazed in an area covering 133 acres throughout the year. Stocking rate in the past 10 years is about 6.6 animals per ha $^{-1}$ area (K'Otuto et al. 2012) and is likely to rise due to increased human settlement and agriculture.

To exclude the desired amount of ambient rainfall or increase the amount of rain input, the RMPs (6 m x 3 m wide) were demarcated. Rainfall reduction by 50% was achieved using rain exclusion gutters constructed from strips (30 cm width) of 6 mm UV-transparent plastic sheets intermittently stretched (inclined at 14°) to cover 50% of the total plot/ground surface (10 strips were used). The strips, laid on wire mesh were stretched over 2 m high metal frames to allow free movement of grazing animals over the plots (Figure 1b, c). To increase the ambient rainfall by 50%, the excluded rainwater was redirected on to open plots, thus raising ambient rain (100%) by 50%, giving 150% rainfall amount (Figure 1). Portable VWC sensors were used a day after rainfall event to test the homogeneity in soil water distribution within the RMPs. Trenches (50 cm deep and 30 cm wide), reinforced with plastic sheets buried in soil, were dug between plots to reduce lateral water flow across plots. The rain shelters had open sides to reduce the greenhouse effect from gutters. Light and temperature sensors were installed under the RMPs to monitor the influence of the gutters. The shelters were set up in a gently sloping (3-5°) open field at the valley bottom.

Microclimate and soil volumetric water content (VWC)

Rainfall, air temperature, humidity, and light intensity were logged from three automatic microclimate stations (AWS-WS-GP1, Delta-T Devices, Cambridge, UK), installed 2 m aboveground, at the study site. VWC was measured using 5TE probes connected to EM50 data loggers (Decagon Devices Inc., Washington, USA) at 20 cm soil depth. Three probes were installed in each plot to log data at 30 minutes' interval between 15/9/2015 to 2/6/2016 (Figure 12).

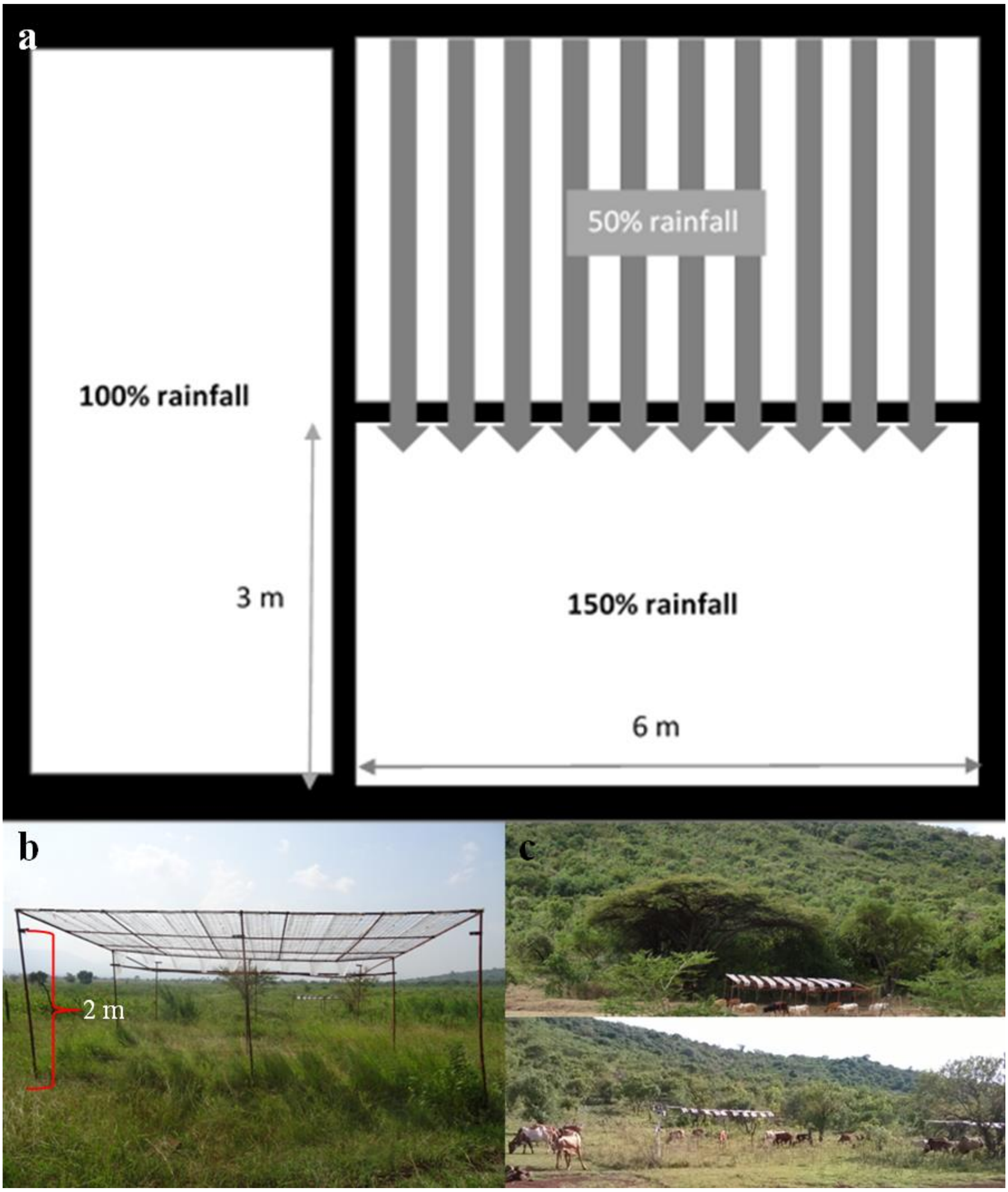

Figure 11: Layout of the rainfall manipulation plots (**a**) separated by trenches (50 cm deep and 30 cm wide) shielded by polythene to prevent lateral flow of water. The grey parallel arrows show the flow of 50% rainwater to enhance the plot designed to receive 150% of the total amount of rainfall through gravity. Rainfall manipulation plot (**b**) partially covered with intermittently spread polythene sheets on a slanting roof (14°) to aid the flow of rainwater. Livestock grazing (**c**) within the rainfall manipulation plots and their surroundings.

Herbaceous community assessment

We monitored the herbaceous species seasonally, in September 2015, January 2016, and May 2016. The species ground cover within plots (1 m x 1 m) was determined using point frame method (Bonham, 1989). The pinholes on the frame were set 10 cm apart. The relative species abundance was calculated from the total count of individuals as outlined in Table 2. To assess changes in richness, diversity, and evenness, we used the Margalef's richness index (D_{mg}), Shannon's diversity (H), and Pielou's evenness (J), respectively (Magurran, 2004). The indices were computed from abundance data using the respective formula in Table 2.

Aboveground biomass (AGB)

AGB was sampled both destructively and non-destructively from every plot. Two plots (40 x 40 cm) were demarcated on opposite sides of every 1 x 1 m, vegetation monitoring plots for destructive and non-destructive estimation of AGB, respectively. A total of 18 plots were used for destructive sampling of AGB. We used the photographic method for non-destructive estimation of biomass using a digital camera (Tackenberg, 2007). The photographic images were calibrated using AGB destructively sampled from selected plots at different times. The validation was done by comparing the exact biomass destructively sampled and their corresponding pixels from the images taken, using linear regression model. Subsequently, the vertical distribution of plant matter in terms of characterized pixels, was evaluated. The images were shot by high-resolution digital camera (20.4 mega-pixels) at 0.5–1.5 m height (depending on the height of the herbaceous stand) against a dark background with a scale.

The standing plant mass was then harvested at the ground level and weighed to quantify the fresh AGB. The two most dominant species from the grazed and ungrazed plots were sorted from the harvested samples and their masses established relative to the total AGB. The samples were later oven dried at 80°C for 48 hours. The AGB estimations in the subsequent seasons were done using the non-destructive method. All images were saved in JPG format for analysis using Image J 1.46 software (Schneider et al., 2012).

Table 2: Formula for calculating species diversity parameters.

Index	**Formula**
Ground Cover	$Cover(\%) = \frac{number\ of\ hits\ of\ species\ x}{total\ number\ of\ hits\ for\ all\ species} * 100$
Margalef index of Richness	$D_{Mg} = \frac{(S-1)}{1nN}$
Shannon Index of Diversity	$H = -\sum \left(\frac{ni}{N}\right) 1n \left(\frac{ni}{N}\right)$ or $-\sum Pi\ 1n\ Pi$
Pielou's evenness	J = H/*1n*S

S - Total number of plant species
N - Total number of individuals
1n - Natural log
N*i* - important value index of the ith species

Statistical analysis

The effects of grazing, rainfall manipulation, seasonality in rainfall, and their interaction on VWC, AGB, S, D_{mg}, H, and J were tested using factorial ANOVA (fully crossed) at a significance level of $p \leq 0.05$. The possible interaction of factors tested included: Grazing X rainfall manipulation; grazing X seasonality in rainfall; rainfall manipulation X seasonality in rainfall, and grazing X rainfall manipulation X seasonality in rainfall. Owing to the large dataset, the real-time VWC (logged every 30 minutes throughout the measurement period) was analysed separately using repeated measure ANOVA. We aggregated the VWC data sets into daily (to minimize the effect of peak VWC values resulting from higher rainfall intensity) and seasonal (September, January, and May) means (± SD) to facilitate the subsequent analysis. Generalized linear mixed model (GLMM) assuming a fixed effect was used to test the influence of VWC as a fixed variable on the AGB, S, D_{mg}, H, and J. The multiple comparison of means was performed using Tukey HSD, when the ANOVA was significant. These analyses were done using JMP 14 Statistical software, SAS Inc.

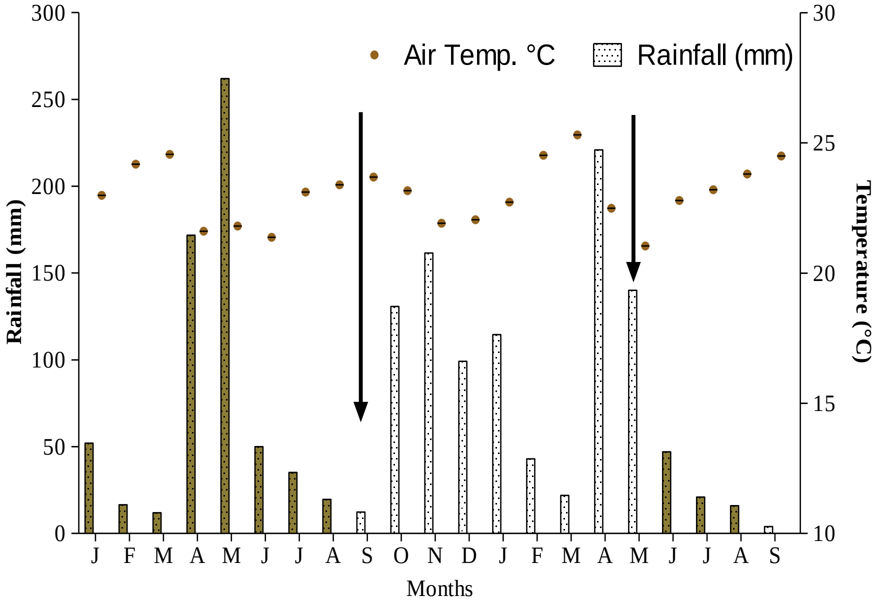

Figure 12: Pattern of air temperature and rainfall from the microclimate station at the study site beginning January 2015 to September 2016. The unshaded bars highlighted between the two arrows pointing downwards represent the study period.

Complex relationships amongst VWC, biomass, and species diversity parameters were evaluated using structural equation modelling (SEM) (Grace et al., 2010). The direct and indirect (with mediation) effects of VWC on herbaceous biomass and diversity were determined using path analysis in the AMOS 25 software (Arbuckle, 2017). Out of the many models tested to predict the effect of VWC on herbaceous biomass and diversity, only one, having D_{mg}, and AGB as mediators passed the model fit test. We tested the models' fit using the chi-square goodness of fit (chi-square = 2.0–5.0; p > 0.05), confirmatory fit index (CFI >

0.95), and root mean square error of approximation (RSMEA < 0.05). Subsequently, covariances that displayed stronger relationships were introduced to modify the model. The Preacher and Hayes (2008) approach using a bootstrap test with bias corrected (BC) percentile method (95%) was applied to demonstrate mediation. Subsequently regression analysis was conducted using JMP 14 Statistical software to test the extent to which AGB influenced H.

Results

Effect of rainfall manipulation and grazing on soil water status

The pattern of soil VWC at the 20 cm depth corresponded to the changes in rainfall amount during the measurement period (Figure 12; Figure 13a, b). The VWC increased with the amount of rainfall allowed into the plots along a gradient of 50%, 100%, and 150% (Figure 13a, b; Table 3). The lowest mean VWC for the period was 9.78% ± 0.82 in September 2015 whereas, the highest was 27.75% ± 0.88 in May 2016 from G50% and U150% plots, respectively. Grazing had a lower mean effect on VWC in the grazed (17.46% ± 3.86) compared to the ungrazed (22.31% ± 5.00) plots (Figure 13b). Rainfall manipulation significantly (f = 96.72; $p < 0.05$) influenced VWC in both the grazed and ungrazed plots (Figure 13b). Naturally, VWC varied seasonally and was lowest in September and highest in May, corresponding to the dry and wet seasons, respectively (Figure 13b). During the dry season, VWC varied significantly between 50%, 100%, and 150% plots of the ungrazed sites, but not in the grazed site (Figure 13b). In the rainy season, there were no differences in VWC between 100% and 150% plots of grazed and ungrazed sites. However, the 50% plots had lower VWC. Both grazing and seasonality in rain significantly ($p < 0.05$) interacted with rainfall manipulation to alter the VWC (Table 3).

Table 3: Full factorial repeated measures ANOVA, f statistics with p values (in parenthesis, bold values indicate significance) showing how various parameters are influenced by grazing - G (grazed and ungrazed), rainfall manipulation - RMP (50%, 100%, and 150%) across 3 seasons (dry season of September 2015; wet seasons of January and May 2016) and the interaction of the three variables. The last row outlines the outcome of one-way ANOVA indicating the subsequent effect of VWC on the measured parameters.

Parameters	**df**	**VWC** (Volumetric water content**)**	**S** **(**Number of species**)**	**D_{mg}** **(**Margalef's index of richness**)**	**H** **(**Shannon's index of diversity**)**	**J** **(**Pielou's evenness**)**	**AGB** **(**Aboveground biomass**)**
Grazing (G)	1	154.12 (<**.0001**)	199.55 (<**.0001**)	267.85 (<**.0001**)	277.98 (<**.0001**)	190.96 (<**.0001**)	385.40 (<**.0001**)
RMP	2	96.72 (<**.0001**)	256.64 (<**.0001**)	238.97 (<**.0001**)	63.57 (<**.0001**)	12.83 (<**.0001**)	157.76 (<**.0001**)
Grazing*RMP	2	14.46 (<**.0001**)	6.50 (**0.0039**)	7.37 (**0.0021**)	13.12 (<**.0001**)	10.57 (**0.0002**)	18.88 (<**.0001**)
Seasonality in rain	2	114.58 (<**.0001**)	16.99 (<**.0001**)	19.70 (<**.0001**)	4.74 (**0.0149**)	0.88 (0.4255)	110.78 (<**.0001**)
Grazing*Season	2	1.47 (0.2430)	4.756 (**0.0147**)	1.97 (0.1543)	0.23 (0.7936)	0.16 (0.8544)	15.61 (<**.0001**)
RMP*Season	4	2.74 (**0.0436**)	1.59 (0.1988)	1.25 (0.3072)	1.05 (0.3964)	0.54 (0.7093)	7.13 (0.0002)
G*RMP*Season	4	0.95 (0.4477)	9.45 (<**.0001**)	9.27 (<**.0001**)	0.85 (0.5005)	0.14 (0.9675)	10.04 (<**.0001**)
VWC		–	1.65 (0.21)	4.26 (**0.044**)	8.18 (**0.006**)	12.75 (**0.0008**)	147.81 (<**.0001**)

Table 4: Relative abundance (mean and SD) showing the distribution of plant species present in plots from grazed and ungrazed areas sampled in September (2015), January and May (2016). The first four species represent the two most numerically dominant plant species, each from grazed (*Bothriochloa insculpta* and *Paspalum dilatatum*) and ungrazed (*Brachiaria decumbens* and *Hyparrhenia fillipendula*).

	Plant species	**Ground Cover (%)**					
		G50%	**G100%**	**G150%**	**U50%**	**U100%**	**U150%**
1	*Bothriochloa insculpta* (A. Rich) A. Camus	31.11 ± 3.97	27.59 ± 3.68	27.32 ± 4.82	–	1.11 ± 0.96	–
2	*Paspalum dilatatum* Poir	11.87 ± 3.75	18.61 ± 3.48	23.02 ± 4.87	0.62 ± 0.99	0.41 ± 0.62	0.43 ± 0.65
3	*Brachiaria decumbens* Stapf	2.51 ± 1.61	3.50 ± 1.04	1.86 ± 0.78	27.72 ± 5.54	18.63 ± 4.61	28.75 ± 8.14
4	*Hyparrhenia fillipendula* (Hochst) Stapf.	12.46 ± 3.46	10.59 ± 2.66	10.82 ± 4.68	54.06 ± 8.30	43.33 ± 9.58	56.47 ± 10.02
5	*Acacia* spp.	–	–	–	–	0.39 ± 0.59	–
6	*Agrostis palustris* Huds	–	–	–	–	0.30 ± 0.60	–
7	*Aspilia pluriseta* Schweinf	3.26 ± 1.62	2.69 ± 2.75	1.72 ± 0.46	2.43 ± 1.56	4.78 ± 2.00	1.88 ± 1.09
8	*Berlaria acanthoides* Vahl.	1.49 ± 1.14	1.15 ± 1.01	1.69 ± 1.23	1.61 ± 0.41	0.68 ± 1.07	1.07 ± 1.01
9	*Cajanus cajan* L. Millsp	–	0.80 ± 1.30	0.36 ± 1.09	1.09 ± 1.14	0.74 ± 1.41	0.36 ± 0.54
10	*Cynodon dactylon* (L) Pers	2.35 ± 0.85	1.28 ± 0.54	1.92 ± 0.97	–	1.78 ± 0.89	0.32 ± 0.97
11	*Desmodium gangeticum* (L.) D.C.	–	0.41 ± 0.62	0.93 ± 1.49	1.47 ± 1.05	1.85 ± 1.47	0.37 ± 1.11
12	*Digitaria sanguinalis* (L) Scop	1.86 ± 0.34	1.88 ± 0.91	1.59 ± 0.41	–	0.40 ± 0.85	0.74 ± 1.56
13	*Euphorbia hirta* Linn.	0.71 ± 1.07	1.44 ± 0.25	1.32 ± 1.47	0.96 ±0.96	0.40 ± 0.85	0.40 ± 0.85
14	*Hoslundia opposita* Vahl.	–	1.26 ± 0.53	–	–	1.80 ± 1.11	–
15	*Hypoestes aristata* Soland ex Roem & Schalt	0.77 ±1.18	0.68 ± 0.90	0.69 ± 1.10	–	1.24 ± 1.2	0.75 ± 1.24
16	*Hypoestes forskaolii* (Vahl) R.Br.	–	0.45 ± 0.68	–	1.3 ± 1.11	0.43 ± 0.65	0.81 ± 0.62
17	*Indigofera arecta* Hochst ex. A. Roch.	–	1.44 ± 0.25	1.32 ± 1.10	–	1.20 ± 0.92	–
18	*Indigofera brevicalyx* Bak.	–	0.37 ± 0.97	0.97 ± 0.75	–	0.43 ± 0.65	–
19	*Ipomoea tenuirostris* Steud ex Choisy	4.32 ± 2.03	1.49 ± 0.83	0.41 ± 0.62	3.09 ± 1.23	1.38 ± 1.12	1.18 ± 1.12
20	*Justicia striata* Vahl	4.38 ± 2.03	3.03 ± 1.60	3.27 ± 1.82	2.61 ± 1.72	1.62 ± 1.65	1.48 ± 1.84
21	*Lantana triifolia* L.	–	0.35 ± 1.06	–	–	0.96 ± 0.82	–
22	*Leonotis nepetifolia* (L) R.Br.	–	–	–	–	1.21 ± 0.62	–
23	*Ocimmun kilimandscharicum* Guerke	–	0.58 ± 0.87	–	–	1.10 ± 0.43	–

24	*Panicum maximum* Jacq.	–	–	–	–	1.10 ± 0.43	–
25	*Rhynchosia minica* (L.) DC.	–	0.86 ± 0.65	–	0.99 ± 0.75	1.53 ± 0.91	1.07 ± 0.84
26	*Sida acuta* Burm. F	1.62 ± 0.69	1.29 ± 0.87	0.77 ± 0.96	–	–	–
27	*Solanum incanum* Linn	–	1.44 ± 0.25	–	–	0.73 ± 1.19	–
28	*Sonchus schweinfurthii* Oliv.	–	0.85 ± 0.89	0.55 ± 0.83	–	–	–
29	*Sphaeranthus suaveolens* (Forsk) DC	–	1.44 ± 0.25	–	–	–	0.38 ± 0.80
30	*Sporobolus agrostoides* Chiov.	10.86 ± 3.10	4.63 ± 2.38	12.85 ± 3.29	–	0.43 ± 0.65	–
31	*Striga asiatica* (L) Kuntze	0.62 ± 0.96	0.45 ± 0.68	0.41 ± 0.62	–	–	–
32	*Themeda triandra* Forssk	–	0.58 ± 0.87	–	0.77 ± 1.36	0.80 ± 0.85	1.09 ± 1.41
33	*Triumphetta rhomboidae* Jacq.	1.62 ± 0.69	0.98 ± 1.20	0.48 ± 0.73	1.27 ± 0.82	3.18 ± 1.76	2.08 ± 0.95
34	*Urena lobata* L.	1.47 ± 0.88	1.44 ± 0.25	0.41 ± 0.62	–	1.19 ± 0.85	0.36 ± 0.54
35	*Vernonia glabra* (Steetz) Vatke	5.09 ± 2.24	5.42 ± 2.44	4.56 ± 2.12	–	4.86 ± 2.15	–
36	*Waltheria indica* Bak.	1.62 ± 0.69	1.04 ± 1.07	0.75 ± 1.25	–	–	–

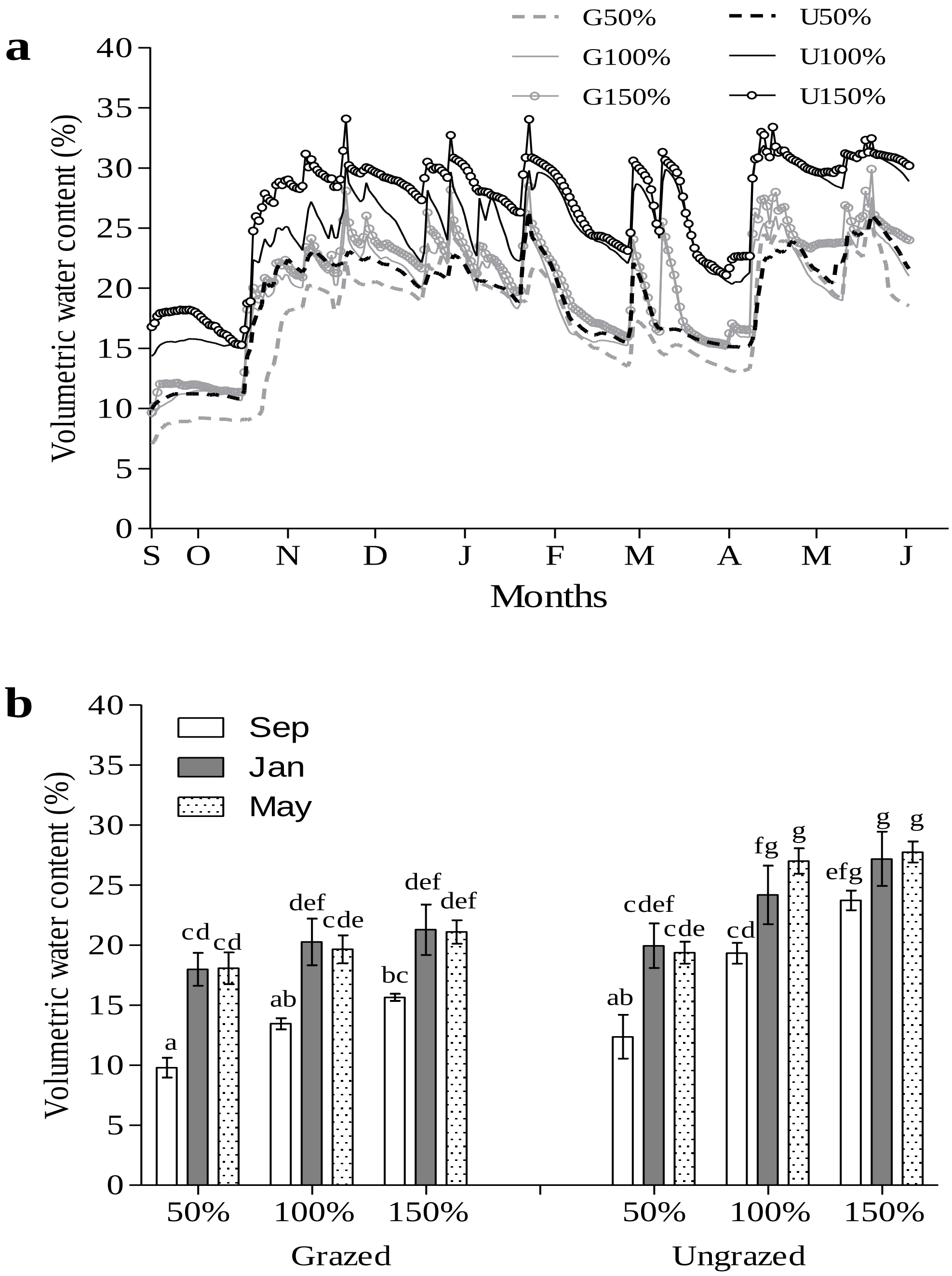

Figure 13: Pattern of the mean daily volumetric water content of grazed and ungrazed plots for the entire measurement period (**a**) and its seasonal variations (**b**) among the treatment plots (50%, 100%, and 150%). Different letters show significant variation in means ($p < 0.05$) among treatments. The error bars in the graph represent mean ± SD.

Herbaceous vegetation response to rainfall manipulation and grazing

Table 4 shows the herbaceous species composition and their distribution in the treatment plots. *Hyparrhenia fillipendulla* (Hochst) Stapf. and *Brachiaria decumbens* Stapf. dominated the ungrazed plots whereas *Bothriochloa insculpta* (A. Rich) A. Camus and *Paspalum dilatatum* Poir were dominant in the grazed plots. The highest number of species (S) occurred in the G100% and U100% plots (Table 4).

Both addition (150%) and reduction (50%) of ambient rainfall lowered S, D_{mg}, H, and J in grazed and ungrazed plots (Figure 14). Higher S and D_{mg} were reported in the 100% rainfall plot compared to the 50% and 150% plots in both grazed and ungrazed sites (Figure 14a, b). H and J displayed a similar pattern, only in the ungrazed site, given that, no mean differences were observed among the grazed plots (Figure 14c, d). The means of S, D_{mg}, H, and J between the 50% and 150% plots in both grazed and ungrazed sites did not vary. Livestock grazing, rainfall manipulation and seasonality in rainfall influenced the changes in S, D_{mg}, and H (Table 3). Various interactions especially between grazing and rainfall manipulation additionally affected the patterns of S, D_{mg}, H, and J (Table 3).

The highest S (24.67 ± 0.57) and D_{mg} (5.38 ± 0.06) were observed in the G100% plot in January 2015 (Figure 14a). The lowest H was in U50% (1.35 ± 0.26) and U150% (1.11 ± 0.17) plots in May 2016 compared to their counterparts in the grazed plots (Figure 14c). J ranged from 0.50 ± 0.08 (U150%) to 0.82 ± 0.02 (G100%), with no significant mean differences among the grazed plots, unlike in the ungrazed plots where J reduced with 50% and 150% rainfall amounts. The influence of grazing on herbaceous community was in the order: H (47.62%) > D_{mg} (45.06%) > S (35.89%) > J (32.09%).

Aboveground biomass (AGB)

The AGB destructively sampled was linearly correlated with their corresponding photographic images (pixels) in both grazed ($r^2 = 0.74$–0.87; $p < 0.05$) and ungrazed ($r^2 = 0.83$–0.91; $p < 0.05$) sites. AGB declined with grazing but increased with rainfall amount (Table 3).

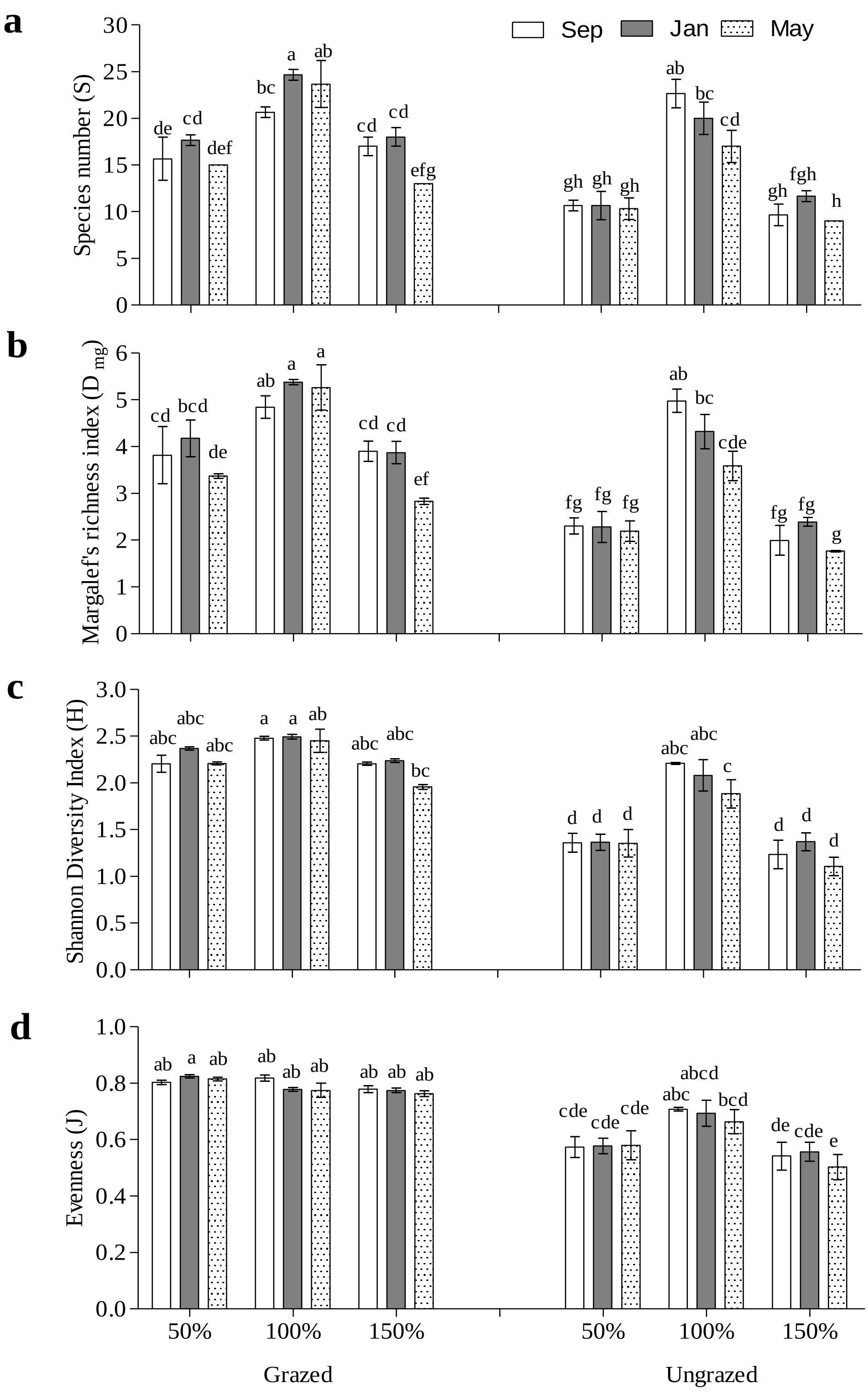

Figure 14: Changes in species number (S, **a**), richness (D_{mg}, **b**), diversity (H, **c**), and evenness (J, **d**) with grazing, rainfall manipulation, and seasonal variation. Different letters show significant variation in means ($p < 0.05$) among treatments. The error bars in the graph represent mean ± SD.

The G50% and U50% had the lowest AGB of 333.74 ± 5.27 g m^{-2} and 604.86 ± 89.48 g m^{-2} from grazed and ungrazed respectively, in September 2015 (Figure 15a). The highest mean seasonal AGB was reported in the U100% plot, in May 2016 (Figure 15a). However, for the entire measurement period, the U150% plot had more AGB of 1150 ± 119 g m^{-2} compared to the other plots (Figure 15b). Mean AGB were different among the plots, except between G100% and G150% ($p = 0.96$). AGB was influenced by grazing, rainfall manipulation, seasonality in rain, and their interactions (Table 3). AGB sharply increased from the dry season (September) to the wet season (January), however, no significant difference was observed between the two wet seasons (January and May) (Figure 15a). *H. fillipendula* and *B. decumbens* constituted 66–75% of AGB from the ungrazed plots whereas *P. dilatatum* and *B. insculpta* contributed 26–36% of AGB in the grazed area (Figure 15b).

Relationships among parameters

The SEM used to predict the effect of VWC on herbaceous AGB and diversity had a good fit to the data ($x^2 = 2.98$; $p = 0.84$; RMSEA < 0.05) (Figure 16). However, we excluded the number of species (S) from the statistics, for the model to fit. Nevertheless, both D_{mg} and J indices still represented S (Table 2). VWC had no direct effect on H and J but increased AGB and decreased D_{mg} (Figure 16). On the contrary, the mediated (indirect-only mediation) effect of VWC on H and J through AGB and D_{mg} were significant ($p < 0.05$). Both H and J increased with D_{mg} but reduced significantly ($p < 0.05$) as AGB increased (Figure 16). The changes in H were strongly correlated with J in our model (Figure 16). Increased AGB significantly lowered H ($r^2 = 0.32$; $p < 0.05$), particularly in the ungrazed plots (Figure 17). The highest H was reported at an AGB range of 400–800 g m^{-2} in the grazed plot.

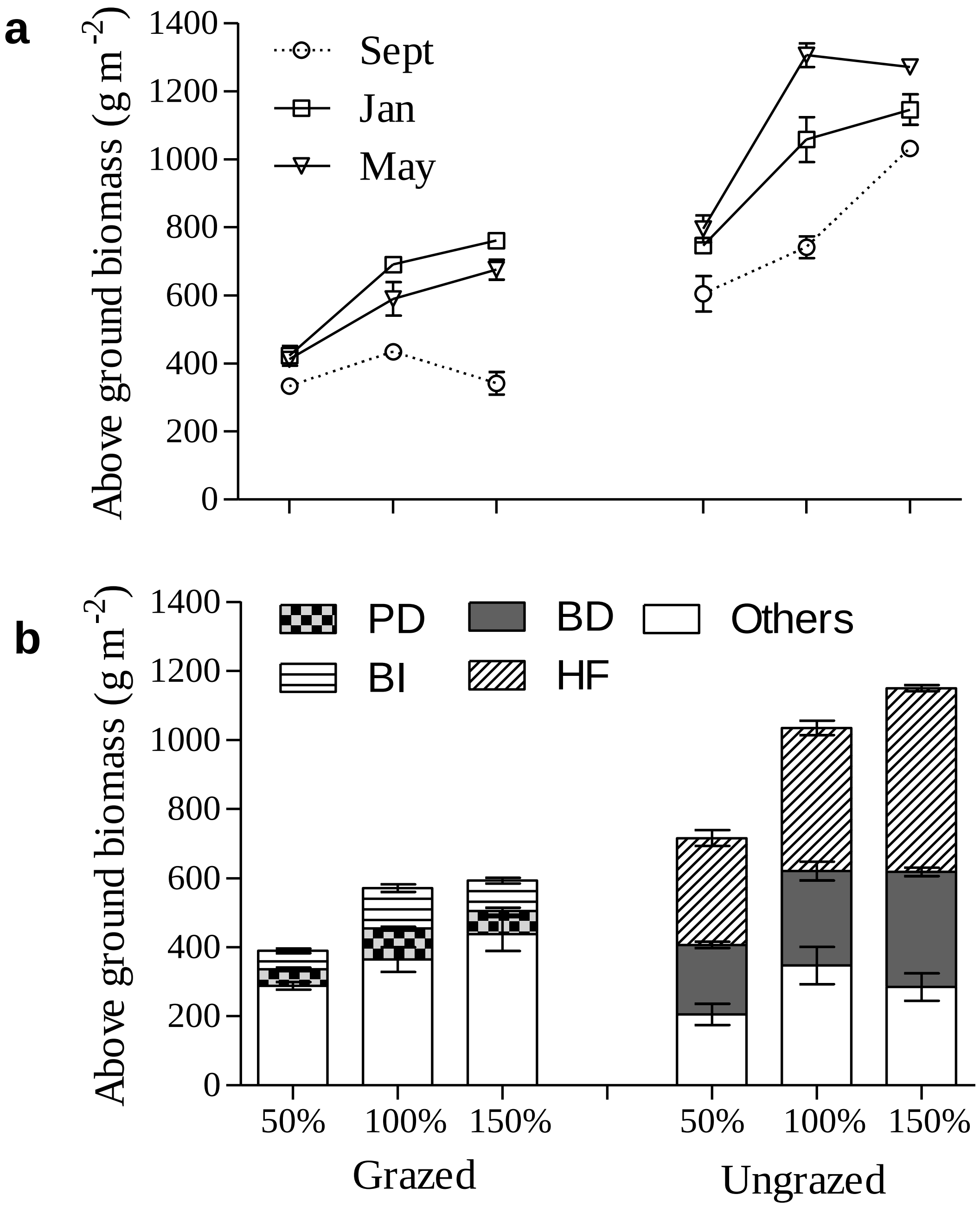

Figure 15: Seasonal changes in mean (plus SD) AGB (**a**) showing variation between grazed and ungrazed plots. AGB increased significantly from the grazed to ungrazed along a rainfall gradient. The contribution of two most dominant species (**b**) from grazed; *Paspalum dilatatum* (PD), *Bothriochloa insculpta* (BI) and ungrazed; *Brachiaria decumbens* (BD) and *Hyparrhenia fillipendula* (HF) to AGB. Rainfall manipulation plots: 50%, 100%, and 150%.

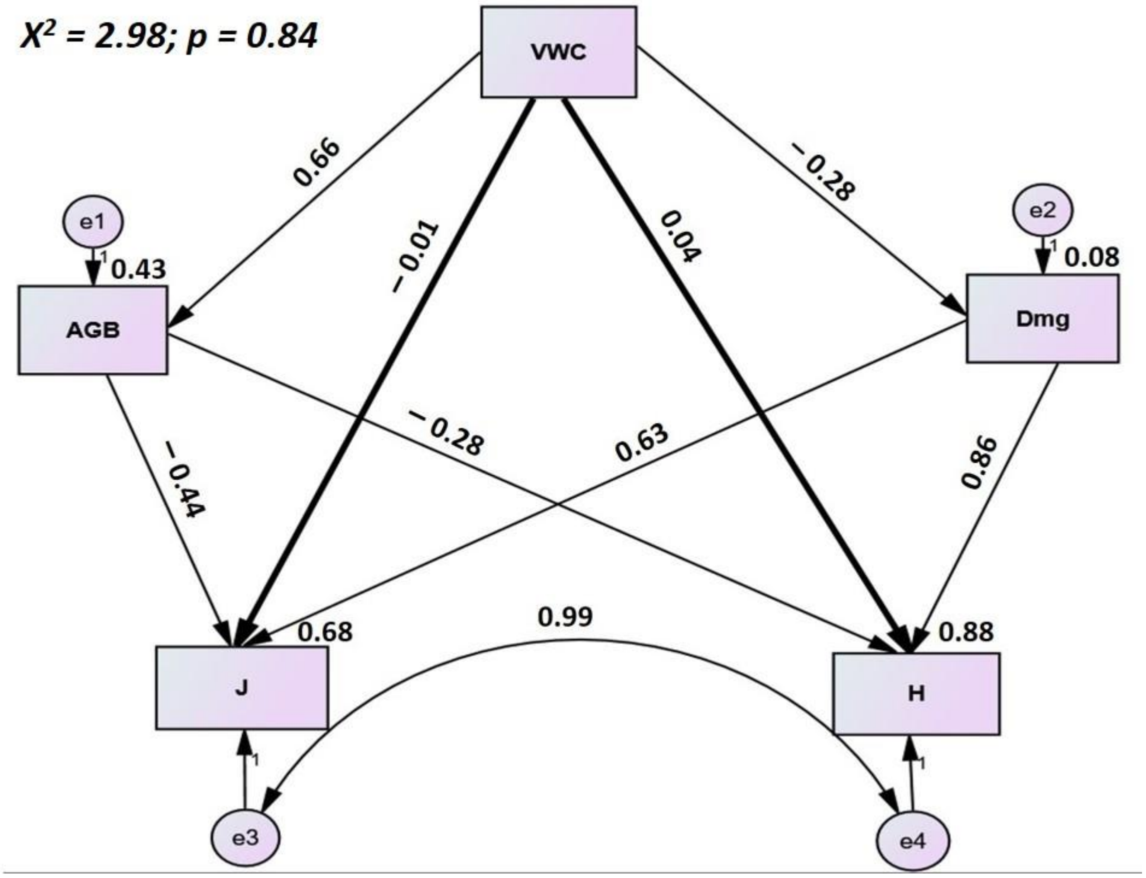

Figure 16: Structural equation model (SEM) showing the effect of volumetric water content (VWC) on species diversity (H) and evenness (J) mediated by aboveground biomass (AGB) and the Margalef's richness (D_{mg}). The chi-square value ($X^2 = 2.98$; $P = 0.84$) expresses the model fit. The values presented alongside the arrows stand for the standardized regression coefficients. The e1–e4 attached to the rectangles are the error terms for every variable tested. The r^2 values above the rectangles show the amount of variation explained by the model, while the thick arrows indicate the lack of significant effect where $P > 0.05$.

Discussion

Patterns in soil water status

Changes in VWC (at 20 cm soil depth) in the plots were correlated with the amount of rain, an indication that rainwater was the main source of moisture input for soil and vegetation. On the other hand, livestock grazing modified the herbaceous structure and reduced the VWC through trampling and clipping of the vegetation. This exposed the soil surface, and accelerated soil moisture loss through evaporation, particularly during drought. Moreover, soil compaction by herbivores reduces the soil water holding capacity, hence, lowering the moisture levels in the grazed savanna ecosystems (Holdo and Mack, 2014). The interaction between grazing and variable rainfall input additionally accounts for the soil moisture variations in our plots (Table 3). Studies that support our findings show increased sensitivity of grazed ecosystems to changes in precipitation compared to their ungrazed counterparts (Frank, 2007; Polley et al., 2008; Skinner et al., 2002). Such changes result from increased water deficit in the soil, prolonged drought (Frank, 2007; Skinner et al., 2002), and effect of high radiation load (Polley et al., 2008).

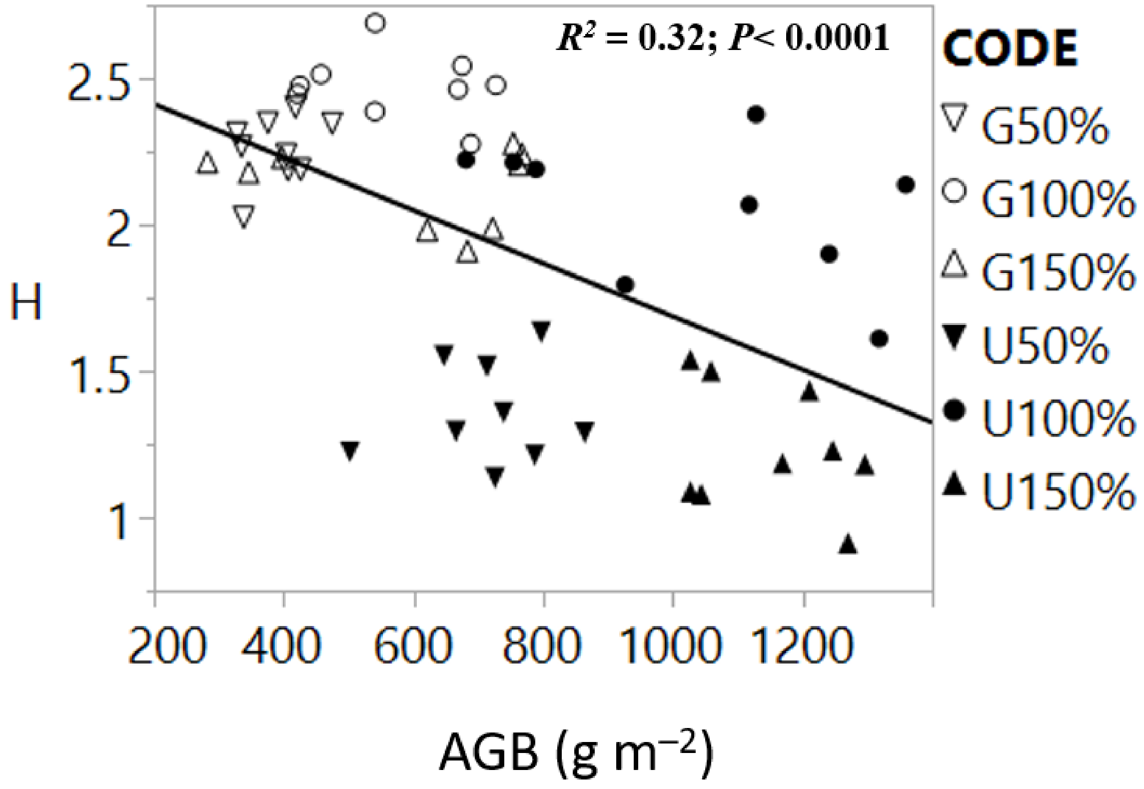

Figure 17: Linear regression showing relationship between aboveground biomass (AGB) and Shannon diversity index (H) plotted from grazed and ungrazed. The line is the significant regression fit ($R^2 = 0.32$; $P< 0.0001$) across data points from all the plots sampled.

Our findings revealed that, during drought, grazing had no effect on the changes in VWC at the 20 cm soil depth. This is shown by the lack of variation in VWC between G50% and U50% plots (Figure 13a and b) in September 2015, contrary to our expectation. We anticipated that, the denser herbaceous canopy in the U50% plot compared to the G50% would aid in conserving soil moisture during drought. Conversely, the manipulative reduction of ambient rainfall dried up the soils, irrespective of whether the plots were grazed or not. According to Maestre et al. (2009), belowground competition by overlapping niches during drought diminishes the positive effects of dense plant canopies on soil moisture availability. Furthermore, modified microclimate conditions such as grazing exclusion to conserve soil water are less likely to remedy the effect of intense drought on the herbaceous layer community (Porensky et al., 2013). These findings partly explain the lack of variation in VWC between the G50% and U50% plots. We additionally suggest that the reduction of ambient rainfall during drought in the U50% plot triggered defoliation and plant death, making the soils vulnerable to water losses. Scholes and Archer (1997) in support of our results show that, physiological stress resulting from drought causes premature leaf senescence and plant death, therefore, exposing the soils to higher evaporation rates due to reduced vegetation cover.

Studies from other ecosystems that conform to our findings, reveal that during drought, soil moisture between grazed and ungrazed sites do not vary (K’Otuto et al., 2012; Sarmiento et al., 2004). According to Cingolani et al. (2005), Gu et al. (2006) and Skinner et al. (2002), the grazing history, functional group traits, variation in the Bowen ratio and root architecture of vegetation, largely account for soil moisture availability across ecosystems. Some belowground soil factors not tested by our study, such as niche differentiation and soil microbial activities (McCulley et al., 2007; Sankaran et al., 2004) explain further the soil moisture pattern between the G50% and U50% plots.

Changes in the herbaceous community composition and diversity

S, D_{mg}, H, and J declined in the rainfall manipulation plots, regardless of the decrease (50%) or increase (150%) in ambient rainfall (Figure 14). We observed no effect of the interaction between rainfall manipulation and seasonality in rainfall on S, D_{mg}, H, and J. Consequently, our hypothesis that, the herbaceous species richness and diversity patterns positively correlate to rainfall gradient (Adler and Levin., 2007; Cleland et al., 2013; Cornwell and Grubb, 2003) was not supported. Nevertheless, livestock grazing interacted with rainfall manipulation and seasonality in rainfall to enhance S and D_{mg} in the herbaceous community. Grazing significantly ($P < 0.05$) influenced vegetation response to rainfall manipulation as depicted by the variation in D_{mg}, H, and J (Table 3). Our results agree with Skinner et al. (2002) who observed that grazing modified species composition following supplemental summer precipitation. Anderson et al. (2007), on the other hand, showed that rainfall and soil phosphorous (P) strongly modulated the effect of grazing on the herbaceous species diversity. In our case, livestock grazing, influenced changes in the herbaceous community by regulating the distribution of biomass through changes in soil moisture.

In an *Acacia*-dominated savanna in Kenya, cattle grazing, in combination with periodic drought, enhanced plant diversity by creating open niches (micro-sites) for the cryptic species (Porensky et al., 2013). Their results partly explain the patterns of D_{mg}, H, and J reported in our grazed plots despite the reduced ambient rainfall or drought conditions in September (Figure 14b, c and d). Gao et al. (2009), however, indicated that under short-term (2 year) exposures, the combined effect of grazing and drought lowered diversity and increased dominance compared to when such factors acted independently. This supports some of our observations. Our study did not compare the long and short-term effects of the interaction between grazing and rainfall variability on herbaceous diversity. Therefore, we were unable to determine the extent to which the herbaceous diversity shifted over long time.

The reduction of D_{mg}, H, and J in the 50% and 150% plots compared to the ambient in the ungrazed site (Figure 14a, b, c) conforms to the findings of Anderson et al. (2007). Species richness declined at both the lower and higher rainfall sites along an annual precipitation gradient of 40–100 cm due to the shifting patterns of soil P following herbivore exclusion (Anderson et al., 2007). Consequently, grazing exclusion enhanced local extinction of species and reduced their colonization rates. We suggest that the lower diversity in U50% and U150% plots resulted from the inability of the rare species to compete for vital resources such as light and nutrients, and partly due to soil water stress, especially in the U50% plot. Porensky et al. (2013) report that, in the absence of grazing and drought, the more dominant perennial grasses and forbs out-compete the non-dominant species. Over time, grazing exclusion, potentially establishes a more stable, but, relatively homogenous herbaceous community (Anderson et al., 2007; Skinner et al., 2002).

The lower H, as observed in the ungrazed plots indicated the declining species number and evenness due to the absence of livestock, thus favouring the predominance of *B. decumbens* and *H. fillipendula* (Figure 14b, c; Table 4). Livestock, by preferentially feeding on the dominant *B. decumbens* and *H. fillipendula* allows the establishment of other species, that would otherwise succumb to intense competition for resources. Preferential feeding on grasses by herbivores increases richness and evenness of forbs therefore modifying the herbaceous community structure (Augustine and Frank, 2001; Koerner and Collins, 2014). Despite resisting grazing pressure, the presence of *B. insculpta* and *P. dilatatum* as the most dominant species in the grazed plots did not suppress the less dominant species (Table 4). Consequently, this enhanced the coexistence amongst the herbaceous species, therefore, increasing their diversity. The stronger gap colonization potential and prostrate growth habit exhibited by the less dominant species (Gao et al., 2009), explain the pattern of diversity in our grazed plots. These strategies enhance herbaceous diversity by enabling species to withstand grazing pressure (Adler et al., 2001; Osborne et al., 2018). Numerous studies on plant community dynamics in the East Africa savanna (Anderson et al., 2007; Oba et al., 2001) and elsewhere (Bakker et al., 2003; Koerner and Collins, 2014; Osem et al., 2002) agree with our findings.

Aboveground biomass dynamics (AGB)

Rainfall manipulation, grazing, seasonality in rainfall, and their interactions influenced the changes in AGB (Table 3). This is consistent with studies in savanna ecosystems that demonstrate the role of livestock grazing, rainfall, and its seasonality in regulating the herbaceous biomass (Anderson et al., 2007; Bat-Oyun et al., 2016; Metzger et al., 2005; Porensky et al., 2013). We attribute the significant drop in AGB in the grazed plots to clipping as earlier reported for the Lambwe Valley ecosystem (K'Otuto et al., 2012), in other parts of Kenya (Bat-Oyun et al., 2016; Kioko et al., 2012), and in savanna ecosystems elsewhere (Dangal et al., 2016; Koerner and Collins, 2014). AGB linearly responded to changes in VWC along a rainfall gradient of 50% to 150% (Figure 15), an indication that the lower VWC from the grazed plots compared to the ungrazed contributed to the reduced AGB. Consequently, AGB decreased by 31.2% and increased by 8.47% due to the reduction and addition of ambient rain, respectively. This implies that future reduction in rainfall would compromise sustainable biomass production.

Past studies which support our findings, conducted in the same area (K’Otuto et al., 2012; Otieno et al., 2010; 2011) showed that the annual AGB pattern strongly shifted with varying rainfall amounts. In our case, therefore, rainfall regulated AGB development, whereas grazing and seasonality in rainfall moderated the growth pattern of species that highly contributed to AGB. This was evident with the decline in AGB in September compared to January and May (Figure 15) due to lower rainfall amount (Figure 12). During this dry spell in September, mean AGB amongst the grazed plots (G50%, G100%, and G150%) were not significantly different due to intensified grazing on the lowly available vegetation. We expected increased AGB from

G150% plot at this time compared to the other grazed plots (Figure 15a) due to its higher VWC (Figure 13b), but that was not the case. The G150% plot was most likely overgrazed due to its palatable foliage during drought resulting from conserved soil moisture.

B. decumbens and *H. fillipendula* contributed a greater proportion of AGB in the ungrazed plots, unlike in the grazed plots where livestock suppressed their dominance and allowed other species to flourish. Quattrocchi (2006) and Coughenour et al. (1985) reported that light grazing, high nitrogen concentration, and increased soil moisture promoted biomass development in *B. decumbens* and *H. fillipendula*. This explains the higher AGB of *B. decumbens* and *H. fillipendula* in our ungrazed plots, especially with 150% rainfall (Figure 15b). Grasses dominated our ungrazed plots unlike in the grazed plots where grasses and forbs coexisted.

The herbaceous community dynamics

Our model (Figure 16) potentially explains the role of soil moisture as a regulator of the properties and functions of the herbaceous community in the Lambwe Valley savanna. Contrary to our expectations, there was no direct effect of VWC on H and J (Figure 16). However, the mediated responses triggered by changes in AGB and D_{mg} explained the indirect influence of VWC on herbaceous diversity. By increasing AGB, both H and J declined, contrary to our expectation that higher AGB would enhance herbaceous species diversity due to improved soil moisture availability. The reductive influence of VWC on $D_{mg,}$ however, increased H and J. The strong effect of livestock grazing on our sites, and other confounding factors, not tested in our study, explain these patterns. The lower VWC and AGB in our grazed plots hindered the establishment of predominant species, therefore increasing D_{mg}, H, and J (Figure 13, 14, 15), which enhanced the herbaceous species diversity.

The negative correlation between VWC and D_{mg}, and the lack of direct effect of the former on H and J (Figure 16) was surprising. Knapp et al. (2002) reported increased species diversity along a soil moisture gradient in a mesic grassland. Koerner and Collins (2014) however, showed that, acting independently, drought minimally influenced the plant community structure due to the stronger effect of grazing. Similarly, higher rainfall in a savanna ecosystem reduced species diversity compared to lower rainfall amount (Barbosa da Silva, 2016). These findings partly explain the trend in correlation of VWC to D_{mg}, H, and J especially, under manipulated rainfall amount. The positive correlation between VWC and AGB (Figure 16) shows the importance of soil moisture as a major driver of herbaceous biomass development. Ecosystems with similar attributes like those of Lambwe Valley report higher AGB with increasing soil moisture (Augustine and McNaughton, 2006; Frank, 2005).

The number of species, abundance and evenness in their distribution were significant in driving herbaceous species diversity (H). This was demonstrated by the stronger correlations amongst D_{mg}, H, and J (Figure 16), emphasizing the role of grazing (Table 3) in modifying the herbaceous community structure by reducing the dominance of *B. insculpta* and *P. dilatatum*. The lower H (Figure 14) in the ungrazed plots resulted from the dominance of *B. decumbens* and *H. fillipendula*. These species imposed competitive advantage in resource utilization over the less dominant species, mostly forbs, hence their higher proportion of AGB (Figure 15b). Empirical studies that support our results show that dominance thrives on greater competitive ability of species in resource utilization, whereas, varying grazing intensities facilitate species diversity and richness (Adler et al., 2011; Augustine and Frank, 2001; Bakker et al., 2003). However, these explanations only apply to moderately grazed ecosystems, since intensive grazing hinders species dominance due to selective clipping (Fraser et al., 2013; Graham and Duda, 2011; Tilman et al., 2012). Higher diversity occurred in the grazed plots, characterized by lower AGB (Figure 17), suggesting that livestock grazing moderated the herbaceous community structure. Findings from grass-dominated ecosystems (Loreau et al., 2001; Schläpfer and Schmid 1999) reveal positive correlations between aboveground biomass and species diversity due to facilitation and niche complementarity. In Kruger National Park in South Africa, the herbaceous diversity declined with increasing biomass in the absence of grazing (van Coller et al., 2013). This agrees with our current findings. The reduction in biomass and canopy cover due to grazing promotes spatial heterogeneity in resources, enhancing the coexistence of herbaceous species and species diversity (Bakker et al., 2003). Studies conducted in East Africa and other sub-humid and semi-arid ecosystems elsewhere demonstrate the positive role of moderate grazing on the herbaceous species diversity (Anderson et al., 2007; Oba et al., 2001; Osem et al., 2002; Dingaan et al., 2016; Koerner and Collins, 2014).

Conclusion

Our results demonstrate that rainfall amount and its seasonality are key determinants of changes in the herbaceous community structure with grazing as a modifier. The effect of grazing on vegetation enhances herbaceous species diversity through reduced competition for resources by the dominant species: *B. decumbens* and *H. fillipendula*. We illustrate that ambient rainfall favours higher diversity, with a sharp decline in the latter resulting from reduced or increased rainfall amounts. From our findings, the aboveground biomass positively correlated with soil moisture, a function of rainfall input. However, aboveground biomass outside the 400–800 gm^{-2} range lowered the herbaceous species diversity.

We project lower herbaceous species diversity and aboveground biomass in the Lambwe Valley ecosystem following decreased rainfall from the current amount. By enhancing evenness through facilitated coexistence of species, livestock grazing will increase species diversity at ambient rainfall. The interaction between grazing and rainfall manipulation will drive the changes in diversity and aboveground biomass. The mediated responses of the aboveground biomass and species composition to varying soil moisture, will additionally enhance the herbaceous species diversity. This research provides a basis for future studies on the implications of livestock grazing and rainfall variability on sustainable management of savanna ecosystems.

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Chapter 4

Manuscript 3: Livestock grazing and rainfall manipulation alter the patterning of CO_2 fluxes and biomass development of the herbaceous community in a humid savanna

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Abstract

Overgrazing by livestock and the changing patterns of rainfall, characterized by severe drought and floods during dry and wet seasons, respectively, threaten the sustainable productivity of the savanna ecosystems. To understand the implications of such changes in Lambwe Valley - Kenya, we simulated 50% decrease (50%) and increase (150%) in ambient rainfall (100%), respectively, in grazed (G) and ungrazed (U) sites during dry and wet months. CO_2 exchange and biomass production were quantified using chamber method and direct biomass sampling technique, respectively. Plots were named by combining the first letters of the sites followed by rainfall amount i.e. U150%. Soil moisture (VWC) increased along a rainfall gradient of 50–150%. Grazing reduced the VWC, net ecosystem exchange (NEE) and total biomass by 19.07%, 57.14%, and 37.03% respectively, with severe effects during the dry months. 50% rainfall strongly influenced the VWC, NEE (negative and positive signs indicate CO_2 uptake and net carbon loss, respectively), and biomass compared to 150% rainfall. The U150% plot reported the highest mean NEE (–8.80±2.26 μmol m^{-2} s^{-1}), AGB (1208.41 g m^{-2}) and total biomass (1589.06 g m^{-2}) during the wet months. Lower VWC in the G50% plot triggered a net carbon loss of 3.68±0.81 μmol m^{-2} s^{-1} (NEE). Our results show that livestock grazing during the dry months hinders herbaceous CO_2 uptake and biomass production. Proper understanding of the interaction between livestock grazing and rainfall variability in humid savanna ecosystems is essential for sustainable management strategies to regulate the herbaceous productivity.

Keywords

Defoliation, productivity, rainfall variability, respiration, soil volumetric water content.

Introduction

The effect of grazing on primary production in savanna ecosystems depends on the type of herbivores, canopy structure and grazing intensity (Bremer et al. 1998; Frank 2007; Owensby et al. 2006). In the African savanna ecosystems, past researches have mostly focused on the impacts of wild herbivores on the ecosystem structure and function (Augustine and McNaughton 2004; Bardgett and Wardle 2003; Koerner and Collins 2014). These studies show either positive, negative, or neutral effects of herbivores on primary production depending on grazing intensity, nutrient availability, rainfall variability and other trade-off mechanisms. Less attention has, however, been given to the role of livestock, despite currently being the most dominant herbivores in the African savanna ecosystems (K'Otuto et al. 2012; Osborne et al. 2018; Owensby et al. 2006).

Existing studies show that livestock grazing reduces plant productivity (K'Otuto et al. 2012; Otieno et al. 2011); enhances species diversity (Augustine and Mc Naughton 2006); increases soil bulk density and decreases soil moisture availability (Holdo and Mack 2014). The extent to which such changes modify the structure and function of the herbaceous layer community depends on grazing intensity (Osborne et al. 2018; Savadogo et al. 2008). However, long-term grazing has little or no effect on the herbaceous community following the adaptability of plants to grazing pressure and the creation of nutrient hotspots that produce high quality forage (Adler et al. 2011; Marshall et al. 2018; van der Waal et al. 2011). The effect of livestock grazing on CO_2 exchange and biomass production (K’Otuto et al. 2012; Owensby et al. 2006) regulates the net carbon (C) emission (Grace et al. 2006) by balancing gross primary production (GPP) and respiration (Otieno et al. 2011; Wilsey et al. 2002).

Coupled model Inter-comparison Project (CIMP3) and Meteorological Research Institute-Global Climate Model (MRI-CGCM3) monitor climate change in East Africa. These models predict a 5-10% decrease in rainfall during the dry periods and an increase of 5-20% during the wet seasons by 2050 (Hulme et al. 2001; Conway et al. 2009; Taylor et al. 2012; Yang et al. 2015). These changes are likely to alter soil moisture distribution (Conway et al. 2009; Funk et al. 2005) and air temperature (Shongwe et al. 2011). Higher radiation load during drought increases evapo-transpiration and reduces soil moisture availability, particularly in the shallow soil layers (Otieno et al. 2004), thus limiting plant water relations and ecosystem functions. Most herbaceous plants of the savanna ecosystems suffer from physiological stress during drought (K'Otuto et al. 2012; Mordelet et al. 1997) given that >60% of their roots dominate the 0-20 cm soil depth (Mordelet et al. 1997). Fluctuation in soil moisture in this layer influences the pattern of CO_2 uptake and biomass production (van der Molen et al. 2011).

Distinct seasonality in rainfall, modifies the spatio-temporal distribution of soil moisture and its availability to the vegetation (Knapp et al. 2008; Risch & Frank 2007; William and Albertson 2004). This affects C uptake, soil organic matter decomposition, and biomass production, which are strongly dependent on soil moisture (Ago et al. 2015; Grace et al. 2006; Hovenden et al. 2014; Kutsch et al. 2008). However, soil properties, plant functional types, habitat, and prevailing microclimate conditions confound the ecosystem's response to seasonal rainfall variability (Zeppel et al. 2014). Despite the existing knowledge on the impact of abiotic conditions on plant performance, the extent to which predicted rainfall variability will affect herbaceous productivity of most savanna ecosystems is still unclear (Beier et al. 2012).

Rainfall manipulation experiments (Beier et al. 2012; Miranda et al. 2011) potentially predict the impacts of rainfall variability on primary production (Fay et al. 2000; Knapp et al. 2008; Yahdjian and Sala 2002), soil characteristics (English et al. 2004; Huxman et al. 2005) and species diversity (Koerner and Collins 2014). For instance, productivity increases (Knapp et al. 2008; Yahdjian and Sala 2002) or decreases (Fay et al. 2000) with changes in rainfall along an experimental precipitation gradient. The success of rainfall manipulation experiments in humid (Otieno et al. 2010) and dry (Koerner and Collins 2014; February et al. 2013) savanna ecosystems of Africa enhances comprehensive analysis of present and future climatic scenarios. This is essential for ecosystem planning, policy formulation, and sustainable management. However, sufficient data on rainfall manipulation experiments still lacks for the African ecosystems (Beier et al. 2012). In a humid Kenyan savanna, herbaceous biomass, net ecosystem exchange (NEE), and respiration (R_{eco}) decreased by 38.5%, 32.6% and 25.6%, respectively under 20% reduction of ambient rainfall (Otieno et al. 2010).

Overgrazing of livestock and other human activities such as agriculture have degraded the Lambwe Valley ecosystem (Muriuki et al. 2005) following human resettlement in the 1960's (Wellde et al. 1989)**.** The effects of increased human and livestock population over time on biodiversity and sustainability of this ecosystem is yet to be fully documented, despite the recommendations by Maitima (1998). However, K'Otuto et al. (2012) and Otieno et al. (2010), reported that livestock grazing, and drought decreased gross primary production; biomass, and soil C-storage. These studies did not, however tackle the interactive effects of rainfall variability and livestock grazing on herbaceous productivity. According to Zeppel et al. (2014), sustainable ecosystem functions depend on multiple ecological drivers acting together, therefore necessitating investigations on the interactions amongst biotic and abiotic factors.

We manipulated ambient rainfall amount in areas grazed by livestock and those ungrazed (livestock excluded) and tested our design during dry and wet months. Our hypothesis included: (i) by enhancing VWC, the interaction of grazing, rainfall manipulation and seasonality in rainfall increases the NEE, R_{eco}, GPP, and total biomass; (ii) increased soil moisture along a precipitation gradient (50%, 100%, 150%) and during the wet months alleviates the adverse effects of grazing on the herbaceous CO_2 fluxes and biomass.

Materials and methods

Study area

The study was conducted in the Lambwe Valley ecosystem (0°30´ 0°45´ south; 34°10´ 34°20´ east), a humid savanna in Kenya covering 324 km^2 and hosts Ruma National Park (120 km^2). The Valley is located in Homa Bay County, 10 km east of Lake Victoria at an altitude of 1200–1600 m ASL. It is surrounded by Gembe and Gwasi Hills to the west, and Kanyamwa escarpment on the east. The annual rainfall is 700–1100 mm in two seasons: April to June and October to December, with mean air temperature of 25º C. The soils at the valley bottom are Vertisols with biotite rock (Allsopp and Baldry, 1972). The landscape is dominated by *Hyparrhenia fillipendula*, with thickets of *Acacia* and other shrubs. Peasant farming and livestock keeping are the common economic activities in the area. Measurements were done in selected open areas neighbouring Ruma National Park, on land belonging to the National Youth Service (NYS).

Experimental design

The design was a split plot factorial setup with 2 levels of grazing and 3 levels of rainfall manipulation. Grazing was categorized into grazed (G) and ungrazed (U) as the main sites (plots) split into 3 levels of rainfall achieved through manipulating ambient rainfall (100%), by reducing 50% (50%) and increasing 50% (150%) respectively (Figure 18a). Each set up, comprising the 50%, 100% and 150% rainfall plots were replicated three times in both grazed and ungrazed sites, giving a total of 6 rainfall manipulation plots (RMPs) used during dry and wet months. The grazed and ungrazed sites were separated by a farm road, however the closest RMPs in both sites were 30 m apart. The RMPs, constructed 10-20 m apart, within respective sites, allowed free movement of livestock (Figure 18b, c), and were ready 3 months before the measurement period (15th September 2015 to 2nd June 2016). We considered months with less than 60 mm of rainfall as dry and those with higher rainfall (>60 mm) as wet (Figure 18a, b) (Mc Knight et al. 2000). September 2015 marked the end of prolonged dry season (Figure 18a), whereas, January and May characterized the end of two rainy seasons, interrupted by short dry spell in February and March 2016 (Figure 18a b). The plots were abbreviated using the first letters of the grazing level (G or U) followed by rainfall amount (50%, 100% and 150%) i.e. G50%, U150%. In 2013, open fields regularly grazed by livestock (G) were fenced with a 2 m high-chain link to exclude livestock and create ungrazed site (U). Soil type, drainage, terrain, and vegetation distribution and structure were considered when fencing the ungrazed site to minimize the effects of confounding factors. Livestock included 180 goats and 130 cattle, randomly grazed in an area covering 133 acres throughout the year. Stocking rate in the past 10 years is about 6.6 animals per ha $^{-1}$ area (K'Otuto et al. 2012) and is likely to rise due to increased human settlement and agriculture.

To exclude the desired amount of ambient rainfall or increase the amount of rain input, the RMPs (6 m x 3 m wide) were demarcated. Rainfall reduction by 50% was achieved using rain exclusion gutters constructed from strips (30 cm width) of 6 mm UV-transparent plastic sheets intermittently stretched (inclined at 14°) to cover 50% of the total plot/ground surface (10 strips were used). The strips, laid on wire mesh were stretched over 2 m high metal frames to allow free movement of grazing animals over the plots (Figure 18b, c). To increase the ambient rainfall by 50%, the excluded rainwater was redirected on to open plots, thus raising ambient rain (100%) by 50%, giving 150% rainfall amount (Figure 18). Portable VWC sensors were used a day after rainfall event to test the homogeneity in soil water distribution within the RMPs. Trenches (50 cm deep and 30 cm wide), reinforced with plastic sheets buried in soil, were dug between plots to reduce lateral water flow across plots. The rain shelters had open sides to reduce the greenhouse effect from gutters. Light and temperature sensors were installed under the RMPs to monitor the influence of the gutters. The shelters were set up in a gently sloping (3-5°) open field at the valley bottom.

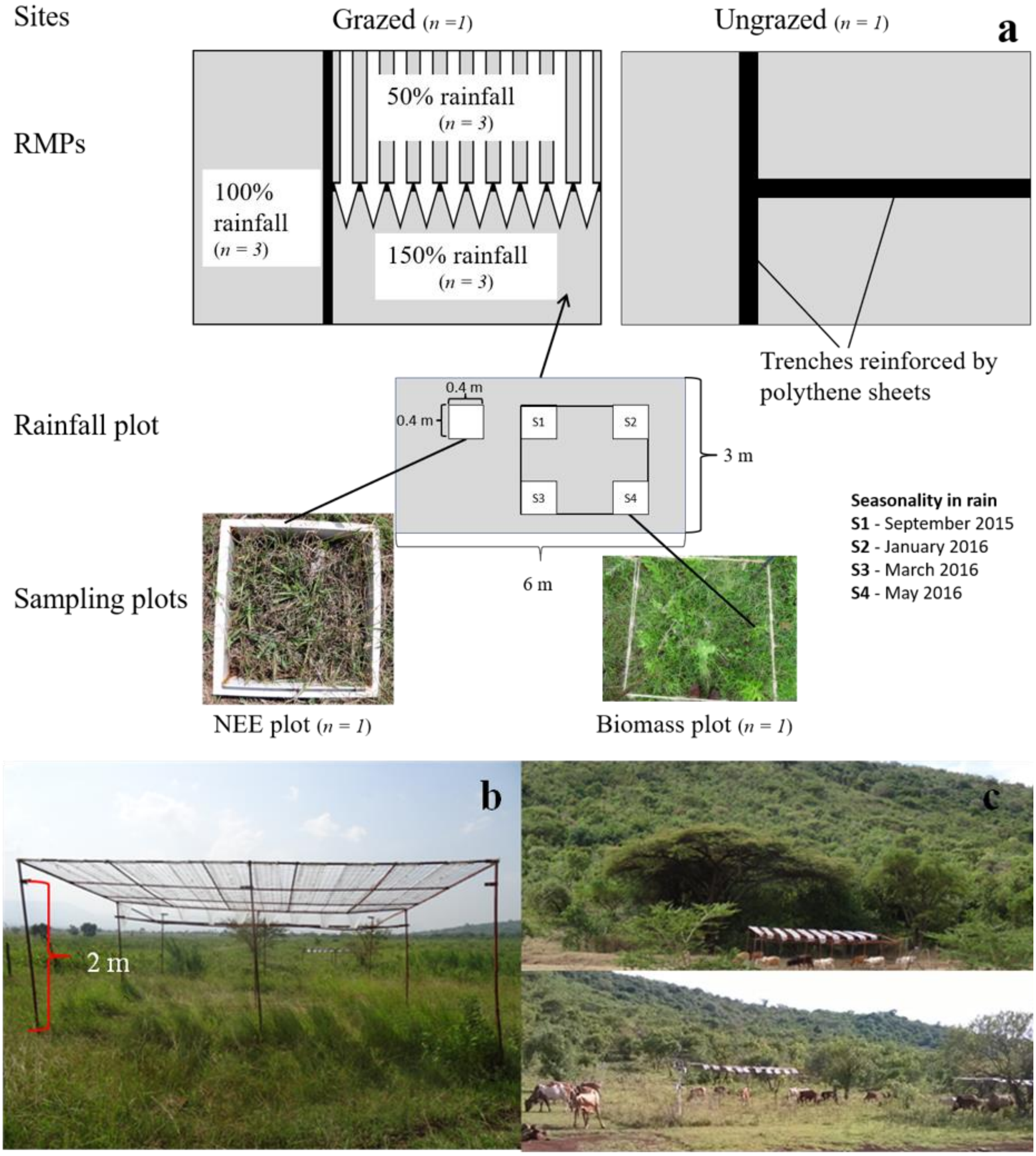

Figure 18: Layout of rainfall manipulation plots. The white parallel arrows represent polythene strips for excluding 50% rainfall and redirecting it to the 150% rainfall plot. The pictures show sampling plots (a) for monthly NEE, Reco, and seasonal biomass. The raised RMP roof (b) facilitates free movement of livestock (c) when grazing.

Microclimate and soil volumetric water content (VWC)

Rainfall, air temperature, humidity and light intensity were logged from three automatic weather stations (AWS-WS-GP1, Delta-T Devices, Cambridge, UK), installed 2 m aboveground on the study site. Two of these weather stations were erected in the open fields within the grazed and ungrazed sites, while the other was installed in the elevated neighbourhood of the study sites. VWC was measured using 5TE probes connected to EM50 data loggers (Decagon Devices Inc., Washington, USA) at 20 cm soil depth. Three probes were installed in every RMP to log data at 30 minutes' interval between 15/9/2015−2/6/2016. The probes were strategically positioned in areas whose biomass were not to be harvested to minimize damages from the soil corer and interference from confounding factors related to the loss of vegetation cover.

NEE, R_{eco}, and GPP

NEE, R_{eco}, and GPP were measured every month from September 2015 to May 2016. Considering the variations in the microclimate, CO_2 flux measurements were taken at 3 various times of the month (early, mid and later days). NEE was measured using a transparent (Plexiglas) gas chamber (3mm XT-20070, 95% light transmission efficiency). R_{eco} was measured with an opaque (PVC) chamber insulated with reflective aluminium foil to maintain the internal chamber conditions. Each chamber had a base area of 40 cm^2 (reinforced with a rubber gasket) and 54 cm height. The chambers were fitted with a thermometer (T-107 Campbell Scientific, USA) installed inside it at a height of 30 cm above the soil surface. A second thermometer was installed outside, at the same height to compare the variation in temperature with the inner chamber. To aid in chamber ventilation and air mixing within the chamber, 3 fans with 1.5 m s^{-1} flow speed were installed inside the chamber. A small opening on top of the chamber allowed for pressure balancing within the head space shortly before measurements were taken. Portable gas exchange analyser (LI-COR 820, USA) connected to the chamber using Bev-A-line tubes (1/4’’ OD; 15 cm length), detected changes in CO_2 concentration. Soil frames (38.5 cm^2), for mounting the chambers were permanently fixed 3 cm into the ground, 3 weeks before the first measurements were taken. This was intended to minimize gas leakage through the soil during the measurements period. To measure the CO_2 fluxes, the chambers were mounted on the soil frame and tightened using elastic bands. CO_2 fluxes were measured every hour from 07:00-18:00 hrs and daily averages calculated. The temperature within the chamber was maintained at 3 °C compared to the ambient, using ice packs. Photosynthetic active radiation (PAR) within the chamber was monitored using a quantum sensor (LI-190, LI-COR, USA), towering above the enclosed vegetation. Soil temperature at the specific time of measurement was extracted from the EM50 data loggers. Records for the CO_2 fluxes and PAR (in the case of NEE) were taken 30-60 seconds after placing the chamber on the soil frame and recorded every 15 seconds for 2 minutes and 15 seconds. CO_2 fluxes were obtained from the time dependent change in CO_2 concentration within the chambers ($r^2 > 0.95$) and flux rate ($F\mathrm{CO}_2$) calculated using the equation below:

$$F\mathrm{CO}_2 = k\mathrm{CO}_2 \frac{273.15}{\mathrm{T}air} \frac{\mathrm{V}}{\mathrm{A}} \frac{dc}{dt}$$

where: $F\mathrm{CO}_2$ - CO_2 flux density (mg CO_2-C m^{-2} h^{-1}); $k\mathrm{CO}_2$ - gas-constant (conversion factor) at 273.15 $k = 0.536$ [µg C μl^{-1}]; T_{air} - air temperature in chamber (k); V - chamber volume (l); A - collar area (m^2); dc/dt - CO_2 concentration change in chamber (CO_2: ml l^{-1} h^{-1}).

We calculated R_{eco} based on regressions between respiration rates and air temperature (Lloyd & Taylor 1994) as shown in the formula below:

$$\mathrm{R}_{eco} = \mathrm{R}_{ref}\, e^{\mathrm{E}_o\left(\frac{1}{\mathrm{T}_{ref}} - \mathrm{T}_0\right) - \left(\frac{1}{\mathrm{T}_{soil}} - \mathrm{T}_0\right)}$$

where: R_{ref} is the respiration at the reference temperature (CO_2-C mg m^{-2} h^{-1}); E_o is the activation energy (K); T_{ref} is the reference temperature = 283.15 (K); T_0 is the temperature threshold of biological processes; T_{soil} is the soil temperature.

NEE was calculated according to Gilmanov et al. (2003) as summarized in the formula below:

$$\mathrm{NEE} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma$$

Where: α is the initial slope of the light response curve and an approximation of light use efficiency (CO_2 m^{-2} s^{-1}/μmol m^{-2} s^{-1}); β is the maximum rate of carbon fixation at infinite PPFD (CO_2 m^{-2} s^{-1}); Q is the photosynthetic photon flux density (μmol m^{-2} s^{-1}); γ is the average daytime respiration.

Subsequently, GPP was calculated from the general equation below:

$GPP = NEE - R_{eco}$

The meteorological sign convention was used to characterize the CO_2 fluxes, where positive (R_{eco}) and negative fluxes (GPP and NEE) indicated the loss of CO_2 to the atmosphere and flow of CO_2 into the plant leaves (Skinner and Adler 2010).

Biomass

Biomass was estimated seasonally in 40 x 40 cm plots at the end of the dry (September 2015, March 2016) and wet (January 2016, May 2016) months. 4 biomass plots were designated in every rainfall plot and each was marked with 4 wooden pegs at the corners (90° angle) (Figure 18a). The plots were labelled: S1(September, 2015), S2 (January, 2016), S3 (March, 2016), and S4 (May 2016) to represent the end of various seasons, and to avoid repeated biomass harvesting in the subsequent seasons. *Brachiaria decumbens* Stapf and *Hyparrhenia fillipendula* (Hochst) Stapf dominated the ungrazed plots (66-75%) while *Bothriochloa insculpta* (A. Rich) A. Camus and *Paspalum dilatatum* Poir (26-36%) were more abundant in the grazed plots. AGB was harvested to the ground surface whereas BGB down to 20 cm soil depth was obtained using a root sampler (8 cm diameter). Three soil cores were randomly obtained per plot and the samples washed, and seived (2 mm mesh) to extract the roots. The plant materials were oven dried at 80°C for 48 hours. Total Biomass was calculated from the sum of the AGB and BGB whereas R:S ratio was obtained by dividing BGB by AGB.

Statistical analysis

The effects of grazing, rainfall manipulation, seasonality in rainfall, and their interaction on VWC, NEE, R_{eco}, GPP, AGB, BGB, total biomass, and R:S were tested using full factorial repeated measures ANOVA in JMP 14 Statistical software, SAS Inc. The factors crossed included: Grazing X rainfall manipulation; grazing X seasonality in rainfall; rainfall manipulation X seasonality in rainfall and grazing X rainfall manipulation X seasonality in rainfall. Significance levels were set at $p \leq 0.05$ for all the above effects. Some Missing BGB data for March 2016 were handled using imputation for partial least squares (PLS). The VWC was analyzed using the daily averages obtained from the 30 minutes intervals measured data to minimize the outlier VWC values (>50%) from heavy rain. Subsequently, the daily VWC, similarly to CO_2 fluxes (sampled 3 time every month) were summarized into monthly and seasonal values to facilitate further analysis. The seasonal values were intended to facilitate the correlation of VWC to the total biomass sampled, once every season. Multiple comparison of means was by Tukey HSD, when the ANOVA was significant. The dependence of NEE, R_{eco}, GPP and total biomass on VWC was tested using linear regression.

Table 5: Full factorial repeated measures ANOVA, *F* statistics with *P* values (in parenthesis, bold values indicate significance) showing the effects of grazing (grazed and ungrazed), rainfall manipulation - RMP (50%, 100% and 150%), seasonality in rainfall (dry and wet months) and their interactions on soil volumetric water content (VWC), net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), gross primary production (GPP) aboveground (AGB), belowground (BGB) biomass, and root to shoot biomass ratio (R:S)

Factors	**VWC**	**NEE**	**R_{eco}**	**GPP**	**AGB**	**BGB**	**Total biomass**	**R:S**
Grazing (G)	448.4 **(<0.05)**	121.5**(<0.05)**	44.7**(<0.05)**	119.4**(<0.05)**	433.9**(<0.05)**	2.4 (0.12)	290.4**(<0.05)**	180.5**(<0.05)**
Rainfall manipulation (RMP)	216.0 **(<0.05)**	39.5 **(<0.05)**	13.6**(<0.05)**	37. 4**(<0.05)**	78.9**(<0.05)**	51.7**(<0.05)**	95.1**(<0.05)**	0.4 (0.6)
Grazing*RMP	45.8**(<0.05)**	0.7(0.50)	0.7 (0.49)	1.0(0.36)	12. 9**(<0.05)**	4.6 **(<0.05)**	4. 7**(<0.05)**	10.4**(<0.05)**
Seasons (S)	329. 9**(<0.05)**	369.6**(<0.05)**	94.2**(<0.05)**	519.7**(<0.05)**	216. 5**(<0.05)**	97.3 **(<0.05)**	259.6**(<0.05)**	4.5 **(<0.05)**
Grazing*Seasons	8.8 (<**0.05**)	9.2 **(<0.05)**	0.1(0.86)	1.9 (0.17)	6.4 **(<0.05)**	0.3 (0.57)	4.9 **(<0.05)**	3.5(0.06)
RMP*Seasons	2.0 (0.14)	0.1(0.94)	1.2(0.28)	1.0 (0.11)	11.3 **(<0.05)**	23.4 **(<0.05)**	18.4 **(<0.05)**	3.8**(<0.05)**
G x RMP x S	1.86 (0.15)	0.7 (0.49)	1.6(0.21)	2.1 (0.13)	9.5**(<0.05)**	0.4 (0.66)	6.3**(<0.05)**	5.8 **(<0.05)**

Results

Volumetric water content (VWC)

Daily VWC at the 20 cm soil depth, across plots, increased in October 2015 and April 2016, after the dry months (Figure 19b) and was linearly correlated to the amount of soil moisture predicted by the model ($RMSE = 3.55$; $r^2 = 0.61$; $P < 0.05$) (Figure 20a). The VWC reduced by 19.07% due to livestock grazing but increased by 23.67% from the dry to wet months (Figure 20b, Table 5). The 50% reduction of ambient rainfall had a stronger effect on VWC (19.29%) compared to an increase (7.34%), especially in the ungrazed site (Figure 19b; Figure 20b). The grazed site did not, however, report an increase in VWC in the G150% plot from ambient (Figure 20b). The significant interaction ($p < 0.05$) of rainfall manipulation with either livestock grazing or seasonality in rainfall, further influenced the pattern of VWC (Table 5). For instance, VWC decreased by 9.6%, 24.70%, and 25.13% in the G50%, G100%, and G150% plots, respectively, compared to their counterparts in the ungrazed site due to the combined effect of grazing and rainfall manipulation (Figure 20b). Livestock grazing during the dry months decreased the VWC by 25.88% compared to the 16.62% reported during the wet months. Mean VWC ranged from 13.99±3.15% in the G50% plot to 28.05±4.21% in the U150% plot during the dry and wet months respectively (Figure 20b).

NEE, Reco and GPP

NEE steadily increased (Negative sign) from 08:00−12:00 hrs with photosynthetic photon flux density (PPFD) (Figure 21). Further increase in PPFD (>2000 μmol m^{-2} s^{-1}), especially after 12:00 hrs gradually decreased NEE. The U150% plot reported the highest mean diurnal NEE of −12.31±2.90 μmol m^{-2} s^{-1} and −17.79±4.63 μmol m^{-2} s^{-1} during the dry and wet months respectively (Figure 21). The monthly pattern of NEE across plots varied with changes in rainfall (Figure 19a, 22a, b).

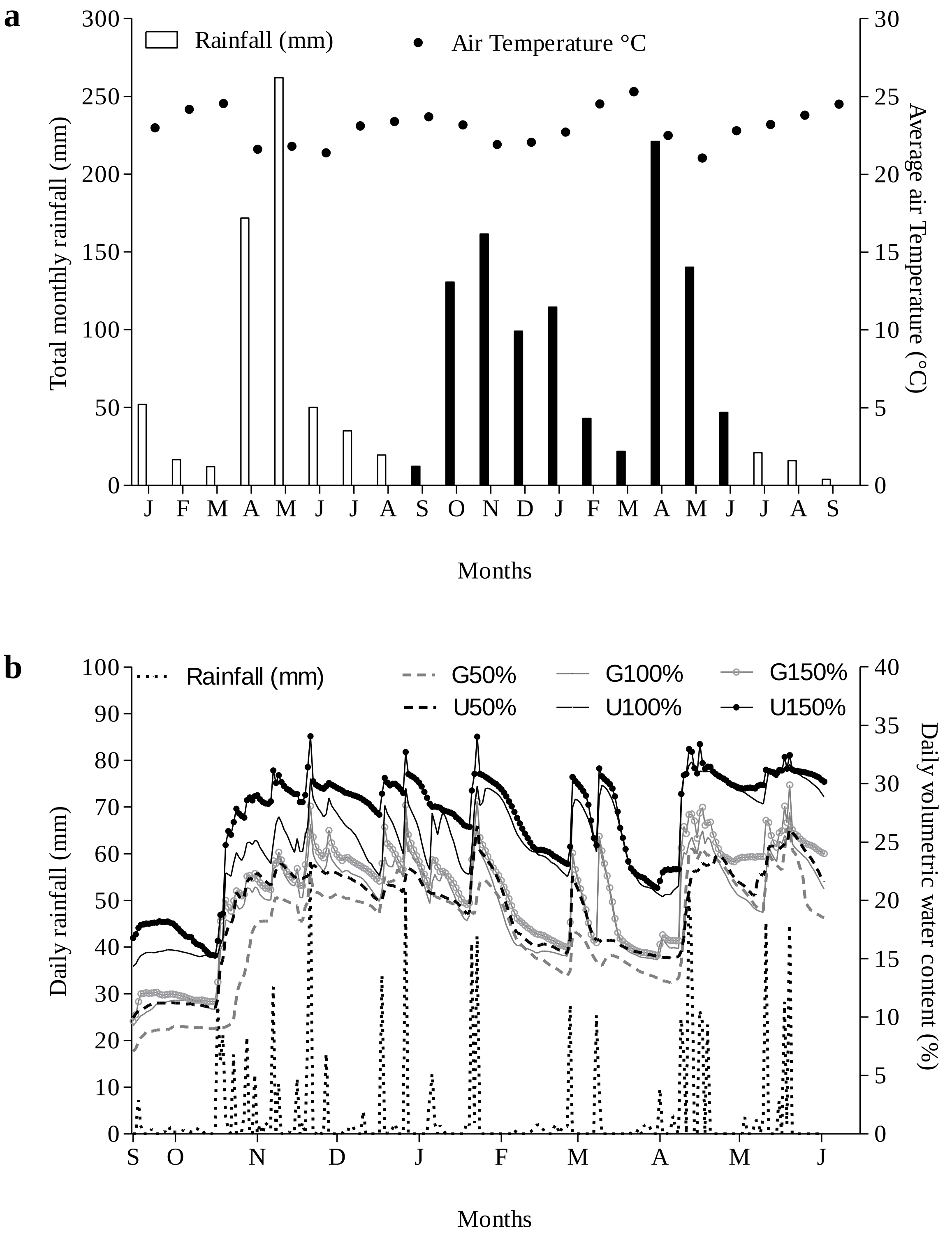

Figure 19: Monthly rainfall and air temperature (**a**) during the measurement period (15/9/2015−2/6/2016 - black bars). Daily rainfall amount and corresponding pattern in VWC (**b**) of grazed and ungrazed plots during the measurement period.

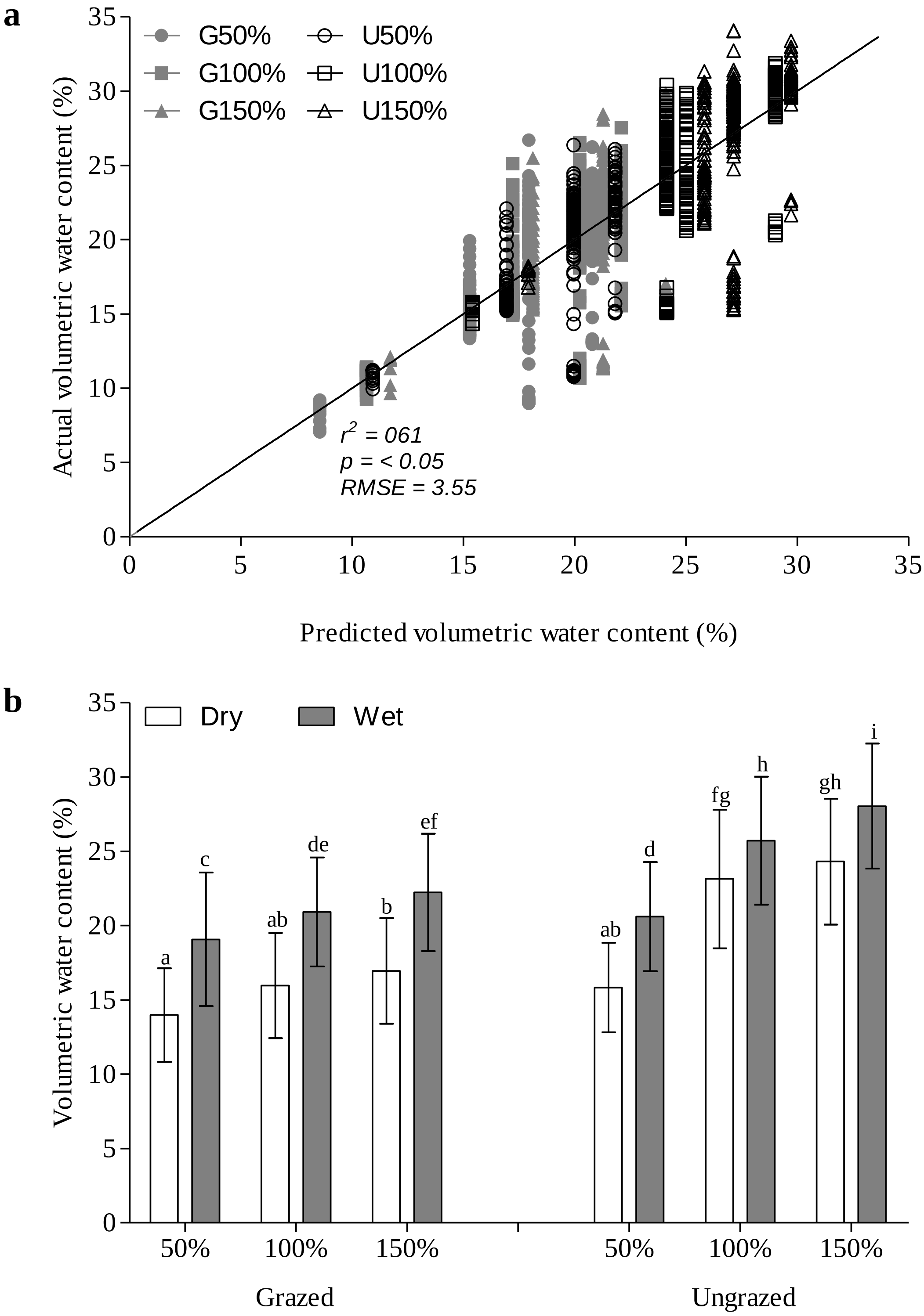

Figure 20: Comparison (**a**) between actual versus predicted volumetric water content - VWC (%). The effect of seasonality of rainfall on VWC (**b**) in grazed and ungrazed sites. Different letters show significant mean (±SD) differences ($p < 0.05$) among treatments.

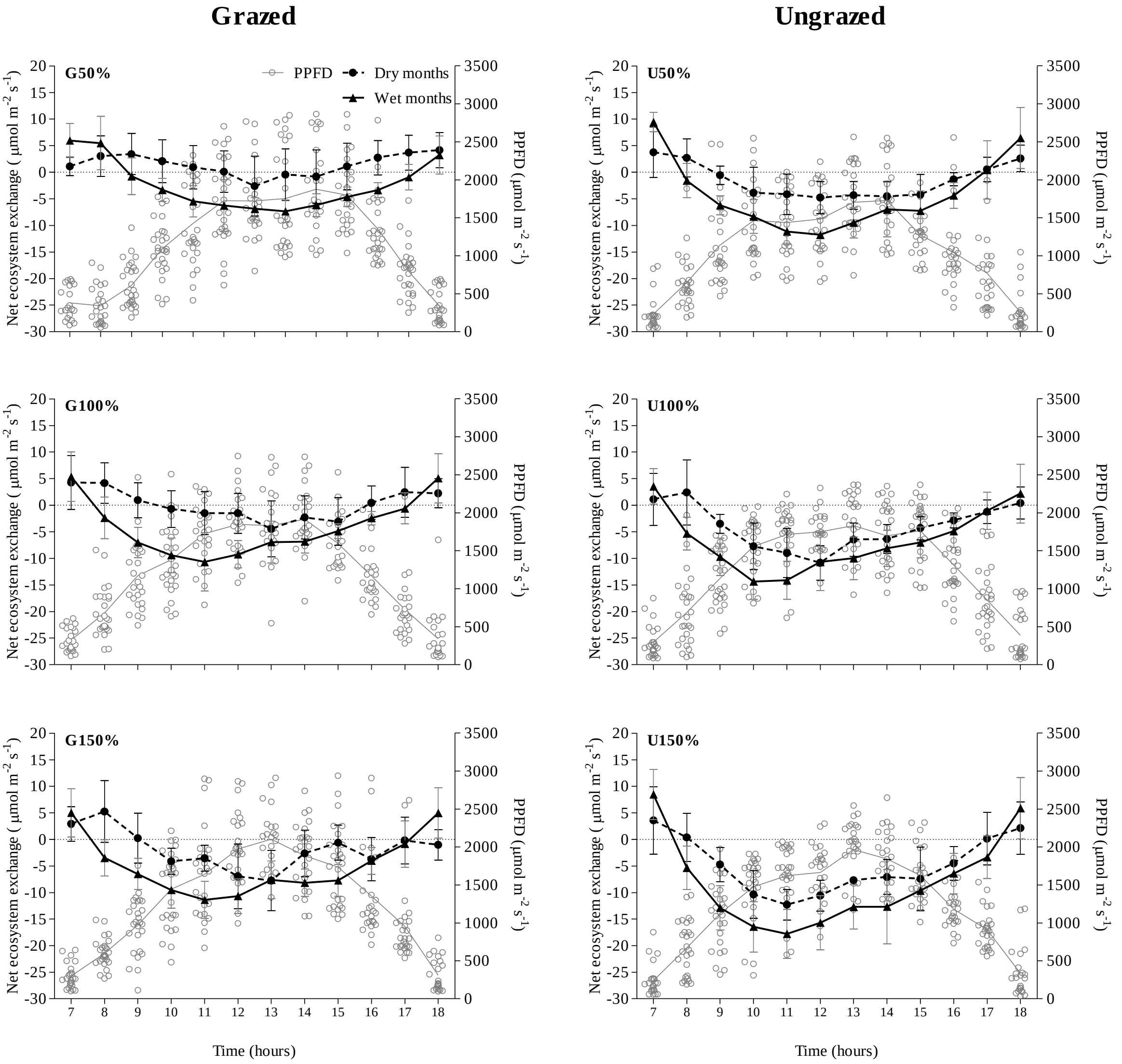

Figure 21: Mean diurnal variation of NEE (negative –ve sign shows CO_2 uptake) and PPFD in grazed and ungrazed plots.

Livestock grazing lowered NEE, R_{eco}, and GPP by 57.14%, 28.61%, and 37.51% respectively (Figure 22; Table 5). Similarly, the effect of rainfall manipulation on the pattern of NEE, R_{eco}, and GPP was significant (Table 5). Overall, NEE, R_{eco}, and GPP decreased with 50% rainfall reduction. However, at seasonal scale, only GPP and NEE declined during the wet months (Figure 22b, f). Conversely, only GPP increased with 150% rainfall amount during the wet months (Figure 22f). NEE increased from 0.09±2.69 µmol m^{-2} s^{-1} during the dry months to

−5.27±2.02 μmol m^{-2} s^{-1} during the wet months (Figure 22b). Similarly, R_{eco} and GPP sharply increased during the wet months (Figure 22c, d; e, f) in all the plots.

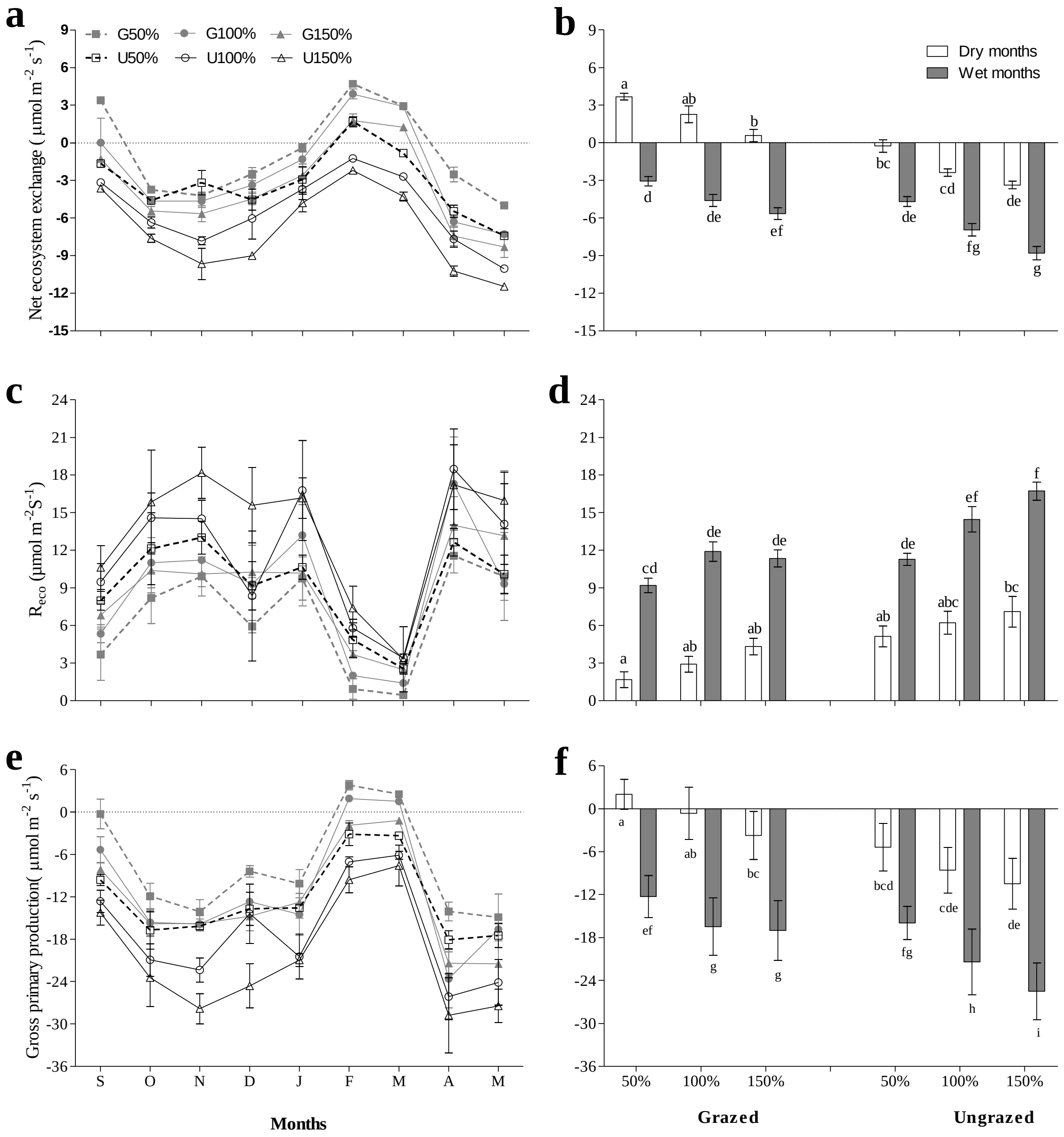

Figure 22: Monthly and seasonal NEE (CO_2 uptake), R_{eco}, and GPP (carbon assimilation) of grazed and ungrazed plots. The negative and positive fluxes denote CO_2 flow into and out of the leaves respectively. Different letters show significant mean (±SD) differences ($p < 0.05$) among treatments.

The highest mean: NEE, -8.80 ± 2.26 µmol m^{-2} s^{-1}; R_{eco}, 16.72 ± 3.05 µmol m^{-2} s^{-1}; and GPP, -25.52 ± 3.97 µmol m^{-2} s^{-1} observed in the U150% plot during the wet months, dropped by >50% during the dry months (Figure 22b, d, f). Grazing, interacting with seasonality in rainfall, reduced NEE, especially during the dry months (Figure 22b; Table 5). R_{eco} and GPP did not change with any interaction.

Total, above- and belowground biomass

Livestock grazing reduced AGB by 46.62% and total biomass by 37.03% but had no effect on BGB ($f = 2.4$, $p = 0.12$) (Figure 23a, b, c; Table 5). Further reduction in AGB, BGB, and total biomass were observed in the 50% rainfall plots (Figure 23a, b, c) following the significant effect of rainfall manipulation (Table 5). 150% rainfall amount increased AGB and BGB in the ungrazed site by 33.91% and 19.26% respectively during the dry months, with no effect during the wet months. During the dry months AGB, BGB, and total biomass declined significantly in all the plots (Figure 23a, b, c).

The interactions among grazing, rainfall manipulation, and seasonality in rainfall influenced further changes in AGB and total biomass (Table 5). For instance, AGB and total biomass largely reduced during the dry months especially in the 100% and 150% rainfall plots of grazed and ungrazed sites (Figure 23a, c; Table 5). Grazing reduced AGB by 50.76% and total biomass by 40.24% during the dry months. However, during the wet months, 43.81% and 34.89% of AGB and total biomass reduced, respectively due to grazing. On the contrary, BGB was only affected by rainfall manipulation interacting with either grazing or seasonality in rainfall (Table 5). Mean total biomass ranged from 476.10 g m^{-2} in the G50% during the dry months to 1589.06 g m^{-2} in the U150% during the wet months (Figure 23c). The R:S biomass ratio increased due to grazing (Figure 24; Table 5) and during the dry months (Table 5).

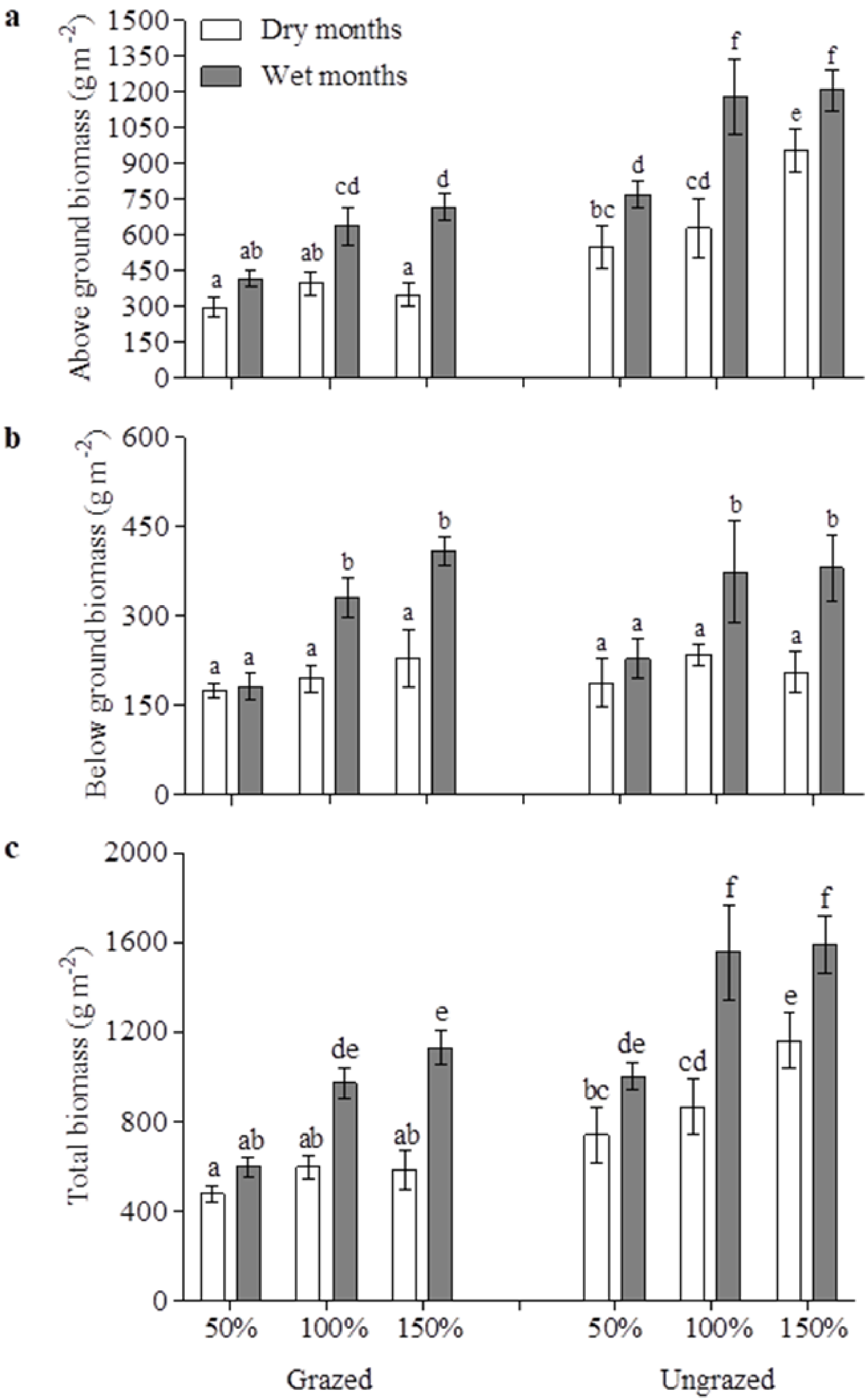

Figure 23: Pattern of (**a**) aboveground biomass, (**b**) belowground biomass, and (**c**) total biomass in grazed and ungrazed plots at different seasons. Different letters show significant mean (±SD) differences ($p < 0.05$) among treatments.

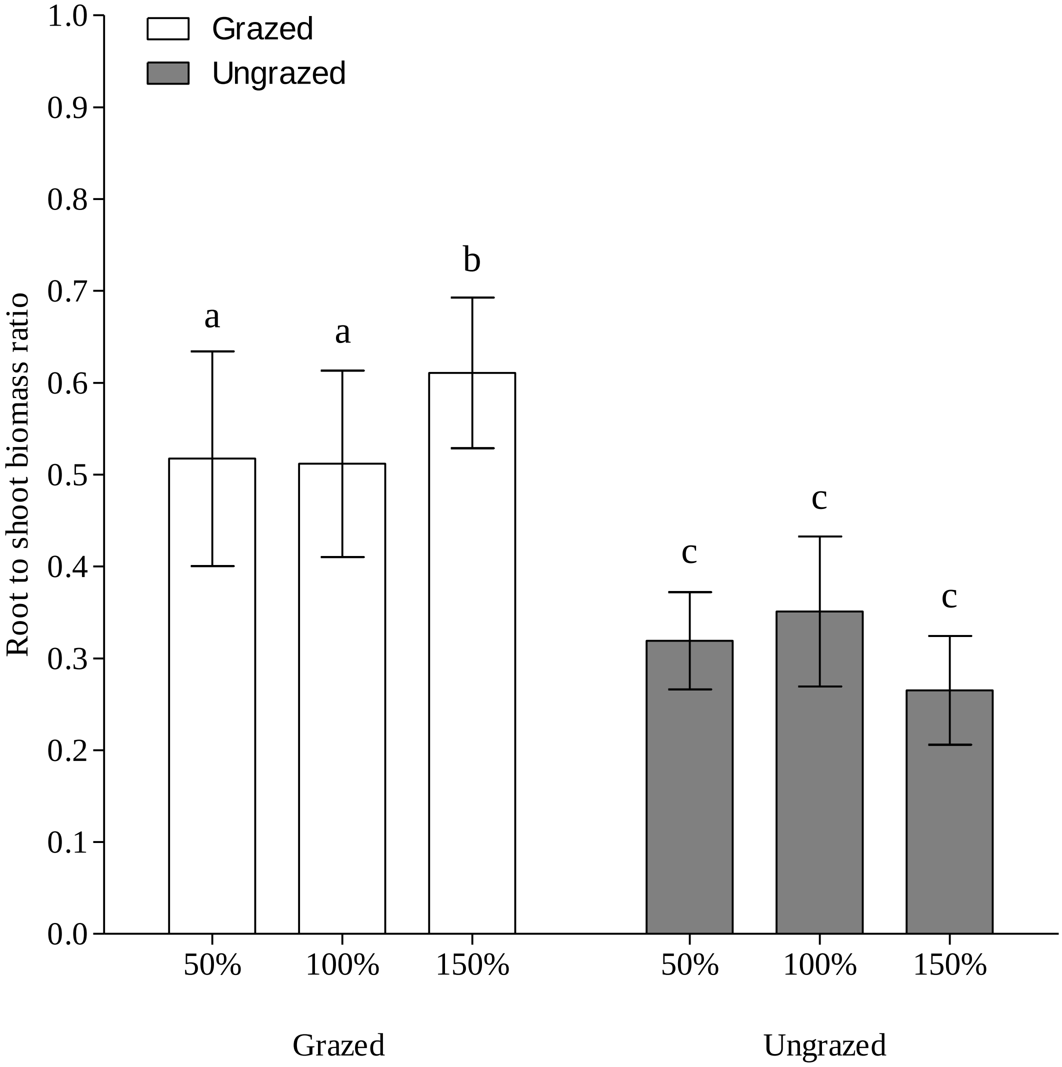

Figure 24: Root to shoot ratio showing variation ($p < 0.05$) among treatments from 50%, 100% to 150% rainfall amount. Different letters show significant mean (±SD) differences.

Discussion

Our findings illustrate that livestock grazing, rainfall manipulation, and seasonality in rainfall independently influenced the patterns of VWC, CO_2 fluxes, and biomass production (Table 5). Specifically, GPP, NEE, R_{eco}, total biomass, and VWC, decreased by 37.51%, 57.13%, 28.61%, 37.04%, and 19.07%, respectively, due to grazing (Figure 20; 21; 22; 23; Table 5). Severe effects of grazing on CO_2 exchange rates and biomass production were however, experienced during the dry months (< 60 mm rainfall) compared to the wet months (Figure 21; 22; 23).

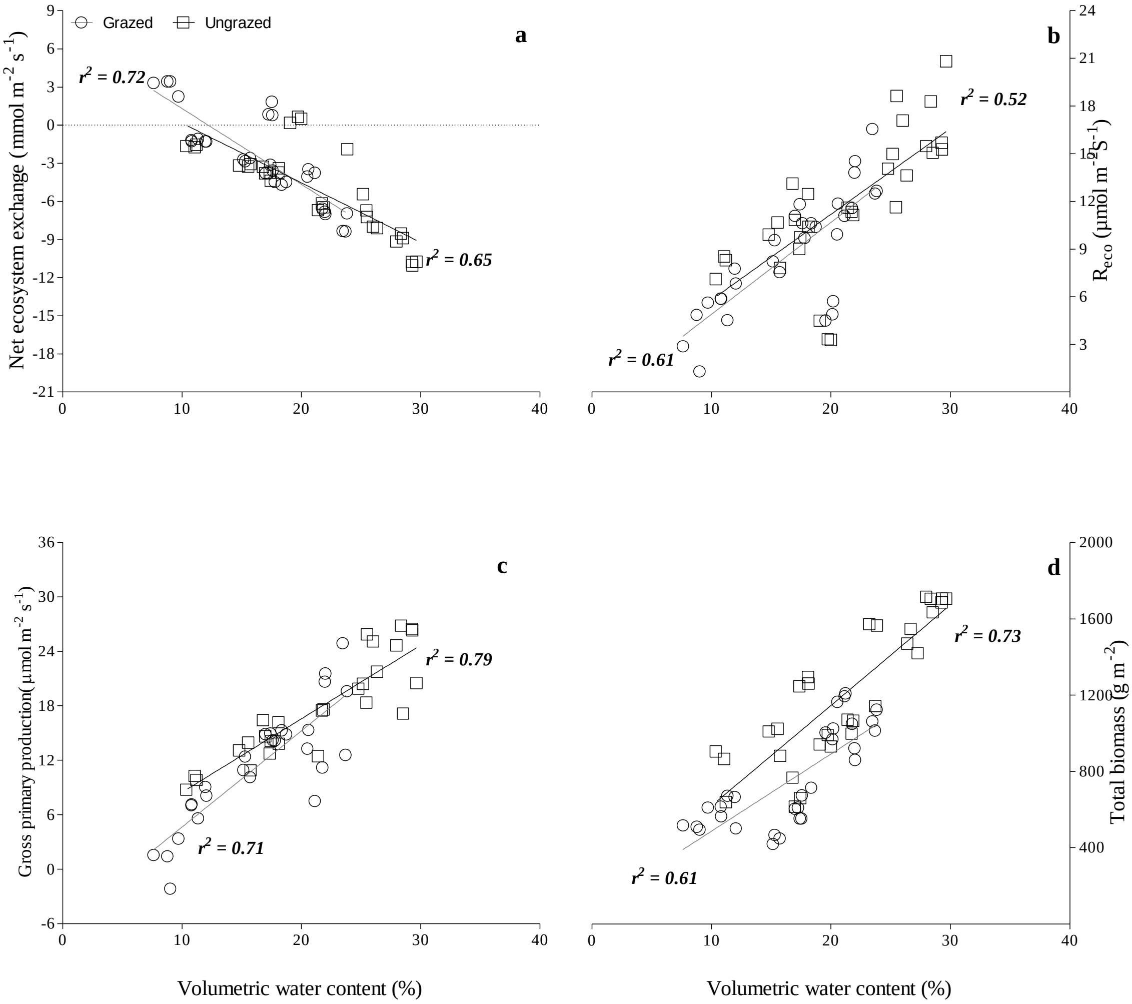

Figure 25: Linear regression showing the influence of volumetric water content (VWC) on: (a) NEE; (b) R_{eco}; (c) GPP (d) total biomass. The negative and positive fluxes denote CO_2 flow into and out of the leaves respectively.

VWC increased ($p<0.05$) along a rainfall gradient of 50%, 100%, and 150% (Figure 19, 20a, b; Table 5), consequently increasing GPP, NEE, R_{eco} (Figure 21, 22), AGB, and total biomass (Figure 23, 24). This shows that rainfall is a major source of water in the 20 cm soil depth, and its variation between plots strongly influence the patterns of CO_2 exchange rates and biomass production. The patterning of the herbaceous CO_2 fluxes and total biomass correlated to the changes in VWC (Figure 25). These results imply that VWC drives the spatio-temporal dynamics of the herbaceous community in Lambwe Valley, however, the negative effects of livestock grazing threaten the sustainable productivity and C storage capacity.

VWC significantly reduced: in the grazed plots; when ambient rainfall decreased by 50%; and during the dry months (Figure 19b; 20a b). The hypothesis that the interaction of grazing, rainfall manipulation, and seasonality in rainfall increases the VWC, was not supported (Table 5). However, grazing influenced the effects of either seasonal or manipulated rainfall input on VWC, showing a linear increase in soil moisture (Figure 20a). Our results, additionally, show a larger effect of grazing on VWC in the 100% and 150% rainfall plots compared to the 50% rainfall plots (Figure 20b). Similarly, the effects of grazing on NEE, R_{eco}, GPP (Figure 21), AGB, and total biomass (Figure 21) were higher in the 100% and 150% rainfall plots. In contrast, there were no changes in BGB between plots of the grazed and ungrazed sites. We attribute the changes in VWC and its effects on CO_2 fluxes and biomass production to the higher soil bulk density at the 20 cm soil depth of the grazed plots and clipping by livestock (Arnhold et al. 2015; K'Otuto et al. 2013).

The changes in VWC, CO_2 fluxes, and biomass observed in our plots show that the variation in rainfall amount influenced the patterning of soil moisture availability in the grazed and ungrazed sites. This indicates that the impact of grazing is more pronounced at higher rainfall amounts, where trampling by livestock intensely compacts the soil, reducing the infiltration rate of rainwater (Holdo and Mack 2014), thus, accounting for the wider differences in VWC between the grazed and ungrazed plots. Consequently, the lower soil moisture availability in the grazed compared to the ungrazed plot reduced the CO_2 exchange rates and biomass production. We further established that, despite the negative effects of grazing on the herbaceous layer community, an increase in rainfall from 50–100% raised the VWC, therefore, promoting CO_2 exchange rates and biomass build-up in both grazed and ungrazed sites. However, regrowth resulting from improved soil moisture at higher rainfall amounts (100% and 150%) did not compensate the herbivore intake, thus lowering the productivity potential of the grazed plots. For instance, NEE, R_{eco}, and GPP reduced by 75.01%, 28.43%, and 42.38%, respectively in the G100% plot, and by 58.37%, 34.21%, and 42.90% respectively, in the G150% plots due to grazing (Figure 22).

Our findings conform to studies that show that grazing and rainfall variability interact to regulate soil moisture patterns and other related ecosystem processes (Bat-Oyun 2016; Koerner and Collins 2014). This interaction influences soil moisture availability (Holdo and Mack 2014; Savadogo et al. 2007) through changes in the: infiltration rate of rainwater; evapotranspiration of soil water; structure of the herbaceous community (Holdo and Mack 2014; Owensby et al. 2006). For instance, Koerner and Collins (2014) show a 90% increase of aboveground net primary production (ANPP) in the ungrazed sites that received ambient rainfall (100%), a variation that resulted from drought (50% of ambient rainfall) by grazing interaction. Dangal et al. (2016), however, reported that improved soil moisture availability marginally impacted on the larger effect of grazing on aboveground production, witnessed at higher rainfall amount. This resulted from the overarching role of livestock grazing in reducing biomass compared to the effect of soil moisture in promoting plant growth and recovery of the clipped foliage.

Further results show that livestock grazing, particularly during the dry months, intensified the loss of AGB and total biomass, consequently reducing CO_2 uptake due to soil water stress. We attribute the > 50% decline in NEE during the dry months (Figure 22b) to the interactive effect of grazing and seasonality in rainfall on the VWC and AGB production (Table 5). Considering that NEE and biomass depended on soil moisture availability (Figure 25a, d), the lower VWC during the dry months (Figure 20b), combined with grazing of livestock had deleterious effects on plant growth and their photosynthetic capacity. However, during the wet months, the herbaceous vegetation resumed their active CO_2 uptake (Figure 22b) and biomass build-up (Figure 23a, b) in both the grazed and ungrazed plots. The variation in NEE and biomass, resulting from the interaction of grazing and seasonality in rainfall, had ramifying effects on the patterning of GPP (Figure 22f) but not R_{eco} (Figure 22d). Findings from other savanna ecosystems (Furley 2006; Koerner and Collins 2014; Merbold et al. 2009) support our results on the spatio-temporal variation of VWC, CO_2 uptake, and AGB. Intense solar radiation during the dry months most likely compounded the changes in NEE (Figure 21), by decreasing light use efficiency and CO_2 assimilation rates under lower soil moisture conditions as previously shown in Lambwe Valley by Otieno et al. (2010).

We suggest that soil water stress in the grazed plots contributed to the drying up of the herbaceous foliage, reducing their biomass and the ability to exchange CO_2 with their surrounding. This explains the lower NEE (net carbon loss, +ve) reported in the grazed compared to the ungrazed plots during the dry months (Figure 22b). Despite the negative effects of grazing during the dry months on productivity, our grazed plots still maintained AGB above 300 gm^{-2}. This was due to *Vernonia glabra* (Steetz) Vatke (Forsk) DC, a non-palatable forb, whose occurrence contributed to a sizeable proportion of the AGB. It is highly likely that *V. glabra* had a lower potential for CO_2 uptake compared to the C4 grasses that constituted >70% of AGB in the ungrazed plots (Okach et al. 2019), leading to the net carbon loss in the grazed plots during the dry months (Figure 21; 22b). Sankaran et al. (2019) show that increased defoliation and plant death during the dry seasons, typical of the herbaceous communities in savanna ecosystems particularly the C4 grasses, reduced productivity due to the interaction of multiple factors including rainfall, herbivory, and inter-life form competition.

The negative effects of grazing under dry conditions on CO_2 exchange rates result from reduced AGB and decreased soil microbial activities (Bremer et al. 1998; Dangal et al. 2017; Grace et al. 2006; Ondier et al. 2019; K'Otuto et al. 2012). According to Dangal et al. (2017) grazing decreases biomass, lowering substrate availability for soil microbes, hence reducing R_{eco}, with no long-term effect on NEE. In our case, however, grazing during the dry months reduced AGB but had no effect on BGB (Figure 23a, b; Table 5), showing less likelihood for substrate depletion within the plots. This is further demonstrated by the higher R:S biomass ratio in the grazed compared to the ungrazed plots (Figure 24). K'Otuto et al. (2012) reported that grazing reduced GPP and NEE but had no effect on R_{eco}, during both dry and wet seasons. Contrarily, other studies show that grazing reduces both GPP and R_{eco}, but, either increases (Gomez-Casanovas et al. 2012; Owensby et al. 2006; Wilsey et al. 2002) or decreases NEE (Tagesson et al. 2015) depending on the developmental stages of the herbaceous canopy and grazing intensity (Osborne et al. 2018; Räsänen et al. 2017). Biomass reallocation, soil moisture availability, and variation in soil microbial activities at spatial and temporal scales (McCulley et al. 2007; Räsänen et al. 2017) explain the disparities between the NEE and R_{eco} within our plots. R_{eco} is largely driven by soil respiration, which depends on belowground components including biomass and root exudates (Gomez-Casanovas et al. 2012; Ondier et al. 2019; Trumbore 2006). Given the marginal effect of grazing on BGB, it is likely that the rate of R_{eco} in our plots resulted from confounding abiotic and biotic factors (McCulley et al. 2007).

Conclusion

This study shows that herbaceous production declined due to the significant loss of biomass, reduced CO_2 uptake and C assimilation rates resulting from soil water stress caused by livestock grazing, 50% reduction of ambient rainfall, and during the dry months. This underscores the role of soil moisture in regulating ecosystem processes and functions, implying that, its reduction threatens sustainable herbaceous productivity and carbon storage in the Lambwe Valley ecosystem. Interactions between grazing, rainfall manipulation, and seasonality in rainfall moderated CO_2 exchange rates and biomass development. The effects were deleterious during the dry months, when the herbaceous productivity was lower, however, the subsequent increase in rainfall during the wet months facilitated recovery of the herbaceous vegetation from the effects of drought. Proper understanding of the interaction between livestock grazing and rainfall variability in humid savanna ecosystems is therefore essential for sustainable management strategies to regulate the herbaceous productivity.

Conflict of interest: The authors declare that they have no conflict of interest.

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Appendix

Additional publications not included in this thesis

Ondier, J., Okach, D.O., John, O.C., Otieno, D.O. 2019. Influence of rainfall amount and livestock grazing on soil respiration in a moist Kenyan savanna. African Journal Ecology. Http://doi.org/10.1111/aje.12670.

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