Environmental and Sustainability Indicators 9 (2021) 100095

Contents lists available at ScienceDirect

Environmental and Sustainability Indicators

journal homepage: www.journals.elsevier.com/environmental-and-sustainability-indicators/

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

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ARTICLE INFO

Keywords:
Rainfall
Grazing
CO_2 exchange
Productivity
Savanna

ABSTRACT

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

1. Introduction

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

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

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https://doi.org/10.1016/j.indic.2020.100095
Received 11 January 2020; Received in revised form 19 December 2020; Accepted 21 December 2020

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

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

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

2. Materials and methods

2.1. Study site

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

2.2. Microclimate

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

2.3. Experimental design

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

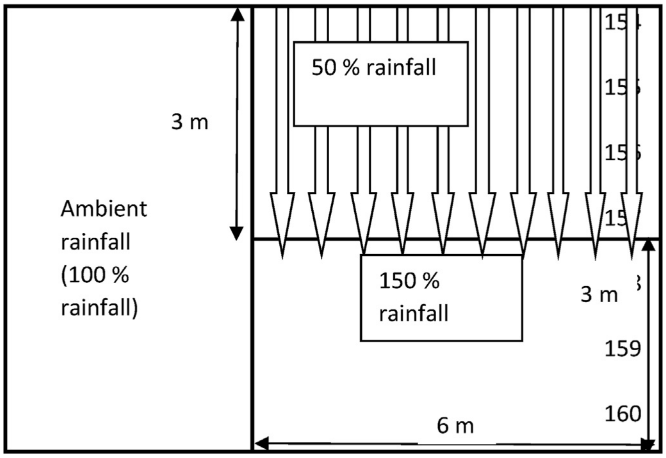

Fig. 1. A bird's eye view of an experimental plot. Open block arrows show transparent plastic sheets used to simulate reduced rainfall and direction of excluded rain water (to increased rainfall plot/150% rainfall).

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

2.4. Soil water content and bulk density determination

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

2.5. Ecosystem CO_2 exchange in the herbaceous layer

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

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

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

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

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

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

2.6. Gross primary production

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

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

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

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

2.7. Plant biomass determination

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

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

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

2.9. Statistical analysis

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

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

3. Results

3.1. Microclimate of the study region

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

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

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

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

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

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

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

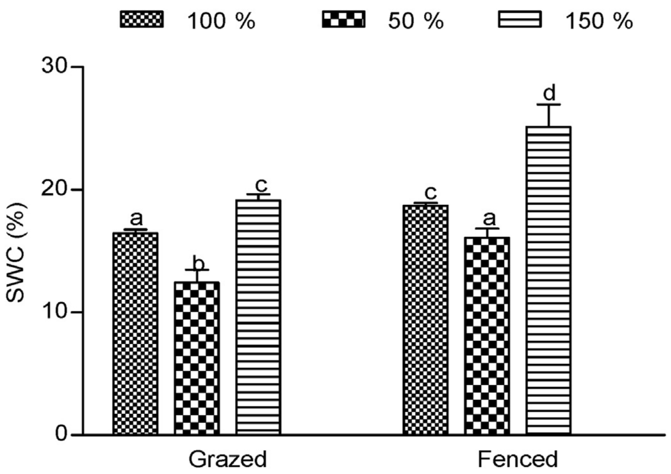

Fig. 3. Mean soil water content (%) in grazed and fenced plots at ambient rainfall (100%), fifty percent rainfall reduction (50%) and fifty percent rainfall increment (150%) for the entire study period. Different letters indicate significant differences ($p \leq 0.05$) in treatments across plots. Bars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

3.1.4. Relationship between CO_2 exchange and SWC

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

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

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

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

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

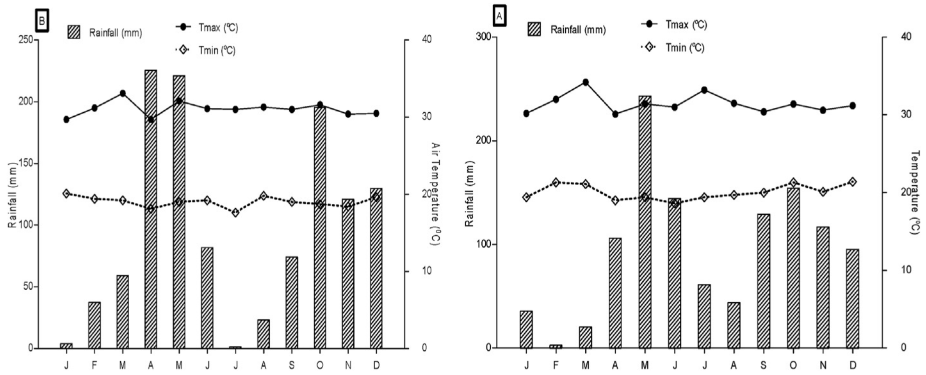

Fig. 2. Monthly rainfall amount (mm) and average maximum and minimum air temperature, T_{air} (^{0}C) recorded in the study site in (A) 2014 and (B) 2015 when measurements were conducted.

Table 1

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

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

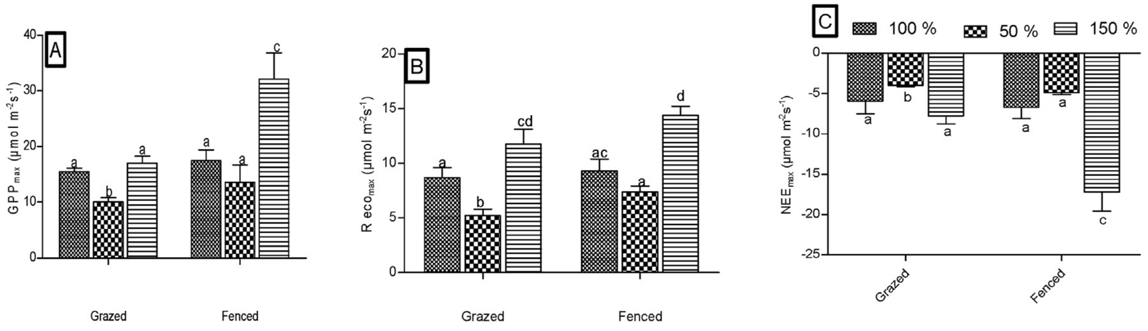

Fig. 4. GPP (a), R_{eco} (b) and NEE (c) in grazed and fenced plots at ambient rainfall (100%), fifty percent rainfall reduction (50%) and fifty percent rainfall increment (150%) for the entire study period. Different letters indicate significant differences ($P < 0.05$) in treatments across plots. Bars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

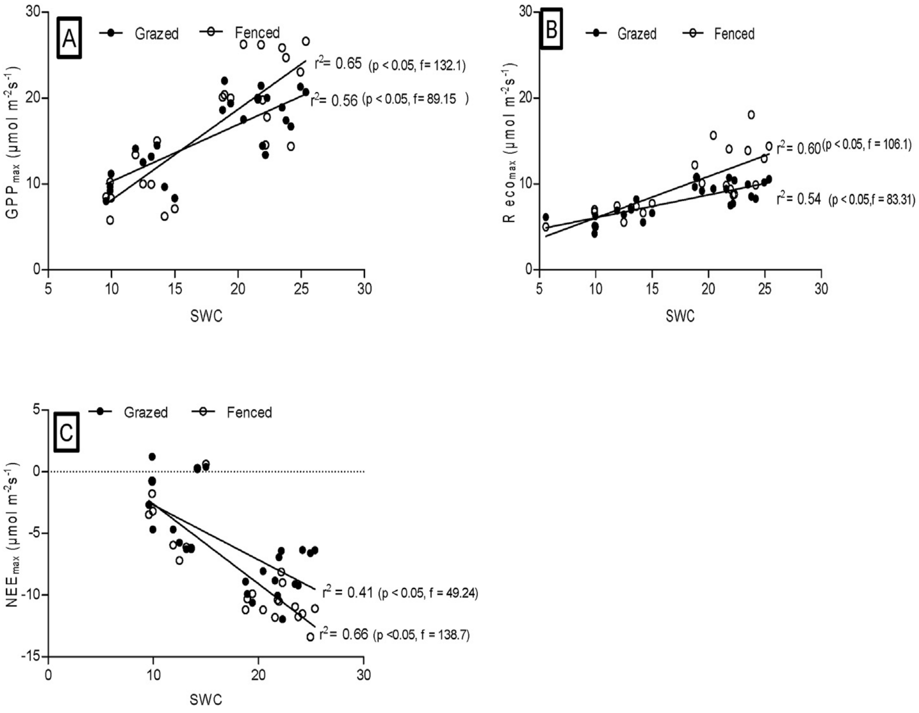

Fig. 5. Relationships between (A) GPP, (B) R_{eco}, (C) NEE and SWC within the 0–30 cm soil profile in the grazed and fenced plots, for the entire measurement period.

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

4. Discussion

4.1. *Influence of livestock grazing on aboveground biomass*

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

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

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

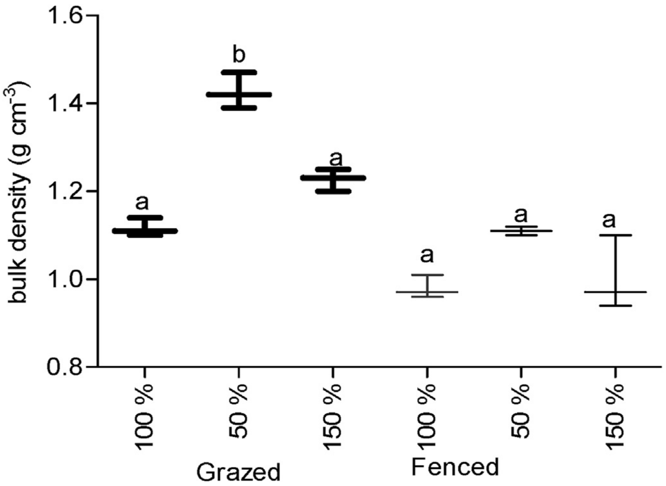

Fig. 6. Mean soil bulk density (g cm^{-3}) in grazed and fenced plots and at ambient rainfall, fifty percent rainfall reduction and fifty percent rainfall increment for the study period. Differences in letters indicate significant differences ($p < 0.05$) in treatments across plots.

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

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

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

4.3. Influence of grazing on ecosystem CO_2 exchange

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

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

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

5. Conclusion

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

Abbreviations

Not applicable.

Ethical approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

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

Funding

This study was funded by International Foundation for Science (IFS), under grant number I-1-D-6174-1 and National Research Fund, Kenya (NRF), 2016/17 FY.

Authors' contributions

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

Conflict of interest

Non declared.

Declaration of competing interest

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

Acknowledgement

We thank the Kenya National Youth Service (NYS) Lambwe Unit for allowing us to conduct experiments on their land.

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