Effects of livestock and wildlife grazing intensity on soil carbon dioxide flux in the savanna grassland of Kenya

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ABSTRACT

Although grazing is the primary land use in the savanna lowland of southern Kenya, the effects of grazing on soil carbon dioxide flux (R_S) remain unclear. A 12-month study was conducted from January to December 2020 on the effects of six grazing intensities sites (overgrazed (OG), heavily grazed (HG), moderately grazed (MG), moderately to lightly grazed (M-LG), lightly grazed (LG) and no grazing (NG)) on R_S on. A camera trap was used to monitor the total number of animals at each site, indicating the grazing intensity. Weekly measurements of R_S were taken using static greenhouse gas chambers along with simultaneous measurements of soil temperature (T_S) and volumetric soil water content (W_S) (depth of 5 cm). Mean R_S at HG, MG, M-LG and LG sites was approximately 15–25% higher than at NG and OG sites ($p < 0.001$). Mean W_S increased with decrease in grazing especially in the dry season, while T_S increased with increase in grazing. We observed bimodal temporal variation in R_S and W_S due to two wet seasons in the year. Thus, variation in R_S across the study period followed the changes in W_S rather than those in T_S. Mean values of R_S in the wet seasons were significantly higher ($> 45\%$) than those in the dry seasons, and W_S accounted for 71% of the temporal variability in R_S ($p < 0.05$). In addition, the enhanced vegetation index (EVI, interpreted as a proxy for vegetation cover) explained 60% of the variance of R_S, and W_S and EVI together explained 75%. EVI showed a negative relationship ($p < 0.05$) with animal intensity, indicating that more grazing reduced vegetation cover and, consequently, soil organic carbon and biomass. Soil bulk density was lower at less grazed sites. While R_S variability was unaffected by total nitrogen content, pH, and texture, correspondence analysis demonstrated that the main factors influencing R_S dynamics across the year under different grazing intensities were W_S and vegetation cover. Our results contribute to closing the existing knowledge gap regarding the effects of grazing intensity on R_S in East Africa savannas. Therefore, this information is of great importance in understanding carbon cycling in savanna grassland, as well as the identification of the potential consequences of increasing land pressure caused by rising livestock numbers, and will assist in the development of climate-smart livestock management in East Africa.

1. Introduction

Savanna grasslands cover ca. 50% of the African continent (Scholes et al., 1997; Castaldi et al., 2006). Covering such a huge area, they have the potential to affect atmospheric carbon dioxide (CO_2) concentrations, net ecosystem productivity and the carbon balance at local, regional and global scales (Scholes et al., 1997; Castaldi et al., 2006; Raich and Schlesinger, 1992). Soil respiration also referred to as the soil CO_2 flux (R_S) including root and microbial respiration is the single largest soil-atmosphere carbon flux from savanna grasslands (Makhado and Scholes, 2012). Key environmental factors that control R_S in the savanna grasslands include precipitation, soil moisture (W_S) and soil temperature (T_S) (Davidson et al., 1998; Lloyd and Taylor, 1994; Merbold et al., 2009), as well as vegetation and substrate availability (Wan and Luo,

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2003). Nevertheless, land use types and management practices, such as grazing can modify these factors and further alter R_S and carbon cycles (Wang and Fang, 2009). Thus, accurate assessment of R_S and its controlling factors are crucial for understanding carbon cycling in savanna (Bond-Lamberty and Thomson, 2010, 2018).

Grazing by both livestock and wildlife is an important component of savanna grasslands (Abdalla et al., 2018). Each animal species differs in terms of its nutritional requirements, jaw anatomy, and grazing habits (Olff and Mark, 1998). Additionally, animal grazing dynamics are influenced by forage and water availability, which varies depending on productivity (Begzsuren et al., 2004). Thus, animal grazing, feeding preferences, and trampling may alter grass cover, vegetation composition, and microclimate, in turn altering R_S and its controlling factors (Patton et al., 2007).

Grasses rather than large shrubs or trees dominate grassland (Grace et al., 2006). Thus grazing may reduce vegetation cover especially the grass cover, thereby reducing above- and belowground carbon and nutrient allocation to plants, root respiration and production, and soil organic matter, depending on the intensity (Abdalla et al., 2018; Carbone et al., 2008; Wang et al., 2017). A reduction in vegetation cover exposes soil to direct sunlight, which increases soil surface temperatures and evapotranspiration, and reduces W_S, and further alters metabolic activity of microbes and plant roots (Carbone et al., 2011; Bond-Lamberty and Thomson, 2010, 2018; Grace. et al., 2006). Moreover, trampling of soil increases soil bulk density (BD), which reduces water infiltration and water availability for root and soil microbes (Patton et al., 2007; Tollner et al., 1990) and diffusion of gases in/out of the soil (Li et al., 2008; Patton et al., 2007; Tollner et al., 1990). All these factors may have a direct or indirect effect on R_S (Cao et al., 2004). Moreover, dung and urine deposition by animals provide easily degradable carbon and nitrogen resources, which can stimulate plant and microbial growth, further affecting R_S. (Janssens et al., 2001; Davidson and Ivan, 2006).

The essential mechanisms driving the responses of R_S to grazing are still not fully understood, as contradictory results have been reported from a range of studies (Cao et al., 2004; Wang et al., 2020). While some have reported an increase in R_S with increased grazing in China (Dong et al., 2000), in the northern great plains and south-central North Dakota grasslands of the USA (Frank, 2002; Patton et al., 2007), others have reported a decrease in R_S with decreased grazing in a humid savanna in Kenya (Ondier et al., 2020), the Kalahari desert in southern Africa (Thomas, 2012), alpine meadows and semiarid grasslands in China (Cao et al., 2004; Wang et al., 2020) and managed pastures in Brazil (Brito et al., 2015). Yet others found no effect of grazing on R_S in a semi-arid savanna in South Africa (Munjonji et al., 2020), as well as a grassland and an alpine meadow in China (Ling-Hao et al., 2000; Cui et al., 2014).

The inconsistencies between these results suggest that the effect of grazing on R_S is complex and might be ecosystem-dependent. The reason may be that different grasslands respond differently to grazing depending on the vegetation type, the animal type, and the feeding preferences, all of which depend on the history, management practices, and levels of grazing utilization of the grasslands (Cao et al., 2004; Frank et al., 2002; Jia et al., 2007; Patton et al., 2007). In addition, the effects of grazing are combined with and are affected by other biotic and abiotic factors that vary with climate zones (Cao et al., 2004; Frank et al., 2002; Jia et al., 2007). The majority of these studies are from temperate grasslands that have soil rich in organic carbon and abundant grass growth (Dong et al., 2000; Frank et al., 2002; Cao et al., 2004; Patton et al., 2007), but such studies from savanna landscapes in Africa remain scarce (Grace et al., 2006), even less is reported for savanna grasslands in the Sub-Saharan Africa (Oduor et al., 2018).

Savanna grasslands unlike temperate grasslands, have low soil carbon (Grace et al., 2006) and are characterized by unpredictable rainfall and variations in vegetation growth, which combined with grazing leads to highly dynamic environments (Grace et al., 2006; Broadl et al., 2018). Rainfall and W_S are major determinants of primary productivity (Grace

et al., 2006). The availability of WS increases microbial activity and decomposition of soil organic matter, which stimulates grass growth and root growth, thereby stimulating R_S (Carbone et al., 2011; Orchard and Cook, 1983). While active roots contribute directly to R_S, dead roots and root exudates provide carbon as a source of energy and nutrients for soil microbial biomass (Tufekcioglu et al., 2001). Previous studies in savanna grasslands have shown that W_S and vegetation status significantly influences R_S variations, but T_S has a marginal effect on R_S because of its marginal intra-annual variation in the tropics (Grace et al., 2006; Ardö et al., 2008; Broadl et al., 2018). The effect of grazing on soil and vegetation, however, is one of the critical factors that alters productivity, microclimates, and eventually R_S in savanna grassland.

In the savanna grasslands of Sub-Saharan Africa, grazing intensity has increased due to an increase in demand for livestock products as a result of population growth (Osborne et al., 2018). This has seen an increase in the number of grazing livestock over the years (Osborne et al., 2018), and as a result, overgrazing due to overstocking is a major cause of soil and vegetation degradation (Abdalla et al., 2018; Patton et al., 2007). Overgrazing reduces ground cover and thus exposes the soil to more radiation, leading to higher evapotranspiration and erosion (Abdalla et al., 2018). Furthermore it leads to less inputs of organic matter as litter, nutrients, and biotic activity, which consequently affects R_S (Abdalla et al., 2018).

In Kenya, savanna grasslands cover more than 80% of the landscape and contain approximately 50% of the total livestock population, primarily within pastoral communities. Similarly they are home to nearly 80% of the total wildlife population (Kinyenze et al., 2019). Given the vast area covered by this ecosystem, any effects of grazing on R_S are likely to influence the local, regional, and global carbon cycles (Scholes et al., 1997; Castaldi et al., 2006; Raich and Schlesinger, 1992). To the best of our knowledge, only a few studies have been conducted in Kenya and in East Africa on the response of R_S on restored communal grazing lands (Oduor et al., 2018) and the interactive effects of grazing, rainfall and drought on R_S (Ondier et al., 2020; Munjonji et al., 2020). Nonetheless, no such study has been conducted on the effects of different levels of grazing on R_S in the savanna grasslands.

To contribute to closing this knowledge gap, we measured R_S under five different levels of grazing in the savanna grasslands of southern Kenya. In addition, a control site with no grazing was established in a fenced enclosure meant for restoration purposes. This study aimed at (i) evaluating the effects of different grazing intensities on R_S, (ii) assessing the temporal variations in R_S at each grazing site for a full year and (iii) identifying key environmental variables driving the response of R_S to variations in grazing. We hypothesized that grazing exclosure and lighter grazing sites would have higher R_S rates than heavily grazed and overgrazed sites due to the effects of grazing on vegetation cover and W_S. Furthermore, we hypothesized that W_S pulses, such as occurring during the rainy seasons, are an important driver of R_S, with T_S being of lower priority due to its low seasonal variation in the tropics.

2. Methodology

2.1. Site characteristics

The experimental site was located in the lowlands of Taita–Taveta County in southern Kenya (38° 8′E, 3° 28′ S, about 800–1000 m above mean sea level). The site is an expansive lowland with a slope of less than 5%. About 89% of county area is considered to be arid and semi-arid land (ASAL). The Tsavo East and Tsavo West national parks cover ca. 62% of the county area (CIDP, 2014), but private sanctuaries, such as the Taita Hills Wildlife Sanctuary (THWS) and LUMO Community Wildlife Sanctuary (an amalgamation of three ranches, namely Lualenyi, Mramba and Oza, hence the name LUMO), increase the land area under conservation. There are 28 ranches designated for livestock production in the county.

The local climate is tropical with two rainy seasons: a long rainy

season between March and May (with a peak in April) and a short rainy season between October and December (with a peak in November). January and February are dry and hot months, while June to September are dry and cool months (Pellikka et al., 2018). The mean annual rainfall in these lowlands is about 500 mm and the mean annual air temperature is 23 °C, with mean daily minimum and maximum temperatures of 16.7 °C and 28.8 °C, respectively (Pellikka et al., 2018). The dominant soil type is rhodic ferralsol, which is characterized by very deep, acidic, dark red, weathered sandy clay soil (CIDP, 2014).

For this study, grazing sites were located in both THWS and LUMO, which covers a wide range of grazing intensities.These sanctuaries consist of open savanna grassland, with areas of open woodland and shrublands with *Acacia* spp. as the main trees, having an extensive variety of herbaceous vegetation dominated by *Chloris roxburghiana*, *Schmidtia bulbosa* and *Cenchrus ciliaris* grass species. THWS (900–1100 m a.s.l.; covering an area of ca. 110 km^2) is a conservation area under private management for wildlife conservation only, and grazing is thus light to very light. LUMO (850–1050 m a.s.l; covering approximately 460 km^2), on the other hand, is a conservation area with some areas dedicated for livestock management (Amara et al., 2020). It is located between Tsavo West National Park and THWS and is a communally owned (GoK, 2013) for community livestock grazing and also wildlife. Large herds roam within LUMO, causing overgrazing, which is enhanced by illegal herders, who mainly enter the conservancy with their livestock in the dry season (CIDP, 2014). Conservation, on the other hand, has reduced the woody vegetation cover due to the large browser population, especially in the THWS (Amara et al., 2020). Our control site was located in a fenced reforestation project area located in THWS that was established in 2010. The electric fence and open soil around it prevents grazing livestock, other larger mammals and lizards, as well as fire, from entering this 13 hectare area (Fig. 1).

2.2. Experimental design

In November 2019, six sampling sites were established to represent different levels of grazing, and subsequent R_S measurements were taken

at these sites (see Table 1; Fig. 1). Because the differences in vegetation cover in the study area are primarily caused by grazing and browsing, the sites were selected using satellite and airborne remote sensing data (Amara et al., 2020). This was supported by field observations, the number of animals captured at each site by wildlife cameras, and consultation with the management from THWS and LUMO. At each site, four circular stainless steel chamber collars (21 cm in diameter and 10 cm in height) were randomly installed in January 2020. The collars were inserted into the soil to a depth of up to 5–6 cm one week prior to the first R_S concentration measurements to avoid disturbance of the measurements due to collar installation. The collars were left in the ground for the entire study period (Søe et al., 2004). Collars that were interfered with or damaged by animals were replaced at least 24 h

Table 1
Characteristics of the six grazing sites.

Site	Code	Description
Overgrazed	OG	Overgrazed by livestock throughout the year due to the proximity of watering points. Occasional visits by wildlife. The land is mostly bare, with exposed soils for most of the year.
Heavily grazed	HG	Heavily grazed by livestock and wildlife in the LUMO community grazing area.
Moderately grazed	MG	Medium grazing by livestock in LUMO, but also accessed by wildlife due to the vicinity of the THWS border. Livestock grazing is discouraged due to wildlife tourism.
Moderately to lightly grazed	M-LG	Minimal grazing by wildlife within THWS. Occasional grazing by cattle and more frequent grazing by wildlife compared to LG due to the vicinity of a water reservoir. Located 100 m from the NG control site.
Lightly grazed	LG	Minimal grazing by wildlife only in the THWS. This area is guarded and is therefore not accessible by livestock.
No grazing	NG	Control site: fenced reforestation enclosure excluding larger animals and fire. Small mammals, birds, reptiles and insects can enter.
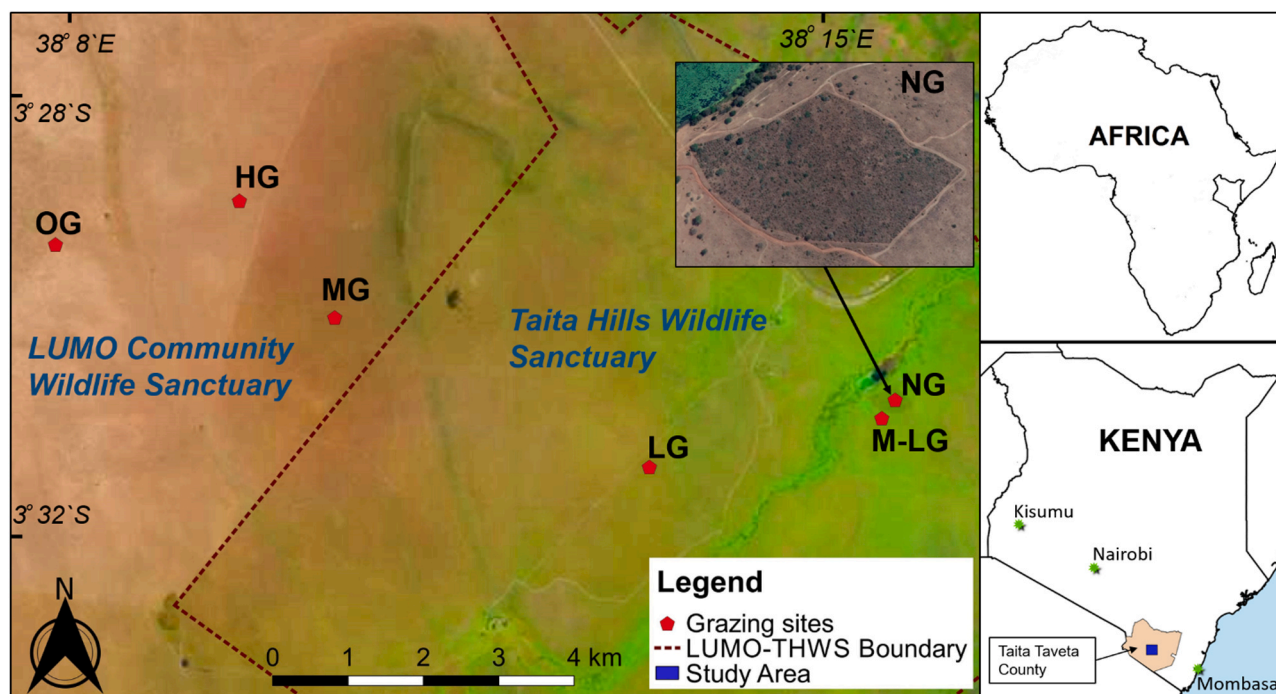
Fig. 1. Study sites with varying grazing intensity located in LUMO and THWS in Southern Kenya. OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG - moderately to lightly grazed, LG - lightly grazed and NG - no grazing (see Table 1 for details). Sentinel-2A satellite image, 20 December 2020, Sentinels Scientific Data HubCE4 (ESA, 2015).

before the next gas sampling took place. Over the length of the study period, the heavy grazing (HG) site was affected by wildfire between 8 and 9 August 2020.

2.3. Measurements of soil CO₂ concentrations and flux calculation

Field measurements of R_S were carried out weekly from 14 January to 22 December 2020. On each of the gas sampling days, the chamber collars were enclosed using a matching lid (internal diameter = 20 cm; height = 24.5 cm) covered with reflective aluminum foil to minimize heating inside the chamber during the period of actual measurements (Fig. 2B). In addition, the duration of the measurement was 5 min at maximum to avoid saturation effects. A small fan was mounted on the chamber ceiling to circulate the air within the chamber and ensure a well-mixed gas sample. The chamber lid had a small vent on it to prevent pressure build-up in the chambers during measurements. The lid was fitted with a CO₂ probe (Vaisala CARBOCAP® GMP343, CO₂ sensor, Vaisala Oyj, Helsinki, Finland) and a temperature probe (HMP75, Vaisala Oyj, Helsinki, Finland). The CO₂ sensor measured the CO₂ concentration in parts per million (ppm). CO₂ has a characteristic absorbance band in the infrared (IR) region at a wavelength of 4.26 μm. Therefore, when IR radiation is passed through a gas containing CO₂, part of the radiation is absorbed. The CO₂ and temperature probes were connected to a Vaisala MI70 indicator to measure changes in the temperature and CO₂ concentration at the same time for 5 min at an interval of 15 s per chamber closure time, giving us 20 readings per chamber deployment time. R_S was calculated using linear least squares regression

of CO₂ concentration within the chamber headspace versus time. The first 20 s of data points were discarded due to noise, as recommended by the manufacturer, ensuring that we used the linear portion of the curve. Individual chamber fluxes were calculated if the linear regression for each individual CO₂ yielded R² > 0.9 or normalized root mean square error < 0.2 (Christiansen et al., 2011). We also discarded data points for which the rate of change of CO₂ was negative, as photosynthesis can be assumed to be zero inside an opaque chamber. Therefore, R_S was calculated using Eq. (1) as follows:

$$R_S = \frac{(\Delta c/\Delta t) \quad \times \quad V_{ch} \quad \times \quad M_w}{A_{ch} \quad \times \quad M_v \quad 60 \times 10^6} \tag{1}$$

where $\Delta c/\Delta t$ is the change in the chamber headspace CO₂ concentration over time (i.e., slope of the linear regression), V_{ch} is the volume of the chamber headspace (m³), M_w is the molar weight (g mol⁻¹) of C for CO₂ (12), A_{ch} is the area covered by the chamber (m²) and M_v is the pressure- and temperature-corrected molar volume (see details in Brümmer et al., 2008a, 2008b). The values 60 and 10⁶ are constants used to convert minutes into hours and grams into micrograms, respectively. Fluxes are expressed as mg C m⁻² h⁻¹.

2.4. Microclimate data

Soil temperature (T_S, °C) and volumetric soil water content (W_S, %) at the depth of 0–5 cm were measured next to the collars using a handheld data logger connected to a GS3 sensor (ProCheck, METER Group, Inc., USA) on each gas sampling day. The air temperature and
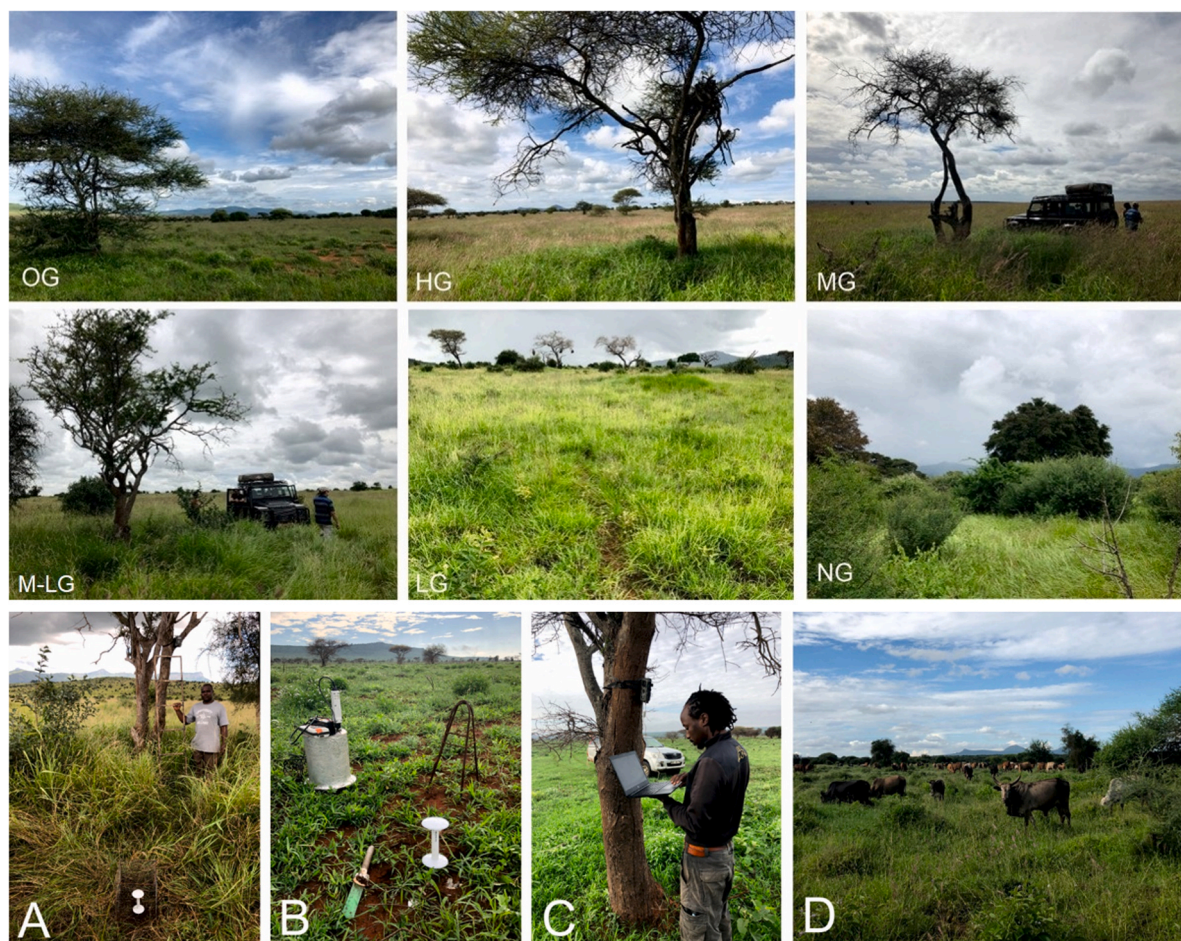

Fig. 2. Grazing sites (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing (see Table 1 for a detailed explanation). (A) TMS-4 data logger, (B) Vaisala chamber with the TMS-4 in front, (C) camera trap set up and (D) livestock grazing in OG. (Photos taken on 20 November 2019 during the wet season by Petri Pellikka).

atmospheric pressure were recorded using a handheld digital thermometer and Garmin GPSMap 64. Daily rainfall (mm) over the year was measured with a tipping bucket (ARG100, Campbell Scientific, USA) and air temperature (T_A, °C) with a digital thermometer. Both were installed at a weather station installed at site LG in THWS in an open area to avoid interference from trees. Measurements were taken every 5 min, averaged and stored every 30 min on a data logger (built in CR200X, ARG100, Campbell Scientific, USA). In addition, continuous T_A, T_S and surface temperature (T_{Surf}), and W_S measurements were taken at 15-minute intervals in the proximity of the collar chambers using TMS-4 data loggers (TOMST®, Czech Republic). The TMS-4 has three temperature sensors for T_A, T_{Surf} and T_S respectively positioned at + 15, 0 and − 8 cm relative to the soil surface (Wild et al., 2019). The W_S sensor, located in the bottom part of the TMS logger probe, measures volumetric soil moisture at a depth of about − 14 cm (Wild et al., 2019). The sensors were kept in place and fenced using wire cages to prevent interference by animals (Fig. 2B). However, we had to replace the TOMST sensors at the HG site after they were burnt in a wildfire in August 2020.

2.5. Evaluating the intensity of animal use at each grazing site

In order to monitor and estimate the intensity of animal use at each site, we installed motion-activated wildlife cameras (APEMAN Trail Cam H45, China) to record the number of animals visiting the sites during the study period. The cameras had a detection angle of 90° and a field of view (FOV) of 73°. They were fixed on a tree (2.5–3 m above ground) to avoid disturbance by animals that typically scratch their body against the trees. We set the cameras to record three consecutive images with a 3-s interval each time the sensor was triggered by animal movement within the camera's detection zone. The recovery time was set at 1 min in order to record images of the same animal or group of animals passing in front of the camera only once (Van Berkel, 2014).

We defined the intensity of animal use as the total number of animals captured in an image at any given time during the whole study period at each site. In addition to counting, we recorded the type of animal species and whether it was grazer or browser, the time and date, and the total number of animals in each image. When a group of animals such as a herd of livestock triggered a camera, the intensity of use (number of animals) was recorded as the maximum number of individuals in that image. This was then binned into the total and mean per month to evaluate the number of animals at each site and across the year to assess the effect on the monthly vegetation index (a proxy of vegetation status) and monthly R_S. Data were downloaded and the batteries and memory card were checked every month.

2.6. Measurements of vegetation characteristics at GI sites

Since the differences in vegetation cover between the sites were mostly caused by grazing and browsing, changes in the remotely sensed vegetation index (Huete et al., 2002) were assumed to reflect the grazing intensity (Ma et al., 2019). Therefore, to investigate differences in the vegetation status and its effect on R_S at each site, we used remotely sensed composite enhanced vegetation index (EVI) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data calculated by the following equation (Eq. (2)):

$$EVI = G(\rho NIR - \rho red)/\rho NIR + C_1 \times \rho red - C_2 \times \rho blue + L$$

(2)

where $\rho blue$, ρred and ρNIR are atmospherically corrected surface reflectance in blue, red and near infrared (NIR) wavelength bands, respectively, L is the canopy background adjustment factor (L = 1), C_1 and C_2 are coefficients of the aerosol resistance terms (C1 = 6 and C2 = 7.5), and G is a gain factor (G = 2.5) (Huete et al., 2002).

We acquired MOD13Q1 (MODIS Level 3 products) EVI data generated at 16-day intervals with a 250-m spatial resolution from *https://ladsweb.modaps.eosdis.nasa.gov* on 23 January 2021. To maintain temporal consistency with the gas sampling data, we selected EVI data captured closest to the gas sampling day or at maximum 5 days before or after this day, assuming that no substantial change in vegetation would have occurred in such a time. We extracted EVI pixel values closest to each site based on their latitude and longitude.

In addition to the EVI data, five (1 m × 1 m) quadrats were randomly selected at each site to assess the herbaceous aboveground biomass (AGB). This was done by clipping all the grasses and small shrubs within the quadrats to ground level (< 1 cm) using hand shears. Sampling was carried out monthly from April to December 2020. The fresh weight of the samples was recorded, and after drying the samples in an oven at 70 °C for 48 h, the dry weight to the nearest 0.01 g was recorded. The biomass of the five quadrats per site was averaged to represent the biomass of each site.

2.7. Soil sampling and analysis

Soil sampling was conducted in April and June 2020 at each site by randomly collecting four soil samples at a depth of 0–20 cm using a soil auger (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). All samples were mixed in a bucket, and all plant debris and roots were removed. A composite soil sample (500 g) was taken and stored in airtight polyethylene bag. This exercise was repeated three times, giving us three composite soil samples per site. Another sample (at a depth of 0–5 cm) was taken using a bulk density ring (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) for bulk density and water content assessment. The samples were labeled accordingly and transported in cooler boxes to the Mazingira Centre at ILRI (Nairobi, Kenya) for the analysis. In the laboratory, the samples were stored at 4 °C until processing within 14 days. The subsample of field moist soil was air-dried at room temperature and sieved using a 2-mm sieve to determine soil organic carbon (SOC), the total nitrogen content (TN), soil pH and texture. Soil texture was determined using the hydrometer technique (Reeuwijk, 2002; Scrimgeour, 2008) and soil pH was measured in a soil:distilled water suspension (1:2.5) using a pH meter (3540 pH and conductivity meter, Bibby Scientific Ltd, UK). To determine SOC and TN, a duplicate of 20 g of the fresh sample was oven-dried at 50 °C for 48 h and then pounded into a fine powder (< 0.25 mm) using a ball mill (Retsch ball mill, Haan, Germany) followed by analysis using an elemental analyser (Vario MAX Cube Analyzer Version 05.03.2013). BD were determined by drying soil samples collected with bulk density rings of known volume at 105 °C for 48 h.

2.8. Data analysis

Descriptive statistics (mean ± SE and coefficient of variation (CV)) were used to examine differences in the measured variables between the sites and seasons. Monthly and seasonal variations in R_S were calculated from the daily arithmetic mean of hourly R_S, which were the averages of all chamber measurements taken on each gas sampling day. R_S data were tested for normality (Kolmogorov–Smirnov coefficients) and equality of variance (Levene test) before and after data transformation. R_S data were not normally distributed and data transformation (log and square root) did not improve data normality, therefore the original data were used for statistical analyses. We used boxplots (displaying the minimum, first quartile (Q1), median, third quartile (Q3), and maximum of data) to examine the temporal variability of R_S, W_S and T_S between sites across the study year. The effects of (i) grazing site and (ii) month on R_S were tested using a generalized linear mixed model (GLMM) fit by maximum likelihood (Gbur et al., 2012). Grazing sites were treated as fixed effects and the months of the year as random effects in the model. A distribution test revealed gamma distribution to provide a good fit for the R_S data and therefore a GLMM Gamma model was used.

The mathematical representation of the model is presented by the equation (Eq. (3)), therefore the model using Rstudio package *lme4* (Bates et al., 2014).

$$log f_0(y) = \beta_0 + \beta_1 x + \mu + \varepsilon \qquad (3)$$

where y = response variable, x = explanatory variables, μ = random effects and ε = error term.

Another GLMM model was developed using W_S, T_S and EVI as fixed effects and grazing sites as random effects to examine the effect of environmental variables on R_S. Spearman correlation coefficients were applied to assess the relationship between the cumulative monthly and annual mean R_S (calculated by trapezoidal integration of daily fluxes with time) against animal intensity of use and environmental variables that were measured once or twice during the study period, including soil pH, BD, soil texture, SOC and TN, herbaceous AGB. The aim was to identify the most significant variables driving the spatial and temporal variation in R_S. All statistical tests were performed at the 5% level of significance. Summary values are expressed as the mean value ± standard error of the mean (SE). Statistical procedures and plotting were performed using the software packages in R 3.5.2.

3. Results

3.1. Effects of grazing intensity on soil CO_2 flux

Soil CO_2 efflux (R_S) rates measured during the study period at all sites ranged from 10 to 356 mg C m^{-2} h^{-1}. Overall, mean R_S was lowest at OG (59 ± 7 mg C m^{-2} h^{-1}) and NG (67 ± 7 mg C m^{-2} h^{-1}) and highest at MG (96 ± 9 mg C m^{-2} h^{-1}) (Table 2). With sites as the fixed effect and the month of year as the random effect, a GLMM model revealed that the difference in grazing sites had a significant effect on R_S (p-values < 0.001; Table 3) accounting for ca. 60% of the spatial variation in R_S. A post hoc analysis that involved a pairwise comparison of the R_S across the sites revealed that OG and NG were significantly lower than all the other grazed sites (HG, MG, M-LG, LG), and the pairs M-LG and HG, M-LG and MG were significantly different. We considered individual months across the year, and observed a significant increase of approximately 10–25% in R_S with the decrease in the grazing evident in January, February, May and November (OG < HG < MG < M-LG < LG; Fig. 3c). In April, no significant differences between the sites was observed, however, in the months of June, July and December, R_S increased with decrease grazing (OG < HG < MG) and thereafter gradually decreased in M-LG and LG. This only applied to the grazed sites, as we observed a decrease in R_S at NG throughout the rainy season months. On average, R_S was lowest at OG in the dry season months and at NG site in the rainy season months. In dry months, during the earliest months of the dry season in June and July, the highest R_S was from MG but latter months in September and October the highest was from NG.

3.2. Temporal variations in soil CO_2 flux

Overall, R_S displayed a bimodal pattern for all sites throughout 2020 (Fig. 3d), with a CV ranging between 60% and 80%. Mean R_S values

Table 3
Results of generalized linear mixed model (GLMM) showing effect of grazing sites on mean soil CO_2 flux (R_S) with the month of the year as random factor.
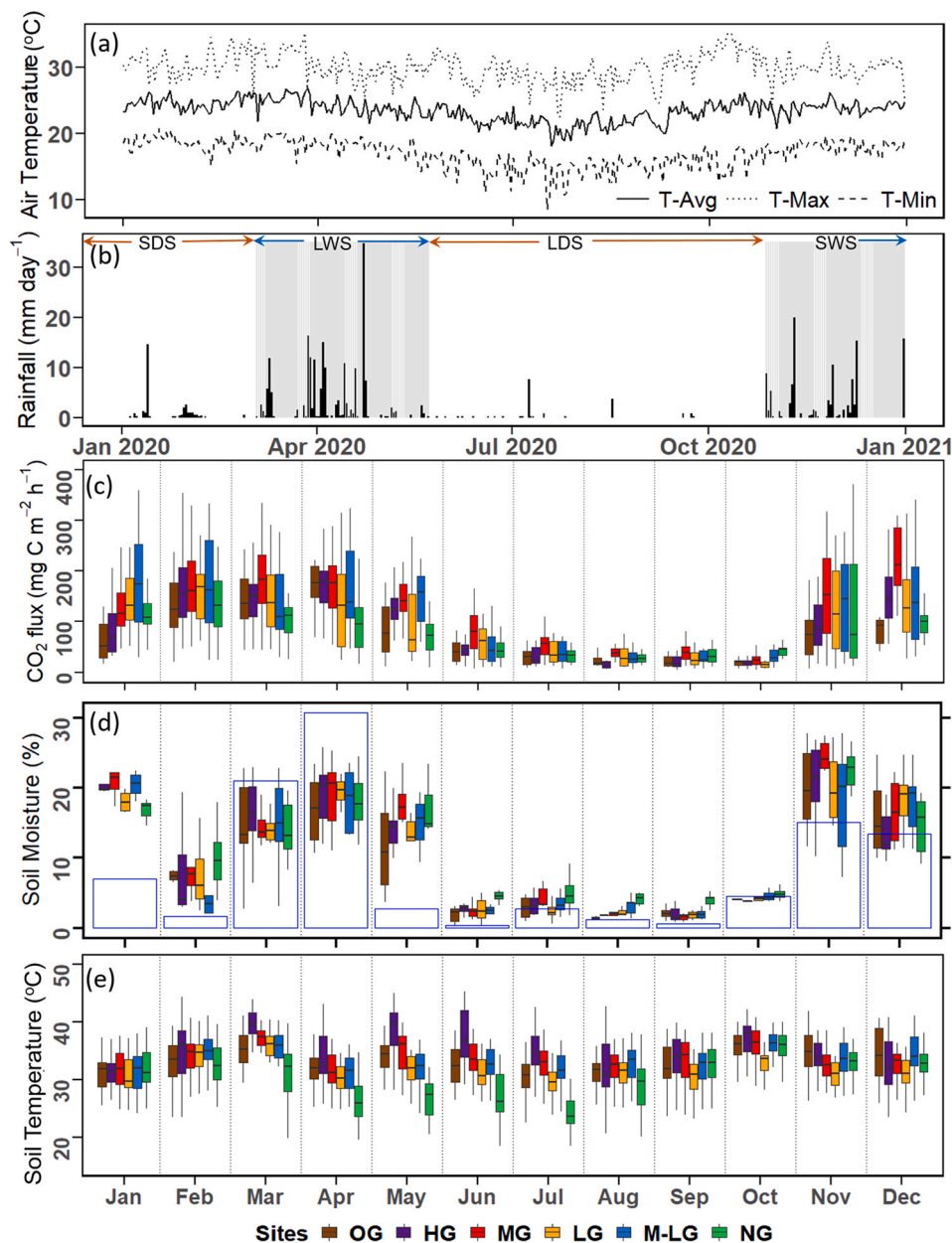
Grazing sites	Estimate	Std. Error	t value	Pr (>|z|)	Significance
OG	3.723	0.151	24.631	< 2e-16	***
HG	0.375	0.069	5.447	5.12e-08	***
MG	0.616	0.067	9.264	< 2e-16	***
M-LG	0.307	0.068	4.529	5.91e-06	***
LG	0.388	0.068	5.747	9.10e-09	***
NG	0.384	0.071	5.417	6.07e-08	***
Random effect		Variance	Std. Dev		
Month (Intercept)		0.152	0.390		
Residual		0.207	0.455		

AIC = 2304, R^2 = 0.62, Significance code: p < 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***.

significantly differed across the seasons ($p < 0.01$), with the highest R_S ranging from 50 to 356 mg C m^{-2} h^{-1} occurring in the two wet seasons (rainy seasons) and in the short dry season (SDS) (mean R_S for each site per season is provided in Table 2). During the expected SDS, sporadic rainfall were observed from last week of January, which led to higher W_S (12–18%) and thus higher R_S. On the other hand, the lowest R_S values (ranging from 5 to 60 mg C m^{-2} h^{-1}) were observed in the long dry season (LDS), which lasted from June to the third week of October. The observed variation in R_S for all the sites followed the changes in W_S (Fig. 3d) rather than those in T_S, and thus R_S substantially increased with the onset of rainfall events (Fig. 3b). W_S at 5 cm also followed a bimodal seasonal pattern, with higher W_S (mean from 15% to 30%) during the long wet season (LWS: long rainy season from end of March to May) and short wet season (SWS: short rainy period from November to December) and the lowest W_S (< 10%) during the February in the short dry season (SDS: period between January to end of February) and LDS, with a high temporal CV across the study period ranging between 60% and 75% at different sites. On the other hand, temporal CV for T_S across the study period was low ranging between 15% and 25% at different sites The difference in R_S between the LWS and SWS was not significant, but R_S in the SDS was 50% higher than in the LDS. Overall, the mean R_S in the combined LWS and SWS period was not significantly different to SDS, but > 45% higher than in the LDS.

3.3. Effects of volumetric soil moisture and soil temperature on soil respiration

Overall mean W_S (13 ± 3%) did not differ between the sites during the study period (Fig. 3d). However, during the dry season (LDS), W_S was slightly higher at NG than the grazed sites, but throughout, OG had the lowest W_S. Soil T_S, on the other hand, was slightly higher at OG and HG (ca. 33 ± 7 °C) and the lowest at NG (29 ± 6 °C) (Fig. 3e) through the study period. Site NG had tall shrubs and bushes, which might have caused shading, thereby cooling the soils compared to the other sites. Surface temperature (T_{Surf}) was also lowest at the NG site (Fig. A1). W_S was found to have a linear relationship with R_S, (p-value = <2e-16). The random effect of the grazing sites were found to be significant due to its large variance of 4.97. Parallel slopes were therefore produced for the different grazing sites to summarize the relationship between W_S and R_S

Table 2
Seasons and annual mean soil CO_2 flux (mg C m^{-2} h^{-1}) per grazing site across the study year. Mean values marked with the different alphabetical letters are statistically different between the sites.

Grazing sites	Short dry season	Long wet season	Long dry season	Short wet season	Max	Min	Annual Mean	CV
OG	111.7 ± 15.1*a*	111.1 ± 10.4*a*	20.2 ± 2.2*a*	58.9 ± 8.1*a*	162.2	9.9	58.7 ± 6.8*a*	78.0
HG	177.7 ± 40.7*b*	155.9 ± 13.3*b*	25.7 ± 2.4*a*	115.2 ± 18.9*b*	293.8	13.1	90.1 ± 11.1*b*	80.2
MG	131.6 ± 25.3*c*	140.9 ± 9.9*cb*	44.8 ± 5.3*b*	146.4 ± 21.5*c*	220.7	16.0	95.8 ± 9.1*b*	63.4
M-LG	142.1 ± 22.6*c*	134.7 ± 19.3*c*	30.5 ± 3.9*c*	87.6 ± 21.4*d*	245.1	11.7	75.3 ± 9.2*c*	81.2
LG	159.0 ± 35.7*db*	143.4 ± 17.3*cb*	30.0 ± 4.2*c*	115.7 ± 22.7*b*	243.1	10.2	86.4 ± 10.4*cb*	80.8
NG	100.2 ± 17.8*a*	87.4 ± 9.9*a*	38.5 ± 3.3*b*	92.3 ± 27.6*db*	213.4	18.6	66.5 ± 6.7*a*	65.4

Fig. 3. Variation in (a) daily maximum, average and minimum air temperatures, (b) total daily rainfall (long (LWS) and short (SWS) wet seasons are indicated with gray areas, while the areas between these are the short (SDS) and long (LDS) dry seasons, (c) mean monthly soil CO_2 flux (R_S), (d) mean monthly volumetric soil moisture and rainfall (blue bars), and (e) mean monthly soil temperature (taken at a depth of 5 cm) at each site (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) from January to December 2020. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
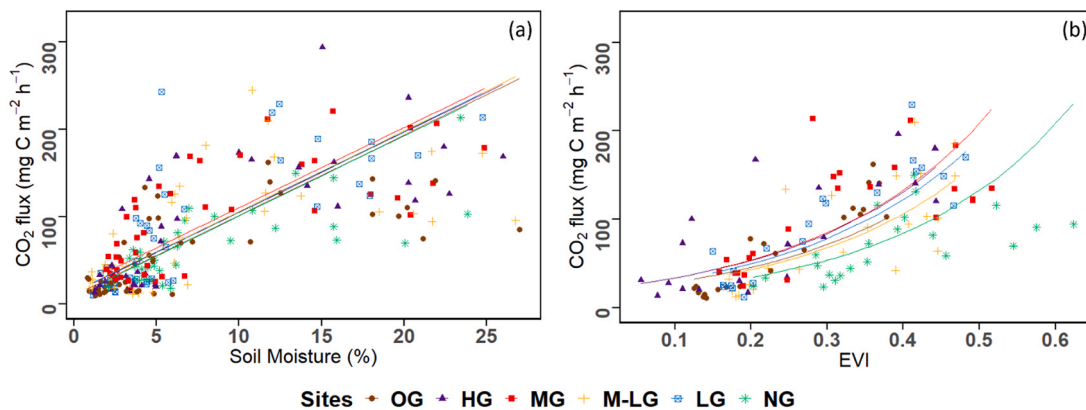
Fig. 4. Relationship of soil CO_2 flux and volumetric (a) soil moisture (W_S) and enhanced vegetation index (EVI) at each grazing site (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) obtained from generalized linear mixed effect model (GLMM). (See Tables 4 and 5 for model parameter).

Table 4

Results of generalized linear mixed model (GLMM) showing effect estimate of the soil moisture on mean soil CO_2 flux (R_S) with the grazing sites as random factor.

Predictors	Estimates	Std. Error	t value	p value	Significance
Intercept	13.4644	3.925	3.43	6.03e-04	***
Soil moisture	9.175	0.699	13.119	< 2e-16	***
Random effects		Grazing sites	Coefficient	Variance	Std. Dev
		OG	10.04		
		HG	13.33		
		MG	18.71		
		M-LG	14.5		
		LG	13.91		
		NG	9.13		
Grazing sites (Intercept)				21.235	4.608
Residual				0.331	0.575

AIC 2377, R^2 = 0.71, Significance code: p < 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***.

(Fig. 4a; Table 4). W_S in M-LG and LG sites led to higher amounts of R_S while W_S levels in NG had the least R_S. Overall, the field measurements of W_S account for about ca. 70% (Table 4) of the variation in the R_S. Soil T_S, on the other hand, did not show any significant ($p > 0.09$) relationship with R_S within each site and across months during the study year. Our results indicate that W_S was essential in controlling the seasonal dynamics of R_S overall and at each site. Combining the effects of W_S and T_S on R_S did not improve the model with W_S as a single factor.

3.4. Intensity of animal use at each grazing site

Altogether, the camera traps at all sites captured a total of 12,711 animals from last week of January to December 2020. We experienced camera failures for a week in August at the HG due to a wildfire (8–9 August), and in October at M-LG, LG and NG due to a failure of the memory card and/or batteries, which might have affected the data for that period of time. However, the frequency of animal use (images captured) was the highest at OG (ca. 33% of the animals) and HG (ca. 23%) and the lowest at MG (ca. 6%) (Table A1). About 97% of the of the animal captured were grazers and browsers, while 3% were predators, such as lions or hyenas, or baboons and stray dogs. Furthermore, 78% of the grazers and browsers were livestock, including cattle (89% of the livestock), sheep and goats. The total number of animal recorded were highest at OG, HG and MG compared to M-LG and LG (no livestock were photographed at the LG). At the MG, 85% of the livestock were captured between 26 September and 28 October, and at NG, about 142 cattle intruded the site at night between 3 and 8 September due to a damaged fence (Table A1). Overall, the highest number of wildlife grazers and browsers was recorded at LG, the number decreasing with increasing

grazing by cattle (Fig. 5b). Buffalos were the most abundant (ca. 39%) wildlife captured, of which about 62% predominantly occurred at the LG. Over the year, the results from OG showed a trend towards a higher intensity of animal use between May and August followed by a drop in September and October and then a slight increase in November and December (Fig. 5a). The reason for the drop is evidently that in September to October the land is mostly barren.

3.5. The effects of grazing intensity on vegetation

Overall, mean EVI values across the study period were highest at the NG (0.39 ± 0.02), with the least disturbance, and the lowest at OG (0.24 ± 0.02) (Fig. 6b). HG had a significantly higher EVI ($p = 0.02$) than other sites in January and February, while during the rest of the year, the highest EVI was generally at NG and MG. NG had a greater cover of shrubs and smaller trees because grazing and browsing were prohibited. Although cattle intruded on the NG in September, this had no observable effect on the EVI. At all sites, we observed an increase in the EVI at the onset of the rainy season in March, but at OG, there was a gradual decline in EVI as the number of animals increased from April and May (Fig. 5a). The herbaceous ranged between 200 and 1200 g dry weight (DW) m^{-2} across the sites. AGB was slightly significantly highest at the MG and lowest at the OG and HG (Fig. 6a; $p < 0.05$). Still, EVI and AGB at HG were affected by a wildfire in August. Therefore, HG recorded the lowest EVI (Fig. A2) in August and September. Overall, the mean herbaceous AGB displayed a positive relationship with the mean EVI (Fig. 6d; $p < 0.05$; $R^2 = 0.31$). Mean animal count (Fig. 6c) revealed a negative relationship against mean AGB (Fig. 6e; $p < 0.05$; $R^2 = 0.26$) and mean EVI (Fig. 6f; $p < 0.05$; $R^2 = 0.58$), indicating that an increase in the number of animals led to a decrease in the mean EVI and AGB. Across the year, the highest EVI values were observed from January to the end of May, and they decreased in June at the onset of the LDS, reflecting the variation in eco-climatic conditions across the year. GLMM results of R_S against EVI with grazing sites as random effect revealed a positive relationship ($p < 0.05$) with the EVI explaining about 60% of the variation in R_S across the year (Fig. 4b; Table 5). Furthermore, including the EVI and W_S in the model led to the explanation of 76% of the variability in R_S (Table A2).

3.6. The effects of soil properties on soil CO_2 efflux

Soil organic carbon (SOC) concentrations were significantly higher at NG, LG and M-LG compared to OG and HG, with the corresponding total nitrogen (TN) content exhibiting a similar trend (Table 6). Bulk density (BD) increased with increased grazing. OG showed a higher (approximately 10%) BD ($p < 0.05$) than the NG, and declined with a lower grazed sites. However, the other soil properties did not differ significantly between the sites and thus were minor in explaining the difference in R_S between the sites.
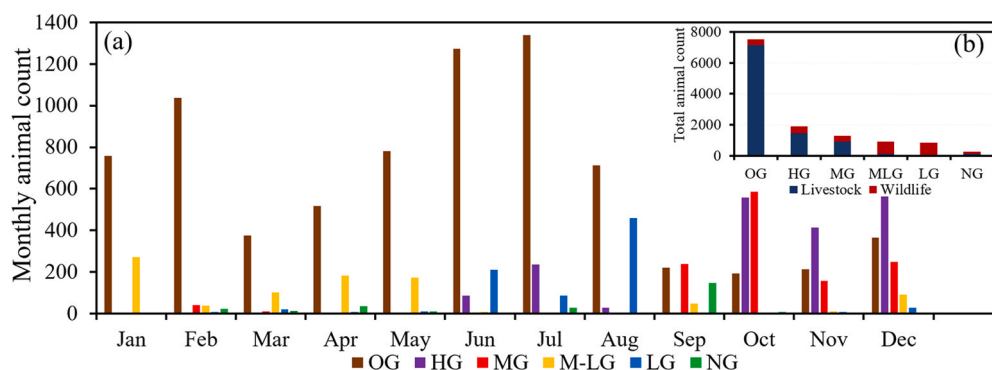
Fig. 5. Variation in (a) the total monthly animal count captured (intensity of use) at each site and (b) the total animal count (livestock and wildlife) at each site (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) over the study periods.
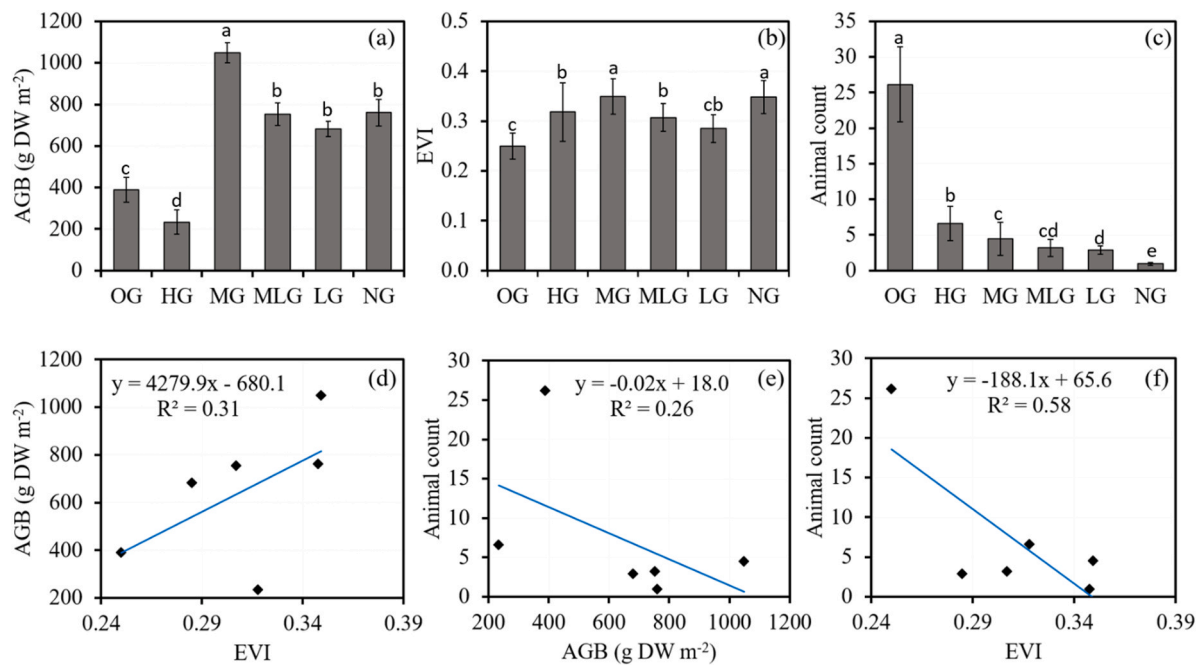
Fig. 6. Variation in the mean (a) herbaceous aboveground biomass (AGB in g DW m^{-2}), (b) enhanced vegetation index (EVI), and (c) animal count between the sites differing in grazing intensity (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) across the study period. The relationship between (d) AGB and the EVI, and between the mean animal count and (e) AGB and (f) the EVI. The solid line is the linear regression line.

Table 5
Results of generalized linear mixed model (GLMM) showing effect estimate of the EVI on mean soil CO_2 flux (R_S) with the grazing sites as random factor.

Predictors	Estimates	Std. Error	t value	p value	Significance
Intercept	2.926	0.169	17.59	< 2e-16	***
EVI	4.501	0.532	11.42	< 2e-16	***
Random effects		Grazing sites	Coefficient	Variance	Std. Dev
		OG	2.89	0.029	0.169
		HG	3.06		
		MG	3.05		
		M-LG	2.83		
		LG	2.97		
		NG	2.59		
Grazing sites (Intercept)				0.029	0.169
Residual				0.283	0.532

AIC 2377, R^2 = 0.60, Significance code: p < 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***.

4. Discussion

In southern Kenya, we studied soil CO_2 flux (R_S) at five grassland sites under different levels of grazing and one enclosed control area. Overall, R_S values from all grazing sites were ranging from 10 to 356 mg C m^{-2} h^{-1}. These results are within the range of previous studies in the same region (Wachiye et al., 2020, 2021) and from other land use types in tropical savanna ecosystems similar to our study (Ardö

et al., 2008; Livesley et al., 2011). Low R_S values from tropical savanna ecosystems have often been related to a low SOC (Grace et al., 2006; Scholes et al., 1997), as observed in this study (Table 6).

4.1. Effects of grazing intensity on vegetation, soil and soil respiration

Grazing can alter vegetation cover and biomass, specifically grass cover, and soil properties, depending on the intensity of grazing and management practices, which in turn can affect on R_S (Cao et al., 2004; QingJi et al., 2009; Wang et al., 2016). Few data are available for a detailed comparison of R_S under different levels of grazing in East Africa (Oduor et al., 2018). In this study, difference in grazing sites were significant in explaining 60% of the spatial variation in R_S. Generally, R_S were significantly lower in heavier grazed OG than the less grazed sites (HG, MG, M-LG and LG), which agrees with previous similar studies in other savannas in Kenya (Oduor et al., 2018; Ondier et al., 2020), and also studies by Cao et al. (2004) and Abagandura et al. (2019). In their study, the authors attributed this to the lower SOC at intensively grazed sites, and we also found a significantly lower (p = 0.02) SOC at the OG in comparison to the less grazed sites (Table 6).

In the OG, vegetation cover was lowest on average (based on EVI, which is a proxy for vegetation cover), and increased to MG dropped in M-LG and LG, suggesting that heavy grazing greatly reduced aboveground vegetation. Mean AGB was also lowest at OG and higher at less grazed sites (Fig. 6a). This was supported by a negative relationship

Table 6
Soil characteristics at different grazing intensities (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) at 20 cm soil depth (mean ± standard error). (n = 5).

GI	TN	SOC	Bulk density (g/cm^3)	pH	% Sand	% Silt	% Clay
OG	0.1 ± 0.1	1.2 ± 0.3	1.22 ± 1.2	6.5 ± 0.2	63.5 ± 0.2	4.4 ± 0.4	31.5 ± 0.2
HG	0.2 ± 0.1	2.7 ± 1.2	1.01 ± 0.1	5.8 ± 0.2	60.5 ± 1.4	7.9 ± 0.5	31.6 ± 0.9
MG	0.2 ± 0.1	1.9 ± 0.7	0.99 ± 0.6	6.6 ± 0.2	67.5 ± 0.3	4.7 ± 0.3	27.5 ± 0.3
M-LG	0.2 ± 0.1	2.8 ± 1.1	0.97 ± 0.1	5.8 ± 0.6	68.5 ± 0.5	5.3 ± 0.0	26.3 ± 0.5
LG	0.2 ± 0.1	2.3 ± 0.8	0.96 ± 0.2	6.2 ± 0.9	71.6 ± 0.5	2.0 ± 0.6	26.4 ± 0.2
NG	0.3 ± 0.1	4.9 ± 1.6	0.94 ± 0.5	6.6 ± 1.1	75.8 ± 0.5	3.3 ± 0.0	20.9 ± 0.7

observed between the number of animal counts and the EVI and AGB (Fig. 6e & f). Therefore, observed lower R_S in OG could be a result of reduced above- and below-ground biomass and subsequent litter deposition, which reduces the supply of substrates for decomposition thus lowering SOC (Cao et al., 2004). In addition, a lower degree of vegetation cover in OG could reduce root biomass thus lower root respiration, as well as root exudation (an important source of carbon and energy for soil microorganisms) and hence reduce R_S (Li et al., 2018).

In the private wildlife sanctuary THWS hosting M-LG and LG, the intensity of grazing is low, since only wild mammals are allowed to graze and browse, causing less damage to the vegetation cover and biomass compared to that LUMO community grazing area (OG, HG and MG), which is frequented by both livestock and wildlife (Fig. 5b; Table A1). Comparatively to THWS sites, OG and HG wildlife cameras captured large herds during study period (Fig. 5b; Table A1). OG and HG also had large patches of bare soil, which indicated heavy grazing. However, the number of animals captured at the LG site was lower than at MG (Table A1) but LG displayed a lower EVI and R_S than MG (Fig. 6b). We noted that most of the animals at LG were buffalos (*Syncerus caffer*), which might have caused more destruction on the grass cover through trampling than other animal species at the other sites. A previous study also showed that megaherbivores, such as elephants and buffalos were the cause of damage on woody biomass in THWS (Amara et al., 2020).

Heavy grazing can shift plant species composition by replacing highly palatable grass species with undesirable plants (Klumpp et al., 2009). This might be the case at OG, where Sodom apple (*Solanum incanum* L) plants are densely spread throughout the site. Although native to East Africa, Sodom apple is considered among the 100 worst invasive plants in the region (Pringle et al., 1785). At HG, we observed *Indigofera tinctoria*, which was extremely dense, especially during the wet season. As a species that is undesired by cattle, it displayed a high EVI at this site between January and May (Fig. A2). This shift in plant species can affect the soil organic matter and root biomass (Klumpp et al., 2009), and may also respond differently to the onset of the rainy season compared to grasses that are known to respond quickly than shrubs (Merbold et al., 2009), thus affecting overall R_S.

Regarding the effect of dung and urine deposition on R_S, we cannot draw any conclusions, since animal excreta were not visible in any of our chambers during the measurement of R_S. In addition, soil pH and TN did not differ significantly between the sites. Nonetheless, BD was higher at OG and dropped with decreased grazing, thus providing an additional explanation for the lower R_S at OG (Bahn et al., 2008; Cao et al., 2004). Increased grazing increases BD through animal trampling, thus reducing water infiltration and gas diffusion in and out of the soil (Jafari et al., 2014; Li et al., 2008; du Toit et al., 2009; Oduor et al., 2018). This in turn reduces the diffusion of R_S in soil, resulting in a lower mean R_S at the OG site compared to the other grazed sites (Cao et al., 2004).

With grazing and browsing prevented due to animal exclusion by fencing, NG showed signs of recovery of the degraded grazing land, since this site had a higher cover of shrubs and small trees compared to the other sites (mean EVI was the highest in NG). The forest restoration enclosure was established in 2010 in a similar landscape to the M-LG site. Although cattle intruded into NG in September, this was not enough to cause a notable change in EVI, since the disturbance only lasted for a few days.

Site NG recorded the lowest R_S, which was opposite to our expectations and contradicts several earlier studies that have reported higher R_S values at ungrazed sites (Oduor et al., 2018; Jia et al., 2006). According to these studies, higher R_S at ungrazed sites was explained by higher vegetation cover, biomass, W_S and SOC, and reduced BD (Yan et al., 2015; Wang et al., 2016), which was also true in this study, however, due to the resultant shading, there was less herbaceous understorey compared to the other sites. Shading might have interfered with the growth and regrowth of herbaceous vegetation below the canopies, and therefore, there is a likelihood that root production in the other open grazed areas was higher (Janssens et al., 2001), although we

cannot confirm this since we did not measure root biomass. Additionally, due to the higher trees and shrubs canopy coverage, the NG site also recorded the lowest soil and surface temperatures overall (Fig. 3d & Fig. A1). Hence, while W_S was adequate to support biological activity, T_S became an important determinant of R_S (Carbone et al., 2011).

After the wildfire on 8–9 August at the HG, vegetation and animal use remained low during September and October but increased once the rainy season began in November (Fig. 5a). Burning releases most carbon, destroys aboveground vegetation, thus affecting carbon allocation and root respiration. Previous studies reported lower R_S values in burned areas a few weeks after fire events in Congo (Castaldi et al., 2010), Ethiopia (Andersson et al., 2004; Michelsen et al., 2004) and Brazil (Poth et al., 1995). In the present study, we did not detect any effects of the wildfire on R_S, even after the onset of the rainy season. This agrees with studies carried out in Nigeria (Adedeji, 1983) and South Africa (Zepp et al., 1996). Since the fire occurred in the dry season, most grasses were dry and W_S was already very low (below 10%), which may have overridden any effects of the fire on R_S.

4.1.1. Temporal variation in soil respiration

Temporal variation in R_S at all sites showed a clear bimodal pattern that mirrored the variation in W_S and rainfall over the year. The highest R_S values were observed during the two rainy seasons (LWS and SWS), and also in the expected short dry season (SDS) due to sporadic rainfall that occurred in January, which resulted in relatively high W_S at all sites. The lowest R_S was observed in the long dry seasons (LDS) when W_S was the lowest at all sites. Overall, W_S explained about 71% (Fig. 4; $p < 0.05$) of the seasonal variation in R_S, which is within the range of previous reports (Frank et al., 2002; Wachiye et al., 2020). Other African savannas have also reported higher R_S results during rainy seasons due to an increase in W_S (Castaldi et al., 2010; Livesley et al., 2011; Wachiye et al., 2020; Pinto et al., 2002). An increase in W_S increases microbial activity, which speeds up the decomposition of soil organic matter and stimulates plant and root growth, thus increasing root respiration (Carbone et al., 2011; Orchard and Cook, 1983). On the other hand, T_S showed no significant influence on seasonal variation in R_S due to its narrow temporal variation, and the same result has been observed in other studies of savannahs (Castaldi et al., 2006; Grover et al., 2012; Livesley et al., 2011; Wachiye et al., 2020).

Furthermore, higher EVI values were observed during the rainy seasons at all sites, indicating a greater amount of vegetation and thus more root respiration since grasses sprout more rapidly with the first rains (Merbold et al., 2009). Results from the GLMM model revealed a positive relationship (ca. 60%; $p < 0.05$; Fig. 4b) between R_S and the EVI at all sites. The inclusion of W_S in the model further improved the relationship, explaining 76% of the variation in R_S. According to these findings, seasonal variation in R_S was therefore strongly dependent on the vegetation status and W_S at high grazing intensity sites, as well as over a broader area.

During the wet season, the differences in R_S between the sites HG, MG, M-LG and LG due to grazing were more apparent. Similarly, EVI significantly differed, with the lowest value at OG and values increasing as a function of decreasing grazing intensity. We assume that vegetation recovered more quickly in less grazed areas because the vegetation was not as heavily damaged by animals grazing and trampling as in heavily grazed areas. Moreover, OG and HG sites displayed more large patches of bare soil. Furthermore, in heavily grazed areas, the higher soil bulk density due to animal trampling, increased evaporation and soil erosion of nutrients lead to drier and nutrient-poor soils, which may limit plant establishment and growth (Belnap et al., 2009; Wang et al., 2016).

At OG, EVI increased at the onset of the rainy season in March but started to gradually decline as the number of animals started to increase from April onwards (Fig. 5a). While conducting gas sampling exercises during this period, we often encountered large herds of livestock. Large patches of bare soil were more visible throughout the overgrazed areas, especially in the dry season. According to the management of the LUMO

community grazing area, local herders not only bring their livestock there but also neighboring communities use the area for their livestock during the dry season. LUMO is a common location for herders to move their cattle to find better forage and water when they have exhausted forage on their land and have most of their land under crop production.

In the dry season, a drop in W_S causes senescence of the grass layer, which in turn reduces root respiration (Pinto et al., 2002). The drying of grasses and other plant tissues was evident in the progressive reduction in the EVI, as well as a decline in W_S and R_S. Reduced W_S can suppress root growth, as a decline in W_S affects the diffusion of organic C substrate, resulting in microbial stress and reduced plant growth (Li et al., 2018; Orchard and Cook, 1983).

Soil W_S was slightly higher at the NG in the dry season an indication that shading provided by shrubs and bushes allowed soils to cool, minimizing evaporation, as NG recorded the lowest T_S (Fig. 3e) and T_{Surf} (Fig. A1). During the latter months of the dry season in September and October, R_S was slightly highest in NG. At all grazing sites and even in NG, grass cover had dried out by this time, reducing R_S, but since the roots of shrubs and trees in NG are deeper than grass roots, they could tap into deeper soil moisture (Carbone et al., 2011). Microbial activity is highest and most variable in the upper soil layers, which are first wetted up and first to dry down, but deeper roots can access to water reserves in deeper soil, which takes longer to exhaust and therefore and so remain active during the dry season (Carbone et al., 2011).

5. Conclusion

This study examined soil carbon dioxide flux (R_S) under various grazing intensities in the savannah lowlands of southern Kenya. Overall, results indicated that R_S decreased with greater grazing intensity, because higher grazing intensity reduced vegetation cover, increased bulk density, and reduced herbaceous aboveground biomass, resulting in a lower R_S. Additionally, SOC was lower on highly grazed sites compared to less grazed sites, supporting these findings. The variations in volumetric soil water content (W_S) and vegetation cover (EVI) were prominent factors in explaining temporal variations in R_S during the study period. Results presented here could be integrated into the management of savannah grasslands in East Africa to identify the potentially adverse consequences of expanding livestock numbers and create climate-smart pastoral practices.

CRediT authorship contribution statement

SW: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Funding acquisition, Writing – review & editing. **PP**: Conceptualization, Writing – review & editing. **JR**: Writing – review & editing. **JH**: Formal analysis, Writing – review & editing. **SA**: Writing – review & editing. **LM**: Conceptualization, Data curation, Formal analysis, Writing – review & editing.

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.

Data availability

The data associated with the manuscript can be obtained from https://figshare.com/articles/dataset/Effects_of_livestock_and_wildlife_grazing_intensity_on_soil_carbon_dioxide_efflux_in_the_savanna_grassland_of_Kenya/14791380.

Appendices.

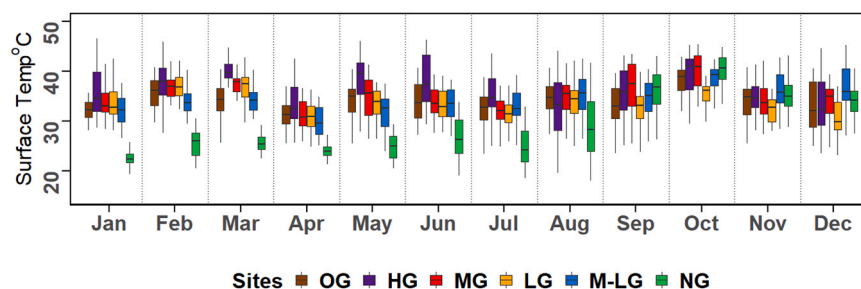See Figs. A1 and A2 and Tables A1 and A2.

Fig. A1. Variation in surface temperature (at < 1 cm above the soil surface) in each grazing site (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) from January to December 2020.
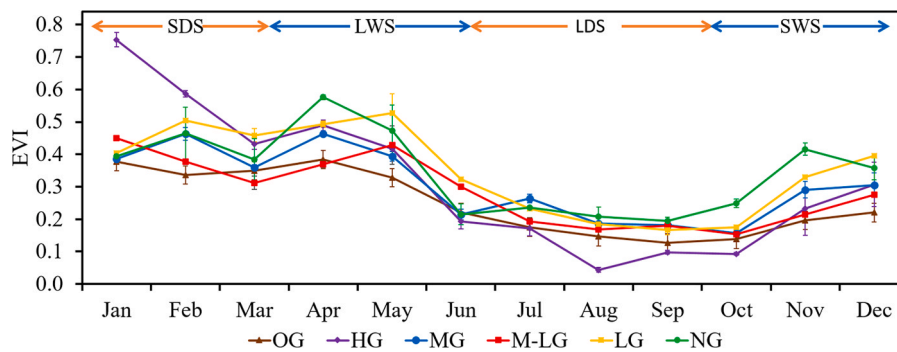
Fig. A2. Variation in EVI in each grazing sites (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) from January to December 2020.

Table A1

Intensity of animal use in relation to grazing intensity (OG - overgrazed, HG - heavily grazed, MG - moderately grazed, M-LG – moderately to lightly grazed, LG - lightly grazed and NG - no grazing) from January to December 2020 as captured by wildlife cameras.

Grazing intensity	Cattle	Sheep	Goats	Total livestock count	Zebra	Buffalos	Elephant	Other wildlife	Total wildlife count	Total animal count
OG	6062	217	876	7155	258	0	6	107	371	7532
HG	1451	5	2	1458	111	3	22	295	431	1889
MG	911	0	0	911	1	283	4	77	365	1287
M-LG	125	0	0	125	19	142	0	632	793	918
LG	0	0	0	0	25	714	5	89	833	833
NG	142	0	0	142	0	0	0	127	127	269
Total	8691	222	878	9791	414	1142	37	1327	2920	12,711

Table A2

Results of generalized linear mixed model (GLMM) showing effect estimate of the soil moisture on mean soil CO_2 flux (RS) with the grazing sites as random factor.

Predictors	Estimates	Std. Error	t value	p value	Significance
Intercept	2.874	0.153	18.801	< 2e-16	***
EVI	3.089	0.391	7.899	2.82e-15	***
Soil moisture	0.049	0.007	6.638	3.18e-11	***
Random effects		Variance	Std. Dev		
Grazing sites (Intercept)		0.018	0.135		
Residual		0.191	0.437		

AIC = 1288, R2 = 0.76, Significance code: p < 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***.

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