Interactive effects of livestock and trees on nutrients and herbaceous layer production in a humid Kenyan savanna

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Abstract: Savannas are key ecosystems that provide vital services such as fodder for wild and domestic animals, recreation, biodiversity habitats, CO_2 sequestration and timber. Their characteristics and distribution make them relatively susceptible to disturbances such as land-use and climate change. This study was carried out to monitor seasonal changes in soil moisture, soil and plant nutrients, and grass primary production as well as establish the impacts of grazers and *Acacia* trees on ecosystem processes in a humid tropical savanna. Soil moisture, soil and plant N/C content and grass biomass were monitored in grazed, non-grazed, under canopy and open locations. Soil moisture was monitored through core method, N and C concentrations (%) were determined by means of elementary analysis while biomass was assessed through harvest method. The results indicated an increase in above ground biomass with progression of wet season with peaks of 1757.63±46 and 1906.75±115 g/(m^2•a) recorded in grazed and non-grazed plots respectively. Understorey sites recorded significantly ($p<0.001$) higher peak aboveground biomass compared to open sites. Significantly higher soil and shoot N content, 0.35±0.1 and 0.93±0.28 %, respectively were observed in the understorey sites, while %C content declined with progress of wet season. In this humid ecosystem, grazers were responsible for keeping grasses low during the dry season; however, they had minimum influence on primary production during the growing season. *Acacia* species strongly influenced organic matter accumulation, soil moisture and biomass production under their canopies. The observed trends created a unique production mosaic of ecosystem function and productivity in the humid savanna. This ecosystem can therefore be a significant source and sink of both N and C with processes that control their emissions being complex and influenced by a variety of interrelated factors such as quality and rates of organic matter turn over. Therefore, processes in humid savannas are not a simple function of rainfall patterns or herbivory, but regulated by interactive effects of grazing and nutrients with trees acting as modifiers.

Keywords: Grazing, Understorey, Primary production, Nutrients, Ruma national park

1. Introduction

Savanna ecosystem is characterized by the co-existence of grasses and trees (Isichei, 1995; Chidumayo, 2001; Lloyd *et al.,* 2008; Kalwij *et al.,* 2010), a stable structure that is largely determined by facilitation, competition and disturbances (Okin, *et al.,* 2008). The contrasting plant life form of trees, shrubs and grasses, cover approximately an eighth of the global land surface

(Sankaran *et al.,* 2004; Otieno *et al*., 2005), which translates to 25% of terrestrial biomes and thus second to tropical forests in their contribution to terrestrial primary production. They support a considerable proportion of the world's human population and a majority of their rangeland and livestock (Sankaran *et al.,* 2004), as well as a continuous layer of drought resistant herbaceous plant and scattered woody species (Fitzgerald, 1973) due to their unique climate.

In Kenya, savanna occupies over one third of the total land area, dominating regions that are characterized by alternating humid and dry seasons and a stable, though considered pre-climax vegetation (Hubbell, 2001). Most of the Kenyan savanna experience warm continental climate, with unreliable precipitation ranging between 150 - 500 mm per annum (Otieno *et al*., 2005), and seasonal fluctuations. However, savannas found in the western part of the country, bordering the tropical rain forest, receive relatively high rainfall amounts that can reach 1500 mm per annum (Otieno *et al.,* 2010). The soil of the savanna is porous, with rapid drainage of water. It has only a thin layer of humus, which provides vegetation with nutrients.

A large number of wild herbivores are found in African savannas with major effects on ecosystem structure and functioning by influencing plant growth and development (Leriche *et al.,* 2003; Kalwij *et al.,* 2010). Herbivory of both wild and domestic ungulates induces changes in soil and vegetation, which in turn may promote or deter further foraging (Skarpe, 1991; Cech *et al*., 2010). Herbivores can control the ecosystem function through modification of feedbacks between dominant plant species and nutrient cycles (Cech *et al.,* 2008; Coetsee *et al.,* 2010), as well as increase tissue loss rates of plant species that tolerate herbivory but have nutrient rich tissues (Augustine and McNaughton, 2006; Cech *et al.,* 2008). Previous studies in semi arid savannas (Augustine and McNaughton, 2004, 2006), indicated that herbivores spatial pattern of habitat use for feeding and excretion affects nutrient distribution. However, domestic herbivores are less mobile than many wild species, which may impede large-scale selectivity when kept at low density. This conclusion is supported by the observed migratory behavior of ungulate species in the Serengeti (Tanzania) and Yellowstone (South Africa) National Parks in response to spatiotemporal gradients of plant productivity and nutrient content (Augustine and McNaughton, 2006).

Due to high organic matter accumulation and reduced evaporation under trees, rapid nutrient movement is anticipated under trees compared to open locations outside tree canopies (Bernhard and Poupon, 1980; Smith, 1999). Thus, compared to neighboring grasslands, soils under tree crowns (canopies) are likely to have higher concentrations of available N (nitrogen) and other important nutrients, higher biodiversity, and faster water infiltration (Belsky *et al.,* 1993). Savanna trees provide a browsing habitat for herbivores and fuel wood for human harvesting (Wang *et al.,* 2009b). They also ameliorate environmental stress under their canopies (Hussain *et al.,* 2009), which may stimulate primary production in the herbaceous layer.

It has been increasingly clear that there exist predictable, yet largely unresolved variations in nutrient balance in humid tropical savannas (Lalljee and Facknath, 2000). Since nutrients and soil water are important limiting factors on

primary production in this ecosystem (Isichei, 1995), a better understanding of ecosystem processes related to their availability may help in designing appropriate management policies that ensures ecosystem sustainability. Several studies have indicated that N nutrient is most often limited in the soil (Belsky *et al*., 1993; Wang *et al.,* 2009; Cech *et al.,* 2010), and thus necessitating clear understanding of its dynamics from grazer to plant, plant to soil and finally to the atmosphere. Recent studies have shown that N dynamics are initiated at the beginning of humid seasons when moisture availability stimulates bioactivity and release of nutrients from detritus as well as translocation of the organic carbon (C) from plant roots (Smith, 1999; Cech *et al.,* 2008; Cech *et al.,* 2010).

In most savannas, the major constraint on soil N availability is an increased leaching during rainfall periods (Cech *et al.,* 2008). However, other studies have shown that under increased temperature and carbon dioxide (CO_2) levels (Isichei, 1995), interactions between C and N dynamics have impacts on ecosystem function and C storage. Nitrous oxide (N_2O) in the atmosphere has been increasing at an average rate of 0.2 to 0.3 % per year (Watson *et al.,* 1990; Serca *et al.,* 1998), with major sources being land-use conversion and vegetation disturbances (Serca *et al.,* 1998; Otieno *et al.,* 2010). This is expected to impact negatively on global climate, resulting in water scarcity and even greater limitation to plant productivity across an increasing amount of land in the savanna. Therefore, an informed knowledge on the processes involved in input, losses and utilization of N through interacting components of this ecosystem will aid in sustainable management decisions.

In this paper, seasonal biomass and nutrient quantities are determined as driven by ungulates. A change in soil properties is also established through long term monitoring as well as the role of trees is defined. Further examination on the underlying mechanisms responsible for any observed changes were carried out by conducting experiments on the relationships among ecosystem components. We hypothesized that primary production in this ecosystem is controlled by soil moisture but accelerated by herbivory. Land use practices, such as increased grazing pressure have been associated with shifting savanna ecosystems from grass to woody plant domination (Archer, 1995), with other interacting factors that includes climate change (Otieno *et al.,* 2010). However, Aranibar *et al.* (2004) found that photosynthetic machinery in plants accounts for more than half of the N in the leaves. Therefore, knowledge of the N cycle in ecosystems is crucial for investigating the effects of global change on vegetation and C cycle since photosynthesis is strongly affected by N availability.

Due to their expansive nature, tropical savanna grasslands play an important role in the annual C balance (Hanan *et al.,* 1998; Ardö *et al.,* 2008), and hence providing a significantly larger photosynthetic surface compared to trees. At the moment, proper studies are scarce on this humid savanna (Muriuki *et al.,* 2003), but results presented by Otieno *et al.* (2010) seems to point out the mechanisms that concentrate nutrient flux at the soil-plant interface. However, the mechanism at soil-plant-herbivore interface has not been well documented and, therefore, the effects of manipulating the carrying

capacity on nutrients cannot be predicted.

2. Material and Methods

Study site

Lambwe valley, Ruma National Park, (00° 35'27.72" S & 34° 18'81.64" E) is located in Suba District, Nyanza Province, Kenya (Fig. 1). The altitude of the area is 1400 meters above sea level. The Park is situated about 10 km east of Lake Victoria in Western Kenya, southwest of Homa Bay town and east of Gembe and Gwasi Hills. The park (formerly Lambwe Valley National Reserve) was established in 1966 but its isolation, and consequent lack of income, ensured a very slow pace of development. With its elevation into a National Park since 1983, game viewing tracks and general Park maintenance have been established.

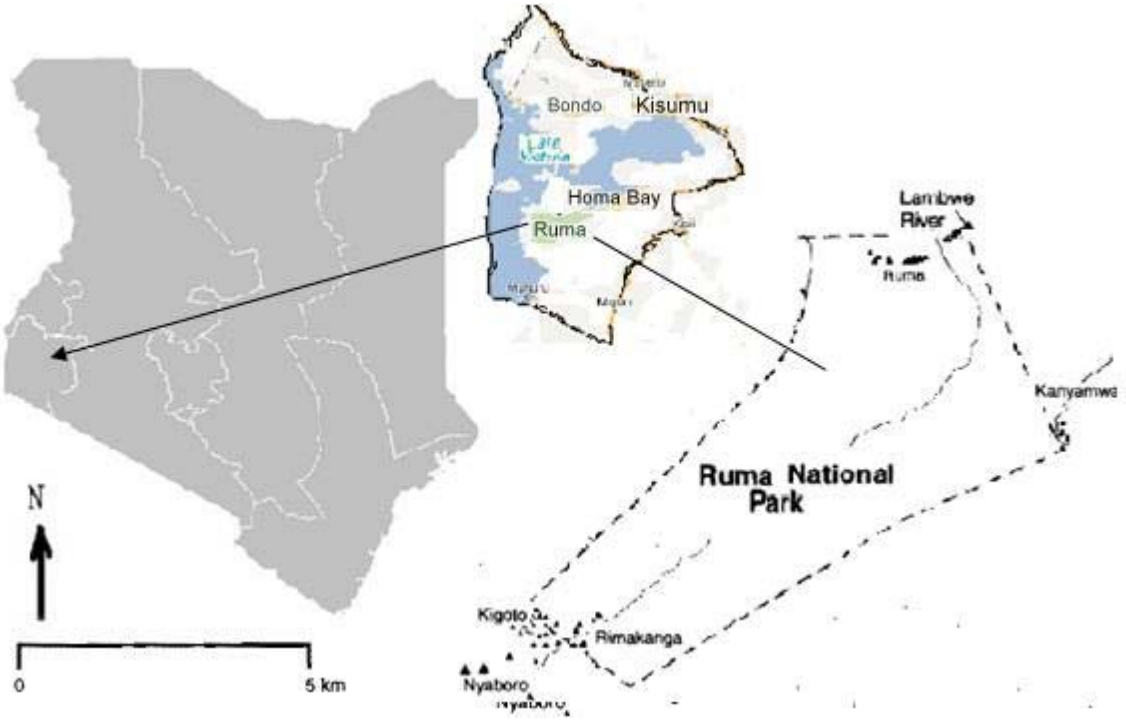

Figure 1 Map showing the study site at Ruma National Park, (00° 35'27.72" S & 34° 18'81.64" E).

The terrain is mainly rolling grassland, with tracts of open woodland and thickets dominated by species of *Acacia, Rhus* and *Balanites* (Table 1). Located just south of the equator and adjacent to Lake Victoria, the area experiences a warm and humid climate, and is classified as sub-humid to semi-arid (Muriuki *et al.,* 2005). The recorded metrological variables are presented in figure 2. Soils are largely "black cotton" clays corresponding to Vertisols according to WRB soil classification. The area around the park is settled with a mix of small-scale cultivation and grassy pastureland. Main grazing animal populations within the Park consist of roan antelope (*Hippotragus equinus*) and Jackson's hartebeest (*Alcelaphus buselaphus*), a larger and redder species than Coke's which is found in most Kenya parks, Oribi (*Ourebia ourebi*), one of the smallest of the antelope family and

Rothschild giraffes (*Giraffa camelopardalis rothschildi*). The park has a perimeter fence around it, which keeps the game animals within. Included within the park but separated by the perimeter fence is a section owned by the Kenya National Youth Service (NYS), which acts as a youth training camp. Our experimental plots were located within the NYS section of the Park, which was grazed mainly by domestic animals; the Zebu (*Bos Indicus*) cattle consisted of drought resistant Sahiwal and Boran breeds.

Table 1 List of plant species growing in the different locations categorized according to the physical feature or land use practice. Vegetation sampling was conducted during the month of March 2008.

Grazed	Fenced		Acacia understory
Acacia ancistroclada	*Acacia ancistroclada*	*Leucas calostachyus*	*Acacia ancistroclada*
Aspilia asperifolia	*Acacia gerarrdii*	*Nuxia congesta*	*Albizia coriaria*
Balanites aegyptica	*Acmella calirrhiza*	*Panicum maximum*	*Aspilia asperifolia*
Conyza floribunda	*Albizia coriaria*	*Pilliostigma thonningii*	*Balanites aegyptica*
Eragrostis atrovirens	*Aspilia asperifolia*	*Pseudathria hookeri*	*Berkeya spekeana*
Kyllinga bulbosa	*Balanites aegyptica*	*Psidium guajava*	*Cordia ovalia*
Panicum maximum	*Berkeya spekeana*	*Rhus natalensis*	*Leucas calostachyus*
Pseudathria hookeria	*Commiphora myrrha*	*Rhus vulgaris*	*Panicum maximum*
Psidium guajava	*Conyza floribunda*	*Solanum incanum*	*Rhus vulgaris*
Striga asiatica	*Cordia ovalis*	*Steganotaenia araliacea*	*Themeda triandra*
Themeda triandra	*Crotalaria pallida*	*Themeda triandra*	*Urena lobata*
	Dyschoriste radicans	*Tithonia diversifolia*	
	Hyparrhenia hirta	*Lantana camara*	
	Indigofera arrecta	*Lantana trifoliate*	

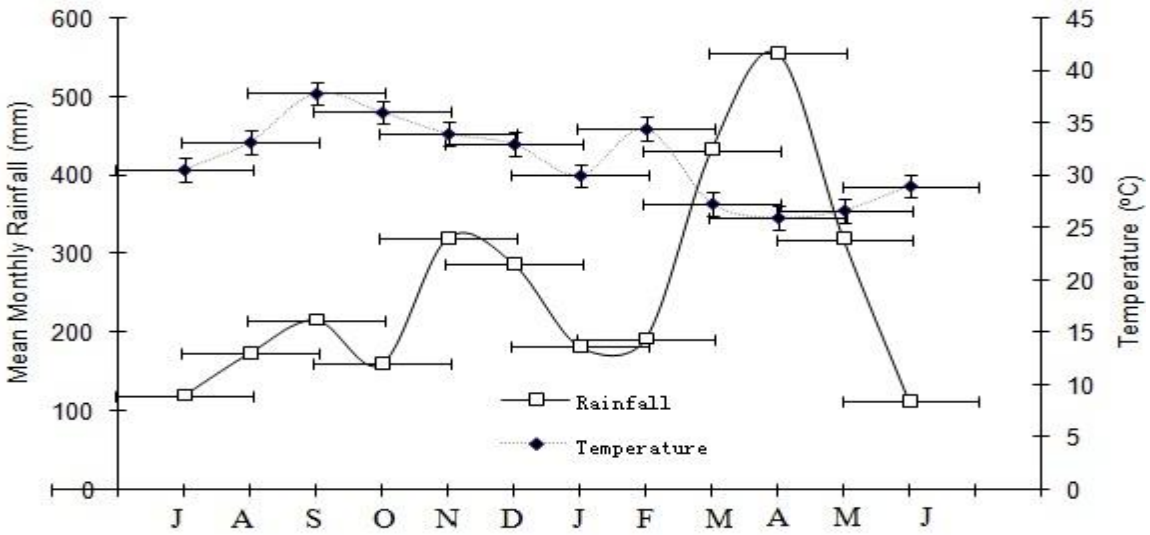

Figure 2 Rainfall and temperature during the growing season of 2007, 2008. Horizontal and vertical bars represent SE.

Experimental design

Experimentation at this site has been going on since 2006. We report here the results of an intensive study carried out between November 2007 and July 2008. Two plots measuring 50 × 50 m were established within *Acacia* woodlands. One plot was enclosed using a 2 m high fence (to exclude grazing), and the other plot was left open to grazing and was strategically located at the intensively grazed site. The animals passed over this area at least 2-3 times a week, with the intensity of grazing increasing during the dry season, when grass was limited elsewhere. They could spend approximately 10-20 minutes feeding on the same area and moving on to other locations since the grazing area was expansive. Within the plot, (grazed and fenced), we randomly established ten (10) 3 × 3 m measurement units, i.e., (5 units) under canopy and (5 units) in open grassland.

Measurements

Weather conditions were continuously recorded at a mini-meteorological station set up at the field site. Air temperature (T_{air}) and humidity (Fischer 431402 sensor, K. Fischer GmbH, Drebach, Germany) data were measured every 5 min, averaged and logged every half-an-hour by data logger (DL2e, Delta-T Devices Ltd. Cambridge UK). In addition, temperature (T_{air}) above grass height (Digital thermometer, Conrad, Hirschau, Germany) and soil temperature (T_{soil}) at 10 cm depth (Einstichthermometer, Conrad, Hirschau, Germany) data were recorded every 15 seconds.

Soil water content

Soil samples were collected with a 3 cm diameter core sampler at the middle of the collars down to 30 cm and the soil cores divided into three layers from 0-10, 10-20 and 20-30 cm from fenced and grazed site. This was done on a monthly basis where two replicates from each collar per sampling date and hence ten replicates in total from each location (open and under canopy) in both grazed and fenced plots. Each sample (layer) was immediately weighed to determine its fresh weight before oven drying at 105ºC for 48 hours and determining the dry weight. Gravimetric soil moisture content was determined as the relative change between fresh weight and the weight difference between the fresh and dry soils as follows:

$$SMC = \left[\frac{(Weig\ ht\ of\ wet\ soil) - (weig\ ht\ of\ dry\ soil)}{(weig\ ht\ of\ dry\ soil)}\right] \times 100\%$$

(1) Bulk density, Plant and Soil N

The second soil sampling was done at the middle of the collars located in both grazed and fenced plots, down to 30 cm and the soil cores divided into three parts from 0-10, 10-20 and 20-30 cm. In each plot, 10 samples were collected; 5 samples under canopy and 5 samples from open sites per sampling date. These set of samples were used for the determination of N content where soil and plant samples were dried and homogenized in a ball mill. The homogenized samples were re-dried in a desiccator to eliminate all the water. A portion of the dried samples, 4–5 and 15–100 mg of plant and soil samples, respectively were analyzed to determine their N and C concentrations (%) by means of elementary analysis (Markert, 1996). Total N content was determined from the total weight of the aboveground biomass and expressed as $g.m^{-2}$. Similarly, total root N content was calculated from the total weight of belowground biomass. A similar

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procedure was followed to determine the total N content (%) in soil. Bulk density was determined by core method where a fixed volume of soil samples from different depths were weighed after drying at 100ºC.

Biomass measurements

Collars measuring 38 × 38 cm were used to demarcate aboveground grass biomass for harvesting every month in each measurement unit. Each month, five replicate collars were sampled from open and under canopy locations in both grazed and fenced plots. The harvested biomass was sorted into green and dead material before oven drying at 80°C for 48 hours and weighing by use of an electronic weighing balance (Denver Instrument Model XL-3100D). Root biomass was sampled with an 8 cm diameter soil cores down to 30 cm, from the same plots after removal of the aboveground biomass. The sampled soil cores were separated into three different layers (0–10, 10–20 and 20–30 cm). Roots from each of the layers were carefully removed from the soil and washed under running tap water using micro-pore (<2 mm) soil sieves. The sieved samples were then oven-dried at 80 °C for 48 h before determining dry weights. Due to difficulty in separating dead and live biomass, the reported results include profile averages for combined dead and live biomass.

Data Analysis

A one way ANOVA was applied to compare differences between means in nutrients, biomass and water content with treatments (plots) as the fixed effects using statistical software SPSS (SPSS 15.0 for Windows, SPSS Inc., Chicago, USA). In case of significant effects, means were compared using least significant difference (LSD) (as described by Little and Hill, 1978) with significance level set at $P \leq 0.05$. Best fits for nutrients, biomass and moisture response curves for grazed and fenced locations were performed using Sigma Plot version 8.0.

3 Results and Discussions

Climate and Soil Properties

The region had a bimodal rainfall pattern with long rains from March to June and short rains in November and December. April was a comparatively wet month with an average monthly rainfall of >500mm while February was the driest month (Fig. 2). Mean monthly temperatures ranged between 38^{o}C and 23^{o}C with lowest temperatures recorded during the wet season. Soil moisture increased with progression of the wet season in all sites, with grazed sites recording higher values compared to fenced sites (Table 2, Fig. 3). Understorey had significantly higher soil moisture 23.83±2.0% compared to open sites 16.79±2.5%. In grazed plot, soil moisture increased with increase in depth during the wet season, however, there was no clearly defined trend in fenced plot (Fig. 3). During the long rain, an increase in soil moisture led to an initial increase in soil N content with highest soil N content 0.32±0.07 recorded between the months of April and May (Fig. 4). In understorey soils, significantly higher N content was exhibited than open locations when data was pooled together, but declined in June and July. However, there was a spiked increase in soil N at the beginning of wet season which later declined with progression of wet season. Soil N at fenced plots was significantly higher than grazed plots during the study

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period except in the month of February. In open grassland sites, there was a uniform increase in soil N throughout the study period.

Table 2 Summary of results of different parameters measured in the different locations/treatments. ± 1 standard deviation from the mean.

	Grazed	Nongrazed	Understorey (Acacia)	Open	No. of replicates	*P*
SWC (%)	*25.61±2.2*	*28.44±2.5*	*23.83±2.0*	*16.79±2.5*	*40*	*<0.001*
Bulk Density (g cm^{-3})	*1.19±0.08*	*1.08±0.05*	*1.54±0.01*	*0.73±0.02*	*6*	*<0.001*
Soil N (%)	*0.22±0.01*	*0.32±0.07*	*0.35±0.1*	*0.15±0.1*	*40*	*<0.001*
Soil pH.	*6.4±0.10*	*6.4±0.15*	*6.5±0.31*		*40*	*=0.014*
Plant N %	*0.44±0.01*	*0.55±0.11*	*0.93±0.28*	*0.41±0.01*	*48*	*<0.001*
Total N content g m^{-2} yr^{-1}	*757.15*	*661.49*	*769.36*	*210.82*	*Biomass* %N*	
Soil C (%)	*3.40±0.2*	*4.84±1.5*	*4.90±0.7*	*2.54±0.20*	*40*	*<0.002*
C: N ratio	*45: 1*	*35:1*	*-*	*-*	*=18*	
Peak aboveground biomass g/(m^2•a)	*1757.81±46*	*1906.75 ±115*	*1137.5 ±25*	*815.625±31*	*40*	*<0.001*
Peak belowground biomass g/(m^2•a)	*862.5±12*	*787.5±53*	*687.05±15*	*334.38±1*	*36*	*<0.001*
Dead biomass g/(m^2•a)	*-*	*-*	*195±39*	*181.25±02*	*<12*	*<0.001*

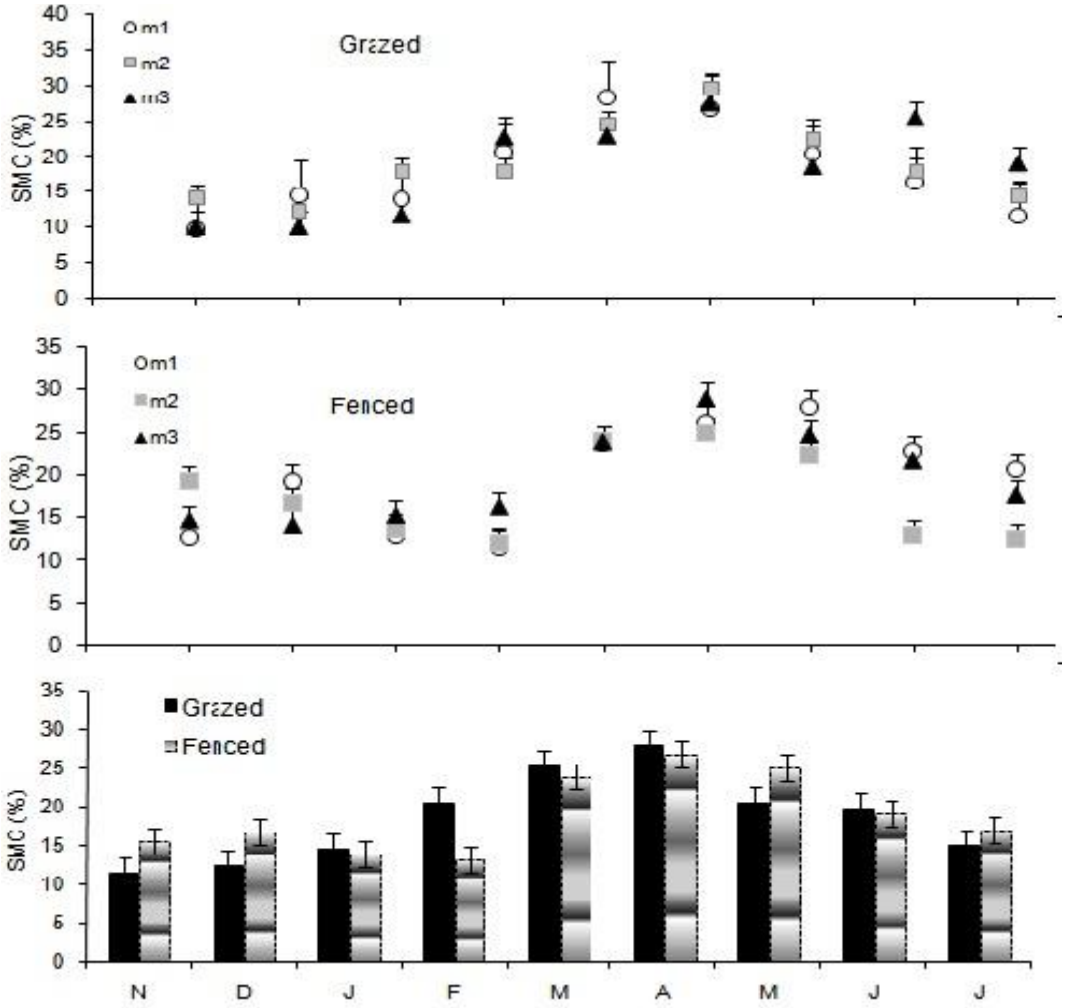

Figure 3 Seasonal Soil Water Content (%) between November 2007 and July 2008 in grazed and fenced sites; m1 (0-10cm depth), m2 (10-20cm depth) and m3 (20-30cm depth). Error bars show ±1 SE based on months variations.

There were seasonal differences in soil C content with lower values recorded during the dry season as well as site differences with grazed plots recording lower values (3.40±0.2%) than fenced plots (data not shown). Understorey sites had significantly higher soil C (4.90±0.7%) compared to open sites (2.54±0.20%) (Table 2). Bulk density was significantly higher at understorey sites (1.54±0.01 gcm^{-3}) compared to open sites (0.73±0.02 gcm^{-3}) (Table 2). Despite the noted differences in bulk density between surface and deeper soils in fenced plots, no significant differences were vivid between grazed and fenced plots..

Plant nutrients

Foliar N content was significantly ($p<0.001$) higher in the grazed plot than fenced plot throughout the growing season (Fig. 5) with values of (0.55±0.11%) and (0.44±0.0%), respectively. Foliar C increased in the fenced site with the progress of the wet season. Equilibrium was attained in the month of April, coinciding with the highest rainfall month. Foliar C/N ratios between plots had a unique trend with 54:1 and 36:1 occurring in the grazed

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and fenced plots, respectively (Table 2). Site differences may have been caused by different biomass developmental stages where most leaves were newly formed after tiller removal by herbivores and hence the high C/N ratio.

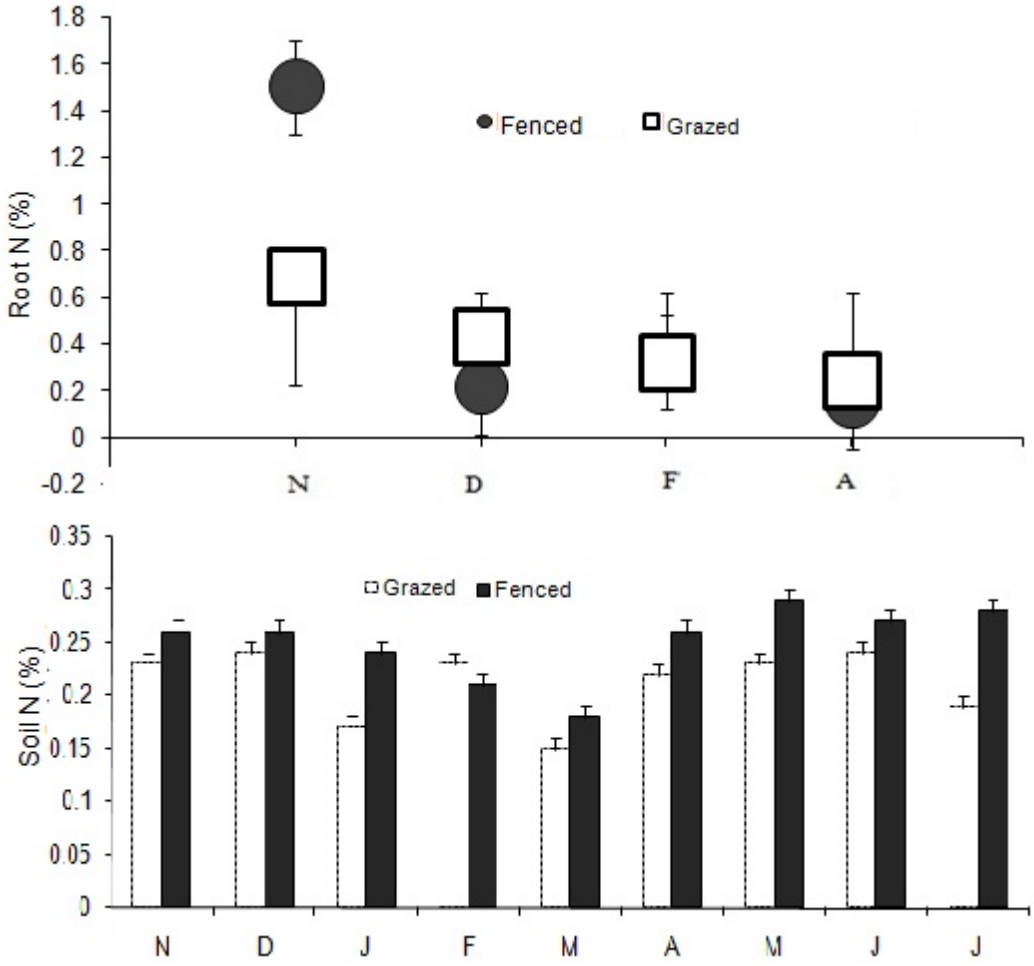

Figure 4 Soil Nitrogen content at understorey vs open sites and grazed vs fenced sites. Error bars show ±1 SE based on months variations.

Root N content in the non-grazed plot was higher than in the grazed plot during the dry season with values ranging between 0.2 to 1.5%, while there was a steady decline from November to April in the grazed plot (Fig. 4). When root C was assessed during the wet and dry seasons, fenced sites had higher content than the grazed sites. Variability of C and N content across sites and profile depths probably reflected the intensity of leaching of manure and urine input from herbivores and organic matter thus leading to lower soil ionic strength.