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The effects of herbivory and nutrients on plant biomass and carbon storage in Vertisols of an East African savanna

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ABSTRACT

Herbivory and nutrients are major ecosystem drivers in African tropical savanna. Although previous studies have determined the influence of herbivory on carbon storage in savanna ecosystems, little is known about the interactive effects of nutrients and herbivory. We determined the effects of long term grazing and short-term factorial nitrogen (N) and phosphorus (P) additions on aboveground biomass, soil organic matter (SOM) content, and plant nutrient storage. Grazing reduced aboveground biomass, foliar P and N stocks by 45%, 38% and 45%, respectively, compared to ungrazed plots, although the foliar P concentration was 20% greater in grazed plots. There was no significant increase in the aboveground biomass after nutrient addition despite increases in foliar N and P concentrations, suggesting that productivity was limited by a different resource (e.g., moisture). There were no significant interactions between nutrient enrichment and grazing. We conclude that grazing reduced aboveground biomass, but improved grass quality through increased foliar P concentration.

1. Introduction

Herbivory and soil nutrients are among the major determinants of tropical savanna function, influencing both plant primary productivity and carbon storage. Nitrogen (N) and phosphorus (P) can limit plant primary productivity in tropical savanna (Augustine et al., 2003; Thornley et al., 1991). The limitation to plant productivity by a specific nutrient is diagnosed when the addition of the given nutrient results in an increase in net primary production (Lebauer and Treseder, 2008). The nutrient limitation on plant production can also impact the herbivore production, as it has been observed that some grazers exhibit N and P deficiency in their diet (Ngatia et al. unpublished data).

Large mammalian herbivores could have positive, neutral or negative effects on annual net aboveground plant production in different ecosystems, depending in part on their direct effects on the availability of key nutrients (Bagchi and Ritchie, 2010). Previous studies have indicated that grazing increases primary productivity in some tropical areas (Pandey and Singh, 1992) while decreasing it in others (Wilsey et al., 2002). Similar findings were reported in temperate grasslands, with reports of grazing leading to decreases (Coughenour, 1991; Pucheta et al., 1998; Singer and Schoenecker, 2003) and increases (Coughenour, 1991; Frank and McNaughton, 1993; Pandey and Singh, 1992) in productivity. Holland et al. (1992) argued that the capacity of herbivores to increase primary production is due to increased nutrient turnover rates. However, the mechanisms/factors resulting to such contrasting findings are not yet clear.

In natural grasslands, productivity and soil fertility are mainly maintained by recycling of nutrients through plant litter decomposition and herbivore fecal matter (Grant et al., 1995). Nutrient limitation to plant productivity varies spatially across the African savanna. Foliar N:P ratios have been widely used as an indicator of nutrient limitation, whereby an N:P ratio >16 indicates P limitation to plant growth, <14 indicates N limitation, and ratios between 14 and 16 suggest that plant growth can be co-limited by N and P (Gusewell, 2004; Koerselman and Meuleman, 1996). Previous studies reported contrasting results on nutrient limitation to plant productivity. Ludwig et al. (2001) reported N limitation under open canopy and P limitation under sub-canopy. Ries and Shugart (2008) indicated N and P co-limitation, while

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O'Halloran et al. (2010) found luxury nutrient uptake. This indicates that N and P limitation to plant productivity in savanna is case specific and there is need for more studies in order to have a better understanding of nutrient limitation to plant production that would inform the management practices.

Although rainfall is a key determinant of productivity in African savanna (Sankaran et al., 2005) there is much less known about nutrients and grazing. Previous studies have focused on nutrients (Ludwig et al., 2001; Ries and Shugart, 2008) or herbivory (Grace et al., 2006) separately as major factors influencing plant productivity and C storage, but few studies have considered the interactions of the two factors in East African savanna. Considering the projected increases in atmospheric CO_2 (Stokes et al., 2005), increasing herbivores populations especially domestic animals and some wild animals (Kinnaird et al., 2010; Thornton, 2010) and soil nutrient limitation to plant production in the savanna (Augustine et al., 2003), it is important to consider the effects of nutrient availability and herbivory on plant quality, production and C storage.

The objectives of this study were to: (1) determine the effects of long term grazing on the grass aboveground biomass, soil C and nutrient storage, and (2) to determine how N and P enrichment affect grass aboveground primary production, biomass and soil nutrient storage and (3) examine the interactive effects of herbivory and nutrient enrichment between grazed and ungrazed ecosystems. We hypothesized that: (1) grazing reduces grass C and nutrient storage but increases soil organic matter (SOM) and soil nutrients, (2) grazing improves grass quality by increased foliar N and P due to herbivory accelerating nutrient cycling and stimulating new shoots regrowth and (3) N and P enrichment favors grass productivity in the non-grazed plots compared to grazed plots, because natural nutrient cycling has been facilitated through fecal matter deposition in grazed plots.

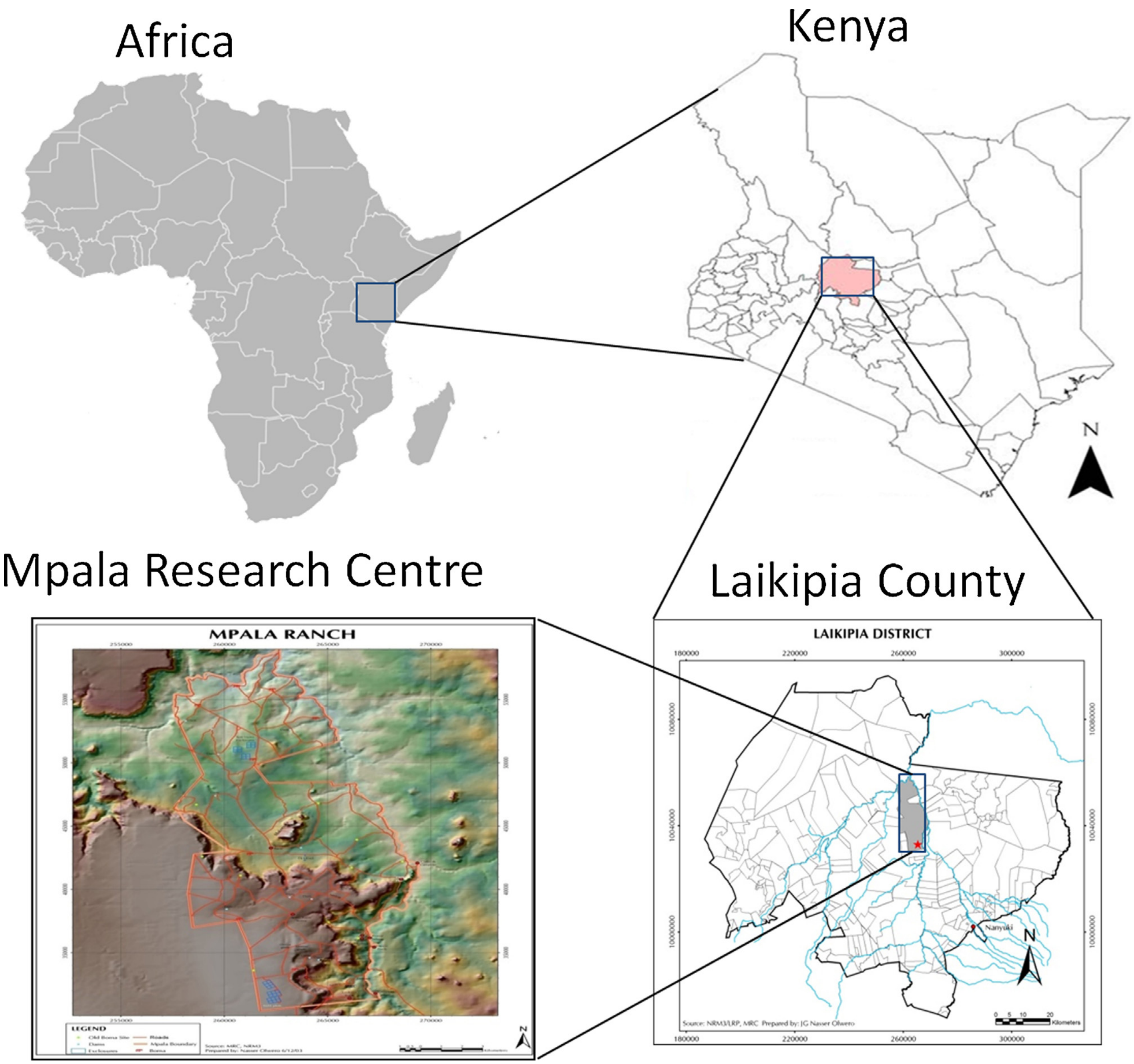

Fig. 1. Study site.
Maps source. Africa map; adapted and modified from Boone et al. (2005). Quantifying declines in livestock due to land subdivision (Page 525, Fig. 1). Rangeland Ecology and Management Journal publication. Kenya map; adapted from Graham, (2006). PhD dissertation, (page 8, Figs. 1 and 2). King's College, University of Cambridge. Laikipia district and Mpala Research Centre maps are unpublished maps from Mpala Research Centre.

2. Materials and methods

2.1. Study site

Mpala Research Centre and Conservancy is located in a semi-arid tropical savanna in Laikipia County, Kenya (37°E, 0°N; 1800 m elevation) and is associated with Mpala ranch covering 190 km^2 (Fig. 1) (Augustine and McNaughton, 2004). The mean annual rainfall is ~~550 mm at the study site (Veblen, 2012). Mpala Research Centre is managed for both livestock production and wildlife conservation. Some of the resident wild large herbivores include elephants (*Loxodonta africana*), hartebeests (*Alcelaphus buselaphus*), giraffes (*Giraffa camelopardalis*), buffaloes (*Syncerus caffer*), Grant's gazelles (*Gazella grantii*), zebras (*Equus burchelli*), impalas (*Aepyceros melampus*) and elands (*Taurotragus oryx*) (Young et al., 1998). The livestock herbivores are mainly cattle (*Bos taurus*) and camels (*Camelus dromedaries*).

The study site is underlain by (black cotton soils) with a pH-H_2O of 6.2 before nutrient enrichment and bulk density of 1 $g\,cm^{-3}$. Vertisols cover approximately 43% of the Laikipia ecosystem (Ahn and Geiger, 1987). The whistling thorn *Acacia* (*Vachellia*) *drepanolobium* is the dominant tree species on Vertisols, accounting for 97% of the overstory, while more than 90% of the understory consists of five grass species and two forb species (Young et al., 1998). Rainfall is weakly trimodal with a distinct dry season from January to March (Georgiadis et al., 2007).

2.2. Experimental design

2.2.1. Grazing experiment

This study was conducted in the Kenya long-term exclusion experiment (KLEE). KLEE is a herbivore exclusion experiment established in 1995 that uses semi-permeable barriers to exclude different guilds of large mammals arranged in a three replicate blocks (Young et al., 1998). In October 2010 four 16 m^2 plots were established in each of the three blocks, within plots that exclude all large herbivores (complete exclosure) and plots where all herbivores are allowed to graze (open). The large herbivores included both wild and domestic animals. At the start of the experiment, the center 1 m^2 in each 16 m^2 plot was clipped to ground level, and the grass dried and weighed. This provided an estimate of the effect of 17 years of herbivore exclusion on standing grass biomass and foliar nutrients. At the same time, a composite soil sample (0–10 cm depth) was collected within each 16 m^2 plot (four separate cores in each composite) to estimate soil carbon and nutrient concentrations.

2.2.2. Nutrient enrichment experiment

After grass clipping and soil sampling, four fertilization treatments were established: N alone, P alone, a mixture of N and P, and a control (hereafter referred to as N, P, NP and control). The four fertilizer treatments were applied in the four 16 m^2 plots that had been established in the grazed and non-grazed plots (i.e., each replicate herbivory plot contained one 16 m^2 plot of each treatment). The fertilizer application included N (urea) at 100 kg N ha^{-1} and/or P (triple super phosphate) at 50 kg P ha^{-1}, applied in late October 2010 and mid March 2011. After fertilizer application a 1 m^2 area in both grazed and ungrazed plots was caged to exclude all vertebrate herbivores (i.e., including hares and rodents). Soil was sampled in the 16 m^2 plot and aboveground regrowth biomass in the 1 m^2 subplots was harvested in early May 2011. The grass biomass was dried at 60 °C (Wrench et al., 1996) to constant weight and then ground. Soil samples were air dried for 12 days at 25 °C (Wrench et al., 1996). All samples were analyzed in the University of Florida Wetland Biogeochemistry Laboratory.

2.3. Nutrient analysis in soil and plant tissue

Plant and soil total C and N were determined using a Thermo-Electron Flash 1112 elemental analyzer. Organic matter was measured by loss on ignition from 0.5 g samples of dried soils. The samples were placed in a muffle furnace and heated to 250 °C for 30 min. The furnace temperature was then increased to 550 °C for 4 h (Anderson, 1976). Organic matter content was calculated as the mass loss on ignition on a dry weight basis (Luczak et al., 1997). Total P was determined using ignition at 550 °C followed by acid extraction in 1 M H_2SO_4. Digested solutions were analyzed colorimetrically using Shimadzu UV–vis recording spectrophotometer UV-160. Extractable P, potassium, calcium, magnesium, iron and aluminum were determined using Mehlich 1 method as outlined by (Kuo, 1996). Nutrient ratios C:N, C:P and N:P were calculated on a mass basis. $NH^+{}_4$-N and $NO^-{}_3$-N were extracted using 2 M KCl. The samples were filtered through a 0.45-μm membrane filter (Pall Corporation) and analyzed colorimetrically (White and Reddy, 2000).

2.4. Statistical analysis

Statistical analyses were conducted using JMP (version 7.02; SAS Institute, 2007). Significant differences among the treatments for the variables were determined by one-way analysis of variance for grazing versus non-grazed treatment before nutrient enrichment and two-way ANOVA after nutrient enrichment using Tukey HSD test and *t*-test at $\alpha = 0.05$.

2.5. Determination of nutrient use efficiency (NUE) and apparent nutrient recovery (ANR)

The difference method was used to determine apparent nutrient recovery and nutrient use efficiency. Apparent nutrient recovery reflects plant ability to acquire applied nutrient from soil (Baligar et al., 2001) and is determined as $(U_N - U_O)/F_N$, where U_N and U_O are the nutrient uptake by grass with and without the applied nutrient, and F_N is the amount of nutrient applied all in kg ha^{-1}; the results are expressed as a percentage. Nutrient use efficiency (NUE) is defined as the amount of forage (dry matter) that is produced for each unit of applied N or P (Fageria and Baligar, 1999; Zemenchik and Albrecht, 2002). Nutrient use efficiency (NUE) is determined as $(Y_N - Y_O)/F_N$, where Y_N and Y_O, are the grass

Table 1
Foliar nutrient concentration under herbivory and nutrient enrichment.

	N ($g\,kg^{-1}$)	P ($g\,kg^{-1}$)	C:N	C:P	N:P
Herbivory (before fertilization)					
Grazed	9.7 ± 0.5^a	0.58 ± 0.01^a	42 ± 2^a	700 ± 10^a	17 ± 0.83^a
Ungrazed	9.4 ± 0.3^a	0.53 ± 0.02^b	42 ± 1^a	760 ± 38^a	18 ± 0.85^a
t- ratio	0.54	5.7	0.02	2.4	0.74
P-value	0.47	0.03	0.90	0.14	0.40
Nutrient enrichment (after fertilization)					
Control	19 ± 1^c	1 ± 0.03^b	21.4 ± 0.9^a	393 ± 10^a	18.5 ± 0.9^b
N	25 ± 1^b	1 ± 0.05^b	16.0 ± 0.7^b	401 ± 18^a	25.1 ± 0.9^a
P	17 ± 0.6^c	2.6 ± 0.3^a	23.4 ± 0.8^a	162 ± 18^b	7.0 ± 0.8^d
NP	28 ± 0.8^a	2.1 ± 0.1^a	14.0 ± 0.4^b	190 ± 7^b	13.6 ± 0.5^c
F- ratio	40	26	38	81	91
P-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means of the N and P concentration and C:N, C:P and N:P ratios between grazed and ungrazed plots before and after fertilization. Before fertilization the grazed and ungrazed plot means were replicates of twelve ($n = 12$). The fertilization includes addition of N only, P only, N + P and control (where no nutrients were added). After fertilization the grazed and ungrazed plots were not significantly different and hence results were combined for statistical analysis. The means were from 6 replicates ($n = 6$). The data indicate mean ± SEM (Standard error of mean). The different superscript letters after SEM within a column indicate significant difference between treatment means at $P < 0.05$.

Table 2
Grass biomass and biomass nutrients under herbivory.

	Aboveground biomass (kg ha^{-1})	C (kg ha^{-1})	P (kg ha^{-1})	N (kg ha^{-1})
Grazed	2214 ± 212^a	889 ± 84^a	1.3 ± 0.1^a	27 ± 3^a
Ungrazed	4030 ± 417^b	1569 ± 148^b	2.1 ± 0.3^b	49 ± 5^b
t- ratio	15	16	10	15
P-value	0.0008	0.0006	0.004	0.0008

Means of grass biomass and biomass nutrients between grazed and ungrazed plots before fertilization. The mean were from 12 replicates the data indicate mean ± SEM. The different superscript letters after SEM within a column indicate significant difference between treatment means at $P < 0.05$.

Table 3
Soil parameters under herbivory before nutrient enrichment.

	Grazed	Ungrazed	*t*- ratio	*P*-value
SOM (%)	15.6 ± 0.3^a	15.0 ± 0.2^a	2.1	0.16
Total C (g kg^{-1})	21 ± 1^a	24 ± 1^a	3.5	0.08
Total N (g kg^{-1})	2.0 ± 0.1^a	2.2 ± 0.1^a	2.3	0.15
Total P (mg kg^{-1})	139 ± 5^a	142 ± 2^a	0.3	0.62
Extractable K (mg kg^{-1}	847 ± 50^a	875 ± 34^a	0.2	0.65
Extractable P (mg kg^{-1})	6.0 ± 0.5^a	6.1 ± 0.4^a	0.03	0.86
NH_4^+-N (mg kg^{-1})	5.9 ± 0.3^a	6.1 ± 0.3^a	0.2	0.68
NO_3^--N (mg kg^{-1})	6.2 ± 1.0^a	5.8 ± 0.7^a	0.1	0.8
Extractable Ca (mg kg^{-1})	4139 ± 200^a	3999 ± 190^a	0.26	0.62
Extractable Mg (mg kg^{-1})	883 ± 25^a	894 ± 17^a	0.1	0.70
Extractable Fe (mg kg^{-1})	30 ± 3^a	42 ± 4^b	6.6	0.02
Extractable Al (mg kg^{-1})	478 ± 21^a	532 ± 17^a	4.0	0.058

Means of the soil parameters between grazed and ungrazed plots before fertilization. There were 12 replicates for each treatment mean. The data indicate mean ± SEM. The different superscript letters after SEM within a row indicate significant difference between treatment means at $P < 0.05$.

biomass with and without the nutrient being tested all in kg ha^{-1} and F_N is as indicated above (Guillard et al., 1995; Syers et al., 2008).

3. Results

3.1. Effects of long term grazing on aboveground biomass and soil nutrients

Seventeen years of grazing increased the foliar P concentration in grass by 20% compared to the ungrazed plots ($t = 5.7$ $P = 0.03$; Table 1). Foliar N was also higher in grazed plots, but not significantly so ($P > 0.05$; Table 1). Grazing reduced aboveground grass biomass by 45% compared to ungrazed plots ($t = 15$; $P = 0.0008$; Table 2). The stocks of aboveground grass biomass C ($t = 16$; $P = 0.0006$), N ($t = 15$; $P = 0.0008$) and P ($t = 10$; $P = 0.004$) were therefore, significantly greater in the non-grazed plots than in the grazed plots, despite a reduction in foliar nutrient concentrations; grazed plots contained 55% of the biomass N and 60% of the biomass P of the ungrazed plots (Table 2). The grass C:N, C:P and N:P ratios did, not differ significantly between the grazed and ungrazed plots. The C:N and C:P ratios were >40 and >700, respectively, in both grazed and ungrazed plots, while the N: P ratio was ~17 (Table 1).

There were no significant differences in soil nutrients between grazed and ungrazed plots, including total C, N, P, extractable P, K, Ca, Mg, Al, NO_3^--N, and NH_4^+-N (Table 3). Only extractable Fe was greater in the ungrazed plots (by 38%; $t = 6.6$, $P = 0.02$) than grazed plots (Table 3).

3.2. Nutrient enrichment effects on soils and aboveground biomass

A two-way ANOVA indicated foliar nutrient concentrations, biomass C, N and P stocks and soils nutrients were not significantly different between grazed and ungrazed plots after nutrient addition. There were no significant interactions between nutrient enrichment and grazing. Therefore, data from above parameters from grazed and ungrazed plots were combined when conducting the statistical analysis.

After nutrient enrichment soil total P, available P, NH_4^+-N and NO_3^--N changed significantly (Fig. 2). However, there were no significant changes in soil C or total N (Table 4). Soil total P doubled under P and NP treatments ($t = 16$; $P < 0.0001$) compared to the control and N treatments (Table 4; Fig. 2A). Available P was also significantly greater under P and NP treatments ($F = 15$; $P < 0.0001$) than in control and N treatments (Fig. 2B). The NH_4^+-N ($F = 31$; $P < 0.0001$) and NO_3^--N ($F = 50$; $P < 0.0001$) were significantly greater in N and NP treatments compared to control and P treatment (Fig. 2C and D). After nutrient enrichment the soil C:N was significantly lower in the N treatment ($F = 7$; $P = 0.0023$) compared to other treatments (Table 4). The soil C:P ratio was significantly lower in P and NP treatments ($F = 30$; $P = 0.0001$) than other treatments (Table 4).

Two-way ANOVA indicated that the nutrient enrichment had a significant effect on foliar N ($F = 40$; $P < 0.0001$) and P ($F = 26$; $P < 0.0001$) concentrations (Table 1). For the NP, N and P treatments, foliar N concentration changed by +53%, +33% and −10%, respectively, and foliar P concentration changed by +110%, +0% and +155%, respectively compared to the control plot grass.

Application of N and/or P fertilizer did not have a significant effect on grass biomass or biomass C, but significantly increased N and P stocks (Fig. 3A–D). With N + P fertilizer addition there was a significant increase in biomass N and P, addition of N alone did not have a significant difference from control or N + P treatment in terms of biomass N. Also addition of P alone did not have a significant difference from control or N + P treatment in terms of biomass P (Fig. 3C and D) indicating interactions between N and P in improving biomass N and P. The N and P interaction was further supported by the N:P ratio decreasing significantly when P and NP were added (<14) and increasing when N was added (>16) (addition significantly averaged the N:P ratio (13.6, P Table 1). The grass C:N, and C:P ratios were significantly different across the treatments after nutrient enrichment (Table 1). The grass C:N ratio was significantly lower in the N and NP treatments (<20) than in the control and P treatments (>20; $F = 38$; $P < 0.0001$; Table 1). The grass C:P ratio was reduced by P addition (<200) compared to no-P plots (>300; $F = 81$; $P < 0.0001$; Table 1).

3.3. Apparent nutrient recovery (ANP), nutrient use efficiency (NUE) and physiological nutrient efficiency (PNE)

After nutrient enrichment apparent N and P recovery were not significantly different between N and NP treatments (Table 5) although apparent N was more than two times higher under NP treatment compared to N treatment. Both N and P use efficiency were not significantly different between N and NP treatments (Table 5); however, P addition had a negative effect while NP addition had a positive effect on nutrient use efficiency. Nitrogen use efficiency was more than three times higher under the NP treatment compared to N treatment.

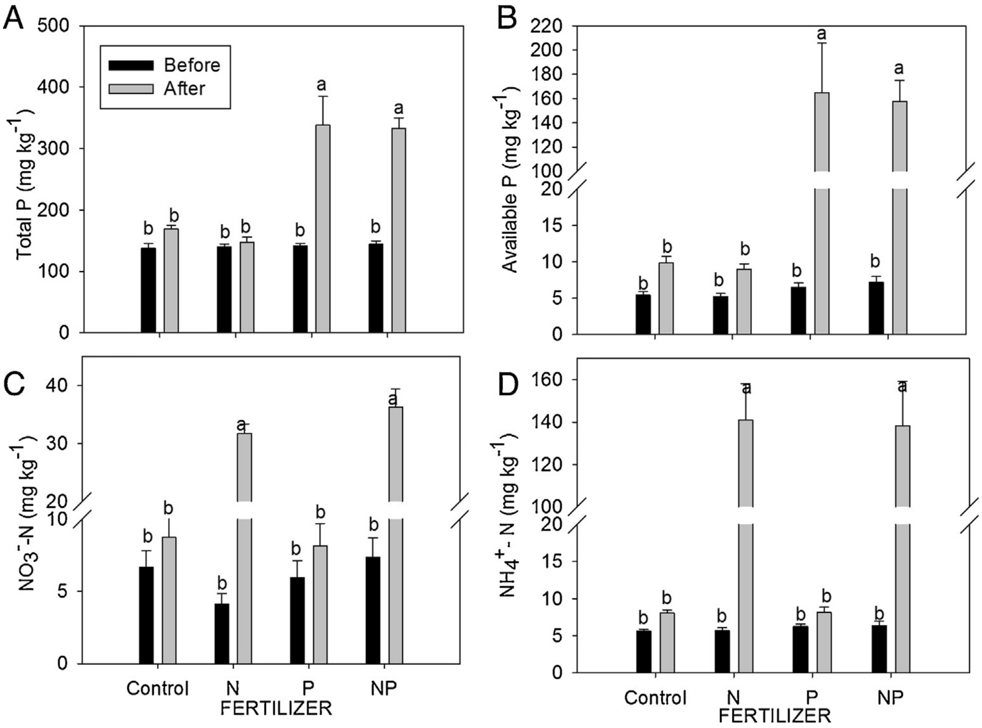

Fig. 2. Soil nutrients before and after nutrient enrichment. (A) Total P. (B) Available P. (C) Nitrate-N. (D) Ammonium-N before and after fertilization. Bars represent mean and error bars represent SEM. Means are from six replicates. The different letters indicate significant difference between treatments for before and after fertilization means at $P < 0.05$.

4. Discussion

4.1. Grazing effects on soil and plant nutrients and aboveground grass production

This observation of decreased aboveground grass biomass (45%) under grazing is consistent with similar observation in South Africa semi-arid savanna (Mbatha and Ward, 2010) and in Rocky Mountain National Park, Colorado (Singer and Schoenecker, 2003). Pucheta et al. (1998) reported a 33% decrease in standing biomass under grazing in central Argentina compared with an area that had been excluded from grazing for two years. Cui et al. (2005) data indicated that grazing decreased aboveground biomass by 65–79% after 25 years of herbivore exclusion in Mongolia. The large decrease was suggested to be due to the intensity of current grazing, although grazing reduced biomass by 18–32% in a degraded/overgrazed site where herbivores had been excluded for 10 years (Cui et al., 2005). This suggests that the period of herbivore exclusion, quality of the grass and the intensity of grazing determine the quantity of the standing aboveground biomass (Pandey and Singh, 1992). However, the study findings contrast with those of Frank and McNaughton, (1993), who reported a 47% increase in aboveground grass biomass in grazed plots in Yellowstone National Park, Wyoming, USA. However, Yellowstone is a temperate area and grazing only occurred over the winter season (7 months), unlike in our study in savanna which indicated lower grass biomass production in the grazed plots where grazing occurred throughout the year.

Our study findings contrasted with our hypothesis that grazing would improve soil organic matter. This could be due to soil cover differences between grazed and ungrazed plots which could influence the soil temperature. Grazing reduces the soil cover, leading to increased soil temperature, which is likely to accelerate the organic matter decomposition rate and reduce the SOM (Haynes et al., 2014). The deposition of fecal matter and urine with high N content during grazing could also have a priming effect on existing soil C, accelerating the organic matter decomposition and reducing soil C (Fontaine et al., 2004; Ngatia et al., 2014). In addition, it is notable that cattle are the dominant herbivores in the study site and after feeding on a free range system during the day they are enclosed in cattle corrals (bomas) at night where the soil accumulates a lot of C and other nutrients (Augustine et al., 2003). This means some of the C is translocated by cattle from the grazing site to the bomas.

Table 4
Soils parameters after nutrient enrichment.

Treatment	Total carbon (g kg^{-1})	Total nitrogen (g kg^{-1})	Total phosphorus (g kg^{-1})	C:N	C:P
Control	22 ± 2^a	2.1 ± 0.2^a	0.17 ± 0.01^b	10.5 ± 0.4^a	130 ± 7^a
N	20 ± 1^a	2.3 ± 0.1^a	0.15 ± 0.01^b	8.4 ± 0.2^b	135 ± 10^a
P	23 ± 1^a	2.2 ± 0.1^a	0.34 ± 0.05^a	10.0 ± 0.4^a	74 ± 11^b
NP	21 ± 2^a	2.25 ± 0.1^a	0.33 ± 0.02^a	9.1 ± 0.4^{ab}	63 ± 3^b
F-ratio	1.1	0.7	16	7.0	30
P-value	0.39	0.58	<0.0001	0.0023	<0.0001

Both grazed and ungrazed were statistically analyzed together because they were not significantly different. There were 6 replicates for each treatment mean. The data indicate mean ± SEM. The different superscript letters after SEM within a column indicate significant difference between treatment means at $P < 0.05$.

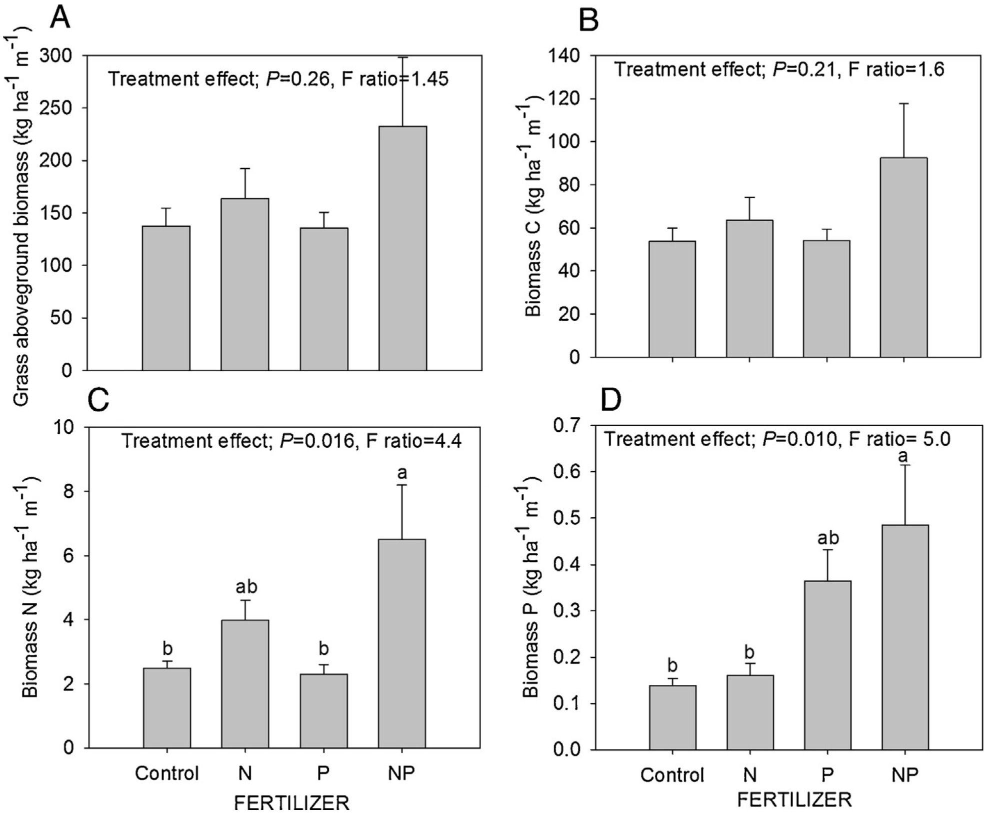

Fig. 3. Grass biomass and nutrients storage after nutrient enrichment. (A) Above ground biomass. (B) Biomass C. (C) Biomass N. (D) Biomass P in a hectare of land per month after fertilization. Bars represent mean and error bars represent standard error of mean from six replicates. The different letters indicate significant difference between treatments means at $P < 0.05$.

This study found no significant difference in foliar N concentrations between grazed and ungrazed plots, which contrasted studies showing increased/decreased foliar N with grazing (Coughenour, 1991; Singer and Schoenecker, 2003; Turner et al., 1993). However, there was a trend of greater foliar N concentration in the grazed grass. Grazing can increase soil N through N rich urine and feces (Augustine et al., 2003; Stark et al., 2002) in a more easily decomposable form, which bypass the slow litter decomposition pathway (Coughenour, 1991). This increases nutrient uptake by plants (Ruess, 1984) and increases the shoot nitrogen content (Knapp et al., 1999). However, in this study site it is possible that the grazers are mining the nutrients from the grazed plot grasses and depositing them elsewhere, as indicated by a trend toward lower soil N concentration in the grazed plots. The dominant grazers at the study site are cattle, which feed throughout the rangeland all day, but then are kept in bomas at night, where a large amount of dung accumulates. Hence there is a flow of nutrients from the nutrient poor bushland to nutrient rich bomas. Overnight cattle bomas are abandoned after a period of use and they naturally convert to nutrient rich glades, whose high nutrient status is maintained by wild animals that spend lot of time on them while feeding or resting. (Augustine et al., 2003; Veblen, 2012).

Table 5

Apparent nutrient recovery (ANR; %) and nutrient use efficiency (NUE)

Treatment	ANR (%)	NUE
Nitrogen		
N	4.5 ± 1.9^{a}	0.8 ± 1^{a}
NP	12.0 ± 5.1^{a}	2.9 ± 2.1^{a}
F-ratio	1.9	0.8
P-value	0.20	0.39
Phosphorus		
P	1.4 ± 0.5^{a}	−0.12 ± 1.6^{a}
NP	2.1 ± 0.8^{a}	5.7 ± 4.2^{a}
F-ratio	0.6	1.7
P-value	0.44	0.22

NUE (kg of grass biomass produced for each unit of applied N or P) following nutrient addition treatments. Values are means of six replicates, mean ± SEM are presented. The different superscript letters after SEM within a column indicate significant difference between treatment means at $P < 0.05$.

The observation of higher foliar P in grazed plots is similar to patterns found by Turner et al. (1993) in Kansas where herbivores were excluded for 10 years and Chaneton et al. (1996) in temperate subhumid grassland in Argentina where herbivores were excluded for eight years. The light grazing intensity employed in this study site does not change the grass species composition. Therefore, there could be two reasons leading to higher foliar P observed in grazed plots. First, higher P could be due to grazer defoliation stimulating grass regrowth (Luo et al., 2012) producing new shoots with higher P while the ungrazed plots retain older grass shoots that persist for a long time until litter fall. Second, herbivory could accelerate P mineralization (Vadigi and Ward, 2014). Soil nutrient cycling through litter decomposition is referred to as the slow cycle, herbivores short circuit the slow cycle when feeding and accelerate nutrient release back to the soils (Belovsky and Slade, 2000). It has been observed that approximately 75–90% of the nutrients consumed by grazing animals are cycled back to the soil in urine and feces (McKenzie et al., 2003). Approximately 50–90% of P in manure is plant available (Dou et al., 2001). Unlike fecal N which can be volatilized from the soils after deposition, P is not volatilized or easily lost due to poor drainage system in the Vertisols, and is therefore easily available to the plants (Miola et al., 2015). Phosphorus availability to plants can be reduced by adsorption onto clays or metal oxides (Perkins and Underwood, 2001). This seems not the case in this study because the increased foliar P suggest that grazing enhanced the rate of P cycling, with more P allocated aboveground supporting shoot regrowth. Hence, the younger tissues generated after grazing have higher P contents than mature or senescent tissues that persist in absence of grazing (Zheng et al., 2012). In this P limited savanna ecosystem, the capacity of grazing to enhance vegetation quality in terms of improving foliar P is important.

The large variation in reported effects of grazing of rangeland soils and vegetation in this study and others (Cui et al., 2005; Pucheta et al., 1998; Singer and Schoenecker, 2003; Turner et al., 1993) suggests strong site effects and study effects that we do not as yet understand, and the number of studies is still too small to discern generalized explanations for this variation. Clearly, more data is needed from other sites to help understand the effects of grazing on rangeland soils and vegetation.

4.2. Effects of nutrient enrichment on soil and plant nutrient concentration, grass primary production and carbon storage

Soil and biomass parameters in the grazed and ungrazed plots did not respond significantly differently to nutrient enrichment. This was due to similarity in soil parameters even before nutrient enrichment, and also perhaps because the aboveground biomass was clipped to ground level before nutrient enrichment.

The foliar N:P ratio has widely been used as an indicator of nutrient limitation (Koerselman and Meuleman, 1996). This study findings of 17–18 foliar N:P ratio before nutrient enrichment suggested N and P co-limitation to primary productivity. However, the luxurious uptake of both N and P in this study without significant increase in biomass production was consistent with previous findings in South African savanna (O'Halloran et al., 2010), but contrasted previous findings by Augustine et al. (2003) in neighboring alfisols where plant production increased with increased plant nutrient uptake. These findings suggest that the plants are either inefficient in nutrient utilization, or are adapted to low soil nutrients status, or that there are other factors, such as moisture that limit plant production (Berendse and Aerts, 1987). Baligar and Bennett (1986) suggested that for an efficient plant, increased nutrient uptake should translate to increased biomass production, and failure to increase production indicates plant inefficiency and the possibility that the plant has slow growth rate.

The study observation of increased foliar P with increasing soil P concurred with the results of previous studies (Ludwig et al., 2001; Ries and Shugart, 2008), while the study observation of increased foliar N concentration with increasing soil N was similar to Ludwig et al. (2001) in Tanzanian savanna but contrasted Ries and Shugart (2008) findings in African woodland savanna in Botswana.

Although the NP treatment in this study increased aboveground biomass by +42%, this increase was low compared to a +220% aboveground biomass increase in Botswana savanna after applying similar quantities of N and P as in this study (Ries and Shugart, 2008). However, Ries and Shugart (2008) reported that the foliar N concentration in their study did not differ significantly from the control, while in this study there was luxury uptake of both N and P after nutrient enrichment. The study findings of reduced C:N ratio after soil N enrichment contrasted with the results in Botswana savanna (Ries and Shugart, 2008). The Botswana study site was dominated by a different grass species and had higher rainfall (698 mm). The different grass species in the two sites could be having different physiological responses to resources availability and nutrient use efficiency (Zemenchik and Albrecht, 2002).

4.3. Effects of nutrient enrichment on ANR and NUE

This study found relatively higher N use efficiency in NP than N treatment which contrasts with the findings of Snyman (2002) that N use efficiency was higher in the N fertilization than NP fertilization in South Africa savanna. We observed lower apparent N recovery compared to an average of 21–27% when N was added alone and 36–45% when N and P were added together in maize farm in coastal savanna of West Africa (Fofana et al., 2005). In addition, Fofana et al. (2005) indicated that addition of N and P together significantly improved the apparent N uptake compared to adding N alone, which was not the case in this study. We broadcasted the fertilizer without manually mixing the fertilizer with the soils. Hence because the root occupies around 1–2% of the soil surface volume and the amount and proportion of added nutrients that reach roots determines the efficiency of nutrient uptake (Baligar and Bennett, 1986), there is a possibility that this application method limited the apparent nutrient recovery. Furthermore, in the tropics large N losses occur through leaching, denitrification and ammonium volatilization, while P is fixed by adsorption on amorphous Fe and Al oxides and hydroxides and are tied up preventing immediate availability to plants. Baligar and Bennett (1986) further indicated that nutrient uptake capacity is determined by the ability of the soils to supply nutrients and the capacity of plant to uptake them. This is influenced by genetic makeup of the plant and interactions with environmental factors, such as rainfall, solar radiation and temperature, since NUE depends on the (1) uptake efficiency (acquiring nutrient from soil), (2) incorporation efficiency (transport to shoots and leaves) and (3) utilization efficiency (Baligar et al., 2001). The increased foliar N and P and unaffected primary production after nutrient enrichment indicate that the species in this study were inefficient in utilizing the added and absorbed nutrients.

5. Conclusion

Grazing improves the quality (in term of foliar P) while reducing the quantity of the aboveground biomass in this ecosystem. In this study, aboveground biomass, foliar nutrients and soil nutrients responded similarly upon N and/or P addition in both grazed and ungrazed plots (this is based on the assumption of biomass clipped to ground level before addition of the nutrients in grazed and ungrazed plots). The luxury uptake of both N and P without increasing plant biomass suggests that other resources, for example soil moisture limitation or adaptation of plant species to low nutrient conditions, could limit plant production in response to nutrient addition. Comparing our study with other previous studies it is clear there are inconsistent responses by both soils and vegetation to herbivory and N or/and P addition. The mechanism/s behind the inconsistencies is not yet clear; more studies in different rangelands are required to address this ambiguity. In addition it would be helpful for future research to focus on the interactions of the belowground biomass and aboveground biomass under herbivory and nutrient enrichment.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.04.025.

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