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Seasonal response of Carbon and Nitrogen to Ungulate Activities in a Kenyan Savanna

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Abstract: Classical perception of savanna structure and function proposes equilibrium between woody and herbaceous species, mediated by differential access to ecosystem resources. We report here the first disequilibrium linkages between the carbon (C) and nitrogen (N) pools as impacted by water to determine the frequency and intensity of grazing. Generally, grazing influenced accumulation of root and shoot N, C/N ratios and biomass. The response of C and N to grazing depended on availability of soil water. Positive response of C, N was vivid during the wet season while undefined response was observed during the dry season. Soil and root N, root C, root and shoot C/N ratios increased while shoot N, soil C and C/N ratio decreased with the increase in soil water. In absence of grazers, biomass was positively correlated to soil, root shoot C/N ratios with significant correlation ($P<0.05$) at root and shoot scales. Intense grazing led to lowered soil C/N ratios regardless of season but adjustment of root and shoot C/N ratios was apparently an integral response feature to driving variables as influenced by grazers and moisture availability. Since ungulate activities did not significantly alter soil C and N pools, the long-term implications on regional biogeochemical attributes of humid savannas cannot be exclusively conditioned to land use changes, especially when sufficient moisture is available. However, this study has shown the potential for N and C immobilization within roots and shoots by grazers, which is an important attribute for regulating their cycles and hence C/N ratios avails the potential of tracking grazing intensity in humid savannas.

Keywords: C/N ratio; Biomass; Savanna; Land use

1. INTRODUCTION

Savannas contrasting plant life form of trees, shrubs and grasses cover approximately an eighth of the global land surface (Smith, 1999; Belsky, 1994), which translates to 25% of terrestrial biomes and thus second to tropical forests in their contribution to terrestrial primary production (Sankaran *et al.*, 2004; Grace *et al.*, 2006). 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 (Isichei, 1995; Porensky and Veblen, 2012). In Africa, savannas cover ~600 million hactares of land, which translates to about 40% of the continents area. Although the general factors controlling the stable expansive grass and scattered trees have been identified as climate, fire and herbivory (Smith, 1999), researchers from different parts of this region have differed in their approach on the ecosystem variables. For instance, studies from Eastern region have focused on migratory habit of wild angulates (Augustine and McNaughton, 2006), Western and Northern parts focused on rainfall and domestic herbivores (Isichei 1995), while the Southern parts focused on rainfall and trees (Aranibar *et al.*, 2004; Caylor *et al.*, 2005; Wang *et al.*, 2009). However, all these variables interact with a high degree of uncertainty due to land use changes (Ludwig *et al.*, 2004; Cech *et al.*, 2010).

Grazing by both domestic and wild hervores within savannas alters caborn (C) and nitogen (N) pools (Augustine and McNaughton, 2006; Cech *et al.*, 2008; Coetsee *et al.*, 2010), which has long-term implications on resource use efficiency and regional biogeochemical attributes in the vast savanna biome (Douglass *et al.*, 2011). Due to their vast extent, tropical savannas are bound to influence the feedback between global C and N cycles as driven by the predicted global warming (Isichei, 2005; Douglass *et al.*, 2011) and land use changes. Although soil C feedback influnces global C cycle while N remains the most important nutrient in growth and development (Wang *et al.*, 2009; Otieno *et al.*, 2010), the potential biodiversity benefits resulting from managing existing habitat to increase C and N stocks in humid tropical savannas remains largely unresolved.

Since the mechanism that regulate these processes is crucial for improving fodder production for grazers as well as conservation of biodiversity (Augustine and McNaughton, 2006; Douglass *et al.*, 2011), decreasing environmental losses and increasing the primary production requires cordinated management of C and N cycles within savannas (Hudak *et al.*, 2003). Angulate grazing reduces biomass accumulation and causes soil damage, with potential consequences of releasing stored C and hence decreasing the ecosystems' sequestration capacity (Ardö *et al.,* 2008; Wang *et al.,* 2009). Although interactions between C and N dynamics have impacts on the general ecosystem functions (Hudak *et al.,* 2003), C storage capacity is influenced by changes in temperature, rainfall and CO_2 levels (Isichei 1995; Otieno *et al.,* 2010). Since the future climate has been predicted to worsen due to global warming and affect C balance within savannas (Watson *et al.,* 1990; Douglass *et al.*, 2011), site-specific C and N balance as driven by land management such as grazing are urgently needed.

Nitrous oxide (N_2O) in the atmosphere has been increasing at a rate of 0.2 to 0.3 % per year (Watson *et al.*, 1992; Serca *et al.*, 1998), with major sources being land-use conversion and vegetation disturbances (Serca *et al.*, 1998). Furthermore, a considerable effect on the stratospheric ozone is inevitable with subsequent alteration of global warming due to the use of synthetic N, which has risen from 12 to 1,004 Tg year^{-1} in the past four decades (Sardans *et al.*, 2012). This is expected to impact negatively on global climate, resulting into greater limitation on plant productivity across an increasing amount of land in the savanna. However, land use change probably has more influence on regional C balance than climate change (Wang *et al.*, 2009). Since savannas occupy over one third of the total land area in Kenya, dominating regions that are characterized by alternating humid and dry seasons (Hubbell 2001; Otieno *et al.*, 2005), an informed knowledge on the drivers of C and N balance and their interaction is essential for making decisions on sustainable management. In addition, any effort to manipulate these fluxes under conditions of changing land use must be based on an understanding of underlying mechanisms, since fluxes of C and N are sensitive to changes in ecosystem drivers such as grazing and climate (Chidumayo, 2001; Siopiñeiro *et al.*, 2006).

The classical perception of savanna structure and function proposes an equilibrium between woody and herbaceous species mediated by differential access to soil resources (Sankaran *et al.*, 2004; Porensky and Veblen, 2012). While regional approach may differ in perceptions of mutual coexistance and the drivers of the stable ecosystem, our general hypothesis in this study is that those perceptions are not mutually exclusive and that they in fact form end-points in the gradients of land use changes in humid savannas. We propose a disequilibrium approach where the linkages between C and N cycles as driven by soil attributes determines the frequency and intensity of grazing. In particular, we expected that the herbivores spatial pattern of habitat use for feeding and excretion will reduce C/N ratios during the growing season. The objective of this study was to establish the extent to which C/N ratios could be applied as an indicator of humid savannas' stability under ungulates activities. While many approaches of estimating productivity and savannas health seems feasible, they involve long time continuous monitoring and often destructive to the entire ecosystem (Augustine, 2003; Cech *et al.*, 2008). Although other approaches like remote sensing seems appropriate as applied in other ecosystems (Grace *et al.*, 2007), they have not been embraced in savannas on a wide scale due to prohibitive costs. Therefore, this study was motivated by the need of finding an alternative, rapid, more efficient and less destructive approach that will be viable for detecting biodiversity health in humid savannas.

2. MATERIAL AND METHODS

2.1. Study site

The study site was located within Ruma National Park, (00° 35'27.72" S & 34° 18'81.64" E) 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 (Maina, 2010; Otieno *et al.*, 2010). The terrain is mainly rolling grassland, with tracts of open woodland and thickets dominated by species of *Acacia*, *Rhus* and *Balanites* (Otieno *et al.*, 2010; Maina *et al.*, 2012). The soils are largely "black cotton" clays corresponding to Vertisols according to WRB soil classification. The surrounding area is settled, with a mix of small-scale cultivation and grassy pastureland with the main grazing animal populations within the Park consisting the roan antelope (*Hippotragus equinus*) and Jackson's hartebeest (*Alcelaphus buselaphus*), and Rotschild 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 Inducus*) cattle that consisted drought resistant Sahiwal and Boran breeds. Two plots measuring 50 m × 50 m were established in the open but close proximity to *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. Cattle passed over this area at least 2-3 times a week, with the intensity of grazing increasing during the dry season. This grazing density in this ecosystem was about 0.25 head ha^{-1}, which we termed as low to medium since they spend approximately 5-10 minutes feeding on the same area before moving to other expansive locations. Within each plot, five replicate sampling units measuring 3 m ×3 m were randomly selected for sampling every specific day of the year.

2.2. Microclimate and soil properties

Weather conditions were continuously recorded at an automatic meteorological station set up at the field site. Air temperature (T_{air}) and humidity (Fischer 431402 sensor, K. Fischer GmbH, Drebach, Germany) were automatically measured every 5 min, averaged and logged every half-hour by data logger (DL2e, Delta-T Devices Ltd. Cambridge UK). In addition, temperature (T_{air}) at 20 cm height just above the vegetation (Digital thermometer, Conrad, Hirschau, Germany) and soil temperature (T_{soil}) at 10 cm depth (Einstichthermometer, Conrad, Hirschau, Germany). Rainfall and temperature data within the study period are presented in Otieno *et al.* (2010). Soil water was determined gravimetrically with a 3 cm diameter core sampler. Soil physical properties such as moisture, bulk density, and pH were determined based on samples collected from both fenced and grazed plots (Otieno *et al.*, 2010; Maina *et al.*, 2012).

2.3. Biomass measurement

Collars measuring 38 cm x 38 cm were used to demarcate grass for harvesting on each day of year during the wet and dry seasons. Five replicate collars were sampled from each plot (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). Below ground, (root) biomass was sampled with an 8 cm diameter soil corer down to 30 cm, from the same plots after removal of the aboveground (shoot) biomass. 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 their dry weights. Due to difficulty in separating dead and live biomass, as well as soil profile roots, the reported results are pooled profile average and combined dead and live shoot biomass.

2.4. Soil and plant N and C

The second soil sampling was done at the middle of each collar down to 30 cm and the soil cores divided into three parts from 0-10, 10-20 and 20-30 cm. This set of sample was used for the determination of soil and root C and N 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 C and N concentrations (%) by means of elementary analysis (Markert, 1996). Total N content was determined from the total weight of the aboveground biomass as expressed in g m^{-2}. Similarly, total root N content was calculated from the total weight of belowground biomass. Similar procedure was followed to determine the total N content (%) in soil.

2.5. Data Analysis

The relationship between biomass, C and N was the main interest in this study. Values were analyzed for seasonal variance followed by a pair-wise comparison, using LSD at 5% probability level. Pearson’s correlation analysis was performed to test the significance of correlations between C, N and other ecosystem variables.

3. RESULTS

3.1. Meteorological parameters

Daily mean maximum air temperatures (Tair) during the study period did not vary greatly between the wet and dry seasons, with ranges of 24.59 ºC and 36.9 ºC, respectively. The site displayed bimodal rainfall pattern as is the normal case around the equator with rainfall average of 381.33 mm p.m during the wet season and 145 mm during the dry season (Table 1). Rainfall events were erratic during the dry season with most weeks experiencing no rain. PPFD values depended on the time of the day with maximum diurnal averages of 1429 µmol $m^{-2}s^{-1}$, recorded during the dry season and 1179 µmol $m^{-2}s^{-1}$ recorded during the wet season. Soil temperature varied depending on depth as well as soil depth and soil water content. The trends in rainfall, temperature and PPFD are presented in Otieno *et al.* (2010). Wide variation in number of rainy days in a month were observed with April receiving the highest rainfall. June to September were the driest months, April to July were the coldest months while March and August were the hottest months. Soil moisture varied depending on the season, with wet season recording highest moisture content of 28% by weight (Fig. 2*A*). During the dry season, moisture content was greatly reduced to 11% by weight. There were no observable deferences in moisture content between grazed and fenced plots.

3.2. C, N and C/N ratio response to grazing and seasonal changes

Increase in soil N concentration led to a decrease in soil C/N ratios in both fenced and grazed plots during the wet season (Fig. 2*B*). This occured when the ecosystem soil water was lowest. During the entire measurent period, soil and shoot N were consistently higher in fenced plot, while root N was higher in grazed plot (Fig. 2*B*). Shoot N decreased significantly during the dry season while root N increased within the fenced plots. Soil C was higher in fenced plot during the dry season but lower in grazed plot. No significant ($P<0.05$) differences were observed between soil C in grazed and fenced plots during the wet season. This probably was the main reason for the changes in root and shoot C/N ratio (Fig. 3). A slight increase in root and shoot C was observed at the beginning of the wet season. As the season progressed, shoot C deceased in grazed plot, while root C remained stable in both grazed and fenced plots. At the end of the dry season, root and shoot C within the fenced plots decilned while grazed plot values remained stable. C/N ratios maintained a decreasing trend with progression of the wet season (Fig. 3). However, as soil moisture content decreased during the dry season, soil C/N ratio reversed to an increasing trend. Although the ratio was parallel between the plots during the measurement period, consistent higher values were recorded in grazed plot. Root C/N was cosistently higher in fenced plot during the measurement period. As soil water decreased, root C/N ratio decreased steadily in the fenced plot. However, the ratio was stable with a slight increase at the end of the dry season in grazed plot. Dry season root C/N ratio was slightly higher compared to wet season. In fenced plot, the ratio ranged between 70 and 290 while in grazed plot the ratio ranged between 25 and 70. Shoot C/N ratio was consistently higher in grazed plot compared to fenced plot during the entire period (Fig 3). The ratio increased slightly in fenced plot during the wet season before decreasing steadily throughout the dry season. However, a steady increase was observed at the end of the dry season. In grazed plot, the ratio was steady during the entire season except towards the end of the dry season where a sharp increase was observed.

The relationship between the C/N ratios and N, C differed between soil root and shoot in both fenced and grazed plots, with season as the main factor. Soil, root and shoot N were all negatively correlated to respective C/N ratios regadless of plot differences. However, no significant correlation was exhibited in these relationships (Fig. 4*A*). Furthermore, soil, root and shoot C were all positively correlated in both grazed and fenced plots but significant correlation (R^2 = 0.0003, *P* = 0.01) was observed only at shoot scale in grazed plot.

3.3. Response of biomass to C and N.

Fenced plot recorded higher shoot biomass during the wet season compared to grazed. However, biomass within the grazed plot increased beyond the wet season up to the month of July (end of the growing season), before decreasing steadily. This was thought to be a response to soil moisture availability. On the other hand, biomass in fenced plot kept fluctauating but eventually declined at the end of the growing season (Fig. 3 *D*). Root biomass increased slightly at the beginning of the wet season before stablizig in both grazed and fenced plots.

Progression of the dry season did not have much influence on the root biomass content.

The correlation coefficients between biomass and the measured parameters differed depending on plot and season. Fig. 4 *B*. shows relationship between above ground biomass and C/N ratios. The relationship was expressed at three scales; soil, roots and shoot in fenced and grazed plots. At each scale, the slope of correlation differed between fenced and grazed plots. The C/N ratio was negatively correlated with biomass in grazed plot at soil and shoot scales but positively correlated in fenced plot. Positive correlation was vivid between biomass and C/N ratio at root scale in grazed plot but negatively correlated in fenced plot. Furthermore, significant correlation was only found in fenced plots at soil scale ($R^2 = 0.007$, $P<0.05$) and shoot scale ($R^2 = 0.0006$, $P<0.05$). When we assessed the ralationship seasonally (Table 2), no significant correlation was found between biomass and soil C/N ratio, root C/N ratio, shoot C/N ratio, soil C, soil N and root N in both wet and dry seasons during the measurement period. However, significant correlation was found in fenced plot between biomass and root C ($R^2 = 0.02$, $P<0.05$), shoot C ($R^2 = 0.00008$, $P<0.001$) and shoot N ($R^2 = 0.003$, $P<0.05$) during the wet season, and shoot C ($R^2 = 0.001$, $P<0.01$) during the dry season in grazed plot.

Relationship between root biomass, C, and N revealed mixed results as presented in table 3. Root biomass was positively correlated to C/N ratios at soil and root scales in both grazed and fenced plots but negatively correlated to soil N in both grazed and fenced plots. Correlation between soil C was negative in grazed plot but positive in fenced. There was no signifcant correlation between root biomass, soil C/N ratio and N content at both soil and root scales (Table 3). However, the correlation was signficant in soil C ($R^2 = 0.01$, $P = 0.05$) during the wet season, root C ($R^2 = 0.12$, $P = 0.01$) during the dry season in fenced and root C/N ratio ($R^2 = 0.005$, $P = 0.05$) in grazed plot.

4. DISCUSSION

The relationship between grass primary production, N and C within savannas have been dynamic (Laclaua *et al.*, 2002; Okin *et al.*, 2008; Wang *et al.*, 2009), with most studies attributing the overall ecosystem health on effects from trees (Ludwig *et al.*, 2004; Lloyd *et al.*, 2008; Fornara and Tilman 2008), fire (Cech *et al.*, 2008,

2010) herbivory (Waldram *et al.*, 2008; Augustine and McNaughton 2006) and/or precipition treatment (Aranibar *et al.*, 2004; Otieno *et al.,* 2010). In the current study, biomass, C and N content presented seasonality as well as site differences. Biomass was negatively correlated to C/N ratio, N content with significant correlation during the dry season. Most studies have ndicated that the pools of N within the soil are regulated by the rate at which mineral N enters the soil via urine, dung, litter decomposition and taken up by plants (Ruess and McNaughton, 1987; Coetsee *et al.,* 2010). Although higher soil N content was expected in grazed plot (Cech *et al.*, 2008; Coetsee *et al.*, 2010), N was consistently lower while soil C/N ratio remained higher throughout the growing season. Furthermore, there were no differences in soil C content between the fenced and grazed plots during the study period. Changes in soil moisture as driven by rainfall seemed to affect soil N cycling processes more than grazers in this study. This finding may perhaps not be surprising since grazing pressure in this ecosystem was considered as moderate to low in comparison to other grazing experiments (Sankaran *et al.*, 2004; Augustine and Mcnaughton, 2004). Results from this study strongly suggested that there is differentiation in nutrient partitioning between soil, roots and shoots depending on grazing, soil water content, temperature and stage of growth. Since previous studies in relatively similar humid savannas have shown that long term grazing and continous monitoring significantly effected soil N (Augustine, 2003; Cech *et al.*, 2010), our findings may only present partial effects of grazers since time scale over which these processes were considered was much shorter.

Although angulates affects N within savannas, most studies have been inconsistent with some attributing the reported results to the type and duration of herbivory (Augustine and McNaughton, 2006; Cech *et al.*, 2010) or interactive effects on litter quality (Belsky *et al.*, 1993; Ruess and McNaughton 1987). The reported results for soil N content of 0.17 - 0.29 % in this ecosystem were within the reported ranges in a semi arid savanna of 0.10 - 0.20 % (Kioko *et al.*, 2012) and an oak savanna of 0.15 – 0.20% (Mitros *et al.*, 2002), although their studies were based on long periods of grazing and fire treatment, respectively. Other studies in a Tanzanian savanna reported soil N content of 0.4 – 0.8 g Kg^{-1} at Saadani game reserve (Cech *et al.*, 2010) and 1-4 g kg^{-1}

in Serengeti grasslands (Ruess and McNaughton, 1987). However, differences in measurement units may present unjustified conclusion if the observed contrast is to be used to assess the differences in land use patterns.

Sufficient soil moisture after the long rains accelerated N investment in physiological processes which led to higher shoot biomass in both plots. These interrelated processes had effects of increasing the amount of C fixed per unit of N uptake. When input of N was synchronized with moisture availability as observed during the wet season in this ecosystem, its requirement was shifted at each stage of growth, while soil resources dictated the ability of grasses to store, mobilize and subsequently re-use the same N. Similar finding have been reported under prostrate grazing in some semi arid savannas (Augustine and McNaughton, 2006; Conrad and Tischew, 2011). Since variation in moisture and temperatures influences the rate of decomposition in most ecosystems (Salamanca *et al.*, 1998), temperature changes within the Kenyan savanna reduced C/N ratios at each stage of growth by effecting organic matter accumulation through increased soil warming, accelerated litter decomposition, higher N mineralization and ultimately reducing soil C pools. These feedback attributes obviously modified soil organic matter in presence of sufficient moisture and favorable temperature during the wet season and may tranform the entire ecosystem into a C sink. Therefore, soil C/N ratio in this ecosystem can be used to estimate the quantity of mineralizeable N per unit C respired since it influnces the amount of this N that is immobilized by decomposers during the wet season.

C/N ratio was critical for predicting the level of disturbance since the results indicated a negative correlation between root biomass and soil C content. Based on the current results, a decrease in soil C/N ratio during the wet season was caused by an increase of organic matter quality caused by grazer activities, which subsequently increased gross N mineralization. Therefore, disturbances on biomass can easily be determined by estimating the rate of organic matter decomposition and N cycling in humid savannas. Although these argument may indicate that grazers should have reduced the overall soil C/N ratio, the relationship between C assimilation and water consumption must have been balanced to optimize the utilization of soil resources and hence higher soil C/N ratio, which was similar to other semi arid ecosystems

(Aranibar *et al.,* 2004; Otieno *et al.,* 2005; Ardö *et al.,* 2008). We must note that the current findings in relation to grazers may not present a clear reliable condition albeit convincing results during the wet season. Seasonal response of soil C/N ratio may require many years of grazing due to slow turn over of organic matter in disturbed ecosystems as has been observed under simulation grazing where overall C/N ratio decresed over time (Siopiñeiro *et al.*, 2006; Conrad and Tischew 2011).

Absence of grazers led to higher soil and shoot N, root C and C/N ratio, and biomass during the wet season. Although these may result in greater C accumulation in the soil (Fornara and Tilman, 2008), we found C content to decrease the entire wet season. Such decrease acompanied by a decrease in C/N ratio during the wet season in this ecosystem was interpreted to indicate an accelerated decomposition of litter in presence of sufficient moisture and favorable temperature, which mobilization of soil resources and hence higher overall biomass. Furthermore, the positive correlation between biomass and N content implied that sufficient moisture induced changes within the root system. Over time such effects altered the response of grasses in presence of grazers and hence reduced the N-uptake capacity as observed from a sequential increase of C/N ratio from soil<root<shoot, within the grazed plot. The reported of root and shoot % C ranges of 33 – 45 % and 40 – 43% , respectively are consistent with previous studies of mixed forest litter (Salamanca *et al.*, 1998) where the values ranged between 42 – 52 %. This results implied that sufficient mositure with ungulate activities ensured that more C was stored within the soil and hence excess carbon would be sequestered, which may ultimately mitigate carbon climate driven changes. However, more C was stored within the root system in absence of herbivore as observed from higher C/N ratio in roots within the fenced plot. Since the increase in C-rich secondary compounds has effects of reducing N-rich metabolites (Sardans *et al.*, 2012), higher C content within the roots in both grazed and fenced plots revealed a dilution effect on N, thereby decreasing the C/N ratios in shoots compared to roots. Since grasslands have been known to cover one fifth of the worlds terestrial surface (Isichei, 1995) and contributes ~10% of soil C budget (Wang *et al.*, 2009), the losses of C through conversion of grasslands to other land uses such as grazing will dramatically shift N dynamics because C

and N dynamics are tightly linked as observed in this study.

During the dry season, the effects of hebivores on soil N was apparent due to significant differences between the fenced and grazed plots. Although we did not assess decomposition rate nor N content within the herbivore dung, it has been found that soils originating from grazer dung had higher N content than soil from litter alone due to high metabolism within the ruminant digestive system (Ruess and McNaughton, 1987). Soil C within grazed and fenced plot ranged from 2.80 to 3.89%, which were slightly higher than reported ranges in some semi arid savannas (Kioko *et al.*, 2012) of 0.10 to 2.09%. In an attempt to unravel the plot differences during the dry season, we found the C/N ratios to increase possibly as a results of transfer of available nutrients into plant materials. This was relevant since the differences observed in the two plots was consistent with the relative availability of N within grass component as observed from similar trend in C/N ratios of roots and shoots. Since soil compaction from grazer hooves may interfere with root biomass accumulation and nutrient acquisition by inhibiting on rooting depth and density (Ruess and McNaughton, 1987; Augustine and McNaughton, 2006), the grasses within the fenced plot did not fix similar rates of CO_2 per unit loss of water compared with grasses from the grazed plot during the dry season. This was observed in significant reduction of shoot biomass during the dry season in grazed plot. These results revealed that the overall efficiency during the wet season in grazed plot reflected an optimum use of resources in presence of disturbance but regular removal of plant material increased the demand for N by the same clipped grass during the dry season and hence more N was transfered from to soil to roots and shoots. Since C4 grasses are known to reduce the concentration of soil NO_3^- to lower levels than other species (Fornara and Tilman, 2008), this phenomenon may reduce leaching loss of N from the soil in the long run. However, if plant N uptake is reduced due to changes in climate or grazing pressure i.e., during the dry season, soil NO_3^- may increases, leading to signifcant losses. Therefore C/N ratios can be measured regularly in order to predict mineralization and decomposition rates as an alternative way of determining the extend of land use changes in humid savannas.

Some studies have suggested that land use changes such as grazing may be associated with conversion of grasslands to woodlands (Archer, 1995; Sankaran *et al.,* 2004). Such findings can be justified if the grazing pressure is relatively high and synchronized with a uniform rainfall pattern. Although the study site exhibited a bimodoal pattern in rainfall (Maina, 2010; Otieno *et al.,* 2010), pressure from herbivory were elusive in this ecosystem since biomass increased with progression of the wet season. This implied that grasses compansated for herbivory by differential allocation of nutrients at each stage of growth as stated above and hence shelving off the pressure from grazers. However, we can not conclussively attribute such increase to rainfall in isolation since soil moiture, nutrients, and tree/grass variables are all interelated in savannas (Hudak *et al.,* 2003; Wang *et al.,* 2010). Furthermore, the current study shows that the onset of rains triggered an increase in N content in both grazed and fenced plots. We are compelled to infer that N limitation can not be replenished by ungulate activities within this ecosystem.

Although we did not consider trees perse, the density of *Acacia* species was relatively high and hence our sampling points were in close proximity to these trees. It has been agreed that presence of C4 grass species together with legume species is a key cause of greater soil C and N accumulation in both higher and lower diversity plant assemblages (Grace *et al.,* 2006; Fornara and Tilman, 2008). Therefore, we cannot exclude trees in our dscussion nor can we conclusively attribute the observed changes in soil and grass C/N ratios to trees since it has been previously observed that presence of trees affects litter input into the soil system, controls of microclimate under their caonopies and fixes N (Ludwig *et al.,* 2004; Sankaran *et al.,* 2004; Lloyd *et al.,* 2008). Although such contribution by N fixation may be justified during the wet season, an enhanced C inputs in the soil through decomposing litter may also lead to an increased C/N ratio in soil, roots and shoots during the same season. This complementary effects of *Acacia* species may eventually ensure an increased N in roots and grass shoots, hence higher C/N ratios and biomass (Belsky *et al.,* 1993; Cech *et al.,* 2008). But since we did consider N input under canopy nor estimate N fixation, our conclusion may not be irrefutable without including the actual biologically fixed N data. Furthermore, without actual fixed N data by trees, as well as output data such as volatilization of ammonia, the estimated N pools within the soil may not reflect the ecosystems capacity in a cordinated approach against climatic changes and land use changes such as grazing. In addition, we have presented pooled data for N and C at soil and root scales. This may be misinterpreted since mineralization and mobilization of soil biota depends not only on soil water but also on the depth (Augustine and McNaughton, 2006). Until these uncertainties are clarified, the ecological significance of findings in such ecosystem in relation to *Acacia* species remains theoretical on a long-term basis. Future studies should aim at presenting C/N ratios for discrete grass species, incorporate trees as well as present data depth-wisely.

5. CONCLUSION

The major difference in C/N ratio in the three components (soil, root and shoot) of the ecosystem was observed during the dry season with high C/N ratio in the soil and shoot materials. Although gazers did not affect biomass directly during the wet season, presence of sufficient moisture mobilized the added nutrients, which significantly shifted the fraction of the whole-carbon budget partitioning between roots and shoot plant tissues. Since this study focused on the possibility of applying C and N pools to determine the effects of grazers in humid savannas, cycling of these nutrients within soil-plant-herbivores interface could have economics value if it could be proved that such conversion resulted a reduction of N_2O emissions and CO_2 accumulation within the stratospehere. We have however shown that C/N ratio can not be used in isolation under land use but soil moisture affects differentiation of pools at soil, root and shoot scales. It is therefore possible to design management activities that are both sustainable and more compatible with native biodiversity conservation as well as critically analize the seasonal shifts in relevant pools of C and N within the humid savanna. Further studies should focus on integrating legumes since they have a unique access to N, which will no doubt influence C and N balance and eventaully control primary production (Ludwig *et al.*, 2004; Lloyd *et al.*, 2008).

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TABLES AND FIGURES

Table 1. Plot charateristics during the measuremnt period

Season	T_{air} (°C)	Rainfall (mm)	PPFD (µmol m^{-2} s^{-1})	Humidity (%)	Soil mositure (%)	Soil bulk density	Soil PH
Wet	24.59	381.33	1178	28.54	25.64(80)	1.13 (42)	5.32 (12)
Dry	23.9	145	1429	21.13	12.12(80)	0.85(42)	4.09 (12)

Values represent seasonal average (number of replicates) for wet and dry season.

Table 2. Relation between shoot biomass and soil, root and shoot C, N and C/N ratios. Values are correlations coefficients (R^2, $P<0.5$, 0.01, 0.001) obtained from regression lines.

Site	Season	Soil C/N	Root C/N	Shoot C/N	Soil C	Soil N	Root C	Root N	Shoot C	Shoot N
Grazed	Rain	0.36	0.39	0.18	0.97	0.07	0.56	0.08	0.89	0.64
	Dry	0.11	0.27	0.28	0.27	0.03	0.32	0.27	0.001**	0.31
Fenced	Rain	0.12	0.76	0.03	0.04	0.21	0.02*	0.99	0.00008***	0.003*
	Dry	0.97	0.73	0.27	0.72	0.35	0.47	0.48	0.95	0.54

* Significant at *P<0.05*; ** Significant at *P<0.01*; *** Significant at *P<0.001*; blank - Not significant

Table 3. Relatioship between root biomass and soil C, N and C/N ratios. Values are correlations coefficients (R^2, P<0.5, 0.01, 0.001) obtained from regression lines.

Site	**Season**	Soil N	Soil C	Root N	Root C	Root C/N	Soil C/N
Grazed	Rain	0.76	0.06	0.39	0.25	0.29	0.4
	Dry	0.74	0.68	0.52	0.06	0.62	0.84
	Total	0.64	0.001**	0.03	0.23	0.005*	0.5
Fenced	Rain	0.34	0.01*	0.24	0.2	0.1	0.14
	Dry	0.29	0.6	0.16	0.12**	0.12	0.18
	Total	0.42	0.12	0.07	0.001*	0.02	0.08

* Significant at *P<0.05*; ** Significant at *P<0.01*; blank - Not significant

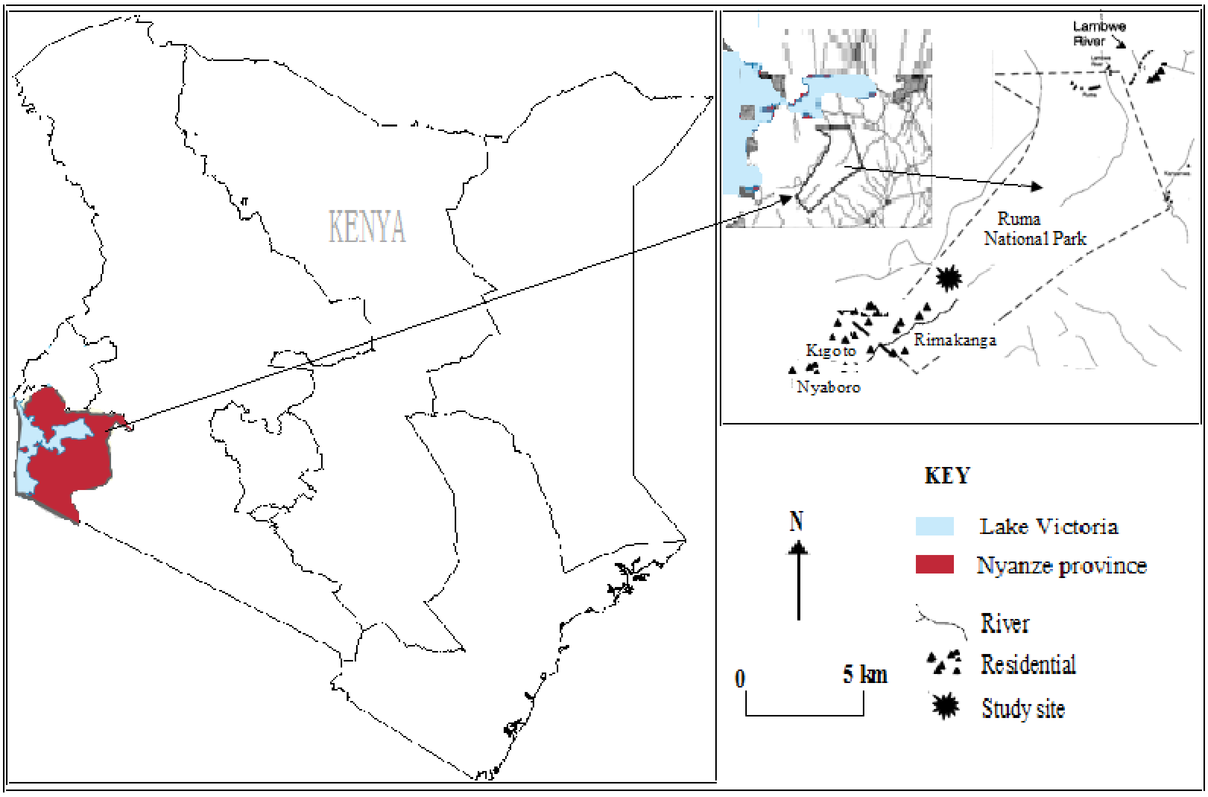

Fig. 1. Location of Ruma national park in western Kenya

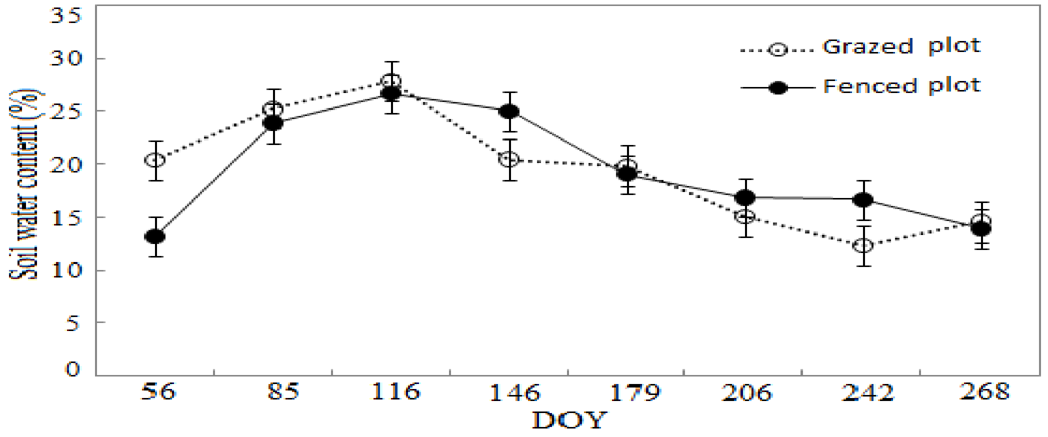

Fig. 2 a. Soil water content within the grazed and fenced plots during the measurement period. Values are means (n = 6) ± error bars for each day of year (DOY).

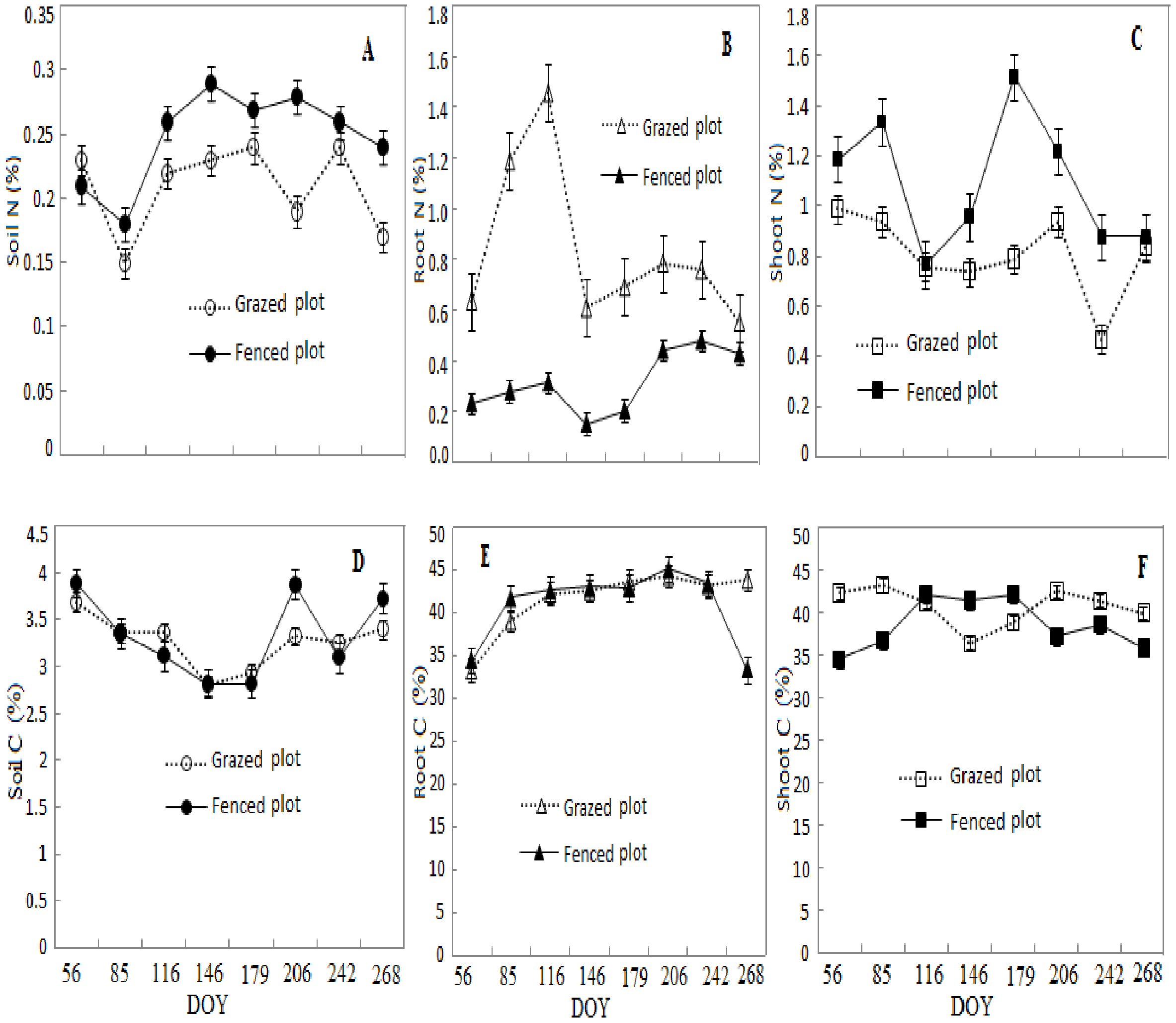

Fig. 2 b. Soil (A), root (B) and shoot (C) nitrogen content (%,)and soil (D) , root (E) and shoot (F) carbon content (%) during the measurement period in grazed and fenced plots.Values represent means (n = 6) ± error bars for each day of year (DOY).

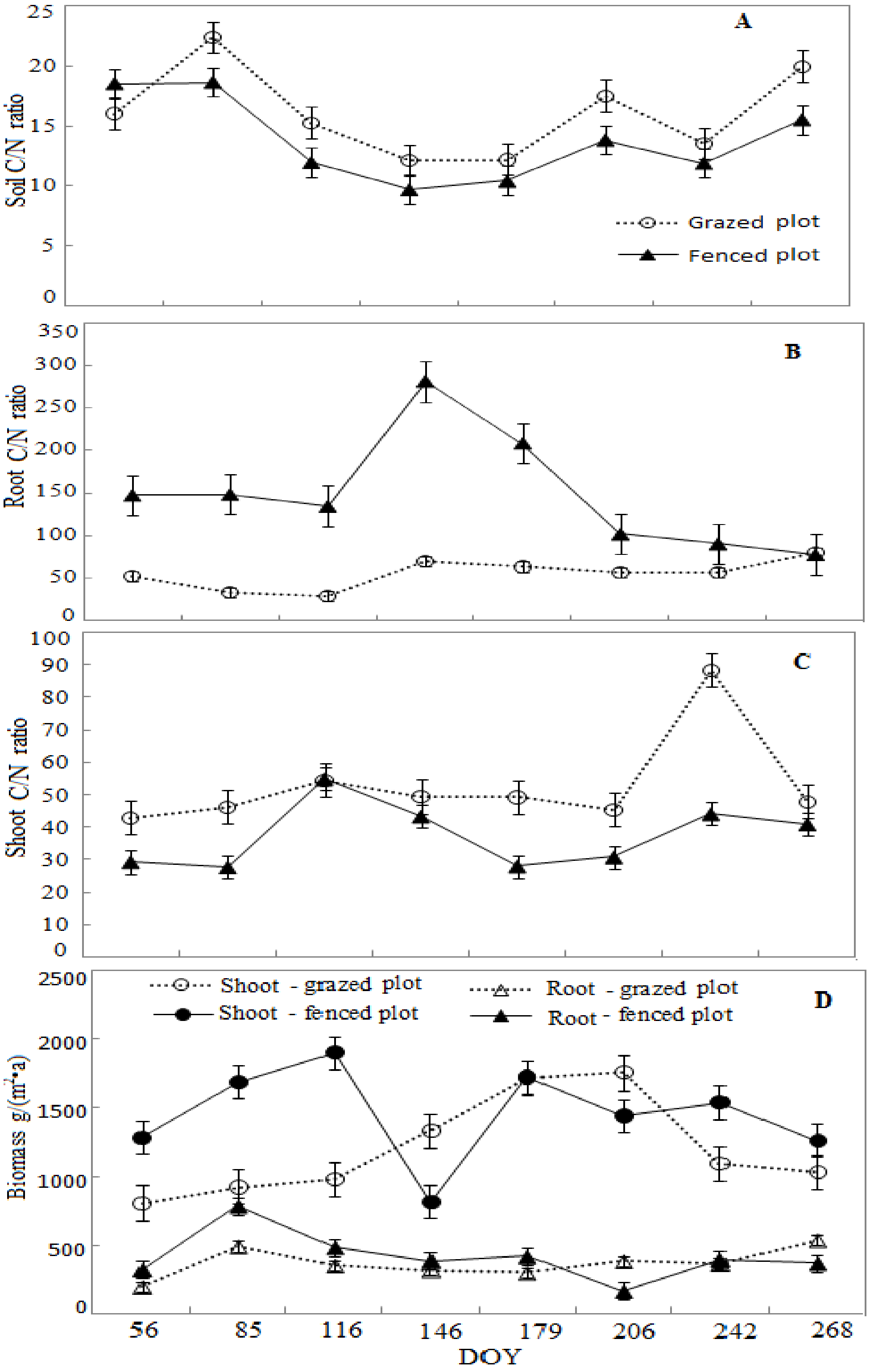

Fig. 3. Soil (A), Root (B) and Shoot (C) C/N ratios and biomass grass (D) during the measurement period in grazed and fenced plots. Values represent means (n = 6) ± error bars for each day of year (DOY).

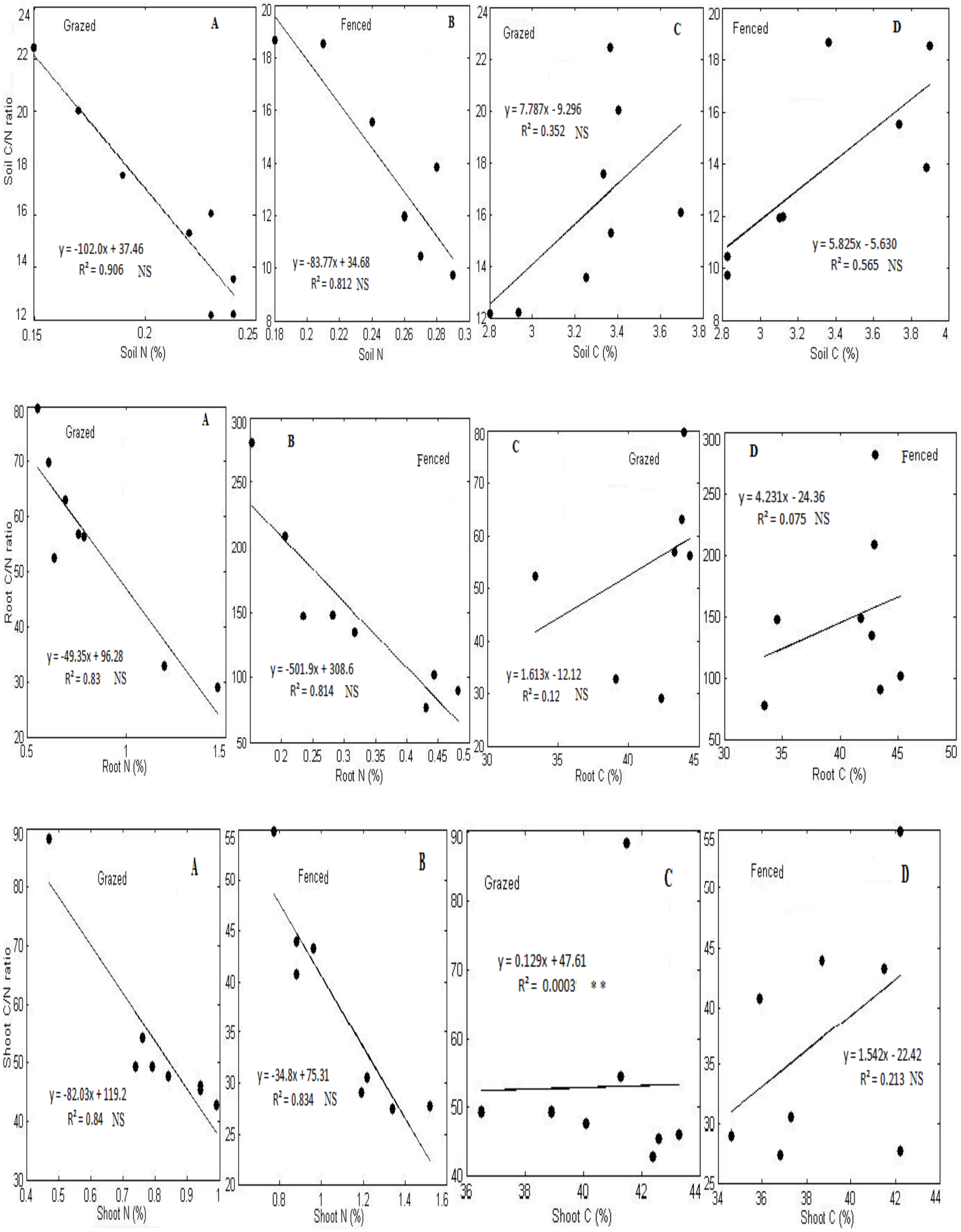

Fig. 4a. Relationship between C, N and C/N ratio in soil, roots and shoots in grazed and fenced plots. ** - Significant at P<0.01; NS – not significant.

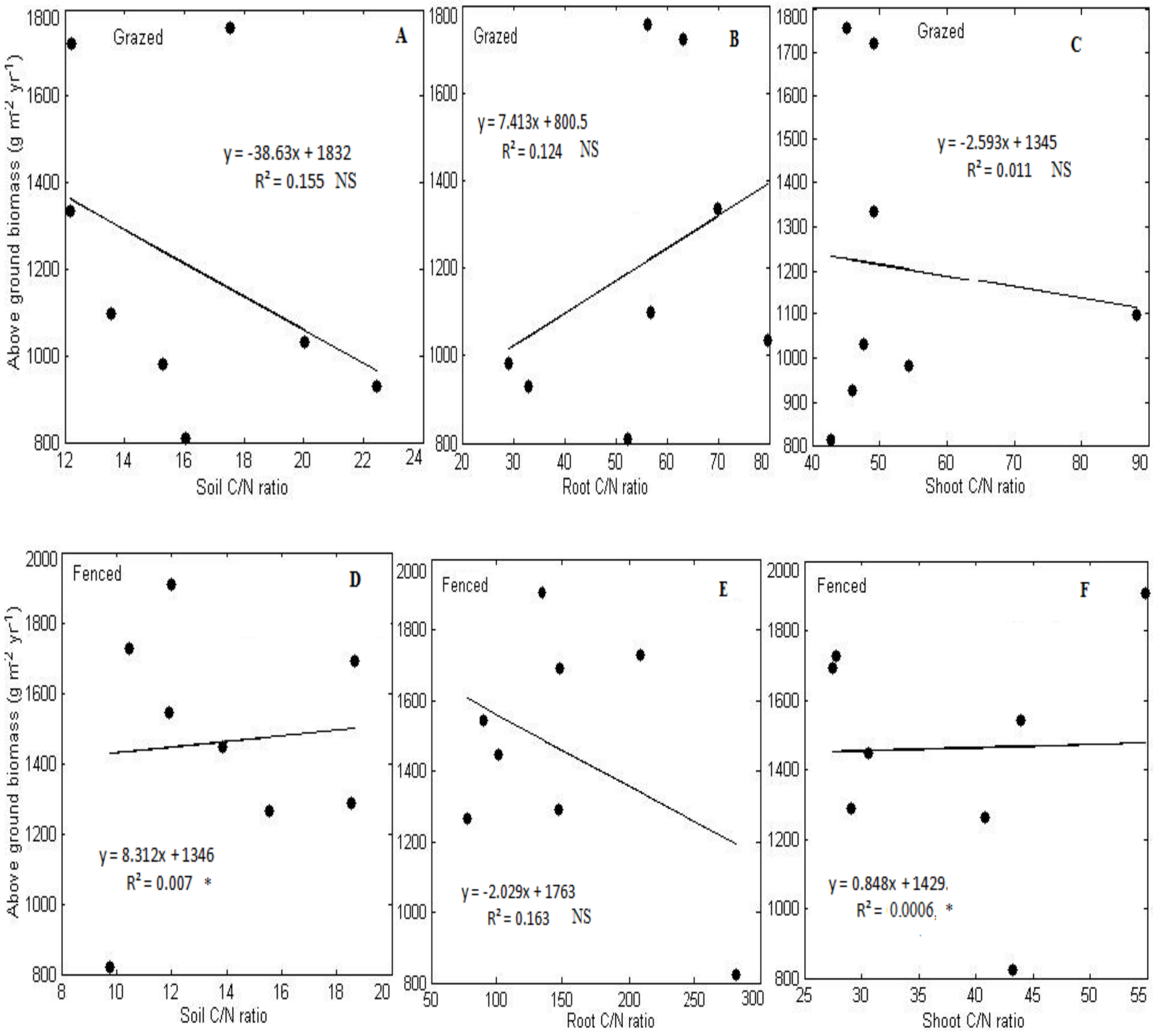

Fig. 4b. Relationship between above ground biomass and C/N ratio in soil, roots and shoots under grazed (A, B, C) and fenced (D, E, F) conditions.

***** - significant at P<0.05; NS - not significant*.