

**EFFECTS OF UNGULATE  
HERBIVORY AND TREE CANOPY ON  
ECOSYSTEM PROCESSES IN RUMA  
NATIONAL PARK, KENYA**

**By**

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## ABSTRACT

Herbivores and tree canopies may have significant influences on savanna ecosystem functioning that are not yet clearly understood. Positive influences of grazers and trees may be associated with fecal deposition and the ability to fix atmospheric nitrogen respectively. On the other hand, grazers could negatively influence savanna functioning through trampling and vegetation removal, while negative influence of trees could be through shading, which reduces the amount of photosynthetic photon flux density (PPFD) reaching the understory. Field studies were carried out in a humid tropical savanna in Ruma National Park, Kenya to understand how grazing by domestic animals and the *Acacia* trees influence ecosystem processes in the herbaceous layer community. The objectives of the study were; to monitor microclimate and soil moisture during an annual growth period, to measure the amount of biomass and nitrogen concentration in the soil and herbaceous layer vegetation during an annual growth period, to measure net ecosystem CO<sub>2</sub> exchange (NEE) and ecosystem respiration (R<sub>eco</sub>) during the vegetative period and to determine how trees and grazing influence soil moisture, N distribution, biomass development and ecosystem CO<sub>2</sub> exchange. Soil moisture was measured through gravimetric method, plant and soil nutrients were monitored through elementary analysis, biomass was measured using harvest method while CO<sub>2</sub> exchange was determined through gas chamber method. Measurements were stratified so that locations under the trees (understory) and in the open, outside the tree canopies were monitored separately to understand the interactive role of trees. Significant ( $p \leq 0.001$ ) differences in peak aboveground biomass at the different locations was recorded with highest peak aboveground biomass of  $902.7 \pm 115 \text{ g m}^{-2}$  recorded in non grazed plots. Trees had significant influence on soil moisture content as well as biomass production in both grazed and non-grazed plots. Plants in the non grazed plots exhibited significantly ( $p \leq 0.001$ ) higher N content compared to those in the grazed plots and similar trends were also observed in the soil N content. Soil moisture, soil N, biomass production and ecosystem CO<sub>2</sub> fluxes exhibited seasonality. Highest N concentration both in the plant material and in the soil occurred during the rainy period and higher N concentrations were observed in the tree understory compared to the open locations outside tree canopies. Significant seasonal changes were observed for NEE, R<sub>eco</sub> and GPP with Net ecosystem CO<sub>2</sub> exchange increasing during the rainy season up to  $15 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Highest R<sub>eco</sub> values occurred during the rainy season, with values of  $20.4 \pm 0.5$  and  $23.5 \pm 0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in grazed and non grazed plots respectively. The study showed that grazing affects soil moisture and soil nutrient content and may significantly influence the savanna ecosystem functioning. This influence is however, modified by the *Acacia* trees through improved soil N content and reduced PPFD in the understory. The observed trends create a unique production mosaic (understory and open locations) of ecosystem function and productivity in the humid savanna. Humid tropical savanna 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 input to the soil, soil chemical status, soil moisture status and soil temperature with herbivory acting as modifiers. These findings indicate that plant dynamics in humid tropical savannas are not a simple function of rainfall patterns or herbivory, but regulated by interactive effects of rainfall, grazing pressure and soil nutrients.

# CHAPTER 1: INTRODUCTION

## 1.1 BACKGROUND

Savannas are rolling grasslands scattered with shrubs and isolated trees, found between the tropical rainforest and desert biome (Smith, 1999). The contrasting plant life forms – trees, shrubs and grasses, cover approximately an eighth (see Appendix 4) of the global land surface (Otieno *et al.*, 2005, Sankaran *et al.*, 2004), which translates to 25% of terrestrial biomes and thus second to tropical forests in their contribution to terrestrial primary production. They support a large 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.

Savanna vegetation is characterized by the co-existence of grasses and trees (Chidumayo, 2001) and largely the key determinants of structure and function are water and nutrients with herbivory and fire acting as modifiers of their distribution and availability (Lehmann *et al.*, 2009; Sankaran *et al.*, 2004; Maranga, 1986). On the African continent, the properties of this ecosystem are highly dynamic and influence the regional as well as the global climate (Lata *et al.*, 2004) with predominant impacts on social and economic environment of more than half of the Africa's continent.

Large portion of savanna occur in Africa (Grace *et al.*, 2006) in two broad belts on each side of the equator (Brewer, 2002; Chapman and Reiss, 1995; Hubbell, 2001) occupying over one half of the continent's total land mass (Otieno *et al.*, 2005; Scholes and Archer, 1997). They are characterized by alternating wet and dry climate type with stable, though considered pre-climax vegetation (Hubbell, 2001). They experience warm continental type of climate with most of the areas receiving rainfall amounts between 150 and 500mm per year, falling within relatively short time period and the ratio of precipitation to potential evaporation (PET) ranging from 0.05 to 0.65 (Otieno *et al.*, 2005), with extreme seasonal fluctuations (Pomeroy and Service, 1986; Smith, 1999; Ewusie, 1993). Mean annual temperature is 27°C with peaks of 33°C in March and September (Brewer, 2002; Woinarski *et al.*, 2004). In Kenya, savanna occupies over one half of the total land area of the country (Otieno *et al.*, 2005). Savanna soils vary according to bedrock and edaphic conditions (Hubbell, 2001) with most soils being oxisols (Brewer, 2002;

Hubbell, 2001) although some areas are covered largely with black cotton soil. They have undergone long period of weathering, denitrification and leaching activities (Smith, 1999; Lata *et al.*, 2004) and also organic matter accumulation is very slow.

It is becoming increasingly clear that there exist dazzling, predictable, yet largely unresolved variations in nutrient balance in wet tropical savannas (Lalljee and Facknath, 2000). Nutrient dynamics are initiated at the beginning of wet season when moisture availability stimulates bioactivity and release of nutrients from materials accumulated in the dry season as well as translocation of the stimulated organic carbon from plant roots (Smith, 1999). Moist soils due to organic matter accumulation and reduced evaporation under trees enable rapid nutrient movement (Smith, 1999; Bernhard and Poupon, 1980). Compared to neighboring grasslands, soils under tree crowns (canopies) have higher concentrations of organic matter, higher concentrations of available N (nitrogen) and other important nutrients, better physical structure, and faster water infiltration (Belsky *et al.*, 1993). Nitrogen is the basic constituent of amino acids and the production of proteins in vegetation is directly proportional to nitrogen availability and reaction (Beadle *et al.*, 2001; Hall *et al.*, 1986) and thus an important component in biomass production. It is also a constituent of chlorophyll, the intermediates of chloroplast electron transport chain and enzymes of carbon reduction (Beadle *et al.*, 2001; Pandey, 2002).

Nitrogen inputs into savanna, is either by deposition or as a result of biological fixation (Beadle *et al.*, 2001). However, high rates of nitrogen input resulting from biological fixation may not reflect an increase in nitrogen content over the long-term assessment in savanna soils due to depletion by non N-fixing species within the ecosystem and losses from ecosystem respiration (Shannon *et al.*, 2005; Caylor, 2005). N fixation rates also seem to be controlled by other factors including soil P availability. Since P availability is generally low in the highly weathered soils and this deficiency might be one of the factors limiting the rate of nitrogen fixation in tropical legumes (Bustamante *et al.*, 2006). Several studies have shown that there is a relationship between below ground productivity and nitrogen dynamics in savanna, which contributes to the overall net primary productivity (Woinarski *et al.*, 2004). The ability of grasses to store, mobilize and subsequently re-use nitrogen nutrients may contribute to competitive advantage of grasses over woody vegetation and this could be an important factor in determining the species composition and productivity of savanna grasslands (Thornton *et al.*, 2002). It has

been shown that savannas are highly dynamic on all temporal and spatial scales, and vary with changes in climate, soil nutrient content, and herbivory (Scholes and Archer, 1997; Bond *et al.*, 2001; Skarpe, 1992). Essentially they result as interactions between soil water and nutrient availability with herbivores acting as modifiers.

Long-term landscape health can only be achieved if the basic ecosystem services of capturing and cycling water and nutrients are maintained. Use of savanna landscapes for pastoral production involves disturbances such as grazing (Belsky *et al.*, 1993), clearing and fire (Cech *et al.*, 2008), which can significantly alter the ability of a landscape to retain water, nutrients and carbon. However, we have a poor understanding of how these disturbances affect these key landscape processes at scales ranging from small patches to whole landscapes. Without this knowledge it is difficult to develop sound recommendations to help land managers maintain healthy landscapes. 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 has been implicated as a key mechanism maintaining the functional properties of grazing ecosystems (Augustine and McNaughton, 2006). This conclusion is supported by the long term declines in primary productivity, nutrient retention, and secondary productivity that some savanna ecosystems have experienced in response to increased densities and reduced migratory behaviour of domestic livestock.

Another proposed determinant of herbivore effects on ecosystems is soil fertility (Ritchie *et al.*, 1998). Both theoretical arguments and some empirical evidence indicate that nutrient availability in an ecosystem determines the degree to which plants invest in chemical defenses on both evolutionary and ecological time scales to prevent herbivory. Daniel (2002) in his study discovered an existence of interspecific differences in growth in response to nutrients, which is likely to be an important determinant of species distribution across natural fertility gradients. Tree crowns and roots also reduce soil and plant temperatures, reduce water-loss due to evapotranspiration, and reduce erosion. In addition, trees provide forage for browsing animals and in some cases, increase understorey herbaceous productivity and forage quality (Belsky *et al.*, 1993). *Acacias*, the quintessential African trees, are important components of natural areas in tropical savannas. They are foci for birds and many are nitrogen fixers (Midgley and Bond, 2001). Global biological N fixation (BNF) in terrestrial ecosystems has been estimated at

128 Tg N/yr), supplying ~15% of the N requirement across all biome types. According to this estimate, about 70% of BNF occurs in regions with warmer climates, for instance Africa (25.9 Tg N/yr) (Bustamante *et al.*, 2006). Besides the need for N fixation by the plant, the magnitude of nodulation depends on the density of bacteria populations, and on the physical and chemical properties of soil. Factors such as P and Ca limitation, high soil acidity, Al saturation, and seasonal water stress may constrain BNF in tropical savannas. It has also been noted that higher carbon and nitrogen densities in understorey soils may reflect differences in abiotic conditions under (Scholes and Archer, 1997), and away from trees and the fact that trees have foliage with higher nutrient content, higher litter inputs, and/or lower decomposition rates than the plants in the herbaceous layer. However, until the uncertainties in the biological N fluxes are clarified, the ecological significance of these *Acacia* trees on ecosystem function in the long-term remains unclear.

Increased dry-matter yield increases the proportion of available soil N that the plants recover in the herbage (Wilkins *et al.*, 2000), which helps to reduce immediate losses of N and improves its recycling. While effects of herbivory in causing savanna change have been documented in a number of studies (Cech *et al.*, 2008; Naiman *et al.*, 2003), few have attempted to quantify their significance relative to other determinants such as nitrogen dynamics in causing vegetation change. For instance, (Georgiadis *et al.*, 1989) found that above-ground grass production was stimulated by moderate grazing in Amboseli National park.

Tropical savannas play a major but poorly defined role in the global carbon (C) cycle (Parton *et al.*, 1997) since they contain approximately 30% of global soil C stocks (Anderson, 1991). The dynamics of these ecosystems are often jointly controlled by climate and biogeochemical factors. The interaction of these factors control fluxes of C through plant and soil organic matter (SOM) in grasslands. The magnitude of the fluxes and storages of C in these ecosystems however have been little studied, especially in the humid savanna. The herbaceous layer plays an important role in the annual carbon balance in the wet tropical savanna due to its drought tolerance ability. Few studies have characterized CO<sub>2</sub> exchange and productivity of this layer.

It is becoming increasingly clear however, that tropical savannas have a greater productivity (Grace *et al.* 2006), higher biodiversity and potentially larger impact on global carbon cycles than previously realised (Scholes & Hall, 1996; Chidumayo, 2001).

Information available on the possible impacts of climate change on grassland ecosystems is also conflicting. For example, studies indicate that increased temperature is likely to lead to increased respiration in grasslands (Weltzin *et al.* 2003). Other studies in Nairobi National Park, (Hall and Scurlock, 1991) have shown that net loss of soil carbon and nitrogen may result, depending upon the frequency of fire, overgrazing and drought. Therefore knowledge of the nitrogen nutrient status of the various plant organs and soil, and their changes during the growing season, and relationship with CO<sub>2</sub> exchange and productivity in the savanna is a necessary basis for a proper judgment of the effect of these changes on the functioning of the ecosystem.

## **1.2 STATEMENT OF RESEARCH PROBLEM**

Savanna characteristics and distribution make them relatively susceptible to disturbances such as land-use and climate change. Responses and adaptation to such disturbances in the wet savanna however, are not well understood. Limited knowledge also exists on the processes that regulate ecosystem N balances, its input into the soil, its uptake by the herbaceous layer vegetation and how N availability interacts with community composition and herbivory to determine ecosystem CO<sub>2</sub> exchange and biomass production in the wet savanna. Better understanding of ecosystem processes related to N availability and CO<sub>2</sub> fluxes may help design appropriate management policies that ensure ecosystem sustainability as well as continued supply of vital ecosystem services.

## **1.3 JUSTIFICATION**

Savanna are key ecosystems that provide vital services such as fodder for wild and domestic animals, recreation, biodiversity habitats, CO<sub>2</sub> sequestration, timber etc. The herbaceous layer for example is vital as a source of fodder for large ungulate community and supports the tourism sector, a key source of foreign income in most African governments as well as a vital source of proteins for the human population. Primary production, which ensures fodder availability, however, relies heavily on N availability and CO<sub>2</sub> exchange processes. Understanding of processes that regulate primary production as well as the linkages among the ecosystem domains is key to savanna management and sustainability.

## 1.4 HYPOTHESES

1. Moderate grazing stimulates tillering of the grasses, increase N input through dung deposition and improve primary production in wet savanna.
2. Acacia trees improve soil nitrogen, reduce soil and air temperatures and reduce rate of soil moisture loss leading to higher productivity in herbaceous layer under the tree crowns.

## 1.5 OBJECTIVES

1. To monitor the microclimate and soil moisture during an annual growth period.
2. To measure the amount of biomass and nitrogen concentration in the soil and herbaceous layer vegetation during an annual growth period.
3. To measure net ecosystem CO<sub>2</sub> exchange (NEE) and ecosystem respiration (R<sub>eco</sub>) during the vegetative period.
4. To determine how trees and grazing influence soil moisture, N distribution, biomass development and ecosystem CO<sub>2</sub> exchange.



## CHAPTER 2: LITERATURE REVIEW

### 2.1 Nitrogen Nutrition in the Savanna.

Nitrogen is taken up by plants predominantly as ammonium ( $\text{NH}_4^+$ ) or nitrate ( $\text{NO}_3^-$ ) ions and is supplemented in leguminous plants by direct fixation of atmospheric nitrogen into ammonia (Larcher, 2003; Kormondy, 2001; Percy *et al.*, 1997). Most plants prefer ( $\text{NO}_3^-$ ) as long as the pH in the rooting zone remains favourable. In nutrients poor acid and wet soils, plants take up mostly ( $\text{NH}_4^+$ ). Nitrogen absorption like all other ions require energy and thus is a function of respiration (Larcher, 2003), and other disturbances such as water stress (Jeffrey *et al.*, 2001), although the relationship between water availability and Nitrogen balance has not been adequately investigated in wet tropical savanna.

Inorganic N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) and organic nitrogen are the major forms in which fixed nitrogen occurs in most environments (Adeniyi, 2006; Kormondy, 2001). Ammonium (the most reduced form of nitrogen) and nitrates (the most oxidized form of nitrogen) are the most important forms in which nitrogen is fixed in biological processes (Adeniyi, 2006), although the importance of biological processes in savanna productivity has not been described adequately. Nitrogen nutrient input to the soil is also through rain, canopy leaching with through fall and stem flow and via litter fall (Schulze and Martyn, 1997). Several studies have shown that the atmosphere provides a ready source of N to the N-depleted systems through biological fixation of  $\text{N}_2$  (Welch, 1993). This occurs under aerobic conditions and requires the presence of heterocystous blue-green algae and/or Rhizobium which is dominant in soils depleted in N.

Other studies have shown that grasses are capable of absorbing N from gases ( $\text{NO}_2$ ,  $\text{NH}_3$ ) via their stomata, or as ions ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ) via the young stem or needles (Schulze *et al.*, 2005). However, it has been noted that N can be lost from savanna soil through gaseous emissions ( $\text{NH}_3$ ,  $\text{N}_2\text{O}$ ,  $\text{NO}_2$ ), leached as  $\text{NH}_4^+$  and  $\text{NO}_3^-$  ions, immobilized for longer or shorter periods through plant fixation and microbial growth (Kristina, 2005; Kormondy, 2001). Absorbed N is incorporated as amino groups into carbon compounds, forming amino acids and amides (Larcher, 2003). Amino acids are basic compounds for the biosynthesis of p-proteins, nucleic acids and nitrogen compounds of secondary

metabolism. During its assimilation, nitrogen is reduced from nitrate to nitrite by catalysis of nitrate reductase (Larcher, 2003; Kormondy, 2003; Brewer, 2002; Chapman and Reiss, 1995) and the ammonium taken up is assimilated via glutamine synthesis (Larcher, 2003). Nutrient balance estimates in root and leaf litter have indicated that there's loss of nitrogen, probably due to leaching activities (Schmidt and Lamblea, 2005), although this has not been investigated in the savanna. It has also been shown that both foliar N and its resorption in trees are related to climatic factors and therefore leaf litter N is climate dependent.

## 2.2 Soil moisture and nitrogen

Both soil microclimate and organic matter quality control nitrogen turn-over (Kormondy, 2001), with soil microclimate limiting mineralization mostly at the beginning of a rainy season. The input of rainfall to the subcanopy habitat via stemflow and throughfall however depends on the size and intensity of rainfall events and the size, bark characteristics, canopy architecture, and leaf area of the tree (Scholes and Archer, 1997). It is only during this time that soil organic matter exerts control, although the actual influence has not been investigated in wet tropical savannas. Topoedaphic gradients of soil texture, moisture, redox values, and carbon (C) and N content play important roles in determining N cycling in grassland landscapes (Douglas *et al.*, 2000).

The accumulation and decomposition of organic matter and subsequent release of mineral nutrients are strongly related to soil water status (Holtgrieve *et al.*, 2006; Boutton *et al.*, 2008). Other studies indicate that in the open pastures, nitrates ( $\text{NO}_3$ ) are leached from the surface soil to greater depth where they are stored as a result of sorption to positively charged surfaces. Therefore pasture in such soils results in the formation of a subsoil nitrogen reservoir, which still may be recycled to the surface by plants (Lilienfein *et al.*, 2003) although the studies on soil water status and trees of wet savannas is still inadequate. Soil moisture and soil nutrients are the key environmental variables regulating productivity and relative abundance of savanna vegetation (Walter, 1971). It has been observed that plants that manage to grow on dry and nutrient-poor soils are generally less palatable and have lower nutritional value to herbivores than those from wet nutrient-rich soils (Lilienfein *et al.*, 2003). Therefore, the moisture and nutrient status of the soil has some effect on the carrying capacity of the savanna (Werner, 1991).

Nitrogen content in grasses has been shown to decline with maturity, season, and this in turn lowers grass palatability (Beadle *et al.*, 2001; Henry and Lynn, 2000). Studies at Nairobi National parks and Masai Mara Game Reserve in Kenya (Boutton *et al.*, 2008), shows that nutrient changes in grasses is related to alternation of wet and dry seasons.

Although other studies have suggested a wide acceptance of competition as a major force structuring the distribution and abundance of species along environmental gradients (Bond *et al.*, 2001), grasses have been shown to access and deplete nutrients that are mineralized in the topsoil more than trees because they are shallow-rooted and fast-growing (Sankaran *et al.*, 2004). The interspersion of grasses and woody plants also alters the hydrology of the savanna at a landscape scale by influencing horizontal patterns of water distribution (Scholes and Archer, 1997). However, in cases where trees significantly depress herbaceous production, bare ground may increase, making sites more susceptible to losses of water and nutrients via surface flow. The availability of nutrients to either vegetation component also depends on the soil type. Soil that is readily leached may be advantageous for trees (Schmidt and Lamblea, 2005; Sankaran *et al.*, 2004), although this has not been established in the savanna. It has also been suggested that grasses and trees avoid competition by differentially utilizing surface and subsurface soil resources respectively (Wilson and Bowman, 1994). In some cases, the presence of trees helps to maintain ground cover (Scholes and Archer, 1997), since tree cover is less variable between years and less easily removed by herbivores or fire, and tree leaf litter is more persistent than grass litter.

### **2.3 Herbivory in the savanna**

Herbivores have been found to indirectly control the form and function of savanna ecosystem through limiting the abundance of one or a few important plant species that control resource abundance like the nitrogen fixers and other efficient nutrient competitors (Ritchie *et al.*, 1998; Sterling, 2004; Herbert *et al.*, 1993; Fitzgerald, 1973). They modify the ecosystem feedback between dominant plant species and nutrient cycles through effects on nutrient uptake, relative growth rates, and tissue nutrient concentrations which in turn yield faster litter decomposition (Ritchie *et al.*, 1998; Belsky, 1994; Manuel and Molles, 2003; Sterling, 2004; William *et al.*, 1998). Some animals like black rhinos are known to eat an extremely wide range of plant species,

ranging from trees to shrubs and herbs (Birkett, 2002). This seems likely that most animals may compensate for loss of *Acacia* trees by switching to other species. Indigenous herbivores and perhaps some highly mobile nomadic livestock (Ellis & Swift 1988) may have comparatively little influence on the vegetation composition and production. Other studies in Amboseli National Park (Georgiadis *et al.*, 1989), have shown that above-ground grass production can be stimulated by grazing although this depends on complex interaction of ecological factors. Similar results have also been reported in united states grasslands (Singer and Schoenecker, 2003). It has also been suggested that in the short growing period after rain, palatable fodder is abundant, and in the dry season most animals become inactive or migrate in pursuit of water and fodder (Skarpe, 1992) while other herbivore populations in preserves for example Nairobi National Park, may be limited by shortages of nutritionally adequate food during dry seasons (Boutton *et al.*, 2008). Selective herbivory can limit the abundance of nitrogen-fixing species, a key functional group in many ecosystems, thereby reducing soil nitrogen availability (Ritchie *et al.*, 1998). Naiman *et al.* (2003) found that large mammalian herbivores influence terrestrial ecosystem processes both directly by consuming plant material and indirectly by altering litter quality and nutrient cycling. However, herbivores actual influence on the nitrogen turnover rate has not been delineated in Ruma National Park. Grazing induces changes in reallocation of nutrients within individual plants and indirectly stimulates soil mineralization processes. Lalljee and Facknath (2000) found that there's a higher rate of nutrient cycling in undisturbed ecosystem than in the disturbed ecosystem. These are conflicting findings since they suggest that the type of resource limiting plant growth may determine the effects of herbivores on nitrogen cycling.

## **2.4 Savanna Trees**

The effects savanna trees have on understorey grass productivity have been a focus of research for decades, and both negative and positive effects have been described (Ludwig *et al.*, 2001; Herbert *et al.*, 1993; Scholes and Archer, 1997), although insufficient literature exists about how these effects interact in humid tropical savannas. The effects of trees on grasses ranges from positive to neutral to negative, and these may depend on the ecophysiological or specific characteristics of the tree and grass (Scholes and Archer,

1997), availability of resources in terms of variability in the amount and seasonality of precipitation and extent of selective grazing and frequency and, intensity (Belsky, 1994; Scholes and Archer, 1997). Trees reduce grass growth by competing with grasses for water, light and nutrients, and can also improve grass production through hydraulic lift, reduced evapotranspiration and increased nutrient availability (Fulco *et al.*, 2007; Scholes and Archer, 1997), but the consequences of this competition on vegetation shift remain largely unquantified in humid tropical savanna.

Studies have also shown that there is a higher grass productivity under savanna trees, which is often attributed to an increase in soil fertility (Sankaran *et al.*, 2004; Treydte *et al.*, 2009), although well documented exceptions to this generalization indicate that assessments should be made on a case-by-case basis. The productivity of areas under tree canopies may be enhanced by improved water and nutrient status (Scholes and Archer, 1997), but be suppressed by low irradiance and competition between trees and grasses for belowground resources. Other studies in southern Kenyan rangeland (Wasonga *et al.*, 2003) have shown that tree canopy enhances grass biomass during the dry than the wet season, while in Kruger National park in a South African savanna (Treydte *et al.*, 2009), trees have been shown to further increase grass species diversity and patchiness by favouring shade-tolerant species. Above ground production appears to be limited primarily by nitrogen content in the soil in open grasslands (Maginniss, 2002). Earlier studies have shown that increased herbaceous production beneath tree canopies in a Kenyan savanna was associated with lower soil temperatures, lower plant water stress, and greater soil organic matter concentrations (Belsky *et al.*, 1989; Weltzin and Couehenour, 1990), mineralizable N, and microbial biomass compared to those of adjacent grassland away from tree canopies. Variations in soil nutrient concentration in open grasses and understorey sites is likely to affect the extent of nutrient limitation in grasses (Ludwig *et al.*, 2001), but this has not been investigated adequately in the humid tropical savanna. Savanna trees have been shown to compete more intensely with understorey plants at wetter sites (Otieno *et al.*, 2005), where their roots terminated in or near crown zones, than at drier sites, where their roots extended further into open grassland (Ludwig *et al.*, 2003; Nygren *et al.*, 2007). Although little is known in Kenyan humid savanna, earlier studies have shown that modest reductions in radiant energy associated with tree shading can lower soil temperatures, reduce evaporative demand and

water stress on understory plants (Belsky *et al.*, 1989; Scholes and Archer, 1997), and enhance subcanopy soil moisture storage, availability, and plant water-use efficiency. Nutrients added by trees at crown zones in the form of tree litter increases understorey productivity by fertilizing nutrient limited soils (Ludwig *et al.*, 2003).

Some trees have been shown to have greater influence on soil nutrient status than others (Midgley and Bond, 2001) and it has also been demonstrated that shade contributes more to re-growth after severe defoliation than to growth under more normal conditions (Belsky, 1994; Manuel and Molles, 2003; Schmidt and Lambalea, 2005). *Acacia* trees have been described to increase the quantity and influence the dynamics of nitrogen in grasses through production of litter rich in nitrogen. This has been enabled through the mutualistic relationship with nitrogen fixing bacteria (Manuel and Molles, 2003). However, this has not been investigated in Ruma National Park. Skarpe (1992) demonstrated that trees themselves improve the nutrient conditions in their immediate environment. When such fertile patches shift as trees die and others establish in other places, they form a patch-dynamic system, and in a longer time perspective will increase the overall nutrient level in the ecosystem. The abundance and distribution of savanna trees is significantly affected by the activities of herbivores. Trees dispersed to and capable of establishing in grass-dominated zones can provide vertical structure attractive to perching birds that disseminate seeds of other woody species (Scholes and Archer, 1997). It has been shown that much greater amounts of N accumulate in the bush land than in the open grassland it replaces (Cech *et al.*, 2008), although this has not been investigated in humid tropical savanna. Previous studies which compared forage quality under trees and in the open field reported higher forage quality under *Acacia* trees (Belsky, 1992). Increased forage quality is probably caused by higher soil nutrient concentrations under tree canopies (Belsky *et al.*, 1989; Scholes and Archer, 1997), although this has not been investigated in humid tropical savanna of Kenya. A recent study in Namibia showed that the number of large trees was reduced by 50% over the last 36 years due to pressure from wild animals while the extent of shrubland dramatically increased (Fulco *et al.*, 2007). They also delineated that outside protected areas, the situation was often even more dramatic, with most of the large trees being removed by local people for production of charcoal (Fulco *et al.*, 2007; Keller *et al.*, 1992). The effects of such activities on herbivore food quality and availability however is not clear in

humid tropical savannas of Kenya. Other studies in the Middle Awash Valley of Ethiopian have shown that the nutrient status of soil under the canopies of woody species were higher than the open grassland (Abule *et al.*, 2005), especially with regard to soil pH, total N and organic carbon.

## **2.5 Carbon dioxide exchange in the savanna**

The chemical composition of the atmosphere is changing rapidly with increasing industrial emissions and changes in land use (Eugenio and Magaly, 1993). Considerable change in land use is occurring in the tropical region, of which the conversion of natural savanna ecosystems to agricultural soils is the most significant (Keller *et al.*, 1992; Xiaoyong *et al.*, 2003). Due to the expansive area savannas occupy, their management may influence the regional and possibly global energy, water and carbon balances (Santos *et al.*, 2004), and the products of their combustion may profoundly influence atmospheric chemistry.

Savanna burning results in an efflux of carbon to the atmosphere, although this is made up of an unknown proportion of 'natural flux' associated with natural fires, and 'anthropogenic influences' including management for grazing, and land-use change (Grace *et al.*, 2006). Savanna ecosystem are under great pressure due to their ability to provide pasture for cattle grazing, wood extraction, charcoal for smelting and land for agriculture (Grace *et al.*, 2006; Keller *et al.*, 1992) although the magnitude of land-use change is not well known. Tropical savannas are remarkably biodiverse, and they contain a high degree of endemism with a wide range of life form (Harris, 1979), and increasingly, savanna lands are being brought into intensive use, and these may have consequences of environmental risks. Due to warming and drying, previous studies have predicted that savanna burning may increase greatly over the next century as a result of climate change (Grace *et al.*, 2006).

Studies have shown that ecosystem productivity and CO<sub>2</sub> fixation and assimilation rates in the understory locations may be influenced by soil moisture regime, light intensity (Kinyamario *et al.*, 1993) and species composition between the canopy and open grassland. Although vegetation under the trees is subjected to alternate sun and shade periods, which could reduce the amount of CO<sub>2</sub> fixed, increased efficiency in utilizing diffused light and the extended favourable edaphic and microclimatic conditions that

prolong the productive period may result into increased production in the tree understorey (Hussain *et al.*, 2009). However, the effect of canopy on amount of CO<sub>2</sub> fixed has not been demonstrated in humid tropical savanna. Recent studies on carbon balance of a tropical savanna of Australia (Xiaoyong *et al.*, (2003) has revealed that the savannas became a carbon sink during the wet season, but a weak source during the dry season. However, the different response of vegetation to CO<sub>2</sub> between seasons is not clear in humid topical savannas of Kenya.



## CHAPTER 3: MATERIALS AND METHODS

### 3.1 Study site



Plate 1a: Location of Ruma National Park ( $00^{\circ} 35' S$  &  $34^{\circ} 12' E$ )  
*Ruma National Park is located in Nyanza province, Suba District, in western Kenya (see Plate 1a). The altitude of the area is 1400 meters above sea level.*

The study site was located within Ruma National Park, ( $00^{\circ} 35' S$  &  $34^{\circ} 12' E$ ) in Nyanza Province, Suba District, in western Kenya (see Plate 1a). The altitude of the area is 1400 meters above sea level. It 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 terrain is mainly rolling grassland, with tracts of open woodland and thickets dominated

by species of *Acacia*, *Rhus* and *Balanites*. The surrounding area is settled, with a mix of small-scale cultivation and grassy pastureland, (see Plate 1b). 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. Main grazing animal populations consist of Roan antelope and Jackson's hartebeest, a larger and redder species than Coke's which is found in most Kenya parks, Oribi, one of the smallest of the antelope family and Rothschild giraffes.



Plate 1b: Grazers found within the park surrounding

*The park surrounding is greatly influenced by livestock farming. The livestock cause disturbance to the vegetation through overgrazing as well as influence the cycling of nitrogen through defecation and vegetation removal.*

The study site was located within the NYS (National Youth Service) section of the park, on the flat floor of the Valley, bordered by escarpments at an altitude of approximately 1400 meters a.s.l. and includes a section of Lambwe Hills Forest Reserve to the southeast. The soils are largely "black cotton" clays. The climate is hot and humid with a mean annual air temperature of 30°C and mean annual rainfall of approximately 1200-1600 mm with a bimodal distribution pattern between April - June and September - November. January - March are usually the driest and hottest months.

### ***Experimental design***

Two plots measuring 50 x 50 m were established within *Acacia* woodlands. One plot was enclosed using a 2 m high fence (to exclude grazing) (see Plate 2), 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 5-10 minutes feeding on the same area and moving on to other locations since the grazing area was expansive. Within the plots, we randomly established 3 m<sup>2</sup> measurement units under canopy and in the open grassland.



Plate 2: Fenced (non grazed) study plot

*Perimeter fence separating grazed and non grazed plots where measurements were conducted. Solar panel (inset) and other equipments were installed within the fenced plot.*

## 3.2 MEASUREMENTS

### 3.2.1 Microclimate

Weather conditions were continuously recorded at a meteorological station set up at the study site within the fenced plot during the study period. Precipitation (RG3 HOBO pedant rain gauge, HOBOware, Eichstetten, Germany), global radiation, photosynthetic photon flux density (PPFD) (HOBO pedant, HOBOware, Eichstetten, Germany), (*see plate 4*), air humidity and temperature at 2 m high (FUNKY-Clima, ESYS, Berlin, Germany), (*see plate 3*). Measurements were taken every 5 minutes, averaged and logged every half-an-hour by data logger (DL2e, Delta-T Devices Ltd. Cambridge UK). Additional, discontinuous recording of microclimate data within and outside the CO<sub>2</sub> flux chambers during gas exchange measurements were conducted. Recorded information included PPFD (LI-190, LI-COR, USA) within the transparent chambers, just above the

herbaceous vegetation (0.5-2.0 m above ground surface),  $T_{\text{air}}$  at 20 cm height inside and outside the chambers (Digital thermometer, Conrad, Hirschau, Germany) and soil temperature ( $T_{\text{soil}}$ ) at -10 cm soil depth (Einstichthermometer, Conrad, Hirschau, Germany) inside the soil frames/chambers. Data were recorded every 15 seconds alongside  $\text{CO}_2$  fluxes. This allowed closer monitoring of the microclimate within plots and to relate the fluxes to actual conditions within the chambers during measurements.



Plate 3: Humidity sensor (Fischer 431402)

*Passive radiation shield with preinstalled RHT sensor. The Radiation Shield was used to protect the Temperature Sensor and the RH/Temp Sensor from ambient interference. Without proper protection, the sensor could give inaccurate readings.*



Plate 4: Hobo Pedant, temperature/Light sensor

*The hobo equipment was used to measure light under shade (canopy) and in the open grassland. This was necessary to estimate the photosynthetic active radiation available for the vegetation.*

E) and ecosystem respiration ( $R_{\text{eco}}$ ) were measured on a monthly basis (1 week in a month, with 3 days of measurements) between February and October 2008 using ecosystem gas measurement chambers (see Plate 6). A set of 6 soil collars, 3 in non-grazed grass (fenced) plots and 3 in grazed (open) plots were established a month before the

measurements were conducted. Both the grazed and non-grazed plots were dominated with *Acacia*. Selective vegetation removal was avoided in order to maintain the natural conditions of the plots. Each soil frame constituted a measurement plot and hence on each measurement week, 3 grazed and 3 non grazed plots were measured on day 1 and 2 completing the measurements at ~18:00 hr each day. New plots were then established for the next cycle of measurements. During any single measurement day, NEE and  $R_{\text{eco}}$  were directly measured with a systematic rotation over all plots using manually-operated, closed gas exchange chambers modified from the description given by Droesler (2005), as used in central European bogs and alpine grasslands (Otieno *et al.*, 2009; Hussain *et al.*, 2009). The 38 x 38 x 54 cm chambers (see Plate 6) of the system were constructed of transparent plexiglass (3 mm XT type 20070; light transmission 95%). Dark chamber for measuring  $R_{\text{eco}}$  was constructed of opaque PVC, and covered with an opaque insulation layer and with reflective aluminium foil. Using extensions, chamber height was adjusted to the canopy height. Chambers were placed on the plastic frames/collars (see Plate 7), that were inserted 4 cm into the ground a month ahead of the measurements. They were sealed to the chamber with a flexible rubber gasket and the chamber firmly secured using elastic bands strapped onto the ground from its two sides. Tests indicated that leakage did not occur (see Droesler, 2005 for details), however, this could not be examined regularly in the case of systematic field measurements and required that each set of data be scrutinized for abnormalities.

Increased air pressure in the chambers was avoided by a 12 mm opening at the top of the chamber which was closed after the chamber had been placed onto the frame and before any measurements were taken. Circulation of air within the chamber was provided by three fans yielding an air flow speed of  $1.5 \text{ ms}^{-1}$ . Change in chamber  $\text{CO}_2$  concentration over time was assessed with a portable, battery operated IRGA (Li-Cor 820) (see plate 5). Measurements were carried out in most cases within 3 - 5 minutes of placing the chamber on the frames. Once steady state was attained, data were logged every 15 s for 2 minutes and  $\text{CO}_2$  fluxes were calculated from a linear regression describing the time dependent change in  $\text{CO}_2$  concentration within the chamber. By mounting frozen ice packs inside and at the back of the chamber in the air flow, temperature during measurements was maintained within  $2^\circ\text{C}$  relative to ambient. Air (at 20 cm above the ground surface) and soil (at -10 cm) temperatures inside and outside of the chambers were monitored during

measurement and data logged at the onset and end of every round of NEE measurement on each plot. Similarly, light levels within the chamber, and above the vegetation (canopy) were monitored using a quantum sensor (LI-190, LI-COR, USA) and data logged every 15 seconds. Tests conducted in a controlled climate chamber showed that vapour pressure deficit (VPD) changes within the CO<sub>2</sub> measurement chambers were limited to 1 hPa during the period (~3 min) when the chambers were placed on the vegetation. We therefore assumed that such small VPD changes might not affect CO<sub>2</sub> exchange via stomatal effects. During each measurement series, repeated light and dark chamber measurements were conducted from sunrise to sunset over single days comparing three non-grazed and three grazed plots. Eight to eleven measurement cycles were accomplished on individual days. The frames were removed and replaced for the next set of measurements. Between February and October, both grazed and non-grazed plots were only measured once and a new set of 3 plots each measured on the next day. This step was taken to avoid possible reductions in fluxes that may arise from previous disturbances on the tall grass. A database was compiled with the observed environmental conditions. To estimate Gross Primary Production (GPP), ecosystem respiration was estimated for each NEE observation time by linearly extrapolating between dark chamber observations ( $R_{\text{eco}}$ ), and then adding it to NEE (cf. Li *et al.* 2008). Measurements of NEE and  $R_{\text{eco}}$  were closely associated in time, thus the corrections made in  $R_{\text{eco}}$  were very small. The measurements of NEE and  $R_{\text{eco}}$  were closely associated in time, thus the corrections made in  $R_{\text{eco}}$  were very small. Measurements were conducted from the end of February until October in order to develop a picture of the seasonal dynamics of CO<sub>2</sub> exchange. Limitation in manpower to carry out the labour intensive chamber measurements and the nature of the experimental site prevented continuation of the observations with chambers during night time periods.

### **3.2.3. Biomass estimation.**

After gas exchange measurements on each plot, all the aboveground biomass within the 39.5 x 39.5 cm<sup>2</sup> area enclosed by the collars was harvested to ground level. The harvested biomass was sorted into green and dead material before being oven dried at 80°C for 48 hours and weighed to obtain the live and dead dry weight. The harvested plots were clearly marked and numbered to avoid repeated harvesting. Leaf area of the grass was

determined by use of leaf area meter (CI-202, CID, Camas, WA) (see Plate 8). Leaf area was then used to determine leaf area index (LAI).



Plate 5: Infrared gas analyzer.

*Infrared gas analyzer IRGA (Li-Cor 820) used for recording gas flux in real time. The IRGA was battery powered and was connected to the chambers via rubber tubes of around 2 mm in diameter, which were gas tight and resistant to UV-radiation.*

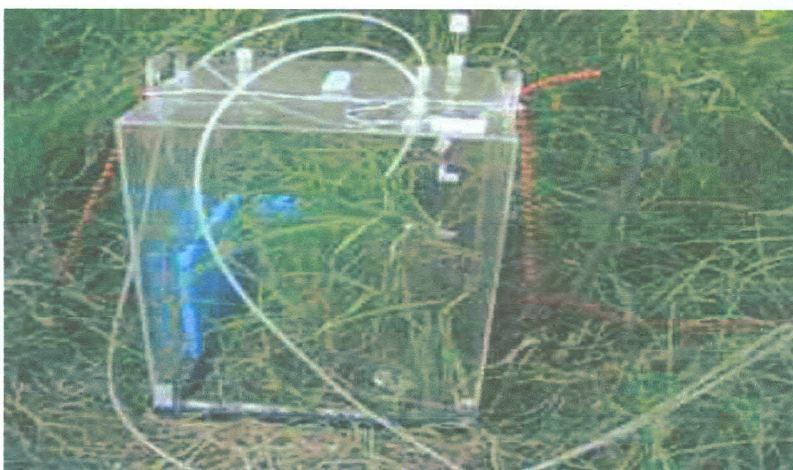


Plate 6: Gas chamber

*Gas chamber (Light) made of 3 mm thick Plexiglas used to enclose a volume of air over the vegetation. To ensure gas tightness, the different materials for the chamber (Plexiglas) was sealed (closed-cell rubber) and collar (PVC-hard) were gas tight.*



Plate 7: Square Collar

*40cm x 40 cm square collar built using 3 mm thick PVC, fixed into the ground. Two types of collars had walls of 10 cm high and were surrounded by a 3 cm wide platform, 3 cm below the top. The chamber with its sealing was placed on this platform during the measurement.*



Plate 8: Leaf meter

*Leaf area meter was used to measure the area of green leaf plades after harvesting.*

### 3.2.4. Soil water content

From the same plots of CO<sub>2</sub> measurements, soil sampling was done with a 3 cm diameter core sampler at the middle of the frame down to 30 cm and the soil cores divided into



three layers from 0-10, 10-20 and 20-30 cm. This was done on a monthly basis same as the biomass by sampling two replicates per sampling date. Each sample (layer) was immediately weighed to determine its fresh weight before oven drying at 105°C for 48 hours and dry weight determined. Gravimetric soil moisture content was determined as the relative change in weight between fresh/wet and dry soil samples (Eq. 1).

$$\text{Soil water content(\%)} = \frac{(\text{Soil(wet)} - \text{soil(dry)})}{\text{soil(dry)}} \times 100\%$$

*Equation 1*

### **3.2.5. Soil pH, CEC, Bulk density, Soil and Plant nutrients**

The second soil sampling was done with a 3 cm diameter core sampler at the middle of the frame down to 30 cm and the soil cores divided into three layers from 0-10, 10-20 and 20-30 cm. After root removal, soil samples (fresh) from the respective plots and depths were divided into two equal parts. One set of samples was used for the determination of soil nitrogen, while the other set was used for the determination of soil pH and bulk density. Soil pH was determined by filling fresh ground 50 g homogenised soil into plastic bottles with 100 ml of distilled water and shaken for 1 hour. A calibrated pH-meter was used for pH determination. CEC was determined based on TSBF Hand book of methods (see Anderson and Ingram, 1993). Bulk density was determined by core method where fixed volume of soil samples at different depths was calculated after drying at 100°C.

A portion of 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 then analyzed to determine their N and C concentrations (%) by means of elementary analysis (see Markert, 1996). Total N uptake was determined from the total weight of the aboveground biomass and expressed as  $\text{gm}^{-2}$ . Similarly, total root N uptake was calculated from the total weight of below ground biomass. Similar procedure was followed to determine the total nitrogen content (%) in soil.

### **3.3 Data analysis**

Statistical analyses were performed using the standard statistical packages, i.e. SPSS and General Linear Models program of SAS (SAS Institute, 2000). The threshold for

potentially significant at  $< 0.05$  interactions was used, while planned contrasts of grazing effects within the plot was evaluated with a three-sided t-test using the mean squared error. A factorial mixed-design analysis of variance was performed on the samples for the different processes against grazing. In case of significant effects, means were compared using least significant difference (LSD) at  $P < 0.05$  (as described by Little and Hill, 1978). Three replicate soil cores per plot were summed to give the number of cores ( $n$ ) per treatment per study period as the data set used for statistical tests, and this was repeated for grasses.

Higher light intensities and temperatures were used in the field compared to the laboratory situation. On 6 occasions, the experimental conditions were set to periods with maximum light intensities of approximately 1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and temperatures averaged in the laboratory to 20  $^{\circ}\text{C}$  and 25  $^{\circ}\text{C}$  respectively. The experimental periods started between mid-morning and mid-afternoon to allow for a temperature of 15  $^{\circ}\text{C}$  and 25  $^{\circ}\text{C}$  respectively. Maximum light intensity was maintained throughout the study. The ambient temperature was recorded every 15 minutes during the study.



Fig. 1. Monthly variation of temperature (°C) and relative humidity (%) during the study period in the field.

## CHAPTER 4: RESULTS

### 4.1: Microclimate

Ruma National Park displayed bimodal rainfall pattern with great variation between seasons. Long rains were received from March to May while short rains were received from September to December (Fig. 1), with the month of April experiencing the highest rainfall. June to August was relatively a dry period. Precipitation declined while radiation, air temperature ( $T_{air}$ ), and VPD increased with progressing rainy season. Higher light intensities and temperatures occurred in the open compared to the understory sites. On a daily basis, the open locations experienced longer periods with maximum light intensities averaging  $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$  (Table 2), while maximum averages in the understory were  $250 \mu\text{mol m}^{-2}\text{s}^{-1}$ . Daily humidity of Ruma National Park varied between understory and open sites. Understorey plots experienced  $84.82 \pm 0.01\%$  and  $39.22\%$  maximum and minimum humidity respectively, while open grassland experienced  $81.66 \pm 0.1\%$  and  $59.7\%$  maximum and minimum humidity respectively (Table 2). Daily ambient air temperatures ranged between  $22^\circ\text{C}$  and  $40^\circ\text{C}$  with maximum occurring during the mid day.

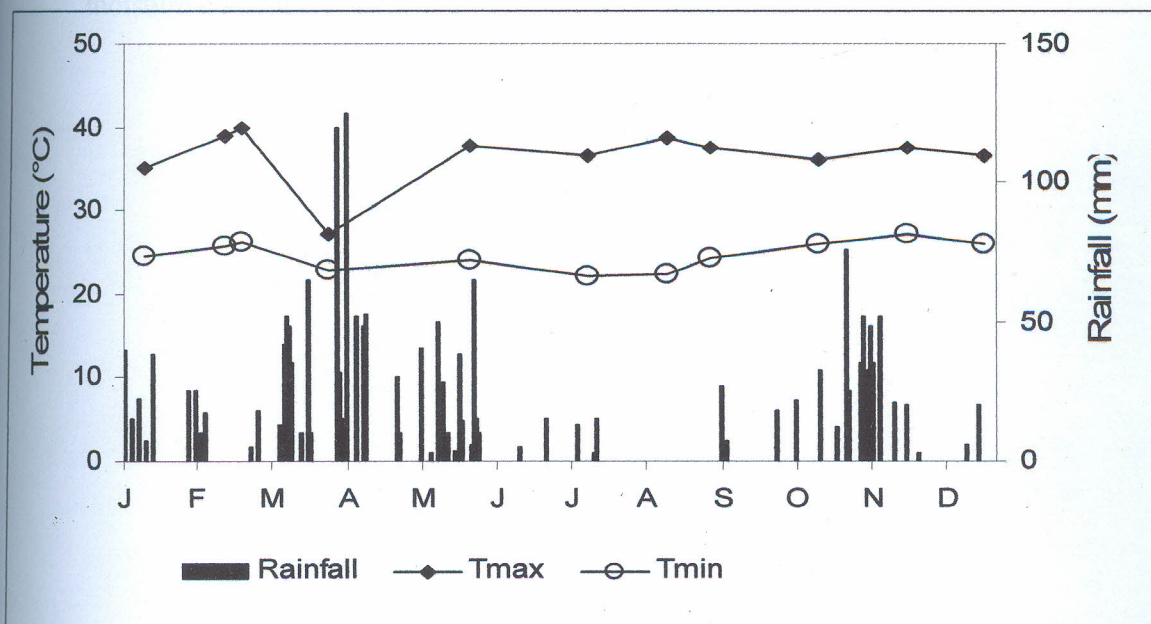


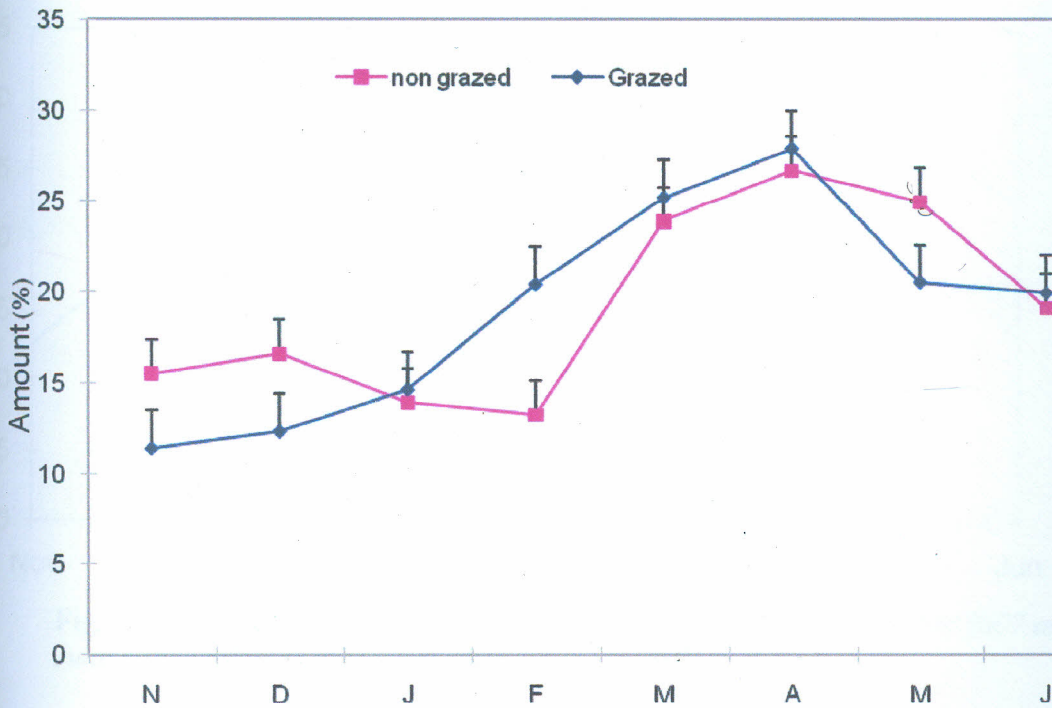
Fig. 1. Daily rainfall amounts (mm), maximum temperature ( $T_{max}$ ) and minimum temperature ( $T_{min}$ ) prevailing in Ruma National Park during 2008.

Daily ambient air temperatures ranged between 22 °C to 40 °C with maximum occurring during the mid day. February and April were the hottest and the coolest months coinciding with the dry and rainy seasons respectively. During gas exchange measurements over the field period, the temperature inside the chamber was maintained close to the ambient air temperature by use of cool packs and a fan. Soil temperature was greatly affected by the intensity of overhead sun and the wind speed, and ranged between 16 and 27 °C (Fig. 20).

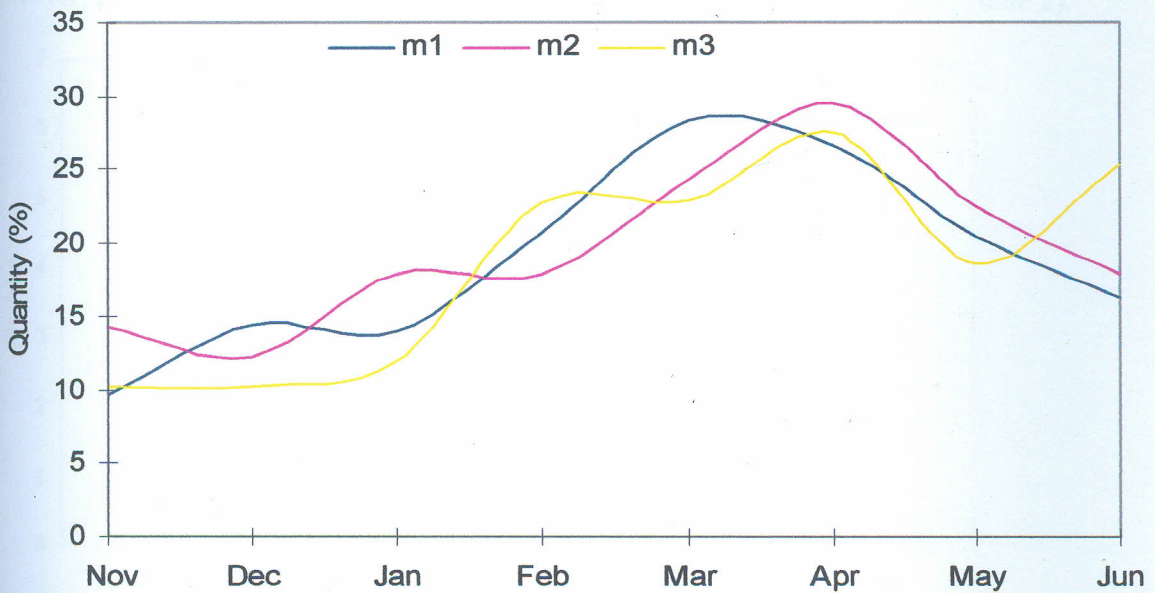
## **4.2: Soil Properties**

### **4.2.1. Soil moisture**

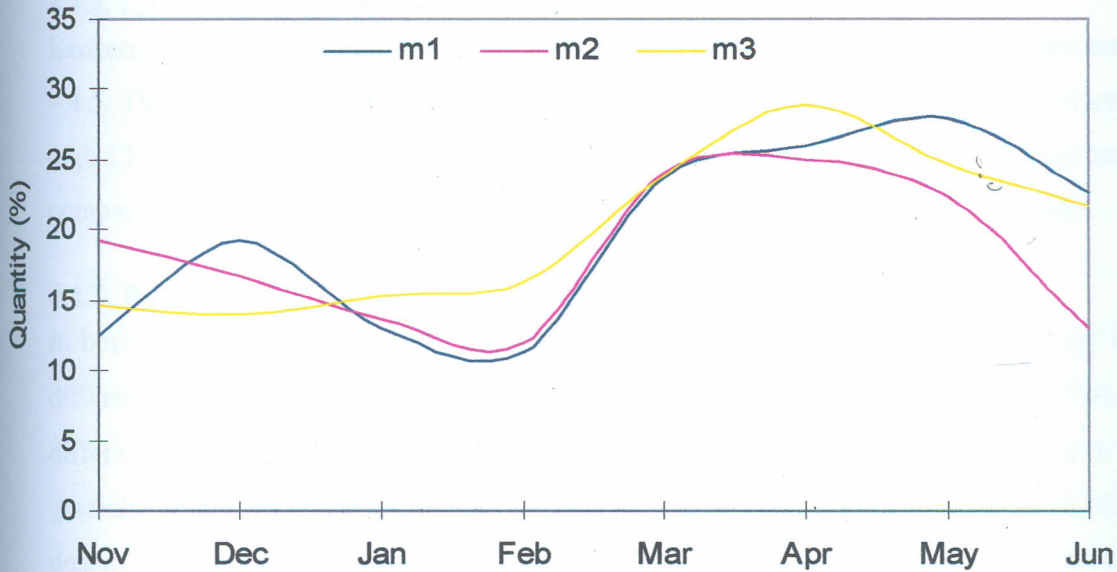
Soil moisture was significantly ( $p < 0.001$ ) higher in non grazed plot  $28.44 \pm 2.5$  compared to grazed plot (Table 2). Differences in soil moisture was also observed in understory sites. Understory sites (*Acacia*) had significantly ( $p < 0.001$ ) higher soil moisture compared to open sites (see Appendix 2). Highest soil moisture content was recorded in April (Fig. 2) coinciding with highest rainfall (Fig. 1). Lowest soil moisture content ~11.4% was recorded in February in non grazed plot (Fig. 2, 3, 4) Soil moisture content however, increased significantly with increase in depth (Fig. 4), with deeper layer recording highest moisture content.



**Fig. 2:** Seasonal Soil Water Content (%) between November 2007 and June 2008 from grazed and non-grazed sites. Error bars are standard deviations.



**Fig. 3:** Gravimetric soil Water Content (%) for grazed plot between November 2007 and June 2008 at depths of 0-5cm (m1), 5-10cm (m2) and 10-15 (m3).

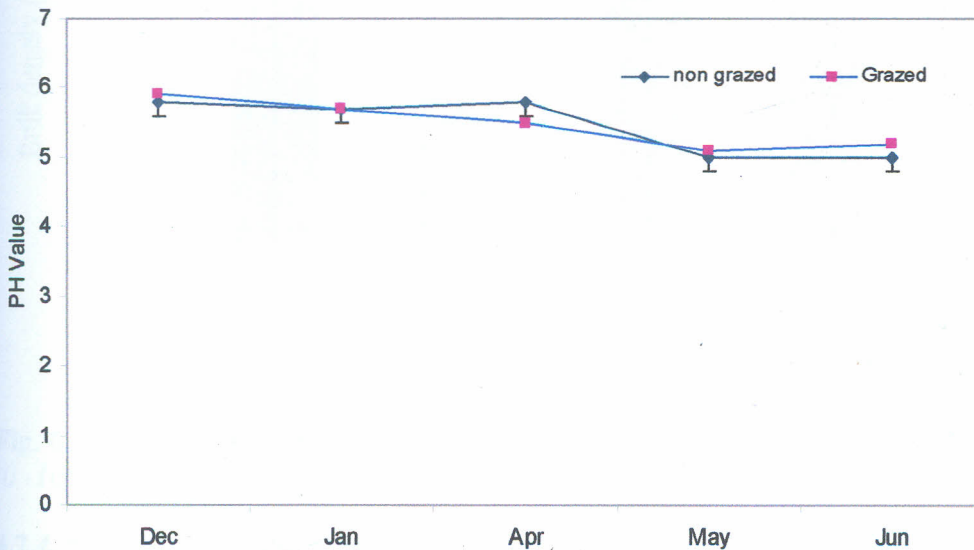


**Fig. 4:** Soil Water Content (%) for non-grazed plots between November 2007 and June 2008 at depths of 0-10cm (m1), 10-20cm (m2) and 20-30 (m3).

#### 4.2.2. Soil pH

There was no significant ( $p > 0.014$ ) difference in pH between soil samples from grazed and non grazed plots and remained at  $\sim 6.00$  throughout the study period (Fig. 5).

However, pH values significantly ( $p < 0.014$ ) increased under canopy  $6.5 \pm 0.31$  (Table 2).



**Fig. 5:** Soil pH measured in grazed and non grazed sites between December 2007 and June 2008. Error bars are standard deviations.

#### 4.2.2. Cation Exchange Capacity

Exchange acidity (CEC) in mg/20000g for Ruma National Park soils ranged between 0.5 – 4.5. There was a decrease in CEC with increase in depth with rainy season experiencing high CEC (Fig. 9). Non grazed plots had significantly ( $p < 0.001$ ) higher exchange acidity compared grazed plots, with open grassland location having the lowest CEC values.

#### 4.2.3. Bulk density

In both grazed and non-grazed plots, soil bulk densities were not significantly ( $p > 0.05$ ) different with values of  $1.19 \pm 0.08$  and  $1.08 \pm 0.05$  respectively (Table 2). This was different in open grassland where bulk density ranged between 0.97 to 1.07 in open non-grazed site and 1.07 to 1.08 in open grazed site. Significant ( $p < 0.05$ ) differences in bulk density were noted between surface and deeper soils in non grazed plot (Fig. 6) where bulk density decreased from surface to deeper soils during the rainy season. However, there was but no significant ( $p > 0.05$ ) difference between depths in grazed plots.

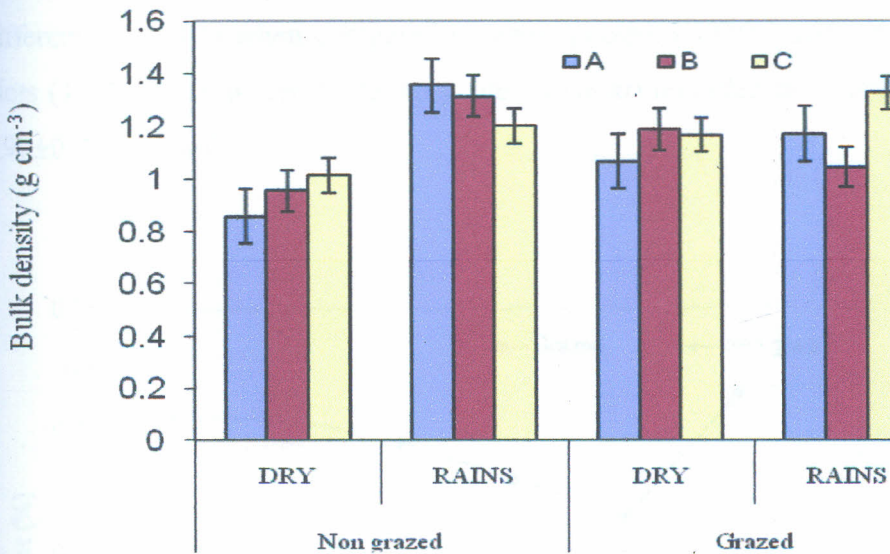
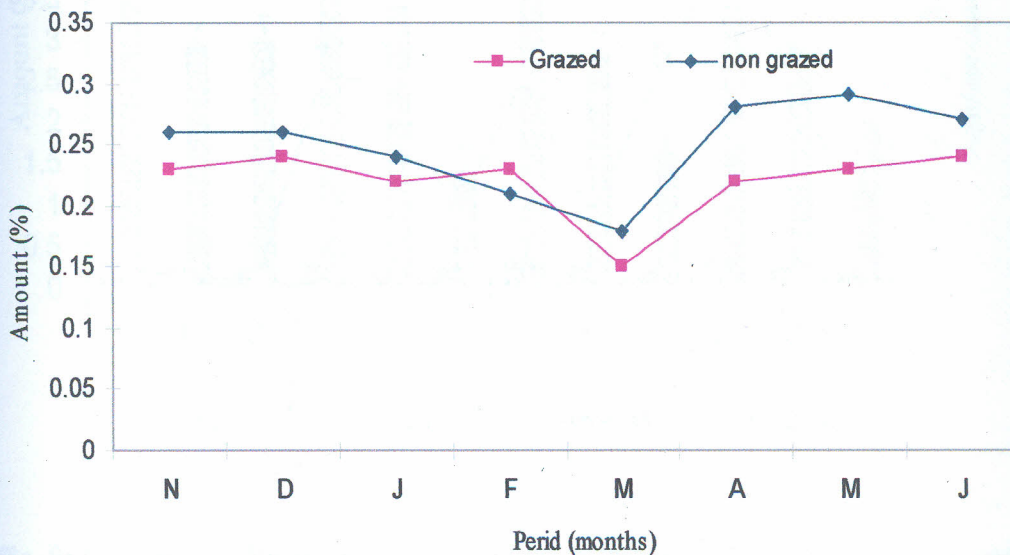


Fig. 6. Seasonal soil bulk density (g cm<sup>-3</sup>) in February (dry) and April (rains) at depths A (0 -10cm), B (10 – 20cm) and C (20 -30cm). Error bars are standard deviations.

#### 4.2.4. Soil Nitrogen and Carbon

Soil nitrogen content was significantly different ( $p < 0.001$ ) in grazed and non-grazed plots with values of  $0.22 \pm 0.01$  and  $0.32 \pm 0.07$  respectively (Table 2). However, there was a decrease in soil nitrogen content in both grazed and non-grazed plots (Fig. 7) from November to March. Soil N was significantly ( $p < 0.05$ ) higher in non grazed than grazed

plots except in the month of February. A significant steady increase in soil N was observed from March to June during the rainy season with April and May recording the highest content  $\sim 0.33\%$ . The understory (*Acacia*) had significantly higher ( $p < 0.001$ ) soil N than the open locations (Table 2). In both understory and open grassland sites, the percentage N content in the soil remained constant during the dry season from November to January. Nitrogen content was not significantly ( $p > 0.001$ ) different between understory and open grassland in January. However, open grassland soils experienced a significant ( $p < 0.001$ ) increase in N content between January and February before decreasing in March (Fig. 8). During the rainy season, understory sites had significantly ( $p < 0.05$ ) higher soil N compared to open sites except in February. In all plots and sites considered, N content declined with increase in depth (0 - 30 cm). Soil carbon was significantly ( $p < 0.002$ ) different between depths (see Appendix 3) with high carbon recorded in top layer (Fig. 9). The top soil layers (0-10cm) registered an average of 4% while the deeper soil layers (20 - 30cm) recording an average of 1.5%. Carbon content was significantly different ( $p < 0.001$ ) when compared between grazed  $3.40 \pm 0.2$  and non grazed  $4.84 \pm 1.5$  plots (Table 2). However, understory sites (*Acacia*) recorded the highest carbon content  $4.90 \pm 0.7$  in the soil.



**Fig. 7:** Soil Nitrogen Content (%) from grazed and non-grazed plots between November 2007 and June 2008. Error bars are standard deviations.



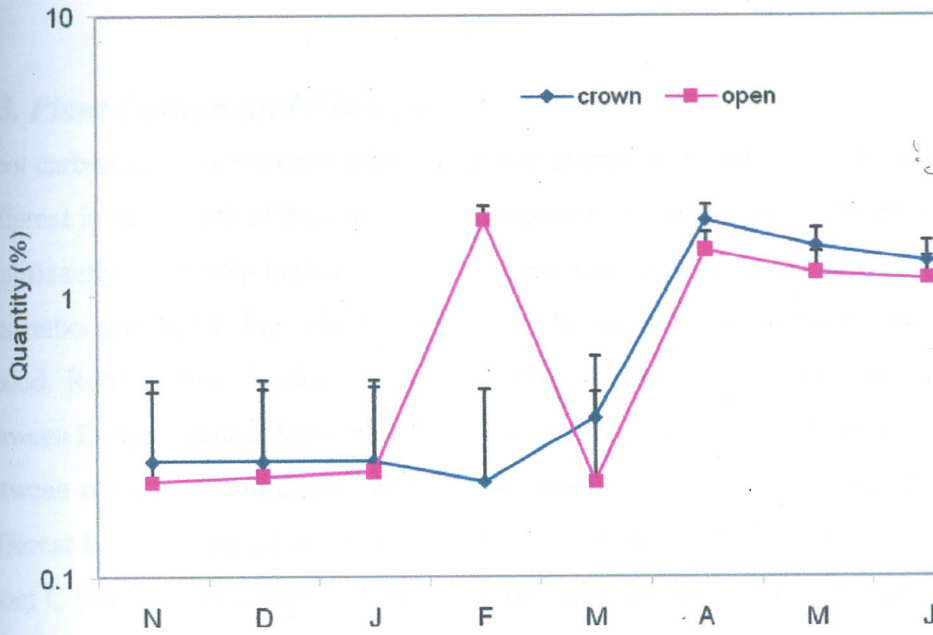


Fig. 8: Soil nitrogen content (%) conducted between November 2007 and June 2008 in understory (crown) and open grassland sites. Error bars are standard deviations.

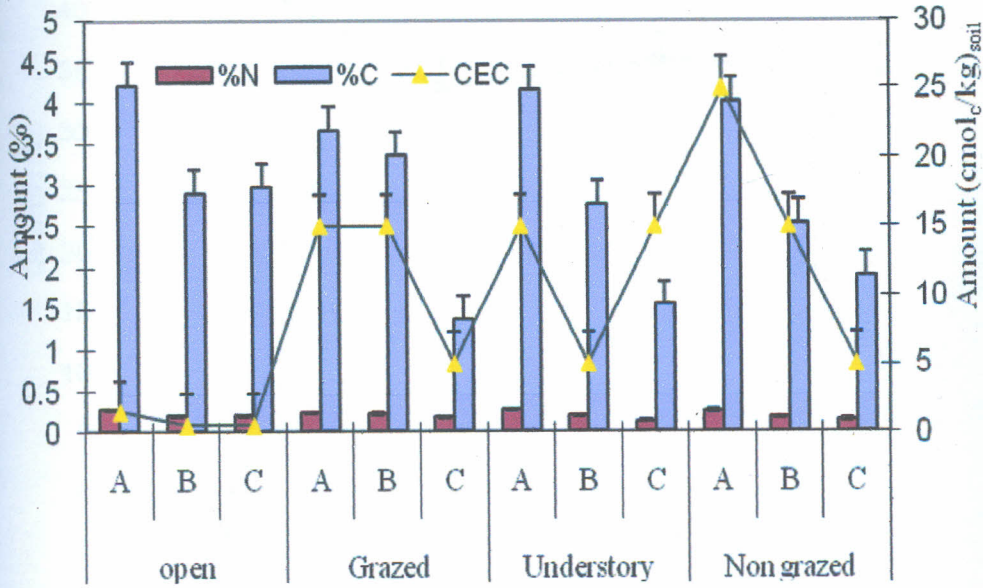
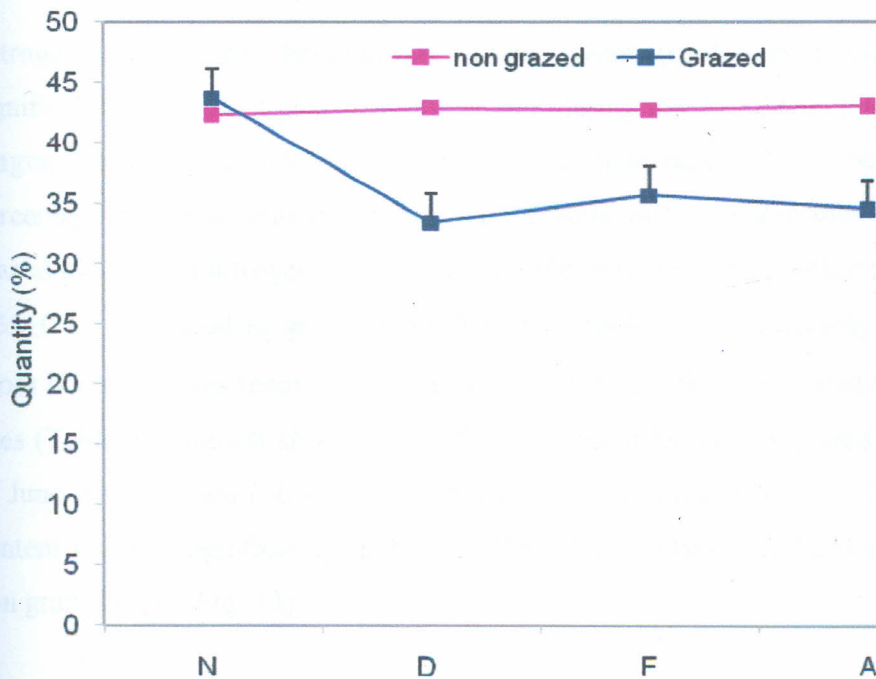


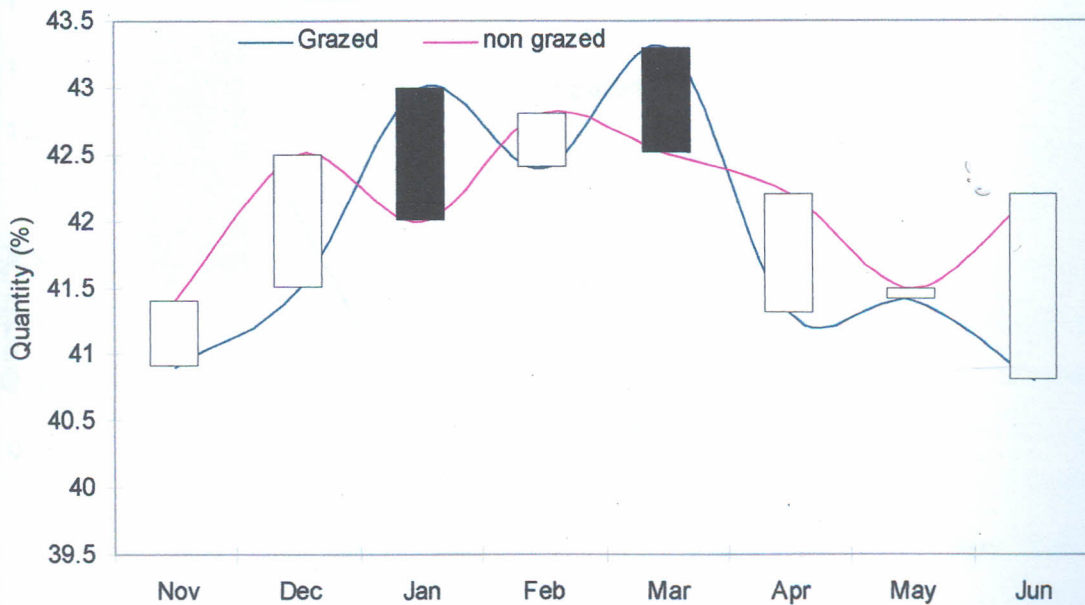
Fig. 9: Carbon (C), Nitrogen (N) and Cation exchange capacity (CEC) from soils from different sampling sites in March 2008 at depths of A(0-10cm) B (10-20cm) and C(20-30cm). Error bars are standard deviations.

### 4.3. Plant Carbon and Nitrogen

Root carbon content between grazed and non grazed plots was not significantly ( $p>0.05$ ) different in the month of November (*see Appendix 3*). However, root carbon content was significantly ( $p<0.05$ ) higher in non grazed plot compared to grazed plot between December and April (*Fig. 10*). Values ranged between 30 - 45% during the measurement period. Root carbon declined from November to December before increasing slightly between December and April. However, no significant ( $p>0.05$ ) differences was observed between seasons in non grazed plot. Shoot carbon content was not significantly ( $p>0.05$ ) different between grazed and non grazed plots during the study period (*Fig. 11*). Highest shoot C (~43%) and lowest (~41%) were recorded in March and November respectively in grazed plots.

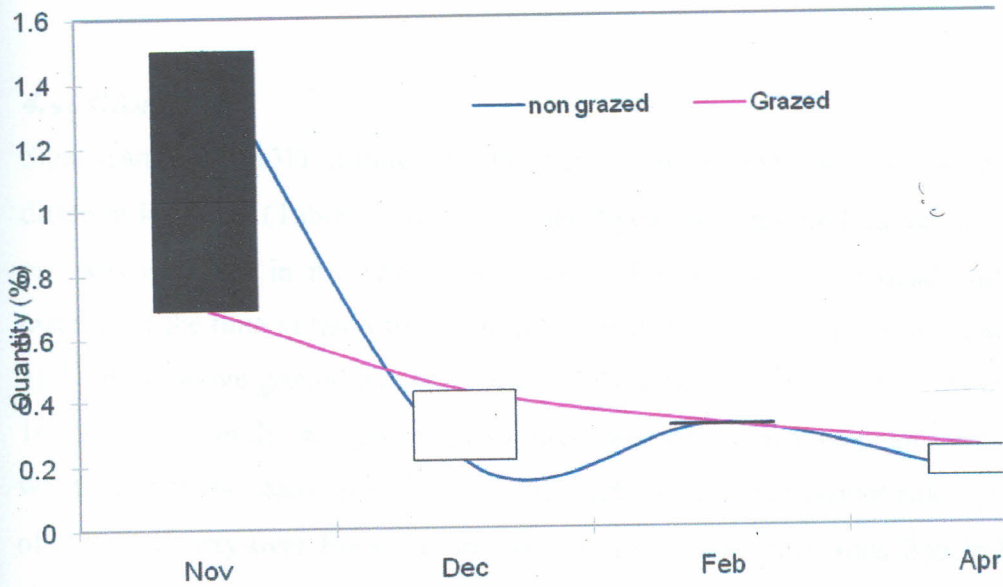


**Fig. 10:** Carbon Content (%) for underground grass material (Root) between November 2007 and April 2008. Error bars are standard deviations.

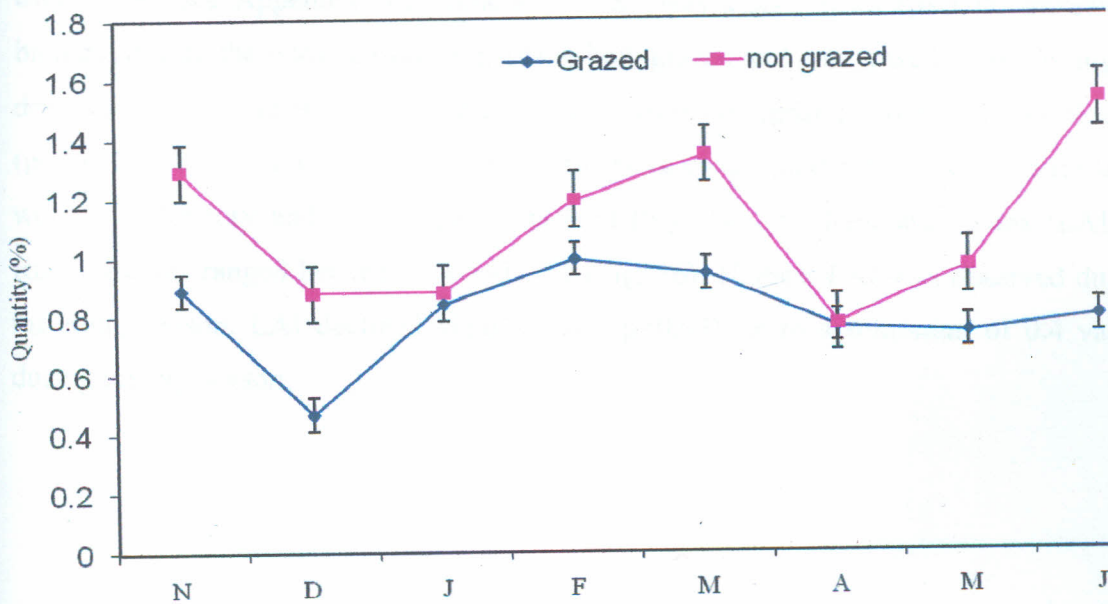


**Fig. 11:** Carbon Content (%) for above ground (shoot) plant material in grazed and non-grazed between November 2007 and June 2008. Up/Down bars represent data points.

Nitrogen content for belowground plant tissue (roots) in non-grazed plot was significantly ( $p < 0.05$ ) higher than grazed plot during the dry season (Fig. 12) with values ranging between 0.2 -1.5% during the measurement period. From November to April, percentage nitrogen content declined significantly in the grazed plot compared to non-grazed plot. Shoot nitrogen content was significantly ( $p < 0.001$ ) higher in non-grazed plot  $0.55 \pm 0.11$  compared to grazed  $0.44 \pm 0.0$  plot (Table 2). Significantly ( $p < 0.001$ ) higher shoot N content was recorded in understory  $0.93 \pm 0.28$  sites compared to open  $0.41 \pm 0.01$  sites (Table 2). Highest shoot N ( $\sim 1.55\%$ ) was recorded in non grazed plot in the month of June while lowest ( $\sim 0.4\%$ ) in grazed plot in December (Fig. 13). However, shoot N content was not significantly ( $p < 0.05$ ) different in January and April in both grazed and non grazed plots (Fig. 13).



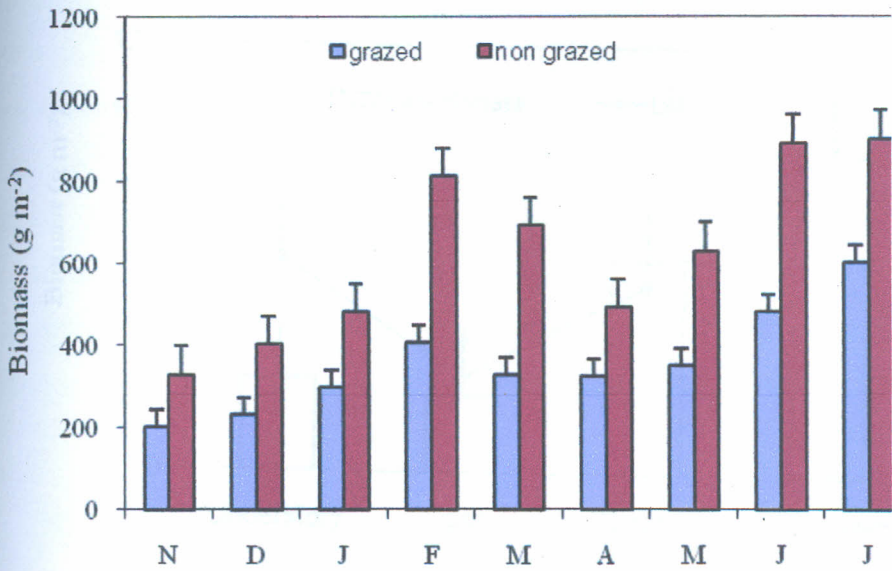
**Fig. 12:** Nitrogen Content (%) for below ground (Root) plant material from grazed and non-grazed sites between November 2007 and April 2008. Up/Down bars represent data point.



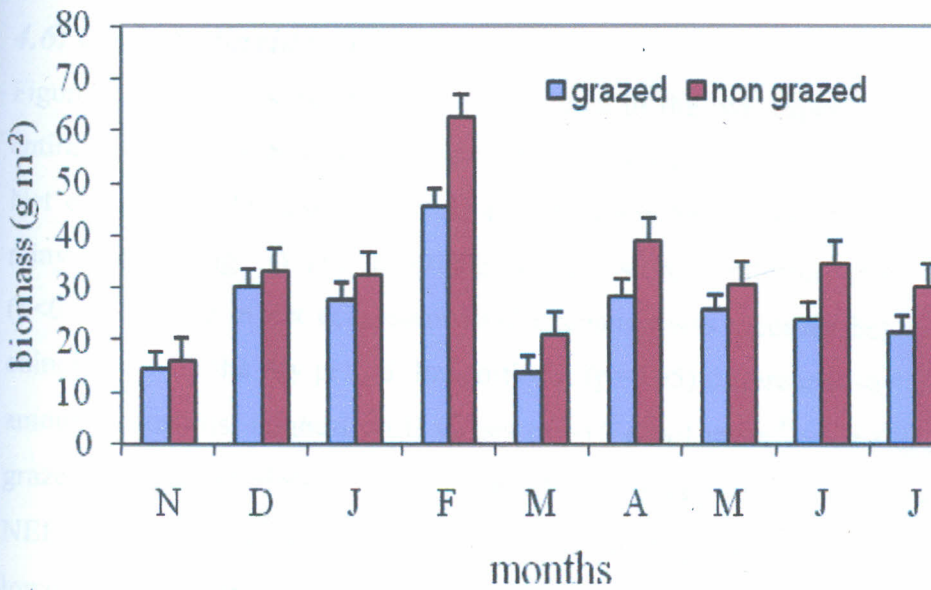
**Fig. 13:** Nitrogen Content (%) for above ground (shoot) grass material from grazed and non-grazed plots between November 2007 and June 2008. Error bars are standard deviations.

#### 4.4. Biomass

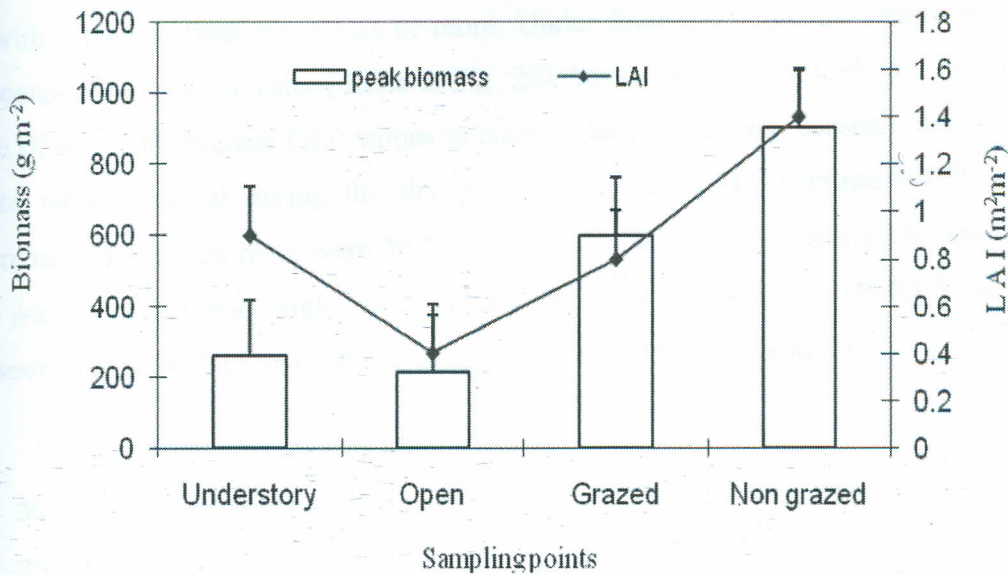
Significant ( $p < 0.001$ ) differences in peak aboveground biomass were observed at different locations (Table 2, Fig. 16). Highest peak aboveground biomass of  $902.7 \pm 115 \text{ g m}^{-2}$  was recorded in the non grazed plots. This included both dead and living plant material at the time of harvesting. Ruma National Park had unique flora at all sites (Table 1). Highest above ground was recorded in July at the end of end of growing season (Fig. 14). However, in the non grazed plots, there was no removal of plant material and since we did not assess decomposition rates of dead biomass, we cannot rule out a possibility of biomass carry-over from the previous season. Understory sites  $256.3 \pm 72 \text{ g m}^{-2}$  had significantly ( $p < 0.001$ ) higher peak above ground biomass compared to open grasslands  $214.2 \pm 63 \text{ g m}^{-2}$  (Table 2, Fig. 16, appendix 1b). In the grazed sites however, no significant difference ( $p > 0.5778$ ) between crown and open grassland sites was established (*see* Appendix 1e). Generally, there was a significant ( $p < 0.05$ ) increase in biomass during the rainy season (Fig. 14) in both grazed and non grazed plots. During the dry season, November to February, biomass from non-grazed plots was significantly ( $p < 0.05$ ) different from grazed plots for both above ground and below ground material as well as understory and in the open grassland (Fig. 14, 15). Leaf area index (LAI) of Ruma grasses ranged between 1.4 and 0.4 (Fig. 16). Highest LAI was observed during the rainy season. LAI declined significantly ( $p < 0.05$ ) up to a minimum of 0.4 values during the dry season.



**Fig. 14.** Above ground (shoot) biomass production ( $\text{g dwt.m}^{-2}$ ) in grazed and non-grazed sites between November 2007 and July 2008. Solid bars represent average monthly biomass production. Error bars are standard deviations.



**Fig. 15.** Below ground (root) biomass production ( $\text{g dwt.m}^{-2}$ ) in grazed and non-grazed sites between November 2007 and July 2008. Solid bars represent average monthly biomass production. Error bars are standard deviations.

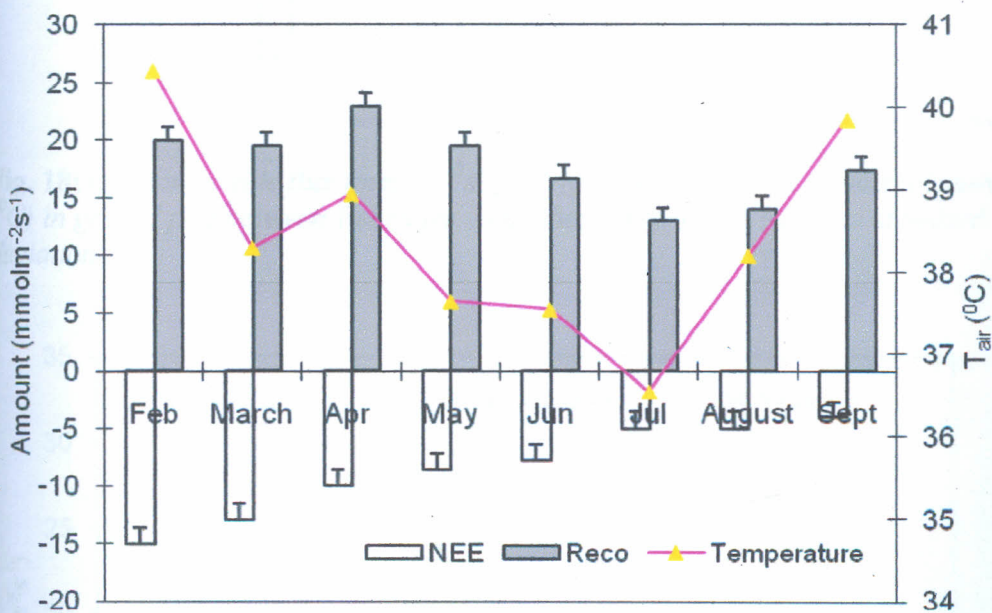


**Fig. 16.** Peak Biomass and Leaf Area Index during July harvested from the respective treatment locations at the study site. Error bars are standard deviations.

#### 4.6: Carbon dioxide flux

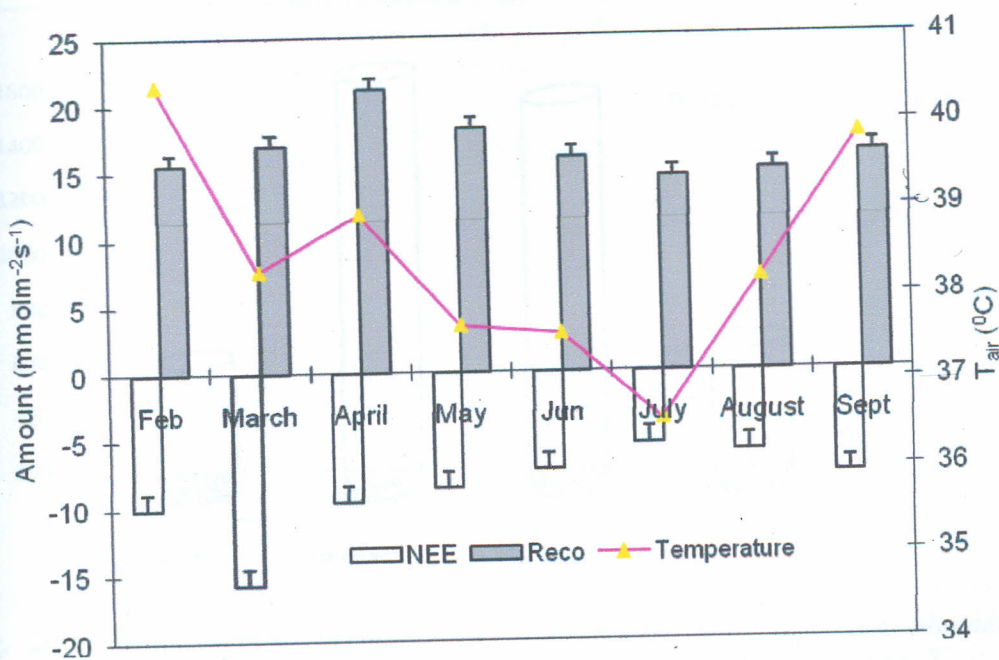
Figure 17, 18 shows trends of CO<sub>2</sub> exchange in the two experimental plots during the entire study period. Significant seasonal changes were observed for NEE, R<sub>eeco</sub> and GPP. Net ecosystem CO<sub>2</sub> exchange increased between March and May coinciding with the rainy period (Fig. 1) and favorable soil moisture conditions (Fig. 2). A significant ( $p < 0.05$ ) decline in net ecosystem CO<sub>2</sub> exchange was recorded between May and July coinciding with the dry period. Insignificant ( $p = 0.05$ ) differences in NEE were observed among treatments. Highest NEE values of  $-15 \mu\text{mol m}^{-2} \text{s}^{-1}$  were recorded in both non grazed and grazed plots and this occurred in February and March respectively. Lowest NEE ( $-5 \mu\text{mol m m}^{-2} \text{s}^{-1}$ ) occurred in July, coinciding with the period of lowest rainfall, lowest soil moisture content. Rates of R<sub>eeco</sub> were significantly ( $p < 0.001$ ) different between grazed plots ( $9.73 \pm 5.68$ ) and non grazed plots ( $7.64 \pm 1.06$ ) (Table 2). However, seasonal trends were similar (Fig. 17, 18). Highest R<sub>eeco</sub> occurred during the rain events and the seasonal patterns resembled those of NEE. Highest R<sub>eeco</sub> values occurred during the rain season, with values of  $20.4 \pm 0.5$  and  $23.5 \pm 0.5 \mu\text{mol m m}^{-2} \text{s}^{-1}$  in grazed and non grazed plots respectively. On a daily basis, under favorable soil moisture conditions, R<sub>eeco</sub> increased from morning hours attaining maximum at around 14:00 hours and then

declining to morning values (data not presented). This trend resembled that of daily NEE but with a lag of about two hours or more. Under favorable moisture conditions, NEE was coupled to light intensity (Table 2, Fig. 20). Seasonal trends of GPP were similar to those of  $R_{eco}$  with highest GPP values occurring during the rainy seasons, while lowest values were recorded during the dry periods (Fig. 19). The maximum GPP values recorded in the grazed plots were  $30.3 \pm 2.01 \mu\text{mol m}^{-2} \text{s}^{-1}$  and occurred in April when soil water content was high. GPP values were not significantly ( $P=0.67$ ) different between grazed ( $4.07 \pm 5.76$ ) and non grazed ( $3.33 \pm 2.50$ ) plots (Table 2).

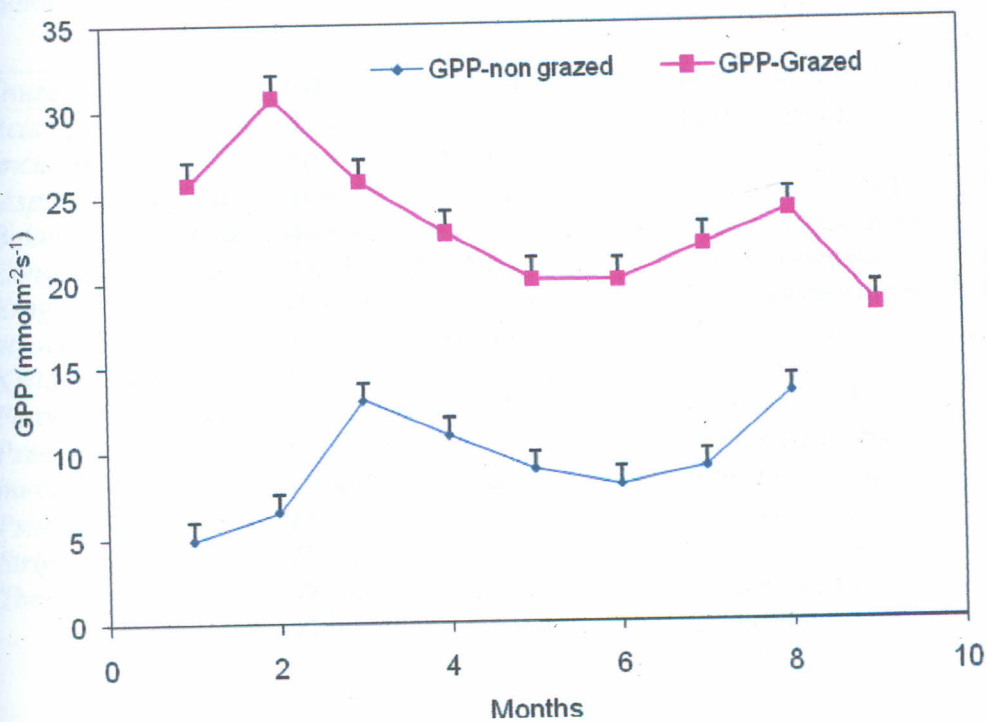


**Fig. 17:** Carbon dioxide flux ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) i.e. NEE and  $R_{eco}$ , and air temperature,  $T_{air}$  ( $^{\circ}\text{C}$ ) from non-grazed plot between February – October 2008. Error bars are standard deviations.





**Fig. 18:** Carbon dioxide flux ( $\text{mmolm}^{-2}\text{s}^{-1}$ ) i.e.  $\text{NEE}$  and  $\text{Reco}$ , and air temperature,  $T_{\text{air}}$  ( $^{\circ}\text{C}$ ) in grazed plot between February – October 2008. Error bars are standard deviations.



**Fig. 19:** Gross Primary Production ( $\text{mmolm}^{-2}\text{s}^{-1}$ ) from grazed and non-grazed plots between February – October 2008. Error bars are standard deviations.

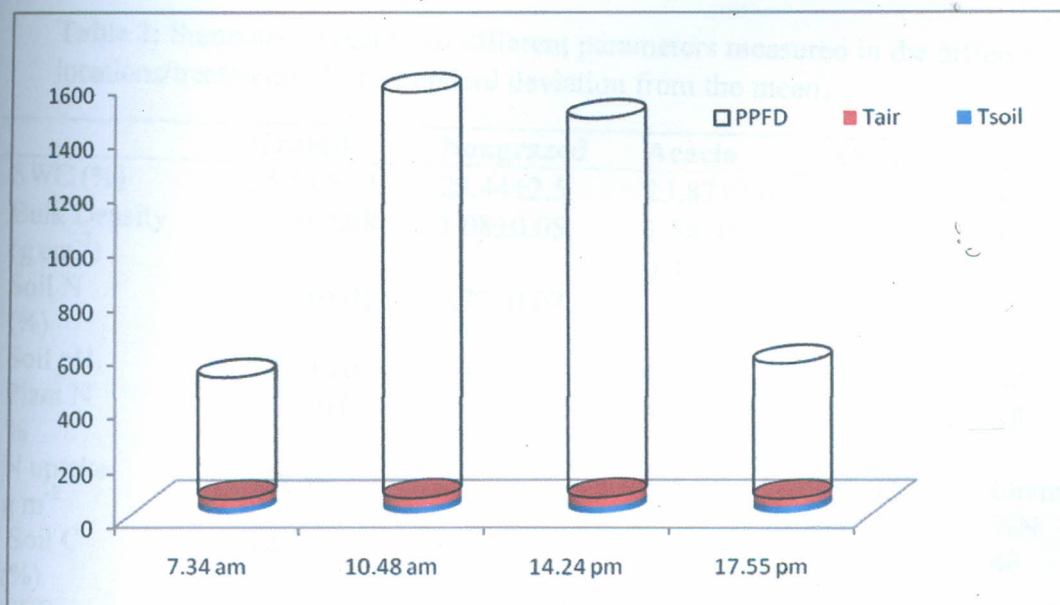


Fig. 20: Diurnal courses of prevailing microclimatic conditions, i.e. photosynthetic photon flux density (PPFD), ambient temperature ( $T_{air}$ ) & soil temperature ( $T_{soil}$ ).

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

| Grazed                       | Non grazed/Fenced            | Non grazed/Fenced              | Acacia understory           |
|------------------------------|------------------------------|--------------------------------|-----------------------------|
| <i>Acacia ancistroclada</i>  | <i>Acacia ancistroclada</i>  | <i>Indigofera arrecta</i>      | <i>Acacia ancistroclada</i> |
| <i>Aspilia asperifolia</i>   | <i>Acacia gerarrdii</i>      | <i>Lantana camara</i>          | <i>Albizia coriaria</i>     |
| <i>Balanites aegyptica</i>   | <i>Acmella calirrhiza</i>    | <i>Lantana trifoliata</i>      | <i>Aspilia sperifolia</i>   |
| <i>Conyza floribunda</i>     | <i>Albizia coriaria</i>      | <i>Leucas calostachyus</i>     | <i>Balanites aegyptica</i>  |
| <i>Eragrostis atrovirens</i> | <i>Aspilia asperifolia</i>   | <i>Nuxia congesta</i>          | <i>Berkeya spekeana</i>     |
| <i>Kyllinga bulbosa</i>      | <i>Balanites aegyptica</i>   | <i>Panicum maximum</i>         | <i>Cordia ovalia</i>        |
| <i>Panicum maximum</i>       | <i>Berkeya spekeana</i>      | <i>Pilliosigma thonningii</i>  | <i>Leucas calostachyus</i>  |
| <i>Pseudathria hookeria</i>  | <i>Commiphora myrrha</i>     | <i>Pseudathria hookeri</i>     | <i>Panicum maximum</i>      |
| <i>Psidium guajava</i>       | <i>Conyza floribunda</i>     | <i>Psidium guajava</i>         | <i>Rhus vulgaris</i>        |
| <i>Striga asiatica</i>       | <i>Cordia ovalis</i>         | <i>Rhus natalensis</i>         | <i>Themeda triandra</i>     |
| <i>Themeda triandra</i>      | <i>Crotalaria pallid</i>     | <i>Rhus vulgaris</i>           | <i>Urena lobata</i>         |
|                              | <i>Dyschoriste radicans</i>  | <i>Solanum incanum</i>         |                             |
|                              | <i>Hyparrhenia hirta</i>     | <i>Steganotaenia araliacea</i> |                             |
|                              | <i>Themeda triandra</i>      |                                |                             |
|                              | <i>Tithonia diversifolia</i> |                                |                             |

**Table 2:** Summary of results of different parameters measured in the different locations/treatments.  $\pm$  are standard deviation from the mean.

|  | Grazed          | Nongrazed       | Acacia           | Open            | N              | P      |
|--|-----------------|-----------------|------------------|-----------------|----------------|--------|
| SWC (%)  | 25.61 $\pm$ 2.2 | 28.44 $\pm$ 2.5 | 23.83 $\pm$ 2.0  | 16.79 $\pm$ 2.5 | 40             | <0.001 |
| Bulk Density<br>(g cm <sup>-3</sup> )                              | 1.19 $\pm$ 0.08 | 1.08 $\pm$ 0.05 | 1.54 $\pm$ 0.01  | 0.73 $\pm$ 0.02 | 6              | <0.05  |
| Soil N<br>(%)  | 0.22 $\pm$ 0.01 | 0.32 $\pm$ 0.07 | 0.35 $\pm$ 0.1   | 0.15 $\pm$ 0.1  | 40             | <0.001 |
| Soil pH.   | 6.4 $\pm$ 0.10  | 6.4 $\pm$ 0.15  | 6.5 $\pm$ 0.31   |                 | 40             | =0.014 |
| Plant N<br>%   | 0.44 $\pm$ 0.01 | 0.55 $\pm$ 0.11 | 0.93 $\pm$ 0.28  | 0.41 $\pm$ 0.01 | 48             | <0.001 |
| N uptake<br>g m <sup>-2</sup>                                      | 128.84          | 496.49          | 238.36           | 87.82           | biomass*<br>%N |        |
| Soil C<br>(%)  | 3.40 $\pm$ 0.2  | 4.84 $\pm$ 1.5  | 4.90 $\pm$ 0.7   |                 | 40             | <0.002 |
| NEE<br>( $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> )               | 5.91 $\pm$ 2.27 | 4.32 $\pm$ 2.03 |                  |                 | >15            | <0.001 |
| R <sub>eco</sub><br>( $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> )  | 9.73 $\pm$ 5.68 | 7.64 $\pm$ 1.06 |                  |                 | >15            | <0.001 |
| GPP<br>( $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> )               | 4.07 $\pm$ 5.76 | 3.33 $\pm$ 2.50 |                  |                 | >15            | =0.067 |
| Peak biomass<br>(g m <sup>-2</sup> )                               | 292.81 $\pm$ 46 | 902.7 $\pm$ 115 | 256.3 $\pm$ 72   | 214.2 $\pm$ 63  | 40             | <0.001 |
| Humidity(%)  | -               | -               | 84.82 $\pm$ 0.01 | 81.66 $\pm$ 0.1 | >30            | <0.001 |
| Light<br>Intensity( $\mu$ mol<br>m <sup>-2</sup> s <sup>-1</sup> ) | -               | -               | 250 $\pm$ 2.0    | 1000 $\pm$ 2.5  | >15            | <0.001 |

Values are means ( $\pm$ SE) of two blocks.  $P < 0.001$ ,  $P < 0.05$ ,  $P < 0.002$ ,  $P = 0.014$ ,  $P = 0.067$  indicate significant differences between sites within blocks.

## CHAPTER 5: DISCUSSIONS

### *5.1. Nutrient dynamics and Soil moisture*

The uptake of cations and anions as plant nutrients is directly related to their concentration in soil solution. This has been demonstrated not only in solution culture but also in soil solution (Agbenin, 2003). Since ion uptake rate by plants is determined by diffusive and convective movement of ions in soil solution to plant roots, only a small quantity of ion uptake in Ruma National Park soils was accounted for by root interception, which was a direct exchange between plant roots and ion exchange sites in the soil. With low soil moisture content across the profile in Ruma National Park due to inadequate rainfall throughout seasons, there is oftentimes an abundance of air which may have limited the accumulation of organic matter by accelerating decomposition and further perpetuate the low level of soil colloids and therefore profoundly increase plant available N.

It has also been shown that precipitation is a major means by which many nitrogen compounds are lost into the atmosphere and/or produced within it are returned to the earth's surface. Since tropical savanna ecosystems are controlled by the interactions between water and nutrient availability (Walter, 1971), Ruma results suggests that the amount and distribution of rainfall, infiltration and evapotranspiration determined the soil moisture regime and nitrogen levels in the soil. The root niche separation model assumes that water is the primary limiting factor, and thus trees and grasses have differential access to this resource because of spatial differences in their rooting profiles (Sankaran *et al.*, 2004). Since savanna vegetation often occurs either on weathered soils with low nutrient availability or regions of limited rainfall, or both (Bustamante *et al.*, 2006), both periodic water shortage and low soil nutrient content have been considered as the major limiting factor for biomass production (Mordelet *et al.*, 1993; Caylor *et al.*, 2004). As evidenced from Ruma National Park, humid tropical savannas are water-limited for a greater part of the year, as the climate is characterized by the alternation of a dry and a rainy period and therefore the reason for highest N content coinciding with rainy season. The distribution of water in grazed, non grazed plots, understory and open grassland in Ruma determined nutrient availability for plant uptake since accumulation and decomposition of organic matter and subsequent release of mineral nutrients is strongly

related to soil water status (Holtgrieve *et al.*, 2006). In grazed plots, low soil moisture may have been caused by trampling by grazers and continuous tiller removal through grazing. Since soil moisture controls microbial activity i.e. nutrient release and water infiltration, leading to the redistribution of nutrients in the soil along the profile depth similar to soil moisture content.

High soil moisture and N at understory sites may have been caused by presence of *Acacia* trees. Trees have been shown to improve grass production through hydraulic lift, reduced evapotranspiration and increased nutrient availability (Fulco *et al.*, 2007; Scholes and Archer, 1997). *Acacia* trees had been previously described to increase the quantity and influence the dynamics of nitrogen in grasses at crown sites through production of litter rich in nitrogen. This has been enabled through the mutualistic relationship with nitrogen fixing bacteria (Manuel and Molles, 2003) and thus their capability to biologically fix nitrogen (Cech *et al.*, 2008). Understory affected the distribution of water by modifying soil water content dynamics through modification on both inputs and outputs. This was done through effects on rainfall interception, evapotranspiration and water infiltration. According to the level of each of this process, tree canopy may have lead to various complex and contrasting situation observed, for example; during the dry season in Ruma (November to February), rain interception is likely to partly account for the discrepancy in soil moisture content between the open grassland and understory sites. Similar results had been observed beneath the canopy in a humid savanna of West Africa (Mordelet *et al.*, 1993), and Amoseli National Park in Kenya (Georgiadis *et al.*, 1989) where plant production responses to defoliation was found to vary widely, contingent upon a complex interaction of ecological factors.

Low pH in the different sites (disturbed and undisturbed) in Ruma soils illustrate inadequate availability of  $\text{Ca}^{++}$  and  $\text{Mg}^{++}$  ions. With continuous decrease in soil pH, it's expected that the number of  $\text{H}^+$  ions and  $\text{Al}^{+++}$  ions will increase. This may lead to limited availability of mineral nutrients to the plant and the soil's inefficient ability to hold applied nutrients. Plants therefore may exhaust a fair amount of energy (that might otherwise have been used for growth, flowering, seed production or root development) scrounging the soil for mineral nutrients. This variability across the field and profile depth probably reflects the intensity of leaching of manure input from herbivores and organic matter thus leading to lower soil ionic strength in grazed plots. These results are

however in discord with the fact that humid tropical savanna soils have adequate Ca, Mg and K saturation of CEC (Agbenin, 2003), even though soil pH varies between mildly acidic (6.63 - 4.93) during dry season to strongly acidic (4.4 - 5.56) during the rainy season.

The spatial pattern of habitat use for feeding (Augustine and McNaughton, 2006; Augustine and McNaughton, 2004) and excretion may contribute to low nutrient levels and this may be a reason for low N in grazed plots in Ruma National park. As studied earlier in an East African savanna (Augustine, 2003), results on nutrient distribution in grazed plots in Ruma may imply that herbivores re-distributed nutrients by feeding in certain areas while depositing their excreta in others thus causing local depletion or enrichment of nutrients. Other studies however, have shown that some herbivores feed and return their excreta in the same intensively used areas, thereby potentially maintaining nutrient rich patches in otherwise nutrient-poor vegetation (Augustine, 2003; Cech *et al.*, 2008) and this may explain high N content recorded in February in grazed plots. Previous studies in Tsavo National Park shows that N may be recycled faster in grazed system than in non-grazed system by going from plant to grazer then back to plant through urination and defecation (Belsky *et al.*, 1993). Also herbivores may have a positive net effect on the soil N pool by reducing the amount of biomass exposed to fire, and thereby reducing the associated losses to the atmosphere. Hence, depending on the patterns of grazing and excretion, herbivory has a neutral effect (Cech *et al.*, 2008) on the ratio of nutrient availability (defoliation) or potentially shifts the nutrient balance towards N-limitation in a humid tropical savanna. The lowest soil C contents and the lowest C-to-N ratios were found in the soils in grazed plots and in deeper profile. Since soil solution is a source of plant nutrients and a medium for all reactions, and nutrient cycling, cation exchange capacity and organic C of Ruma National Park soils decreased with increase in depth, indicating high potential for microbial activity and higher soil respiration at the top layer than layers beneath. The highest cation exchange capacities (CEC) contents registered in the soils under tree crowns shows inadequacy of Ca and Mg in the exchange complex and thus confirms that humid tropical savanna soils have limited nutrient reserves to meet forage nutrition. Differences in exchange acidity between disturbed and undisturbed sites and low CEC (less than 5 meg/20000g) proved the lower quantities of clay and organic matter in Ruma soils. Soil fertility and nutrient availability are closely

connected to the SOM content and its mineralization (Glaser *et al.*, 2001) and, also N is incorporated into soil microbial biomass to a higher extent than C. Soil N and C data shows that mineralization and nitrification of organic matter were most rapid following the wetting of the soil after a period of drying and therefore the more severe the drying, the greater and subsequent formation of inorganic nitrogen. Higher total carbon was recorded at understory sites in Ruma. Since organic carbon not only depends on storage capacity but also on input (Glaser *et al.*, 2001), it's therefore imperative to conclude that larger proportion of C came from bird droppings, ungulate dung and through-fall leachates from tree canopies. Leaf fall is considered to be the main source of carbon input under tree crowns.

Studies have shown that soils are significant sources and sinks for both  $N_2O$  and  $CH_4$ . It has been estimated that soil emissions account for approximately 65% of global  $N_2O$  emissions through aerobic nitrification and anaerobic denitrification (Smith, 1999). Total organic N was greater under tree crowns but the difference between canopy and open grassland was higher than for total carbon and this lead to a higher C/N ratio of 30:1 under tree crowns. However, the difference between crown and open sites could not be explained by the C/N differences in the organic matter originating from tree and grass material. Organic matter in the open grassland mainly came from grasses while a higher proportion under tree crowns came from tree material with a lower C/N ratio contributed to soil organic matter, which consequently led to a lower C/N ratio.

## ***5.2. Biomass production***

The productivity of savannas is normally attributed to the generally lower precipitation, the occurrence of a pronounced and prolonged dry season, or in some cases the result of soil characteristics in relation to water-holding capacity. In savannas, linear relationships have been found between biomass and precipitation (Skarpe, 1992), and days of water stress, although from place to place productivity may be strongly affected by biomass burning, which reduces the duration of leaf area and thus limits productivity. Above ground was the sum of stem, cumulative leaf mass and standing dead averaged monthly from each plot and expressed per unit area. There was more leaf mass in non-grazed plots especially in understory sites than in open grassland and also reduced above ground leaf mass in grazed plots. Standing dead mass was greatly reduced in grazed plots especially

in open grassland probably due to continuous removal of tillers by grazers thus reducing accumulation of dead mass.

Below ground biomass depicted a unique dimension both in grazed and non-grazed plots. There was more root concentration in the top layer in non-grazed plots. Roots however, were distributed uniformly at understory sites in probably to tap more nutrients and water, although little differences were observed in root mass for both grazed and non-grazed plots. Therefore, grazing profoundly affected morphological components of yield and productivity and also increased the amount of green leaf tissue while reducing the amount of non-photosynthetic tissue (stem, standing dead). In non-grazed plots, there was different allocation of biomass resulting from canopy closure. Trees have been shown to improve soil resources under their canopies (Mordelet *et al.*, 1993; Belsky *et al.*, 1993), and to have beneficial effects on the herbaceous layer production in savannas. This is done by adding organic matter and nutrients through leaf-fall, by reducing soil temperatures and water loss due to evapotranspiration, and by attracting birds and large mammals that add nutrients to the soil in their droppings. These effects cannot easily be separated from each other since earlier studies at the low and high rainfall sites in Tsavo West National Park showed the individual benefits of increasing herbaceous productivity due to increased N-input from trees (Belsky *et al.*, 1993) and at crown shade (Belsky, 1994). Within the non grazed plots, the areas under tree crowns had a unique understory flora, lower bulk densities, high biomass and mineralizable N than open grasslands. In the grazed plots, few differences between crown and open grassland sites were observed. Possible explanations for soil enrichment include removal of nutrients from deeper soil profile (Dunham, 1991), or from topsoil outside the tree's canopy by lateral roots stretching beyond the crown. These nutrients would enter the topsoil under trees as a result of leaf-fall and subsequent decomposition. This lack of significant differences does not, however, exclude the possibility that the trees would have a positive effect on understory biomass production if grazing pressure was reduced. Similar observation had been previously found in Middle Awash Valley of Ethiopia where high nutrients were recorded under canopy in moderately grazed areas (Abule *et al.*, 2005), but heavy grazing proved to be a strong overriding effect of the positive influences of the woody plants. It has also been shown that arid and semi-arid systems where the annual coefficient of variation in rainfall exceeds 30% are best described by non-equilibrium relations between



plants and herbivores (Ellis and Swift, 1988), since annual fluctuations in plant production may become so great that herbivore populations are incapable of tracking primary production and hence have no significant effects on plant dynamics. Plant-available moisture has been shown to reduce the nutrient content of plants but increases productivity (Hans *et al.*, 2002). Organic matter turnover in savannas is controlled by interactions between water and nutrient availability, and this basic environmental structure is modified by fire frequency and land management practices (Bustamante *et al.*, 2006). As shown by (Jian, 2004), the analysis of climate vs productivity correlations implies that aboveground productivity appears to be more controlled by rainfall whereas below ground and total productivity is more influenced by temperature. Ruma National Park data shows more control of above ground biomass by rainfall since precipitation and temperature are major controlling climate factors for vegetation structure along longitude and latitude respectively in humid tropical savanna.

Enhanced decay rates with higher temperatures may lead to more nitrogen being released from litter and this may ultimately influence productivity (Biello, 2007), of which high temperature are attributes of savanna ecosystems. Many factors affect the quantities and spatial distribution of nutrients in savanna soils (Cech *et al.*, 2008), with fire, herbivory and atmospheric N<sub>2</sub> fixation being particularly important. Global biological N fixation (BNF) in terrestrial ecosystems has been estimated at 128 TgN /yr), supplying 15% of the N requirement across all biome types. According to this estimate, about 70% of BNF occurs in regions with warmer climates (Bustamante *et al.*, 2006) for instance Africa (25.9 Tg N/yr). Nitrogen is however critical for plant growth and development, hence ecosystem productivity (Cech *et al.*, 2008). Therefore, the high primary production under tree canopy both in grazed and non-grazed plots observed in Ruma Park signifies the role of leguminous plants in fixing nitrogen. Patterns of LAI resembled biomass development. Decreased leaf longevity causes an immediate and sustained decrease in LAI. When LAI fell below the equilibrium state in grazed plots, evapotranspiration also decreased. In the short term, faster mineralization produces large amounts of soil mineral N, substantial amounts of which were leached, partly because the drop in LAI resulting in decreased evapotranspiration and increased drainage (Thornley and Cannell, 1997). In the longer term at equilibrium, higher temperatures decreased the amount of soil mineral N. Although mineralization occurred faster at higher temperatures, the total soil organic

matter pool was smaller, more N was continually being lost by leaching, and higher temperatures increased N losses by ammonium volatilization. In the short term, high soil mineral N levels resulted in increased assimilates partitioning to shoots and an increase in shoot root ratio.

The immediate evidence of grazing impact is the low peak biomass but continued removal of biomass has the consequences of declining soil N and lowering photosynthetic surface area due to clipping that may result into low ecosystem productivity in the long-term. Similar results have been reported in Rocky mountain and Yellowstone National Parks in western United States grasslands (Singer and Schoenecker, 2003). The grazed plots in the study site were used continuously but abandoned if the grass grew above the critical height. Such sites would then not be grazed again until the dry season or accumulated biomass was removed by fire (personal observations). This was observed both inside and outside the Park. This pattern of habitat use by both domestic and wild herbivores which has also been observed in humid African savanna (Cech *et al.*, 2008), may explain why the grazed plots was only moderately enriched with N content and hence low biomass compared to non grazed plots.

### 5.3. $CO_2$ exchange

Savanna carbon fluxes are highly seasonal, and are characterized by high interannual variability caused by fire (Grace *et al.*, 2006). Compared to  $C_4$  plants,  $C_3$  plants have lower temperature optima for growth and net assimilation, lower water and nitrogen use efficiencies and lower net assimilation that saturates at lower light intensities (Ehleringer & Pearcy 1983; Sikolia *et al.*, 2009). With an altitude of 1400 m a.s.l and mean temperature of  $30^\circ C$ ,  $C_4$  plants are favoured in Ruma National Park and therefore the reason for high primary production. Biomass influences NEE and GPP since it determines the photosynthetic surface area (Otieno *et al.*, 2009; Hussain *et al.*, 2009). Mean seasonal maximum NEE for Ruma National Park were around  $12 \mu mol m^{-2} s^{-1}$  for grass, while the GPP averaged at  $35 \mu mol m^{-2} s^{-1}$ . These are within the range of  $-10.0$  and  $23 \mu mol m^{-2} s^{-1}$  reported for mountain peatland grasses (Otieno *et al.*, 2009). We also observed a strong relationship between  $R_{eco}$  and GPP in our site, although the exact contribution of the vegetation to the total ecosystem respiration is not known. This suggests that a significant proportion of respiration was autotrophic.

From the results temperature plays a significant role in determining CO<sub>2</sub> exchange processes since it sets the upper limit of NEE, which increases steadily with increasing temperature to an optimum of 30°C. Since there is an exponential increase in R<sub>eco</sub> with increasing temperature, rapid decline in NEE above 30°C could be a result of an increasing respiration rate over CO<sub>2</sub> assimilation (Otieno *et al.*, 2009). This indicates that at low temperatures, humid tropical savannas are likely to become CO<sub>2</sub> sinks. Generally, savannas are less productive despite having C<sub>4</sub> grasses. When well-managed, as in derived pastures, C<sub>4</sub> grasses in savanna environments can be very productive (Santos *et al.*, 2004). But in the natural state, they sometimes have a remarkably low foliar nitrogen concentration, which limits the rate of photosynthesis. Plant production is linear function of light (particularly C<sub>4</sub> species), depending upon leaf area index (biomass) and canopy nutrition (Hussain *et al.*, 2009). Therefore high light intensities recorded in open location lead to higher NEE compared to the understory where soil moisture was high. Ecosystem respiration of the understory during the period when soil moisture was high was driven by soil temperature, with similar responses in both locations.

Previous studies on savanna woody expansion had concentrated on increasing global level of atmospheric CO<sub>2</sub> (Sankaran *et al.*, 2004). These studies had assumed competition based models of savanna and posit that decreased transpiration rates under elevated CO<sub>2</sub> increased subsoil moisture (Bond *et al.*, 2001), and thereby increasing woody cover which results from increased belowground carbohydrate storage of trees. We also anticipate that differences in dominant species composition as shown between the canopy and open grazed locations are likely to influence CO<sub>2</sub> assimilation rates (Kinyamario *et al.*, 1993) as supported by our GPP results. Our results show a different structure and functionality in the *Acacia* understory that is likely to influence the overall ecosystem CO<sub>2</sub> budget. Since primary production is a key variable of terrestrial ecosystems and an important component of the global carbon cycle (Jian, 2004; Scurlock *et al.*, 2002), the current study confirms previously studies (Jian, 2004; Parton *et al.*, 1996), which acknowledged the importance of biomass knowledge as essential to understanding the terrestrial carbon cycle, biosphere-atmosphere interaction and response of ecosystem function to climate change and CO<sub>2</sub> fertilization. Like other tropical savanna ecosystem, there is a clear distinction in biomass between dry and rainy season in Ruma National Park. These results are in concord with the differences in nitrogen and carbon levels

throughout the seasons. During dry season however, CO<sub>2</sub> fixation and ecosystem productivity in the canopy locations was likely limited by low light intensity (Kinyamario *et al.*, 1993).

## CHAPTER 6: CONCLUSIONS & RECOMMENDATIONS

### 6.1. CONCLUSIONS

Low soil moisture in Ruma National Park influenced N distribution, reduced CO<sub>2</sub> assimilation, biomass development and overall ecosystem productivity. However, soil N availability was less sensitive to soil moisture changes. Its availability to plants was impaired by low soil moisture availability, likely through reduced decomposition (N release), reduced uptake and transport. Grazing potentially reduced soil moisture storage and soil N. These changes were,

however, modified by the presence of *Acacia* trees. Therefore, the presence of farming activities impact on soil structure and vegetation composition, CO<sub>2</sub> exchange and overall ecosystem productivity. The effects of these and other determinants on tree-grass balance in savannas are useful for future researchers interested in finding ways of combating bush encroachment.

R<sub>eco</sub> was the dominant factor influencing GPP and was sensitive to precipitation amounts through changes in soil moisture status. This suggests that changes in soil C and N dynamics may have enormous influence on global carbon and nitrogen cycle and thus mitigating the impacts of global warming. Decline in precipitation therefore, may lead to increased C investment into the roots, reduced decomposition rates and hence higher C storage in the soil. GPP and R<sub>eco</sub> were strongly regulated by climate and therefore the ecosystem was a net CO<sub>2</sub> source during drought.

Trees with low, dense, evergreen canopies enhanced morning and afternoon light levels, facilitated establishment of unique grasses, and increased total herbaceous biomass beneath the tree canopy. In other cases, browsing may have stimulated tree growth and thus suppress grasses. Ruma tree canopies affected herbaceous phenology, production, and biomass allocation (root/shoot) as well as species composition. Since trees have historically been viewed as competitors with grasses and are widely regarded as having a negative impact on herbaceous production, particularly where livestock production is a primary land use, this study has revealed that productivity of areas under tree canopies may be enhanced by improved water and nutrient status but be suppressed by low irradiance and competition between trees and grasses for belowground resources.

Exclusion of herbivore through fencing in Ruma Park strongly increased herbaceous cover and biomass and a few species of woody plants. These effects were associated with greater aboveground standing biomass, reduced belowground biomass, and reduced light penetration to the ground surface. Herbivore exclusion also modified N cycling through greater N content in live aboveground plant tissue during the rainy season, and more litter and belowground tissue late in the rainy season and also increased soil nutrient concentrations. These findings indicate that plant dynamics in humid tropical savannas are not a simple function of rainfall patterns or herbivory, but regulated by interactive effects of rainfall, grazing pressure and soil nutrients.

## **6.2. RECOMMENDATIONS**

Savanna is highly structured with micro-organisms and the production of organic and inorganic compounds (such as ammonium) are concentrated close to roots. Therefore, an increase in plant biomass could potentially increase ammonium availability in the soil through an increase of root-derived carbon. Since various studies have shown that large tree cover is decreasing in several African savannas due to high elephant pressure and frequent fires within national parks and game reserves and also outside protected areas the situation is often even more dramatic, with most of the large trees being removed by local people for production of charcoal, reduction in tree cover could have serious consequences since trees have a positive effect on herbivore food quality and availability. The vast cover of savanna vegetation may significantly contribute to the global carbon budget and related gaseous fluxes. In order to assess the role of these ecosystem in global change, a better knowledge of these gas fluxes is necessary to strengthen the reporting of trace gas emissions in relation to national commitments under the Kyoto Protocol. It is important to ensure that there is;

1. Controlled grazing which balances the herbivores within the savanna ecosystem based on the available herbage with an ultimate goal of maintaining the carrying capacity.
2. Increase leguminous plants population, which in turn will reduce atmospheric carbon and nitrogen. All this combined with proper management will ensure grasslands fulfill their significant role in the global carbon cycle.

3. Obtain realistic data on the rates of trace gas exchange between the biosphere and the atmosphere, as well as conducting diurnal gas measurement for the herbaceous layer for day and night during dry and rainy seasons.

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