Carbon dioxide exchange and biomass productivity of the herbaceous layer of a managed tropical humid savanna ecosystem in western Kenya

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Abstract

Aims

Humid savannas, as a result of high precipitation amounts, are highly productive. They are also hotspots for land use change and potential sources of carbon dioxide (CO_2) due to the large soil carbon (C) stocks. Understanding how ecosystem CO_2 exchange is influenced by changes arising from agricultural land use is vital in future management of these ecosystems and in responding to the ongoing shifts in management and climate. The aim of this study was to identify how ecosystem CO_2 exchange and biomass productivity of the herbaceous layer of a humid savanna in Kenya respond to current management practices.

Methods

We used flux chambers to quantify CO_2 fluxes, while monthly harvests were undertaken to determine biomass development of the herbaceous layer of three sites that were (i) fenced to exclude livestock grazing, (ii) subjected to grazing by livestock and (iii) abandoned after being cultivated for maize production and also open to grazing by livestock.

Important findings

The peak aboveground biomass ranged between 380 and 1449 g m^{-2} and biomass production was significantly ($P < 0.05$) lower in the grazed and abandoned plots. The maximum gross primary production (GPP) and net ecosystem CO_2 exchange (NEE) ranged between 21.8 ± 1.3 to 32.5 ± 2.7 and -9.6 ± 0.7 to -17.9 ± 4.8 µmol m^{-2} s^{-1}, respectively. Seasonal NEE fluctuations ranged between 10 and 21 µmol $m^{-2}s^{-1}$, while spatial (among sites) differences ranged between 2 and 10 µmol m^{-2} s^{-1}. Ecosystem respiration (R_{eco}) fluctuated between 5 and 10 µmol m^{-2} s^{-1} during the growing season. R_{eco} was, however, not significantly different among the sites. Unlike in other similar ecosystems where ecosystem respiration is determined by the ambient temperature, we did not find any relationship between R_{eco} and temperature in this savanna. Instead, soil moisture accounted for 38–88% of the spatial and seasonal fluctuations in ecosystem CO_2 fluxes and aboveground biomass production. Management influenced the maximum GPP and NEE rates through modification of soil moisture, plant species composition and aboveground biomass. We concluded that soil moisture is the key determinant of ecosystem CO_2 exchange and productivity in this tropical savanna. Management, however, significantly modifies C fluxes and productivity through its influence on soil moisture, plant species composition and aboveground green biomass and should be taken into consideration in future similar studies.

Keywords: tropical humid savanna • abandoned croplands • biomass production • ecosystem CO_2 exchange • livestock grazing • soil water content

INTRODUCTION

Large quantities of carbon (C) are continuously exchanged between the atmosphere and the terrestrial biosphere (Hall 1989; Mooney *et al.* 1997; Schimel *et al.* 2001). Tropical savannas, which cover one-sixth of the world's land surface and account for about 30% of the global terrestrial primary production (Grace *et al.* 2006; Scurlock and Hall 1998), play a

crucial role in the carbon exchange process. In Africa, savanna covers about two-thirds of the land surface and plays an important role in the local and regional C budget (Ciais *et al.* 2011; Grace *et al.* 2006; Williams *et al.* 2007). Carbon exchange and storage in the African savanna is, however, still poorly understood (Ciais *et al.* 2009, 2011; Williams *et al.* 2007).

The most significant joint effort to assess the African carbon budget has been that of the CarboAfrica project (http://www.carboafrica.net), which provided crucial data on CO_2 fluxes from some isolated savanna sites, including southern Africa, West Africa and the Sudan. The savannas of Africa, however, are very diverse, meaning that studies conducted in one part may not be universally representative (Ardö *et al.* 2008). So far, little is known about CO_2 exchange in the East African savanna (Kinyamario and Imbamba 1992), despite its wide coverage and high diversity, both in structure and function. Multiple site-specific studies are therefore required to accurately determine the CO_2 exchange and regional C budget of this ecosystem.

The natural Africa savanna ecosystems are undergoing change as a result of conversion into grazing fields for large-scale livestock production, shifting cultivation for crop production and urbanization (Bombelli *et al.* 2009; Ciais *et al.* 2009; DeFries *et al.* 2002). The transition from natural tree–grass mixture to agro-ecosystems leads to a vegetation dominated by grasses and other herbaceous plants that function differently (Hoffman and Jackson 1999; Woomer 1993) compared with the natural savanna. Savanna soils are generally poor in nutrients (Cech *et al.* 2010), and without fertilizer input, as is common in most African farmlands, they are rapidly depleted and can only support crop production for a short period (2–3 years), before they become unproductive. The fields are then abandoned and require extended fallow intervals (abandonment) in order to regain fertility. Large tracts of fallow land, overgrown by agricultural weeds have therefore become a common feature in the African savanna landscape. Although these changes are impacting the ecosystem's capacity for C exchange and storage (Ciais *et al.* 2011; DeFries *et al.* 2002), their influence in this regard is still poorly understood.

Most C in grasslands is stored underground as soil C pool (Eswaran *et al.* 1993; Jenkinson *et al.*1999; Parton *et al.* 1994) and is supplied by an actively photosynthesizing aboveground biomass (Kuzyakov and Gavrichkova 2010; Otieno *et al.* 2010). The amount of stored C in the soil is determined by the balance between photosynthetically derived C inputs and C losses (Jastrow *et al.* 2007). Clearing of the natural savanna vegetation for the establishment of maize-based agriculture lowers the photosynthetic C inputs into the soil and increases soil C losses, reducing the ecosystem C storage (Jastrow *et al.* 2007; McCulley *et al.* 2007; Muniafu and Kinyamario 2007). Woomer (1993) reported a decline of about 70% in total soil organic carbon after 50 years of cultivation, while Zingore *et al.* (2005) reported a 40% decline in 10 years. In comparison, the conversion of natural savanna into livestock grazing fields at high stocking rates leads to excessive removal of the aboveground biomass and the reduction of photosynthetic leaf area (Leriche

et al. 2003; Skarpe 1991; Turner *et al.* 1993). Poor grazing management, associated with overstocking of livestock, leads to excessive trampling and inflict physical injury to the vegetation (Abdel-Magid *et al.* 1987a; Hodgkinson *et al.* 1989; Patton *et al.* 2007), increase soil bulk density and decrease soil water infiltration (Abdel-Magid *et al.* 1987b; Patton *et al.* 2007). As a result, there are changes in plant species composition, decrease in leaf photosynthetic rates and a drop in C storage by the ecosystem (Hodgkinson *et al.* 1989; Leriche *et al.* 2003). Light grazing on the other hand may stimulate aboveground biomass growth through enhanced tillering of grasses (Patton *et al.* 2007; Silva and Raventós 1999; Turner *et al.* 1993). Enhanced sprouting of young shoots from the tillers increases the generation of fresh actively photosynthesizing green vegetation (Leriche *et al.* 2003; Turner *et al.* 1993), which, coupled with the low accumulation of dead biomass, improves light penetration into the canopy and increases CO_2 uptake and C storage by the grasslands (Silva and Raventós 1999).

The two commonly used methods for direct measurements of ecosystem CO_2 exchange are the eddy covariance (EC) and chambers (Aubinet *et al.* 2000, Wohlfahrt *et al.* 2005). Both methods have been compared in detail by Wohlfahrt *et al.* (2005). The EC technique applies best on relatively flat terrain to minimize convective error, with vegetation structure over a given fetch where fluxes are easily related to clearly defined vegetation types or footprint locations (Aubinet *et al.* 2000). Thus, EC applies best in monocultural landscapes, or where separation of fluxes among ecosystem components (patches) is not an objective. The technique is, however, not appropriate in heterogeneous landscapes when the focus is to separate fluxes from the different ecosystem patches. In such cases, the chamber technique is employed (Long *et al.* 1992; Li *et al.* 2008a). Large chambers that enclose "ecosystem monoliths" directly measure CO_2 exchange within the defined enclosed area, allowing for the spatial evaluation of CO_2 fluxes. We used chambers to measure CO_2 fluxes of the herbaceous understory of a humid savanna subjected to grazing by livestock and an abandoned field that was formally used for growing maize. Similar chambers have widely been used for CO_2 measurements in the temperate (Li *et al.* 2008a), Mediterranean (Hussain *et al.* 2009; Li *et al.* 2008b), peatlands (Otieno *et al.* 2009) and in the African savanna (Otieno *et al.* 2010, 2011) ecosystems, and the results compare favourably with eddy data when both are used in parallel (Li *et al.* 2008a, 2008b). We hypothesized that changes in the ecosystem structure and function due to heavy cattle grazing and shifting cultivation for maize production (abandoned fields) lower ecosystem CO_2 exchange and productivity of the savanna herbaceous layer and hence ecosystem C storage.

METHODS

Study site

The study was conducted in Ruma National Park (00° 34′ S and 34° 22′ E), 10 km east of Lake Victoria, in Nyanza

province, Kenya. The park lies within the Lambwe valley at an elevation of between 1200 and 1300 m.a.s.l. It is bordered by Kanyamwa escarpment (1722 m.a.s.l.) to the east and Gwasi hills (2270 m a.s.l.) to the west. The valley slopes gently in an E-W direction. Gwasi hills and the Kanyamwa escarpment support largely ferruginous tropical soils and halomorphic soils on rocks rich in ferromagnesium. On the escarpment and in the foothills, mixed soil formations of red-brown friable clays, grey mottled clays and grey compacted loamy sands predominate. Levels of exchangeable sodium, magnesium and calcium are high in these formations and hence the valley soils have high mineral content and are alkaline. The higher parts of the hills support shallow stony soils and dark brown loams with numerous rock outcroppings, particularly where the underlying stratum is of lava (Allsopp and Baldry 1972; Atlas of Kenya 1962).

The climate is hot and humid with a mean air temperature of 22.5°C. The mean annual rainfall for the last 15 years is 1346 mm, with a bimodal distribution pattern between April–June and September–November. The terrain is mainly rolling grassland with tracts of open woodland and thickets. The dominant tree species are *Acacia ancistroclada, A. gerarrdii, Rhus natalensis, R. vulgaris, Pilliostigma thonningii* and *Belanites aegyptica*. The herbaceous layer comprises a rich mix of grass and herbs (see Otieno *et al*. 2011 for full plant species list and distribution). The dominant grass species in the open grazed field were *Themeda triandra* Forssk. and *Panicum maximum* Jacq., while the abandoned field was dominated by *Amaranthus hybridus* L., a common agricultural weed in this region.

Experimental site and study design

An observational plot of 40 ha was established within the land belonging to the Kenya National Youth Services (NYS). Three different sites, based on the common land use practice namely fenced (control), grazed and abandoned farmlands were identified and demarcated for measurements (See Fig. 1). The sites measured approximately 70 m by 50 m each, lying in close proximity to each other, so that they shared similar soils and climate. The site characteristics were examined and described in detail by Otieno *et al*. (2011). The fenced site was established in 2006 by erecting a 2-m high perimeter fence to exclude livestock. The grazed site was an open savanna subjected to grazing by livestock (stocking rate = 6.6 animal units ha^{-1}). Livestock grazed the demarcated study site at least twice a week. At any grazing event, they stayed on the site for not more than one hour. The abandoned site was previously planted with maize (*Zea mays*), after conversion from natural savanna. Maize had been grown on the field for 10 years before abandonment in 2006 (communication from the National Youth Services). Maize was planted bi-annually (April–June and October–December). There were no records of artificial fertilizer/manure application during this period. Since 2006, the site had been left fallow to regain fertility. This field was located on the eastern side of the fenced and grazed sites, at a slope of 2°. Both the abandoned and grazed sites were open to grazing by livestock. Field measurements were conducted between March 2008 and November 2009, except in the abandoned site, where they started in August 2008.

Measurements

Microclimate

A microclimate station was set up within the study site in an open area to avoid interference from trees. Weather parameters measured were rainfall (RG3 HOBO pedant rain gauge, HOBOware, Eichstetten, Germany), air temperature and humidity (FUNKY-Clima, ESYS, Berlin, Germany) and global radiation (HOBO pedant, HOBOware, Eichstetten, Germany) at 2 m above the ground. Measurements were taken every 30 s and averaged and stored every 30 min using in-built data loggers. Discontinuous measurements of soil temperature at 10-cm depth were carried out on the three sites during CO_2 flux measurements using digital thermometers (Einstichthermometer, Conrad, Hirschau, Germany).

Determination of soil bulk density and soil water content

We used an 80-mm diameter sturdy ring corer to obtain soil samples, down to 30 cm, for soil moisture and soil bulk density determination. During any sampling event, five (5) samples were obtained randomly (between 10:00 and 12:00) from each of the sites. Each sample was checked for soil compaction before removing the sampler from the soil, by inspecting the relative height of soil inside and outside the sampler. A 90-mm diameter section of polyvinyl chloride plumbing pipe, cut longitudinally in half, was used as a cradle to hold the soil cores when they were ejected from the sampler. The soil cores were separated into 0–10, 10–20 and 20–30 cm depths using a sharp knife to cut through the cylindrical sample and immediately weighed to determine their fresh weights. The samples were later oven-dried at 105°C to constant weight and re-weighed to determine dry weight. Gravimetric soil water content was determined as the relative change in weight between fresh and dry soil samples. Soil bulk density was calculated by dividing oven dry weight of the composite soil samples by the total volume of soil sampled at each depth.

Ecosystem CO$_2$ exchange

Net ecosystem CO_2 exchange (NEE) and ecosystem respiration (R_{eco}) were measured monthly using chambers (see Li *et al*. 2008b for full chamber description). A set of soil frames measuring 39.5 × 39.5 cm (See Fig. 1b) were inserted 4 cm into the soil at least 3–4 weeks before the measurements were conducted. Three soil frames were randomly established in each of the sites (pseudo replication) every month. Spacing between them was >10 m, in order to ensure representative site sampling. The soil frames provided a base onto which the chambers were affixed (See Fig. 1c) to ensure airtight conditions between the chamber and the soil. During any single measurement day, NEE and R_{eco} were sequentially measured in a systematic rotation in the three sites using
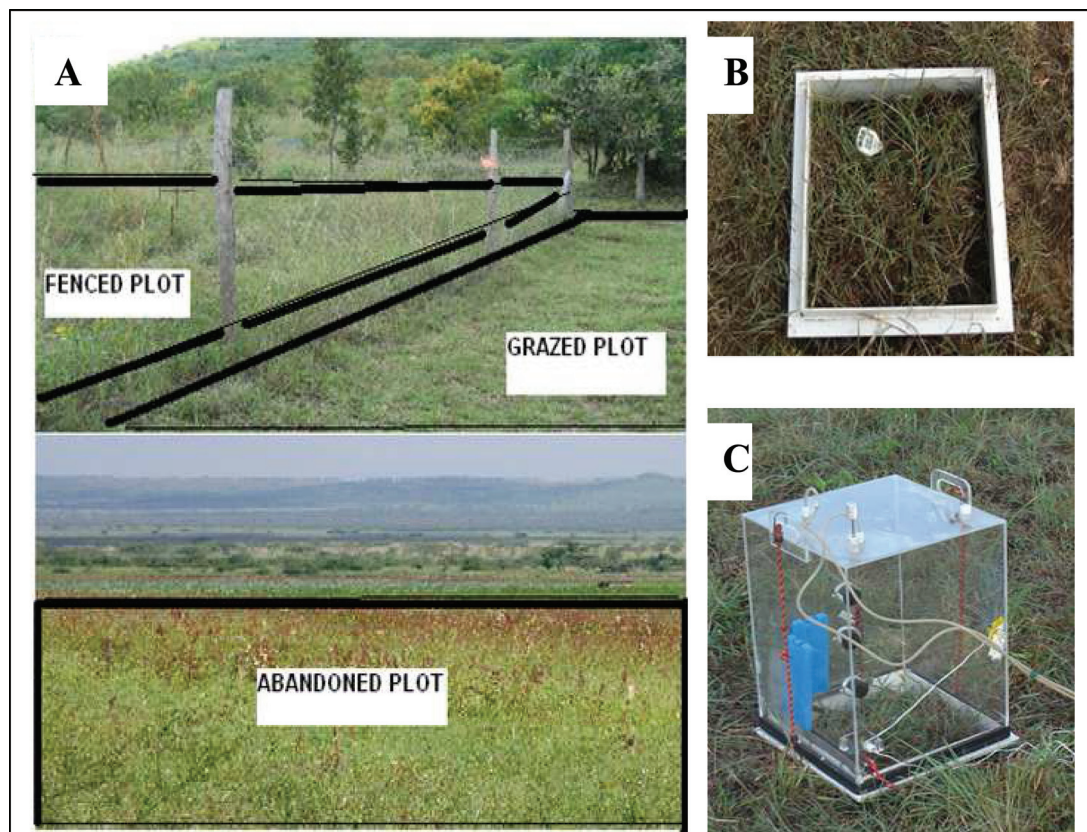
Figure 1: (a) pictorial representation of the study site, showing land use types on which measurements were conducted. (b) Soil frames onto which chambers were fixed for ecosystem CO_2 measurements as demonstrated by the (c) light/transparent chamber.

manually operated, closed gas-exchange chambers. During the serial CO_2 flux measurements, it took between 3–5 min to change from one frame to the other. The time lapse between NEE and R_{eco} measurements on each plot was between 20–30 min, with NEE measurements taken upfront. The 40 × 40 × 54 cm chambers of our system were constructed from transparent plexi-glass (3 mm XT type 20070; light transmission 95%) for measuring NEE (See Fig. 1c) and from opaque polyvinyl chloride, covered with an opaque insulation layer and reflective aluminium foil, for measuring R_{eco}.

The chamber height was adjusted to the canopy height using extension frames of different sizes. Chambers were sealed to the frames inserted into the soil with a flexible rubber gasket and the chamber firmly secured using elastic straps fastened onto the ground from two sides (Fig. 1c). Tests indicated that leakage did not occur, 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. Increment in air pressure in the chamber headspace 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 records were taken. Circulation of air within the chamber was provided by three fans yielding a wind speed of 1.5 m s^{-1}. Changes in chamber

CO_2 concentration over time were read from a portable IRGA (Infra Red Gas Analyzer) (LI-COR 820, USA). Measurements were carried out within 3 min of placing the chamber onto the frames. Once steady rate of change in CO_2 concentration was attained, usually 1 min after placement of chamber onto the frames, data were logged every 15 s for 2 min. CO_2 fluxes were calculated from a linear regression describing the time-dependent change in CO_2 concentration within the chamber. By mounting dry ice packs inside and at the back of the chamber in the air flow, internal chamber temperature was maintained within 2°C relative to ambient during the measurements. Air (at 20 cm above the ground surface) and soil (at 10-cm depth) temperatures inside and outside of the chamber were monitored during measurements and data logged at the onset and end of every round of NEE measurement on each frame. Similarly, light intensity within the chamber and above the vegetation (canopy) was monitored using a quantum sensor (LI-190, LI-COR, USA), and data logged every 15 s alongside the CO_2 concentration data.

Tests conducted in a controlled-climate chamber showed that vapour pressure deficit (VPD) changes within the 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 will not

affect CO_2 exchange *via* stomatal effects. Effects of decreasing CO_2 concentrations on the vegetation during measurements were assumed. These effects were, however, minimized by reducing the time interval during which the vegetation was enclosed in the chamber. On each measurement day, hourly measurements were conducted from sunrise (07:00) to sunset (18:00) over the same frames in each site. Eleven rounds of measurement were accomplished on each single day, giving a total of 198 complete chamber records per day and a non-stop 9.9 chamber hours.

Gross Primary Production (GPP) was estimated *via* the general equation (Gilmanov *et al.* 2007):

$$GPP = R_{eco} - NEE \qquad (1)$$

After CO_2 flux measurements, all the aboveground biomass from each of the frames was cut to ground level and the positions clearly marked to avoid repeated measurements. The frames were removed and randomly reinstalled onto new locations for the next round of monthly measurements.

Aboveground biomass

The harvested biomass from the frames (for CO_2 flux measurements) was separated into live and dead biomass. Live biomass constituted green standing plant material, while the dead biomass consisted of brown standing and non-standing (on the ground) plant material. The aboveground biomass samples were then oven-dried at 80°C for 48 h, before determining their dry weights.

To compare the sites, GPP was normalized with green biomass (expressed per unit gram biomass) in order to remove the differences in GPP arising from biomass differences among the sites.

Soil and plant nitrogen and carbon

Monthly soil samples for C/N determination were extracted down to 30 cm using 1.5-cm diameter soil corer. Three samples were obtained from each of the sites (one sample per CO_2 flux measurement site), separated into 0–10, 10–20 and 20–30 cm depths. The holes were re-filled with soil after removal of the sample cores. The samples were sieved through a 0.2-mm wire mesh to remove roots and stones. The sieved samples were then oven-dried at 80°C for 48 h. Approximately 20 g soil from each layer was then used for C/N determination. Plant material for C/N analysis was derived from the biomass samples, after dry weight determination. All the samples (shoots, roots and soil) were separately homogenized in a ball mill and re-dried in a desiccator to eliminate all water. About 5 g of the dried soil and 1 g of the dried plant material were then analysed to determine their C and N concentrations (%) by means of elemental analysis (Markert 1996).

Statistical analysis

Group means from the three different sites were compared using one-way analysis of varience (ANOVA), with sites as the fixed effects, using statistical software SPSS (SPSS 15.0 for Windows, SPSS Inc., Chicago, USA). Pairwise tests of the means were conducted using Tukey-LSD (least significant difference) to compare between the sites. Significance level was set at $P \leq 0.05$. Interactions between factors were assessed through regression analyses and also using Generalized Linear Model. We checked the normality of the model residuals visually. We assured the homogeneity of variances and goodness of fit of the models by plotting residuals versus fitted values.

RESULTS

Microclimate

The total amount of rainfall received during the measurement period was 820 and 1100 mm in 2008 and 2009, respectively. These amounts were lower than the 15-year average of 1346 ± 54 mm. The long rains occurred between April and June, while the short rains occurred from October to December (Fig. 2). January–March and July–September were dry. The mean diurnal air temperature was 25.3 ± 5°C. The highest and lowest mean daily maximum air temperatures were 35 ± 1.5°C in 18 March ± 1.1°C in July, respectively. Diurnal temperature fluctuations were larger than the annual fluctuations.

Soil bulk density, water content and temperature

Soil bulk densities of the top 10 cm soil profile were 1.1 ± 0.1, 1.2 ± 0.1 and 1.3 ± 0.2 g cm^{-3} in the fenced, grazed and abandoned sites, respectively. As expected, the gravimetric soil water content (SWC) within the 0–30 cm soil profile increased during the rains and declined during drought (Figs. 3a and b). Differences among the sites were significant (ANOVA, $F = 0.27$, $P < 0.01$). The highest and lowest SWC were recorded in the fenced and abandoned sites, respectively. Soil temperatures at 10-cm depth in the fenced site were lower compared with the other two sites (Fig. 3c and d).

Soil nitrogen and carbon concentrations

Total nitrogen (N) within the top 30-cm soil profile did not differ significantly among the sites (Fig. 4a). Percentage (%) N within this layer was 0.24 ± 0.02, 0.22 ± 0.03 and 0.24 ± 0.03, translating into 2.6 ± 0.2, 2.4 ± 0.3 and 2.9 ± 0.4 t N ha^{-1} in the fenced, grazed and abandoned sites, respectively. There was a consistent decrease in soil N concentrations with increasing soil depth. The respective percentage C concentrations in the top 30-cm layer were 4.6 ± 0.4, 4.3 ± 0.5 and 3.2 ± 0.2 in the fenced, grazed and abandoned sites, resulting into 52.2 ± 2.8, 46.2 ± 5.8 and 41.3 ± 3.3 t C ha^{-1}, respectively. Compared with the other two sites, soil C concentration within the top 10 cm profile in the abandoned site was significantly (ANOVA, $F = 45.8$, $P < 0.001$) lower (Fig. 4b). The highest soil C concentration occurred in the fenced site.

Plant nitrogen and carbon

Nitrogen content in the aboveground biomass varied significantly during the year, with plant N content increasing
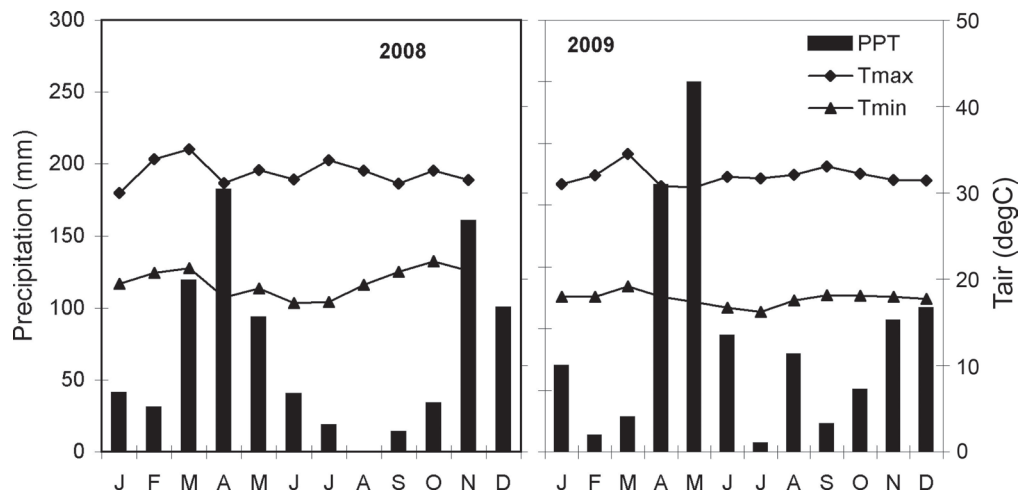
Figure 2: monthly rainfall amounts and mean maximum and minimum monthly air temperatures at Ruma during 2008 and 2009 when the measurements were conducted.
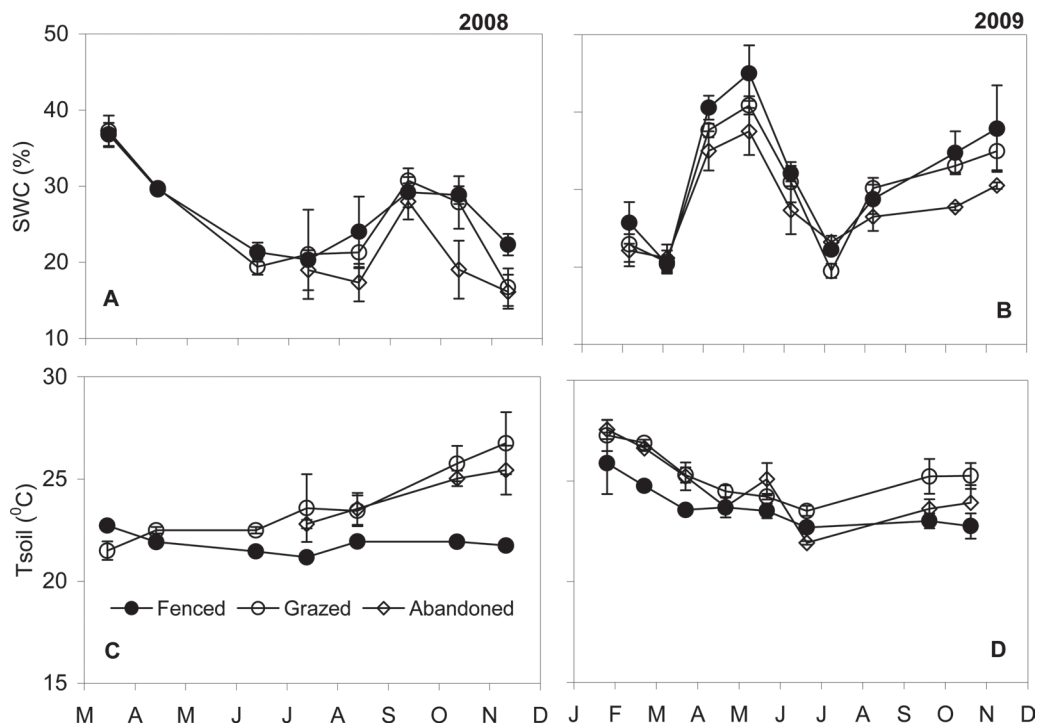

Figure 3: SWC within the 0-cm- to 30-cm soil depth in the fenced, grazed and abandoned sites during (a) 2008 and (b) 2009 and monthly mean soil temperatures in 10-cm depth in the respective plots during (c) 2008 and (b) 2009 ($n = 3$).

during the rainy periods, associated with active plant growth, and declining during drought (Fig. 5a). Compared with the other two sites, the vegetation on the abandoned site had significantly (ANOVA, $F = 3.7$, $P = 0.04$) higher tissue N content. Except in the grazed site, root N content increased significantly during the growing period (Fig. 4c). The lowest ($F = 3.5$, $P < 0.05$) C:N ratio occurred in the abandoned site (Fig 4b).

Aboveground biomass development

Aboveground biomass development was seasonal, with 2 peaks during the year (Fig. 6). Mean annual aboveground biomass production was 1449 ± 330, 303 ± 118 and 380 ± 230 g m^{-2} in the fenced, grazed and abandoned sites, respectively. Differences among the sites were significant. Due to persistent livestock grazing, biomass in the grazed site was kept low most of the year.
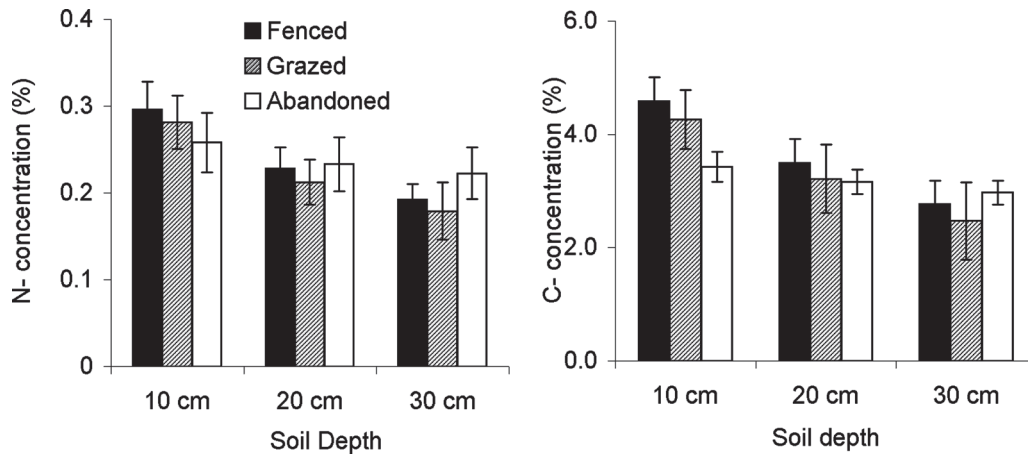
Figure 4: (a) soil nitrogen and (b) carbon concentrations within the top 0–30 cm soil profiles of the fenced, grazed and abandoned sites. Bars are ±SE ($n = 3$).
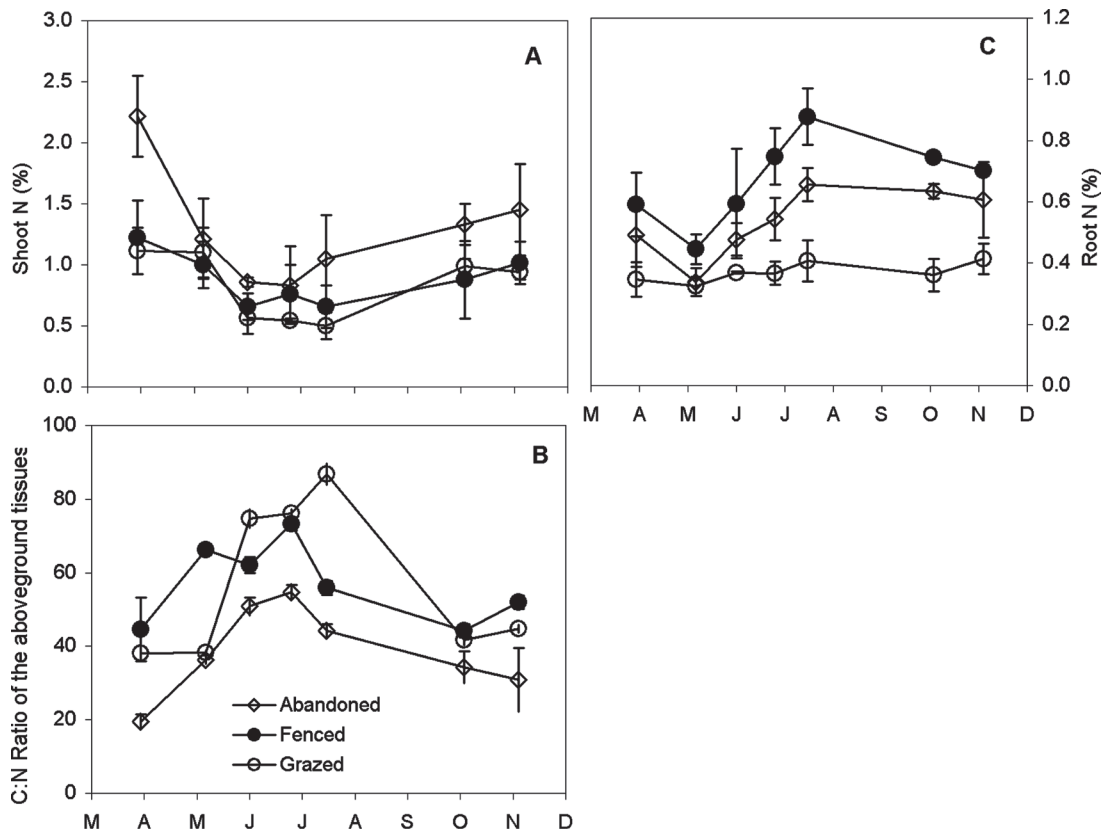

Figure 5: (a) seasonal trends of shoot (b) root nitrogen uptake and (d) C:N ratio of the aboveground tissue at the respective sites. Bars are ±SE ($n = 3$).

Ecosystem CO_2 exchange

GPP and R_{eco} increased during the rainy seasons and declined during the dry periods (Fig. 7). The lowest GPP ranged between 2 and 5 μmol m^{-2} s^{-1} during the dry period, while the highest rates ranged between 21.8±1.3 and 32.5±2.7μmol m^{-2} s^{-1} during the rainy periods (Fig 7a).

In most instances, GPP in the grazed sites was significantly ($F = 9.9$, $P < 0.001$) lower compared with the two other sites. Biomass-normalized GPP was higher in the grazed > abandoned > fenced sites in the order (Fig. 8). Differences between the grazed and abandoned sites were, however, not significant ($P > 0.05$).
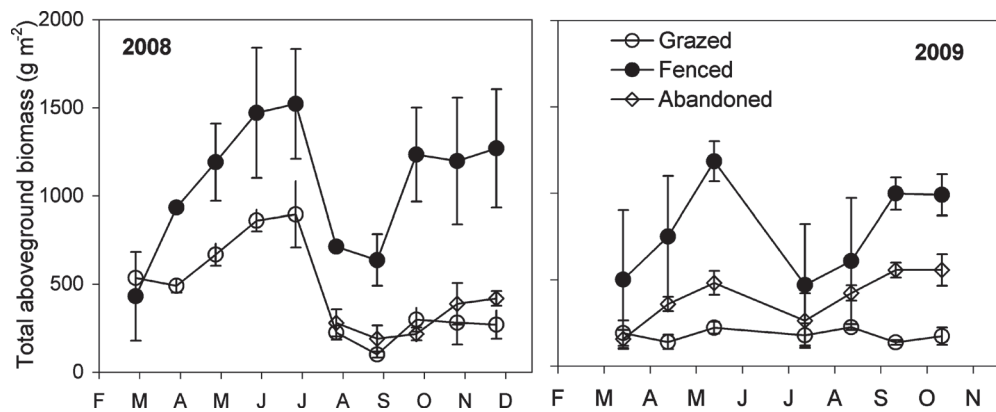
Figure 6: seasonal trend of aboveground biomass in the respective sites during (a) 2008 and (b) 2009. Bars are ±SE (*n* = 3).

Ecosystem respiration (R_{eco}) increased during the rains and declined during drought (Fig. 7b). The highest R_{eco} recorded during the measurements were around 15 ± 2 μmol m^{-2} s^{-1}, occurring during the rainy periods. There were no differences among the studied sites. GPP and R_{eco} contribute to NEE, hence NEE increased (more negative) during the rainy periods and declined during drought (Fig. 7c). The lowest NEE was around 5 ± 2 μmol m^{-2} s^{-1}, occurring during the dry periods, while highest rates of between -9.6 ± 0.7 and -17.9 ± 4.8 μmol m^{-2} s^{-1} were recorded during the rains. During the second year of measurements, the grazed site registered significantly ($F = 25.9$, $P < 0.001$) lower NEE compared with the other two sites. The abandoned and fenced sites were, however, not different and NEE rates were higher than the previous year.

NEE, R_{eco} and GPP were linearly and significantly correlated with SWC in all the three sites (Fig. 9). GPP and NEE responded more rapidly to changes in soil moisture in the abandoned compared with the other two sites (Figs. 9a and c). The strongest ($R^2 = 0.88$ and $R^2 = 0.59$ for NEE and GPP, respectively) relationship occurred in the fenced site, while the weakest ($R^2 = 0.43$ and $R^2 = 0.38$ for NEE and GPP, respectively) occurred in the grazed site. In all the sites, R_{eco} was positively and significantly correlated ($R^2 = 0.69$) with SWC (Fig. 9b), with no differences among the sites. Soil temperature at 10-cm depth did not influence ecosystem respiration in all the sites. The interaction term in the model relating SWC, soil temperature and CO_2 flux parameters was also not significant ($P > 0.05$), indicating no interaction between SWC and soil temperature on their influence on the ecosystem parameters.

DISCUSSION

Aboveground biomass ranged between 380–1449 g m^{-2}, characterized by strong spatial and seasonal differences (Fig 6). Spatial differences in biomass (among sites) were likely as a result of biomass removal by livestock, differences in SWC and in the dominant species. Cattle grazing was associated with active biomass removal and a drop in the aboveground biomass, thus accounting for difference in biomass between grazed and non-grazed plots. Differences arising between the grazed and abandoned plots were attributed to the dominant plant species, which likely respond differently to grazing (preference by the grazing livestock). SWC was also different among the sites (Fig 3) and may contribute to both the spatial, as well as temporal variations in biomass (Otieno *et al.* 2010, 2011).

Biomass production at our study site, however, is within the range of the aboveground biomass reported in other humid savannas receiving similar amounts of rainfall. Scurlock *et al.* (2002) analyzed aboveground net primary production (ANPP) of different grasslands of the world and reported biomass range between 300–900 g m^{-2} year^{-1} for tropical humid savannas, with annual precipitation of 580–1926 mm. ANPP values of 160–1440 g m^{-2} year^{-1} have been reported for humid savannas in Africa receiving annual precipitation of 610–1700 mm and subjected to different management options (Cech *et al.* 2010; Mordelet and Menaut 1995). The mean aboveground biomass reported for the understory of a humid savanna in Brazil, with an annual rainfall between 1100 and 1700 mm ranged between 137 and 817 g m^{-2} (Barbosa and Fearnside 2005).

Soil moisture also explained most of the temporal variations in GPP, R_{eco} and NEE within the sites (Figs 7 and 9), with GPP, R_{eco} and NEE increasing with increasing SWC. There were however, significant variations in the responses to soil moisture among the sites. Compared with the other two sites, at similar SWC, the abandoned site exhibited significantly higher GPP rates (Fig. 9), which may be linked to higher leaf N content in the vegetation (Fig. 5a), promoting higher photosynthesis rates (Jackson *et al.* 1988). However, the lower C:N ratio compared with the native C4 grasses (grazed and fenced sites, Fig. 5b) infers low N use efficiency by the vegetation, which maybe an ecological disadvantage in an ecosystem like moist savanna, which is N limited (Cech *et al.* 2008, 2010). This may be one of the reasons why the dominant species in the abandoned sites are not common in the climax communities of the herbaceous layer in this savanna (Otieno *et al.* 2011).
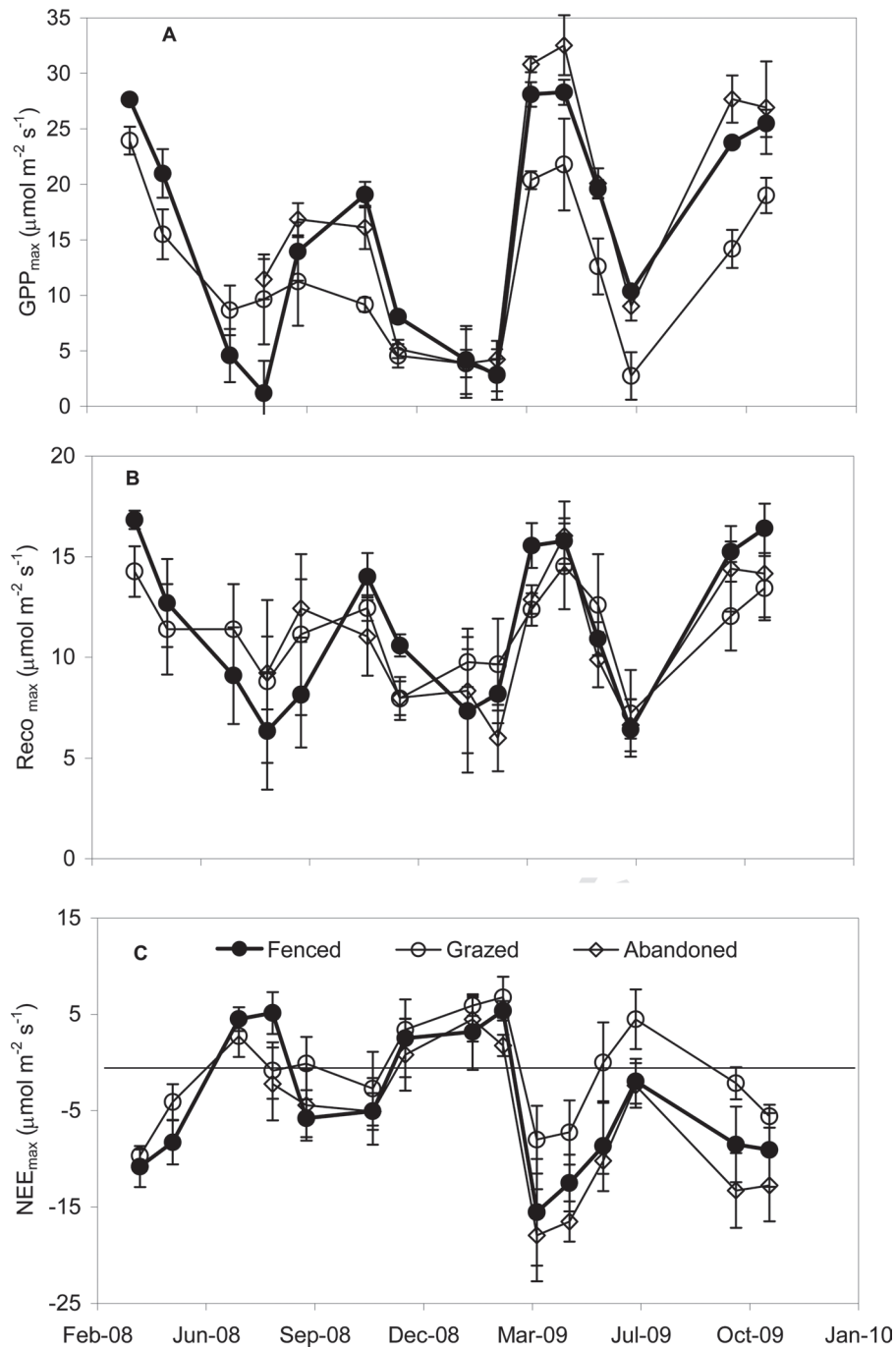
Figure 7: (a) maximum GPP (b) Ecosystem Respiration (R_{eco}) and (c) Net Ecosystem CO_2 Exchange (NEE) in the fenced, grazed and abandoned sites between 2008 and 2009. Bars are ±SD ($n = 8$).

Root N in the grazed sites was relatively constant and significantly lower throughout the vegetative period (Fig. 5c). This may be because of constant clipping by the grazing animals, which promotes continued shoot growth and a continuous demand N. There is, therefore, no relocation of N to the plant roots, as is always the case in senescing perennial grasses (Jackson *et al.* 1988). We speculate that the young plant tissues, stimulated by grazing, promote CO_2 uptake and

is the reason for the higher normalized GPP recorded in the grazed site (Fig. 8). Grazing enhances tillering and sprouting of young shoots, while improving the light environment within the stand (Patton *et al.* 2007; Silva and Raventós 1999), factors that promote higher photosynthesis (Leriche *et al.* 2003; Turner *et al.* 1993). The total ecosystem GPP in the grazed site is, however, low (Fig. 7), despite higher leaf photosynthetic efficiency (Fig. 8) due to the low photosynthesizing biomass
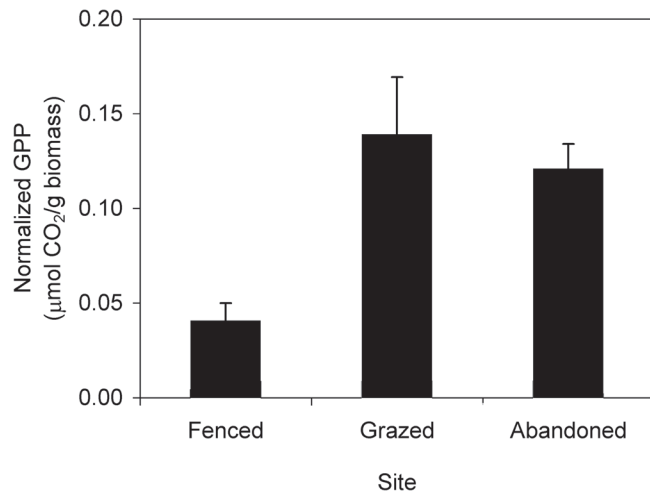
Figure 8: biomass-normalized GPP (mean values) during the growing periods between April–June and September–November in the fenced, grazed and abandoned sites. Letters indicate significant differences. Bars are ±SE (*n* = 8).

(Otieno *et al.* 2009). This leads to an overall lower NEE in the grazed plots.

Seasonal (between wet and dry seasons) fluctuations in NEE were much larger (10–21 µmol m^{-2} s^{-1}) compared with the spatial (among site) differences (2–10 µmol m^{-2} s^{-1}). Thus, although changes in NEE arising from seasonal fluctuations in soil moisture dictate the annual ecosystem C balance, a drop in daily NEE of about 2–10 µmol m^{-2} s^{-1} as a result of management (largest drop in the grazed plots) may result into huge losses in ecosystem's C storage capacity, when the entire growing period is taken into consideration. On the other hand, higher water use efficiency (higher GPP at similar SWC) demonstrated by the abandoned site promotes C storage and water saving by the ecosystem, resulting in higher NEE during the vegetative period (Fig. 7 and 9). Changes in the ecosystem arising from management, therefore, modify the rate of CO$_2$ exchange and C storage by the ecosystem and also how the ecosystem will respond to changes in SWC. These adjustments are important since they determine the overall NEE. The nature of our measurements, however, could not enable us calculate the total C stored in the respective ecosystem patches of the herbaceous layer, thus we cannot provide an estimate of changes in ecosystem C balance resulting from management. Our peak CO$_2$ exchange rates and the observed fluctuations in CO$_2$ fluxes, however, are within the range of values reported for African savannas elsewhere (Archibald *et al.* 2009; Ardö *et al.* 2008; Kutsch *et al.* 2008; McCulley *et al.* 2007; Veenendaal *et al.* 2004; Williams and Albertson 2004; Williams *et al.* 2009) and demonstrate the significant impacts of both management and soil moisture on ecosystem CO$_2$ exchange and biomass production.

Despite differences in soil temperature among the sites and also during the year (Fig. 3), soil temperature showed no
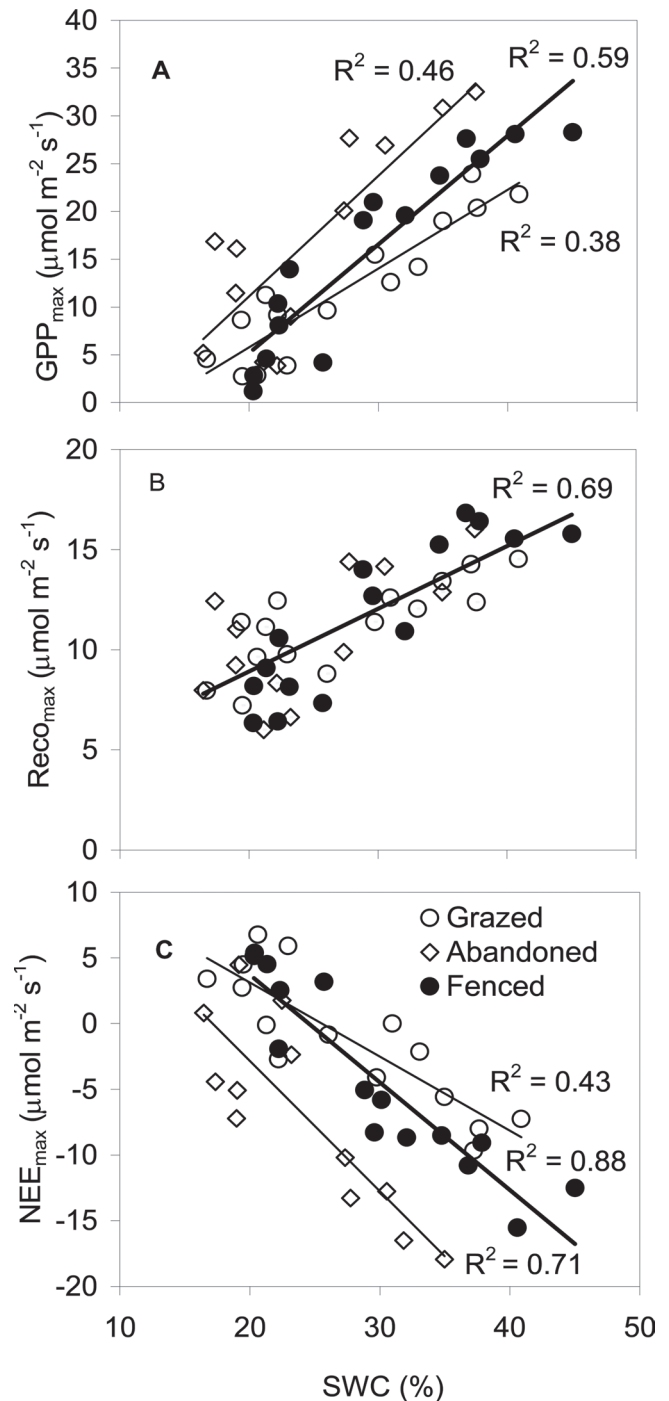

Figure 9: relationship between (a) GPP, (b) R_{eco}, (c) NEE and SWC within the 0–30 cm soil profile in the fenced, grazed and abandoned sites, for the entire measurement period.

significant influence on R_{eco}. This is a departure from some of the earlier studies in some African savannas (Williams *et al.* 2009; Kutsch *et al.* 2008; Merbold *et al.* 2008; Williams and Albertson 2004), which show temperature dependence of R_{eco}. Our results are, however, in agreement with recent studies (Grover *et al.* 2012; Otieno *et al.* 2010; McCulley *et al.* 2007), which show that soil temperature has insignificant

influence on R_{eco} in tropical savannas. The influence of temperature is likely masked by the strong dependence of ecosystem respiration on SWC ($R^2 = 0.69$, Fig 9c) and the antagonistic trends of both temperature and soil moisture. Temperature declined during the rainy periods and increased during drought (Fig. 2). Daily temperature fluctuations were much larger than seasonal changes, which could affect the long-term impact of temperature on R_{eco}. R_{eco} responses to the daily soil temperature changes were however undefined and insignificant. Otieno et al. (2010) found no relationship between soil temperature and R_{eco} in a rain exclusion experiment performed in a moist African savanna. Grover et al. (2012) and McCulley et al. (2007) reported lack of responses of R_{eco} to changes in soil temperature and instead emphasized soil moisture as the main factor regulating R_{eco} in the Australian savannas. Tang et al. (2005) observed that respiration in the understory of an oak-savanna was decoupled from soil temperature but was instead more coupled to the crown assimilation. These results are a strong pointer to possible functional differences among savanna types, emphasizing the need for site-specific studies in the estimation of regional C balance for the African savannas. Insensitivity of R_{eco} to soil temperature, as reported in this humid savanna, also provides a new research frontier, given that most global change studies predict increased R_{eco} in responses to global warming (IPCC 2007).

CONCLUSION

Soil moisture determined the magnitudes of ecosystem CO_2 exchange and productivity. Temporal (due to rainfall seasonality) and spatial (due to management) changes in SWC resulted into differences in net ecosystem CO_2 exchange and biomass production. Management modified ecosystem CO_2 exchange and ecosystem productivity through alteration in soil moisture, nutrient uptake, plant species and aboveground biomass. Spatial and temporal differences need therefore to be considered in future studies aimed at understanding CO_2 exchange and C storage and productivity of this, and similar savannas elsewhere. Unlike in other ecosystems, we did not observe any influence of soil temperature on ecosystem respiration. Management showed a significant effect on ecosystem CO_2 exchange. Accurate determination of C balance of the African savanna must therefore consider differences in C storage as a result of ecosystem modification arising from management.

REFERENCES

Abdel-Magid AH, Trlica MJ, Hart RH (1987a) Soil and vegetation responses to simulated trampling. *J Range Manage* **40**:303–6.

Abdel-Magid AH, Schuman GE, Hart RH (1987b) Soil bulk density and water infiltration as affected by grazing systems. *J Range Manage* **40**:307–9.

Allsopp W, Baldry AT (1972) A general description of the Lambwe valley area of South Nyanza District, Kenya. *Bull Wld Hlth Org* **47**:691–7.

Archibald SA, Kirton A, van der Merwe MR, et al. (2009) Drivers of inter-annual variability in net ecosystem exchange in a semi-arid savanna ecosystem, South Africa. *Biogeosciences* **6**:251–66.

Ardö J, Mölder M, El-Tahir BA, et al. (2008) Seasonal variation of carbon fluxes in a sparse savanna in semi arid Sudan. *Carbon Balance Manag* **3**:7. doi:10.1186/1750-0680-3-7.

Atlas of Kenya (1992) *Survey of Kenya*. Government Press, Nairobi, 46.

Aubinet M, Grelle A, Ibrom A, et al. (2000) Estimates of the annual net carbon and water exchange of the European forests: the EUROFLUX methodology. *Adv Ecol Res* **30**:113–75.

Barbosa RI, Fearnside PM (2005) Above-ground biomass and the fate of carbon after burning in the savannas of Roraima, Brazilian Amazonia. *For Ecol and Manage* **216**:295–316.

Bombelli A, Henry M, Castaldi S, et al. (2009) An outlook on the Sub-Saharan Africa carbon balance. *Biogeoscience* **6**:2193–205.

Cech PG, Ventrink HO, Edwards PJ (2010) N and P cycling in Tanzanian humid savanna: influence of herbivores, fires, and N2-fixation. *Ecosystems* **13**:1079–96.

Cech PG, Kuster T, Edwards PJ, et al. (2008) Effects of herbivory, fire and N2-fixation on nutrient limitation in a humid African savanna. *Ecosystems* **11**:991–1004.

Ciais P, Bombelli A, Williams M, et al. (2011) The carbon balance of Africa: synthesis of recent research studies. *Philos Transact A Math Phys Eng Sci* **369**:2038–57.

Ciais P, Piao S-L, Cadule P, et al. (2009) Variability and recent trends in the African terrestrial carbon balance. *Biogeosciences* **6**:1935–48.

DeFries RS, Bounoua L, Collatz GJ (2002) Human modification of landscape and surface climate in the next fifty years. *Glob Change Biol* **8**:438–58.

Eswaran H, van den Berg E, Reich P (1993) Organic carbon in soils of the world. *Soil Sci Soc Amer J* **57**:192–4.

Gilmanov TG, Soussana JE, Aires L, et al. (2007) Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agric Ecosyst Environ* **121**:93–120.

Grace J, San Jose J, Meir P, et al. (2006) Productivity and carbon fluxes of tropical savannas. *J Biogeogr* **33**:387–400.

Grover SPP, Livesley SJ, Hutley LB, et al. (2012) Land use change and the impact on greenhouse gas exchange in north Australian savanna soils. *Biogeosciences* **9**:423–37.

Hall DO (1989) Carbon flows in the biosphere: present and future. *J Geographical Soc, Lond* **146**:175–81.

Hodgkinson KC, Ludlow MM, Mott JJ, *et al.* (1989) Comparative responses of the savanna grasses *Cenchrus ciliaris* and *Themeda triandra* to defoliation. *Oecol* **79**:45–52.

Hoffman WA, Jackson RB (1999) Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. *J Climate* **13**:1593–602.

Hussain MZ, Otieno DO, Mirzaei H, *et al.* (2009) CO_2 exchange and biomass development of the herbaceous vegetation in the Portuguese montado ecosystem during spring. *Agric Ecosyst and Environ* **132**:143–52.

IPCC (2007) *Climate Change 2007: the Physical Science Basis*. Geneva: Intergovernmental Panel on Climate Change.

Jackson LE, Strauss RB, Firestone MK, *et al.* (1988) Plant and soil nitrogen dynamics in Californian annual grassland. *Plant Soil* **110**:9–17.

Jastrow JD, Amonette JE, Bailey JL (2007) Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. *Climatic Change* **80**:5–23

Jenkinson DS, Meredith J, Kinyamario JI, *et al.* (1999) Calculating the annual input of organic matter to soil from measurements of total organic carbon and radiocarbon. *European Journal of Soil Science*, **45**:167–74.

Kinyamario JI, Imbamba SK (1992) Dry savanna, Kenya. In Long SP, Jones MB, Roberts M (eds). *Primary Productivity of Grass Ecosystems of the Tropics and Sub-Tropics*. London: Chapman and Hall, 123–40.

Kutsch WL, Hanan N, Scholes RJ, *et al.* (2008) Response of carbon fluxes to water relations in a savanna ecosystem in South Africa. *Biogeosciences* **5**:4035–69.

Kuzyakov Y, Gavrichkova O (2010) Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. *Glob Change Biol* **16**:3386–406

Leriche H, Le Roux X, Desnoyers E, *et al.* (2003) Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecol Appl* **13**:1346–54.

Li Y-L, Tenhunen J, Owen K, *et al.* (2008a) Patterns in CO_2 gas exchange capacity of grassland ecosystems in the Alps. *Agric For Meteorol* **148**:51–68.

Li Y-L, Tenhunen J, Mirzaei H, *et al.* (2008b) Assessment and upscaling of CO_2 exchange by patches of the herbaceous vegetation mosaic in a Portuguese cork oak woodland. *Agric For Meteorol* **148**:1318–31

Long SP, Jones MB, Roberts MJ (1992) *Primary Productivity of Grass Ecosystems of the Tropics and Sub-Tropics*. Chapman & Hall, London.

McCulley RL, Boutton TW, Archer SR (2007) Soil respiration in a sub-tropical savanna parkland: response to water additions. *Soil Sci Soc Am J* **71**:820–8

Markert B (1996) *Instrumental Element and Multi-Element Analysis of Plant Samples-Methods and Applications*. New York: John Wiley and Sons.

Merbold L, Ardö J, Arneth A, *et al.* (2008) Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosci Discuss* **5**:4071–105.

Mordelet P, Menaut J-C (1995) Influence of trees on above-ground production dynamics of grasses in a humid savanna. *J Veg Sci* **6**:223–8.

Mooney HA, Vitousek PM, Matson PA (1987) Exchange of materials between terrestrial ecosystems and the atmosphere. *Science* **238**:926–32.

Muniafu M, Kinyamario JI (2007) Soil nutrient content, soil moisture and yield of Katumani maize in a semi-arid area of Kenya. *African J Environ Sci Technol* **1**:81–5.

Otieno DO, K'Otuto GO, Ja´kli B, *et al.* (2011) Spatial heterogeneity in ecosystem structure and productivity in a moist Kenyan savanna. *Plant Ecol* **212**:769–83.

Otieno DO, K'Otuto GO, Maina JN, *et al.* (2010) Responses of ecosystem carbon dioxide fluxes to soil moisture fluctuations in a moist Kenyan savanna. *J Trop Ecol* **26**:605–18.

Otieno DO, Wartinger M, Nishiwaki A, *et al.* (2009). Responses of CO_2 exchange and primary production of the ecosystem components to environmental changes in a mountain peatland. *Ecosystems* **12**:590–603.

Parton WJ, Scurlock JMO, Ojima DS, *et al.* (1994) Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Glob Biogeochem Cycles* **7**:785–809.

Patton BD, Dong X, Nyren PE, *et al.* (2007) Effects of grazing intensity, precipitation, and temperature on forage production. *Rangeland Ecol Manage* **60**:656–65.

Schimel DS, Cias P, Peylin P, *et al.* (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414**:169–72.

Scurlock J, Hall D (1998) The global carbon sink: a grassland perspective. *Glob Change Biol* **4**:229–3.

Scurlock JMO, Johnson K, Olson RJ (2002) Estimating net primary productivity from grassland biomass dynamics measurements. *Glob Change Biol* **8**:736–53.

Silva JF, Raventós J (1999) Effects of end of dry season shoot removal on the growth of three savanna grasses with different phonologies. *Biotropica* **31**:430–38.

Skarpe C (1991) Impact of gazing in savanna ecosystems. *Ambio* **20**:351–56.

Tang J, Baldochchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. *Glob Change Biol* **11**:1298–304.

Turner CL, Seastedt TR, Dyer MI (1993) Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. *Ecol Appl* **3**:175–86.

Veenendaal EM, Kolle O, Lloyd J (2004) Seasonal variation in energy fluxes and carbon dioxide exchange for broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. *Glob Change Biol* **10**:318–28.

Williams CA, Hanan N, Scholes RJ, *et al.* (2009) Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna. *Oecologia* **161**:469–80.

Williams CA, Hanan NP, Neff JC, *et al.* (2007) Africa and the global carbon cycle. *Carbon Balance Manag* **2**:3.

Williams CA, Albertson JD (2004) Soil moisture controls on canopyscale water and carbon fluxes in an African Savanna. *Water Resource Res* **40**:W09302. doi:10.1029/2004WR003208,2004.

Wohlfahrt G, Anfang CH, Bahn M, *et al.* (2005) Quantifying ecosystem respiration of a meadow using eddy covariance, chambers and modelling. *Agric For Meteorol* **128**:141–62.

Woomer PL (1993) The impact of cultivation on carbon fluxes in woody savannas of Southern Africa. *Water Air Soil Pollu* **70**:403–12.

Zingore S, Manyame C, Nyamugafata P, *et al.* (2005) Long-term changes in organic matter of woodland soils cleared for arable cropping in Zimbabwe. *Eur J Soil Sci* **56**:727–36.