INTERACTIVE EFFECTS OF QUANTUM FLUX, TRANSPIRATION RATES AND LEAF STOMATA CONDUCTANCE ON NET CO2 ASSIMILATION RATES OF SAVANNAH GRASSES IN KENYA

Dr. Elias K. Maranga[1]*

[1]*Senior Lecturer/Consultant, Natural Resources Ecology &Microclimatology, Department of Natural Resources, Egerton University, P.O Box 536-20115, Egerton, Kenya*

***Corresponding Author: -**
Email:-ekmaranga@yahoo.com*

Abstract:-

The current study was conducted to investigate the interactive effects of quantum flux, transpiration rates, and leaf stomata conductance on net CO_2 assimilation rates of Panicum maximum beneath Acacia tortilis canopies and disturbed micro sites where these trees were removed. A randomized complete block design was used to measure the treatment effects created by cutting Acacia tortilis trees on CO_2 assimilation rates of Panicum maximum. The mean quantum fluxes for the canopy micro sites and disturbed micro sites were 694.8μmol m^{-2} s^1 and 1184.5μmol m^{-2} s^{-1}, respectively. The average leaf stomata conductance values for Panicum maximum in the exposed and canopy micro sites were 249.6 mmolm^{-2}s^{-1} and 332.8mmol m^{-2} s^{-1} respectively. These average leaf stomata conductance values were significantly different at p≤ 0.05 Transpiration means for Panicum maximum in the exposed micro sites (4.0 mgcm^{-2}s^{-1}) and canopy micro sites (4.2mg cm^{-2}s^{-1}) were not significantly different at P≤ 0.05. Panicum maximum in the disturbed micro sites exhibited significantly lower (p≤0.05) net CO_2 assimilation rates (mean of 1.4μmolCO_2 m^{-2} s^{-1}) than the rates measured for the same species (mean of 9μmolCO_2 m^{-2} s^{-1}) in the canopy micro sites. These findings suggest that induced disturbances created by clearing of Acacia tortilis trees in the long term will cause shifts in micro environmental fluxes of energy, water and CO_2 exchange with significant implications on herbaceous under storey productivity.

Keywords:- *Acacia tortilis, Panicum maximum, net CO_2 assimilation rates, savannah, environmental fluxes, productivity*

1.0 INTRODUCTION

The primary objective of this study was to investigate the interactive effects of quantum flux (photosynthetically active radiation), transpiration rates and leaf stomata conductance on net carbon assimilation rates of *Panicum maximum* in disturbed and undisturbed microenvironments (canopy micro sites). The effects of fire, defoliation, soil texture, soil nutrients, radiation and water in relation to the dynamics of tree-grass co-existence in natural ecosystems have been studied (Belsky *et al.* 1990, 1993, 1994, Higgins *et al.* 2000, Ludwig *et al.* 2004, Tietjen and Jeltsch, 2007, Lortie and Callaway 2006, Maranga, 1986, Muthuri *et al.* 2009, Murphy and Bowman 2012, Ward *et al.* 2013, Bertness and Altieri, 2013 and Dohn, 2015). However, little is known about the interacting effects of these variables in altered environmental conditions due to human activities. The current study was designed to contribute to our understanding of the ecological consequences of cutting *Acacia tortilis* trees on the primary productivity of *Panicum maximum* which is a dominant species beneath *Acacia tortilis* canopies in the semi-arid ecosystems in Kenya. It was hypothesized that shifts in the climate beneath *Acacia tortilis* due to clearing of these trees would affect CO_2 fixation rates of *Panicum maximum.* These effects would in turn have significant implications on primary productivity and longevity of *Panicum maximum.* Information on the influence of trees on soil fertility, soil water status, plant water status, plant species composition, and CO_2 assimilation rates of herbaceous under storey is necessary in the development of tree-grass management interventions and shaping of natural resource management policy.

2.0 MATERIALS AND METHODS

2.1 Study Sites

The study locations were two contrasting micro sites (*Muuni* and *Four Corners*) with four plots in each location located in a semi-arid ecosystem in south central Kenya on the Kenya Agricultural and Livestock Research Organization (KALRO), National Range Research Centre, Kiboko.

The microclimate beneath *Acacia tortilis* trees supported a dense matrix of *Panicum maximum* Jacq. The sun tolerant grasses outside the canopy area of *Acacia tortilis* trees included *Chloris roxburghiana*, *Themeda triandra*, *Digitaria milanjiana*, and *Cenchrus ciliaris.* Isolated bushes with dominants such as *Commiphora riparia, Commiphora africana, Acacia senegal, Acacia mellifera, Grewia bicolor* and *Duosperma species* were interspersed with *Acacia tortilis* trees. The study area receives bimodal rainfall characterized by well-defined precipitation periods. The long rainfall season spans the period from March to May and the short rains from October to December. A short dry season occurs between June and September. Makindu surface weather station about 3 kilometres from the study locations receives a mean annual rainfall of 600mm (based on 70 years of rainfall data). Ambient air temperatures range from 28.6 °C (mean maximum) to 16.5 °C (mean minimum). The month of February is characterized by the highest temperatures (36.1°C) whereas the lowest temperatures occur in July (8.8 °C). Relative humidity varies between 78% at 0600 GMT and 47% at 1200 GMT. The soils are classified as acri-rhodic ferralsols, deep and reasonably well drained (Michieka and Van der Pour, 1977). Water stress is a common feature during the dry season (Fig.1). Tree felling and herbivory characterize the ecological dynamics of the study locations.
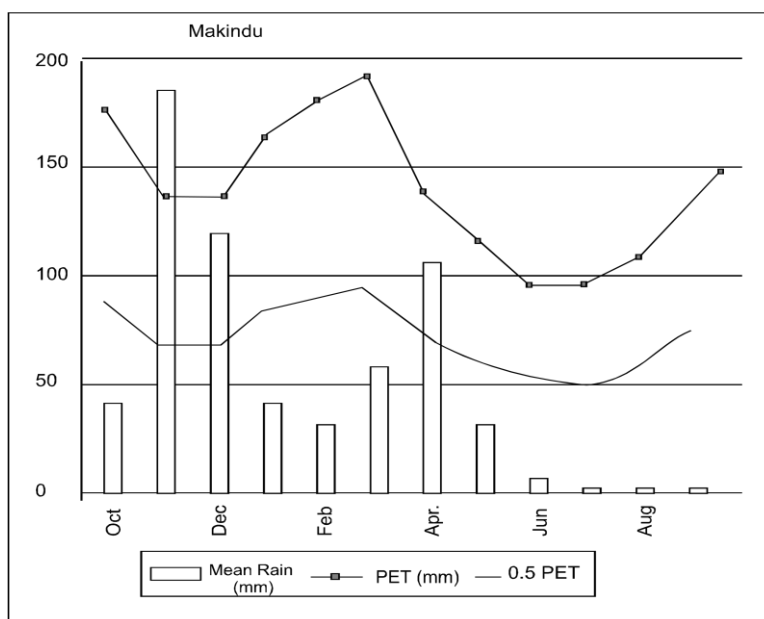

Fig 1: Water balance of the study locations on the National Range Research Centre, Kiboko Source: **Adapted from Gichuki (2000).**

2.2 Field Studies

Field studies were conducted on two sites with four micro sites in each site. One of these sites represented the control where *Panicum maximum* coexisted with *Acacia tortilis* beneath the canopies of these trees (canopy micro sites). *Acacia tortilis* were removed in the other site to expose *Panicum maximum* to the sun and alter micro environmental fluxes

(disturbed micro sites). Environmental measurements of quantum flux, coupled with measurements of transpiration rates, leaf stomata conductance and CO_2 assimilation rates of *Panicum maximum* were monitored in the course of the bimodal dry and wet phases. Quantum flux was measured by means of a cosine corrected quantum sensor. Transpiration rates were measured by a Li- Cor LI- 1600 steady state porometer. Leaf stomata conductance was measured by means of a pressure chamber membrane (Scholander, 1964). Net CO_2 assimilation rates were calculated using equations modified by Long and Hällgren 1985. Net CO_2 exchange of healthy newly expanded leaves of *Panicum maximum* were measured by a means of a portable infrared gas analyser fitted with a modified narrow leaf chamber for grasses (ADC LCA, Analytical Development Co. Ltd., Hertfordshire UK). To minimise variations in ambiet CO_2 concentrations, sample air was provided to the analyser by means of a mast extending above the grass canopy. In the course of measurements, the gas analyser was operated in the variable differential mode with a constant flow rate (Long and Hällgren 1985).

Net CO_2 assimilation rates (A) ($\mu mol\ m^{-2}\ s^{-1}$) was calculated using the equations adapted from Von Caemmerer and Farquhar (1981) and as modified by Long and Hallgren (1985) as follows:

CO_2 assimilation rates (A) = F/s x   c…………………….. (1)
Where   F   =   mole flow of air ($mol\ s^{-1}$)
               s   =   leaf surface area (m^2)
               c   = CO_2 differential between reference and analysis streams ($mol\ mol^{-1}$).

A correction factor was used because of increase in water vapour resulting from transpiration of the leaf. Including the correction factor in equation 1, then,

A   =   F/s   x   c   x   1-We/1-Wo……………………………… (2)

Where   We =   mole fraction of water vapour at the leaf chamber inlet ($mol\ mol^{-1}$)
               Wo =   mole fraction of water vapour at the leaf chamber outlet ($mol\ mol^{-1}$).
Wo and We were calculated from the saturation vapour pressure at the measured leaf temperature given the relative humidity (RH%) from the analyzer(Long and Hällgren 1985).

Thus, Wo/We = Ls/100 x RH ………………………… (3)

The correction factor 1-We /1-Wo was further simplified since the infra-red gas anayser accessed dry air into the Parkinson chamber thus permitting the system to operate under isothermal conditions (i.e We =o) and 1-Wo≈1 (Jones 1992). The correction factor was approximated to 1/1-Wo, where RH (relative humidity) of existing air =Wo/Ls; thus, Wo = Ls x RH%. The term 1 –Wo in the denominator of equation 2 adjusts the flow rate for the amount of water vapour input via transpiration from the leaf. This correction is of the order of 2-4% and is only important for accurate work particularly where it may be needed to calculate intercellular space CO_2 concentration.

The following equation (see Long and Hällgren 1985) was used to convert measured volumetric flow (moles) to mole flow of air in $mol\ s^{-1}$, that is:

F   =   fv/1000   x   1/22.4   x 273.15/273.15+T x   p/101.3   x 1/60   ……… (4)

Where   F   =   mole flow of air ($mol\ s^{-1}$)
               fv   =   volumetric flow of air ($cm^3\ min^{-1}$)
               22.4   =   volume in dm^3 of one mole of air at standard temperature and pressure
               T   =   temperature recorded during measurement
               P   =   atmospheric pressure during measurements (KPa).

Leaf stomata conductance (Sc) was calculated using equation 5 (Long and Hällgren   1985):

       Sc   =   E/Ls (L_T – Wo) ………………………… (5)
       where E (transpiration) = F/A (Wo/1-Wo) in m mol $m^{-2}\ s^{-1}$
       Ls   =   Saturation vapour pressure that is, mole fraction of water vapour at saturation

L_T = Parkinson chamber temperature assuming the leaf is saturated with water vapour at the actual leaf temperature, L_T Quantum flux, transpiration rates, leaf stomata conductance and CO_2 assimilation data were statistically analyzed using analysis of variance methods (Little and Hills, 1975). Duncan Multiple Range Test was used in separating means that were significantly different at p ≤0.05.

3.0 RESULTS AND DISCUSSION
3.1 Quantum Flux and Leaf Stomata Conductance
The diurnal course of quantum flux during the wet season (April) between 1.00pm and 7.00pm in the canopy micro sites indicated that the maximum value of 900$\mu mol\ m^{-2}\ s^{-1}$ (900$\mu Em^{-2}\ s^{-1}$) occurred at 3.00pm (Fig. 1). The maximum quantum

flux value in the disturbed micro sites where *Acacia tortilis* were removed was 1900 µmol m^{-2} s^{-1} (1900µEm^{-2}s^{-1}). The differences in quantum flux between the canopy and disturbed micro sites were significantly different at p≤ 0.05. During the dry phase in June (Fig.2) quantum flux peaked at 4.00 pm. Maximum values during this period were 400 µ mol m^{-2} s^{-1} (400µEm^{-2}s^{-1}) and 1000µ mol m^{-1} s^{-1} (1000µm^{-2}s^{-1}) for the canopy and disturbed micro sites respectively.
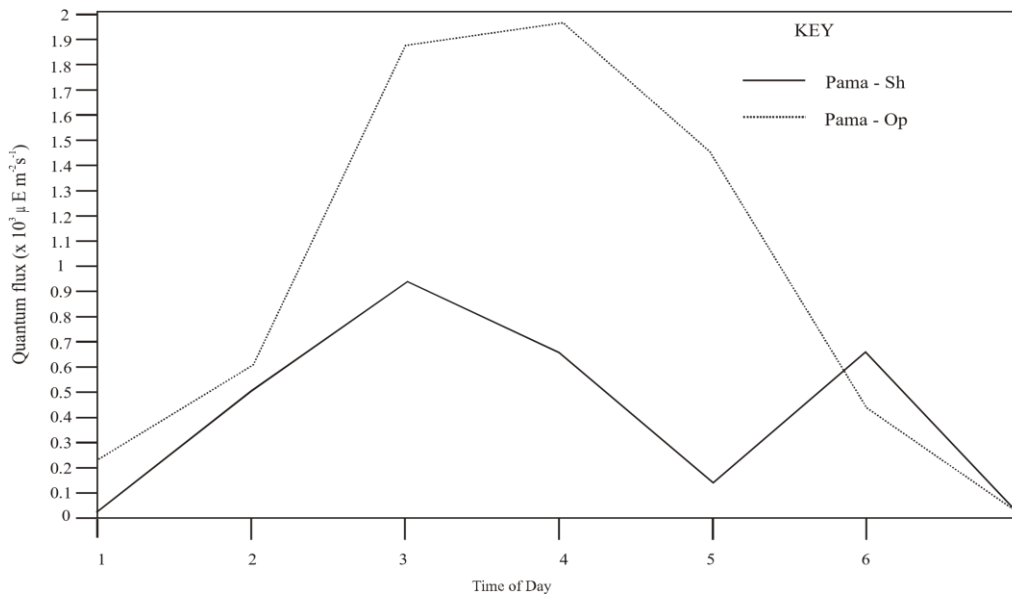
Fig. 2: Diurnal course of quantum flux in the non-disturbed (Pama- sh –trees intact) and disturbed (Pama- Op-trees cleared) micro sites in April
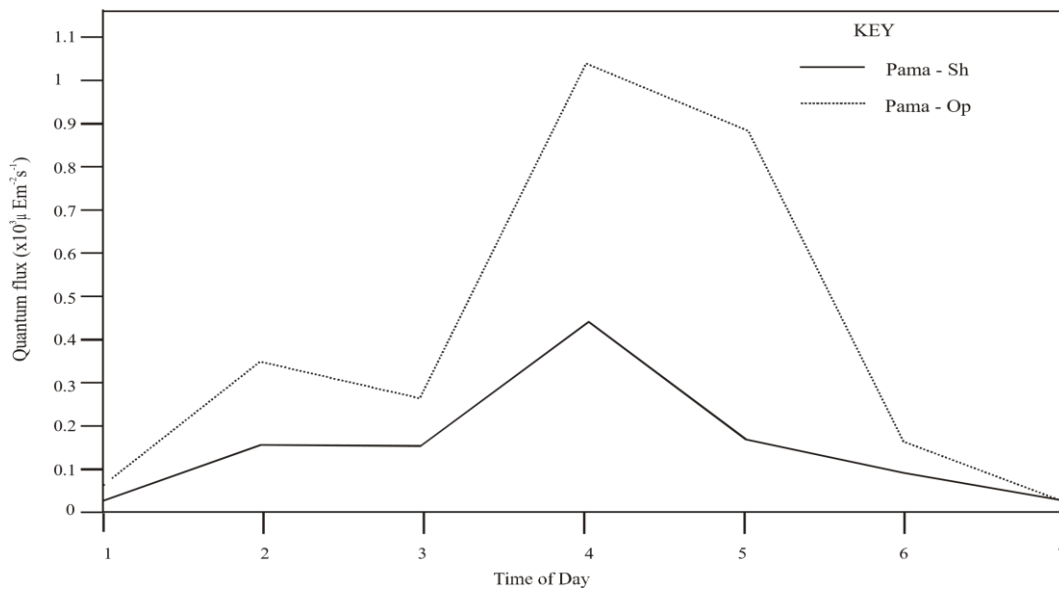

Fig. 3: Diurnal course of quantum flux in the non-disturbed (Pama- sh –trees intact) and disturbed (Pama- Op-trees cleared) micro sites in June

The seasonal course of quantum flux in the disturbed and canopy micro sites in *Muuni* and *Four Corners* study sites indicated that the exposed micro sites received higher quantum flux than the canopy micro sites. Maximum values of the order of 2000µmol m^{-2} s^{-1} occurred at the height of the dry phase in February and May. The lowest values of quantum flux in the disturbed micro sites occurred in late January and early June with values between 100µmol m^{-2} s^{-1} and 700µmol m^{-2} s^{-1} respectively (Fig. 4a). The mean quantum fluxes for the canopy micro sites and disturbed micro sites were 694.8µmol m^{-2} s^{-1} and 1184.5µmol m^{-2} s^{-1}, respectively. These means were significantly different at p ≤ 0.05.
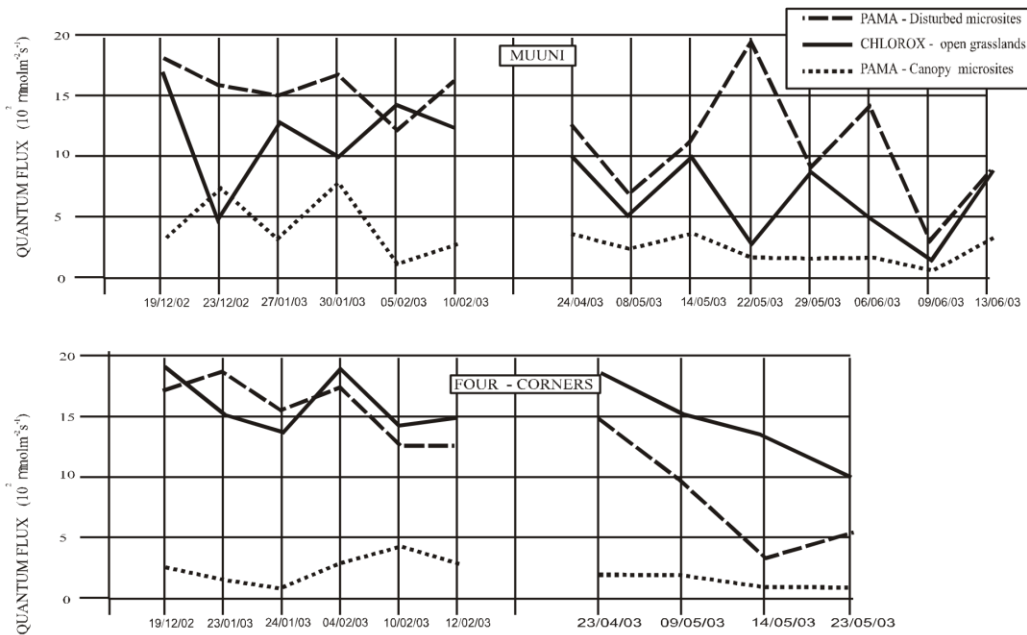
Fig 4 a   Seasonal trends of quantum flux in the disturbed and canopy microsites of *Panicum maximum* (PAMA) and *Chloris roxburghiana* (Chlorox) at the Muuni and Four Coners study sites, KARI, Kiboko, Kenya
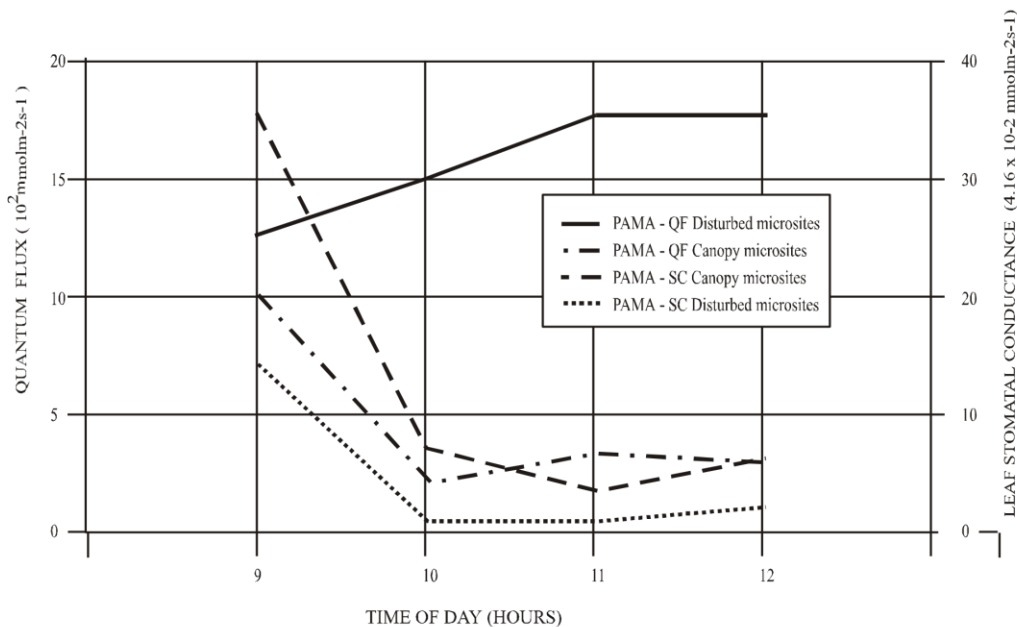

Fig 4 b   Changes in quantum flux (QF) and leaf stomatal conductance (SC) in the canopy and disturbed microsites associated with *Panicum maximum* (PAMA) at the Muuni study site, KARI, Kiboko, Kenya

Differences in quantum flux regimes have been invoked to explain differences in photosynthetic capacities for sun and shade-adapted species (Bjorkman 1981, Oguchi *et al.* 2003, Timperio *et al.* 2007, Marek Zivcak *et al.* 2014). Jones (1992) showed that differences in photosynthetic responses of sun and shade-adapted species involve adaptations of all components of the photosynthetic system that can occur within days of alterations of irradiance. Such adaptations include thicker leaves with a greater internal surface area for sun-adapted leaves as well as increased carboxylase (RubiSCO) concentration (see Stitt and Schulz 1994). In shade-adapted leaves, the overall capacity for electron transport in cyclic and non-cyclic photophosphorylation is markedly reduced due to the reduction of cytochrome f and b components of the transport chain (Stitt and Schulze 1994; Schluter *et al.* 2003). Adaptations of *Panicum maximum* in the disturbed micro sites including the capacity to fix CO_2 under higher levels of quantum flux may have been associated with adjustments of light and temperature compensation points. Those adaptations may be invoked to explain the observed differences in CO_2 assimilation rates (discussed in detail in later subsection) of *Panicum maximum* in the contrasting micro sites. Berry and Downton (1982) found that C_4 herbaceous plants attained high CO_2 assimilation rates at high temperatures. Mooney and West (1964) also reported evidence that temperature acclimation periods of 3-8 weeks were adequate to induce changes in photosynthetic rates. Differences in quantum flux have been shown to bring about differences in diffusive resistance and transpiration rates (Davies and Kozlowski 1974, Kinyamario *et al.* 1995).

In this study, significant differences in leaf stomata conductance of *Panicum maximum* were obtained for non-disturbed micro sites and disturbed micro sites. The average leaf stomata conductance values for *Panicum maximum* in the exposed

and canopy micro sites were 249.6 mmolm^{-2}s^{-1} and 332.8mmol m^{-2} s^{-1} respectively. Higher values of stomata conductance were associated with *Panicum maximum* that received lower quantum flux (canopy micro sites). The magnitude of quantum flux in the canopy micro sites was of the order of 450µmol m^{-2} s^{-1} at 1100 hours compared to 1600µmol m^{-2} s^{-1} at the same time in the disturbed micro sites (Fig.4b).

3.2 Transpiration rates

The diurnal course of transpiration rates in the exposed and canopy micro sites exhibited similar trends (Figs 5 and 6). Transpiration rates were generally higher in the exposed micro sites than the canopy micro sites. The maximum values of transpiration rates were 6.5mg cm^{-2}s^{-1} and 5.3 mg cm^{-2}s^{-1} in the exposed and canopy micro sites respectively. In the course of the dry period, (June) diurnal trends of transpiration for *Panicum maximum* in the canopy micro sites remained generally higher compared to those of the exposed micro sites (Fig 6).

Transpiration means for *Panicum maximum* in the exposed micro sites (4.0 mgcm^{-2}s^{-1}) and canopy micro sites (4.2mg cm^{-2}s^{-1}) were not significantly different at P≤ 0.05. It is likely that the higher rates of transpiration for *Panicum maximum* in the canopy micro sites may be due to higher soil water potentials because of the effect of shade in these habitats compared to those prevailing in the exposed micro sites.
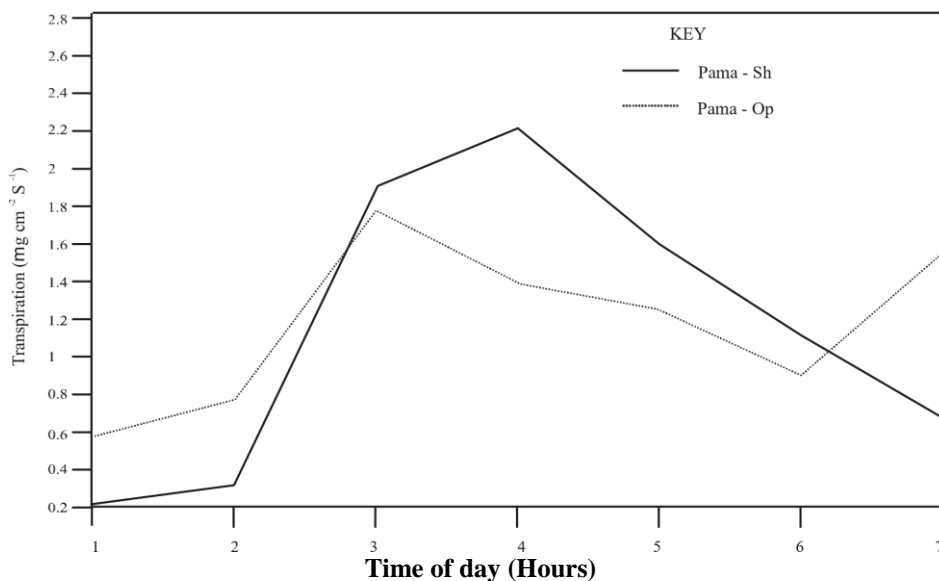

Fig. 5: Diurnal transpiration rates of *Panicum maximum* in the shade (Pama- sh-trees intact) and sun (Pama – Op-trees cleared) in April (wet phase)
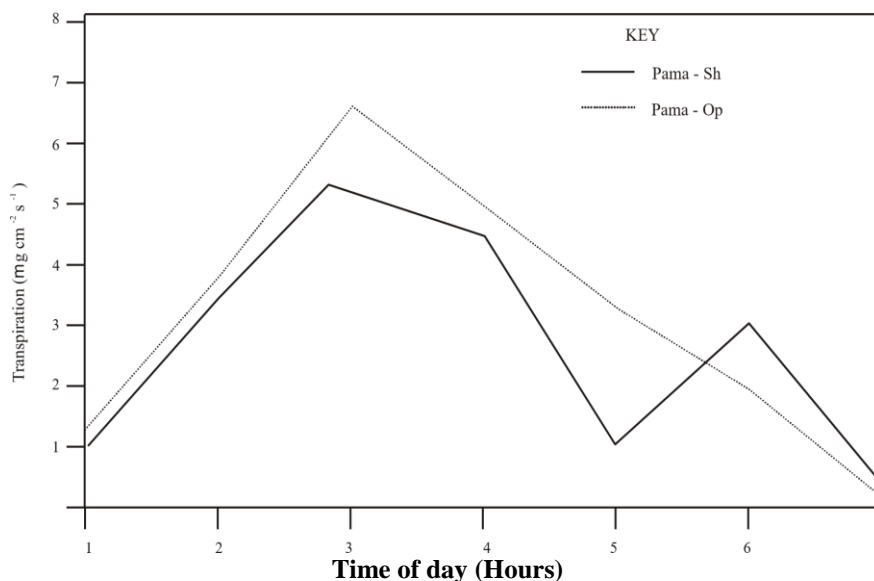

Fig.6: Diurnal transpiration rates of *Panicum maximum* in the shade (Pama- sh-trees intact) and sun (Pama- Op-trees cleared) in June (dry phase)

3.3 Net CO$_2$ assimilation rates

Panicum maximum in the disturbed micro sites exhibited significantly lower (p≤0.05) net CO$_2$ assimilation rates (mean of 1.4µmolCO$_2$ m^{-2} s^{-1}) than the rates measured for the same species (mean of 9µmolCO$_2$ m^{-2} s^{-1}) in the canopy micro sites. These CO$_2$ assimilation rates are lower than those obtained by Kinyamario *et al.* 1995 in their CO$_2$ studies of C$_4$

species in the Nairobi National Park. Kinyamario *et al.*1995 found that under low light intensities beneath tree canopies, net CO_2 assimilation rates for *Panicum maximum* was 11.2 $\mu molCO_2$ m^{-2} s^{-1}. CO_2 assimilation rates for *C. roxburghiana* (a sun adapted C$_4$ grass species) ranged between 4.9$\mu molCO_2$ m^{-2} s^1) and 12.3μmol CO_2m^{-2} s^1). The temporal trend of CO_2 gas exchange for *Panicum maximum* indicated that maximum photosynthetic rates occurred in the canopy and disturbed micro sites during periods of plentiful soil moisture supplies. The correspondence between high CO_2 assimilation rates, transpiration rates and leaf stomata conductance illustrates the significance of leaf water status in the regulation of stomata activity that controls CO_2 uptake and subsequent CO_2 fixation into carbohydrates.

It is unlikely that these differences would be due to variations in light intensity alone. Synergistic effects due to morphological variations and variations in soil nitrogen capital, soil moisture and leaf water status in the contrasting environments may have contributed to the differences in CO_2 assimilation rates (see also Oguchi *et al.* 2003 , Marek Zivcak *et al.* 2014). Stitt and Schulze (1994) found that light intensity influenced the allocation of nitrogen to RubisCO, which, in turn, exerted a large limitation to CO_2 assimilation rates. Higher rates of water use efficiency have been reported with nitrogen sufficiency than that of nitrogen limiting conditions (Stitt and Schulze 1994). The likelihood of higher nitrogen capital and evidence of higher leaf water status and lower quantum fluxes in this study may be invoked to account for higher net CO_2 assimilation rates of *Panicum maximum* in the canopy micro sites. Acclamatory processes resulting in the adjustments of light and temperature compensation points for *Panicum maximum* are likely to have occurred as a result of higher light energy and temperature regimes in the exposed micro sites. Berry and Downton (1982) adduced evidence that leaves from sun and shade adapted plants achieve approximately the same efficiencies in net solar energy conversion over the ranges of light intensities prevailing in the local habitats. They argued that it is the net efficiency rather than maximum possible rate of net CO_2 uptake that would impart a competitive advantage in a given habitat.

4.0 Conclusions

The findings of this study suggest that the main reason for the differences in net CO_2 assimilation rates for *Panicum maximum* in the canopy and disturbed micro sites is that different resources limit CO_2 assimilation rates at different times and spatial scales and ,therefore, primary productivity. Lower light intensities and higher leaf stomata conductance coupled with soil moisture and nutrient availability during the wet seasons account for the higher CO_2 assimilation rates in the canopy micro sites than the disturbed micro sites. Lower CO_2 assimilation rates in the dry periods in the disturbed micro sites are due to restricted CO_2 uptake caused by decreased stomata conductance and increased diffusive resistance. Experimental data is required for conclusive evidence of the role of increased light and temperature compensation points on the growth adjustment process associated with *Panicum maximum* in the exposed micro sites. These results suggest that clearing of *Acacia tortilis* trees in the long term will cause shifts in microenvironmental fluxes of energy, water and CO_2 exchange with significant implications on herbaceous under storey productivity.

5.0 References

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