LEAF STOMATA CONDUCTANCE, LEAF WATER POTENTIAL AND SOIL WATER STATUS IN *PANICUM MAXIMUM* (JACQ.) IN DISTURBED AND NON-DISTURBED MICROSITES IN A SEMI-ARID ECOSYSTEM IN KENYA

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Abstract
Tropical semi-arid ecosystems are intricate ecosystems characterized by alternating dry-wet cycles. The question of how trees and grasses coexist under a considerable range of environmental and management conditions has been referred to as the "savanna problem" The practical significance of understanding the dynamics of natural ecosystems in relation to disturbances induced by herbivory, changing land use patterns or climate change is increasingly being recognized. Natural resource conservationists, range managers, and other custodians of natural resources require concrete information bases for land use policy formulations and as a means of regulating land use systems for sustainable resource use and development. An experiment using a randomised complete block design was set up to measure the effects of induced disturbances on ecosystem components and concomitant plant physiological responses. Analysis of variance techniques were used to determine the presence or absence of significant treatment effects. Disturbed micro-sites (manipulated treatments where *Acacia tortilis* trees were removed) demonstrated contrasting results compared to the non-disturbed micro-sites (*Acacia tortilis* trees left intact).The disturbed sites had less average moisture content in the 10cm soil profile (14.4%) than the non-disturbed sites(18.8%). *Panicum maximum* had an average stomata conductance of a magnitude of $0.65 cms^{-1}$($270 mmolm^{-2}\ s^{-1}$) for the disturbed microsites and $0.75 cms^{-1}$($312 mmolm^{-2}s^{-1}$) for the non-disturbed sites. There were no significant treatment effects in transpiration rates and leaf water potential of *Panicum maximum* in the disturbed and non-disturbed sites. This analysis demonstrates that long term changes in microenvironmental conditions of soil and plant water status due to tree removal is likely to cause shifts in botanical composition of graminoid species with direct implications on nitrogen sequestration, species biodiversity, and productivity.

Key words: *Panicum maximum*, semi-arid ecosystems, soil water status, stomata conductance, tree-grass interactions, micro-environmental fluxes

1.0 Introduction

Tropical semi-arid ecosystems are intricate ecosystems characterized by alternating dry-wet cycles (Maranga *et al.* 1983; Kinyamario *et al.*1995; Higgins *et al*. 2000; Ludwig *et al*. 2004; Tietjen and Jeltsch 2007 and Muthuri *et al.* 2009). The question of how trees and grasses coexist under a considerable range of environmental and management conditions has been referred to as the "savanna problem" (Sarmentio 1984). Trees may influence microenvironmental conditions of temperature, light distribution, wind regimes, soil and water status (Maranga *et al*. 1983; Anderson *et al*. 2001 and Ludwig *et al.* 2004). Maranga *et al*. (1983) and Kinyamario *et al*. (1995) found that *Panicum maximum* predominantly occurred under the extended canopies of *Acacia tortilis* trees in Kenya. This influence of trees on the distribution of understorey grasses was explained in terms of improved water status beneath their canopies. Light energy interception by tree canopies reduced evapotranspiration, however, the reduction of rainfall due to interception was compensated by reduced water loss due to the presence of the canopy shade. Specialized habitats beneath tree canopies may explain the special mix of graminoid species associated with these microsites (Belsky *et al*. 1989; Ludwig *et al.* 2001, Anderson *et al*. 2001, Ludwig *et al.* 2004, Otieno *et al*.2005).

The effect of trees on microenvironmental fluxes of water, light and temperature of understorey species have been studied in situations involving intact isolated trees with distinct "within canopy" and "outside canopy" microsites (Maranga *et al*. 1983; Belsky 1990, 1994; Kinyamario *et al.* 1995; Le Roux *et al.* 1995; Scholes and Archer 1997; Ludwig *et al.* 2004;Tietjen and Jeltsch 2007). Although these studies have adduced evidence that suggested that light intensity had both negative and positive effects on graminoid understorey productivity, it is not clear how increased light intensity (full sun) and evapotranspiration rates would impact the soil and plant water status of shade adapted plants in situations where trees are removed to give way to alternative land uses as is the case in Kenyan semi-arid ecosystems.

The present study was designed to establish the dynamics of soil and plant water status of understorey species associated with selective removal of trees.

2.0 Material and Methods

2.1 Study Sites

The study was conducted in a semi-arid ecosystem in south central Kenya on the Kenya Agricultural Research Institute (KARI), National Range Research Centre, Kiboko (NRRC). The research station facility covers about 25,000 ha and lies between latitude 2^0 20'S and longitude 37^0 50' E with an elevation of approximately 1000m above sea level.

The study sites were approximately 10 kilometers away from the station headquarters. These were at Muuni and Four Corners area. The salient floristic and

physiognomic attributes of the vegetation include scattered overstorey trees of *Acacia tortilis* with large umbrella shaped canopies. *Acacia tortilis* trees often reached a height of 5metres with canopy diameters exceeding 10metres. The dominant grasses were *Panicum maximum* (beneath the canopy of *Acacia tortilis* trees) and *Chloris roxburghiana*, *Themeda triandra*, *Digitaria macroblephora*, *Cenchrus ciliaris* found in the sunny habitats. Interspersed with *Acacia tortilis* were isolated bushes comprising of *Commiphora riparia*, *Commiphora_africana*, *Acacia senegal*, *Acacia mellifera*, *Grewia bicolor* and *Duosperma* species. Bimodal rainfall regime is typical of the study area. The meteorological data used in this study was obtained from Makindu and Spray Race weather stations within the Kiboko station facility and about 3 kilometres away from the study sites.

Well-defined precipitation periods include the long rainfall season from March to May and the short rains from October to December. These wet periods are interrupted by a short dry season between June and September. The mean annual rainfall for Makindu Weather Station about 3 kilometres from the study locations is 600mm (based on 70 years of rainfall data). Ambient air temperatures range from 28.6^0C (mean maximum) to 16.5^0C (mean minimum). The lowest temperatures occur in July (8.8^0C) and the highest in February (36.1^0C). Relative humidity varies between 78% at 0600 GMT and 47% at 1200 GMT. Soils are acri-rhodic ferralsols, deep and reasonably well drained (Michieka and Van der Pouw, (1977)). Significant water stress during the dry season coupled with tree felling and herbivory characterizes the ecological dynamics of the study sites.

2.2 Field Experimentation

Field studies were conducted on four micro-sites with replicates located at Muuni and Four Corners areas in the southern part of Kiboko National Range Research Station land facility. Two of these micro-sites represented treatments (undisturbed microsites) where *Panicum maximum* coexisted with *Acacia tortilis* beneath the canopies of these trees. *Acacia tortilis* were removed in the other two micro-sites to simulate conditions in the sun (disturbed microsites). Here *Panicum maximum* was exposed to conditions under full sun.

Insitu measurements of leaf transpiration, ambient air temperature, leaf temperature and relative humidity were taken on fully expanded leaves of *Panicum maximum* by means of a Li-Cor LI-1600 steady state porometer. Data from these measurements were used in the calculation of stomata conductance as described by Long and Hällgren 1985. Six leaf samples from each sampling location in the disturbed and non disturbed sites were identified for porometric measurements.

After in *situ* measurements were taken, leaves were immediately cut and their water potential measured with a pressure chamber (PMS Instrument Company,

Corvallis, Oregon, USA) as described by Scholander, *et al.* 1964. Measurements were carried out once or twice a week between 1100hrs and 1400hrs for a period including one short rainfall season and long rainfall season. The period of measurements spanned the time frame including November 2002 to mid December 2002. Data collection ceased after mid December because of the short dry season and recommenced with the onset of the long rainfall season in April 2003 and continued up to June 2003. Leaf stomata conductance (Sc) was calculated using the equation of Long and Hällgren 1985 as follows:

$$Sc = E/Ls\ (L_T - W_O) \quad \text{.....(i)}$$

Where E = transpiration in m mol m^{-2} s^{-1} ,

Ls =Saturation vapour pressure, that is, mole fraction of water vapour at saturation,

$\text{Log}_{10}\ Ls = 0.02604T + 0.82488$ (Rosenberg, 1974),

Where T = ambient air temperature (^{0}C),

L_T = Leaf chamber temperature assuming its leaf is saturated with water vapour at the actual leaf temperature,

W_O = mole fraction of water vapour at the leaf chamber outlet (mol mol^{-1}).

Soil moisture samples were obtained at short term intervals with frequencies running between 3 days and 14 days. Sampling for soil moisture commenced with the onset of the short rains. The initial samples were taken on 18th of November for the short rains and 24th of April for the long rains. Sampling was stopped when differences in soil moisture content ceased with progressive drying around 13th of December for the short rains and 9th of June for the long rains. Soil moisture status was determined gravimetrically by drying samples in the oven at 105^{0}C for 24hours. The difference between the field weights and the oven dry weights constituted the moisture content of the samples (AOAC, 1975).

A randomized complete block research design was used in this experiment. The study was replicated twice. Treatments comprised of microsites with intact *Acacia tortilis* canopy environments (undisturbed microsites) and where these trees had been removed to expose *Panicum_maximum* to the full sun (disturbed microsites), and time. Analysis of variance was conducted on leaf water potential, transpiration, leaf stomatal conductance and soil moisture content using analysis of variance methods (Little and Hills 1975). Duncan Multiple Range Test was used in separating means that were statistically different at $p \leq 0.05$.

3.0 Results

3.1 Rainfall

The rainfall distribution in the study sites that influenced the soil moisture supplies is shown in Fig 1. Relatively higher rainfall amounts were recorded for the study sites (Makindu and Spray Race) in the short rainfall season (October - December) compared to the long rainfall season (March - May). The highest rainfall amounts were received in the second week of December with single rainfall events contributing more than 100mm. The seasonal rainfall totals received at the Makindu Weather Station near the study experimental plots for the short rainfall season and long rainfall seasons during the study period (2002-2003) were 257mm and 112mm respectively. There were no rains in January and February.

3.2 Soil Moisture

Seasonal trends of soil moisture distributions in the (average values of soil moisture for each sampled date and sampling depth) 10cm and 30cm soil profiles (Fig 2a and 2b) reflect the pattern of soil moisture replenishment through rainfall.

The onset of the short rainfall season was associated with considerable soil moisture infilling in both the disturbed and non-disturbed microsites. However, there was a slight but conspicuous increase in wetting intensity between November and December in the non-disturbed microsites compared to the disturbed microsites in the 10cm and 30cm soil depths. Mean soil moisture content calculated from pooled seasonal data for each profile and associated Duncan Multiple Range Test in the disturbed and non-disturbed areas (76 observations for all sampled dates in the disturbed sites and 25observations for the non-disturbed sites) are shown in Table 1c. Statistical parameters for seasonal soil moisture data are depicted in Table 1a.

In the second wetting phase (April-May) and beginning of the drying cycle (mid-June) differences in soil moisture between microsites in the surface layers were less apparent. In the deep soil profiles (90cm) the seasonal course of moisture distribution (Fig 2c) during the short rainfall season indicated that non-disturbed microsites were drier than the disturbed microsites (Table 1a).

3.3 Leaf Water Potential (Ψ_l)

Progressive increase in soil dryness in the disturbed and non-disturbed microsites was occasioned by increase in divergence in leaf water potential of *Panicum maximum* in these microsites. On 21st January (short dry phase) the leaf water potential of *Panicum maximum* in the non-disturbed microsites was -1.5MPa whereas in disturbed microsites, it was -2.2MPa. At the peak of the short dry season around 7th and 14th February, *Panicum maximum* in the non-disturbed microsites exhibited a leaf water potential of

-6.3 MPa whereas in the disturbed microsites, it reached -7.0 MPa (Fig 3). The leaf water potential means in the contrasting microsites were not significantly different ($p \leq 0.05$) (see Table1c).

3.4 Transpiration

The highest transpiration rates were recorded for *Panicum maximum* (Figs. 4and 5) in the disturbed microsites (full sunlight). In the course of the dry period, mean transpiration values for *Panicum maximum* (4.2mmol H_2O m^{-2} s^{-1}) in the non-disturbed microsites remained relatively higher compared to those of *Panicum maximum* (4.0mmol H_2O m^{-2} s^{-1}) in the disturbed microsites. Statistical parameters for transpiration data are depicted in Table 1b. Transpiration means in the disturbed and non disturbed microsites were, however, not significantly different at $p \leq 0.05$.

3.5 Leaf Stomata Conductance

Variations in leaf stomatal conductance in *Panicum maximum* in disturbed and non-disturbed microsites were similar to those of transpiration rates (Figs.4a, 4b, 5a and 5b). Leaf stomata conductance increased during the wet phases and decreased with the advancement of the dry season in the contrasting microsites. Mean leaf stomata conductance of 0.75cms^{-1} (312 mmolm^{-2} s$^{-1)}$ was recorded in *Panicum maximum* in the non-disturbed microsites whereas *Panicum maximum* in the disturbed microsites registered a mean value of 0.65cms^{-1} (270 mmolm^{-2} s^{-1}.) Leaf stomata conductance means in the contrasting microsites were significantly different ($p \leq 0.05$). Standard errors for seasonal leaf stomata conductance data and other relevant statistical parameters are shown in Table 1b.

PET refers to potential evapotranspiration

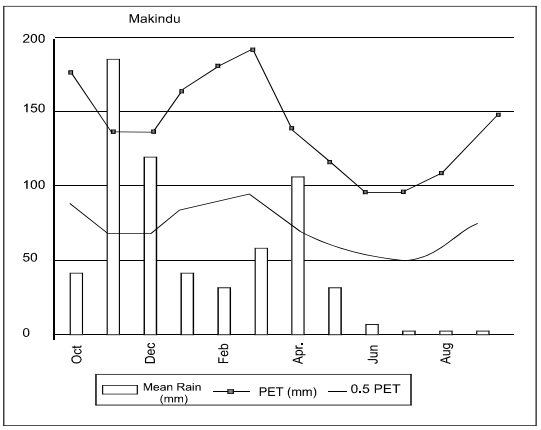

Fig.1a :Water balance of the study locations, National Range Research Centre, Kiboko

Source:Adapted from Gichuki, (2000).

Table 1a: Summary of averages (M) and standard errors (SE) of moisture content (%) at 10cm (SM1), 30cm (SM2) and 90cm (SM3) soil depths in disturbed and non-disturbed microsites during the Nov-Dec.2002 and April-June 2003growth cycle at the Muuni study site, KARI, Kiboko, Kenya

Date	Disturbed Microsite						Non-Disturbed Microsite					
	SM1		SM2		SM3		SM1		SM2		SM3	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
18/11/02	18.5	5.5347	10.7	3.1275	10.1	3.1171	35.8	8.0500	22.7	0.8500	22.6	4.1000
29/11/02	19.9	7.9146	7.5	2.4044	14.2	3.5327	17.0	3.0000	18.6	3.5999	10.4	1.3000
13/12/02	37.4	2.0895	36.3	2.9091	34.2	2.8634	49.1	8.4430	45.2	4.3444	40.1	5.6888
24/04/03	14.1	2.0436	12.3	1.6711	8.8	0.6052	20.4	3.6500	13.7	3.6500	9.4	3.3500
08/05/03	15.1	1.3960	14.9	0.8593	14.3	1.3561	16.5	0.7929	13.7	0.6500	15.7	0.8071
22/05/03	10.2	1.1482	10.8	0.9373	13.7	0.5582	9.2	0.8500	10.9	0.2828	13.1	0.9000
28/05/03	11.5	0.6731	12.3	1.1734	9.7	2.0642	14.8	1.5513	12.1	1.2223	11.4	0.4898
06/06/03	11.9	0.2788	10.0	1.8857	13.1	0.4618	10.1	0.6499	11.7	1.6499	11.4	0.6499
09/06/03	10.5	0.6753	11.0	0.5404	11.5	1.9539	11.6	3.3843	9.8	0.1999	11.3	0.0999
17/06/03	11.3	0.4314	10.9	0.5056	11.3	0.8582	8.4	1.6499	9.7	0.3000	14.0	3.9500

Table 1b. Summary of averages (M), standard deviations(SD) and standard errors(SE) of transpiration rates(TS) mmol H_2O m^{-2} s^{-1} and stomatal conductance (SC) cms^{-1} of Panicum maximum at the Muuni study site,KARI, Kiboko, Kenya

Date	DISTURBED MICROSITE						NON-DISTURBED MICROSITE					
	TS			SC			TS			SC		
	M	SD	SE	M	SD	SE	M	SD	SE	M	SD	SE
19/12/02	11.9	0.44	0.1258	1.3	0.13	0.0368	10.2	0.50	0.1462	1.5	0.31	0.0900
23/12/02	7.4	1.61	0.6569									
23/01/03							3.4	2.50	0.7219	0.6	0.53	0.1530
24/01/03	1.1	1.36	0.5146	0.2	0.30	0.1150	4.9	1.73	0.4619	0.8	0.48	0.1292
04/02/03	0.5	0.35	0.1025	0.1	0.05	0.0131	0.6	0.32	0.0927	0.1	0.03	0.0091
10/02/03	0.8	0.39	0.1585	0.1	0.03	0.0105	0.5	0.18	0.0519	0.0	0.01	0.0037
23/04/03	0.3	0.24	0.0767	1.0	0.03	0.0084	0.6	0.43	0.1229	0.1	0.07	0.0019
09/05/03	0.9	0.82	0.2365	0.1	0.12	0.0033						
14/05/03	4.2	1.48	0.4260	0.5	0.20	0.0589	7.2	1.41	0.4058	0.8	0.17	0.0478
23/05/03	7.3	1.27	0.3661	1.2	0.29	0.0845	8.2	0.73	0.2102	1.2	0.18	0.0505
29/05/03	10.3	1.53	0.4429	1.6	0.24	0.0700	8.0	0.56	0.1614	1.4	0.08	0.0243
06/06/03	9.2	1.50	0.4342	1.7	0.30	0.0874	8.3	0.98	0.2834	1.2	0.11	0.0316
09/06/03	7.0	0.27	0.0788	1.5	0.12	0.0356	6.9	0.30	0.0873	1.5	0.09	0.0255
13/06/03	7.7	2.12	0.6133	0.0	0.30	0.0879	8.5	0.46	0.1341	1.4	0.13	0.0385

Table 1c: Physiological responses of Panicum maximum as influenced by the environmental conditions in the disturbed and non-disturbed microsites

Variable	Disturbed microsite	Non-disturbed microsite
Air temperature(C^0)	617	587 Duncan= Duncan Multiple Range Test
N	30.8	29.0
Mean	a	b p≤0.05
Duncan		
		587 Means followed with the same letter
Leaf temperature	617	29.6 are not significantly different
N	31.9	b
Mean	a	
Duncan		
Soil moisture (%)	76	25
10cm soil depth	14.4	18.8
N	a	b
Mean		
Duncan		
Soil moisture (%)	76	25
30cm soil depth	14.7	15.1
N	a	a
Mean		
Duncan		
Soil moisture(%)	76	26
90cm soil depth	13.8	14.1
N	a	a
Mean		
Duncan		
Transpiration(mmol$H_2Om^{-2}s^{-1}$)	617	587
N	4.47	4.61
Mean	a	a
Duncan		
Leaf stomata conductance		
(mmol$m^{-2}s^{-1}$)	617	587
N	270	312
Mean	a	b
Duncan		
Leaf water potential(MPa)		
N		
Mean	1122	1018
Duncan	-2.3	-2.26
	a	a

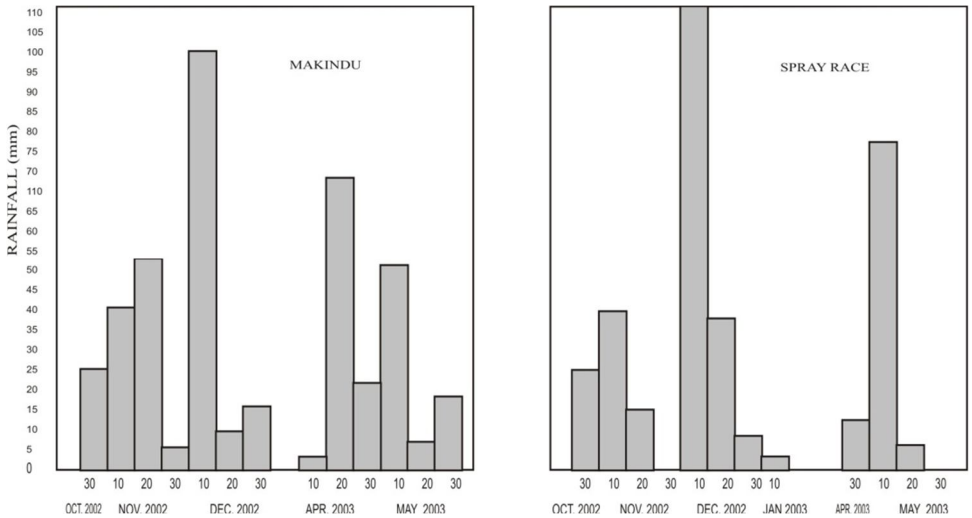

Fig.1b Rainfall distribution in the study area during the study period (2002 – 2003) for Makindu Meteorological Station and Spray Race within the Study sites

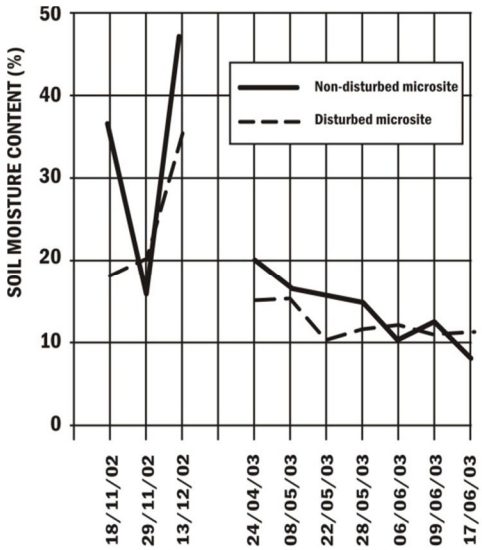

Fig 2a Gravimetric soil moisture distribution in the disturbed and undisturbed microsites at 10 cm depth during the Nov-Dec. 2002 and April-June 2003 growth cycle at the Muuni study site, KARI, Kiboko, Kenya

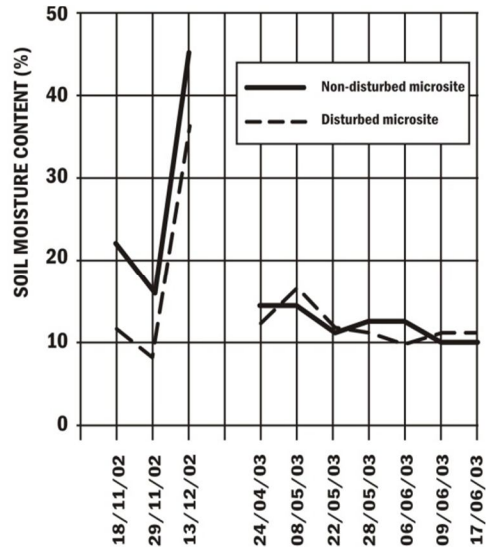

Fig 2b Gravimetric soil moisture and undisturbed microsites at 30 cm depth during the Nov-Dec. 2002 and April-June 2003 growth cycle at the Muuni study site, KARI, Kiboko, Kenya

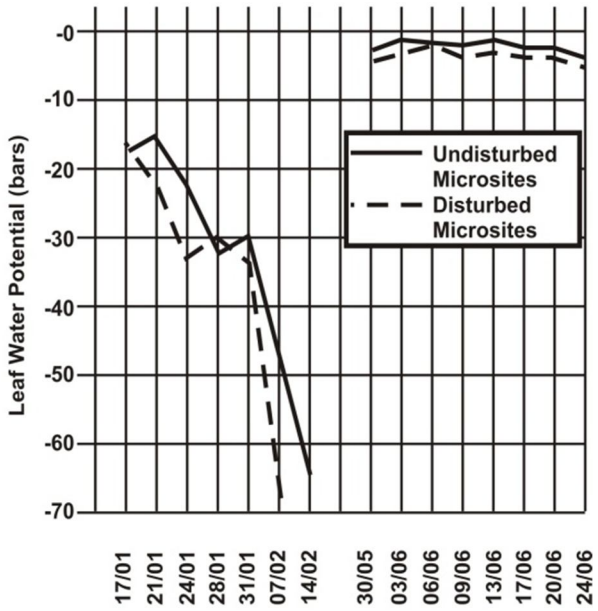

Fig 2c : Gravimetric soil moisture distribution in the disturbed microsites and undisturbed microsites at 90 cm depth during the Nov-Dec. 2002 and April-June 2003 growth cycle at the Muuni

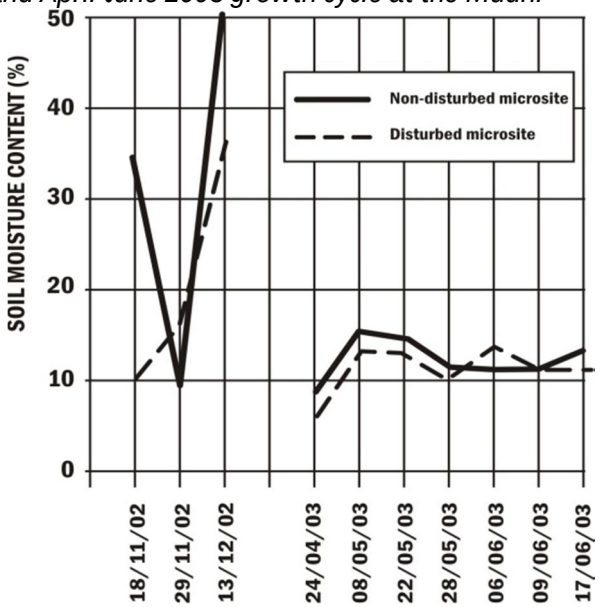

Fig 3 : Leaf water potential in the disturbed and undisturbed microsites for Panicum maximum at the Muuni study Site, KARI, Kiboko, Kenya

4.0 Discussion

Temporal patterns of soil moisture, leaf water status, leaf stomatal conductance and transpiration suggested the presence of shifts in environmental conditions in the disturbed and non-disturbed microsites that were superimposed on physiological responses of *Panicum maximum*. Similarities in soil wetting patterns in the contrasting microsites in the course of the bi-modal wet-dry cycle were clearly reflected in patterns of leaf stomatal conductance, leaf water potential and transpiration rates. This illustrates the role of synergistic mechanisms in the environmental modulation of plant physiological responses. Davies and Kozlowski (1974), Kinyamario *et al.* (1995) and Ludwig *et al*. (2004) reported that differences in light energy regimes were responsible for differences in diffusive resistance and transpiration rates. In this study, significant differences in soil water status in the shallow soil profiles (10-30cm) may be attributed to differential heating and consequent evapotranspiration variations in the contrasting microsites. Higher transpiration rates were associated with lower diffusive resistance recorded in *Panicum maximum* in the disturbed microsites (full sunlight). Higher leaf stomata conductance was observed in *Panicum maximum* in non-disturbed microsites.

A coupling of soil moisture availability with leaf water potential was clearly evident in this study. The phase of intense soil moisture - infilling (November-December) was associated with smaller divergence in leaf water potential in *Panicum maximum* in the disturbed and non-disturbed microsites. The coupling of soil moisture with leaf water potential is due to the fact that the level of tissue hydration determines cell turgidity, which is in turn dependent on soil moisture availability (Kramer 1983). Higher leaf water potential in *Panicum maximum* in the non-disturbed microsites in the course of the early part of the dry season may be due to lower vapour pressure deficits irrespective of the highest transpiration rates recorded at this time at the diurnal level. These findings are in agreement with the evidence adduced by Drake *et al.* (1970) and Maranga (2007) that plants growing in wet environments exhibited high transpiration rates. Mwangi *et al.* (1999) found that transpiration was related directly to the air vapour pressure deficit and stomata conductance to water vapour. Evidence was also adduced in this study that suggested a strong coupling of soil moisture availability with transpiration in *Panicum maximum* in the contrasting microsites. This relationship suggested the significance of soil profile moisture availability and profile partitioning in relation to the use of water by shallow rooted graminoid species. This was indicated by the achievement of maximum transpiration rates early in the day during the wet season when moisture was non-limiting compared to the dry phase when the wetting front moved away from the zone of maximum density. Differences in the seasonal soil moisture cycle in the contrasting microsites meant that the relatively stable soil moisture supply into the dry phase for the non-disturbed microsites permitted. *Panicum maximum* to remain physiologically active over a longer period compared to *Panicum maximum* in the disturbed microsites. A detailed study of

the implications of the extension of physiological activity into the dry season in the non-disturbed microsites in relation to net CO_2 assimilation rates is the subject of another technical paper to be considered for publication in this series.

4.0 Conclusion and Recommendations

Evidence from this study that demonstrated:

(i) That there was a significant difference in soil moisture status in the contrasting microsites suggested that tree removal in semi-arid environments may accelerate soil dryness with consequent negative effects on plant water status and physiological processes that control productivity.

(ii) That there was a significant difference in the stomata conductance of *Panicummaximum* in the disturbed and non-disturbed microsites suggested that tree removal had a negative impact on the water relations of *Panicum maximum.* Continuous exposure of *Panicum maximum* to full sun under conditions of limited soil moisture availability is likely to cause tissue dehydration with consequent implications on CO_2 uptake carbohydrate metabolism and plant productivity.

(iii) Efforts to arrest indiscriminate tree removal and overexploitation of tree resources in the semi- arid ecosystems are critical in the dynamics of soil and plant water resources that regulate tree- grass co-existence and productivity.

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