PRIMARY PRODUCTIVITY IN RELATION TO ENVIRONMENTAL VARIABLES OF A SEMI-ARID GRASSLAND ECOSYSTEM IN KENYA

by

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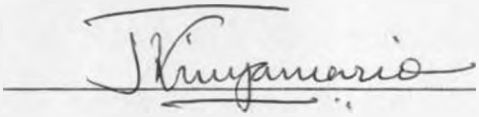
DECLARATION

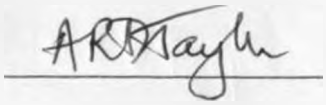
I, Jenesio Ikindu Kinyamario, hereby declare that this thesis is my original work and has not been presented for a degree in any other University. All sources of information have been acknowledged by means of references.



Jenesio Ikindu Kinyamario

This thesis has been submitted for examination with our approval as University supervisors.

Professor S.K. Imbamba



Dr. A.R.D. Taylor

DEDICATION

To my parents, Samuel Kithumbu and Leah Nditi for sacrificing a lot for my education.

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ABSTRACT

A semi-arid grassland was investigated for biomass production and the factors that influence its productivity. Live aboveground biomass ranged from 73 g m^{-2} in October 1984 to 338 g m^{-2} in April 1985. Peak live biomass was attained during the rainy season. Peak dead aboveground biomass was attained during the dry season. Dead aboveground biomass ranged from 66 g m^{-2} in December 1984 to 651 g m^{-2} in September 1985. From September 1985 dead aboveground biomass kept a constant trend fluctuating between 400 and 600 g m^{-2}. Standing dead biomass ranged between 19 and 457 g m^{-2} while litter biomass ranged between 50 and 190 g m^{-2}.

Stratified clipping revealed that most of the live aboveground biomass (64%) occured in the first 0-20 cm canopy layer above the soil surface. Individually, *T. triandra* contributed 35% of total aboveground live biomass, *P. mezianum* 26%, other grasses combined 21% and dicots with sedges 18%.

Belowground live biomass was highest during the dry season and ranged between 60 and 260 g m^{-2}. Dead belowground biomass ranged between 12 and 345 g m^{-2}.

Relative decomposition rate ranged between 0.023 and 0.18 g g^{-1} mon^{-1} for aboveground dead herbage and

0.076 and 0.335 g g^{-1} mon^{-1} for belowground dead.

Net primary productivity was 1332.4 g m^{-2} yr^{-1} (3.65 g m^{-2} d^{-1}) for aboveground compartment while it was 965.8 g m^{-2} yr^{-1} (2.65 g m^{-2} d^{-1}) for belowground compartment. Monthly net primary production ranged between 9 and 324 g m^{-2} for aboveground material and between 8 and 357 g m^{-2} for belowground material.

Turnover rates for different plant materials ranged between 0.4 for aboveground dead and 2.5 for the litter.

Leaf area index ranged from 0 to 3.09 while stem and sheath indices ranged from 0 to 0.95 and 0 to 1.53 respectively. Total area index ranged between 0 and 5.57.

Total solar radiation averaged 19.7 MJ m^{-2} d^{-1} at the top of plant canopy. 64% (or 12 MJ m^{-2} d^{-1}) was intercepted by the plant canopy during the growing season. The efficiency with which the intercepted energy was used to produce new dry matter ranged from 0 to 0.31 g MJ^{-1}.

Soil moisture content ranged from 6% (during the dry season) to 35% (during the wet season) in the first 0 - 5 cm of the soil column. Rainfall amounts ranged from 0 to 212.6 mm.

Field measurements of physiological variables showed that seasonal rates of photosynthesis ranged

from 0 to 26.8 μmol m^{-2} s^{-1} in *T. triandra* and 0 to 27.1 μmol m^{-2} s^{-1} in *P. mezianum* at midday. At the same time seasonal rates of transpiration ranged from 0.83 to 9.51 mmol m^{-2} s^{-1} in *T. trindra* and 0.93 to 16.2 mmol m^{-2} s^{-1} in *P. mezianum*. Stomatal conductance ranged from 0.095 to 0.533 cm s^{-1} in *T. triandra* and 0.148 to 1.1 cm s^{-1} in *P. mezianum*. Leaf water potential ranged from -2 MPa to <-4 MPa at midday. Air temperatures were optimum and ranged between 30 and 35°C at midday while vapour pressure deficit ranged from 30 to 40 mbars.

Top leaves in the plant canopy possessed the highest rates of photosynthesis (22 - 27 μmol m^{-2} s^{-1}) followed by the middle canopy leaves (10 - 12 μmol m^{-2} s^{-1}) and finally by the bottom canopy leaves (8 - 10 μmol m^{-2} s^{-1}). Diurnal course in photosynthetic rates showed that the highest values were attained between 11.00 and 12.00 hours during the growing season. During the early dry season peak values occured early in the morning hours (10.00 hours) and evening hours (16.00 hours) with a midday stomatal closure. The same trend of one-peaked trend during the growing season and two-peaked trend during the dry season was observed for transpiration rate and stomatal conductance.

Laboratory work was carried out on stomatal count, chlorophyll determination and photosynthesis by

different plant structures (leaf blades, stems, sheaths and inflorescences). Stomatal count revealed that all structures contained stomata which ranged between 836 cm^{-2} in stems of *T. triandra* to 29866 cm^{-2} on the adaxial surface of leaf blade of *T. triandra*. Total chlorophyll ranged from 0.18 mg g^{-1} fresh weight in the stem of *R. repens* to 2.49 in the leaf blade of *T. triandra*. Ratio of chlorophyll *a/b* was lowest (2.55) in the sheath of *C. caesius* and highest (5.73) in the leaf blade of *P. mezianum*. Mean photosynthetic rates ranged from 0.38 µmol m^{-2} s^{-1} in the inflorescence of *C. caesius* to 28.68 µmol m^{-2} s^{-1} in the leaf blade of *T. triandra*.

Water stress experiment showed that photosynthesis decreased with water stress effects. Mean rates of CO_2 assimilation decreased by 47% in *T. triandra*. The decrease was by 100% in *P. mezianum*. With rewatering, photosynthetic rates increased by 49% in *T. triandra* and by 100% in *P. mezianum*. Both leaf water potential and chlorophyll levels decreased with increase in water stress. Leaf water potential decreased from between -1.08 and -1.48 MPa to between -1.6 and <-4 MPa while total chlorophyll decreased from between 1.14 and 2.52 mg g^{-1} to between 0.99 and 1.76 mg g^{-1}. However, after rewatering leaf water potential increased to between -1.39 and 3.24 MPa while total

chlorophyll increased to between 1.05 and 2.1 mg g^{-1}.

Leaf anatomy of the grass species used in the water stress experiment revealed that the grass species were either NADP-me or PEP-ck C_4 Kranz sub-types. NADP-me species included *T. triandra, P. mezianum, C. caesius* and *C. ciliaris* while PEP-ck species were *R. repens, E. paspaloides* and *D. aegyptium*. Scanning electron micrographs of two grasses; *T. triandra* and *P. mezianum* confirmed that stomata occured on both adaxial and abaxial surfaces of leaf blade. Stomata were often found in crypts in *T. triandra*. Except in the stem, epidermal cells of *T. triandra* possessed protrusions called papillae. Epidermal surfaces of leaf blade, stem, sheath and inflorescence possessed numerous stomata, prickles, microhairs and waxy cuticle.

Spectral reflectance ratio (SRR) data revealed that there was a good correlation ($r = >-0.8$) between SRR data and live aboveground biomass during the growing season and that the method was a good predictor of live aboveground biomass. However, during the dry season when plant leaves were senescent, the correlation was poor ($r = <-0.5$) and SRR was not a good method to predict the amount of live aboveground plant biomass from the SRR data.

CHAPTER 1

INTRODUCTION

1.1. General Distribution of Grasslands

The grasslands of the world cover approximately 24 million km², spanning over all the continents (Whittaker 1975). It is believed that grasslands might have spread worldwide during the Cretaceous period. Pollen records show that grasslands, similar to the present ones, covered much of Africa since the Upper Tertiary (Van der Hammen 1983). Tropical grassslands, with or without trees or shrubs are the most extensive, covering approximately 15 million km² in Africa, South America, Asia and Australia. Tropical grasslands are more extensive in Africa where they lie between the rainforests and the deserts on both sides of the equator from about 29°S to about 16°N. Tropical grasslands are characterized by a continuous graminoid stratum, alternating wet and dry seasons, large animal biomass (especially in Africa) and frequent occurence of fires that prevent the intrusion of woody species (Menault *et al.* 1984).

1.2. Primary Production and Importance of Grasslands

Primary production of tropical grasslands vary

widely worldwide. In Indian grasslands peak aboveground live biomass range from 76 to 1974 g m^{-2} (Singh *et al.* 1984) while in South America, Hadley and Buccos (1967) recorded a peak of 354 g m^{-2}. Ohiagu and Wood (1979) in the Guinea savanna of Nigeria observed peak live aboveground biomass of 273 g m^{-2}. In the Nairobi National Park, Deshmukh (1986) calculated peak live aboveground biomass to be 332 g m^{-2}. These wide variations are due to biotic, soils and environmental factors.

Grasslands are extensively utilized for the production of milk and meat products worldwide. Van Dyne *et al.* (1974) estimated that at the world level the milk production had increased by 8% and meat production by 25% since 1964. This indicated an intensification of grassland usage for livestock production. With the ever increasing growth of the human population worldwide, there will be increasing demand for milk and meat. This will result in more intensive utilization of grasslands. Therefore, adequate knowledge of the functional ecology of these grassland ecosystems will be required, especially in the developing countries.

Grasslands, wooded grasslands and bushed grasslands form a major component of the East African rangelands. They are very important ecosystems in the

East African environment where they form major grazing areas (Pratt *et al.* 1966). Kenya alone has approximately 490,000 km² of rangeland which cover 80% of the land area of the country. These rangelands carry 60% of the country's estimated 9.0 million heads of cattle, 70% of the estimated 8.5 million sheep and goats, nearly 100% of the estimated 1.0 million camels (Ayuko 1978) and almost all the wildlife population (Talbot and Stewart 1964, Sinclair 1975 and McNnaughton 1979a). This large animal biomass depends largely on the primary producers for their food requirements (Sinclair 1975). Plants produce this food material through the process of photosynthesis (Hall and Rao 1981).

Primary production and the factors that influence it have been studied in various grassland ecosystems of the world (Hadley and Buccos 1967, San Jose and Medina 1976, Laurenroth and Whitman 1977, Sims *et al.* 1978, and Sims and Singh 1978a, 1978b). Few studies have, however, dealt with tropical grasslands (Cassady 1973, Ohiagu and Wood 1979 and Singh and Joshi 1980). Only a few studies have included some important aspects of primary production measurements, such as, below-ground biomass and decomposition rates of dead materials (Mall and Billore 1974, Strugnell and Pigott 1978, and Ohiagu and Wood 1979). Hence, some previous estimates of net primary productivity of tropical

grasslands are probably underestimates of the true values. Information on belowground biomass, canopy architecture and photosynthesis would contribute greatly to the understanding of the structures and production capacities of these ecosystems.

Plant biomass production results from the process of photosynthesis. Higher plants are divided into three distinct photosynthetic groups according to their mode of photosynthetic pathway. They are described as either C_3 or C_4 species depending on whether the first product of photosynthetic CO_2 assimilation is a C_3 or C_4 compound (Hatch and Slack 1970). The third group of plants is one in which the species assimilate CO_2 through the crassulacean acid metabolism (CAM). Plants belonging to this group are normally succulents and inhabit arid environments.

The C_4 species are further subdivided into three categories (the Kranz subtypes) on the basis of their leaf anatomy and biochemistry (Tregunna *et al.* 1970). These are the "NADP-me type" (NADP-malic enzyme species), the "NAD-me type" (NAD-malic enzyme species) and the "PEP-ck type" (PEP-carboxykinase species) (Gutierrez *et al.* 1974 and Hatch and Osmond 1976). This classification is based on the decarboxylation reaction of the C_4 acids in the bundle sheath cells of leaves yielding a 3-carbon compound and

CO_2.

While studying photosynthetic pathways and the geographical distribution of grasses in southern Africa, Ellis *et al.* (1980) observed that malate formers (NADP-me species) increased with increasing rainfall whereas the aspartate formers (PEP-ck and NAD-me species) showed the opposite trend. However, the PEP-ck species formed a group intermediate between the NADP-me and NAD-me species. Tieszen *et al.* (1979) in their studies on the ecological distribution of grasses in Kenya, found that no C_3 grasses occured at low altitudes in which a great portion of our semi-arid lands lie whereas the C_4 grasses dominated the above arid lands. Although it has been established that in the arid areas of East Africa the three Kranz subtypes dominate (Tieszen *et al.* 1979), there is lack of quantitative information on the contribution of individual species or genera on the primary production of these arid zones. Macharia (1981) working in various grassland ecosystems of Kenya found *Sporobolus rangei* Pilg. (NAD-me species) and *Sporobolus marginatus* A. Rich. (PEP-ck species) to be the dominant species in Amboseli National Park in terms of dry matter production. Deshmukh (1986) found *Themeda triandra* Forssk. (NADP-me species) to be the most dominant in terms of biomass production in the Nairobi National Park. The

Nairobi and Amboseli National Parks receive total annual rainfall of about 790 and 610 mm, respectively.

1.3. Influence of Some Environmental Factors on Primary Production

1.3.1. The Role of Moisture on Grassland Primary Production

Studies have shown that environmental factors, such as water, light and temperature are important integrators in primary production. The amount of seasonal precipitation has great influence on biomass production (Mall and Billore 1974, Sims and Singh 1978a). In East Africa, several investigators have also reported similar observations (Cassady 1973, Strugnell and Pigott 1978, Owaga 1980 and Macharia 1981). It has also been shown that belowground biomass changes with rainfall patterns in grassland ecosystems (Singh and Yadava 1974). Pandey and Sant (1980) working in an Indian grassland ecosystem found that peak biomass of the aboveground portion was high during the rainy season and that of the belowground during the dry season. In the work of Singh and Yadava (1974) the biomass production dynamics revealed that productivity was more aboveground directed during the rainy season and belowground directed during the dry season.

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Drought effects on primary production may be ascertained through experimentation on the effects of water stress on net photosynthesis. Many studies have shown that lowering of leaf water potential decreases net photosynthesis and plant growth (Brix 1962, Boyer 1970a and 1970b, Hsiao 1973, Hsiao and Avecedo 1974, and Bunce 1977). Knapp (1985) working with *Andropogon gerardii* Vitman and *Panicum virgatum* L. observed that when water stress was severe (ψleaf -4 to -6 MPa), photosynthesis declined to near zero. Yet following a substantial late season precipitation, photosynthesis increased from 28% to 48% of the early season rates in both grasses. However, *A. gerardii* maintained high rates of photosynthesis under water stress unlike *P. virgatum*. It was, therefore, concluded that *A. gerardii* was dominant in the tallgrass prairie, partly, because it was able to maintain high rates of carbon gain over a greater range of lower water potential. In another earlier experiment on controlled burning Knapp (1984) observed some reduction in above-ground biomass in unburned compared to burned prairie. It was also observed that plants in the unburned prairie exhibited lower early season water potentials than burned prairie plants. This reduction in above-ground biomass was attributed to the observed lower early season leaf water potentials in unburned prairie.

Water stress affects CO_2 assimilation by reducing the regeneration of ribulose bisphosphate (RubP) substrate. The CO_2 assimilation process results in a net production of dry matter where CO_2 is combined with the RubP to form sugars through complex biochemical reactions (Beadle *et al.* 1985). Palta (1983) concluded from water stress experiments on cassava leaves that internal factors other than stomatal closure (such as, internal rate of CO_2 evolution, increase in chemical resistance to CO_2 fixation, and changes in the carboxylation reactions) were responsible for the reduction in net photosynthesis. Palta (1983) arrived at this conclusion after noting a high correlation ($r = 0.830$) between leaf internal CO_2 conductances and leaf water potential.

O'Toole *et al.* (1976), Bunce (1977) and Setter *et al.* (1980) found that low leaf water potential (about -1.2 to -4.0 MPa) caused a reduction in net photosynthesis. This was attributed to increased resistance to CO_2 diffusion in the liquid phase from the mesophyll walls to the chloroplasts. Mathews and Boyer (1984), however, concluded that in the studies of O'Toole *et al.* (1976) and Bunce (1977), nonstomatal inhibition of photosynthesis at low leaf water potential was due probably to losses in chloroplast activity and not to a decrease in leaf diffusive

conductance. In addition to the noted biochemical changes in the leaves of water stressed plants, Morgan and Willis (1983) observed a reduced leaf area index and net photosynthesis. Aparicio-Tego and Boyer (1984) found that water stressed maize plants (Ψleaf of -1.8 to -2.0 MPa) had less dry matter accumulation when compared to non-stressed plants.

1.3.2. The Role of Light on Grassland Primary Production

The amount and quality of solar radiation received by a plant community influences primary production (Idso and Baker 1968, Macharia 1981 and Brewster 1982). Brewster (1982) working on onions, found that dry matter yields were linearly related to the total radiation intercepted during bulb growth. In a Minnesota tallgrass prairie, Bohdan (1981) found that, among other factors, PAR contributed significantly to the variability in dynamics of aboveground biomass components.

1.4. Influence of Plant Morphological Factors on Primary Production of Grasslands

Different plant communities intercept different amounts of light depending on the density of the canopy. Leaf area index (LAI) is a useful measure of canopy density and has been shown to be an important

factor influencing primary production in several plant communities (Brougham 1960, Loomis and Williams 1963, Redman 1975, and Rath and Misra 1981). This influence is primarily due to the amount of light intercepted by the canopy and used in photosynthesis. LAI values at which a plant community attains the highest crop growth rate values can be regarded as optimal; and in grasses and fodder crops the optimal values are usually between 6 to 11 (Sestak *et al.* 1971).

High LAI values usually do not result in high production in most plant communities. This is because of light attenuation within the plant canopy due to canopy depth and leaf architectural arrangements (Loomis *et al.* 1967). Horizontally arranged leaves result in the greatest loss of PAR in the plant canopy due to absorption by the leaves in the upper plant canopy, while vertically arranged leaves allow deeper canopy penetration by light. The fraction of light absorbed by the plant canopy layer is termed as the extinction coefficient for that plant canopy. For grass type canopies, this value ranges from 0.3 to 0.5 (Loomis *et al.* 1967).

Leaves from different canopy layers or heights exhibit light response curves of varying degree depending on the degree of shading by leaves in the upper layers. Boller and Nosberger (1985) demostrated

that bottom leaves showed low rates of net photosynthesis and light saturation, while the unshaded upper leaves appeared not to be light saturated. Middle layer leaves showed an intermediate response. The distribution of irradiance over the individual leaves of the plant canopy and the photosynthetic response of these leaves to irradiance is known to influence CO_2 flux into a canopy (Sheehy and Cook 1977).

1.5. Contribution of Different Plant Organs to Primary Production of Grasslands

The contribution to net photosynthesis and hence to primary production by other green plant organs other than leaf-blades has been demonstrated by several workers on crop plants. In barley, Thorne (1959) showed that apparent photosynthesis of sheath and enclosed stem was about 50% of that of the lamina of the same leaf. These measurements were taken on one side of the leaf lamina and the outer exposed surface of the sheath. Thorne (1965) also demonstrated that 60% of the ear carbohydrate could be accounted for by barley ear photosynthesis. In finger millet, inflorescences are photosynthetically active at most stages of development; at early anthesis they contributed about 40% of the measured photosynthesis (Tieszen and Imbamba 1978). The presence of other green structures, such as, awns

have also been shown to enhance ear photosynthesis and grain filling (Olugbemi *et al.* 1976). Nalborczysk *et al.* (1981) found that in wheat leaf blades contributed about 60% of overall photosynthesis while in rye they contributed only 20%. This study also showed that in wheat the highest photosynthetic activity (35.5%) occured in the flag leaf. In the same study, panicle contribution to total photosynthesis was 12% for wheat, 23.3% for rye, 28.9% for barley and 40.7% for oats. Overall, the stems with sheaths contributed about 31% in wheat, 56.6% in rye, 17.7% in barley and 21.5% in oats. From the above, it appears that leaves during maturation stages lose a substantial role in photosynthesis especially where they grow in dense stands and are partly shaded. Eventually, the stems, sheaths and the ears become even more important in photosynthesis as the grasses mature.

1.6. The Role of Transpiration on Grassland Primary Production

The role of panicle transpiration in influencing dry matter accumulation has been noted in grasses. Rami (1984) working on rice found this crop did not have any mechanisms of controlling panicle transpiration. It was noted that maximum transpiration rates occured around panicle initiation and heading time. O'Toole *et al.*

(1984) also noted the lack of the ability of the rice panicle to impede water loss when the water deficits coincided with flowering. This was because the rice panicles transpired at rates that were independent of panicle water potential. Therefore, water relations of reproductive organs in grasses may vary significantly from those of leaves. This may cause lower biomass accumulation if the soil does not provide enough water to balance the enhanced transpiration rates caused by panicle initiation in grasses.

1.7. Anatomy of Plants in Relation to Primary Production of Grasslands

In order to carry out photosynthesis, the green plant structures must possess functional stomata. The distribution of stomata has been shown to play some role in photosynthesis. Heichel (1971) showed that in two maize varieties, net photosynthesis was inversely related to stomatal frequency measured on the same leaf *in situ*. Simultaneous measurements of transpiration and photosynthesis on the two maize varieties showed there were no differences in transpiration rates to infer that stomatal resistance led to the noted differences in net photosynthesis. It was concluded that mesophyll resistance was apparently responsible for the differences between the maize varieties used. This may

lead to the possibility that species with higher stomatal frequencies may possess higher mesophyll resistances to explain this noted phenomenon. Mott and O'Leary (1984) found in amphistomatous sunflower leaves that the adaxial leaf diffusive conductances generally exceeded the abaxial leaf diffusive conductances. However, despite this phenomenon, the study did not find any significant differences in CO_2 uptake by the two leaf surfaces. It was concluded that there were extremely low resistances to CO_2 diffusion through the mesophyll in sunflower which precluded any differences in CO_2 uptake. This conclusion was reached despite possible nonhomogeneity of the mesophyll. This was also noted by Farquhar and Raschke (1978) in cotton and maize leaves.

Wood (1934) showed that though it may be expected from the laws of multi-perforate diffusion that transpiration would be less in leaves in which stomata are closer together (high densities), it was evident from his results that mean transpiration value in any group of plants with non-succulent leaves is approximately the same. Parkhurst (1978) using models based on mass-transfer physics concluded that mesophyll thickness is the key variable determining stomatal distribution, with thick leaves tending to be amphistomatous. It was noted that although stomatal

distribution may prove to be poorly related to climate, selective pressure for high CO_2 uptake for each unit of water lost may be greatest in xeric environments which may lead plants growing there to possess amphistomatous leaves.

1.8. The Role of Decomposition on Grassland Primary Production

Decomposition of plant material is an important process in the recycling of nutrients in natural ecosystems. Decomposition rates influence the release of nutrients to the active pool as well as the level of litter and nutrients accumulation in the litter layer. In addition, plant material decomposition rates are essential in calculating the overall net primary productivity of a plant community (Roberts *et al.* 1985). The rate of decomposition of herbage materials helps in the determination of turnover rates of biomass in a plant community. Rates of herbage decomposition are found to be highest during the growing season (Sims *et al.* 1978, Sims and Singh 1978a, George and Smeins 1982). Macharia (1981) noted higher initial decomposition rates and lower subsequent rates.

1.9. The Role of Grazing on Grassland Primary Production

Several studies have attempted to show the effects of grazing on plant community production. Most of these studies were, however, based on clipping experiments (Vogel and Bjugstand 1968, Lorenz and Rogler 1973 and Macharia 1981). Varied results from clipping studies are obtained depending on the frequency and level or height of plant removal. Plants clipped too close to the ground produced less dry matter. Edroma (1981) found that when *Imperata cylindrica* (L.) Raeuschel plants were clipped at a height of 15 cm above the ground their biomass production decreased by about 45%. Defoliation frequency has also been shown to reduce growth and a pronounced diversion of carbohydrates from the roots following defoliation (Kinsinger and Shaulis 1961, and Ryle and Powell 1975). Clipping has also been shown to stimulate new production (Owaga 1980). This production is usually caused by increased assimilate demand in the meristem of the remaining shoot. Defoliation of plants, whether by grazing or clipping, to remove stem apices stimulate tillering by removing a major source of auxin, which inhibits lateral bud development. However, defoliation to remove only leaves retards tillering by reducing photosynthetically active tissue with a

consequent reduction in CO_2 assimilation and, therefore, biomass production. Clipping or grazing may further increase the rates of photosynthesis in the remaining tissue due to reduced mutual leaf shading and hence more light penetration (Brown and Blaser 1968). Sosebee and Wiebe (1971) found an interaction betwen defoliation and soil moisture, whereby reduced water supply increased translocation of assimilates to the roots and crowns, while partial defoliation increased translocation to younger leaves.

Grazing intensity by animals is partially determined by the nutritive value of forages. Forages of high nutritive values are highly preferred by herbivores and are, therefore, grazed more readily than poor quality forages (Topps 1969). This preference of the more palatable plants by herbivores is known to affect primary production through the removal of palatable plants from the plant community relative to the less preferred species. Strugnell and Pigott (1978) found that in a Ugandan grassland community, significant increases in the amount of *Heteropogon contortus* (L.) Roem. & Schult., *Cenchrus ciliaris* L. and *Bothriochloa insculpta* (A. Rich.) A. Camus occured while *Sporobolus pyramidalis* P. Beauv. and *Chloris gayana* Kunth decreased, apparently due to selective grazing.

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The effect of grazing on primary production can be investigated more readily by use of exclosures. Strugnell and Pigott (1978) found a reduction in grass production outside the exclosure which was attributed to grazing pressure. Tueller and Tower (1978) found the production of shrubs to be lower inside the exclosure and higher outside. On the other hand, grasses and forbs showed a definite increase in total forage produced due to protection from grazing in the same study.

1.10. The Role of Plant Mortality on Grassland Primary Production

The significance of plant mortality in estimating primary production in grassland ecosystems has been recognized by Macharia (1981) and Deshmukh and Baig (1983). Biomass accumulation is affected by both tiller mortality and decomposition rates of the dead plant materials. Macharia (1981) observed that accumulation of dead foliage and progressive sward age reduced plant productivity and increased dead biomass.

1.11. The Objectives of the Study

The objectives of this study are, therefore:

(1) to assess the influence of environmental variables on the net primary production of a grassland

ecosystem;

(2) to assess the contribution of different plant organs to overall net photosynthesis of the dominant grass species in the ecosystem;

(3) to determine the turnover rates and times of different plant materials;

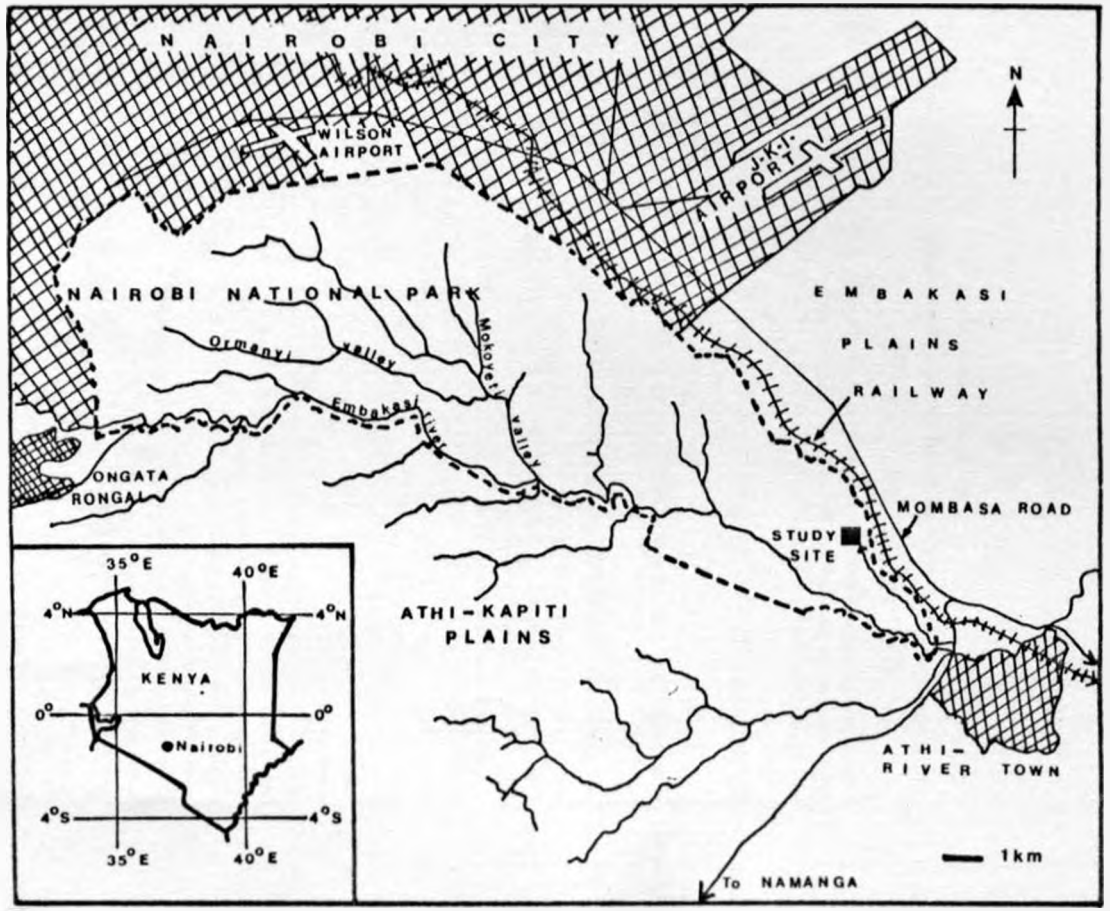
(4) to determine the rates of CO_2 assimilation by individual leaves located at different positions in the plant canopy;

(5) to evaluate the effects of water stress on CO_2 assimilation rates in the dominant arid grass species; and

(6) to assess the extent of light interception by the plant canopy.

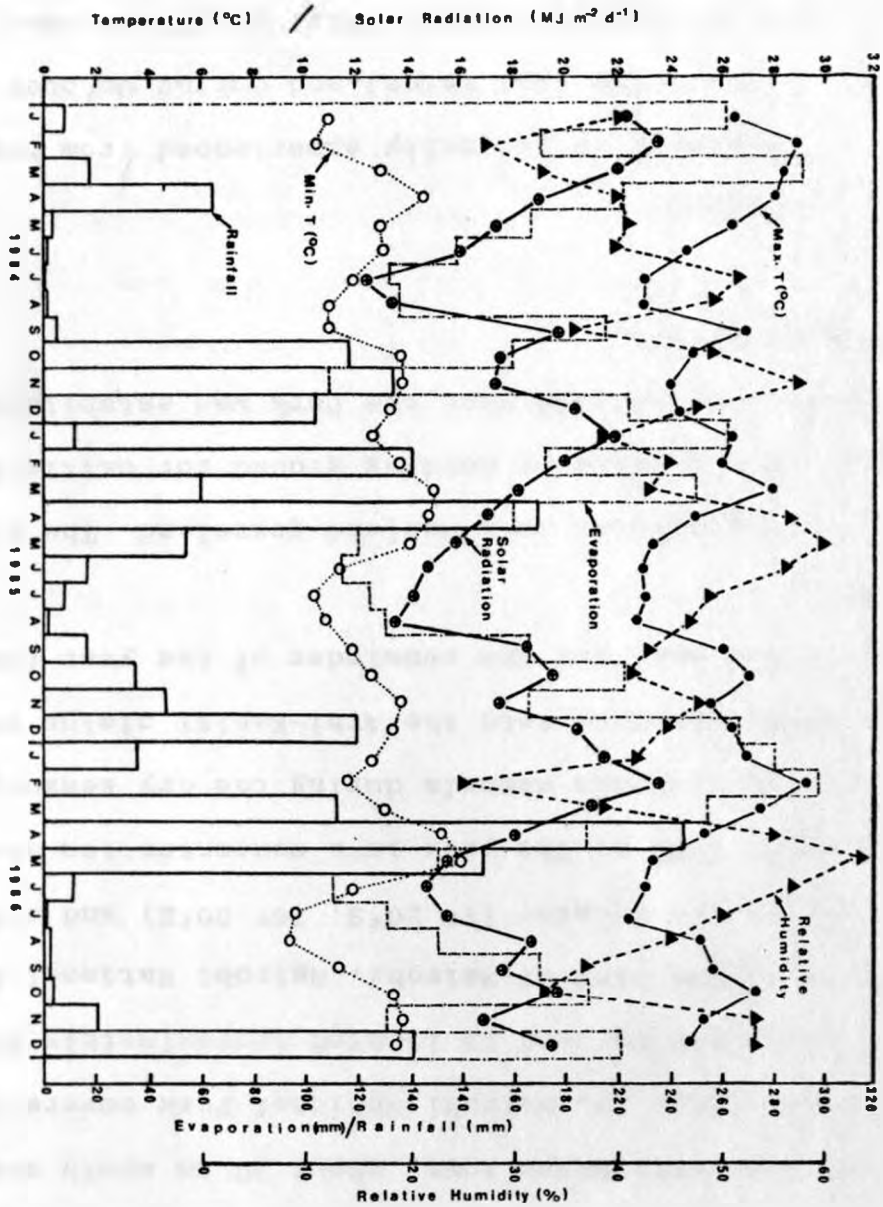
(7) This project also formed a part of a larger study on bioproductivity of tropical grassland ecosystems sponsored by UNEP.

Fig. 1. The general study area showing the location of the study site.


NAIROBI CITY
WILSON AIRPORT
J.K.I. AIRPORT
N
NAIROBI NATIONAL PARK
Ormanyi valley
Mokoyeti valley
Embakasi river
EMBAKASI PLAINS RAILWAY
ONGATA RONGAI
MOMBASA ROAD
STUDY SITE
ATHI-KAPITI PLAINS
ATHI-RIVER TOWN
1km
To NAMANGA
35°E
40°E
4°N
0°
4°S
KENYA
Nairobi

①

Fig. 2. Climatic trends in temperature, solar radiation, rainfall, pan evaporation and relative humidity for the JKI Airport near the study site from 1984 to 1986.


Temperature (°C)
Solar Radiation (MJ m⁻² d⁻¹)
Min. T (°C)
Max. T (°C)
Rainfall
Solar Radiation
Evaporation
Relative Humidity
1984
1985
1986
Evaporation (mm)/Rainfall (mm)
Relative Humidity (%)

CHAPTER 2

2. THE GENERAL STUDY AREA

2.1. Introduction

The study site is located in the Nairobi National Park near Athi River town, about 30 km south east of Nairobi (Fig. 1). Nairobi National Park covers an area of about 112 km² and is located approximately 10 km south of the city of Nairobi. Nairobi National Park lies close to the Equator (1° 20'S, 36° 50'E) and altitude of about 1600 m. The park is a concentration area for large herbivorous mammals during the dry season, most of which disperse into the Athi-Kapiti plains to the south and east for the remainder of the year (Desmukh 1986).

This habitat is a derived grassland. The area was used as a grazing or holding ground for cattle for many years prior to 1946 when the Park was established (Lusigi 1978).

2.2. Climate

Rainfall is generally experienced from March through May (the long rains) and during October and November (the short rains) (Fig. 2). The normal rainfall for the area is approximately 800 mm per year, but with

large variations from year to year. Mean annual temperature for Nairobi is around 19.6°C with monthly maxima and minima in the ranges 23-28 and 12-14°C respectively (Lusigi 1978 and Deshmukh 1986).

2.3. Drainage

Most of what is known about soils, topography and drainage of this area is due to the work of Scott (1963). In his presentation, the Nairobi National Park is topographically divisible into three types of landscapes: the upland area to the west and north west, approximately 1700-1800 m above sea level; the central undulating plains, about 1600 m above sea level; and the flat plains to the south, north and north east about 1500 m above sea level.

The upland area is part of the high ground of the eastern flank of the Rift Valley and the area receives the highest (700-900 mm per year) amount of annual rainfall in this ecosystem. The upland area has a steep downward slope in an easterly direction and terminates with the Athi-Kapiti plains. The drainage follows the slope and comprises numerous streams giving rise to parallel ridges.

The central undulating plains extend from the Embakasi river to the south and are underlain by phonolite lava and tuff (Scott 1963). They are

dissected by down cutting streams which flow into the Athi river. With the exception of the Embakasi river bordering the Park to the south, most of the rivers dry up during the dry season. These undulating plains occur under rainfall of between 500-750 mm per year.

The flat plains cover most of the Park and extend to the Kapiti plains. The underlying rocks are volcanic lavas, tuffs and basement complex (Scott 1963). They are flat and end up in bluffs overlooking the Athi in the east.

2.4. Soils

The soils of the upland area are polygenitic in origin derived from a number of intermittent volcanic ash showers (Scott 1963). The red friable clays are the dominant soils on the upper and middle slopes. The lower slopes are dominated by shallow brown to yellow friable clays overlying a laterite horizon or rock. Vlei soils, the dark greyish-brown mottled clays, occur in the depressions. These soils are thought to have been formed due to impeded drainage and are characterised by high acidity and mottling. Shallow stony soils with rock outcrops occur here. They are usually covered with *Acacia* thickets.

The major soils of the central undulating plains are dark greyish-brown calcareous clays or "Black

Cotton Soil", the dark greyish-brown calcareous clays with light textured top soil, reddish-brown sandy clay loams and the alluvial soils. The dark greyish-brown calcareous clays overlie secondary limestone. They have appreciable amounts of coarse stones which are not present in the underlying limestone, and are probably of lacustrine origin. It is possible that this was the lowest part of a lake where, on finally drying out, deposits of limestone were laid down within the underlying porous tuff (Lusigi 1978). These soils have a high content of exchangeable bases. The dark greyish-brown calcareous clays with light textured top soil are situated on summits and crests of undulations but may occur on lower slopes. The alluvial soils are confined to the Athi river and its tributaries where flooding occurs during the wet seasons. On these undulating plains shallow stony soils with rock outcrops usually with thicket cover occur. Shallow stony soils are also found on slopes.

The soils of the flat plains are black to dark grey clays, grumsolic soils; shallow yellow to yellow-red friable clays overlying a laterite horizon or rock; shallow soils on steep slopes and alluvial soils. The black to dark grey clays, grumsolic soils are the most dominant. They have equal exhangeable

bases of calcium, magnesium, potassium and sodium. These soils crack when dry and are sticky when wet. There seems to be no agreement on their origin. The soils are best utilized for dry season grazing since during the wet season they become very sticky.

2.5. Vegetation

The area is semi-arid hence it does not support forest, except for a ground water or riverine forest which is found along river valleys. The dry upland forest found in the north west of the area is the lower end of the higher rainfall area of the highlands east of the Rift Valley. The area has large expanses of open grasslands with scanty woody vegetation found mainly on the flat and undulating plains which are associated with impeded drainage or volcanic ash. However, grassland is not considered a climax vegetation for this area (Lusigi 1978). There is a strong trend towards woody vegetation and woodland could be considered to be the potential climax vegetation. The open grassland with scattered woody vegetation is, therefore, the result of several forces which include moisture availability, grazing, burning and poorly drained soils. All these ecological forces have been in functional balance in this area over a long time. The vegetation, therefore, could be considered a functional sub-climax (Lusigi

1978).

The dominant vegetation of the area is a derived grassland with varying degrees of scattered trees and bushes. Depending on the amount of wooded vegetation present, it is possible to divide this grassland into open grassland, wooded grassland, and bushed grassland. Almost half of the area is occupied by open grassland. The dominant floral elements of this community are *Acacia drepanolobium* Harms ex Sjostedt and four grass species, *Themeda triandra* Forssk., *Pennisetum mezianum* Leeke, *Dichanthium insculptum* (A. Rich) W. D. Clayton and *Digitaria macroblephara* (Hack.) Stapf. *T. triandra*, a perennial grass reaching a height of about 1 m is the most widely distributed grass. A wooded grassland in the area is found immediately north of Athi River town where the vegetation is dotted with trees such as *Balanites aegyptica* (L.) Del., *Acacia gerradii* Benth., *Acacia mellifera* (Vahl) Benth. and *A. drepanolobium*. Bushed grassland type is recognisable in the north east part of the Park where *A. drepanolobium* occurs.

This vegetation supports large herds of Thomson's and Grant's gazelle (*Gazella thomsoni* Gunther and *Gazella granti* Brooke), wildebeest (*Connochaetes taurinus* Burchell) Coke's hartbeest *Alcelaphus buselaphus* Gunther and migratory herds of eland (*Taurotragus oryx* Lyddeker), zebra (*Equus burchelli*

Gray), buffalo (*Syncerus caffer* Sparrman), giraffe (*Giraffa camelopardalis* Matschie) and some waterbuck (*Kobus defassa* Rupell) which occur near river valleys. This ecosystem is also inhabited by several species of bi such as ostrich (*Struthio camelus* Linnaeus), vultures (*Torgos tracheliotus* Forster), eagles (*Polemaetus bellicossus* Daudin) and bustards (*Eupodotis senegalensis* Reichenow) (Lusigi 1978).

2.6. The Study Site

The study site is located in the southern area of the Park near Athi River town, 30 km from Nairobi city (Fig. 1). The vegetation cover of the study site consists of almost pure stands of grasses with some few scattered woody plants. The major grass species are *T. triandra*, *P. mezianum*, *Pennisetum stramineum* Peter, *D. macroblephara*, *Eustachys paspaloides* (Vahl) Lanza & Mattei, *Cymbopogon caesius* (Hook & Arn.) Stapf, *Rhynchelytrum repens* (Willd.) C. E. Hubbard, and *Cenchrus ciliaris* L. Some woody species which occur on the plots are *A. mellifera*. The climate of the study area is dry and semi-arid. It has two distinct seasons, dry and wet, in a year (see 2.1.2. above). The topography of the study site is flat to undulating. The site has shallow greyish clay soil which becomes water-logged when wet and cracked when dry.

Fig. 3. Study site, showing a layout of paths and potential quadrats. The latter are shown stippled in the enlarged inset. The area is divided into quarters or blocks (B1 to B4), each quarter containing 19 columns of potential quadrats running parallel to the paths and numbered from left to right (x): 1,2,3,... etc. Each column contains 46 potential quadrats, numbered from top to bottom (y): 1,2,3,... etc. Quadrats for harvesting are selected by random x and y co-ordinates within each block.

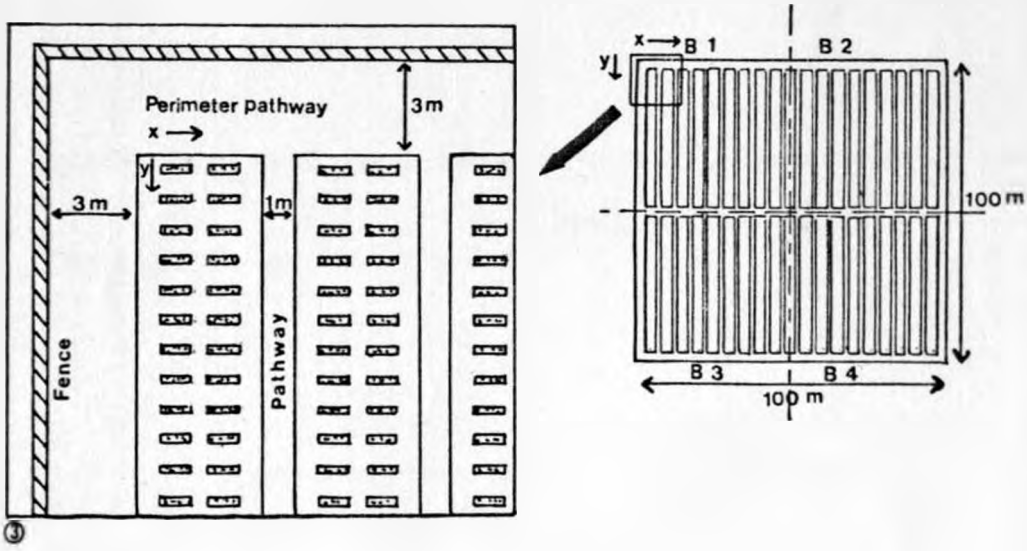
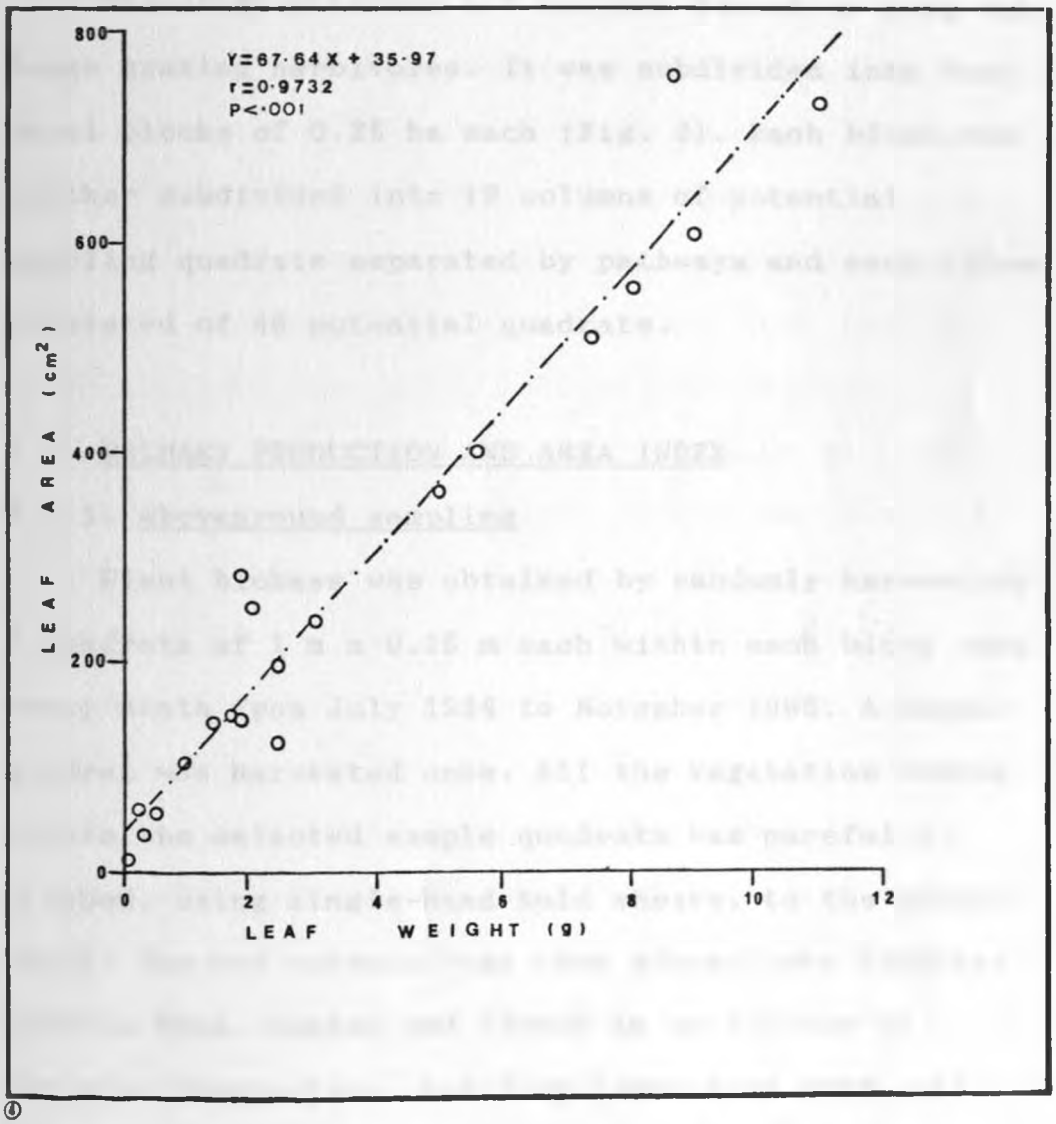

Perimeter pathway
x
y
3 m
3 m
1m
Fence
Pathway
x
B 1
B 2
y
100 m
B 3
B 4
100 m

Fig. 4. Relationship between leaf area and leaf weight during October 1984.


Y=67·64 X + 35·97
r=0·9732
P<·001
LEAF AREA (cm²)
800
600
400
200
0
0
2
4
6
8
10
12
LEAF WEIGHT (g)

CHAPTER 3

3. MATERIALS AND METHODS

The study site was a 1 ha plot fenced to keep out large grazing herbivores. It was subdivided into four equal blocks of 0.25 ha each (Fig. 3). Each block was further subdivided into 19 columns of potential sampling quadrats separated by pathways and each column consisted of 46 potential quadrats.

3.1. PRIMARY PRODUCTION AND AREA INDEX

3.1.1. Aboveground sampling

Plant biomass was obtained by randomly harvesting 5 quadrats of 1 m x 0.25 m each within each block once every month from July 1984 to November 1986. A sample quadrat was harvested once. All the vegetation rooted within the selected sample quadrats was carefully clipped, using single-hand held shears, to the ground level. The cut material was then placed into labelled plastic bags, sealed and stored in an ice-box to minimize dessication, awaiting laboratory work. All lying litter was also collected and placed into separate labelled bags.

The clipped material once in the laboratory was then separated into key species (*T. triandra* and *P. mezianum*). All the remaining plant material was

separated into categories of "other" grasses, sedges and dicots. Subsamples (of between 1 to 800g fresh weight) of live leaf lamina for each plant species and category, were removed and their projected areas determined using a Delta-T leaf area meter (Model AMT/2). Once the subsampled leaf lamina had their areas determined they were oven dried at 80°C for 24 hours and their dry weights determined. A linear regression line was then obtained by plotting leaf areas against leaf weights (Fig. 4). This line was then used later to calculate leaf areas from leaf weights. A line was obtained for every clipping period where live leaves were encountered. From the calculated leaf areas, leaf area indices were calculated. From March 1985, areas of sheath and photosynthetic stem (see 4.1.6) were calculated in this manner and then their area indices obtained. The remaining material was separated into live and dead. Dead material was pooled regardless of species or plant category. Stems, leaf blades and sheaths were considered dead when a proportion of yellow/brown tissue exceeded 50%. Each category of material was then oven dried at 80°C for 24 hours.

Stratified canopy sampling was also carried out for the assessment of aboveground biomass and leaf area indices. Briefly, the method was as follows: a wooden board was marked into segments of 20 cm each (0, 20,

40, >40 cm). The 0 cm mark corresponded to the ground or clipping level. After clipping the plant material was placed on the 0 cm mark as accurately as possible. This process was carried out in the field during sampling. No attempt was made to straighten the plant materials as this would tend to lengthen their heights than they were in the plant canopy. The material on the board was then cut at each appropriate level with a sharp knife depending on its height.

For each canopy layer plant material was separated into plant species and categories as described earlier. Projected areas of leaf lamina, green stems and sheaths were determined with the leaf area meter as described above. From these areas, LAI was calculated for each canopy layer.

3.1.2. Belowground sampling

Belowground biomass sampling was determined by taking soil cores of 5 cm diameter to a predetermined depth of 15 cm from each clipped quadrat during each harvest. Preliminary sampling showed that 95-97% of belowground plant biomass occured in the first 15cm depth. The extracted soil cores were then washed through a 2 mm wire mesh tray to remove soil particles. By use of vital staining with 2,3,5-triphenyltetrazolium chloride (2,3,5-TTC), the washed root material was separated into live and dead portions (Knievel 1973).

Tetrazolium salts act as terminal

electron acceptors in respiration and are reduced to their coloured form in living tissue. Roots were immersed in a 1% 2,3,5-TTC solution in distilled water at room temperature and kept in the dark for about 8 hours or more. Dead roots remained unstained. Where roots were covered with brown to dark dead layer of material, they were sectioned with a blade to expose the inner tissues so that any staining could be noted. Dry weights were determined as for aboveground material.

3.1.3. Decomposition of Dead Plant Materials

The rate of decomposition or disappearance of dead plant materials was determined using the litter bag technique (Wiegert and Evans 1964). Sub-samples of dead roots and shoots were obtained during the monthly harvest period. 2 g dry weight of each category of dead plant materials were placed in litter bags made of nylon of 2 mm mesh. After filling the bags with dead plant materials, the bags with shoot material were placed on the soil surface under the plant canopy while the bags with dead root materials were buried 5 cm under the soil surface in the field. The bags were placed in the field during each monthly harvest and retrieved during the coming harvest with an interval of one month. After removal from the field the remaining plant materials in bags were oven-dried and

their dry weight obtained. The change in weight was calculated so that the relative rate of decomposition, r, was calculated using the following formula:

$$r = \log n (Di / Di+1) / (ti+1 - ti)$$

where r = instantaneous rate of disappearance of dead plant parts ($g\ g^{-1}\ day^{-1}$)

Di = mean dry weight of dead material at ti

Di+1 = mean dry weight of dead material at ti+1

(ti+1 - ti) = harvest interval

3.1.4. Net Primary Production

Net primary production rates were calculated using the equations of Roberts *et al.* (1985) as follows:

$$Pn = \Delta B + dl + dg + de$$

where, Pn = net primary production ($g\ m^{-2}\ d^{-1}$)

ΔB = change in biomass ($g\ m^{-2}$)

dl = losses due to death, shedding or decomposition ($g\ m^{-2}$)

dg = loss to grazing ($g\ m^{-2}$)

de = loss to root exudation ($g\ m^{-2}$)

Losses due to death and shedding are as follows:

$$dl = \Delta D + r \cdot t \cdot D$$

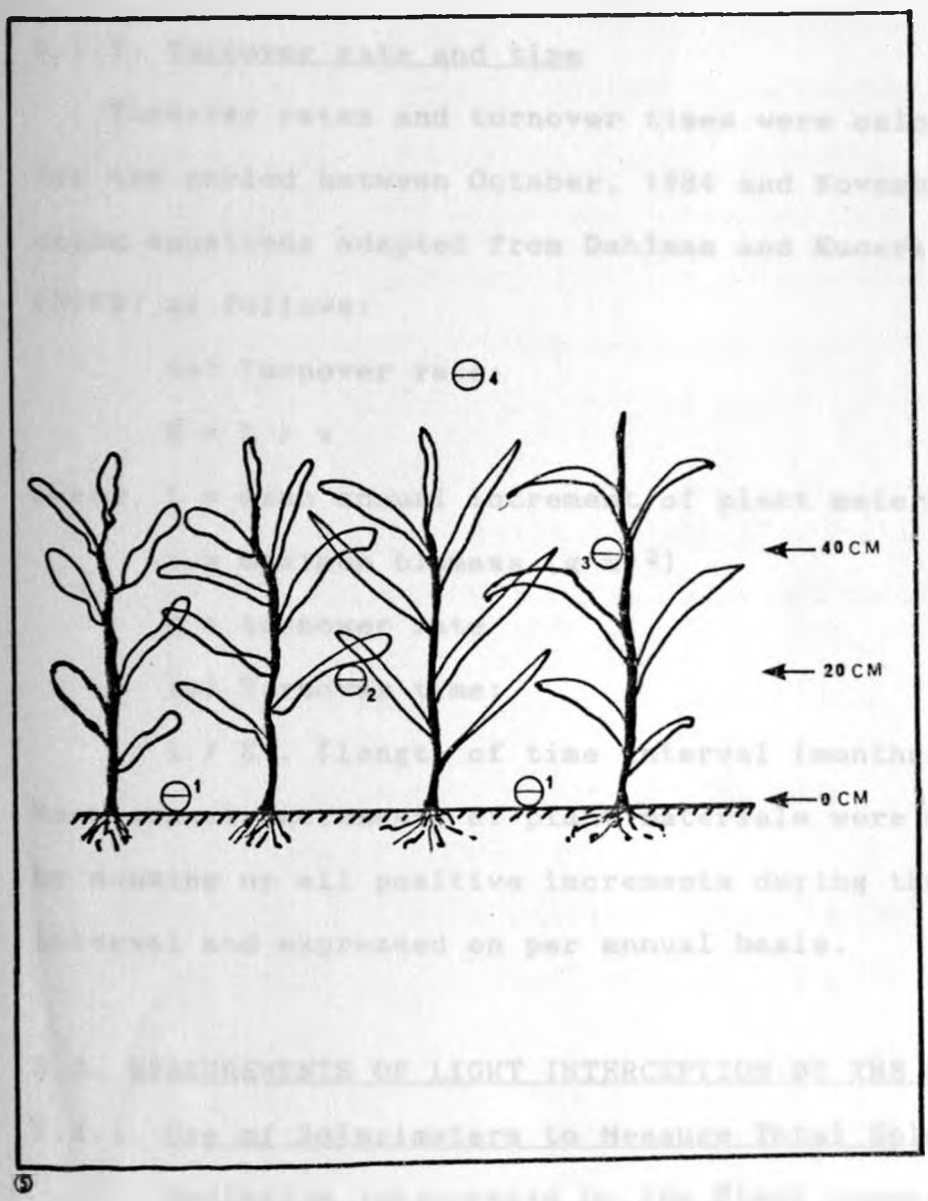
where, ΔD = change in dead biomass ($g\ m^{-2}$)

t = length of time interval (days)

D = mean quantity of dead material ($g\ m^{-2}$)

Only positive values of ΔB and ΔD were used and negative values were ignored during the

Fig. 5. The arrangement of tube solarimeters within the plant canopy (1-3) and above the plant canopy (4) for measurement of total solar radiation.


Θ4
Θ3
Θ2
Θ1
Θ1
40 CM
20 CM
0 CM

summation of net primary production (Milner and Hughes 1968, Deshmukh 1986). Losses to root exudation were not estimated in this study. Since the site was fenced to keep off grazing herbivores, dg was assumed to be zero.

3.1.5. Turnover rate and time

Turnover rates and turnover times were calculated for the period between October, 1984 and November, 1986 using equations adapted from Dahlman and Kucera (1965) as follows:

(a) Turnover rate:

$K = L / x$

where, L = mean annual increment of plant material (g m^{-2})

x = maximum biomass (g m^{-2})

K = turnover rate

(b) Turnover time:

1 / K . [length of time interval (months)]

Mean annual increments of plant materials were calculated by summing up all positive increments during the same time interval and expressed on per annual basis.

3.2. MEASUREMENTS OF LIGHT INTERCEPTION BY THE CANOPY

3.2.1. Use of Solarimeters to Measure Total Solar Radiation Intercepted by the Plant Canopy

Tube solarimeters (Model TSL, Delta-T devices) were used to measure solar radiation received by the plant canopy (Szeicz *et al.* 1964). Tube solari-

meters were placed in the plant canopy at appropriate levels (Fig. 5). Two solarimeters were placed at the base of the canopy, one was placed at 20 cm level and another was placed at 40 cm level. A single solarimeter was placed above the canopy to record the incident solar radiation. The output from the solarimeters was continuously accumulated on electronic integrators (Delta-T devices) which were read biweekly. From the measurements the transmitted fraction of radiation (T) was calculated for each canopy level and the fraction of solar radiation intercepted by the plant canopy was assumed to be 1 - T.

3.2.2. Light Energy Conversion Efficiency

Light energy conversion efficiency (ε) was calculated as follows:

$$\varepsilon = B / I$$

where, B = mean monthly net increase in live biomass ($g\ m^{-2}$)

I = solar radiation received by the canopy during a given time interval (1 month), $MJ\ m^{-2}$

3.3. SOIL MOISTURE CONTENT

Soil moisture content was determined from fresh soil samples collected from the field at different soil depths (0-5 cm, 5-10 cm and 10-15 cm) and placed in labelled air tight plastic bags. Samples were taken to the laboratory for analysis. Soil moisture content was determined by weighing a fresh soil sample, drying it in an oven at 100°C to remove water and weighing again after 48 hours (Milford 1976). The loss in weight on drying was the weight of water originally present. This weight was expressed as a percentage of the oven dry weight of the soil (Pw). Pw is the ratio of the weight of the soil water to weight of oven dry soil multiplied by 100, using the formula:

$$Pw = \frac{\text{Wt. soil water (g)}}{\text{Wt. oven dry soil (g)}} \times 100$$

Soil moisture content was determined for dry and wet seasons.

3.4. SPECTRAL REFLECTANCE RATIO

Spectral reflectance ratios of the vegetation were taken during the period from June to December 1986 to determine the appropriateness of using spectral reflectance ratio (SRR) in estimating plant biomass. A portable spectrophotometer (Skye Instruments, Scotland)

was used for this experiment. The instrument consists of a light sensor which contains two similar planar diffused silicon photocells, which are exposed to filtered light with band centres at 660 nm (red wave band) and 730 nm (near-infrared wave band). These photocells produce a current, which is converted to a voltage, with the amount of voltage depending on the level of light. The voltage is then amplified by an electronic unit to give a direct readout of 660/730 nm photon flux density ratio readings. Photon flux density ratio was converted to spectral reflectance ratio (where reflectance is the ratio of PFD from the vegetation to that of a Lambertian reflector, Kodak Gray Card, Eastman Kodak Company, USA) by dividing canopy PFD ratio values by the PFD ratio of light reflected from the grey card.

Thus:

$$SRR = \frac{\text{reflectance at 660 nm relative to grey card}}{\text{reflectance at 730 nm relative to grey card}}$$

However, since the field of view of the sensor head is very wide, it was found necessary to concentrate on a limited field of view or radius of scan. Therefore, a field stop was fitted to the sensor head. This consisted of a simple tube made of optically black plastic material. An acceptance angle of 40° (20° either side of the vertical) was utilized and the

length of field stop was calculated to be 6 cm long.

Before readings were taken, the sensor head was placed at an appropriate height above the plant canopy depending on the relative canopy height. Again this was arrived at by deciding on the acceptance angle and radius of scan or field of view. Once the acceptance angle and radius of scan had been decided upon the height was arrived at trigonometrically using the formula:

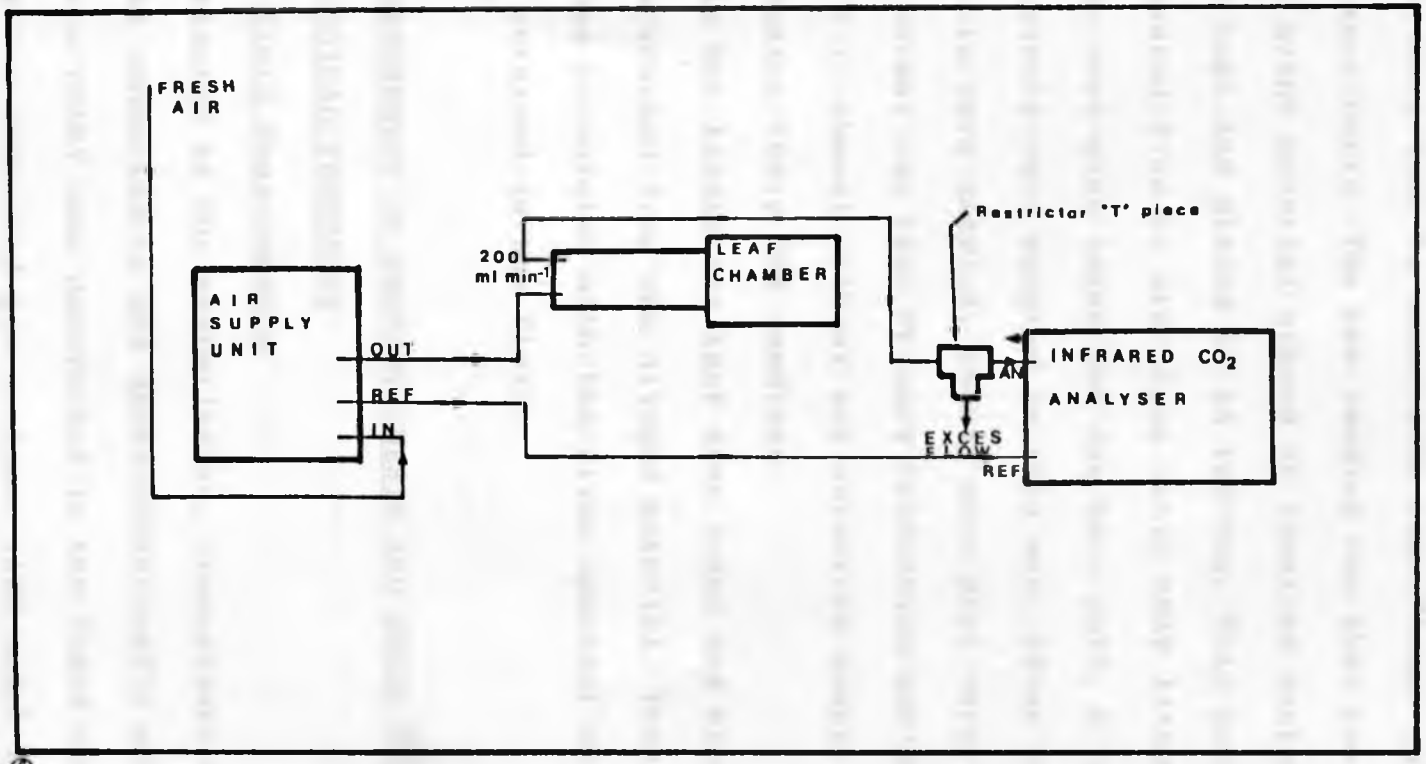
$$\text{Height} = \text{radius} / \tan 20^{\circ}$$

A height of 1.37 m was utilized so as to scan a radius of 50 cm (1 m diameter).

The sensor was mounted on an adjustable tripod and placed directly over the center of the circular quadrat, using a plumb line. A suitable tripod stand was made for the sensor using some special laboratory clamps as swivel joints. These allowed independent adjustment of the sensor head and the grey card, both of which were fitted with spirit levels to ensure accurate adjustment of position. To take the reference readings, the grey card was swung in and out of the field of view without disturbing the sensor.

After assembly of the apparatus, a reading was taken directly from the instrument. After taking the

Fig. 6. The arrangement of portable IRGA system (ADC model LCA2) showing the general flow of gas within the system (see text for details).


FRESH AIR
AIR SUPPLY UNIT
OUT
REF
IN
200 ml min⁻¹
LEAF CHAMBER
Restrictor 'T' piece
AN
EXCES FLOW
REF
INFRARED CO_2 ANALYSER

⑥

reading, the plot confined in the circular quadrat was selectively clipped to remove some bit of plant material at a time to cause some significant change in reflectance ratio. The new reading was then recorded and all plant material placed in labelled sealed plastic bags and placed in an ice-box. This process was repeated five or six times until only litter remained. Readings were also taken for the bare soil. A total of five quadrats were sampled in this way. After these five plots were sampled, twenty more plot were clipped in the normal way (see Primary Production and Area Index, 3.1. above) without any selective sampling while taking their SRR readings.

In the labolatory leaf area index and biomass were determined from the clipped material. These values were then correlated with the given spectral reflectance ratios obtained in the field.

3.5. MEASUREMENT OF PHOTOSYNTHESIS AND OTHER RELATED PHYSIOLOGICAL PROCESSES

3.5.1. Field Measurements

Estimates of CO_2 assimilation, transpiration rates, stomatal conductances and photosynthetically active radiation (PAR) were determined in the field with an open system infra-red gas analyser (ADC model LCA2) with a hand held cuvette. The analyser was used in a

constant flow rate variable differential method. In this method air of known or measured CO_2 concentration was passed at a known and controlled flow rate (using the ADC air supply unit type ASU) into a Parkinson leaf chamber (Model PLC). Air was sampled from the leaf chamber using the restrictor T piece (LCA-135) supplied at the analysis input (see Fig. 6). Air was drawn from 3.6 m height through a sampling tube. It was then drawn through the air supply unit and divided into two streams. The reference stream was passed directly to the analyser while the out stream was passed through the leaf chamber where temperature and humidity sensors are located. After passing through the leaf chamber it entered the analyser as the analysis stream where it was analysed for CO_2 concentration. Differential reading was obtained when analysis and reference air streams were compared.

In the leaf chamber CO_2 exchange between the air and the leaf took place and the difference in CO_2 concentration between the sample and the reference stream recorded. The leaf chamber also contained the PAR sensor. The temperature sensor was a Fenwal LTN-1 precision thermistor. The light sensor was a filtered selenium photocell while the humidity sensor was made of a Vaisala element.

Physiological measurements were carried out each

month when plants possessed green leaves. Additionally, attempts were made to measure the variation of photosynthetic rates within the plant canopy at different canopy levels for various grass species. Leaves were randomly selected for each species at the top, middle and bottom levels of the plant canopy. Neutral density fibre glass filters were used to vary the amount of photon flux density. Leaves were fully exposed to light by separating the dense grass cover. Attempts were also made to conduct a diurnal course in physiological processes (photosynthesis, transpiration, stomatal conductance and leaf water potential).

Leaf water potentials (MPa) were determined with a portable pressure chamber (PMS Instruments, Corvallis, Oregon) using the method of Scholander *et al.* 1965. A leaf was cut from a plant and placed in the chamber with the cut end projecting through the hole in a rubber bung. Pressure was applied to the cut leaf using nitrogen gas from a portable gas cylinder. The pressure applied to the leaf to return the water interface to where it was before leaf detachment, is equal and opposite to the tension in the xylem of the intact plant.

Calculations of CO_2 assimilation rates, transpiration rates and stomatal conductances of single leaves were calculated using flux equations adapted

from von Cammerer and Farquhar (1981) and Long and Hallgren (1985). Briefly CO_2 assimilation rate (Fc) ($\mu mol\ m^{-2}\ s^{-1}$) was calculated using the formula:

$$Fc = f / s \,.\, \Delta c$$

where, f = mole flow of air ($mol\ s^{-1}$)

s = leaf surface area (m^2)

Δc = CO_2 differential between reference and analysis streams ($mol\ mol^{-1}$)

However, a correction for the increase in water vapour by transpiration of the leaf was needed:

$$Fc = f / s \,.\, \Delta c \,.\, [(1 - Xe) / (1 - Xo)]$$

where, Xo = mole fraction of water vapour at leaf chamber outlet ($mol\ mol^{-1}$)

Xe = mole fraction of water vapour at leaf chamber inlet ($mol\ mol^{-1}$)

Xo and Xe are calculated from saturation vapour pressure (Xs) at the measured leaf temperature, given the relative humidity:

$$Xo \text{ or } Xe = Xs \,.\, RH / 100$$

Transpiration rate (E) was calculated using the following equation:

$$E = f / s \,.\, [(Xo - Xe) / (1 - Xo)]$$

where, E = transpiration rate ($mmol\ m^{-2}\ s^{-1}$)

Stomatal conductance (gs) was calculated following the equation:

$$gs = (E / Xs,Tl - Xo) / 0.4$$

where, gs = stomatal conductance (cm s^{-1})

Tl = chamber temperature (^{o}C)

Xs,Tl = saturation vapour pressure at chamber temperature (^{o}C)

0.4 = to convert mol m^{-2} s^{-1} to cm s^{-1}

Vapour Pressure Deficit (VPD) calculations followed the method of Buck (1981), appendix 6.

3.5.2. Laboratory Measurement of CO_2 Assimilation Rate by Different Plant Organs

Four dominant East African grass species at the study site (*T. triandra*, *P. mezianum*, *C. caesius* and *R. repens*) were collected from the field and potted in their original soil type and placed in a shade house at the Chiromo campus, University of Nairobi. They were watered until establishment.

CO_2 assimilation of attached leaf blade, sheath, stem, flag leaf and inflorescence were monitored in an open gas exchange system (Long and Hallgren, 1985) with an ADC Infrared Gas Analyser (Model 225) connected to a TOA recorder (Model EPR-1FA) and a Cambridge Dewpoint Hygrometer (Model 880). Assimilation chamber temperature was controlled at 30^{o}C by circulating thermostatically warmed water through a water jacket surrounding the leaf chamber and was monitored by thermocouple wires appressed on one side of the plant organ. This was then read using a Keithley Digital Multimeter (Model 60B). Gas flow rates were monitored by an ADC Sample Selector

(Model WA 161). The assimilation chamber was 8 cm long, 3.5 cm wide and 1 cm deep, made of metal base with plexiglass cover, equipped with a small air stirrer and a water jacket around it. Light of 1800 μmol m^{-2} s^{-1} was provided by a Tungsten Halogen Lamp, and was filtered through 15 cm deep water. The irradiance level was attained by use of a Zenith Variac control and measured by a Lambda Quantum Sensor (Model LI 188).

Air containing approximately 330 ppm CO_2 was pumped from outside the laboratory, bubbled through cold water to lower the dew point and passed through the assimilation chamber (as sample air) and the other through the Dewpoint Hygrometer to the analyser (as reference air). The incoming and outgoing dew points were set by using the reference and sample air respectively. The CO_2 assimilation rates were calculated as follows:

(i) CO_2 assimilation (Fc) (μmol m^{-2} s^{-1});

$$Fc = \frac{\text{---div.} \times SF \times 1.178 \times 10^{-4} \times Fr}{\text{Leaf area } (dm^2)} / 1.584$$

Where, ---div = number of chart divisions.

SF = Scaling factor.

Fr = Flow rate (ml min^{-1}).

1.178×10^{-4} = amount of mg(CO_2) assimilated in (60 mins.) per dm^2 of leaf surface.

1.584 = to convert mg(CO_2) dm^{-2} hr^{-1} to μmol m^{-2} s^{-1}.

Prior to determination of CO_2 assimilation rates of different plant organs, the occurence and level of chlorophyll content and the distribution of stomata in these tissues were determined. Chlorophyll extraction method followed that of Arnon (1949) and level of chlorophyll was determined with a Pye Unicam spectrophotometer (model SP 500). Stomatal count was done from replica slides made of nail varnish (Sampson 1961) using a compound light microscope. The area of field of view was calculated using an eyepiece micrometer.

3.5.3. Water Stress Effects on CO_2 Assimilation and Other Associated Physiological Processes

For this experiment the plant material used included *T. triandra*, *P. mezianum*, *R. repens*, *E. paspaloides*, *C. caesius* and *C. ciliaris* which were collected from the study site at Athi River. *Dactyloctenium aegyptium* (L.) Willd. was also used in this experiment and was collected from Magadi. They were potted in their original soil types and placed in the shade house at the Chiromo campus (as in section 3.5.2). They were watered to establishment. Prior to imposing the water stress treatment, determination of leaf water potential (using a portable pressure chamber), CO_2 assimilation rate and other related physiological processes were carried out in the laboratory as previously described.

Plants were water stressed by with-holding water for 15 days. Physiological data were collected as for control plants. Chlorophyll levels were monitored for both control and water stressed plants using the same leaves used for the determination of CO_2 assimilation rates. Chlorophyll determination followed the method of Arnon (1949). Levels of chlorophyll were determined with a Pye Unicam Spectrophotometer (Model SP 500).

3.6. LEAF ANATOMY

3.6.1. Light Microscopy

Fresh grass leaf material of the dominant C_4 species (*T. triandra*, *P. mezianum*, *C. caesius*, *C. ciliaris*, *R. repens*, *E. paspaloides* and *D. aegytium*) were collected from potted plants, cut into small portions of about 1 cm long and fixed in 70% alcohol. In the laboratory, they were dehydrated in alcohol and xylene series and embedded in paraffin wax. Transverse sections, about 12 µm were cut using a microtome and then mounted on slides previously smeared with dilute egg albumen and dried on a warm plate. Wax was removed in xylene and subsequently stained in safranin and light green. Permanent mounting was done with DPX.

Transverse sections of the leaves were examined under a Leitz largefield photomicroscope (Model

"Orthoplan") and photographs taken with a 35 mm camera attached to the microscope.

3.6.2. Scanning Electron Microscopy

Fresh grass materials of *T. triandra* and *P. mezianum* were obtained from the potted plants (see section 3.5.2.). The plant materials consisted of stems, sheaths, leaf blades and inflorescences (floral parts of *P. mezianum* were too minute to manipulate for this work). These plant specimens were cut into 2 mm thick slaps with sharp lazor blade and immersed in a 1% buffered glutaraldehyde fixative solution (Robards 1978). The plant specimens were left for about 8 hours at room temperature in order to enhance the penetration of the fixative into the tissue. From the fixative plant materials were dehydrated in a series of acetone solution. Finally the specimens were stored in 100% acetone in sealed bottles and sent to the EM laboratory at the University of Sussex, England. Samples before analysis were critical-point dried with CO_2 and then sputter-coated with gold dust to enhance quality. Photographs of the plant specimens' epidermal surfaces were taken at 20 kV on a JEOL 100C electron microscope with the ASID-4D scanning attachment. SEM photo-micrographs were analysed for their diagnostic characters according to the criteria of Palmer and Tucker (1981).

Fig. 7. Changes in above- and belowground live biomass from October 1984 to November 1986 (vertical bars are SE).

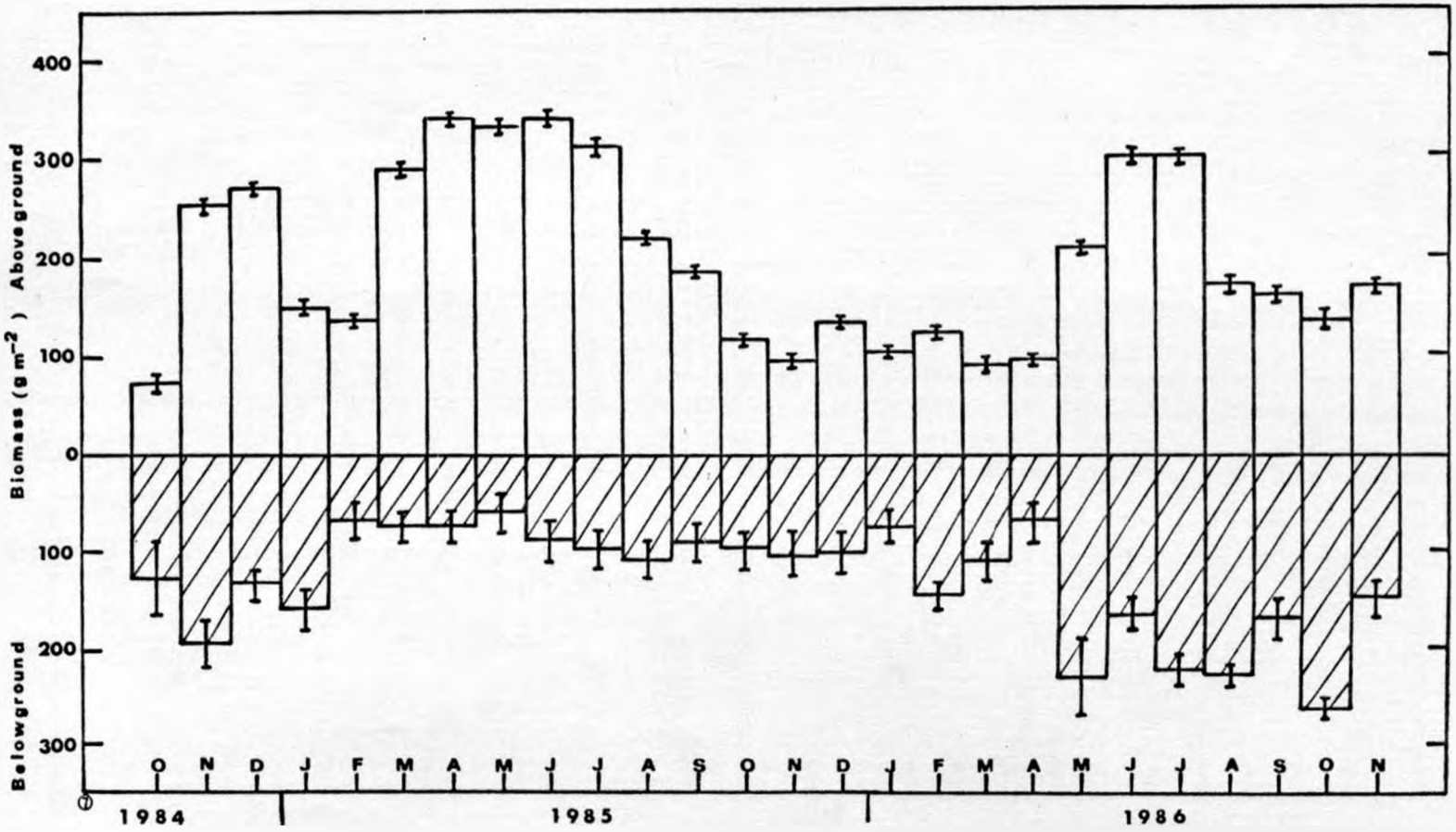

Biomass (g m⁻²)
Aboveground
Belowground
400
300
200
100
0
100
200
300
O N D J F M A M J J A S O N D J F M A M J J A S O N
1984
1985
1986

Fig. 8. Changes in above- and belowground dead biomass from October 1984 to November 1986 (vertical bars are SE).

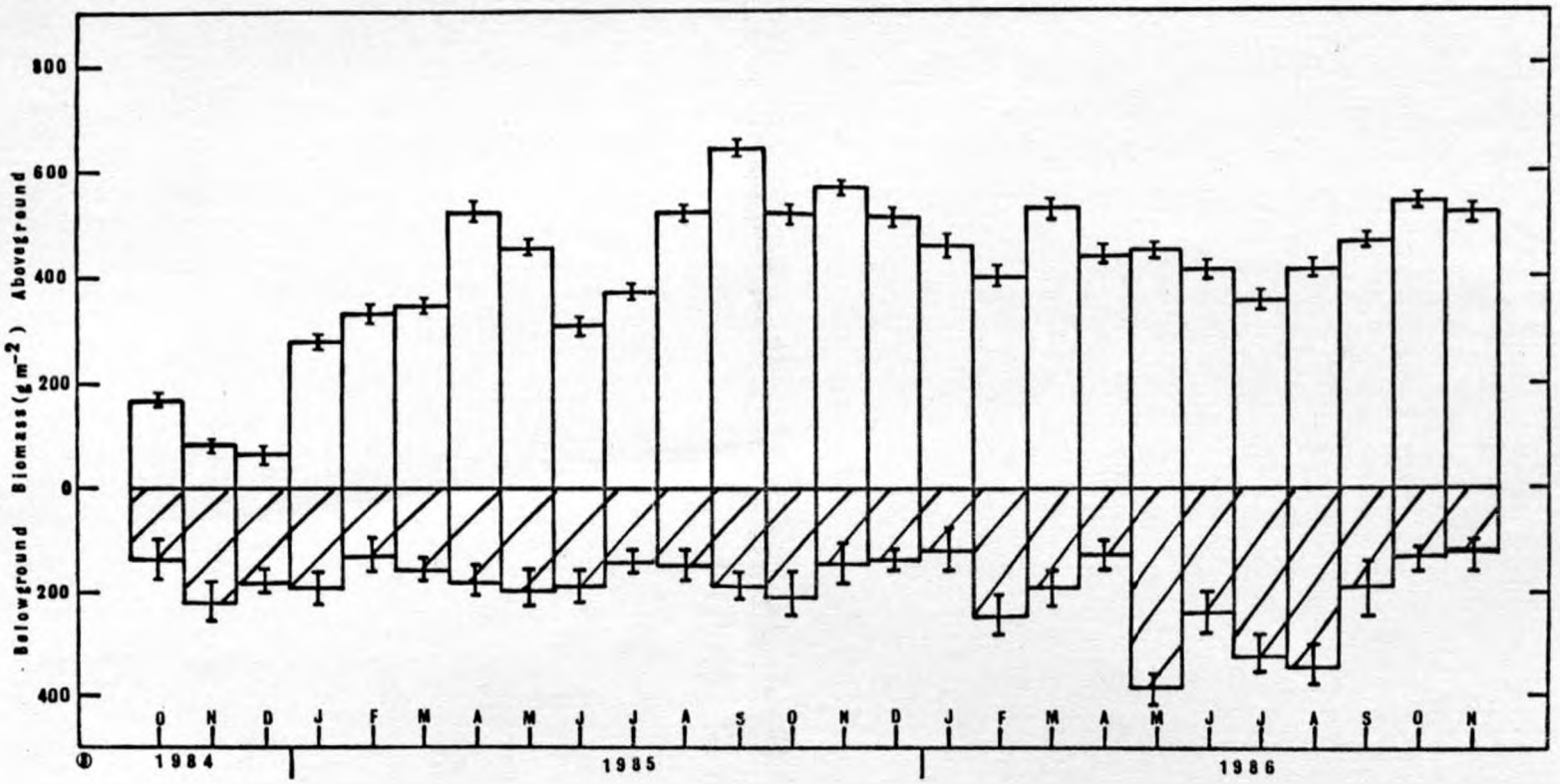
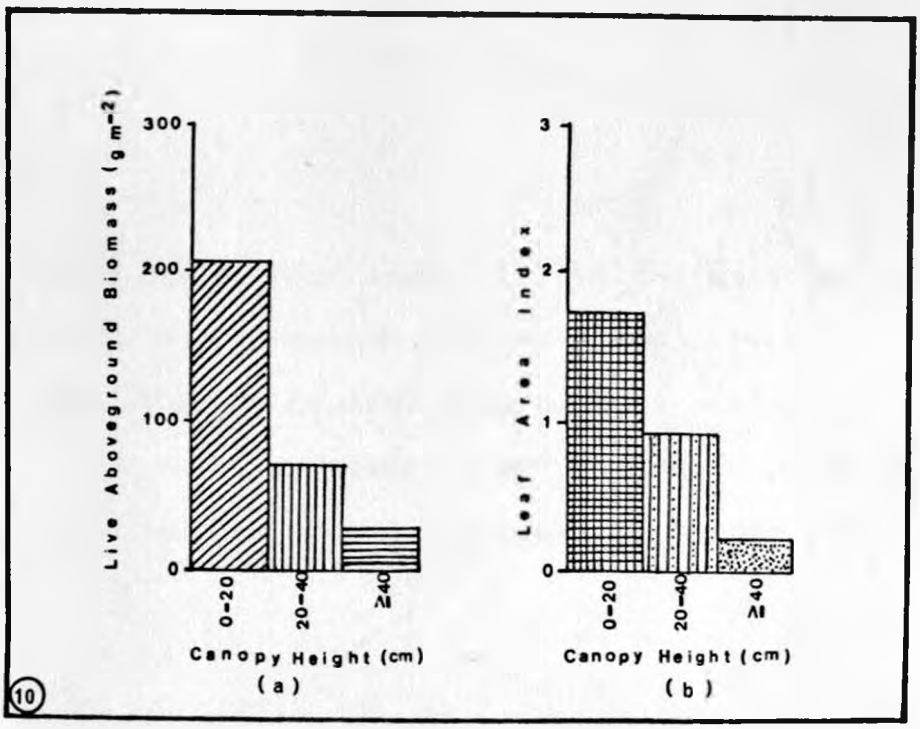

800
600
400
200
0
200
400
Belowground Biomass(gm^{-2}) Aboveground
O N D J F M A M J J A S O N D J F M A M J J A S O N
1984
1985
1986

Fig. 9. Monthly trends in aboveground biomass and rainfall. (●) live biomass; (■) standing dead (○) litter and (+) rainfall.

RAIN FALL (mm) /
BIOMASS (g m-2)
0
100
200
300
400
500
1984
1985
1986
O N D J F M A M J J A S O N D J F M A M J J A S O N

Fig. 10. Vertical distribution of (a) live aboveground biomass and (b) leaf area index (LAI) within the plant canopy (June 1986).


Live Aboveground Biomass ($g\ m^{-2}$)
300
200
100
0
0-20
20-40
≥40
Canopy Height (cm)
(a)
Leaf Area Index
3
2
1
0
0-20
20-40
≥40
Canopy Height (cm)
(b)

10

Fig. 11. Contribution of individual species and plant categories to overall aboveground live biomass from October 1984 to November 1986. (●) *T. triandra*, (○) *P. mezianum*, (▲) "other" grasses, (△) dicots and (◆) sedges.

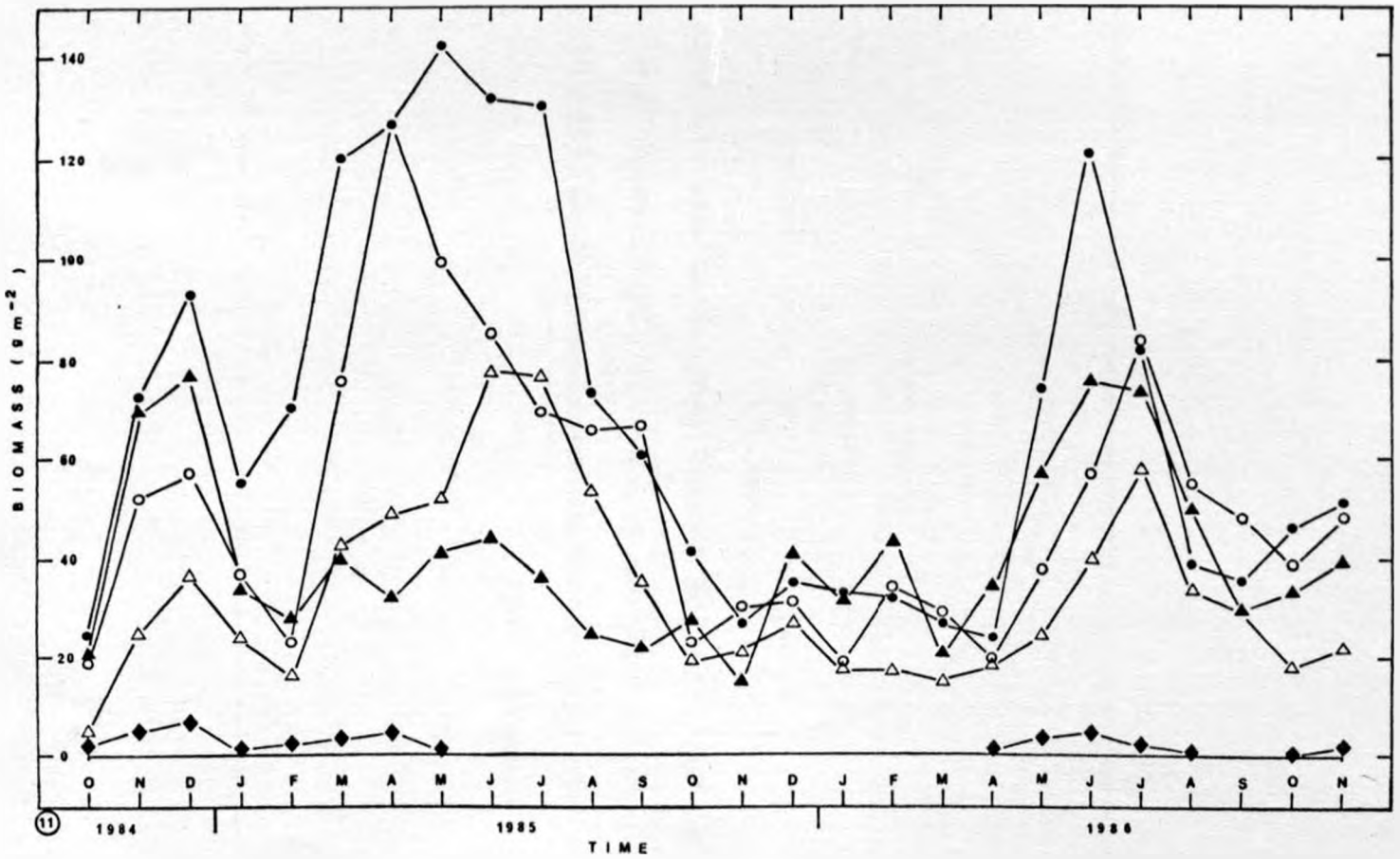
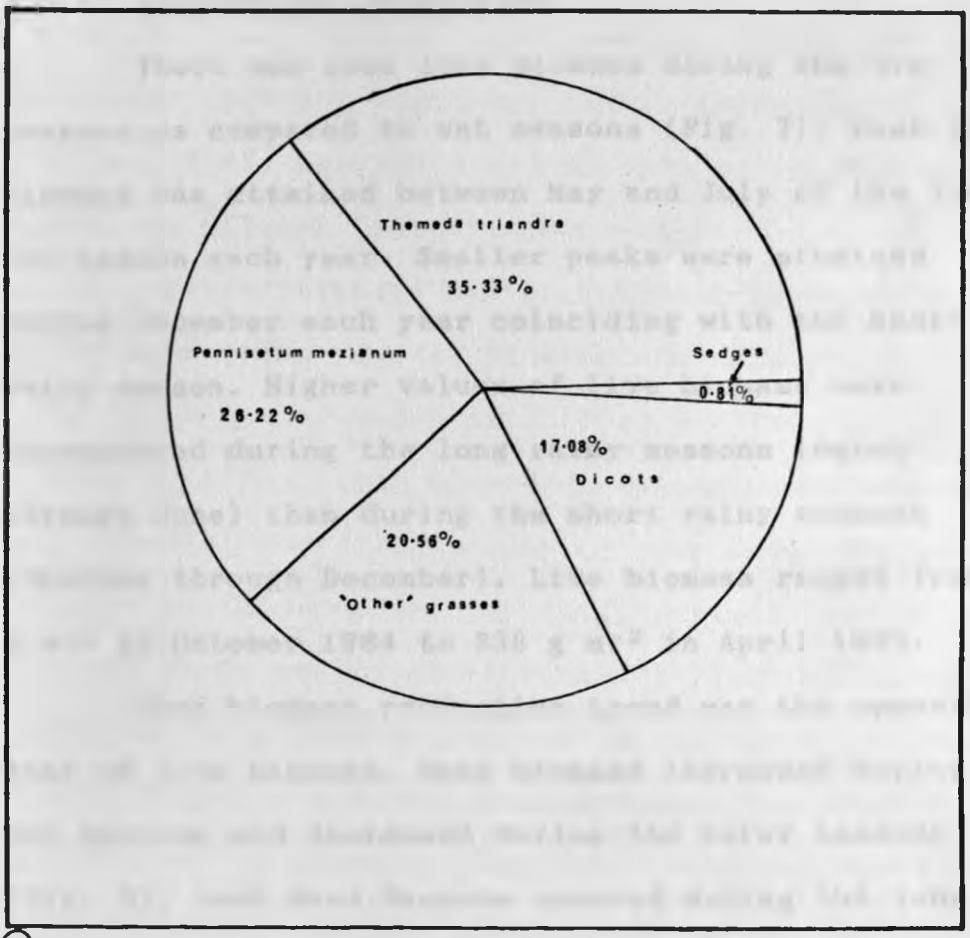

BIOMASS (g m⁻²)
140
120
100
80
60
40
20
0
O N D J F M A M J J A S O N D J F M A M J J A S O N
1984
1985
1986
TIME

Fig. 12. Contribution (%) of individual species and and categories to overall aboveground live biomass production between October 1984 and November 1986.


Themeda triandra
35·33 %
Pennisetum mezianum
26·22 %
Sedges
0·81%
17·08%
Dicots
20·56%
"Other" grasses

(12)

CHAPTER 4

4. RESULTS

4.1. BIOMASS PRODUCTION AND AREA INDEX

4.1.1. Aboveground Production

There was less live biomass during the dry seasons as compared to wet seasons (Fig. 7). Peak live biomass was attained between May and July of the long wet season each year. Smaller peaks were attained during December each year coinciding with the short rainy season. Higher values of live biomass were encountered during the long rainy seasons (March through June) than during the short rainy seasons (October through December). Live biomass ranged from 73 g m^{-2} in October 1984 to 338 g m^{-2} in April 1985.

Dead biomass production trend was the opposite that of live biomass. Dead biomass increased during the dry seasons and decreased during the rainy seasons (Fig. 8). Peak dead biomass occured during the long dry seasons (August through October). Results show that the amount of dead biomass kept on a steady increase from a low value of 66 to a high value of 651 g m^{-2} in December 1984 and September 1985, respectively. From September 1985 dead biomass production maintained a constant trend fluctuating between about 400 and 600 g

m^{-2} with minor drops and peaks during wet and dry seasons, respectively.

Standing dead biomass increased steadily from December 1984 until March 1985 (Fig. 9). However, throughout the rest of the study period it remained about constant, fluctuating between about 200 and 400 g m^{-2}. Standing dead biomass ranged between 19 and 457 g m^{-2} in December 1984 and September 1985, respectively. Peak values of 457 and 440 g m^{-2} occured during September 1985 and October 1986, respectively.

Litter biomass was at a higher level in October 1984 than standing dead biomass and this trend continued upto January 1985 (Fig. 9). However, from February 1985 litter biomass remained lower than that of standing dead fluctuating between about 100 and 190 g m^{-2} over the rest of the study period. Over the entire study period since February 1985 the average standing dead biomass remained about 340 g m^{-2} while that of litter biomass remained about 130 g m^{-2}. Standing dead biomass, therefore, remained more than twice that of litter biomass over the entire study period from October 1984 to November 1986.

Stratified clipping revealed that most of live aboveground biomass occured in the bottom 0-20 cm canopy layer followed by the middle 20-40 cm layer and lastly the upper >40 cm canopy layer (Fig. 10a). During

June 1986, 68% (or 203 g m^{-2}) of total live above-ground biomass occured in the 0-20 cm canopy layer, 23% (or 70 g m^{-2}) in the 20-40 cm canopy layer, and only 9% (or 27 g m^{-2}) occured in the >40 cm canopy layer.

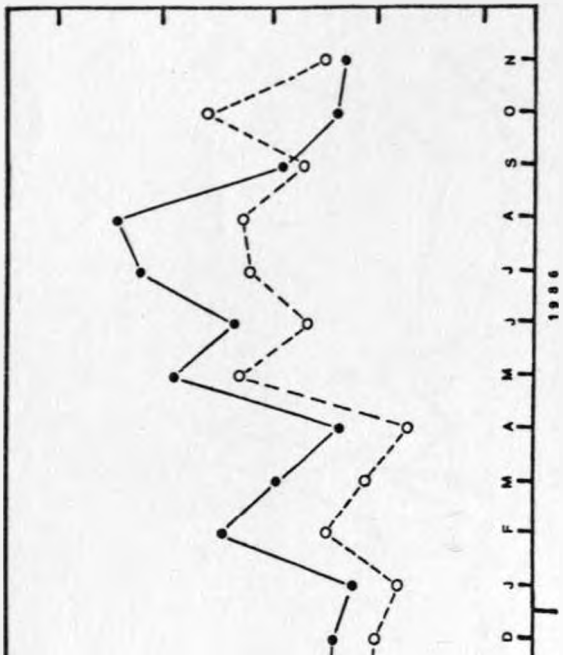
4.1.1.a. Contribution of individual plant species and plant categories to overall aboveground standing live biomass

T. triandra and *P. mezianum* contributed the most to standing live biomass in this grassland ecosystem (Fig. 11). All "other" grasses came next in this aspect. Dicots, which included several annuals, are important constituents of this plant community where in some months they contributed more to live aboveground biomass than all "other" grasses category. This is notable during March through September 1985. Sedges contributed the least to standing live biomass. On an overall basis of standing live biomass, *T. triandra* contributed 35%, *P. mezianum* 26%, all "other" grasses 21%, dicots 17% and sedges 1% between October 1984 and November 1986 (Fig. 12).

4.1.2. Belowground Production

Belowground live biomass was highest during the dry seasons. However, peak values of live biomass occured just before the end of the growing season or at the start of the dry season. This trend was evident during November 1984 (195) and May 1986 (230

Fig. 13. Monthly trend in mean live and dead below-ground biomass from October 1984 to November 1986. (o) live biomass and (•) dead biomass.


D J F M A M J J A S O N
1986

BELOWGROUND BIOMASS (gm⁻²)
0
100
200
300
400
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1984
1985

Fig. 14. Relationship between above- and belowground dead materials decomposition rates and rainfall. (▲) aboveground dead material decomposition rate, (●) belowground dead material decomposition rate, and (◆) monthly rainfall.

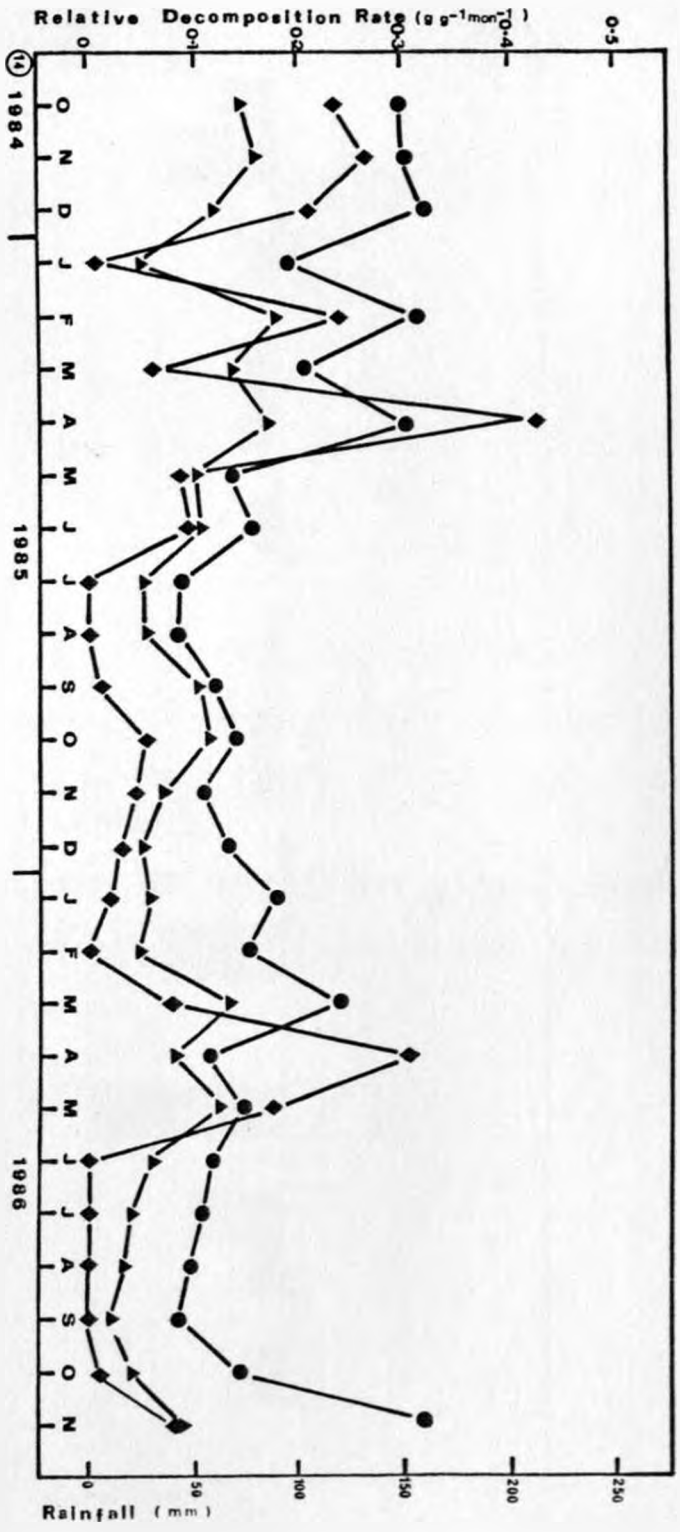

Relative Decomposition Rate (g g⁻¹mon⁻¹)
0
0·1
0·2
0·3
0·4
0·5
1984
1985
1986
O N D J F M A M J J A S O N D J F M A M J J A S O N
0
50
100
150
200
250
Rainfall (mm)

Fig. 15. Relationship between aboveground (□) and belowground (■) monthly Net Primary Production rate ($g\ m^{-2}\ mon^{-1}$) and rainfall (o).

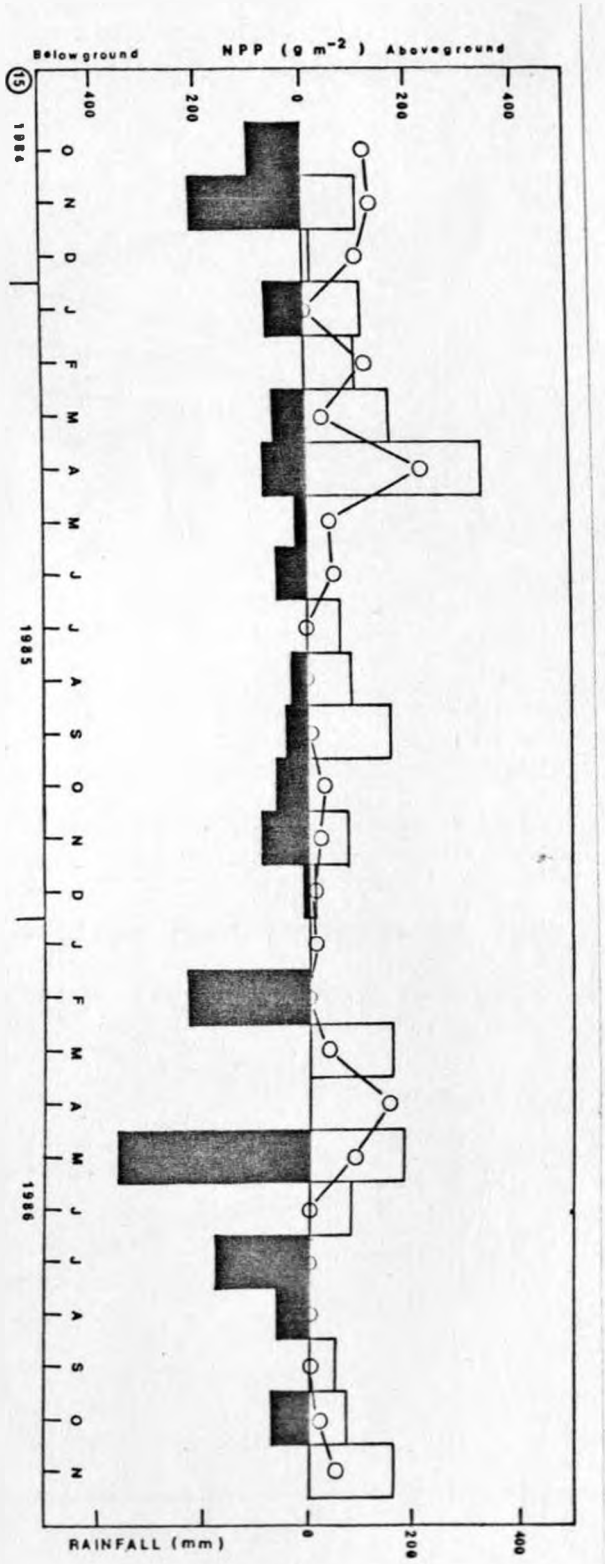
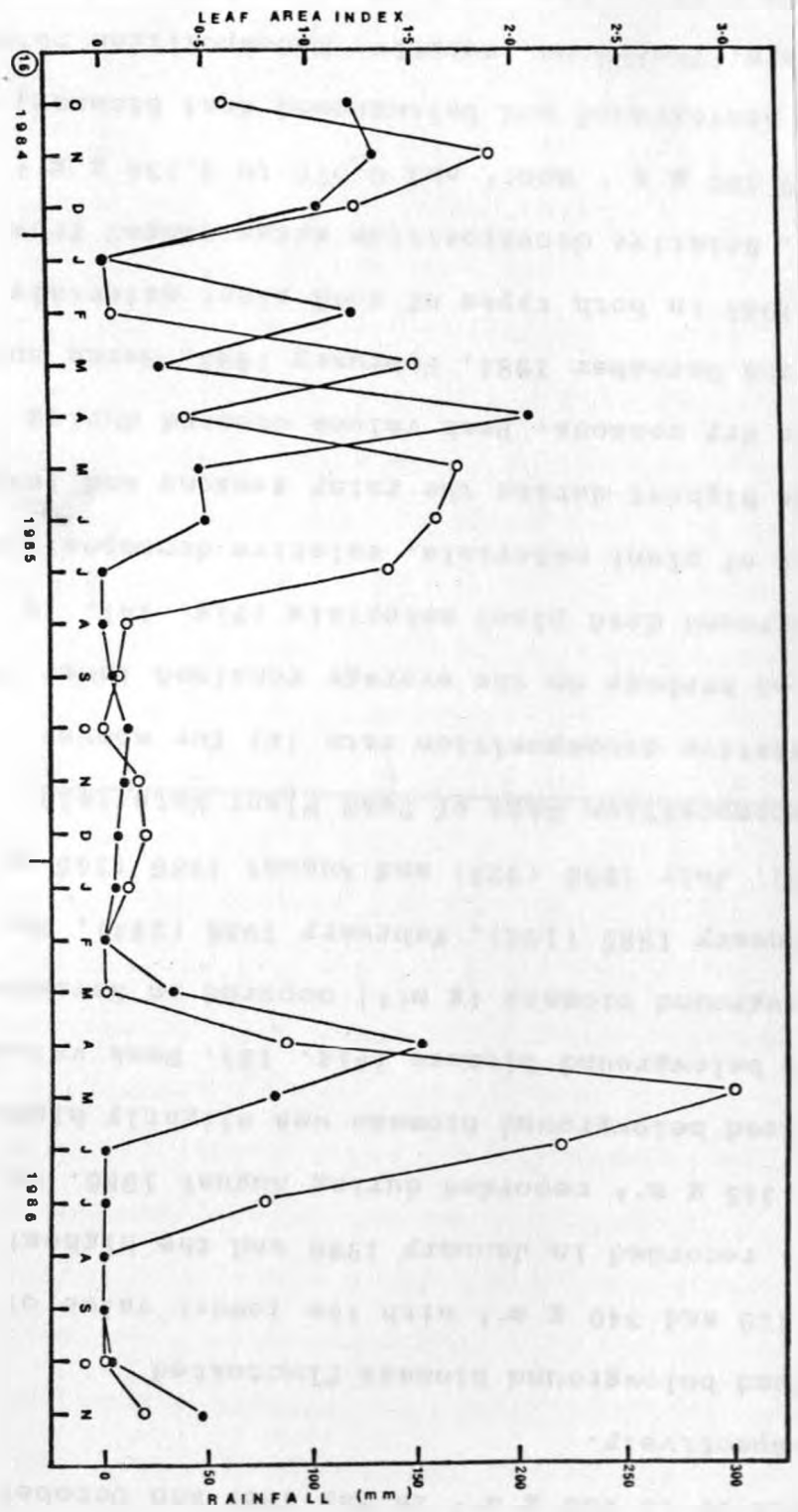

Belowground
NPP (g m^{-2}) Aboveground
400
200
0
200
400
(15)
1984
O N D J F M A M J J A S O N D J F M A M J J A S O N
1985
1986
RAINFALL (mm)
0
200
400

Fig. 16. Leaf area index (o) and rainfall (•) trend from October 1984 to November 1986.


LEAF AREA INDEX
0
0·5
1·0
1·5
2·0
2·5
3·0
(16)
1984
O N D J F M A M J J A S O N D J F M A M J J A S O N
1985
1986
0
50
100
150
200
250
300
RAINFALL (mm)

g m^{-2}), Fig. 7. Live belowground biomass ranged from about 60 to 260 g m^{-2} in May 1985 and October 1986, respectively.

Dead belowground biomass fluctuated between 120 and 340 g m^{-2} with the lowest value of 121 g m^{-2} recorded in January 1986 and the highest value of 345 g m^{-2} recorded during August 1986. On the average dead belowground biomass was slightly higher than live belowground biomass (Fig. 13). Peak values of dead belowground biomass (g m^{-2}) occured in November 1984 (220), January 1985 (192), February 1986 (244), May 1986 (289), July 1986 (323) and August 1986 (345 g).

4.1.3. Decomposition Rate of Dead Plant Materials

Relative decomposition rate (r) for aboveground dead herbage on the average remained lower than for belowground dead plant materials (Fig. 14). In both types of plant materials, relative decomposition rates were highest during the rainy seasons and lowest during the dry seasons. Peak values occured during November and December 1984, February 1985, March and November 1986 in both types of dead plant materials (Fig. 14). Relative decomposition rates ranged from 0.023 to 0.180 g g^{-1} mon^{-1} and 0.076 to 0.335 g g^{-1} mon^{-1} for aboveground and belowground dead biomass, respectively. Therefore, relative decomposition rate ranged from 2.3% to 18% and 7.6% to 33.5% per month for

above- and belowground dead biomass, respectively.

4.1.4. Net Primary Production

Over the period between October 1984 and November 1986 aboveground net primary production rate was 1332.4 g m^{-2} yr^{-1} (3.65g m^{-2} d^{-1}) while that of belowground material was 965.8 g m^{-2} yr^{-1} (2.65g m^{-2} d^{-1}). Therefore, total net primary production rate of the plant community was about 2298.2 g m^{-2} yr^{-1} (6.3 g m^{-2} d^{-1}). Monthly net primary production rate ranged between about 9 and 324 g m^{-2} for aboveground material and 8 and 357 g m^{-2} for belowground material (Fi 15). The trend in monthly net primary production followed closely after that of rainfall, which ranged from 0 to 21 mm (Fig. 15). At the start of rains, belowground compartment accumulated more material than aboveground compartment, hence, there was a net primary production in belowground material during the first or second month after the rains fall. For example, this occured in October 1984 (98 g m^{-2}), March 1985 (61 g m^{-2}), October 1985 (55 g m^{-2}), May 1986 (356 g m^{-2}) and October 1986 (68 g m^{-2}). It is after this increase in belowground net primary production that aboveground net primary production peaked. This happened during or after the month the rainfall occurs (Fig. 15).

4.1.5. Turnover rate and time

Results of turnover rate and time of different

plant materials are presented in Table 1. Litter had the highest turnover rate (2.5) followed by aboveground live biomass (2.08) and standing dead biomass (2.0). Total aboveground dead biomass had the lowest turnover rate (0.4). Dead belowground biomass had a turnover of 1.95 while that of live belowground biomass was lower at 1.85.

From Table 1 it can be noted that plant materials with the lowest turnover rate had the highest turnover time. Total aboveground dead biomass had the highest turnover time of 64 months followed by belowground live biomass (14 months) and total belowground biomass (14 months). The turnover time for all plant materials averaged about 12 months in this plant community.

4.1.6. Area Index

Higher values of leaf area index (LAI) were encountered during the wet seasons than during the dry seasons (Fig. 16). LAI values ranged from 0.0 (in most dry months) to 3.09 (in May 1986). LAI values trend lagged closely behind, about one month, that of rainfall. Peak values occured in November 1984 (1.9), March 1985 (1.5), May 1985 (1.7) and May 1986 (3.1).

Stratified canopy sampling showed that most of the LAI occured in the bottom 0-20 cm canopy layer followed by the middle 20-40 cm canopy layer and lastly by the top >40 cm canopy layer (Fig. 10b). In June 1986, about

Table 1. The maximum biomass, mean annual increment and turnover rate and time for different plant materials (October, 1984 - November, 1986).

Plant material	Maximum biomass ($g\ m^{-2}$)	Mean annual increment ($g\ m^{-2}\ yr^{-1}$)	Turnover rate	Turnover time (mons)
AGB*	338.35	705.57	2.08	12
SDB	457.22	917.00	2.00	13
Litter	196.32	492.58	2.50	10
Total AGD	650.58	262.32	0.40	64
BGB	262.39	485.75	1.85	14
Dead BG	344.86	672.58	1.95	13
Total BG	571.03	1087.22	1.90	14

* Plant material:
AGB = aboveground biomass
SD = Standing dead
Total AGD = Total aboveground dead (Standing dead + Litter)
BGB = belowground biomass
Dead BG = Dead belowground
Total BG = Total belowground (live + dead)

Fig. 17. Solar radiation absorption profile within the plant canopy (vertical bars are S.E.).

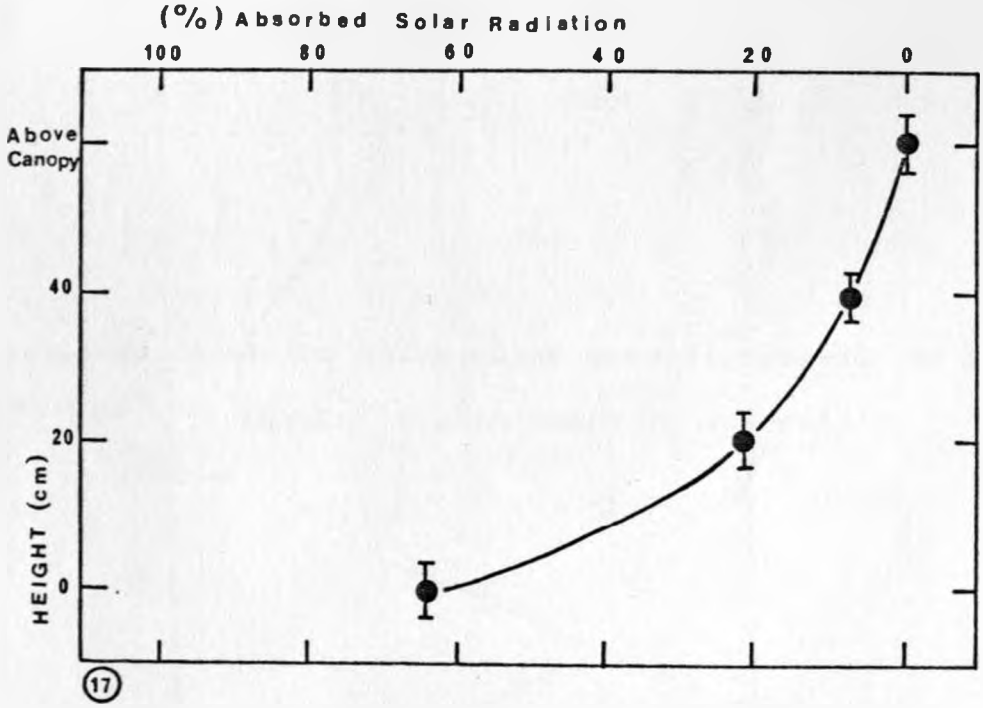

(%) Absorbed Solar Radiation
100
80
60
40
20
0
Above Canopy
40
20
0
HEIGHT (cm)
17

Fig. 18. Changes in mean daily solar radiation received at the top of plant canopy between 1984 and 1986.

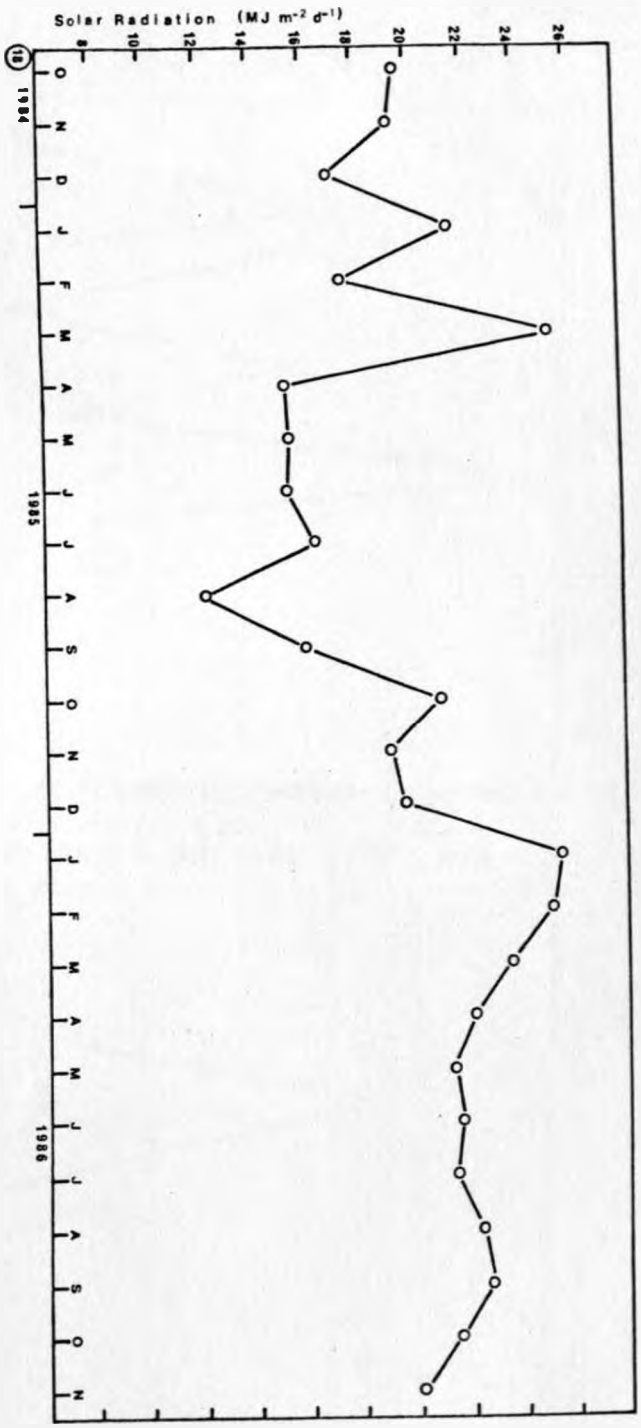

Solar Radiation (MJ m-2 d-1)
8
10
12
14
16
18
20
22
24
26
1984
1985
1986
O N D J F M A M J J A S O N D J F M A M J J A S O N

Fig. 19. Relationship between light use efficiency for total biomass (•) and rainfall (+).

Light Use Efficiency (g MJ⁻¹)
0·5
0·4
0·3
0·2
0·1
0
Rainfall (mm)
200
160
120
80
40
0
O N D J F M A M J J A S O N D J F M A M J J A S O N
1984
1985
1986
(19)

Table 2. Leaf, sheath, stem and total area indices from March, 1985 to November, 1986.

MONTH	LEAF AREA INDEX	SHEATH AREA INDEX	STEM AREA INDEX	TOTAL AREA INDEX
MAR/85	1.50	0.32	0.11	1.93
APR/85	0.40	0.16	0.02	0.58
MAY/85	1.71	1.21	0.03	2.95
JUN/85	1.61	0.59	0.09	2.29
JUL/85	1.36	0.05	0.02	1.43
AUG/85	0.17	0.02	0.01	0.20
SEP/85	0.07	0.02	0.01	0.09
OCT/85	0.00	0.00	0.00	0.00
NOV/85	0.18	0.02	0.01	0.21
DEC/85	0.20	0.03	0.02	0.25
JAN/86	0.12	0.01	0.01	0.14
FEB/86	0.00	0.00	0.00	0.00
MAR/86	0.00	0.00	0.00	0.00
APR/86	0.82	0.49	0.27	1.58
MAY/86	3.09	1.53	0.95	5.57
JUN/86	2.16	1.29	0.66	4.11
JUL/85	0.86	0.51	0.20	1.57
AUG/86	0.00	0.00	0.00	0.00
SEP/86	0.00	0.00	0.00	0.00
OCT/86	0.05	0.00	0.00	0.05
NOV/86	0.49	0.16	0.01	0.66

56% (or 1.73) of LAI occured in the 0-20 cm canopy layer, 30% (or 0.93) in the 20-40 cm layer and only 14% (or 0.43) occured in the top >40 cm canopy layer.

Stem and sheath area indices were monitored from March 1985. Stem area index was always lower than leaf or sheath area index (Table 2). This was because only areas of photosynthetic stems were determined for area indices. Stem area index ranged from 0.0 during the dry season months to 0.95 in May 1986 while sheath area index ranged from 0.0 during the dry seasons to 1.53 in May 1986. Total area index, the total of leaf blade, sheath and photosynthetic stems area index, was highest during the long rainy season months. Highest value was 5.57 in May 1986 and the lowest values of 0.0 were encountered during the dry season months.

4.2. LIGHT ENERGY INTERCEPTION BY THE PLANT CANOPY

4.2.1. Total Solar Radiation

The amount of total solar radiation received by the plant canopy decreased with the depth of the canopy in all months (Appendix 1). The amount of total solar radiation received over the entire period from October 1984 to November 1986 averaged about 19.7 MJ m^{-2} d^{-1} at the top of the plant canopy (Appendix 1). The trend in daily amounts received at the top of the canopy is shown in Fig. 18.

The amount of percentage solar radiation intercepted by the plant canopy increased with canopy depth (Fig. 17). During March through June 1986 growing season about 7% of solar radiation was intercepted by the plant canopy at height level of 40 cm. This amount increased to about 21% at 20 cm canopy level and about 64% (about 12.6 MJ m^{-2} d^{-1}) at the bottom of canopy. Therefore, only about 36% (about 7.1 MJ m^{-2} d^{-1}) of solar energy managed to penetrate to the ground level in this plant community.

4.2.2. Light Energy Conversion Efficiency

Light energy conversion efficiency (ε) is the efficiency with which intercepted solar energy is used to produce new dry matter by a plant community. The highest values of ε occured during the rainy seasons (Fig. 19). ε values ranged between 0.00 and 0.31 g MJ^{-1}. Highest value for aboveground biomass was 0.31 g MJ^{-1} in November 1984 and 0.15 g MJ^{-1} for belowground biomass in October 1986. Aboveground biomass was closely correlated with rainfall with the highest ε occuring during or just after the month with the highest rainfall amount (Fig. 19). Light energy conversion efficiency for belowground biomass was more pronounced during the dry season months.

Fig. 20. Relationship between Spectral Reflectance Ratio (SRR) and live plant biomass during various months at the Study Site.

(△) - Jun(CD) --- June, 1986, calibration experiment, r = -0.959, P<.01

(×) - Jun --- June, 1986, normal harvest data, r = -0.923, P<.01

(⊕) - Jul --- July, 1986, r = -0.555

(◉) - Sep --- September, 1986, r = -0.112

(+) - Oct --- October, 1986, r = -0.004

(o) - Nov --- November, 1986, r = -0.815, P<.01

(●) - Dec --- December, 1986, r = -0.869, P<.01

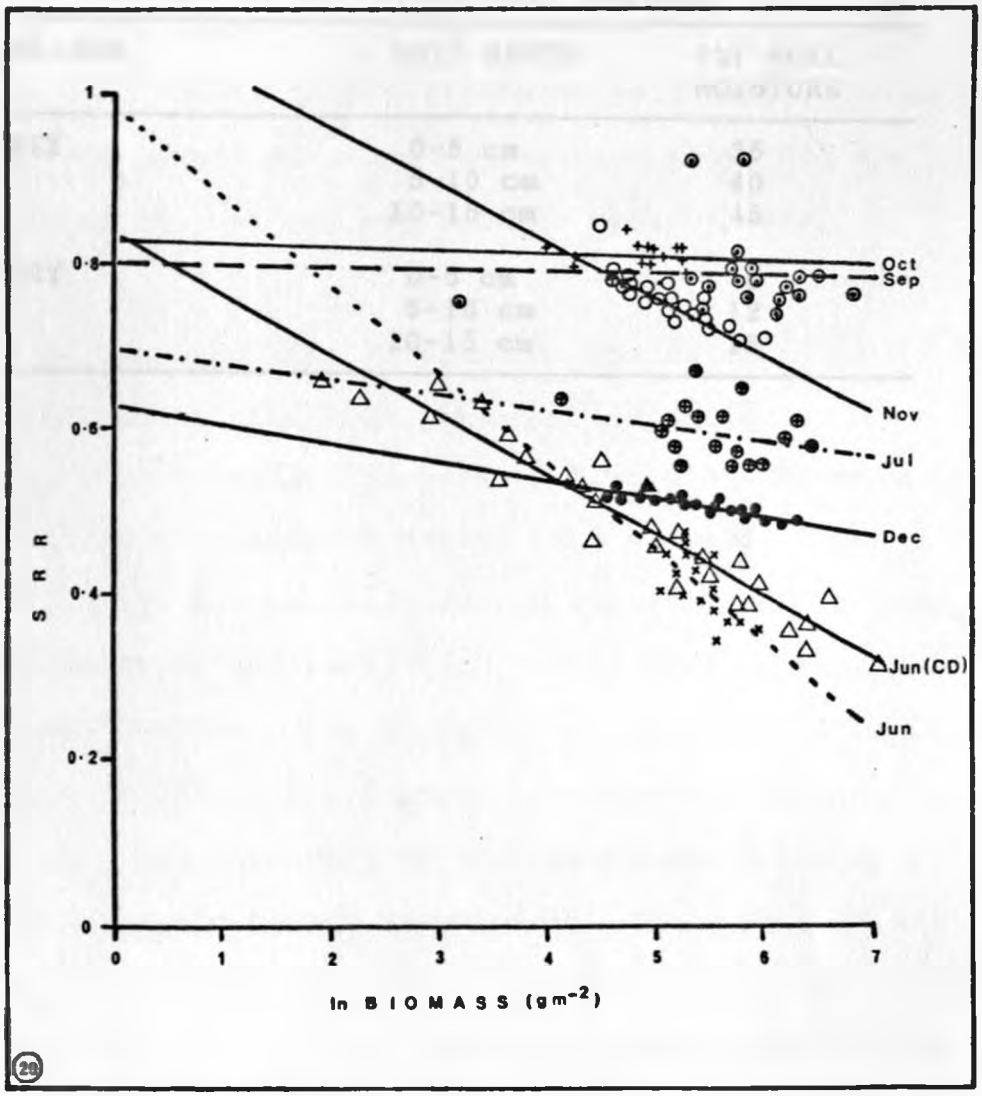

1
0·8
0·6
0·4
0·2
0
S R R
0
1
2
3
4
5
6
7
ln BIOMASS (gm⁻²)
Oct
Sep
Nov
Jul
Dec
Jun(CD)
Jun
29

Table 3. Soil moisture content (%) for different seasons and at different soil depths.

SEASON	SOIL DEPTH	(%) SOIL MOISTURE
WET	0-5 cm	35
	5-10 cm	40
	10-15 cm	45
DRY	0-5 cm	6
	5-10 cm	12
	10-15 cm	15

4.3. SOIL MOISTURE CONTENT

Soil moisture content was high during the wet season and low during the dry season (Table 3). Wet season mean values ranged from 35% (0-5 cm depth) to 46% (10-15 cm depth). However, these values dropped during the dry season to low values which ranged from 6% (0-5 cm soil depth) to 15% (10-15 cm soil depth). On the average, soil moisture content was about 40% and 11% during the wet and dry seasons respectively.

4.4. RELATIONSHIP BETWEEN SPECTRAL REFLECTANCE RATIO (SRR) AND ABOVEGROUND LIVE PLANT BIOMASS

The relationship between live plant biomass and SRR was strongly correlated ($r = -0.959$) on June 4th, 1986 for the calibration experiment (Fig. 20). After about two weeks (June 16th, 1986) during the normal harvest, the correlation was still strong ($r = -0.923$) but different from that of the calibration experiment. However, as the vegetation dried up this relationship became less evident (July, $r = -0.555$; September, $r = -0.112$ and October, $r = -0.004$). During the same period there was a corresponding reduction in the amount of live plant biomass (Appendix 2).

After the onset of rains and initiation of plant growth in November 1986 the relationship between live plant biomass and SRR improved (November, $r = -0.815$ and

December, r = -0.869). It is, therefore, apparent that the relationship between SRR and plant biomass may vary from season to season depending on the amount of infrared and red radiation reflected by the green plant canopy (Fig. 20). As the mean live plant biomass decreased with prevailing dry weather conditions the mean SRR increased (Appendix 2). The trend was reversed after the onset of rains which enhanced plant growth.

4.5. PHOTOSYNTHESIS AND RELATED PROCESSES

4.5.1. FIELD MEASUREMENT OF PHYSIOLOGICAL PROCESSES

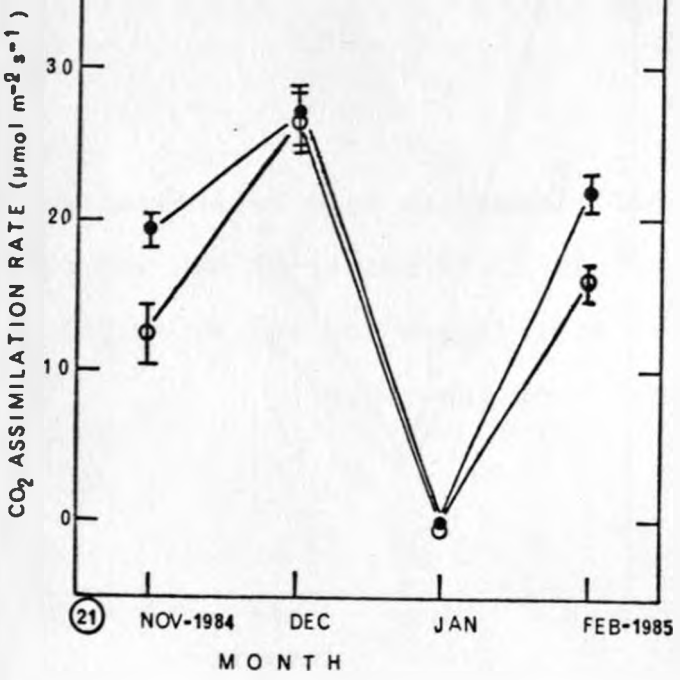
4.5.1.a. Seasonal rates of photosynthesis

Mean rates of CO_2 assimilation between November 1984 and February 1985 ranged from 0.00 to 26.83 µmol m^{-2} s^{-1} for *T. triandra* and 0.00 to 27.06 µmol m^{-2} s^{-1} for *P. mezianum* at 12.00 hours (Fig. 21). The lowest rates, for both key species, were recorded during January 1985 when the vegetation was drying up due to the prevailing dry weather conditions. The highest rates were recorded during December 1984 for both key species.

4.5.1.b. Seasonal rates of transpiration

Mean rates of transpiration ranged from 0.83 to 9.51 mmol m^{-2} s^{-1} for *T. triandra* and 0.93 to 16.20 mmol m^{-2} s^{-1} for *P. mezianum* during the period between November 1984 and February 1985 around 12.00 hours

Fig. 21. Seasonal changes in mean CO_2 assimilation rate (measured at 12.00 hours) of the two key species, *T. triandra* (○) and *P. mezianum* (●) (vertical bars are S.E.).


CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
30
20
10
0
21
NOV-1984
DEC
JAN
FEB-1985
MONTH

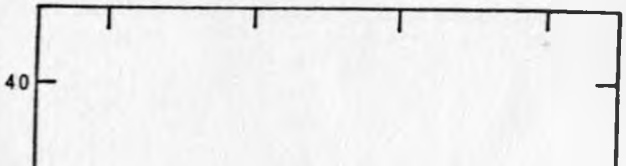

40

Fig. 22. Seasonal changes in mean transpiration rate (measured at 12.00 hours) of the two key species, *T. triandra* (O) and *P. mezianum* (●) (vertical bars are S.E.).

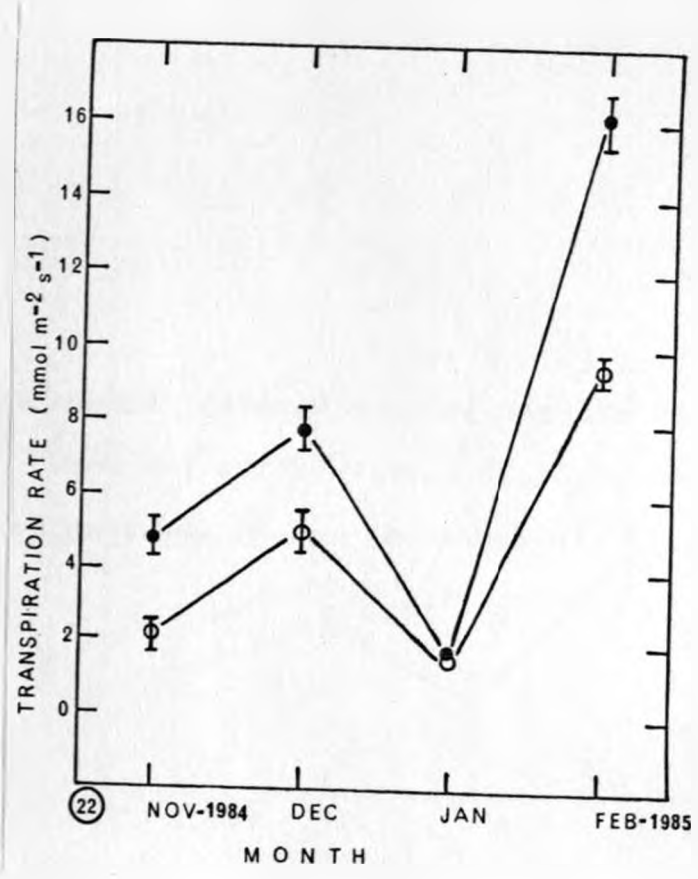
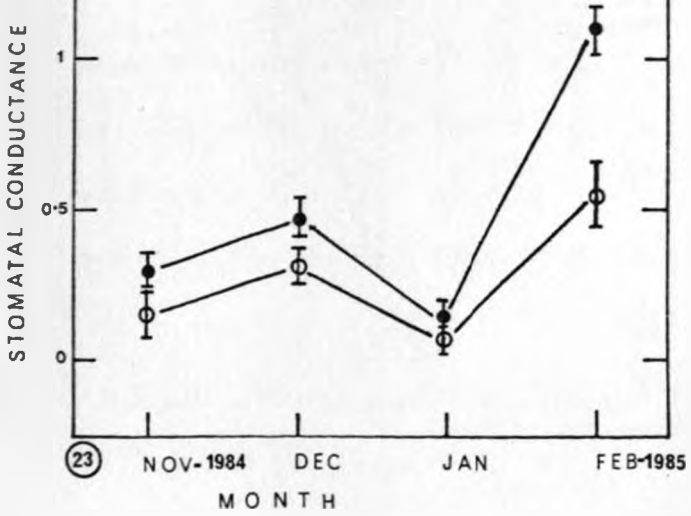

TRANSPIRATION RATE (mmol m-2 s-1)
16
14
12
10
8
6
4
2
0
22
NOV-1984
DEC
JAN
FEB-1985
MONTH

Fig. 23. Seasonal changes in mean stomatal conductance (measured at 12.00 hours) of the two key species, *T. triandra* (o) and *P. mezianum* (•) (vertical bars are S.E.).


STOMATAL CONDUCTANCE
1
0·5
0
23
NOV-1984
DEC
JAN
FEB-1985
MONTH

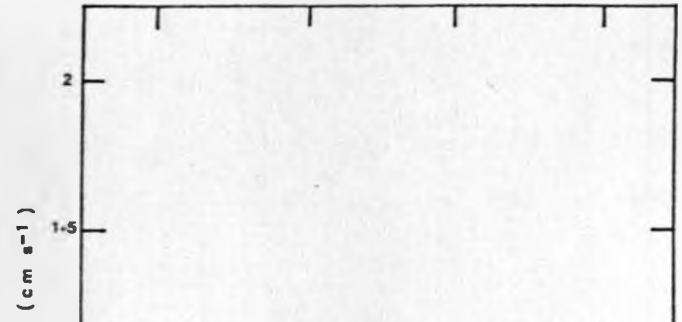

2
1·5
(cm s⁻¹)

Fig. 24. Seasonal changes in mean monthly leaf water potential (measured at 12.00 hours) of *T. triandra* (○) and *P. mezianum* (●); air temperature (◇) and vapour pressure deficit (▲) (vertical bars are S.E.).

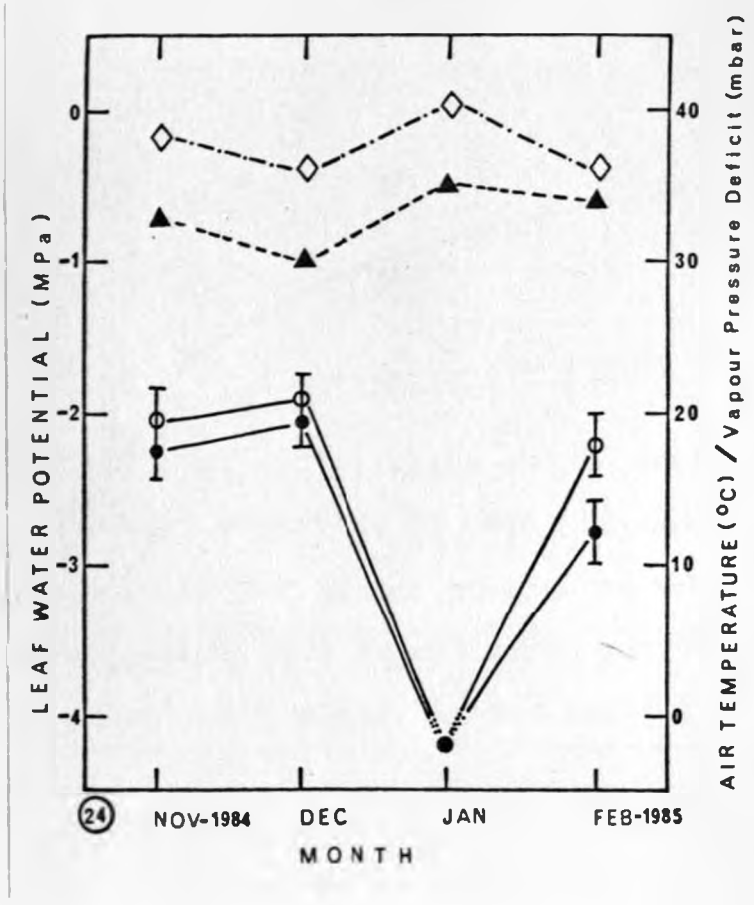

LEAF WATER POTENTIAL (MPa)
0
-1
-2
-3
-4
40
30
20
10
0
AIR TEMPERATURE (°C) / Vapour Pressure Deficit (mbar)
24
NOV-1984
DEC
JAN
FEB-1985
MONTH

Fig. 25. Response of CO_2 assimilation rate to photon flux density (PFD) of different leaves of *T. triandra* at various canopy levels in the plant canopy [top canopy level (+), middle canopy level (●) and bottom canopy level (○)].
Data taken on 6.5.1986

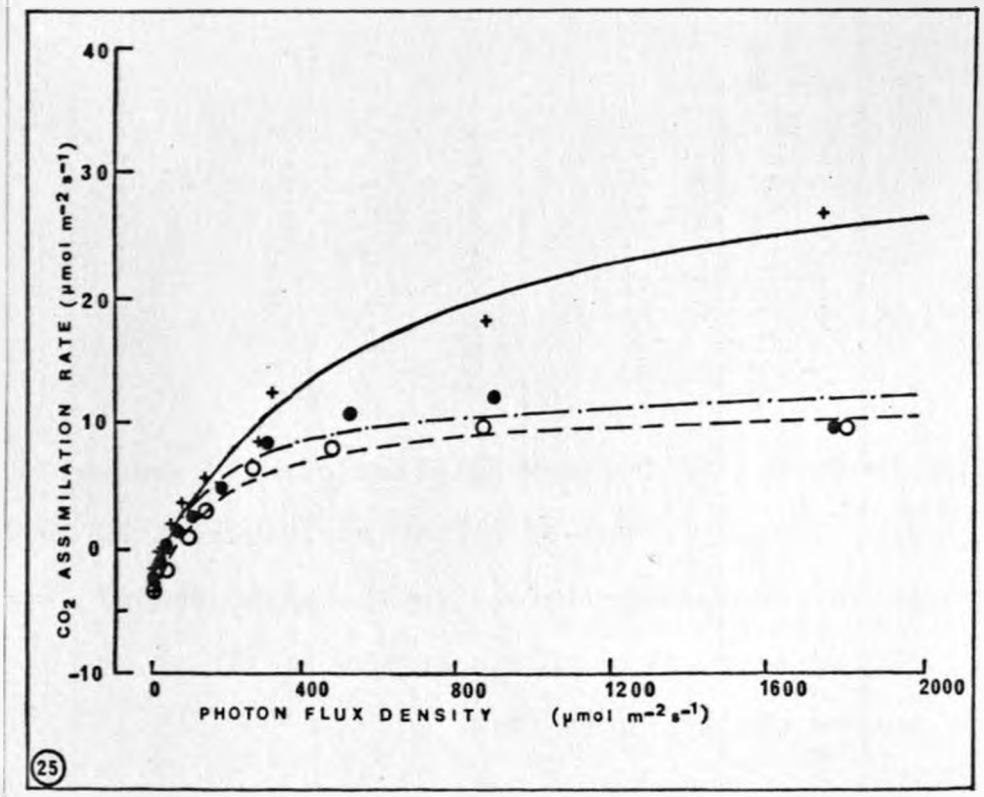

40
30
20
10
0
-10
CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol m^{-2} s^{-1})
25

Fig. 26. Response of CO_2 assimilation rate to photon flux density (PFD) of different leaves of *P. mezianum* at various canopy levels in the plant canopy [top canopy level (+), middle canopy level (●) and bottom canopy level (○)]. Data taken on 6.5.1986

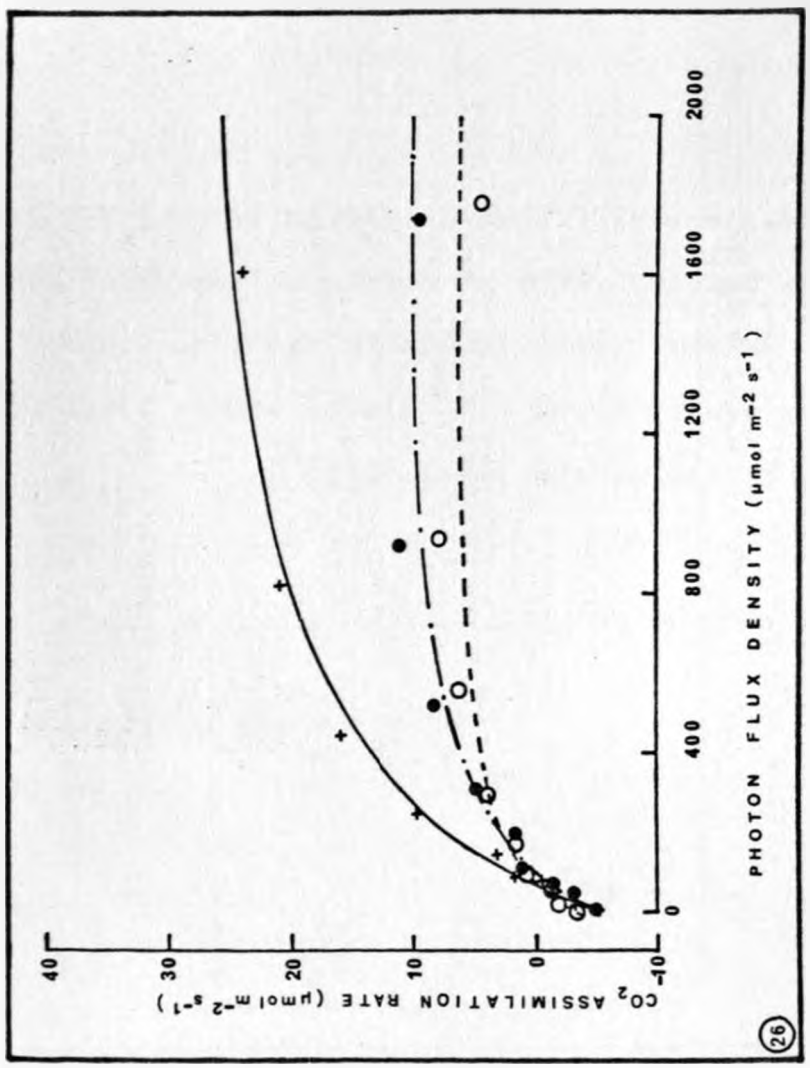
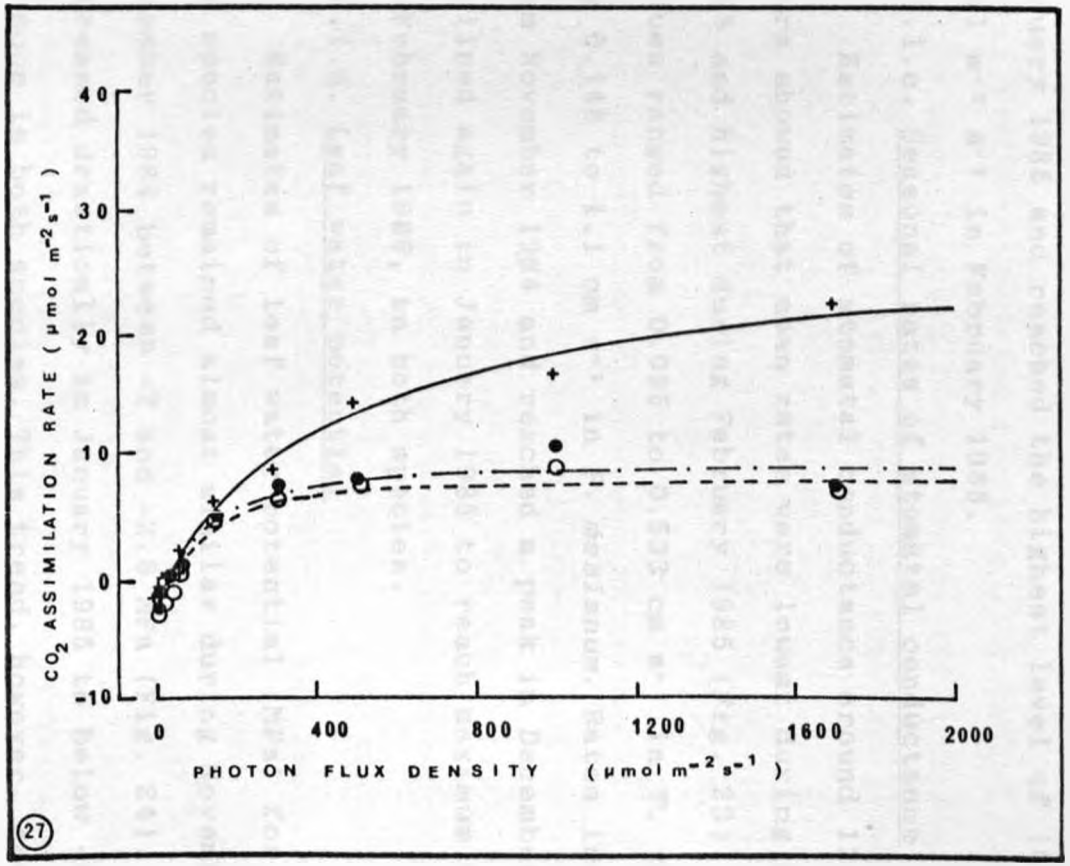

CO2 ASSIMILATION RATE (μmol m-2 s-1)
40
30
20
10
0
-10
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol m-2 s-1)
26

Fig. 27. Response of CO_2 assimilation rate to photon flux density (PFD) of different leaves of *C. caesius* at various canopy levels in the plant canopy [top canopy level (+), middle canopy level (•) and bottom canopy level (o)]. Data taken on 6.5.1986


40
30
20
10
0
-10
CO_2 ASSIMILATION RATE (μmol $m^{-2}s^{-1}$)
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol $m^{-2}s^{-1}$)
27

(Fig. 22). Rates of transpiration were lowest during January 1985 and the highest rates were recorded in February 1985 for both species. Transpiration rates increased from 2.32 mmol m^{-2} s^{-1} in November 1984 reached a peak in December 1984 declined again in January 1985 and reached the highest level of 16.20 mmol m^{-2} s^{-1} in February 1985.

4.5.1.c. Seasonal rates of stomatal conductance

Estimates of stomatal conductance around 12.00 hours showed that mean rates were lowest during January 1985 and highest during February 1985 (Fig. 23). Mean values ranged from 0.095 to 0.533 cm s^{-1} in *T. triandra* and 0.148 to 1.1 cm s^{-1} in *P. mezianum*. Rates increased from November 1984 and reached a peak in December 1984 declined again in January 1985 to reach maximum rates in February 1985, in both species.

4.5.1.d. Leaf water potential

Estimates of leaf water potential (MPa) for both key species remained almost similar during November and December 1984 between -2 and -2.5 MPa (Fig. 24). Values decreased drastically in January 1985 to below -4.0 MPa at noon in both species. This trend, however, changed in February 1985 when values increased to -2.2 and -2.8 MPa in *T. triandra* and *P. mezianum*, respectively.

4.5.1.e. Air temperature

Air temperature at around noon (12.00 hours) did not show large variations between months (Fig. 24). Air

temperatures ranged from 30 to 35°C. During December 1984 air temperatures were the lowest at about 30°C at 12.00 hours. Temperatures were highest (35°C) during January 1985 when the weather was dry.

4.5.1.f. Vapour Pressure Deficit (VPD)

Vapour Pressure Deficit at midday over the period between November 1984 and February 1985 ranged from about 30 mbar to about 40 mbar (Fig. 24). VPD was highest in January 1985 at about 40 mbar and lowest in December 1984 at about 30 mbar.

4.5.1.g. Light response curves of leaves at different canopy levels

CO_2 assimilation-light response curves of individual leaves of three grass species (*T. triandra*, *P. mezianum* and *C. caesius*) at different canopy levels had the typical hyperbola shape. Leaves in the top canopy layer exhibited higher rates of CO_2 assimilation at higher photon flux density (PFD) in the three grass species (Figs. 25, 26, 27).

Top leaves of *T. triandra* reached a maximum CO_2 assimilation rate of 26.83 μmol m^{-2} s^{-1} which declined with reduction in PFD (Fig. 25). Top leaves did not light saturate even at PFD rates near 2000 μmol [PAR] m^{-2} s^{-1}. Middle canopy layer leaves possessed lower maximum photosynthetic rates even at higher PFD rates and only attained a maximum photosynthetic rate of

about 12 μmol m^{-2} s^{-1} at PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1}, nearly half of that of top canopy layer leaves. Middle canopy leaves light saturated at PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1}. Bottom canopy leaves of *T. triandra* had the lowest maximum photosynthetic rates overall with a maximum of about 9.6 μmol m^{-2} s^{-1} at PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1}. Bottom canopy layer leaves light saturated at lower PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1} similar to middle layer leaves. Results of Fig. 25 show that bottom and middle canopy layer leaves showed a decline in photosynthetic rates when PFD rates were beyond about 1000 μmol [PAR] m^{-2} s^{-1}.

Photosynthetic rate trend in different leaves of *P. mezianum* at different canopy levels behaved in a similar way to those of *T. triandra* (Fig. 26). Top canopy layer leaves showed no evidence of light saturation while middle and bottom level leaves light saturated at PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1}. Maximum photosynthetic rates of about 24, 11, and 8 μmol m^{-2} s^{-1} were recorded for top, middle and bottom canopy layer leaves, respectively. Maximum photosynthetic rates of top canopy layer leaves were nearly as twice as those of middle canopy layer leaves.

Leaves of *C. caesius* did not behave differently in terms of CO_2 assimilation rates at different

2000
1600
1200
800
400
0
PHOTON FLUX DENSITY (μmol m^{-2} s^{-1})
8-00
10-00
TIME (Hrs)

12·00
14·00
16·00
0
8
16
24
32
40
CO_2 ASSIMILATION RATE ($\mu mol\ m^{-2}\ s^{-1}$)

Fig. 28. Diurnal course in PFD [PAR] (o) and CO_2 assimilation rate (•) in leaves of *T. triandra*.

Data taken on 12.2.1985

2000
1600
1200
800
400
0
PHOTON FLUX DENSITY (μmol m⁻² s⁻¹)
8·00
10·00
12·00
14·00
TIME (Hrs)

40
32
24
16
8
0
1600
CO_2 ASSIMILATION RATE ($\mu mol\ m^{-2}\ s^{-1}$)

Fig. 29. Diurnal course in PFD [PAR] (o) and CO_2 assimilation rate (•) in leaves of *P. mezianum*
Data taken on 12.2.1985

2000
1600
1200
800
400
0
PHOTON FLUX DENSITY (μmol m⁻² s⁻¹)
8·00
10·00
12·00
TIME (Hrs)

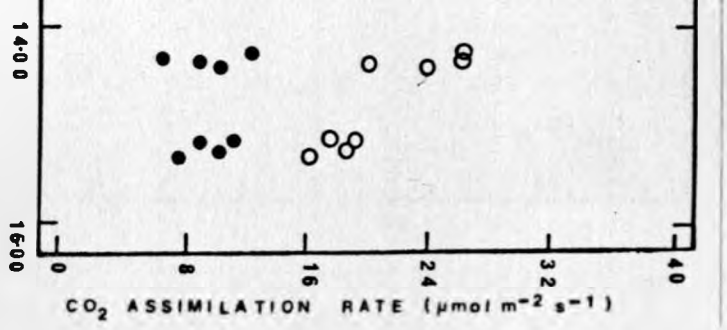

14·00
16·00
0
8
16
24
32
40
CO2 ASSIMILATION RATE (μmol m-2 s-1)

Fig. 30. Diurnal course in mean CO_2 assimilation rate of leaves of *T. triandra* (o) and *P. mezianum* (•) (vertical bars are S.E.). Data taken on 12.2.1985

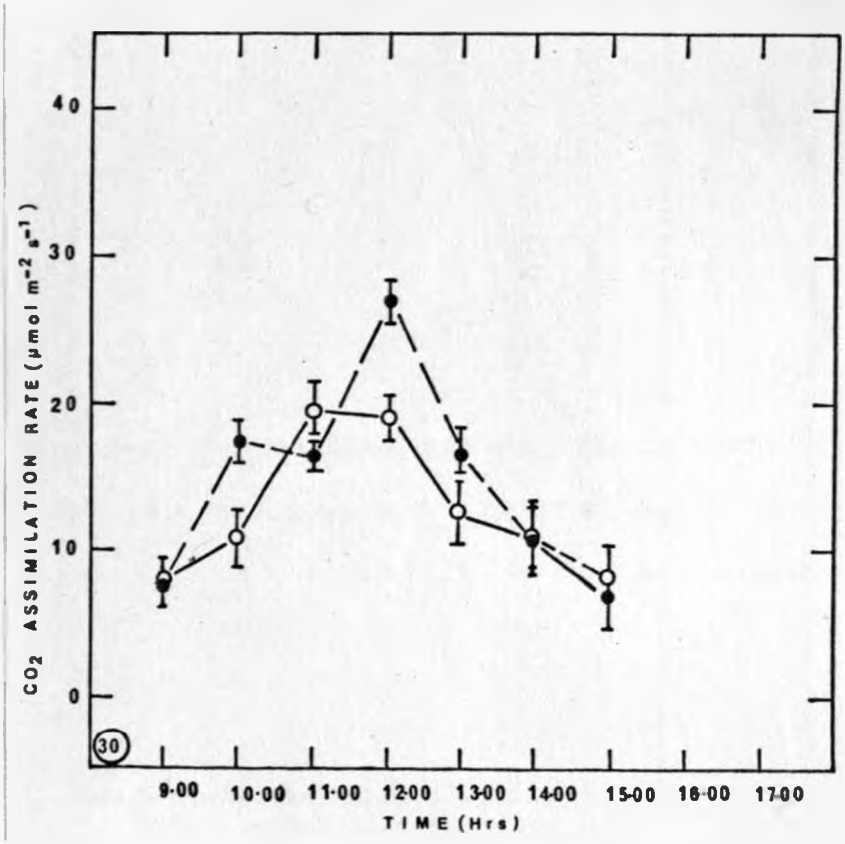

40
30
20
10
0
CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
30
9·00
10·00
11·00
12·00
13·00
14·00
15·00
16·00
17·00
TIME (Hrs)

Fig. 31. Diurnal course in air temperature (o), leaf water potential (Δ), transpiration (▲) and leaf temperature (●) of *P. mezianum* (vertical bars are S.E.). Data taken on 12.2.1985

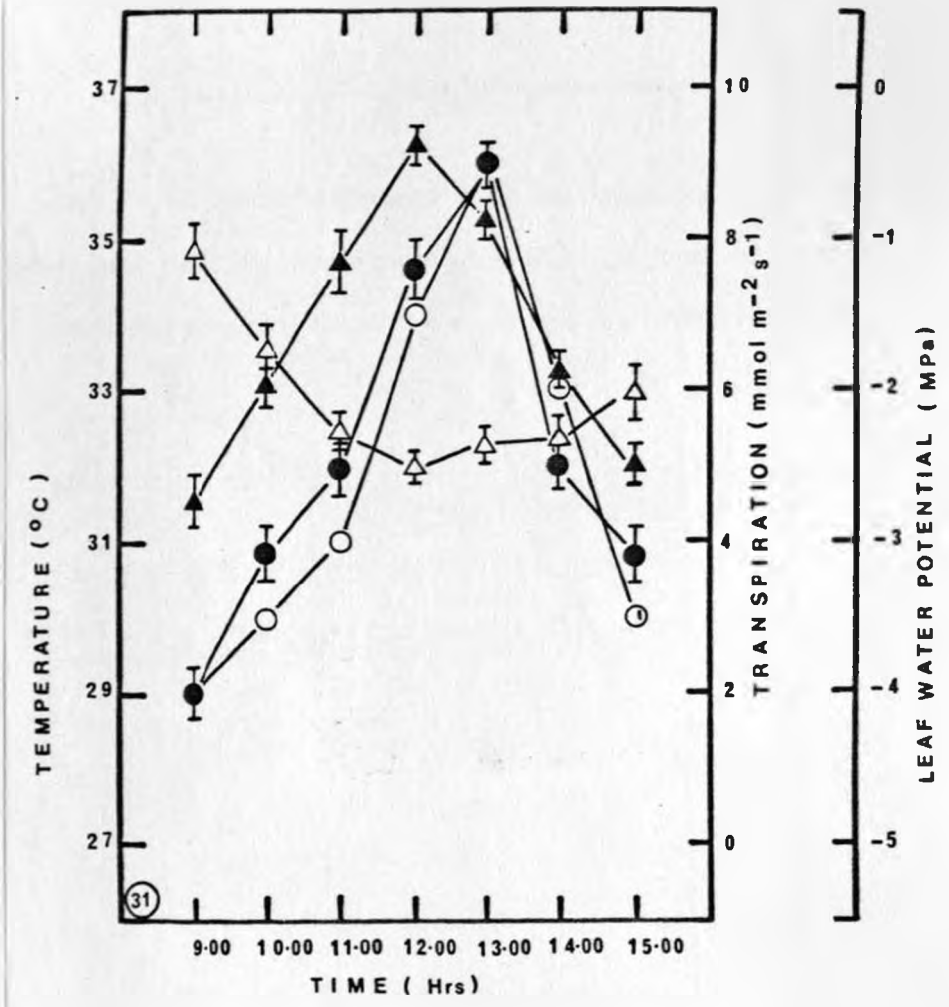

TEMPERATURE (°C)
37
35
33
31
29
27
TRANSPIRATION (mmol m⁻² s⁻¹)
10
8
6
4
2
0
LEAF WATER POTENTIAL (MPa)
0
-1
-2
-3
-4
-5
(31)
9·00
10·00
11·00
12·00
13·00
14·00
15·00
TIME (Hrs)

Fig. 32. Diurnal course in air temperature (O), leaf water potential (Δ), transpiration (▲) and leaf temperature (●) of *T. triandra* (vertical bars are S.E.). Data taken on 12.2.1985

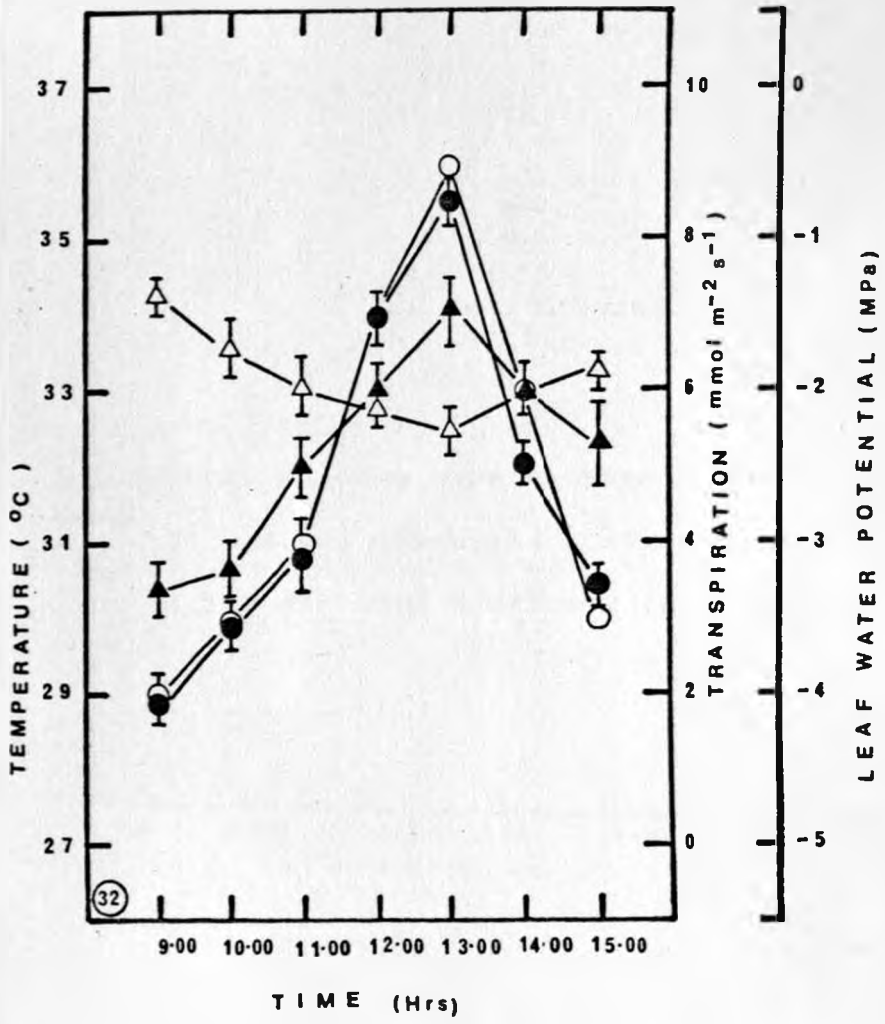

37
35
33
31
29
27
TEMPERATURE (°C)
10
8
6
4
2
0
TRANSPIRATION (mmol m⁻² s⁻¹)
0
-1
-2
-3
-4
-5
LEAF WATER POTENTIAL (MPa)
32
9·00
10·00
11·00
12·00
13·00
14·00
15·00
TIME (Hrs)

Fig. 33. Diurnal course in mean stomatal conductance of *T. triandra* (●) and *P. mezianum* (○) (vertical bars are S.E.). Data taken on 12.2.1985

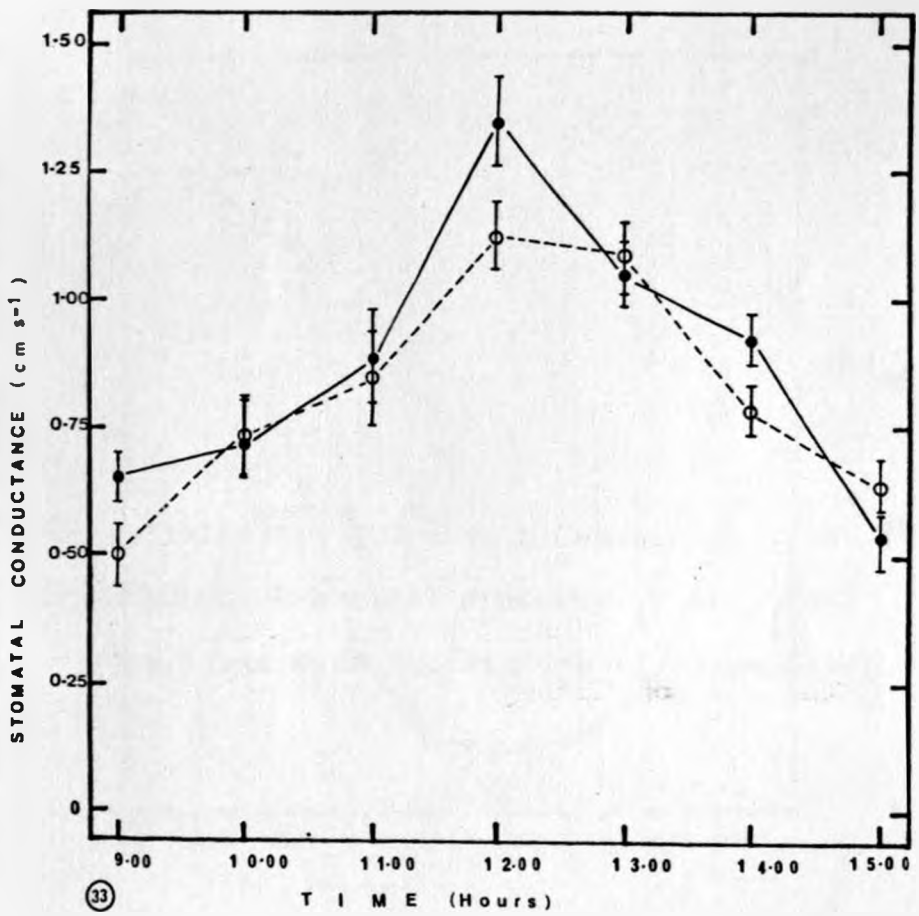

1·50
1·25
1·00
0·75
0·50
0·25
0
STOMATAL CONDUCTANCE (cm s⁻¹)
9·00
10·00
11·00
12·00
13·00
14·00
15·00
TIME (Hours)
33

Fig. 34. Diurnal course in mean CO_2 assimilation rate of leaves of *T. triandra* (•) and *P. mezianum* (o) in January 1985 (vertical bars are S.E.).

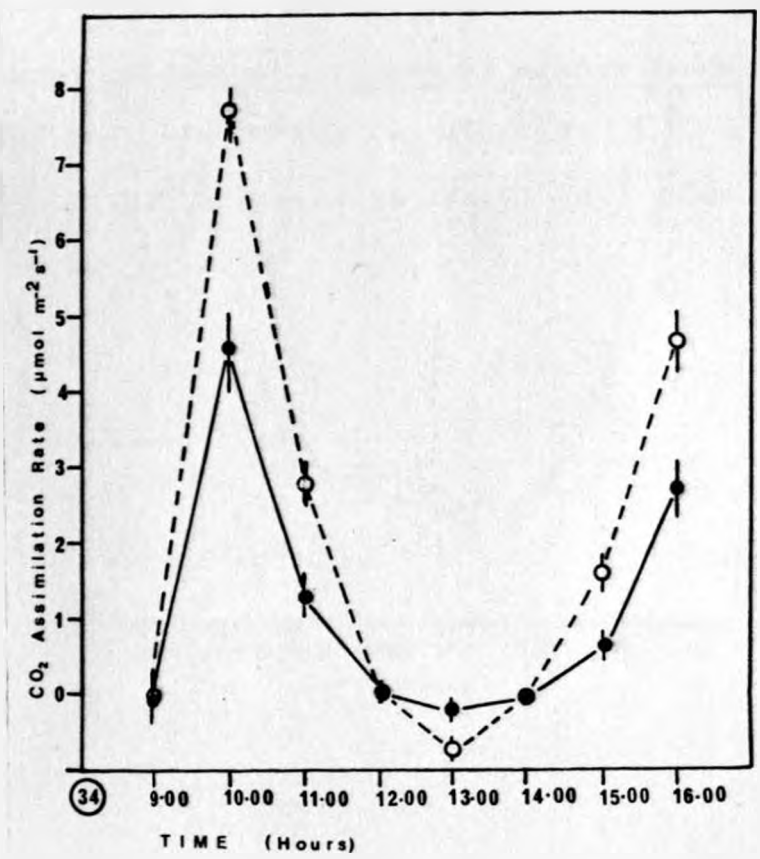

8
7
6
5
4
3
2
1
0
CO_2 Assimilation Rate (μmol m^{-2} s^{-1})
(34)
9·00
10·00
11·00
12·00
13·00
14·00
15·00
16·00
TIME (Hours)

Fig. 35. Diurnal course in mean transpiration rate of leaves of *T. triandra* (●) and *P. mezianum* (○) in January 1985 (vertical bars are S.E.).

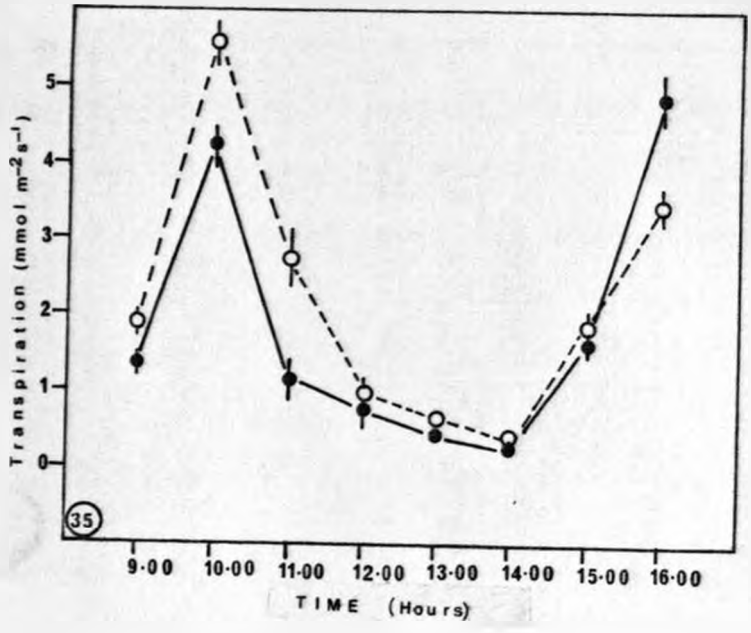
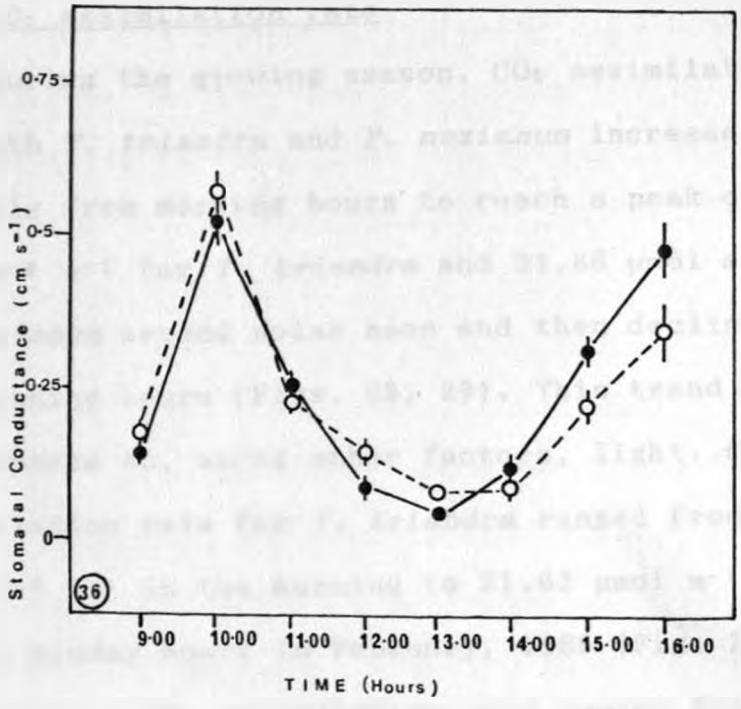

Transpiration (mmol m⁻² s⁻¹)
0
1
2
3
4
5
35
9·00
10·00
11·00
12·00
13·00
14·00
15·00
16·00
TIME (Hours)

Fig. 36. Diurnal course in mean stomatal conductance of leaves of *T. triandra* (●) and *P. mezianum* (○) in January 1985 (vertical bars are S.E.).


0·75
0·5
0·25
0
Stomatal Conductance (cm s⁻¹)
36
9·00
10·00
11·00
12·00
13·00
14·00
15·00
16·00
TIME (Hours)

canopy levels from those of *T. triandra* and *P. mezianum* (Fig. 27). Maximum CO_2 assimmilation rates of about 22, 10 and 9 μmol m^{-2} s^{-1} for top, middle and bottom canopy layer leaves were recorded, respectively. Middle and bottom canopy layer leaves light saturated at PFD rates of about 1000 μmol [PAR] m^{-2} s^{-1}, while top canopy layer leaves did not light saturate.

4.5.1.h. Diurnal course in some physiological variables

(i) CO_2 assimilation rate

During the growing season, CO_2 assimilation rates for both *T. triandra* and *P. mezianum* increased steadily from morning hours to reach a peak of 21.63 μmol m^{-2} s^{-1} for *T. triandra* and 31.86 μmol m^{-2} s^{-1} for *P. mezianum* around solar noon and then declined towards the evening hours (Figs. 28, 29). This trend was clearly in response to, among other factors, light. CO_2 assimilation rate for *T. triandra* ranged from 2.77 μmol m^{-2} s^{-1} in the morning to 21.63 μmol m^{-2} s^{-1} during midday hours in February, 1985 (Fig. 28). In *P. mezianum*, CO_2 assimilation rate ranged from 6.42 to 31.86 μmol m^{-2} s^{-1} during morning and midday, respectively. Mean values for *P. mezianum* were highest at around 12.00 hours at 27 μmol m^{-2} s^{-1} which dropped to a low value of 7 μmol m^{-2} s^{-1} around 15.00 hours (Fig. 30). *T. triandra* had a lower maximum value of about 20 μmol m^{-2} s^{-1} which was attained earlier

in the day (11.00 hours) than that of *P. mezianum*.

During the start of the dry season in January 1985 both key species exhibited a two-peaked diurnal course in CO_2 assimilation rates (Fig. 34). For both species, the first peak occured during the morning hours around 10.00 hours. During this peak *T. triandra* had photosynthetic rate of 4.52 μmol m^{-2} s^{-1} while *P. mezianum* had 7.83 μmol m^{-2} s^{-1}. There was a midday total cessation in photosynthetic process in both species due to stomatal closure. During the evening hours (around 16.00 hours) some photosynthetic activity was recorded.

(ii) Transpiration rate

Mean values of transpiration rate increased steadily to reach a maximum rate at about 13.00 hours in both *P. mezianum* and *T. triandra* during the growing season (Figs. 31, 32). Thereafter, during the remainder of the day, transpiration decreased in both species. At most times *T. triandra* transpired at higher rates than *P. mezianum* and the maximum mean values were 9.30 mmol m^{-2} s^{-1} and 7.11 mmol m^{-2} s^{-1}, respectively, for the two species. At the start of the dry season in January 1985, both key species exhibited a two-peaked diurnal course similar to that of CO_2 assimilation (Fig. 35). Plants transpired more during the morning and evening hours with little transpiration recorded during

midday hours due to stomatal closure. *T. triandra* exhibited transpiration rate of about 4.23 mmol m^{-2} s^{-1} and *P. mezianum* had about 5.55 mmol m^{-1} s^{-1} during the morning hours. These values dropped drastically at midday to about 0.35 mmol m^{-2} s^{-1} and 0.38 mmol m^{-2} s^{-1} for *T. triandra* and *P. mezianum* respectively. Rates of transpiration regained during the evening hours after stomatal opening in both species.

(iii) Stomatal conductance

During the growing season, mean values of stomatal conductance in both species (Fig. 33) increased with the time course. However, after 12.00 hours stomatal conductance decreased towards the evening hours. In *T. triandra*, stomatal conductance increased from 0.665 cm s^{-1} to reach a maximum of 1.355 cm s^{-1} at 9.00 and 12.00 hours, respectively. In *P. mezianum* it increased from 0.503 cm s^{-1} at 9.00 hours to 1.115 cm s^{-1} at 12.00 hours. On the average *T. triandra* possessed slightly higher values than *P. mezianum*. During January 1985, the two grass species exhibited a two-peaked diurnal regime of stomatal opening (Fig. 36). Stomata of both grass species exhibited maximum conductance during the morning hours, around 10.00 hours. There was a severe stomatal closure during the midday in both grass species. However, stomatal opening was recorded in the evening hours. *T. triandra* recorded values of 0.518,

0.050 and 0.463 cm s^{-1} around 10.00, 13.00 and 16.00 hours, respectively. *P. mezianum* recorded values of 0.570, 0.073 and 0.413 cm s^{-1} at around 10.00, 13.00 and 16.00 hours, respectively.

(iv) Leaf water potential

With the course of the day, mean leaf water potential dropped slowly from a value of -1.35 MPa at 9.00 hours to a low value of -2.23 MPa at 13.00 hours in *T. triandra* while in *P. mezianum* it dropped from -1.05 at 9.00 hours to -2.5 MPa at 12.00 hours (Figs. 31, 32). Generally, *P. mezianum* was more water stressed than *T. triandra* during the course of the day. However, both species recorded lowest water potentials around midday. Leaf water potential began to increase again towards the evening hours to morning levels.

(v) Air and leaf temperatures

Mean air temperatures climbed sharply from around 29°C at 9.00 hours to reach a peak of about 36°C at 13.00 hours (Fig. 31). In comparison, mean leaf temperatures for *T. triandra* climbed with the air temperature but remained slightly lower and ranged from 29°C at 9.00 hours to a maximum of about 35°C at 13.00 hours. Leaf temperatures for *P. mezianum* (Fig. 32) remained only slightly higher than those of *T. triandra*. In both species, leaf temperature declined with the course of air temperature.

4.5.2. STOMATAL COUNT, TOTAL CHLOROPHYLL CONTENT AND PHOTOSYNTHETIC RATES OF DIFFERENT PLANT ORGANS

4.5.2.a. Stomatal density

The distribution of stomata in different plant parts was variable (Table 4). Leaf blades of all species possessed stomata. All species contained appreciable numbers of stomata in their stems and sheaths.

4.5.2.b. Total chlorophyll in tissue

In all cases the amount of chlorophyll *a* was higher than that of chlorophyll *b* in different plant organs (Table 5). Hence the ratio of chlorophyll *a:b* was in excess of 3:1 in most cases. Leaf blades possessed the most chlorophyll. There was no noticeable chlorophyll in the stems of *T. triandra* and *C. caesius*.

4.5.2.c. CO_2 Asssimilation Rate

(i). Leaf blade

Of all the plants organs examined, leaf blades exhibited the highest levels of CO_2 assimilation rates (Table 6). *T. triandra* had the highest rate (28.68 μmol m^{-2} s^{-1}) followed by *P. mezianum* (19.26 μmol m^{-2} s^{-1}), *C. caesius* (18.27 μmol m^{-2} s^{-1}) and lastly *R. repens* (14.84 μmol m^{-2} s^{-1}).

Table 4. Number of stomata cm^{-2} in different plant organs of some grass species at the study site (±S.E., n=8)

SPECIES	LEAF BLADE		SHEATH	STEM	INFLORE-SCENCE
	ABAXIAL	ADAXIAL			
T. triandra	29866 ±433	7466 ±552	6929 ±216	836 ±216	10513 ±443
P. mezianum	9677 ±584	9796 ±564	8492 ±335	17800 ±786	*
C. caesius	21742 ±761	2150 ±239	14574 ±951	2031 ±335	11923 ±1544
R. repens	12185 ±782	16844 ±476	12066 ±569	5801 ±823	*

* - Structures too minute for analysis

Table 5. Amount of chlorophyll and ratio of chlorophyll a:b in different species and plant organs (mg g^{-1} fresh weight; ± S.E.; n = 4).

SPECIES	PLANT ORGAN	CHLOROPHYLL *a*	CHLOROPHYLL *b*	TOTAL Chl. *a+b*	RATIO *a:b*
T. triandra	Leaf blade	2.00	0.52	2.52	3.85
	Sheath	0.67±0.01	0.13±0.01	0.80±0.02	5.15±0.18
	Inflorescence	0.52±0.01	0.16±0.01	0.68±0.02	3.25±0.17
P. mezianum	Leaf blade	1.79	0.31±0.01	2.10±0.01	5.77±0.11
	Sheath	0.57±0.01	0.17±0.01	0.74±0.01	3.35±0.07
	Stem	0.36±0.01	0.10	0.46±0.01	3.59±0.07
C. caesius	Leaf blade	1.55	0.42	1.97±0.01	3.69
	Sheath	0.37±0.02	0.15±0.02	0.52±0.02	2.47±0.16
	Inflorescence	0.49±0.01	0.13±0.01	0.62±0.01	3.77±0.09
R. repens	Leaf blade	1.63±0.01	0.32±0.01	1.95±0.03	5.09±0.17
	Sheath	0.53	0.16±0.01	0.69±0.01	3.31±0.20
	Stem	0.14	0.05±0.01	0.19±0.01	2.80±0.17

Table 6. Mean Photosynthetic rate* (μmol m^{-2} s^{-1}) for different plant parts of some grass species at the study site ($\bar{X}$ ± S.E.).

SPECIES	LEAF BLADE	SHEATH	STEM	FLAG LEAF	INFLORESCENCE
T. triandra	28.68 ±1.14	10.41 ±1.47	-3.20 ±0.63	8.85 ±0.37	8.23 ±1.54
P. mezianum	19.77 ±0.37	13.54	4.99 ±0.98	10.93 ±2.57	-4.68 ±0.55
C. caesius	18.57 ±0.12	6.25 ±1.48	-2.60 ±0.37	5.21 ±2.21	0.38 ±0.10
R. repens	14.84 ±2.76	7.29 ±0.73	9.23 ±1.33	2.08	-7.14 ±0.84

* - PFD = 1800 μmol m^{-2} s^{-1}
T = 30°C
n = 4

(ii). Sheath

Sheaths of *P. mezianum* exhibited the highest rate (13.54 μmol m^{-2} s^{-1}) among the four grass species (Table 6). *T. triandra* ranked second (10.41 μmol m^{-2} s^{-1}) followed by *R. repens* (7.29 μmol m^{-2} s^{-1}) and lastly *C. caesius* (6.25 μmol m^{-2} s^{-1}).

(iii). Stem

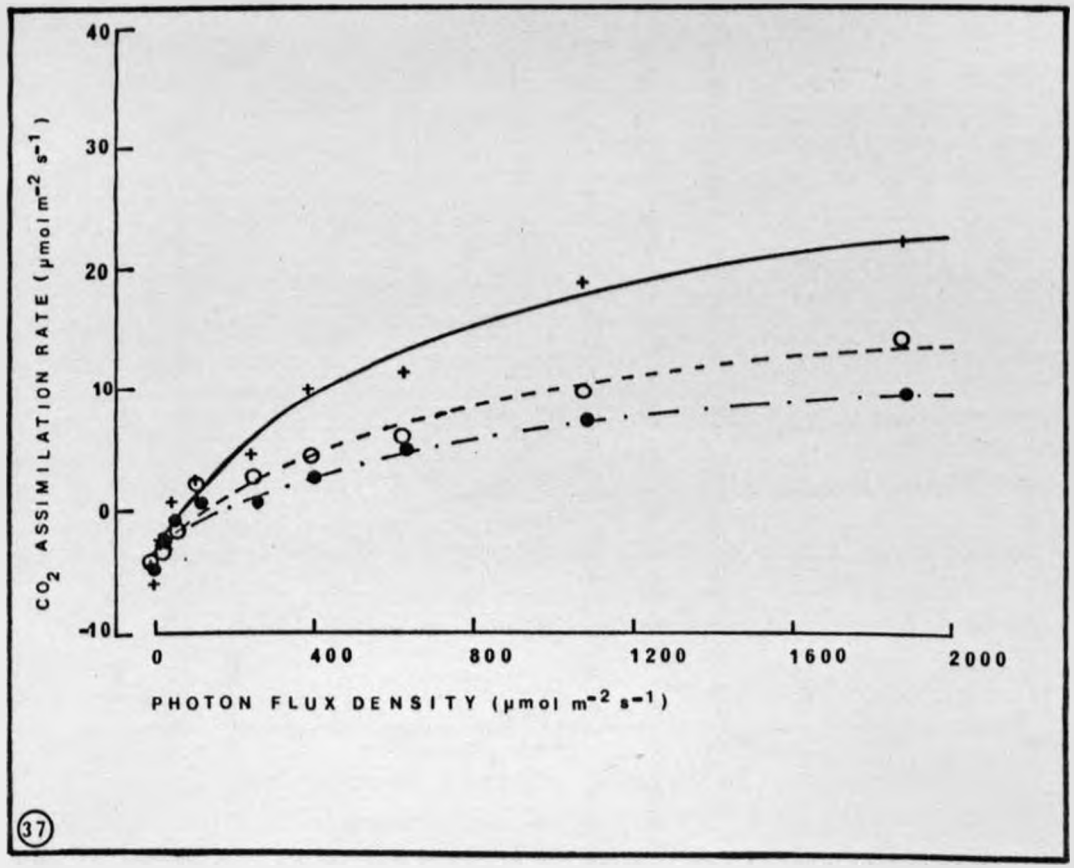
Only stems of *P. mezianum* and *R. repens* exhibited some photosynthesis, with 4.99 and 9.23 μmol m^{-2} s^{-1}, respectively (Table 6). Stems of *T. triandra* and *C. caesius* had only respiratory losses of 3.20 and 2.60 μmol m^{-2} s^{-1}, respectively.

(iv). Flag leaf blade

Flag leaf blade of *P. mezianum* exhibited the highest rate (10.93 μmol m^{-2} s^{-1}) among the four grass species (Table 6). This rate was nearly 50% of that exhibited by leaf blade of the same species. Flag leaf blade of *T. triandra* had 8.95; *C. caesius*, 5.21; and *R. repens*, 2.08 μmol m^{-2} s^{-1}. Overall, flag leaf blades were third to leaf blades and sheaths in terms of CO_2 assimilation.

(v). Inflorescence

Inflorescences of *T. triandra* and *C. caesius* exhibited some CO_2 assimilation rates, 8.23 and 0.38 μmol m^{-2} s^{-1}, respectively (Table 6). Respiratory losses were recorded for *P. mezianum* (4.68 μmol m^{-2} s^{-1}) and *R. repens* (7.14 μmol m^{-2} s^{-1}).


40
30
20
10
0
-10
CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol m^{-2} s^{-1})
37

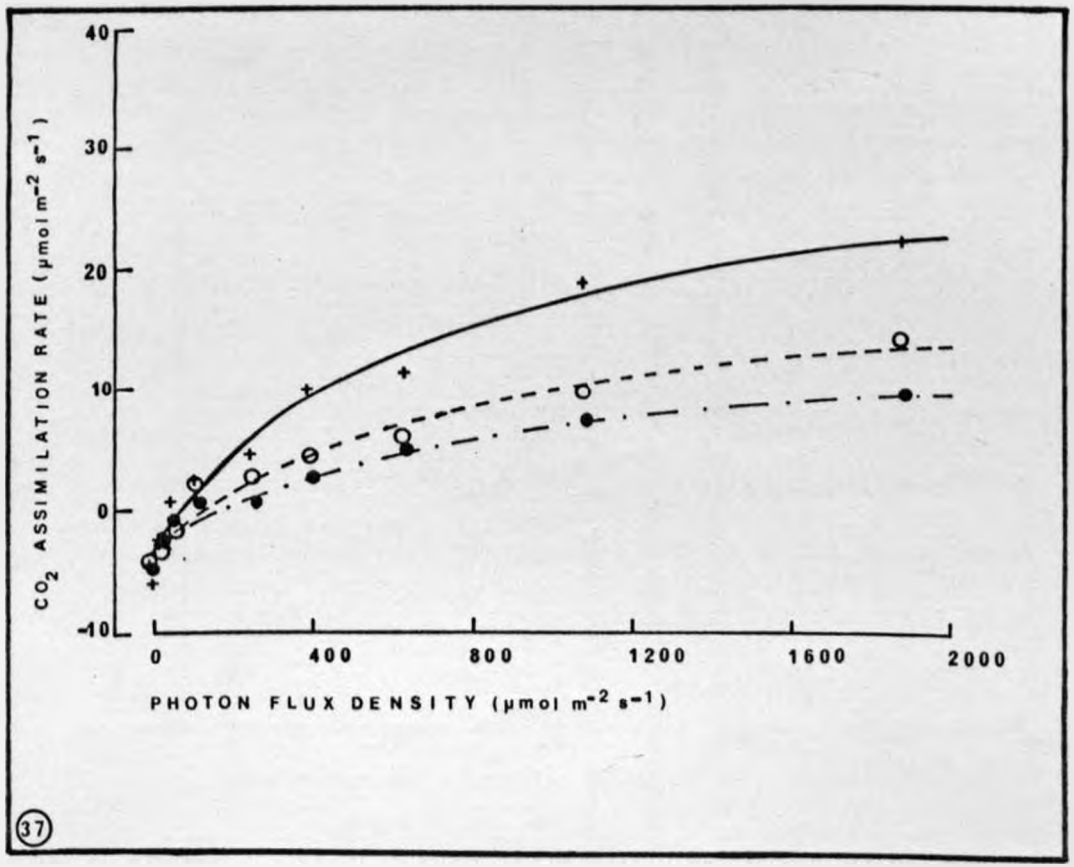
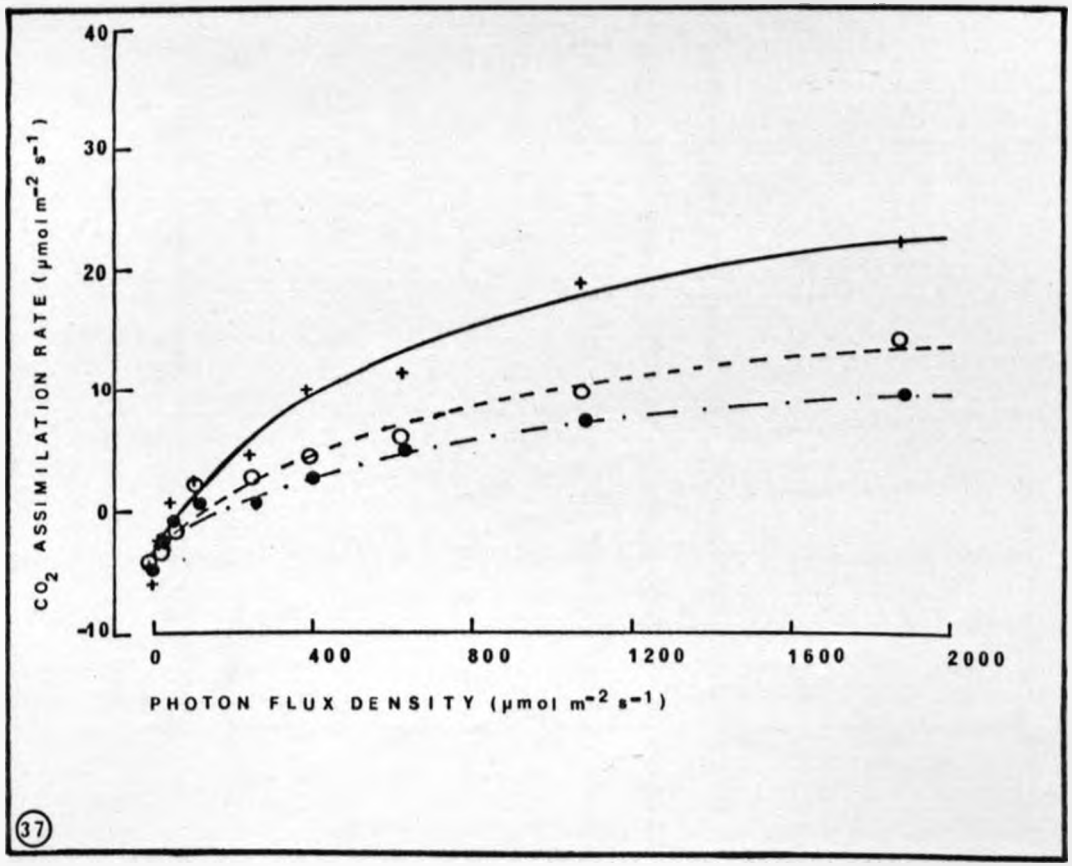
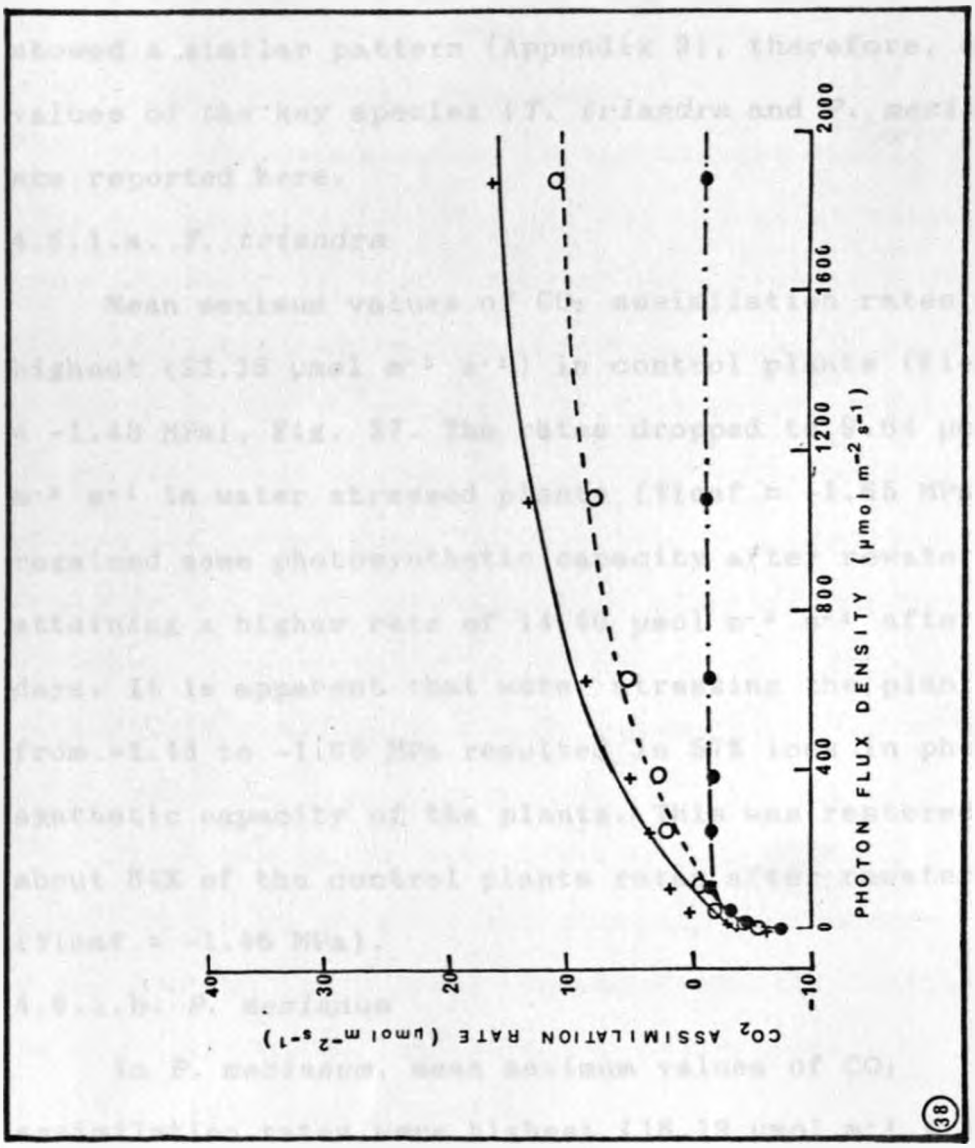

40
30
20
10
0
-10
CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol m^{-2} s^{-1})
37

Fig. 37. Response curves of CO_2 assimilation rate of leaves of *T. triandra* to PFD under (+) control conditions (Ψleaf = -1.48 MPa), (●) water stress (Ψleaf = -1.65 MPa) and (o) rewatered conditions (Ψleaf = -1.46 MPa).


40
30
20
10
0
-10
CO_2 ASSIMILATION RATE (μmol m^{-2} s^{-1})
0
400
800
1200
1600
2000
PHOTON FLUX DENSITY (μmol m^{-2} s^{-1})

(37)

Fig.38. Responses curves of CO_2 assimilation rate of leaves of *P. mezianum* to PFD under (+) control conditions (Ψleaf = -1.38 MPa), (●) water stress (Ψleaf = <-4.0 MPa) and (○) rewatered conditions (Ψleaf = -3.24 MPa).


CO2 ASSIMILATION RATE (μmol m-2 s-1)
40
30
20
10
0
-10
PHOTON FLUX DENSITY (μmol m-2 s-1)
0
400
800
1200
1600
2000
38

4.6. WATER STRESS EFFECTS ON SOME PLANT PHYSIOLOGICAL PROCESSES

4.6.1. CO_2 Assimilation Rate

Trend in photosynthetic rates in all grasses showed a similar pattern (Appendix 3), therefore, only values of the key species (*T. triandra* and *P. mezianum*) are reported here.

4.6.1.a. *T. triandra*

Mean maximum values of CO_2 assimilation rates were highest (22.35 µmol m^{-2} s^{-1}) in control plants (Ψleaf = -1.48 MPa), Fig. 37. The rates dropped to 9.64 µmol m^{-2} s^{-1} in water stressed plants (Ψleaf = -1.65 MPa) but regained some photosynthetic capacity after rewatering by attaining a higher rate of 14.40 µmol m^{-2} s^{-1} after 5 days. It is apparent that water stressing the plants from -1.48 to -1.65 MPa resulted in 57% loss in photosynthetic capacity of the plants. This was restored to about 64% of the control plants rates after rewatering (Ψleaf = -1.46 MPa).

4.6.1.b. *P. mezianum*

In *P. mezianum*, mean maximum values of CO_2 assimilation rates were highest (16.19 µmol m^{-2} s^{-1}) in control plants, when leaf water potential was -1.38 MPa (Fig. 38). Water stressed plants (Ψleaf = <-4.00 MPa) exhibited negative values of CO_2 assimilation, showing

a complete loss of their photosynthetic capacity. However, plants regained their photosynthetic capacity after rewatering (Ψleaf = -3.24 MPa) and attained mean maximum rates of 10.99 μmol m^{-2} s^{-1}. This was about 68% of the control plants rates.

4.6.2. Leaf Stomatal Conductance

Watered plants exhibited the highest values of both CO_2 assimilation rate and leaf stomatal conductance (Appendix 3). Leaf stomatal conductance in the control plants ranged from 0.540 cm s^{-1} in *R. repens* to 0.895 cm s^{-1} in *T. triandra*. Leaf stomatal conductance decreased with a corresponding increase in plant water stress and ranged from 0.160 cm s^{-1} in *D. aegyptium* to 0.420 cm s^{-1} in *P. mezianum*. Leaf stomatal conductance increased substantially in all rewatered plants and ranged from 0.413 cm s^{-1} in *R. repens* to 0.555 cm s^{-1} in *C. caesius*.

The trend in CO_2 assimilation rate shows a close relationship to that of leaf stomatal conductance. It is clear that photosynthesis was substantially inhibited by the decrease in leaf stomatal conductance.

4.6.3. Leaf Water Potential

The trend in leaf water potential in response to water stress was the same in all plants (see Appendix 4). Therefore, only values for the key species (*T. triandra* and *P. mezianum*) are reported here.

Table 7: Chlorophyll levels in control, water stressed and rewatered plants ($\bar{X}$ ± S.E.; n = 3)

Amount of Chlorophyll *a* (mg g^{-1} fresh weight)

Species	Control	Stressed	Rewatered
T. triandra	2.00	1.44 (0.04)[1]	1.60
P. mezianum	1.79	1.18	1.44
E. paspaloides	1.47 (0.04)	1.41 (0.02)	1.43 (0.02)
C. ciliaris	1.44 (0.03)	1.27	1.37 (0.02)
C. caesius	1.55	1.40 (0.03)	1.42 (0.01)
R. repens	1.63 (0.01)	1.26 (0.04)	1.37
D. aegyptium	0.88 (0.02)	0.76 (0.03)	0.80 (0.02)

Amount of Chlorophyll *b* (mg g^{-1} fresh weight)

Species	Control	Stressed	Rewatered
T. triandra	0.52	0.32 (0.01)	0.50
P. mezianum	0.34	0.15 (0.02)	0.31 (0.01)
E. paspaloides	0.45 (0.06)	0.34 (0.05)	0.37
C. ciliaris	0.48 (0.04)	0.27 (0.02)	0.33 (0.01)
C. caesius	0.42	0.36 (0.04)	0.37 (0.01)
R. repens	0.32	0.28	0.30
D. aegyptium	0.26 (0.08)	0.23 (0.02)	0.25 (0.01)

Ratio of Chlorophyll *a:b*

Species	Control	Stressed	Rewatered
T. triandra	3.85	4.50 (0.90)	3.20
P.mezianum	5.77 (0.18)	7.87 (0.40)	4.65 (0.30)
E. paspaloides	3.29 (0.29)	4.15 (0.62)	3.86 (0.05)
C. ciliaris	3.00 (0.40)	4.70 (0.43)	3.70 (0.08)
C. caesius	3.69	3.89 (0.40)	3.84 (0.02)
R. repens	5.09 (0.17)	4.80 (0.20)	4.57 (0.46)
D. aegyptium	3.38 (0.47)	3.30 (0.19)	3.20 (0.04)

[1] - Values in brackets are S.E.

4.6.3.a. *T. triandra*

Leaf water potential for *T. triandra* ranged from -1.48 MPa in control plants and -1.46 MPa in rewatered plants to -1.65 MPa in stressed plants. It is evident that there was a small drop in leaf water potential during water stress which later increased after watering of plants.

4.6.3.b. *P. mezianum*

Leaf water potentials dropped drastically from a high value of -1.38 MPa in control plants to <-4.0 MPa in water stressed plants. After rewatering, the plants exhibited a mean value of -3.24 MPa. This was more than for the stressed plants but less than for the control plants.

4.6.4. Chlorophyll Levels in Plant Leaves

The amount of chlorophyll *a* in plant leaves was variable (Table 7). Watered or control plants generally had higher chlorophyll *a* levels than water stressed plants. After rewatering, chlorophyll *a* content increased in all plants. The levels ranged from 0.88 to 2.00 mg g^{-1} fresh weight in control plants, 0.76 to 1.44 mg g^{-1} in water stressed plants and 0.80 to 1.60 mg g^{-1} in rewatered plants.

The level of chlorophyll *b* dropped with water stress (Table 7). Watering of the plants increased the content of chlorophyll *b* in all cases. The levels

ranged from 0.26 to 0.52 mg g^{-1} fresh weight in control plants, 0.15 to 0.36 mg g^{-1} in water stressed plants and 0.25 to 0.50 mg g^{-1} in rewatered plants.

The ratio of chlorophyll *a:b* in control plants was always greater than 3.00 in all cases (Table 7). Under water stress conditions this ratio increased in most species except in *R. repens* and *D. aegyptium* where it dropped from 5.09 to 4.80 and 3.38 to 3.30, respectively. After rewatering of the plants, the ratio dropped in all plants. Ratio of chlorophyll *a:b* ranged from 3.00 to 5.77 in control plants, 3.30 to 7.87 in water stressed plants and 3.20 to 4.65 in rewatered plants.

4.7. LEAF ANATOMY

4.7.1. Light Microscopy

All the seven grass species examined were found to be C_4 species. Five of the grasses were NADP-me and three were PEP-ck type. C_4 grasses are characterized by the presence of a Kranz or chlorenchymatous sheath of enlarged cells and containing specialized chloroplasts distinct from those of the mesophyll (Ellis *et al.* 1980). NADP-me type grasses included *T. triandra*, *P. mezianum*, *C. caesius* and *C. ciliaris* (Plates 1-4, respectively). PEP-ck type grasses were *R. repens*, *E. paspaloides* and *D. aegyptium* (Plates 5-7,

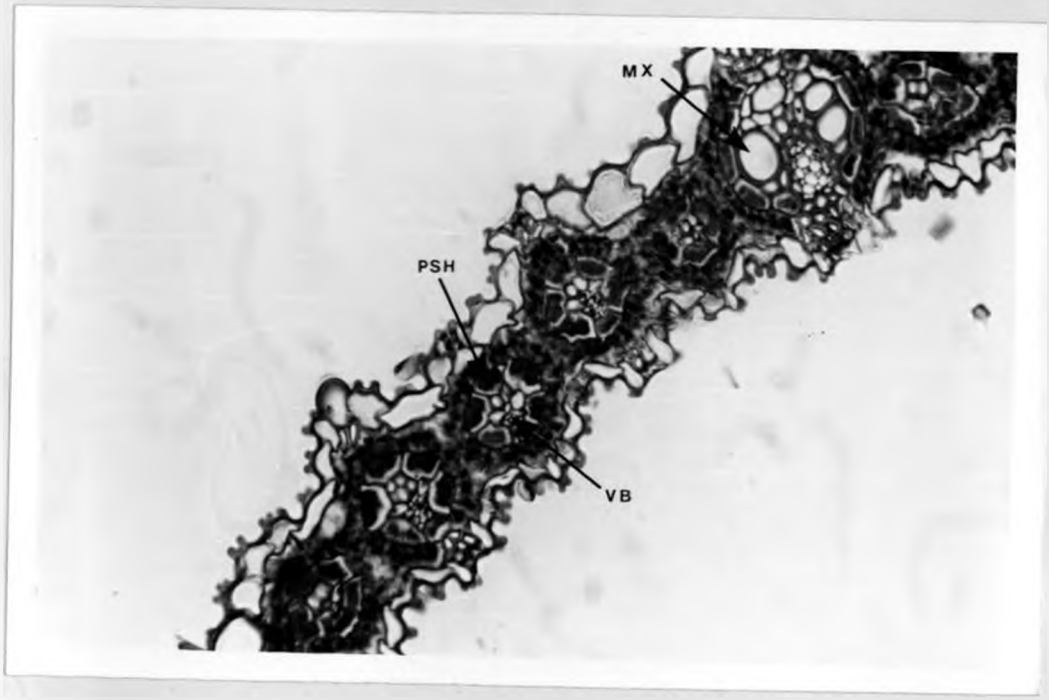

MX
PSH
VB

Plate 1. *Themeda triandra* is an NADP-me Kranz sub-type species with a single parenchyma bundle sheath (PSH) surrounding a vascular bundle (VB). No mestome sheath between the metaxylem vessel elements and the parenchyma sheath cells. Note that the chloroplasts in the PSH are in the centrifugal position. MX = metaxylem.

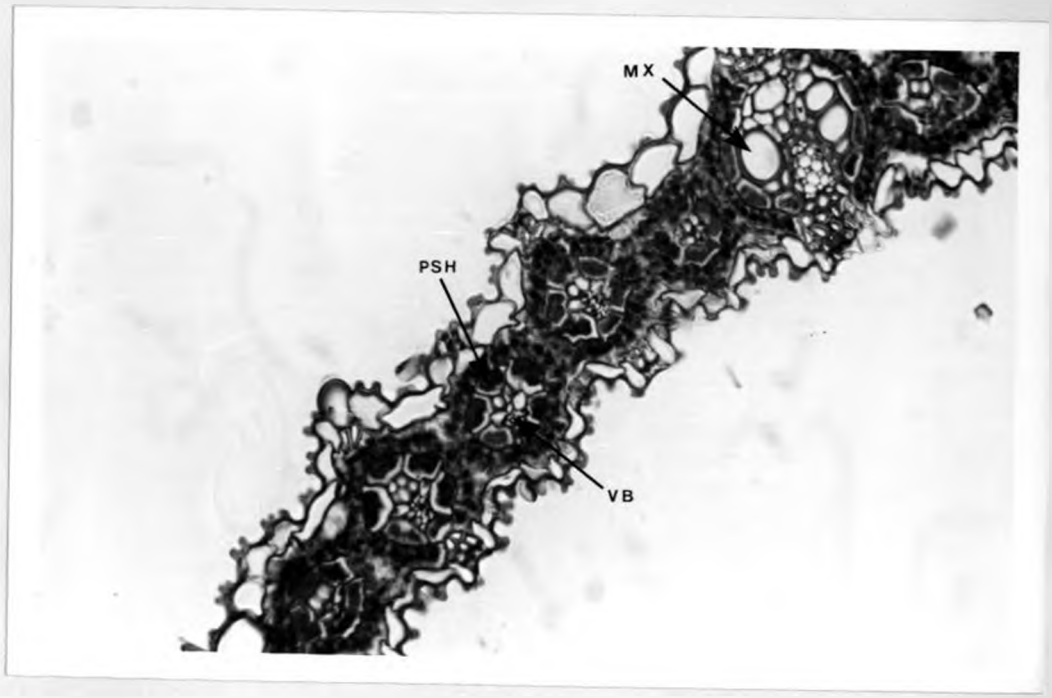

MX
PSH
VB

Plate 2. *Pennisetum mezianum* is a typical C_4 panicoid species with a single bundle sheath with specialized chloroplasts. It has a characteristic NADP-me Kranz sub-type anatomy with a parenchyma bundle sheath (PSH) surrounding a vascular bundle (VB).

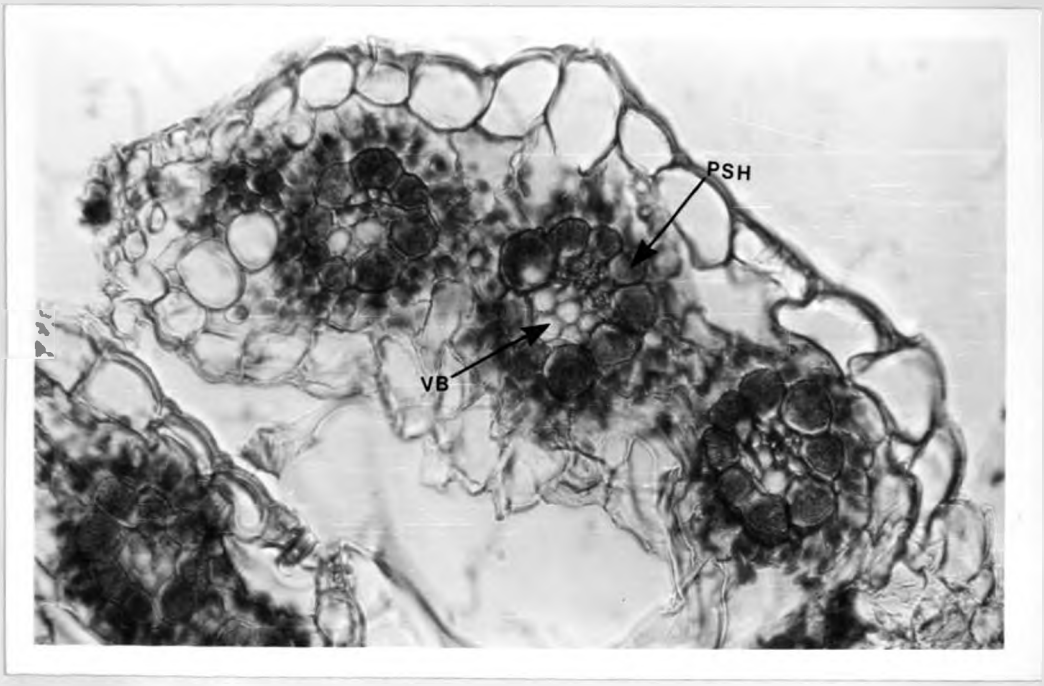

PSH
VB

Plate 3. *Cymbopogon caesius* is a typical NADP-me Kranz sub-type species with a single parenchyma bundle sheath (PSH) surrounding a vascular bundle (VB).

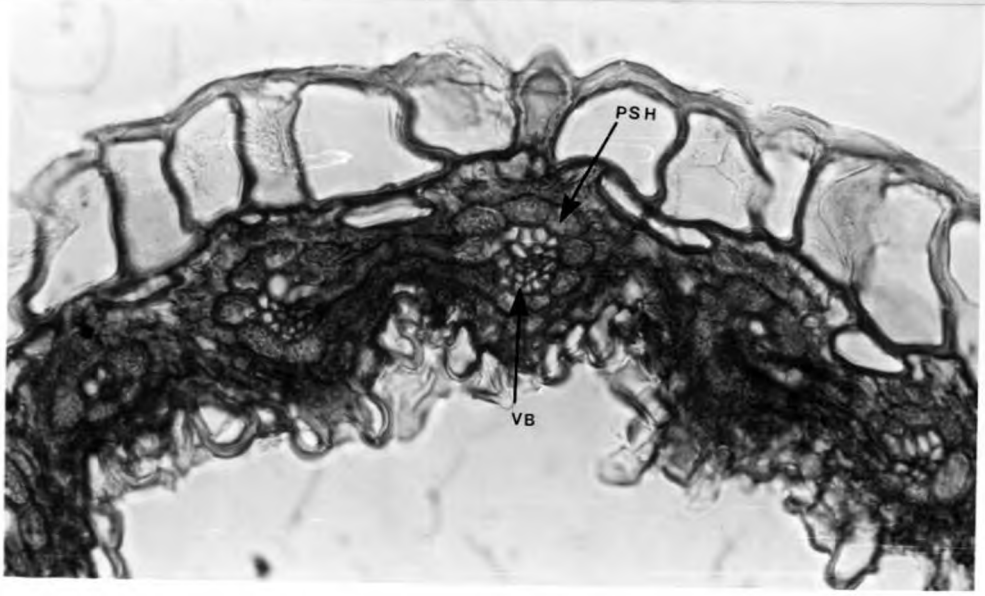

PSH
VB

Plate 4. *Cenchrus ciliaris* has a single parenchyma bundle sheath (PSH) surrounding a vascular bundle (VB) typical of NADP-me Kranz sub-type species.

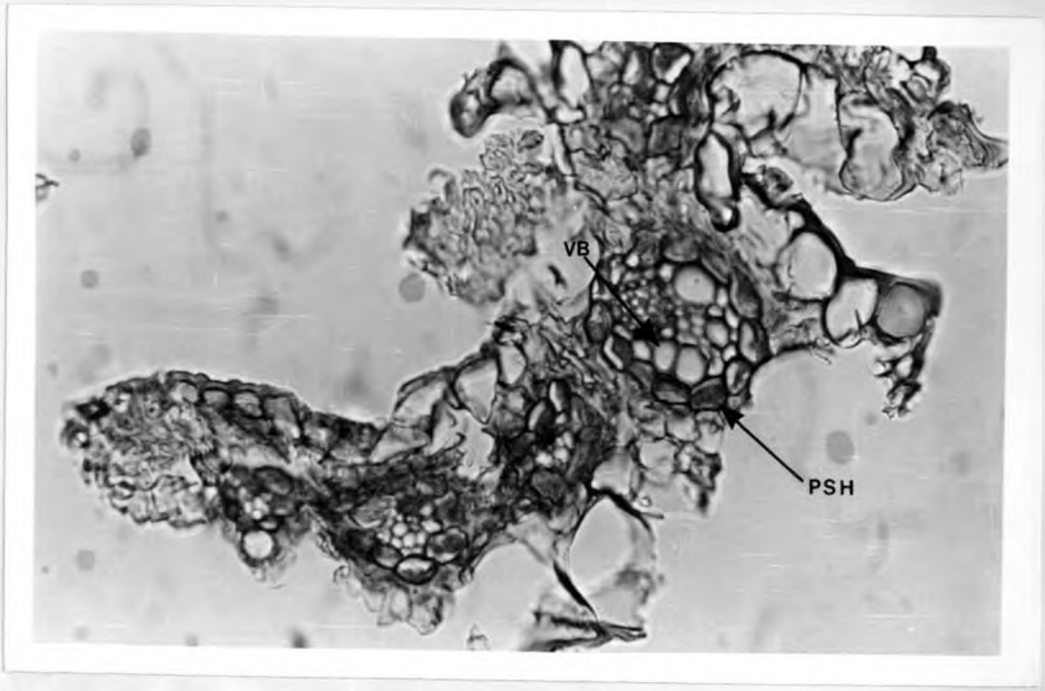

VB
PSH

Plate 5. *Rhylchelytrum repens* is a C_4 species with prominent grana in the parenchyma bundle sheath (PSH). A typical mestome sheath (MSH) is present and no chloroplasts are present in this tissue. The species is a PEP-ck Kranz sub-type. VB = vascular bundle.


VB
MSH
PSH

Plate 6. *Eustachys paspaloides* is a typical PEP-ck Kranz sub-type. Bundle sheath cells are of different sizes. MSH = mestome sheath; PSH = parenchyma bundle sheath and VB = vascular bundle.

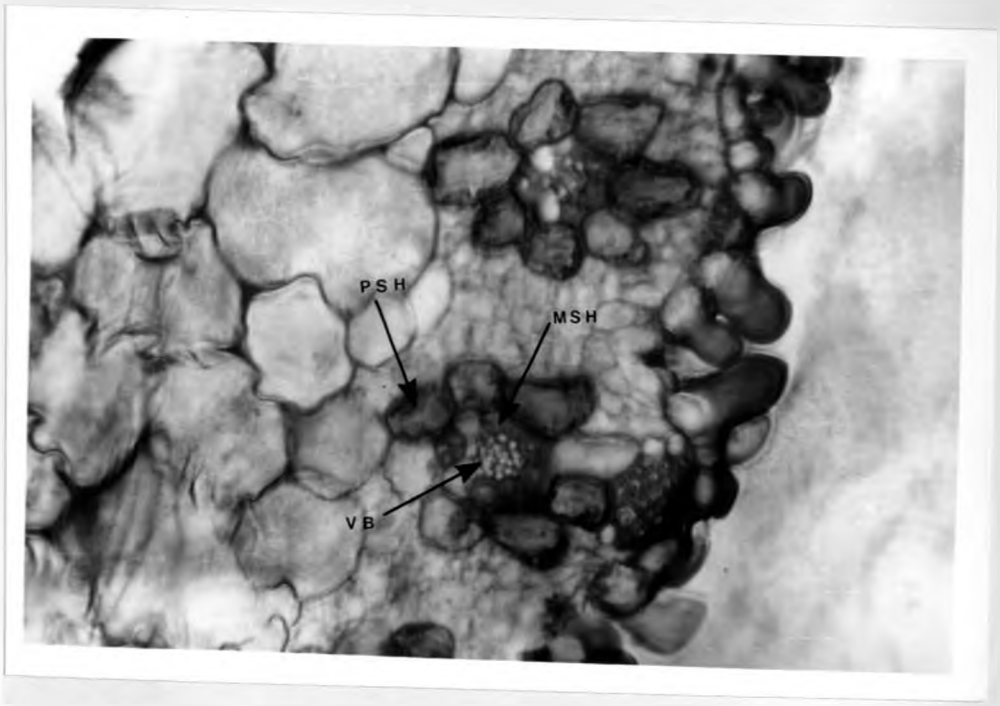

PSH
MSH
VB

Plate 7. *Dactyloctenium aegyptium* has anatomy typical of PEP-ck grasses. VB = vascular bundle; MSH = mestome sheath and PSH = parenchyma bundle sheath.

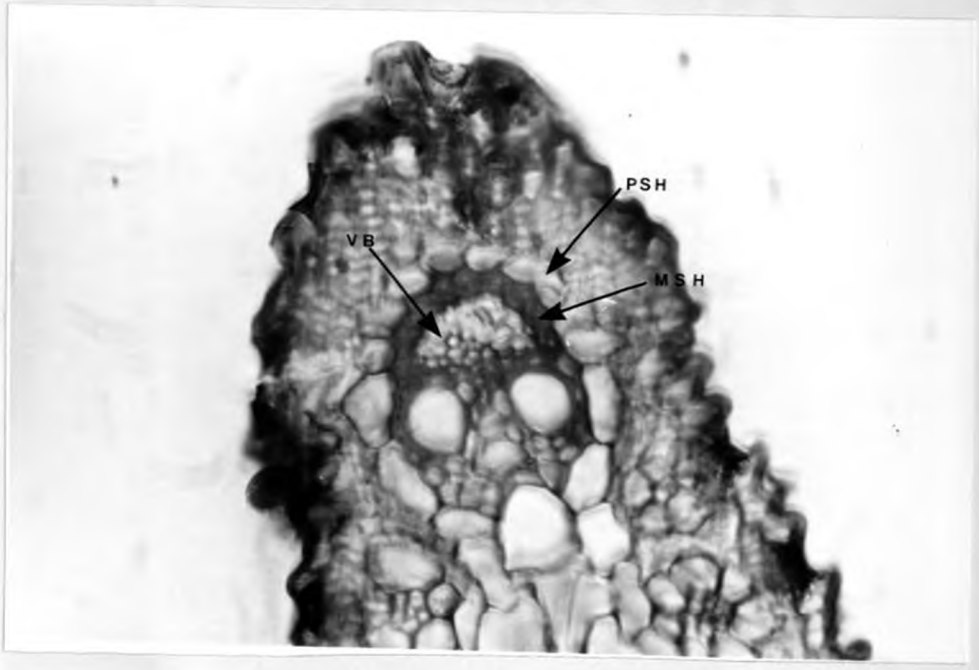

PSH
VB
MSH

Plate 8. An overview (x415) of the adaxial epidermis of *T. triandra* leaf blade. Pr, prickle; S, stoma.

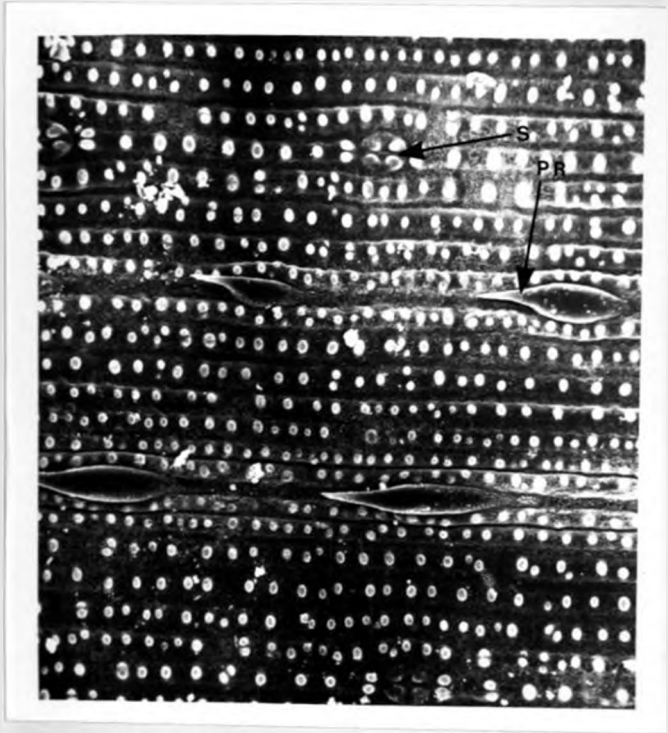

S
PR

Plate 9. An overview (x415) of the abaxial epidermis of *T. triandra* leaf blade. S, stoma; M, microhair and P, papilla

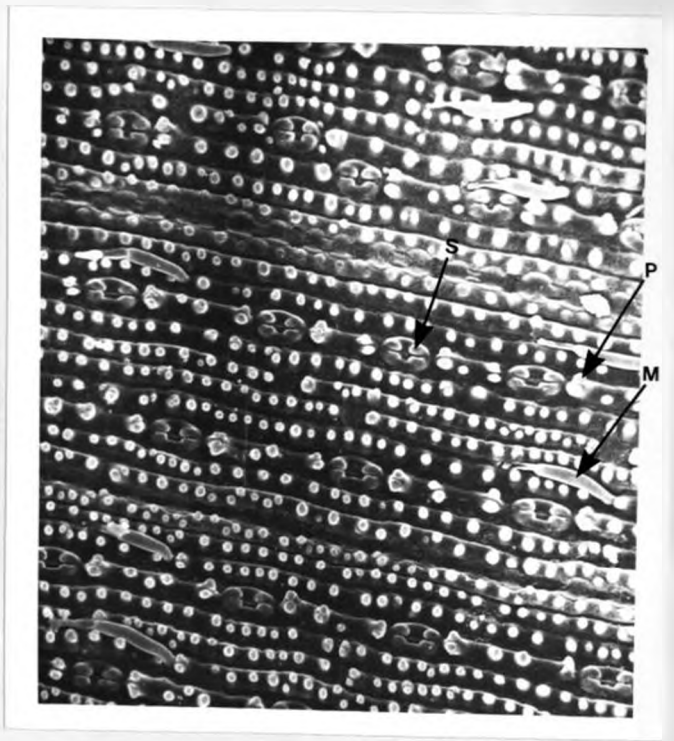

S
P
M

Plate 10. An overview (x415) of the abaxial epidermis of *P. mezianum* leaf blade. S, stoma; M, microhair and Pr, prickle.

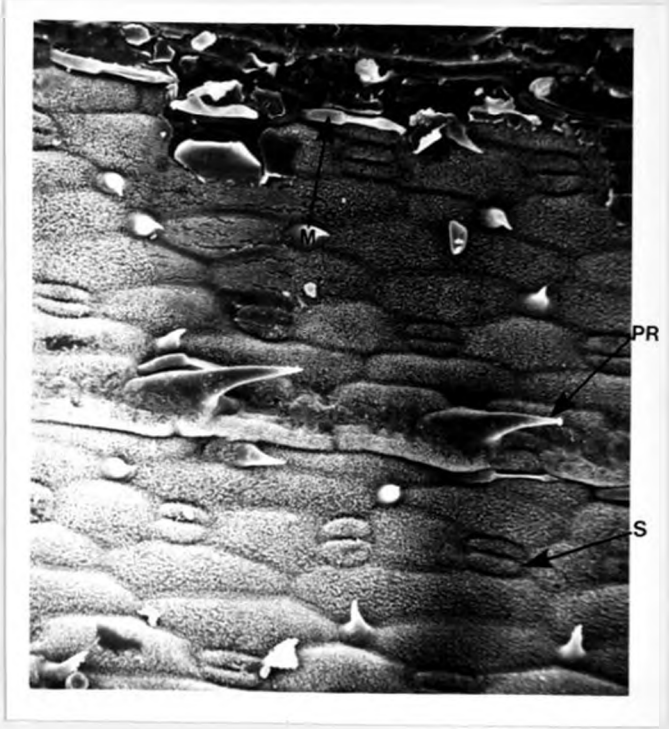

M
PR
S

Plate 11. An overview (x415) of the adaxial epidermis of *P. mezianum* leaf blade. S, stoma; M, microhair and Pr, prickle.


S
PR

Plate 12. A close-up view (x4150) of a stoma of *T. triandra* leaf blade. GC, guard cell; SP, stomatal pore and SC, subsidiary cell.

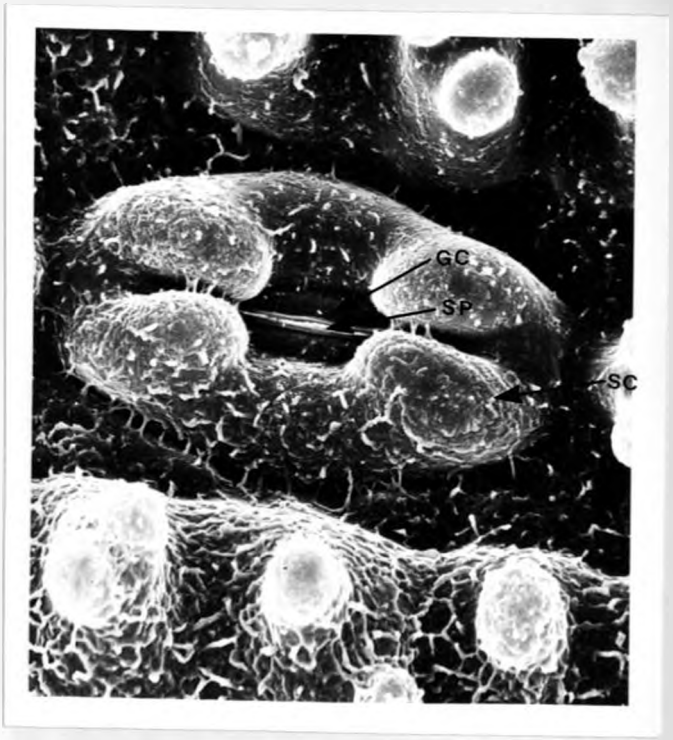

GC
SP
SC

Plate 13. A close-up view (x1090) of abaxial epidermis of *P. mezianum* showing the wax coated stoma (S), microhair (M) and prickle (Pr).


S
M
Pr

Plate 14. An overview (x415) of sheath of *P. mezianum* showing stoma (S), microhair (M) and prickle (Pr).

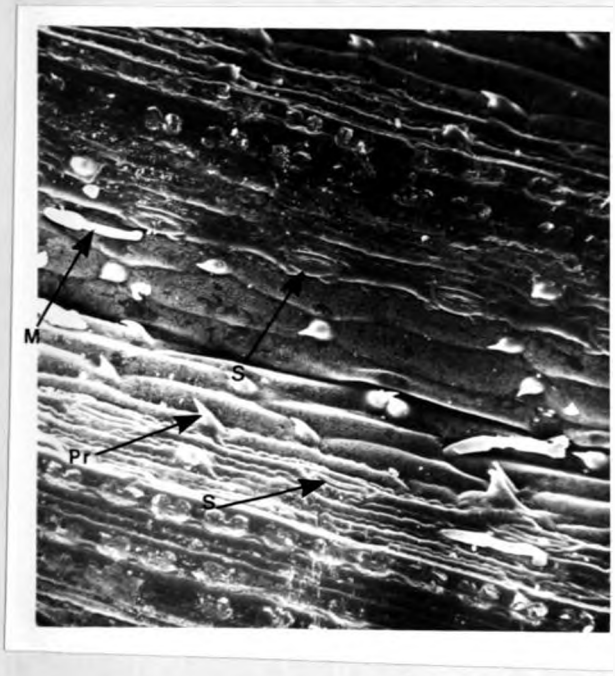

M
S
Pr
S

Plate 15. A close-up view (x4150) of a stoma of *T. triandra* stem. SP, stomatal pore (closed); GC, guard cell; SC, subsidiary cell and W, wax coat.


W
SP
GD
SC

Plate 16. An overview (x415) of stem of *P. mezianum* showing occurence of numerous stomata (S).

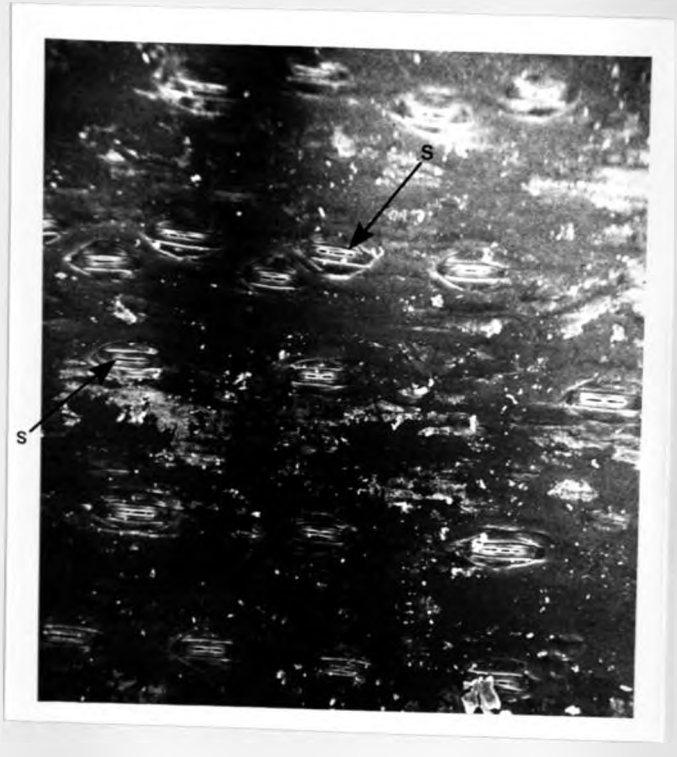

S
S

Plate 17. A close-up view (x700) of inflorescence of *T. triandra* showing macrohair (H) and macrohair base (B). M, microhair.

respectively).

The NADP-me Kranz sub-type species have one sheath surrounding the vascular bundle and are malate formers while the PEP-ck Kranz sub-type species have two sheaths and are aspartate formers (Gutierez *et al.* 1974). The bundle sheaths of NADP-me and PEP-ck grass species have centrifugal (i.e. located towards the outer tangential wall) chloroplasts.

4.7.2. Scanning Electron Microscopy

4.7.2.a. Leaf Blade

On the average, stomata were more frequent on the abaxial than on the adaxial surface of *T. triandra* (Plates 8, 9). However, in *P. mezianum* stomatal frequency was nearly as high on the abaxial surface as on the adaxial surface (Plates 10, 11). Stomata of *T. triandra* were situated in crypts created by the papillate subsidiary cells (Plate 12). No crypts were encountered in *P. mezianum* (Plate 13).

In *P. mezianum*, microhairs and prickles occured on both the adaxial and abaxial surfaces. However, in *T. triandra* prickles occured only on the adaxial surface, while microhairs occured on the abaxial surface. The epidermal cells on both leaf surfaces of *T. triandra* possessed epidermal wall protrusions (papillae). Papillae did not occur in *P. mezianum*. The epidermal surfaces of both *T. triandra* and *P. mezianum* were

heavily coated with wax (Plates 12, 13). In *T. triandra* both the adaxial and abaxial epidermal cells were long and narrow in shape. However, in *P. mezianum* the abaxial epidermal cells were short, wide and rectangular in shape while the adaxial epidermal cells resembled those of *T. triandra*, except that they lacked papillae.

4.7.2.b. Sheath

The sheath surface of *T. triandra* closely resembled that of its leaf blade and possessed numerous stomata, long and narrow epidermal cells and lots of papillae. Stomata were located in crypts created by the papillate subsidiary cells. The epidermal surface of sheath of *P. mezianum* resembled more the adaxial leaf surface than the abaxial surface. However, its epidermal cells were of two types, namely, short and rectangular and long and narrow in shape (Plate 14). In *P. mezianum* the sheath possessed numerous stomata and no crypts were present. The sheaths of both species possessed microhairs and prickles. In both species the sheath was heavily covered with wax.

4.7.2.c. Stem

The stem of *T. triandra* was heavily coated with wax. Stomata were few and heavily coated with wax (Plate 15). Epidermal cells were not papillate like those of the leaf blade and sheath. The stem of *P. mezianum*, however, possessed more stomata than

those found on the leaf blade (Plate 16). The stem of *P. mezianum* was further covered with a coat of wax. In both species neither microhairs nor prickles were present on the stems.

4.7.2.d. Inflorescence

The inflorescence of *T. triandra* showed the presence of numerous papillate stomata, prickles microhairs and macrohairs (Plate 17). Stomata were located in crypts created by the papillate subsidiary cells like in the leaf blade and sheath.

CHAPTER 5

5. DISCUSSION

5.1. Aboveground biomass production

The trend in live biomass showed that production coincided with rainfall availability. Peak live biomass values were obtained during the long rainy seasons when rainfall amounts were high. Shoot growth in semi-arid grasses is basically dependent on the availability of soil moisture (Cassady 1973, Mall and Billore 1974, Sims and Singh 1978a, Strugnell and Pigott 1978 and McNaughton 1979b). The peak live biomass occured during the long rainy seasons and ranged from about 300 to 338 g m^{-2} in 1985 and 1986. These ranges were within those reported by several workers in the Nairobi National Park ecosystem. Owaga (1980) reported peak values of about 309 and Deshmukh (1986) that of 332 g m^{-2} inside exclosures. In other East African grass ecosystems, Sinclair (1975) reported a peak value of 115 g m^{-2} in the Serengeti while in the Ruwenzori National Park, Uganda, Strugnell and Pigott (1978) reported a peak value of 405 g m^{-2}.

Apparently, in the later part of this study period live biomass appeared to stagnate, attaining values below 200 g m^{-2} in most months after September 1985.

Due to lower rainfall amounts during the long rainy season of 1986 as compared to 1985, live biomass levels for 1986 did not reach the 1985 levels. This again may be due to vegetation stagnation (Tueller and Tower 1979). Vegetation stagnation is sometimes caused by smothering of live shoots by the accumulation of standing dead biomass due to the exclusion of grazers from the vegetation (McNaughton 1979b). Grazing is known to remove this effect through stimulation of growth by the removal of leaf shading by the dead biomass (McNaughton 1979b). On the average, over the entire study period, live biomass production accounted for only 32% of the total aboveground production, reflecting a great degree of accumulation of dead biomass after fencing of the study site.

Dead biomass production results from the transfer of live biomass material to the dead biomass compartment (Sims and Singh 1978b). Therefore, high peak values of dead biomass were encountered during the dry seasons of the year. This is in line with the findings of Singh *et al.* (1978), Strugnell and Pigott (1978), Macharia (1981), Deshmukh and Baig (1983), Deshmukh (1986). In this ecosystem, Deshmukh (1986) encountered a peak dead biomass of 374 g m^{-2} while the present study encountered a peak of about 651 g m^{-2}. Owaga (1980) working in the same ecosystem reported values of 93 g m^{-2}. These differences in the same

ecosystem may be due to the fact that these studies took different lengths of time, whereby most of them took one year or less while the present study monitored biomass for more than two years and hence had more time to encounter more variability in production levels of this semi-arid ecosystem.

Levels of standing dead biomass production were lowest in December 1984 following the rains. Much of the standing dead material in the absence of large grazers is broken down by decomposers, insects, wind and raindrops to form litter which in turn undergoes decomposition mostly during the rainy season. By January 1985 when the rains had stopped, there was a transfer of live biomass to the standing dead compartment through leaf death. This is reflected by an increase in standing dead materials during this period. Standing dead production kept a steady increase with a small drop during the May and June 1985 rainy season. Standing dead material is known to be broken down by raindrops and wind to form litter during rainy seasons. Rain water is also known to leach most soluble nutrients which form part of structural material of standing dead biomass. This process is known to be faster in dead plant materials than live ones (Tukey and Mecklenburg 1964). After July 1985 standing dead biomass kept a constant trend fluctuating between about 200 and 400 g m^{-2}. This indicated that

inside the exclosure, levels of standing dead biomass had stabilized and changed only according to the time of the rainy periods.

Litter was at higher levels than that of standing dead in October 1984 to January 1985. This reflected the pre-fencing conditions where most of the standing dead biomass was broken down to litter through trampling by grazing herbivores since this is a dry season concentration area for the grazing herbivores of this ecosystem (Lusigi 1978, Owaga 1980, and Deshmukh 1986). However, after fencing of the study site any accumulated standing dead materials could only be broken down by rain water and wind. Since this is a slow process, standing dead biomass stayed at an higher level than litter after January 1985. After this month, litter kept a constant but fluctuating pattern, increasing and decreasing, depending on the amount of standing dead transferred to the litter compartment and that lost through decomposition. It is, therefore, evident that any amount of litter encountered at any particular period is a balance between the amount added from the standing dead compartment and that lost into decomposition process (Sims and Singh 1978a, 1978b).

Most biomass occured in the first 20 cm above the ground canopy layer reflecting the growth pattern of these grasses. Most tropical grasses have co-evolved

with grazing herbivores and because of the consistent effect of grazing down to the ground level, the grasses do not elevate their apical meristems above the ground until prior to the flowering phase. Stapledon (1928) argues that one of the principal responses of grasses to herbivory is selection for the prostrate rapidly growing genotypes. Morphological evolution leading to meristem protection by physical isolation has been a major feature of grass evolution (McNaughton 1979b). Therefore, much of the foliage, consisting mostly of leaves, are found in the first 20 cm above the ground surface. It is only prior to the flowering phase that current season culms and nodal tillers are formed and elevated above the 20 cm level of the plant canopy. However, since most of these grasses are perennial, those culms formed in the last growing season which are not grazed still remain. These culms with progressive age become very fibrous and unpalatable to the grazers but they may carry current season nodal tillers, for example in *P. mezianum*, which provide comparatively more nutritious forage for grazers during the dry season (Kinyamario *et al.* 1984). Some of the culms remain as standing dead for the rest of the time until broken down into litter.

In any ecosytem, a species or several of them may dominate depending on the biotic and/or abiotic factors

that favour them. These factors may include fire, soil, rainfall and grazing. Plants that are resistant to grazing and fire pressures dominate in most semi-arid East African grasslands (McNaughton 1979b). It has been reported that *T. triandra* is a dominant species in this and similar plant communities because it is resistant to burning and grazing in contrast to other grass species (Strugnell and Pigott 1978). Lusigi (1978) and Deshmukh (1986) have reported that *T. triandra* contributed the highest amount of biomass in this ecosytem. In this study, dicots made a substanti contribution to biomass and this was most pronounced between March and November 1986 (Fig. 11). Most of these dicots, which included *Indigofera volkensii* Taub., *Dolichos formosus* A. Rich., *Sida schimperiana* A. Rich., *Vigna frutescens* A. Rich., *Clitoria ternata* L. and *Neonotonia wightii* (Wight Arm.) Leckey were creepers or of short habit found in the first 20 cm canopy layer above the soil surface. The fact that most of these dicots were in the first 20 cm canopy layer above the soil surface is probably an adaptation to grazing pressure. A fundamental botanical difference between dicots and monocots is that dicots grow from terminal meristems, which are highly susceptible to herbivore destruction through grazing while the monocots grow from basal intercalary meristems that are

that favour them. These factors may include fire, soil, rainfall and grazing. Plants that are resistant to grazing and fire pressures dominate in most semi-arid East African grasslands (McNaughton 1979b). It has been reported that *T. triandra* is a dominant species in this and similar plant communities because it is resistant to burning and grazing in contrast to other grass species (Strugnell and Pigott 1978). Lusigi (1978) and Deshmukh (1986) have reported that *T. triandra* contributed the highest amount of biomass in this ecosytem. In this study, dicots made a substantial contribution to biomass and this was most pronounced between March and November 1986 (Fig. 11). Most of these dicots, which included *Indigofera volkensii* Taub., *Dolichos formosus* A. Rich., *Sida schimperiana* A. Rich., *Vigna frutescens* A. Rich., *Clitoria ternata* L. and *Neonotonia wightii* (Wight Arm.) Leckey were creepers or of short habit found in the first 20 cm canopy layer above the soil surface. The fact that most of these dicots were in the first 20 cm canopy layer above the soil surface is probably an adaptation to grazing pressure. A fundamental botanical difference between dicots and monocots is that dicots grow from terminal meristems, which are highly susceptible to herbivore destruction through grazing while the monocots grow from basal intercalary meristems that are

less accessible to large herbivores (Branson 1953 and Rechenthin 1956).

During October 1984, after fencing of the site, dicots contributed a small proportion to biomass production (Fig. 11). However, after October 1984 their contribution increased. This demonstrates that without the exclosure dicots were readily grazed. Owing to the fact that growth of dicots is from terminal buds, their growth was curtailed and hence this accounts for their low contribution to the overall biomass production prior to site fencing.

5.2. Belowground Biomass Production

It appears that a larger amount of material is translocated and accumulated in the roots during the dry season than during the favourable wet season. It has been documented in other grassland ecosystems (Whalley and Davidson 1968, Singh and Yadava 1974 and Pandey and Sant 1980) that towards the end of the growing season, there is an accumulation of reserve carbohydrate material in the stem bases and roots. Sims and Singh (1978b) proposed that this noted increase of root biomass could again be attributed to the decreased rate of decomposition of dead roots during the dry

season. The stem bases and roots remain alive during the unfavourable dry spells and new growth occurs from meristematic buds on these structures at the beginning of the next growing season. This growth draws on the reserve carbohydrates and results in a decrease in live belowground biomass at the beginning of the growing season. This process of drawing food reserves from the roots for early initial growth of grasses is termed root "draw down" (McNaughton 1979b). This process is a critical feature of grass physiology determining species success in these grasslands. Grass species in this ecosystem such as *P. mezianum* which have low abundance under heavy grazing, but become fairly abundant when grazing pressure is removed, probably suffer fatal root reserve depletion or "draw down" under intense grazing pressure (McNaughton 1979b). In Fig. 11, *P. mezianum* at the start of the study, October 1984 ranked third in biomass production but at the end of the study, November 1986, ranked second overall after *T. triandra*. This may explain partly why *T. triandra* is the dominant species in this ecosystem where grazing can be very severe (McNaughton 1979b and Boutton *et al.* 1986). Therefore, a critical feature of grazing resistance in grasses undoubtedly is the ability to maintain a high enough shoot biomass to sustain root reserves.

One essential feature of root "draw down" in grass growth is that the mobilized food reserves are used in the initial phase of shoot growth early in the growing season until the shoots have developed a fully functional photosynthetic apparatus. After this phase of development, the shoot is able to manufacture enough food material for its subsequent growth. Any extra food material after this stage which is not used for growth is again stored in the stem bases and roots, for example, during November 1984, April 1985, May 1986 and October 1986 (Fig. 13). However, one notable phenomenon which occurs in this grassland community is a depression of live root biomass at the end of the growing season such as during December 1984 and June 1986. This feature can be explained through the growth patterns of these semi-arid grasses. At the end of the growing season, plants are in their last phase of growth, that is flowering and seed ripening. Therefore, some food reserves may be drawn for the formation of seeds (Strugnell and Pigott 1978). After seed ripening any extra manufactured food material plus that mobilized from the senescent leaves are translocated to the roots and stem bases, hence the noted increase in live belowground biomass during the dry seasons.

Dead belowground biomass was higher than live belowground biomass and followed closely the trend of

live biomass (Fig. 9). This shows that live biomass may have been disappearing into the dead biomass compartment at a higher rate than the disappearance of dead belowground biomass through decomposition. This aspect, however, was not reflected by their respective turnover rates which were nearly equal (Table 1).

Although the magnitude of belowground biomass in East African grasslands is not well documented, the range of values in this study are within those reported by Strugnell and Pigott (1978). They reported ranges of 512 and 2007 g m^{-2} for total root biomass in enclosed sites of the Ruwenzori National Park, Uganda. The values of 197 to 517 g m^{-2} total root biomass in the present study are on the lower scale of those of Strugnell and Pigott (1978). The apparent high limit found in their study may be due to their study site having deep soils which permitted the authors to sample roots to a depth of 60 cm. This study and that of Strugnell and Pigott (1978) clearly demonstrate that root dynamics are a critical aspect of East African grasslands especially where grazing is intense. Hence, more work needs to be done on root dynamics of East African grasslands.

5.3. Decomposition Rate of Dead Plant Materials

Decomposition of plant materials is very much a function of the type of plant material, climatic

factors (rainfall, temperature, etc.,) and the type of decomposers. In East African grasslands, which fall under the tropical climates, temperature is never limiting for effective decomposition to take place. However, rainfall is usually the limiting factor for this process especially during the dry seasons (Ohiagu and Wood 1979). The trend in decomposition rates followed that of rainfall with highest rates during the wet season (Fig. 14) (Abouguendia and Whitman 1979).

Decomposition data for East African grasslands are few and are usually low (Macharia 1981 and Deshmukh 1985). Macharia, in several grassland ecosystems, found that decomposition rates varied from site to site depending on rainfall. At the Nairobi National Park site average values of 0.018 g g^{-1} mon^{-1} were reported, while at the Masai Mara site it was about 0.02 and at Amboseli about 0.009 g g^{-1} mon^{-1} for aboveground dead herbage. Our monthly average value of 0.09 to 0.18 g g^{-1} mon^{-1} for aboveground material were much higher than those reported by Macharia (1981) but compare well with those reported for other grassland ecosystems of the world. George and Smeins (1982) reported an average value of 0.07 g g^{-1} mon^{-1} for aboveground herbage in Texas. Abouguendia and Whitman (1979) reported values ranging from 0.018 to 0.128 g g^{-1} mon^{-1} in ungrazed

mixed prairie in western North Dakota, USA. Ohiagu and Wood (1979) in Nigeria reported an average of 13.2% (about 0.132 g g^{-1} mon^{-1}) loss of litter weight due to decomposition for an ungrazed plot. None of these studies, however, reported any values for belowground plant materials. Comparisons of decomposition rates between different studies in tropical Africa is difficult because most of these studies fail to specify the mesh size of their litter bags to determine whether they allowed large detrivorous organisms to enter their bags. Ohiagu and Wood (1979) used unspecified type of wire mesh cages which allowed access to termites.

On an average percentage basis aboveground dead herbage was lost at about 9% rate per month to the decomposers while belowground dead materials were lost at about 18% rate. This compares with 13.2% for aboveground dead herbage for West African grasslands investigated by Ohiagu and Wood (1979).

5.4. Net Primary Production

The aboveground net primary production (NPP) rate of 1332.4 g m^{-2} yr^{-1} (about 3.65 g m^{-2} d^{-1}) was much higher than those reported by different authors in this ecosystem. Lusigi (1978) reported values of 394.7 g m^{-2} yr^{-1}, Owaga (1980) 447.9 g m^{-2} yr^{-1}, Macharia

(1981) 364 g m^{-2} yr^{-1} and Deshmukh (1986) 1071 g m^{-2} yr^{-1}. These authors grossly underestimated net primary production rate of this ecosystem because they used either the "Peak biomass" method, the "Maximum-Minimum biomass" method or the "standard IBP method" of Milner and Hughes (1968). All these methods have serious shortcomings because either they do not account for simultaneous occurrence of death and growth or they ignore the role of decomposition (Table 8).

Since biomass changes as well as losses through death were measured in this study at regular intervals we can use these data to determine what would be obtained with the "standard IBP" method and the "Maximum-Minimum biomass" method used by many grassland ecologists. This comparison (Table 8) shows that the "standard IBP" and the "Max.- Min." methods underestimated productivity by 89% and 88% respectively, in comparison with present study method estimates which accounted for both losses through death and decomposition and belowground production. It can be seen that failure to account for belowground production resulted in about 42% underestimation while failure to account for decomposition losses accounted for about 34% underestimation. Accounting for plant mortality for aboveground production only (Deshmukh 1986) resulted in an underestimation of 60% of NPP. It can, therefore, be

Table 8. Net primary productivity (g m^{-2} yr^{-1}): a comparison of the estimates obtained by taking account of mortality, decomposition and belowground production, with estimates from aboveground biomass change alone.

Methodology	Net Primary Productivity
1. Present Study Method	
a) Accounting for mortality and decomposition (including roots and rhizomes)	2298
b) Accounting for mortality alone (including roots and rhizomes)	1518 (34%)*
c) Accounting for mortality and decomposition (shoot production only)	1332 (42%)
d) Accounting for mortality alone (shoot production anly)	921 (60%)
2. Standard IBP method (shoots only)	254 (89%)
3. "Maximum - Minimum" method (shoots only)	266 (88%)

* Values in brackets are levels of underestimation as % of 1.a)

Table 9 . Net primary productivity (g m^{-2} yr^{-1}) in different African Tropical Grasslands.

Place	Vegetation Type	Annual Rainfall (mm)	NPP	Author
Ghana	Savanna woodland	153	763	Nye & Greenland (1960)[1]
Senegal	Tree savanna	300	42	Morel & Bourliere (1962)[1]
Nigeria	Savanna woodland	1168	680	Hopkins (1965)
Cote d'Ivoire	Grassland	1300	550	Cesar (1971)[1]
Senegal	Tree savanna	435	150	Bille (1973)[1]
Kenya	*Themeda* grassland	560	500	Cassady (1973)
Kenya	Wooded grassland	680	450	Cassady (1973)
Zaire	Miombo woodland	950	222	Freson (1973)[1]
Kenya	*Themeda* grassland	560	648	Phillipson (1975)
Tanzania	Short-grassland	613	470	Sinclair (1975)
Tanzania	Long-grassland	905	598	Sinclair (1975)
Kenya	*Themeda* grassland	900	395	Lusigi (1978)
Uganda	*Hyparrhenia*/ *Themeda* grassland	600	553	Strugnell & Pigott (1978)
Uganda	*Sporobolus*/ *Chloris* grassland	600	536	Strugnell & Pigott (1978)
Nigeria	Savanna grassland	1115	231	Ohiagu & Wood (1979)
Kenya	*Themeda* grassland	600	402	Owaga (1980)
Kenya	*Themeda* grassland	1034	810	Macharia (1981)
Kenya	*Themeda* grassland	729	364	Macharia (1981)
Kenya	*Themeda* grassland	850	1071	Deshmukh (1986)
Kenya	*Themeda* grassland	800	1332	Present Study[2]
Kenya	*Themeda* grassland	800	2298	Present Study[3]

[1] Cited by Ohiagu and Wood (1979)

[2] Net Primary Production for shoot production only

[3] Total Net Primary Production for shoot and root production

concluded that most results of NPP in most tropical African grasslands are gross underestimates of their true values (Table 9).

Studies in other tropical African grasslands again show a lot of variability in aboveground net primary production (Table 9). This variability is due to the methodology used for assessing net primary production and the inherent climatic conditions, especially rainfall amounts and other environmental factors prevailing in these grasslands. The aboveground NPP daily average rate of 3.65 g m^{-2} d^{-1} found in this study included both the dry and wet seasons. However, higher rates were obtained during growing season months, for example, values of 6.54 g m^{-2} d^{-1} in November 1984, 10.80 g m^{-2} d^{-1} in April 1985 and 6.12 g m^{-2} d^{-1} in May 1986. When the above- and belowground rates are added together for each month, very high rates of 13.64 in November 1984, 13.53 in April 1985 and 17.63 in May 1986 were obtained. In the Serengeti, McNaughton (1979b) obtained extremely high short-term aboveground productivities during the wet season with the highest value of 40 g m^{-2} d^{-1} recorded. However, during the growing season values were consistently above 20 g m^{-2} d^{-1} suggesting that East African grasslands may be among the most productive in the world.

Besides the present study, only the study of

Strugnell and Pigott (1978) dealt with belowground production among the studies in Table 9. Strugnell and Pigott (1978) estimated an annual net primary production rate of roots at about 1500 g m^{-2} yr^{-1} and emphasized that this value did not include short-term loss and replacement of roots. Their study was based on the "Maximum-Minimum biomass" method. The value of 966 g m^{-2} yr^{-1} from the present study demostrates clearly that the belowground compartment of these grasslands is fairly productive and, therefore, an essential component for the functioning of these ecosystems.

The dependence of net primary production on rainfall is depicted in Fig. 15. However, the level and time of positive net primary production for above- and belowground plant materials varied with time. There was a positive NPP in belowground biomass at the start of rainy season. This may be caused probably by the plants initiating growth in the roots first before that of shoots to form a large network of root to enable the plants to absorb large quantities of soil water at the start of the rainy season. Since most of the roots are found in the first 15 cm layer of the soil column this could be a survival mechanism for these semi-arid grasses. During this initial stage of plant growth these semi-arid plants invest more in the formation of a viable and large root network to maximize rain water

interception and absorption during the usually short rainy periods. Taerum (1970) reported that *Eragrostis superba* Peyr. and *T. triandra* send some roots to depths of at least 2 m but retain the bulk of their roots near the soil surface, where they can make maximum use of light rainfall.

5.5. Turnover rate and time

Turnover rate of live aboveground biomass was high (208%) due to the fact that a lot of live plant material is usually transferred to the standing dead compartment during the dry season (Deshmukh and Baig 1983). Every 12 months there was a complete turnover of live aboveground material. Turnover rate for standing dead compartment was comparatively low (200%). Due to the fact that the effect of trampling and breaking down of standing dead material to litter by grazing herbivores was removed after fencing, this category of biomass had low turnover rates (Rath and Misra 1980). Only rain drops, wind and decomposition may have contributed to any significant breakdown of standing dead plant materials. The high turnover rate of litter biomass (250%) was due to breakdown of litter by microbial decomposers, a process which was rapid during the wet seasons. It is worth noting that approximately every one year there was a complete replacement of live, standing dead and litter

Table 10. Turnover rate of different grassland communities.

Place	Plant community	Turnover rate (%)						Authority
		LAB[1]	SDB	Litter	LBB	DBB	TBB	
USA	Prairie	97	--	45	---	---	47	Ovington *et al.*, (1963)[2]
USA	Savanna	98	--	45	---	---	46	"
USA	*Andropogon* grassland	90-92	--	--	---	---	48-62	Golley (1965)[2]
USA	"	--	--	--	---	---	26	Dahlman & Kucera (1965)
India	*Dichanthium* grassland	--	--	--	---	---	51-64	Singh (1967)[2]
India	*Heteropogon* grassland	--	--	--	---	---	83	Jain & Misra (1972)[2]
India	*Dichanthium* grassland	--	--	82	---	---	45	Misra (1973)[2]
India	Grassland	99	--	96	---	---	47	Mall & Billore (1974)
Uganda	Grassland	174-188	--	--	---	---	--	Strugnell & Pigott (1978)
India	Grassland	77	--	119	---	---	52	Misra & Misra (1979)
Kenya	Savanna	92-208	69-200	127-250	92-185	131-195	88-190	Present Study

[1] LAB = Live aboveground biomass
SDB = Standing dead biomass
LBB = Live belowground biomass
DBB = Dead belowground biomass
TBB = Total belowground biomass

[2] Cited by Misra and Misra (1979)

biomass in this plant community. Other authors have found a more or less similar pattern and magnitude in turnover rate and time for other tropical grasslands (Misra and Misra 1979 and Rath and Misra 1980), Table 10.

Litter biomass exhibited the highest (250%) turnover rate in this ecosystem. There was a complete turnover of live biomass every 10 months. The turnover rate of dead belowground biomass was slightly lower (195%) with a turnover time of 13 months. This reflects a situation where more plant material was transferred from the live biomass compartment to the dead compartment than that lost through decomposition of dead materials. This explains why dead belowground biomass was always higher than live biomass (Fig. 13) during most of the study period.

5.6. Area Index

Maximum growth of plants is realized during the rainy seasons and it is during these periods that shoot growth is maximal due to the greater availability of soil moisture in most East African grasslands (McNaughton 1979b). Therefore, during these times shoots carry a lot of foliage and hence high LAI values are realized (Strugnell and Pigott 1978).

Stratified canopy sampling showed that LAI was highest in the first 20 cm above the ground canopy layer

followed by the second 20 cm canopy layer. This is true for many grazed grasslands because much of the above-ground biomass is distributed in a similar manner (Fig. 10b). Again, in this and similarly grazed ecosystems grasses do not elevate much of their meristematic apices above the soil surface until during the flowering phase to avoid damage by grazers (McNaughton 1979b).

The range in LAI values (0 - 3.1) is similar to that reported by Strugnell and Pigott (1978) (0 - 3.0) for a *T. triandra* dominated grassland in the Ruwenzori National Park, Uganda, in an enclosed site. LAI generally did not exceed 3.0 except during May, 1986 and highest values were recorded during the long wet season each year. Thus, LAI values varied sinusoidally from below 1.0 in the dry season to between 2.0 and 3.0 during the wet seasons showing a relationship between LAI and rainfall (Fig. 16).

This study is the first to examine the contribution of the stem and sheath area indices after confirming that these plant organs photosynthesise (see 4.5.2.c.). Although stem area index ranged from 0 to 0.95 while that of sheath ranged from 0 to 1.53 they, nevertheless, contributed greatly to the total area index with the highest value recorded of 5.57 in May 1986. Leaf area index alone was about 3.1 during May 1986. The stems and sheaths of grasses, therefore,

provided additional photosynthetic surfaces important in primary production.

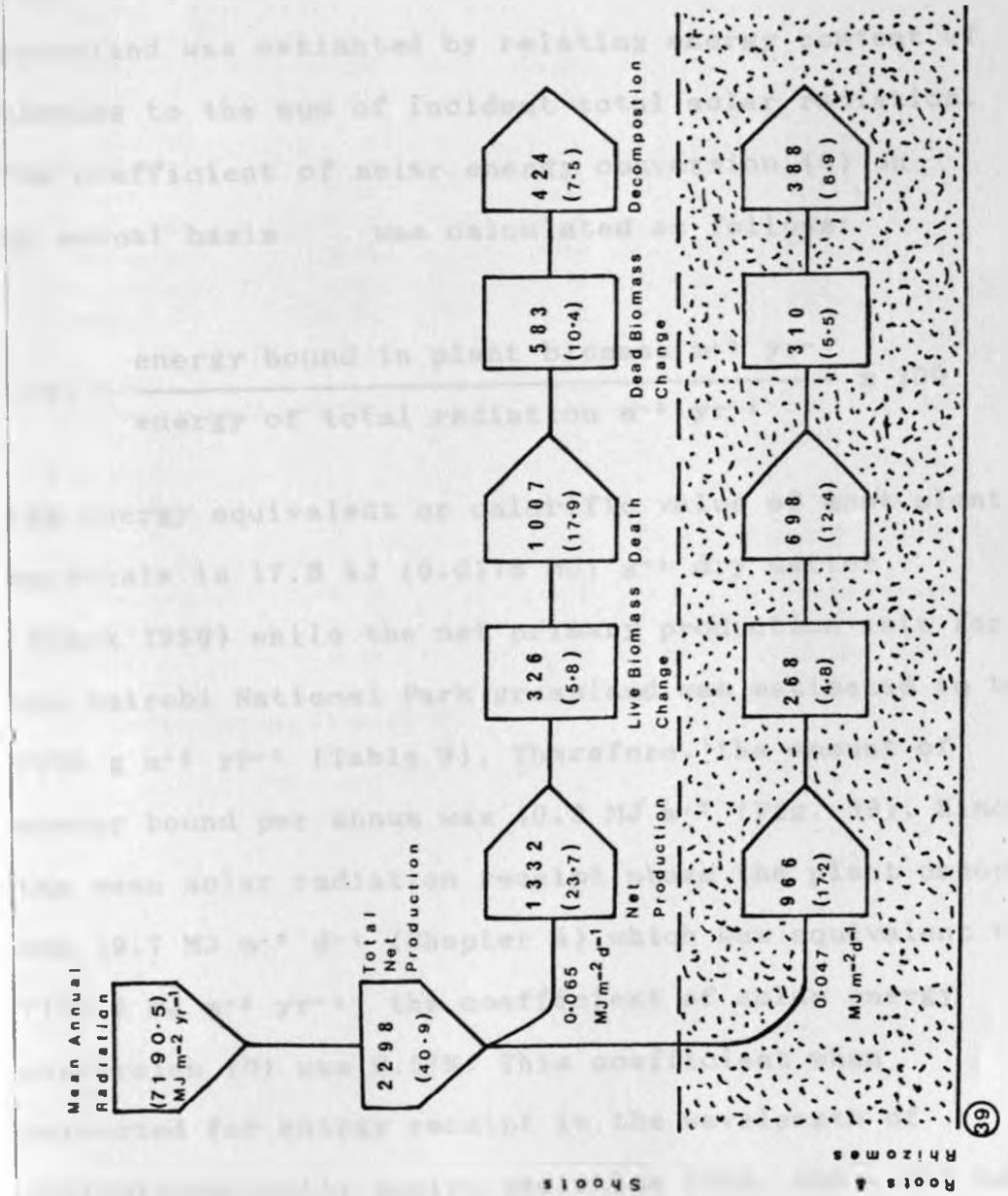
5.7. Total Solar Radiation

The daily average total solar radiation (350-2500 nm) received by the plant canopy of 19.7 MJ m^{-2} for the period under study was within the range for most tropical areas (Cooper 1975). Daily average total solar radiation ranges from about 14 to 21 MJ m^{-2} d^{-1} (3288 to 4932 cal cm^{-2} d^{-1}) in tropical areas depending on cloudiness and elevation (Landsberg 1965 and Cooper 1975). In East Africa, Strugnell and Pigott (1978) reported daily mean value of 20.2 MJ m^{-2} d^{-1} in the Ruwenzori National Park and Muthuri (1985) reported a value of 18.2 MJ m^{-2} d^{-1} in the papyrus swamp of Lake Naivasha. However, the values quoted by Macharia (1981) for four grassland ecosystems in Kenya were too low. His study gives values of about 13.7 to 15.8 cal cm^{-2} d^{-1} (0.57 - 0.66 MJ m^{-2} d^{-1}).

Solar radiation attenuation within the plant canopy is characteristic of tussock or bunch forming grasses due to mutual leaf shading (Caldwell *et al.* 1983). Tillers in some grasses, such as *T. triandra*, are clustered together resulting in a compact architecture. The magnitude of attenuation depends on the level of LAI. In March 1986, when LAI was low (Fig. 16) less

energy was intercepted by the plant canopy (Appendix 1). However, as LAI levels increased the amount of solar radiation intercepted increased. During May 1986, when LAI values were highest less energy penetrated to the ground surface and most of it was intercepted by the plant canopy. This general attenuation pattern is characteristic of grassland and other canopies where mutual leaf shading is common (Caldwell *et al.* 1983 and Jones 1986).

There is change in the solar radiation measured at the top of the plant canopy both in intensity and spectral composition from that which reaches the plant at the lower canopy levels (Nobel and Long 1985). This change is known to induce characteristic differentiation of leaf structure with high and low light intensities resulting in the so called sun and shade leaves on one plant (Bolhar-Nordenkampf 1985). Sun leaves have relatively lower chlorophyll content per plastid, higher ratio of chlorophyll a/b and higher net leaf photosynthesis than shade leaves. Shade leaves are adapted to low light intensities and, therefore, cannot make full use of high light intensities. High production rates of some plant communities have been associated with efficient interception and use of incoming solar radiation (Jones 1986).


Mean Annual Radiation
(7190·5) MJ m⁻² yr⁻¹
2298 (40·9)
Total Net Production
1332 (23·7)
326 (5·8)
1007 (17·9)
583 (10·4)
424 (7·5)
Shoots
Live Biomass
Death
Dead Biomass
Decomposition
Net Production
Change
0·065 MJ m⁻² d⁻¹
966 (17·2)
268 (4·8)
698 (12·4)
310 (5·5)
388 (6·9)
0·047 MJ m⁻² d⁻¹
Roots & Rhizomes
39

5.8. Coefficient of Solar Energy Conversion

Net efficiency of solar energy conversion is a factor attributed to high primary production in plant communities. Net efficiency of solar energy capture or conversion by the Nairobi National Park grassland was estimated by relating energy content of biomass to the sum of incident total solar radiation. The coefficient of solar energy conversion (η) on an annual basis was calculated as follows:

$$\eta(\%) = \frac{\text{energy bound in plant biomass } m^{-2}\ yr^{-1}}{\text{energy of total radiation } m^{-2}\ yr^{-1}} \times 100$$

The energy equivalent or calorific value of most plant materials is 17.8 kJ (0.0178 MJ) g^{-1} dry matter (Black 1956) while the net primary production rate for the Nairobi National Park grassland was estimated to be 2298 g m^{-2} yr^{-1} (Table 9). Therefore, the amount of energy bound per annum was 40.9 MJ m^{-2} (Fig. 39). Since the mean solar radiation receipt above the plant canopy was 19.7 MJ m^{-2} d^{-1} (Chapter 4) which was equivalent to 7190.5 MJ m^{-2} yr^{-1}, the coefficient of solar energy conversion (η) was 0.57%. This coefficient when corrected for energy receipt in the wavelength of photosynthetically active radiation (PAR, 400 - 700 nm) was 1.26%, assuming that PAR was 45% of total radiation (Dykyjova 1978 and Sims and Singh 1978c).

Table 11. Productivity and energy conversion efficiency (η) of some tropical and temperate grassland ecosystems.

Grassland Type	NPP (MJ m^{-2} yr^{-1})	(%) Efficiency of Energy Capture	Authority
Tropical			
semi-arid	3.87	0.12	*
sub-humid	25.95	0.81	*
Humid	19.82	0.69	*
Temperate			
desert	5.44	0.17	*
shortgrass	16.38	0.70	*
mixedgrass	18.86	1.03	*
tallgrass	16.09	0.72	*
mountain	25.28	1.02	*
Tropical			
Indian grassland	14.97	0.32-0.33	Naik & Mishra (1977)
East African grassland	9.54	0.29	Strugnell & Pigott (1978)
E.A. grassland			
-aboveground	23.70	0.73	Present study
-belowground	17.20	0.53	Present study
-total	40.90	1.26	Present study

* Cited by Sims and Singh (1978b)

The value of 1.26% energy conversion effeciency based on total net primary production and PAR obtained in this study compares well with those of other grassland ecosystems of the world (Table 11). Since most of these studies did not report values for belowground production it can be assumed that total community energy conversion efficiencies would have been higher in these studies. However, based on the aboveground production rates alone, the value of 0.73% obtained in this study compares well with those reported in tropical and temperate grasslands of the Indian sub-continent and USA (Sims and Singh 1978b). Botkin and Malone (1968) reported an annual efficiency rate of 1.8% based on PAR. However, they reported a 10% rate for the growing season. These differences arise because conditions for primary production are not favourable during much of the year. However, when conditions allow primary production to occur, the efficiency can be considerable, in terms of energy intercepted. On the African continent, using the annual net primary production data and the amount of solar radiation of Strugnell and Pigott (1978) corrected for PAR, a value of 0.29% was obtained.

The high rates of efficiency of energy capture obtained in this study are due to several factors. Virtually all the plants in this community are C_4

plants with high rates of CO_2 assimilation during the growing season. C_4 plants are known to fix high levels of CO_2 at high levels of ambient temperatures and radiant energy, factors abundant in this tropical ecosystem.

The percentage of energy captured in the above- and belowground biomass was 0.73% and 0.53%, respectively, based on PAR (45% of total solar radiation) (Table 11). This was a low proportion of the total solar energy received by the plant community and confirms that a majority of the energy in solar radiation was not utilized by grassland plants in their net production. However, it shows that a relatively large proportion of the energy flowed through the dead compartment (including decomposition) of the grassland ecosystem. This was 0.54% for aboveground and 0.38% for belowground production. Sims and Singh (1978b) in North American grasslands found the same trend of energy flow but more energy through the belowground pathway (0.065 MJ m^{-2} d^{-1}) than aboveground pathway (0.023 MJ m^{-2} d^{-1}) in ungrazed grasslands.

5.9. Use of Spectral Reflectance Ratio (SRR) to Estimate Aboveground Plant Biomass

Results of this study show that during the growing season when foliage was green there was a strong

correlation ($r = >-0.8$) between SRR and aboveground live biomass (Fig. 20). However, as the vegetation dried up, during the dry season, the relationship was less evident ($r = <-0.5$). This lack of correlation when the vegetation is dry and senescent between spectral reflectance ratio and live plant biomass lies in the mode of reflectance of solar radiation from the vegetation. In the visible portion of the spectrum the leaf reflectance is quite low (about 10%) with a peak at about 550 nm in the green region of the spectrum (Knipling 1970). There is maximum absorption (about 90%) at about 660 nm of solar radiation while the maximum reflectance centred at 730 nm is about 50% (Roberts *et al.* 1985).

The high absorption of radiant energy in the visible spectral region is due to leaf pigments, primarily the chlorophylls, although the carotenoids, xanthophylls and anthocyanins also have an effect (Rabideau *et al.* 1946). Chlorophyll *a*, the major pigment in higher plants, has absorption maxima at 660 nm. Leaf pigments absorb much of the solar radiation in the red (640-740 nm) portion of the spectrum and as a result reflectance is small. In contrast, reflectance in the near infra-red (740-1100 nm) is much greater so that the ratio of red to near infra-red in the reflected light varies as a function of the amount of green

foliage present. The reflectance ratios are all affected, not only by the amount of green foliage, but also by differences in reflectance from bare soil and from both green and dead foliage (Huete *et al.* 1985 and King *et al.* 1986). However, soils only show a small gradual increase in reflectivity across the spectrum and the spectral characteristics will, therefore, change as vegetation changes (Steven *et al.* 1985).

It has been further documented that the high infra-red reflectivity around 730 nm by leaves is caused by the internal cellular structure of leaves since the cuticular wax on a leaf is nearly transparent to visible and infra-red radiation and very little of the solar energy incident to the leaf is reflected directly from its surface (Knipling 1970). Radiation is diffused and scattered through the cuticle and epidermis to the mesophyll cell and air cavities in the interior of the leaf where it is further scattered as it undergoes multiple reflections and refractions. There are refractive index differences between air (1.0) and hydrated cellulose walls (1.4) inside the leaf. Knipling (1970) noted that during leaf senescence cell walls break down resulting in a decrease in reflectance of radiation from the leaves. This phenomenon may explain why the SRR values in this study increased with leaf age and death and were highest during the dry season when no

green plant materials were present.

Several workers have found good relationships between spectral reflectance and green plant biomass (McNaughton 1976 and Boutton and Tieszen 1983). However, the utility of spectral reflectance data in assessing standing crop biomass depends on the relationship of green leaves to the standing crop biomass (Tucker 1980). It, therefore, follows that these spectral reflectance data are not always related to standing crop biomass at a given point in time. Boutton and Tieszen (1983) found in the Masai Mara Gam Reserve that spectral reflectance ratio measurement of the vegetation was a reliable indicator of green biomass. However, significant errors in the biomass estimates were obtained in plots which contained less than 30% of green biomass. They recommended that where green biomass is in excess of 30% and where standing dead biomass is low, spectral reflectance ratio data can be used to estimate standing crop of a rangeland o pasture. Lamprey and de Leeuw (1986) using a modified spectral reflectance ratio called normalized differenc vegetation index (NDVI) found a highly significant relationship between NDVI and green plant biomass. They, however, found great interseasonal variability in NDVI and biomass estimate values.

Spectral reflectance ratio method can, however,

provide important data quickly for gross surveys of green biomass, for detecting large seasonal variations in green biomass during peak plant growth over large areas such as rangelands. The method would be less useful during the dry season for precise measurements in plant community productivity studies. Therefore, improvements of the method for assesment of biomass during dry months is recommended.

5.10. PHOTOSYNTHESIS AND RELATED PROCESSES

5.10.1. Field Measurements of Photosynthesis and related Processes

Maximum photosynthetic rates of 26.83 and 27.06 μmol m^{-2} s^{-1} for *T. triandra* and *P. mezianum* respectively, compare well with those quoted by Medina (1986) of between 2.2 and 43.9 μmol m^{-2} s^{-1} for African and South American C_4 grasses. However, values were much higher than those obtained from the field which were quoted by Medina (1986) to range from 2.2 to 7.9 μmol m^{-2} s^{-1}. Seasonal rates of CO_2 assimilation in this study were highest during the growing season and lowest during the dry season for both key species. This trend was due to the magnitude of rates of CO_2 conductance into leaf tissues through stomatal opening. Stomatal conductance rates were highest (between 0.533 and 1.1 cm s^{-1}) during the growing season and lowest (between

0.095 and 0.148 cm s^{-1}) during the dry season for both species. Although maximal rates of stomatal conductance were encountered during February 1985 in contrast to other months between November 1984 and January 1985, maximal rates of CO_2 assimilation were not attained during this month. The non-attainment of maximal CO_2 assimilation rates during February 1985 was probably due to the fact that plants had not fully recovered from the January 1985 drought conditions and did not fully regain their photosynthetic capacity during February 1985. Boyer (1971) reported similar observations.

The decrease in leaf water potential from high values of about -2 MPa to <-4 MPa for both key species from December (growing season) to January (dry season) reflected a decrease in the internal water status of plants. This decrease was followed by a decrease in CO_2 assimilation rates due to water stress. However, after late season rains of February 1985, the water status of plants improved. Photosynthetic rates increased from 2.17 to 16.86 µmol m^{-2} s^{-1} in *T. triandra* and from 10.40 to 23.73 µmol m^{-2} s^{-1} in *P. mezianum* during the same period. Water stress affects photosynthesis by reducing stomatal conductance to CO_2 from the atmosphere to the carboxylation sites within the leaf mesophyll tissue. Guard cells lose their turgor pressure which leads to closure of the stomata (Beadle

et al. 1985). Moreover, most of the photosynthetic tissue in this study during January 1985 was mature and senescent and leaves are known to lose a substantial amount of their photosynthetic capacity with age (Ticha *et al.* 1985). During the brief period of leaf expansion, photosynthetic capacity of leaves increases after which maximal photosynthetic rate remains relatively constant and then steadily declines with leaf age (Woledge and Parsons 1986). Decline in both stomatal and mesophyll conductances with leaf age have been reported to contribute to this fall in photosynthetic rates (Woledge 1972). This is also paralled by a decline in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity (Treharne and Eagles 1970).

Seasonal rates of transpiration were also highest during the rainy season and lowest during the dry season months. Maximal rates of transpiration were recorded during February 1985 (9.51 and 16.20 mmol m^{-2} s^{-1} for *T. triandra* and *P. mezianum* respecively). This was due to maximal rates (0.533 and 1.1 cm s^{-1} for *T. triandra* and *P. mezianum* respectively) of stomatal conductance encountered during the month. Leaf water potential estimates were highest (around -2 MPa for both key species) during the rainy season and lowest (<-4 MPa for both species) during the dry season due to depletion in soil moisture content. Soil water content

fell from an average of 40% during the growing season to about 11% during the dry season (Table 3). Rainfall which fell during the month of February 1985 for several days raised the plant water status from low values of <-4.0 MPa in January 1985 to -2.2 and -2.8 MPa in *T. triandra* and *P. mezianum* respectively. During the growing season leaf water potential of grasses remained more or less the same (about -2 MPa at midday) except at the end of the growing season when it dropped to <-4 MPa due to leaf age (Ticha *et al.* 1985) and soil water depletion (Knapp 1985). High seasonal leaf water potential values coincided with high values of photosynthetic rates and stomatal conductances. In the North American tallgrass prairie, Knapp (1985) found that during severe seasonal water stress (leaf water potential of <-6.00 MPa), photosynthesis decreased to zero, yet following a substantial late season rainfall photosynthesis increased from about 28 to 48% of early season rates.

Differences in leaf water potential among plants under longterm drought are mainly due to differences in rooting depth and root density and the regulation of transpiration at the stomata and canopy level. The extent to which leaf water potential declines and to which soil water is depleted in the root zone during the day is determined by the transpiration rate of the

whole plant (Schulze and Hall 1982). Leaf water potential dependence on changes in transpiration explains variations in diurnal and seasonal leaf water potential (Kappen *et al.* 1975). This explains partly why leaves of stressed and non-stressed plants may have the same leaf water potential but at different levels of transpirational water loss.

Air temperatures between months did not vary much but were slightly higher during the dry season with about 5°C difference. However, though mean temperatures were lower during the growing season they were an average of 35°C at midday. These temperatures were not limiting to plant growth and CO_2 assimilation process since most of the grasses were C_4 species (Black 1973).

Air relative humidity is an indicator of vapour pressure deficit (VPD) since it is the ratio of the actual vapour pressure to the saturated vapour pressure at the dry bulb temperature (Jones 1985). Plants do not respond directly to relative humidity but to vapour pressure deficit between the leaf and the air. Vapour pressure deficit is an index of the drying power of the air; the higher the deficit the greater the evapotranspiration. Highest seasonal rates of CO_2 assimilation for both key grasses occured during December 1984 (Fig. 19) when VPD was lowest (36 mbar) at midday. The month of January 1985 was very dry with VPD of about

40 mbar at midday and CO_2 assimilation rates were at very low levels for both *T. triandra* (2.17 μmol m^{-2} s^{-1}) and *P. mezianum* (10.40). This decrease in net photosynthesis was attributed to decrease in leaf stomatal conductance due to increase in VPD. Bunce (1984) found in sunflower that net photosynthetic rates decreased as VPD increased. In maize, Bunce (1982) found that stomatal conductance was reduced from 0.71 to 0.53 cm s^{-1} when VPD was 10 and 25 mbar respectively. At the same time photosynthesis was reduced from 39 to 33 μmol m^{-2} s^{-1} at the two respective VPD levels. Other authors have found large differences in vapour pressure deficits to cause reduced stomatal conductance in many species, both C_3 and C_4 (Lange *et al.* 1971, Cowan 1977 and Long and Woolhouse 1978). Leaf water potential, temperature and ambient humidity change in synchrony in natural environments and it is not known which of these factors is responsible for change in stomatal conductance that occur (Schulze and Hall 1982).

Light response curves for CO_2 assimilation rates of individual leaves of three grass species exhibited typical hyperbola shapes with CO_2 assimilation rates increasing with increase in light intensity. Leaves from the top canopy layer possessed higher rates of CO_2 assimilation (ranged from 22 to 24 μmol m^{-2} s^{-1}) than the

leaves from the middle and bottom canopy layers. Bottom canopy level leaves had the lowest maximal rates (ranged from 8 to 10 μmol m^{-2} s^{-1}) of photosynthesis in the three grasses, *T. triandra*, *P. mezianum* and *C. caesius* (Figs. 25, 26, 27). Although the leaves used were more or less of the same age, they had developed under different environmental conditions due to differences in the microclimate within the plant canopy. Top canopy layer leaves can be regarded as sun leaves while the bottom canopy layer leaves as shade leaves which behave differently in their photosynthetic activity at higher PFD values (Bolhar-Nodenkampf 1985). Woledge and Parsons (1986) noted that it was the difference in light received during leaf development and expansion that causes the difference in the photosynthetic capacity between shade and sun leaves. Prioul *et al.* (1980) found that chloroplast structure and Rubisco activity, both important determinants of photosynthetic capacity, appeared to be controlled by the amount of light directly reaching the leaf during leaf development. Other studies (Wilson and Cooper 1969, and Woledge 1971, 1973) have shown that grass leaves developed in dim light possess lower rates of photosynthesis per unit leaf area at light saturation, but similar or even higher rates at low light levels than leaves developed in high light intensities. Top canopy layer leaves did not light saturate at high PFD

rates (>1800 μmol [PAR] m^{-2} s^{-1}) and are, therefore, adapted to high light intensity environment for photosynthesis. This is unlike the lower canopy layer leaves which could not fully utilize high light intensities and appeared to suffer from photo-inhibition. Powles and Critchley (1980) noted that a common factor in photo-inhibition is an over-energization of the photosystem reaction centres resulting either from absorption of unusually high photon fluxes or from inadequate supply of electron acceptors, CO_2 and O_2, which act as sinks for photo-chemically generated energy (NADPH and ATP). This appears to be the case in the middle and bottom canopy leaves of the three grass species of the present study.

Boller and Nosberger (1985) found a similar pattern of light response curves for white clover (*Trifolium repens* L.) leaves from three different levels of the plant canopy. Light interception is a function of canopy architecture which may determine photosynthetic production of whole grass stands by either limiting light interception of young stands or by allowing light to penetrate more or less easily into the dense foliage of older plant stands. Results show that although the leaves used in the study were more of the same age, they possessed different photosynthetic capacities depending on their relative

position in the plant canopy. These differences in photosynthetic rates per unit leaf area are again due to structural and biochemical features of these leaves. Other studies have shown that both stomatal and mesophyll conductances are usually greater in leaves grown in bright light than those grown in dim light (Woledge 1977). Wilson and Cooper (1969) and Prioul *et al.* (1980) noted that in ryegrass such leaves possessed more stomata per unit leaf area, more mesophyll cells, more and larger chloroplasts and a greater activity of Rubisco. Recently, Raus *et al.* (1986) found that leaves of wheat developed in full sunlight exhibited less intercellular air space than those which developed in the shade. This was accompanied by increases in the number of chloroplasts with increasing canopy height suggesting a more compact arrangement of photosynthetic apparatus with canopy height. Top canopy leaves possessed higher grana numbers than bottom canopy leaves. Dunstone *et al.* (1973) also found that photosynthesis increased with canopy height. Decrease in distance between veins and between chloroplasts as found with increasing canopy height in wheat by Raus *et al.* (1986) is thought to facilitate the transport of water and photosynthetic assimilates (Parker and Ford 1982). This is correlated with higher photosynthetic activity in leaves in the upper canopy layer.

It has already been pointed that photosynthetic capacity of leaves growing within plant canopies may be reduced by the dim light prevailing during their development (Woledge 1977). Results of the present study show that there were reductions of about 50% in CO_2 assimilation rates in the middle canopy leaves and about 70% in bottom canopy leaves of the three grass species due to leaf shading. Reductions of up to 30% in canopy photosynthesis due to leaf shading during sward development as leaf area index increases have also been reported in temperate grasslands (Woledge and Leafe 1976). Reduced availability of solar radiation incident on young shoots shaded by standing dead biomass has been reported to reduce photosynthetic production in grasslands (Old 1969, Woledge 1973, Woledge and Leafe 1976 and Knapp 1984). This aspect of reduced solar energy in shaded areas plus the fact that these shaded leaves possess smaller photosynthetic capacities means that as the grass stands get older and accumulate more and more standing dead biomass, photosynthetic production will decline as a greater proportion of light is intercepted by dead or senescent leaf materials (Woledge and Parsons 1986).

Diurnal course in CO_2 assimilation rates for both *T. triandra* and *P. mezianum* showed a steady

increase during the morning hours to reach a peak around midday and a declined towards the evening hours. This was due to variability in prevailing environmental conditions. Air temperature (Fig. 24) and light intensity (Figs. 28, 29) increased with the course of the day and declined towards the evening hours after midday. An increase in leaf stomatal conductance during the course of the day upto midday (Fig. 33) favoured increased rates of CO_2 assimilation. However, plants suffered decreased water status at around midday (Figs. 31, 32) but not low enough to limit CO_2 assimilation when measurements were taken during the growing season. The two key grass species exhibited a one-peaked CO_2 assimilation pattern (Fig. 30) (Schulze and Hall 1982). One-peaked daily courses of both C_3 and C_4 plants are frequently observed with well-watered plants. Pearcy *et al.* (1974) reported one-peaked diurnal courses in leaf conductance in *Phragmites communis* Trin. growing in a moist habitat but under extremely high evapo-transpirational demands. In irrigated *Tidestromia oblongifolia*, Bjorkman *et al.* (1972) also noted a one-peaked daily course of CO_2 uptake and transpiration rates. Jones (1987) noted a similar trend in *Cyperus papyrus* L. in Lake Naivasha, Kenya.

Plants in this study exhibited two-peaked daily course in their physiological processes (photosynthesis

and stomatal conductance) during the dry season in January 1985 (Figs. 34 and 36 respectively). The first peak was noted in the morning hours followed by a mid-day stomatal closure. The second peak was noted in the evening hours. Two-peaked daily course in CO_2 exchange has been noted in C_3 and C_4 plants especially in arid environments (Pearcy *et al.* 1974). CO_2 uptake increases to high rates early in the morning, but stomatal closure at midday occurs to such a degree that CO_2 assimilation is restricted. Stomata open again in the late afternoon, resulting in a second peak of CO_2 uptake.

Leaf temperature of *T. triandra* increased with that of the air but remained slightly lower. It, therefore, appears that this species exhibited a lower leaf temperature regime than the ambient air. However, although *P. mezianum* transpired at slightly higher rates than *T. triandra* its leaf temperature remained slightly higher than that of *T. triandra*.

5.10.2. Photosynthetic Capacity of Different Plant Organs

This study found that all plant organs studied possessed appreciable numbers of stomata. Stomata act as passages for gaseous exchange between the plant and the atmosphere. They are thus important passages for CO_2 during the process of photosynthesis. In all cases, except in the stems of *T. triandra* and *C. caesius*,

plant organs possessed chlorophyll. Chlorophyll *a/b*-protein complex is important during photosynthesis since it is involved in the transfer of excitation energy during cyclic and non-cyclic photophosphorylation (Hall and Rao 1981).

This study confirmed that photosynthetic activity occurs in green plant organs (stems, sheath and inflorescences) of grasses other than leaf blades. Leaf blades as CO_2 assimilatory organs had the highest levels of photosynthesis in all grasses which ranged from 14.84 to 28.68 μmol m^{-2} s^{-1}. Photosynthesis of sheath with enclosed stem was in excess of 34% of that of leaf blade in all grasses and ranged from 6.25 to 13.54 μmol m^{-2} s^{-1}. Photosynthesis of inflorescence of *T. triandra* was 8.23 μmol m^{-2} s^{-1} about 29% of that of leaf blade. Again in the green stems of *P. mezianum* and *R. repens*, stem photosynthesis was about 25% and 62% of that of leaf blade photosynthesis, respectively . Data from Tieszen and Imbamba (1978) indicated that the finger millet inflorescence carried about 6% of leaf blade photosynthesis. This study is the first to deal with the contribution of various CO_2 assimilatory organs into the total photosynthetic activity of natural grassland species. Other studies have dealt with agronomic crops such as barley (Thorne 1959, 1965), finger millet (Tieszen and Imbamba 1978),

wheat and oats (Nalborczysk *et al.* 1981). Nalborczysk *et al.* (1981) found that in wheat the flag leaf contributed the most in photosynthetic activity while in oats, both the flag leaf and the second leaves exhibited similar photosynthetic activity at certain stages of plant development. The contribution of stem with sheath ranged from about 20% in barley to 60% in rye.

It is, thus, clear that other green plant organs including the stem, sheath with enclosed stem, and inflorescence are significant sources of products of photosynthesis. In evaluating the photosynthetic production of plants, it is, therefore, not enough to base the production on leaf blade photosynthesis alone as other green plant organs contribute a substantial proportion of the overall gross photosynthetic production in most natural grasslands.

5.10.3. Effects of Water Stress on Photosynthesis

The results presented in this study show that there was a corresponding decrease in CO_2 assimilation rate following a decrease in stomatal conductance due to plant water deficit after imposing water stress treatment. The drop in CO_2 assimilation rates due to water stress treatment ranged from 30 to 100% among the species (see section 4.6.1.). After rewatering the

stressed plants, CO_2 assimilation rates and leaf stomatal conductance increased substantially, recovering after about 5 to 8 days. CO_2 assimilation rates were restored with rewatering the water stressed plants and the degree of recovery ranged from 47 to 90% of the control values. There was an apparent dependence of CO_2 assimilation on the magnitude of leaf stomatal conductance in all plant species.

Stomatal closure is the primary factor associated with inhibition of CO_2 assimilation during the initial phases of plant water deficit. Boyer (1970b) showed that as the leaf water potential declined with increasing water stress, stomatal conductance progressively decreased. Other authors (Collatz *et al.* 1976 and Schulze and Kuppers 1979) have also shown that stomatal conductance is reduced by reduction in leaf water potential in several plant species during progressive water stress. However, Schulze and Hall (1982) argued that reduction of leaf stomatal conductance due to decline in leaf water potential is not a universal phenomenon in plants, and that a clear relationship between leaf stomatal conductance and leaf water potential is sometimes lacking. Results of this study, however, demonstrate that there was a clear relationship between leaf stomatal conductance and CO_2 assimilation rate on one hand and between stomatal conductance and leaf water

potential on the other hand.

Water stressing the plants led to reduced rates of CO_2 assimilation and the degree of reduction depended partly on the level of leaf water potential and partly on the particular plant species examined. It appears that plants behave differently to the effects of water stress depending on their biochemical make-up. Results of this study showed that NADP-me species (*P. mezianum, C. caesius and C. ciliaris*) suffered more loss of their photosynthetic activity due to water stress in the excess of 90%, with the exception of *T. triandra* (57%), see section 4.6.1 and Appendix 3. The rest of the species (*R. repens, E. paspaloides* and *D. aegyptium*), which were PEP-ck species, suffered less loss of their photosynthetic activity (<75%) except in *D. aegyptium* (100%). However, all species whether NADP-me or PEP-ck were able to regain their photosynthetic activity in excess of 50% of the control values after rewatering except *D. aegyptium* (47%). Giles *et al.* (1974) reported that the mesophyll chloroplasts of C_4 plants are more readily disorganized or their activity disrupted at low leaf water potentials than are chloroplast in the bundle sheath. Since NADP-me species do not have grana in their bundle sheath chloroplasts and that they lack PS II activity, their cyclic and non-cyclic photophosphorylation activities are

curtailed under water stress more than those of NAD-me or PEP-ck species which possess both PS I and PS II. During photosynthesis, NADP-me species generate the NADP to reduce oxaloacetate to malate in the mesophyll cells. On the other hand NAD-me and PEP-ck species do not use any NAD in the mesophyll cells during the conversion of oxaloacetate to aspartate. In the bundle sheath cells NADP-me species use more reducing power to reduce phosphoglyceric acid (3-PGA) to 3-phosphoglyceraldehyde while aspartate formers use the reducing power in the bundle sheath cells in two steps, namely, to reduce oxaloacetate to malate and 3-PGA to 3-phosphogryceraldehyde in the Calvin cycle. It has already been pointed that water stress affects more the mesophyll chloroplasts of C_4 plants by disrupting their activity than bundle sheath chloroplasts (Giles *et al.* 1974). Thus, in NADP-me species, one essential step in their photosynthesis is curtailed by water stress, that is, oxaloacetate is not reduced to malate in the disrupted mesophyll cells. This is because the generating process of NADPH, the Hill reaction in mesophyll cells, is curtailed during water stress. Again NADP-me species lack Hill reaction in their bundle sheath chloroplast (Downton *et al.* 1970 and Osmond 1974). In NAD-me and PEP-ck reducing power can still be generated in bundle sheath chloroplasts

which remain relatively intact during water stress and possess Hill reaction. This may explain why NAD-me and PEP-ck species are more drought avoiding and are, therefore, found in drier environments than NADP-me species (Ellis *et al.* 1980).

Boyer (1971) found that stomatal closure was not sufficient to account for the reduction in net photosynthetic rate in sunflower at low water potential. A parallel fall in the rate of photosynthetic electron transport was observed in the same experiment though the eventual decline of photosynthesis to zero was later found only to be correlated with cyclic and non-cyclic photophosphorylation (Keck and Boyer 1974). This reduction in photosystem I and II activity has been observed over a range of water stress treatments in wheat, barley and cotton (Nir and Poljakoff-Mayber 1967 and Fry 1970). The observed loss in photosynthetic activity in grasses of this study during water stress may have been caused by reduction of photosynthetic RubP substrate regeneration. The initial biochemical effect of water stress in plants is a reduction in the capacity of ribulose-1,5-bisphosphate (RubP) substrate regeneration during the dark reaction of photosynthesis and this results in reduction in net photosynthetic CO_2 uptake (Farquhar and Sharkey 1982).In the reductive pentose phosphate pathway (Calvin cycle) CO_2 is fixed

into sugars. This process occurs in four phases, namely carboxylation, reduction, regeneration and product synthesis, and is the only form of CO_2 carboxylation which results in a net production of dry matter or biomass. In the carboxylation phase CO_2 is added to the 5-carbon sugar, RubP to form two molecules of phosphoglyceric acid (PGA). PGA is reduced to glyceraldehyde using the assimilatory power of NADPH and ATP, a process which takes two steps, first phosphorylation, adding on a Pi from ATP and then reducing with NADPH (Hall and Rao 1981). The enzyme responsible for the carboxylation of CO_2 with its substrate RubP is Rubisco. The 3-carbon PGA is either used to regenerate the 5-carbon substrate RubP for further CO_2 fixation reactions or leaves the cycle as a 6-carbon sugar. Therefore, when water stress reduces the capacity for RubP substrate regeneration it reduces CO_2 carboxylation. The reduction in CO_2 carboxylation (photosynthesis) will depend on the degree of water stress and the plant species; for example in *D. aegyptium* there was a total reduction in CO_2 assimilation while in *R. repens* only about 30% of photosynthetic capacity was lost although *R. repens* was more water stressed. Internal factors (such as internal CO_2 evolution, increase in chemical resistance to CO_2 fixation, etc.) other than stomatal closure have been

found to limit net photosynthesis (Palta 1983). Chloroplasts have also been shown to lose their photosynthetic activity causing reduction in the net photosynthesis with water stress (Mathews and Boyer 1984).

Rewatered plants in this study exhibited varying degree of recovery of their photosynthetic capacity after water stress treatment. It can be seen (see section 4.6.1. and Appendix 3) that recovery depended primarily on the degree of the preceding plant water deficit. Where plant water deficit was too severe, incomplete recovery was encountered (for example in *P. mezianum* and *D. aegyptium*). Photosynthetic CO_2 assimilation did not recover fully in all plants for upto 5 days after rewatering. Boyer (1971) also found that photosynthetic CO_2 uptake in leaves of sunflower in high irradiance did not fully recover from a water deficit for one to two days after rewatering. However, it has been reported that frequent rapid recovery of photosynthesis after a period of water stress is due to the fact that chloroplast function is still maintained during the period of water stress (Ludlow and Ng 1974). It has been hypothesized that leaf ageing is suspended during the periods of water stress and that after rewaterings plants still have the capacity for photosynthesis commensurate with their physiological age (Quarie and Jones 1977). However, recovery of photo-

synthetic CO_2 assimilation is often delayed owing to after effects of water stress which prevent full stomatal opening.

Results of the present study show that total chlorophyll (*a*+*b*) content declined with water stress by between 9 and 38% for all species under study. This general decrease in levels of chlorophyll *a*/*b* during water stress found in the present study has been observed in other plants by several authors. Alberte *et al.* (1975) demonstrated that there was at least 50% inhibition of chlorophyll *a*/*b*-protein complex synthesis under mild leaf water stress (0.8 MPa) conditions. Alberte *et al.* (1977) observed in maize a drop in leaf total chlorophyll content during water stress conditions. Rewatering the stressed plants resulted in a rapid chlorophyll accumulation after a lag period. These authors also noticed that water stressed leaves had much higher (4.4) ratios of leaf chlorophyll *a*/*b* than the controls (3.0). This trend was also noted by Conroy *et al.* (1986) in the *Pinus radiata* needle leaves. Alberte *et al.* (1977) attributed the loss of chlorophyll during water stress to loss of pigment in the light-harvesting chlorophyll *a*/*b*-protein which resulted in an elevated chlorophyll *a*/*b* ratios. They postulated that the losses in the lamellar content of the light-harvesting chloropyll *a*/*b*-protein in response to water

stress can be attributed either to greatly enhanced catabolism of the protein complex or to severe retarda tion of synthesis (assuming rapid turnover under norma growing conditions). Hsiao (1973) reported that one of the most common and major consequences of tissue water stress is destruction of intracellular membrane systems. Because the light-harvesting chlorophyll *a/b*-protein complex is a major intrinsic membrane constituent, it is possible, therefore, that losses in this component may lead not only to perturbation of the structural organization of the chloroplast membrane, but also to a reduction in the efficiency of the membrane-dependent electron transport system of photo-synthesis. Alberte *et al.* (1977) suggested that the rapid breakdown of the chlorophyll *a/b* protein complex under water stress suggests strongly the use of this complex as a readily mobilized source of amino nitrogen for maintenance protein synthesis as well as a source of carbon for energy production during water stress. It has already been pointed out that plant water stress affects cyclic and non-cyclic photophosphorylation in stressed plants (Keck and Boyer 1974). Chlorophyll *a/b*-protein complex is involved in the transfer of excitation energy during cyclic and non-cyclic photo-phosphorylation (Hall and Rao 1981). Cholorophyll *a/b*-protein complex molecules are located in the

intracellular thylakoid membranes which are specific targets for water stress (Hsiao 1973 and Alberte *et al.* 1977).

Some authors (Ghorashy *et al.* 1971) have noted a complete cessation of photosynthetic activity in plants subjected to severe water stress and ultimate reduction in growth as a result of restricted supply of photosynthates. Water stress not only limits the photosynthetic capacity of leaves but also reduces leaf growth, and LAI. Thus,canopy photosynthesis is further reduced (Ripley and Redman 1976).

5.11. LEAF ANATOMY

C_4 plants are divided into three Kranz subtypes on the basis of bundle sheath decarboxylating enzymes namely; NADP-malic enzyme, NAD-malic enzyme and PEP-carboxykinase (Gutierrez *et al.* 1974). The authors noted that NADP-me species lacked well-developed grana in bundle sheath chloroplasts and that the bundle sheath chloroplasts were in the centrifugal position. NAD-me species had bundle sheath chloroplasts in the centripetal position and they contained grana. PEP-ck species had bundle sheath chloroplasts in the centrifugal position and they contained grana.

All the seven grass species studied were found to be C_4 species. Four of the grasses were NADP-me and

three were PEP-ck Kranz sub-type species. None of the grasses belonged to the NAD-me Kranz sub-type. From the Athi River site NADP-me grasses included *T. triandra*, *P. mezianum*, *C. caesius* and *C. ciliaris* while *R. repens* and *E. paspaloides* were PEP-ck Kranz sub-type species. *D. aegyptium* from around Magadi was also a PEP-ck Kranz sub-type.

C_4 grasses are associated with high temperature and light regimes and low soil water availability (Laetsch 1974, Tieszen *et al.* 1979, and Ellis *et al.* 1980). Laetsch (1974) noted that C_4 plants and their leaf structural features are adaptations for efficient carbon fixation in regions with intermittent aridity.

The epidermis of the four grasses possessed thick lignified epidermal walls which enables the plants to exist in dry environments by minimizing water loss through transpiration. This is a characteristic feature of xerophytes (Esau 1960). In addition to the thick epidermal cell walls found in the grass leaves, the leaves lacked conspicuous intercellular air spaces. The intercellular air spaces constitute a large surface area in plant leaves, especially in mesophytes (Esau 1958). The ratio of internal to external surface area differs with plants from different environments. Esau (1958) notes that mesomorphic leaves have ratios of between 11.6 and 19.2 while it is between 17.2 and 31.3

for xeromorphic leaves. Therefore, xeromorphic leaves contain less intercellular air space. The ratio of internal to external surface is positively correlated with the rate of transpiration (Turrell 1944) so that the structure favourable for photosynthesis induces at the same time a high loss of water.

Scanning electron micrographs of the dominant grass species showed the presence of stomata on both sides of the leaf blade (adaxial and abaxial). Stomata were additionally found in the sheaths, stems and inflorescences of the grass species except *P.mezianum*. Stomata act as passages for CO_2 and water vapour exchange during photosynthesis and transpiration process. Stomatal openings were frequently found in crypts (see Appendix 5). The presence of crypts is an adaptation in plants to reduce transpirational losses by creating a large boundary layer around the stomatal openings.

Plants adapted to regimes of high evaporative demands such as those found in arid environments show the presence of hairs on their surfaces, a feature termed as pubescence. Gates (1968) noted that pubescence can potentially reduce the heat load of leaves by increasing the reflectance from the leaf surface, which reduces the amount of radiation absorbed. There is a great adaptive value of a reduced radiation load to plants growing in hot or semi-arid

environments in terms of reduced leaf water losses and hence leading to better water use efficiencies of these plants. Ehleringer *et al.* (1976) found that leaf pubescence in some desert plants reduced radiation (PAR) absorbance by as much as 56%. However, they found this reduction in PAR led to a reduction in the photosynthetic rate caused by decreased light absorption rather than decreased CO_2 conductance through the boundary layer. Pubescence also creates a large boundary layer around the leaf surface thereby reducing transpirational losses. The protrusions (papillae) found on the epidermal cells of *T. triandra* may also act the same way as hairs by creating a large boundary layer above the leaf surface and especially around stomatal apertures leading into reductions in transpirational losses.

There was a heavy coat of wax in all the plant species examined. Wax drastically cuts transpirational losses from plant tissues by rendering surfaces less permeable to water (Esau 1960). Once the stomata are closed, little water is lost through the wax covered cuticle of epidermal cells.

Some of arid grasses have bulliform cells located on the upper surface of leaves between the vascular bundles. One of the grasses, *R. repens* is a good example. Bulliform cells cause leaf rolling during

water stress (Stover 1951). When bulliform cells lose their turgidity with water stress by losing water to the mesophyll cells and the intercellular spaces, the turgidity of the cells of the lower side of the leaf causes the leaf to fold or roll, depending on the number of rows of the bulliform cells. This cuts transpirational losses by reducing the effective leaf area and increasing boundary layer resistance (Beadle *et al.* 1985).

CHAPTER 6

GENERAL CONCLUSIONS

The results obtained from this study show that East African grasses are among the most productive of those in the tropical African grasslands. The aboveground net primary production (Pn) rate of 1332 g m^{-2} yr^{-1} or 3.65 g m^{-2} d^{-1} obtained in the study is the highest reported for tropical African grasslands (Table 9, Chapter 5). This study, beside that of Strugnell and Pigott (1978) is the only study in tropical African grasslands to report estimate of belowground net primary production. The belowground net primary production rate in this study was 965.8 g m^{-2} yr^{-1} or 2.65 g m^{-2} d^{-1}. Therefore, the net primary production rate for both above- and belowground compartments was 2298 g m^{-2} yr^{-1} or 6.3 g m^{-2} d^{-1} in the present study. Since most studies did not ascertain the magnitude of belowground Pn, most of the values quoted are underestimates of the true values. Results of this study show that the level of underestimation due to non-determination of belowground biomass would have ranged from about 88% to 89%, respectively. Moreover, the methods used to estimate Pn in most tropical African grasslands may have led to underestimation of its true values since the methods either did not include plant mortality and decomposition or belowground biomass. The level of underestimation due

to not accounting for plant mortality, decomposition of dead plant materials and accounting for shoot production only ranged from 34% to 89% (see Table 8, Chapter 5). It is thus, quite clear from the results presented herein that the role of plant mortality and decomposition in estimation of Pn is important.

The role of rainfall in influencing primary production was shown to be crucial. The overall Pn for the entire period was calculated to be 6.3 g m^{-2} d^{-1} for both above- and belowground compartments. However, during the rainy season, when the soil moisture was high due to rains, Pn values ranged between 13 and 18 g m^{-2} d^{-1} (see section 5.4., Chapter 5). McNaughton (1979b) obtained higher values (20-40 g m^{-2} d^{-1}) during the growing season in the Serengeti grassland. The present study demonstrated that during the dry season Pn was belowground directed while it was aboveground directed during the growing season.

Results show that the plant canopy intercepted about 64% of total solar radiation during the growing season (Chapter 4). This shows that there was enough solar radiation, from an average of 20 MJ m^{-2} d^{-1}, intercepted for biomass production in this ecosytem. The coefficient of solar energy conversion (η) on an annual basis based on PAR (about 0.73% for aboveground and 0.53% for belowground) compares well with those of

other grasslands of the world which ranged from 0.12% for arid grasslands to 1.03% for temperate mixedgrass prairie (Table 11, Chapter 5). The values of the present study are among the highest mainly due to the methodology of estimating Pn in which account was taken of the amount of production in the belowground compartment and that lost through plant mortality and decomposition.

The noted high rates of Pn in the present study was, as already mentioned, also due to the high rates of CO_2 assimilation rates exhibited by the C_4 grasses which dominated the grassland. Their maximum rates (about 27 μmol m^{-2} s^{-1}) compare well with 2.2 to 43.9 μmol m^{-2} s^{-1} quoted for African and South American grass species by Medina (1986). In the present study, CO_2 assimilation rates were highest during the growing season which coincided with high soil moisture content and leaf stomatal conductance. This resulted in the high Pn rates observed during the growing season.

Most studies have shown that leaf area index is an important variable in grassland productivity measurements (Loomis and Williams 1963, Redman 1975, and Rath and Misra 1981). However, no study has demonstrated the importance of other green plant structures (stems, sheaths and inflorescences) in measurements of productivity of natural grasslands. Therefore, the present

study has demonstrated that these green plant structures are important sources of products of photosynthesis in natural grasslands. The SEM micrographs and chlorophyll determinations demonstrated that these structures contained stomata and chlorophyll (except the stems of *T. triandra* and *C. caesius*). Since these green structures contained chlorophyll and stomata they were shown to carry out photosynthetic activity. Photosynthetic rates of green stems ranged from 25% to 62% of that of leaf blade while that of sheath was an average of 34%. Photosynthesis of inflorescence was about 29% of that of leaf blade on the average.

This study has clearly demonstrated that in modelling productivity of natural grassland ecosystems account should be taken of other green plant structures such as stems, sheaths and inflorescences. This study, therefore, proposes that a variable termed total area index to include leaf, green stem and inflorescence area indices be used in order to include the contribution of of all green plant structures to net primary production.

Water stress experiment showed the dependence of photosynthesis on plant water status (see Chapter 4). Photosynthetic rates dropped by about 30% to >100% among the plant species due to drop in plant water status. Photosynthetic activity recovered after re-

watering. This is a feature which resembles that found during the growing season of October to December 1984, the drought period of January 1985 and the late dry season rainfall conditions of February 1985. Water stress was shown to act primarily on the leaf stomatal conductance with high levels of water stress resulting in lower leaf stomatal conductances and hence lower photosynthetic rates. This ultimately will result in lower biomass production.

Results of this study again demonstrated that NADP-me species (*P. mezianum*, *C. caesius* and *C. ciliaris*) suffered more loss of their photosynthetic activity due to water stress than were PEP-ck species (*R. repens* and *E. paspaloides*). *T. triandra*, an NADP-me species, lost only about 57% of its photosynthetic activity due to water stress which may show reasons why this species dominated this semi-arid plant community. The reasons why *D. aegyptium* (a PEP-ck species) suffered such a high loss (>100%) in its photosynthetic activity with water stress is not known.

It has been shown that *T. triandra* contributed the most biomass in this ecosystem (see Chapter 4). *T. triandra* was shown to be fairly tolerant to water stress and, therefore, this makes it an important grass species to consider for rehabilitating denuded semi-arid lands with similar climatic conditions.

Moreover, PEP-ck species, *E. paspaloides* and *R. repens* appear to be promising drought resistant species for use in rehabilitating denuded semi-arid lands.

Results of this study showed that spectral reflectance ratio (SRR) to estimate live biomass is a promising method in grassland production ecology. There was a good relationship between SRR and green biomass during the growing season (section 4.4., Chapter 4). However, the relationship was poor during the dry season when leaves were senescent. It became evident from the results that spectral reflectance ratio data were not always related to standing biomass at a given point in time, especially during the dry season.

In conclusion, the results of this study show that East African grasslands are among the most productive of tropical grasslands. This productivity is mainly limited by failure of rainfall during the dry seasons. Conditions that favour high productivities include high rainfall, solar radiation, optimum temperatures and high rates of CO_2 fixation. The study also showed that other green plant structures (stems, sheaths and inflorescences) contributed greately to net primary production. These structures were shown to possess stomata and exhibited photosynthetic activity.

The importance of sampling for belowground biomass has been demonstrated in this study. Below-

ground biomass production has been shown to account significantly (42%) to the total net primary production of these grasslands. Hence, it has been demonstrated clearly that most of the available primary productivity data are gross underestimates of the true values in most tropical grasslands.

This study has also shown the importance of dead material decomposition in estimating net primary production. Decomposition was shown to be high during the growing season in these grasslands. Decomposition is a vital process in nutrient cycling by which nutrients are released into the nutrient pool for uptake by plants during growth. Hence, decomposition contributes greatly to net primary production.

This plant community consisted of both NADP-me and PEP-ck species. It was shown that one NADP-me (*T. triandra*) and two PEP-ck species (*E. paspaloides* and *R. repens*) are fairly drought tolerant. These may be promising species for rehabilitating denuded semi-arid areas due to their resistance to water stress. These species possessed high rates of CO_2 assimilation under water stress conditions.

Results of spectral reflectance ratio data show a promising method for providing important data quickly for gross surveys of biomass over large areas such as rangelands during the growing season.

It is, therefore, the hoped the results of this study will form a basis for modelling productivity of tropical grasslands, as well as helping in the future formulation of management and planning programmes of these grasslands for higher plant and animal productivities.

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Appendix 1. Mean solar radiation (MJ m^{-2} d^{-1}) received at various canopy levels in various months, 1986.

CANOPY LEVEL	MARCH	APRIL	MAY	JUNE	JULY
0 cm	11.07	7.51	7.23	7.40	7.30
20 cm	20.82	17.30	17.47	15.70	14.61
40 cm	22.35	20.50	17.30	19.20	19.10
Above Canopy	23.53	21.93	19.36	19.68	19.32

Appendix 2. Mean values of Live Plant Biomass and SRR ($\bar{X} \pm$ S.E.)

Month	Biomass	SRR
June, 1986	299.96 ± 16.46	0.42 ± 0.008
July, 1986	300.05 ± 6.38	0.58 ± 0.009
September, 1986	160.15 ± 3.70	0.78 ± 0.049
October, 1986	137.78 ± 3.07	0.81 ± 0.017
November, 1986	167.60 ± 6.49	0.76 ± 0.035
December, 1986	243.95 ± 30.15	0.51 ± 0.014

Appendix 3. Mean values of physiological variables[1] for different water stress treatment for various grass species.

SPECIES	CONTROL		STRESSED		REWATERED	
	CO_2	gs	CO_2	gs	CO_2	gs
T. triandra	22.35	0.895	9.64	0.323	14.40	0.438
P. mezianum	16.19	0.628	-1.61	0.420	10.99	0.555
C. ciliaris	34.02	0.728	2.01	0.173	25.44	0.480
C. caesius	25.44	0.623	1.40	0.208	13.58	0.233
R. repens	26.28	0.540	7.23	0.195	16.09	0.413
E. paspaloides	24.61	0.543	17.74	0.328	22.36	0.505
D. aegyptium	23.60	0.770	-2.41	0.160	11.24	0.510

[1] CO_2 = CO_2 assimilation rate ($\mu mol\ m^{-2}\ s^{-1}$)
gs = stomatal conductance ($cm\ s^{-1}$)

Appendix 4. Leaf water potential (MPa) of control, water stressed and rewatered plants ($\bar{X} \pm$ S.D.; n = 5)

Species	Control	Stressed	Rewatered
T. triandra	-1.48 ± 0.31	-1.65 ± 0.10	-1.46 ± 0.33
P. mezianum	-1.38 ± 0.11	<-4.00	-3.24 ± 0.21
E. paspaloides	-1.48 ± 0.08	-1.60 ± 0.24	-1.49 ± 0.09
C. ciliaris	-1.40 ± 0.14	-3.20 ± 0.15	-2.40 ± 0.25
C. caesius	-1.42 ± 0.05	-3.54 ± 0.37	-2.36 ± 0.17
R. repens	-1.44 ± 0.06	-2.52 ± 0.05	-1.46 ± 0.02
D. aegyptium	-1.08 ± 0.28	-1.94 ± 0.13	-1.39 ± 0.39

Appendix 5. SEM diagnostic features encountered in two East African grass species dominant at the Study Site.

PLANT ORGAN	*T. triandra*	*P. mezianum*
Leaf blade	(i) Stomata - adaxial & abaxial (ii) Prickles - adaxial (iii) microhairs - abaxial (iv) Papillae - adaxial & abaxial (v) Stomatal crypts (vi) Subsidiary cells (vii) Wax coat	(i) Stomata - adaxial & abaxial (ii) Prickles - adaxial & abaxial (iii) microhairs - adaxial & abaxial (iv) Heavy wax coat
Sheath	(i) Stomata (ii) Papillae (iii) Microhairs (iv) Prickles (v) Subsidiary cells (vi) Stomatal crypts (vii) Wax coat	(i) Stomata (ii) Microhairs (iii) Prickles (iv) Subsidiary cells (v) Heavy wax coat
Inflorescence	(i) Stomata (ii) Prickles (iii) Papillae (iv) Microhairs (v) Macrohairs (vi) Wax coat	
Stem	(i) Stomata (ii) Subsidiary cells (iii) Heavy wax coat (iv) Stomatal crypts	(i) Stomata (ii) Subsidiary cells (iii) Heavy wax coat

Appendix 6

Calculation of Vapour Pressure Deficit (VPD)

$VPD = e_o - e_s$

where,

e_o = vapour pressure of water of air in cuvette

e_s = saturated vapour pressure at cuvette air temperature

$$e_s = 6.13753 \cdot \text{Exp}(t_a(18.564 - t_a / 2544.4) / (t_a + 255.57)) \cdot 10^{-3}$$

where,

t_a = air temperature

$e_o = e_s \cdot h_c/100$

h_c = % relative humidity in cuvette