A STUDY ON THE GROWTH AND DEVELOPMENT OF GRASSES WITH EMPHASIS ON THEIR ROOT SYSTEMS

BY

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DECLARATION

I declare that this thesis, entitled "A Study on the growth and development of grasses with emphasis on their root systems" has not been submitted for a degree in any other University.

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ABSTRACT

The growth of six grasses, grown as spaced plants under two ecologically different habitats in Kenya, were studied with the object of obtaining basic information on their growth and development. This information is an essential part of general research aimed at the improvement of stability and value of rangelands in East Africa. An introduction to the grass species and the experimental sites is given, and methods employed are described.

Plots of Cenchrus ciliaris var.biloela, Chloris gayana var.mbarara and Panicum maximum var.makueni were established at Muguga in April 1968 and sampled nine times until March 1969. In addition, at Muguga (2,086 m, high rainfall) and Kedong (1,878 m, low rainfall) the above mentioned grasses and Cenchrus ciliaris var.mbalambala, Eragrostis superba and Themeda triandra were sampled five times from April 1967 to February 1968 and subsequently during May to July of the same year.

Comparative dry weight yields and plant part ratios, and comparisons between spaced plants and swards were included in the study.

The evaporative demand on plants was similar at the two sites, but relatively large differences in rainfall and soils were recorded. Yields and growth trends, however, were similar.

Large differences were obtained between species. High shoot yields were recorded for P.maximum and C.gayana while root yields were high in C.gayana

and the two C.ciliaris varieties. In 28 month old sward plots, C.ciliaris var.mbalambala yielded 7,000 kg/ha root dry matter compared to 3,300 kg/ha for P.maximum.

Defoliated plants of P.maximum yielded less above ground, had smaller root yields, shallower rooting depths and less horizontal spread than non-defoliated plants.

The relationship between above and below ground growth expressed as leaf/root and shoot/root ratios was calculated: the C.ciliaris varieties and T.triandra gave low ratios. The ratios in most species varied throughout the growth period. A simplified method for determining relative differences between shoot/root ratios of perennial grasses is given. Shoot/root ratio values of spaced plants, and plants grown in swards were similar; values obtained for spaced plants are, therefore, of direct application to swards.

Mean nodal root diameter and nodal root branching differed greatly from one species to another. C.ciliaris var.biloela had the coarsest but the least branced nodal roots while the opposite was found for P.maximum. The cortex remained intact in both C.ciliaris varieties 14 months from planting. The cortex of nodal roots of P.maximum was lost within 3 months of planting except for short sections behind the root tips. In the other grasses the root cortex was lost, but to a lesser degree. Visual examination at any of the samplings did not reveal any dead roots.

A mucilagenous layer to which soil particles adhered was observed on the roots of E.superba and T.triandra. These two species also had a relatively higher density of roots in the soil surface layer at Kedong as compared to the other grasses. At Muguga (1968-1969) it was shown that the amount of roots present in the

0-20 cm soil layer as a per cent of total roots changed considerably throughout the growth period.

Excavated plants and readings from gypsum resistance blocks indicated that the grasses could be placed in two groups, those that were deep rooting (*C.ciliaris* varieties, *C.gayana* and *P.maximum*) and those which were shallow rooting (*E.superba* and *T.triandra*). Rooting depth was greater under swards as compared to spaced plants.

At Muguga (1968-1969) differences between root volumes were comparable to differences in root yields, except for slight deviations caused by individual changes in the specific weight of roots.

The specific weight of leaves of *C.ciliaris* var. biloela was higher, and for *P.maximum* lower, than that of *C.gayana*. From April to July, the specific weight of leaves increased although both temperature and total light decreased.

The results are discussed in relation to climate and soils, and recommendations, believed to be of value to the planning of future work and range management, are given.

CHAPTER 1

INTRODUCTION

Throughout much out East Africa rainfall is both low in quantity and erratic in distribution with the result that, during consequent periods of low soil moisture, plant growth may be seriously restricted. As plant growth becomes limited, the rangelands are often destroyed through overgrazing, resulting in considerable livestock and wildlife losses.

In East Africa, rangelands are usually characterized as areas receiving less than 760 mm rainfall per annum; areas where rainfall is higher are usually considered as better potential land. According to MacGillivray (1967) approximately 63 per cent (1,052,000 square km) of the total land area in East Africa is available for pasture and range. Improvement in the stability and value of these areas requires intensive research into many fields. Although several means of increasing the potential of the rangelands are available, such as control of the number of animals to avoid overgrazing, control of undesirable bush by the use of fire, chemicals or machines and artificial reseeding, these cannot be used without knowledge of how they should be applied under various environmental conditions. The East African rangelands are characterized by a complex of ecological variables. One example that illustrates this clearly is rainfall. Annual and monthly rainfall for a given location vary greatly from one year to another (Heady 1960). Also, on an East African basis there are great differences as to the season of the year when precipitation occurs

(Walter 1952). Griffiths (1958) divided East Africa into ten different climatic zones. For example, the central region of western Uganda including Ankole has two rainy seasons a year, from February to May and from September to November, while the Karamoja region has only one wet season from April to September. Most rangelands in Kenya have two rainy seasons: March to May and November to December. In Tanzania, the greater part of the drier regions have only one wet season per year, for example the Serengeti receives most of its rainfall during December to May.

In addition to the large variations in rainfall and rainfall pattern, the effectiveness of a given amount of rain will again depend on the capacity of the soils to absorb and store water available to plants, and on the evaporative power of the air.

As the root system of a plant is the main organ through which both nutrients and water are taken from the soil, it is relevant to obtain basic data concerning growth. The need for research into this field in East Africa was stressed at a Pasture Specialist Committee Meeting held at the National Research Station Kitale in June 1964. A recommendation to this effect was made, and this led to the present study undertaken at the East African Agriculture and Forestry Research Organization.

The grasses selected for this study included species important to both rangelands and pasture, and a brief evaluation of these and their distribution is given. In East Africa very little is known about grass roots and their relation to shoot growth. Some studies have been carried out in other parts of Africa, but these have mainly dealt with certain aspects of root growth without considering the above ground parts. Price (1911) studied the anatomy and morphology of roots in grasses growing under desert conditions in North Africa, and Goossens and Stapelberg (1933) and Goossens (1936) carried out similar investigations in South Africa. Also in South Africa, Murray and Glover (1935) classified grasses on the basis of depth and lateral spread of the roots; the root development in grasses under arid conditions in Somalia were described by Glover (1951).

The object of the present study was to determine the growth potentials and behaviour of six important grasses during their establishment year at two locations in East Africa. As far as practical limitations would allow, locations were selected for differences in soils and rainfall. The study was designed to provide information that would enable a prediction to be made as to the use of these grasses in the overall improvement of the East African rangelands. It was decided to carry out the investigation on individual plants although it was realized that by spacing the grasses the effect of competition was removed. In addition to determining yields and growth patterns, studies on distribution of roots in the soil, rooting depth and spread, changes in soil moisture and certain aspects of leaf growth were made.

In the field experiments, wide spacing prevented plant competition. Under sward, relative species growth will change, though relative growth order of species is likely to remain the same as that determined. Many workers including Ahlgren et al. (1945), Kramer (1947), Nissen (1960), Wright (1960) and Lazenby and Rogers (1962), have shown that characters measured on spaced plants may change with plant density. Green and Eyles (1960) found that the yields in five varieties of Lolium perenne grown in a spaced plant culture did not agree with those obtained in broadcast sward. Nevertheless, these authors suggested that spaced plant cultures usually give a better indication of relative growth potential than do swards. For wheat, Puckridge and Donald (1967) reported that plant weight increased with decreasing population density. Maximum differences occured at maturity. Maximum yields were obtained in the higher density stands, but not always in the stand of highest density, suggesting that competitive effects were involved.

When the present study began, individual plant spacing was selected. In comparison with sward cultivation, individual spacing seemed capable of yielding information particularly on roots, that would be more extensive and reproducible. Moreover, relative species growth estimated from the results could be used as a working hypothesis to make a tentative prediction of a mixed sward, or relative growth order of species as single sward components. One attempt was made to compare sward with spaced plants, but due to the limited time available, this work could not be developed. Whereas much of the data, therefore is not of immediate and direct application, the results suggest lines for future research. They also form a basis for a direct appraisal of the effect of various pasture and range management practices on grass growth.

This thesis gives a full account of the results obtained, and includes an evaluation of the methods used. Conclusions and recommendations are deduced from the data.

CHAPTER II

LOCALITIES

Experimental plots were located in Kenya at Muguga and on the East African Agriculture and Forestry Research Organization (EAAFRO) Dryland Research Ranch, Kedong, in the Rift Valley.

Muguga (36°38'E, 1°13'S) lies at an altitude of 2,086 m and the annual rainfall is 1,013 mm (18 years of records) with two main wet periods per year: a long rains in April-May and a short rains in November-December. A short period of mists occurs during August in most years. Further climatic details are given in Table 1.

The whole of the Muguga area was forested (*Juniperus*, *Olea*, *Euclea*, *Teclea*) at the turn of the century but was subsequently cleared for agriculture and is now used as mixed farming land. The soil at Muguga (Kikuyu Red Loam) is derived from both volcanic and basement complex rocks and is a lateritic, weak to moderately developed dark red-brown (5YR 3/3 when moist, Munsell 1949) clay loam of some 50 cm depth overlying medium clay of 10 cm depth; it has a friable consistency and moderate permeability.

The ability of the Kikuyu Red Loam to hold water available to plants, defined as the water held between 1/3 and 15 atmospheres tension, was determined in seven sets of profile samples from five pits at Muguga (data from EAAFRO Physics Division 1969). It was found that this soil profile could hold 229 mm of available water between the soil surface and 195 cm depth; the amount between the soil surface and 315 cm depth was 329 mm (Table 2).

TABLE 1

Monthly means of daily rainfall, maximum plus minimum air temperatures, Penman* estimate of potential evaporation, and monthly means of rainfall for Muguga (18 years of records) and Kedong (7 years of records) including 1968

Date	Rainfall, mm.		Air temperature °C		Pot. evaporation, mm.	
	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong
January 1967	0.0	5.3	17.4	19.5	219	180
February	4.4	39.1	18.2	19.8	204	180
March	21.6	44.7	18.7	20.6	211	206
April	419.2	152.9	17.0	18.8	141	145
May	375.6	275.3	15.5	17.2	103	134
June	30.9	21.8	13.7	15.2	88	108
July	13.4	37.1	13.4	15.0	87	110
August	34.6	15.0	13.2	14.9	108	118
September	34.1	10.7	14.5	15.3	133	142
October	81.0	22.6	15.7	17.7	154	170
November	96.5	63.5	15.8	18.4	140	155
December	49.5	58.2	15.9	18.1	171	152
Total	1,160.8	746.2			1,759	1,800
Mean			15.8	17.5		
January 1968	0.0	8.4	16.9	20.0	197	188
February	108.5	107.2	16.9	19.5	164	139
March	237.6	164.6	15.9	17.6	134	126
April	239.5	256.0	15.5	17.5	115	124
May	218.6	64.8	14.8	17.0	105	111
June	53.9	62.0	13.8	15.8	91	105
July	1.8	3.3	12.4	14.6	74	100
August	0.8	2.0	12.6	14.6	84	103
September	8.5	8.4	14.4	16.1	153	156
October	31.7	47.2	16.2	17.6	167	165
November	212.4	68.6	15.0	18.1	116	147
December	130.1	117.9	15.5	18.0	169	165
Total	1,243.4	910.4			1,565	1,627
Mean			15.0	17.2		
January 1969	65.6	78.5	16.2	18.5	185	178
February	49.0	70.6	16.1	18.2	139	147
March	78.9	14.2	16.6	19.2	155	177
April	60.1	15.0	17.3	19.0	164	169
May	159.4	152.7	15.9	17.3	112	120

Mean rainfall, mm.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Muguga 18 years	59.8	43.7	73.7	247.5	194.4	42.0	20.2	25.0	22.8	52.6	138.1	93.1	1,012.9
Kedong 7 years	59.7	43.9	86.9	231.7	134.5	28.6	31.0	17.1	10.5	32.1	61.9	66.9	804.8

*Penman (1948)

TABLE 2

Soil water held between field capacity and 15 atmospheres tension

Soil depth cm	Available water in mm			
	Muguga		Kedong	
	Per layer	Running totals	Per layer	Running totals
6- 15	18.0		25.9	
15- 45	32.0	50.0	52.0	77.9
45- 75	35.5	85.5	62.4	140.3
75-105	40.3	125.8	55.9	196.2
105-135	34.5	160.3	53.5	249.7
135-165	35.3	195.6	51.2	300.9
165-195	33.0	228.6	53.0	353.9
195-225	29.0	257.6		
225-255	25.5	283.1		
255-285	21.5	304.6		
285-315	24.8	329.4		

Kedong $36^{o}30'$E, $0^{o}55'$S) lies at an altitude of 1,878 m and the mean annual rainfall is 805 mm based on 7 years of records. The seasonal rainfall pattern is essentially that of Muguga but there are no periods of mist. Further climatic details are given in Table 1.

The Kedong area is wooded grassland range with Acacia drepanolobium and Tarchonanthus camphoratus as the dominant species with Themeda triandra as the main grass. The soil at Kedong is volcanic ash and sand of Pleistocene to Recent age. It consists of a structureless to weakly developed, dark grey-brown (10 YR 3/2 when moist) sandy loam 40-50 cm in depth, overlying various layers of fine to coarse lava tuff; its consistency is friable to loose and its permeability is rapid to moderate. At varying depth beneath the surface there is a compact but usually cracked layer in which the soil particles are cemented together by calcium carbonate.

Adjacent to the experimental plots at Kedong two sets of profile samples from three pits were analysed for their available water holding capacity. Field capacity measurements were made after the profiles had been wetted and thereafter drained for two days; tension plates were employed in determining the water content of the soil at 15 atmospheres tension. In the wetting process, open ended halved 44 gallon drums were embedded so that the lower surface was some 10 cm below ground level. The drums were twice filled with water giving a total of 100 cm of water. It proved, however, impossible to saturate the soil to a depth greater than 2 m due to soil compaction layers causing the water to spread outwards rather than downwards. This is reflected in the absence of measurements for Kedong soil depths greater than 195 cm (Table 2).

These measurements indicated that the Kedong soil could hold as much as 354 mm of available water between the soil surface and 195 cm depth.

Chemical analysis of the soils, based on composite samples from four soil cores, are presented in Table 3. In general, the Kikuyu Red Loam had a higher nutritive status than the volcanic ash and sandy soil at Kedong. The soil at Kedong had a slightly higher pH than the soil at Muguga, especially in the deeper layer.

Although Kedong had a higher mean annual air temperature, the Penman estimate of potential evaporation (Penman 1948) was about the same for both locations. The main differences between the sites, therefore, were in rainfall and soils. It would have been desirable to carry out the study under conditions where potential evaporation differences were larger. The plots, however, had to be within a reasonable distance from Muguga because the work had to be carried out with the labour in the Plant Physiology Division. Also, at Kedong the experimental plots were relatively safe from wildlife intrusion, because the ranch and the plots themselves were fenced in, meteorological data were collected and water was available within a short distance.

Chemical analysis of soils

Depth in cm	%N		% Org.C+		pH 1:2.5M/100 $CaCl_2$		Mg per 100 gm air dry soil[x]							
							P		K		Ca		Mg	
	Mug.	Ked.	Mug.	Ked.	Mug.	Ked.	Mug.	Ked.	Mug.	Ked.	Mug.	Ked.	Mug.	Ked.
0- 20	0.43	0.15	3.37	1.54	5.1	5.1	0.50	0.30	69	42	302	176	36	21
20- 40	0.32	0.10	2.39	1.52	5.1	5.4	0.12	0.25	67	43	243	155	38	15
40- 60	0.20	0.07	1.41	0.65	4.9	5.5	0.10	0.30	65	42	191	145	39	13
60-100	0.13	0.02	0.74	0.10	5.9	5.9	0.06	1.00	75	44	219	77	53	5
100-140	0.10	0.01	0.46	0.08	5.9	6.1	0.06	0.60	88	77	176	103	53	2
140-180	0.08	0.02	0.31	0.11	5.8	7.1	0.06	0.35	88	133	150	118	48	4
180-220	0.06		0.23		5.8		0.06		98		134		44	
220-260	0.07		0.18		5.1		0.06		120		113		35	

[+] The Walkley-Black method - Walkley and Black (1934). Organic C values are uncorrected, X 1.33 = organic -C; X 2 = organic matter (approx.)

[x] The Ammonium lactate - Acetic Acid Method by Egner et al. (1960).

CHAPTER III

MATERIALS AND METHODS

3.1 General Information on the Grass Species

Seed stock was obtained from the National Research Station, Kitale, and a brief description of the grasses including their distribution and Kenya Department of Agriculture seed introduction numbers (Bogdan 1965) is given below (K = Kitale, P = Katumani Station, Kenya).

Cenchrus ciliaris L. (African foxtail, Rhodesian foxtail, buffel grass) is distributed throughout the hotter and drier parts of India, the Mediterranean region, tropical and South Africa and has been introduced into Australia and the Americas (Bor 1960). It is one of the most important hay grasses in India (Whyte et al. 1959). In East Africa, this rhizomateous perennial is widespread from sea level to approximately 2,000 m (Napper 1965), but it is not commonly found at Muguga or Kedong. C. ciliaris germinates readily from seed, providing the mature seed has been stored for 12-18 months following harvest (Brzostowski and Owen 1966). Numerous varieties have been selected, some of the better known being biloela, Edwards tall, gayndah, kongwa, mbalambala, molopo, mpwapwa and nunbank. Although there is no complete comparison of these varieties, biloela, molopo and nunbank have given good results in North Tanzania (Naveh and Anderson 1967) while biloela, kongwa and mbalambala are recommended in reseeding work for the drier areas of Kenya (Bogdan and Pratt 1967). The biloela (P.57123 and the mbalambala (K.59203) varieties were used in the present study.

Chloris gayana Kunth (Rhodes grass, grama Rhodes) is a stoloniferous perennial which is found in grassland and open woodland on a wide range of soils throughout East Africa from sea level to approximately 2,400 m (Napper 1965). The grass is widely distributed from Senegal eastwards to the Sudan and South including South Africa (Bor 1960). It has been introduced into North and South America, Australia, North Africa, the Philippines and India and is regarded as one of the best species for rotation grasslands (Whyte et al. (1959). Seed germination is very good and many varieties are obtainable commercially in East Africa. In northern Tanzania, chepararia (Naveh and Anderson 1966) and kongwa (naveh and Anderson 1967) varieties have given good results. Others described by Bogdan (1965) include katambora, masaba, mbarara, mpwapwa, nzoia and rongai. According to Bogdan, the mbarara (K.53166) variety included here has medium herbage quality, forms a dense sward and is very persistent. C.gayana is commonly found at kedong where it occasionally forms pure stands.

Eragrostis superba Peyr. (Wilman lovegrass, Masai lovegrass) is distributed throughout tropical (Bor 1960), South and South-West Africa (Chippindall et al. 1955), and has been introduced into India (Bor 1960). It is a densely tufted perennial which is mainly found in open thicket and grassland on poor sandy soils in East Africa from sea level to approximately 2,000 m (Napper 1965). So far, no varieties have been described for East Africa. Under moderate dry conditions, it is regarded as a safe grass for reseeding used in mixtures with C. ciliaris (Bogdan and Pratt 1967). E. superba has good seeding qualities and is easy to establish from seed (Edwards and Bogdan 1951). The grass is not found at either of the experimental sites. Its seed introduction number was K.6023.

Panicum maximum Jack. (true guinea grass) is widely distributed in tropical Africa (Bor 1960), South Africa except for the greater part of western Cape, and in several districts of South-West Africa (Chippindall et al. 1955). It is believed to have been introduced into India,but was collected there before year 1800 (Bor 1960). P.maximum is a tufted perennial occurring in grassland and open woodland throughout East Africa from sea level to 2,400 m (Napper 1965). Germination from seed is easy and Bogdan and Pratt (1967) recommend the makueni and trichoglume varieties as suitable for reseeding work in Kenya, the latter being the least drought resistant. Numerous varieties have been described by Bogdan (1965) and trials in Northern Tanzania including likoni, makueni, sabi, teso, trichoglume and ulachloa indicated that likoni was good, especially when grown in mixture with legumes (Naveh and Anderson 1967). The makueni (K.6462) variety was included in the present work.

Themeda triandra Forsk. (red oat grass), distributed widely in all warm and tropical regions of the old World (Bor 1960), is a tufted perennial which is common in grassland and open woodland throughout East Africa between altitudes of approximately 450 and 2,000 m (Napper 1965). This grass is found on a variety of soils (Heady 1966) and is the most abundantly occurring grass in the Kedong area where it forms pure stands; it is occasionally found at Muguga.

T.triandra is probably the most widely distributed and important grass of East Africa and appears to be specially adapted to survive fires (Edwards and Bogdan

1951). In South Africa, it is regarded as a climax species, but due to mismanagement it has been reduced and even eliminated in some regions (Chippindall et al. 1955). The grass is difficult to germinate from seed and in this work, germination was less than one per cent. Its seed introduction number was K.53302.

3.2 Outline of Studies, I and II

This thesis comprises the results from two related investigations. Wherever possible, the same methods were used in both studies. The investigations were:

Study I. Intensive studies on C.ciliaris var. biloela, C.gayana and P.maximum grown in experimental plots at Muguga, April 1968 to March 1969.

Study II. Extensive studies on the above mentioned grasses and C.ciliaris var. mbalambala, E.superba and T.triandra grown in experimental plots at Muguga and Kedong, April 1967 to July 1968.

3.3 Methods Common to Both Studies

3.3.1 Seeding and method of planting

To eliminate possible effects of poor germination, the grass seeds were treated with mercuric chloride, seeded and grown in pots in the open, and later planted out at the beginning of long rains. In the plots, to ensure freedom from inter- and intra-specific competition both above and below ground, the spacing between individuals was 2.5 m. In addition, close planted (40 x 40 cm) plots were established at Muguga in 1967.

3.3.2 Root sampling

Various means of root sampling, such as pinboard, a soil-root sampler and the jet-wash method were tried out (Taerum and Gwynne 1969). The main objection to the pinboard was that it sampled only a small part of the root system. In Kikuyu Red Loam, for example, where roots from one grass may have a lateral spread of 2 m and growth to 6 m depth, it would be impossible to give even an approximate estimate of total root weights from pinboard sampling. The soil-root sampler, designed to sample equal volumes of soil from a vertical trench wall, yielded poor results when single plants were sampled. For assessing root biomass under swards, where the root distribution was more uniform, the soil-root sampler technique enables a root distribution pattern to be built up very quickly, where the soil is relatively loose.

Although time consuming, the jet-wash method was found to be the most satisfactory for the present study. It entailed removing the entire root system from the soil in such a way that dry weights, etc. could be determined on a soil layer basis while at the same time enabling a drawing of the root profile to be obtained.

Essentially the plant was washed out of the soil using a fine jet of water from a 1 mm diameter nozzle. The water was gravity fed from a mobile 1000 l water tank giving a drop to ground level of 50 cm, thus ensuring a steady water flow.

The surface soil was first washed away from the base of the plant until a major root was encountered. This root was followed out radially until its growing tip was exposed or until it turned sharply downwards. A small drainage pit and connecting channel were then dug well beyond the root end, after which the radial root channel was gradually enlarged laterally by washing, exposing new roots.

The initial washing resulted in a radial trench with an arc of about 10° (Fig.1a) which gave an indication of the extent of the limit of the observed root direction. Well beyond the limit of the observed root spread a short deep trench was sunk tangential to the radial one, and the two were connected (Fig.1b). Washing then proceeded along the sides of the radial trench gradually enlarging it in width and in depth (Fig.1c).

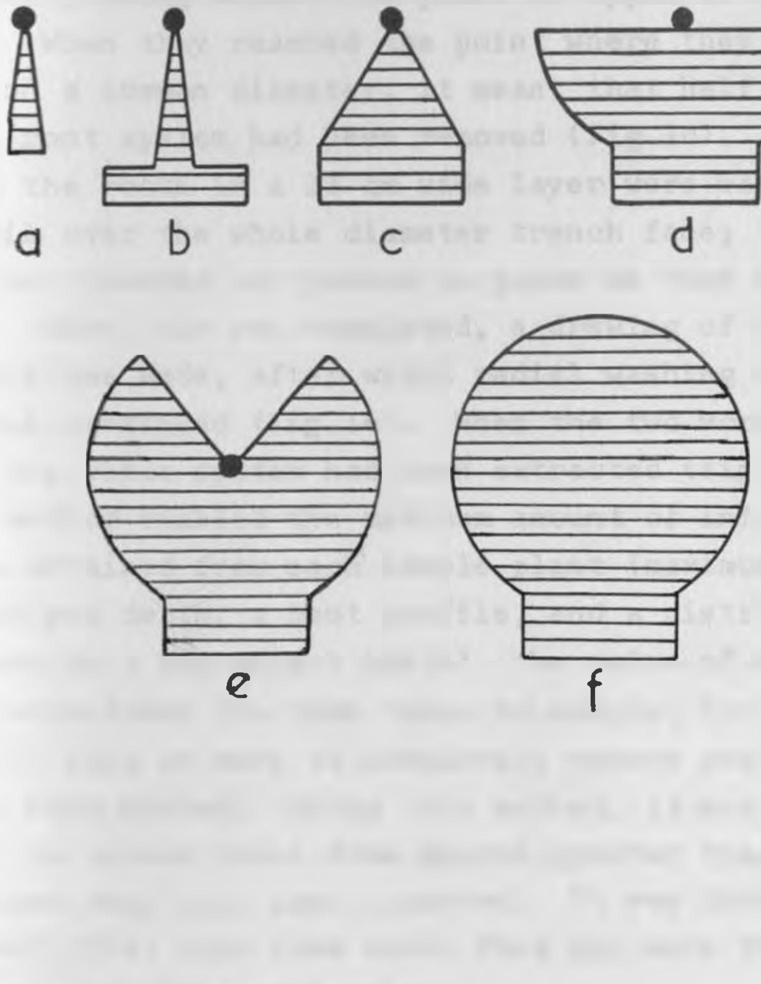

Fig. 1 Vertical plan diagram showing the stages of excavating using the jet-wash method. See text for details.

3.3.3 Shoot sampling

Measurements of the shoots taken in the field were:

a) Tuft spread (diameter of leaf mass)

b) Tuft height (height of leaf table)

c) Record of flower and seed development

When approximately half of the root system of one grass had been removed, its shoots were cut at ground level, sorted into inflorescences, leaf blades and stems, dried at 75°C and weighed. Additional stem material left in the soil below ground level after the initial stem cut were separated out and added to the stem portion at the completion of the root excavation; rhizomes were similarly separated out at this stage.

Because the rhizomes were mainly located below the soil surface, they had no grazing value and were, therefore, excluded when comparisons were made between shoot yields. When examining shoot/root ratios, however, the dry weights of rhizomes were included in the shoot fraction because they are part of the stems, active in transpiration. Dead leaves, not being physiologically active in any way, were excluded from all comparisons.

3.4 Methods Employed in Study I

3.4.1 Planting date and sampling frequency

The four weeks old potted seedlings of the three grasses were planted into the experimental plots on April 1, 1968, during the long rains. Throughout the growth period, April 1968 to March 1969, the grasses were sampled nine times; three individuals of each species were examined each time. The interval between each sampling was 2½ weeks from April to May (two samplings), 5 weeks from May to September (four samplings) and 7½ weeks from September to March (three samplings).

3.4.2 Leaf weight index

The leaf weight index (L_w: leaf dry weight per unit area of ground) was determined in samples taken from April to September. For these determinations the ground area was calculated from tuft spread measurements.

3.4.3 Leaf area index

The leaf area index (L_A: leaf area per unit area of ground) was calculated in samples taken between April and August. The leaf area was estimated from linear measurements using the equation area = 0.905 (LB), where L was length of leaf blade and B leaf width measured at a point halfway along the length of the leaf (Kemp 1960). In early stages of growth, all leaves were measured. When individual sample numbered several thousand leaves, shoots were divided into three parts and the average leaf area determined in one part; this value was used for the estimation of total area. In trials, where the average area was determined in each of the three parts, it was found that the error by using either one was less than 10 per cent.

3.4.4 Specific weight of leaves

The specific weight of leaves (L_S: weight per unit area of leaf) was calculated from leaf dry weight and area measurements in samples taken between April and November.

3.4.5 Defoliation treatment

An additional plot of P.maximum was established to study the effects of defoliation. Most of the leaves and some stem material were removed on all plants on five successive occasions at approximately 5-week intervals from April 25 to September 9. When shoot yields of defoliated plants were compared with those of non-defoliated plants, the mean weight of defoliated material was added to the weight of defoliated plants.

3.4.6 Root volume measurements

After the roots had been washed free of soil, they were shaken lightly to remove excess water and left to dry on an inclined tray for approximately 15 minutes. The damp roots were thereafter lowered into a graduated cylinder filled with a known volume of water to which a liquid soap had been added to reduce surface tension effects. Additionally, a pump, exerting a vacuum of 500 mm Hg was employed before and after the addition of the roots until the ascent of larger air bubbles ceased. The volume of roots was then recorded as the difference between the levels of water in the cylinder. The specific weight of roots was calculated on the basis of root volumes and root dry weights.

3.4.7 Method of indicating significanes in data tables.

In the tables showing statistical analyses, differences are shown by the use of letters; means not followed by the same letter are significantly different at a given level. Using Table 4 as an example, the first letter behind each mean of each species refers to comparisons made between species at the same date or between their growth period means. The second letter in brackets refers to comparisons made vertically. On April 18, none of the species differed: the mean of each species was followed by the same letter. The growth period means, however, differed and P.maximum had a lower mean than any of the other species.

The result of comparisons made between dates (vertically) for each individual species or for all species combined are given in brackets. For example, the yields in C.ciliaris increased significantly from one sampling to the next between April 18 and August 19. From August 19 to September 24, yields did not differ although they did differ between July 14 and September 24.

3.5 Methods Employed in Study II

3.5.1 Planting date and sampling frequency

The potted seedlings of the six grasses were planted into the experimental plots at Muguga and Kedong at 7 weeks of age at the beginning of the long rains April 15, 1967. The first sampling was carried out in May followed by four samplings at about 10-week intervals up to February 1968 and finally the sixth sampling after renewed growth (May-July) following the February to May seasonal rains.

At the two first samplings two individuals of each grass species, except in T.triandra, were examined; subsequently only one and occasionally two were sampled due to the length of time needed to complete each one. Lack of replication at the later stages of growth was unfortunate, but increased sampling time and shortage of labour made it impossible to collect more than one plant.

When comparing yields of the same species at Muguga and Kedong, there was always a considerable timelag between samplings due to limited labour and laboratory facilities. Muguga samplings were always carried out prior to Kedong; the difference in time varied from a few days at the early stages of growth to three weeks at the February 1968 sampling. The data collected at the May-July sampling were not included in the statistical analyses.

3.5.2 Gypsum resistance blocks

The use of uncalibrated gypsum resistance blocks to obtain an indication of the exhaustion of available soil moisture and the attainment of wilting point beneath plants in the field has given useful results under East African conditions (Pereira et al. 1958). The blocks are insensitive to low soil moisture tensions under wet conditions, but they have a theshold value of approximately one atmosphere for their initial change. Such changes of resistance, therefore, indicate soil drying by evaporation only, with reliable assurance that downward drainage has ceased. The soil water extraction pattern is, therefore, obtained by plotting the log-resistance of the gypsum blocks placed beneath the plants, thus showing the times at which the soil moisture tension reached the approximate measurable limits of one and fifteen atmospheres, the range between which half of the available soil moisture has been extracted from the soil, and wilting point.

Although it is possible to calibrate the resistance blocks so that the actual water content could be inferred from resistance readings, this procedure was considered unnecessary for the following reasons[1]: 1) The blocks cannot be recalibrated after installation, 2) Although the blocks have a similar ohmic resistance at the wet and the dry ends, their response to changing moisture content may be different, thus making it necessary to use different calibrations. 3) Response time for these blocks is so long that at best they indicate the average situation over a few days. It would therefore be risky to try and work out rates of water movement from such records.

[1] Wangati, F.J., Physics and Chemistry Division, E.A.A.F.R.O., personal communication.

In both series of experimental plots at Muguga and Kedong gypsum blocks were placed within a 20 cm radius circle around each of two individuals of each grass species at depths ranging fra 30 to 480 cm. Similar blocks were beneath two plots of bare ground at each site and at Muguga beneath swards of each grass species. From graphs of readings taken weekly from May 1967 to May 1969 an indication was obtained as to the availability of soil moisture and the depth during the dry seasons from which the roots were extracting their soil moisture. Where more than one set of blocks were used (around single plants and beneath bare ground) mean readings were calculated. Data for species showing extreme water use patterns have been graphed and are given in the results; other water use data can be found elsewhere (Taerum 1969).

3.5.3 Nodal root diameter

The diameter of the nodal root, all adventitious, crown and secondary but not seminal roots (Troughton 1957), were measured with a micrometer approximately three months after planting; the measurements being taken in each of the four uppermost soil layers immediately after the roots had been excavated.

3.5.4 Swards versus single plants

To determine the relationship of shoot/root ratios in spaced plants to those in swards, a simple experiment was carried out in 28 month old single plant and sward plots of P.maximum and C.ciliaris var.mbalambala. Shoots of plants in these plots were cut at ground level in April 1969 and the sward plots were divided into 120 x 120 cm squares. Four months later, three single plants and three random squares of both species were sampled and shoot/root ratios determined. The spaced plants were sampled in the usual manner; in the swards, the total shoot dry matter within each square was compared with the roots excavated from a 120 x 120 x 300 cm deep soil block. The root yields in the swards were also used in calculating root production per unit area.

CHAPTER IV

STATISTICAL ANALYSIS OF DATA

4.1 Assumptions

For the records on the trial carried out at Muguga and Kedong, 1967 to 1968, two samples were taken for each of five species at two sites and two times. Thus, there was formally a 5 x 2 x 2 design with two replicates. Additional samples, one or two in number, were available for a further species and additional times, but it was not possible to add these to the analysis while retaining the orthogonality. Since analysis of variance was the only appropriate method of getting results from the data, such an analysis was performed on the orthogonal 5 x 2 x 2 array, treating it as a completely randomized design with two replicates. It was assumed that the variability in this array was a true representation on the total variability in the records; thus the standard error obtained from the orthogonal analysis of variance was used to enable conclusions to be drawn from the whole set of data. This assumption was sufficient for the analyses on ratios, which did not vary greatly over the trial period. In order to validate analyses of variance on weight these were assumed to be increasing approximately exponentially: thus, weight data were transformed to logarithmic values before analysis. This transformation had the desired effect of more nearly equalizing the variation between samples for the different treatments.

4.2 Methods

For any of the analyses, on untransformed ratios or transformed weights, the procedure was as follows.

The 5 x 2 x 2 design with two replicates was treated as a completely randomized arrangement, and all the effects were compared with the residual error by means of F-tests. That is to say, there were three main effects, sites and times with one degree of freedom each and species with four; there were also the three possible two-factor interactions and the one, not very important, three factor interaction, leaving 20 degrees of freedom for error (Appendix). Since it was desirable to draw general conclusions from the whole body of data the subsequent procedure was not determined by the significance of the F-tests, which is the most usual way of concluding analysis of variance. Instead, certain predetermined differences, such as a comparison between two particular species at one site or a general comparison of ages, were examined specially. For this purpose many different least significances had to be calculated, because of the unequal replication. These were all derived from the residual variance of the orthogonal anlysis, and applied to means of the data obtained in the appropriate way: if the data for analysis of variance were transformed to logarithmic values, so were the data for which the means were found. As most of the comparisons tended to involve only a small number of means the least significant difference method was used throughout (Fisher 1935): multiple range tests (Duncan 1955) might well be appropriate, especially to comparisons of species, but would be difficult to use on account of the unequal replication. As always, the results from the statistical analyses carried out on the data need to be interpreted in the light of the full knowledge of the experiment and its background.

As mentioned above, several values for least significant differences were obtained within each group of analyses. Since, however, the differences between the values within each group were small and the effects on the result by using either one were negligible, only the highest value obtained within each group was used.

In the 1968-1969 work at Muguga, comprising three grass species, the method described above was employed. In most of the analyses, however, the assumption made above regarding variability was not necessary because replication was similar throughout the experiment.

CHAPTER V

EXPERIMENTAL RESULTS

5.1 General Development of the Grasses

In these experiments, seed formation in all species reached a peak approximately 10 months from planting, coinciding with the dry period following the short rains in November-December. Some seeds were shed before and during the short rains, but large numbers of flowers were still being formed. On the basis of seed formation and shedding, it was concluded that the grasses, during their establishment year, had matured in February. Growth, however, continued throughout this period. Although the dry weight of the dead leaves in some samples exceeded that of green leaves, the dry weight of green leaves and the shoot as a whole increased. The dead leaves were mainly collected from underneath tufts. Observations in plants more than one year old revealed a different growth cycle, in which a complete shedding of seeds occurred before the short rains and again before the long rains.

Visual examination of the roots, even at the May-July 1968 sampling, did not reveal dead root matter. Any increase in root dry matter content, therefore, most likely represented the true expansion of the live root system, active in water and nutrient uptake.

A great volume of growth data was collected throughout the experimental periods: only the major findings are included in this chapter. Complete records of growth data are reported by Taerum (1969).

5.2 Results - Study I

The results of Study I, comprising three grass species grown in experimental plots at Muguga are given below. The term "Growth period mean" used below refers to the mean of all samplings made throughout the growth period, April 1968 to March 1969. For comparison purposes, the rainfall data on a 10-day basis are shown in Fig.2.

5.2.1 Root yields

A summary of the root yield analysis ($P<0.001$) is shown in Table 4; the dry weight data are presented in Fig.3.

Higher mean dry weight values for the growth period were obtained in C.ciliaris var.biloela and C.gayana than in P.maximum, although these differences could not always be established on a sampling date basis, except between C.ciliaris var.biloela and P.maximum during the later half of the growth period.

In C.ciliaris var. biloela, root yields increased significantly between successive samplings from April to August; in C. gayana and P.maximum from April to July. Subsequently, yield increments decreased, although C.gayana and P.maximum again showed high yield increases from November to January. The combined sampling means, however, indicated increased yields from April to January.

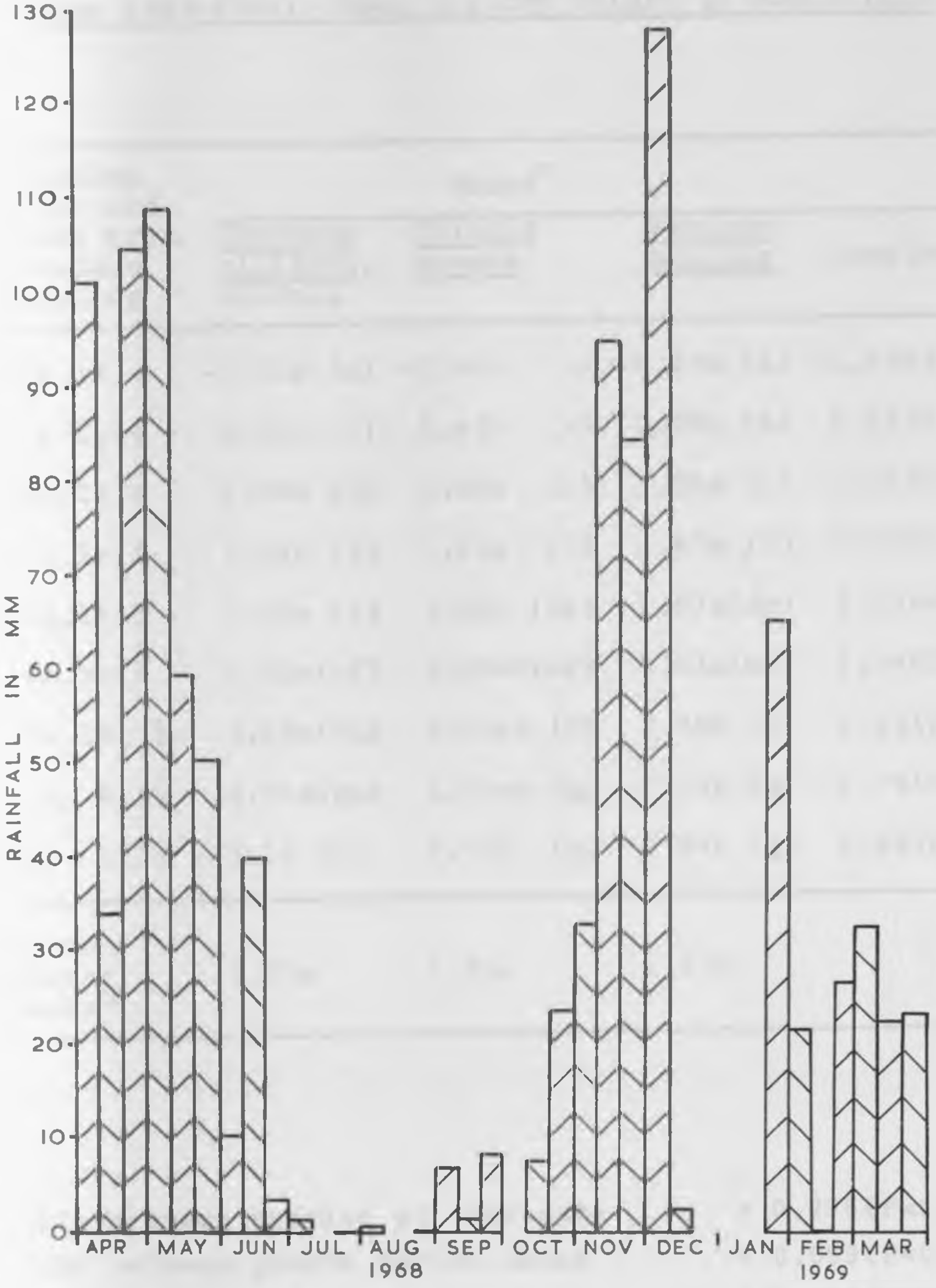

Fig. 2 Muguga: Rainfall on a 10-day basis.

TABLE 4

Muguga 1968-1969: Mean log dry weight of roots (gm)

Sampling dates and weeks from previous sampling	Means^{x}			
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum*	Combined
Apr.18	-0.51a (a)	-0.41a (a)	-0.64a (a)	-0.52(a)
May 6,2½	0.06a (b)	0.43b (b)	0.36b (b)	0.29(b)
Jun.12,5	1.38a (c)	1.35a (c)	1.29a (c)	1.34(c)
Jul.14,5	1.69a (d)	1.81a (d)	1,67a (d)	1.73(d)
Aug.19,5	2.16a (e)	2.06a (de)	1.87a(de)	2.03(e)
Sep.24,5	2.41a(ef)	2.30ab(ef)	2.01b(ef)	2.24(f)
Nov.15,7½	2,65a(fg)	2.37ab (f)	2.28b (f)	2.43(g)
Jan. 6,7½	2.94a(gh)	2.73ab (g)	2.61b (g)	2.76(h)
Mar. 1,7½	3.15 (h)	2.70b (g)	2.64b (g)	2,83(h)
Growth period means^{x}	1.77a	1.70a	1.57b	

^{x}LSD between species at same date = 0.296(P<0.001)
LSD between growth period means = 0.099(P<0.001)
LSD between dates each species = 0.296(P<0.001)
LSD between dates all species combined = 0.171(P<0.001)

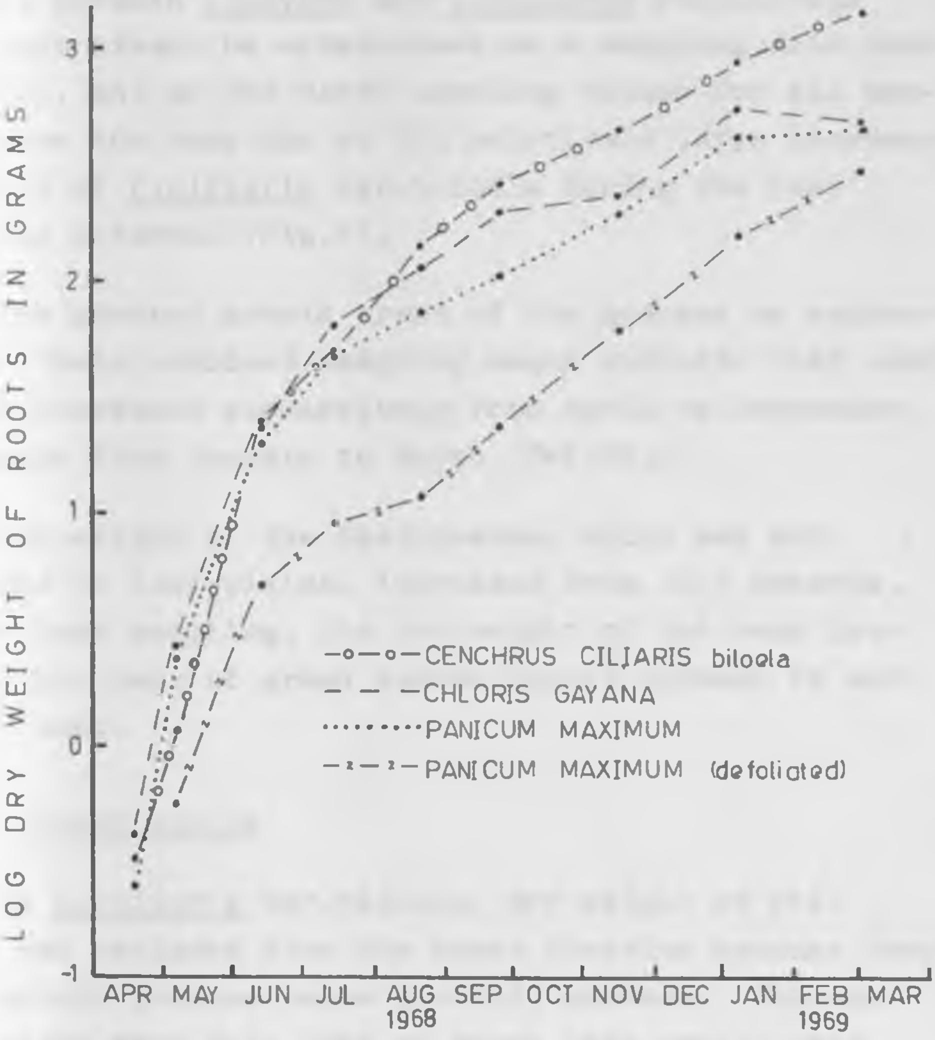

Fig. 3 Muguga: Mean total dry weight of roots.

5.2.2 Leaf yields

Leaf yield analyses (Table 5) indicate that *P.maximum* had a higher growth period mean than *C.gayana*; the mean of the latter species was higher than that of *C.ciliaris* var.biloela ($P<0.001$). The difference between *C.gayana* and *C.ciliaris* var.biloela could not always be established on a sampling date basis ($P<0.01$), and at the March sampling values for all species were the same due to the relatively large increase in yield of *C.ciliaris* var.biloela during the last sampling interval (Fig.4).

The general growth trend of the grasses as expressed in their combined sampling means indicate that leaf yields increased successively from April to September and again from January to March ($P<0.001$).

Dry weight of the dead leaves, which was not included in leaf yields, increased from July onwards. At the last sampling, the dry weight of the dead leaves as per cent of green leaves varied between 46 and 71 per cent.

5.2.3 Shoot yields

In *C.ciliaris* var.biloela, dry weight of rhizomes was excluded from the shoot fraction because they were mainly located below the soil surface. Rhizome dry weight from July 1968 to March 1969 constituted an average of 19.8 (max. 25.4) per cent of the total shoot and rhizome dry weights.

In the analysis of shoot yields ($P<0.001$) the following differences were obtained (Table 6). *C.gayana* and *P.maximum* gave higher growth period means than *C.ciliaris* var.biloela. On a sampling date basis, there were no significant differences at the March sampling.

TABLE 5

Muguga 1968-1969: Mean log dry weight of leaves (gm)

Sampling dates and weeks from previous sampling	Means[x]			
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum*	Combined
Apr.18	-0.31a (a)	-0.22a (a)	-0.27a (a)	-0.27 (a)
May 6,2½	0.25a (b)	0.56b (b)	0.83c (b)	0.55 (b)
Jun.12,5	1.56a (c)	1.63ab (c)	1.81b (c)	1.67 (c)
Jul.14,5	1.82a (d)	2.02ab (d)	2.22b (d)	2.02 (d)
Aug.19,5	2.15a (e)	2.27ab (e)	2.38b (d)	2.27 (e)
Sep.24,5	2.28a(ef)	2.50b (fg)	2.61b (e)	2.47 (f)
Nov.15,7½	2.44a (f)	2.54a (g)	2.76b(ef)	2.58(fg)
Jan. 6,7½	2.53a (f)	2,65ab(gh)	2.81b(ef)	2.66 (g)
Mar. 1,7½	2.77a (g)	2.84a (h)	2.89a (f)	2.84 (h)
Growth period means[x]	1.72a	1.87b	2.00c	

[x] LSD between species at same date = 0.218($P<0.01$)
LSD between growth period means = 0.096($P<0.001$)
LSD between dates each species = 0.218($P<0.01$)
LSD between dates all species combined = 0.165($P<0.001$)

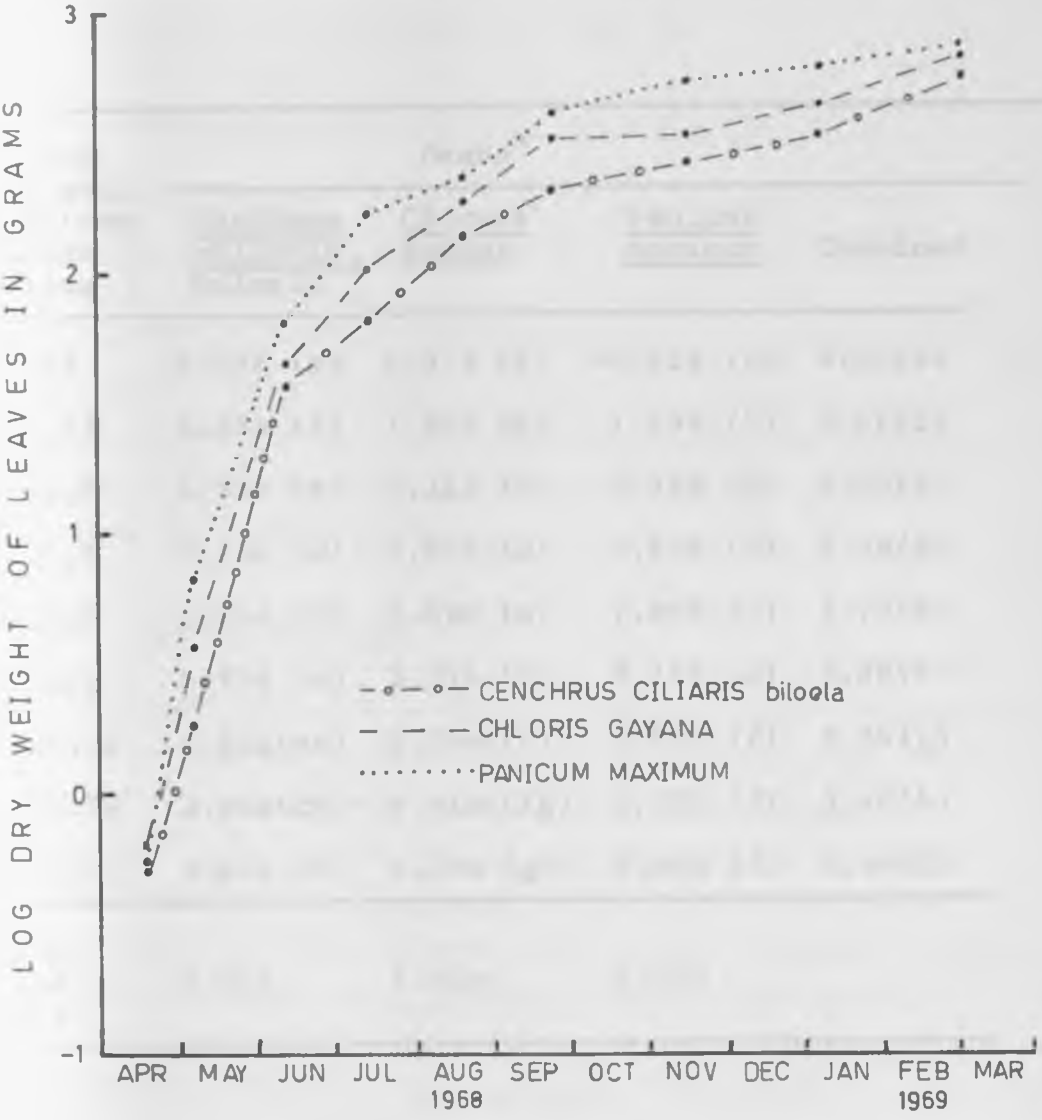

Fig. 4 Muguga: Mean total dry weight of leaves.

TABLE 6

Muguga 1968-1969: Mean log dry weight of shoots (gm)

Sampling dates and weeks from previous sampling	Means[x]			
	Cenchrus ciliaris, biloela	Chloris gayana	Panicum maximum	Combined
Apr. 18	-0.03a (a)	0.07a (a)	-0.01a (a)	0.01(a)
May 6,2½	0.59a (b)	1.00b (b)	1.14b (b)	0.91(b)
Jun.12,5	1.98a (c)	2.11a (c)	2.18a (c)	2.09(c)
Jul.14,5	2.23a (c)	2.60b (d)	2.62b (d)	2.48(d)
Aug.19,5	2.60a (d)	2.88b (e)	2.84b (d)	2.77(e)
Sep.24,5	2.87a (e)	3.21b (f)	3.16b (e)	3.08(f)
Nov.15,7½	3.05a(ed)	3.25ab(f)	3.43b (f)	3.24(g)
Jan. 6,7½	3.26a(df)	3.41ab(fg)	3.53b (f)	3.40(h)
Mar. 1,7½	3.43a (f)	3.58a (g)	3.68a (f)	3.56(i)
Growth period means[x]	2.22a	2.46b	2.51b	

[x] LSD between species at same date = 0.270($P<0.001$)
LSD between growth period means = 0.090($P<0.001$)
LSD between dates each species = 0.270($P<0.001$)
LSD between dates all species combined = 0.155($P<0.001$)

The combined sampling means suggest that the growth rate from June to September was about one fifth of that from April to June; from September to March it decreased further to about one third of the latter. Shoot yield data are given in Fig. 5.

5.2.4 Root and shoot yields, defoliated plants

Mean yields of roots and shoot in defoliated *P.maximum* plants (Figs. 3 and 5) were compared with those of non-defoliated plants (Tables 7 and 8). Non-defoliated plants had a higher mean root yield and highly significant differences ($P<0.001$) occurred at all samplings except the last where the means differed at the 1 per cent level only. Similar differences were obtained for shoot yields.

5.2.5 Leaf/root ratio

The analysis of leaf/root ratios (Table 9) indicate that *P.maximum* had a higher and *C.ciliaris* var. biloela a lower growth period mean than *C.gayana* ($P<0.001$). The ratio in *C.ciliaris* var.biloela differed from that in *P.maximum* at each sampling date, while there was no difference in values between *C.ciliaris* var.biloela and *C.gayana* before August ($P<0.01$). A steady decreasing trend was observed in *C.ciliaris* var.biloela (Fig.6). In *C.gayana*, the ratio in January was lower than most previous ones and in *P.maximum* it increased from April to September and then decreased until January ($P<0.01$). *C.ciliaris* var.biloela showed a high ratio in April, *C.gayana* in June and *P.maximum* in September, although none of these were significant higher ratios.

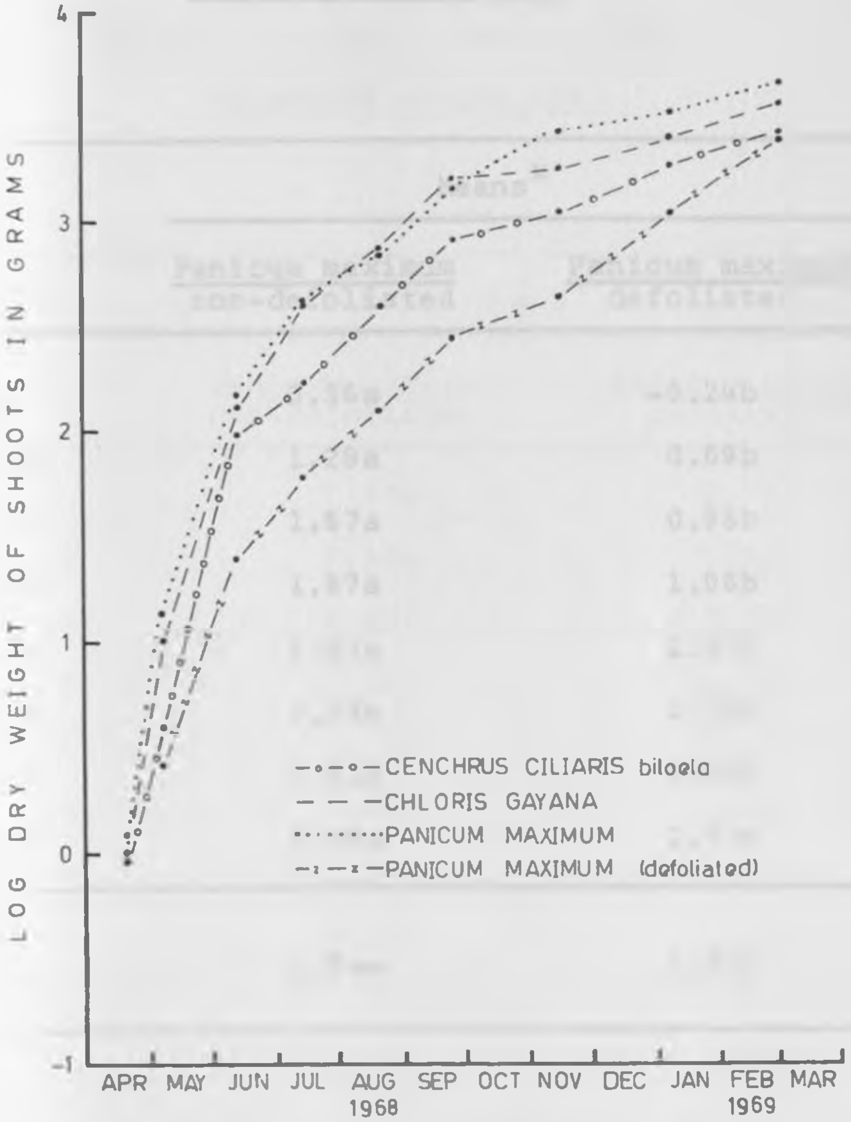

Fig. 5 Muguga: Mean total dry weight of shoots.

TABLE 7

Muguga 1968-1969: Mean log dry weight of roots (gm)

Date	Means[x]	
	Panicum maximum non-defoliated	Panicum maximum defoliated
May 6	0.36a	-0.24b
Jun. 12	1.29a	0.69b
Jul. 14	1.67a	0.95b
Aug. 19	1.87a	1.06b
Sep. 24	2.01a	1.37b
Nov. 15	2.28a	1.79b
Jan. 6	2.61a	2.20b
Mar. 1	2.64a	2.47a
Growth period means[x]	1.84a	1.29b

[x] LSD between treatments at same date = 0.260($P<0.001$)
LSD between growth period means = 0.092($P<0.001$)
LSD (between periods at same date = 0.196($P<0.01$) see text)

TABLE 8

Muguga 1968-1969: Mean log dry weight of shoots (gm)

Date	Means[x]	
	Panicum maximum non-defoliated	*Panicum maximum* defoliated[xx]
May 6	1.14a	0.42b
Jun. 12	2.18a	1.38b
Jul. 14	2.62a	1.78b
Aug. 19	2.84a	2.09b
Sep. 24	3.16a	2.44b
Nov. 15	3.43a	2.63b
Jan. 6	3.53a	3.03b
Mar. 1	3.68a	3.39b
Growth period means[x]	2.82a	2.14b

[x] LSD between treatments at same date = 0.203($P<0.001$)
LSD between growth period means = 0.077($P<0.001$)

[xx] Previously defoliated matter added

TABLE 9

Muguga 1968-1969: Mean leaf/root ratios

Date	Means[x]		
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum*
Apr. 18	1.59a (c)	1.60a (b)	2.35b(bc)
May 6	1.57a (c)	1.36a(ab)	2.91b(cd)
Jun. 12	1.56a (c)	1.95a (b)	3.29b (d)
Jul. 14	1.37a (bc)	1.63a (b)	3.51b(de)
Aug. 19	0.98a(abc)	1.66b (b)	3.33c(de)
Sep. 24	0.76a (ab)	1.64b (b)	4.00c (e)
Nov. 15	0.62a (a)	1.51b(ab)	3.02c(cd)
Jan. 6	0.39a (a)	0.85a (a)	1.57b (a)
Mar. 1	0.42a (a)	1.43b(ab)	1.80b(ab)
Growth period means[x]	1.03a	1.52b	2.86c

[x] LSD between species at same date = 0.672(P<0.01)
LSD between growth period means = 0.292(P<0.001)
LSD between dates each species = 0.672(P<0.01)

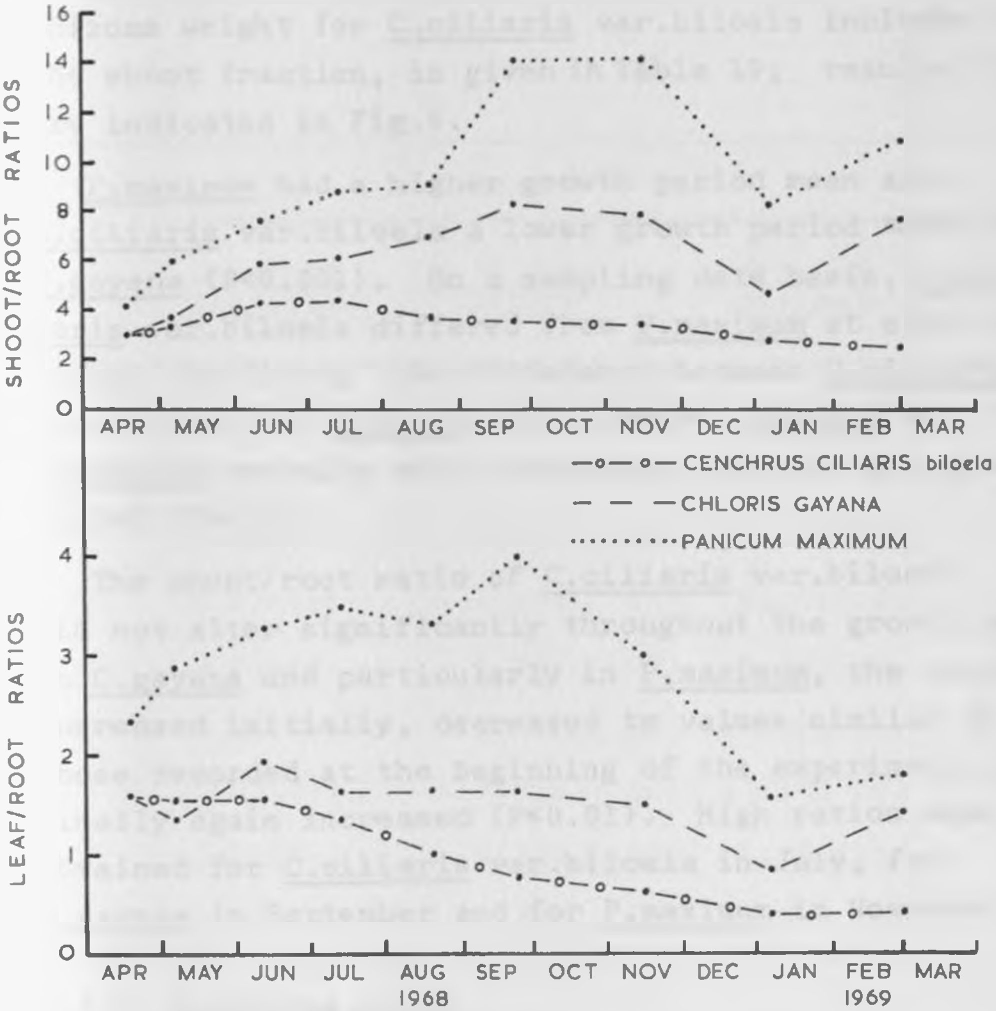

Fig. 6 Muguga: Mean shoot/root and leaf/root ratio trends.

5.2.6 Shoot/root ratio

The analysis of mean shoot/root ratios, with rhizome weight for C.ciliaris var.biloela included in the shoot fraction, is given in Table 10; results trends are indicated in Fig.6.

P.maximum had a higher growth period mean and C.ciliaris var.biloela a lower growth period mean than C.gayana ($P<0.001$). On a sampling date basis, C.ciliaris var.biloela differed from P.maximum at each date except the first; the difference between C.ciliaris var.biloela and C.gayana and between C.gayana and P.maximum becoming more pronounced later in the growth period ($P<0.01$).

The shoot/root ratio of C.ciliaris var.biloela did not alter significantly throughout the growth period. In C.gayana and particularly in P.maximum, the ratios increased initially, decreased to values similar to those recorded at the beginning of the experiment, and finally again increased ($P<0.01$). High ratios were obtained for C.ciliaris var.biloela in July, for C.gayana in September and for P.maximum in November.

5.2.7 Leaf/stem ratio

The leaf/stem ratio analysis (Table 11) shows that C.ciliaris var.biloela and P.maximum had higher growth period means than C.gayana ($P<0.0001$) and that these differences were due to differences obtained during the first half of the growth period ($P<0.01$). In all grasses, the ratio fell rapidly during early stages of growth and subsequently more slowly (Fig.7).

5.2.8 Leaf weight index

A higher overall leaf weight index (mg leaf wt./cm^2 ground area) mean was obtained for P.maximum than

TABLE 10

Muguga 1968-1969: Mean shoot/root ratios

Date	Means^x		
	Cenchrus ciliaris, biloela	Chloris gayana	Panicum maximum
Apr. 18	2.99a(a)	3.14a (a)	4.26a (a)
May 6	3.43a(a)	3.74ab (ab)	5.99b(ab)
Jun. 12	4.30a(a)	5.92ab(bcd)	7.66b(bc)
Jul. 14	4.41a(a)	6.16a (cd)	8.80b(cd)
Aug. 19	3.77a(a)	6.98b (cd)	9.18b(cd)
Sep. 24	3.60a(a)	8.30b (d)	14.16c (e)
Nov. 15	3.43a(a)	7.91b (d)	14.20c (e)
Jan. 6	2.81a(a)	4.77a (abc)	8.33b(bc)
Mar. 1	2.54a(a)	7.72b (d)	10.94c (d)
Growth period means^x	3.48a	6.07b	9.28c

^{x}LSD between species at same date = 2.389($P<0.01$)

LSD between growth period means = 1.042($P<0.001$)

LSD between dates each species = 2.389($P<0.01$)

TABLE 11

Muguga 1968-1969: Mean leaf/stem ratios

Date	Means[x]		
	Cenchrus ciliaris, biloela	Chloris gayana	Panicum maximum
Apr. 18	1.14ab(a)	1.06a (a)	1.22b (a)
May 6	0.86b (b)	0.61a (b)	0.94 b (b)
Jun. 12	0.65ab(c)	0.52a(bc)	0.78b (c)
Jul. 14	0.67b (c)	0.41a(cd)	0.69b(cd)
Aug. 19	0.58b (c)	0.40a(cd)	0.54ab(d)
Sep. 24	0.39a (d)	0.28a(de)	0.37a (e)
Nov. 15	0.34a (d)	0.27a(de)	0.29a(ef)
Jan. 6	0.26a (d)	0.24a (e)	0.25a(ef)
Mar. 1	0.30a (d)	0.24a (e)	0.21a (f)
Growth period means[x]	0.58b	0.45a	0.59b

[x] LSD between species at same date = 0.152(P<0.01)
LSD between growth period means = 0.066(P<0.001)
LSD between dates each species = 0.152(P<0.01)

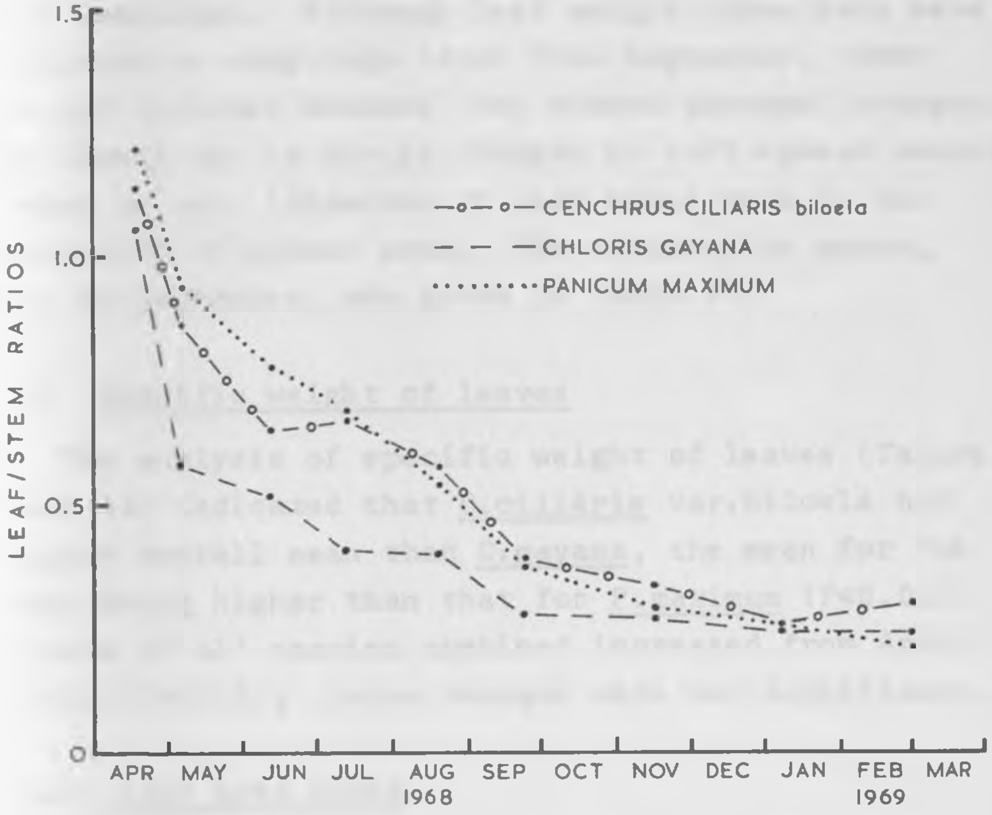

Fig. 7. Muguga: Mean leaf/stem ratio trends.

for C.ciliaris var.biloela and C.gayana ($P<0.05$, Table 12). C.ciliaris var.biloela and C.gayana showed no difference, either at sampling dates, or overall. In all species, the index increased from April to September ($P<0.01$) but the rate of increase was less for later samplings. Although leaf weight index data were calculated at samplings later than September, these were not included because they showed abnormal changes, most likely due to abrupt changes in tuft spread caused by wind or rain (diameter of leaf mass) used in the calculation of ground area. The calculation means, April to September, are given in Table 13.

5.2.9 Specific weight of leaves

The analysis of specific weight of leaves (Tables 14 and 15) indicated that C.ciliaris var.biloela had a higher overall mean than C.gayana, the mean for the latter being higher than that for P.maximum ($P<0.01$). The mean of all species combined increased from April to July ($P<0.05$); later changes were not significant.

5.2.10 Leaf area index

During the period April to August, P.maximum had a higher mean leaf area index than C.ciliaris var.biloela ($P<0.01$), C.gayana being intermediate between the two (Table 16). The differences between C.gayana and either one of the other species was significant at the 5 per cent level only.

5.2.11 Root distribution and rooting depth.

Between species, the mean dry weight distribution of roots in relation to soil depth, expressed as percentage did not differ greatly (Table 17).

TABLE 12

Muguga 1968: Mean log leaf weight index (mg/cm^2)

Date	Means[x]		
	Cenchrus ciliaris, *biloela*	*Chloris gayana*	*Panicum maximum*
Apr. 18	-0.30a (a)	-0.28a (a)	-0.28a (a)
May 6	-0.05a (a)	0.00a (b)	0.17a (b)
Jun. 12	0.67a (b)	0.58a (c)	0.68a (c)
Jul. 14	0.74a(bc)	0.93ab(de)	1.05b(de)
Aug. 19	0.95a (c)	1.13ab(ef)	1.16b (e)
Sep. 24	1.28a (d)	1.32a (f)	1.53 (e)
Overall Means[x]	0.55a	0.61a	0.72b

[x] LSD between species at same date = 0.189($P<0.05$)
LSD between overall means = 0.077($P<0.05$)
LSD between dates each species = 0.253($P<0.01$)

TABLE 13

Muguga 1968: Mean leaf weight index (L_W, mg/cm^2), specific weight of leaves (L_S, mg/cm^2) and leaf area index (L_A, cm^2/cm^2)

Date	Cenchrus ciliaris, biloela			Chloris gayana			Panicum maximum		
	L_W	L_S	L_A	L_W	L_S	L_A	L_W	L_S	L_A
Apr.18	0.52	2.67	0.19	0.53	2.30	0.24	0.54	1.95	0.25
May 6	0.91	3.51	0.25	1.02	2.72	0.36	1.52	2.27	0.59
Jun.12	4.84	3.20	2.06	4.01	3.52	1.56	4.85	2.89	1.54
Jul.14	5.70	5.89	1.08	8.55	5.34	1.79	11.68	3.22	2.23
Aug.19	9.25	5.45	2.19	13.35	4.76	2.63	14.54	3.67	4.10
Sep.24	18.92			21.23			35.21		
Nov.15		5.86			6.06			4.21	
Mean	6.69	4.43	1.15	8.12	4.12	1.32	11.39	3.04	1.74

TABLE 14

Muguga 1968: Mean log specific weight of leaves (mg/cm^2), April to November

	Species		
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum*
Means^x	0.553a	0.492b	0.395c

^{x}LSD = 0.055 ($P<0.01$)

TABLE 15

Muguga 1968: Mean log specific weight of leaves (mg/cm^2), all species combined

Date	Means^x			
Apr.18	0.358)			(a)
	)	L.S.D. 0.040)		
May 6	0.422)	)		(b)
		)		
Jun.12	0.504)	)	L.S.D. 0.049	(c)
	)	)		
Jul.14	0.669)	)		(d)
	)	L.S.D. 0.080)		
Aug.19	0.660)			(d)
	)			
Nov.15	0.725)			(d)

^{x}$P<0.05$

TABLE 16

Muguga 1968: Mean log leaf area index, April to August

	Species		
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum*
Means^x log (L_A X 10)	0.574a	0.685ab	0.792b

^{x}LSD = 0.151 (P<0.01)
LSD = 0.110 (P<0.05, see text)

TABLE 17

Muguga 1968-1969: Dry weight distribution of roots in relation to soil depth. Each percentage value is the mean of 9 samplings (X 3 plants)

Soil depth (cm)	Grass species			
	Cenchrus ciliaris, biloela	Chloris gayana	Panicum maximum non-defoliated	Panicum maximum defoliated
	Mean %	Mean %	Mean %	
0- 20	53.3	57.3	51.7	49.3
20- 40	15.1	15.8	16.3	18.0
40- 60	8.3	9.3	9.8	11.6
60- 80	6.4	5.3	5.8	7.5
80-100	4.4	4.0	4.5	5.2
100-120	3.6	2.6	3.5	4.1
120-140	2.6	2.0	2.6	2.4
140-160	2.1	1.4	2.0	1.1
160-180	1.5	1.0	1.4	0.6
180-200	1.2	0.8	1.0	0.2
200-220	0.6	0.4	0.8	
220-240	0.3	0.1	0.5	
240-260	0.2		0.1	
260-280	0.1			
280-300	trace			

Considerable changes however, occurred throughout the growth period in the percentage of roots collected in the 0-20 cm soil layer while fluctuations in the 20-40 cm soil layer were small (Fig.8). In all species, a large percentage of the root systems was initially collected from the surface layer, followed by a decreasing trend until August-September. At this stage the percentages in the 0-20 cm soil layer began to increase, reached high values in November through December and then decreased again.

Maximum rooting depth in defoliated plants of P.maximum was 200 as compared to 250 cm in non-defoliated plants.

The mean horizontal (diameter) spread of roots (Table 18) was similar in C.gayana and P. maximum throughout the growth period. In C.ciliaris var. biloela, spread was small initially, but greater than that of other species, at later samplings. Horizontal spread in defoliated P.maximum plants was less than that of non-defoliated plants.

5.2.12 Roots as percentage of total plants

Figure 9 shows that the trends in root dry matter yield as a percentage of the total plant for any one species were in general inversely correlated to their shoot/root ratios (Fig.6).

5.2.13 Root volumes and specific weight of roots

Root volume increases (Table 19) throughout the growth period were similar to those obtained for root yields except for small deviations caused by changes in the specific weight of roots. At the March samplings the volume ratio between C.ciliaris var.biloela and C.gayana was 1: 0.49 and between C.ciliaris var.biloela and P.maximum 1: 0.35 while their dry weight ratios were 1: 0.37 and 1: 0.36.

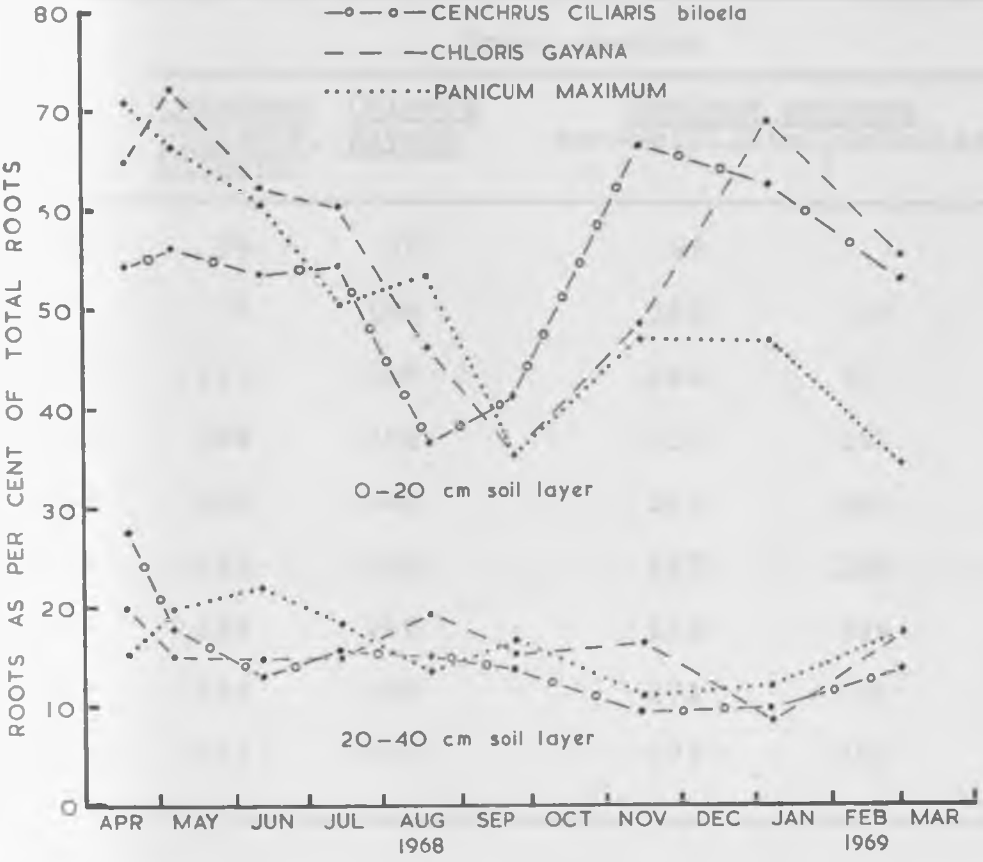

Fig. 8 Muguga: Root dry matter yields in surface soil layers as per cent of total roots; mean of three plants.

TABLE 18

Muguga 1968-1969: Horizontal (diameter).spread of roots (cm); mean of three plants

Date	Grass species			
	Cenchrus ciliaris, biloela	*Chloris gayana*	*Panicum maximum* non-defoliated	*Panicum maximum* defoliated
Apr.18	29	50	55	
May 6	76	108	161	37
Jun.12	152	164	183	127
Jul.14	168	252	216	157
Aug.19	200	245	221	184
Sep.24	231	260	257	188
Nov.15	265	248	251	238
Jan. 6	315	236	271	230
Mar. 1	312	262	273	260

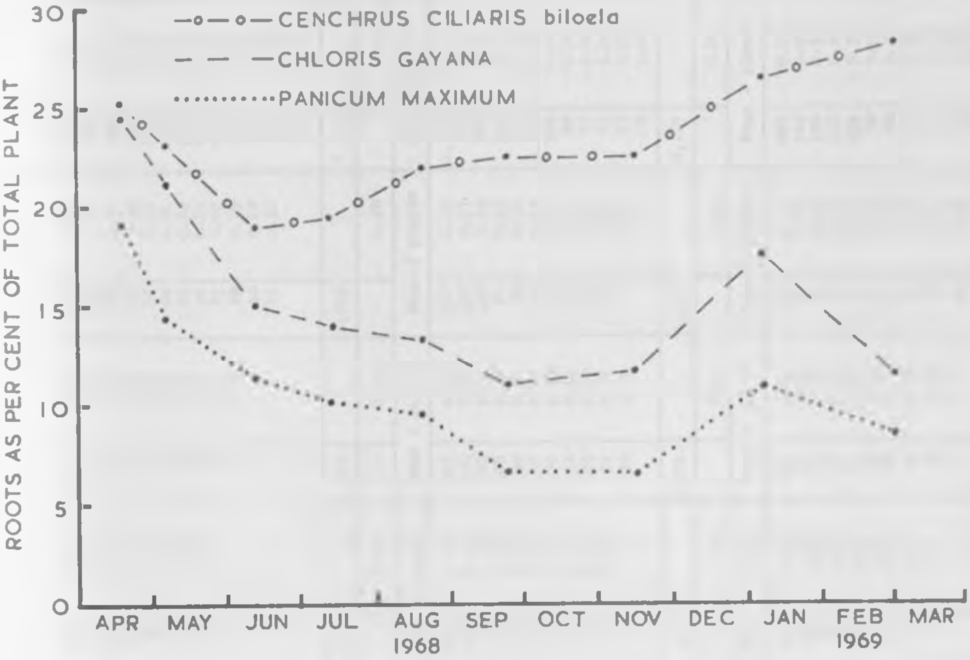

Fig. 9 Muguga: Root dry matter yields as per cent of total plants: mean of three plants.

[illegible] 1968-1969: Root volumes (cm^3) and specific weight of roots (gm/cm^3)

	Soil depth (cm)	June 12		July 14		Aug. 19		Sep. 24		Nov. 15		Mar. [illegible]	
		Vol.	Sp. weight	Vol.	Sp. weight	Vol.	Sp. weight	Vol.	Sp. weight	Vol.	Sp. weight	Vol.	Sp. weight
CENCHRUS CILIARIS VAR. BILOELA		Mean 3 plants		Mean 3 plants		Mean 2 plants		Mean 1 plant		Mean 2 plants		Mean 2 plants	
	0-20	100	0.13	194	0.14	284	0.15	491	0.21	1,403	0.20	3,077	0.24
	20-40	33	0.10	68	0.12	132	0.16	153	0.20	198	0.22	770	0.22
	40-60	17	0.10	41	0.11	79	0.16	132	0.19	89	0.22	387	0.20
	60-80	22	0.10	26	0.10	104	0.15	97	0.18	79	0.21	297	0.20
	80-100	19	0.09	17	0.10	86	0.14	72	0.16	64	0.20	285	0.18
	100-120	13	0.09	17	0.10	74	0.13	74	0.16	57	0.19	249	0.19
	120-140	12	0.10	14	0.11	70	0.14	57	0.15	28	0.21	229	0.18
	140-160	7	0.11	9	0.10	73	0.12	49	0.16	50	0.18	202	0.17
	160-180			10	0.10	60	0.11	44	0.16	55	0.19	202	0.17
	180-200			10	0.10	37	0.12	41	0.15	37	0.20	205	0.16
	200-220							33	0.14	38	0.19	184	0.16
	220-240									10	0.18	60	0.17
	240-260									31	0.22	95	0.20
	260-280											51	0.20
	280-300											26	0.20
	Total	225		406		999		1,243		2,134		6,315	
	Mean		0.10		0.11		0.14		0.17		0.20		0.19
CHLORIS GAYANA		Mean 3 plants		Mean 3 plants		Mean 2 plants		Mean 2 plants		Mean 2 plants		Mean 2 plants	
	0-20	101	0.13	230	0.17	301	0.19	361	0.19	757	0.15	1,712	0.17
	20-40	34	0.12	62	0.16	109	0.18	190	0.18	183	0.17	490	0.16
	40-60	21	0.13	40	0.18	58	0.19	145	0.18	149	0.18	202	0.16
	60-80	9	0.14	28	0.15	32	0.17	106	0.18	87	0.18	163	0.16
	80-100	8	0.13	19	0.14	32	0.17	98	0.17	79	0.18	112	0.16
	100-120	3	0.10	12	0.15	29	0.18	93	0.16	40	0.19	105	0.16
	120-140	2	0.12	6	0.15	24	0.16	70	0.18	34	0.19	109	0.16
	140-160			3	0.11	20	0.15	62	0.18	29	0.17	60	0.16
	160-180					12	0.14	43	0.19	26	0.17	59	0.16
	180-200					8	0.14	32	0.17	18	0.17	62	0.16
	200-220							25	0.16	5	0.18	37	0.17
	220-240											5	0.18
	Total	178		400		625		1,225		1,407		3,119	
	Mean		0.12		0.15		0.17		0.18		0.18		0.18
PANICUM MAXIMUM		Mean 3 plants		Mean 3 plants		Mean 2 plants		Mean 2 plants		Mean 2 plants		Mean 2 plants	
	0-20	92	0.14	136	0.17	221	0.21	181	0.25	603	0.17	885	0.19
	20-40	33	0.13	52	0.17	54	0.20	84	0.28	98	0.23	440	0.20
	40-60	12	0.13	40	0.19	30	0.20	50	0.25	62	0.29	191	0.22
	60-80	7	0.12	14	0.21	34	0.21	44	0.27	36	0.30	133	0.26
	80-100	4	0.11	14	0.18	25	0.20	40	0.24	32	0.31	104	0.27
	100-120	4	0.11	10	0.14	19	0.19	28	0.23	30	0.30	98	0.26
	120-140	2	0.10	5	0.16	13	0.19	23	0.19	27	0.28	78	0.27
	140-160			3	0.11	14	0.17	17	0.20	21	0.27	70	0.24
	160-180			2	0.11	9	0.15	8	0.19	20	0.27	57	0.25
	180-200							4	0.18	11	0.29	60	0.25
	200-220									10	0.25	43	0.26
	220-240									2	0.21	29	0.24
	240-260											21	0.24
	Total	154		276		419		479		952		2,208	
	Mean		0.12		0.16		0.19		0.23		0.28		0.24

During the dry period, June to September, the mean specific weight of roots increased the most in P.maximum and the least in C.ciliaris var.biloela. Subsequently, the mean specific weight of roots remained constant in C.gayana while it continued to increase in C.ciliaris var.biloela and in particular in P.maximum.

Specific root weights decreased with increasing root depth in samples taken from June to September, suggesting that roots at greater depths had a higher moisture content. At later samplings, the trends were irregular and higher specific weights were occasionally recorded at depths well beyond the soil surface layer.

5.3 Results - Study II

A summary of the dry weight data obtained at Muguga and Kedong, 1967-1968, is given in Figs.10 and 11 (values less than 0.1 gm have been omitted).

5.3.1 Root yields

The root system of the grasses increased in dry matter content until the plants reached maturity in February 1968. During the period February to July, however, root growth rates showed a marked decrease in most species (Figs.10 and 11) suggesting that maximum root development coincided with the maturation of the grasses.

The following differences ($P<0.05$) in mean root dry matter yields were obtained (Fig.12) At Muguga, E.superba grew less than all other species; C.gayana yielded more than both T.triandra and C.ciliaris var. mbalambala; and C.ciliaris var.biloela more than the latter. At Kedong, E.superba grew less than all other

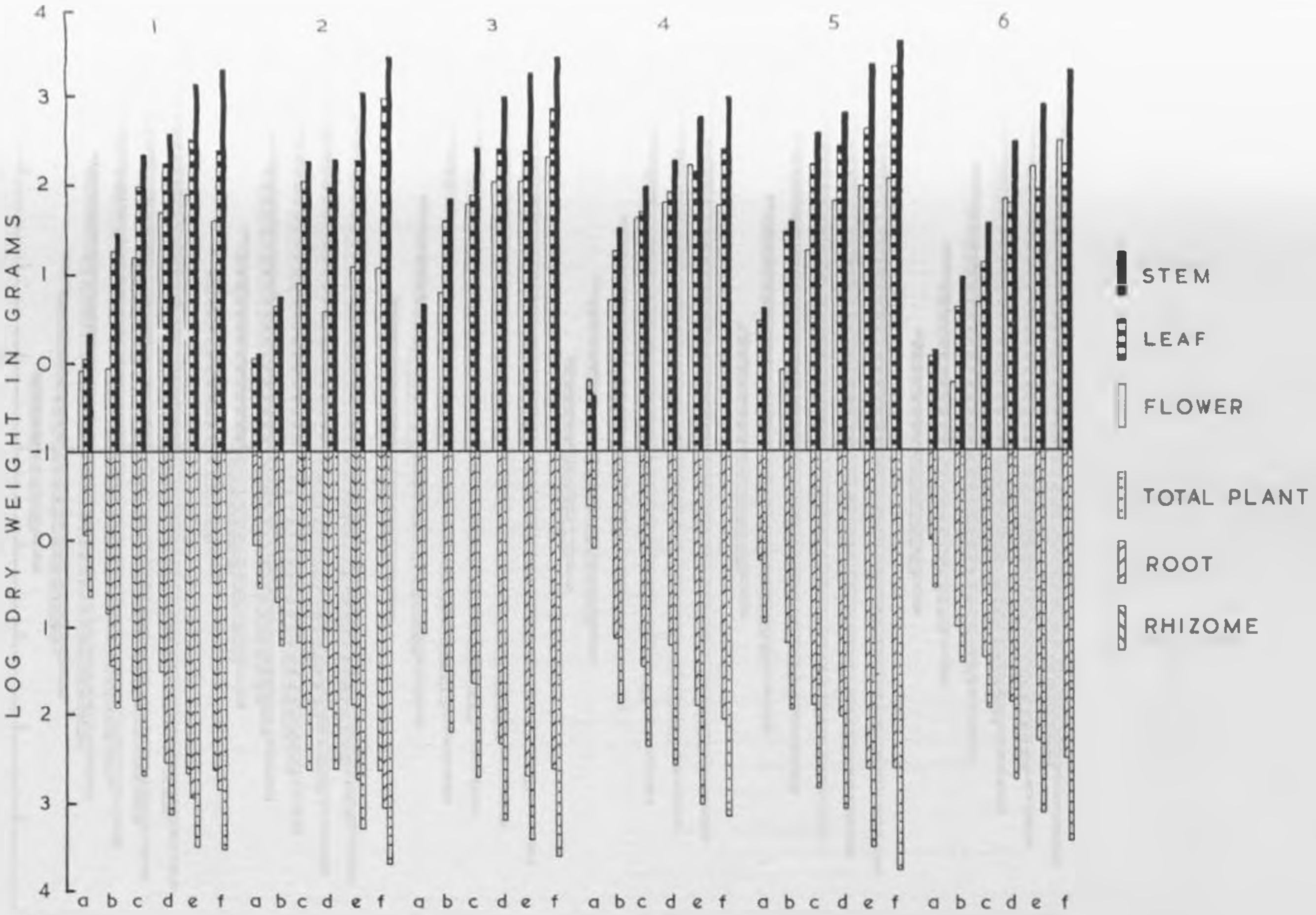

Fig. 10 Dry weights of 1. *Cenchrus ciliaris* var.biloela, 2.*Cenchrus ciliaris* var.mbalambala, 3. *Chloris gayana*, 4. *Eragrostis superba*, 5. *Panicum maximum* and 6. *Themeda triandra* planted at Muguga in April 1967 and sampled in: a) May, b) July, c) September, d) November, 1967 and in e) February and f) June-July, 1968. Dry weights less than 0.1 gm are not shown. Diagrammatic presentation of results has been simplified by giving total weights below the line rather than above.

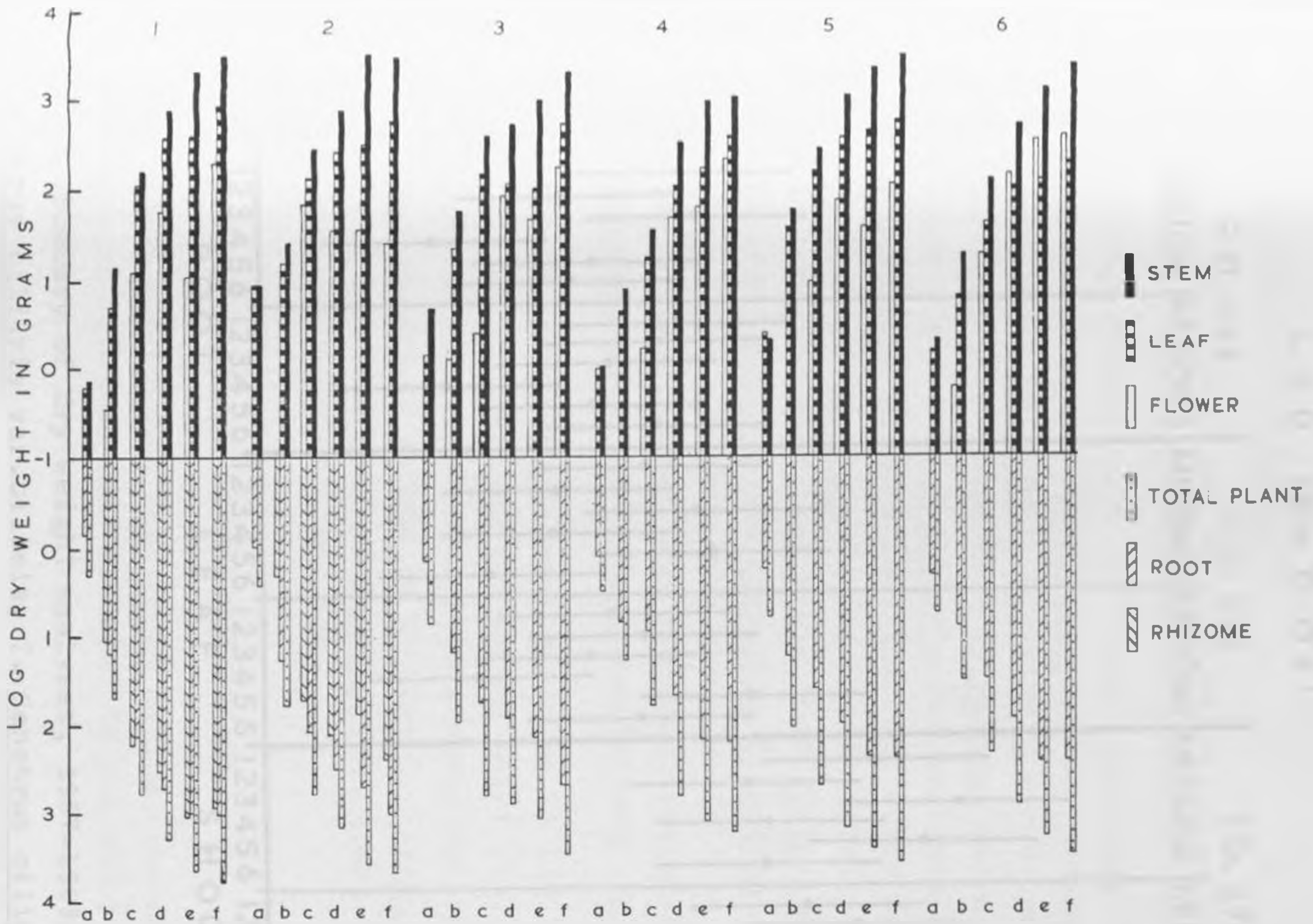

Fig. 11 Dry weights of: 1. Cenchrus ciliaris var.biloela, 2. Cenchrus ciliaris var. mbalambala, 3. Chloris gayana, 4. Eragrostis superba, 5. Panicum maximum and 6. Themeda triandra planted at Kedong in April 1967 and sampled in: a) May, b) July, c) October, d) December, 1967 and in e) February and f) May, 1968. Dry weights less than 0.1 gm are not shown. Diagrammatic presentation of results has been simplified by giving total plant weights below the line rather than above.

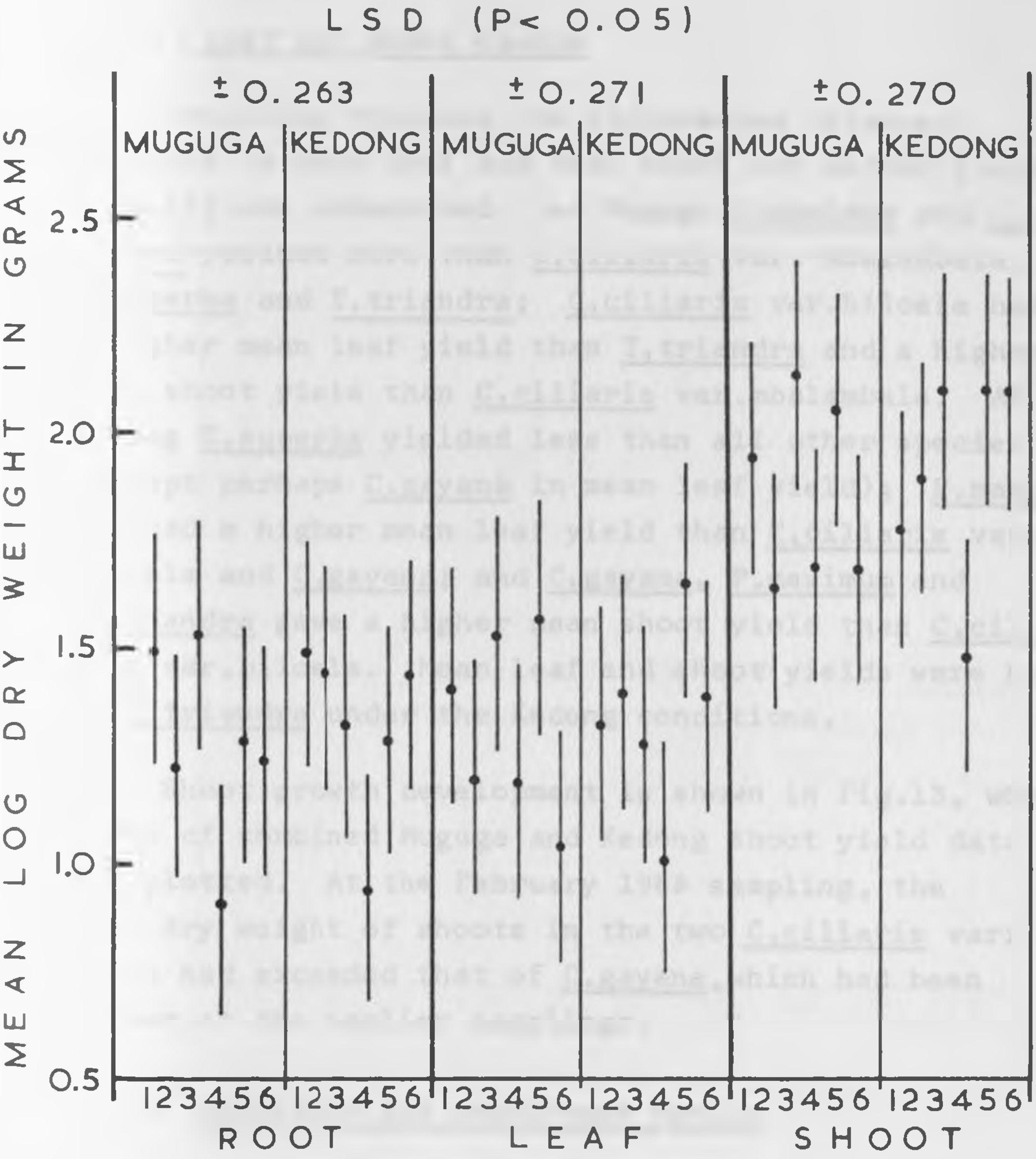

Fig. 12 Summary of dry weight analyses, 1967-1968: 1. Cenchrus ciliaris var.biloela, 2. Cenchrus ciliaris var.mbalambala, 3. Chloris gayana, 4. Eragrostis superba, 5. Panicum maximum and 6. Themeda triandra. Individual species means differ at the 5 per cent level when one mean is not overlapped by the LSD of another.

species; otherwise no differences were obtained. No significant differences were obtained between Muguga and Kedong for any species.

5.3.2 Leaf and shoot yields

Excluding rhizomes the differences obtained ($P<0.05$) in mean leaf and mean shoot dry matter yields (Fig.12) are summarized: at Muguga *P.maximum* and *C. gayana* yielded more than *C.ciliaris* var. mbalambala, *E.superba* and *T.triandra*; *C.ciliaris* var.biloela had a higher mean leaf yield than *T.triandra* and a higher mean shoot yield than *C.ciliaris* var.mbalambala. At Kedong *E.superba* yielded less than all other species (except perhaps *C.gayana* in mean leaf yield); *P.maximum* had a higher mean leaf yield than *C.ciliaris* var. biloela and *C.gayana*; and *C.gayana*, *P.maximum* and *T.triandra* gave a higher mean shoot yield than *C.ciliaris* var.biloela. Mean leaf and shoot yields were higher in *T.triandra* under the Kedong conditions.

Shoot growth development is shown in Fig.13, where means of combined Muguga and Kedong shoot yield data are plotted. At the February 1968 sampling, the mean dry weight of shoots in the two *C.ciliaris* varieties had exceeded that of *C.gayana*,which had been higher at the earlier samplings.

5.3.3 Leaf/root and shoot/root ratios

When determining shoot/root ratios, the dry weights of rhizomes were included in the shoot fraction. During the four last samplings, July 1967 to February 1968, the rhizomes constituted an average of 21 per cent of the total shoot weight in *C.ciliaris* var. biloela at Muguga and 30 per cent at Kedong. The corresponding figures for *C.ciliaris* var. mbalambala

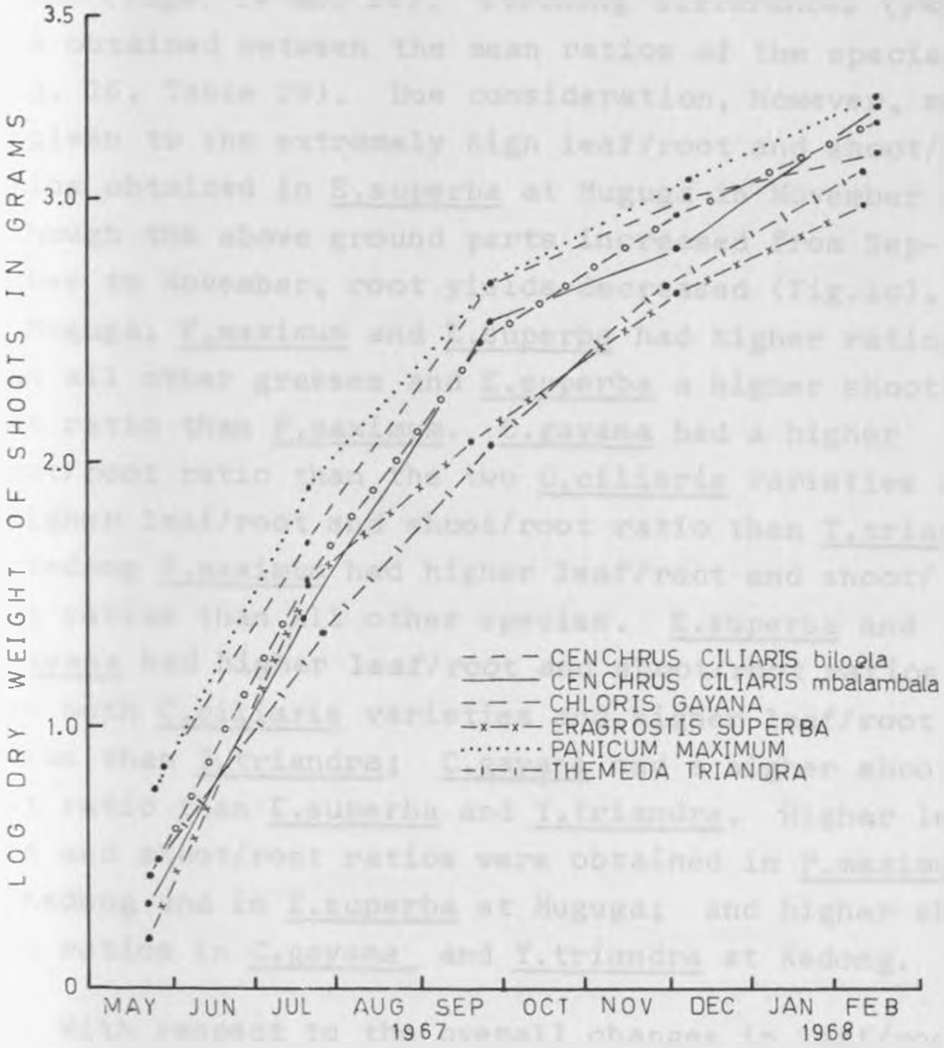

Fig. 13 Combined Muguga and Kedong: Mean dry weight of shoots.

were 4 per cent and 8 per cent.

Each grass species showed very similar leaf/root and shoot/root ratio trends under both experimental conditions (Figs. 14 and 15). Striking differences ($P<0.05$) were obtained between the mean ratios of the species (Fig. 16, Table 20). Due consideration, however, must be given to the extremely high leaf/root and shoot/root ratios obtained in E.superba at Muguga in November for although the above ground parts increased from September to November, root yields decreased (Fig.lo). At Muguga, P.maximum and E.superba had higher ratios than all other grasses and E.superba a higher shoot/root ratio than P.maximum. C.gayana had a higher shoot/root ratio than the two C.ciliaris varieties and a higher leaf/root and shoot/root ratio than T.triandra. At Kedong P.maximum had higher leaf/root and shoot/root ratios than all other species. E.superba and C.gayana had higher leaf/root and shoot/root ratios than both C.ciliaris varieties and higher leaf/root ratios than T.triandra; C.gayana had a higher shoot/root ratio than E.superba and T.triandra. Higher leaf/root and shoot/root ratios were obtained in P.maximum at Kedong and in E.superba at Muguga; and higher shoot/root ratios in C.gayana and T.triandra at Kedong.

With respect to the overall changes in leaf/root and shoot/root ratios throughout the development of the grasses from planting to maturation, the following differences ($P<0.05$) were found (Table 21). Both ratios increased from July to December and then decreased; the leaf/root ratio in February 1968 decreased to a value less than that obtained in May and July 1967.

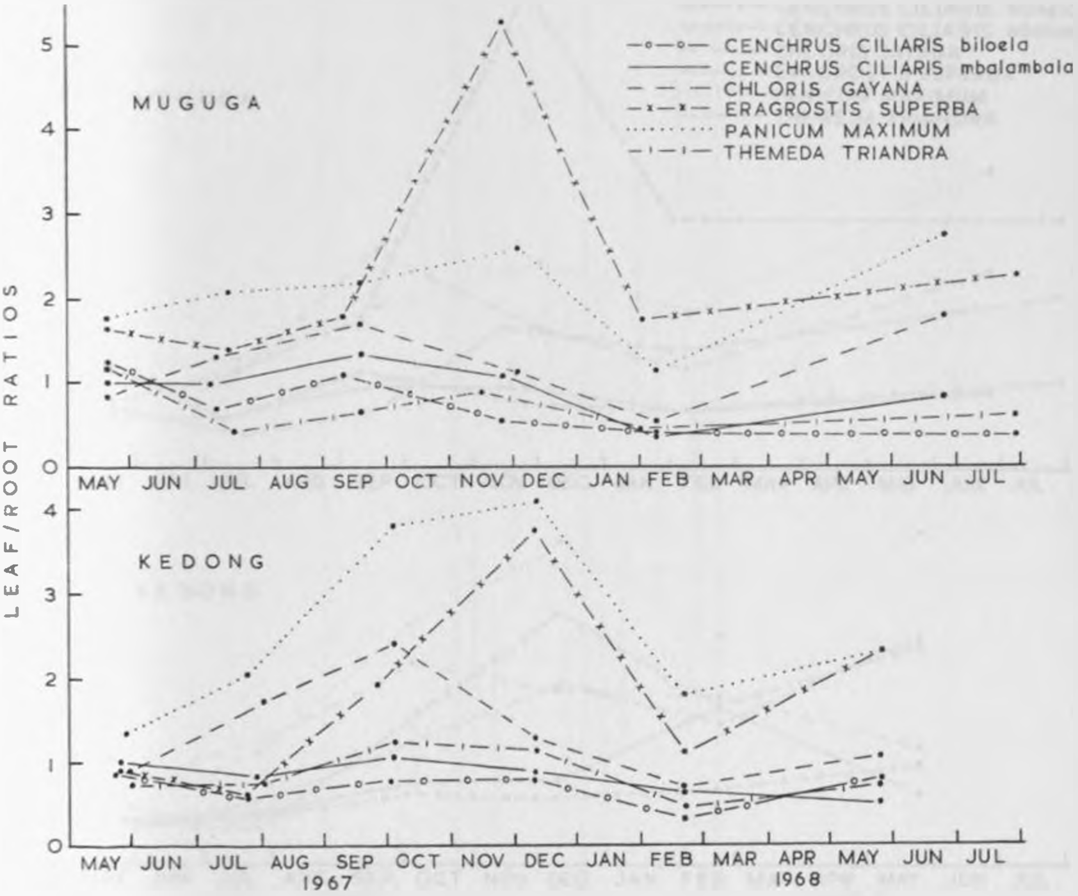

Fig. 14 Mean leaf/root ratio trends.

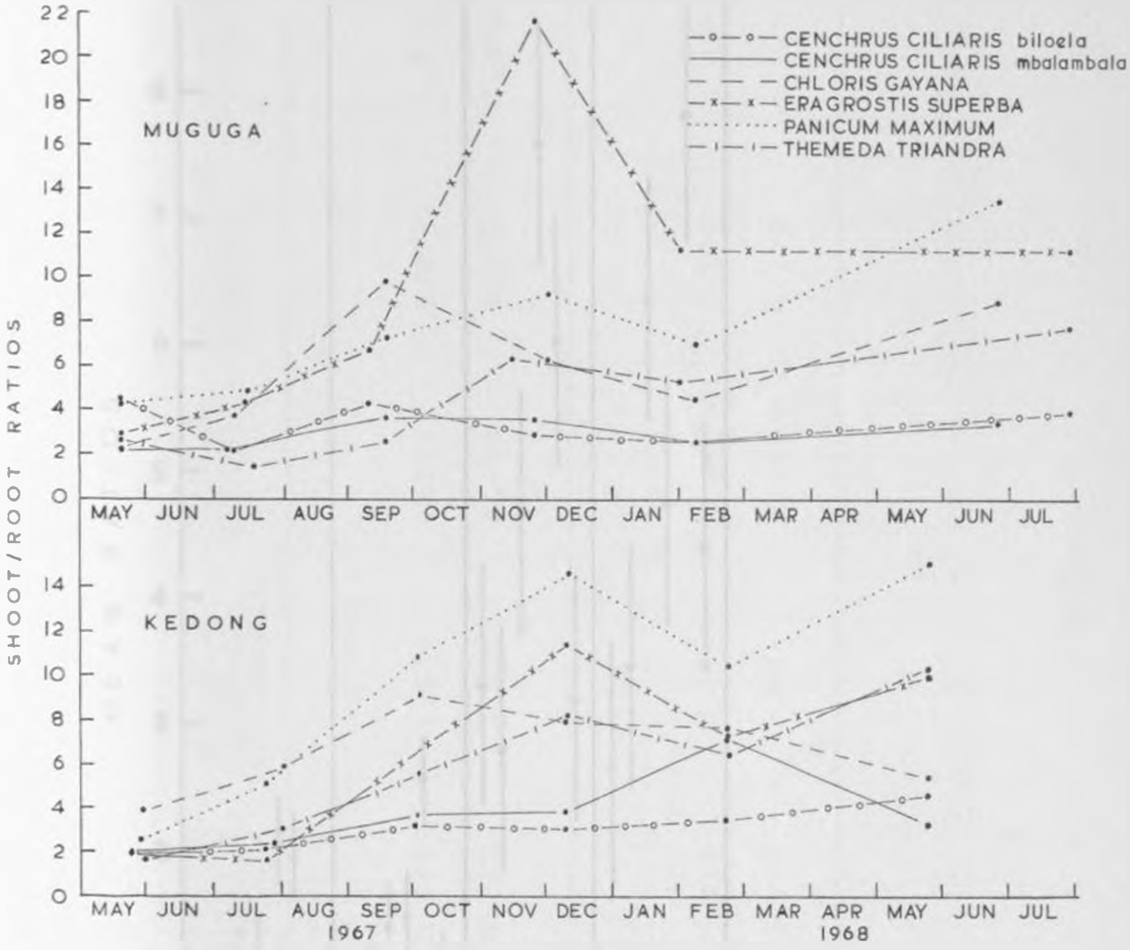

Fig. 15 Mean shoot/root ratio trends.

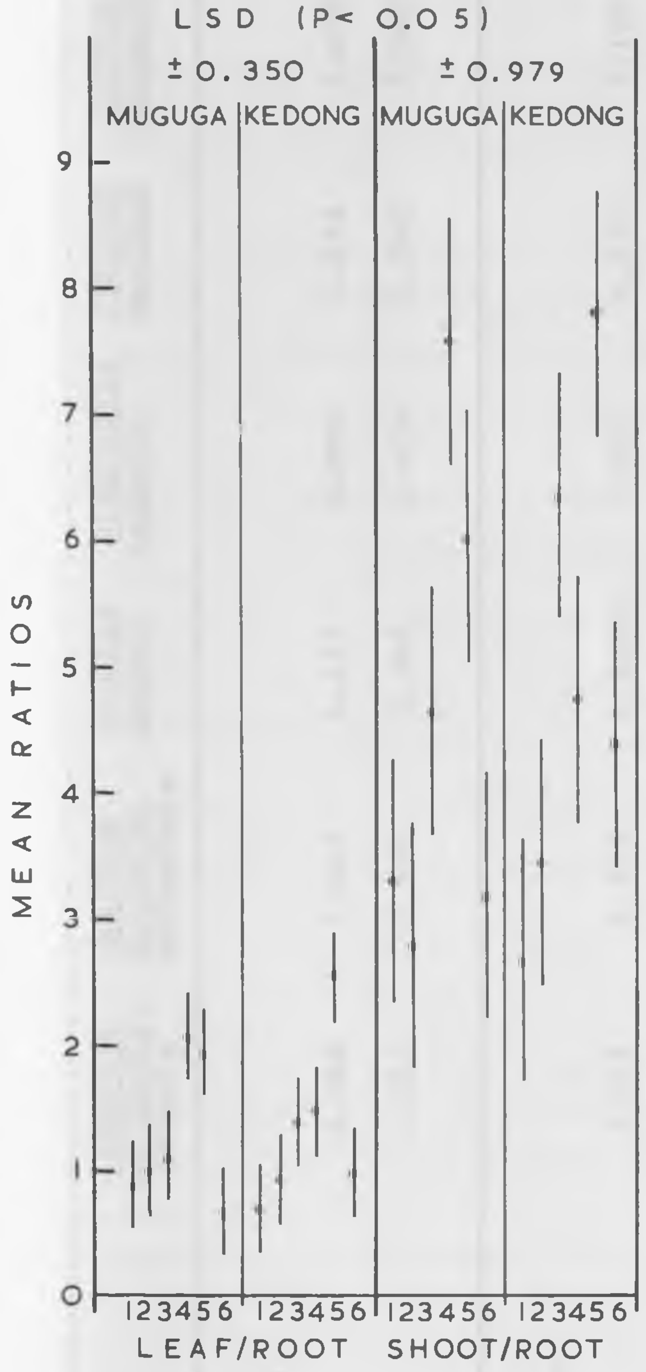

Fig. 16 Summary of ratio analyses, 1967-1968: 1. <u>Cenchrus ciliaris</u> var.biloela, 2. <u>Cenchrus ciliaris</u> var.mbalambala, 3. <u>Chloris gayana</u>, 4. <u>Eragrostis superba</u>, 5. <u>Panicum maximum</u> and 6. <u>Themeda triandra</u>. Individual species means differ at the 5 per cent level when one mean is not overlapped by the LSD of another.

Muguga and Kedong 1967-1968: Mean leaf/root and shoot/root ratios

	Cenchrus ciliaris, biloela	*Cenchrus ciliaris*, mbalambala	*Chloris gayana*	*Eragrostis superba*	*Panicum maximum*	*Themeda triandra*
Leaf/root:						
Muguga	0.888	1.023	1.116	2.098	1.956	0.679
Kedong	0.713	0.930	1.389	1.478	2.540	0.992
Shoot/root:						
Muguga	3.319	2.795	4.660	7.593	6.034	3.194
Kedong	2.675	3.461	6.357	4.746	7.814	4.387

TABLE 21

Combined Muguga and Kedong 1967-1968: Analysis of leaf/root and shoot/root ratio trends

Period	Leaf/root ratio means	L.S.D.($P<0.05$)
May v Jul.	1.144 v 1.147	0.187
Jul. v Sep.	1.147 v 1.616[x]	0.190
Sep. v Dec.	1.616 v 1.993[x]	0.224
Dec. v Feb.	1.993 v 0.820[x]	0.257
May v Feb.	1.144 v 0.820[x]	0.226
	Shoot/root ratio means	L.S.D.($P<0.05$)
May v Jul.	2.762 v 3.274	0.525
Jul. v Sep.	3.274 v 5.707[x]	0.531
Sep. v Dec.	5.707 v 8.278[x]	0.637
Dec. v Feb.	8.278 v 6.367[x]	0.718

[x] Means significantly different ($P<0.05$)

5.3.4 Sward versus single plants

Shoot/root ratios in swards and single plants approximated in values. In C.ciliaris var.mbalambala the shoot/root ratio was slightly higher under sward conditions while in P.maximum both ratios were similar (Table 22).

In the 28 month old sward plots root excavations to 3 m depths indicated that C.ciliaris var.mbalambala yielded approximately 7,000 kg/ha root dry matter compared to 3,300 kg/ha for P.maximum.

5.3.5 Leaf/stem ratio

Combined mean leaf/stem ratios for Muguga and Kedong are given in Table 23, and they suggest that the two C.ciliaris varieties, E.superba and P.maximum have a higher leaf/stem ratio than C.gayana and T.triandra.

5.3.6 Roots as percentage of total plants

The trends in root dry matter yield as a percentage of total plant for any one species were in general inversely correlated to their shoot/root ratios; the values of these are given in Table 24.

The trends for individual species were irregular. However, the sampling means for all species and locations combined give a good indication of events during initial establishment of the grasses under the conditions of the experiment. The means suggest that the roots as a percentage of the total, decrease from May to December, increase slightly from December to February during which time the grasses mature, and then decrease slightly following the long rains and renewed growth in March-April.

TABLE 22

Muguga 1969: Shoot/root ratios for plants grown in swards and for single plants, 28 months from planting

Species	Ratios							
	Sward samples			Mean	Single plant samples			Mean
Cenchrus ciliaris mbalambala	2.60	2.74	3.03	2.79	2.01	2.21	2.75	2.32
Panicum maximum	5.03	4.97	5.16	5.05	5.70	5.06	4.84	5.20

TABLE 23

Combined Muguga and Kedong 1967-1968: Mean leaf/stem ratios

Species	Leaf/stem ratio mean
Chenchrus ciliaris, biloela	0.53
Cenchrus ciliaris, mbalambala	0.60
Chloris gayana	0.33
Eragrostis superba	0.61
Panicum maximum	0.56
Themeda triandra	0.38

Muguga and Kedong 1967-1968: Root dry matter yields as percentage of total plants

Species	Location	Roots, per cent						
		May	Jul.	Sep.	Dec.	Feb.	Mean	May-July
Cenchrus ciliaris, biloela	Muguga	18.1	32.2	19.9	25.7	27.6	24.7	20.4
	Kedong	34.2	31.4	24.3	24.3	21.9	27.2	17.8
Cenchrus ciliaris, mbalambala	Muguga	31.8	32.3	25.2	21.7	27.3	27.7	21.9
	Kedong	33.2	29.1	21.4	20.5	12.0	23.2	22.9
Chloris gayana	Muguga	32.1	21.2	9.2	13.8	18.1	18.9	10.0
	Kedong	22.5	14.9	9.8	11.2	11.4	14.0	15.5
Eragrostis superba	Muguga	25.9	19.4	13.9	4.4	8.1	14.3	8.1
	Kedong	38.2	36.9	15.3	8.0	11.9	22.1	9.1
Panicum maximum	Muguga	18.6	17.0	13.6	9.7	12.5	14.3	6.9
	Kedong	28.0	16.4	8.5	6.4	8.7	13.6	6.2
Themeda triandra	Muguga	27.6	41.8	27.5	13.7	15.9	25.3	11.3
	Kedong	36.5	24.4	15.2	10.9	13.4	20.1	8.8
Sampling Mean:		28.9	26.4	17.0	14.2	15.7		13.2

5.3.7 Root distribution

The dry weight distribution of the various species (April 1967 to May-July 1968) is indicated in Table 25.

At Kedong, all species had a higher mean percentage of their root systems in the 0-20 cm soil layers; very high percentages for these layers were recorded for E.superba and T.triandra. These two species also had higher root yields at Kedong, which indicates even greater root densities. Previous analyses, however, of mean root yields over the period April 1967 to February 1968 did not indicate significant differences between locations. The data obtained when figures for all species are combined (Table 25) show that at Kedong, on a dry weight basis, there was at least 10% more roots in the 0-20 cm soil layer than at Muguga, although C.gayana and P.maximum individually had smaller mean yields.

Rooting depths measured by excavations (Table 25) may not indicate the maximum depth attained since it was impossible to follow and excavate the smallest roots at the distal end of the systems. The depths, however, serve as a basis for comparison and they suggest that all the grasses had a shallower root system at Kedong. At Muguga, C.ciliaris var.biloela, C.gayana and P.maximum roots were followed to 280 cm depths, E.superba to 220 cm and C.ciliaris var.mbalambala and T.triandra to 180 cm. At Kedong, C.ciliaris var.biloela and C.gayana penetrated to 180 cm, E.superba to 160 cm, P.maximum and T.triandra to 140 cm and C.ciliaris var.mbalambala to 120 cm soil depths.

Maximum horizontal spread of roots at any sampling date revealed only small differences between

TABLE 25

Dry weight distribution of roots in relation to soil depth. Each percentage value is the mean of six samples taken between May 1967 and July 1968

Soil depth cm	Grass species: *Cenchrus ciliaris*, biloela Mean %		*Cenchrus ciliaris*, mbalambala Mean %		*Chloris gayana* Mean %		*Eragrostis superba* Mean %		*Panicum maximum* Mean %		*Themeda triandra* Mean %		Mean %, all species	
	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong	Muguga	Kedong
0–20	52.1	56.5	55.7	58.1	67.2	68.5	53.0	72.2	50.8	58.3	45.6	71.1	54.1	64.1
20–40	18.6	18.8	16.3	17.9	12.8	16.2	20.9	17.1	13.9	22.6	21.2	15.1	17.3	18.0
40–60	12.2	11.7	10.9	13.5	5.8	7.3	9.8	7.6	8.2	9.9	14.8	8.6	10.3	9.8
60–80	7.5	5.9	7.1	6.2	4.0	3.3	5.7	2.6	8.1	5.1	11.1	2.2	7.3	4.2
80–100	3.4	3.2	4.2	3.1	2.9	1.5	4.0	0.4	6.2	3.8	4.0	1.5	4.1	2.2
100–120	2.3	2.6	3.1	1.3*	2.0	1.1	3.4	0.2	3.8	1.1*	1.6	1.0	2.7	1.2
120–140	1.0	0.8	1.3		1.0	1.5	1.9	0.1	2.9	Trace	1.3	0.6	1.6	0.5
140–160	0.8	0.5	0.6		1.1	0.5	0.5	0.1	1.9		0.1		0.8	0.2
160–180	0.4	0.2	0.9		0.9	0.1	0.4		1.5		0.6		0.8	0.1
180–200	0.4				0.5		0.3		1.1				0.4	
200–220	0.8				0.4		0.1		0.7				0.3	
220–240	0.2				0.7				0.5				0.2	
240–260	0.3				0.3				0.2				0.1	
260–280	0.2				0.3				0.1				0.1	
Mean dry weight in gm	255.46	314.00	135.93	182.14	148.40	59.91	26.80	43.00	113.55	79.15	57.61	77.43	117.96	125.94

*compact layer

species or locations (Table 26). The mean diameter for all species combined was 255 cm at Muguga and 249 cm at Kedong.

5.3.8 Gypsum resistance block readings

The gypsum resistance block readings in the C.ciliaris var.biloela sward plot at Muguga (Fig.17) show that the whole soil profile was saturated with water following the long rains (April-May: 795 mm) in 1967 (Table 1). By the end of July at least half the available water had been extracted from the surface layer by the grasses; evaporation losses from bare soil being small (Fig.18). By the middle of October most of the available soil water was used to 150 cm depth and heavy uptake was occurring between 150 and 240 cm. The short rains (October-December: 227 mm) wetted the surface layer of the soil but had no noticeable effect below 150 cm. Following the short rains, ending in the first part of December, the soil was drying out rapidly and for approximately three weeks, prior to the onset of the long rains in the middle of February 1968, the entire soil profile to 480 cm depth had reached wilting point. The long rains (February to May: 804 mm), which began approximately four weeks earlier than normal (Table 1), rewetted the soil profile, the surface layer first in the latter part of February and down to 480 cm depth by the beginning of May.

It would appear that the roots must have penetrated below the depth where resistance readings were affected. Though not strictly accurate, minimum rooting for each grass was estimated on the basis of the readings obtained (Table 27). In C.ciliaris var.biloela, relatively high readings obtained at 480 cm soil depth suggested that the grass had rooted to 6 m.

TABLE 26

Horizontal (diameter) spread of root systems (cm), 1967-1968

Species	Muguga	Kedong
Cenchrus ciliaris, biloela	295	291
Cenchrus ciliaris, mbalambala	245	245
Chloris gayana	285	242
Eragrostic superba	220	215
Panicum maximum	245	260
Themeda triandra	240	241
Mean	255	249

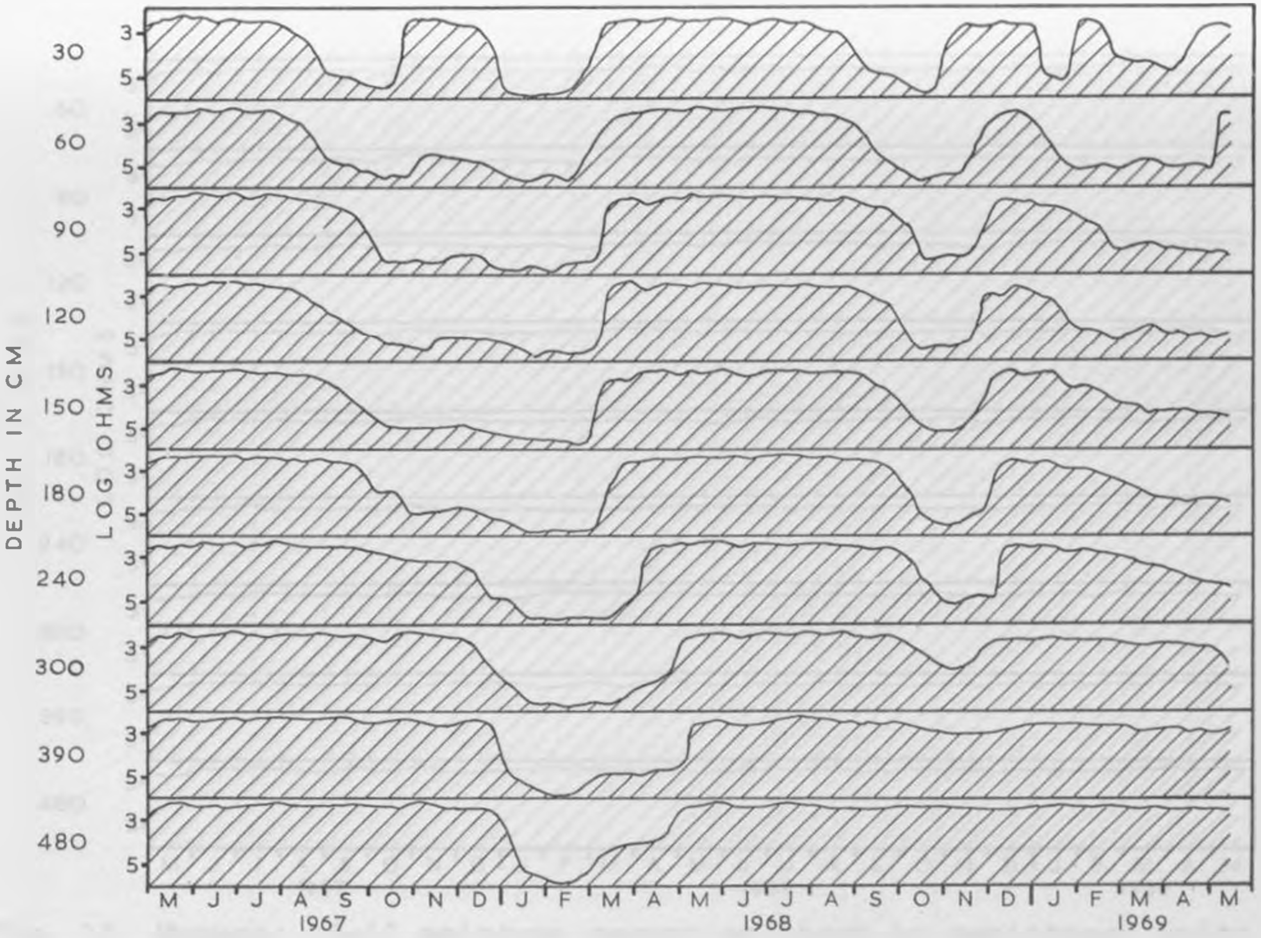

Fig. 17 Muguga : Soil moisture record as shown by resistance units under *Cenchrus ciliaris* var.biloela sward plot.

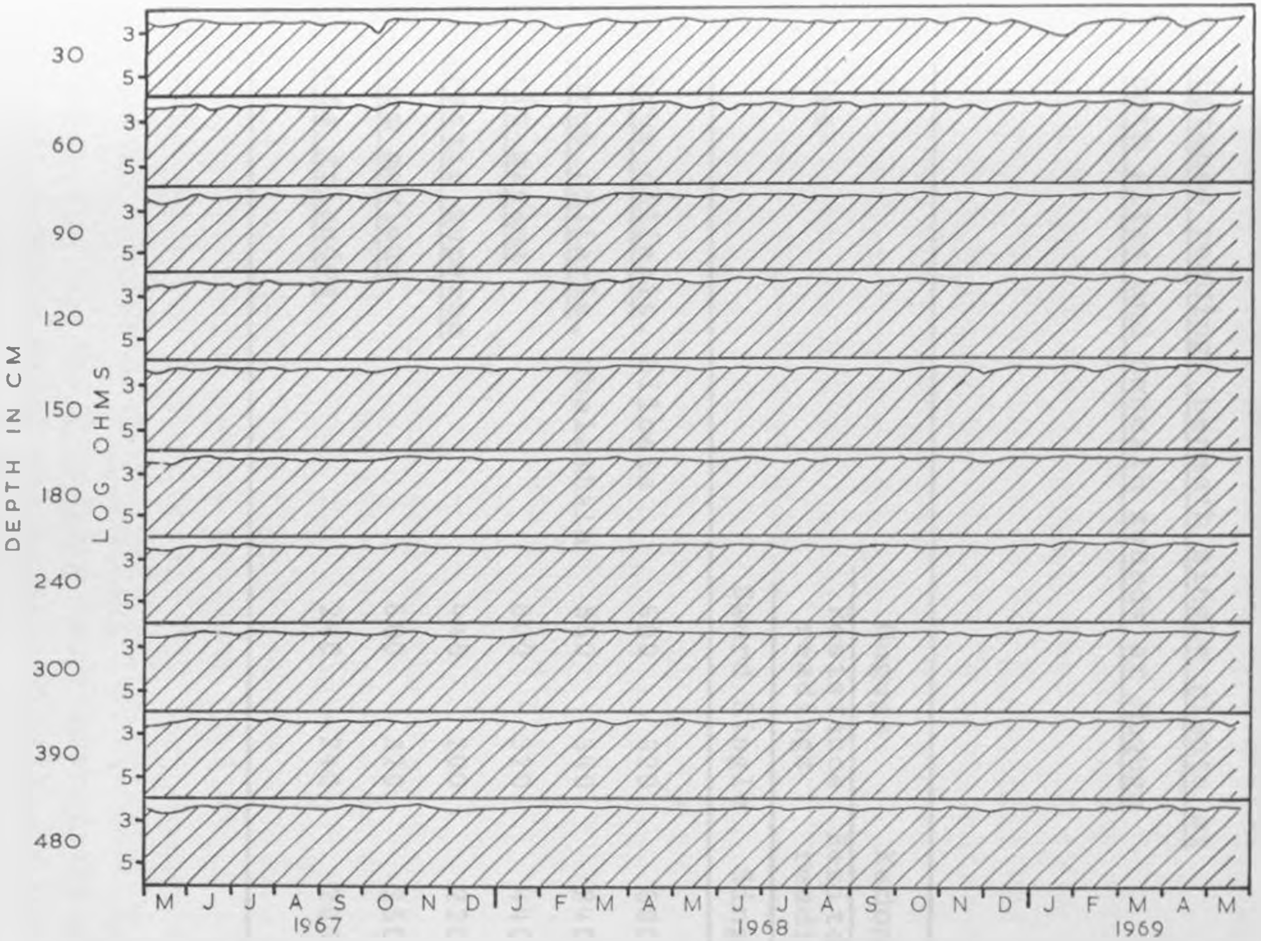

Fig. 18 Muguga: Soil moisture record as shown by resistance units under control plot (bare ground).

TABLE 27

Rooting depths (cm) as estimated from gypsum resistance readings beneath single plants at both sites and beneath swards at Muguga

Species	Muguga		Kedong
	Resistance readings		Resitance readings
	Sward	Single	Single
Cenchrus ciliaris, biloela	600	320	500
Cenchrus ciliaris, mbalambala	550	340	240
Chloris gayana	600	320	440
Eragrostis superba	440	200	220
Panicum maximum	600	320	350
Themeda triandra	240	240	200

This corresponded to a mean growth rate of more than 2 cm per day. Due to heavier short rains (October-December: 374 mm) and also to rains in January and February 1969 (115 mm), the high water deficit in the soil profile obtained in the previous year was not repeated.

Resistance block readings in C.ciliaris var.mbalambala, C.gayana and P.maximum sward plots showed similar trends to those described for C.ciliaris var. biloela. In C.ciliaris var.mbalambala water extraction was not so pronounced between the 290 and 480 cm soil depths, suggesting that the grass did not root quite as deeply as the biloela variety. In E.superba, the readings indicated that wilting point was reached in early February at 240 cm soil depth; minimum rooting depth was estimated as 440 cm. T.triandra extracted water from above 60 cm during July to October 1967 (Fig.19). After the short rains, wilting point was not quite reached at 60 cm, and readings were little affected at 240 cm.

The data from resistance blocks placed around single plants at Muguga generally indicated shallower root systems than in the sward plots. In C.ciliaris var.biloela (Fig.20), wilting point was attained only at 30 cm soil depth during February 1968 while the rooting depth was approximately 320 cm. Comparing the other species with C.ciliaris var.biloela, C.gayana was similar, and P.maximum had higher readings although rooting depth was equal. C.ciliaris var. mbalambala differed in having less pronounced water use in 1967. Readings during the latter part of 1968, however, were higher and rooting depth was estimated as 340 cm. E.superba and T.triandra had much lower readings in all layers and their roots only reached 200 and 240 cm soil depth respectively. In T.triandra

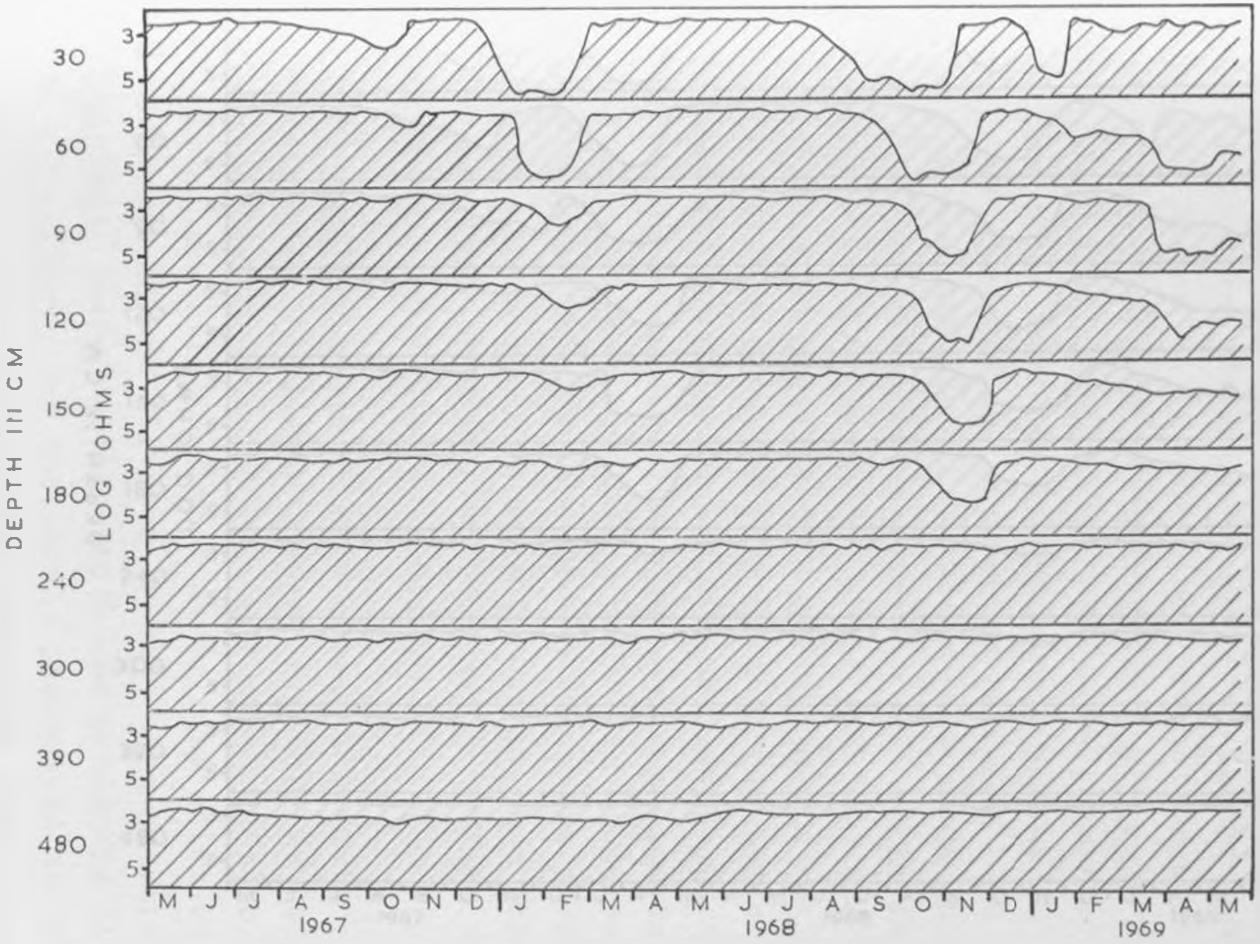

Fig. 19 Muguga: Soil moisture record as shown by resistance units under <u>Themeda triandra</u> sward plot.

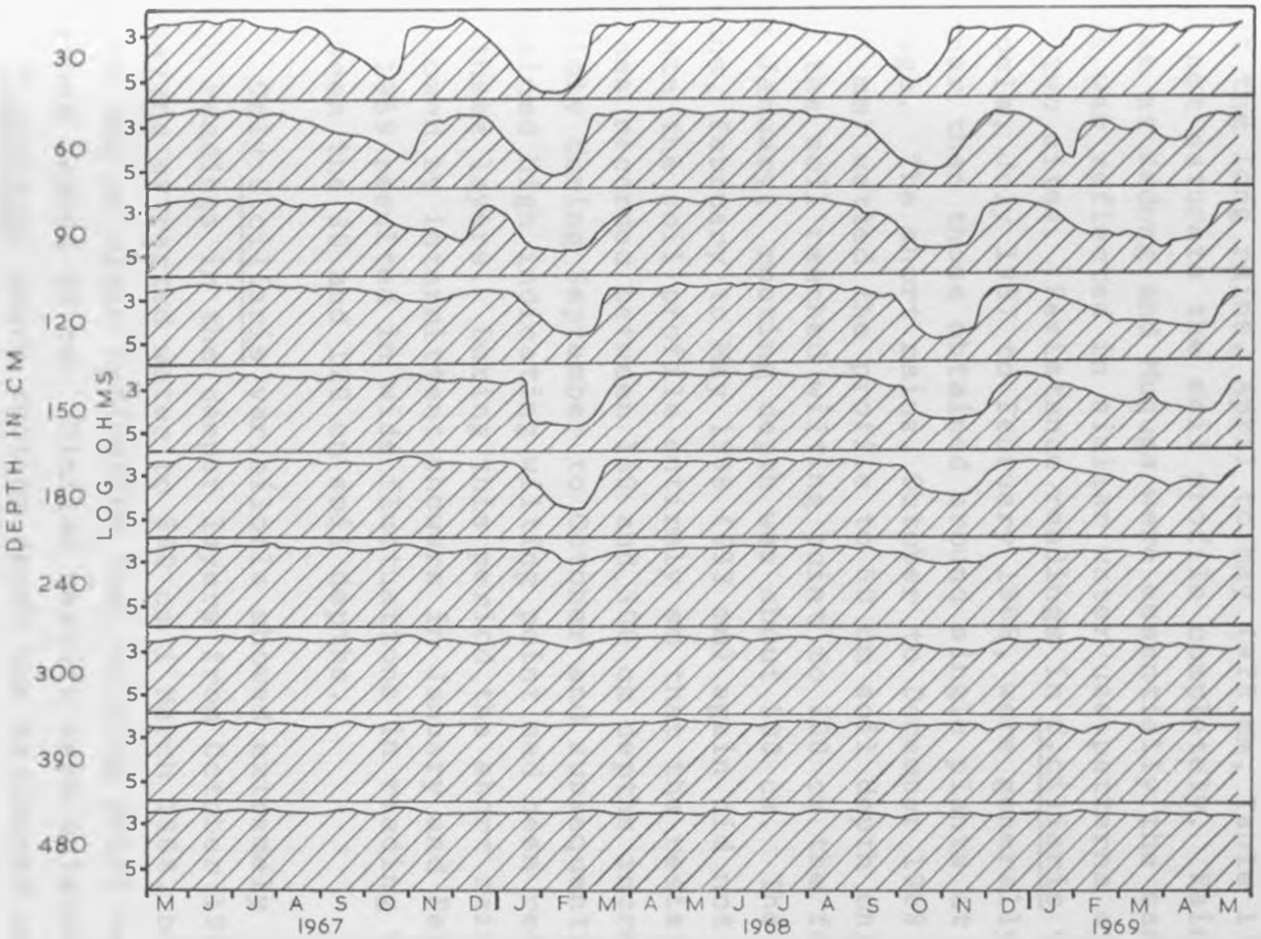

Fig. 20 Muguga: Soil moisture record as shown by resistance units under Cenchrus ciliaris var.biloela single plant plot.

the water use pattern was essentially the same as that obtained in the sward plot (Fig.19).

At Kedong, readings were only taken around single plants. The *C.ciliaris* var.biloela graph (Fig.21) shows that the long rains, April to May (428 mm, Table 1) did not saturate the soil profile completely. Rainfall dates at Kedong and Muguga were essentially the same: this was reflected in similar water use patterns at the two sites. Resistance readings in *C.ciliaris* var. biloela, July 1967 to February 1968, were generally higher than those obtained around single plants at Muguga. The short rains, October to December 1968 (234 mm) wetted the profile to 60 cm soil depth only and the soil reached wilting point to 300 cm the following January; rooting depth was about 500 cm. The long rains, February to May 1968 (593 mm) again did not saturate the soil profile entirely so that the resistance values recorded between 150 and 300 cm depths increased rapidly during September to October and subsequently remained high indicating wilting point had been reached in these layers. During this period the short rains followed by intermittent showers in January and February 1969 resulted in wide fluctuations in reading values between the 30 and 120 cm soil depths.

Only *C.ciliaris* var.biloela showed extremely high readings in the deeper layers from October 1968. *C.gayana* extracted water to 390 cm i March 1968, but there was no clear indication that wilting point was reached beyond 30 cm. Similar results were obtained for *P.maximum*, where rooting depth was estimated as 350 cm. *C.ciliaris* var.mbalambala penetrated to approximately 240 cm and readings were generally lower than in *C.ciliaris* var.biloela. Wilting point was reached at 120 cm soil depth in *E.superba* during February 1968:, its roots penetrated to about 220 cm. The lowest readings

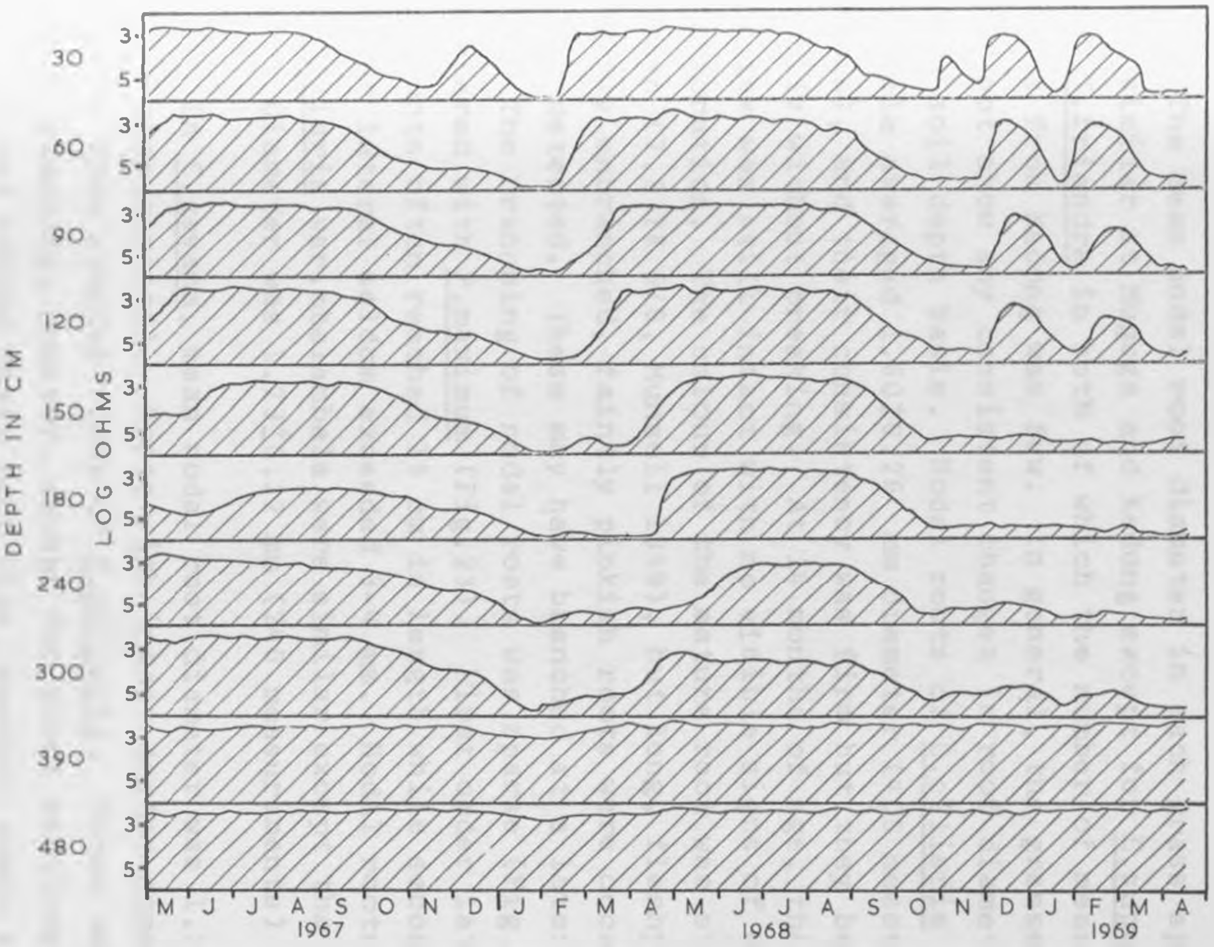

Fig. 21 Kedong: Soil moisture record as shown by resistance units under *Cenchrus ciliaris* var.biloela single plant plot.

were obtained with T.triandra at Kedong, where wilting point was reached at 30 cm in February 1968; rooting depth was estimated as 200 cm.

5.3.9 Root morphology

The mean nodal root diameter in each grass species was similar at Muguga and Kedong except for E.superba and T.triandra in both of which the number of measurements from Kedong was few. In general, the grasses did not show any consistent changes in root diameter on a soil depth basis. Nodal roots of C.ciliaris var. biloela averaged 1.60±0.26 mm diameter (400 measurements), and their consistency was firm but they bent easily without breaking. At 14 months of age, the root cortex was still intact with no visible signs of deterioration. The colour of the mature root was strong brown (7.5 YR 5/6, Munsell 1949), but long, fleshy, mostly unbranched, faintly pinkish roots were occasionally detected. These may have branched at a later stage. The branching of nodal roots was sparse (Fig.22) compared with P.maximum (Fig.23). First order lateral roots often reached 15 cm in length while second order lateral seldom exceeded 3-4 mm. Nodal roots of C.ciliaris var.mbalambala were similar except that their mean diameter was 1.23±0.32 mm (240 measurements).

In C.gayana, mean nodal root diameter was 1.27±0.30 mm (343 measurements). Roots with intact cortex appeared softer than similar roots of C.ciliaris. Three months after planting, however, except for short sections (10-15 cm) behind their root tips, several roots either had lost their cortex entirely or it remained as a thin torn sheath. Mature root clour was brownish-yellow (10 YR 6/8); a few fleshy, whitish, sparsely branched roots were observed occasionally. Branching was more extensive than that observed in C.ciliaris but less extensive than in P.maximum. First order

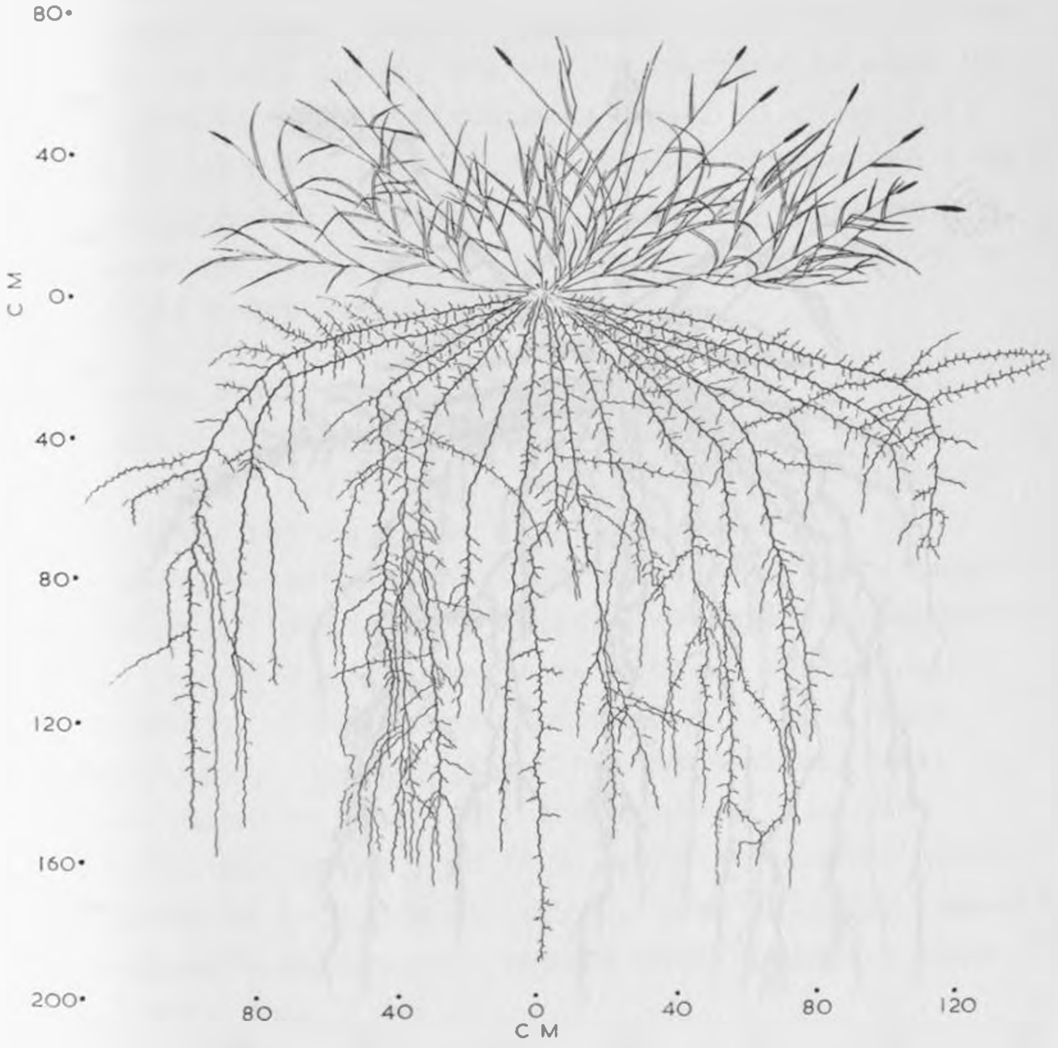

Fig. 22 Muguga: Vertical section showing the root system of <u>Cenchrus ciliaris</u> var.biloela, 7 months after planting.

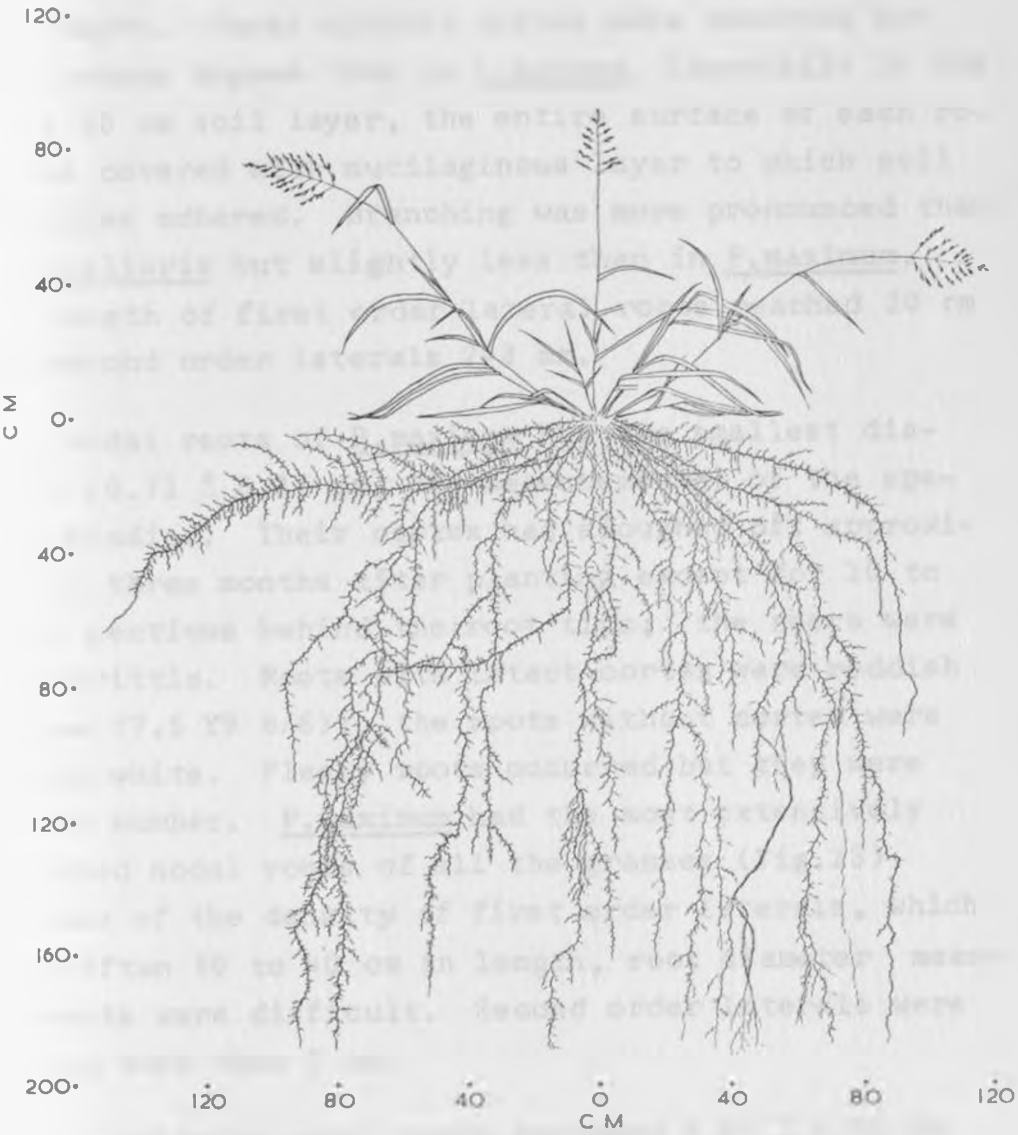

Fig. 23 Muguga: Vertical section showing the root system of Panicum maximum, 7 months after planting.

lateral roots sometimes exceeded 30 cm while second order were usually less than 3 cm.

Mean nodal diameter in E.superba was 1.37 ± 0.31 mm (261 measurements); root colour was dark reddish grey (5 YR 4/2) becoming slightly lighter with increasing depth. Roots without cortex were observed but to a lesser degree than in C.gayana. Especially in the upper 20 cm soil layer, the entire surface of each root was covered with mucilaginous layer to which soil particles adhered. Branching was more pronounced than in C.ciliaris but slightly less than in P.maximum. The length of first order lateral roots reached 20 cm and second order laterals 2-3 mm.

Nodal roots of P.maximum had the smallest diameter (0.71 ± 0.17 mm, 388 measurements) of the species studied. Their cortex had sloughed off approximately three months after planting except for 10 to 15 cm sections behind the root tips; the roots were very brittle. Roots with intact cortex were reddish yellow (7.5 YR 8/6); the roots without cortex were creamy white. Fleshy roots occurred but they were few in number. P.maximum had the most extensively branched nodal roots of all the grasses (Fig.23). Because of the density of first order laterals, which were often 30 to 40 cm in length, root diameter measurements were difficult. Second order laterals were seldom more than 2 mm.

T.triandra nodal roots averaged 0.87 ± 0.21 mm in diameter (260 measurements); their colour was reddish brown (5 YR 5/4). By approximately 4 months from planting several roots had lost their cortex, although this was still intact behind the root tips. A mucilaginous layer was present but, in contrast to E.superba, it was found mainly in the proximity of the root tips at greater depths. Branching was similar to that of C.gayana, first order laterals reached 25 cm and second order laterals 1-2 mm.

CHAPTER VI

DISCUSSION

6.1 Yields: Muguga Versus Kedong

With the exception of T.triandra, all species performed similarly at Muguga and Kedong and in spite of substantial ecological differences in growth habitats the mean yields were not affected. Muguga samplings were always made prior to Kedong; this may have introduced a possible source of error in yield comparisons between the sites. It is clear from Fig. 12 that the time interval between samplings had no effect on the results.

This apparently anomalous result may be explained by considering climate, soil data and experimental procedure. The evaporative demand on the plants at Muguga and Kedong was similar for although higher mean air temperatures were recorded at Kedong, the Penman estimate of potential evaporation (Table 1) was approximately the same at both sites. Soils and rainfall, however, showed greater dissimilarities. The water holding capacity of the Kedong soil to a depth of 195 cm (Table 2) was much higher than that of the Muguga soil. The shallower root systems at Kedong (Table 25) and resistance readings (Fig. 21) which demonstrated that the Kedong soil was far from saturated by the seasonal rains in April-May 1968 (Table 1), suggest that the water supply available to the grasses must have been less than at Muguga (further discussion later). Also, chemical analyses (Table 3) indicated that the Kedong soil was inferior to the Muguga soil. This evidence implies that the Muguga soil was more adequate for plant growth. Spacing the plants, however, removed competition between roots and it is possible that grass growth at Kedong was compensated for by a relatively greater lateral nutrient and water absorption.

6.2 Root Yields

At Muguga and Kedong (1967-1968) maximum root yields were obtained approximately 10 months from planting (Figs. 10 and 11) coinciding with the maturation of the grasses. This was confirmed during the following season (1968-1969) at Muguga where, however, C.ciliaris var.biloela was an exception.

The reduced root yields (Table 7), rooting depth (Table 17) and spread (Table 18) in defoliated P.maximum plants as compared to non-defoliated plants are of significance. Many workers, Nedrow (1937), Jacques (1937), Weaver and Darland (1947), Jameson and Huss (1959) and Humphreys (1967) have observed that defoliation causes reduced root growth and consequently a depletion in the underground reserves (Weinmann 1944 and 1948). The importance of underground reserves in pastures has been questioned by May (1960). He claimed that further work was required to establish the exact role played by reserves in regrowth, and suggests that "accumulates" is probably a better word than "reserves". In deciduous trees, for example, sufficient food exists in young twigs to allow for the development of several leaves in the spring without the utilization of food that is stored in branches, trunks and roots (Curtis and Clark 1950). Recently, Kozlowski and Keller (1966) found a marked depletion of carbohydrates from the stem and roots of woody plants accompanying new shoot growth. In addition, Olofinboba (1969) found that carbohydrates accumulated at leaf fall in the xylem of Antiaris africana became depleted at new flush. For grasses, Baker and Garwood (1961) claimed that there was an association between regrowth and declining carbohydrate content in the stubble. On the other hand, Davidson and Milthorpe (1965) concluded from their work with Dactylis glomerata that carbohydrate reserves alone could not meet the demand for new growth and losses by respiration after severe defoliation and that other fractions, possibly proteins, were remobilized. Davidson (1969) reported a significant positive correlation between root weight and percentage watersoluble carbohydrates in Lolium perenne. He suggested that a high concentration of carbohydrates in autumn is associated with rapid root growth so that the concentration of carbohydrates in the roots may not really be a measure of carbohydrate reserves. Work on Medicago sativa, however, indicated that a bidirectional movement of organic compounds between the root and the shoot took place after defoliation (Hodgkinson 1968). It appeared that carbohydrate reserves in the root contributed to new shoot growth until new leaves began exporting photosynthate.

In summary, present knowledge indicates that seasonal changes occur in carbohydrate content of stems and roots. Because depletion of these substances usually coincides with the onset of new growth it is suggested that the carbohydrates at least partly act as reserves.

In Rajasthan, Dabadghao et al. (1962) found that several grasses, among them C.ciliaris, reached maximum rooting depth within 9 months of growth, an observation in agreement with the present data. Dabadghao et al. believed that forage utilization should be possible during the establishment year. The adverse effects of defoliation on growth indicated above, however, imply that under semi-arid and arid conditions any treatment during the establishment year causing reduced root growth and rooting depth and a depletion in the underground reserves must be disadvantageous, especially if growth conditions during the following year are poor.

On a single plant basis, the grasses differed greatly in mean root dry matter yields. The overall results indicated that *C.ciliaris* var.biloela and *C. gayana* had high yields followed closely by *C.ciliaris* var.mbalambala (Table 4, Fig.12). Intermediate yields were obtained for *P.maximum* and *T.triandra* while *E.superba* was inferior. Although root yields from single plants do not have much meaning, root excavations in 28 month old sward plots to 3 m depth showed that *C. ciliaris* var.mbalambala had produced 7,000 kg/ha root dry matter, compared to 3,300 kg/ha for *P.maximum.*

Grass roots are not harvested and root yields *per se* are therefore of no economic interest. It is generally accepted that grass roots contribute to the development of a good soil structure. Moreover, the overall ameliorative influence of grass roots is manifested in many ways (Russell 1961). Over a longer period of time, root matter will influence soil organic matter; soil fertility and the water holding capacity of the soil being improved. Since many East African soils have a low organic matter content it is believed that grasses producing high root yields are to be preferred.

6.3 Leaf and Shoot Yields

At Muguga and Kedong (1967-1968), *P.maximum* and *C.gayana* were superior to other species in mean leaf and shoot yields (Fig.12). The mean shoot yield data given in Fig.13 (for Muguga and Kedong combined) suggest that the two C.ciliaris varieties at the February sampling had exceeded C.gayana. At Muguga (1968-1969), P.maximum and C.gayana had higher mean shoot yields than C.ciliaris var.biloela; there were significant differences in mean leaf yields between all species, with P.maximum giving the highest yield (Tables 5 and 6). These differences, however, could not be demonstrated clearly on an individual sampling date basis. Leaf and shoot yield differences between C.gayana and C.ciliaris var.biloela were not significant at the last three samplings. At the March sampling, there was no significant differences between any of the species. Also, mean leaf weight index differed between P.maximum and C.ciliaris var.biloela only (Table 12).

These results suggest that above ground yield differences decreased at the last samplings. This agrees with Naveh and Anderson (1966) who, from their cutting trials in northern Tanzania, implied that while C.ciliaris had a slower establishment rate than C.gayana, it would ultimately outyield the latter. Later work (Anderson and Naveh 1968) showed that yield differences between C.gayana and C.ciliaris in a 30 months period from sowing were small, but C.ciliaris was capable of more sustained production during dry periods. From intensive carrying capacity studies under semi-arid conditions in Kenya, Pereira et al. (1961) suggested C.ciliaris to be better than C.gayana.

6.4 Leaf/root and Shoot/root Ratios

Plants adapted to dry climates have been classified in various ways (Parker 1968). According to Levitt et al. (1960) every plant adapted to a dry climate (xerophyte) must be drought resistant, for survival is conditional to growth and development. In Levitt's classification, xerophytism was divided into two categories. The ability to stay alive (drought resistance) and the ability to grow and develop. Drought resistance was subdivided into the ability to prevent reduction in water content (drought avoidance) and the ability to survive reduction in water content (drought tolerance). Drought avoidance was further divided into three categories, the ability to obtain a large amount of water during drought (water spenders: drought evading), the ability to complete life cycle before extreme drought (ephemerals: drought escaping) and the ability to reduce water loss to a minimum (water savers: drought enduring).

In the above classification, drought avoiding plants would probably be most suitable as pasture plants because factors responsible for drought avoidance help to maintain the optium water content for growth, while factors favouring drought tolerance permit survival but growth would be restricted. Where rainfall is seasonal a high and prolonged production of green material can only be achieved if sufficient amounts of water can be supplied by the roots to the transpiring and photosynthesizing shoot. Deep rooting is believed to be an advantage to the growth and survival of a plant where water reserves are available at considerable depths (Burton et al. 1954, Oppenheimer 1960, May and Milthorpe 1962). Plants having a shallow but dense root system, may also be drought resistant and Oppenheimer (1960) suggest that an increased secondary and tertiary ramification of such a root system enables a better utilization of soil water if it becomes immobilized in the wilting range of soil moisture. Hudson, commenting on the paper of Troughton and Whittington (1968), on the other hand, pointed out that a plant with a well developed root system may quickly exhaust the supply of available soil moisture and eventually die. This had been observed in one grass variety growing under low rainfall conditions. When selecting grasses for dry conditions, therefore, it is essential to know the environment for which selection is being made and preferably carry out trials before any recommendation is made. Under East African conditions it is suggested that grasses having low shoot/root and leaf/root ratios are usually better equipped to survive the dry periods between the seasonal rains although it is realized that a high root yield is not necessarily correlated with extensive root distribution and water uptake efficiency. In these respects, the *C.ciliaris* varieties and *T.triandra* (Tables 9 and 10, Fig.16) proved superior to other grasses having low mean ratios. An intermediate ratio was obtained in *C.gayana* while *P.maximum* and *E.superba* had high ratios. This finding confirms the observation made by Owen and Brzostowski (1966) in their pasture trials in central Tanzania (mean annual rainfall 550 mm) where *C.ciliaris* performed well while *C.gayana* suffered greatly during a drought year.

At Muguga and Kedong (1967-1968) most species attained maximum ratios before December (Figs.14 and 15) but the analysis of ratio trends, species and locations combined (Table 21), showed that maximum values were obtained in December. This was the result of the very high ratios attained in December by *P.maximum* and *E.superba*. Very low ratios were obtained at the February sampling, and again most grasses yielded higher ratios at the May-July sampling following the seasonal rains.

In the more intensive work at Muguga (1968-1969) the shoot/root ratios in *P.maximum* and *C.gayana*

(Fig. 6) increased initially, reached high values during September to November, decreased markedly from November to January and then increased again. A similar trend was observed for the leaf/root ratio in P.maximum. Ratios in C.ciliaris var.biloela, however, did not alter significantly throughout the growth period although they showed a decreasing trend.

In general, the results on shoot/root ratios at Muguga suggest that two samplings confined to the September-November period using C.ciliaris var.biloela as an indicator plant, would indicate whether or not a grass has a favourable shoot/root ratio. This supposes that the same experimental procedure is followed. It is possible that this technique could be applied with equal success to other habitats.

Seasonal changes in shoot/root ratio in grasses (in some cases related to specific conditions) have been observed by several workers. Weaver and Himmel (1929), Roberts and Struckmeyer (1946) and Troughton (1960) found that shoot/root ratios increased at the time of flowering. Troughton also noted that a lower ratio was obtained in plants grown under moisture stress as compared to adequate water supply, while decreased light intensity had the opposite effect. Ozanne et al. (1965) found that the ratios increased with increasing maturity, and MacColl and Cooper (1967) observed that the shoot/root ratios increased from spring to winter when the grasses were grown under glasshouse conditions. The growth of the shoot relative to that of the root appears to be controlled genetically (Troughton and Whittington 1968). Furthermore, Eagles (1967) found that increasing temperature resulted in increasing shoot/root ratios in a tetraploid population of Dactylis glomerata from Norway while the ratio decreased in a diploid population from Portugal when grown in controlled-environment rooms. In *Lolium perenne*, Troughton (1961) observed that increasing temperature (10°C - 21°C) resulted in decreasing shoot/root ratios. It is therefore apparant that some exceptions exist to the statement of Brouwer (1966) that the shoot root ratio generally increases with increasing temperature. In the present investigation it was difficult to relate shoot/root ratio changes to any specific conditions. The shoot/root ratio in *C. ciliaris* var. biloela, however, differed from the other grasses, especially at Muguga (1968-1969). Except for a slight initial increase, its shoot/root ratio showed a steadily decreasing trend which was maintained through flower formation, through temperature increase and through decreasing soil moisture availability.

Comparisons between shoot/root ratios in swards and those of spaced plants (Table 22) indicate that these approximate in value. This implies that both the results of, and conclusions drawn from, spaced plants are directly applicable to sward conditions.

6.5 Specific Weight of Leaves

A great volume of work on specific weight of leaves has shown that the ratio is influenced by light and temperature. In *Lolium perenne*, Mitchell (1953) found that specific weight of leaves increased with increase in light intensity or decrease in air temperature. Mitchell concluded that the speed and pattern of morphological development of plants as a whole was determined by contemporary rather than previous light and temperature conditions and that a readjustment could occur within a week. Similar influences of light and temperature on specific weight of leaves were recorded in *Helianthus annuus* by Blackman et al. (1955), and Hunt and Cooper (1967) found that specific weight of leaves in grasses grown under heated glasshouse conditions was higher in May, a time coinciding with high light intensity and low temperature, than in September when light intensity was lower and temperature higher. At Muguga (1968-1969) specific weight of leaves increased from April to July (Table 14). Assuming that the results obtained in Britain are applicable to East Africa, the effect of the 3°C drop in mean air temperature from April to May (Table 1) must have been of greater significance than reduced light, for although light intensity is believed to be much the same during sunshine, radiation decreased from 406 gm/cals/cm^2/day to 291 gm/cals/cm^2/day during the above period (E.A.A.F.R.O. 1969), mainly due to increased cloud cover. Following July, total light (radiation) sunshine hours and temperature increased and in November they were much the same as in April, but there was no further increase in the specific weight of leaves. The possibility, however, that the increased soil moisture tension from June to October and the increased flower and seed formation from July to November may have had certain influences on specific weight of leaves, cannot be excluded.

6.6 Root Distribution - Water use

Roots present in the 0-20 cm soil layer changed proportions throughout the growth period at Muguga (Fig.8). These changes were most probably influenced by water availability; low percentages nearly coincided with high resistance readings (Fig.17) related to low rainfall during the period of measurement (Fig.2). The resistance blocks, however, were placed below the 0-20 cm soil layer and could not give a measurement for this layer. Wilting point was probably reached much earlier than was recorded by the resistance blocks. The root percentages indicate that great errors may be made if conclusions are drawn from the relative amount of roots present in the soil surface layers on the basis of a single sampling.

Results given in Table 27 indicate clearly that under these conditions grasses root deeper when growing in competition. This is contrary to the findings of Pavlychenko (1942) who from Nebraska reported deeper rooting in spaced plants compared with that of plants grown in a sward. Ozanne et al. (1965) found that a fivefold increase in seeding rate of grasses, legumes and herbs, had no significant effect on overall rooting depth in 126 days old plants.

Neither the resistance readings nor the jet-wash root sampling could give accurate information on the rooting depths of these grasses. The gypsum resistance blocks are intensitive to changes in moisture potential under conditions of high soil moisture and when initial changes in resistance readings occur, the soil surrounding the blocks is depleted by approximately half of its available soil moisture (see 3.5.2). A small number of roots, highly active in extracting water, may therefore have been present at the distal end of the root systems without affecting the block readings.

To calculate the water used by plants, relationships between transpiration (E_t) and the Penman estimate of potential evaporation (E_o, given in Table 1) have been found useful; in well-watered Kikuyu grass (Pennisetum clandestinum) at Muguga, consistent values of $E_t/E_o = 0.75$ were obtained (Glover and Forsgate 1964). Similar values have been determined for P.maximum and Cynodon dactylon (Hosegood 1963). Using this relationship to calculate potential transpiration, it can be deduced from Table 1 that transpirational losses from grasses growing at Muguga may be as much as 5 mm per day. As available soil moisture becomes limiting, water movement from deeper layers into the root zone may be of importance. Van Bavel et al. (1968) demonstrated upward movement of water to the root zone at rates up to 4 mm per day for up to 12 days after irrigation. There was, however, an indication in their graphs that this rate was decreasing after this period. The total amount of water that could be transported in this way was therefore, although highly significant, strictly limited by the observed decrease, through several orders of magnitude, of soil moisture conductivity through relatively small decreases in moisture content. At Perkerra in Kenya, Pereira (1958) observed that in spite of the large quantity of water available in the soil profile up to about 180 cm, maize failed to mature because roots could not grow fast enough to occupy the profile where water was available. This would indicate that upward movement of water by capillarity was insufficient to meet the demand of the maize crop.

In the present study, if the bulk supply of water to the root zone was by capillary flow, a very steep gradient of moisture content between the root zone and the water filled soil layers below should have been observed. The resitance readings did not show such a phenomenom. In early February 1968 very little, if any, available water was left in the soil underneath C.ciliaris var.biloela at Muguga (Fig.17) to 480 cm depth. The sward, however, remained green and there was no indication of any drought effects. During the next three weeks before the rains that fell in the latter part of February, transpirational losses, if maximal, were about 100 mm (5 mm per day). Most of this water must have been extracted from the soil below 480 cm depth. With an available water holding capacity of 25 mm per 30 cm soil depth (Table 2), all available water between 480 and 600 soil depth would have been extracted during this period. It seems reasonable, therefore, to suggest that the roots must have penetrated to 6 m depth for although transpirational losses may have been smaller, it is doubtful that a root system in this very uniform and deep soil would end abruptly and use all available water to the same depth. The resistance readings suggest a rather different situation. Figs. 19 and 20 show that the resistance readings changed from 5.8 to 2.6 over a soil profile of at least 150 cm depth. Rooting depths of all grasses at Muguga and Kedong were estimated in a similar way (Table 27). At Kedong, the procedure was somewhat simpler, since roots did not penetrate as deep as at Muguga, the resistance readings gave a more direct indication of rooting depths.

Although the root excavations were carried out with care, it was not possible to follow and collect the very fine roots at the distal end of the root systems and it was not practical to remove roots from depths greater than 3 m. It was thought, however, that the roots collected formed the major part of the roots (Table 25).

Root depths in excavated plants (Table 25) indicated that grasses rooted deeper at Muguga, but resistance reading data did not agree with these observations. As discussed earlier, however, the Kedong soil was far from saturated by the seasonal rains in April-May and measurable changes in soil moisture would therefore be more easily attained at Kedong as compared to Muguga. The results do indicate, however, that the grasses can be placed in two groups: those that are deep rooting (both C.ciliaris varieties,, C.gayana and P.maximum), and those which are shallow rooting (E.superba and T.triandra).

Deep rooting grasses have the advantage of being able to absorb water from great depths during periods of drought. Soil moisture resistance readings suggested that several of the grasses studied rooted to depths of about 6 m at Muguga. After the long rains in April-May 1967, the soil at Muguga was saturated with water (Fig.17), holding about 500 mm of available water to a depth of 6 m (Dagg 1968). Before the long rains which began in the latter part of February 1968, the C.ciliaris varieties, C.gayana, and P.maximum had used all available water to 6 m in addition to the 340 mm of rain which fell between the long rains in 1967 and 1968. During this time interval, the evaporational demand was 1180 mm (Table 1), giving an E_t/E_o value of 0.71. This value, was only slightly lower than the one obtained by Glover and Forsgate (1964) and Hosegood (1963). Evidently the grasses maintained near-potential rates of transpiration until all available water to 6 m soil depth was extracted.

The mean annual potential evaporation for 12 years of records including 1968 (E.A.A.F.R.O., 1969) was 1705 mm giving an average potential transpiration of 1279 mm per year (1705 x 0.75). This is more than the average rainfall of 1013 mm (Table 1), indicating that modulus potential growth rates can seldom be attained. Large soil moisture deficits are therefore likely to develop by the start of the rainy season, especially before the long rains. To compensate for a deficit of 500 mm within a period of two months, a rainfall of about 660 mm is required, allowing 160 mm for evapotranspiration losses. The seasonal rains do not normally compensate for this loss but the long rains in 1967 and 1968 were much higher than normal indicating that through drainage and some contribution to ground water had occurred.

Even greater soil moisture deficits occur before the long rains at Kedong, where the rainfall pattern is much the same as for Muguga. This results in a more pronounced seasonal growth. The mean annual potential evaporation (7 years of records) was 1747 mm (Woodhead 1968), giving an average potential transpiration of 1310 mm (using the same E_t/E_o value as for Muguga). The mean annual rainfall is 805 mm.

Data on mean annual rainfall, potential evaporation and transpiration for Kedong and Muguga allow for a comparison to be made of the two areas in terms of expected growing seasons. If drought occured in only one period during the year, grasses could probably grow for about 8½ months at Kedong in contrast to an expected 10 month growing period at Muguga.

During the experimental period, April 1967 through February 1968, the differences between rainfall and transpiration was 323 mm at Kedong; the long rains did not penetrate much below 2 m soil depth. At Muguga, rainfall exceeded potential transpiration. Yields did not differ between Muguga and Kedong. It was suggested that the spaced plants at Kedong must have had a relatively greater lateral absorption of water although the horizontal spread of roots was much the same (Table 26). This assumption could not be substantiated since water losses from the soils were not measured.

The combined Muguga and Kedong shoot yields (Fig.13) suggested that E.superba and T.triandra were less productive than other grasses. In T.triandra, yield increments were initially much the same as in the other grasses, but from July to November, increments were less. The low yields of E.superba and T. triandra in particular could be a result of having less available water within their root range due to a shallower root system.

The loss of water through surface run-off has not been considered; it was assumed to be negligible in the experimental plots (Pereira et al. 1967). Nevertheless, run-off cause serious reduction in yield in areas such as Muguga and Kedong where rainfall limits growth and heavy seasonal rains occur. Sound management practice should, however, be able to prevent run-off, and thus preclude an associated loss of productivity.

The above discussion demonstrates the important part played by the root system in the adaption of grasses to semi-arid conditions with seasonal rainfall. Deep rooting grasses are necessary to exploit the annual recharge of the soil moisture reserves from the seasonal rains, thereby making the growth season as long as possible. This presupposes more than mere survival. In comparison with shallow rooting grasses, deep rooting grasses should be capable of transforming an increased water uptake into greater yield of dry matter during a given period. Although fluctuation in the water table is to be expected when deep rooting grasses are used, the greater water use must not result in a net loss of ground water reserves. At Muguga, it is believed that the rainfall is adequate to meet the above requirement. At Kedong, further studies on the water use of these grasses in swards are required before any suggestion can be made. It is well known, however, that <u>T.triandra</u> can tolerate very dry conditions, and Bogdan and Pratt (1967) regarded <u>E.superba</u> as a safe grass for use under moderately dry conditions. Although all grasses had a higher percentage of their root systems in the surface layers at Kedong (Table 25), <u>E.superba</u> and <u>T.triandra</u> had the highest. Since these two grasses had higher mean root yields at Kedong, although not significantly different from Muguga, it follows that the root density was much higher in the surface layer, maximum spread of roots being much the same (Table 26). From studies on T.triandra in South Africa, Goossens and Stapelberg (1933) suggested that the heavy concentration of roots in the surface soil layer enabled this species to make the fullest use of all light showers of rain, and to compete favourably with other deeper rooting grasses. Murray and Glover (1935) came to a similar conclusion. The present study supports this hypothesis and indicates that E.superba also has this quality. E.superba has the disadvantage of high shoot/root and leaf/root ratios but is probably more deep rooting than T.triandra.

Competition is one of the underlying principles in plant communities and Donald (1963) defines competition in such a way that it covers all living organisms: "Competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing, and when the immediate supply of the factor or thing is below the combined demand of the organisms". T.triandra often forms large pure stands although other grasses may be present in the vicinity. Possibly this grass in some competitive way withstands intrusion from other grasses, and observations in T.triandra grasslands at Kedong seem to verify this suggestion. Where firebrakes were made, using a disc plough, other grasses (C.gayana in particular) invaded the firebrakes and formed dense stands, displacing T.triandra. A possible explanation for other grasses being unable to compete with T.triandra is that the species uses the soil moisture in the surface layers so effectively that other grasses are unable to establish themselves. T.triandra, therefore, would seem to have a greater ability to survive under conditions of low intermittent rainfall, and shallow soil. It is also possible that the high density of T.triandra roots in the soil surface at Kedong acted as a mechanical barrier to the penetration of the soil profile by the seedling roots of other species. Rhodes (1968) reports on a similar phenomenom in Lolium perenne. Another explanation for the success of T.triandra could be that it has a more effective nutrient absorbing root system. Parsons et al. (1953) give a good example of such competition. They found that Agrostis alba and Poa pratensis took up potassium so readily that Dactylis glomerata, Medicago sativa and Bromus inermis were eliminated from a mixed population.

6.7 Root Morphology

Diameter of nodal roots between 0 and 80 cm soil depth was not influenced by the different growth conditions at Muguga and Kedong. Marked differences, however, were found between species. C.ciliaris var. biloela had the largest diameter (1.60 mm) followed by E.superba (1.37 mm), C.gayana (1.27 mm), C.ciliaris var.mbalambala (1.23 mm), T.triandra (0.87 mm) and P.maximum (0.71 mm). Many of these grasses had large diameter roots when compared with other species. Pavlychenko (1942) recorded diameters between 0.19 and 1.1 mm for ten grass species; Crider (1945) listed root diameters ranging from 0.43 to 1.11 mm for nine-week old plants of twelve grass species grown in pots: Coupland and Johnson (1965), studying root development of native grassland in Saskatchewan, reported root diameters from 0.2 to 1.0 mm. Large root diameters, however, have been observed previously in grasses growing under wet conditions in the grass prairies of the USA where the coarsest roots of Spartina michauxiana measured 3 to 4 mm across (Weaver 1926).

In *P.maximum* roots, the cortex was sloughed off relatively early except for short sections behind the root tips. This was also observed in *C.gayana*, *E.superba* and *T.triandra*, although to a lesser extent. In the two *C.ciliaris* varieties, the cortex was intact, without any sign of deterioration, 14 months from planting. These observations seem to agree with the data obtained on specific weight of roots (Table 19).

Throughout the growth period, mean specific weight of roots was higher in *P.maximum* than in *C.ciliaris* var. biloela; *C.gayana* was intermediate.

The cortex may play an important role in the uptake of nutrients. Earlier, it was thought that nutrients were absorbed mainly in younger tissue a short distance from the root tip (Steward et al. 1942). Recent experiments with barley in solution culture, however, suggest a different situation (Clarkson et al. 1968). In older roots, at least 40 cm from the root tip where the endodermis was heavily thickened, phosphate was absorbed and translocated as readily as in the young tissue, providing the cortex remained intact. Much less is known about other ions, but it seems that the pattern of potassium uptake is comparable to that for phosphate (Clarkson and Sanderson, cited in Russell 1970). If the same situation is generally true for plants growing in soil, *C.ciliaris* would have a great advantage over most of the other grasses included in this work.

On the basis of persistance of the cortex, Goossens and Stapelberg (1933) classified grasses in two groups: those having a soft, early deciduous cortex and those having a more or less hard persistent cortex. Group one included grasses of the dry regions with xerophytic roots; group two consisted of grasses of the moist regions with mesophytic roots.

In this classification, C.ciliaris would seem to belong to group two. However, this work has indicated that C.ciliaris is well adapted to drier regions.

Roots with a mucilagenous layer were observed in E.superba, especially in the soil surface layer, and in T.triandra at greater depth. Similar mucilagenous layers have been described bv Price (1911), Warming (1925), Goossens and Stapelberg (1933) and Arber (1934) but opinions differ as to how they are formed. The sheath, including the mucilage and soil particles, remains on the roots as long as the cortex and Warming (1925) believed that the mucilage protected against a loss of water from the roots into soil when the latter became dried out. Goossens (1936), however, thought that it aided in the absorption of water.

6.8 Tentative Conclusions

Above ground yields in C.gayana and P.maximum exceeded those of the two C.ciliaris varieties under the relatively good rainfall conditions of these experiments. The differences, however, tended to decrease for the later stages of growth. On a dry matter basis, a highly balanced shoot and root development was observed in the two C.ciliaris varieties, while in the other two species, shoot growth was much more rapid during the first 7 months of growth. Assuming that comparative shoot and root growth would be similar under less favourable moisture conditions, it is probable that above ground yield differences would be smaller, even during early stages of growth. Under conditions of moisture stress, it is likely that yields would be reduced earlier in species with high shoot/root ratios. Under severe dry conditions C.gayana and P.maximum would not be able to survive, even if they succeded in establishing themselves. This is supported by the observations of Pereira et al. (1961) and Owen and Brzostowski (1966).

Regeneration, vegetatively or genetically, is a most important factor to be considered when growth may be limited by low or uncertain rainfall. It is postulated that a well adapted grass should have the ability to build up a reserve of seeds in the soil, that is, the seeds must not only maintain their viability but a proportion of them should remain dormant even when moisture conditions are favourable for germination. T.triandra is, ecologically, a highly successful species probably due, in part, to the species ability to build up such a seed reserve. In this work, both C.ciliaris varieties showed poor germination. Brzostowski and Owen (1966), however, found that seeds of this grass germinated readily provided mature seeds were stored for 12 to 18 months after harvest. This suggests that C.ciliaris may be able to store viable seeds over a prolonged period of time and that its establishment is safeguarded even when growth conditions are poor for periods up to 1½ years. Freshly harvested seeds of both C.gayana and P.maximum germinate readily and it is probable that with these grasses no significant seed reserves remain following a good rain.

Observations showed that C.ciliaris var.biloela in particular, and also var.mbalambala, had extensive rhizome systems of great regenerative value. Also, most of the rhizomes were located well below the soil surface, which is of great significance, because the use of fire is generally accepted as a tool for eradicating undesireable vegetation.

Specht (1957) emphasized that interception of rainfall by vegetation is a major factor in any study of the water balance of an ecosystem. Stem flow or foliar drip can be of considerable importance in arid plant communities and has a great influence on distribution of incoming moisture. Glover (1950) found that a number of Somaliland plants had developed extensive shallow lateral root systems as an adaptation to shallow penetration of rain water after sporadic showers. In East Africa, Glover and Gwynne (1962) showed that the maize plant was capable of intercepting light showers of rain and concentrating water in considerable amounts near the base of its stem. A similar phenomenom was described for several grassland communities, including T.triandra in Kenya (Glover et al. 1962), and for Agropyron spicatum in British Columbia (Ndawula-Senyimba 1969).

The aerial part of grasses may therefore be considered as a catchment area which collects rain water and delivers it to the soil at the base of the grasses where it accumulates in amounts greater than those available from bare ground. This supposes that the grasses are distributed singly or in clumps; this is a common type of distribution in drier range regions. Where rain falls upon a uniform closed canopy, no single plant is able to obtain such additional water.

It has been suggested that E.superba and T.triandra, because of their high concentration of roots in the soil surface layer, are capable of utilizing light showers of rain more effectively than other grasses. Undoubtedly, the catchment effect can be included. Also, the mucilagenous root layer observed in E.superba in the top soil may enhance the absorption of small amounts of water.

When studying T.triandra grasslands in East Africa, Heady (1966) found that this grass grew on a variety of soils and did not appear to be closely correlated to rainfall conditions. He also observed that where T.triandra was occurring in abundance, organic matter to a depth of 20 to 50 cm was constantly higher than where the grass was scarce or absent. Although Heady thought that the range of organic matter was a result of differences in the abundance of T.triandra rather than causing it, the findings in this work may suggest the latter.

The success of T.triandra grasslands is undoubtedly the result of a variety of factors. Four of the more important of these include. 1) The relatively shallow root system, which enables the grass to grow equally good on both shallow and deep soils; 2) on deep soils it can compete with more deep rooting grasses providing rainfall is intermittent, because of its ability to utilize light showers of rain more effectively; 3) the grass has a favourable shoot/root ratio, and 4) its establishment is safeguarded by seed reserves in the soil.

CHAPTER VII

CONCLUSIONS AND RECOMMENDATIONS

In East Africa where rangelands are characterized by a complex of ecological factors, management is equally varied and the preference for any one grass may differ over comparatively small areas. The main factor limiting growth is rainfall. Most of the rangelands in Kenya have two rainy seasons a year but large areas of Uganda and Tanzania have only one. Under such conditions of seasonal rains it is very important to find the grass species that will, for each different growth habitat, most effectively exploit and utilize the annual recharge of the soil profile.

Under the conditions described for the experiments, leaf and shoot yields alone would tend to favour P.maximum as a preferred rangeland grass. However, when the high root yields and their possible long term effect on soil fertility and soil water holding capacity are considered, the two C.ciliaris varieties and C.gayana would seem to be better than P.maximum.

In many of the East African soils, organic matter content is low and it is believed that the influence different grasses may have on the soils should be investigated. This research could easily be combined with long term pasture trials.

In more arid conditions, above ground yields, leaf/root and shoot/root ratios, and rooting depth (providing the soils are deep) are factors to be considered. In these respects, the two C.ciliaris varieties proved superior to all other grasses.

If, however, the soils are shallow it is possible that grasses like T.triandra, having low shoot/root ratios and shallow root systems, would be preferable although there is no experimental evidence to suggest that C.ciliaris varieties which have deep root systems would not do equally well under shallow soil conditions.

In this discussion it has been suggested that T.triandra and the two C.ciliaris varieties, due to their intrinsic seed germination properties, are better equipped to reseed the area successfully following prolonged periods of drought than any of the other grasses studied.

These results indicate that future work on improving the rangelands should consider the relationship of above to below ground growth of grasses. This work has shown that such studies can be simplified. Comparisons between shoot/root ratios in swards and those of spaced plants suggest that conclusions drawn from spaced plants are directly applicable to sward conditions. Also, relative differences between shoot/root ratios of perennial grasses can be obtained from spaced plants grown at Muguga, and possibly other locations having similar growth conditions, through two samplings confined to the September-November period, providing the same experimental procedure is followed, and using C.ciliaris var.biloela as a standard. By using the jet-wash method for root excavation, the distribution of the roots in the soil profile could be determined and studies on root morphology could be carried out. An indication of minimum rooting depth can be obtained in swards with the aid of gypsum resistance blocks placed at regular intervals to at least

6 m depth.

During the establishment period of grasses on ranges in semi-arid and arid regions, which lasts approximately 10 months after planting, grazing should be avoided or kept to a minimum. This would allow the grasses to build up their root systems and underground reserves with consequent high subsequent primary and secondary productivity levels.

Knowledge of the many grass varieties in East Africa is scant. A research programme to compare and evaluate the more important grass varieties would certainly provide further valuable data for the overall improvement of East African rangelands.

REFERENCES

Ahlgren, H.L., Smith, D.C. and Nielsen, E.L.N. (1945). Behaviour of various selections of Kentucky Bluegrass, Poa pratensis L., when grown as spaced plants and in mass seedlings. J.Am.Soc.Agron. 37, 268-281.

Anderson, G.D. and Naveh, Z. (1968). Promising pasture plants for northern Tanzania. V. Overall comparisons of promising plants. E.Afr.agric.For.J. 34, 84-105.

Arber, A. (1934). The Gramineae. A study of cereal, bamboo and grass. Cambridge.Camb.Univ.Press.

Baker, H.K. and Garwood, E.A. (1961). Studies on the root development of herbage plants. V. Seasonal changes in fructosan and soluble-sugar contents of cocksfoot herbage, stubble and roots under two cutting treatments. J.Br.Grassld Soc. 16, 263-267.

Blackman, G.E., Black, J.N. and Kemp, A.W. (1955). Physiological and ecological studies in the analysis of plant environment. X.An analysis of the effects of seasonal variation in daylight and temperature on the growth of Helianthus annuus in the vegetative phase. Ann.Bot. 19, 527-548.

Bogdan, A.V. (1965). Cultivated varieties of tropical and subtropical herbage plants in Kenya. E.Afr.agric.For.J. 30, 330-338.

Bogdan, A.V. and Pratt, D.J. (1967). Reseeding denuded pastoral land in Kenya. Nairobi: Minist.Agric.Anim.Husb.

Bor, N.L. (1960). Grasses of Burma, Ceylon, India and Pakistan. Vol.1. Oxford, London, New York, Paris. Pergamon Press.

Brouwer, R. (1966). Root growth of grasses and cereals. In "The growth of cereals and grasses". (Milthorpe, F.L. and Ivins, J.D. eds). Proc. XII Easter Sch.agric.Sci.Univ.Nott. 1965. pp. 153-166.

Brzostowski, H.W. and Owen, M.A. (1966). Production and germination capacity of buffel grass (Cenchrus ciliaris) seeds. Trop.Agric.,Trin. 43, 1-10.

Burton, G.W., de Vane, E.H. and Carter, R.L. (1954). Root penetration, distribution and activity in southern grasses measured by yields, drought symptons and p^{32} uptake. Agron.J. 46, 229-233.

Chippindall, L.K.A., Scott, J.D., Theron, J.J. and Meredith, D. (1955). The grasses and pastures of South Africa. Cape. Cape Times Ltd.

Clarkson, D.T., Sanderson, J. and Russell, R.S. (1968). Ion uptake and root age. Nature, 220, 805-806.

Coupland, R.T. and Johnson, R.E. (1965). Rooting characteristics of native grassland species in Saskatchewan. J.Ecol. 53, 475-507.

Crider, F.J. (1945). Three introduced lovegrasses for soil conservation. Circ. U.S. Dep.Agric. No.730.

Curtis, O.F. and Clark, D.G. (1950). An introduction to plant physiology. p. 437. New York. McGraw Hill.

Dabadghao, P.M., Marwaha, S.P., Gupta, B.S., Das, R.B. and Deb, R.R. (1962). Root ecology of some promising desert grasses of Rajasthan. Ann.Arid Zone, Jodphur, 1. 163-173.

Dagg, M. (1968). Hydrological implications of grass root studies at Muguga. 4th specialist meeting on applied meteorology, Nairobi.

Davidson, R.L. (1969). Effects of edaphic factors on the soluble carbohydrate content of roots of Lolium perenne L. and Trifolium repens L. Ann. Bot. 33, 579-589.

Davidson, J.L. and Milthorpe, F.L. (1965). Carbohydrate reserves in the regrowth of cocksfoot (Dactylis glomerata L.) J. Br.Grassld Soc. 20, 15-18.

Donald, C.M. (1963). Competition among crop and pasture plants. Adv.Agron. 15, 1-118.

Duncan, D.B. (1955). Multiple range and multiple F.tests. Biometrics, 11, 1-42.

E.A.A.F.R.O. (1969). Record of Research, for the year 1968.

Eagles, C.F. (1967). The effect of temperature on vegetative growth in climatic races of Dactylis glomerata in controlled environments. Ann.Bot. 31, 31-39.

Edwards, D.C. and Bogdan, A.V. (1951). Important grassland plants of Kenya. Nairobi. Sir Issac Pitman and Sons, Ltd.

Egner, H., Riehm, H. and Domingo, W.R. (1960). Untersuchungen über die chemische Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes der Böden. II. Chemische Extractionsmethoden zur Phosphor und Kaliumbestimmung. K.LantbrHögsk. Annlr 26, 199-215.

Glover, P.E. (1950). Rain-water penetration in British Somaliland soils. E.Afr.agric.J. 16, 26-33.

Glover, P.E. (1951). The root systems of some British Somaliland plants. II. E.Afr.agric.J. 16, 154-173.

Glover, J. and Forsgate, J. (1964). Transpiration from short grass. Q.Jl R.met.Soc. 90, 320-324.

Glover, J. and Gwynne, M.D. (1962). Light rainfall and plant survival in East Africa. I. Maize. J.Ecol. 50, 11-118.

Glover, P.E., Glover, J. and Gwynne, M.D. (1962). Light rainfall and plant survival in E.Africa. II. Dry grassland vegetation. J.Ecol. 50, 199-206.

Goossens, A.P. (1936). Notes on the anatomy of grass roots. Trans.R.Soc.S.Afr. 23, 1-21.

Goossens, A.P. and Stapelberg, W.J. (1933). A brief note on the macroscopic aspect of some Western Transvaal grasses. S.Afr.J.Sci. 30, 212-219.

Green, J.O. and Eyles, J.C. (1960). A study in methods of grass variety testing. J.Br.Grassld Soc. 15, 124-132.

Griffiths, J.F. (1958). Climate zones of East Africa. E.Afr.agric.For.J. 23, 179-185.

Heady, H.F. (1960). Range management in East Africa. Nairobi. Govt. Printer.

Heady, H.F. (1966). Influence of grazing on the composition of Themeda triandra grassland, East Africa. J.Ecol. 54, 705-727.

Hodgkinson, K.C. (1968). Studies on the physiology of regeneration of lucerne (Medicago sativa L.). J.Aust.Inst.agric.Sci. 34, 221.

Hosegood, J.A. (1963) Record of Research, for the year 1962. E.A.A.F.R.O., p. 9.

Humphreys, L.R. (1967). Grass reaction to grazing and cutting. Trop.Grasslds 1, 65-67.

Hunt, L.A. and Cooper, J.P. (1967). Productivity and canopy structure in seven forage grasses. J.appl.Ecol. 4, 437-458.

Jacques, W.A. (1937). The effect of different rates of defoliation on the root development of certain grasses. N.Z.Jl.Sci.Technol. 19, 441-450.

Jameson, D.A. and Huss, D.L. (1959). The effect of clipping leaves and stems on number of tillers, herbage weights, root weights, and food reserves of little bluestem. J.Range Mgmt 12, 122-126.

Kemp, C.D. (1960). Methods of estimating the leaf area of grasses from linear measurements. Ann.Bot. 24, 491-499.

Kozlowski, T.T. and Keller, T. (1966). Food relations of woody plants. Bot.Rev. 32, 293-382.

Kramer, H.H. (1947). Morphology and agronomic variation in Poa pratensis L. in relation to chromosome numbers. J.Am.Soc.Agron. 39, 181-191.

Lazenby, A. and Rogers, H.H. (1962). Selecton criteria in grass breeding. I. J.agric.Sci., Camb. 59, 51-62.

Levitt, J., Sullivan, C.Y. and Krull, E. (1960). Some problems in drought resistance. Bull.Res. Counc. Israel. 8D, 173-180.

MacColl, D. and Cooper, J.P. (1967). Climatic variation in forage grasses. III. Seasonal changes in growth and assimilation in climatic races of Lolium, Dactylis and Festuca. J.appl. Ecol. 4, 113-127.

MacGillivray, D. (1967). East African livestock survey. Vol.2. Rome. UNDP/FAO.

May, L.H. (1960). The utilization of carbohydrate reserves in pasture plants after defoliation. Herb.Abstr. 30, 239-245.

May, L.H. and Milthorpe, F.L. (1962). Drought resistance of crop plants. Fld Crop Abstr. 15, 171-179.

Marshall, B., Long, M.I.E. and Thornton, D.D. (1969). Nutritive value of grasses in Ankole and the Queen Elizabeth National Park, Uganda, III - In vitro dry matter digestibility. Trop.Agric., Trin. 46, 43-46.

Mitchell, K.J. (1953). Influence of light and temperature on the growth of ryegrass (Lolium spp.) I. Pattern of vegetative developments. Physiologia Pl. 6, 21-46.

Munsell Color Company. (1949). Munsell soil color charts. Baltimore.

Murray, S.M. and Glover, P. (1935). A preliminary study of the root development of certain South African highveld grasses. Jl. S.Afr.Bot. 1, 65-70.

Napper, D.M. (1965). Grasses of Tanganyika with keys for identification. Minist.Agric.For.Wildl. Tanzania, Bull.No.18.

Naveh, Z. and Anderson, G.D. (1966). Selection of promising pasture plants for Northern Tanzania. Part II - a comparison of drought-resistant selections of rhodes grass (Chloris gayana Kunth.) and buffel grass (Cenchrus ciliaris L.). E.Afr.agric.For.J. 32, 96-102.

Naveh, Z. and Anderson, G.D. (1967). Promising pasture plants for northern Tanzania. IV - Legumes, grasses and grass/legume mixtures. E.Afr.agric.For.J. 32, 282-304.

Nedrow, W.W. (1937). Studies on the ecology of roots. Ecology, 18, 27-52.

Ndawula-Senyimba, M.S. (1969). Fenceline ecology in British Columbia. M.Sc.thesis, University of British Columbia.

Nissen, 0. (1960). Testing hay varieties of grasses as spaced plants, in a pure stand or in a mixture with legume. Proc. 8th Int.Grassld Congr. pp. 310-313.

Olofinboba, M.O. (1969). Seasonal variations in the carbohydrates in the xylem of Antiaris africana. Ann.Bot. 33, 339-349.

Oppenheimer, H.R. (1960). Adaption to drought: Xerophytism. In "Plant-water relationships in arid and semi-arid conditions". UNESCO. pp. 105-138.

Owen, M.A. and Brzostowski, H.W. (1966). A grass cover for the upland soils of the Kongwa Plain, Tanganyika. Trop.Agric., Trin. 43, 303-314.

Ozanne, P.G., Asher, C.J. and Kirton, D.J. (1965). Root distribution in a deep sand and its relationship to the uptake of added potassium by pasture plants. Aust.J.agric.Res. 16, 785-800.

Parker, J. (1968). Drought-resistance mechanisms. In "Water deficits and plant growth". (Kozlowski, T.T. ed.). Vol. 1, 195-234. New York, London. Academic Press.

Parsons, J.L., Drake, M. and Colby, Wm.G. (1953). Yield and vegetative and chemical composition of forage crops as affected by soil treatment. Proc.Soil Sci.Soc.Am. 17, 42-46.

Pavlychenko, T.K. (1942). Root systems of certain forage crops in relation to management of agricultural soils. Publs Can.nat.Res.Coun. No. 1088.

Penman, H.L. (1948). Natural evaporation from open water, bare soil and grass. Proc.R.Soc. A. 193, 120-146.

Pereira, H.C. (1958). The limited utility of floodwater in the Perkerra River irrigation scheme, Kenya. E.Afr.agric. J. 23, 246-253.

Pereira, H.C., Wood, R.A., Brzostowski, H.W. and Hosegood, P.H. (1958). Water conservation by fallowing in semi-arid tropical East Africa. Emp.J.exp.Agric. 26, 213-228.

Pereira, H.C., Hosegood, P.H. and Thomas, D.B. (1961). The productivity of tropical semi-arid thorn-scrub country under intensive management. Emp.J.exp.Agric. 29, 269-286.

Pereira, H.C., Hosegood, P.H. and Dagg, M. (1967). Effects of tied ridges, terraces and grass leys on a lateritic soil in Kenya. Expl Agric. 3, 89-98.

Price, S.R. (1911). The roots of some North African desert-grasses. New Phytol. 10, 328-340.

Puckridge, D.W. and Donald, C.M. (1967). Competition among wheat plants sown at a wide range of densities. Aust.J.agric.Res. 18, 193-211.

Rhodes, I. (1968). The growth and development of some grass species under competitive stress. L. Competition between seedlings, and between seedlings and established plants. J.Br. Grassld Soc. 23, 129-136.

Roberts, R.H. and Struckmeyer, B.E. (1946). The effect of top environment and flowering upon top-root ratios. Pl.Physiol., Lancaster. 21, 332-344.

Russell, E.W. (1961). Soil conditions and plant growth. 9th.ed. p. 437. London. Longmans.

Russell, R.S. (1970). Root systems and plant nutrition - some new approaches. Endeavour 29, 60-66.

Specht, R.L. (1957). Dark island heath (Ninety-mile plant, South Australia). IV. Soil moisture patterns produced by rainfall interception and stem flow. Aust.J.Bot. 5, 137-150.

Steward, F.C., Prevot, P. and Harrison, J.A. (1942). Absorption and accumulation of rubidium bromide by barley plants. Localization in the root of cation accumulation and of the transfer to the shoot. Pl.Physiol., Lancaster. 17, 411-421.

Taerum, R. (1969). A report on the growth and development of grasses in Kenya. E.A.A.F.R.O., Muguga.

Taerum, R. and Gwynne, M.D. (1969). Methods for studying grass roots under East African conditions and some preliminary results. E.Afr. agric.For.J. 35, 55-65.

Troughton, A. (1957). The underground organs of herbage grasses. Bull.Commonw.Bur.Past.Fld Crops No. 44.

Troughton, A. (1960). Further studies on the relationship between shoot and root systems of grasses. J.Br.Grassld Soc. 15, 41-47.

Troughton, A. (1961). The effect of photoperiod and temperature on the relationship between the root and the shoot system of Lolium perenne. J.Br.Grassld Soc. 16, 291-295.

Troughton, A. and Whittington, W.J. (1968). The significance of genetic variation in root systems. In "Root growth". (Whittington, W.J. ed.). Proc. XV Easter Sch.agric.Sci.Univ.Nott. pp. 296-314.

Van Bavel, C.H.M., Brust, K.J. and Stirk, G.B. (1968). Hydraulic properties of a clay loam soil and the field measurement of the water uptake by roots: II. The water balance of the root zone. Proc.Soil Sci. Soc.Am. 32, 317-321.

Walkley, A. and Black, I.A. (1934). An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37, 29-38.

Walter, M.W. (1952). A new presentation of the seasonal rainfall of East Africa. E.Afr.agric.For. J. 18, 11-20.

Warming, E. (1952). Oecology of plants. London. Oxf.Univ.Press.

Weaver, J.E. (1926). Root development of field crops. New York. McGraw Hill.

Weaver, J.E. and Himmel, W.J. (1929). Relation between the development of root system and shoot under long and short-day illumination. Pl.Physiol., Lancaster. 4, 435-457.

Weaver, J.E. and Darland, R.W. (1947). A method of measuring vigor of range grasses. Ecology, 28, 147-162.

Weinmann, H. (1944). Root reserves of South African highveld grasses in relation to fertilizing and frequency of clipping. Jl.S.Afr. Bot. 10, 37-54.

Weinmann, H. (1948). Underground development and reserves of grasses. J.Br.Grassld Soc. 3, 115-140.

Whyte, R.O., Moir, T.R.G. and Cooper, J.P. (1959). Grasses in Agriculture, Rome. FAO. Agricultural study No. 42.

Woodhead, T. (1968). Studies of potential evaporation in Kenya. Kenya Minist.Nat.Resources.

Wright, C.E. (1960). The introduction of an associated legume at the progeny testing stage in perennial ryegrass breeding. Proc. 8th Int.Grassld Congr. pp. 313-317.

APPENDIX

EXAMPLE OF STATISTICAL METHOD AND CALCULATION

Shoot/root ratios, Muguga and Kedong 1967-1968
Study II

To indicate the procedure used in the statistical treatment of the data presented in this thesis, the analysis of the shoot/root ratios, obtained at Muguga and Kedong, May 1967 to February 1968, is given as an example. The shoot/root ratios are stated in Table 1. It was assumed (Chapter 4) that the variability between the ratios shown within the double lines in the table indicates a true representation of the total records including T.triandra; thus the standard error obtained through the calculations shown in Tables 2 and 3 was used to draw conclusions from the whole set of data.

To determine differences within groups that proved significant in Table 3, the least significant differences (LSD) test was employed as follows:

$$LSD = t\sqrt{s^2\,\frac{n_1 + n_2}{n_1 n_2}}$$

where
t = tabulated "t" value
s^2 = mean square for error
n = number of observations

Example 1.

Comparing shoot/root ratios between C.ciliaris var.biloela = 2.675 and C.gayana = 6.357 at Kedong.

(Table 1).

t = 2.086 (tabulated "t" value at the 5% level):

s^2= 0.711205 (mean square for error, Table 3).

n_1= 8 (number of observations in C.ciliaris var. biloela).

n_2= 7 (number of observations in C.gayana).

LSD = 0.910

The differences between the means given above is larger than the LSD value obtained indicating that at the 5% level, C.gayana had a higher mean shoot/root ratio than C.ciliaris var.biloela.

Example 2.

Comparing ages, for example May = 2.762 versus July = 3.274 (Table 1).

t and s^2 are the same as in example 1.

n_1= 22 (number of observations in May, all species and locations).

n_2= 23 (number of observations in July).

LSD = 0.525.

This shows that the ratios at the two dates did not differ at the 5% level since the LSD value obtained was slightly larger than the difference between the May and July ratios.

For each analysis of variance, only the species having the same number of observations (n_1 and n_2) overall or for a particular comparison would yield the same LSD. This gave rise to several LSD values within each analysis. Using the shoot/root ratio analysis as an example, these were:

LSD ($P < 0.05$) comparing shoot/root ratio means:

1. Between species at Kedong

(a) Two of *C.ciliaris* var.biloela, *C.ciliaris* var. mbalambala, *E.superba*, *P.maximum*, LSD = 0.880

(b) One of (a) versus *C.gayana*, LSD = 0.910

(c) One of (a) versus *T.triandra*, LSD = 0.950

(d) *C.gayana* versus *T.triandra*, LSD = 0.979

2. Between species at Muguga

(a) Two of *C.ciliaris* var.biloela, *C.ciliaris* var. mbalambala, *E.superba*, *P.maximum*, LSD = 0.880

(b) Two of *C.gayana*, *P.maximum*, *T.triandra*, LSD = 0.940

(c) One of (a) versus (b), LSD = 0.910

3. Between same species at Kedong and Muguga

(a) *C.ciliaris* var.biloela, var.mbalambala, *E.superba*, LSD = 0.880

(b) *C.gayana*, LSD = 0.940

(c) *P.maximum*, LSD = 0.910

(d) *T.triandra*, LSD = 0.979

4. Between ages, all species and locations combined

May versus July, LSD = 0.525

May versus September LSD = 0.537

May versus December or February, LSD =0.631

July versus September, LSD = 0.531

July versus December or February, LSD = 0.626

September versus December or February, LSD = 0.637

December versus February LSD = 0.718

Shoot/root ratios obtained at Muguga and Kedong May 1967 - February 1968

Species	Location	May		Jul.		Sep.		Dec.	Feb.	Species Mean
		Plant		Plant		Plant		Plant	Plant	
		1	2	1	2	1	2	1	1	
Cenchrus ciliaris, biloela	Muguga	4.04	4.16	2.21	1.98	3.07	5.57	2.90	2.62	3.319
	Kedong	1.67	2.23	2.21	2.16	2.56	3.89	3.12	3.56	2.675
Cenchrus ciliaris, mbalambala	Muguga	2.02	2.28	1.61	2.83	1.86	5.50	3.60	2.66	2.795
	Kedong	2.33	1.74	2.57	2.32	4.28	3.29	3.88	7.28	3.461
Chloris gayana	Muguga	1.57	2.95	4.18	3.33	9.82		6.25	4.52	4.660
	Kedong	2.27	5.54	7.00	4.82	9.16		7.96	7.75	6.357
Eragrostis superba	Muguga	2.58	3.21	4.98	3.55	4.80	8.62	21.70	11.30	7.593
	Kedong	2.97	0.96	1.82	1.62	4.43	7.30	11.44	7.43	4.746
Panicum maximum	Muguga	4.35	4.39	4.78	5.03	7.36		9.31	7.02	6.034
	Kedong	2.57	2.57	4.57	5.77	9.94	11.90	14.68	10.51	7.814
Themeda triandra	Muguga	2.63		1.12	1.74	2.53	2.77	6.28	5.29	3.194
	Kedong	1.74		3.10		5.21	5.99	8.21	6.46	4.387
Date mean:		2.762		3.274		5.707		8.278	6.367	

TABLE 2

Uncorrected sums of squares for shoot/root ratios

Total = 471.646600

Places (P) = 396.262250

Ages (A) = 399.449780

Species (S) = 421.372275

P x A = 401.701500

P x S = 437.936050

A x S = 434.725850

P x A x S = 457.422500

Correction factor = 395.263690

TABLE 3

Analysis of variance for shoot/root ratios

Terms	Degrees of freedom	Sums of squares	Mean squares	F(calc)
Places (P)	1	0.998560	0.998560	1.40
Ages (A)	1	4.186090	4.186090	5.89^{x}
Species (S)	4	26.108585	6.527146	9.18^{xxx}
P x A	1	1.253160	1.253160	1.76
P x S	4	15.565215	3.891304	5.47^{xx}
A x S	4	9.167485	2.291871	3.22^{x}
P x A x S	4	4.879715	1.219929	1.72
Error	20	14.224100	0.711205	
Total	39	76.382910		

^{xxx}Significant at the 0.1% level

^{xx}Significant at the 1% level

^{x}Significant at the 5% level