PRIMARY PRODUCTIVITY, ENERGY FLOW AND NITROGEN CYCLING IN A RANGELAND ECOSYSTEM

by

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DECLARATION.

THIS THESIS IS MY ORIGINAL WORK AND HAS NOT BEEN PRESENTED FOR A DEGREE IN ANY OTHER UNIVERSITY.

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THIS THESIS HAS BEEN SUBMITTED FOR EXAMINATION WITH OUR APPROVAL AS UNIVERSITY SUPERVISORS.

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DEDICATION.

This thesis is dedicated to the Ekaya family.

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ABSTRACT.

A study was conducted to estimate and characterize the structure and function of a rangeland ecosystem on the Njemps flats of Baringo District, Kenya. Herbaceous primary production and productivity were estimated, and energy flow and nitrogen cycling characterized over a two-year period.

Total aboveground standing crop ranged from 84.6 g m^{-2} to 295.4 g m^{-2}, with a mean of 162.3±60.6 g m^{-2}. Mean monthly aboveground standing crop for 1992 and 1993 was 142.8 ±53.8 and 178.5±63.3 g m^{-2} respectively. The two values were significantly different ($P<0.10$). Aboveground biomass yield ranged from 17.7 g m^{-2} to 242.7 g m^{-2}, with a mean of 104.3±58 g m^{-2} and a coefficient of variation of 58%. Mean aboveground standing crop was 59±24 g m^{-2}. Monthly values ranged from 28.8 g m^{-2} to 120 g m^{-2}, with a 38% coefficient of variation.

The range for total belowground standing crop was from 83.3 g m^{-2} to 232.7 g m^{-2}, and a mean of 155.2±46 g m^{-2}. The values had a coefficient of variation of 30%. Mean total monthly belowground plant material yield for 1992 and 1993 was 137.6±41 g m^{-2} and 169.9 ±46 g m^{-2}. The coefficients of variation were 59% and 28% respectively. The mean monthly belowground biomass yield was 51.6±33 g m^{-2} with a coefficient of variation of 64%. Mean monthly yield for belowground dead material was 103.7±32 g m^{-2}, with a coefficient of variation of 31%. There was no significant difference ($P>0.01$) in the mean belowground dead material yield between 1992 and 1993.

Aboveground:Belowground plant material ratios ranged from 0.55 to 2.31. Ratios greater than 1.00, thus indicating higher quantity of plant material aboveground than belowground, were observed in March and October of 1992 and July and October of 1993.

Monthly litter production spread from 31.4 g m^{-2} to 130 g m^{-2}. Mean monthly yield was 92.5±26 g m^{-2}, with a 28% coefficient of variation. There was no significant difference ($P>0.01$) in litter yield between 1992 and 1993.

Rate of decomposition for aboveground material ranged from 0.005 g g^{-1} day^{-1} to 0.084 g g^{-1} day^{-1}. The mean annual rate of decomposition was 0.026 g g^{-1} day^{-1}. Belowground plant material rates of decomposition spread from 0.009 g g^{-1} day^{-1} to 0.062 g g^{-1} day^{-1}, with a mean annual rate of 0.041 g g^{-1} day^{-1}. Belowground material consistently decomposed faster than aboveground material. Peaks in both aboveground and

belowground material decomposition rates coincided with rainfall peaks.

In 1992, annual NPP was 439.2 g m^{-2}, giving a net primary productivity of 1.22 g $m^{-2}day^{-1}$. Monthly NPP ranged from 17.2 g m^{-2} to 90.1 g m^{-2}. In 1993, annual NPP was 944.5 g m^{-2}, equivalent to a net primary productivity of 2.62 g m^{-2} day^{-1}. Monthly NPP was between 27.4 g m^{-2} and 548.6 g m^{-2}. Over the 1992-1993 period, NPP was 1383.7 g m^{-2}, equivalent to a productivity of 1.92 g $m^{-2}day^{-1}$. Trends in monthly NPP closely followed the trend in rainfall.

Turnover rates and times varied between years and compartments. Highest turnover rate was for aboveground biomass (0.40), which was closely followed by the grass litter and belowground biomass compartments with 0.32 and 0.30 respectively. Lowest turnover rate (0.13) was recorded from the aboveground dead compartment. The turnover times for the aboveground biomass, grass litter, and belowground biomass compartments were 2.5 years, 3.1 years and 3.3 years respectively. The dead aboveground biomass had a turnover time of 4.5 – 7.7 years. High turnover rates were associated with higher rainfall.

Energy contents in the aboveground and belowground plant materials during both seasons were 17.9 KJ g^{-1} and 21.6 KJ g^{-1} respectively. Aboveground live and dead plant material compartments had one and a half times more standing crop of energy during the dry season compared to the wet season. During the dry season there was net loss of energy from the aboveground dead compartment. The litter compartment had a net loss of energy during both seasons.

Energy content in the belowground live compartment was 1135.0 and 1118.9 KJ m^{-2} for the dry and wet season respectively. There was net loss of energy from this compartment during both seasons. During the dry season, average energy accumulation in aboveground and belowground compartment occurred at a rate of 25.4 KJ m^{-2} day^{-1} and 16.5 KJ m^{-2} day^{-1} respectively. In the wet season, average energy accumulation in aboveground and belowground compartments was 27.8 KJ m^{-2} day^{-1} and 22.0 KJ m^{-2} day^{-1} respectively.

The total standing stock of nitrogen in plant compartments during the dry and wet season was 7700 mg m^{-2} and 9650 mg m^{-2} respectively. The two values were significantly different ($P<0.05$). Among the aboveground compartments, in the dry season, live dicots had the highest nitrogen content (2.4%). The dead dicots and litter compartments had 2% nitrogen. Live plant material had highest nitrogen content (1.8%) among the below ground

compartments. The lowest nitrogen content was recorded in the aboveground dead grass compartment (0.7%). During the wet season, litter compartment had highest nitrogen content (2.9%) whereas the lowest value was for the aboveground dead grass compartment (1.3%). The live belowground material had 3% nitrogen, which was the highest among the belowground compartments.

Incubation of dry season soil revealed that over a period of twelve weeks, and with 7% soil moisture content, the mineralization potential was about 26.0 and 23.0 $\mu g\ g^{-1}$ soil for NH_4^+-N and NO_3^--N respectively. The pH of the incubated soil remained within narrow limits, ranging from 6.4 and 6.8. The mineralization potential for the wet season soil, having 27% moisture content, was estimated to be 35.0 and 28.0 $\mu g\ g^{-1}$ soil for NH_4^+-N and NO_3^--N respectively. Soil pH during wet season soil incubation ranged between 6.9 and 8.8.

Total soil nitrogen pool during the dry season was estimated to be 2847.6 g m^{-2} in the top 30 cm soil horizon. Mineralised nitrogen constituted 0.05%. Standing crop of nitrogen in the aboveground plant material compartments was 2320 mg m^{-2}, 920 mg m^{-2} and 1950 mg m^{-2} for the live material, dead material and litter compartments respectively. An accumulation of nitrogen was evident in the aboveground live compartment.

Standing stock of nitrogen in the belowground plant material compartments was 930 mg g^{-1} and 1580 mg g^{-1} for the live and dead compartments respectively. There was relative accumulation of nitrogen in the mineralized nitrogen pool, whereas the belowground live compartment had a net loss of nitrogen.

Total standing stock of nitrogen in the soil pool during the wet season was 5152.8 g m^{-2} in the top 30 cm soil horizon, which was higher than that recorded during the dry season ($P<0.05$). Mineralized nitrogen constituted 0.07%. Standing stocks of nitrogen in the belowground live and dead compartments were 1550 and 2130 mg m^{-2} respectively. Both values were higher than those recorded during the dry season. There was a net loss of nitrogen from the belowground dead compartment. Standing stocks of nitrogen in aboveground compartments were 2420 mg m^{-2}, 2300 mg m^{-2} and 1050 mg m^{-2} for the aboveground live, dead, and litter compartments respectively. There was a significant difference ($P<0.05$) between standing stock of nitrogen in the aboveground live and dead compartments, and between aboveground dead and litter compartments.

On the whole, structure and function of the Njemps flats rangeland ecosystem was

episodic in nature and closely correlated with the rainfall trend. This was shown by the high variability of the data on aboveground and belowground biomass compartments, NPP, decomposition and turnover rates. The ecosystem was in a non-equilibrium state, having STF values between most compartment being either greater or less than 1.

The high primary productivity reported from this arid rangeland ecosystems puts these areas under focus as CO_2 sinks whose role in the amelioration of the imminent warming of global climate could be more important than is currently thought. In terms of management and utilization by man, the ecosystem characteristics imply a high level of flexibility, the sole objective being to seize opportunities while spreading and reducing risks.

1.0 INTRODUCTION

The arid rangeland environment is, typically, of limited rainfall with annual means falling below 500mm and characterized by erratic distribution within and between seasons and years. Temperatures are high year long, fluctuating around 30°C and the potential evapotranspiration exceeds the annual rainfall resulting in low relative humidity, often less than 30 % (Cocheme, 1966; Stoddart *et al.*, 1975; Pratt and Gwynne, 1977; Musembi, 1986). These characteristics have concert profound effects on both the structural and functional aspects of rangeland ecosystems. The annual growth period may consist of a few to several days or weeks during the expected wet season with subsidiary periods of activity spread over the year. As a result, total annual primary production can be the summation of a limited number of short bursts of growth events randomly distributed in time, and showing high variability. Equally, there are far reaching effects of the seasonality on mineral cycling, energy capture and flow. The overall effect is that ecosystem structure and function is episodic in nature and seldom sustained for long periods of time.

The recycling of nutrients between different parts of any ecological system is a key process to its sustainability. All elements in the ecosystem will cycle to some extent, but emphasis should be given to essential elements because they are responsible for the fuelling of biological activities. Thus, they influence the productivity of an ecosystem within the constraints set by the physical environment. Nitrogen is one of the essential nutrient elements universally often limiting in agricultural and natural lands, particularly in the tropics (Bradshaw *et al.*, 1964; Gill, 1969; Charley, 1977). As Bate (1981) emphasized, the amount of nitrogen available to plants is to a large extent a function of the rate at which organic nitrogen is mineralized by soil micro-organisms. In the savannas, moisture is a limiting factor for microbial activity for a greater part of the year. It would therefore be expected that as soon as moisture becomes available, a surge in the amount of soil nitrogen would occur (Enwezor, 1967). Savanna soils are usually low in total nitrogen, with values ranging from 0.008% to 0.29% (Jones, 1973). Of this, only a small proportion is available for uptake by plants. Jones (1973) and Isichei (1979) estimated this to be about 4% and 2% respectively. Generally, within broad limits, the amount of nitrogen in plant material depends on the amount available in the soil (Isichei, 1980). In the savanna, there exists a

broad relationship between total annual rainfall and plant biomass and concomitant with this is an increase in the amount of organic matter for decomposition, which ultimately results in soil nitrogen. Therefore a decline in soil nitrogen content would likely occur from the moist to the dry natural environments (Jones, 1973; Isichei, 1979).

In tropical forest ecosystems and high potential agricultural and grazing ecosystems that receive frequent bombardments of nitrogen fertilisers, there is plenty of literature on nitrogen transformation and cycling. However, the same subject has received little research attention in the low input moisture-limited range environments (Jordan and Medina, 1977). The same is the case in Kenya's arid and semi-arid areas, hence the scarcity in literature on nitrogen transformation and cycling.

In order to understand the functioning of any ecosystem, it is essential to know how much energy is available to drive that system (de Jager and Harrison, 1982). In an ecological system, the basic energy input comes from the sun. Energy flow within the ecosystem therefore begins with the capture of this solar energy by green plants. Thus the efficiency with which the energy is captured and accumulated is basic to determining the functioning and particularly the productivity of ecosystems. This process is affected by various factors such as leaf morphology and orientation, ratio of photosynthetic to non-photosynthetic tissue, carbon dioxide concentrations, temperature, light and moisture profiles. Although all do play a role, moisture has been identified as a major limiting factor and therefore the driving force in rangeland ecosystems (Douglas and Tedrow, 1959; Whittaker, 1970; Anderson and Coe, 1974; Swift *et al.*, 1979: Musembi, 1986; Kinyamario and Imbamba, 1992). Comprehensive studies on energy capture and flow in the tropical natural ecosystems remain few. These include those by Lamotte (1977,1978 (quoted by Lamotte and Bourliere, 1983)), Singh *et al.*, (1979), and Lamotte and Bourliere (1983). Therefore, an acute shortage of literature on the subject exists, which implies incomplete understanding of the energy flow dynamics in these ecosystems.

Generally, arid rangeland ecosystems are dominated by fortuitous co-occurrence of sequences of events, where each event has a low probability of occurrence (Noble, 1986). This dependence on the co-occurrence of low probability events has two implications. First, models based on continuous variation in these ecosystems are unlikely to be adequate to predict range dynamics over the long-term. Secondly, the occurrence of an event without any discernible impact on the ecosystem does not necessarily imply that the event is

irrelevant. Under different circumstances it may initiate major changes in the ecosystem (Noble, 1986).

2.0 REVIEW OF LITERATURE

2.0.1 Primary production / productivity of African rangelands

Primary production, and to a very little extent productivity, and the factors that influence them have been studied in various grassland ecosystems the world over. However, in Africa, such studies remain few, despite the fact that approximately 36% of the human food originates from herbaceous plants, primarily through a herbaceous-cattle-milk energy flow pathway (Galvin, 1985; Coughenour *et al.*, 1985). The few published studies include those of Cassady (1973), Sinclair (1975), Strugnell and Pigott (1978), Ohiagu and Wood (1979), Owaga (1980), Macharia (1981), Deshmukh (1986), Coughenour *et al.* (1990) and Kinyamario and Imbamba (1992). These studies have reported large fluctuations in primary production, largely linked to rainfall in many instances.

Sinclair (1975) reported a peak biomass value of 115 g m^{-2} in the Serengeti ecosystem. Strugnell and Pigott (1978) reported a peak value of 405 g m^{-2} from the Ruwenzori National Park in Uganda. Ohiagu and Wood (1979) reported from Nigerian grasslands a minimum standing grass biomass at the end of the dry season, with annual production ranging from 50 to 100 g m^{-2}. Large variations were recorded in some locations due to presence of termites, which removed up to 40% of the annual yield of biomass. Owaga (1980) and Deshmukh (1986) recorded peak biomass values of 309 g m^{-2} and 332 g m^{-2} respectively in areas of minimal grazing by large herbivores in the Nairobi National Park. Coughenour *et al.*, (1990) reported herbaceous aboveground biomass values from six different sites in the arid Turkana ecosystem of Kenya. The reported values ranged from 0 g m^{-2} to 214 g m^{-2}. They observed a strong correlation between cumulative aboveground biomass yield and cumulative rainfall. From a semi-arid grassland in the Nairobi National Park, Kinyamario and Imbamba (1992) recorded aboveground biomass values ranging from 73 g m^{-2} to 338 g m^{-2}. Biomass exhibited a seasonal bimodal pattern, with peaks during the wet season.

Fluctuations in biomass are important in determining food habits and habitat utilization of large herbivores (Kutilek, 1979; Ekaya, 1991). This phenomenon is also important in the classification of land for potential and suitability for livestock and wildlife, for example the occurrence of poisonous plants and the presence and distribution of protective cover are important for wildlife. A combination of plant biomass and species

composition therefore determines the species as well as the quantity of animal biomass.

Only a few published studies have investigated the contribution of individual plant species and genera or specific plant categories to the primary production of grasslands in East Africa. In the Amboseli ecosystem, Macharia (1981) found that the genus *Sporobolus* ranked highest in dry matter yield. From the Nairobi National Park, Deshmukh (1986) found *Themeda triandra* to be the most productive species. From the same location but on a different site, Kinyamario and Imbamba (1992) found that *Themeda triandra* made the highest contribution (42%), to the overall standing crop by each plant category followed by *Pennisetum mezianum* (28%), dicots (17%) and other minor grasses grouped together contributed 13%.

Even fewer of the above studies on primary production have included measurements of such important aspects of primary production as below ground biomass and decomposition rates of dead plant materials. These include those by Strugnell and Pigott (1978), Ohiagu and Wood (1979) and Kinyamario and Imbamba (1992). Due to these omissions, some previous calculations of net primary productivity are probably underestimates of the true values. Further, due to the omission of below ground biomass measurements, the reported variability in net primary production with environmental variables could be overestimates. This arises from the fact that many plants in the arid rangeland ecosystems, especially perennial grasses translocate some of their non-structural photosynthetic products to stem bases and roots as they approach dormancy. These reserves are then used for tissue maintenance during dormancy and initiation of growth when environmental conditions become favourable (Trlica, 1977; McNaughton, 1979). Therefore measurement of the aboveground biomass only may show large variability in biomass yield with season when actually the material has been translocated belowground and the actual variability would be less than what is reported if belowground production was included.

Most of the studies cited above dealt with changes in yield of biomass as opposed to productivity. Biomass yield is reported in most of the above studies to have a large difference between the dry and wet seasons. Kinyamario and Imbamba (1992) found that when rainfall was 856 mm the net primary productivity reached 1292 g $m^{-2}y^{-1}$ in the Nairobi National Park. However, this declined to 587 g $m^{-2}y^{-1}$ when rainfall declined to 775 mm. Based on the few studies so far published, and the little quantitative information

available on the wide diversity of tropical grasslands, it can be concluded that the productivity of many tropical grasslands is far from being understood.

2.0.2 Approaches used in estimating primary production

A number of studies have been conducted in tropical grassland / rangeland ecosystems, with an aim of estimating primary production and / or productivity. These include those by individual researchers such as Cassady (1973), Strugnell and Pigott, (1978), Ohiagu and Wood (1979), Owaga (1980), Deshmukh (1986), Kinyamario and Imbamba (1992), or comprehensive and co-ordinated networked research such as that by the International Biological Programme (IBP) studies (Singh and Joshi, 1979), and the UNEP bioproductivity studies (Long and Jones, 1992). In each of the above studies, the methods used are not uniform in their physical conduct and bear with them some shortcomings. Long and Jones (1992) concluded that the methodology used in the earlier studies of the IBP may have led to serious and variable underestimation of production and turnover of plant biomass in the communities in which the studies were based.

Ideally, net primary production is the total gain in biomass due to photosynthesis less the losses due to respiration per unit of ground area (Milner and Hughes, 1968; Cooper, 1975; Linthurst and Reimold, 1978; Coupland, 1979; Roberts *et al.*, 1993). Thus over any interval of time, net primary production must be equal to the change in plant mass plus any losses through death of both aboveground and belowground material.

The main approaches that have been used to estimate primary production and productivity include the following;

(a). Peak standing crop method

The method has been extensively used in tropical grassland research. Studies include those of Bourliere and Hadley (1970) in 22 tropical grasslands and 21 IBP studies on tropical grasslands reviewed by Singh and Joshi (1979). In this approach, net primary production is considered to be equal to the maximum standing crop recorded for any season or year. There are some limitations however;

(i). There is an assumption that during any interval of time between harvests or during the time prior to peak standing biomass, death does not occur if production is occurring and vice versa. This assumption does not hold in natural plant communities that consist of plant

species with different growth patterns, growth stages and life forms.

(ii). The methods fail to take account of the different cycles of growth and death in different species associated together in a community. Therefore species that attain maximum biomass before the community peak biomass or those that attain maximum biomass after the overall peak biomass will be ignored. In rangeland ecosystems characterized by mixtures of species with differing lengths of life cycles, this approach resulted in underestimation of primary production.

(b). Trough-peak method

Trough-peak analysis for the estimation of biomass was widely used by the IBP for the study of tropical grasslands (Milner and Hughes, 1968; Coupland, 1979; Singh and Joshi, 1979). Under this approach, biomass sampling was carried out over time intervals. Where the biomass was found to increase between harvest intervals, production over the interval was considered to equal the increase. Where a decrease or no change was discerned, production was assumed to be zero. The annual production was then obtained by summing up all the positive increments. The analysis assumes that production and death are two discrete processes. Therefore an overlap of the two will lead to an underestimation of biomass (Long and Jones, 1992).

Trough-peak analysis as used by the IBP was later improved by Singh *et al.* (1975), whereby positive increments in biomass were summed, but where positive increments in dead plant material coincide with positive increments in biomass, these were also added to the total. Therefore this procedure corrected for the amount of material lost through death during periods of biomass increase, but only if no decomposition occurs. This is unlikely, and therefore the method still lead to underestimation.

Two assumptions, which can, to a large extent influence the estimate of primary production using the trough-peak method, include the following;

(i). The analysis considers only positive increments, therefore it is assumed that neither aboveground nor belowground production can be negative (Long and Jones, 1992). This assumption clearly oversimplifies the scenario. Tropical grasslands tend to be dominated by perennial species with underground or surface storage organs. It has been reported (Trlica, 1977; McNaughton, 1979) that significant transfers of non-structural assimilates

occur between aboveground and belowground structures. For example, as the dry season approaches, there can be translocation of non-structural matter from the shoots to the belowground storage organs. During this time, the aboveground biomass will decline whereas the belowground biomass will rise. Using the trough-peak analysis, this will give a positive belowground biomass production and zero aboveground biomass, thus a positive net plant production. In reality though, no new material has been formed; the existing material has just been relocated. Similarly, when growth conditions become favourable, the relocated assimilates are re-routed to the aboveground parts for the production of new shoots. The resultant increase in biomass weight would again be recorded as net production of the whole plant, which is an overestimation.

(ii). The second assumption, which can be quite tricky in some environments, is that all increases in biomass represent production. In natural communities, random fluctuations in biomass are not uncommon. Inadequate sampling or flaws in the physical conduct of sampling may further complicate this. Although it can be argued that the random fluctuations can be self-cancelling in the long run, selection of only positive increments will mean that the greater variability between the samples, the greater the overestimation of production (Singh *et al.*, 1975).

One statistical improvement to this assumption has been to compensate for the error by only including positive increments where the biomass on one sampling date is significantly higher ($P<0.10$) than on the previous sampling date (Singh *et al.*, 1975). However, a technical problem does arise at this point in that many, but small real increases in biomass, which is the norm in tropical rangelands, may pass undetected.

Linthurst and Reimold (1978) compared the production estimated from maximum biomass as used by Bourliere and Hadley (1970) and from the trough-peak analysis as used by Singh and Joshi (1979) with a method in which primary production was calculated from changes in biomass corrected for simultaneous losses through death. From this comparative study, it was concluded that both methods underestimated primary production when account was taken of the simultaneous losses of material, by 50-80% and by 10-70% respectively. It was also clearly demonstrated that the degree of overestimation varied markedly with location and with species composition. Bradbury and Hofstra (1976) and Long and Mason (1983) reached similar conclusions. Underestimation of primary production further affected

understanding of ecosystem functioning since the estimated values were used further in the estimation of vegetation death and decomposition in the IBP syntheses of tropical grasslands (Singh *et al.*, 1975). These strong conclusions have lead ecologists to question the IBP estimates of primary production of tropical grasslands. However, in spite of the above flaws and objections, Singh and Joshi (1979), in an evaluation of 30 different methods of computing net primary production concluded that trough-peak analyses were among the superior procedures.

The trough-peak method has over time been improved on by inclusion of corrections due to death and decomposition for both aboveground and belowground material simultaneously coupled with short interval sampling (Long and Jones, 1992). This was through the UNEP research on the productivity of tropical grasslands. The current study employs this improved method as detailed in the materials and methods section.

2.0.3 Plant litter

Litter has been defined in different ways. Medwecka-Kornas (1971) defined litter as that material lying on the soil surface and consisting of dead plants and shed organs but excluding standing dead material. Rodin and Bazilevitch (1967) gave a more comprehensive description. They included all dead organic matter from aboveground and belowground plant parts whether they die naturally or whether they are added to the organic pool as a result of ageing or natural thinning. Heady (1956) reported that in natural grasslands, any dead material above the soil surface are referred to as litter, mulch or plant residue. This material may vary in position, from lying on the soil surface to standing in upright tangled mass of vegetation and may be in various degrees of decomposition. Under natural conditions, total mulch may be categorised into two (Hendrick, 1948; Heady, 1956). These are: (i). fresh mulch and forage residue, which may form part of animals' intake, and, (ii). raw humus, which is the partially decomposed material on the surface. From the above definitions from different authors, one point of consensus is that litter is made of dead material. The rest of the definition will depend on the individual worker and probably the objective.

The major aboveground components that comprise surface litter include leaves, flowers, glumes, seeds, fruits and small twigs. Debris from primary producers accumulates on the soil surface and within mineral horizons along the network of roots and rhizomes

(Medwecka-Kornas, 1971). Part of the litter may be buried in the soil through animal activities, e.g. hoof activity through trampling or arthropod activity.

Litter plays a crucial role in nutrient cycling and soil organic matter build-up in the savanna ecosystems (Isichei, 1980). Hopkins (1965) was also of the view that the amount of litter produced is an indication of the production of vegetation, especially the woody component. Litter increases soil moisture through its effects on infiltration, evaporation and runoff. It tends to stabilize soil moisture and soil temperatures, thus improving conditions for germination, and often the presence of litter alters the botanical composition of a plant community through its effects on soil nutrient status (Mathews and Cole, 1938; Jacks *et al.*, 1955; Geiger, 1965; Abouguendia and Whitman, 1979). All these effects influence the amount of green herbage produced, and green herbage is the source of future litter. Nye and Greenland (1960) reviewed in a general way the role of litter in nutrient cycling in both forest and savanna ecosystems. Hopkins (1966) concluded that litter does not add much organic material to the soil in savanna ecosystems, since annual fires destroy more litter than is decomposed. However, Collins (1977) observed that in the southern and northern zones of Nigeria, most of the litter fell after the annual fires, so that decomposition and consumption by termites account for much of the litter disappearance. Therefore considerable amounts of organic matter and nitrogen may be added or returned by way of litter. A similar view is shared by Isichei (1979).

If not burned, litter can contribute significantly to the accumulation of organic matter in the savanna. Isichei and Sanford (1980) estimated that in southern zones of Nigeria, only about 18.5%, 11.7% and 36.8% of the annual leaf, wood and fruit litter production respectively were burned. Litter-fall peaks were outside the burning periods in most places. Table 1 below shows a summary of some of the known rates of litter fall.

Table 1: Summary of some published litter fall results (g m^{-2}).

Location and zone	Leaf fall	Wood fall	Total	Source
Mokwa, Guinea	238.7	139.1	----	Collins (1977)
Miombo, Zaire	290	440	---	,,
Lamto, Ivory Coast	----	----	480	,,
Fete Ole, Senegal	----	----	160	,,
Olokemeji, Nigeria	90	----	160	Hopkins (1966)

It is a common view amongst rangeland ecologists that nutrient contents of tropical ecosystems are held in the biomass (Isichei, 1980). Litter is, therefore, a very important means of nutrient recycling. In a nitrogen balance study, Isichei (1979) showed that most of the nitrogen in the savanna ecosystem is held in the woody biomass instead of in the herbaceous biomass.

2.0.4 Plant litter decomposition

Decomposition is a complex and continuous process that mainly occurs within the soil body, but is initiated before death (Satchell, 1974). The process of decomposition is central to all aspects of ecology (Barbour *et al.*, 1980). Rate constants are determined by the nature of the substrate, as influenced by environmental factors, which include the following (Bray and Gorham, 1964);

(i). the chemical composition of the litter. This is determined by the species in question as well as the age of the litter,

(ii). the prevailing environmental conditions at the site of litter decomposition. Temperature and moisture are the most important. However, rainfall is usually the limiting factor especially during dry seasons.

(iii). the resident soil micro-flora and –fauna, and

(iv). soil characteristics, with structure and texture being most important. Soil structure reflects pore size, which influences aeration and moisture content.

The assessment of plant material decomposition is important in understanding nutrient cycling in terrestrial ecosystems. Factors affecting decomposition also affect nutrient cycling and therefore primary productivity. In the absence of export from the system, all production in natural ecosystems enters the decomposer system (Bourliere and Hadley, 1970). This organic debris is broken down and simplified by the decomposer organisms, making nutrients available for recirculation (Wood, 1976). The elements retained at the time of death in the various plant parts are circulated and returned to the soil through several stages. It has been reported that in terrestrial ecosystems, the largest portion of aboveground production enters the detritus food chain (Wiegert and McGinnis, 1975). They concluded that the saprophage food chain is more important than biophage food chains. Teal (1962) and Bray and Gorham (1964) reported that 88-99% of the annual net primary production is not consumed by herbivores but enters the soil litter system. This plant debris is an important and major component in nutrient cycling (Odum and de la Cruz, 1963; Odum, 1971). The main source of energy for micro-organisms in the soil system is the chemical energy bound in the organic debris. Heterotrophic organisms use it as a source of energy as well as a nutrient pool (Odum, 1971).

Plant litter consists of six major categories of chemical constituents, namely: cellulose, hemicellulose, lignin, water soluble sugars, amino and aliphatic acids, ether and alcohol soluble components and proteins (Alexander, 1976; Isichei, 1980; Van Soest, 1982). The organisms that contribute to decomposition include micro-organisms and soil microfauna (Dickinson and Pugh, 1974; Alexander, 1976). The micro-organisms include bacteria and fungi (actinomycetes and yeasts) while the soil fauna include nematodes, various worms, insects and rodents (Kevan, 1962; Brandsberg, 1969; Dickinson and Pugh, 1974).

There are two functional groups of soil bacteria (Dickinson and Pugh, 1974); the indigenous population whose numbers in the soil do not change much with the addition of litter material, and the zymogenous flora whose numbers peak with organic matter breakdown and then drop to insignificant levels. Therefore litter decomposition is characterized by periodicity, consisting of the accumulation of a large population of decomposer micro-organisms and the resynthesis of organic compounds which are less

degradable compared to original matter (Alexander, 1976). The role of bacteria in litter breakdown is twofold, i.e. direct breakdown of litter constituents and the indirect degradation of organic constituents that build up as a result of litter decomposition (Eklund and Gyllenberg, 1974).

The actinomycetes have a number of ecological advantages over bacteria (Goodfellow and Cross, 1974). These include;

(i). nutritionally, they are more versatile than bacteria and grow well on both nutritionally rich and poor substrates,
(ii). they are capable of attacking a wide variety of both natural and artificial substrates that are usually resistant to attack by bacteria,
(iii). their ability to produce mycelium allows them to radiate outwards. This enables them to attack organic matter at a distance from their initial growth centre, and
(iv). they yield an array of secondary metabolites including some antibiotically active compounds, which give them competitive advantage.

Actinomycetes and other fungi play an important role in decomposition. On addition of organic matter to the soil, the "sugar fungi" rise up in numbers to utilize easily decomposable organic matter (Dickinson and Pugh, 1974; Pugh, 1974). The fungi, which utilize the more stable substrate such as lignin and cellulose grow more steadily over a longer period of time. Fungi normally constitute the primary decomposer population in most environments and the bacteria appear as a secondary population (Eklund and Gyllenburg, 1974).

Organic matter breakdown provides energy and building blocks for micro-organism tissues (Wiegert *et al.,* 1970). This process may be preceded by ingestion and breakdown by invertebrates. Anderson (1979) identified two cycles of litter decomposition, namely the fast and the slow cycle. In the fast cycle, micro-organisms act on the low molecular weight, easily broken down carbon sources like root exudates, sloughed off cells and amino acids. The slow cycle involves the breakdown of the not-so-easy to decompose constituents like cell walls (Coleman *et al.*, 1982). Anderson (1979) reported that dissolving inorganic phosphates from inorganic detritus proceeds faster and more completely in the presence of bacterial grazers than in the presence of bacteria alone. This means that animals change rates of substrate utilization and mineral nutrient release. The animals mechanically process

litter and detritus and thereby influence organic matter distribution. This affects the decomposition process by bringing about even nutrient distribution at sites of decomposition. In the absence of grazers, therefore, there would be litter accumulation and nutrient immobilization and ultimately a reduction in nutrient turnover.

Barsdate *et al.* (1974) reported that bacteria and fungi release little phosphorus or nitrogen during decomposition because they require it for building their body tissues. They are consequently indirectly responsible for nutrient regeneration. Bacteria consumers which constitute secondary saprophages are important for cycling bacterially-bound nutrients (Wiegert and Owen, 1971).

It has been postulated that nutrient release operates in two stages (Reichle,1977; Coleman *et al.*, 1982). During the first stage, the plant produces a low molecular weight mass of carbon compounds that stimulate and maintain bacterial population growth. Carbon compounds are broken down with release of CO_2 while nitrogen and phosphorus are utilized in the production of new tissue. In the second stage, nematodes and other bacterial grazers with high intake rates and low productivity, consume large amounts of micro-organisms. Most of these are returned to the soil through waste products. The two stages result in high nitrogen turnover and the formation of stable organic mineral complexes. The nutrient cycle through bacteria and bacterial grazers and back into the soil is much faster when all the relevant niches are filled.

Except for a few cases (Macharia, 1981; Deshmukh, 1985; Kinyamario, and Imbamba, 1992), decomposition has been ignored in primary production studies in African grassland ecosystems, thus resulting in underestimation of the net primary production as well. Table 2 below gives the decomposition rates that have been recorded from various locations.

Table 2: Summary of herbaceous plant material decomposition rates (g g^{-1} $month^{-1}$)

Author	Location	Rates
Kinyamario and Imbamba (1992)	Kenya	0.09 - 0.18
Deshmukh (1985)	Kenya	0.08 - 0.10
George and Smeins (1982)	Texas, U.S.A	0.07
Macharia (1981)	Kenya	0.009 - 0.02
Ohiagu and Wood (1979)	Nigeria	0.132

Of these studies, only Kinyamario and Imbamba (1992) reported belowground decomposition rates (0.05 - 0.32 g g^{-1} $month^{-1}$). There is a general agreement, however, that the trend in relative decomposition rates follows that of rainfall, with highest rates during the wet season. However, comparison of decomposition rates obtained from different studies is inconclusive because most of them fail to give part of the details under which the studies were conducted, e.g. sampling intensity, plant species involved, the prevailing environmental conditions, and the mesh size of the litter bags.

2.0.5 Energy flow in tropical rangelands

All organisms above the level of primary producers are dependent on energy supplied by photosynthetic organisms. Thus the measurement of energy fixation by plants provides a starting point for describing the functional aspects of an ecosystem, as opposed to a description of its structural composition (Stewart *et al.*, 1973). Plants differ in their efficiency to capture solar energy due to differences in leaf morphology, leaf area, leaf orientation and inclination, and the ratio of photosynthetic to non-photosynthetic tissue. Efficiency of energy capture at plant community level is further affected by such factors as shading, canopy density, intra and inter-species interactions, light and moisture profiles, temperature and CO_2 concentration (Sims and Singh, 1978a; Kinyamario and Imbamba, 1992).

Accurate description and quantification of energy flow in a tropical rangeland ecosystem is not easy. Although the total number of species of organisms is not as high as

in a rain forest, for example, species richness is nevertheless high (Lamotte and Bourliere, 1983). Furthermore the nutritional requirements or feeding habits of many species of organisms remain poorly understood. However, some long-term and short-term studies have been carried out, which shed some light on the structure and functioning of some savanna ecosystems. It is still an open question whether the results from these studies are representative of all tropical savannas.

Ideally, estimation of energy flow within an ecosystem, implies reliable estimates of a number of population parameters of the major participating species. In addition, measurements are required for other demographic and physiological characteristics, such as age structure, sex ratio, population production and turnover, feeding habits, nutritional requirements and respiration (Lamotte and Bourliere, 1983). The estimation of numbers and standing crop can be satisfactorily estimated for some taxonomic groups of organisms, mainly vertebrates and arthropods living in litter and grass layers. Such estimations are much more difficult for soil micro-organisms, for example fungi and soil invertebrates, as well as of the tree and shrub inhabiting arthropods, for which there are hardly any adequate sampling methods. It is impossible within a short time to identify and quantify the diet of thousands of species, at various stages of their life cycle and during the different seasons of the year. All organisms belonging to a single functional group, e.g. fresh-leaf eaters do not necessarily use the same food and in the same way and with the same efficiency. For example, the ingested energy to assimilated energy ratio greatly differs from one species to another. The ratio is far larger for an elephant than for a Thompson`s gazelle, for example (Lamotte and Bourliere, 1983). Therefore knowledge of the nutritional physiology of the various species in an ecosystem is essential. Seasonal changes in the nutritive value of the diet must be considered, especially of the plant material which loses a large part of proteins and other nutrients once dry (Kamstra *et al.*, 1955; Karue, 1974, 1975; Van Soest, 1982, Leng, 1990; Ekaya, 1991).

One other technical/methodological problem arises from the lack of a clear-cut borderline between some trophic levels. This is the case for the omnivorous animals, which occur among mammals, birds and insects (Lamotte and Bourliere, 1983). The same is the case for decomposers, who although having a small biomass, their role in energy flow is far more important than that of most large animals. Furthermore the estimation of maintenance energy requirements of the various organisms constituting a savanna community would

involve respiration measurements which cannot be carried out easily in the field. Such measurements would entail simulation of field conditions in the laboratory.

From the foregoing, it is apparent that attempts to accurately characterize energy flow in tropical savannas have been faced with two major drawbacks; (i). the large diversity of the ecosystems, coupled with numerous compartments within the ecosystems, and (ii). methodological shortcomings. However despite the drawbacks, many studies have been conducted, mainly covering a few compartments of the ecosystem or parts thereof. The tentative conclusions reported from various studies have tended to stimulate further research.

Most of the world's savannas lie in the inter-tropical zone, where the sun is directly overhead for at least part of the year. These zones therefore benefit from maximum amount of radiant solar energy. Table 3 below shows some reported values of average incident solar radiation from tropical grasslands.

Table 3: A summary of some reported values of incident solar radiation in tropical grasslands.

Location	**Solar radiation**	**Source**
1. Lamto (Ivory Coast)	16.5 GJ m^{-2} yr^{-1}	Lamotte and Bourliere (1983)
2. Lamto (Ivory Coast)	5.69 GJ m^{-2} yr^{-1}	Bony (1974)*
3. North Indian grasslands	6.37 GJ m^{-2} yr^{-1}	Singh *et al.*, (1975)
4. Semi-arid grassland (Kenya)	19.7 MJ m^{-2} day^{-1}	Kinyamario and Imbamba (1992)

*Quoted by Lamotte and Bourliere (1983).

A large part of the incoming solar radiation is, however, reflected upward by the cloud cover, and is therefore unusable for photosynthesis. Indeed, less than half reaches the earth's surface (Lamotte and Bourliere, 1983). Of that amount of energy reaching the earth's surface, only about one half is photosynthetically active, i.e. the wavelength lies between 400 and 700 nm (Long and Jones, 1992). Nevertheless, incoming solar radiation can not be considered as a limiting factor for primary production in tropical savannas;

generally, net primary production is reported to be greater in the humid tropical regions where there is more cloud cover than in drier sun-scorched tropical areas (Lamotte and Bourliere, 1983).

Two approaches have been used in the estimation and characterization of energy flow patterns through the plant components of tropical savannas. The first and commonest approach is the direct measurement of biomass quantities in the different compartments, which are then interpreted to be related to energy flow in the ecosystems. There are many studies reported on standing crop and net primary production of tropical savannas and grasslands (see section 2.0.1). Unfortunately the interpretation of these estimates is made difficult by the variety of the methods used, and by the great variation in the comprehensiveness of the different studies. Estimations of standing crop of plant material are often accompanied by estimations of the amount of plant material consumed by both large and invertebrate herbivores. There are a number of estimates reported from different environments. Table 4 below shows a summary of some of the reported values from tropical grasslands.

Table 4: Estimates of aboveground net primary production consumed by large and invertebrate herbivores.

Location	Community	% Consumed	Source
(a). *Large herbivores*			
Uganda	Savanna	30 - 40	Strugnell and Pigott (1978)
Uganda	Savanna	28	Lamprey (1964)
Tanzania	Savanna	60	Petrides and Swank (1965)
Serengeti	Savanna	66	McNaughton (1985)
Serengeti	Savanna	15 - 39	Norton-Griffin (1979)
Serengeti	Long-Short grass	19 - 24	Sinclair (1975)
Nigeria	Savanna	45	Ohiagu (1979)
South Africa	Broad-leaf savanna	19	Gander (1982)
(b). *Invertebrate animals*			
Serengeti	Savanna	4 - 9	Norton-Griffin (1979)
Serengeti	Short-Long grass	4 - 8	Sinclair (1975)
Kenya	Savanna	6	Coughenour *et al.* (1985)
South Africa	Broad-leaf savanna	7 - 17	Grunow *et al.* (1980)

The figures generally show high variation in the amount of aboveground biomass consumed by both large herbivores and invertebrates, from different communities and locations.

The second approach used is the direct estimation of the energy content (Joules) in ecosystem compartments. The few studies carried out in tropical grasslands using this approach include those by Sims and Singh (1978b), Singh *et al.*, (1979) and Kinyamario and Imbamba, (1992).

In ungrazed North American grasslands, Sims and Singh (1978b) found that the percentage of solar energy captured was 0.64%, indicating that most of the energy was not utilized for net primary production. Energy accumulation in the live shoot and belowground compartments was 22.6 KJ m^{-2} day^{-1} and 75 KJ m^{-2} day^{-1} respectively. Therefore, most of the energy flowing through the grassland followed the belowground pathway.

Singh *et al.*, (1979) synthesized data on energy flow for semi-arid, dry sub-humid,

moist sub-humid and humid grasslands of India, with mean annual rainfall of 1381, 1190, 942 and 492 mm respectively. Their important findings can be summarized as follows:

(i). energy fixation was at a minimum (3871 KJ m^{-2} yr^{-1}) in the water-limited semi-arid zone. It was at a maximum (36213 KJ m^{-2} yr^{-1}) in the dry sub-humid zone,

(ii). the rate of energy fixation was at a maximum during the rainy season for all the grasslands,

(iii). the proportion of solar energy fixed by the vegetation in the semi-arid grassland was lowest, at 0.05%, and highest for the dry sub-humid grassland, at 0.5%,

(iv). in the semi-arid and humid conditions, belowground biomass receives a larger proportion of the energy fixed, 64% and 67% respectively. The converse was true for the dry sub-humid grasslands, and

(v). all the grasslands showed an accumulation of energy (11.33%) over the annual cycle.

It has been observed that generally, the efficiency of energy capture by plants based on the percentage of photosynthetically active radiation is lowest for the arid and semi-arid grasslands. Based on a wide survey of data, Sims and Singh (1978b), calculated efficiency values for semi-arid, sub-humid and humid tropical grasslands to be 0.12%, 0.81% and 0.69% respectively. The efficiency value for the semi-arid grasslands in the USA greatly differs with that of Kinyamario and Imbamba (1992), calculated from a semi-arid grassland in Kenya (0.70%). This exemplifies the role played by local factors in grasslands that may be classified as structurally similar.

Equally few studies have been carried out to estimate energy flow patterns and characteristics through the animal component of tropical savannas. This is attributable to the complicated nature of energy flow through the different animal trophic levels (Lamotte and Bourliere, 1983). In order to estimate the energy flow through the animal trophic levels, it is necessary to measure the animal populations and their fluctuations through the year, plant material intake and assimilation efficiency, the proportion of the energy that is transferred to carnivores and from all consumers to the detritus food chain, and respiratory losses from the ecosystem. The amount of animal tissue synthesized during the year through growth of the parental generations and through production of new individuals has to be evaluated as well (Lamotte and Bourliere, 1983).

Most of the reported studies on energy flow through the animal component deal with energy conversion parameters at population level rather than a complete energy flow budget through the ecosystem. Table 5 below summarizes some reported energy conversion parameters for various savanna organisms.

Table 5: Energy conversion parameters, at population level, for some tropical savanna animals*.

	Assimilation efficiency	Production efficiency	Ecological efficiency	Turnover rate
(a). Herbivores				
Grasshoppers				
Burkea savanna, various spp.	0.32	0.19	0.057	
Acacia savanna, various spp.	0.32	0.21	0.068	
Orthochtha brachycnemis	0.20	0.42	0.085	9.6
Caterpillars				
Cirina forda	0.43	0.15	0.064	
Herbivorous termites				
Trinervitermes geminatus			0.09	1.04
Ancistotermes cavithorax			0.018	9.7
Hodotermes mossambicus	0.61			
Ungulates				
Uganda kob	0.84	0.01	0.01	0.27
Impala	0.59	0.04	0.024	
Domestic cattle	0.57	0.05	0.023	
African elephant	0.30	0.02	0.005	
(b). Carnivores				
Spiders				
Orinocosa celerierae	0.95	0.53	0.50	
Afropisaura valida				6
Lizard				
Mabuya buettneri			0.11	3
(c). Detritivore				
Earthworm				
Millsonia anomala	0.09	0.04	0.006	2

*Data compiled from various sources by Lamotte and Bourliere (1983).

Assimilation efficiencies vary widely among species, mainly depending on taxonomic status and physiological characteristics as well as the trophic category to which the species belong, developmental stage of the animal, seasonal changes in food habits and the nutritive value of the staple food (Lamotte and Bourliere, 1983).

Preference for particular plant species, parts of plants and for living versus dead herbage have been described for many herbivorous species (Bell, 1969; Ng'ethe and Box, 1976; Migongo, 1984; Coppock *et al.*, 1986; Kayongo-Male, 1986; Kinyamario and Muthuri, 1986; Rutagwenda *et al.*, 1990; Ekaya, 1991). The energy expenditure during food search (foraging), which is an important factor in the energy balance of most species, has also been estimated (Cordova *et al.*, 1978; Hanley, 1982). Therefore, the intake and assimilation values obtained in laboratory feeding experiments where dietary selection is restricted, is only an approximate representation of the actual field scenario. Therefore estimation of the average assimilation efficiency in natural populations is a delicate task. The assimilation figures given in Table 5 are similar to those published by Hutchinson and King (1979) for temperate grassland animals.

Production efficiency is very high in invertebrate and cold-blooded vertebrate carnivores, high in invertebrate herbivores and very low in warm-blooded herbivores and invertebrate detritus feeders. The lowest ecological efficiency reported within the animal kingdom is that for the savanna earthworm, *Millsonia anomala* (Lavelle, 1978) (quoted by Lamotte and Bourliere, 1983). This ratio has been attributed to the very low nutritive value of the soil ingested by the worm, about 376 J g^{-1}, and the high temperatures of tropical savanna soils, which increase the respiration of the animals.

The index of efficiency of biomass production, or the biomass turnover rate per year varies widely. Generally, the turnover rate within a given taxonomic group is more rapid as the number of generations per year gets higher (Lamotte and Bourliere, 1983).

Very few attempts have been made to estimate the energy flow through the various levels of animal consumers in tropical savannas. A notable attempt is that by Lamotte (1977,1978) (quoted by Lamotte and Bourliere, 1983) from the Lamto savanna ecosystem in Guinea. The average total standing crop was about 66 t ha^{-1}, out of which 42.6 t ha^{-1} and 23.4 t ha^{-1} was aboveground and belowground respectively. The photosynthetic efficiency was estimated to be 0.67%. This compares well with rates reported from other savanna and even temperate grasslands (Coupland, 1979; Kinyamario and Imbamba, 1992). About 50%

of the aboveground primary production was destroyed by fire. Grasshoppers, foraging termites and rodents were the significant primary consumers in the ecosystem. Table 6 below summarizes the characteristics of the consumers.

Table 6: Average biomass (**B**), annual production (**P**), consumption (**I**) and energy budget for some groups of primary and secondary consumers in the Lamto savanna.

	B	**P**	**I**	**P:I**	**P:B**	**I:B**
Primary consumers						
Rodents	5225	14600	710000	0.02	2	100
Grasshoppers	11700	83600	1254000	0.06	7	104
Termites	23400	234000	16720000	0.014	10	714
Earthworms	752400	1567000	2299000000	0.005	1.8	450
Secondary consumers						
Birds	2341	920	52250	0.02	0.4	22
Lizards	585	1840	18390	0.10	2.8	30
Spiders	13376	96140	313500	0.30	7.0	23
Driver ants	200640	1254000	5016000	0.25	6.2	25

*Estimates in KJ ha^{-1} for biomass, and KJ ha^{-1} yr^{-1} for production and consumption. (Data compiled by Lamotte and Bourliere ,1983).

From the above table, the investigator concluded that the proportion of energy routed through aboveground consumers was very low, less than 260 x 10^6 KJ ha^{-1} yr^{-1}. However, earthworms and fungus-growing termites played a key role in the flow of energy. Earthworms alone consumed about 230 x 10 KJ ha^{-1} yr^{-1} and fungus-growing termites more than 16 x 10^6 KJ ha^{-1} yr^{-1}. However, their ecological efficiency is low, especially that of the earthworms whose P:I ratio averaged 0.006. This was attributed to the non-assimilation of most of the ingested plant material. It was estimated that about 226 x 10^6 KJ ha^{-1} yr^{-1} was excreted, thus remaining available to other detritus feeders. Respiratory loss was low, about 31 x 10^6 KJ ha^{-1} yr^{-1}, due to the fact that most primary consumers in the study site were poikilothermic invertebrates with low maintenance costs (Lamotte and Bourliere 1983).

The biomass of secondary consumers amounted to 217 x 10^6 KJ ha^{-1} yr^{-1}, with most of the standing crop accounted for by driver ants. The various levels of carnivores consumed about 5.4 x 10^6 KJ ha^{-1} yr^{-1} and produced about 1.45 x 10^6 KJ ha^{-1} yr^{-1}. Respiratory losses averaged 2.3 x 10^6 KJ ha^{-1} yr^{-1}. The amount of energy in the rejecta produced was estimated to be 1.7 x 10^6 KJ ha^{-1} yr^{-1}.

The energy equivalent of the plant material which was not used by herbivores was estimated at 67 x 10^6 KJ ha^{-1} yr^{-1}, and that of unassimilated organic material available in the excreta of various herbivores and detritus feeders at 226 x 10^6 KJ ha^{-1} yr^{-1}, making a grand total of 293 x 10^6 KJ ha^{-1} yr^{-1} which was available to micro-organisms, together with the bodies of animals that died.

2.0.6 Nitrogen situation in tropical dryland soils

Except for the dry rangelands of the tropics, the rest of the areas have favourable climatic conditions. These conditions encourage dense vegetation, which enriches the soils with organic matter. However, a majority of tropical soils are very low in nitrogen (Das, 1949; Nye and Greenland, 1960; Webster and Wilson, 1971). Das (1949) reported a total soil nitrogen content of 0.05% from a wide variety of Indian soils, a value that was only one third of that reported from temperate soils (Mochoge,1977). However, in the high altitude tropical regions with higher rainfall, the amount of nitrogen is said to be higher than 0.05% (Harradine and Jenny, 1958; Mochoge, 1977). This scenario appears to be caused by many factors. The virgin lands of the tropics have been cultivated over and over, and thus the output of nutrients has been more than the inputs (Mochoge, 1977) . Moreover, soil management in tropical natural ecosystems is generally poor. This has therefore contributed to the impoverishment of the soils. Nitrogen uptake by plants and micro-organisms is considered a loss from the soil though a temporary one. After death, plants and micro-organisms decompose and release nitrogen to the soil. This temporary lock-up of nitrogen by plants and micro-organisms has a major impact on the cycling of nutrients especially in the drier tropics where productivity and decomposition are limited by a deficiency of moisture (Mochoge, 1977). Apparently, plants in tropical areas do not make proper recovery of available nitrogen due to the deficiency in soil moisture. Rogers (1961) and Viets (1960) indicate that recovery of available soil nitrogen ranges on the average from 50% to 60%. The other 40% and 50% escapes from the soil system in one way or another. The chief loss

has been considered to be transportation of available nitrogen from the root zone, i.e. leaching. Under high rainfall conditions and in friable well drained soils, leaching can be quite rapid. This is common in humid areas of the tropics. However, in low rainfall areas, leaching may be negligible, but other factors may make the nitrogen unavailable to plants.

Volatile loss processes like denitrification and ammonification may account for between 5% and 15% of the available nitrogen (Bartholomew, 1964; Allison, 1966). Loss of ammonia nitrogen through volatilization has been a major route of loss (Mochoge, 1977). This is common in arid and semi-arid rangelands where ammonia-yielding fertilizers have been applied to the surface of sandy soils. In savanna regions of the tropics, where fires are frequent during the dry seasons, there are considerable losses of nitrogen in gaseous form to the atmosphere. Soil erosion resulting from poor agricultural management, e.g. overgrazing, has caused considerable losses of nitrogen in the tropics.

Tropical soils heavily depend on natural means for any gains in soil nitrogen, through symbiotic nitrogen fixation, non-symbiotic nitrogen fixation and precipitation (Mochoge, 1977). When gains are compared to the losses, the semi-arid areas of the tropics are always having a deficit as far as nitrogen content in the soil is concerned (Mochoge, 1977).

2.0.6.1 Nitrogen fixation by free-living organisms

In the arid and semi-arid soils, nitrogen fixation by free-living organisms is insignificant (Mochoge, 1977). The probable reason is that the organisms involved are efficient mainly under less aerobic conditions, such as those that prevail in soils that are saturated for long periods (Jensen, 1940; Dickinson and Pugh, 1974). Moreover, the organic matter residues added to the soil to provide energy for the bacteria responsible for nitrogen fixation is very low, and temperatures a bit high for optimum activity to be reached (Mochoge, 1977). However, Tchan and Beadle (1955) estimated that the maximum contribution of Azotobacter and algae was 0.1 and 3.3 kg ha^{-1} $year^{-1}$ respectively.

2.0.6.2 Symbiotic nitrogen fixation

Adequate soil moisture is the first essential requirement for the symbiotic relationship between the host plant and *Rhizobium*. When moisture deficit becomes severe,

the plant sheds its nodules (Russel, 1973). High soil temperatures also adversely affect nitrogen fixation by nodules. In the semi-arid region of Australia, Meyer and Anderson (1959) found that the nodules of sub-terranean clover were found to fix nitrogen actively at 20^{o}C, with an optimum at 25^{o}C but almost complete cessation at 30^{o}C.

2.0.6.3 Organic nitrogen in semi-arid soils

Due to the low organic matter content in semi-arid soils, they are generally poor in nitrogen content. The areas experience serious droughts for nearly ten months in a year, having only 2-3 months of sporadic rainfall. The rainfall being so low, cannot support a luxurious amount of vegetation, save for tough grasses and shrubs whose annual yield of biomass is extremely low when compared to that of equatorial high rainfall zones of the tropics. Published studies give the organic matter content from tropical African grasslands as lying between 0.36 and 0.75 % carbon (Nye and Greenland, 1960).

2.0.6.4 Inorganic nitrogen in semi-arid soils

Just as is the case with organic nitrogen, semi-arid soils have very low inorganic nitrogen content (Mochoge, 1977). This is a reflection of the low amount of humus available in these regions. However, the amount of inorganic nitrogen varies from season to season and from one soil type to another (Mochoge, 1977).

2.0.7 Nitrogen transformation in rangeland ecosystems

Nitrogen has a unique role among the elements essential for plant growth because of the large amounts required by most plants (Devlin and Witham, 1983; Odhiambo, 1989). Nitrogen is a component of chlorophyll, enzymes, vitamins and hormones. It is essential for carbohydrate utilization, root development and uptake of other nutrients, for example, phosphorus and sulphur (Olson and Kurtz, 1982).

To become available to plants, nitrogen like all other mineral elements has to be mineralized to inorganic forms, otherwise the element remains locked up in undecomposed dead organic matter or immobilized in the tissues of living decomposer organisms (Deshmukh, 1986) The maintenance of soil nitrogen in ionic forms available to plants results from the complex interactions of soil chemistry. The equilibria between the various forms of the element are controlled by plant uptake, return through decomposition and the

physical and the chemical state of the soil pH and whether the environment is reducing or oxidizing (Ladd and Jackson, 1982; Stevenson, 1986; Deshmukh, 1986).

The forms of nitrogen in the soil can be divided into four categories, that is, nitrate nitrogen, ammonia nitrogen, organic nitrogen and molecular nitrogen. Higher plants absorb nitrogen from soil in the form of nitrate (NO_3^-). This form of nitrogen however is not directly used by the plant, but must first be reduced to ammonia (NH_3) before it can be incorporated into plant nitrogenous compounds (Devlin and Witham, 1983). The reduction process requires energy, and it has been observed that, through the breakdown of stored carbohydrates (in respiration) the needed energy is supplied as well as the carbon skeletons necessary for the incorporation of ammonia into plant nitrogenous compounds (Aslam *et al.*, 1973).

The first step in NO_3^- reduction is the conversion of NO_3^- to NO^-_2. This process takes place within the cell cytoplasm and is catalyzed by the enzyme nitrate reductase (Aslam *et al.*, 1973).The NO_2^- produced is then 'transported' into the chloroplast, where the enzyme nitrite reductase catalyses the reduction of NO_2^- to NH_3. This is then used in the synthesis of nitrogenous compounds, for example amino acids and proteins. In the absence of herbivores and fire, these organic nitrogenous compounds finally enter the soil nitrogen cycle when the plants die or their parts are shed and incorporated into the soil.

An internal cycle of nitrogen exists in the soil, which is distinct from the overall cycle of nitrogen but that interfaces with it. The soil nitrogen cycle consists of complex chemical and biochemical transformations that often fall out of the scope of a single research project. The conversion of organic nitrogen to forms available to plants (NH_4^+ and NO_3^-) occurs through biochemical transformations mediated by micro-organisms and is influenced by those factors that affect microbial activity for example, temperature, moisture, pH, etc. (Stevenson, 1986). The first step (ammonification) involves the conversion of organic nitrogen to NH_3 and is carried out by heterotrophic micro-organisms. The subsequent conversion of NH_3 to NO_3^- (nitrification) occurs through the combined activities of two groups of bacteria namely *Nitrosomonas* which converts NH_4^+ to NO_2^- and *Nitrobacter* which converts NO_2^- to NO_3^- (Stevenson, 1986).

Both aerobic and anaerobic micro-organisms are involved in the ammonification process, whereas only aerobes convert NH_4^+ to NO_3^-. Thus, conditions that restrict the supply of oxygen allow NH_4^+ to accumulate. NO_3^- is the predominant available form of

nitrogen in well-aerated soils (Stevenson, 1986). This process whereby organic nitrogen is converted to forms that are available to plants is termed mineralization. The reverse process whereby forms of nitrogen available to plants are converted to unavailable form, e.g. microbial protein, fixation by clay minerals, etc. is termed immobilization.

2.0.8 Non-biological effects on the soil nitrogen cycle

Apart from the nitrogen transformation brought about by soil micro-organisms, non-biological reactions do affect the cycle as well. According to Stevenson (1986), these reactions fall into three categories:

(i). NH_4^+ fixation by clay minerals especially vermiculite and hydrated micas, thus immobilizing the nitrogen,

(ii). NH_3 fixation by soil organic fractions, which supplement biological immobilization since the fixed N is not readily available to plants or micro-organisms, and

(iii). reactions of NO_2^- with organic components, e.g. humic and fulvic acids during which some of the NO_2^- is converted to organic forms and part are lost as nitrogen gases.

2.0.9 Gains in soil nitrogen

Sources of nitrogen input to natural grasslands without intensive management interventions are primarily symbiotic and non-symbiotic fixation and through ambient precipitation (Evans and Barber, 1977; Clark *et al.*, 1980; Stevenson, 1986). Nitrogen contained in faeces of animals, wind and surface water import are supplementary sources. In contrast, in intensively managed grasslands, fertilizers and the legumes in sown legume-grass mixtures are responsible for the major inputs.

The inputs of non-symbiotic nitrogen fixation reported from most tropical grasslands are low; values commonly in the range of 0.1 to 0.2 g $m^{-2}yr^{-1}$ (Steyne and Delwinche, 1970; Reuss, 1971; Vlassak *et al.*, 1973). Of the symbiotic associations, nodulated legumes are the principal agents of fixation with reported values ranging from 10 to 30 g $m^{-2}yr^{-1}$ (Clark *et al.* 1980; Evans and Barber, 1977. The estimated average rates of biological nitrogen fixation for some organisms and associations are shown in Table 7 below.

Table 7: Estimated average rates of biological nitrogen fixation for specific organisms and associations

Organism or system	N_2 Fixed, Kg/ha/Year
Blue - Green algae	25
Free - living organism	
Azotobacter	0.3
Clostridium pasteurianum	0.1 - 0.5
Plant - algal associations	
Ggunnera	12 - 21
Azollas	313
Lichens	39 - 84
Legume - *Rhizobium* associations	
Soybeans	57 - 94
Cowpeas	84
Alfalfa	128-600
Nodulated non legumes	
Alnus	40 - 300
Ceanothus	60

Source: Evans and Barber (1977)

Although the amount of nitrogen contributed annually to dry grassland by symbiotic and non-symbiotic mechanisms are quite low, the cumulative effect over several years can be important in the build up of the organic nitrogen of grassland soil.

It is well documented that precipitation washes down available nitrogen from the atmosphere and plant canopy (UNESCO, 1978; Clark *et al.*, 1980; Bate and Gunton, 1982; Brassel and Sinclair, 1983). Some of the published figures from around the world are shown in Table 8 below.

Table 8: Some values reported for nitrogen in precipitation from various sites.

Nitrogen in precipitation ($g\ m^{-2}\ yr^{-1}$)	Sites
0.40	Pawnee, Colorado
0.32	Matador, Canada
0.30	Curlew valley, Utah
0.35	Kursk, USSR
0.11	Nylsvley, South Africa

Source: Clark *et al.*, (1980); Bate and Gunton, (1982)

The precipitation input is roughly of lower order of magnitude than the input due to biological fixation. A possibility that may have been commonly ignored in the past is that nitrogen measured in the rainwater represents only a part of the nitrogen input to the soil-plant system from the atmosphere. In arid areas, additional nitrogen inputs may occur due to wind erosion. West Africa for example, the harmattan wind that blows from the arid northern areas during the early part of the year carries dust containing silica, calcium and organic matter. This material is deposited in the savanna and forests to the south (Whalley and Smith, 1981).

2.0.10 Nitrogen loss from the soil

Nitrogen is the most mobile nutrient and one that is subject to greatest loss from the soil - plant system (Stevenson, 1986). In grassland ecosystems, under natural setting, nitrogen may be lost by denitrification, volatilization, leaching, wind and water erosion of particulate matter as well as in harvest or animal export (Charley, 1977; Evans and Barber, 1977; Clark *et al.*, 1980). The form of nitrogen commonly lost following these pathways is mineral nitrogen in the form of nitrate and ammonia, which only occur in very limited

amounts in natural grassland soils (Clark *et al.*, 1980). Consequently, nitrogen losses from grassland will usually be far lower than those from cultivated soils.

2.0.10.1 Denitrification

Denitrification occurs in soil when available nitrate is present, aeration is limited, and the soil moisture, temperature and pH are favourable for microbial growth (Clark *et al.*, 1980). Further, easily decomposable organic matter must be available to the micro-organisms (Tanji, 1982). This set of conditions rarely occurs concomitantly in arid grasslands, therefore denitrification in these areas will primarily occur in soils that have been heavily fertilized with nitrate and in which plant growth is insufficient to use the rapidly applied nitrate (Evans and Barber, 1977; Clark *et al.*, 1980). Skujins (1975) indicated the possibility of denitrification occuring in the decomposing algal crusts on rangelands, but confirmatory data are lacking.

The ability to convert NO_3^- to N_2 and N_2O gases is limited to a few organisms that are able to utilize the oxygen from NO_3^- (and NO_2^-) as a substitute for O_2 in conventional metabolism. The organisms primarily involved are heterotrophic and belong to the genera *Alcaligenes, Agrobacterium, Bacillus and Pseudomonas* (Stevenson,1986). Denitrification acts as a balance on biochemical N_2 fixation. Just as organically bound carbon is returned to the atmosphere (as CO_2) through respiration, combined nitrogen is returned through denitrification.

2.0.10.2 Chemodenitrification

The oxidation of NO_2^- to NO_3^- in soil by *Nitrobacter* normally proceeds at a faster rate than the conversion of NH_4^+ to NO_2^- by *Nitrosomonas,* thus NO_2^- seldom persists in detectable amounts (Stevenson, 1986). However, high levels may be detected when NH_3 or NH_4^+ type of fertilizers are applied to alkaline soils at high rates (Nelson, 1982). This has been attributed to the inhibition of the second step of nitrification process presumably due to NH_3 toxicity to *Nitrobacter* (Stevenson, 1986).

The accumulation of NO_2^- is undesirable due to its toxicity to plants at relatively low concentrations (Court *et al.*, 1974), and the ease with which it may undergo a series of reactions with organic matter to yield N gases which are subsequently lost from the soil (Broadbent and Stevenson, 1966; Nelson and Bremner, 1969; Nelson, 1982).

2.0.10.3 Leaching, erosion, and runoff

Nitrogen is leached mainly as NO_3^- although NH_4^+ ions may be lost from sandy soils (Clark *et al.*, 1980). Leaching requires high NO_3^- levels in soil and downward movement of water sufficient to move NO_3^- below the rooting depth (Stevenson, 1986). These conditions are met in soils of the mesic zones and only infrequently if at all in arid and semi-arid ecosystems. Therefore, nitrogen losses in arid grasslands due to leaching are usually low or non-existent. Power (1971) reported that in a semi-arid north Dakota grassland given a heavy application of mineral nitrogen suffered no loss of nitrogen due to leaching in the several following years.

Considerable nitrogen amounts may be lost from the soil due to erosion and surface runoff. In sheet erosion, the eroded fraction may contain several times more N than the original soil. Most of the nitrogen lost by erosion is in organic forms and is eventually deposited in water bodies with little opportunity of being recycled into terrestrial systems (Stevenson, 1986).

2.0.10.4 Ammonia volatilization

The volatilization of ammonia has been known to cause substantial losses of nitrogen from either fertilized or heavily grazed grasslands (Clark *et al.*, 1980). Volk (1959) reported the nitrogen loss during seven days following surface application of urea to grass sods to range from 20 to 30 % of the urea nitrogen applied. The author noted, however, that this high rate of volatilization did not mean equivalent loss to the atmosphere. The ammonia release was almost entirely absorbed by the vegetation canopy. Skujins (1975) reported that as much as 10 - 25% of the nitrogen fixed in algal crusts may undergo volatilization as NH_3 during algal crust decomposition. There is also the possibility that ammonia may be volatilized from higher plants or from amide containing guttations (Martin and Ross, 1968).

2.0.11 Rate limiting steps in the nitrogen cycle

Steele and Vallis (1988) concluded that the productivity of tropical pastures without added fertilizer nitrogen is generally well below potential yield, despite high total nitrogen in the soil-plant system. This is an indication that there is a slow rate of cycling of nitrogen in the system into available form, which limits productivity. Graham *et al.* (1985) reported that pasture deterioration in central Queensland was influenced more by reduced availability

of nitrogen than by changes in nitrogen reserves.

Litter production in semi-arid pastures is small, especially where pasture is burnt or cut for animal feed (Christie, 1979; Hunt, 1983; Bruce and Ebersohn, 1982). The chemical composition of litter determines the balance between mineralization and immobilization of nitrogen (Isichei, 1979; Steele and Vallis, 1988). Vallis (1983) reported that between 10% and 33% of the litter nitrogen becomes available to plants within the first year of deposition, but in subsequent years, less than 5% of the residual nitrogen per year is recycled.

Vallis and Gardener (1984a) observed that passage through livestock increases the rate of conversion of nitrogen in herbage to mineral forms, but at the expense of greater losses from the ecosystem. The few published studies conducted on tropical pastures (Vallis and Gardener, 1984b; Vallis *et al.*, 1985) indicate that the recovery of urinary nitrogen by pasture plants may be even lower than the generally 30% or lower quoted for temperate pastures in New Zealand (Steele and Brock, 1985). Nevertheless, animal excreta, particularly urine is important in maintaining high pasture productivity (Ball, 1979). As pasture productivity and animal stoking rate increase, animal excreta contributes proportionately more to the nitrogen taken up by plants (Steele and Brock, 1985).

Belowground plant material can also contribute considerable amounts of nitrogen to the soil during decomposition, but due to the high C:N ratio of the material, their decay may be associated with net immobilization of soil mineral nitrogen at least during the initial stages of decomposition (Steele and Vallis, 1988). From the humid forest zone of the Ivory Coast, Picard (1979) reported the turnover time for roots of *Panicum maximum* defoliated at six weekly intervals to lie between 0.2 and 0.4 years. The annual input of belowground dry matter was estimated to be between 9 and 16 tonnes per hectare. The pattern of nitrogen release from decomposing roots was similar to that from herbage, that is, a rapid release during the first year followed by a slow release (Moore, 1974).

Soil micro-organisms, apart from being mediators of nitrogen transformations, act as small but important reservoir of nitrogen and comprise a dynamic component with a rapid rate of turnover (Steele and Vallis, 1988). Therefore, they are a key component in grassland nitrogen cycles. The soil fauna, usually dominated by earthworms and / or termites is also important in nitrogen cycling in pastures. In a review of the influence of earthworms and termites on soil nitrogen cycling, Lee (1983) concluded that earthworms are likely to have

an important influence on nitrogen cycling in humid areas, where they may ingest litter at rates exceeding the rate of litter production and return nitrogen to the soil in the form of ammonia, urea, mucoproteins and dead tissues. Termites may also be of similar significance in light-textured semi-arid and desert soils, where the supply of nitrogen is very limited (Steele and Vallis, 1988). From a semi-arid environment in north Queensland, Australia, Holt and Easey (1984) reported that the biomass per hectare of grass for litter-feeding termites was 2-5 times that of the cattle biomass.

2.0.12 Effects of management on nitrogen cycling

Management practices that increase the rate of nitrogen cycling in pastures will inevitably increase the rate of nitrogen loss (Steele andVallis, 1988). This conclusion was based on the assumption that increased uptake of nitrogen by pasture plants is accompanied by greater intake and excretion of nitrogen by grazing animals, thereby increasing nitrogen losses from excreta-affected areas.

The amount of nitrogen passing through plant litter has a major impact on the size of the soil organic matter pool. Increasing pasture utilization by animals reduces the amount of litter in pastures and increases the dependence of pasture plants on mineralization of stable soil organic matter and animal excreta for their nitrogen requirements (Field and Ball, 1982). In cases where nitrogen inputs are insufficient to match the experienced losses, a negative nitrogen balance will inevitably occur.

Rapid decomposition and nitrogen release occurs from plant roots with a C:N ratio below 20-25, whereas immobilization takes place at higher C:N ratios (Whitehead, 1970). Nitrogen cycling is promoted by shifts in botanical composition of pastures towards legumes since legume tissues have C:N ratios generally less than 20, while grasses are generally greater than 30 (Steele and Vallis, 1988). However, this increased cycling carries the risk of greater losses of nitrogen from the ecosystem. Plant species with high C:N ratios reduce nitrogen losses by causing more of the nitrogen to be incorporated into relatively stable organic matter (Van Soest, 1982; Steele and Vallis, 1988).

Surface cultivation of clay soils with high total nitrogen but low in available nitrogen which have been under a tropical grass pasture may stimulate nitrogen cycling (Steele and Vallis, 1988). Catchpoole (1984) reported that the annual dry matter yield and nitrogen content of a stand of *Panicum maximum* was increased from 8 to 10 ton ha^{-1} and

90 to120 kg ha^{-1} respectively by annual surface cultivation. It was further reported that the growth of grass was depressed for several weeks after cultivation, but was subsequently stimulated. In old pastures on soils of low organic nitrogen content, and where most of the nitrogen is contained in pasture roots, surface cultivation may not increase nitrogen cycling (Steele and Vallis, 1988).

In extensively managed pastures, it is common to use fire to remove the excess, inferior quality dead herbage at the start of the wet season. This practice has implications for the nitrogen cycle. Mott (1983) and Filet *et al.*, (1986) reported from central Queensland that burning of litter at the start of the wet season reduced the flow of nitrogen through the litter by 16 kg ha^{-1}, but had no measurable effect on nitrogen uptake by the pasture. It appears that little nitrogen from the decomposing litter was available for plant uptake, in the short term. Regular burning of pastures over many years, however, may deplete the active soil organic matter and ultimately reduce the rate of nitrogen cycling (Steele and Vallis, 1988).

2.0.13 Nitrogen cycling in tropical grasslands

The majority of discussions and simulations of nutrient cycles in natural ungrazed tropical grassland ecosystems have commonly used a skeletal framework based on a nutrient balance approach (e.g. Singh *et al.*, 1979; Rutherford and Panagos, 1982). They have used box and arrow diagrams representing the major state variables and directional transfers between them. These involve flows from an available nutrient pool to the live, dead and litter plant compartments. Thereafter the nutrients flow to one or more reservoirs in the soil, from which there occurs replenishment of the available pool.

This basic cycle may encounter diverse gains and losses (Steyne and Delwinche, 1970; Reuss, 1971; Vlassak *et al.*, 1973, Stewart, 1966). However, uncertainties still remain, for example whether the annual supply of an element comes from the previous year's litter, from litter of several years or primarily from soil humid material (Clark *et al.*, 1980). Nevertheless, since the net annual primary production is measurable, as well as the nutrient content and the release rates of nutrients in that biomass, a specific nutrient cycle can be postulated on a broad scale.

Nutrient cycles describe the route of chemical elements within the ecosystem. Plants obtain these elements in inorganic forms from the atmosphere or from the soil in

solution. Animals and micro-organisms consume the elements in their organic food and through respiration and decomposition, eventually return the elements to the atmosphere or the soil. Due to their key role in non-atmospheric cycles, soils and their biota are important determinants of nutrient cycling. Vegetation is an important store of nutrient especially in the tropics (Deshmukh, 1986).

Energy flow closely parallels the routes of nutrient cycles within the biotic components of ecosystems. However an important distinction between the two processes is the relationship with the abiotic environment. While energy flow is profligate, being driven by an endless solar power supply, nutrient cycling is conservative, with chemical elements being drawn from finite pools and largely retained within ecosystems (Deshmukh, 1986). Nutrient cycling and energy flow both involve storage in living and dead organic matter and rates of flow between the various compartments of ecosystems. To put emphasis on the biological geological and chemical nature of the processes involved in nutrient cycling, they are often referred to as biogeochemical cycles.

Nitrogen cycles are not entirely edaphic but most have an atmospheric component linked to the soil by nitrogen fixation and denitrification (Deshmukh, 1986). Nevertheless plants obtain most of their nitrogen from the soil as nitrate and ammonium ions (Stevenson 1986). Atmospheric nitrogen fixation worldwide accounts for about 10 kg $ha^{-1}yr^{-1}$, representing about 2% of global nitrogen assimilation (Burns and Hardy, 1975). However, most of the nitrogen in soil and biota originated in the atmosphere and has accumulated over the millions of years in which nitrogen fixation has been taking place (Deshmukh, 1986)

According to Rutherford and Panagos (1982), there are two overlapping nutrient cycles in the savannas; a relatively rapid cycle involving herbaceous plants and a slow cycle through the woody component. Nutrient flux through the herbaceous layer is a function of the level of production and biomass turnover, which fluctuate considerably from year to year depending on the amount of annual rainfall and incidence of fire and herbivory. They further state that the relatively small size of the herbaceous nutrient pool means that fluctuations in soil nutrient availability will be rapidly reflected in the mass of nutrients being turned over by herbaceous plants. This suggests that ecosystems dominated by herbaceous biomass have a less stable nutrient cycling system that is susceptible to perturbations (de Angelis, 1980).

There are very few studies on nitrogen cycling in dry tropical ecosystems, and most

of these are concerned with only some of the components of the ecosystem or particular processes. Singh *et al.*, (1979) synthesized data on nitrogen cycling for Indian grasslands studied under the International Biological Programme. The grasslands fell under three categories, i.e. semi-arid, sub-humid and humid. They reported that the annual uptake of nitrogen ranged from 25.6 (sub-humid) to 2.9 g m^{-2} (semi-arid). Cycling of nitrogen was promoted through the belowground parts in semi-arid grasslands whereas shoots played the major role in sub-humid grassland.

Frost (1984) calculated the soil nitrogen pools of an African savanna. Total nitrogen averaged 3654 kg ha^{-1} per metre soil depth, of which 196 kg (36 kg nitrate-N, 160 kg ammonium-N) was available to plants. The study showed that most of the nutrients in the system were in the soil rather than in plant biomass.

Isichei (1979) reported average nitrogen concentration in grasses for various periods of the year from sites in Guinea (Table 9 below).

Table 9. Average nitrogen concentration in aboveground and belowground grass samples during various seasons of the year.

Season	Aboveground	Belowground
Flush stage	0.74	0.53
Mid-growth	0.57	0.49
Peak growth	0.47	0.42
Dry season	0.32	0.58

From the data in Table 9 above, it is clear that there was low aboveground nitrogen content during the dry season, but a rapid increase in concentration at the flush and mid-growth periods. Thereafter there was a steep decline. In belowground biomass, the highest concentration of nitrogen was recorded during the dry season. There was a continuous decline as the season progressed, with lowest value at the peak period. This pattern in

nitrogen content has also been reported by Karue (1974,1975), Haggar (1975), Jihad (1976), and Ekaya (1991). The pattern of nitrogen concentration belowground throughout the year seems to give support to the opinion that there is translocation of nitrogen to the belowground parts, which is again relocated upwards during grass flushing. This has been indicated by Egunjobi (1974) and Morton (1977), from temperate species. From the studies thus far published on nutrient cycling in dryland ecosystems, it is clear that the quantitative and qualitative nature of nutrient cycles in these ecosystems is very diverse.

It is apparent from the above review of literature that plenty of studies have been undertaken in tropical grassland ecosystems to estimate primary production and productivity. However, due to differences in the methods used, and shortcomings associated with the methods, the reported figures show high variability and underestimate the productivity of these grasslands. There is limited literature on both nitrogen cycling and energy flow in African rangeland ecosystems. Furthermore, hardly any simultaneous studies have been carried out on primary productivity, nutrient cycling and energy flow, yet these are closely related and interdependent ecosystem processes that form a unified whole. A sound understanding of the structural and functional dynamics of natural ecosystems is necessary if they are to be managed in a way that provides adequate livelihood for present populations while maintaining management options for future generations. The development of conceptual models that will contribute to the overall understanding of the dynamism in these ecosystems is thus imperative.

Hypotheses;

1. Tropical rangeland ecosystems have higher primary productivity than is currently thought.

2. Energy flow and nutrient cycling in tropical rangeland ecosystems operate in non-equilibrial state.

Overall objective;

To attempt to synthesize a conceptual model of structure and function of tropical rangeland ecosystems using field data collected.

Specific objectives;

The specific objectives were to study;

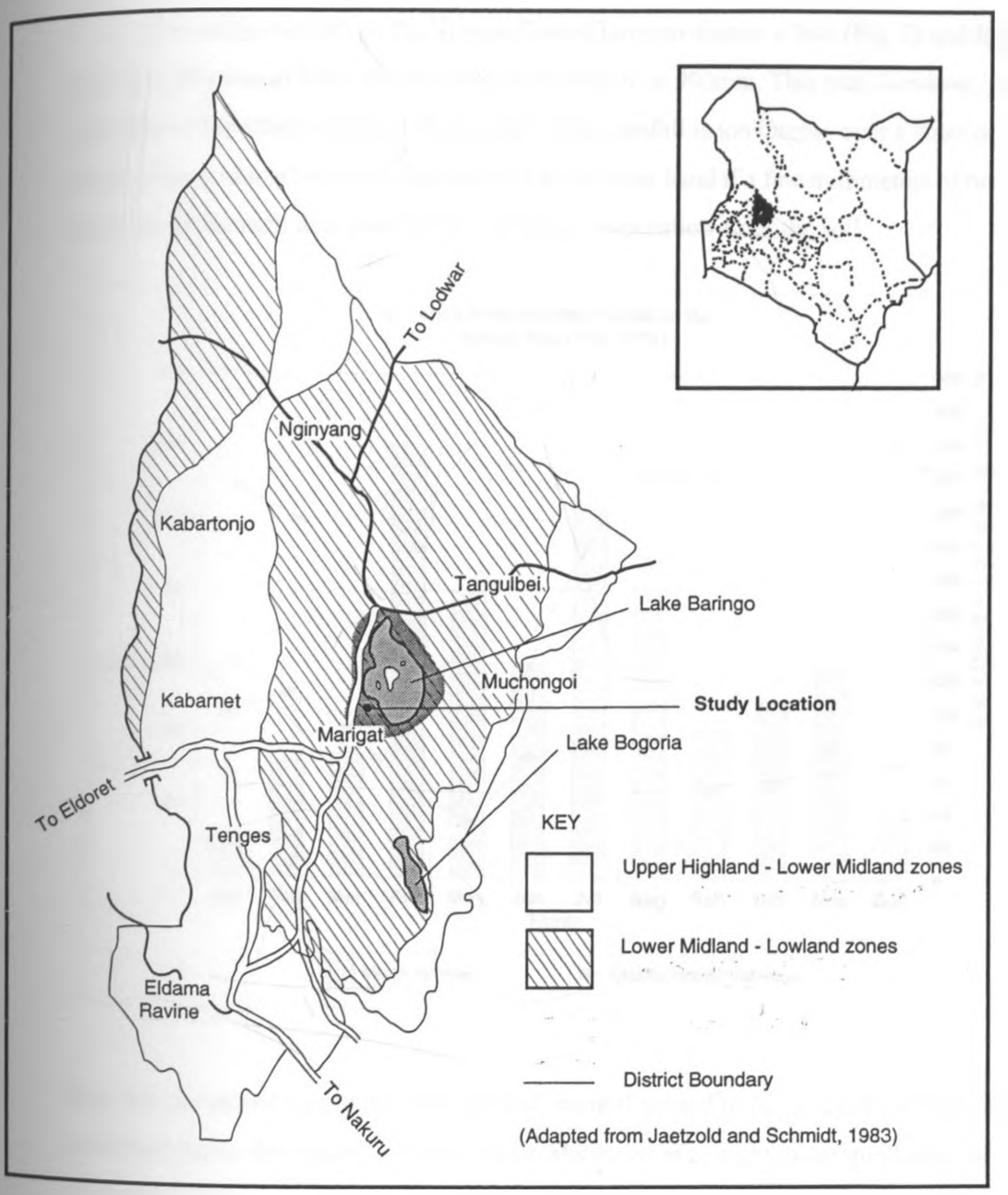
1. Dynamics of herbaceous net primary production and productivity,
2. The capture and flow of energy through the herbaceous layer, and
3. Nitrogen dynamics within the herbaceous layer, with an aim of characterizing the nitrogen cycle.

3.0 MATERIALS AND METHODS

3.0.1 Location of study site

The study was conducted on the Njemps flats of Baringo district in the Rift Valley province of Kenya (Fig. 1). The district covers an area of 9885 km^2 and encompasses a wide diversity of ecological zones, ranging from fertile, well-watered highlands to the arid lowland plains (Jaetzold and Schmidt, 1983). Rangeland constitutes 82% of the district, while high potential land is only 8%. Cropping agriculture (mainly subsistence) and livestock production provide 75% of the district's total income (Anderson, 1980).

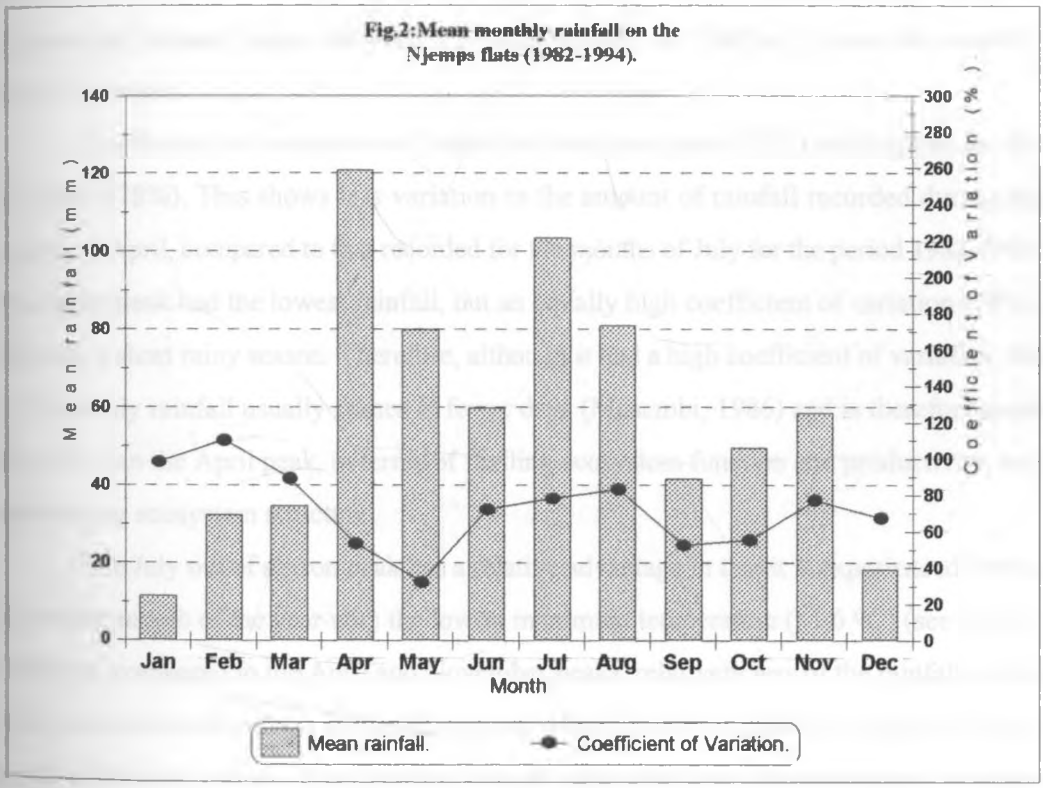
Fig. 1: Map of Kenya showing study area and location



3.0.2 Climatic characteristics of the study site

3.0.2.1 Rainfall

Generally, rainfall on the Njemps flats of Baringo district is low (Fig. 2) and highly localized. The annual total rainfall varies from 600mm to 900mm. This total, however, gives little idea of the effectiveness of the rainfall. If the rainfall is too intense over a short period of time, much of it is lost as surface runoff. On the other hand if a few millimetres of rainfall are received on each day, most of this is lost as evaporation from the soil.



On a few occasions during the study period, rainfall tended to be concentrated into short periods of heavy downpour, occurring in the afternoon or at night under conditions of low wind speed. Large drop sizes resulted in phenomenal surface runoff accompanied by soil loss. More common, however, were light late afternoon showers of 5-10 mm. Most of this rainfall was lost through evaporation especially if there was an interval of dry hot days between the shower events.

Three rainfall peaks are conspicuous (Fig.2). These are in April, July and November

with 10.5mm, 103.1mm and 58.2mm respectively. The April and November peaks are expected because this is when the Inter-tropical Convergence Zone (ITCZ) brings the long and short rains respectively. July is an out of season peak, a phenomenon not uncommon in tropical rangelands (Pratt and Gwynne, 1977; Glover and Robinson. 1953; Kenworthy and Glover, 1958). The three rainfall peaks were accompanied by high monthly evaporative demands of 168 mm, 179.8 mm and 183 mm for April, July and November respectively (section 4.0.1.2). During these months, the evaporative demand was 39%, 74% and 214% higher than the monthly rainfall. Therefore the monthly rainfall fell below the evaporative demand of the ecosystem. This is also the case for the rest of the months where the total evaporation demand ranges between 2.2 (August) and 20 (January) times the monthly rainfall received.

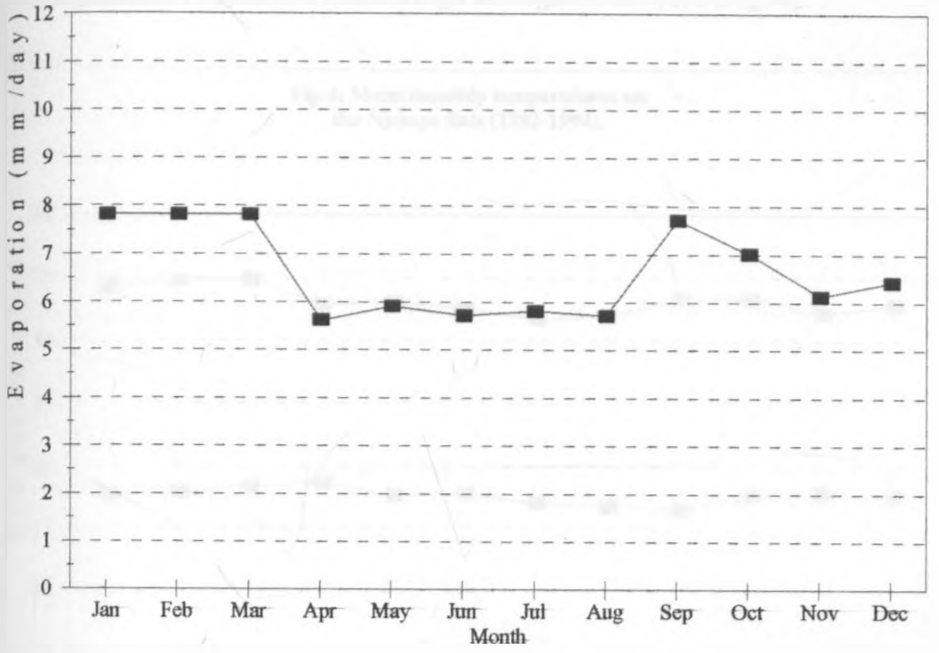
Coefficient of variation was lowest for the April peak (53%) and highest for the July peak (78%). This shows less variation in the amount of rainfall recorded during the months of April, compared to that recorded for the months of July for the period 1982-1994. November peak had the lowest rainfall, but an equally high coefficient of variation (77%). This was a short rainy season. Therefore, although it had a high coefficient of variation, the total monthly rainfall usually comes in fewer days (Musembi, 1986) and is therefore more effective than the April peak, in terms of fuelling ecosystem function and productivity, and determining ecosystem structure.

The July out of season peak has a relative advantage in that it is experienced during the coolest month of the year with the lowest maximum temperature (31.6 ^{o}C) (see Fig. 4). Therefore, compared to the April and November peaks, relatively less of the rainfall would be lost as evapotranspiration during this month. Although some rainfall is experienced each month of the year, however, the potential evapotranspiration far exceeds the actual moisture in the system throughout the year, thus giving a negative moisture balance for a greater part of the year (Jaetzold and Schmidt, 1983).

3.0.2.2 Evaporation rates

Pan evaporation rates are simulations of how rapid a surface of the ecosystem will lose moisture. Figure 3 shows the mean pan evaporation rates (mm/day) on the Njemps flats.

Fig.3: Mean monthly evaporation rates on the Njemps flats (1982-1994).

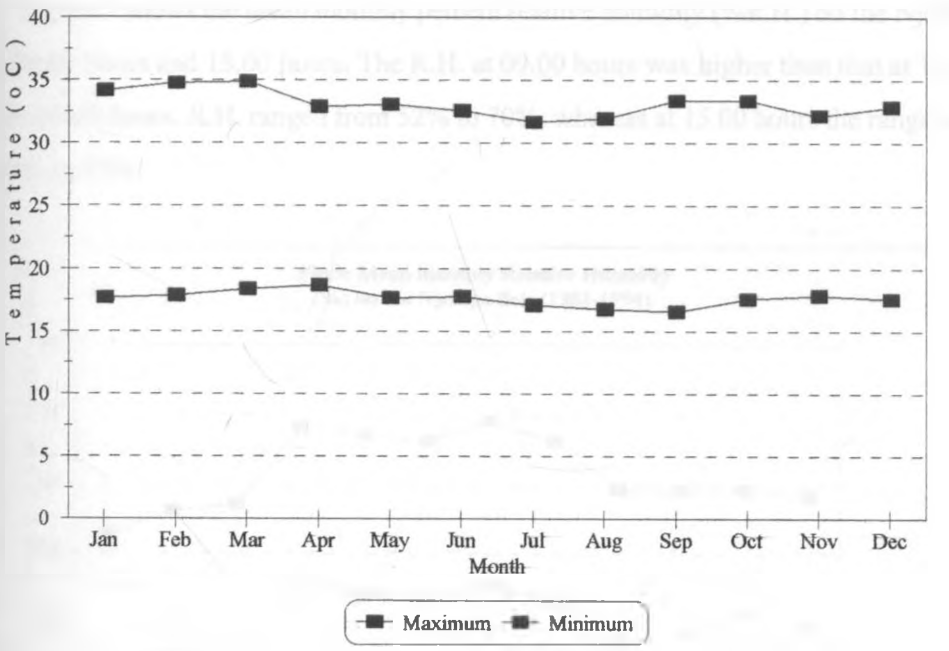


Evaporation rates ranged from 7.9 mm/day to 5.6 mm/day. Highest evaporation rates were recorded in the months of January and March, i.e. 7.8 mm/day, equivalent to 241.8 mm/month. Another evaporation peak was conspicuous in September (7.7 mm/day). These months preceded the rainfall peaks (Fig. 2) and were also the hottest (Fig. 4). This accounts for the high evaporation rates. Rate of evaporation suddenly dropped during the months of April and November, which had rainfall peaks and highest relative humidity. The increased humidity due to additional moisture from rainfall caused a reduction in the rate of evaporation. Months with lowest relative humidity recorded the highest evaporation rates. This was caused by an increase in the atmospheric moisture saturation pressure deficit, causing mass flow of moisture from surfaces into the atmosphere.

3.0.2.3 Temperature

Temperature in the area remains high throughout the year (Fig. 4).

Fig.4: Mean monthly temperatures on the Njemps flats (1982-1994).



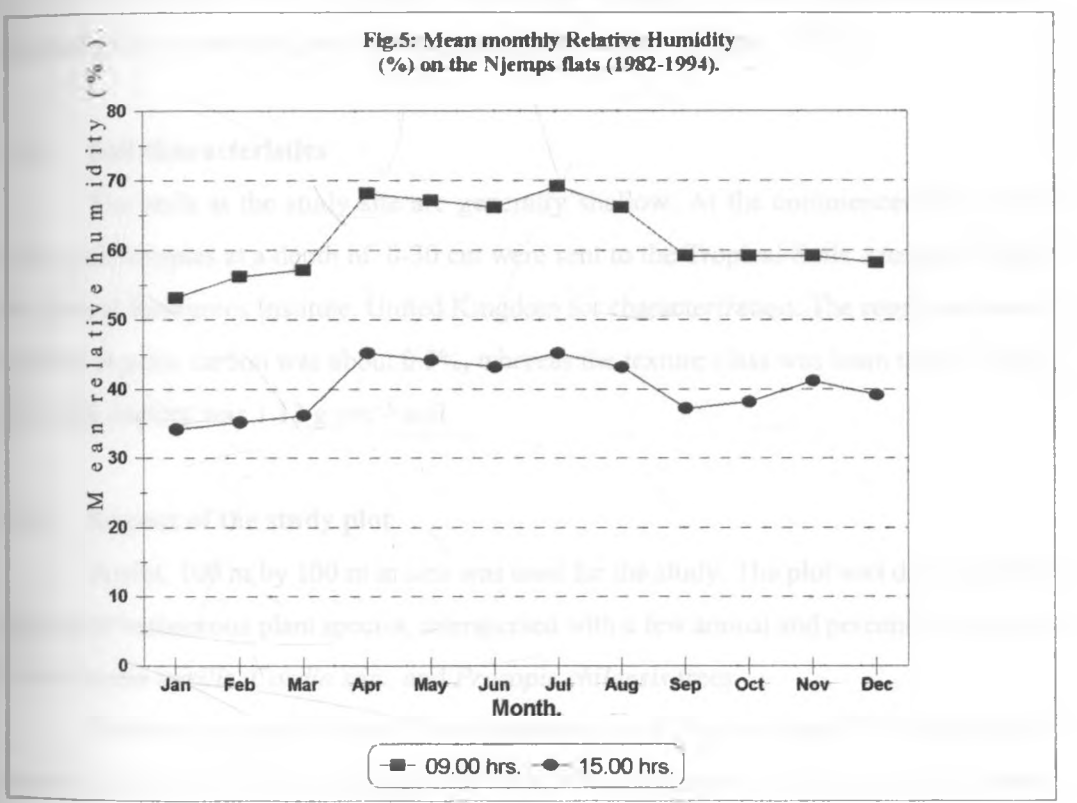
There is only slight variation in the monthly maximum temperatures. These fluctuate between 30°C and 35°C. Temperatures are highest during the months of January to March, which precede the long rains season. Thereafter, temperatures drop to about 31°C in July, which is the coolest month, and gradually rise to 33°C in September/October just before the short rains season. Cloudy skies and the position of the sun (overhead) during these times cause the high temperatures.

Minimum temperatures are experienced in the early hours of the morning, around 02.30 - 04.00 hours. Figure 4 shows that months with the lowest minimum temperatures tended to coincide with months with highest maximum temperatures. This is a phenomenon commonly experienced in arid ecosystems where hottest days are accompanied by coolest

nights. The narrowest range between maximum and minimum temperature coincided with the three rainfall peaks. April had a temperature difference of 14.2°C while November had 14.3°C. The July out of season peak had a 14.6°C temperature difference. The rainfall peaks had the effect of lowering the daily maximum temperature and raising the daily minimum temperature thereby reducing the temperature difference between day and night.

3.0.2.4 Relative humidity

Figure 5 shows the mean monthly percent relative humidity (%R.H.) on the Njemps flats at 09.00 hours and 15.00 hours. The R.H. at 09.00 hours was higher than that at 15.00 hours. At 09.00 hours, R.H. ranged from 52% to 70%, whereas at 15.00 hours the range was from 33% to 45%.



Higher %R.H. is experienced in the morning because this is the time when surfaces, especially of soil and plants, have more moisture to lose, resulting from cooling and at times condensation of air at night due to low ambient temperatures. It is not uncommon to

encounter dew in the early morning. This night condensation raises the %R.H. in the morning when the hot sun rises, thereby causing moisture evaporation. At 15.00 hours, the surfaces have lost most of the moisture into the system, which then dilutes it with dry air brought by winds. The %R.H., therefore, drops by the late afternoon.

Three %R.H. peaks can be identified from the graphs. These occur in April (65% at 09.00 hours and 45% at 15.00 hours), July (71% at 09.00 hours and 45% at 15.00 hours) and November (60% at 09.00 hours and 41% at 15.00 hours). These were the same months that experienced the three rainfall peaks (Fig.2). During this time, more moisture was received in the system, and therefore, it was able to lose higher quantities of moisture due to constantly high temperatures. This gave rise to the observed peaks in %R.H.

Low %R.H. at 15.00 hours, when the sun is hottest, causes a high rate of moisture loss from the system. This, coupled with the low rainfall, causes moisture deficiency, characteristic of semi-arid and arid rangelands (Pratt and Gwynne, 1977).

3.0.3 Soil characteristics

The soils at the study site are generally shallow. At the commencement of this study, soil samples at a depth of 0-30 cm were sent to the Tropical Soils Analysis Unit at the Natural Resources Institute, United Kingdom for characterization. The results indicated that soil organic carbon was about 0.5%, whereas the texture class was loam to silty loam. Soil bulk density was 1.13 g cm^{-3} soil.

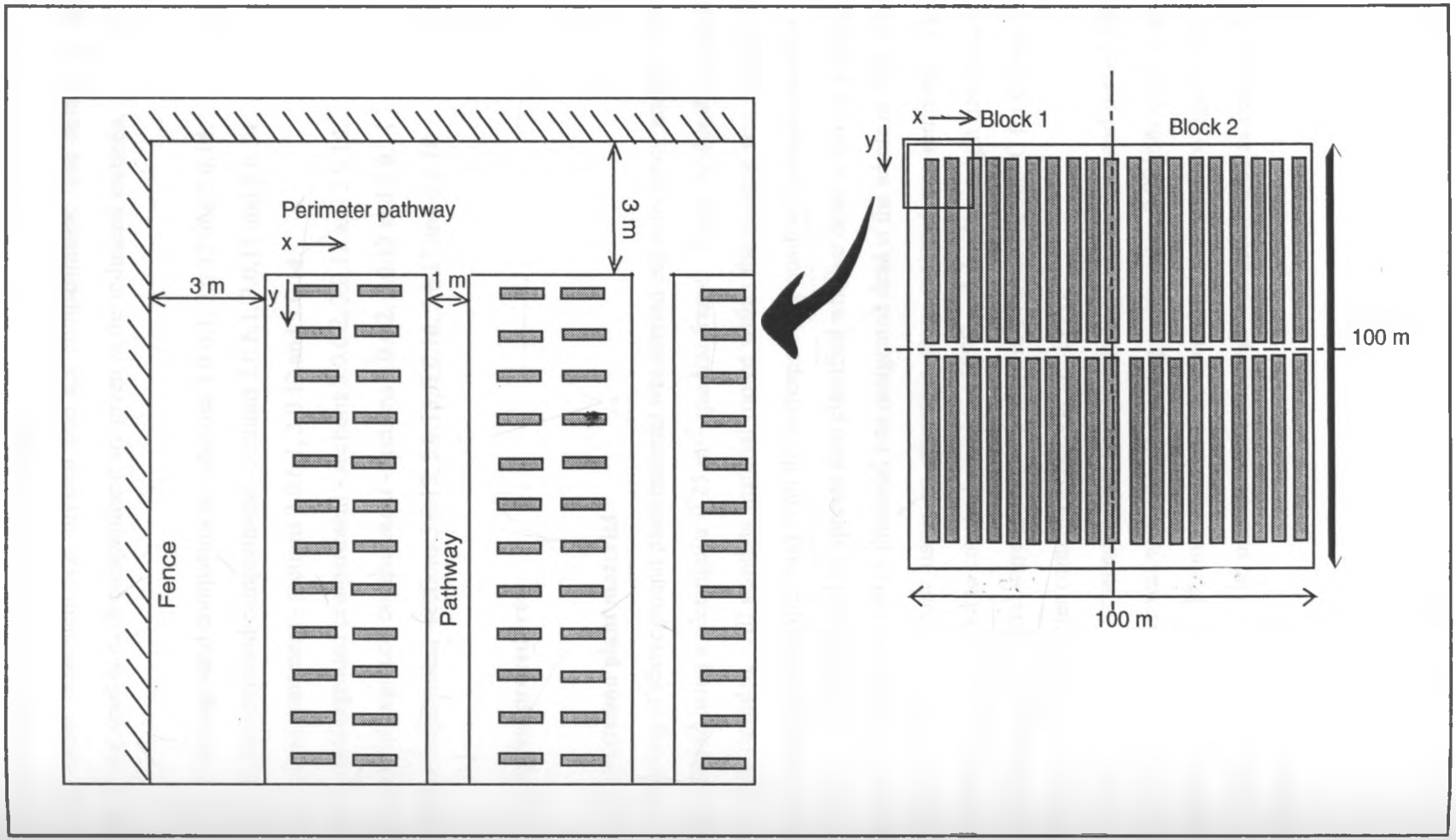
3.0.4 Layout of the study plot

A plot, 100 m by 100 m in size was used for the study. The plot was dominated by ephemeral herbaceous plant species, interspersed with a few annual and perennial herbs and a few *Acacia tortilis, Cordia spp.,* and *Prosopis chilensis* trees.

Twenty-two equally spaced belt transects, each 3 m wide and 90 m long were marked out in the plot using a design from UNEP bio-productivity studies (Fig. 6) (Roberts *et al.*, 1993). These were separated by 1-m pathways, which also enabled access to selected quadrat locations without interference with other quadrats. Within each belt transect there were two columns of potential quadrat locations, half a metre apart. A 25 cm buffer zone was left on either side of the belt transect. All the potential quadrat locations were assigned numbers and a table of random numbers was used to select thirty quadrats for monthly

sampling. To ensure well distributed sampling throughout the study plot, the area was divided into two parts, such that fifteen of the sampled quadrats came from each of the two parts. At each sampling location, a rectangular quadrat, 0.25 m^2 in size was used for sampling.

Fig.6: Design of the study plot showing transects and potential quadrat locations.



3.0.5 Compartmentization of the ecosystem

The study ecosystem was divided into six compartments. The details of the parameters measured in each compartment are given in the indicated sections;

1. Live aboveground compartment - sections 3.0.6.1, 3.0.12 and 3.0.14.
2. Dead aboveground compartment - sections 3.0.6.1, 3.0.12 and 3.0.14.
3. Litter compartment - sections 3.0.6.1, 3.0.12 and 3.0.14.
4. Live belowground compartment - sections 3.0.6.2, 3.0.12 and 3.0.14.
5. Dead belowground compartment - sections 3.0.6.2, 3.0.12 and 3.0.14.
6. Soil compartment -sections 3.0.12, 3.0.13, 3.0.16, 3.0.17 and 3.0.18.

3.0.6 Sampling procedures

3.0.6.1 Aboveground plant material

Sampling of aboveground plant material was carried out at monthly intervals, for a two-year period using a rectangular 0.25 m^{-2} quadrat frame. Thirty randomly selected quadrats were sampled. All standing material rooted within the quadrat was clipped at ground level and put into paper bags with the corresponding quadrat reference numbers. The material was then separated by species then classified whether dead or live by physical examination (Roberts *et al.*, 1993). Material was designated dead if the whole of their area had become necrotic. Necrotic tissue on otherwise green material was removed. The material was then oven-dried to constant weight at 80^{o}C and the dry weight determined. Samples from the dry material were ground and ashed in a furnace at 500^{o}C for 6 hours to determine their organic matter content (Roberts *et al.*, 1993).

Litter, i.e. all shed herbaceous plant parts within the quadrat was hand-picked and bagged separately. The litter was washed with running water over a 2.00 mm sieve to get rid of attached soil particles. The material was then oven-dried to constant weight at 80^{o}C and dry weight determined. The organic matter content was determined as outlined for aboveground biomass.

3.0.6.2 Belowground plant material

Belowground plant material was sampled monthly by using a 5-cm diameter soil corer, to a depth of 30 cm. Soil samples were taken from the centre of plots clipped for aboveground sampling. The samples were then washed over a 1mm sieve to get rid of the soil while retaining roots. Live roots were separated from dead roots by means of the vital staining technique using 2, 3, 5-triphenyl tetrazolium chloride. The salt acts as a terminal electron acceptor during respiration and is reduced to its coloured form (pink) by living tissue (Roberts *et al.*, 1993). The roots were immersed in a 0.01M solution for three days in the dark. Roots having a pink colour were assumed live, whereas unstained roots were assumed dead. These were dried to constant weight at 80°C and their dry weight determined. Samples of these were ashed to determine the organic matter content. All recorded weight values were multiplied by a factor of 509.6 to give the weight of roots per square metre.

3.0.7 Net Primary Production (NPP) and productivity

NPP was calculated using the following equations (Roberts *et al.*, 1993):

$$NPP = \triangle B + dl + dg + de$$

where:

NPP = Net primary production (g m^{-2})

$\triangle B$ = Change in live biomass (g m^{-2})

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

dg = Losses due to grazing (g m^{-2})

de = Losses due to root exudation (g m^{-2})

Losses due to root exudation (de) were not estimated. Losses resulting from death, decomposition and shedding (dl) were estimated using the formula:

$$dl = \triangle D + r.t.\ \bar{D}$$

where:

ΔD = Change in dead plant material (g m^{-2})

t = Length of time interval (days)

r = Relative rate of decomposition of dead material (g g^{-1} day^{-1})

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

Only positive values of ΔB and ΔD were used. Negative values were ignored in the summation process (Milner and Hughes, 1968; Deshmukh, 1986).

Since the study site was free from grazing herbivores throughout the study period, it was assumed that losses due to grazing (dg) was zero.

3.0.8 Decomposition of dead plant Material

The rate of decomposition/disappearance of dead plant materials in the field was determined using the litterbag technique as described by Wiegert and Evans (1964) and Roberts *et al.*, (1993). Sub-samples of dead aboveground and belowground material were obtained during the monthly harvest period. Two grams dry weight of each category of plant material (dead aboveground grass and dicots and dead belowground) was placed in nylon litter bags of 2 mm mesh. The bags containing aboveground material were placed on the soil surface under the canopy while bags with belowground material were buried 5 cm below the soil surface in the field. The bags were placed in the field during each monthly harvest and retrieved during the subsequent harvest with an interval of one month. Any loss in weight was assumed resulting from decomposition (Roberts *et al.*, 1993).

The residual material was washed, oven-dried to constant weight at 80°C and the dry weight determined. Subsamples of the material were ashed to determine the organic matter content. The change in weight was calculated so that the relative rate of decomposition, r, was obtained using the formula below (Roberts *et al.*, 1993):

$$r = \frac{\ln(D_i/D_i + 1)}{((t_i + 1) - t_i)}$$

where:

r = Instantaneous rate of disappearance of dead plant material (g g^{-1} day^{-1})

D_i = mean dry weight of dead material at time t_i

D_{i+1} = mean dry weight of dead material at time t_{i+1}

$t_{i+1} - t_i$ = harvest interval (days)

Due to the long distance between the litter bag preparation site (Botany Department) and the study site, correction factors were calculated on a monthly basis to compensate for loss of plant material from litter bags due to rigours of travelling to and from the study site.

3.0.9 Turnover rate and time

The equations from Dahlman and Kucera (1965) were used to calculate the turnover rates and time.

(i) Turnover Rate (K)

$K = L/X$

where:

K = Turnover rate (% $year^{-1}$)

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

X = Maximum biomass (g m^{-2})

(ii) Turnover Time (T)

T = 1/K x Length of time interval (months)

where:

T = Turnover time (years)

K = Turnover rate

The mean annual increments of plant materials were calculated by summing up all non-negative increments during the sampling time interval and expressed on annual basis.

3.0.10 Equilibrium time

The following formula (Dahlman and Kucera, 1965) was used to estimate Equilibrium Time, that is the time required for 99% equilibrium in a particular

compartment, under the prevailing conditions of growth and decomposition;

$$t\ (\text{years}) = \frac{-\ln \frac{(100-99)}{100}}{k_i}$$

where; k_i = Decomposition rate for compartment *i*.

3.0.11 Species diversity

Species diversity was calculated using Simpson's Index (Simpson, 1949);

$$D_S = 1 - \frac{\Sigma n_i\,(n_i-1)}{N(N-1)} = 1 - \frac{\Sigma n_i^2 - N}{N(N-1)}$$

where; D_S = Simpson's Index of Diversity.

n_i = Importance value of the *ith* species (in this case biomass was used as a measure importance).

N = Total of importance values for all species.

3.0.12 Nitrogen content determination

The nitrogen content of live and dead aboveground, litter, live and dead belowground compartments was determined using the micro-Kjeldahl method (A.O.A.C., 1985). Soil nitrogen was categorised into three fractions:

(i). total nitrogen,
(ii). nitrate nitrogen, and
(iii). ammonium nitrogen

Total nitrogen in soil was determined in accordance with the Kjeldahl method described by Bremner and Mulvaney (1982). Soil samples were air dried then passed through a 2 mm sieve. One gram of the sieved soil was put into a 250-ml digestion flask and 3.5 mls of phenol-sulphuric acid added. Fifteen minutes later, 0.5g sodium thiosulphate was added. After a further fifteen minutes, 0.5g selenium mixture, 0.5g K_2SO_4 and 3.5ml

of concentrated sulphuric acid were added. The mixture was then digested at low temperature (60°C) until clear. The mixture was then allowed to cool after which about 20ml of distilled water was added to prevent solidification of the digest. The digest was transferred into a distillation flask and 40ml of 1.0N sodium hydroxide added. The NH_3 released during the distillation was collected in 20 ml of 1% boric acid with mixed indicator. Titration was done using 0.01N sulphuric acid.

1ml 0.0IN H_2SO_4 = 140 µgN

Nitrate and ammonium nitrogen (plant available nitrogen) was determined following the procedure described by Keeney and Nelson (1982). Ten grams of wet soil was weighed in wide mouthed plastic bottles and 100mls of 2N Potassium chloride added for extraction. The contents were shaken for one hour using a shaker and filtered using Whatman filter paper No. 42. The filtrate was then transferred into a distillation flask, some MgO powder added and distilled. The NH_3 gas released was trapped in 20 ml of 1% boric acid. Upto 150ml of distillate was collected, and stored awaiting titration. This process determined the ammonium nitrogen available in soil.

To determine the nitrate nitrogen content, Devarda's alloy was added to the mixture above and distillation continued to collect another 150ml of distillate. The NH_3 released was collected in a new 20ml of 1% boric acid. Titration was done using 0.01N sulphuric acid.

3.0.13 Mineralizable soil nitrogen

Mineralizable soil nitrogen was determined by the incubation method (Bremner, 1965; Moore and Chapman, 1986). Soil samples were obtained from the top 30cm soil depth and put into polythene bags to avoid moisture loss. These were then thoroughly mixed and passed through a 4.0-mm sieve to eliminate plant litter, roots and pebbles. The soils were then sealed in clear polyethylene bags of 0.02 mm thickness, and incubated in an incubator at 30oC in the laboratory for a period of twelve weeks. The two sets of soil, consisting of twenty-eight bags each for the dry and wet season were replicated four times. The number of bags allowed sampling for analysis without replacement for seven sampling periods.

At an interval of two weeks, starting from week zero (24 hours after onset of

incubation), four replicates of set of incubated soils were removed from the incubator and analysed for exchangeable ammonium and nitrate nitrogen. Whenever analysis could not be carried out immediately, the samples were frozen. The samples were then analysed for ammonium and nitrate nitrogen.

3.0.14 Energy content determination

The gross energy content of all plant materials was determined by bomb calorimetry (A.O.A.C., 1985), for the following ecosystem compartments:

(i). Aboveground (live),
(ii). Aboveground (dead),
(iii). Litter,
(iv). Belowground (live), and
(v). Belowground (dead).

One gram of finely ground sample material was ignited and burned in oxygen under pressure. The gross energy content was calculated as follows (Roberts *et al.*, 1993);

$$V = \frac{W\Delta T - \Sigma C}{G}$$

where:

V = Gross energy content of sample material (J g m^{-1})
W = Water value of the apparatus (J)
ΔT = Rise in temperature of the apparatus (^{o}C)
ΣC = Sum of additional corrections
G = Dry weight of sample (g m)

The water value of the apparatus (W), is the number of joules required to raise the temperature of the water bath by $1^{o}C$. This was determined by burning a small sample of Benzoic acid in the bomb and the increase in water bath temperature measured. W was then calculated as follows (Roberts *et al.*, 1993).

$$W = \frac{VG + \Sigma C}{\Delta T}$$

where:

W = water value of apparatus (J)

V = gross energy content of benzoic acid (J)

G = dry weight of Benzoic acid (g)

ΣC = sum of additional corrections

ΔT = rise in temperature of water bath (^{o}C)

The additional corrections arise from the following:

(i) Electrical ignition: This causes an input of energy which will be measured by blank runs of the calorimeter and an appropriate subtraction/ addition made to the energy content.

(ii) Acid formation: The nitrogen and sulphur produced during combustion are oxidized to form nitric and sulphuric acids. Leith (1968) states that the correction due to acid formation is about 0.1% or less. This value will be used for correction.

3.0.15 System transfer functions

The rates of transfer of energy and nitrogen between ecosystem compartments were defined by system transfer functions. The system transfer function of a particular process is the quantity by which a system block or compartment multiplies the input to generate the output (Golley, 1965). In other words, it is the ratio of the total output of material from the relevant compartment to the total inputs of the same material to the same compartment at a specified time (Sims and Singh, 1978b). The functions express ecosystem functioning, and provide insight into the dynamics of various primary producer compartments. The input, output and their relationship are affected by the abiotic as well as biotic variables. Therefore system transfer functions integrate the effects of abiotic and biotic variables and serve as indices of ecosystem functioning.

A system transfer value of 1 indicates dynamic equilibrium in ecosystem functioning, i.e. the rate at which material enters a compartment equals the rate of exit.

Values in excess of or less than 1 indicate an imbalance in ecosystem functioning, i.e. there is accumulation or depletion of material in some compartments.(Sims and Singh, 1978b).

3.0.16 Soil moisture content

Soil moisture content (gravimetric) was determined at three depths in the field (0 - 10, 10 - 20 and 20 - 30cm). Fresh soil samples were obtained at each quadrat location and placed in air tight plastic bags. Their moisture content was determined by taking a 10g-soil sub-sample and oven-drying to constant weight at 80°C. The loss in weight on drying was the weight of water originally present in the soil. This was expressed as a percentage of the dry weight of the soil, i.e.

$$\% \text{ moisture} = \frac{W_a}{W_b} \times 100$$

where:

W_a = Weight of soil water (g)

W_b = Weight of dry soil (g)

This was carried out on a monthly basis during sampling of plant material.

3.0.17 Soil organic matter content

Soil organic matter at the three soil depths as outlined for soil moisture, was determined by ashing soil sub-samples obtained from the samples used in soil moisture determination at 500°C for six hours. The loss in weight (loss-on-ignition) was assumed to be the organic matter and was expressed as a percentage of the soil dry weight, i.e.

$$\% \text{ organic matter} = \frac{W_L}{D_S} \times 100$$

where:

W_L = Weight loss after ashing (g)

D_S = Weight of dry soil (g)

3.0.18 Soil pH

Soil pH (water) was determined using a pH meter by the procedure of McLean (1982). Ten grams of soil was weighed and transferred into a wide mouthed plastic bottle, then 25 ml of distilled water added. The mixture was then shaken vigorously for 30 minutes using a shaker. The pH reading was then taken after the sample had settled for another 30 minutes. Prior to taking readings, the pH meter was calibrated using buffer solutions.

3.0.19 Climatic data collection

A rain gauge and minimum - maximum thermometer was installed within the study field. Daily values of rainfall, minimum and maximum temperatures were collected throughout the study period. Data on evaporation rates and relative humidity was supplied by the meteorological office at Marigat.

3.0.20 Statistical analysis of data

The data collected was subjected to appropriate standard statistical tests described by Steel and Torrie (1981). Data was tested whether normally distributed then subjected to analysis of variance (ANOVA). Means were separated Duncan's Multiple Range Test. Differences between any two sample means were tested using student's *t*-test.

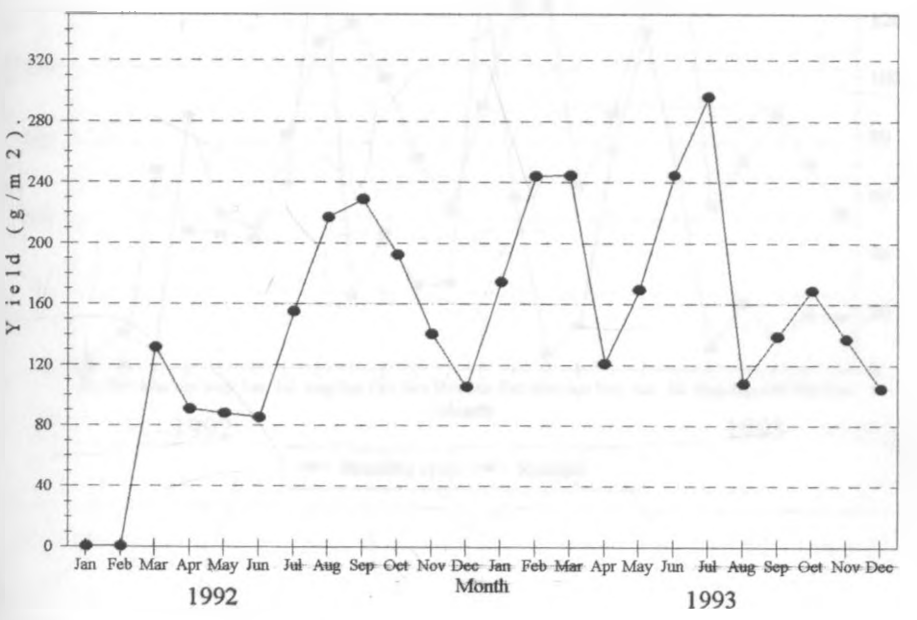
4.0 RESULTS AND DISCUSSION

4.0.1 Net primary production

4.0.1.1 Aboveground standing crop

The trend in aboveground standing crop during the study period is shown in Fig. 7.

Fig. 7: Aboveground plant material yield during 1992 and 1993.

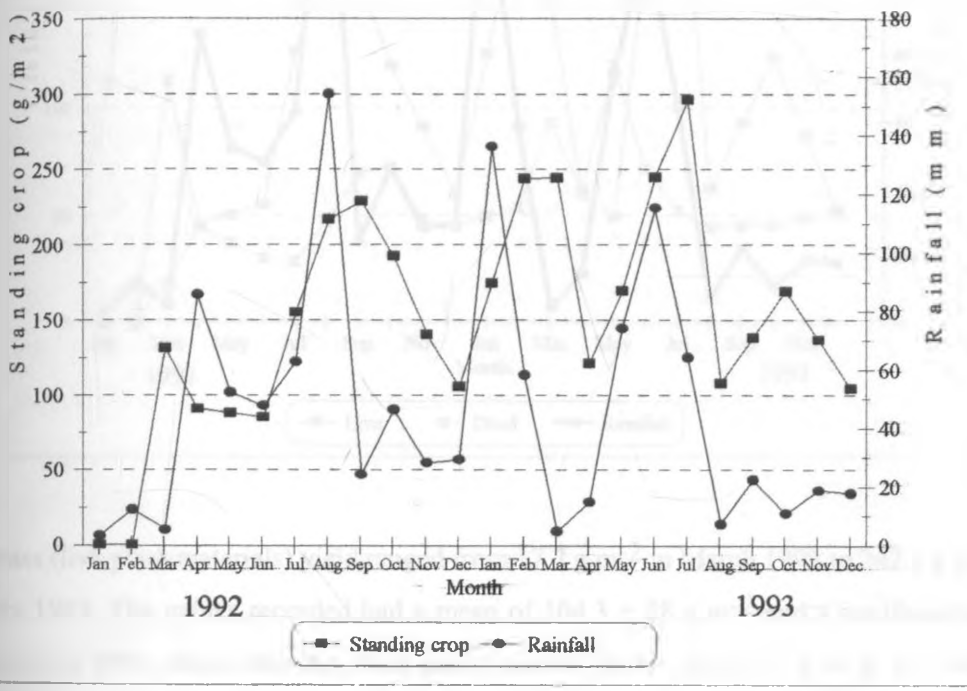


Aboveground standing crop yield showed high variability, ranging from 84.6 g m^{-2} in June 1992, to 295.4 g m^{-2} in July 1993. The values recorded had a mean of 162.3 $\pm$ 60.6 g m^{-2}. Mean monthly aboveground standing crop was 142.8 $\pm$ 53.8 and 178.5 $\pm$ 63.3 g m^{-2} for 1992 and 1993 respectively. The 1993 mean monthly aboveground standing crop was significantly higher ($P<0.05$) than that for 1992. These ranges of figures of total standing crop lie within those reported from other Kenyan range ecosystems. These include those reported by Macharia (1981), Kinyamario and Macharia (1992) and Kinyamario and Imbamba (1992), from the Nairobi National Park ecosystem and Coughenour *et al.* (1990)

from Turkana ecosystem. Other studies with similar results, carried out within African drylands include those by Strugnell and Pigott (1978) and Ohiagu and Wood (1979).

The trend in aboveground standing crop closely followed that of monthly rainfall (Fig.8).

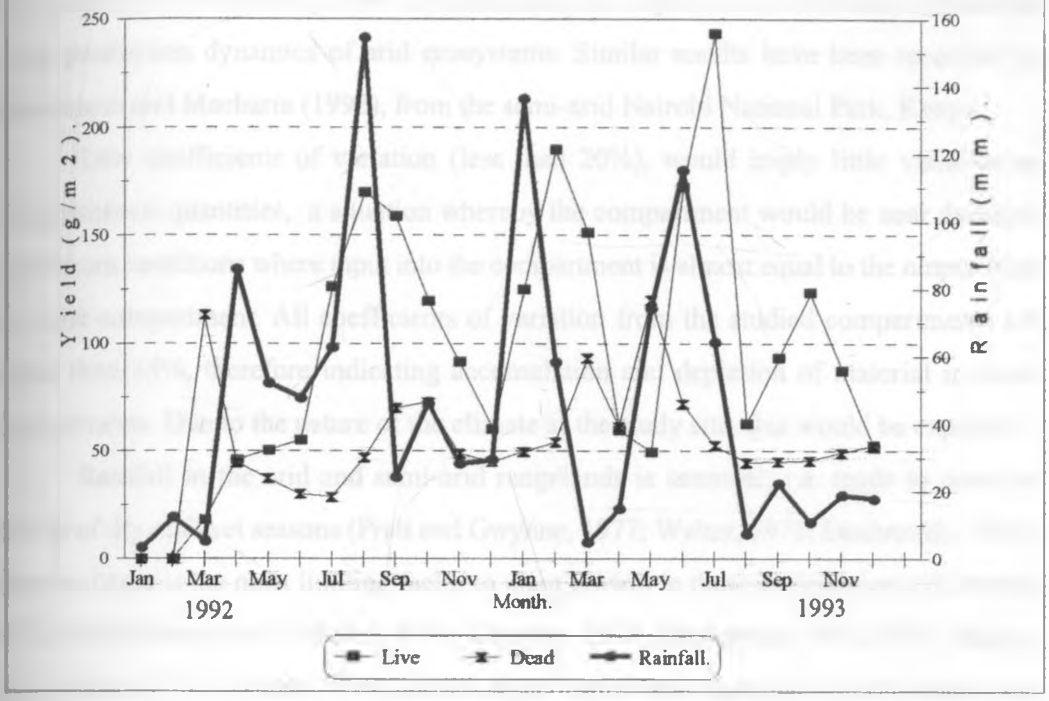
Fig.8: Trends in standing crop and rainfall in 1992 and 1993.



There were three conspicuous rainfall peaks (Fig. 8). These were recorded in August 1992 (154mm), January 1993 (136mm) and June 1993 (115mm). There were also three major conspicuous standing crop peaks. These were recorded in September 1992 (228.2 g m^{-2}), March 1993 (243.7 g m^{-2}) and July 1993 (295.4 g m^{-2}). Each of these biomass peaks was recorded just after a rainfall peak. Similar trends were observed by Cassady (1973), Strugnell and Pigott (1978), McNaughton (1979) and Kinyamario and Macharia (1992) in East African dry grasslands.

Figure 9 below shows the trend for above ground live and dead plant materials.

Fig.9: Trends in live and dead above-ground material yields and rainfall.



Biomass (live plant materials) yield ranged from 17.7 g m^{-2} in March 1992 to 242.7 g m^{-2} in July 1993. The values recorded had a mean of 104.3 $\pm$ 58 g m^{-2} and a coefficient of variation of 58%. Mean standing dead plant material yield was 59.7 $\pm$ 24 g m^{-2} with monthly values ranging from 28.8 g m^{-2} (July 1992) to 120 g m^{-2} (May 1993). The values had a coefficient of variation of 38%.

The total biomass yield during the study period was significantly higher than total standing dead plant material yields ($P<0.01$). Biomass yield was higher than standing dead plant material yield for both 1992 and 1993 ($P<0.05$ and $P<0.01$ respectively). Higher ($P<0.01$) live shoot biomass was recorded in 1993, during which higher rainfall amount was recorded. However, there was no significant difference ($P>0.05$) between dead shoot biomass yield for 1992 and 1993.

Three very distinct aboveground biomass peaks were observed. These occurred in August 1992, February 1993 and July 1993. Similar peaks were observed for aboveground dead plant material, but these came immediately after the aboveground biomass peaks. The live above ground plant material compartment serves as input for the dead aboveground

plant material compartment, thus the lag in dead aboveground plant material peak.

All the aboveground biomass peaks were preceded by rainfall peaks, i.e. in July 1992, January 1993 and May 1993. This indicates the importance of moisture availability to the production dynamics of arid ecosystems. Similar results have been recorded by Kinyamario and Macharia (1992), from the semi-arid Nairobi National Park, Kenya.

Low coefficients of variation (less than 20%), would imply little variation in compartmental quantities, a situation whereby the compartment would be near dynamic equilibrium conditions where input into the compartment is almost equal to the output from the same compartment. All coefficients of variation from the studied compartments are higher than 35%, therefore indicating accumulation and depletion of material in some compartments. Due to the nature of the climate at the study site, this would be expected.

Rainfall in the arid and semi-arid rangelands is seasonal, i.e. tends to occur in periods of dry and wet seasons (Pratt and Gwynne, 1977; Walter, 1971; Deshmukh, 1986). Since moisture is the most limiting factor to plant growth in these environments (Cassady, 1973; Karunaichany and Paliwal, 1993; Charley, 1977; Deshmukh, 1985,1986; Skarpe, 1992, Walter, 1971, Scholes, 1990), it implies that herbaceous plant growth will mainly take place during those times when effective moisture is available to the soil system. This phenomenon is depicted by the large variability in biomass yield and three very distinct peaks of biomass yield, which lagged just behind the rainfall peaks. Similar results have been reported by Cassady (1973), Coughenour *et al.* (1990), Deshmukh, (1986), Kinyamario and Imbamba (1992).

Due to the erratic nature of rangeland rainfall within the wet season or even out of season (Pratt and Gwynne, 1977; Glover and Robinson, 1953; Kenworthy and Glover, 1958), seedling emergence and / or biomass sprouting and subsequent survival is strongly affected by the timing and variation in rainfall. In the current study, this phenomenon is illustrated by the occurrence of peaks of biomass yield, preceded by rainfall peaks (Fig.9). Veenendaal (1991) reported that successful germination in dry rangeland ecosystems with a variable rainfall has to be safeguarded by one or more rainfall events of 'sufficient' quantity. Such a minimum amount may hold for a large number of species in one ecosystem or only for specific species in specific sites.

In the Mojave Desert, Tevis (1958) and Beatley (1974) reported that a minimum amount of precipitation of 25mm at the onset of the rainfall season was necessary to trigger

widespread germination. In the northern Australian tropical habitats, repeated rainfall events in excess of 15mm have been reported to trigger germination in an number of grasses (Mott, 1978; Andrew and Mott, 1983; McKeon *et al.*, 1985). In south-eastern Botswana, Ernst and Tolsma (1988) found that 10mm of rainfall stimulated the germination of the annual grass *Tragus berteronianus.*

In all the above reported studies, once sufficient rainfall was received, germination of herbaceous vegetation occurred rapidly, enabling the seedlings to escape surface drying and competitiveness in dense stands. However, a single large rainfall event, especially if early in the season, followed by a long dry spell caused a high mortality among seedlings (McKeon *et al.*, 1985; Kadman and Schmida, 1990). Veenendaal (1991) advanced the argument that plant species favour to spread the risks of germination over more than one rainfall event at the beginning of the season. Indeed, many studies have reported that in dry rangeland ecosystems, germination is usually spread over several rainfall events (Mott, 1978; Lodge, 1981; Andrew and Mott, 1983; Ernst and Tolsma, 1988).

Angevine and Chabot (1979) proposed that a drought avoidance dormancy syndrome, a high innate dormancy and a gradual decrease of dormancy of seeds ensure germination of plant seeds in arid ecosystems. This syndrome results in a situation whereby during the rainfall season, several rainfall events create germination / establishment opportunities. At each opportunity, that part of the seed bank, which by the time has lost its dormancy, will then germinate. This dormancy pattern ensures that even when the rainy season starts early, a large fraction of seeds remains available for germination. Another factor may be the presence of different age cohorts of seeds in the soil, releasing dormancy at different times (Andrew and Mott, 1983; Ernst and Tolsma, 1988; Veenendaal, 1991). Veenendaal (1991) observed spacing of germination waves in the arid rangelands of Botswana, a mechanism he attributed to the differential breakage of dormancy and seed age cohorts.

The month by month trend in biomass yield closely followed the rainfall trend. The same was observed for the change in dead plant material yield (Fig.9). Peaks in the yield of both live and dead plant material generally followed rainfall peaks. This is due to the effect of rainfall on herbaceous vegetation. Growth and/or regrowth of herbaceous vegetation in arid rangelands depend on the availability of moisture (Deshmukh, 1986; Veenendaal, 1991). Rainfall events therefore stimulate rapid growth of herbaceous vegetation, thereby

increasing the live biomass yield. Overall, the mean aboveground biomass yield was higher than the aboveground dead plant material yield ($P<0.01$). This is attributable to two factors;

(i). the rapid response of herbaceous biomass growth to rainfall events, and
(ii).the rapid disappearance of dead herbaceous biomass due to high rates of decomposition, shedding, and pulverization / abrasion by wind.

During the study period, rainfall was highly localised, tending to occur in patches even over small areas. This caused patchiness in biomass yield over the range space. Similar observations have been reported from African rangelands by Breman and Cisse (1977), Deshmukh (1986), Coughenour *et al.* (1990) and Veenendaal (1991). Further, the rainfall that was received was made less effective for biomass production due to the constantly high daytime temperatures and low relative humidity, giving rise to high rates of moisture loss from soil and plant surfaces. Due to these abiotic characteristics of the rangeland environment working in concert, the total annual primary production consisted of a summation of a limited number of growth events randomly distributed in time and space.

4.0.1.2 Belowground standing crop

Figure 10 below shows the course for monthly total below ground plant material yield. The yield ranged from 83.3 g m^{-2} in October 1992 to 232.7 g m^{-2} in June 1993. The values recorded had a mean of 155.2±46 g m^{-2} with a 30% coefficient of variation. These values closely agree with those of Kinyamario and Imbamba (1992). There were three prominent peaks in belowground biomass yield. These occurred in July 1992 (166.6 g m^{-2}), December 1992 (213.3 g m^{-2}) and in June 1993 (232.7 g m^{-2}). These peaks closely coincided with peaks in total shoot biomass yield, and were preceded by rainfall peaks. The mean total monthly belowground plant material yield for 1992 was 137.6±41 g m^{-2} with a coefficient of variation of 59%. The year 1993 had a mean total monthly belowground plant material yield of 169.9±46 g m^{-2}, having a coefficient of variation of 28%. Belowground biomass yield ranged from 17.6 g m^{-2} in October 1992 to 142.2 g m^{-2} in July 1993 (Fig. 11).

Fig.10: Trend in belowground plant material yield during 1992 and 1993.

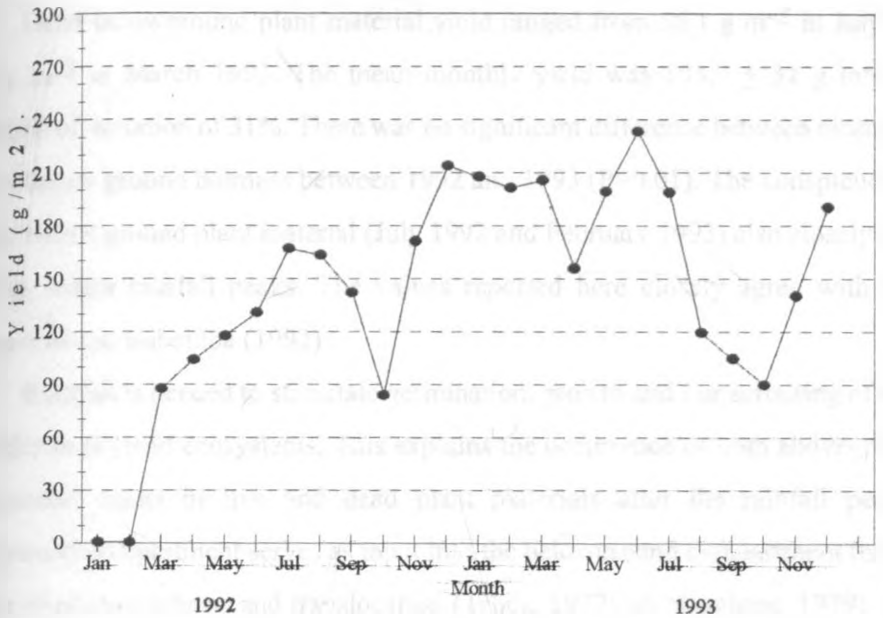
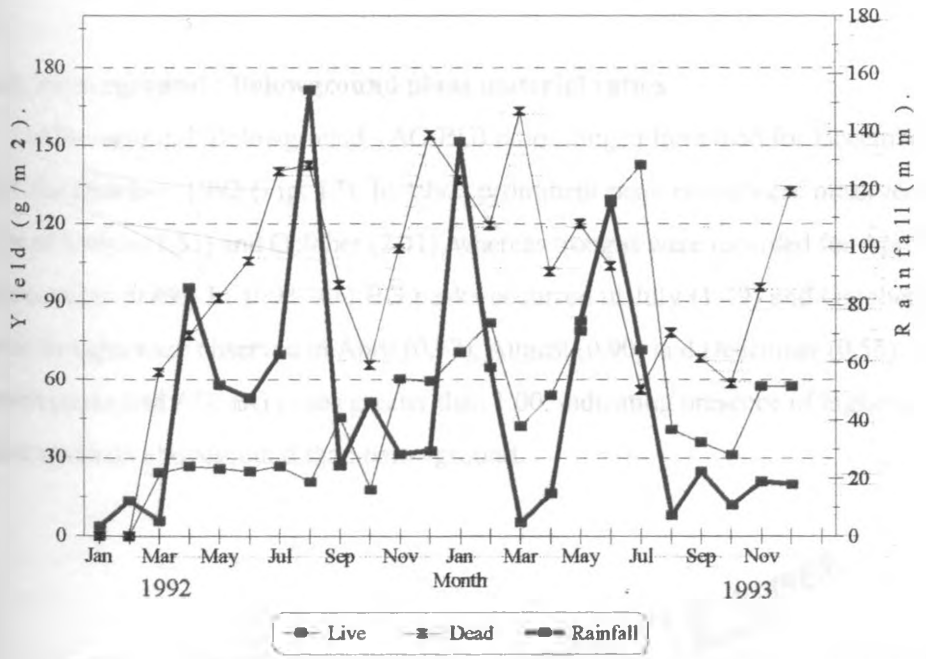


Fig.11: Live and dead plant material yield and rainfall in 1992 and 1993.



The mean monthly yield was 51.6 ± 33 g m^{-2} with a coefficient of variation of 64%. Peaks were recorded in February and July of 1993. Rainfall peaks preceded both peaks. Higher belowground biomass production was recorded for 1993 compared to 1992 ($P<0.05$).

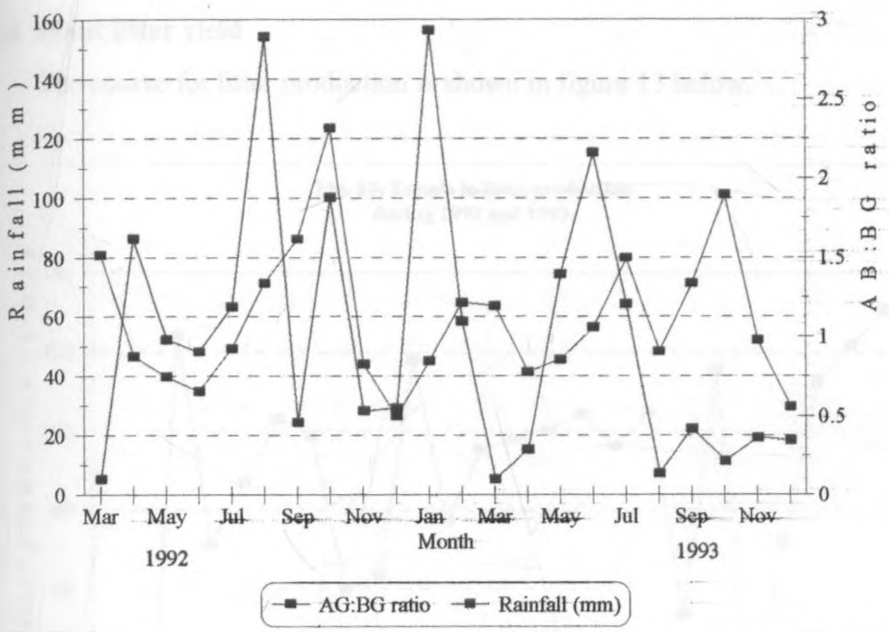
Dead belowground plant material yield ranged from 56.1 g m^{-2} in July 1993 to 163.3 g m^{-2} in March 1993. The mean monthly yield was 103.7 ± 32 g m^{-2}, with a coefficient of variation of 31%. There was no significant difference between mean monthly yield of below ground biomass between 1992 and 1993 ($P>0.01$). The conspicuous peaks in dead below ground plant material (July 1992 and February 1993) also closely followed the three major rainfall peaks. The values reported here closely agree with those of Kinyamario and Imbamba (1992).

Rainfall is needed to stimulate germination, growth and / or sprouting of biomass, especially in dryland ecosystems. This explains the occurrence of both aboveground and belowground peaks in live and dead plant materials after the rainfall peaks. The aboveground compartment serves as input into the belowground compartment through the process of photosynthesis and translocation (Trlica, 1977; McNaughton, 1979). Peaks in aboveground biomass therefore usually precede belowground biomass peaks. For perennial grasses, these materials translocated to and stored in belowground parts are later used to sustain plant tissues during conditions unfavourable for growth, and to initiate sprouting of shoots when conditions become favourable. In dryland ecosystems, conditions become favourable for growth when rainfall is received.

4.0.1.3 Aboveground : Belowground plant material ratios

Aboveground: Belowground (AG:BG) ratios ranged from 0.55 for December,1993 to 2.31 for October, 1992 (Fig. 12). In 1992, prominent peak ratios were observed in the months of March (1.51) and October (2.31), whereas troughs were recorded for April (0.87) and December (0.49). In 1993, AG:BG peaks occurred in July (1.49) and October (1.89) whereas troughs were observed in April (0.77), August (0.90) and December (0.55). All the observed peaks had AG: BG ratios greater than 1.00, indicating presence of higher quantity of plant material aboveground than belowground.

Fig. 12: Aboveground:belowground plant material ratios and rainfall



Except for the October,1993 AG:BG ratio peak, all the other peaks either coincided with or came immediately after a rainfall peak. This is due to plant growth taking place after the rain, thereby shoot material exceeding the belowground material. Part of the belowground material, especially the non-structural carbohydrates was used up during the initial stages of plant growth.

The troughs in AG:BG ratios coincided with or occurred immediately after those months, which had the least rainfall. All values were less than 1.00. This observation is expected in the grass-dominated dryland ecosystems during the dry season when there is translocation of non-structural carbohydrates to underground parts (Trlica, 1977) and the weathering of dead dry aboveground plant material due to physical forces like wind action (Pratt and Gwynne, 1977).

The October 1993 AG:BG ratio peak (1.89) coincided with a low rainfall amount, about 15 mm. During this month, all the rainfall was received over a period of two consecutive days. Therefore, although the amount was little, moisture was injected into the

soil system over a short interval of time, and therefore was more effective in stimulating the growth of ephemeral and annual plant species, hence the observed AG:BG ratio greater than 1.50.

4.0.1.4 Plant litter yield

The course for litter production is shown in figure 13 below.

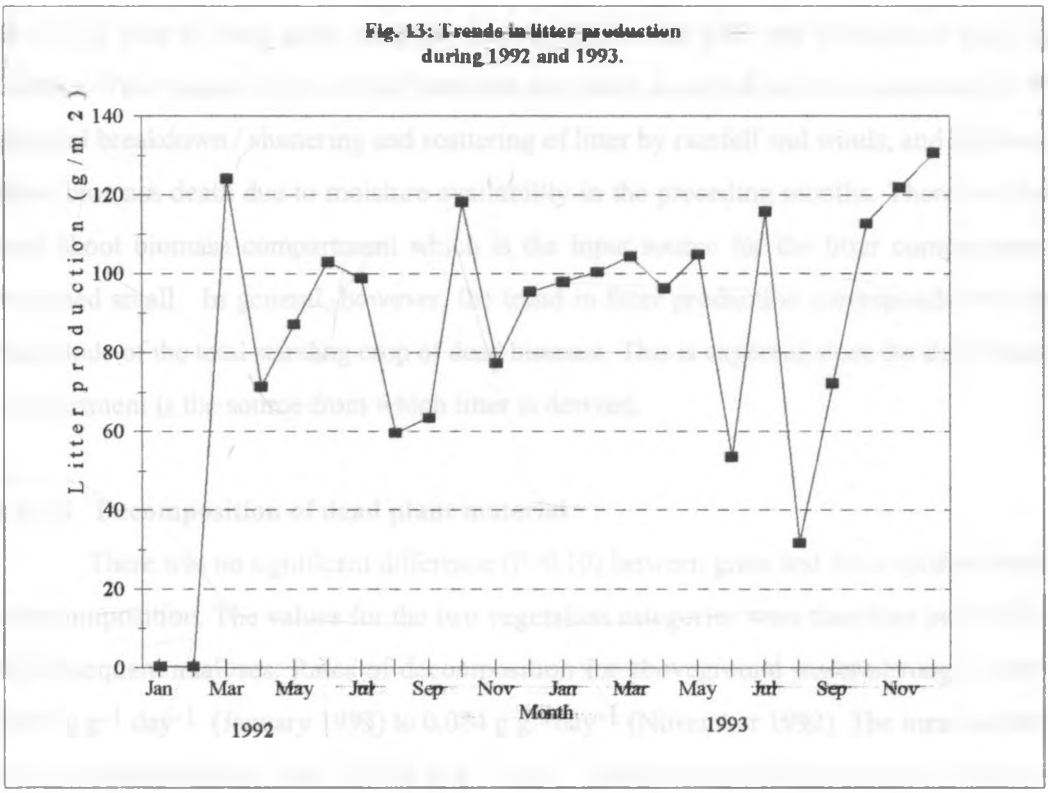


Fig. 13: Trends in litter production during 1992 and 1993.

Monthly litter production ranged from 31.4 g m^{-2} in August 1993 to 130.4 g m^{-2} in December 1993. Mean monthly litter yield was 92.5 $\pm$ 26 g m^{-2} with a coefficient of variation of 28%. There was no significant difference (P>0.01) between litter yield in 1992 and 1993. These range of values for litter yield agree closely with those of Kinyamario and Imbamba (1992).

The trend in litter production was characterized by troughs rather than peaks. There were three conspicuous troughs. These occurred in August 1992 (59.4 g m^{-2}), June 1993 (53.3 g m^{-2}) and the most prominent in August 1993 (31.4 g m^{-2}). The August 1992 and June 1993 troughs coincided with rainfall peaks. However, rates of aboveground biomass

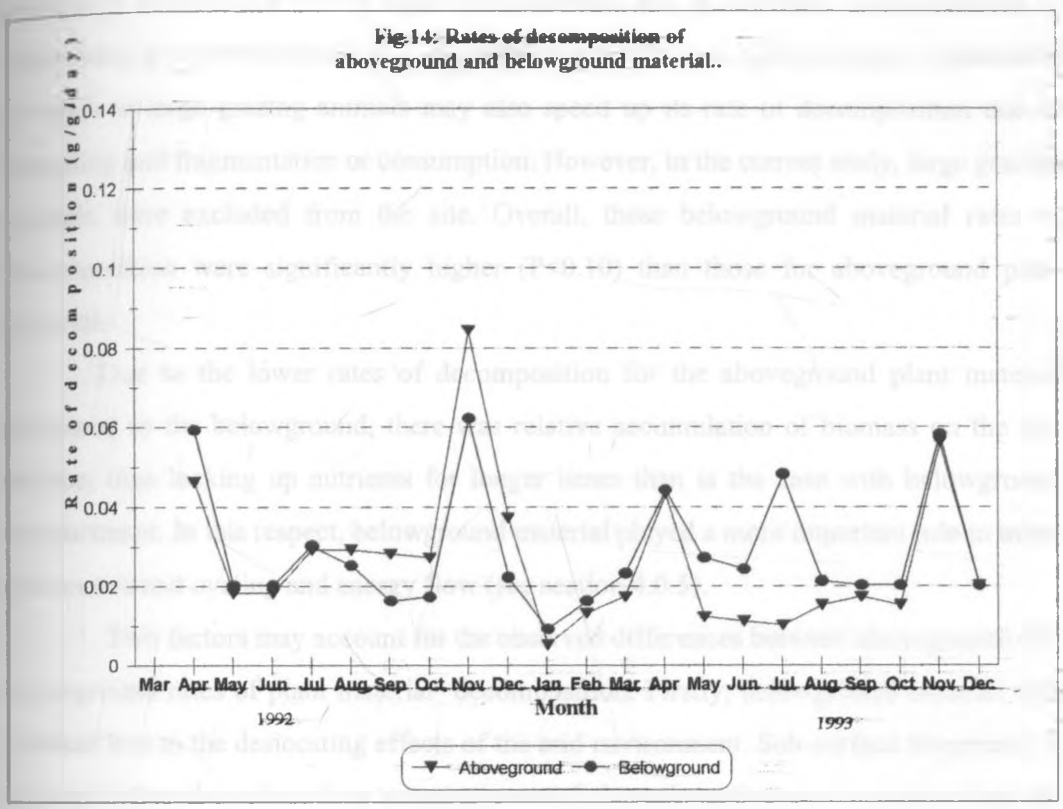
decomposition during the same months were low, averaging 0.034 and 0.013 g g^{-1} day^{-1} respectively (Fig. 14). This implies physical smothering of the brittle litter material by the rainfall received during these peaks in concert with other physical agents like strong winds thus reducing the amount of discernible litter on the ground.

The August 1993 trough, which is the deepest, thus indicating the lowest amount of litter on the ground, was preceded by 74 mm, 115 mm and 64 mm of rainfall in May, June and July respectively. However, the rainfall recorded in August 1993 was very low (7 mm). The rate of dead plant material decomposition was also low throughout May to October. This trough in litter yield therefore may have occurred due to a combination of physical breakdown / shattering and scattering of litter by rainfall and winds, and minimal shoot biomass death due to moisture availability in the preceding months. Therefore the dead shoot biomass compartment which is the input source for the litter compartment remained small. In general, however, the trend in litter production corresponded to the magnitude of the total standing crop of dead biomass. This is expected since the dead shoot compartment is the source from which litter is derived.

4.0.1.5 Decomposition of dead plant material

There was no significant difference ($P>0.10$) between grass and dicot material rates of decomposition. The values for the two vegetation categories were therefore pooled for all subsequent analyses. Rates of decomposition for aboveground material ranged from 0.005 g g^{-1} day^{-1} (January 1993) to 0.084 g $g^{-1}day^{-1}$ (November 1992). The mean annual rate of decomposition was 0.026 g g^{-1} day^{-1}. Belowground plant material rates of decomposition ranged from 0.009 g g^{-1} day^{-1} (January 1993) and 0.062 g g^{-1} day^{-1} (November 1992). The mean annual value was 0.041 g g^{-1} day^{-1}.

Figure 14 shows a graphical trend in rates of decomposition for aboveground and belowground plant material.



Belowground plant material rates of decomposition were consistently above those for aboveground biomass except for only four months, namely September, October, November and December of 1992. For both 1992 and 1993, there were three conspicuous decomposition peaks for both aboveground and belowground plant material. These occurred during the months of April (0.046 g g^{-1} day^{-1}), July (0.029 g g^{-1} day^{-1}) and November (0.084 g g^{-1} day^{-1}). Rates of decomposition for the three peak months were significantly higher ($P<0.10$) than the rest of the months for both 1992 and 1993. For both years, the November peak showed the highest rate of decomposition. The three annual decomposition peaks coincided with the three rainfall peaks in the study area. A sudden increase in the rates of decomposition due to an increase in rainfall is an indicator that moisture deficiency is a limiting factor to plant material decomposition. Similar results were obtained by Abouguendia and Whitman (1979), Ohiagu and Wood (1979), Swift_*et al* (1979) and Kinyamario and Imbamba (1992),

The November peak in rate of decomposition, which is higher than the other two,

is associated with the character of the short rains in dryland ecosystems, whereby the total rainfall is experienced over a short time interval, and is therefore more effective in influencing ecosystem function e.g. decomposition in this case, and structure. Exposure of biomass to large grazing animals may also speed up its rate of decomposition due to trampling and fragmentation or consumption. However, in the current study, large grazing animals were excluded from the site. Overall, these belowground material rates of decomposition were significantly higher ($P<0.10$) than those for aboveground plant material.

Due to the lower rates of decomposition for the aboveground plant material compared to the belowground, there was relative accumulation of biomass on the soil surface, thus locking up nutrients for longer times than is the case with belowground compartment. In this respect, belowground material played a more important role in intra-system nutrient cycling and energy flow (see section 4.0.5).

Two factors may account for the observed differences between aboveground and belowground rates of plant material decomposition. Firstly, belowground material was exposed less to the desiccating effects of the arid environment. Sub-surface temperatures are cooler than the soil surface temperatures and also sub-surface soil is moister than the surface soil. A combination of these factors creates a suitable environment for the decomposer organisms, thus giving higher rates of decomposition (Deshmukh,1986). Secondly, non-woody rangeland vegetation is known to deposit soluble nutrients especially carbohydrates and proteins in their belowground systems at a certain stage of growth just before seed set (Trlica, 1977, McNaughton, 1979). The belowground plant material will therefore at certain stages of growth contain more soluble and easily decomposable material than aboveground material.

The process of plant material decomposition can be divided into non-microbial and microbial decomposition. Non-microbial loss of weight may be caused by leaching of soluble substances and products of breakage by rain and removal of solids from bags by gravity and animals. Microbial decomposition is caused by various groups of micro-organisms including bacteria, fungi and even termites (Witkamp, 1966; St. John, 1980; Deshmukh, 1986). From the foregoing, it is likely that the loss of aboveground plant material was dominated by non-microbial decomposition processes whereas the loss of belowground plant material was mainly caused by microbial decomposition.

Detailed comparisons and / or contrasting of rates of biomass decomposition from the current study with the existing few obtained from different studies is difficult. Most of the other studies fail to give part of the details under which the studies were conducted, for example mesh size of the litter bags, type of plant material and the post-field treatment of the residue material. Also, some of the studies conducted in the drylands of Africa for example Ohiagu and Wood (1979) in West Africa, Morris *et al.*, (1982) in South Africa and Bagine (1982) in East Africa, concern areas where termites are the major decomposers of herbaceous vegetation. Generally, however, the values for rate of decomposition obtained from the current study lie close to those obtained by Macharia (1981), Deshmukh (1985) and Kinyamario and Imbamba (1992) who worked in Kenyan grasslands. The slight differences observed whereby the current study recorded higher values, is due to the fact that the above earlier studies mostly dealt with fibrous perennial grasses, whereas vegetation on the current study site was dominated by less fibrous herbaceous ephemeral and annual grasses, herbs and forbs. These categories of vegetation have low cellulose content and relatively higher nitrogen content compared to the more fibrous perennial grasses. They, therefore, tend to have similar C:N ratios, which are lower than those for perennial grasses. Low C: N ratios are often associated with nutritious and succulent leaves and higher rates of decomposition. High values usually coincide with tough leaves which are high in resistant components such as cellulose and lignin and, especially in early stages of decay, with low palatability to litter decomposing fauna (Witkamp, 1966; Dickinson and Pugh, 1974; Deshmukh, 1986).

A review of literature generally shows that decomposition of dead plant material, especially belowground, has been the last major component of any ecosystem to fall under the searchlight of ecologists. Less than 1% of published papers on terrestrial ecosystems deal with the subject. In the African tropical savannas, only four studies that included biomass decomposition have been published. These are by Ohiagu and Wood (1979), Macharia (1981), Deshmukh (1985) and Kinyamario and Imbamba (1992). Of these, only Kinyamario and Imbamba (1992) estimated decomposition of belowground plant material.

4.0.1.6 Net primary production and productivity

Annual net primary production (NPP) and productivity differed between years. In 1992, annual NPP was 439.2 g m^{-2}, which was equivalent to a net primary productivity of

1.22 g $m^{-2}day^{-1}$. Monthly NPP ranged from 17.2 g m^{-2} in September to 90.1 g m^{-2} in December. In 1993, annual NPP was 944.5 g m^{-2}, equivalent to a net primary productivity of 2.62 g $m^{-2}day^{-1}$. Monthly NPP values ranged from 27.4 g m^{-2} in September to 548.6 g m^{-2} in May. For both 1992 and 1993, lowest NPP was recorded during the month of September, which was a rainfall trough i.e. both August and October had higher rainfall amounts. Highest values of NPP were recorded during the months of December and May for 1992 and 1993 respectively. This was an expected observation since rainfall peaks preceded these months, in November and April respectively. NPP for 1993, which received higher rainfall, was significantly higher ($P<0.05$) than for 1992. During the period March 1992 to December 1993, NPP was 1383.7 g m^{-2}. This was equivalent to a productivity of 1.92 g $m^{-2}day^{-1}$. The trend in monthly NPP closely followed the pattern of rainfall, with peaks in NPP preceded by peaks in rainfall and troughs in NPP preceded by low rainfall.

The annual NPP and productivity values reported in the current study closely agree to those reported by Kinyamario and Imbamba (1992) from a high potential rangeland in the Nairobi National Park, having an annual rainfall of about 800 mm with well defined wet and dry seasons. They used the same methods as in the current study and they reported an annual NPP of 1880 g m^{-2}, which was equivalent to a productivity of 2.6 g $m^{-2}day^{-1}$. These values are higher than those from the current study. This observation can be attributed to the climatic differences between the study sites, especially rainfall. Annual rainfall on the Njemps flats was lower (about 600 mm) and was rendered less effective for biomass production by the poor distribution of occurrence within the years, high temperatures and rates of evaporation. Differences in soils between the two sites further contribute to the differences in biomass production. The site in the Nairobi National Park was dominated by heavy dark grey soils whereas on the Njemps flats site the dominant soils were silty loams with low water holding capacity.

Other studies on production and productivity of East African grasslands include those by Cassady (1973), Sinclair (1975), Lusigi (1978), Strugnell and Pigott (1978), Owaga (1980), Macharia (1981) and Deshmukh (1986). Table 10 below gives a summary of the annual NPP values obtained from these studies.

Table 10: Annual net primary production from East African grasslands.

COUNTRY	AUTHOR	VEGETATION COMMUNITY	NPP ($g\ m^{-2}$)	RAINFALL (mm)
Kenya	Cassady (1973)	*Themeda* grassland	560	500
Tanzania	Sinclair (1975)	Short grassland	470	613
Kenya	Lusigi (1978)	*Themeda* grassland	395	900
Uganda	Strugnell & Pigott (1978)	*Hyperhenia* grassland	536	600
Kenya	Owaga (1980)	*Themeda* grassland	402	600
Kenya	Macharia (1981)	"	365	729
Kenya	Deshmukh (1986)	"	1071	850
Kenya	Kinyamario and Imbamba (1992)	"	1880	815
Kenya	Ekaya (this study)	Ephemeral rangeland	692	582

All the above annual NPP values lie very close to the current study's 1992 annual NPP value of 439.2 g m^{-2}. Those reported by Lusigi (1978), Owaga (1980) and Macharia (1981) are lower despite the study sites having higher annual rainfall amounts (600 mm, 600 mm and 729 mm respectively). The main reason behind this observation is the differences in methods used by Kinyamario and Imbamba (1992) as well as the current study, and previous methods which include maximum standing crop, International Biological Programme standard method and the maximum-minimum method (Roberts *et al.*, 1993). These methods failed to account for losses due to decomposition and any positive increments in biomass prior to peak standing crop. To compound this further, belowground plant material production and decomposition were completely ignored. This led to serious underestimation of annual NPP, and therefore productivity.

In a detailed comparison of annual NPP values recorded from tropical grasslands using the previous methods and that of the current study, Kinyamario and Imbamba (1992) reported that underestimation ranged from 2% to 69%. Due to this flaw in estimating NPP and productivity of tropical grasslands, previous figures are probably underestimates. These ecosystems are therefore more productive than currently thought. This revelation places the

tropical dryland ecosystems into sharp focus as a CO_2 sink, whose role in CO_2 sequestration and amelioration of the imminent climate change due to the green house gas effect has not been well documented, particularly for belowground biomass.

4.0.2 Species diversity

A unique characteristic of the community level of biological organization is species diversity, which is an expression of community structure. A community is said to have a high species diversity when it has numerous equally or almost equally abundant species (Brower *et al.*, 1990). Hurlburt (1971) asserts that species diversity expresses the Probability of Interspecific Encounter (PIE), which is the probability of an individual in the community encountering a member of another species. The encounters will occur in such interactions as competition, predation, synergism and many others, both positive and negative.

Table 11 below shows the month by month indices of species diversity, together with the number of species encountered and the total rainfall received.

Table 11: Monthly species diversity, number of species encountered and total rainfall during 1992 and 1993.

Year	Month	Simpson's Index (PIE)	Number of species	Rainfall (mm)
1992	March	0.77	6	5
	April	0.40	5	85.5
	June	0.54	8	47.5
	July	0.66	11	62.5
	August	0.76	10	154
	September	0.89	14	24
	October	0.92	16	100
	November	0.83	12	28
	December	0.62	12	29
1993	February	0.78	13	58
	March	0.66	8	4.5
	April	0.78	9	14.5
	May	0.78	10	74
	June	0.79	14	64
	July	0.79	13	7
	August	0.65	9	10.5
	October	0.55	5	17.5
	December	0.83	17	115

The highest and lowest PIE values were recorded during the months of October 1992 (0.92) and April 1992 (0.40) respectively. Other high PIE values (>80%) were recorded during September and November of 1992 and December of 1993. PIE values below 60% were recorded during June, 1992 and October, 1993.

For both 1992 and 1993, highest PIE values were recorded during those months with the highest number of species encountered during sampling, that is 16 and 17 species

for 1992 and 1993 respectively. In 1993, the same months, as in 1992, received the highest total rainfall (115 mm). However, in 1992, highest PIE and number of species was recorded during the month that received the second highest total rainfall. This was caused by the distribution of the rainfall within the month. The 100 mm of rainfall received in October occurred over fewer number of days and was therefore more effective in stimulating germination and sprouting of species. Low PIE values were always associated with a low number of species, although this may not have been recorded during months with lowest rainfall, for example April 1992. This was due to the poor rainfall distribution within the months, making it less effective for stimulating ecosystem function, especially plant growth.

High species diversity indicates a highly complex community, since a greater variety of species allows for a larger array of interactions between species. Therefore, population interactions involving energy transfers, predation, competition and niche apportionment are more complex and varied in a community of high species diversity. For arid rangeland ecosystems, in which lack of moisture is a key limiting factor to ecosystem structural and functional dynamism, this scenario occurs during periods of effective moisture injection into the ecosystem. The moisture stimulates growth, increasing the number of species and biomass per species, and therefore PIE.

High species diversity is connected to community stability (Woodwell and Smith, 1969; May, 1975). This occurs in very large areas in which random changes affecting species tend to compensate each other. However, in small areas and in non-equilibrial ecosystems such as the current study site, random changes actually constitute the system.

4.0.3 Turnover rate and time

Turnover time refers to the number of time units required to produce as much plant material as is present in a specified compartment at the time of measuring the standing crop in the same compartment. Turnover rate on the other hand refers to the amount of output plant material from a specified compartment per unit time. The turnover rates and times of the different categories of plant material are shown in Table 12 below.

Table 12: Turnover rate and time of different categories of plant material.

Plant Material	Turnover Rate (year^{-1})		Turnover Time (Years)	
Category	1992	1993	1992	1993
Live aboveground	0.18^{ab1}	0.40^{c2}	5.6	2.5
Dead aboveground	0.13^{a1}	0.22^{ab2}	7.7	4.5
Grass litter	0.32^{d1}	0.15^{a2}	3.1	6.7
Dicot litter	0.21^{bc1}	0.29^{b1}	4.7	3.4
Live belowground	0.30^{cd1}	0.15^{a2}	3.3	6.7
Dead belowground	0.16^{ab1}	0.19^{a1}	6.3	5.3

[abcd]Column values with different letter superscripts differ significantly (P<0.05).

[1,2]Row values with different number superscripts differ significantly (P<0.05).

Aboveground biomass had the highest turnover rate (0.40 - 0.18 y^{-1}), followed by the grass litter and the live belowground compartments with 0.32 - 0.15 y^{-1} and 0.30 - 0.15 y^{-1} respectively. Lowest turnover rate was recorded in the dead aboveground compartment (0.13 - 0.22 y^{-1}). Due to the above turnover rates, aboveground biomass had the lowest turnover time (2.5 - 5.6 years) followed by grass litter (3.1 - 6.7 years) and belowground biomass (3.3 - 6.7 years). The highest turnover time was recorded for the dead aboveground compartment (7.7 years).

The high turnover rate of aboveground biomass is due to the fact that in this arid ecosystem, shoot and root growth takes place rapidly in response to effective rainfall events. Within a short time therefore, there is a sudden increase in the size of the aboveground and belowground biomass compartments. However, the new growth is rapidly transferred to the respective dead plant material compartments when the plants quickly die off due to lack of moisture. Furthermore, most of the species resident in this arid ecosystem are ephemeral and opportunistic. When moisture becomes available, they grow rapidly, produce seeds, shed them and die out within short periods of time, about one week to one month. This further increases the size of the dead aboveground and belowground compartments. The perennial species whose growth curve lags behind that of ephemeral species may die off before

reaching the seeding stage. The new growth is thus rapidly transferred into the dead plant material compartments.

The dead aboveground and belowground compartments had the lowest turnover rates and therefore the highest turnover times (4.5 - 7.7 and 5.3 - 6.3 years respectively) due to the low rates of plant material decomposition for these compartments (0.026 g g^{-1} day^{-1} and 0.041 g g^{-1} day^{-1} respectively). However, the dead belowground plant material had a lower turnover time, associated with the more rapid rate of decomposition. The high turnover time for grass litter is due to slow microbial and non-microbial breakdown processes of plant material in arid environments in general. It is also associated with the rapid shedding of dead standing shoots into the litter compartment due to physical forces, for example strong winds.

Results from the current study do not lie within those from previous studies carried out elsewhere, for example Strugnell and Pigott (1978), Misra and Misra (1979) and Kinyamario and Imbamba (1992). In all the above previous studies, turnover rates ranged from 0.70 yr^{-1} to 1.2 yr^{-1}, giving turnover times as low as 8 months, whereas in the current study, the lowest turnover time was 2.5 years. This difference is due to the fact that all previous studies have been conducted in semi-arid savanna grasslands with higher and well defined rainfall. Therefore growth, decomposition and inter-compartmental transfers of biomass were more rapid. There are also differences in methods and formulae used in estimating turnover rates and times, which also account for part of the differences in the reported values.

4.0.4 Equilibrium time

Equilibrium time is the time required to attain 99% equilibrium under the prevailing conditions of growth and decomposition (Dahlman and Kucera, 1965). Table 13 below shows the equilibrium times for the dead aboveground and belowground compartments.

Table 13: Equilibrium times for dead aboveground and belowground plant materials during 1992 and 1993.

Compartment	Decomposition Rate (R)		99% Equilibrium Time (Years)	
	($R_{max.}$)	($R_{min.}$)	($T_{min.}$)	($T_{max.}$)
Aboveground (dead)	0.099	0.006	46.5	767.5
Belowground (dead)	0.088	0.014	52.3	328.9

These estimates of equilibrium time vary inversely with the corresponding decomposition rate values, thus giving long equilibrium times for low decomposition rates. Low decomposition rates in some compartments means an accumulation of material in the same compartment thus increasing the input:output ratio, thereby increasing the time needed to attain equilibrium. Lowest equilibrium time was recorded for the aboveground compartment (46.5 years). This compartment also had the highest maximum equilibrium time (767.5 years), resulting from the very low decomposition rates. The belowground compartment had 328.9 years as the maximum equilibrium time.

The estimated equilibrium times from the current and previous studies can only be realized under one main assumption; that the main operating factors and the prevailing climatic conditions remain fairly constant over the same time period. Arid rangeland ecosystems are characterized by erraticity rather than anything near constancy (Behnke and Scoones, 1992). Therefore, although equilibrium times have been estimated, these are only theoretical. However they serve as indicators of ecosystems function, when used in combination with other characteristics like decomposition and turnover rates.

4.0.5 Energy content and flow through the herbaceous producer system

The incident solar radiation value of 23.5 MJ m^{-2} used in this study was that calculated by Kinyamario and Imbamba (1992) on a bright cloudless day at the semi-arid Nairobi National Park. Since photosynthetically active radiation (PAR) constitutes about 45% of incoming solar radiation (Sims and Singh, 1978b), the above incoming solar

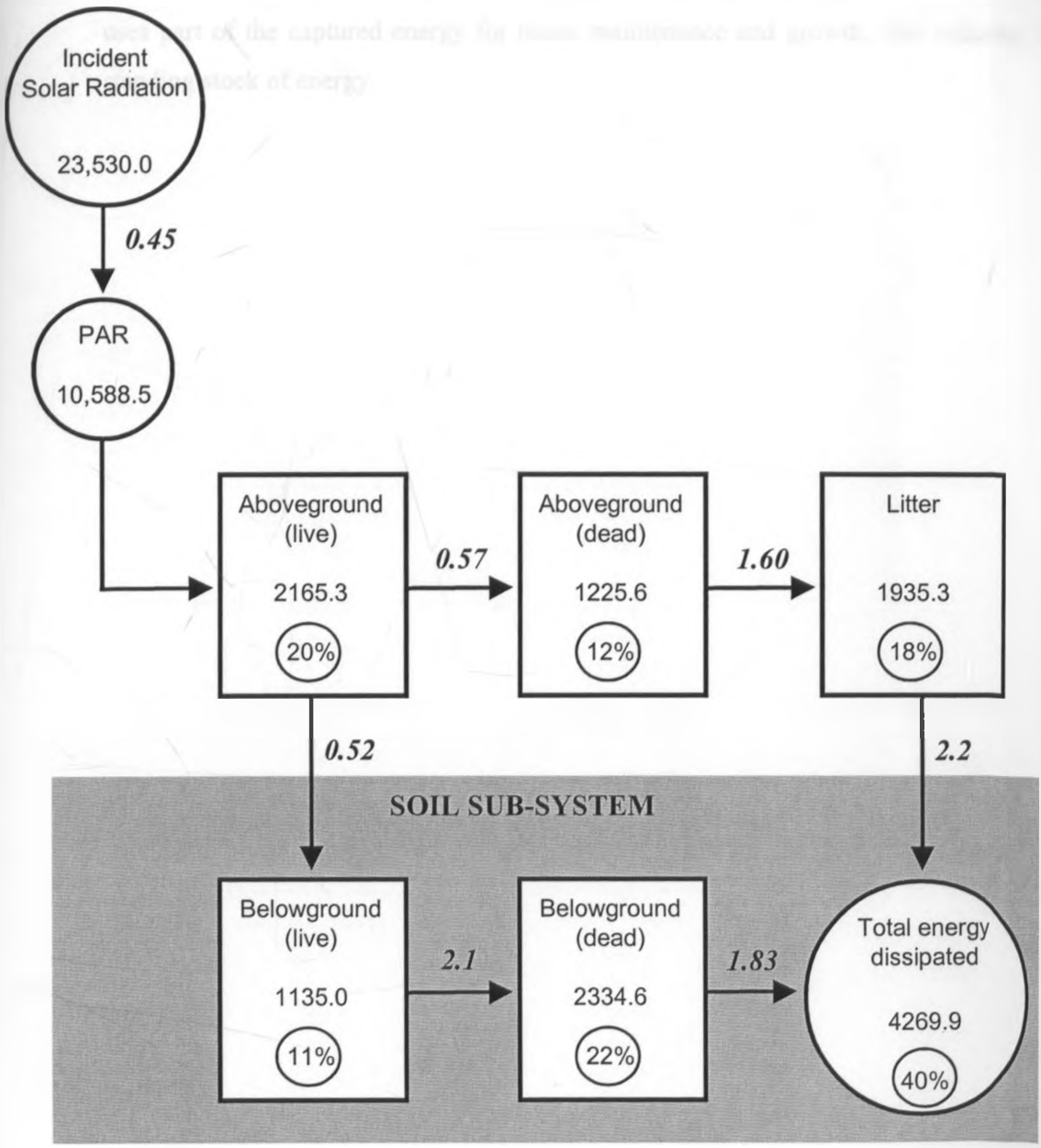
radiation value was reduced by 55% to obtain an estimate of PAR. PAR was thus calculated to be 10,588.5 KJ m^{-2}. It was henceforth assumed that this was the total energy available for capture by the primary producers, and subsequent conversion into biomass.

Aboveground plant material, which consisted of leaves and stems, had a mean energy content of 17.9 KJ g^{-1}, whereas belowground material had a mean energy content of 21.6 KJ g^{-1}. There was no significant difference in energy content ($P>0.05$) between the live and the dead plant material compartments, as well as between the dry and the wet season. Therefore the above mean values of energy content were used for both categories of plant material as well as for both seasons.

Due to the inherent absence of clearly defined wet and dry seasons at the study site, a different approach was used to distinguish between wet and dry season. The months of April, May, July, August and November, which had higher rainfall and biomass yield than the rest of the months were assumed to constitute the wet season. The other months, i.e. January, February, March, June, September, October and December constituted the dry season.

Energy flow through the herbaceous primary producer subsystems on the Njemps flats during the dry and wet season is shown in figures 15 and 16 respectively.

Fig. 15: Energy flow through the herbaceous layer on the Njemps flats ecosystem during the dry season.

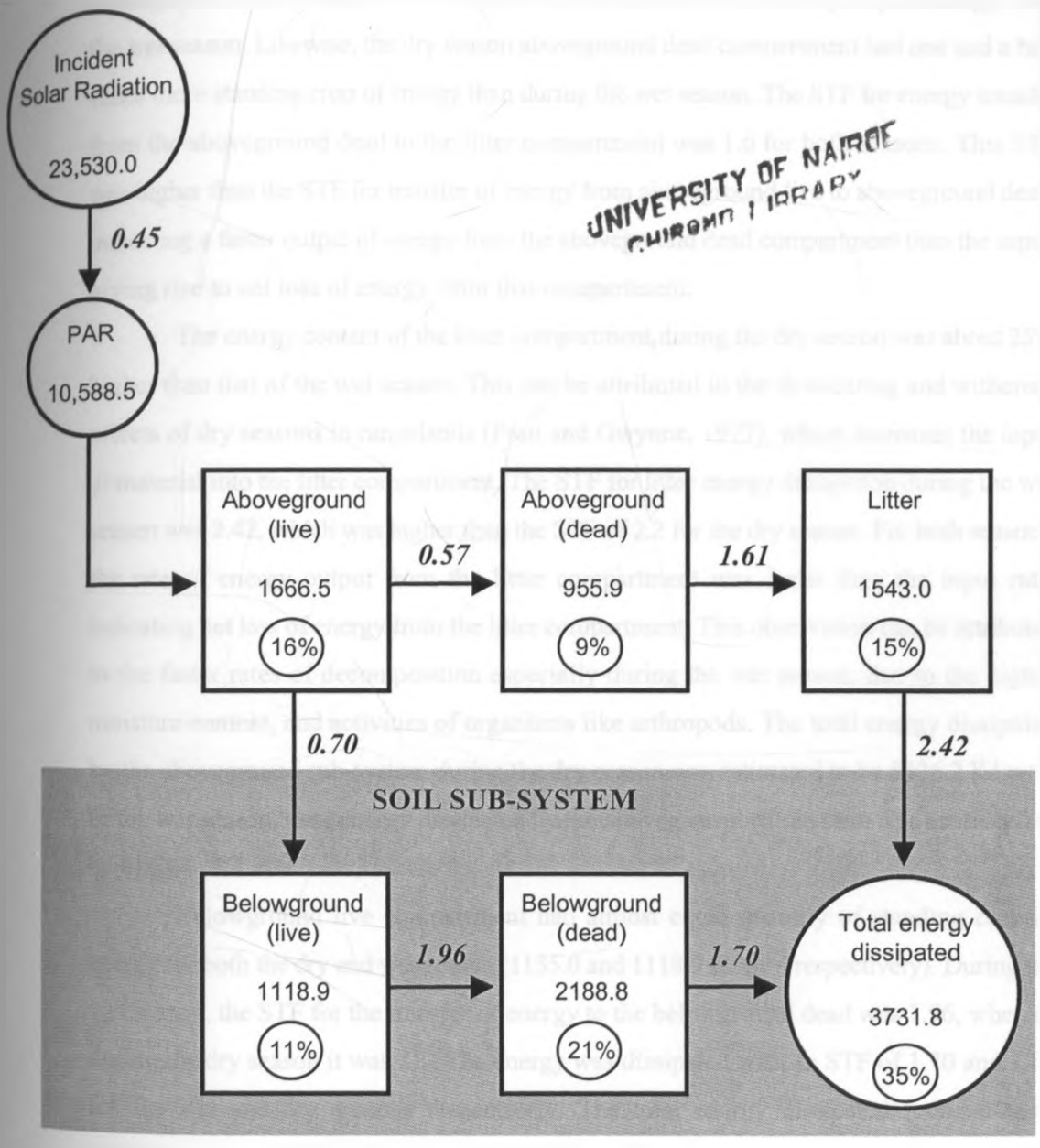


KEY:

1. Values in circles: Energy input to, and output from the system (KJ m^{-2}).
2. Values in boxes: Mean standing stock of energy in compartments (KJ m^{-2}).
3. Values on arrows (italics): System Transfer Functions.

Total standing stock of energy in the producer system during the dry season was about 17% higher than for the wet season. During the wet season, when plant growth is active, the plant uses part of the captured energy for tissue maintenance and growth, thus reducing the standing stock of energy.

Fig. 16: Energy flow through the herbaceous layer on the Njemps flats ecosystem during the wet season.



KEY:

1. Values in circles: Energy input to, and output from the system (KJ m^{-2}).
2. Values in boxes: Mean standing stock of energy in compartments (KJ m^{-2}).
3. Values on arrows (italics): System Transfer Functions.

The System Transfer Function (STF) for energy transfer from the aboveground live to aboveground dead was the same (0.57) for both seasons. However, the dry season aboveground live compartment had one and a half times more standing crop of energy than the wet season. Likewise, the dry season aboveground dead compartment had one and a half times more standing crop of energy than during the wet season. The STF for energy transfer from the aboveground dead to the litter compartment was 1.6 for both seasons. This STF was higher than the STF for transfer of energy from aboveground live to aboveground dead, indicating a faster output of energy from the aboveground dead compartment than the input, giving rise to net loss of energy from that compartment.

The energy content of the litter compartment during the dry season was about 25% higher than that of the wet season. This can be attributed to the desiccating and withering effects of dry seasons in rangelands (Pratt and Gwynne, 1977), which increases the input of material into the litter compartment. The STF for litter energy dissipation during the wet season was 2.42, which was higher than the STF of 2.2 for the dry season. For both seasons, the rate of energy output from the litter compartment was faster than the input rate, indicating net loss of energy from the litter compartment. This observation can be attributed to the faster rates of decomposition especially during the wet season, due to the higher moisture content, and activities of organisms like arthropods. The total energy dissipated by the aboveground sub-system during the dry season was estimated to be 5326.2 KJ m^{-2}. In the wet season, total energy dissipated by the aboveground sub-system was estimated to be 4165.4 KJ m^{-2}.

Belowground live compartment had almost equal quantity of standing crop of energy for both the dry and wet season (1135.0 and 1118.9 KJ m^{-2} respectively). During the wet season, the STF for the transfer of energy to the belowground dead was 1.96, whereas during the dry season it was 2.1. The energy was dissipated with an STF of 1.70 and 1.83 for the wet and dry seasons respectively. The total energy dissipated (compartment summation) was 3731.8 KJ m^{-2} and 4269.9 KJ m^{-2} for the wet and dry season respectively. The higher energy dissipated during the dry season is due to low rates of decomposition during this season, coupled with higher stock of compartmental energy contents than during the wet season.

During the dry season, average energy accumulation in all the aboveground

compartments occurred at 25.4 KJ m^{-2} day^{-1}. The average energy accumulation in all belowground compartments occurred at 16.5 KJ m^{-2} day^{-1}. During the wet season, average energy accumulation in all belowground compartments occurred at 27.8 KJ m^{-2} day^{-1} whereas in the aboveground compartments, accumulation was 22.0 KJ m^{-2} day^{-1}. Therefore, irrespective of season, a relatively larger proportion of the energy that flowed through the rangeland ecosystem followed the aboveground pathway. These findings are in conflict with those by Sims and Singh (1978b) and Singh *et al.*, (1979). Sims and Singh (1978a) attributed this phenomenon to low, erratic rainfall, in which case the vegetation growth is adapted to respond quickly to available water. Products of photosynthesis are concentrated in aboveground parts i.e. leaves, flowers and seeds. As a result there is a lower percentage of belowground material mass and therefore less energy in belowground compartments.

Overall, for both the dry and wet season, and with respect to energy flow, the system is not in dynamic equilibrium. This arises out of the varying STFs between the different compartments. For both the dry and the wet season, the STF between the aboveground live and aboveground dead was less than 1. This implies some net accumulation of energy in the aboveground live compartment. The rest of the STFs ranged from 1.5 to 2.5, which means net loss of energy from the relevant compartment.

4.0.6 Nitrogen dynamics through the herbaceous producer system

The mean standing crop of plant material and nitrogen content of different plant compartments and categories during the dry and wet seasons are shown in Table 14 below. For both seasons, material classified as grass constituted 39.8% of the total aboveground plant material, whereas material classified, as dicots constituted 60.2%.

Table 14: Mean standing crop and nitrogen content of plant categories and compartments during the dry and wet season.

Compartment	Mean standing crop (g m^{-2})		Mean % nitrogen content	
	Dry season	Wet season	Dry season	Wet season
Aboveground (live) grass	43.5	37.1	1.7^{c1}	2.3^{c2}
Aboveground (live) dicots	65.8	56.0	2.4^{f1}	2.8^{e2}
Aboveground (dead) grass	24.6	21.3	0.7^{a1}	1.3^{a2}
Aboveground (dead) dicots	37.3	32.1	2.0^{de1}	2.4^{d2}
Belowground (live)	51.4	51.8	1.8^{cd1}	3.0^{fg2}
Belowground (dead)	105.6	101.3	1.5^{b1}	2.1^{b2}
Litter	97.7	86.2	2.0^{de1}	2.9^{ef2}

^{abcdef}Column means with different letter superscripts differ significantly ($P<0.05$).

^{1,2}Row means with different number superscripts differ significantly ($P<0.05$).

During the dry season, the highest percent nitrogen content was recorded in the aboveground live dicots (2.4%). This was closely followed by the aboveground dead dicots and litter compartments both with 2% nitrogen. Belowground live material also had a high value of 1.8%. The lowest nitrogen content was recorded in the aboveground dead grass compartment (0.7%).

The higher nitrogen content of the dicot compartments compared to the grass compartments is related to the inherent higher nitrogen content of the former (Dougall *et al.*, 1964; Van Soest, 1982). Previous studies that have reported similar trends especially during the dry season include those by Dougall and Bogdan (1958), Otsyina and McKell (1985), Tessema (1986) and Ekaya (1991). The high nitrogen content of the litter compartment could partly be due to the contamination by nitrogen from litter-decomposing micro-organisms (Coupland, 1973a, 1973b) as well as the presence of dicot plant litter, since in the current study litter was not separated into different categories.

The high nitrogen content of the belowground live material during both the dry and wet season (1.8% and 3.0% respectively) can be attributed to the inherent high nitrogen

content of dicot plant material and the contamination of root material by soil micro-organisms, especially for dicots, which may have symbiotic relationships with nitrogen fixing bacteria (Burns and Hardy, 1975; Bate, 1981). The low nitrogen content of the aboveground dead grass material is attributable to the rapid decline in nitrogen content as the plants advance in maturity, due to the increasing dilution of nitrogen by an increasing percentage of non-nitrogenous organic matter including cellulose and lignin material (Dougall *et al.*, 1964; Van Soest, 1982) and the retranslocation of nitrogen out of organs before abscission.

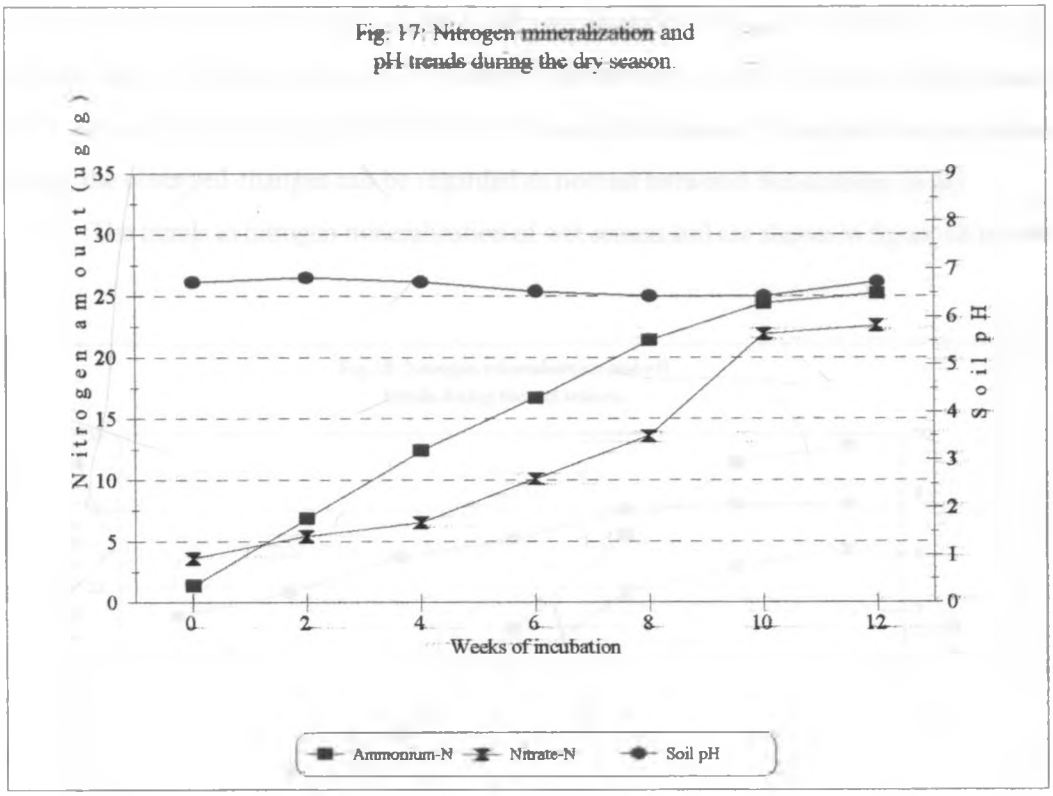
During the wet season, highest nitrogen contents were recorded in the belowground live (3.0%), litter (2.9%) and aboveground dead dicots (2.8%) compartments. The value of nitrogen recorded in the belowground live compartment is attributable to plant synthesis processes, this being a growing season, as well as by contamination by soil micro-organisms associated with belowground plant parts especially roots. The litter nitrogen content was contributed to by decomposer organisms due to an increase in the moisture content of litter and soil during the wet season. The low nitrogen content of the aboveground dead grass is attributable to mature senescent ephemeral grasses whose nitrogen content had rapidly declined (Karue, 1974, 1975; Van Soest, 1982).

Overall, the mean standing stocks of nitrogen in the herbaceous layer during the dry and wet seasons were 7700 mg m^{-2} and 9650 mg m^{-2} respectively. The wet season had a higher standing crop of nitrogen ($P<0.05$) than the dry season.

4.0.7 Soil nitrogen mineralization

The trend in mineral nitrogen content and pH of dry season soil incubated for a period of twelve weeks is shown in Fig. 17 below.

Fig. 17: Nitrogen mineralization and pH trends during the dry season.



After 24 hours of stabilization incubation, the ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) levels were at 1.3 and 3.6 $\mu g\ g^{-1}$ soil respectively. Within a period of two weeks ammonification was favoured, raising the NH_4^+-N content to 6.8 $\mu g\ g^{-1}$ while NO_3^--N only rose to 5.4 $\mu g\ g^{-1}$. This lower rate in NO_3^--N production is attributable to the concomitant slight increase in pH, which favours nitrogen immobilization or reduced nitrification (Laura, 1977; Keeney, 1980). Thereafter, mineral nitrogen showed a steady increase up to the 10th week of incubation. The NH_4^+-N levels for weeks 4-10 were 12.3, 16.1, 21.3 and 24.3 $\mu g\ g^{-1}$ respectively, whereas NO_3^--N levels were 6.5, 10.1, 13.6 and 21.9 $\mu g\ g^{-1}$ of soil respectively. From the second week of incubation onwards, the NH_4^+-N levels were consistently higher than NO_3^--N levels. The highest difference between NH_4^+-N and NO_3^- -N levels was recorded at the 6th week of incubation (6.6 $\mu g\ g^{-1}$). There was a marked decline in the rate of production of both NH_4^+-N and NO_3^--N after the 10th week of incubation, showing an increase of only 0.8 and 0.7 $\mu g\ g^{-1}$ for NH_4^+-N and NO_3^--N respectively. Generally, ammonification was favoured over nitrification.

Soil pH remained within narrow limits throughout the 12-week incubation period,

ranging from 6.4 to 6.8. A slight decline in pH was recorded between the 2nd and 10th week of incubation, with values at 6.8, 6.7, 6.5 and 6.5 respectively. At the 12th week, pH increased to 6.7. Due to the narrow range within which the soil pH remained throughout the incubation period, the observed changes can be regarded as normal intra-soil fluctuations in pH.

The trends in nitrogen mineralization of wet season soil are shown in figure 18 below.

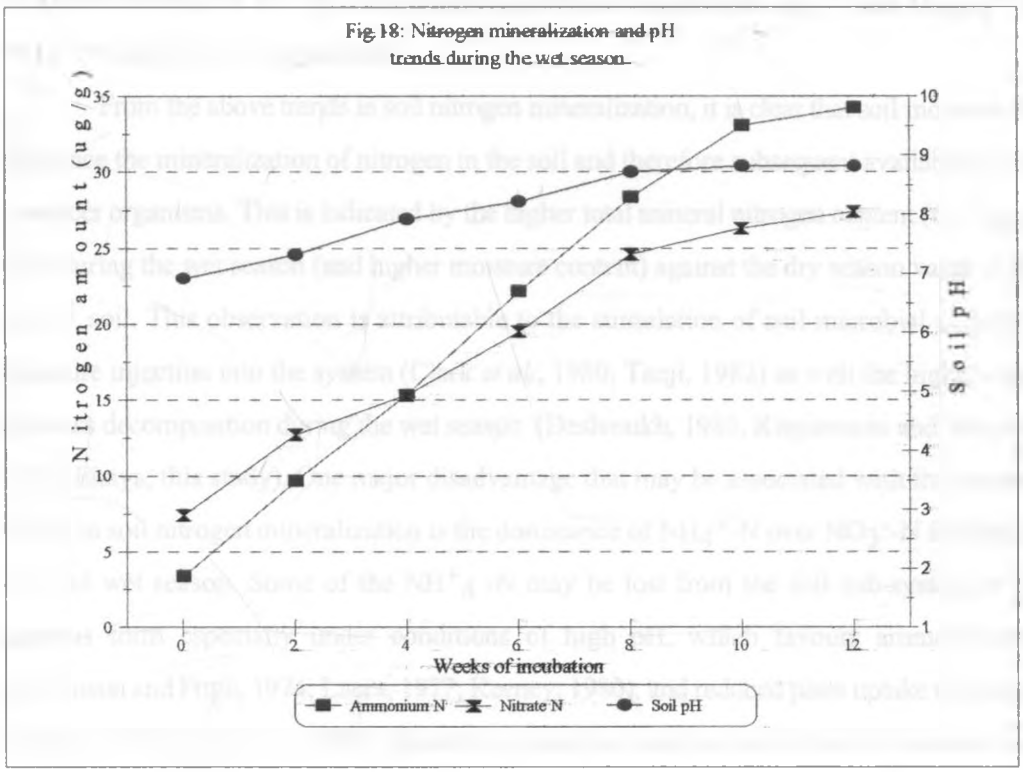


Fig 18: Nitrogen mineralization and pH trends during the wet season

At the onset of incubation, the soil NO_3^--N content was more than twice the NH_4^+-N content, i.e. 7.4 μg g^{-1} soil and 3.3 μg g^{-1} soil respectively. After a period of two weeks the NH_4^+-N and NO_3^--N content was 9.6 μg g^{-1} soil and 12.7 μg g^{-1} soil respectively. The soil pH had risen from 6.9 at the start of the incubation, to 7.3 at the second week of the experiment. There were equal amounts of NH_4^+-N and NO_3^--N in the soil after four weeks of incubation, i.e. 15.3 μg g^{-1}. Soil pH had risen to 7.9. From week four up to the end of incubation at week twelve, ammonification was favoured. NH_4^+-N contents were consistently higher than

NO_3^--N contents. Soil pH during the same period steadily rose from 7.9 at week 4 to 8.8 at the 12th week, through 8.2, 8.7 and 8.8 at weeks 6, 8 and 10 respectively.

Due to the minor increase in the mineralized nitrogen between the 10th and 12th week of the experiment, it was approximated that during the wet season, with the soil having a mean moisture content of 27%, the NH_4^+-N and NO_3^--N mineralization potential was about 35 μg g^{-1} and 28 μg g^{-1} soil respectively. During the dry season, with the soil having a mean soil moisture content of 6.7%, the mineralization potential was about 26 μg g^{-1} and 23 μg g^{-1} for NH_4^+-N and NO_3^--N respectively.

From the above trends in soil nitrogen mineralization, it is clear that soil moisture does influence the mineralization of nitrogen in the soil and therefore subsequent availability to the producer organisms. This is indicated by the higher total mineral nitrogen content (61.6 μg g^{-1} soil) during the wet season (and higher moisture content) against the dry season value of 47.7 μg g^{-1} soil. This observation is attributable to the stimulation of soil microbial activity by moisture injection into the system (Clark *et al.*, 1980; Tanji, 1982) as well the higher rate of biomass decomposition during the wet season (Deshmukh, 1985, Kinyamario and Imbamba, 1992, Ekaya, this study). One major disadvantage that may be associated with the observed trends in soil nitrogen mineralization is the dominance of NH_4^+-N over NO_3^--N for both the dry and wet season. Some of the NH^+_4 -N may be lost from the soil sub-system in the gaseous form especially under conditions of high pH, which favours ammonification (Dickinson and Pugh, 1974; Laura, 1977; Keeney, 1980), and reduced plant uptake (Evans and Barber, 1977; Clark *et al.*, 1980). However, ammonia volatilization is mainly favoured when aeration is limited (as is the case in waterlogging), and the soil moisture, temperature and pH are favourable for the growth of micro-organisms (Clark *et al.*, 1980; Tanji, 1982).

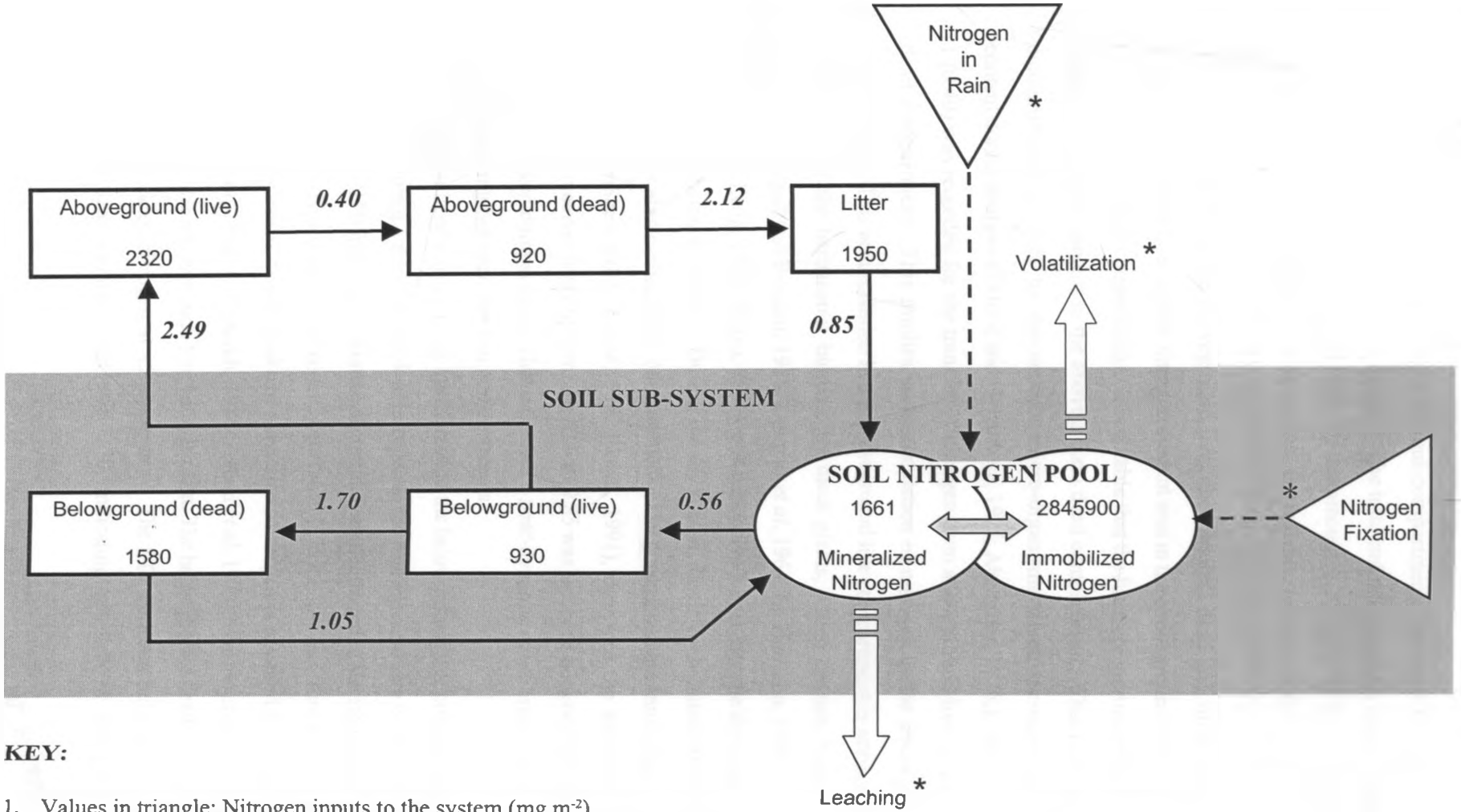
4.0.8 Synthesis of the nitrogen cycle

Plant nitrogen pools were based on average values for the concentration of nitrogen in the different plant compartments during the dry and wet seasons. The total soil nitrogen pool and the two soil nitrogen sub-compartments, i.e. mineralized and immobilized nitrogen pools were estimated based on a nutrient balance approach (Clark *et al.*, 1980). Total soil nitrogen as well as mineralized nitrogen during the two seasons was determined in the laboratory by chemical analysis. Immobilized nitrogen was assumed to be the difference between total soil nitrogen and mineralized nitrogen for soil samples taken during

the same season.

Figure 19 below shows a synthesis of the nitrogen cycle during the dry season. In synthesizing the cycle, it was assumed that nitrogen losses through leaching, denitrification and volatilization were negligible, and that input of nitrogen through precipitation was minimal for this arid rangeland ecosystem.

Fig. 19: Schematic synthesis of the nitrogen cycle on the Njemps flats ecosystem during the dry season.



The standing stock of nitrogen in the various compartments and the STFs with which the system cycles this element were estimated. The total soil nitrogen pool was estimated to be 2847.6 g m^{-2} in the top 30 cm soil layer. Of this amount, 1.70 g m^{-2} (0.05%) was in mineral form, whereas 2845.9 g m^{-2} was in the unavailable or immobilized form. In the aboveground sub-system, the standing stocks of nitrogen were 2320 mg m^{-2}, 920 mg m^{-2} and 1950 mg m^{-2} for the aboveground live, aboveground dead and litter compartments respectively. Therefore highest nitrogen content was in the aboveground live compartment followed by the litter compartment. It is notable that the litter compartment had more than twice the nitrogen content in the aboveground dead compartment. This is attributable to contamination of litter by decomposer micro-organisms which increases the nitrogen content during analysis (Eklund and Gyllenberg, 1974; Alexander, 1976;). An STF less than 1 (0.40) was recorded for the transfer of nitrogen from aboveground live to aboveground dead compartment. This implies an accumulation of nitrogen in the aboveground live compartment. This accumulation in the aboveground live compartment is attributable to the dominance of the herbaceous biomass by dicot plants, which contain higher nitrogen contents (Dougall and Bogdan, 1958; Dougall *et al*, 1964; Le Houerou, 1980; Otsyina and Mckell, 1985; Leng, 1990; Ekaya, 1991), and which live longer into the dry season than the annual and ephemeral grasses. During the dry season, dicots contributed 60% of the total biomass in the aboveground live compartment. The grasses contain much less nitrogen at maturity (VanSoest,1982; Karue,1974, Ekaya, 1991), therefore the aboveground dead compartment receives less nitrogen. An STF of 0.85 was recorded between the litter and the mineral nitrogen compartment This indicated a near-dynamic equilibrium with respect to nitrogen cycling between the two compartments.

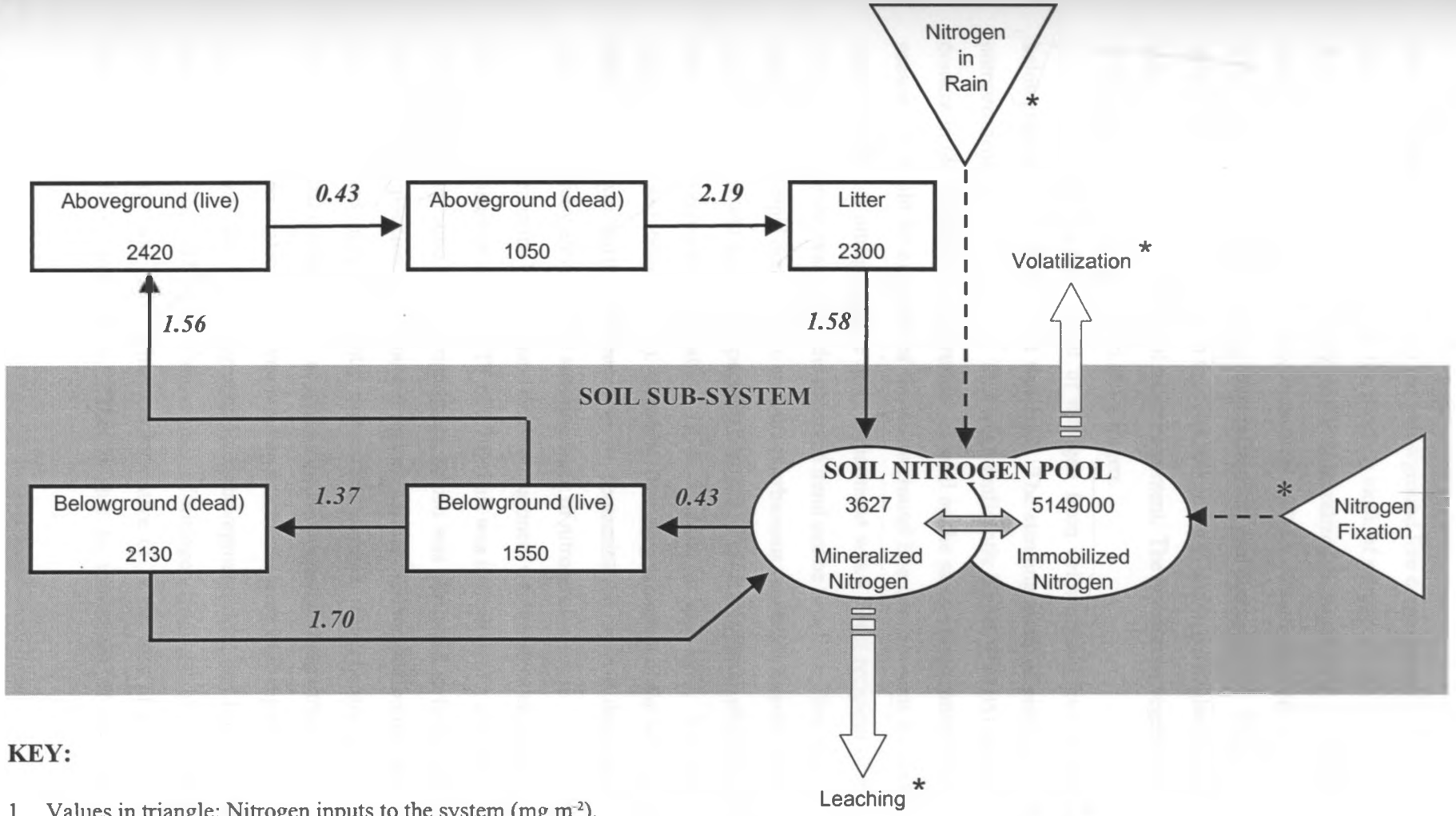
Mineralized nitrogen was transferred to the belowground live compartment with an STF of 0.56 giving a standing stock of nitrogen in the belowground live compartment of 930 mg m^{-2}. This STF indicates a relative accumulation of nitrogen in the mineralized nitrogen compartment. This observation is partly attributable to the low moisture content of the soil during the dry season, hence uptake of mineralized nitrogen is impeded (Ladd and Jackson, 1982; Stevenson 1986, Deshmukh, 1986; Aslam *et al*, 1973), concomitant with the uptake of nitrogen by the aboveground live compartment. The belowground dead compartment had a standing stock of nitrogen at 1580 mg m^{-2}. The STF between belowground live and belowground dead compartment was 1.70, indicating net loss of nitrogen from the

belowground live compartment. This observation may also be caused by nitrogen accumulation in the belowground dead compartment, mainly due to the accumulation of decomposer organisms, thus contaminating the analysed dead plant material. This was further contributed to by the lower rates of decomposition during the dry season, implying a slow rate of nutrient release from the dead material.

On the whole, during the dry season, the belowground plant material compartments were more important in nitrogen cycling than the aboveground compartments. Except for 0.56, the rest of the STF values from belowground compartments were greater than 1, indicating no net accumulation of nitrogen. In contrast, net accumulation of nitrogen was recorded in the aboveground live compartment, which had an STF value of 0.40. These results concur with decomposition estimates obtained in this study in which during the dry season, the belowground plant material had higher rates of decomposition than aboveground material.

Figure 20 below shows nitrogen cycling model during the wet season. The total soil nitrogen pool was 5152.8 g m^{-2} in the top 30 cm soil depth. Out of this, 3.63 g m^{-2} (0.07%) was in mineralized form whereas 5149.1 g m^{-2} was in the immobilized form. Total soil nitrogen during the wet season was significantly higher ($P<0.05$) than that during the dry season.

Fig. 20: Schematic synthesis of the nitrogen cycle on the Njemps flats ecosystem during the wet season.



KEY:

1. Values in triangle: Nitrogen inputs to the system (mg m^{-2}).
2. Values in boxes: Mean standing stock of nitrogen in compartments (mg m^{-2}).
3. Values on arrows (italics): System Transfer Functions.

* Not estimated in this study (negligible).

The standing stock of nitrogen in the belowground live compartment was 1550 mg m^{-2}, which was higher ($P<0.10$) than the standing stock of nitrogen in the same compartment during the dry season (930 mg m^{-2}). Mineralized nitrogen was transferred to the belowground live compartment with an STF of 0.43. This was indicative of a relative accumulation of the element in the mineralized nitrogen compartment. This observation is attributable to a flush increase in the total soil nitrogen and in particular mineral nitrogen content as a result of increased soil moisture content. The herbaceous vegetation was unable to take up this sudden increase in soil nitrogen.

The STF for movement of nitrogen from belowground live compartment to belowground dead compartment was 1.37. The standing stock of nitrogen in the latter compartment was 2130 mg m^{-2}. This was significantly higher ($P<0.05$) than the nitrogen content in the preceding compartment, as well as the same compartment during the dry season. It would be expected of the belowground live compartment to contain higher standing stock of nitrogen, since this compartment was a direct recipient of mineralized nitrogen. However, reasons for the observed trend can be two-fold. First, this being a wet season, there is rapid opportunistic growth of herbaceous vegetation thereby rapidly drawing on any belowground nutrients especially nitrogen. This is a common phenomenon in arid and semi-arid ecosystems (Beatley, 1974; Stoddart *et al.*, 1975; Veenendal, 1991; Karunaichamy and Paliwal, 1993). Secondly, the nitrogen content of the belowground dead compartment was partly contributed to by contamination by soil decomposer micro-organisms, thereby elevating the standing stock of nitrogen.

Nitrogen in the belowground dead compartment was translocated to the mineralized nitrogen compartment with an STF of 1.70. This was indicative of a net loss of nitrogen from the belowground dead compartment, which was attributed to faster rates of plant material decomposition during the wet season. Overall, the wet season increased the total soil nitrogen, and more importantly, mineralized nitrogen which became an input for the two belowground compartments, as well as the aboveground compartments.

Nitrogen contents of aboveground compartments were 2420 mg m^{-2}, 1050 mg m^{-2} and 2300 mg m^{-2} for the aboveground live, aboveground dead and litter compartments respectively. The STF for the movement of nitrogen from the belowground live to aboveground live was 1.58. This was indicative of a net loss of nitrogen from the belowground live compartment. This is due to movement of nitrogen into the

photosynthetic tissues in the aboveground live material (Aslam *et al* ., 1973; Devlin and Witham, 1983; Stevenson, 1986) since the wet season is a period of rapid growth of herbaceous vegetation in dryland ecosystems. An STF value of 0.43 was recorded between aboveground live and aboveground dead compartments of plant material. Therefore nitrogen was accumulated in the aboveground live compartment during the wet season, when plants are young and lush (Van Soest, 1982, Ekaya, 1991). From the aboveground dead compartment to the litter compartment, nitrogen was transferred with an STF value of 2.19, showing a rapid transfer of nitrogen from the aboveground dead compartment to the litter compartment. Therefore, a net loss of nitrogen from the aboveground dead compartment is implied. This can be attributed to both the rapid shedding of plant parts into the litter compartment as well as the elevation of the nitrogen content of the litter compartment due to contamination by the litter-decomposing organisms.

Nitrogen in litter was mineralized and transferred to the mineralized soil nitrogen pool with an STF of 1.58. This was an indication of net loss of nitrogen from the litter compartment. This is attributable to the higher rates of plant material decomposition recorded in this study during the wet season compared to the dry season, and the rapid entry of mineralized nitrogen into the mineral nitrogen pool, concomitant with the slow uptake by the belowground live compartment.

On the basis of the higher decomposition rates of both belowground and aboveground plant material during the wet season, as well as the STF values between compartments during the same season, it can be concluded that the cycling of nitrogen through the herbaceous layer was faster during the wet season. It can also be added that during the dry season, some plant material compartments essentially locked up nitrogen due to the lower rates of decomposition.

Although the nitrogen budget drawn up from this study is based on some assumptions, there are certain clear points that need to be stressed. First, most of the nitrogen in the system is in the soil rather than in the plant material. The plant material compartments accounted for only 0.003% and 0.002% of the total nitrogen during the dry and wet season respectively. This trend is a contrast to the pattern found in tropical forests, where the plant material contains a far higher proportion of the nutrients (Dickson and Pugh, 1974; Frost, 1984). The exchangeable fraction of the soil nitrogen pool is also relatively small.

Secondly, a higher proportion of the cycled nitrogen went through the aboveground compartments. During the dry season, 67% of the nitrogen in the plant material was in the aboveground compartments, whereas in the wet season, aboveground compartments cycled 62% of the nitrogen. These findings are in agreement with those on energy flow in this study. However, they conflict with those of Singh *et al.*,(1979) who reported that 53%-73% of the cycled nitrogen in Indian semi-arid grasslands followed the belowground pathway. This difference in findings is related to the differences in herbaceous vegetation types. The Indian semi-arid grasslands were dominated by perennial grasses which accumulate nutrient reserves in their root systems especially during the dry season (Trlica, 1977; Stoddart *et al.*,1975). At the onset of the wet season, the plants draw on the reserves at the start of regrowth. In the current study, however, the herbaceous vegetation was mainly annual and ephemeral. These are opportunistic in their growth such that when conditions are favourable, they dedicate a lot of their energy to the aboveground photosynthetic tissues for maximum growth in order to complete their life cycle before harsh environmental conditions set in (Beatley, 1974; Angevine and Chabot, 1979; Breman and Cisse, 1979; Ernst and Tolsma, 1988; Veenendaal, 1991). Therefore, more nutrients will be found in the aboveground biomass.

Thirdly, that the plants do not make full use of the available nitrogen may reflect limitations on nutrient uptake arising from relatively low soil moisture level especially during the dry months of the year. Frost (1984) recorded similar findings from the *Burkea* savanna ecosystem in southern Africa.

According to de Angelis (1980), the rate at which an ecosystem recovers from perturbations to its nutrient cycle(s) is related to the turnover times of nutrients in that system. For the Njemps flats ecosystem, the nitrogen cycle through the herbaceous layer is unstable and quite susceptible to perturbations because of the relatively small plant nutrient pool and the sensitivity of herbaceous production to rainfall variations as well as other forces like fire and herbivory. However, compared to the general nitrogen cycle in a forest ecosystem, which is characterized by a higher proportion of nutrients in aboveground plant material and a low rate of nutrient turnover, the more rapid rate of nutrient turnover in the herbaceous layer would counterbalance the lowered stability of the system by speeding up its rate of recovery from perturbation. The same phenomenon has been observed in tropical

grasslands dominated by perennial grasses (Isichei, 1980; Hunt, 1983; Frost, 1984; Filet *et al.*, 1986).

5.0 SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

The structure and function of a rangeland ecosystem on the Njemps flats of Baringo district was studied with the aim of developing a conceptual model. Primary production and productivity, and the energy flow and nitrogen cycling characteristics of the herbaceous layer were estimated.

The study site was characterized by low, erratic and localized rainfall, which was equal to about only one third of the evaporative demand in the area. Temperatures remained high year long, whereas relative humidity was generally low. This combination of climatic factors implied a high rate of moisture loss from soil and plant surfaces, thereby increasing the deficiency in moisture. Higher relative humidity tended to coincide with wet months. Soils at the study site were silty loams with low mean nitrogen and organic matter contents.

Primary production exhibited high variability, and closely followed but lagged behind the rainfall trend. Rainfall peaks preceded peaks in both aboveground and belowground standing crop. Peaks in aboveground standing crop closely followed peaks in rainfall. This was also the case for the belowground standing crop. Higher aboveground primary production was recorded in 1993, during which there was a higher total rainfall amount than in 1992.

Peaks in total belowground standing crop coincided with peaks in aboveground standing crop, and were all preceded by rainfall peaks. The same was the case for belowground live and dead standing crop.

Peak Aboveground:Belowground plant material ratios in 1992 occurred in March and October whereas in 1993, peaks were recorded in April, August and December. All the peaks had ratios greater than 1.00, meaning presence of higher quantity of aboveground standing crop than belowground. All peaks either coincided with or closely followed the rainfall peaks.

Over the two years of study, troughs rather than peaks characterized the trend in litter production. These troughs in litter production coincided with rainfall peaks. However, the low quantity of discernible litter on the ground may have been caused by smothering of litter by physical agents like rainfall and strong winds, since during the same months, the rate of decomposition of plant material was low.

Dicot and grass material had similar rates of decomposition. Except for only four

months, rates of decomposition for belowground material were consistently higher than those for aboveground material. The three conspicuous decomposition peaks coincided with rainfall peaks, thus indicating that availability of moisture stimulates decomposition of plant material. In other words moisture is limiting for the decomposing of plant material during certain times of the year, when rainfall is not received. Due to this, there is accumulation of plant material on the soil surface, which means that nutrients are locked up in the material. From the findings of this study, therefore, belowground material was more important in intra-system nutrient release and cycling and energy flow. This conclusion is in agreement and further supported by findings on nitrogen cycling in this study.

Higher NPP and primary productivity was recorded in 1993, during which higher rainfall amount was received. Rainfall peaks preceded all peaks in NPP. Annual NPP values from the current study are higher than those reported from a number of east African grasslands, despite the latter having higher rainfall. This is attributable to the flawed methods used in the previous studies. The methods include maximum standing crop method, International Biological Programme Standard method and the maximum-minimum method (Roberts *et al.*, 1993). These methods ignored belowground plant material as well as decomposition. Underestimation of NPP and productivity of tropical grasslands due to the shortcomings of the methods previously used is estimated to lie between 2% and 69% (Kinyamario and Imbamba, 1992). Tropical grassland ecosystems are therefore more productive than is currently thought. This high primary productivity puts the areas under sharp focus as potential CO_2 sinks, thus playing a significant role in the amelioration of climate change resulting from the green house effect. Research is imperative, in order to understand the role of these ecosystems in global climate amelioration.

Species diversity was high during and/or immediately after the wet months, when number of species were highest. High species diversity is indicative of complexity in community, due to the larger array of interactions between species. The interactions involve energy transfers, predation, competition and niche apportionment which are more complex and varied under diversity (Brower *et al.*, 1990; Hurlburt, 1971). High species diversity has been linked to community stability (Woodwell and Smith, 1969; May, 1975) in that random changes affecting species tend to compensate each other.

Turnover rate and time varied between years and compartments. Aboveground biomass had the highest turnover rate, closely followed by the grass litter and live

belowground compartments. The dead aboveground compartment recorded the lowest turnover rate. The high turnover rate of the aboveground biomass is attributable to the rapid plant growth response to rainfall in dryland ecosystems, resulting in a sudden increase in the size of the biomass compartments. Due to the short lifespan of the dominant ephemeral plants, the biomass is quickly transferred to dead plant material compartments. The low turnover rates of dead aboveground and belowground compartments are primarily due to their low rates of decomposition reported in this study. Climatic and methodological differences between the current study and previous ones, e.g. Strugnell and Pigott (1979), Misra and Misra (1979) and Kinyamario and Imbamba (1992), explain the differences in the reported values. Turnover time was highest for those compartments with the lowest turnover rates.

Aboveground live and dead plant material compartments had one and a half times more standing crop of energy during the dry season compared to the wet season. There was net loss of energy from the aboveground dead compartment during the dry season. During the dry season, the litter compartment had more standing crop of energy than during the wet season. There was net loss of energy from the litter compartment during both seasons. This is attributable to decomposition of litter by micro-organisms and arthropods. Higher amount of energy was dissipated from the system during the dry season.

Belowground live compartment had similar quantity of standing crop of energy during both seasons, during which there was net loss of energy from the aboveground live compartment. Higher quantity of energy was dissipated from the belowground dead compartment during the dry season compared to the wet season. This is attributable to the lower decomposition rates during the dry season coupled with higher stocks of compartmental energy contents during the same season. For both the dry and wet season, a larger proportion of the energy that flowed through the ecosystem followed the aboveground pathway.

Overall, irrespective of season, the rangeland ecosystem was in a non-equilibrium state with respect to energy flow. This is as a result of net accumulation of energy in the aboveground live compartment during both seasons, and net loss of energy from other compartments.

During the dry season, highest nitrogen content in the aboveground plant

compartments was recorded in the live dicots. In the belowground compartments, the live material had the highest nitrogen content. Overall, lowest compartmental nitrogen content during the dry season was in the aboveground dead grass compartment. The higher nitrogen content of dicot compartments is related to their higher nitrogen content as compared to grasses. The high nitrogen content of the litter compartment is attributable to contamination by litter decomposing micro-organisms as well as the presence of dicot plant material.

During the wet season, highest nitrogen content among aboveground compartments was recorded in the litter compartment. The lowest value was for the aboveground dead grass compartment. Among the belowground compartments, the live material had highest value. The low nitrogen content of the dead grass compartment is attributable to the rapid decline in nitrogen content of grasses with advancement in age. Overall, the herbaceous layer had higher standing crop of nitrogen during the wet season.

Incubation of dry season soils generally revealed that ammonification was favoured over nitrification. NH_4^+-N values were consistently above those of NO_3^--N up to the end of incubation at the 12^{th} week. Soil pH remained within narrow limits throughout the incubation period.

At the start of incubation of the wet season soil, the NO_3^--N content was more than double the NH_4^+-N content. This trend was maintained up to the 6^{th} week, from which NH_4^+-N content was consistently above that of NO_3^--N. Higher soil mineral nitrogen content was recorded during the wet season. This was attributed to the increased soil microbial activity and plant material decomposition during the wet season due to injection of moisture into the system. Moisture plays a significant role in dryland ecosystem function.

During the dry season, mineralized nitrogen constituted 0.05% of the total soil nitrogen pool. Among the aboveground plant material compartments, highest standing crop of nitrogen was in the live material compartment, followed by the litter compartment and the dead plant material compartment. The high value recorded for the litter compartment is attributable to the contamination of litter by decomposer micro-organisms.

There was an accumulation of nitrogen in the aboveground live compartment. This is attributed to the dominance of the herbaceous vegetation by dicots, which contain higher nitrogen contents and live longer into the dry season than annual and ephemeral grasses. Generally, there was an accumulation of nitrogen in the mineralized nitrogen pool, partly

attributable to the low soil moisture content during the dry season, and transfer of nitrogen from the belowground live compartment to the aboveground live compartment.

There was a net loss of nitrogen from the belowground live compartment. Overall, during the dry season, belowground plant material compartments were more important in nitrogen cycling than aboveground compartments. This is further enhanced by the faster rates of belowground plant material decomposition during the dry season.

During the wet season, mineralized nitrogen constituted 0.07%. Standing stock of nitrogen in the belowground live compartment was higher than that in the same compartment during the dry season. A net loss of nitrogen from the belowground dead compartment was recorded, and was attributed to the faster rates of plant material decomposition during the wet season. Among the aboveground compartments, the live material compartment had the highest nitrogen content. This was followed by the litter and the dead plant material compartments. There was accumulation of nitrogen in the aboveground live compartment. A net loss of nitrogen was recorded in the aboveground dead compartment.

On the basis of the higher decomposition rates of both belowground and aboveground plant material during the wet season, and the recorded STF values, cycling of nitrogen through the herbaceous layer was faster during the wet season than during the dry season. During the dry season, nitrogen was locked up in some plant material compartments due to the lower rates of decomposition. Certain key points characterize the synthesized nitrogen cycle;

(a) a larger proportion of the nitrogen was held in the soil rather than in the vegetation,

(b) a larger proportion of the cycled nitrogen went through the aboveground compartment. However, due to the faster decomposition rates of belowground plant material, the belowground component played a more significant role in the cycling of nitrogen throughout the year, and

(c) plants do not make full use of the available (mineralized) nitrogen apparently partly due to moisture deficiency, thus limiting both primary production and the need for, as well as the uptake of nitrogen.

Overall, the structure and function of the herbaceous layer on the Njemps flats rangeland ecosystem is episodic in nature and closely correlated with the rainfall trend. The annual growth period consists of a few to several days within the expected wet season, with

subsidiary growth periods randomly spread over the year. The dominant ephemeral and annual plants are short-lived and the nutritious green tissues senesce rapidly. Rhythms of rainfall and herbaceous production are not necessarily uniformly distributed over large areas. As a result, total annual NPP consists of the summation of short pulses of growth events that are randomly distributed within the year following rainfall events. Trends in the yields of all categories of plant material and decomposition of dead plant material closely followed the rainfall trend, higher values being recorded during the wet months. Ecosystem function was in a non-equilibrium state, with net accumulation and net loss of energy and nitrogen occurring in some of the ecosystem compartments.

The structural and functional characteristics dictate that management and utilization will not be a matter of adhering to a single pre-planned rigid strategy, which will apply in all circumstances. Instead, management and utilization will be highly flexible and opportunistic in nature, the object of which should be to seize opportunities and to reduce risks as much as possible. A key risk management mechanism would be the opportunistic harvest of energy and nutrients by herbivore species through mobility in search of plant biomass, and multi-species grazing for efficient use of the various species of plant biomass. Others include various buffer mechanisms such as multiple-use alternatives of dryland ecosystems e.g. dryland farming in suitable areas, bee-keeping, eco-tourism and integration into the mainstream economies of the countries as a buffer against changing ecological, socio-economic and socio-political environment.

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7.0 APPENDICES

Appendix 1: A list of plant species encountered at the study site.

(a). Trees and shrubs

Acacia tortilis
Acacia reficiens
Prosopis chilensis
Cordia sinensis

(b). Non-woody dicots

Aerva lanata
Berlaria arcanthoides
Cassia spectabilis
Hibiscus aponeurus
Hibiscus micranthus
Indigofera erecta
Indigofera tinctoria
Justicia flava
Ruellia patula
Solanum incanum
Tephrosia pumila
Ocimum kilimandscharicum

(c). Grasses

Aristida keniensis
Brachiaria pubifolia
Cenchrus cilliaris
Chloris pychnothrix
Chloris virgata
Cymbopogon caesius
Cynodon dactylon
Digitaria velutina
Eragrostis cillianensis
Setaria verticillata
Tetrapogon tenellus
Heliotropium steudneri

Appendix 2: Aboveground and belowground dead plant material rates of decomposition (g g^{-1} day^{-1})

	(i). Aboveground plant material.		(ii). Belowground plant material	
1992			1992	
	Jan.	—	Jan.	—
	Feb.	—	Feb.	—
	Mar.	—	Mar.	—
	Apr.	0.046	Apr.	0.059
	May	0.018	May	0.020
	Jun.	0.018	Jun.	0.020
	Jul.	0.029	Jul.	0.030
	Aug.	0.029	Aug.	0.025
	Sep.	0.028	Sep.	0.016
	Oct.	0.027	Oct.	0.017
	Nov.	0.084	Nov.	0.062
	Dec.	0.037	Dec.	0.022
1993	Jan.	0.005	1993 Jan.	0.009
	Feb.	0.013	Feb.	0.016
	Mar.	0.017	Mar.	0.023
	Apr.	0.043	Apr.	0.044
	May	0.012	May	0.027
	Jun.	0.011	Jun.	0.024
	Jul.	0.010	Jul.	0.048
	Aug.	0.015	Aug.	0.021
	Sep.	0.017	Sep.	0.020
	Oct.	0.015	Oct.	0.020
	Nov.	0.056	Nov.	0.058
	Dec.	0.020	Dec.	0.020

Appendix 3: Quantification of the soil nitrogen compartments during the dry season.

(i). Total soil nitrogen (from laboratory analysis) = 0.84% = **0.0084 g N/g soil.**

(ii). Unit volume of soil used (basis of quantification) = 1m x 1m x 30cm = **300,000 cm^3**

(iii). Bulk density of the soil = **1.13 g/cm^3**

(iv). Therefore, weight of the soil in the unit volume = 300000cm^3 x 1.13 g/cm^3

=339,000g

(v). Total nitrogen in the soil ($g\ m^{-2}$) = 0.0084 $g\ g^{-1}$ soil x 339000 $g\ m^{-2}$ = **2847.6 $g\ m^{-2}$**

(vi). Mineralized nitrogen (from mineralization experiment) = 4.9 $\mu g\ g^{-1}$ soil;
Therefore, total mineralized nitrogen/m^2 = 4.9 $\mu g\ g^{-1}$ x 339,000g= 1661100 µg
= 1661.1 mg m^{-2}

(vii). Immobilized nitrogen therefore = 2847.6 $g\ m^{-2}$ – 1.661 $g\ m^{-2}$ = **2845.9 $g\ m^{-2}$**

Appendix 4: Quantification of the soil nitrogen compartments during the wet season.

(i). Total soil nitrogen (from laboratory analysis) = 1.52% = **0.0152 g N/g soil.**

(ii). Unit volume of soil used (basis of quantification) = 1m x 1m x 30cm = **300,000 cm^3**

(iii). Bulk density of the soil = **1.13 g/cm^3**

(iv). Therefore, weight of the soil in the unit volume = 300000cm^3 x 1.13 g/cm^3
=339,000g

(v). Total nitrogen in the soil ($g\ m^{-2}$) = 0.0152 $g\ g^{-1}$ soil x 339000 $g\ m^{-2}$ = **5152.8 $g\ m^{-2}$**

(vi). Mineralized nitrogen (from mineralization experiment)= 10.7 $\mu g\ g^{-1}$ soil;Therefore, total mineralized nitrogen/m^2 = 10.7 $\mu g\ g^{-1}$ x 339,000 $g\ m^{-2}$ = 3627300 µg
= 3627.3 $mg\ m^{-2}$

(vii). Immobilized nitrogen therefore = 5152.8 $g\ m^{-2}$ – 3.627 $g\ m^{-2}$ = **5149.1 $g\ m^{-2}$**

Appendix 5: Mineralizable soil nitrogen content (μg g^{-1}) and pH of soil during the dry season.

Time (weeks)	Ammonium N	Nitrate N	pH (water)
0	1.3	3.6	6.7
2	6.8	5.4	6.8
4	12.3	6.5	6.7
6	16.6	10.1	6.5
8	21.3	13.6	6.4
10	24.3	21.9	6.4
12	25.1	22.6	6.7

Appendix 6: Mineralizable soil nitrogen content (μg g^{-1}) and pH of soil during the wet season.

Time (weeks)	Ammonium N	Nitrate N	pH (water)
0	3.3	7.4	6.9
2	9.6	12.7	7.3
4	15.3	15.3	7.9
6	22.1	19.5	8.2
8	28.3	24.6	8.7
10	33.0	26.3	8.8
12	34.2	27.4	8.8