# FORAGE INTAKE AND NUTRITIVE VALUE OF SHEEP AND GOAT DIETS IN SOUTH-EASTERN KENYA



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

To my parents, brothers and sisters whose constant encouragement since childhood has enabled me to reach this level of academic achievement.

**ABSTRACT**

The forage intake, botanical composition and nutritive value of diets selected by free-ranging sheep and goats grazing together in south-eastern Kenya were determined. Forage intake was estimated using chromium sesquioxide orally administered daily to the animals. Dietary botanical composition was determined using the microhistological faecal analysis technique, whereas quality of simulated diet samples was determined by chemical analysis for crude protein, neutral detergent fibre, acid detergent fibre, lignin, total ash and *in vitro* dry and organic matter digestibilities.

Dry matter intake in g/day was similar ($P > 0.05$) for sheep and goats within a given season, but in terms of metabolic bodyweight (g/kg $W^{0.75}$), it was significantly lower ($P < 0.05$) for goats compared to sheep during the dry season. Dry matter intake averaged 471.3 g/day or 2% of bodyweight and 500.3 g/day or 2.5% of bodyweight for goats and sheep, respectively. The lowest levels of intake for both species (1.6% for goats and 2.0% for sheep) were recorded during the wet season. Overall, sheep consumed 53.0 g/kg $W^{0.75}$ while goats had an average intake of 43.6 g/kg $W^{0.75}$.

Goats selected diets that were higher ($P < 0.05$) in crude protein than did sheep i.e 16.4% and 13.5%, respectively when averaged across the two seasons. Sheep diets had lower ($P < 0.05$) levels of lignin during the wet season compared to goats but the lignin contents for both were the same during the dry season. Goats, however, selected diets lower in neutral detergent fibre and

acid detergent fibre than did sheep. Goats were found to be better adapted for survival in this environment than sheep.

*In vitro* dry matter digestibility of simulated diets were not different between goats and sheep i.e 56.2% and 55.6%, respectively. *In vitro* organic matter digestibility also did not differ between the two livestock species i.e 55.1% and 56.5% for goats and sheep, respectively. Digestibility coefficients of the diets of both animal species were significantly higher ($P < 0.05$) for the wet season than the dry season diets.

Goats' diets consisted mainly of browse (> 81%) while those of sheep comprised mainly grasses (> 77%) during both seasons. Goats consumed very little forbs (> 2%) whereas browse was the least utilized forage category by sheep (< 8%). Neither species showed significant change ($P > 0.05$) in the proportions of grass, forbs or browse in their diets with change of season, and no single plant dominated the diets of either livestock species. Sheep and goats were therefore complimentary in their feeding in both seasons.

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TABLE OF CONTENTS

## LIST OF FIGURES

## LIST OF TABLES

## LIST OF APPENDICES

# 1. INTRODUCTION

The arid and semi-arid areas cover about 47% of the total land mass of the world (Heady 1975). In Kenya, they comprise more than 80% of the country's total land surface (Pratt and Gwynne 1977) and carry over 25% of the human population and more than half of the livestock population (Government of Kenya 1989). These areas are characterised by inadequate rainfall to support rainfed agriculture and are therefore of low production potential, being used predominantly for pastoralism, tourism and recreational activities.

Bernstein and Jacobs (1983) reported that about 50% of Kenya's cattle herd, 78% of small stock, 99% of the camels and over 90% of the wildlife populations are found in the rangelands, where they depend almost entirely on natural vegetation for their nutritional requirements and production. These domestic animals play a major role in both local and national economies. Mostly, local breeds which are of low productivity in terms of birthweight, growth rate, weaning and mature weights and carcass quality are raised.

Rangelands support a very heterogenous vegetation including grasses, forbs, shrubs and trees. The rangelands also support an equally diverse population of wild and domestic herbivores with varying grazing habits and plant species preferences. Sheep and goats are dominant livestock species of the world's rangelands where they are usually herded together with cattle and camels especially in Africa where they compete for various forage resources. They play a special role in the socio-economic aspects of pastoral and agro-pastoral communities. Under typical pastoral production systems, when the large domestic ruminants have migrated to the dry season grazing areas, sheep and goats are usually left behind to provide milk and meat to the family, utilizing forage resources around the homesteads.

Knowledge of the food habits (forage consumption, diet selection and quality, etc) of herbivores is essential for improvement of their nutrition and efficiency of utilization of range resources. Such information could contribute to better understanding of the dietary interrelationships and potential food competition between animals to better utilize the range vegetation. This would assist range managers in planning multiple use of the range while sustaining these resources. Data on comparative diet selection by sheep and goats would permit better estimation of grazing capacity on common use ranges. Otherwise, without due regard to sustainable resource utilization, efforts to maximize immediate production without proper grazing management results in depleted range (Ayuko 1978, Bernstein and Jacobs 1983), and the selection patterns of the livestock are inadvertently altered (Mnene and Stuth 1986).

Data on nutrient intake by free-ranging animals from the range is necessary to establish whether their nutrient requirements are being met. Implementation of effective grazing management systems requires that this information be coupled with data on nutrient requirements of the various kinds and classes of animals. Unfortunately, such data is not readily available for Kenya's diverse arid and semi-arid regions.

Efficiency of animal production is closely related to the nutritional value of the available forage. However, owing to the low and erratic rainfall regimes in range areas, there is a wide seasonal fluctuation in quantity and quality of forage which poses a major problem to livestock production since animals occasionally undergo periods of nutritional stress particularly during the dry season (Kayongo-Male and Field 1981, Loosli and McDowell 1985, McDowell 1985). Under such conditions, the survivability of goats has been higher than other domestic livestock possibly due to their unique aspects of diet selection and feeding behaviour, thus requiring minimal supplemental feeding. Hansen et al. (1986) observed that the nutritional characteristics of the diets selected by range livestock from various vegetation types during different seasons are not adequately known, hence the need for more research.

Forage quality is a function of its nutrient content, digestibility and intake by the animal. Consumption sets the limit to input of all nutrients including minerals and under extensive grazing conditions herbage intake is usually the main factor affecting animal performance. Intake and digestibility of grazed forages have been areas of interest and challenge to animal nutritionists for a long time and substantial research has been carried out. However, although volumes of data are available for animal responses to pen-feeding trials, only meagre information is available about animals that graze the natural vegetation (Hansen et al. 1986). Inferences made from studies using confined animals or those carried out in different ecological areas are not directly applicable to the extensive grazing systems encountered in our range areas.

It was against this background that this study was conceived and designed with the following objectives:

1. To determine the seasonal forage intake of free-ranging sheep and goats.
2. To determine the botanical composition of the diets selected by free-ranging sheep and goats.
3. To determine the nutritive value of the diets selected on a seasonal basis by free-ranging sheep and goats in Kibwezi area within the southern rangelands of Kenya.

# 2. LITERATURE REVIEW

## 2.1 Nutrient intake

The major factor limiting animal production from natural forage is the quantity of useful energy consumed by the ruminant (Crampton 1957). Feed intake and quality are two major controlling factors to livestock production because they determine liveweight gain and reproductive success of the animal (Crowder 1985). When animals are maintained under normal conditions, dry matter intake is influenced primarily by body size, energy density of the diet and the rate of digestion or fermentation (McDowell 1985). Nutrient intake is a function of daily dry matter consumed and the portion of that dry matter which is digested (Van Soest 1982). As observed by Blaxter (1962) and Soneji (1970), the most efficient animals are likely to be those that consume most feed per unit bodyweight.

In range areas, pasture quality and quantity change with seasons (Karue 1975, Kayongo-Male and Field 1981), hence intake, digestibility and chemical composition of the diets selected by livestock are expected to vary accordingly. Mnene (1985), working with cattle at Kiboko in south-eastern Kenya, found that season had a strong effect on dietary crude protein and energy intakes but had little effect on *in vitro* digestibility of the diets. Cattle had near or below maintenance levels of crude protein and energy intake during the dry and beginning of the wet seasons, respectively. Despite high dietary crude protein during the wet season, energy concentration was low, resulting in reduced organic matter intake. The existence of a significant difference in dietary crude protein between the wet and dry seasons, alone or together with *in vitro* organic matter digestibility, could have caused a significant decline in intake. Pfister and Malechek (1986) in Brazil reported that the lowest levels of feed intake by local sheep and goats were found during the wet season when nutritional quality of the forage was highest. Animal activity and weight responses suggested that low intake of digestible energy was seriously limiting animal performance during the dry season.

Forage intake and digestibility are both related to various forage characteristics particularly the chemical composition. Homb and Brierem (1952), Van Soest (1982) and Tessema (1986) reported a high correlation between dietary crude protein with digestibility, suggesting that intake is directly related to diet quality and that crude protein was a better predictor of digestibility than any of the other components of the diet. Both intake and digestibility are depressed when crude protein level falls below 7% which is the minimum nitrogen requirement of rumen bacteria (Migongo-Bake 1984, Milford and Minson 1966, Tessema 1986). A low protein diet reduces microbial fibre digestion in the rumen leading to a fall in cellulose and hemicellulose digestion (Smith *et al*. 1971, 1972). This seriously affects the proportion of energy intake used for maintenance and, in most cases, causes animals to lose weight (Provenza and Malechek 1984). Since dietary crude protein in the rangelands varies with seasons (Kibet 1984, Olubajo and Oyenuga 1974), herbage intake would subsequently be expected to vary.

There is a decline in digestibility with increasing fibre content of the diet (Van Soest 1965). Of the various fibre components, Tessema (1986) found that cellulose was the most negatively correlated (r = -0.86) to digestibility, exceeding lignin (r = -0.78). Proportional increases in the quantity of indigestible fibrous residues accompany decreases in digestibility resulting in greater retention time of the ingesta and consequently, a decline in herbage intake (Blaxter et al. 1961, Van Soest 1965).

The relationship between various forage constituents and intake ultimately depends on their association with plant structural components. Thus, cellulose is more closely related to intake than to digestibility as an aspect of bulk; conversely, lignin is more closely related to digestibility than to intake (Van Soest 1982). In all, total structural carbohydrates, i.e. plant cell wall, are the most consistent factors related to intake (Van Soest 1965, Osbourn et al. 1974). As this fraction increases beyond 55 to 60% of the dry matter, voluntary intake decreases at an increasing rate. Milford and Minson (1965a) reported that the cell wall content of tropical grasses is more or less constant and is, therefore, a less critical variable as far as ingestion of these plant species is concerned. Intake is also limited by dietary bulk and subsequent distension of the digestive tract, although bulk volume is less well related to voluntary intake than cell wall content (Van Soest 1982).

The inter-relationships between forage intake, digestibility and chemical composition are species-specific. For instance, although legumes and browse have higher lignin contents than grasses, they are consumed more than grasses of comparable digestibility (Crampton 1957, Bogdan and Mwahka 1970, Milford and Minson 1966, Van Soest 1982). Intake is dependent upon the structural volume and therefore cell wall content, while digestibility is dependent upon both cell walls and their availability to digestion as determined by lignification and other factors.

Intake and digestibility are closely interrelated such that digestibility is depressed at higher intakes due to competition between digestion and passage rates, the influence of which is largest upon the slowest digesting fraction contained in the plant cell wall (Van Soest 1982). If poor quality feeds contain factors limiting intake such as bulk or dietary deficiency, a positive relationship exists between herbage intake and digestibility (Conrad 1966). He suggested that the point of maximum dry matter intake occurred at about 67% apparent digestibility when concentrate-alfalfa combinations were fed to lactating dairy cattle. Other studies suggest that this point is not fixed, but is dependent upon the nutrient/energy density of the diet and the energy demand of the animal. When availability is not limiting, intake increases until it reaches a critical herbage allowance where the animal is at or near maximum intake, at which point herbage digestibility becomes the governing factor (Jamieson and

Hodgeson 1979). Assuming that animals eat to satiety, the consumption of a less digestible diet must be more than a more digestible one in order to achieve the required level of digestible calories. However, this assumption is refuted by the fact that the linear relationship between herbage digestibility and intake has been shown to hold true even at 53 to 63% digestibility range of forages (Hodgeson et al. 1977, Van Soest 1982).

Advance in maturity of forage has been shown to depress mean voluntary intake (Dougall and Bogdan 1958, Pieper et al. 1959, Cordova et al. 1978), and most patterns of forage consumption could be explained in terms of plant maturity. Intake reaches a peak with the new growth after the rainy season starts and declines thereafter. Data from studies utilizing native Hyparrhenia rufa pasture showed that Bos indicus steers consumed dry matter equivalent to 1.2% of their body weight when herbage contained 50% digestible organic matter, but as the dry season progressed, intake of that forage fell to 0.8% of body weight when digestible organic matter dropped to 38% (Smith 1962). It is possible, however, that good correlation between intake and digestibility of forage as plants mature may be coincidental rather than a cause-and-effect relationship. In most cases, correlation coefficients between the two are too low to suggest that digestibility per se is the only or even the primary factor controlling forage intake (Cordova et al. 1978). The relationship between intake and forage maturity is apparently more variable than that between digestibility and forage maturity (Milford and Minson 1965a, Heaney et al. 1966).

A major limitation to nutritional studies with grazing ruminants is that there is no simple and reliable technique for measuring intake and digestibility of forage by free-grazing animals (Gwaiseuk and Holmes 1986, Leaver 1982). One of the factors affecting precision of intake measurements is the high individual variability between animals, thus necessitating large numbers of animals to detect significant differences between treatments when evaluating forages and pastures (Van Dyne and Meyer 1964). Several workers have shown that more animals are required to study intake than other parameters of animal grazing behaviour (Van Dyne and Meyer 1964, Obioha et al. 1970). However, cost and management of such large numbers of animals might be prohibitive.

## 2.2 Diet quality

The importance of plants as a source of forage for both livestock and wildlife is determined by their availability, palatability and nutritive value (Lusigi et al. 1984). The quality of forage may be viewed in terms of the concentration of digestible nutrients and concentration of components that limit digestibility such as fibre, lignin, silica and tannins (Hart et al. 1983). It is also affected by factors such as climate and soil conditions (Semenye 1987), plant species and part and the stage of maturity of the plants (Hart et al. 1983, Stobbs and Minson 1979).

The utility derived from forage eaten by herbivores largely depends on the availability of the various nutrients to the animal's body. This is affected by the concentration of secondary components like tannins, lignin and cutin which are associated with plant cell walls and are almost indigestible (Provenza and Malechek 1984, Hansen et al. 1973). These compounds physically inhibit the digestion of the enclosed cell nutrients and thus decrease the amount of substrate accessible for bacterial action (Stobbs and Minson 1979, Jung and Vogel 1986, Leng 1990). Other secondary plant metabolites such as volatile oils and alkaloids interfere with digestion mechanisms in the animal due to their toxic effects or through enzyme inhibition and substrate binding in the digestive tract (Reed 1984, Van Soest 1982). This in effect reduces the microbial populations and subsequently the digestibility of the diet. Tannins also have a protein-precipitating action which reduces the level of available nitrogen for rumen micro-organisms.

Although both grasses and browse show an increase in lignin with advancing maturity, browse plants contained two to three times more lignin than grasses at comparable stages of growth (Ekaya 1991). Jung and Vogel (1986) attributed this to contamination of acid detergent lignin with cutin, which occurs in high levels in browse plants. In vitro digestibility subsequently declines due to lignification of the cell walls in combination with inadequate nitrogen for rumen microbes due to low crude protein in mature forages.

The leaf to stem ratio has been reported to influence the nutritive value of the herbage consumed by animals (Wallace et al. 1972, Milford and Minson 1965a,b). More leaves in the diet implies better quality since leaves are more nutritious (higher crude protein and lower total fibre) and are of higher digestibility than stems (Milford and Minson 1965b), although in a few cases no relationship could be found between the leaf to stem ratio and nutritive value of tropical grasses. Furthermore, reduced herbage availability resulting from intense forage use leads to selection of diets low in digestibility and crude protein due to increased stems in the diet (Hodgeson et al. 1977, Heady 1964).

Mnene and Stuth (1986) concluded that season was the single most important factor determining the amount of available herbage, browse, leaf and live components of the forage. Consequently, season influenced the composition and nutritive value of the diets selected by cattle. Selection of more leaf and live components by the animals during the wet season did not affect the diet digestibility, mainly because of high content of browse which contains digestibility depressants. Therefore, while wet season diets may be nutritionally superior to the dry season diets, the presence of high amounts of browse could hinder availability of the nutrients to the animal.

Most forage plants in the range areas have high proportions of structural carbohydrates which are deposited in the plant tissues at an early vegetational stage. As seasons progress and plants mature, the nutritive value of range forages generally declines. This is often associated with a decrease in crude protein, phosphorus and digestible dry matter, coupled with an increase in crude fibre and lignin (Stobbs and Minson 1979, Milford and Minson 1965a, Hart et al. 1983). Since rangeland vegetation types differ in botanical composition and phenology during different seasons, diet quality is expected to fluctuate accordingly. Range forage quality is highly correlated with progression in plant phenology, and large ungulates which utilize the range on a seasonal or year-round basis tend to follow this progression by selective grazing (Schwartz and Ellis 1981).

The dry season is therefore a potential period of nutrient deprivation for range animals due to forage maturity and the inevitable decline in quality, often to levels that are unable to support the energy requirements of grass-dependent ruminants (Karue 1974, 1975; Van Soest 1982, Tessema 1986, Shaabani et al. 1986). This is especially so for grasses than for browse; the latter are much higher in crude protein content at all stages of growth (Otsyina and McKell 1985) and the decline in their crude protein content is more gradual. The time of high nutritional value for grasses is limited to a short period of rapid growth during the vegetative stage and their crude protein content shows the greatest change per unit of time (Tessema 1986, Ekaya 1991). A critical level of crude protein in mature grass was given by Stobbs and Minson (1979) as between 6 to 8% of the dry matter. However, most of the grass species found in arid and semi-arid lands are deficient in protein during the dry season (Kirui 1995).

The relative digestive abilities of sheep and goats is controversial. Devandra (1978), Gihad (1976), Sharma and Rajora (1970) and Migongo-Bake et al. (1986) found that goats digest fibre better than sheep or cattle, a factor which probably enables goats to adapt better to poor environments where they convert low quality materials into products needed for human use. On the other hand, Pfister and Malechek (1986) found evidence to the contrary with sheep selecting diets lower in lignin, equal levels of cell wall fibre and higher *in vitro* organic matter digestibility compared to goats. Goats, however, selected diets higher in crude protein than did sheep.

## 2.3 Diet selection by sheep and goats.

A conceptual framework for understanding the reasons why ungulates select the kinds of food that they do was put forward by Hanley (1982) and tested by Hanley and Hanley (1982). It consists of four morphological parameters namely body size, type of digestive system, rumino-reticular volume to bodyweight ratio and mouth size. According to Hanley (1982), diet selection may be viewed as both a strategic and tactical adaptation. Strategies include optimizing energy expended in food gathering, minimizing feeding time and ensuring a balanced intake of nutrients. This view-point emphasizes that certain ultimate strategies of diet selection arose as a result of natural selection. Tactics vary with species and environment, and the major dietary selection components are food availability, consumer food preference, food requirements and consumer selectivity.

Under most circumstances, therefore, livestock graze selectively, preferring certain plant species and parts to others; thus, the quality and botanical composition of the diets selected by grazing animals differ from forage available in the pastures (Arnold 1960, Hardison et al. 1954, Kibet 1984). Forage selectivity is determined by preference and palatability factors (Heady 1964). Palatability factors are attributes of plants that affect their acceptability to grazing animals including availability, chemical composition, proportion of plant parts, phenology, external plant form and associated feed elements. Preference factors are attributes associated with the grazing animal that control food acceptability such as internal animal factors (senses and physiological condition), learned or evolved behaviour and environmental influence (Heady 1964, Arnold 1981, Holechek et al. 1982).

The composition of herbivore diets varies considerably within and between seasons, even within the same range. Kibet (1984) observed that heifer diets contained a great diversity of plant species when forages were green but were limited to what was available when species were mature during the dry season. In their study, Galt et al. (1969) reported that leaves comprised the majority of plant parts in cattle diets. However, as the dormant season advanced more stems were consumed. The increase in stem component has also been observed as vegetation matures or as intensity of grazing increases (Allison and Kothman 1979). During the dry season when herbaceous vegetation is either dormant or dead, any plant part may be consumed (Theron and Booysen 1966). Differences between seasons in dietary selection have been associated with mainly a decrease in certain species of grass or forbs and an increase in shrubs in the diets.

Goats have a reputation for survival on harsh degraded rangelands partly due to unique dietary selection (Devandra 1978) and partly due to their relatively unspecialized feeding habits, eating a wider array of plant species than other livestock (French 1970, Wilson et al. 1975, Peters 1987, Skea 1988). Increased specialization implies fewer plant species or parts eaten. Conversely, Van Soest (1982) stated that goats should have more specialized feeding habits than do sheep based on body size, gastrointestinal capacity, nutrient requirements and feeding strategy. He classified goats as forb-or-browse preferring intermediate feeders and sheep as grass-preferring intermediate feeders. This definition has also been supported by Papachristou and Anastasios (1993), Pfister and Malechek (1986) and Kamau (1986), all of whom tend to confirm that goats are generally browsers or intermediate feeders, although the browse component of their diets varies with site and time of the year. They all concluded that goats are opportunist feeders since they adapt their diets with changing seasons and according to forage class availability and quality.

Pfister and Malechek (1986) reported a large degree of dietary overlap between sheep and goats during the dry season when they limited their grazing to the same vertical space resulting in severe competition for a limited number of palatable plant species. Competition was considerably reduced during the wet season given the large amount of forage available, differences between sheep and goats in partitioning their vertical grazing space and differences in dietary preferences.

Changes in vegetation structure and composition are thought to affect dietary selection and quality during certain periods of the year. By increasing the proportion of herbaceous species and decreasing the shrubby components, dietary selection of the herbaceous species would be favoured (Papachristou and Anastasios 1993).

## 2.4 Markers and estimation of intake

The indirect estimation of the intake of grazing animals depends on estimating the daily faecal output and digestibility of the diet consumed. Faecal output can be estimated by administration of a suitable external marker, collection of representative samples of faeces and determination of marker concentration in the faeces. Digestibility of the diet may be estimated from samples of herbage collected by simulation or by oesophageal/rumen fistulated animals, or from the faecal nitrogen index method (Wanyoike and Holmes 1981, Greenhalgh 1982).

Since a significant linear relationship between faecal output and dry or organic matter digestibility is an established fact, then by using diet digestibility data and indigestible markers, voluntary intake can be quantified using the formulae below (McCullough 1959, Ellis et al. 1982, Van Soest et al. 1983, Hodgeson and Rodriguez 1971, Greenhalgh 1982):

$$\text{Faecal output (g/day)} = \frac{\text{Weight of marker given (g/day)}}{\text{Mean conc. of marker in faeces (g/g)}}$$

$$\text{Dry matter intake (g/day)} = \frac{\text{Faecal output (g/day)}}{\text{\% indigestibility.}}$$

Direct weighing of consumed forage is impractical under range grazing conditions and total faecal collection is laborious and interferes with normal grazing behaviour of the animals. The advantages of estimating faecal output by marker dilution technique include flexibility in the number and sex of the animals, small investment of time by field staff and minor interference with grazing.

Ideal qualities of markers to estimate faecal output include indigestibility, lack of diurnal variations in excretion, ease of measurement and non-toxicity (Kotb and Luckey 1972). The marker technique has been used extensively despite inability to sample grazed herbage accurately, lack of completely indigestible markers and diurnal fluctuations in concentration of marker in faeces, leading to an overall reduced precision (Warner 1969, Ellis et al. 1982, Kotb and Luckey 1972).

Insoluble markers such as rubber, plastics, Sudan II and chromic oxide have problems of cyclic fluctuations in excretion, incomplete mixing with ingesta and dissociation from the particulate matter of the ingesta (McRae 1974). Basically, they do not have the same physical properties as feed particles such as density, ease of rumination, etc and therefore yield only relative data. Lignin is not completely indigestible (Van Dyne and Meyer

1964, Wallace and Van Dyne 1970) whereas the recovery of silica is not quantitative in all conditions due to longer retention time, absorption and excretion in urine. Hence, estimates of forage intake using silica are more variable and higher than even those obtained using lignin (Van Dyne and Meyer 1964, Kotb and Luckey 1972).

Other soluble markers such as polyethylene glycol (PEG) used to quantify faecal output have been reported to show confusion with respect to their utility based on variation in attachment to particulate matter (Alexander et al. 1969). Use of chelated markers has been discouraged since they appear in urine of dosed animals as a result of displacement of the marker metal by hydrogen (Miller and Byrne 1970).

Rare earth metals with large molecular size and reduced displacement by hydrogen have been considered safe (Uden et al. 1980) and complete recovery of the rare earths in faeces has been achieved (Ellis and Huston 1968). Among the rare earth elements, Ytterbium (Yb) and Erbium (Er) are the best compromises so far, with many of the qualities of effective indicators. They both are indigestible and associate well with feed residues, a property which minimizes diurnal variations in faecal marker concentration attributable to differential flow of feed residue and marker from the rumen (Corbett et al. 1958, McRae 1974), and thus simplify the dosing and sampling procedures currently necessary with $Cr_2O_3$. Ytterbium is also comparatively inexpensive and can be detected using atomic absorption equipment (Teeter et al. 1979).

Prigge et al. (1981) reported that diurnal excretion patterns for Yb and chromic oxide ($Cr_2O_3$) differed significantly, but the variation observed for both markers within dosing schedule was as great for Yb as it was for $Cr_2O_3$. Although faecal output was accurately estimated from Yb with one simultaneous collection and dosing period, the response may have been due to time of collection rather than to an actual reduction in diurnal variation. He concluded that Yb was as effective as $Cr_2O_3$ as a faecal indicator. However, further experimental evaluation is needed before conclusive assessment on the usefulness of rare earths with free-grazing animals.

Chromic oxide (chromium sesquioxide, $Cr_2O_3$) is currently the most widely used marker to measure faecal output for both confined and grazing ruminants, despite such shortcomings as incomplete recovery and the administration of discrete doses once or twice daily. The diurnal variations in concentration of the indicator hence leads to difficulties in estimating the mean concentration in faeces (Hardison and Reid 1953, Hardison et al. 1959). However, incomplete recovery of the individual doses does not invalidate the technique if percent recovery is constant and can be reasonably quantified.

McRae (1974) and Langlands (1975) indicated that $Cr_2O_3$ does not associate itself well with the particulate phase of the digesta in the gastro-intestinal tract resulting in variations in excretion. Because of the cyclic fluctuations in the excretion of this marker, techniques have been devised based on dosing, faecal collection times or mathematical models that permit determination of representative concentration in the faeces. Thus, in most cases, frequent or specifically timed doses and/or collections are necessary for effective use of $Cr_2O_3$ as a quantitative faecal indicator (Prigge et al. 1981).

In studies with ruminants, $Cr_2O_3$ can be given in capsules, impregnated paper, pellets or incorporated in feed. Corbett et al. (1958) and Hardison and Reid (1953) found that the flow of chromic oxide through the duodenum was more regular when it was administered in impregnated paper and this reduced diurnal variation in excretion and slightly improved the accuracy of estimation. However, Valderrabano (1979) found little difference between $Cr_2O_3$ capsules and $Cr_2O_3$ given in paper. Thus, the substances used as carriers for $Cr_2O_3$ and the patterns of dosing and sampling should be designed to minimize or take into account these fluctuations in chromic oxide excretion.

A preliminary dosing period is required for the marker to equilibrate throughout the gut prior to sampling faeces. The time required is influenced by the level of intake and by the characteristics of the feed, as the rate of excretion of the marker is related to the rate of passage through the digestive tract. In practice a minimum of 7 days is recommended (Penning and Le Du 1982, Wanyoike and Holmes 1981, Hardison et al. 1959).

Faecal samples should be taken at times when the concentration of the marker is similar to the mean daily value. Lambourne (1957) concluded that an unbiased estimate of the mean marker concentration was obtained by dosing animals and taking samples of faeces at 9- and 15- hour intervals. Coop and Hill (1962), using this dosing and sampling pattern, confirmed that marker concentration was within 1% of the mean concentration although faecal samples taken at two-hour intervals showed a diurnal variation of ± 12% from the mean. More frequent dosing appears to eliminate diurnal variations but it may not be practical.

Penning and Le Du (1982) found the mean recovery rate of $Cr_2O_3$ from 55 experiments reported in the literature to be 96.5% ± 5.6%. These experiments included cattle and sheep, different types of feed, carriers for $Cr_2O_3$, preliminary dosing periods and frequencies of dosing and sampling. Calculations from the data in the literature were also made of the total faeces production estimates by $Cr_2O_3$ concentration compared with measured faecal output; the mean figure found was 96.1% ± 6.2%.

It is therefore concluded that using $Cr_2O_3$ as a marker will generally estimate faecal output to within 6% of the mean. The Grassland Research Institute (Penning and Le Du 1982, Hodgeson and Rodriguez 1971) recommended a preliminary dosing period of 7 days with animals being dosed twice daily at approximately 8- and 16-hour intervals and faecal samples taken at the same time over at least a 5-day period. The 0800 and 1600 hours were chosen for dosing and collection because they represent a good compromise between convinience and accuracy for estimating faecal output with $Cr_2O_3$, and have been used by numerous investigators (Prigge et al. 1981).

# 3. MATERIALS AND METHODS

## 3.1 The study area

The study was conducted at Kibwezi Dryland Field Station situated in Makueni District, Eastern Province, Kenya. It is about 250 km south of Nairobi along the Nairobi-Mombasa highway. It lies between 37° 55'E to 38° 05'E and 2° 28' to 2° 35'S at an altitude of 700-800 metres above sea level (Figures 1 and 2).

The Station falls under agro-ecological zone V (Pratt and Gwynne 1977), characterized by low and erratic rainfall with a bimodal distribution pattern. The long rains come between March and May and the short rains between October and December. The long-term mean annual rainfall is 600 mm (Kenya Meteorological Department 1991). Mean annual temperature is about 23°C. During the study period there was a lot of rainfall in the short rains while very little rainfall was recorded in the long rainy season, the latter which comprised the "dry" season in this study. The climatic data for the period 1982-1991 and for the study period (1992-1993) is presented in Figure 3.

The soils are derived from metamorphic rocks composing the basement complex. The main soil types are sandy clays, calcareous alkaline soils (along the slopes) and alluvial soils along the river beds and valley bottoms, and they are generally well drained (Touber 1983). According to Pratt and Gwynne (1977) and Touber (1983), this is a typical semi-arid rangeland dominated by *Commiphora* spp., *Acacia* spp. and allied genera, many of shrubby habit. Baobab trees (*Adansonia digitata*) are common. Perennial

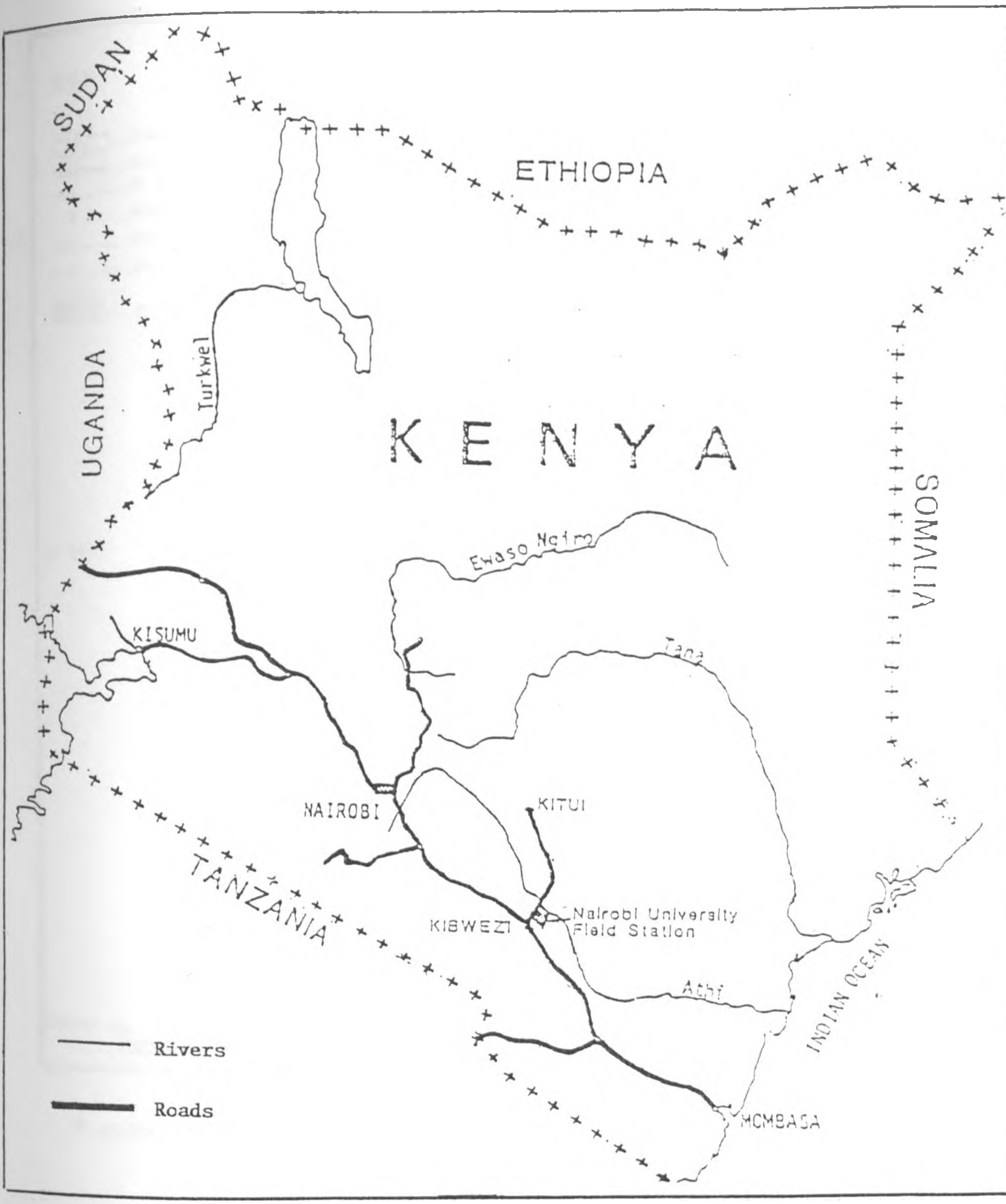


Figure 1: Location of the Kibwezi Dryland Field Station, Kenya

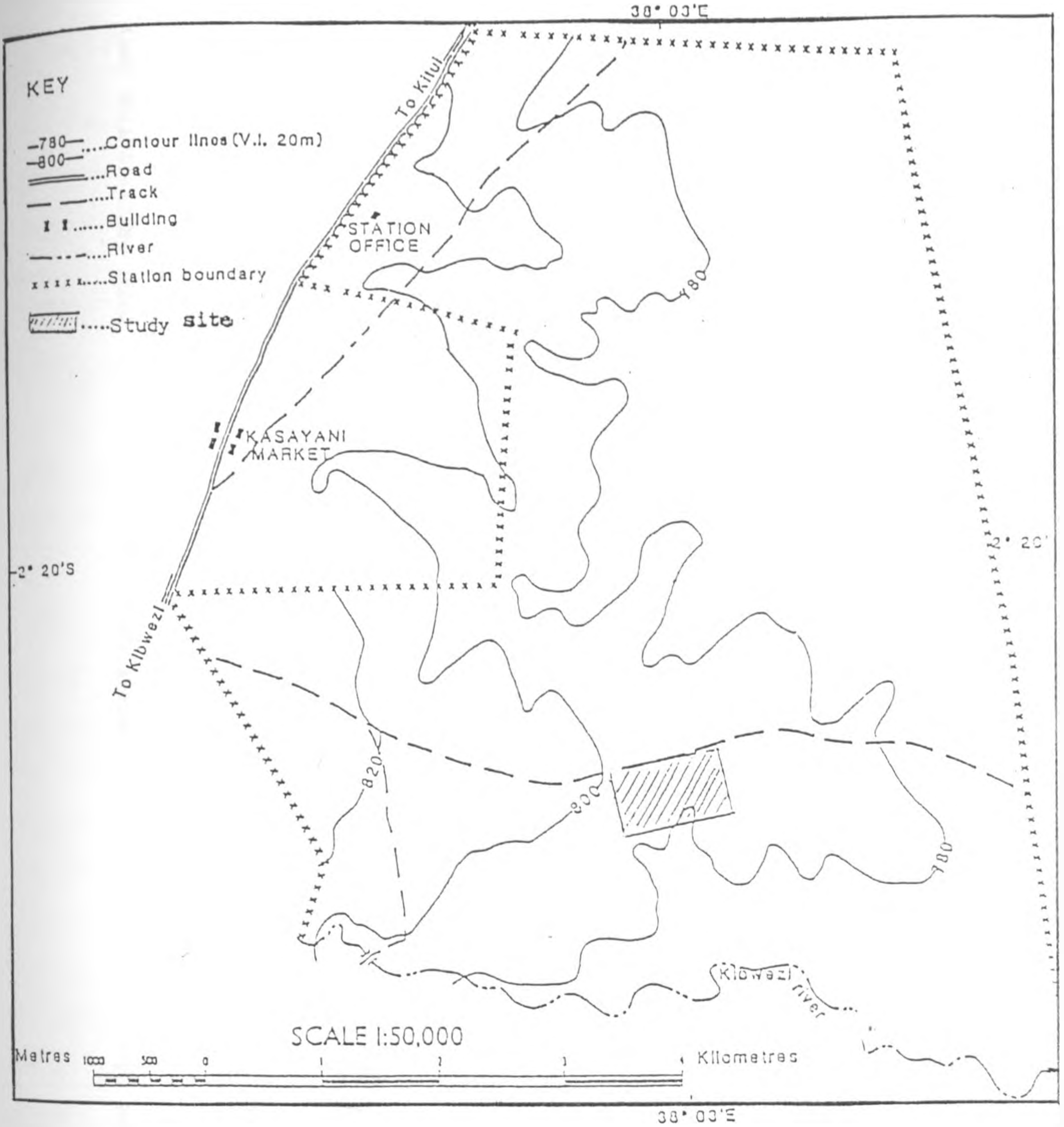


Figure 2: Location of experimental site at the Kibwezi Dryland Field Station.

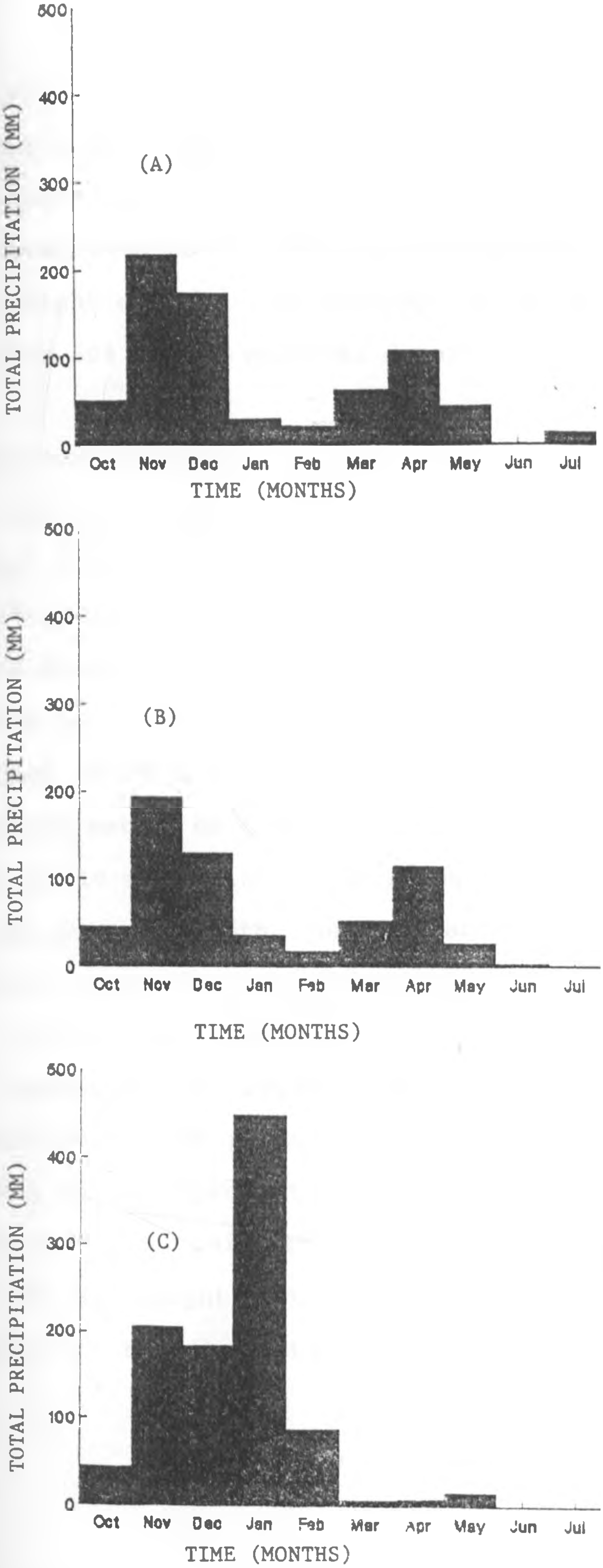


FIG 3: The 10-year mean monthly rainfall for Kibwezi DWA Plantation Limited (A) and Makindu Meteorological Station (B). The monthly precipitation for Kibwezi Meteorological Station (October, 1992 - July, 1993) is shown in (C).

grasses include Cenchrus ciliaris, Chloris roxburghiana and Enteropogon macrostachyus.

The study was confined to a 50-hectare portion of land which had been bush-cleared in 1989. The shrubs were slashed to a goat browsing height and the tree density reduced as necessary but not by more than 50% of the original density.

### 3.2 Vegetation inventory

Ten 100-metre systematic transects were laid out in the entire study area. The density of trees and shrubs was determined by the point-centred quarter (PCQ) method as described by Dieter and Heinz (1974) and Pieper (1978). Points were selected along each transect at 10-metre intervals to give a total of 100 sampling points.

Herbage biomass in the study area was estimated using the hand-clipping method on a monthly basis. A square quadrat of $0.25m^2$ was laid at 10-metre intervals along each transect to give 10 samples per transect. Both the grass and forb species present were recorded and percent relative frequency determined. All herbage was clipped at 0.5cm above the ground and the fresh and oven-dried weights recorded. To avoid sampling the same plots in the subsequent months, the points were sequentially moved by about one metre. The biomass production of small shrubs within browsing height was estimated using the reference unit method by multiplying the unit foliage weight of the reference shrub for each species by the respective density estimate (Mueller-Dombois and Ellenberg 1974).

## 3.3. Dry matter intake study

Fifteen female Maasai sheep of about 20 kg bodyweight and 15 Small East African female goats of about 24 kg average bodyweight were used in the study. The animals were selected from the existing flocks on the basis of age, bodyweight and sex.

The dry matter intake was determined from mean faecal output and in vitro dry matter digestibility of simulated diet samples. Faecal output was estimated from eight animals of each species randomly selected from the experimental group using the chromium sesquioxide dilution technique (Hodgeson and Rodriguez 1971). Dosing and sampling were done on a monthly basis from December 1992 to July 1993.

During each sampling period (month), one gram of chromic oxide wrapped in tissue paper was administered orally to each animal using a balling gun twice daily at 0700-0800 hours and 1600-1700 hours for twelve consecutive days. Faecal grab samples were taken manually from the rectum of each animal, at the times of dosing, during the last five days of each sampling period. The faecal samples were composited by animal species on a daily basis.

The faecal grab samples were weighed when fresh and after they were oven-dried to constant weight at 60°C for 48 hours. The samples were then ground in a Wiley mill to pass through a 1mm screen. Analysis for chromic oxide concentration was done using atomic absorption spectrophotometry as described by Kimura and Miller (1957). Faecal output was then calculated from the ratio of the amount of marker given daily to the mean concentration of marker in the faeces.

Other analyses done on the faecal samples included determination of dry matter (DM), organic matter (OM) and total ash contents.

### 3.4. Sampling the animals' diets

Dietary samples selected by the animals were obtained by simulation using six animals of each species. Each animal was observed separately for 10 minutes and samples of the plant species and parts consumed were harvested in proportion to the amount eaten by the animal. The two animal species were observed alternately.

The diet samples were collected during the last five days of each sampling period, and were composited by animal species and day. The samples were air-dried and later oven-dried to constant weight at 60°C for 48 hours, ground in a Wiley mill over a 1 mm screen and aliquots taken for subsequent analyses.

Dry matter and organic matter digestibilities of each composite sample were determined using the two-stage *in vitro* fermentation method (Tilley and Terry 1963). Rumen liquor was obtained from a rumen-fistulated steer fed on good quality hay to ensure that nitrogen supply was adequate to provide a highly viable rumen microflora. Dry matter intake was calculated as described earlier in Section 2.4 on a monthly basis.

The diet samples were analysed for neutral detergent fibre, acid detergent fibre and lignin using the procedures outlined by

Goering and Van Soest (1970). Other determinations included dry matter, organic matter, crude protein and total ash contents (AOAC 1970). Percent nitrogen was determined using the micro-kjeldahl technique and then converted to an estimate of dietary crude protein through multiplying by a factor of 6.25.

### 3.5 Diet botanical composition

The botanical composition of the diets selected by each animal species during the four months of each collection season were determined according to their corresponding relative densities using the microhistological faecal analysis technique (Hansen 1971). The faecal samples were dried, ground through a 1mm screen, and species composition determined following the procedures outlined by Sparks and Malechek (1968). Five slides were prepared for each composite faecal sample and twenty systematically selected fields observed per slide under a compound binocular microscope at x40 magnification. Plant species identification involved matching epidermal characteristics of faecal samples with reference slides prepared from all plant species occurring in the pastures utilized by the animals (Hansen 1971, Davies 1959, Ng'ethe and Box 1976). Plant species were recorded as being either present or absent until a total of 100 observations per sample were made. Animal diets were classed into grasses, forbs and browse components for each month and season.

## 3.6 Statistical analysis

Comparisons were made for intake and *in vitro* digestibility between sheep and goats within and among seasons by one-way analysis of variance. The botanical and chemical compositions of the diets were also compared between months and seasons within and between animal species. Student's t-test (Steel and Torrie 1980) was used to compare proportions of grass, forbs and browse in the diets of the animals during the two seasons.

The study comprised a nested design with days being nested within months, months within seasons and seasons within animal species . Duncan's New Multiple Range Test (Steel and Torrie 1980) was used to separate main effect means at 5% level of significance.

# 4. RESULTS

## 4.1 Forage production

Figure 4 shows the monthly biomass production of grasses, forbs and shrubs on the experimental site during the study period from December 1992 to July 1993. During the wet season (December - March), forbs were the dominant component of herbage i.e 1517 kg/ha and 1478 kg/ha for forbs and grasses, respectively, whereas during the dry season (April - July), grasses contributed more biomass (1543 kg/ha) than forbs (1384 kg/ha). Shrubs contributed the least biomass in both seasons. The minimum total dry matter yield was 2657 kg/ha in December 1992 and the maximum dry matter yield of 5183 kg/ha was recorded in March 1993.

## 4.2 Botanical composition of the herb layer

The species composition of the herbaceous layer in the study area during the two seasons is presented in Table 1. The major grass species were Enteropogon macrostachyus, Cenchrus ciliaris, Chloris roxburghiana, Eragrostis caespitosa and Digitaria velutina. Dominant forb species included Brepharis integriifolia, Commelina benghalensis, Macrotylomma axillare, Ipomea mombasana, Cassia spp. and Justicia disclipteroides in decreasing order. Forbs were more abundant than grasses in both seasons (67.8% and 60.0% for the wet and dry seasons, respectively) compared to grasses which made up the remaining fraction during the respective seasons. There was a slight increase in the proportion of grasses from the wet to the dry season whereas the opposite was true of the forbs.

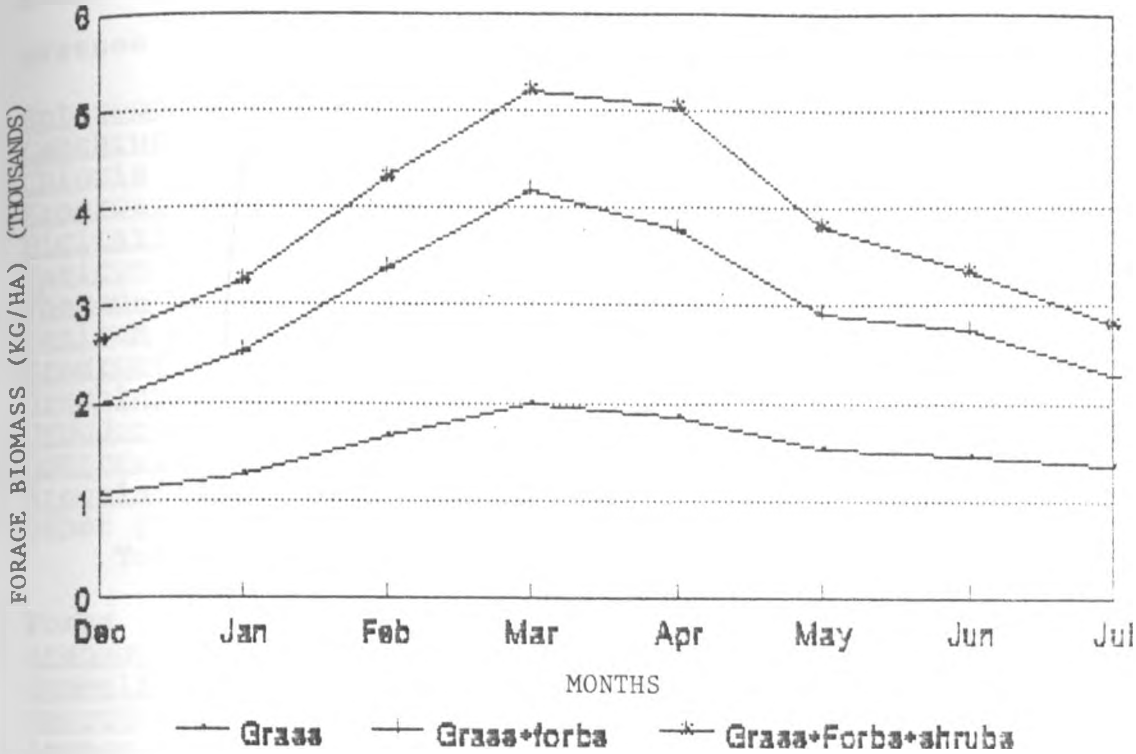


Figure 4: Cumulative biomass (kg/ha) as made up of different forage classes in the study area from December 1992 to July, 1993.

Table 1. Mean percent relative frequency of the major grass and forb species by season

| Plant Species | % relative frequency | | | |
|---|---|---|---|---|
| | Wet Season | | Dry Season | |
| **Grasses** | Mean | S.D. | Mean | S.D. |
| *Enteropogon macrostachyus* | 6.1 | 1.5 | 14.5 | 2.0 |
| *Cenchrus ciliaris* | 3.0 | 0.7 | 3.5 | 0.7 |
| *Chloris roxburghiana* | 1.8 | 0.7 | 4.0 | 1.1 |
| *Eragrostis caespitosa* | 1.5 | 0.5 | 2.7 | 0.7 |
| *Digitaria velutina* | 2.1 | 0.8 | 1.1 | 0.4 |
| *Panicum maximum* | 1.0 | 0.3 | 2.0 | 0.9 |
| *Themeda triandra* | 1.3 | 0.4 | 1.1 | 0.9 |
| *Panicum deustum* | 0.4 | 0.6 | 1.9 | 1.0 |
| *Eragrostis superba* | 1.3 | 0.8 | 0.7 | 0.5 |
| *Brachiaria reptans* | 1.8 | 0.7 | 0.2 | 0.5 |
| *Cynodon plectostachyus* | 1.0 | 0.2 | 1.6 | 0.9 |
| *Rottboelia exaltata* | 1.4 | 0.3 | 0.4 | 0.7 |
| *Brachiaria serrata* | 1.1 | 0.8 | 0.1 | 0.3 |
| Other grasses | 8.4 | 1.7 | 6.2 | 1.1 |
| **Total grasses** | 32.2 ± | 1.2 | 40.0 ± | 2.7 |
| **Forbs** | | | | |
| *Brepharis integriifolia* | 6.9 | 1.0 | 11.9 | 1.6 |
| *Commelina benghalensis* | 8.2 | 1.1 | 9.8 | 1.0 |
| *Macrotylomma axillare* | 6.4 | 1.5 | 7.5 | 1.5 |
| *Ipomea mombasana* | 3.3 | 1.1 | 6.4 | 0.9 |
| *Cassia* spp. | 5.3 | 1.3 | 1.6 | 1.0 |
| *Justicia disclipteroides* | 4.3 | 0.9 | 2.1 | 1.1 |
| *Achyranthes aspera* | 1.5 | 0.5 | 3.0 | 0.8 |
| *Pupalia lupacea* | 1.2 | 0.8 | 2.8 | 0.8 |
| *Oxygonum sinvatum* | 3.3 | 0.6 | 0.5 | 0.8 |
| *Crabbea velutina* | 2.2 | 0.9 | 0.6 | 0.7 |
| *Leucas glabrata* | 3.0 | 0.9 | 0.6 | 0.7 |
| *Crotalaria incana* | 1.3 | 0.6 | 2.0 | 1.2 |
| *Polygala* spp. | 1.9 | 0.6 | 0.7 | 0.6 |
| *Vernonia aemulans* | 0.6 | 0.3 | 1.9 | 0.6 |
| *Ocimum basilicum* | 1.5 | 0.5 | 0.7 | 0.5 |
| *Acanthosperma hispidum* | 1.7 | 0.8 | 0.1 | 0.4 |
| *Kotstachys* spp. | 1.6 | 0.3 | 0.1 | 0.4 |
| Other forbs | 13.6 | 1.0 | 7.7 | 2.0 |
| **Total forbs** | 67.8 ± | 1.2 | 60.0 ± | 2.7 |

## 4.3 Density of trees and shrubs

The total density of the trees and shrubs encountered in the study area was 1804 plants per hectare. The density of the shrubs (1270 shrubs/ha) was more than that of trees (534 trees/ha). This was as expected considering that the vegetation type in the area is classified as dense thicket to sparse woodland. The dominant trees were Commiphora riperia, Acacia tortilis and Commiphora campestris in decreasing order. Among the shrubs, Duosperma kilimandscharicum, Premna hildebrandtii and Ochna insculpta were the most common.

## 4.4 Nutritional Characteristics of Simulated Diets

The nutritional properties of the simulated diets for the two animal species during the two seasons are presented on the basis of each nutrient in Tables 2 to 6.

### 4.4.1 Crude protein content (CP)

Crude protein values were divergent for the two animal species in both seasons. On the whole, goats selected diets significantly higher ($P < 0.05$) in crude protein than did sheep (16.4% and 13.6%, respectively) when averaged over the two seasons (Table 2). Both sheep and goats maintained crude protein levels above 15.0% during the wet season and above 12.0% during the dry season.

Crude protein levels were significantly different ($P < 0.05$) between seasons for both animal species, being higher in the wet than in the dry season diets. Goats selected diets with 18.5% and 14.2% CP during the wet and dry seasons, while sheep diets contained 15.2% and 12.0% CP during the wet and dry seasons, respectively.

Goat diets had significantly higher ($P < 0.05$) CP content than sheep in all months in both seasons. However, crude protein content of the diets selected by both sheep and goats was similar for all months constituting the wet season for each species unlike during the dry season when it differed significantly ($P < 0.05$) between most of the months.

Table 2: Mean percent crude protein content of simulated diets for sheep and goats

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E* | Mean | S.E |
| Dec | 18.7[a1] | 0.6 | 15.8[b1] | 0.4 |
| Jan | 18.6[a1] | 0.2 | 15.4[b1] | 0.5 |
| Feb | 18.5[a1] | 0.3 | 15.2[b1] | 0.5 |
| Mar | 18.0[a1] | 0.5 | 14.6[b1] | 0.3 |
| | 18.5[a] ± | 0.2 | 15.2[b] ± | 0.2 |
| Dry Season | | | | |
| Apr | 16.1[a3] | 0.3 | 14.1[b3] | 1.0 |
| May | 15.5[a3] | 0.3 | 13.0[b23] | 0.1 |
| Jun | 13.6[a2] | 0.3 | 11.9[b2] | 0.4 |
| Jul | 11.6[a1] | 0.5 | 8.9[b1] | 0.2 |
| | 14.2[a] ± | 0.4 | 12.0[b] ± | 0.5 |

[ab] Means in the same row with different letter superscripts differ ($P < 0.05$)

[123] Means in the same column within a season with different numeral superscripts differ ($P < 0.05$)

* S.E: standard error of the mean

### 4.4.2 Neutral detergent fibre (NDF)

The simulated diet samples of goats had significantly lower ($P < 0.05$) levels of NDF than those of sheep in all months except June when they were similar (Table 3). The percentage of NDF showed significant variation ($P < 0.05$) between the two seasons for both animal species. It was lower in the wet season than in the dry season diets. The NDF content of goat diets was 38.2% and 45.2% for the wet and dry seasons, respectively, whereas sheep selected diets containing 46.6% and 53.3% NDF during the wet and dry seasons. The overall average was 41.7% for goats and 49.9% for sheep.

The NDF content of the simulated diets for goats was similar ($P > 0.05$) for all the other months apart from June and July. Sheep diets had similar NDF content during the wet season months but were different between some of the months comprising the dry season.

### 4.4.3 Acid detergent fibre (ADF)

The ADF content of the simulated diets (Table 4) varied between animal species, seasons and months within seasons. Goats selected diets with significantly lower ($P < 0.05$) levels of ADF than did sheep in both seasons and in all months except July. The percentage of ADF was also strongly affected by season, being lower in the wet season than in the dry season diets for both animal species. The ADF content of the diets varied significantly between most of the months for both sheep and goats but were similar in the wet season months for goat diets. Goat diets contained 26.2% average ADF whereas sheep diets had an average ADF level of 30.5%.

Table 3: Percent neutral detergent fibre content of simulated diets for sheep and goats during wet and dry season.

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | $37.6^{a1}$ | 0.4 | $44.6^{b1}$ | 2.4 |
| Jan | $37.6^{a1}$ | 1.6 | $46.4^{b1}$ | 1.5 |
| Feb | $38.6^{a1}$ | 0.6 | $47.7^{b1}$ | 0.9 |
| Mar | $38.9^{a1}$ | 0.8 | $47.5^{b1}$ | 1.1 |
| | $38.2^{a}$ | ± 0.5 | $46.6^{b}$ | ± 0.8 |
| Dry Season | | | | |
| Apr | $39.7^{a1}$ | 0.9 | $50.5^{b1}$ | 2.4 |
| May | $41.4^{a1}$ | 1.2 | $53.0^{b12}$ | 2.5 |
| Jun | $49.5^{a2}$ | 0.7 | $52.8^{a12}$ | 0.6 |
| Jul | $50.3^{a2}$ | 1.7 | $56.9^{b2}$ | 2.0 |
| | $45.2^{a}$ | ± 1.2 | $53.3^{b}$ | ± 1.1 |

[ab] Means in the same row with different letter superscripts differ ($P < 0.05$)

[12] Means in the same column within a season with different numeral superscripts differ ($P < 0.05$)

Table 4: Percent acid detergent fibre content of simulated diets during wet and dry season.

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | $23.0^{a1}$ | 0.4 | $27.4^{b1}$ | 1.3 |
| Jan | $23.9^{a1}$ | 0.2 | $29.3^{b12}$ | 0.6 |
| Feb | $24.5^{a1}$ | 1.0 | $29.2^{b12}$ | 1.0 |
| Mar | $25.3^{a1}$ | 1.8 | $29.4^{b2}$ | 1.1 |
| | $24.2^{a}$ | ± 0.5 | $28.8^{b}$ | ± 0.5 |
| Dry Season | | | | |
| Apr | $25.0^{a1}$ | 0.9 | $29.8^{b1}$ | 0.6 |
| May | $27.6^{a12}$ | 0.8 | $31.1^{b12}$ | 0.8 |
| Jun | $28.2^{a2}$ | 0.7 | $33.7^{b23}$ | 0.4 |
| Jul | $32.1^{a3}$ | 1.0 | $34.0^{a3}$ | 0.6 |
| | $28.2^{a}$ | ± 0.7 | $32.2^{b}$ | ± 0.5 |

[ab] Means within a row with same letter superscripts do not differ ($P > 0.05$)

[123] Means in the same column within a season followed by the same numeral superscripts do not differ ($P > 0.05$).

### 4.4.4. Acid detergent lignin (ADL)

Sheep diets had significantly lower ($P < 0.05$) lignin contents than goat diets during the wet season but were similar during the dry season (Table 5). Lignin contents did not differ ($P > 0.05$) for the two animal species in all months, although values for goats were higher compared to those of sheep during the wet season months. Percentage lignin in the simulated diets was different between some of the constituent months, and hence the seasons, for both sheep and goats. Overall, goats selected diets with 5.5% lignin whereas sheep diets contained 5.0% lignin.

### 4.4.5 Total ash

Total ash content was the same for both the animal species and seasons as shown in Table 6. Significant variation ($P < 0.05$) was however observed between some months during the wet season for sheep and goats, but the dry season months were all similar for each of the two animal species. For goats, total ash content averaged 12.6% and for sheep 12.8% over the study period.

Table 5: Mean percent acid detergent lignin content of simulated diets during wet and dry season

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | $4.0^{a1}$ | 0.2 | $3.6^{a1}$ | 0.3 |
| Jan | $4.9^{a12}$ | 0.2 | $4.0^{a12}$ | 0.1 |
| Feb | $5.1^{a12}$ | 0.6 | $4.3^{a12}$ | 0.2 |
| Mar | $5.8^{a2}$ | 0.8 | $4.8^{a2}$ | 0.4 |
| | $5.0^{a}$ ± | 0.3 | $4.2^{b}$ ± | 0.2 |
| Dry Season | | | | |
| Apr | $5.2^{a1}$ | 0.2 | $5.1^{a1}$ | 0.5 |
| May | $5.1^{a1}$ | 0.5 | $5.4^{a12}$ | 0.2 |
| Jun | $6.4^{a2}$ | 0.2 | $5.7^{a12}$ | 0.1 |
| Jul | $7.3^{a2}$ | 0.2 | $6.5^{a2}$ | 0.6 |
| | $6.0^{a}$ ± | 0.2 | $5.7^{a}$ ± | 0.2 |

[ab] Means in the same row with different letter superscripts differ ($P < 0.05$)

[12] Means in the same column within a season having different numeral superscripts differ ($P < 0.05$).

Table 6: Mean percent total ash content of simulated diets during wet and dry seasons

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | 15.1[a2] | 1.1 | 14.5[a2] | 0.8 |
| Jan | 12.1[a1] | 0.4 | 13.6[a2] | 0.7 |
| Feb | 11.5[a1] | 0.4 | 10.3[a1] | 0.2 |
| Mar | 11.3[a1] | 0.6 | 11.2[a1] | 0.6 |
| | 12.5[a] ± | 0.5 | 12.4[a] ± | 0.5 |
| Dry Season | | | | |
| Apr | 12.3[a1] | 0.8 | 12.4[a1] | 0.5 |
| May | 12.6[a1] | 0.3 | 13.2[a1] | 0.6 |
| Jun | 13.4[a1] | 0.6 | 13.3[a1] | 0.8 |
| Jul | 12.9[a1] | 0.5 | 13.1[a1] | 0.5 |
| | 12.8[a] ± | 0.3 | 13.0[a] ± | 0.3 |

[ab] Means in the same row with the same letter superscript do not differ (P > 0.05)

[12] Means in the same column within a season with the same numeral superscript do not differ (P > 0.05)

## 4.5 *In Vitro* dry matter digestibility (IVDMD)

The *in vitro* dry matter digestibilities of the simulated diets are presented in Table 7 showing similar ($P > 0.05$) values for sheep (55.6%) and goat diets (56.2%) on average. However, season had a strong effect on IVDMD, with the wet season diets being more digestible ($P < 0.05$) than dry season diets for the two animal species. Within a given season, the digestibilities were similar ($P > 0.05$) for both sheep and goats. Goat diets had IVDMD values of 60.2% and 52.1% during the wet and dry seasons, respectively, while sheep diets had digestibility values of 61.3% and 49.9% over the same period, respectively. *In vitro* dry matter digestibilities of the diets were similar for the wet season months in the case of sheep and the dry season months for goats. There was a consistent decline in IVDMD as seasons progressed and as plants matured, the drop being more dramatic for sheep (22.1%) than for goats (14.9%) between December and July.

Table 7: Mean percent in vitro dry matter digestibility of simulated diets

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | $63.6^{a2}$ | 4.4 | $67.0^{a1}$ | 0.6 |
| Jan | $61.8^{a12}$ | 1.5 | $62.8^{a1}$ | 1.6 |
| Feb | $59.3^{a12}$ | 3.3 | $60.0^{a1}$ | 2.0 |
| Mar | $55.8^{a1}$ | 3.7 | $55.8^{a1}$ | 1.2 |
| | $60.2^{a}$ ± | 1.7 | $61.3^{a}$ ± | 1.1 |
| Dry Season | | | | |
| Apr | $53.9^{a1}$ | 2.0 | $53.4^{a2}$ | 2.9 |
| May | $54.1^{a1}$ | 2.7 | $52.1^{a12}$ | 1.9 |
| Jun | $51.9^{a1}$ | 2.2 | $49.4^{a12}$ | 1.4 |
| Jul | $48.7^{a1}$ | 1.6 | $44.9^{a1}$ | 1.8 |
| | $52.1^{a}$ ± | 1.1 | $49.9^{a}$ ± | 1.2 |

[ab] Means in a row with the same letter superscripts do not differ ($P > 0.05$)

[12] Means in a column within a given season with same numeral superscripts do not differ ($P > 0.05$)

## 4.6 In Vitro organic matter digestibility (IVOMD)

In vitro organic matter digestibility (Table 8) generally declined with advance in forage plant maturity. It was similar ($P > 0.05$) for the two animal species over the study period (56.5% and 55.1% for sheep and goats, respectively). On average, sheep diets had slightly higher IVOMD than goat diets while the reverse was true in the case of IVDMD. Goat diets were 58.2% and 51.9% digestible during the wet and dry seasons, respectively, compared to sheep diets which had IVOMD values of 61.2% and 51.8% in the wet and dry seasons. The drop in IVOMD from the wet to the dry season was greater for sheep (9.4%) than goats diets (6.3%). Differences were also noted between the sampling dates (months) comprising the seasons apart from the dry season in the case of goats when they were similar.

Table 8: Mean percent in vitro organic matter digestibility of simulated diets

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | $64.8^{a2}$ | 4.1 | $68.4^{a2}$ | 0.6 |
| Jan | $59.6^{a12}$ | 3.2 | $61.4^{a1}$ | 2.9 |
| Feb | $55.2^{a1}$ | 2.2 | $61.0^{a1}$ | 1.5 |
| Mar | $53.4^{a1}$ | 3.2 | $53.9^{a1}$ | 1.7 |
| | $58.2^{a}$ | ± 1.8 | $61.2^{a}$ | ± 1.5 |
| Dry Season | | | | |
| Apr | $54.4^{a1}$ | 1.8 | $56.2^{a2}$ | 2.9 |
| May | $53.1^{a1}$ | 2.6 | $56.6^{a2}$ | 1.1 |
| Jun | $51.6^{a1}$ | 2.2 | $49.2^{a12}$ | 1.4 |
| Jul | $48.3^{a1}$ | 1.6 | $45.5^{a1}$ | 1.7 |
| | $51.9^{a}$ | ± 1.1 | $51.8^{a}$ | ± 1.4 |

[ab] Means in the same row with different letter superscripts differ ($P < 0.05$)

[12] Means within a row in a given season with different numeral superscripts differ ($P < 0.05$)

## 4.7 Dry matter intake

The daily dry matter intake data are shown in Tables 9 to 11. The mean dry matter intake in g/day was similar ($P > 0.05$) for sheep and goats within a given season although values for sheep were slightly higher than those for goats (Table 9). It was significantly lower ($P < 0.05$) during the wet compared to the dry season for both species. Differences were also observed between months within seasons for each species except during the wet season in case of sheep. Intake averaged 471.3 g/day and 500.3 g/day for goats and sheep respectively over the entire study period. This translated to 2.0% for goats and 2.5% for sheep in terms of percent bodyweight (Table 11). Sheep had an intake of 394.8 g/day and 579.3 g/day during the wet and dry seasons, respectively, whereas goats consumed 387.0 g/day and 534.5 g/day of dry matter during the respective seasons.

Dry matter intake in metabolic bodyweight basis (g/kg $W^{0.75}$) was similar ($P > 0.05$) for sheep and goats during the wet season but significantly lower ($P < 0.05$) for goats than sheep in the dry season (Table 10). It differed significantly between most of the months comprising the respective seasons for both animal species except during the wet season for sheep when they were similar between the three months. Overall, sheep consumed 53.0 g/kg $W^{0.75}$ while goats had an intake of 43.6 g/kg $W^{0.75}$.

A summary of the various nutritional variables for sheep and goats during the two seasons of the study is given in Table 12.

Table 9: Dry matter intake in g/day for sheep and goats during the wet and dry seasons.

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | N/A[1] | | N/A[1] | |
| Jan | 345.6[a1] | 17.4 | 366.8[a1] | 19.1 |
| Feb | 454.5[a2] | 33.3 | 426.8[a1] | 10.4 |
| Mar | 361.0[a12] | 28.7 | 390.7[a1] | 11.5 |
| | 387.0[a] ± | 19.5 | 394.8[a] ± | 10.1 |
| Dry Season | | | | |
| Apr | 434.3[a1] | 26.3 | 520.1[a1] | 38.9 |
| May | 447.6[a1] | 25.9 | 545.0[b12] | 35.6 |
| Jun | 575.3[a2] | 33.6 | 624.0[a2] | 45.0 |
| Jul | 680.6[a3] | 25.6 | 628.6[a2] | 44.8 |
| | 534.5[a] ± | 26.4 | 579.3[a] ± | 21.9 |

N/A[1] Data not recorded

[ab] Means in the same row with the same letter superscripts do not differ ($P > 0.05$)

[123] Means in the same column within a season having similar numeral superscripts do not differ ($P > 0.05$).

Table 10: Dry matter intake as percent bodyweight for sheep and goats during the wet and dry seasons.

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | N/A[1] | | N/A[1] | |
| Jan | $1.4^{a2}$ | 0.1 | $1.8^{a1}$ | 0.1 |
| Feb | $1.9^{a12}$ | 0.1 | $2.1^{a1}$ | 0.1 |
| Mar | $1.5^{a1}$ | 0.1 | $2.0^{a1}$ | 0.1 |
| | $1.6^{a}$ ± | 0.1 | $2.0^{b}$ ± | 0.1 |
| Dry Season | | | | |
| Apr | $1.8^{a1}$ | 0.1 | $2.6^{b1}$ | 0.2 |
| May | $1.9^{a1}$ | 0.1 | $2.7^{b1}$ | 0.2 |
| Jun | $2.4^{a2}$ | 0.1 | $3.1^{b2}$ | 0.2 |
| Jul | $2.8^{a2}$ | 0.1 | $3.1^{a2}$ | 0.2 |
| | $2.2^{a}$ ± | 0.1 | $2.9^{b}$ ± | 0.2 |

N/A[1] Data not recorded.

[ab] Means in the same row with the same letter superscript are similar ($P > 0.05$)

[12] Means within a column in a given season with same numeral superscripts are similar ($P > 0.05$)

Table 11. Dry matter intake in g/kg metabolic bodyweight for sheep and goats during the wet and dry seasons.

| | Goats | | Sheep | |
|---|---|---|---|---|
| Wet season | Mean | S.E | Mean | S.E |
| Dec | N/A[1] | | N/A[1] | |
| Jan | $31.5^{a1}$ | 1.6 | $38.9^{a1}$ | 2.0 |
| Feb | $42.4^{a2}$ | 4.6 | $45.2^{a1}$ | 1.1 |
| Mar | $33.9^{a12}$ | 2.7 | $41.4^{a1}$ | 1.3 |
| | $35.9^{a}$ | ± 2.3 | $41.9^{a}$ | ± 1.1 |
| Dry season | | | | |
| Apr | $40.2^{a1}$ | 2.4 | $55.0^{b1}$ | 4.1 |
| May | $41.2^{a1}$ | 2.4 | $57.9^{b12}$ | 3.8 |
| Jun | $53.4^{a2}$ | 3.1 | $66.0^{b2}$ | 4.8 |
| Jul | $62.8^{a2}$ | 2.4 | $66.4^{a2}$ | 4.7 |
| | $49.4^{a}$ | ± 2.5 | $61.3^{b}$ | ± 2.3 |

N/A[1] Data not recorded

$^{ab}$ Means in the same column with same letter superscripts are similar ($P > 0.05$)

$^{12}$ Means in a column within a given season with same numeral superscript are similar ($P > 0.05$)

Table 12: Summary of the mean dry matter intakes, chemical composition and digestibility of simulated diets for sheep and goats during the study period.

| | Goats | | | | Sheep | | | |
|---|---|---|---|---|---|---|---|---|
| | Wet | | Dry | | Wet | | Dry | |
| Variable | Mean | S.E. | Mean | S.E | Mean | S.E. | Mean | S.E. |
| CP(%) | 18.5[a] | 0.2 | 14.2[b] | 0.4 | 15.2[b] | 0.2 | 12.0[c] | 0.5 |
| NDF(%) | 38.2[a] | 0.5 | 45.2[b] | 1.2 | 46.6[b] | 0.8 | 53.3[c] | 1.1 |
| ADF(%) | 24.2[a] | 0.5 | 28.2[b] | 0.7 | 28.8[b] | 0.5 | 32.2[c] | 0.5 |
| ADL(%) | 5.0[b] | 0.3 | 6.0[c] | 0.2 | 4.2[a] | 0.2 | 5.7[c] | 0.2 |
| ASH(%) | 12.5[a] | 0.5 | 12.8[a] | 0.3 | 12.4[a] | 0.5 | 13.0[a] | 0.3 |
| IVDMD(%) | 60.2[b] | 1.7 | 52.1[a] | 1.1 | 61.3[b] | 1.1 | 49.9[a] | 1.2 |
| IVOMD(%) | 58.2[b] | 1.8 | 51.9[a] | 1.1 | 61.2[b] | 1.5 | 51.8[a] | 1.4 |
| DMI (g/day) | 387.0[a] | 19.5 | 534.5[b] | 26.4 | 394.8[a] | 10.1 | 579.3[b] | 21.9 |
| DMI (% BW) | 1.6[a] | 0.1 | 2.2[b] | 0.2 | 2.0[b] | 0.1 | 2.9[c] | 0.1 |
| DMI ($g/kgW^{0.75}$) | 35.9[a] | 2.3 | 49.4[b] | 2.5 | 41.9[a] | 1.1 | 61.3[c] | 2.3 |

[abc] Means in the same row with same letter superscripts do not differ ($P > 0.05$)

## 4.8 Diet composition

The mean percentages of grass, forbs and browse in the livestock diets during the wet and dry seasons is shown in Table 13.

During both seasons, there was a large divergence in the composition of sheep and goat diets. In the wet season (December 1992 - March 1993), sheep selected a significantly higher ($P < 0.05$) percentage of grass (81.7%) compared to goats (17.2%). Little browse (6.3%) and forbs (12.0%) were consumed by sheep during this season. During the dry season (April 1993 - July 1993) sheep consumed slightly less but not significantly different ($P > 0.05$) proportion of grass (77.7%) and slightly more forbs (13.1%) and browse (9.2%) compared to the wet season. Hence, sheep did not show a significant change ($P > 0.05$) in the composition of their diets with change of season.

Goat diets comprised higher ($P < 0.05$) percentage of browse component and significantly less ($P < 0.05$) forbs and grass than sheep in the two seasons. Goat diets consisted of 17.2% grass, 1.5% forbs and 81.3% browse during the wet season and 15.5%, 2.8% and 81.7% of grass, forbs and browse, respectively, during the dry season. Goats therefore browsed more than sheep did. Forbs were the least utilized forage class by goats during either season.

Generally, the plant species in the diets of the two livestock species were dissimilar throughout the study period. The most preferred plant species by sheep were all grasses in both seasons, while goats primarily consumed browse species.

Table 13. Mean percent grass, forbs and browse constituting livestock diets during the wet and dry seasons.

| | Grass | Forbs | Browse |
|---|---|---|---|
| **Goats** | | | |
| Wet season | $17.2^{a1}$ | $1.5^{b1}$ | $81.3^{c2}$ |
| Dry season | $15.5^{a1}$ | $2.8^{b1}$ | $81.7^{c2}$ |
| **Sheep** | | | |
| Wet season | $81.7^{a2}$ | $12.0^{b2}$ | $6.3^{c1}$ |
| Dry season | $77.7^{a2}$ | $13.1^{b2}$ | $9.2^{b1}$ |

$^{ab}$ Means in the same row with different letter superscripts differ ($P < 0.05$)

$^{12}$ Means in the same column with different numeral superscripts differ ($P < 0.05$)

# 5. DISCUSSION

## 5.1 Forage production

The dense vegetation tended to favour forbs more than grasses during the wet season. During the dry season, forbs were actively sought after by the animals possibly due to their higher palatability. Consequently, they contributed less to available herbage compared to grasses. The grasses, being coarse and hence less palatable, persisted longer during the dry period.

Despite its relatively lower contribution to total forage, browse constitutes an important part of the diets of domestic livestock and wildlife. This is particularly true when grass is scarce due to climatic and management factors (Otsyina and McKell 1985). Browse is an important feed component especially during the dry season when the herbaceous layer dries up or is depleted through grazing. Animals could be seen picking up dried leaves and pods from under the trees and shrubs at that time.

## 5.2 Chemical composition

Influence of season on the dietary nutritional characteristics of both animal species was observed. There was a consistent decline in crude protein and in vitro dry and organic matter digestibilities accompanied by an increase in the fibre fraction in the animals' diets from the wet season to the dry season as plants matured. The decline in CP content was more dramatic than the increase in fibre level. The seasonal influence on chemical composition and digestibility of the simulated diets was consistent with previous reports (Karue 1974, 1975), with the dry season corresponding to the lowest levels of nutritional quality for sheep and goat diets. The changes in CP, NDF and ADF values occurred over a short period of time which is in agreement with fast plant growth and rapid decline in quality of range plants (Tessema 1986, Mbui and Stuth 1986, Mnene and Stuth 1986).

The observed differences in the characteristics of the animals' simulated diets were due to the nutrient dynamics of the forages preferred by each animal species over the two seasons. High diet quality values occurred during the wet season which was a period of active plant growth when the grazing animals would have been actively selecting for leafy, green plant material (Mnene 1985, Milford and Minson 1965a,b; Tessema 1986). Periods of advanced plant maturity have been documented as periods of low CP and organic matter digestibility (Smith et al. 1971, Heitschmidt et al. 1982, Haggar et al. 1971). As plants mature, the percentage CP content declines as this fraction becomes increasingly diluted by non-nitrogenous organic matter including crude fibre (Dougall et al. 1964), leading to a decline in nutritive value. The grazing animals' diets have high stem to leaf ratio (Kibet 1984) and the levels of dietary quality during the dry periods were indicators of reduced live plant materials in the diets (Mnene 1985). Structural material is synthesized at the expense of cellular contents as plants age physiologically (Van Soest 1982, Crowder 1985, Short 1971, Johnston et al. 1968), and this explains the increase in NDF and ADF contents. Grasses, however, show higher values of fibre than browse at comparable stages of growth (Tessema 1986, Kirui 1995); thus, sheep diets which were dominated by grasses in both seasons had higher total fibre content.

Selective feeding behaviour and shifting between forage classes enables animals to take advantage of plants with higher feed quality, hence be able to cope better with the temporal trend in the quality of available forage. The dependence on grasses by sheep is a great disadvantage in the dry season during which time mature range grasses have low CP content (often as low as 4%) and high fibre content. This accounts for the much lower CP and higher NDF and ADF of sheep diets in the dry season. Since goats depended more on browse species which contain higher CP, cell solubles, are more digestible and show a slower decline in quality with advancing maturity than grass species(Kirui 1995, Ekaya 1991), they were able to ingest diets of better nutritional quality than sheep. With respect to ADL, goat diets contained higher amounts than sheep diets probably because of the high proportion of browse. As expected, this fraction was lower in the wet season diets since young plants have lower lignin contents compared to mature ones. The fibre content of goat diets was lower than the findings of Kirui (1995). Goats were therefore able to maintain a relative advantage over sheep by selecting diets lower in fibre.

The results of this study support those of Van Soest (1982) but are contrary to the findings of Pfister and Malechek (1986). The former author reported that goats selected diets of higher nutritional quality than did sheep, while the latter found only minor differences in the dietary selections made by sheep and goats, and that goats did not select a more nutritious diet than sheep. Schwartz et al. (1986) in Northern Kenya found the CP content to be higher in goats' diets but not significantly different from that of sheep and that sheep selected marginally superior diets than goats only during two months at the peak of the growing season when over 50% of intake consisted of young grasses and forbs. During the dry season, protein content in grasses can be potentially limiting to the utilization of range forage by sheep and supplementation may be necessary. However, the CP content in the diets of both sheep and goats in this study was adequate for animal maintenance even during the dry season.

### 5.3 In vitro digestibility

The in vitro dry and organic matter digestibility values were higher in the wet season as expected because at this time dietary CP content was high and the degree of lignification was lower since plants were young. Various authors (Milford and Minson 1966, Migongo 1984, Van Soest 1982) report dietary CP of 7-8% as the critical minimum for efficient microbial activity including maintenance of positive nitrogen balance, below which digestibility and intake decline. However, this study was terminated before the peak of the dry season when CP would be expected to drop below the critical level.

These findings are similar to those of Schwartz et al. (1986) who found no evidence that goats are more efficient converters of low quality forages than sheep. He concluded that highly selective behaviour rather than a better digestive efficiency gives goats an advantage over sheep on semi-arid and arid dwarf shrub pastures in Northern Kenya i.e. goats had a behavioural rather than a physiological adaptation to that environment. However, if a physiological adaptation was effective, it would give an added advantage to the goat.

On the contrary, other researchers (Huston 1978, Devandra 1978, Migongo-Bake *et al*. 1986), reported higher digestibility of fibre by goats than sheep, and that this efficiency enables goats to adapt better to poor environments. Migongo-Bake *et al*. (1986) reported linear correlation coefficients ($r^2$) of 0.95, 0.97 and 0.96 between rumen digestive efficiencies of sheep, goats and camels, respectively, relative to steers. The lines for sheep and goats were parallel, indicating that the goat is a more efficient digester of the forages tested regardless of the digestibility of the forage. This supported work by Devandra (1978) who showed that goats had a higher digestibility of fibre than sheep. Huston (1978) reported that the order of decreasing digestive ability was cattle, sheep, goats and deer, an order inverse to their respective abilities for selective feeding, and that the disparity increases with poor quality diets. The *in vitro* digestibility results were only slightly higher than those reported by Kirui (1995) in the case of goats.

Goats had slightly lower *in vitro* digestibility values in the wet season and slightly higher values during the dry season compared to sheep. Consumption of more browse by goats might have yielded greater amounts of digestibility depressants. Pfister and Malechek (1986) reported that in addition, the source of rumen inoculum may have been inappropriate for the browse-containing diets of goats. The donor animal (steer) was maintained on grass hay, and the rumen liquor probably did not have appropriate microbial populations for in vitro digestion of materials high in browse, but was probably appropriate for the grass-dominated samples from sheep.

Leng (1990) described any forages with dry matter digestibility values less than 55% and CP below 8% as low quality in terms of meeting the nutrient requirements of ruminants. Using this criterion, dry season diets for both animal species had less than optimum digestibilities, although CP was apparently sufficient. The relationship between dietary CP and digestibility was positive whereby diets lower in CP were less digestible as reported by Van Soest (1982) and Mnene (1985). Miller (1969) recommended 50% organic matter digestibility for maintenance of tropical grazing beef cattle, and this was barely achieved in the dry season in the case of sheep and goats. It should however be noted that these diet samples were obtained by simulation, and the animal often appears to select material higher in in vitro digestibility and nitrogen percent than the human sampler as shown by Gibb and Treacher (1976).

## 5.4 Dry matter intake

The results of this study showed that sheep had a higher voluntary intake (2.5% bodyweight) than goats (2.0%) when averaged over the whole study period. This was contrary to the findings of Pfister and Malechek (1986) who showed that forage intake of sheep (2.2%) was approximately equivalent to that of goats (2.1%).

As with Pfister and Malechek (1986) and Mnene (1985), the lowest levels of intake (1.6% for goats and 2.0% for sheep) were found during the wet season when nutrient quality of the forage was highest. The diets consumed during the wet season had higher water content (hence less dry matter) than those selected during the dry season. High dietary water content may lead to gut fill but actually low DMI (Mnene, 1985). Mugerwa et al. (1975) working with dairy cattle on improved pasture in Uganda reported that dry matter content had influence on herbage dry matter intake by the animals, whereby intake increased by 5.19g per 1% increase in dry matter content of the plants. Wet season intakes were the lowest, attributable to the low dry matter content. The high dry matter intake during the dry season may also have been due to the bulky nature of the herbage as indicated by the high fibre levels. Bulky feeds have low nutrient density which must have necessitated the animals to ingest more feed to meet their energy requirements (Kayongo-Male and Field 1981).

In ruminants, herbage intake depends on the capacity of the digestive tract, particularly the rumen (Crowder 1985). The animal eats until a certain degree of gastro-intestinal "fill" is reached and then rests and/or ruminates until the fill is reduced as a result of digestion and movement of the ingesta to the lower digestive tract. The higher voluntary intake of sheep compared to goats was probably because of their greater gut capacity. Hanley (1982) reported that sheep have a higher rumino-reticular volume to bodyweight ratio (relative to goats) which is an adaptation to a high cellulose diet, typically a diet consisting mainly of grasses. Cellulose digestion is a time-dependent process and such animals would have a slow rumen turnover rate, hence be able to retain food longer in the rumen despite having a high rate of food consumption. Sheep diets were of lower quality compared to those of goats and this might explain their higher consumption. Under grazing conditions, availability of forage, low protein content, supplements, mineral deficiencies as well as environmental conditions significantly alter intake.

Intake estimates for grazing animals have been very variable but those considered most valid for cattle and sheep grazing ranges in the United States generally range from 40 to 90 $gDM/_{kg}\ W^{0.75}$ or from 1 to 2.8% of body weight (Cordova et al. 1978). Therefore the intake data obtained in the current study do not deviate significantly from other reported data in the literature.

**5.5 Dietary selection**

No single plant species dominated the diets of either sheep or goats during both seasons. This may have been due to the ready availability of palatable alternatives among or within the preferred forage classes.

Goats made greater use of a bipedal stance while foraging, thus increasing the volume of browse potentially available to them. Sheep virtually never used a bipedal stance to feed, and the shrubs they consumed in appreciable amounts had low growth forms and retained their leaves well into the dry season. However, Pfister and Malechek (1986) suggested that the presence of palatable and attainable overhead green forage would presumably be necessary for goats to gain a nutritional advantage over sheep because of bipedal feeding, especially during periods of nutritional stress. This further explains why their diets consisted of more than 81% browse compared to about 8% for sheep on average.

Diet studies have typically shown large seasonal variation in the diets of sheep and goats (Pfister and Malechek 1986, Bryant et al. 1979, Knight 1964, Kirui 1995). The latter, working in Kibwezi, found that goats primarily consumed browse in both dry and wet seasons, but the proportion of this forage class varied widely from the dry season (77.7%) to the growing season (61.3%), the remainder being made up of grass. The findings of the current study were contrary to those above but agree with Migongo-Bake (1984) who reported sheep to be largely grazers and goats to be browsers irrespective of season. Taylor and Kothman (1990) and Bryant et al. (1979) had reported that grass was more than browse in the diets of goats. Hence Van Soest's (1982) classification of goats as intermediate browsers and sheep as grazers appears appropriate in this case.

There was very little dietary overlap between sheep and goats throughout the study period and their order of preferences for plant species were negatively correlated, i.e. of the plants consumed by both, those most preferred by sheep were the least preferred by goats. Thus the two animal species were complementary feeders, hence their grazing together should lead to more efficient and proper utilization of available forage. Other studies (Pfister and Malechek 1986, Ekaya 1991, Papachristou and Anastasios 1993) have shown goats and sheep to be competitors particularly during the dry season when sheep consume more browse, resulting in a high degree of dietary overlap. Migongo-Bake (1984) working in Rendille part of Kenya and Lusigi et al. (1984) in Marsabit found the lowest dietary overlap between sheep and goats but clear overlaps existed between sheep and cattle and also goats and camels. Ekaya (1991) found cattle to be complementary in their feeding to both sheep and goats during the dry season in Kiboko, Kenya.

Fruits and flowers were seasonally important in the animals' diets. Malechek and Provenza (1983) commented that these parts may be crucial to animal survival at times of nutritional stress. This may be true even though fruits and flowers represent a very small fraction of the diets, because these parts are high in nutrients (Schwartz and Said 1981, Papachristou and Anastasios 1993).

Some hypothesized aspects of diet selection in relation to rumino-reticular volume advanced by Hanley (1982) were supported.

He maintained that the rumino-reticular volume to body weight ratio of a ruminant determines the type of food items the ruminant is most efficient in digesting. High rumino-reticular volume to bodyweight ratio as in sheep is an adaption to a high cellulose content diet, typically a diet consisting primarily of grasses. Hanley and Hanley (1982) found sheep diets to be generally intermediate, being composed primarily of graminoids and forbs but also containing appreciable proportions of browse.

On the other hand, low rumino-reticular volume to bodyweight ratio as for goats is an adaptation to a high cellular content and/or high lignin diet, typically a diet composed primarily of young grasses, forbs and browse (Hoffmann and Stewart 1972). Plant cellular contents are digested very rapidly (Van Soest 1965) whereas lignin is not only indigestible, but also interferes with cellulose digestion. Hence the rapid passage of lignified cell walls would be beneficial to an animal with a small rumen. Differences in rumen volume and turnover rate have been suggested as being important factors in resource partitioning in ungulate communities (Hanley 1982).

# 6. CONCLUSIONS AND RECOMMENDATIONS

The findings of this study revealed some important differences between the feeding behaviour of sheep and goats. Forage intake as percent bodyweight for sheep (2.5%) was higher than for goats (2.0%) and intake was much lower in the wet season than in the dry season for both. Goats selected nutritionally superior diets than sheep with higher crude protein, similar digestibility and lower fibre content. Goats' diets however contained more lignin than sheep diets. Diet quality declined as seasons progressed, which is inevitable as plants mature.

Overall, sheep and goat diets were adequate for animal maintenance in terms of crude protein throughout the study period. Dry season diets were nevertheless lower in nutritional value than those of the wet season. In case of prolonged drought the results show that sheep are more likely to be disadvantaged than goats which were able to select diets higher in crude protein and thus showed superiority to sheep in coping with this season. The combination of low forage quality and low availability makes the dry season the most stressful nutritional period. Hence, management strategies aiming at improving the production of these animals should consider forage quality for goats and both quantity and quality for sheep.

The two species of small ruminants were consistent in their dietary selections with sheep showing preference for grass, whereas goats preferred mainly browse irrespective of season. Thus, the two showed complementarity in feeding in both seasons. Since the area is used by the two kinds of livestock, diet overlap where it occurs should be considered while recommending stocking rates. Manipulation of the range for better primary production should take into account the needs of different livestock species on a common use range. For instance, bush control and management in Kibwezi and similar environments should be judiciously done so as to reduce thickets of bush and replace the undesirable woody vegetation with more preferred species. Such species would include the already existing Acacia spp., Acalypha fruticosa, Combretum spp., Duosperma kilimandscharicum, Grewia spp. and Hermania alhiensis among others. Thus, selective bush clearing is recommended since browse formed the bulk of goat diets in both seasons. These findings form a guideline for range managers in assessing the usefulness of the vegetation to sheep and goat nutrition and how the two species exploit the resource.

Although of limited duration, this study indicated that goats were better adapted for survival in this environment than sheep. However, follow-up studies should be carried out to pursue and investigate the animal and vegetational responses over a longer time and especially in relation to the highly variable climatic conditions of this semi-arid region. Moreover, other aspects of goat and sheep survival mechanisms and production trends need to be studied, including water economy, resistance to starvation during drought periods and ability to forage over long distances.

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Appendix I. Percent relative frequency of forbs and grasses occurring in the study area by month.

| Plant Species | Dec '92 | Jan 93 | Feb | Mar | Apr | May | Jun | Jul '93 |
|---|---|---|---|---|---|---|---|---|
| | **Wet season** | | | | | **Dry season** | | |
| **Grasses** | | | | | | | | |
| Brachiaria reptans | 1.8 | 2.4 | 2.0 | 1.1 | 0.4 | 0.3 | | |
| Brachiaria serrata | 2.0 | 1.4 | 0.8 | 0.4 | 0.2 | | | |
| Cenchrus ciliaris | 2.8 | 3.1 | 3.5 | 2.5 | 3.1 | 4.2 | 3.6 | 3.0 |
| Chloris roxburghiana | 1.5 | 1.5 | 1.5 | 2.6 | 2.5 | 3.5 | 4.7 | 5.1 |
| Cynodon dactylon | 0.6 | 1.1 | 0.5 | 0.4 | 0.4 | 0.3 | 0.3 | |
| Cynodon plectostachyus | 1.0 | 1.0 | 1.0 | 1.1 | 0.7 | 1.8 | 1.2 | 2.7 |
| Dactyloctenium aegyptica | 1.5 | 0.6 | 1.0 | 0.4 | 0.4 | 0.1 | | |
| Digitaria macroblephara | 1.9 | 1.7 | 2.1 | 1.5 | 2.1 | 1.2 | 2.4 | 3.1 |
| Digitaria velutina | 2.1 | 1.8 | 3.0 | 1.5 | 1.1 | 1.3 | 1.2 | 0.9 |
| Echnochloa haploclada | 0.3 | 0.3 | 0.3 | 0.3 | 0.4 | 0.3 | 0.3 | 0.4 |
| Enteropogon macrostachys | 4.6 | 4.1 | 6.3 | 9.2 | 9.6 | 13.0 | 17.7 | 17.6 |
| Eragrostis caespitosa | 1.7 | 1.2 | 1.3 | 1.8 | 2.1 | 2.5 | 2.9 | 3.1 |
| Erogrostis superba | 1.4 | 2.2 | 1.0 | 0.7 | 1.1 | 0.8 | 0.6 | 0.5 |
| Panicum deustum | 0.2 | 0.3 | 0.3 | 1.1 | 1.1 | 1.5 | 1.8 | 3.3 |
| Panicum maximum | 1.0 | 0.9 | 1.0 | 1.1 | 1.1 | 1.5 | 2.4 | 3.1 |
| Rottboelia exaltata | 1.5 | 1.5 | 1.3 | 1.5 | 1.1 | 0.6 | | |
| Themeda triandra | 1.2 | 1.1 | 1.3 | 1.5 | 1.8 | 1.8 | 0.6 | 0.3 |
| Other grasses | 7.4 | 5.5 | 3.0 | 2.6 | 1.1 | 4.7 | 4.1 | 3.6 |
| **Total grasses** | 34.5 | 31.7 | 31.3 | 31.3 | 30.3 | 39.4 | 43.8 | 46.7 |
| **Forbs** | | | | | | | | |
| Acanthosperma hispidum | 2.1 | 1.9 | 2.0 | 0.7 | 0.4 | | | |
| Achyranthes aspera | 1.4 | 1.5 | 1.3 | 1.8 | 2.1 | 3.5 | 3.1 | 3.1 |
| Barleria spp. | 0.6 | 0.7 | 0.8 | 0.6 | 0.2 | 0.2 | | |
| Bidens pilosa | 2.0 | 1.1 | 1.5 | 0.7 | 0.4 | 0.2 | | |
| Boerhavia diffusa | 0.3 | 0.5 | 0.5 | 1.5 | 1.8 | 1.8 | 0.6 | 0.3 |
| Brepharis integriifolia | 5.4 | 6.9 | 7.0 | 8.1 | 9.6 | 10.1 | 12.9 | 14.8 |
| Cassia spp. | 5.3 | 6.5 | 6.5 | 3.0 | 2.8 | 2.1 | 1.2 | 0.4 |
| Commelina benghalensis | 6.6 | 8.2 | 8.8 | 9.2 | 11.0 | 10.1 | 9.4 | 8.7 |
| Crabbea velutina | 2.8 | 2.1 | 2.8 | 1.1 | 1.1 | 0.8 | 0.6 | |
| Crotalaria incana | 1.4 | 1.6 | 1.5 | 0.7 | 0.7 | 1.5 | 3.4 | 3.4 |
| Dyschoriste procumbens | 0.7 | 0.8 | 0.5 | 2.2 | 1.8 | 1.2 | 0.6 | 0.3 |
| Hypoestes verticillaris | 0.7 | 0.6 | 0.6 | 1.0 | 0.8 | 0.6 | 0.6 | 1.4 |
| Ipomea mombasana | 2.5 | 2.6 | 2.8 | 5.2 | 5.9 | 5.4 | 7.1 | 7.1 |
| Justicia disclipteroides | 5.2 | 4.5 | 4.0 | 3.3 | 3.6 | 2.5 | 1.2 | 1.3 |
| Kotstachys spp. | 1.7 | 1.6 | 1.5 | 1.5 | 0.4 | 0.2 | | |
| Leucas glabrata | 3.6 | 3.2 | 3.5 | 1.8 | 1.1 | 1.0 | 0.3 | |
| Macrotylomma axillare | 4.0 | 5.4 | 6.8 | 9.2 | 10.0 | 8.9 | 6.1 | 5.1 |
| Ocimum bacilicum | 1.8 | 1.3 | 1.3 | 1.5 | 1.1 | 0.8 | 0.6 | 0.5 |
| Oxygonum sinvatum | 3.6 | 3.1 | 3.5 | 2.9 | 1.1 | 1.0 | | |
| Plectranthus canabinus | 1.1 | 0.8 | 0.8 | 0.4 | 1.1 | 0.1 | | |
| Polygala spp. | 2.2 | 2.2 | 1.8 | 1.5 | 1.0 | 1.0 | 0.6 | 0.2 |
| Pupalia lupacea | 1.0 | 1.0 | 0.8 | 2.2 | 2.5 | 2.2 | 3.5 | 3.1 |
| Stylosanthes fruticosa | 0.3 | 0.6 | 0.5 | 0.4 | 0.7 | 0.7 | 0.6 | |
| Tephrosia spp. | 1.6 | 1.6 | 1.6 | 2.6 | 1.4 | 1.6 | 0.6 | 0.3 |
| Vernonia aemulans | 0.5 | 0.5 | 0.5 | 0.7 | 2.1 | 2.2 | 1.8 | 1.3 |
| Vigna spp. | 1.0 | 0.5 | 0.8 | 0.4 | 0.4 | 0.4 | 0.6 | 1.1 |
| Other forbs | 6.0 | 7.0 | 4.7 | 4.5 | 4.6 | 0.6 | 0.7 | 1.0 |
| **Total forbs** | 65.4 | 68.3 | 68.7 | 68.7 | 69.7 | 60.7 | 56.2 | 53.3 |

Appendix II. Density of trees and shrubs

| Plant species | Relative density(%) | Plants/hectare |
|---|---|---|
| **Trees** | | |
| Acacia mellifera | 2.3 | 41 |
| Acacia nilotica | 1.4 | 25 |
| Acacia senegal | 0.4 | 8 |
| Acacia tortilis | 6.4 | 115 |
| Adansonia digitata | 0.1 | 2 |
| Albizia antihelmintica | 0.8 | 14 |
| Commiphora africana | 0.4 | 8 |
| Commiphora baluensis | 0.9 | 16 |
| Commiphora campestris | 4.5 | 82 |
| Commiphora riperia | 6.8 | 123 |
| Lannea traphylla | 0.7 | 13 |
| Lonchocarpus bussei | 0.9 | 16 |
| Ormocarpum kirkii | 0.9 | 16 |
| Psychotria kirkii | 2.2 | 40 |
| Sterculia rhynchocarpa | 0.8 | 15 |
| Total trees | 29.6 | 534 |
| **Shrubs** | | |
| Abutilon mauritianum | 0.3 | 5 |
| Acacia brevispica | 1.4 | 25 |
| Acalypha fruticosa | 1.3 | 24 |
| Asparagus racemosus | 0.1 | 2 |
| Boscia angustifolia | 0.4 | 8 |
| Boscia coriaceae | 1.8 | 33 |
| Canthium sordidum | 0.4 | 8 |
| Combretum aculeatum | 1.4 | 25 |
| Combretum exalatum | 2.7 | 49 |
| Dichrostachyus cinera | 5.0 | 90 |
| Duosperma kilimandscharicum | 16.4 | 295 |
| Entada abyssinica | 1.7 | 31 |
| Grewia bicolor | 0.9 | 16 |
| Grewia similis | 0.9 | 16 |
| Grewia villosa | 1.8 | 33 |
| Grewia hexaminta | 0.2 | 3 |
| Hermania alhiensis | 3.2 | 57 |
| Hibiscus calophyllus | 1.4 | 25 |
| Hibiscus micranthus | 0.4 | 8 |
| Hibiscus aponeurus | 0.8 | 14 |
| Hoslundia opposita | 0.7 | 13 |
| Hypoestes aristata | 0.4 | 8 |
| Indigofera lupatena | 0.4 | 8 |
| Lantana verbenoides | 1.8 | 33 |
| Lippia javanica | 0.8 | 15 |
| Maerua edulis | 0.9 | 16 |
| Mondulea sevicea | 0.9 | 16 |
| Ochna inermis | 0.9 | 16 |
| Ochna insculpta | 5.9 | 107 |
| Pavonia patens | 3.7 | 66 |
| Premna hildebrandtii | 9.1 | 164 |
| Solanum incanum | 1.4 | 25 |
| Tenantia senii | 0.9 | 16 |
| Total shrubs | 70.4 | 1270 |
| **Grand total** | **100.0** | **1804** |

Appendix III. Percentages of plant species in livestock diets during the wet (December 1992 - March 1993) and dry seasons (April - July 1993).

| | Sheep | | | | | | | | Goats | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Wet season | | | | Dry season | | | | Wet season | | | | Dry season | | | |
| Plant Species | Dec 92 | Jan 93 | Feb 93 | Mar 93 | Apr 93 | May 93 | Jun 93 | Jul 93 | Dec 92 | Jan 93 | Feb 93 | Mar 93 | Apr 93 | May 93 | Jun 93 | Jul 93 |
| **Grasses** | | | | | | | | | | | | | | | | |
| Aristida keniensis | 1.1 | 2.5 | 3.9 | 1.1 | | 1.0 | 3.2 | 2.0 | 1.1 | | | | | | | 1.2 |
| Brachiaria spp. | 5.5. | 4.4 | | 1.1 | 2.3 | 2.9 | 1.0 | 6.1 | | | | | | | | |
| Cenchrus ciliaris | 12.1 | 11.5 | 12.6 | 13.8 | 5.8 | 6.8 | 10.5 | 8.1 | 1.1 | | 1.2 | 4.7 | 2.5 | 1.2 | 2.5 | 1.2 |
| Chloris roxburghiana | 1.1 | 1.6 | 1.9 | 6.3 | 3.5 | 1.0 | 1.0 | 2.0 | 7.9 | 3.4 | 2.3 | 1.1 | | 1.1 | 1.3 | |
| Cynodon dactylon | 4.4 | 4.4 | 7.8 | 2.1 | 1.2 | 8.7 | 5.4 | 13.1 | 4.5 | 1.1 | 1.2 | 1.2 | 1.3 | | 2.5 | |
| Cynodon plectostachys | 3.3 | 6.2 | 8.7 | 8.5 | 1.2 | 1.9 | 1.1 | 2.0 | 3.4 | 1.1 | | | | 1.2 | | 1.2 |
| Dactyloctenium aegyptica | 4.4 | 2.5 | | 3.2 | 3.5 | 1.0 | | 1.0 | | | | | | | | |
| Digitaria macroblephara | 4.4 | 2.6 | | 4.3 | 3.5 | 4.9 | 2.1 | 5.1 | | 1.1 | 1.2 | | | | | |
| Eragrostis caespitosa | 8.8 | 13.0 | 13.6 | 9.6 | 11.6 | 13.6 | 8.4 | 14.1 | | 2.4 | 3.4 | 2.3 | 2.5 | 4.7 | | 3.6 |
| Eragrostis superba | 13.2 | 8.5 | 5.8 | 9.6 | 8.1 | 12.6 | 12.6 | 11.1 | 3.3 | 1.1 | 1.2 | 3.5 | 5.1 | 5.8 | 3.8 | 1.2 |
| Enteropogon macrostachys | 9.9 | 8.4 | 4.9 | 6.3 | 12.8 | 10.7 | 4.2 | 5.1 | | | | 2.4 | | | | 1.2 |
| Panicum maximum | 4.4 | 1.6 | 2.9 | 1.1 | 1.2 | 1.0 | 2.1 | | | | 1.2 | | | | 1.3 | 2.4 |
| Panicum deustum | 1.1 | | | | 2.3 | 1.9 | | 1.0 | | 1.1 | | | | | | |
| Setaria pallidesfusca | | | | | 1.2 | | | | | | | 1.2 | | | | 1.2 |
| Themeda triandra | 4.4 | 6.8 | 7.8 | 3.2 | 5.8 | 3.9 | 9.5 | 6.1 | | | | 1.2 | 1.3 | | | |
| Other grasses | 9.9 | 9.3 | 7.7 | 7.4 | 13.9 | 8.7 | 11.6 | 3.0 | 2.3 | 3.5 | 1.1 | | 2.5 | 2.3 | 2.5 | 3.6 |
| **Total grasses** | 88.0 | 83.4 | 77.7 | 77.6 | 77.9 | 80.6 | 72.7 | 79.8 | 22.5 | 15.9 | 12.8 | 17.6 | 15.2 | 16.3 | 13.9 | 16.8 |
| **Forbs** | | | | | | | | | | | | | | | | |
| Achyranthes aspera | | | | | | | | | 1.1 | | | | | | | 2.4 |
| Amaranthus spinosus | | | | | | | | | | 1.1 | | 1.2 | | | 2.5 | |
| Bidens pilosa | 1.1 | | | 1.1 | | | 1.0 | | | | | | | | | |
| Cassia mimosoides | | 1.6 | | | | 1.0 | 1.1 | | | | | | | | | |
| Commelina benghalensis | 1.1 | | 1.0 | 1.1 | | 1.0 | 1.0 | | | | | | | | | |
| Ipomea mombasana | | 1.6 | | | | 3.9 | 2.1 | 2.0 | | | | | | | | |
| Oxygonum sinvatum | 1.1 | 2.5 | 1.9 | 2.1 | 2.3 | 1.9 | 1.1 | 4.0 | | | | | | | | |
| Stylosanthes fruticosa | | | 1.0 | 2.1 | | 1.9 | 3.2 | | | | | | | | | 2.4 |
| Tephrosia spp. | | | 1.0 | 2.1 | | | 1.0 | 1.0 | | | | | | | 2.5 | |
| Other forbs | 5.4 | 5.0 | 8.7 | 6.4 | 3.5 | 6.7 | 8.4 | 4.1 | | 1.2 | | 1.2 | | | | 1.2 |
| **Total forbs** | 8.7 | 10.8 | 13.6 | 14.9 | 5.8 | 16.4 | 18.9 | 11.1 | 1.1 | 2.3 | 0.0 | 2.4 | 0.0 | 0.0 | 5.0 | 6.0 |

Appendix 111 continued.

| Plant Species | Sheep | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Wet season | | | | Dry season | | | |
| | Dec 92 | Jan 93 | Feb 93 | Mar 93 | Apr 93 | May 93 | Jun 93 | Jul 93 |
| **Trees and Shrubs** | | | | | | | | |
| *Acacia brevispica* | | | | | | | 1.0 | |
| *Acacia mellifera* | | | | | | | | |
| *Acacia nilotica* | | | | | | | | |
| *Acacia tortilis* | | | | | 1.2 | | | |
| *Acalypha fruticosa* | | | | | | | | 1.1 |
| *Balanites aegyptica* | | | | | | | | |
| *Boscia angustifolia* | | | | | | | | |
| *Cadaba farinosa* | | | | | | | | |
| *Combretum aculeatum* | | | | 1.1 | | | | |
| *Combretum exalatum* | | 1.6 | | | 2.3 | | | |
| *Duosperma kilimandscharicum* | | | | | 1.2 | | | |
| *Grewia bicolor* | | | | | | | | |
| *Grewia similis* | | | | | | | | |
| *Grewia villosa* | | | | | 1.2 | | | |
| *Hermania alhiensis* | 1.1 | 2.6 | 5.8 | 2.1 | 2.3 | 1.0 | 3.2 | 2.0 |
| *Hibiscus calophylus* | | | | | 1.2 | 1.0 | | |
| *Hibiscus micranthus* | | | | | | | | |
| *Indigofera* spp. | | | | | | | 1.0 | 3.0 |
| *Pavonia patens* | | | 1.0 | | | 1.0 | | |
| *Sida ovata* | 1.1 | 1.6 | 1.9 | 4.3 | 3.5 | | 1.1 | 3.0 |
| *Solanum incanum* | 1.1 | | | | 1.2 | | 2.1 | |
| Other trees & shrubs | | | | | 2.3 | | | |
| **Total trees & shrubs** | 3.3 | 5.8 | 8.7 | 7.5 | 16.3 | 3.0 | 8.4 | 9.1 |

**Goats**

| Wet season | | | | Dry season | | | |
|---|---|---|---|---|---|---|---|
| Dec 92 | Jan 93 | Feb 93 | Mar 93 | Apr 93 | May 93 | Jun 93 | Jul 93 |
| 1.1 | 1.1 | | 1.2 | | | | 2.4 |
| 3.4 | 2.3 | | 3.5 | | 3.5 | | 2.4 |
| 4.5 | 2.3 | | 2.3 | 3.8 | 5.8 | 8.9 | 3.6 |
| 9.0 | 8.0 | 7.0 | 7.1 | 8.9 | 3.5 | 6.3 | 2.4 |
| 5.6 | 10.2 | 13.9 | 5.8 | 10.1 | 10.5 | 5.1 | 8.5 |
| 2.3 | | 1.2 | 1.2 | | | | 2.4 |
| 1.1 | 1.1 | 1.2 | 2.3 | 1.3 | 1.1 | 2.5 | |
| 1.1 | | | | | 1.2 | 5.1 | |
| 2.3 | 1.1 | 1.2 | 1.2 | 3.8 | 2.3 | 1.3 | 2.4 |
| 4.5 | 3.4 | 5.8 | 7.1 | 7.6 | 7.0 | 10.1 | 12.1 |
| 4.5 | 3.4 | | | 1.3 | 2.3 | 3.8 | 10.8 |
| 4.5 | 9.1 | 11.6 | 8.2 | 7.6 | 9.3 | 8.9 | 7.3 |
| 7.9 | 8.0 | 11.6 | 11.8 | 13.9 | 11.6 | 13.9 | 4.9 |
| 1.1 | 1.1 | 1.2 | 7.1 | | 7.0 | | |
| 5.6 | 9.1 | 11.6 | 8.2 | 2.5 | 4.7 | 1.3 | 2.4 |
| 3.4 | 2.3 | 2.3 | 2.4 | 2.5 | 2.3 | | |
| | 3.4 | 4.7 | | | 2.3 | 1.3 | 1.2 |
| 1.1 | 1.1 | | 1.2 | 1.3 | | | |
| 1.1 | | | | 5.0 | | | |
| 4.5 | 3.4 | | | 5.0 | 1.1 | | 2.4 |
| 1.1 | 2.3 | 2.3 | 2.3 | 1.3 | 3.5 | | |
| 6.7 | 9.1 | 11.6 | 7.1 | 8.9 | 4.7 | 12.7 | 12.0 |
| 76.4 | 81.8 | 87.2 | 80.0 | 84.8 | 83.7 | 81.1 | 77.2 |