FORAGE INTAKE AND FREE-RANGING RUMINANTS: A TROPICAL PERSPECTIVE

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ABSTRACT
Grasslands in tropical environments are characterized by greater diversity than is found in temperate areas. In South Africa, greater diversity is found with the seasonally limited production which occurs on dystrophic soils under humid conditions in the sourveld, as opposed to the year round production that occurs on eutrophic soils under warm and drier conditions in the sweetveld. Most of the animal and plant characteristics that affect the intake of pasture plants in the temperate regions and in the sweetveld are involved in tropical areas and in the sourveld as well. However, some of these characteristics assume much greater significance in the tropics compared to temperate grasslands. In tropical areas, the grazing cutoff, or the amount of total herbage that must be present for any intake to occur, takes place with herbage yields below 500 kg dry matter (DM) ha^{-1} for immature forage whereas it occurs with yields of over 1500 kg DM ha^{-1}, when the forage is mature. Quality factors reducing intake of tropical pastures may be attributed to their relatively high content of fibre and to the unique plant anatomy of tropical forages, which combine to reduce the degradation rate, particularly of grass species, in the rumen. Sward greenness is also an important characteristic affecting intake. Gross modelling of performance of ruminants on tropical pastures demonstrated that stocking rate was negatively related to daily gain of cattle and plant species composition had very little effect on animal performance under conditions of overstocking. Analysis of results from mixed grazing studies, with sheep and cattle, found that systems with sheep only or ratios of cattle to sheep of less than 3:1, were less productive in terms of pasture output than systems where the cattle to sheep proportion was 3:1 or greater.

KEYWORDS
Tropical pastures, intake, forage species, forage quality, modelling, mixed species grazing, stocking rate

INTRODUCTION
Tropical vegetation typically occurs in areas with distinct moist (usually summer) and dry (usually winter) seasons, and is dominated by C4 grasses. A wide range of vegetation types occur: from humid woodlands and grasslands through savannas and semi-arid grasslands to deserts (e.g. Tainton & Walker, 1993). All tropical vegetation types are characterised by large fluctuations in the quantity and/or quality of herbage available to free-ranging ruminants. Such fluctuations influence intake and thus livestock production potential. Animal performance on tropical forages is thus generally less than half the genetic potential of the animals due mainly to the poor quality characteristics of forage on offer (t'Mannetjie, 1982).

The purpose of this paper is to highlight animal and plant factors which influence intake in tropical/sub-tropical environments and to illustrate how these factors may provide understanding of herbivore dynamics. While a wide range of literature was consulted, much of the discussion is based on southern African experiences. In this region the terms sweetveld and sourveld are used to describe rangelands with differing forage producing characteristics. We consider the contrast between these two broad categories of vegetation to be useful in describing the forage producing characteristics (mainly in terms of quality on offer to the animal) of most tropical environments. In general, sweetveld occurs in warm, arid and semi-arid environments, on eutrophic soils with high base saturation, where the plants are slow to reach maturity and thus maintain their quality. Sweetveld also occurs in areas where rainfall is distributed throughout the year. Here, since plant growth may take place at any time of the year, immature palatable herbage may be available at any time. By contrast, sourveld occurs in humid areas, usually on dystrophic soils with low base saturation. Plant growth is restricted to the spring and summer months and grasses mature in mid- to late-summer. Herbage in the sourveld provides good quality grazing in spring and summer but becomes increasingly less palatable in autumn and winter.

ANIMAL FACTORS
Preference and selection behaviour. Food preference depends not only on taste, but the interaction between taste and the postingestive consequences of ingesting a particular food by the grazing animal (Provenza, 1995a). Food selection involves smell and sight to distinguish between foods that cause positive or negative postingestive effects. In general, animals prefer foods that cause satiety (Provenza, 1995b), but acquire aversions to foods that cause malaise, feelings of discomfort from excesses of toxins or nutrients. In tropical rangelands, typical aversions and therefore decreased voluntary intake may result from alkaloids (Olson & Ralphs, 1986; Thompson & Stuedemann, 1993), condensed tannins (Provenza et al., 1990), saponins and coumarins (Rankins et al., 1993) and deficits (Ternouth, 1991; Anil et al., 1993; Wallis de Vries, 1994) of energy, nitrogen, amino acids and minerals, particularly phosphorus.

Animal species and foraging strategy would influence selection patterns. In general, the diet selected by sheep is of higher quality than that selected by cattle across vegetation communities, ranging from temperate grasslands (Grant et al., 1985) and sown pastures (Duzinski & Arnold, 1973) to semi-arid (Zeeman et al., 1983; 1984) and humid rangelands (O'Reagain, 1994). This reflects the greater selective ability of sheep arising from fundamental differences in muzzle width, curvature of the incisor arcade, lip mobility and grazing method between the two animal species (e.g. Gordon & Illius, 1988). Furthermore, small herbivores, such as sheep, are adapted to grazing more closely than cattle (Heinemann, 1970; Mentis, 1980). It has been suggested that cattle cannot graze closer than approximately 1.3 to 1.5 cm from the soil (Voison, 1959; Heinemann, 1970), whilst sheep may graze to soil level (Hafez & Scott, 1962). Comparing cattle-only versus sheep-only grazing of a humid sub-tropical grassland with both species stocked at the same number of animal unit equivalents per hectare, 30% of the experimental area allocated to sheep was grazed to < 1cm whereas for the cattle less than 1% of the treatment area was grazed to <1cm (Hardy, 1995).

Voluntary intake. Potential intake is determined by factors such as animal size and physiological state. Voluntary intake, i.e. the quantity of forage consumed by the animal, is influenced by complex interactions among dietary preferences and selection habits, and ingestive and digestive constraints to intake (e.g. Illius, this conf.). Ultimately, animal production on pasture is primarily a function of voluntary intake which is, in turn, inextricably linked to forage quality (digestibility) which, in the ruminant, reflects reticuloruminal rates of fermentation and passage.

Plant structure and composition. In general, animals select plants with nutritious high quality leaves which are rapidly digested in the rumen, e.g. Heady (1964). However, preference is also strongly influenced by plant structure in terms of the effects of this variable on ingestion rate (O'Reagain, 1993). Amongst grazers, animals thus tend to select species which are non-stemmy and which have accessible leaves of high nutrient content and low tensile strength (O'Reagain & Mentis, 1989). Conversely, low quality, stemmy species with inaccessible leaves of high tensile strength are avoided (O'Reagain, 1993). For browsers, intake has been positively related to leaf weight per unit length of shoot and the ease of harvesting leaf material, but the relationship was modified by browse-induced tannin levels and the overall digestibility of leaves and shoots (Teague, 1989). Plant selection thus appears to be based largely upon the interplay between plant structure which determines intake rate and leaf quality which determines nutrient content.

PLANT FACTORS

Voluntary intake. The most important factors determining intake are the quantity (e.g. Ulyatt, 1973) and quality (e.g. Noy-Meir, 1975) of herbage on offer. In rangelands these are, in turn, affected by factors such as plant species composition, plant and plant-community structure, season (herbage maturity) and the grazing or browsing history of the site in question.

Theoretically, species composition could affect intake at two levels. At the plant level, species could differ in potential rates of intake due to differences in bite size and or biting rate arising through differences in plant structure or morphology. At the patch or community level, intake could also be affected through the differences in the proportion and distribution of the different species present. Here intake would be a function of time required to locate different species in the sward (Spalinger & Hobbs, 1992).

In general, intake increases dramatically with increased height and density of the sward, and therefore available herbage e.g. Hodgson (1982); Fox (1987). Intake rate rises asymptotically until bite size is restricted by mouth dimensions (Allden & Whittaker, 1970) and/or biting rate becomes limited by chewing rate (Spalinger & Hobbs, 1992). This resembles the Type II functional response (Holling, 1959) with intake increasing as a decelerating function of available forage (Figure 1). Distinct functional responses exist for different animals according to body mass, mouth dimensions and foraging efficiencies (Short, 1985).

The Type II functional response may, in certain circumstances, be replaced by a quadratic function (O'Reagain et al., 1996). For example, sheep intake rates on sourveld showed a curvilinear response to plant height, with intakes declining on very tall swards. This effect may be attributed to the reduced biting rates observed on very tall swards which possibly result from the increased search and handling times required to locate and prehend highly dispersed items of food in these relatively low quality swards (O'Reagain et al., 1996). The present effect is important as it highlights the inability of the functional response to cope with the interaction between food quality and availability.

Quantity of drymatter intake increases with nutritive value of the feed and energy uptake by the animal also increases with increase in nutritive value up to approximately 9.2 MJME kgDM^{-1} (Ulyatt, 1973). Since apparent digestibility in a subtropical grassland such as sourveld rarely exceeds 65% (^{3} 9.2MJME kgDM^{-1}) (Hardy, 1986; O'Reagain & Owen-Smith 1996), the voluntary intake of cattle grazing on sourveld will be restricted by virtue of the poor quality forage on offer. The only time when the nutritive value may exceed 9.2 MJME kgDM^{-1} is when the grass is fresh and young at the very start of the growing season, in which case the amount of herbage on offer will be limiting (Mentis, 1982). Thus the limiting effects of quantity and quality on intake will act simultaneously and jointly impose gradual increasing restriction on intake. This is a necessary consequence of selective feeding by animals whose ingesta are generally of a higher quality than that of the sward as a whole.

Moreover, in many grazing systems, and for cattle grazing on sourveld in particular, there is likely to be a grazing cutoff (Noy-Meier, 1975; Walker, 1980; Mentis & Tainton, 1981). The grazing cutoff is the herbage mass below which no grazing occurs because the grass is inaccessible to the grazer, or because it is of such low value that the grazer will not eat it (Figure 1). Hardy & Mentis (1986) incorporated a grazing cutoff in a model which predicted steer performance in sourveld. The proportion of forage (F) in the total above-ground herbage mass (V) through a growing season was modelled as: F = BV where B is the grazing cutoff factor and is a linear function of sward maturity (t), viz. $B = 0.71 -7.74*10^{-4}t$. So, in the early season (t=60) when V=1000 kg.DMha^{-1}, approximately 660 kgDMha^{-1} could be considered forage. Similarly, at the end of the season (t = 200) and V=3000 kg.DMha^{-1}, F=1680 kg.DMha^{-1}. The grazing cutoff was also quantified by Turner & Tainton (1989). Thus forage may be distinguishable from herbage as that part of the herbage ingested by the animal. As herbage matures it becomes progressively less acceptable to the animal. It follows that, for certain vegetation types, the proportion of forage in the herbage decreases with the maturity of the herbage (Figure 2).

QUALITY OF INTAKE

Tropical and sub-tropical vs temperate forages. Compositional constituents that limit intake of tropical and subtropical forages are primarily those associated with the cell wall. In general, intake is limited by cell wall above neutral detergent fibre (NDF) concentrations of 550 - 600 g per kg dry matter (DM), but not below (Meissner et al., 1991). Most subtropical grasses would contain higher NDF concentrations than this indicator level, whereas NDF in most temperate grasses and legumes would be lower.

Tropical forages are not only more stemmy but their leaves contain more cell wall than temperate species. This results in lower digestibility, slower fermentation and slower particle size reduction in the reticulorumen which in turn reduces the rate of passage of digesta from this organ (see reviews of Minson, 1981; 1990 and Meissner, 1988). These structural characteristics also cause resistance to comminution during mastication and rumination further limiting particle breakdown and hence intake.

However, the major differences in degradability between tropical and temperate species result from the basic dichotomy in leaf anatomy between C3 and C4 species. In C3 grasses, loosely-packed mesophyll cells and widely spaced vascular bundles allow rapid microbial degradation of the leaf substrate while, in C4 species, the typical Kranz anatomy reduces microbial access to interior mesophyll cells. The leaf epidermis of most C4 grasses is also more resistant to degradation than C3 species (Watson & Dallwitz, 1980). Further, shedding of the leaf epidermis to allow easy breakdown of particles, does not occur easily in most tropical grasses because the abaxial and adaxial epidermis is linked to the vascular bundles by thick-walled, lignified sclerenchyma and parenchyma bundle sheath cells (Wilson et al., 1989). Large differences in leaf quality have also been recorded between different C4 species. For example, different sourveld grasses vary markedly in both their rate and extent of DM degradation in the rumen (O'Reagain et al., 1995). Thus species such as *Eragrostis plana* and *Microchloa cafra* are poorly digestible while species such as *Themeda triandra* and *Alloteropsis semialata* have very favourable digestion characteristics and degrade rapidly under rumen conditions. Interestingly, these differences appear to be partly associated with differences in leaf tensile strength among grass species which is largely determined by the concentration of cellulose and the amount of sclerenchyma tissue present in the leaf (Evans, 1964; Wilson, 1965). In all species tested there was a marked decline in the potentially digestible fraction, an increase in the indigestible fraction and a general decline in the degradation rate of DM as the plants matured from spring through to winter (O'Reagain et al., 1995).

The degradation rates of all sourveld species (O'Reagain et al., 1995) were markedly lower than those recorded for temperate species. Even in spring when sourveld grasses are most digestible, cell wall degradation rates are usually less than half those for C3 species when measured at the same physiological state (Hoffman et al., 1993). In general, degradation rates of C3 grasses only appear to decline to the levels recorded for C4 grasses following anthesis, e.g. Lentz & Buxton (1992).

Sward structure. Sward structure is a major determinant of diet quality for grazing herbivores on both tropical and temperate pastures. However, of the different sward structure variables, sward greenness probably has the major effect on diet quality e.g. Hamilton et al. (1973); Chacon et al. (1978). For example, on sourveld, sward greenness was found to be the single most important determinant of diet quality in both cattle and sheep (O'Reagain & Owen-Smith, 1996). This relation is logical; green leaf is the highest quality component within the sward (Juko & Bredon, 1961) and dietary quality is strongly correlated with the amount of leaf in the diet (O'Reagain & Mentis, 1988). Interestingly, the relation between diet quality and sward greenness appears to be non-linear, at least on sourveld, with the major response to this variable occurring at high greenness values (O'Reagain & Owen-Smith, 1996). Forbes and Coleman (1993) similarly noted that cattle grazing *Bothriochloa* pastures were able to harvest diets of similar digestibilities over a wide range of green leaf availabilities in the sward. This suggests that animals are, to a certain extent, able to mitigate the effects of decreasing green leaf availability by becoming increasingly selective. This is corroborated by the fact that for cattle on sourveld biting rates generally decline with decreasing greenness (O'Reagain et al., 1996), presumably because animals spend more time searching for or manipulating bites.

Dietary quality is negatively related to herbage mass and sward height, at least within the growing season (Chacon et al., 1978; O'Reagain, 1990, O'Reagain et al., 1996). Short swards provide a dense, concentrated layer of high-quality leaf but as swards increase in height and available herbage, shading increases leaf senescence, diluting the availability and accessibility of greenleaf to the grazing animal. Leaf quality declines with increasing height and mass e.g. Grieve & Osbourn (1965) due to increased lignification with leaf age (Wilson, 1973; Wilson & t'Mannetjie, 1978).

Dietary quality will decline with increasing stemminess (Chacon et al., 1978; O'Reagain & Owen-Smith, 1996). While young stems may be reasonably digestible (Norton, 1982), stems are lignified and of poor quality (Juko & Bredon, 1961). Although stems tend to be avoided forming less than 20% of cattle diets (O'Reagain & Mentis, 1988), at high stem densities, animals are possibly unable to select leaf without consuming a certain amount of stem. Also, stemmy swards tend to be in a late stage of maturity resulting in overall lower digestibility of leaf. In addition, stemminess may restrict access to leaf within the tuft (Arnold, 1962) forcing animals to consume lower-quality dead or partly-senescent herbage.

Seasonal effects. Marked seasonal changes in the quality of intake have been recorded in humid tropical environments, with crude protein content and digestibility of ingesta being highest in spring and lowest in autumn and winter (Table 1). These changes largely reflect seasonal changes in leaf quality and accessibility to the grazing animal (O'Reagain, 1994). Early in the growing season, swards are open and leaf is accessible, allowing selection of a high-quality diet. As the season progresses however, swards become increasingly stemmy, the proportion of leaf present declines and becomes increasingly dispersed resulting in an overall reduction in leaf accessibility. This is parallelled by increasing consumption of dead herbage (O'Reagain & Mentis, 1988) and an associated decline in dietary quality. In autumn, widespread leaf senescence occurs, in response to low soil moisture or periodic frosts (Wilson & Ng, 1975; Wilson & t'Mannetjie,1978), forcing animals to subsist on a diet of predominantly dead herbage of low quality (O'Reagain & Mentis, 1988). These effects are frequently exacerbated by the concomitant decline in the quality of available leaf over the grazing season observed with many sourveld grasses e.g. O'Reagain et al. (1995).

In many tropical rangelands intra-seasonal fluctuations in dietary quality may also occur e.g. McKay & Frandsen (1969); Dradu & Harrington (1972). These fluctuations appear to reflect temporal patterns in rainfall distribution. For example in a study on sourveld, dietary quality was observed to drop sharply during a short, mid-season drought but subsequently recovered when soil moisture levels were replenished (O'Reagain, 1994). These trends are possibly linked to soil wetting and drying cycles and their effect on N availability for the plant. Inter-seasonal fluctuations in forage quality also occur in many rangelands with the general observation that provided herbage availability is not limiting, animal production is relatively better in dry than in wet years due to the relatively higher quality of herbage in dry years. For example, sheep grazing on sourveld during a dry year (67% of mean annual rainfall) showed a 100 to 200% improvement in livemass gain per animal relative to livemass gains recorded during 'normal' (800mm annual rainfall) years (Hardy & Tainton, 1995). This response occured despite dry matter production being 50% lower than that expected during 'normal', wet years (Hardy, 1994).

Species composition. In sourveld, the different degradability characteristics of grass species such as, for example, *Eragrostis plana* and *Microchloa cafra* (which tend to be abundant in "poor" condition, over- grazed rangeland), and *Themeda triandra* (which is abundant in range which is considered to be in "good" condition), it would be expected that range condition (based on species composition) would influence diet quality and thus animal performance (Hardy & Mentis, 1986; O'Reagain et al., 1996). This is corroborated by simulation models which indicate that species composition has the potential to have a major effect on animal performance on sourveld (O'Reagain, 1996 a&b). While the studies of Mentis (1982), O'Reagain and Mentis (1990) and O'Reagain and Owen-Smith (1996) found no relation between species composition and the quality of intake by steers, Hardy (1986) reported that, depending on season, species composition influenced the quality of diet selected by cattle on sourveld swards. Sensitivity analyses showed that the difference in the digestibility of the selected diet could be as much as 10 percentage points. Species composition therefore appears to be important, in humid, sourveld regions, because the inherent quality and relative abundance of the species present ultimately fix the potential dietary quality available to the animal, and the extent to which this quality can be maintained through the grazing period.

By contrast, in arid and semi-arid sweetveld regions species composition does not appear to have a major influence the quality of diet selected by grazers. Danckwerts (1989), working in a semi-arid sweetveld area, reported that OMD declined from spring (65% OMD) to winter (55%OMD) and that digestible crude protein content in the diet was unaffected by time of year remaining at approximately 8%CP. Range condition, as indexed by species composition, had a small, significant effect on the quality of diet. It was concluded that, in this sweetveld region, forage availability would have a greater influence on animal performance than forage quality (Danckwerts, 1989).

ESTIMATING INTAKE AND ANIMAL PERFORMANCE

Understanding what determines and limits intake is important to optimizing utilisation of the resource. Voluntary intake has a direct bearing on grazing capacity and therefore on stocking rate and rangeland management. Stocking rate may be calculated as a function of energy requirements of grazing herbivores, but modified through the voluntary intake of the herbage on offer, in terms of the amount and quality of the herbage consumed (Meissner, 1994). These modifications are particularly important in multiple-species grazing systems where positive and negative interactions may occur between bulk grazers, concentrate grazers and browsers. One suspects these influences to be more important to managing savanna and mixed rangeland in the tropics and sub-tropics than management systems elsewhere.

Two main approaches to predicting intake have been taken. First, detailed process-based models predict nutrient intake from the specific characteristics of individual plant species or groups of plant species and the foraging behaviour, digestive function and metabolic requirements of the animal concerned. Second, "gross" empirically-based models predict nutrient intake from basic animal characteristics and the overall quality and quantity of forage on offer (e.g. Hardy & Mentis, 1986; Meissner & Paulsmeier, 1995).

A series of process-based models were developed by O'Reagain (1996 a & b) to predict cattle and sheep performance on sourveld. The models were based on the digestive and ingestive characteristics of a range of sourveld grasses and quantified the effects of species composition, sward structure and season on potential animal production. Dietary quality, through its effect on digestion rate, was found to be of greater importance than the rate of dry matter ingestion in determining animal production. Under nearly all circumstances the potential rate of dry matter ingestion for both cattle and sheep exceeded potential digestion rates in the rumen, suggesting that diet quality is the major determinant of dietary intake on sourveld. Species composition was found to have a major effect on predicted animal production due mainly to large differences in quality among grass species.

"Gross" approaches to predicting or estimating intake have provided useful insights into optimal utilization of fodder resources. Hardy and Mentis (1986) developed a model to predict the performance of steers grazing on sour grassveld. The quality of intake was modelled as a function of sward maturity, species composition and immediate grazing history, while the quantity of intake was modelled as a function of sward maturity and the amount of forage on offer. A grazing cutoff was included to distinguish forage from herbage. Animal based factors such as 1) daily energy requirement for maintenance, 2) energy available for production 3) efficiency of energy utilization for gain, and 4) net energy stored (Anon., 1975; Kearl, 1982) were integrated with the models predicting the quality and quantity of intake to predict daily mass gain per animal for animals of a given mass, within a given management system, at a given stocking rate, for a given grazing season. Sensitivity analysis showed that where stocking rates were set at levels used in commercial livestock production systems, species composition through its effects on the quality of forage ingested had a major effect on the performance of the steers (Figure 3). Where stocking rates were set at high levels aimed at maximising livestock numbers rather than individual animal performance, as is the case in many subsistence grazing systems, species composition had a negligible influence on steer performance (Figure 3). At the stocking rates the sward is kept short maintaining the herbage in a young, nutritious state. Thus the quantity of herbage on offer would limit the number of animals which could be carried at maintenance.

A posteriori estimates of forage utilization by individual animals in a multi-species grazing system has proved useful in considering the appropriate animal species mixes and the sustainable use of resources. Hardy (1994; 1996) analysed data derived from a mixed-species grazing trial which monitored the performance of, and the quality of forage selected by, cattle and sheep for various cattle to sheep ratio treatments, with each treatment stocked at the same metabolic mass ($W^{0.75}$) per hectare at the start of the grazing season. Given the animal's mass, physiological status, average daily gain and the quality of intake over time, daily dry matter intake per animal could be estimated from feeding standards (e.g. Meissner et al., 1983).

Estimates of daily dry matter intake per hectare by cattle and sheep in each ratio treatment are presented in Figures 4a to 4d. Clearly, where the cattle and sheep started at the same metabolic mass per hectare (Figures 4a & 4c), or where sheep were in higher proportion to cattle (Figure 4d), estimated daily intake by cattle and sheep varied considerably. Only in the 3:1 ratio were the relative intake rates of the cattle and sheep similar (Figure 4b). The estimated total apparent intake for each of the cattle-to-sheep ratio treatment (from cattle-only to sheep-only) was 1779, 1696, 1602, 1504 and 1287 kgDM ha^{-1} a^{-1}, supporting the general observation of decreasing apparent intake with increasing proportion of sheep in the species mix. Sheep-only grazing removed approximately 28% less dry matter per hectare than cattle-only grazing.

The demand for forage by sheep was low relative to that of cattle. As the proportion of sheep in the species mix increased more herbage became available for the remaining cattle. With an increasing availability of dry matter on offer per animal, individual livemass gains of the cattle would increase (Hardy & Tainton, 1995). However, sheep performance appears to be influenced more by sward structure, and thus by quality rather than the quantity of herbage on offer. Sward structure is, in turn, a function of animal species mix and stocking rate. Severe patch grazing is a common feature of sheep-only grazing in both sweet- and sourveld and the sheep tend to restrict their grazing to the patches (Hardy, 1995; Danckwerts, unpublished data). For sheep-only grazing in sourveld, Hardy (1995) showed that approximately 65% of the sward remained ungrazed (non-patch areas) with a modal leaf table height (LTH) of 26cm for the non-patch grazed area. By contrast where cattle were stocked at the same metabolic mass as in the sheep-only system, non-patch areas comprised approximately 20% of the sward with a modal LTH of 12cm. Modal LTH of patch-grazed areas was < 4cm in both the sheep-only and cattle-only systems. Where cattle were stocked in high proportion to sheep a sward structure similar to that of cattle-only grazing developed (Hardy 1995). In this latter circumstance the sheep would therefore have had access to a sward comprising mainly short, relatively immature grass. Thus at a ratio of 3 AU cattle to 1 AU sheep, not only would the sheep have had a greater opportunity for selection, but there would have been a greater quantity of high quality herbage on offer to them relative to ratios with a greater proportion of sheep.

These results provide insights into the management requirements of rangelands. For example, a common factor among all methods for defining grazing capacity is the animal unit (AU). The AU provides a point of reference against which animals of different species, and classes within a species, may be equated. Various definitions for the AU have been proposed. These relate to 1) the expected dry matter intake of an animal according to its livemass (e.g. de Leeuw & Tothill, 1993), 2) the energy requirements of an animal based on its metabolic mass (e.g. Mentis, 1981), and 3) the energy requirements of an animal of a specified mass and a specified level of performance (Meissner et al.,1983). It should be noted here that central to these definitions is that the amount of herbage consumed by herbivores is equated across animal types. This has generally been taken to imply an equivalent impact on the sward. When presenting their definitions of AU and grazing capacity, few authors have stressed the differences in feeding habits between different species of herbivore and the different potential effects of these different feeding habits on range condition. Cattle and sheep cannot be equated in terms of their potential demands on forage (Figures 4 a, c & d), except in certain circumstances (e.g. when cattle are stocked in high proportion to sheep, Figure 4b). Sustainability of the system may also be affected due to differences in the grazing/browsing impact among herbivores. For example, sheep tend to repeatedly and severely graze individual plants and selected patches in the sward (Hardy et al., 1994; Hardy, 1995). Under such circumstances range condition would be expected to deteriorate thus negatively influencing the sustainability of the system.

CONCLUSIONS

Large fluctuations in the quality and quantity of forage produced in tropical environments impose severe limitations to intake by free-ranging ruminants. Despite the general recognition of such limitations, few studies have been conducted on tropical forages, particularly in respect of free-ranging ruminants, to obtain a predictive understanding of the interactions between plant and animal factors and their influence on voluntary intake. Such understanding is necessary to predict the consequences of various grazing/browsing systems on the economic and environmental sustainability of the animal production system.

The models predicting intake and animal performance discussed in this paper are based on averages and do not cope with the structural, spatial and temporal heterogeneous nature of forage production. They also do not cope with constraints to intake as influenced by the "state" or physiological condition of the animal. Moreover, most research has been conducted on small paddocks which may have had an influence on the relation between, for example, the quality of intake and sward maturity. A greater predictive understanding is required which incorporates such animal and sward variability. When developing models for estimating intake, the methods applied must be appropriate to the extensive grazing systems practised in most tropical environments.

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Table 1
Mean organic matter digestibility (%OMD) and crude protein (%CP) content of ingesta (dry matter basis) selected by cattle from spring through winter in a humid (sourveld) subtropical grassland (after Hardy, 1994; O'Reagain, 1994)

Season	%OMD	%CP
Spring	65	11
Summer	55	7
Autumn	45	5
Winter	40	3

Figure 1
Intake increasing as a decelerating function of herbage mass (HM) for a) immature, high quality herbage where HM>2000kg DMha^{-1} is theoretical since at such levels the herbage would be mature and of low quality, and b) mature, low quality herbage. A grazing cutoff is also shown for each of a) & b) at a_1 and b_1. The grazing cutoff is the HM below which no grazing occurs because the herbage is inaccessible to the grazer or of such low quality that the grazer would not eat it (after Hardy & Mentis, 1986)

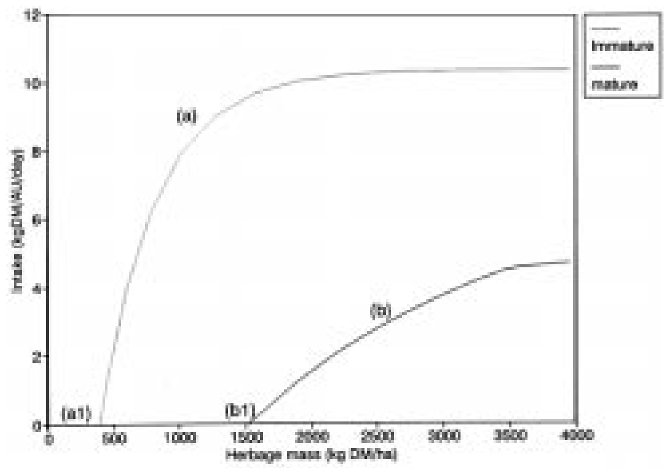

Figure 2
Functions describing a) undisturbed herbage production for sourveld, and b) the decreasing proportion of forage in the herbage with increasing herbage maturity (after Hardy & Mentis, 1986)

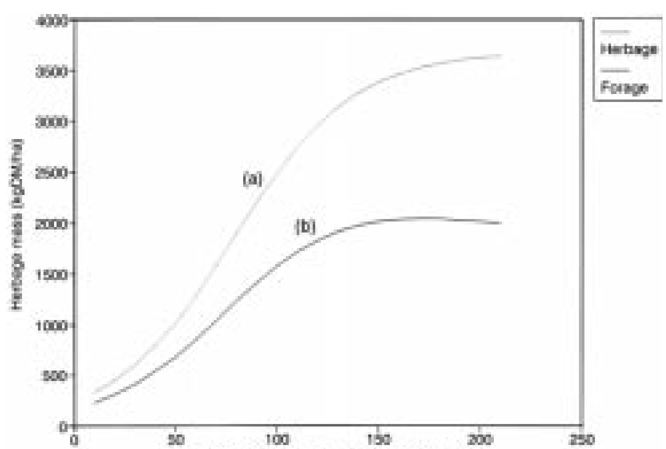

Figure 3
Isoclines showing the interaction of species composition and stocking rate on the production (expressed in terms of average daily gain - ADG) of steers (starting mass = 300kg) for a 7 month grazing season on sourveld (adapted from Hardy & Mentis, 1986).

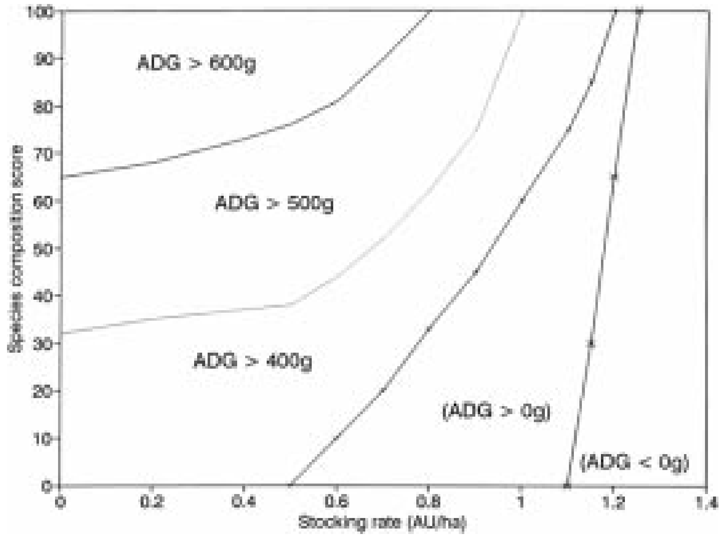

Figure 4
Seasonal trends in daily dry matter intake per hectare by cattle and sheep for each of five cattle-to-sheep ratios. The 1:0 and 0:1 ratios have been shown on a single figure for ease of comparison