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THE EFFECT OF SWARD STRUCTURE AND SPECIES COMPOSITION ON DIETARY QUALITY AND INTAKE IN CATTLE AND SHEEP GRAZING THE DOHNE SOURVELD

Peter John O'Reagain

A thesis submitted to the Faculty of Science,
University of the Witwatersrand, Johannesburg,
in fulfilment of the requirements for the degree
of Doctor of Philosophy

Stutterheim 1994

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted for any degree in any other University.

P.J. O'Reagain

28 June 1994

ABSTRACT

This study investigated the potential effects of species composition and sward structure on dietary quality and intake in cattle and sheep grazing the Dohne Sourveld. In the main experiment, animals were confronted with a range of sward structures at four different sites at different times through the grazing season. Species composition and hence, veld condition, were found to have no clear effect on dietary quality in either cattle or sheep. Conversely, sward structure had a major effect on dietary quality in both animals, with dietary crude protein and *in vitro* digestibility being strongly related to sward greenness but negatively related to sward height and herbage mass. Dietary quality was also significantly higher in sheep than in cattle and was markedly higher in the year of the burn than in the subsequent year.

Species composition and veld condition were also found to have no measurable effect on the rate of DM intake in cattle and sheep. In contrast, sward height had a major effect on intake rate but other sward structure components like greenness, stemminess and herbage density had no clear effect on this variable. For both animals, intake rate increased two to six fold with increasing sward height, reaching an asymptote or maximum at a height of 10-15 cm for sheep and 20-25 cm for cattle.

Cattle and sheep both followed a distinct sequence of species selection over the grazing period. In general, preferred species were defoliated first followed by less preferred species but avoided species were generally not consumed until the majority of tillers (> 60%) of the preferred species had been defoliated and a considerable proportion of these tillers regrazed. Overall, the frequency of tiller defoliation was the same under both cattle and sheep grazing but sheep consistently defoliated tillers at a lower height and removed relatively more of a tiller, than did cattle.

In two separate but related trials the potential ingestion and digestion rates of different sourveld grass species were investigated. Although some significant between-species differences were evident, measured rates of DM intake from different sourveld grasses were surprisingly similar. However, there were major differences in ruminal degradation rates and in the size of the digestible and indigestible fractions present in different sourveld grasses. Large seasonal differences were also evident with degradation rates declining, and the indigestible fraction increasing, from spring through to winter.

In a series of simulation models, dietary quality, through its effects on digestion rate, was found to be of greater importance than ingestion rate in determining animal production on sourveld. Species composition was found to be a major determinant of predicted animal production, due to large differences in the rate and extent of digestion between grasses. Sward structure was also found to be an important determinant of animal production on sourveld through its effects on dietary quality and intake. Optimum heights during the growing season for animal production were 6 - 8 cm for sheep and 10 - 12 cm for cattle, but these would be expected to become progressively lower through the season as quality declined and the digestive constraint on intake increased. Overall, a strong interaction between species composition and sward structure was evident with the optimum sward height varying with species composition while the species composition where animal production was maximised also varied with sward structure. Accordingly, an optimum species composition and sward structure cannot be specified as these variables are both conditional upon each other as well as the season, the objectives of the grazier and the animal species involved.

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ABBREVIATIONS

CP = crude protein

df = degrees of freedom

DM = dry matter

IVD = *in vitro* digestibility

min. = minute

N = nitrogen

n = sample size

OM = organic matter

SS = sums of squares

% = percent

* = (P≤0.05)

** = (P≤0.01)

*** = (P≤0.001)

CHAPTER 1

INTRODUCTION

An ability to predict the potential of an area of rangeland to support animal production would be a major practical and theoretical advance. Practically, this would enable a monetary value to be attached to rangeland which would have major consequences for resource conservation and legislation. Such knowledge would also facilitate strategic and tactical decision making by the grazier in terms of financing, marketing and basic animal and range management. Theoretically, predicting the animal production potential of different areas of rangeland would allow their resource value to the animal to be assessed. This would be valuable in addressing such issues as the distribution of animals in relation to the available resources, e.g. the ideal free distribution (Fretwell & Lucas 1970) and the patch selection and departure rules used by foraging animals.

In South Africa, rangeland has traditionally been assessed on the basis of its species composition and basal cover, quantified in terms of a 'veld condition score' or 'veld condition index'. The first quantitative methods of assessing veld condition were based on the increaser-decreaser concept of Dyksterhuis (1958) where the vegetation of a site was rated relative to the benchmark or potential species composition of that particular area (Foran 1976; Tainton *et al.* 1978; Tainton *et al.* 1980). Later methods involved giving each species a score with the veld condition index being determined as the sum of the products of the abundance and score of each species at a particular site, e.g. Heard *et al.* (1986). These methods, or derivations of these methods, are widely accepted and employed in resource assessment and monitoring in southern Africa.

Although the original concept of range condition was defined as the 'state of health' of the vegetation (Stoddart & Smith 1955) it was later assumed that a direct relation existed between range condition and the potential of that site to support animal production, e.g. Tainton (1986); Tainton (1988). As an example, in the method of Tainton *et al.* (1980), grazing capacity, and by inference animal production, is held to be a function of species composition, modified by slope, basal cover and soil erodibility; if the latter factors are held constant then grazing capacity is a direct function of species composition. This assumption is based on the tenet that there is "a close relationship

between the ecological status of a plant community and its value for the production of forage" (Tainton 1986).

A direct relation between veld condition and animal production does appear to hold, at least in the arid and semi-arid grasslands of South Africa (locally termed sweetveld). For example, Danckwerts (1982) recorded a linear relation between veld condition and carrying capacity over seven sites in the semi-arid sweetveld of the eastern Cape. Similarly, in the same area, herbage production from veld in 'good' condition was found to be nearly double that from veld in 'poor' condition (Danckwerts & Barnard 1981). Such a relation is, however, to be expected in these environments in that animal production is generally limited by forage quantity rather than quality (Danckwerts 1984), while any decline in range condition often involves an increase in the relative abundance of annual grasses such as *Tragus koeleroides* (Martens 1992) with logical consequences for long-term herbage production.

The situation in the lower quality, mesic grasslands of South Africa (locally termed sourveld) is, however, notably different. First, most, if not all, sourveld grasses are perennial, so a decline in veld condition does not necessarily involve a change to species with a different life history strategy. Second, in sourveld, animal production is most commonly limited by herbage quality rather than quantity so the amount of herbage produced is not as critical as its nutritive value.

Accordingly, there is little to substantiate the contention that animal production is a function of veld condition in the sour grasslands, and, in fact, most evidence is to the contrary. Turner (1990), for example, recorded significantly higher animal production on medium- than on good condition sourveld in northern Natal. Further, three separate studies on sourveld indicated that there was no overall relation between veld condition and the quality of diet selected by cattle on this veld type (Mentis 1982; Hardy 1986; O'Reagain & Mentis 1990). There also appears to be no relation between veld condition and herbage production, at least in the Dohne Sourveld (Willis 1990). However, possibly the strongest evidence is that of Gillard (1961; cited by Roux 1969 p.121) at Frankenwald; here, cattle mass gains increased progressively over time as the range deteriorated under heavy stocking from the climax 'purple veld' to a degraded sward dominated by *Eragrostis* and *Cynodon* species. After five years, gains on the degraded site were more than 50 percent greater than those on the adjacent climax veld

regarded as being in 'good' condition (Gillard *loc. cit.*).

The apparent lack of a relation between animal production and range condition on sourveld may be attributed to two possible factors. In the first instance, it is suggested (O'Reagain 1989) that current methods of rating species to determine a condition score are done according to criteria which are largely meaningless to the grazing animal. In particular, contrary to the claims of Tainton (1988), the categorisation of species into ecological groups, i.e. Increasers or Decreasers, does not necessarily reflect their value to the animal either in terms of palatability (O'Reagain 1989) or forage production (Stoltz & Danckwerts 1990). Furthermore, the assignment of limits (Foran *et al.*, 1978) or scores (Vorster 1982) to these species is subjective and unsubstantiated by empirical evidence. For example, in the weighted quantitative climax method (Tainton *et al.*, undated, cited by Heard *et al.*, 1986) *Hyparrhenia hirta* is assigned a score of four, while *Eragrostis capensis* and *Bothriochloa insculpta* are both given a score of seven. Yet *H. hirta* is far more palatable and productive than either of the latter species (Tainton *et al.* 1976; O'Reagain 1989; O'Reagain unpub. data).

The introduction of the Weighted Palatability (Barnes *et al.* 1984), Weighted Productivity (Heard *et al.* 1986) and Forage Factor (Trollope 1986) methods, was an attempt to remedy this situation by subjectively rating the agronomic value of species on the basis of their palatability and perceived forage production potential. Although an improvement, these methods are still simplistic and suffer from a number of shortcomings. First, palatability is a poor indicator of agronomic value as it gives no indication of the actual bulk of forage removed in grazing. Second, the forage production potential of a species is only a gross indication of the quantity of material that it is capable of producing and is not necessarily an index of what is actually available to the grazing animal.

However, possibly the major shortcoming of these methods is their failure to assess the value of a forage within the context of the morphological, nutritional and digestive constraints imposed, through evolution, on the grazing animal. Dietary selection is not simply a problem of maximising dietary quality and intake but rather involves optimisation of these two variables within the many constraints under which the animal operates. Other factors which should therefore be used in determining the utility of a species are (i) the quality of the forage in terms of its ability to satisfy the

digestible energy and protein requirements of the animal, (ii) the handling costs in terms of the time and energy associated with harvesting that forage, and (iii) the processing costs of the forage in terms of its degradation rate and retention time in the rumen. The relative importance of these factors will vary according to the particular time-energy constraints (Hanley 1982) under which an animal operates. Due to the nature of the allometric relations between body size and metabolic rate, gut capacity and mouth dimensions, these constraints are unique for a particular body size (Demment 1983). The relative importance of these constraints in determining the utility of a food to an animal, will therefore vary so that the 'value' of a species should, theoretically, depend upon the animal concerned. This suggests that any index of veld condition should be conditional upon the animal species involved. For example, Novellie (1990) reported that while the veld condition score appeared to be a good index of habitat suitability for grazing ungulates like zebra and hartebeest, it was a poor index for other grazers like wildebeest and springbok.

A second explanation for the apparent absence of a relation between animal production and veld condition may possibly be that, in sourveld, sward structure overrides any effect of species composition on animal production. Sward structure directly affects dietary quality through its effects on plant part selection (Barthram 1981) with quality being highest on green, leafy swards but declining rapidly as swards mature and become tall and stemmy (Hamilton *et al.* 1973; O'Reagain 1990) or when swards are very short (O'Reagain 1989). Sward structure also directly determines intake through its effects on bite size and bite rate. Sward structure may restrict bite size by reducing leaf accessibility and restricting bite depth and hence bite volume on short swards (Illius & Gordon 1987) or by reducing leaf density and hence bite mass (Demment *et al.* 1987). Bite size and intake rate increase with sward height in temperate (Allden & Whittaker 1970; Hodgson 1981; Burlison 1989) and tropical pastures (Stobbs 1973b; Stobbs & Hutton 1974; O'Reagain 1990) but may decline above a certain height due to a decrease in leaf density (Stobbs 1973b). Sward structure may restrict biting rates by increasing the handling or search time per bite (Ruyle *et al.* 1987; Demment *et al.* 1987). Where bite size is restricted, animals may compensate by either extending grazing time, increasing biting rate, or both (Allden & Whittaker 1970; Chacon *et al.* 1978; O'Reagain 1990) but the extent to which these strategies can compensate for

reduced bite size is limited. Bite size is therefore the major determinant of intake (Hodgson 1981).

Unfortunately, the heights at which bite size and bite quality are maximised are seldom likely to coincide, given the general negative relation between sward height and forage quality reported for most pastures, e.g. Grieve and Osbourn (1965). There should therefore be some height where the opposing constraints of dietary quality and intake are optimised and animal production, which is a function of both of these variables, is maximised.

In practice, animal production, at least on temperate pastures, appears to be maximised at a sward height of between 8-10 cm (Ernst *et al.* 1980; Wright & Russel 1987). Wright and Whyte (1989) observed that live weight gains in beef cows on ryegrass were maximised at a height of 9 cm but declined thereafter. In contrast, sward heights of 4-6 cm (Parsons *et al.* 1986) and 5-7 cm (Parker & McCutcheon 1992) have been suggested as being optimal for sheep on ryegrass. Conversely, Chestnutt (1992) reported that over a range of heights on ryegrass-clover pastures, continuously stocked ewes and lambs performed best at a sward height of 9 cm.

Although the concept of sward structure is implicitly accepted as being an important determinant of animal production on sourveld, e.g. Edwards (1981); Barnes (1989), optimum heights for production have yet to be quantified. Similarly, while conventional grazier wisdom states that swards should be kept 'short' or 'long' for sheep and cattle respectively, these terms are relative and have not been objectively defined. Management recommendations by advisory staff are vague, stating only that veld should be grazed when it is 'ready' (Barnes 1989) or 'grazeable' (Edwards 1981). While it has been rigidly asserted that sourveld should only be grazed at a height of 10-15 cm, particularly after a burn (Venter & Drewes 1969; Trollope 1984; Tainton 1987), this recommendation is aimed at minimising the impact of grazing on the grass layer *per se* rather than maximising animal production.

In practice, there is unlikely to be a single optimum sward height for animal production, as a strong interaction possibly exists between this factor and species composition, i.e. the optimum sward height for veld in poor condition could be markedly different from that for veld in so-called good condition. Given differences in mouth anatomy, grazing behaviour and digestive constraints the optimal sward structure is also

likely to be dependent upon animal type. The recommended sward height is therefore likely to be different for cattle and sheep on swards of different species compositions.

The primary objectives of the present study were therefore to:

(i) quantify the effects of sward structure and species composition on dietary quality and intake for cattle and sheep grazing sourveld, and

(ii) synthesise these relations into a simulation model to predict animal production on sourveld based on the sward structure and/or species composition of a site.

To achieve these objectives, two approaches, focused at two different hierarchical scales in the system, were adopted. In the first instance, a gross, sward-oriented approach was taken with attention being focused at the sward level in terms of its structure and species composition, and its resultant effects on dietary quality and intake in the grazing animal. In the second instance, a more reductionistic, species-oriented approach was followed with attention being focused on the properties of individual grass species and their potential dietary quality and rate of DM intake available from these grasses.

These two approaches are reflected in the basic organisation of this document. Accordingly, in chapter 2, the effects of sward structure and species composition on dietary quality in cattle and sheep are examined over two consecutive years at four different sites on the Dohne Sourveld. In chapter 3, the effects of sward structure and species composition on bite size, bite rate, intake rate and grazing time in cattle and sheep are examined at the same four sites. In both chapters the sward approach is adopted with dietary quality and intake being measured on a number of swards of different structure and species composition at various times through the grazing season.

In contrast, chapters 4, 5 and 6 reflect the reductionistic, species based approach. Thus, in chapter 4, the sequence and extent to which individual species are defoliated by cattle and sheep through a period of occupation in a paddock is determined. In chapter 5, the potential ingestion rates of a number of different sourveld species by cattle and sheep are determined for a number of different sourveld species. Finally, in chapter 6, the forage fractions and potential degradation rates of these species in the rumen at four different times through the grazing season, are assessed.

In the final section of the thesis (Chapter 7), data and relations presented in

previous sections are synthesised into a series of simulation models in an attempt to elucidate the relative effects of sward structure and species composition on predicted animal production on sourveld. This chapter again reflects the species and sward approaches adopted in the study with two separate series of models, based on data derived from individual species and swards respectively, being constructed. However, in the final model, an attempt is made to integrate the species and sward approaches into a single model to predict animal production on swards of different species composition. In the relatively short chapter 8, an attempt is made to extend the present results to the field by revising the recommended forage factors of the different sourveld species on the basis of their acceptability and potential ingestion and digestion rates. The thesis concludes with chapter 9 in which the main findings of the study are discussed, achievements and shortcomings of the study are highlighted and suggestions are made for future research.

Finally, it should be noted that in writing the thesis, an attempt was made to organise the document into a set of self-contained chapters in the hope that this would expedite their future publication in the literature as a series of separate but related papers. A certain amount of repetition between chapters was consequently unavoidable, especially with regard to the introduction and procedure sections of the different chapters.

CHAPTER 2

THE EFFECT OF SPECIES COMPOSITION AND SWARD STRUCTURE ON THE QUALITY OF DIET SELECTED BY CATTLE AND SHEEP GRAZING THE DOHNE SOURVELD

2.1 Objectives

The specific objectives of this experiment were to:

(i) determine the relative impact of species composition and sward structure on the quality of diet selected by cattle and sheep on Dohne sourveld, and

(ii) define in quantifiable terms any relation which might exist between the quality of diet selected and species composition and sward structure.

2.2 Introduction

Local graziers have traditionally termed grassveld either sweet or sour depending upon the inherent quality of the constituent grass species. Sweetveld is, by definition, palatable and largely retains its quality throughout the year. Sourveld, in contrast, although being of fairly high quality early in the grazing season, rapidly declines in palatability and quality as the season progresses. By winter, herbage quality is insufficient for maintenance requirements and unsupplemented animals experience severe loss of body mass. Dietary quality is therefore the major limitation to animal production on sourveld.

Sward species composition is held to be a major determinant of animal production on sourveld and it has been implied (Tainton *et al.* 1980; Tainton 1988) or explicitly stated (Tainton 1986) that a direct linear relation exists between veld condition score of a site and potential animal production. This appears to be based on the assumption that the seral stage of a community or species is a direct reflection of its forage value (Tainton 1986; 1988). Unfortunately, these assertions remain unsubstantiated. Contradictory evidence, in fact, exists which suggests that species composition or veld condition has no effect on dietary quality in sourveld (Mentis 1982; Hardy 1986;

O'Reagain & Mentis 1990).

It has been suggested that, in sourveld, sward structure overrides any potential effect of species composition on dietary quality (O'Reagain & Mentis 1990). This is logical; differences in quality between plant parts of the same species usually exceed differences in quality between the same parts of different species (Juko & Bredon 1961) and dietary quality is strongly correlated with plant part selection (O'Reagain & Mentis 1988). Sward structure has also been found to be an important determinant of dietary quality in both temperate and tropical pastures (e.g. Hamilton *et al.* 1973). The importance of sward structure has also been intuitively recognised by local graziers. Fire has long been used to remove moribund material and supply green grazing while graziers recommend that swards be kept 'sheep short' or even 'trampled sweet' to provide nutritious forage for sheep.

The relative effect of sward structure and species composition on dietary quality will also be dependent upon the animal species involved. Animals of different body mass function under different time-energy constraints due to the allometric scaling of morphological and physiological factors with body size (Hanley 1982). Cattle and sheep, which are the two most common domestic grazers in sourveld, vary widely in physiological requirements and selective ability. Consequently, the optimum species composition or sward structure for dietary quality is likely to be different for the two animals.

2.3 Procedure

2.3.1 Study area

The experiment was conducted at the Dohne Agricultural Development Institute (32°31'S, 27°28'E, elevation 899 m) situated 8 km north of the town Stutterheim, South Africa. Mean annual rainfall is 752 mm (40 year mean), largely distributed between October and March. During the period of the study, rainfall was below average in both years, i.e. 613 and 671 mm in the 1990-91 and 1991-92 seasons respectively. Rainfall distribution was also markedly different between the two years of the study (Fig. 2.1). In the first season, spring and early-summer rainfall were below average but February was very wet with almost double the average monthly rainfall. Conversely, the second season had a very wet spring but monthly rainfall was well below average thereafter.

Mean maximum and minimum air temperatures are 25°C and 14°C respectively in summer, and 18°C and 7°C respectively in winter (Fig. 2.1). Frosts are common between May and September.

Soils are mesotrophic sandy loams, being largely derived from shales and sandstones. Most soils are generally of shallow to intermediate depth with a fluctuating water table. The vegetation is an open grassland termed the Döhne Sourveld (Acocks 1988) and consists of a dense, perennial grass community of medium height dominated by C_4 tussock grasses such as *Themeda triandra* and *Tristachya leucothrix* (nomenclature follows Gibbs Russel *et al.* 1990). As its name implies, it is regarded as being relatively unpalatable and of low nutritional quality. especially during the dormant season. The area has been subjected to domestic pastoralism and frequent fires for at least the last three centuries, but in the past was probably only utilized by pastoralists and migratory ungulates during the growing season.

2.3.2 Experimental design

The experiment was laid out as a simulation trial with the specific objective of achieving as wide a combination of sward structures and species compositions as possible. Four sites varying widely in species composition were selected for the study. These were (i) a flat previously over-grazed site dominated by *Eragrostis plana* (termed eragrostis camp) (Table 2.1), (ii) a previously under-utilized site, dominated by *Tristachya leucothrix* situated about 200 m north-east of eragrostis camp on a gentle (<5%) north-facing slope (sheep shed camp), (iii) a secondary grassland community dominated by *Hyparrhenia hirta* on a previously (>10-year) cultivated land about 1 500 m east of sheep shed (old lands camp), and (iv) a previously well-managed site dominated by *T. triandra* and *T. leucothrix* situated on a gentle north-facing slope (<5%) about 1 500 m south-east of eragrostis camp (bush camp). Sites were burnt in September 1990 to remove residual material and then fenced into six equal-sized blocks each measuring 24 x 50 m. All blocks at a particular site had similar species compositions (Appendix 2.1).

Veld condition scores were calculated for each block as the sum of the products of the proportional abundance of each species multiplied by its forage factor, as recommended for the Dohne Sourveld by Danckwerts (1987). Forage factors are

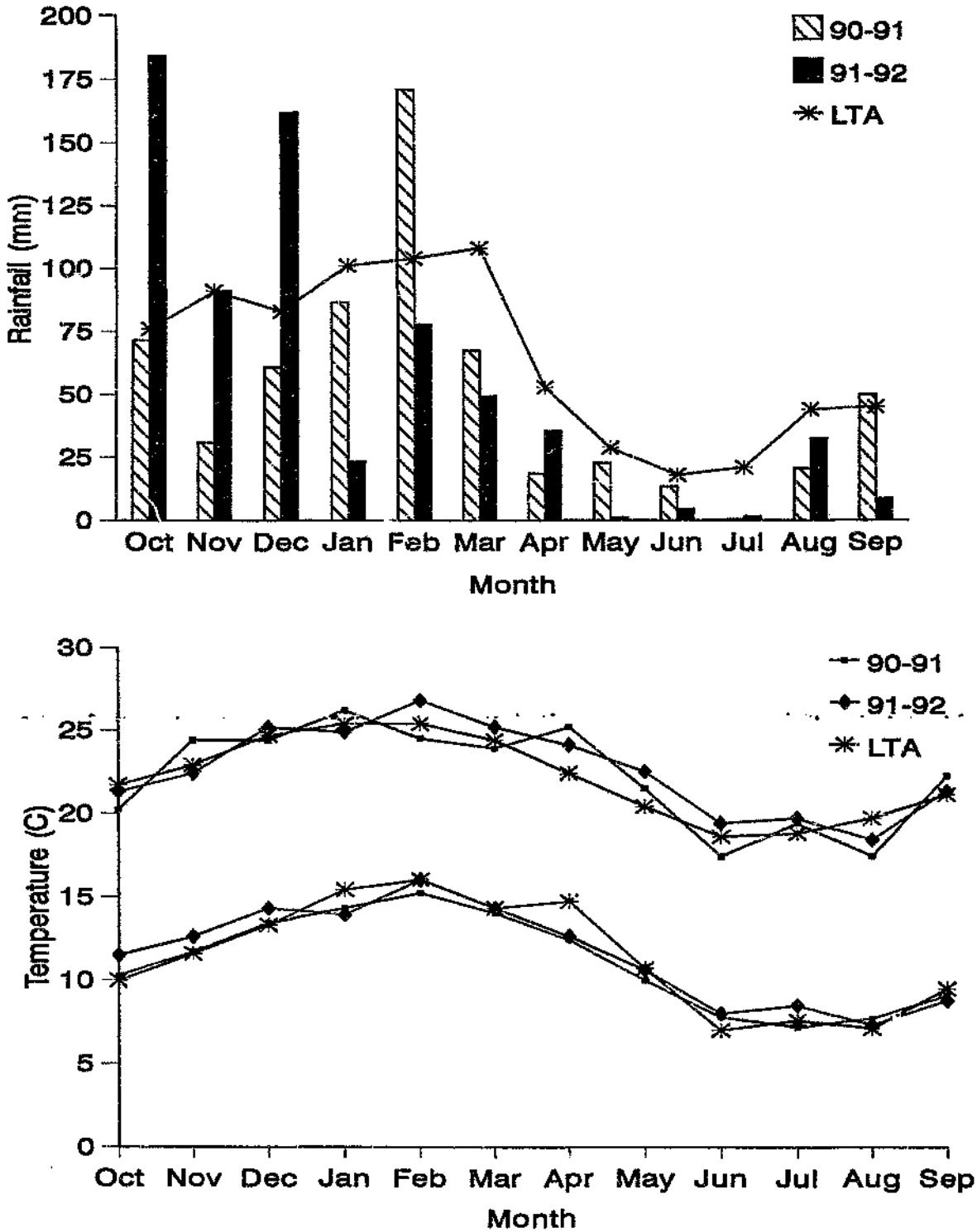

Figure 2.1 Long-term average (LTA) monthly rainfall (Top) and maximum and minimum air temperatures (Bottom) at Dohne and over the experimental period.

Table 2.1 Proportional species compositions (%) and veld condition score of the 4 sites selected on the Dohne sourveld. Individual species scores (forage factors) are given in brackets

Species	Site			
	Eragrostis	Sheep shed	Bush	Old lands
Alloteropsis semialata (2)	4	13	6	
Andropogon appendiculatus (7)	19	10	12	
Cynodon dactylon (2)	4			11
Elionurus muticus (0)		1	3	
Eragrostis capensis (2)			2	2
Eragrostis chloromelas (4)	6			2
Eragrostis curvula (4)	3	1		8
Eragrostis plana (2)	37		5	9
Eragrostis racemosa (2)			2	
Harpochloa falx (4)	3	5	4	
Heteropogon contortus (7)	1	8	3	13
Hyparrhenia hirta (4)				46
Microchloa caffra (0)		7	1	
Sporobolus africanus (7)	5	2	6	9
Themeda triandra (10)	15	10	27	
Tristachya leucothrix (7)	3	43	29	
TOTAL	100	100	100	100
VELD CONDITION SCORE	487	584	678	424

subjective estimates of the agronomic ability of a species to produce grazeable forage (Danckwerts 1987), derived from a combination of the estimated productivity and palatability of a species.

A specific objective of the trial was to confront animals with as wide a range of sward structures as possible. To achieve this, each block at each site was grazed in a

simulated rotational grazing system using 1 of 6 possible frequencies of grazing, i.e. every 3, 5, 8, 11, 16 or 20 weeks, starting from the beginning of the growing season (subjectively defined as 1 October). For example, the 3-week block was first grazed 3 weeks after the start of the growing season and thereafter every 3 weeks. Similarly, the 20-week rotation was first grazed 20 weeks after the start of the season and thereafter had another 20-week period of uninterrupted growth before being grazed again. Blocks were not necessarily sampled at each grazing. In practice, the period between grazings was often extended, especially where growth was slow, so as to achieve the desired sward structure.

Blocks were grazed by a mixture of cattle and sheep at the recommended ratio of 6:1 (Barnes 1989) with the objective of achieving as even a sward utilization as possible. At the end of the first grazing season, i.e. August 1991, all camps were grazed down by cattle in an attempt to reduce the carry-over of residual material into the next season. The experiment was repeated over the subsequent season (October 1991- July 1992) without burning.

2.3.3 Sward measurements

Immediately prior to grazing in each block, the physical structure of a number of individual grass species was measured in detail. Species selected were *T. triandra* and *E. plana* (eragrostis camp), *H. hirta* and *H. contortus* (old lands camp), *T. leucothrix, A. appendiculatus* and *A. semialata* (sheep shed camp) and *T. triandra, T. leucothrix* and *A. appendiculatus* (bush camp). Species were chosen on the basis of their abundance and/or palatability. In addition, at old lands and eragrostis camps, measurements were also taken at random of any remaining species in each particular block. These measurements were simply termed 'sward'.

Fifty tufts of each species were randomly selected in each block and the following variables measured:

- plant height, defined as the extended height above ground level of the tallest leaf on a vegetative tiller;
- leaf table height, defined as the height below which 80 % of the plant's leaves were subjectively judged to occur;
- stemminess, subjectively estimated on a scale of 0 to 5 where 0 = no stems and

5 = many stems;

- greenness, subjectively estimated on a scale of 0 to 5 where 0 = no green leaves present in the tuft and 5 = only green leaves present in the tuft.

Herbage mass of the sward as a whole was estimated using the pasture disc meter calibrated for each block on the basis of 30 clipped quadrats (Bransby & Tainton 1977).

2.3.4 Animal measurements

Two oesophageally fistulated Bonsmara steers (mean mass 400 kg) and three Dohne Merino wethers (mean mass 50 kg) were used to collect dietary samples. Animals had been raised on sourveld and were well adapted to local conditions. Animals were supplemented with a mineral-phosphate lick until autumn with provision of a urea lick thereafter. In between sampling, animals grazed veld similar in composition to the study sites.

Animals generally grazed the same block in different camps within the same week according to the following schedule ; sheep shed (Tuesday), eragrostis (Wednesday), bush (Thursday) and old lands (Friday). This schedule was chosen to minimise walking distances and hence disturbance to experimental animals. Animals were penned and fasted overnight (16:00-06:30) prior to sampling so as to ensure collection of adequate samples. Short-term fasting appears to have no effect on the quality of diet selected by fistulated animals (Langlands 1967; Jung & Koong 1985). Grazing began at 06:30 and continued until fistula bags were full (about 20 minutes). Samples contaminated with rumen contents were discarded. Solid-fraction fistula samples were frozen and then freeze-dried (48 hours), milled (1 mm sieve) and stored in sealed plastic bags for analysis. Discarding the liquid fraction of fistula samples may depress digestibility estimates by 3 to 4 units (Minson *et al.* 1976). Samples were analyzed for *in vitro* digestibility (IVD) (Tilley & Terry 1963, modified by Engels & Van der Merwe 1967) at the Glen Agricultural Development Institute. Crude protein (CP) analyses were conducted by the soils laboratory at Dohne using the Macro-Kjeldahl procedure (AOAC 1970) but on a few occasions samples were only large enough to permit IVD analysis.

The digestion rates (expressed as mean retention time (h)) of about 100 samples were also determined using an *in vitro* gas production method (Pienaar & Kuhn 1991; Pienaar 1994) at the Animal and Dairy Science Research Institute, Irene. Analyses were

restricted to relatively few samples due to the cost associated with the procedure. Due to the incomplete nature of this data, these results are not presented in this chapter but are presented in Appendix Tables 1.1 - 1.4 and analyzed for modelling purposes in Appendix 6.

2.3.5 Soil moisture

A simple soil water balance model was constructed in order to predict the available soil water (SW) when any block was grazed and the potential growth days between grazings. Available SW was calculated as the difference between inputs (rainfall) and outputs (transpiration and drainage). Soil water holding capacity for the top soil layer and wilting point, based on a clay content of 15 % and a depth of 500 mm, were calculated using soil water retention curves derived by Fouché (1992), i.e.

$$FC = WHC/100 * SD$$

where FC = field capacity, SD = soil depth and WHC = water holding capacity calculated as :

$$WHC = (0.138 + (0.00416* \% \text{ clay}))*100$$

Soil data were taken from soil survey data of the area. A constant crop factor of 0.5 was assumed for all swards. A daily time step was used based on meteorological data from the Döhne weather station. Available soil water (SW) was defined as all soil moisture above wilting point and below field capacity. Potential growth days were defined as days when soil moisture exceeded wilting point and average air temperature was greater than 12°C. Total growth days were calculated as the sum of all potential growth days between successive defoliations of a particular block.

2.3.6 Statistical analysis

At each sampling date, measurements of CP and IVD were meaned across animals for both cattle and sheep, while sward structure variables were meaned across tufts (n = 50) for each species. Percentage data for CP was arcsine-transformed but not IVD, as nearly all the latter data fell between 30 to 70 % (Sokal & Rohlf 1981). The sward structure data for each camp were initially explored using principal components (PRINCOMP; SAS (1991)) and correlation analyses (CORR; SAS (1991)) in order to identify the most important determinants of sward structure and to determine the

relationship between the different sward structure variables. These indicated, first, that most of the variability in the data could be explained in terms of 'height' and 'greenness' axes and second, that most sward structure parameters were strongly inter-correlated (Table 2.7). Correlation analyses also indicated that dietary quality was correlated with general groups of sward structure variables. Furthermore, the more palatable grasses may be logically expected to exert a greater influence on animal foraging than others. Accordingly, to facilitate data presentation, the original set of 14 sward structure variables at each camp was reduced to four; total herbage mass and the plant height, stemminess and greenness of the most palatable species in the sward. These species were *T. triandra*, *T. leucothrix*, *H. hirta* and *T. triandra* for bush, sheep shed, old lands and eragrostis camps, respectively.

To investigate the effect of camp, year and animal type on dietary quality, an analysis of covariance was conducted with 'greenness' as covariate using the GLM procedure of SAS (SAS 1991). The relation between dietary quality and veld condition score, and dietary quality and sward structure was explored using correlation and regression analysis (CORR, REG; SAS (1991)). Residuals and studentized residuals were examined to identify observations having undue influence on parameter estimates and, if necessary, excluded from models.

For the analysis of the effects of sward structure on dietary quality, data were separated into the growing season (greenness score >3) and the dormant season (greenness score <3) with analyses being performed separately on each group. Perusal of the scatter plots of the relation between dietary quality and the selected parameters of sward structure indicated a general similarity of response for all camps. Furthermore, as there appeared to be little difference between camps in terms of dietary quality, it was considered justified to combine the data from all camps for each year in order to facilitate data presentation and interpretation. Accordingly, the 'greenness', 'stemminess' and 'height' variables in this combined data set are a combination of the measurements of four different species in a single variable, i.e. *T. triandra* for bush and eragrostis, *T. leucothrix* for sheep shed and *H. hirta* for old lands.

2.4 Results

2.4.1 Effect of year on dietary quality

Overall, 'year' had a major effect ($P \leq 0.0001$) on dietary quality (Appendix Table 2.2) with both cattle and sheep selecting diets of significantly ($P<0.05$) higher IVD and CP in year 1 than in year 2 (Table 2.2). However, this difference was not consistently evident with diets selected in the late spring-early summer (50-100 days) and winter (>250 days) periods tending to be of similar quality in both years (Figs. 2.2 & 2.3). The major between-year differences in quality occurred, first, in early spring (0-50 days) when the quality of diet selected on burnt regrowth was markedly higher than on unburnt regrowth the subsequent year and second, in mid-season (100-250 days), when the IVD and CP of diets selected in year 1 were usually 10-15 % and 3-4 % higher, respectively,than in year 2. Accordingly, the hypothesis that dietary quality is higher in the year of the burn than in the following grazing season is accepted. However, it is recognised that this difference is not consistent, being more pronounced at certain times of the year than at others.

2.4.2 Effect of animal on dietary quality

In general, sheep selected a diet of significantly ($P \leq 0.0001$) higher quality in terms of both CP and IVD (Appendix Table 2.2) than did cattle (Table 2.2) This difference was consistent across all 4 sites, both years and most sward structures (Figs. 2.2 & 2.3). However, there were instances where sheep did select diets of considerably lower quality than cattle, particularly on long, rank swards with a large mass of herbage. For example, at all four sites in year 2, the IVD of diets selected by sheep (circled points: Fig. 2.5) was considerably lower (mean: 40.63 vs 45.09 %) than that selected by cattle when grazing the tall, infrequently grazed herbage of the 20-week block. The data are still, however, consistent with the hypothesis that in general, sheep select a diet of higher quality than cattle and the hypothesis is accordingly not refuted.

2.4.3 Effect of season on dietray quality

Dietary quality, in terms of CP and IVD, declined over the grazing season for both cattle and sheep (Figs. 2.2 & 2.3). Dietary quality was highest in spring with extrusa digestibilities in excess of 65 % but was lowest in winter with digestibilities of less than

Table 2.2 Mean *in vitro* digestibility (IVD) and crude protein (CP) content of diets selected by cattle and sheep at four sites in the Dohne sourveld. Means in the same row with the same superscript are not significantly different at the 5 % level

Animal	Variable	Year	CAMP			
			Bush	Eragrostis	Lands	Shed
			% DM			
Sheep	IVD	1	56.48^{a}	58.41^{a}	57.43^{a}	58.79^{a}
		2	50.89^{b}	52.91^{ab}	55.51^{a}	51.64^{ab}
Cattle	IVD	1	54.21^{ab}	53.2^{b}	54.86^{ab}	56.35^{a}
		2	48.17^{b}	49.90^{ab}	52.46^{a}	49.61^{ab}
Sheep	CP	1	7.12^{b}	7.48^{ab}	8.33^{a}	7.31^{b}
		2	5.21^{a}	5.78^{a}	5.88^{a}	6.01^{a}
Cattle	CP	1	6.77^{a}	6.98^{a}	7.09^{a}	7.07^{a}
		2	4.85^{a}	4.81^{a}	5.40^{a}	5.45^{a}

45 % being recorded at some sites. Similarly, in both animals, dietary CP was highest in spring (>10 %) but lowest in winter when CP levels frequently declined to below 4 % (Fig. 2.3). As expected, dietary quality was negatively correlated with days (P<0.0001) since the start of the season, with this variable accounting for between 61 % to 79 % of the variation in the data in both years (Table 2.3 & 2.4). These trends corroborate the hypothesis that in sourveld, there is a general decline in dietary quality over the grazing season.

Despite this general consensus, the actual pattern of change over the season varied markedly between years (Figs. 2.2 & 2.3). In year 1, dietary quality initially declined from spring through to early summer before increasing to a second peak in mid-season. The quality of diet selected thereafter fluctuated within relatively narrow limits until autumn (*c.* 200 days), whereafter it steadily declined to low winter levels. In contrast, dietary quality in year 2 showed a steady decline almost from the start of the season to reach a minimum around March (*c.* 150 days) whereafter it remained fairly constant. Consequently, in year 2 dietary quality reached minimum 'winter' levels

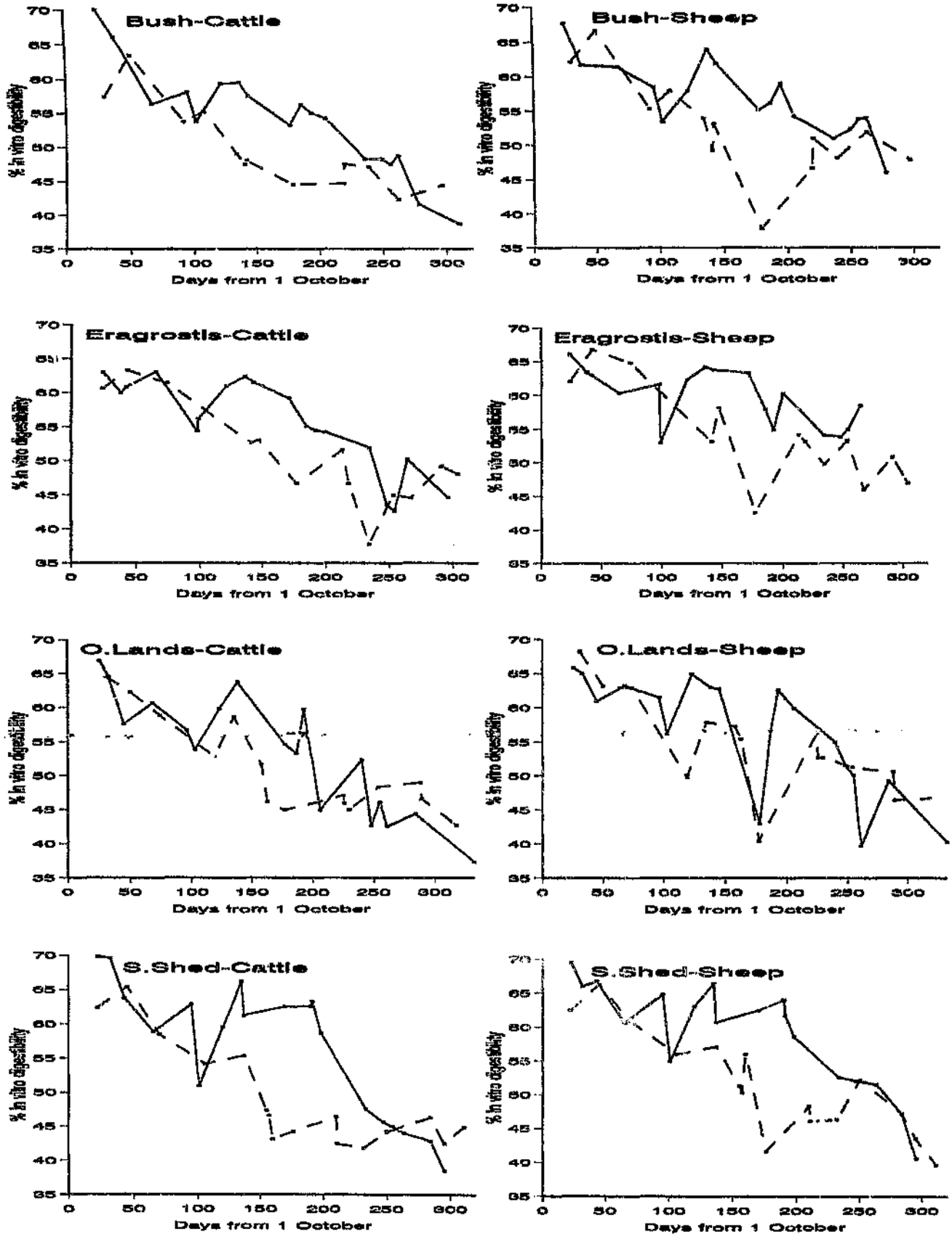

Figure 2.2 Seasonal changes in the *in vitro* digestibility (IVD) of diets selected by cattle and sheep over the grazing season at four sites in the Dohne Sourveld in year 1 (solid) and year 2 (dotted).

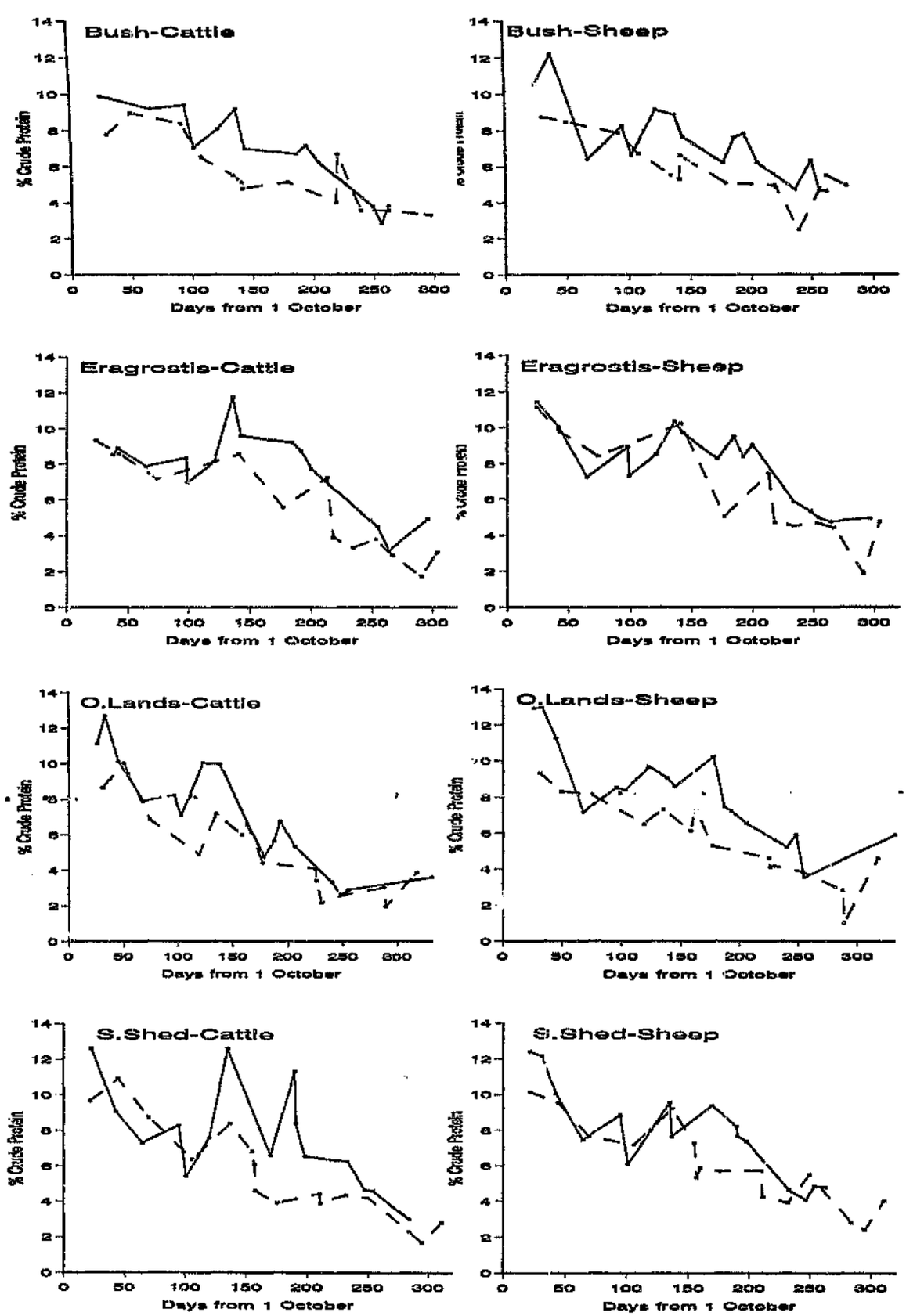

Figure 2.3 Seasonal changes in the crude protein (CP) content of diets selected by cattle and sheep over the grazing season at four sites in the Dohne Sourveld in year 1 (solid) and year 2 (dotted).

Table 2.3 Linear regression equations for the relationship between the *in vitro* digestibility (IVD) and crude protein (arcsine transformed) content of diets (CP) selected by sheep over the whole grazing season and soil water content (SW), sward greenness (GR), herbage mass (HM) and days from the start of the grazing season. Non-significant relations are not shown

Variable	Equation	
Year 1: IVD		
Day	67.66 - 0.0585x	r^2 = 0.61; F = 110; ***
GR	44.91 + 3.77x	r^2 = 0.69; F = 153.96; **
HM	64.55 - 0.0041x	r^2 = 0.22; F = 19.29; ***
SW	55.11 + 0.101x	r^2 =0.22; F = 19.92; ***
Year 2: IVD		
Day	65.24 - 0.0643x	r^2 = 0.74; F = 151.14; ***
GR	48.91 - 3.53x + 1.34x^2	r^2 = 0.62; F = 43.28; ***
HM	58.82 - 0.00339x	r^2 = 0.11; F = 6.67; *
SW	47.28 + 0.186x	r^2 = 0.72; F = 134.03; ***
Year 1: CP		
Day	0.0346 - 0.0000431x	r^2 = 0.68; F = 135.24; ***
GR	0.0169 + 0.00292x	r^2 = 0.67; F = 130.24; ***
HM	0.032 - 0.00000294x	r^2 = 0.23; F = 19.60; ***
SW	0.0249 + 0.0000647x	r^2 = 0.23; F = 19.26; ***
Year 2: CP		
Day	0.0321 - 0.0000453x	r^2 = 0.74; F = 151.03; ***
GR	0.0161 + 0.00263x	r^2 = 0.64; F = 100.24; ***
SW	0.0205 + 0.00011x	r^2 = 0.54; F = 63.84; ***

almost 100 days sooner than in year 1. These differences suggest that the simple linear decline in dietary quality which is commonly assumed to hold for sourveld may not always occur, and that a bimodal trend may be evident in some situations.

In both years dietary quality fluctuated sharply over short time periods within the grazing season in apparent response to changes in sward structure and/or rainfall distribution. The effects of these variables on dietary quality will be examined further in sections 2.4.5 and 2.4.6 respectively.

2.4.4 Effect of species composition on dietary quality

Overall, there was no significant difference in dietary IVD or CP between the different camps (Appendix table 2.2) in either of the years studied. This indicates that species

Table 2.4 Linear regression equations for the relation between the *in vitro* digestibility (IVD) and crude protein (arcsine transformed) content of diets (CP) selected by cattle over the whole grazing season and soil water content (SW), sward greenness (GR), herbage mass (HM) and days from the start of the grazing season. Non-significant relations are not shown

Variable	Equation	
Year 1: IVD		
Days	68.22 - 0.0827x	r^2 = 0.75; F = 216.7; ***
GR	37.68 + 5.03x	r^2 = 0.77; F = 236.4; ***
HM	62.27 - 0.0047x	r^2 = 0.16; F = 14.05; ***
SW	49.91 + 0.146x	r^2 = 0.27; F = 26.24; ***
Year 2: IVD		
Days	62.02 - 0.0658x	r^2 = 0.71; F = 134.66; ***
GR	48.71 - 6.94 + 1.99x^2	r^2 = 0.70; F = 61.74; ***
HM	55.59 - 0.0029x	r^2 = 0.08; F = 4.97; *
SW	43.92 + 0.193x	r^2 = 0.77; F = 181.66; ***
Year 1: CP		
Days	0.0341 - 0.0000513x	r^2 = 0.66; F = 106.88; ***
GR	0.0130 + 0.00359x	r^2 = 0.78; F = 192.79; ***
HM	0.0324 - 0.00000427x	r^2 = 0.27; F = 20.74; ***
SW	0.0235 + 0.000086x	r^2 = 0.21; F = 15.56; ***
Year 2: CP		
Days	0.0321 - 0.0000532x	r^2 = 0.79; F = 204.17; ***
GR	0.014 + 0.00291x	r^2 = 0.70; F = 129.16; ***
SW	0.0183 + 0.000132x	r^2 = 0.59; F = 79.21; ***

composition had little effect on dietary quality in either cattle or sheep. However, when compared on the basis of individual camps, the quality of diet selected on some camps was, on certain occasions,
significantly higher ($P < 0.05$) than that selected on others (Table 2.2).

There was no relation whatsoever between veld condition score and the quality of diet selected by either cattle or sheep (Table 2.5). This was evident whether the data were analyzed over the growing season, dormant season or over the grazing season as a whole. The hypothesis that species composition has an effect on dietary quality in sourveld is therefore rejected.

Table 2.5 Correlation coefficients for the relation between veld condition score and the *in vitro* digestibility (IVD) and crude protein (CP) content of diets selected by cattle and sheep grazing the Dohne Sourveld in the growing season, dormant season and over both of these seasons

	Year 1			Year 2		
	Growing season	Dormant season	Both	Growing season	Dormant season	Both
Sheep: IVD	-0.013	0.201	0.032	-0.172	-0.144	-0.081
CP	-0.147	-0.089	-0.105	-0.069	0.049	0.069
Cattle: IVD	0.107	0.071	0.033	-0.178	-0.258	-0.08
CP	-0.109	0.087	-0.037	0.01	0.023	0.105

2.4.5 Effect of sward structure on dietary quality

2.4.5.1 Analysis of sward structure

Principal components analysis indicated that at all sites the majority (>70 %) of variance in the sward structure data could be accounted for by the first two ordination axes (Table 2.6). Similarly, at all sites, herbage mass, plant height and leaf table height were all correlated with axis 1 while greenness was positively correlated with axis 2. Stemminess was not consistently correlated with either axis (Table 2.6).

The first axis therefore appears to represent a gradient from short swards where herbage mass was low, to tall swards with a large mass of accumulated herbage. In contrast, axis 2 appears to represent a gradient of sward greenness from swards comprised almost entirely of green leaf to those largely dominated by senescent material. These trends are illustrated in Figure 2.4 with short, frequently-grazed blocks on the left, and tall, infrequently-grazed blocks on the right of the ordination diagram. Similarly, a distinct seasonal gradient was evident through axis 2, from blocks grazed in spring at the top going down successively through those grazed in summer, autumn and finally winter at the bottom of this axis. Stemminess did not appear to be an important component of sward structure, largely because of the very low levels of stemminess encountered at most sites.

Inter-parameter correlations for sward structure and other variables in the

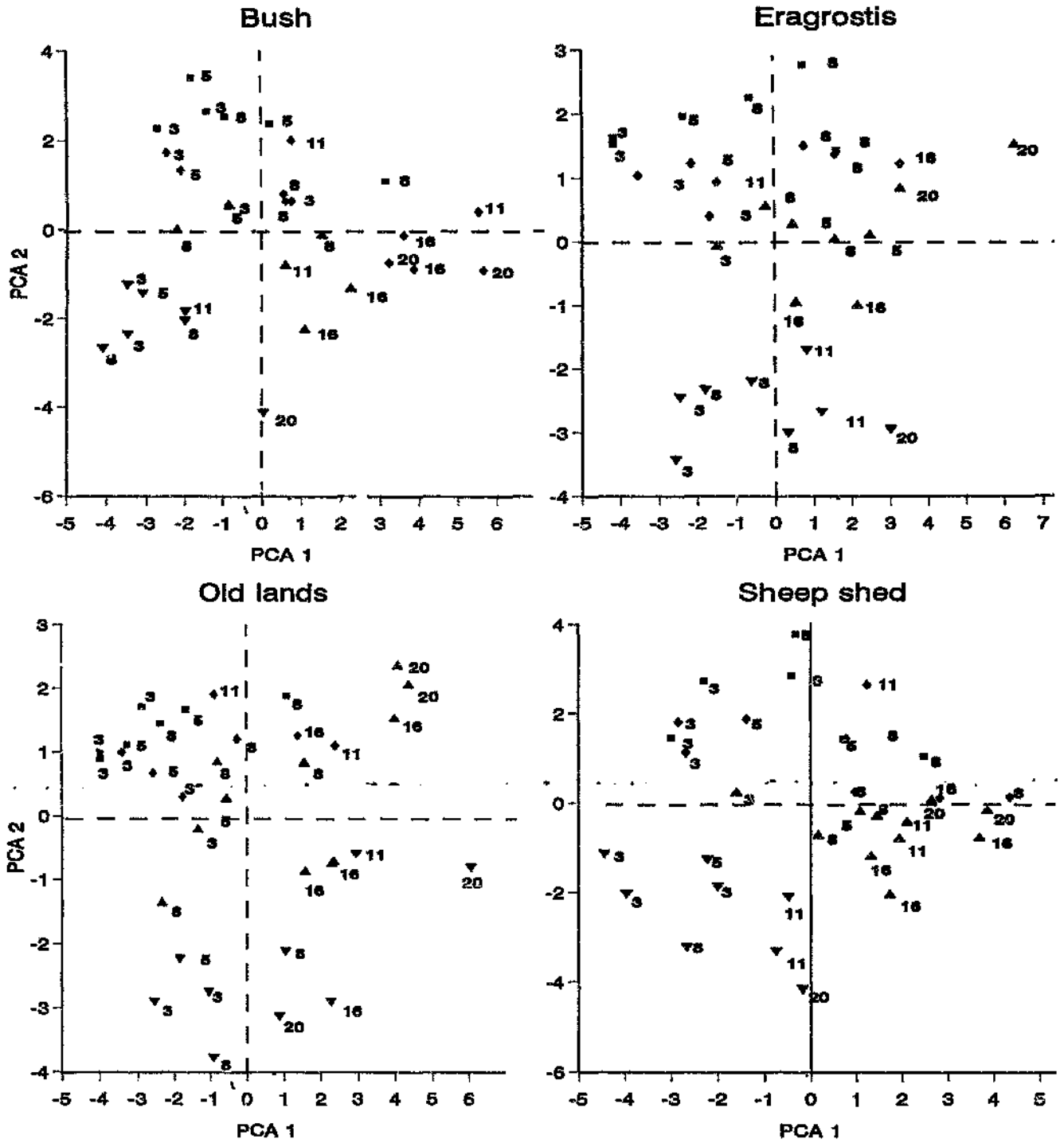

Figure 2.4 Principal components analysis of sward structure data at bush, eragrostis, old lands and sheep shed camps in years 1 and 2 (■ = spring; ♦ = summer; ▲ = autumn and ▼ = winter). Numbers refer to the average grazing frequency of blocks in weeks- see text for details.

growing and dormant seasons are presented in Tables 2.7(a) and 2.7(b). As would be expected, the proportion of green leaf in the sward declined as plant height and herbage mass increased in the growing season. Similarly, greenness tended to decline while herbage mass accumulated with time through the season. Greenness was negatively correlated with total growing days in the growing season when herbage mass would tend to accumulate under favourable growing conditions (Table 2.7) but, interestingly, was positively correlated with this variable in the dormant season. This is presumably because favourable conditions late in the season would not stimulate growth but would tend to maintain leaf viability, delaying senescence until later in the season.

2.4.5.2 Effect of sward structure on dietary quality

Dietary quality in terms of CP and IVD was strongly ($P \leq 0.0001$) correlated with sward greenness but negatively correlated with herbage mass during the growing season (Table 2.8). These relations were significant for both cattle and sheep, and across both years. In certain cases, dietary quality was also negatively correlated with plant height (Table 2.8). The relation between stemminess and dietary quality was inconsistent (Table 2.8), possibly due to the very low levels of stemminess encountered in most blocks. However, dietary quality did appear to decline with increasing stemminess above a stemminess score of about 1.5. (Fig.2.7).

Within the dormant season, dietary quality showed a general, positive relation ($P \leq 0.05$) with sward greenness but the relation was weaker than that observed in the growing season. Plant height, herbage mass and stemminess appeared to have no effect on dietary quality in the dormant season (Table 2.8). When considered over the whole grazing season, i.e. the growing and dormant seasons, dietary quality showed a similar, positive ($P \leq 0.0001$) response to sward greenness but declined ($P \leq 0.05$) with increasing herbage mass for both animals (Tables 2.3 & 2.4). Overall, greenness accounted for the largest proportion of the variability in the data (r^2 = 0.62 - 0.77) of all variables. Multiple linear combinations of other structure variables both with and without greenness failed to improve on the predictive power of the former variable and these models are consequently not presented.

growing and dormant seasons are presented in Tables 2.7(a) and 2.7(b). As would be expected, the proportion of green leaf in the sward declined as plant height and herbage mass increased in the growing season. Similarly, greenness tended to decline while herbage mass accumulated with time through the season. Greenness was negatively correlated with total growing days in the growing season when herbage mass would tend to accumulate under favourable growing conditions (Table 2.7) but, interestingly, was positively correlated with this variable in the dormant season. This is presumably because favourable conditions late in the season would not stimulate growth but would tend to maintain leaf viability, delaying senescence until later in the season.

2.4.5.2 Effect of sward structure on dietary quality

Dietary quality in terms of CP and IVD was strongly ($P \leq 0.0001$) correlated with sward greenness but negatively correlated with herbage mass during the growing season (Table 2.8). These relations were significant for both cattle and sheep, and across both years. In certain cases, dietary quality was also negatively correlated with plant height (Table 2.8). The relation between stemminess and dietary quality was inconsistent (Table 2.8), possibly due to the very low levels of stemminess encountered in most blocks. However, dietary quality did appear to decline with increasing stemminess above a stemminess score of about 1.5. (Fig.2.7).

Within the dormant season, dietary quality showed a general, positive relation ($P \leq 0.05$) with sward greenness but the relation was weaker than that observed in the growing season. Plant height, herbage mass and stemminess appeared to have no effect on dietary quality in the dormant season (Table 2.8). When considered over the whole grazing season, i.e. the growing and dormant seasons, dietary quality showed a similar, positive ($P \leq 0.0001$) response to sward greenness but declined ($P \leq 0.05$) with increasing herbage mass for both animals (Tables 2.3 & 2.4). Overall, greenness accounted for the largest proportion of the variability in the data (r^2 = 0.62 - 0.77) of all variables. Multiple linear combinations of other structure variables both with and without greenness failed to improve on the predictive power of the former variable and these models are consequently not presented.

Table 2.6 Correlation coefficients of different sward structure variables with principal component axes 1 and 2 for the different sites used in the experiment. (For sheep shed, 1 = *T. leucothrix*, 2 = *A. appendiculatus* and 3 = *A. semialata*. For eragrostis, 1 = *E. plana*, 2 = *T. triandra* and 3 = 'sward'. For lands, 1 = *H. hirta*, 2 = *H. contortus* and 3 = 'sward'. For bush, 1 = *T. triandra*, 2 = *A. appendiculatus* and 3 = *T. leucothrix*)

	CAMP							
	BUSH		ERAGROSTIS		OLD LANDS		SHEEP SHED	
VARIABLE	AXIS 1	AXIS 2	AXIS 1	AXIS 2	AXIS 1	AXIS 2	AXIS 1	AXIS 2
Herbage mass	0.315	-0.219	0.353	-0.136	0.341	-0.005	0.175	-0.326
Plant height 1	0.352	-0.162	0.382	-0.028	0.350	0.122	0.333	0.109
Leaf table height 1	0.363	-0.114	0.387	-0.003	0.338	0.161	0.381	0.112
Stemminess 1	0.099	0.207	0.055	0.173	0.325	-0.178	0.079	0.287
Greenness 1	0.128	0.505	-0.080	0.529	-0.196	0.471	0.128	0.469
Plant height 2	0.363	-0.103	0.369	-0.029	0.366	0.031	0.382	-0.184
Leaf table height 2	0.368	-0.599	0.349	0.119	0.339	0.181	0.404	-0.085
Stemminess 2	0 266	0.077	0.086	-0.187	-0.053	0.196	0.182	0.092
Greenness 2	0.141	0.491	-0.058	0.523	-0.159	0.506	0.112	0.476
Plant height 3	0.359	-0.069	0.345	0.161	0.338	0.133	0.383	-0.185
Leaf table height 3	0.331	0.051	0.371	0.131	0.305	0.238	0.404	-0.118
Stemminess 3	0.041	0.321	0.198	0.168	0.075	0.106	0.120	0.04[illegible]
Greenness 3	0.130	0.497	-0.054	0.522	-0.098	0.537	0.088	0.488
% Variance accounted for	0.543	0.249	0.460	0.247	0.536	0.234	0.420	0.282

Table 2.7a Inter-parameter correlation coefficients for the growing season in year 1 (n = 3[illegible], and year 2 (n = 24). Data are from all sites

	Day	Soil water	Growing days	Herbage mass	Plant height	Stemminess
Year 1						
Soil water	0.198					
Growing days	0.697***	0.473**				
Herbage mass	0.814***	0.338*	0.821***			
Plant height	0.457**	0.445**	0.745***	0.677***		
Stemminess	0.278	0.164	0.265	0.218	0.519**	
Greenness	-0.927***	-0.159	-0.656***	-0.718***	-0.456**	-0.422*
Year 2						
Soil water	-0.892***					
Growing days	0.359	-0.475				
Herbage mass	0.428*	-0.433*	0.801***			
Plant height	0.284	-0.350	0.833***	0.858***		
Stemminess	-0.198	0.091	0.112	0.126	0.403*	
Greenness	-0.790***	0.816***	-0.458*	-0.483*	-0.450*	-0.093

Table 2.7b Inter-parameter correlation coefficients for the dormant season in year 1 (n = 14) and year 2 (n = 19). Data are from all sites

	Day	Soil water	Growing days	Herbage mass	Plant height	Stemminess
Year 1						
Soil water	-0.181					
Growing days	-0.489	-0.375				
Herbage mass	-0.242	-0.100	0.700**			
Plant height	-0.135	-0.278	0.572*	0.562*		
Stemminess	0.364	-0.315	0.194	0.100	0.686**	
Greenness	-0.654*	0.185	0.155	0.127	-0.042	-0.612*
Year 2						
Soil water	0.330					
Growing days	-0.610**	-0.039				
Herbage mass	0.103	0.765***	0.333			
Plant height	-0.201	0.433	0.543*	0.841***		
Stemminess	-0.160	0.549	0.210	0.013	0.764***	
Greenness	-0.777***	-0.247	0.623**	-0.007	0.164	0.013

The above results are expected and are in general agreement with the hypothesis that dietary quality should be positively related to sward greenness but negatively related to herbage mass and plant height. Accordingly, the hypothesis that sward structure has a major effect on dietary quality is not refuted. However, the nature of the relationship between dietary quality and greenness is surprising; intuitively a linear response would be expected with quality a constant function of the proportion of green leaf in the sward. In practice, with the exception of sheep IVD in year 1, a strong curvilinear or threshold response was evident (Figure 2.5 & 2.6). Dietary quality showed a strong linear response to the proportion of green leaf in the sward above a greenness score of 3-3.5. However, below this level, the response was considerably weaker, e.g. cattle IVD (year 1), while in some cases dietary quality remained almost constant over a range of greenness values, e.g. sheep CP (year 1).

The similarity in response to sward structure by cattle and sheep is also surprising. Although sheep appeared to be marginally more sensitive to plant height and herbage mass (Table 2.8), dietary quality in both animals generally reacted in a very similar fashion to changes in sward structure.

2.4.6 Effect of soil moisture on dietary quality

The seasonal changes in dietary quality presented in section 2.4.3 appeared to reflect, in part, changes in rainfall distribution over the grazing season. This aspect was further investigated by plotting dietary quality against daily soil moisture balance through the two years of the study (Figs. 2.8 & 2.9). For both cattle and sheep, dietary CP and IVD appeared to respond strongly to changes in soil water balance, generally increasing as available moisture increased but declining as the soil profile dried out during mid-season droughts or towards the end of the growing season. This is best illustrated in the 1990/1991 season when dietary CP declined by nearly 50 % during an early summer drought but recovered sharply when soil moisture was replenished (Figs. 2.8 & 2.9). Surprisingly, dietary quality in the growing season was only correlated with soil moisture content in year 2 with no relation being evident in year 1. This probably reflects differences in sward structure resulting in considerable fluctuations in dietary quality at fairly constant soil moisture levels. Dietary quality was also unrelated to soil moisture in the dormant season, possibly reflecting the uniformly low levels of both

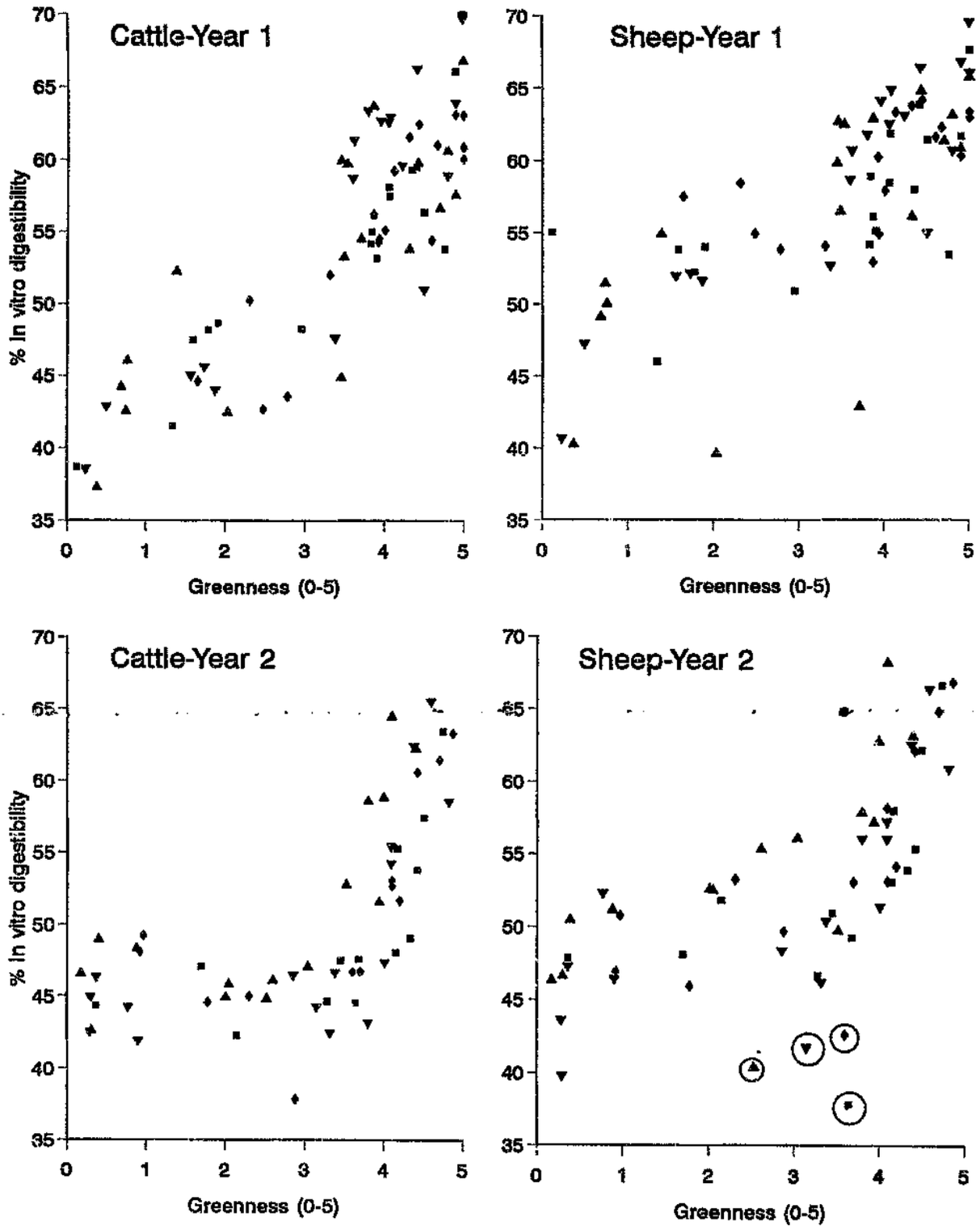

Figure 2.5 The relation between dietary *in vitro* digestibility (IVD) in cattle and sheep and sward greenness in year 1 (Top) and year 2 (Bottom). Data are from all camps and the whole grazing season (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

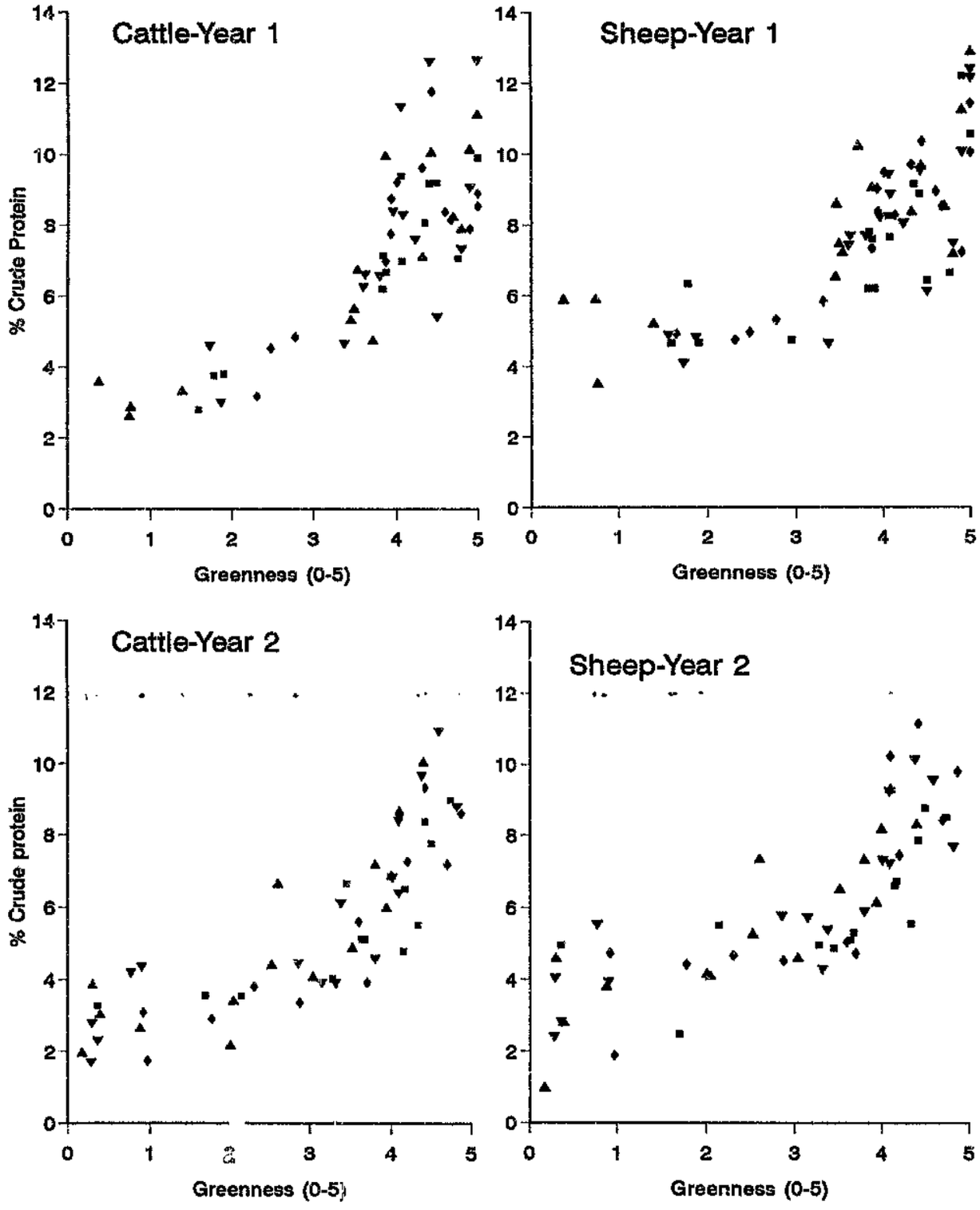

Figure 2.6 The relation between dietary *crude protein* (CP) content in cattle and sheep and sward greenness in year 1 (Top) and year 2 (Bottom). Data are from all camps and the whole grazing season (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

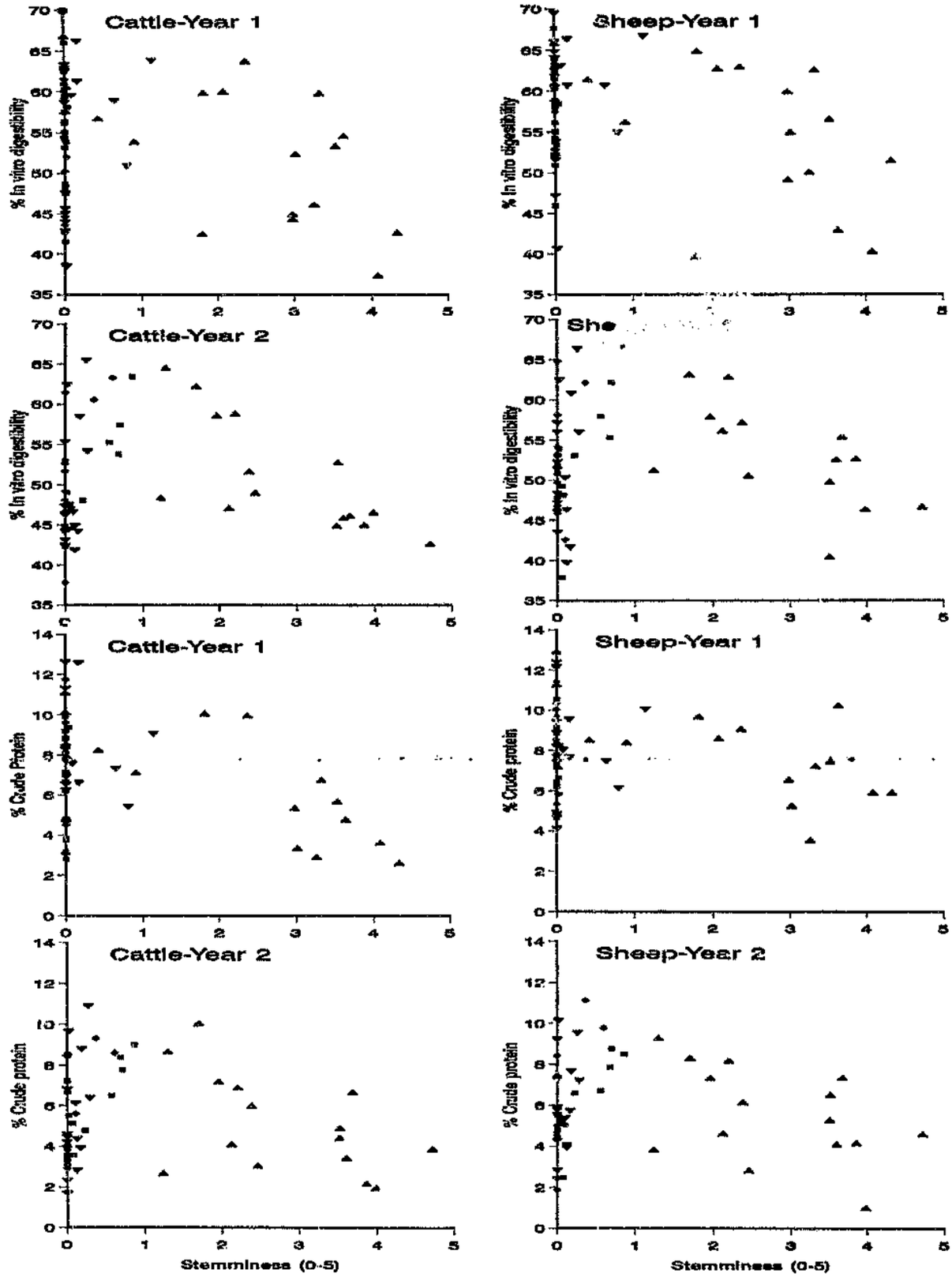

Figure 2.7 The relation between dietary *in vitro* digestibility (IVD) and crude protein (CP) content in cattle and sheep and stemminess in years 1 and 2. Data are from all camps and the whole grazing season (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

Table 2.8 Correlation coefficients for the relation between the *in vitro* digestibility of diets selected by sheep and cattle with plant height, herbage mass, stemminess and greenness. Data are from all sites

	GROWING SEASON		DORMANT SEASON	
	Year 1	Year 2	Year 1	Year 2
Sheep: IVD	(n=53)	(n=35)	(n=19)	(n=22)
Plant height	-0.348*	-0.370*	0.027	-0.153
Herbage mass	-0.413**	-0.435**	0.065	0.027
Stemminess	-0.235	0.230	-0.275	0.116
Greenness	0.530***	0.753***	0.541*	0.357
Sheep: CP	(n=52)	(n=34)	(n=15)	(n=22)
Plant height	-0.132	-0.425*	0.307	0.085
Herbage mass	-0.419**	-0.431**	-0.110	0.209
Stemminess	-0.084	0.059	0.201	-0.008
Greenness	0.614***	0.772***	-0.093	0.555**
Cattle: IVD	(n=53)	(n=35)	(n=21)	(n=22)
Plant height	-0.215	-0.256	-0.054	-0.066
Herbage mass	-0.347*	-0.338*	-0.001	-0.078
Stemminess	-0.248	0.270	-0.108	0.128
Greennes	0.569***	0.782***	0.543*	-0.227
Cattle: CP	(n=46)	(n=34)	(n=12)	(n=22)
Plant height	-0.210	-0.410*	-0.180	0.234
Herbage mass	-0.350*	-0.473**	0.232	0.371
Stemminess	-0.364*	0.013	-0.466	0.154
Greenness	0.600***	0.787***	0.586*	0.527*

quality and soil moisture at this stage.

Dietary quality was negatively correlated with total growing days between defoliations during the growing season in both years (Table 2.9) presumably because herbage mass would tend to accumulate with increased growing days. Conversely, there was a positive relation between dietary quality and this variable during the dormant season.

2.5 Discussion

Sward structure had a major effect on dietary quality in both cattle and sheep. Of the

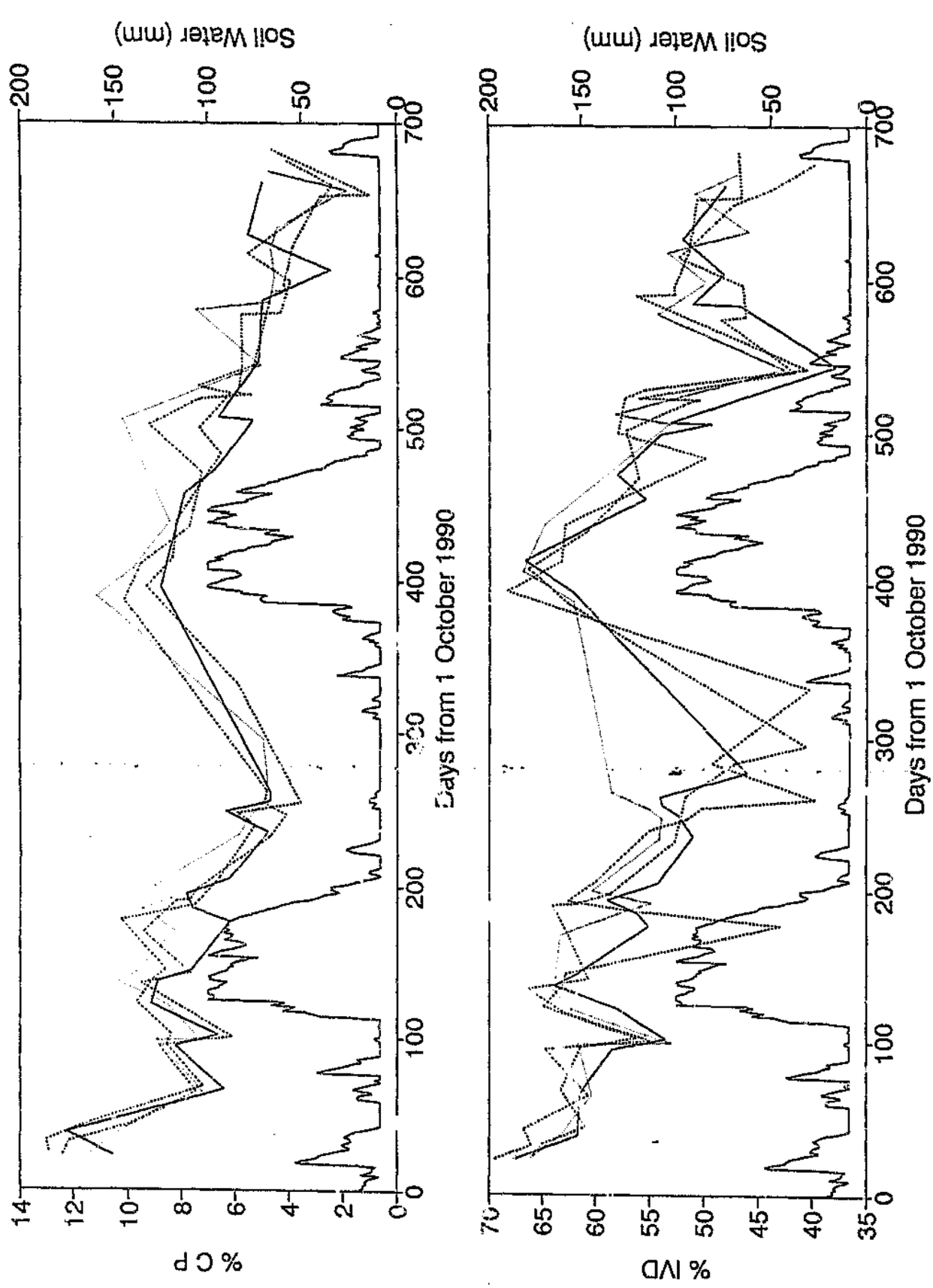

Figure 2.8 Changes in soil water content (bottom solid line) and the *in vitro* digestibility (IVD) and dietary crude protein (CP) of diets selected by sheep at 4 sites (top four lines) over 2 grazing seasons in the Döhne Sourveld.

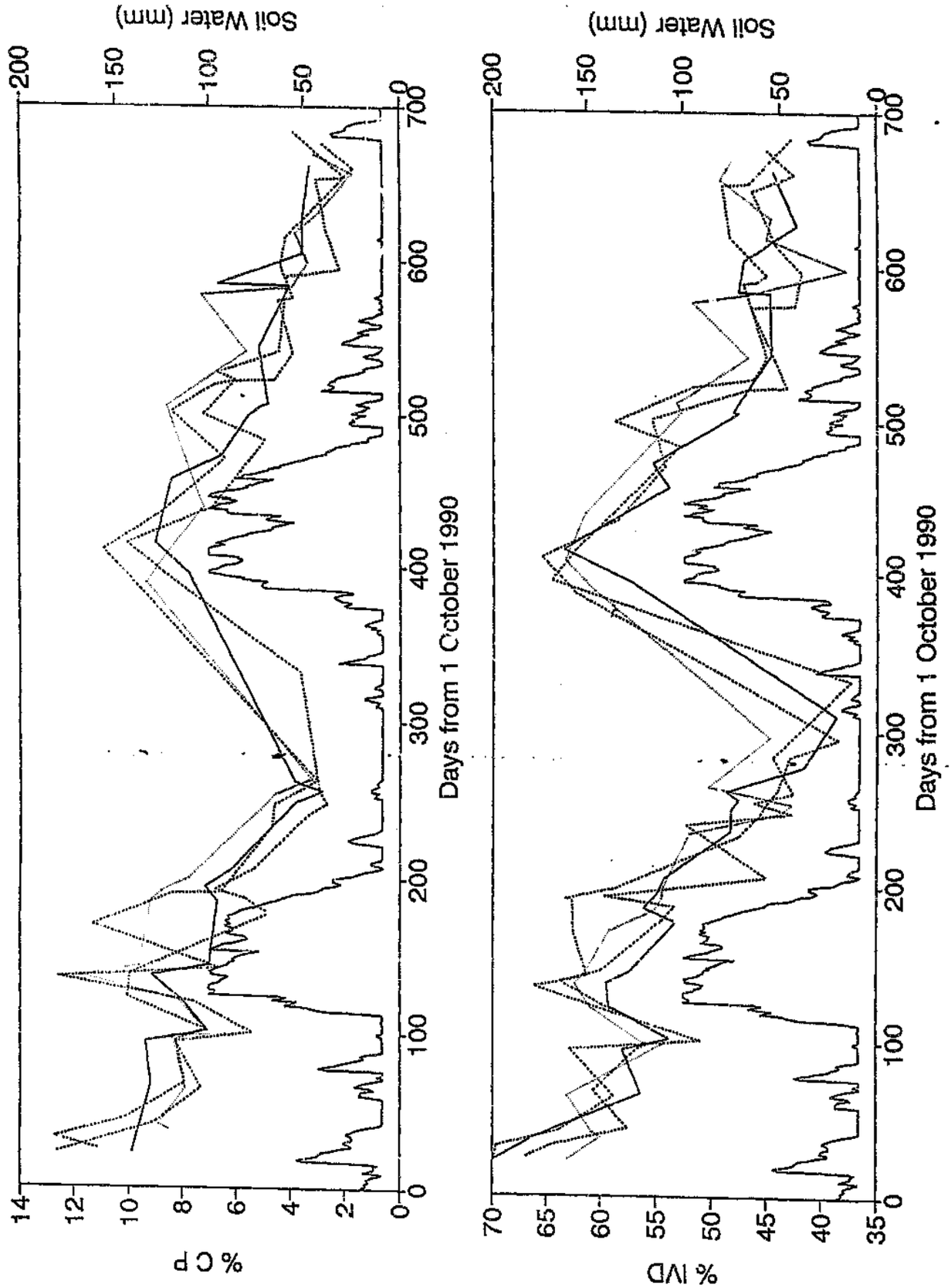

Figure 2.9 Changes in soil water content (bottom solid line) and the *in vitro* digestibility (IVD) and dietary crude protein (CP) of diets selected by cattle at 4 sites (top four lines) over 2 grazing seasons in the Döhne sourveld.

Table 2.9 Correlation coefficients for the relation between soil moisture content and total growing days between defoliations, and the *in vitro* digestibility (IVD) and crude protein content (CP) of diets selected by cattle and sheep in the growing and dormant seasons

	Year 1		Year 2	
	Growing season	Dormant season	Growing season	Dormant season
Sheep: IVD				
Soil water	0.144	0.191	0.810***	0.034
Growing days	-0.455***	0.283	-0.646***	-0.026
Sheep: CP				
Soil water	0.173	-0.292	0.740***	0.272
Growing days	-0.345*	0.153	-0.457**	0.424*
Cattle: IVD				
Soil water	0.245	0.152	0.832***	-0.153
Growing days	-0.341*	0.228	-0.437**	-0.384
Cattle: CP				
Soil water	0.259	-0.163	0.764***	0.376
Growing days	-0.343*	0.055	-0.434*	0.534

sward structure variables considered, sward greenness was the single most important determinant of dietary quality in both animals, in agreement with findings on other tropical and temperate pastures (Hamilton *et al.* 1973; Chacon *et al.* 1978; Forbes & Coleman 1993). 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 1989). At high greenness values, swards were relatively undiluted by senescent material, allowing selection of a high leaf-high quality diet. Conversely, at low values, green leaf was scarce and highly dispersed amongst low quality dead material, depressing the average quality of bites available to the animal. Interestingly, the response to greenness was non-linear with the major response occurring above a greenness level of 3 - 3.5 (Figs. 2.4 & 2.5). Below this level, the response was considerably weaker, and in some cases almost non-existent. Forbes and Coleman (1993) similarly noted that cattle grazing *Bothriochloa* pastures were able to

harvest diets of equivalent digestibilities over a wide range of green leaf availabilities. This suggests, in agreement with Topps (1962), that animals are, to a certain extent, able to mitigate the effects of declining green leaf availability by becoming increasingly selective. This is corroborated by the fact that for cr[illegible], biting rates generally declined with decreasing greenness (Section 3.4.1.2) presumably because animals spent more time searching for and/or manipulating bites.

Dietary quality was negatively related to herbage mass and sward height, at least within the growing season. This concurs with findings on other tropical (Chacon *et al.* 1978; O'Reagain 1990) and temperate pastures (Arnold 1960; Hamilton *et al.* 1973). Short, frequently-grazed swards provide a dense, concentrated layer of high-quality leaf material. As swards increase in height and available herbage, however, shading increases leaf senescence, diluting the availability and accessibility of green leaf in the sward (Table 2.7). Increasing sward height, may also affect bite size and plant part consumption by the grazing animal. On short swards, bite depth is restricted, limiting grazing to the upper horizon which is the highest quality substrate within the sward (Hodgson & Maxwell 1981). However, with increasing height, animals would have extended bite depth, increasing consumption of underlying pseudostem and dead material (Barthram 1981) with a consequent decline in dietary quality.

Leaf quality is also likely to decline with increasing herbage height and mass (Grieve & Osbourn 1965; Muldoon & Pearson 1977; Minson 1984) due to increased lignification with leaf age (Wilson 1976; Wilson & t'Mannetjie 1978). Later leaves of higher insertion on the tiller are also likely to be of relatively lower quality than earlier ones produced lower down (Wilson 1973; Wilson 1976; Wilson & Ng 1975). Large leaves on tall swards also have a relatively greater cell wall content due to their greater demands for structural strength (Wilson 1976).

Dietary quality also declined as swards became increasingly stemmy but this only occurred at old lands camp where the stem densities of *H. hirta* approached levels sufficient to affect bite quality (Fig. 2.7). This is in agreement with the findings of Chacon *et al.* (1978) for cattle grazing a *Setaria sphacelata* pasture. While young stems may be reasonably digestible (Norton 1981) stems are generally lignified and of poor quality (Juko & Bredon 1961). Generally, stems are avoided, forming less than 20 % of cattle diets (O'Reagain & Mentis 1988) and less in sheep (O'Reagain; unpublished data)

so it is unclear why increasing stemminess should depress dietary quality. However, at high stem densities, animals may be unable to select leaf without consuming a certain amount of stem. Alternatively, stemminess may restrict access to leaf within the tuft (Arnold 1962) forcing animals to consume lower-quality dead or partly-senescent material. Thus, on some occasions, cattle at old lands camp were observed to consume large amounts of stem without attempting to graze the leaf clusters at the base of the plants. Whatever the explanation, the site in question is atypical of sourveld, and it may be concluded that under most circumstances, stemminess is not an important determinant of dietary quality on this veld type.

There were marked seasonal changes in dietary quality over the grazing season with CP and IVD being highest in spring but lowest in winter for both cattle and sheep. This trend is characteristic of sourveld (Tainton 1981) and has been widely reported in other sourveld areas, e.g. Smith (1961b); Elliot *et al.* (1965); Shackleton & Mentis (1992). The present trends largely reflect seasonal changes in leaf quality and accessibility to the grazing animal. Early in the season swards are open and leaf is accessible, allowing selection of a high-quality diet. As the season progresses the increasing maturity of the grass layer results in a gradual decline in the proportion and accessibility of the available leaf. This is paralleled by increasing consumption of dead material (O'Reagain 1989) and an associated decline in dietary quality. In autumn, widespread leaf senescence in response to low soil moisture and periodic frosts occurs (Wilson & Ng 1978; Wilson & t'Mannetjie 1978) forcing animals to subsist on a diet of predominantly dead material (O'Reagain 1989) of low quality.

There are also marked changes in leaf quality over the grazing season. In spring, soil wetting after the dry winter leads to rapid microbial mineralization of organic matter releasing a large pulse of available nitrogen (Birch 1958) which may vary from 13 to 183 kg of N per hectare (Semb & Robinson 1969). This is rapidly absorbed by plants producing high quality herbage. As pulse size is directly dependent upon the length of the dry cycle (Birch 1960), it is suggested that shorter wetting and drying cycles later in the season produce less N possibly explaining the relatively low quality of green herbage at this time. Leaves produced later in the season may also be of lower quality due to their higher insertion in the grass tiller (Wilson 1973; Wilson 1976). The mass translocation of herbage N and carbohydrates to below-ground roots and crowns

in the late season (Clark 1977), a characteristic of perennial grasses, is likely to depress herbage quality further as winter approaches.

In winter, the quality of standing herbage may be further reduced by adverse weather conditions. Frosting of green leaves leads to a sharp drop in digestibility and nitrogen content (Wilson & t'Mannetjie 1978) while freezing and thawing of senescent material may lead to respiration and leaching losses of more digestible tissue constituents (Ocumpaugh & Matches 1977; Wilson 1981). Such losses may be exacerbated by rainfall and increased temperatures (Hart *et al.* 1969).

Within the growing season, marked intra-seasonal fluctuations in dietary quality were also evident. Aside from the effects of sward structure, these fluctuations appear to reflect temporal patterns of rainfall distribution through the season as reported on other subtropical pastures (McKay & Frandsen 1969; Dradu & Harrington 1972). This effect was particularly pronounced in year 1 when dietary quality dropped sharply during a mid-season drought but subsequently recovered when soil moisture levels were replenished. Similarly, in year 2, quality closely paralleled declining soil moisture levels after the cessation of rain in mid-season (Figures 2.8 & 2.9). Although moisture stress accelerates leaf senescence (Wilson & Ng 1975; Wilson & t'Mannetjie 1978) this did not appear to occur in the present study where leaves rolled and wilted but largely remained green during dry spells.

These patterns appear to conflict with accepted theory that herbage quality generally improves under conditions of moisture stress (Wilson 1981 but see Wilson & Ng 1975). However, the majority of evidence (Wilson *loc. cit.*) is derived from cultivated pastures where soil nutrient levels are generally adequate. In contrast, on most rangeland soils N is released in conjunction with soil wetting and drying cycles (Birch 1958) with N-availability declining as soils dry out (Millbank 1956; Birch 1960). This possibly accounts for the relatively lower herbage quality observed in the present study under dry conditions. Growth also slows down with restricted soil moisture and may reduce herbage quality as cell wall contents tend to be higher when growth is slow (Wilson 1976). The decline in leaf appearance rates (Wilson & t'Mannetjie 1978) would also reduce quality by increasing mean leaf age in the sward.

In apparent contradiction to the above, dietary quality was negatively related to total growing days between defoliations, a variable largely dependent upon soil

moisture. However, herbage mass and height increased with growing days resulting in a probable decline in herbage quality due to a change in sward structure. This supports the observation by graziers that provided herbage availability is not restricted, animal production is relatively better in dry than in wet years (t'Mannetjie, cited by Wilson 1981).

Fire had a major effect on dietary quality with diets selected in the year of the burn being of significantly higher quality than those selected the subsequent year. This substantiates results from other grassland areas, e.g. Mes (1958); Tainton *et al.* (1977); Svejcar (1988); Shackleton & Mentis (1992), although in these studies the effects of fire were found to be relatively transient and mainly confined to the early season. In the present study, aside from the spring, the major difference occurred in mid-season with quality declining to winter levels approximately 100 days sooner in the non-burn year (Figures 2.2 & 2.3). However, due to the marked differences in rainfall distribution between the two years (Figure 2.1) this difference cannot be solely attributed to the effects of fire.

The effects of fire on dietary quality may be partly attributed to its effects on sward structure; burning prevents the carry-over of poor-quality residues into the next season resulting in concentrated leafy regrowth uncontaminated by stem or senescent material. However, the main impact of burning probably results from its effects on nutrient cycling. Burning releases large amounts of nutrients tied up in senescent material and litter, increasing the availability of N and other soil nutrients (Sharrow & Wright 1976; Kellman *et al.* 1985; Stock & Lewis 1986). Excluding volatilisation losses, estimates of N-input vary from 23 kg N/ha for prairies (Sharrow & Wright 1976) to 60 kg N/ha for macchia (Stock & Lewis 1986) but are probably close to the former level for sourveld. Such nutrients are rapidly absorbed (Sharrow & Wright 1976; Kellman *et al.* 1985) and shunted into the leaves (Clark 1977) producing herbage of high nutrient quality (Shackleton & Mentis 1992). Although the results are equivocal, e.g. Sharrow & Wright (1976), the effects of fire on soil nutrient levels do not appear to be transient and may still be detected some months after burning (Kellman *et al* 1985; Stock & Lewis 1986). A gradual wind-down in herbage quality with subsequent seasons after the burn may be expected, resulting from the accumulation of senescent material and N-immobilization in this fraction (Clark 1977).

harvest diets of equivalent digestibilities over a wide range of green leaf availabilities. This suggests, in agreement with Topps (1962), that animals are, to a certain extent, able to mitigate the effects of declining green leaf availability by becoming increasingly selective. This is corroborated by the fact that for cattle, biting rates generally declined with decreasing greenness (Section 3.4.1.2) presumably because animals spent more time searching for and/or manipulating bites.

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Dietary quality also declined as swards became increasingly stemmy but this only occurred at old lands camp where the stem densities of *H. hirta* approached levels sufficient to affect bite quality (Fig. 2.7). This is in agreement with the findings of Chacon *et al.* (1978) for cattle grazing a *Setaria sphacelata* pasture. While young stems may be reasonably digestible (Norton 1981) stems are generally lignified and of poor quality (Juko & Bredon 1961). Generally, stems are avoided, forming less than 20 % of cattle diets (O'Reagain & Mentis 1988) and less in sheep (O'Reagain; unpublished data)

harvest diets of equivalent digestibilities over a wide range of green leaf availabilities. This suggests, in agreement with Topps (1962), that animals are, to a certain extent, able to mitigate the effects of declining green leaf availability by becoming increasingly selective. This is corroborated by the fact that for cattle, biting rates generally declined with decreasing greenness (Section 3.4.1.2) presumably because animals spent more time searching for and/or manipulating bites.

Dietary quality was negatively related to herbage mass and sward height, at least within the growing season. This concurs with findings on other tropical (Chacon *et al.* 1978; O'Reagain 1990) and temperate pastures (Arnold 1960; Hamilton *et al.* 1973). Short, frequently-grazed swards provide a dense, concentrated layer of high-quality leaf material. As swards increase in height and available herbage, however, shading increases leaf senescence, diluting the availability and accessibility of green leaf in the sward (Table 2.7). Increasing sward height, may also affect bite size and plant part consumption by the grazing animal. On short swards, bite depth is restricted, limiting grazing to the upper horizon which is the highest quality substrate within the sward (Hodgson & Maxwell 1981). However, with increasing height, animals would have extended bite depth, increasing consumption of underlying pseudostem and dead material (Barthram 1981) with a consequent decline in dietary quality.

Leaf quality is also likely to decline with increasing herbage height and mass (Grieve & Osbourn 1965; Muldoon & Pearson 1977; Minson 1984) due to increased lignification with leaf age (Wilson 1976; Wilson & 'tMannetje 1978). Later leaves of higher insertion on the tiller are also likely to be of relatively lower quality than earlier ones produced lower down (Wilson 1973; Wilson 1976; Wilson & Ng 1975). Large leaves on tall swards also have a relatively greater cell wall content due to their greater demands for structural strength (Wilson 1976).

Dietary quality also declined as swards became increasingly stemmy but this only occurred at old lands camp where the stem densities of *H. hirta* approached levels sufficient to affect bite quality (Fig. 2.7). This is in agreement with the findings of Chacon *et al.* (1978) for cattle grazing a *Setaria sphacelata* pasture. While young stems may be reasonably digestible (Norton 1981) stems are generally lignified and of poor quality (Juko & Bredon 1961). Generally, stems are avoided, forming less than 20 % of cattle diets (O'Reagain & Mentis 1988) and less in sheep (O'Reagain; unpublished data)

so it is unclear why increasing stemminess should depress dietary quality. However, at high stem densities, animals may be unable to select leaf without consuming a certain amount of stem. Alternatively, stemminess may restrict access to leaf within the tuft (Arnold 1962) forcing animals to consume lower-quality dead or partly-senescent material. Thus, on some occasions, cattle at old lands camp were observed to consume large amounts of stem without attempting to graze the leaf clusters at the base of the plants. Whatever the explanation, the site in question is atypical of sourveld, and it may be concluded that under most circumstances, stemminess is not an important determinant of dietary quality on this veld type.

There were marked seasonal changes in dietary quality over the grazing season with CP and IVD being highest in spring but lowest in winter for both cattle and sheep. This trend is characteristic of sourveld (Tainton 1981) and has been widely reported in other sourveld areas, e.g. Smith (1961b); Elliot *et al.* (1965); Shackleton & Mentis (1992). The present trends largely reflect seasonal changes in leaf quality and accessibility to the grazing animal. Early in the season swards are open and leaf is accessible, allowing selection of a high-quality diet. As the season progresses the increasing maturity of the grass layer results in a gradual decline in the proportion and accessibility of the available leaf. This is paralleled by increasing consumption of dead material (O'Reagain 1989) and an associated decline in dietary quality. In autumn, widespread leaf senescence in response to low soil moisture and periodic frosts occurs (Wilson & Ng 1978; Wilson & 'tMannetje 1978) forcing animals to subsist on a diet of predominantly dead material (O'Reagain 1989) of low quality.

There are also marked changes in leaf quality over the grazing season. In spring, soil wetting after the dry winter leads to rapid microbial mineralization of organic matter releasing a large pulse of available nitrogen (Birch 1958) which may vary from 13 to 183 kg of N per hectare (Semb & Robinson 1969). This is rapidly absorbed by plants producing high quality herbage. As pulse size is directly dependent upon the length of the dry cycle (Birch 1960), it is suggested that shorter wetting and drying cycles later in the season produce less N possibly explaining the relatively low quality of green herbage at this time. Leaves produced later in the season may also be of lower quality due to their higher insertion in the grass tiller (Wilson 1973; Wilson 1976). The mass translocation of herbage N and carbohydrates to below-ground roots and crowns

in the late season (Clark 1977), a characteristic of perennial grasses, is likely to depress herbage quality further as winter approaches.

In winter, the quality of standing herbage may be further reduced by adverse weather conditions. Frosting of green leaves leads to a sharp drop in digestibility and nitrogen content (Wilson & 'tMannetje 1978) while freezing and thawing of senescent material may lead to respiration and leaching losses of more digestible tissue constituents (Ocumpaugh & Matches 1977; Wilson 1981). Such losses may be exacerbated by rainfall and increased temperatures (Hart *et al.* 1969).

Within the growing season, marked intra-seasonal fluctuations in dietary quality were also evident. Aside from the effects of sward structure, these fluctuations appear to reflect temporal patterns of rainfall distribution through the season as reported on other subtropical pastures (McKay & Frandsen 1969; Dradu & Harrington 1972). This effect was particularly pronounced in year 1 when dietary quality dropped sharply during a mid-season drought but subsequently recovered when soil moisture levels were replenished. Similarly, in year 2, quality closely paralleled declining soil moisture levels after the cessation of rain in mid-season (Figures 2.8 & 2.9). Although moisture stress accelerates leaf senescence (Wilson & Ng 1975; Wilson & 'tMannetje 1978) this did not appear to occur in the present study where leaves rolled and wilted but largely remained green during dry spells.

These patterns appear to conflict with accepted theory that herbage quality generally improves under conditions of moisture stress (Wilson 1981 but see Wilson & Ng 1975). However, the majority of evidence (Wilson *loc. cit.*) is derived from cultivated pastures where soil nutrient levels are generally adequate. In contrast, on most rangeland soils N is released in conjunction with soil wetting and drying cycles (Birch 1958) with N-availability declining as soils dry out (Millbank 1956; Birch 1960). This possibly accounts for the relatively lower herbage quality observed in the present study under dry conditions. Growth also slows down with restricted soil moisture and may reduce herbage quality as cell wall contents tend to be higher when growth is slow (Wilson 1976). The decline in leaf appearance rates (Wilson & 'tMannetje 1978) would also reduce quality by increasing mean leaf age in the sward.

In apparent contradiction to the above, dietary quality was negatively related to total growing days between defoliations, a variable largely dependent upon soil

moisture. However, herbage mass and height increased with growing days resulting in a probable decline in herbage quality due to a change in sward structure. This supports the observation by graziers that provided herbage availability is not restricted, animal production is relatively better in dry than in wet years ('t Mannetje, cited by Wilson 1981).

Fire had a major effect on dietary quality with diets selected in the year of the burn being of significantly higher quality than those selected the subsequent year. This substantiates results from other grassland areas, e.g. Mes (1958); Tainton *et al.* (1977); Svejcar (1988); Shackleton & Mentis (1992), although in these studies the effects of fire were found to be relatively transient and mainly confined to the early season. In the present study, aside from the spring, the major difference occurred in mid-season with quality declining to winter levels approximately 100 days sooner in the non-burn year (Figures 2.2 & 2.3). However, due to the marked differences in rainfall distribution between the two years (Figure 2.1) this difference cannot be solely attributed to the effects of fire.

The effects of fire on dietary quality may be partly attributed to its effects on sward structure; burning prevents the carry-over of poor-quality residues into the next season resulting in concentrated leafy regrowth uncontaminated by stem or senescent material. However, the main impact of burning probably results from its effects on nutrient cycling. Burning releases large amounts of nutrients tied up in senescent material and litter, increasing the availability of N and other soil nutrients (Sharrow & Wright 1976; Kellman *et al.* 1985; Stock & Lewis 1986). Excluding volatilisation losses, estimates of N-input vary from 23 kg N/ha for prairies (Sharrow & Wright 1976) to 60 kg N/ha for macchia (Stock & Lewis 1986) but are probably close to the former level for sourveld. Such nutrients are rapidly absorbed (Sharrow & Wright 1976; Kellman *et al.* 1985) and shunted into the leaves (Clark 1977) producing herbage of high nutrient quality (Shackleton & Mentis 1992). Although the results are equivocal, e.g. Sharrow & Wright (1976), the effects of fire on soil nutrient levels do not appear to be transient and may still be detected some months after burning (Kellman *et al* 1985; Stock & Lewis 1986). A gradual wind-down in herbage quality with subsequent seasons after the burn may be expected, resulting from the accumulation of senescent material and N-immobilization in this fraction (Clark 1977).

In general, sheep selected diets of higher CP and IVD than cattle, in agreement with findings from other vegetation communities ranging from temperate grasslands (Grant *et al.* 1985) and sown pastures (Dudzinski & Arnold 1973) to semi-arid rangelands (Zeeman *et al.* 1983; 1984). 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 animals (Owen-Smith 1982; Chambers *et al.* 1981; Grant *et al* 1985; Gordon & Illius 1988). Despite this, it is surprising that in the present study, the two animals appeared to be equally vulnerable, in terms of dietary quality, to changes in sward structure. It is particularly noteworthy that sheep appeared to be particularly sensitive to very tall, rank swards and, on occasion, selected diets of considerably lower quality on these swards, than did cattle. Sheep graze deeper into the sward profile than do cattle (Forbes 1982 cited by Grant *et al.* 1985) and on tall swards may have inadvertently consumed lower quality leaf or senescent material in the sub-canopy. In contrast, if cattle were grazing in the top horizon as observed by Forbes (*loc. cit.*), they would have rejected the higher quality green leaf which is usually concentrated at the top of the canopy. This suggests that sheep have an innate, relatively inflexible foraging strategy, e.g. graze short grass, which is normally successful for their foraging niche, but which fails is less effective when they are forced to forage on swards to which they are ill-adapted.

The results of the present study suggest that in sourveld sward species composition has little or no effect on dietary quality. Dietary quality was also unrelated to veld condition score in both the growing and dormant seasons, in general agreement with findings in other sourveld regions in South Africa. Mentis (1982), working in the moist tall grassveld of Natal, reported that while the quality of diet selected by cattle was strongly related to time since the start of the grazing season, it was unrelated to species composition. Hardy (1986), repeated Mentis's (*loc. cit.*) experiment on a different sourveld type, but could also not detect any relation between dietary quality and species composition over the grazing season as a whole, although a significant relation was detected in summer (Hardy 1986). O'Reagain and Mentis (1990) also failed to find any relation between dietary quality in cattle and veld condition even when a variety of methods were used to index species composition. The present results therefore appear to confirm the assertion that the effects of species

composition on dietary quality are negligible in sourveld (O'Reagain & Mentis 1990) and largely overridden by sward structure and season.

Unfortunately, a major shortcoming of the present study is that dietary quality was estimated from fistula samples collected within the first 20-30 minutes of occupation in a particular block. Over this short time period, animals would have had the opportunity to be extremely selective and graze only the highest quality species present. This is likely to have occurred even on swards with a preponderance of unpalatable species, thereby masking any potential longer-term effect of species composition on dietary quality. This is supported by the observation that dietary CP and IVD appeared to decline more in certain camps over extended periods of occupation than in others (section 4.4.4) suggesting that the effects of species composition may become apparent over longer time periods when animals are forced to consume less palatable, lower quality species.

In practical terms, animals on Döhne Sourveld will be on a declining plane of nutrition from midsummer onwards. As quality declines, voluntary intake will be restricted leading to deficiencies in both digestible energy and protein, with subsequent loss of body mass and condition. The timing and rate of this decline appears to depend upon rainfall and the burning history of a particular site. Quality appears to decline later on burnt than on unburnt swards and this difference is likely to be more pronounced as the period between burns is extended. Quality may also decline sooner and faster in very wet years when growth is excessive leading to rank swards, and in very dry years when premature leaf senescence occurs in response to low soil moisture. Assuming maintenance protein requirements of 6 % for cattle and sheep (Kearl 1982) animals on the present trial were on sub-maintenance levels from May onwards in the year of a burn and as early as February in the subsequent year. This is likely to occur even sooner under on-farm conditions given the higher maintenance requirements of reproductive animals (Kearl 1982) and the decline in dietary quality with continuing periods of occupation in a camp (e.g. O'Reagain & Mentis 1988). This is substantiated by the poor reproductive performance reported by most graziers for animals on Döhne Sourveld (A.M. Grenfell pers. comm[1].). Depending upon rainfall, it is consequently

[1] P.O. Box 116, Stutterheim, 4930.

recommended that N- supplementation of animals be initiated as early as April on burnt veld and even earlier on unburnt veld. Counter to current recommendations, mid-season supplementation of N may also be necessary during mid-season droughts.

Within the growing season, potential exists to improve dietary quality by manipulating sward structure through strategic grazing management. Swards should be kept in a short, actively-growing phase to maximise the quality and accessibility of leaf available to the grazing animal. Extended periods of regrowth between defoliations should be avoided to minimise the accumulation of low-quality herbage while, contrary to current recommendations (Anon. 1988), swards should be utilized as soon as possible after burning to take advantage of the inherent high quality of post-burn regrowth. Within the dormant season, however, herbage quality appears to decline to some uniform low level irrespective of management and there appears to be little potential to improve dietary quality through manipulating sward structure.

In conclusion, the following conceptual model of dietary quality on sourveld is proposed. During the growing season, i.e. when temperatures are adequate for growth and over the normal duration of the rains, dietary quality will be relatively high. Here, quality is dependent upon sward structure, being highest on short, leafy swards and lowest on tall, rank swards with a low green:dead ratio. To a lesser extent, dietary quality will also be dependent upon rainfall distribution, declining during droughts but increasing when moisture levels are replenished. The limits to these responses will be determined, first, by burning history in terms of the initial input of nutrients into the system and second, by total rainfall in terms of ratio of metabolic:cell wall constituents (*sensu* Bell 1982) with herbage quality being lower with above-average rainfall and vice versa. At the end of the growing season a transition occurs with extensive translocation of herbage nutrients to storage organs in response to declining temperatures and/or low soil moisture levels, followed by extensive leaf senescence at the start of the dormant season. This precipitates a major decline in dietary quality to low winter levels. Although sward structure may have an effect on quality at this stage, its effects are likely to be marginal. Dietary quality in the growing season is therefore determined by a combination of environmental and management factors. In the dormant season, in contrast, quality appears to be totally under the control of environmental factors and is largely unaffected by management.

2.6 Conclusions

2.6.1 Species composition had no measurable effect on dietary quality in either cattle or sheep. Dietary quality was also unrelated to veld condition score whether considered over the growing, dormant or entire grazing season.

2.6.2 Sward structure had a major effect on dietary quality in both animals. Dietary CP and IVD were strongly correlated with sward greenness but negatively correlated with herbage mass and height.

2.6.3 Fire had a major effect on dietary quality with CP and IVD being significantly higher in the year of the burn than in the subsequent year.

2.6.4 Dietary quality showed a strong seasonal trend being highest in spring and lowest in winter. Within this trend marked intra-seasonal variations in quality were also evident in response to fluctuations in rainfall and soil moisture.

2.6.5 The quality of diet selected by sheep was significantly higher than that of cattle. This difference was consistent across all species compositions, sward structures and across both years. An exception was on very tall, rank swards when sheep selected diets of considerably lower quality than did cattle.

2.6.6 It is proposed that in the growing season, dietary quality is determined by a combination of environmental and management factors and is therefore amenable to manipulation through grazing management. Conversely, in the dormant season, dietary quality is determined by environmental factors which are beyond the control of the grazier.

CHAPTER 3

THE EFFECT OF SPECIES COMPOSITION AND SWARD STRUCTURE ON THE INGESTIVE BEHAVIOUR OF CATTLE AND SHEEP GRAZING DOHNE SOURVELD

3.1 Objectives

The specific objectives of this experiment study were to:

(i) determine the relative effects of species composition and sward structure on the ingestive behaviour of cattle and sheep on Dohne Sourveld;

(ii) define in quantifiable terms any relation that might exist between ingestive behaviour and species composition and sward structure.

3.2 Introduction

Sward species composition is assumed to be a major determinant of animal production on rangeland, e.g. Tainton 1986. Consequently, species composition should have a major influence on dietary quality or intake or both. In sourveld, however, species composition appears to have no effect on dietary quality (Mentis 1982; Hardy 1986; O'Reagain & Mentis 1990) while the relation with intake is obscure. Efforts to relate intake to species composition in sourveld (Mentis 1982; Hardy 1986) have been unsatisfactory due in part to methodological problems but, more importantly, because little attempt has been made to gain a mechanistic understanding of the basic processes involved at the plant:animal interface.

Ignoring the effects of herbage quality on passage rate, intake may be defined as the product of bite size, bite rate and grazing time (Allden & Whittaker 1970; Hodgson 1981). Theoretically, numerous combinations of bite size, biting rate and grazing time could give the same intake (Greenwood & Demment 1988) but in practice bite size is the major determinant of intake with biting rate and grazing time being largely compensatory variables (Hodgson 1981). Bite size is determined by the dimensions of the buccal cavity and the depth, area and density of herbage prehended (Black & Kenney 1984; Burlison *et al.* 1991). Biting rate basically reflects the ease with

which herbage can be prehended but is also determined by chewing rate as the two are considered to be competing processes (Spalinger & Hobbs 1992). Grazing time may be adjusted to compensate for bite size but is constrained by other activities such as rumination and thermo-regulation (Belovsky 1978; Demment *et al.* 1987).

Species composition on rangeland could conceivably 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. These could arise through differences in plant morphology or growth form. At the patch or community level, intake could be affected through differences in the proportion and distribution of different species present. Here, intake would be a function of the search time and encounter rate of different species in the sward (Spalinger & Hobbs 1992).

Sward structure could also have a major effect on intake for animals on rangeland. There is compelling evidence from other native and cultivated pastures to show that bite size, and hence intake, increases dramatically with increasing height and density of the sward, e.g. Allden & Whittaker (1970); Jamieson & Hodgson (1979); Burlison *et al.* (1991). Generally, intake rate increases until a limit is reached where bite size is restricted by the dimensions of the buccal cavity (Allden & Whittaker 1970; Black & Kenney 1984; Hudson & Nietfeld 1985) and/or biting rate becomes limited by chewing rate (Spalinger & Hobbs 1992). This resembles the classic Type II functional response (Holling 1959) where intake increases as a decelerating function of forage availability until an asymptote is reached (Short 1985; Spalinger & Hobbs 1992; Gross *et al.* 1993). Distinct functional responses exist for different animals according to body mass, mouth dimensions and foraging efficiencies (Allden & Whittaker 1970; Wickstrom *et al.* 1984; Short 1985).

Conceptually, sward species composition and structure could therefore both be important determinants of intake on sourveld and the potential also exists for an interaction between these variables. The magnitude and nature of any effect these variables might have is also likely to vary with the animal species involved. Quantification of these effects for individual animal species is therefore important to allow the accurate prediction of animal production on this range type.

3.3 Procedure

3.3.1 Study area

The study was conducted at the Dohne Agricultural Development Institute situated 10 km north of Stutterheim, in the Dohne Sourveld (Acocks 1988). A detailed description of the study area and experimental conditions is provided in section 2.3.1.

3.3.2 Experimental design

3.3.2.1 Cattle

Cattle data were collected from the simulation trial described in section 2.3.2. Briefly, the trial consisted of four sites termed bush, eragrostis, old lands and sheep shed camps, all of which varied widely in species composition (Table 2.1). Each camp was divided into six equal sized blocks which were then subjected to different frequencies of grazing i.e., approximately every 3, 5, 8, 11, 16, or 20 weeks, in order to achieve a range of sward structures. Cattle intake data were collected in the 1990-1991 and 1991-1992 grazing seasons, hereafter referred to as years 1 and 2 respectively.

3.3.2.2 Sheep

Initially, sheep data were collected using oesophageally fistulated animals in conjunction with the cattle trial described above. However, due to extremely variable recovery rates of fistula samples, the data were considered to be insufficiently precise to allow accurate estimates of intake and were discarded. A new data set for sheep was therefore collected using the methodology described below.

In this new trial, sheep data were collected from the same experimental areas described for cattle (*3.3.2.1*) but during the 1992-1993 grazing season. All four sites were burnt in September 1992 before data collection commenced in order to remove the residual effects of previous seasons' grazing. Blocks were then grazed at different intervals after the burn using different frequencies of grazing to achieve as wide a range of sward structures as possible. On occasion, blocks were strategically grazed by cattle to ensure a uniform sward structure.

3.3.3 Sward measurements

Measurements of plant height, leaf table height, greenness and stemminess for three

selected grass species at each site, as well as an estimate of herbage mass for the sward as a whole, were made in each block as described in section 2.3.3. Herbage density (mg.DM/cm^{-3}) was estimated by dividing total herbage mass by the leaf table height of the most preferred species in the sward (section 3.3.5).

3.3.4 Animal measurements

3.3.4.1 Cattle

Fistula samples were collected and processed as described in section 2.3.5. Biting rates were recorded using a stop-watch for a minimum of 20 consecutive prehension bites with recording being suspended if the animal raised its head and moved to a new feeding station. A total of 30 observations, equally divided between the two experimental oxen, were made for each sampling episode. Total bites were estimated from the product of biting rate and sampling (grazing) time. Bite size was calculated as total fistula extrusa (dry mass) divided by total bites. Intake rate (IR) was calculated by dividing total fistula extrusa by sampling time. Average daily grazing time was estimated using a Kienzle[1] vibracorder attached to a single steer of similar mass and age to the fistulated animals. Dietary quality data for cattle were obtained from section 2.4.

A problem with the use of fistulated animals is that of incomplete recovery of ingested material, leading to underestimates of intake. Stobbs (1973a) advocated the use of foam rubber plugs in the oesophagus to ensure complete recovery of fistula samples and reported recovery rates of 90 - 100 % using this method. However, personal experience is that animals suffer considerable discomfort with the method and, in many cases, refuse to eat (O'Reagain 1989). A similar lack of success with the method has also been noted by Zinnerman (1983) and Penning and Hooper (1985). Accordingly, while it was accepted that the fistula method was likely to underestimate intake, it was assumed that this would occur to an equal extent under all conditions and would not affect the nature of any sward structure-ingestive behaviour relation *per se*.

3.3.4.2 Sheep

Herbage intake was estimated using the method of Erizian (1932), as used by Allden

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[1] Tachograph Sales and Services, PO Box 1547, East London, 5200.

(1962), Allden and Whittaker (1970) and modified by Penning and Hooper (1985). Intake was calculated using the equation:

$$I = (W_2 + F + U + IWL) - W_1 \quad (1)$$

where I = intake, W_1 and W_2 = mass of animal before and after grazing, F = weight of faeces produced, U = weight of urine produced and IWL = insensible weight loss (Erizian 1932, cited by Penning & Hooper 1985). Field tests indicate that the method provides comparable estimates of intake to traditional marker methods, e.g. chromic oxide (Penning & Hooper 1985). The latter techniques were considered inappropriate for the present study due to the short periods of occupation (<24 hours) on different blocks. Preliminary trials with animals being fed a known mass of feed indicated that the present method provided consistent, accurate estimates of intake (O'Reagain unpublished data).

Four Dohne merino ewe lambs (average mass 40 kg) and a single non-reproductive, 6-tooth ewe (mass 63 kg) were used in the study. All were sourveld-raised and well adapted to range conditions. Prior to sampling, animals were fasted overnight to stimulate appetite. Any effects of hunger on foraging behaviour were assumed to be constant over all sward structures. Sampling began at 06·30 each morning. Animals were first fitted with canvas faeces bags which were double-lined with plastic and contained vermiculite to absorb urine. Animals were then weighed in the field using a Mettler[2] KC 300 electronic scale (range 0-300 kg, sensitivity 10 g) attached to a Mettler ID1 terminal and powered by a portable generator. A minimum of 10 consecutive weighings were taken for each animal with the time of weighing recorded to the nearest minute. Wind interference was minimised by enclosing the weighing area with iron sheeting, but under extreme conditions weighing was abandoned.

Immediately after weighing, animals were released as a group and allowed to graze for a set, recorded time (usually about 60 minutes). Biting rate was estimated from the time taken to achieve a minimum of 20 consecutive prehension bites without the animal raising its head and moving to a new feeding station. A total of 20-30 such observations were made in each sampling. Animals were then re-weighed and intake calculated from total mass change adjusted for herbage DM% and total IWL between

[2] Microsep (Pty) Ltd.,PO Box 2288, Pinetown, 3600.

initial and final weighings. IWL was calculated as:

$$IWL\ (g/min.) = 1.209 + 0.117\ T + 0.0331\ M \quad (2)$$

where T = ambient air temperature and M = animal mass (r^2 = 0.815; $P \leq 0.0001$). Equation 2 was derived from IWL measured over a range of air temperatures (Appendix 3.1). Intake rate (IR) was calculated as total DM intake divided by grazing time and was expressed as both an absolute, i.e. g.DM/minute, and relative value, i.e. per unit of body mass (g.DM/min./kg). Bite size was calculated from total DM intake divided by the estimated total number of bites, i.e. biting rate x sampling (grazing) time.

3.3.5 Statistical analyses

At each sampling date, measurements of bite size, bite rate and intake rate were meaned for both cattle (n=2) and sheep (n=5). The mean of each sward structure variable was also calculated across tufts (n = 50) for each grass species. Correlation and principal components analysis of sward structure data indicated that the majority of variables were strongly inter-correlated (Tables 2.6 & 2.7). Accordingly, 3 variables were selected for further consideration, i.e. plant height, herbage density and greenness. Stemminess was also considered, but only for old lands camp as this was the only site where this variable reached levels sufficient to have any noticeable effect on sward structure. Because animals may be expected to concentrate on the most preferred species present, only plant height and greenness from the most preferred species in a camp were considered. These species were *T. triandra* (bush), *T. triandra* (eragrostis), *H. hirta* (lands) and *T. leucothrix* (sheep shed).

Data were initially tested for normality (UNIVARIATE; SAS [1991]). The variables plant height and cattle bite size were not normally distributed and were log- and square-root-transformed respectively. To investigate the effect of species composition ('camp') on ingestive behaviour, an analysis of covariance was conducted using plant height as a covariate (GLM; SAS [1991]). A similar analysis using data from individual sheep was conducted to determine the effect of 'animal' on intake rate.

Initial exploration of cattle data indicated first, that there was little difference between camps in terms of ingestive behaviour and second, that there was a degree of variability in estimates of bite size and intake rate in these animals. To facilitate data presentation and interpretation, cattle data from the different camps were therefore

grouped into a single data set for each year. However, there were cases where individual relations were thought to be of interest, e.g. for modelling, and these are presented individually for the four different camps. In contrast, the sheep data appeared to be relatively precise and less variable than those for cattle and here it was considered appropriate to conduct and present all analyses on a camp-by-camp basis.

Relations between sward structure and ingestive behaviour were investigated using correlation analysis (CORR; SAS [1991]) as well as linear and polynomial regression (REG; SAS [1991]). Where appropriate, the Michelis-Menton function was fitted (NLIN; SAS [1991]) after first standardizing plant height to zero.

3.4 Results

The basic, unprocessed ingestive behaviour and sward structure data for both cattle and sheep is presented in Appendix 1.

3.4.1 Cattle

3.4.1.1 Effect of species composition on ingestive behaviour

Overall, 'Year' had a significant ($P \leq 0.05$) effect on bite size (Appendix 3.2) with the size of bite harvested in year 2 being larger (0.332 g vs 0.290 g) than that harvested in year 1 (Table 3.1). 'Year' also had a significant ($P \leq 0.05$) effect on intake rate (IR) with the average IR being 2-3 g/minute higher in the second year.

Table 3.1 Mean bite size, bite rate and intake rate for cattle grazing four sites in the Dohne Sourveld in year 1 and 2. Within a row, means with the same superscripts are not significantly different ($P \leq 0.05$)

Variable	Year	CAMP			
		Bush	Eragrostis	Lands	Shed
Bite size (g.DM)	1	0.266^{a}	0.316^{a}	0.293^{a}	0.285^{a}
	2	0.348^{a}	0.361^{a}	0.306^{a}	0.313^{a}
Bite rate (bites/minute)	1	59.11^{a}	53.58^{b}	54.14^{b}	56.73^{ab}
	2	57.05^{ac}	51.02^{b}	54.07^{bc}	57.80^{a}
Intake rate (g.DM/minute)	1	15.45^{a}	16.36^{a}	15.45^{a}	15.97^{a}
	2	20.28^{a}	18.63^{ab}	16.05^{b}	18.53^{ab}

Species composition, expressed as 'camp' had no effect on the size of bite harvested by cattle in either year (Appendix 3.3), but had a significant effect on biting rate in both year 1 ($P \leq 0.05$) and 2 ($P \leq 0.01$). On average, biting rates were lower ($P \leq 0.05$) in eragrostis and old lands than in the other camps in both years (Table 3.1). Species composition had no overall effect on intake rate, although some between-camp differences were significant in year 2 (Table 3.1) with average intake rates being highest and lowest on bush and old lands camps respectively.

3.4.1.2 Effect of sward structure on ingestive behaviour

In year 1, cattle bite size was strongly correlated ($P \leq 0.0001$) with plant height (Table 3.2). Taken over all camps the relation was non-linear ($P \leq 0.0001$) with bite size increasing from about 0.12 g to a maximum of 0.4 g as plant height increased from 6 to 25 cm (Fig 3.1). Above this height bite size remained relatively constant. However, for individual camps the relation was generally linear with height accounting for up to 60 % of the variability in bite size at certain sites (Table 3.3). No relation between bite size and plant height was evident in year 2 with bite size showing no consistent response to height over the entire range of heights encountered (Fig. 3.1). Bite size was not related to herbage density in either year but was negatively correlated ($P \leq 0.01$) with sward greenness in year 2 (Table 3.2).

Intake rate also responded strongly to plant height in year 1 (Table 3.2), increasing from about 6 g DM/minute to an intake of nearly 20 g DM/minute over the

Table 3.2 Correlation coefficients for the relation between the different components of ingestive behaviour in cattle and plant height, herbage density and greenness in year 1 and 2 on Dohne Sourveld. Data are from all sites

	Plant height		Herbage density		Greenness	
Year	1	2	1	2	1	2
Bite size	0.609***	0.200	0.017	0.076	-0.155	-0.388**
Bite rate	-0.458***	-0.275*	0.126	0.044	0.387***	0.793***
Intake rate	0.538***	0.055	0.070	0.038	0.024	0.147
Grazing time	-0.607***	-0.0614	-0.020	0.166	0.412*	0.407*

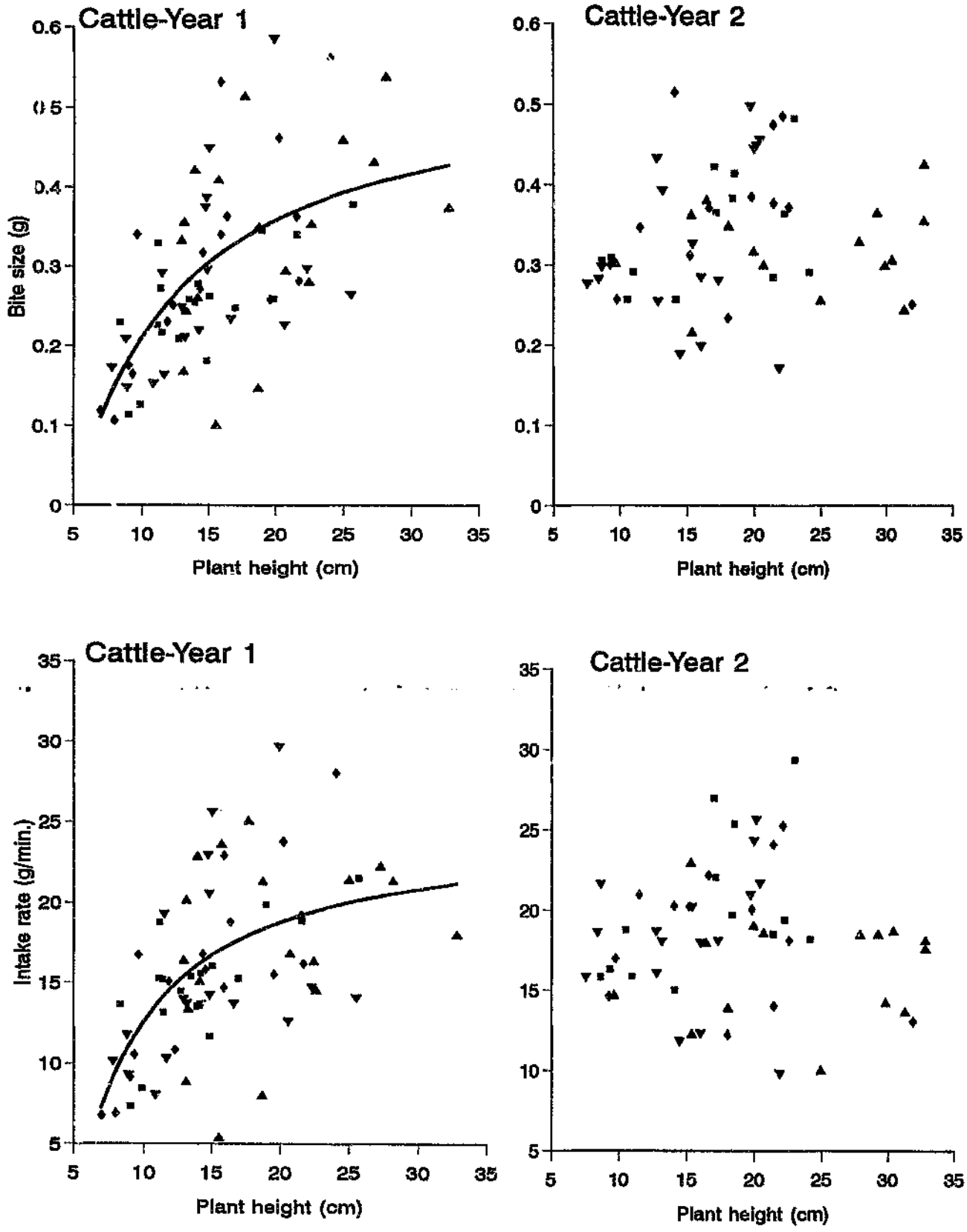

Figure 3.1 The relation between bite size and plant height (top), and intake rate and plant height (bottom) for cattle grazing 4 sites on Dohne Sourveld in year 1 and 2 (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

range of heights encountered (Fig. 3.1). As with bite size, the overall relation was non-linear ($P \leq 0.0001$) with IR reaching a maximum at a height of about 20 - 25 cm. With the exception of old lands camp, IR increased linearly with plant height in all camps (Table 3.3). As with bite size, there was no apparent response to height in year 2 with IR fluctuating between 10 and 25 g/minute over a range of heights from about 6 to 30 cm (Fig. 3.1). Intake rate showed no response to herbage density and greenness in either year (Table 3.2).

Table 3.3 Linear regression equations for the relation between bite size and intake rate with plant height for cattle at four sites in the Dohne Sourveld in year 1

Camp	Equation	
	Bite size	
Bush	$y = 0.0695 + 0.162x$	$r^2 = 0.49$; $F = 13.56$; **
Eragrostis	$y = -0.120 + 0.249x$	$r^2 = 0.61$; $F = 24.23$; ***
Lands	$y = 0.109 + 0.157x$	$r^2 = 0.41$; $F = 3.34$
Sheep shed	$y = -0.120 + 0.245x$	$r^2 = 0.39$; $F = 9.32$; **
All camps	$y = 0.551x/(8.068+x)$	$r^2 = 0.42$
	Intake rate	
Bush	$y = -4.71 + 7.43x$	$r^2 = 0.39$; $I = 10.34$; **
Eragrostis	$y = -17.24 + 12.55x$	$r^2 = 0.67$; $F = 30.45$; ***
Lands	$y = 2.57 + 5.04x$	$r^2 = 0.07$; $F = 1.22$
Sheep shed	$y = -17.79 + 12.99x$	$r^2 = 0.33$; $F = 7.02$; *
All camps	$y = 24.89x/(4.91+x)$	$r^2 = 0.38$

In contrast to bite size, biting rates declined with increasing sward height in both years (Fig. 3.2), with this effect being particularly evident in year 1 (Table 3.2). Conversely, biting rates were positively correlated with greenness and showed a marked linear ($P \leq 0.0001$) response to this variable, particularly in the second season (Fig. 3.2). In old lands camp, stemminess had little effect on biting rates in year 1 ($r=-0.304$; $P \leq 0.219$) but biting rates appeared to be restricted by increasing stemminess ($r=-0.458$; $P \leq 0.085$) levels in year 2 (Fig. 3.3). However, the effects of stemminess may be confounded with those of greenness as the stemmiest swards happened to be grazed in

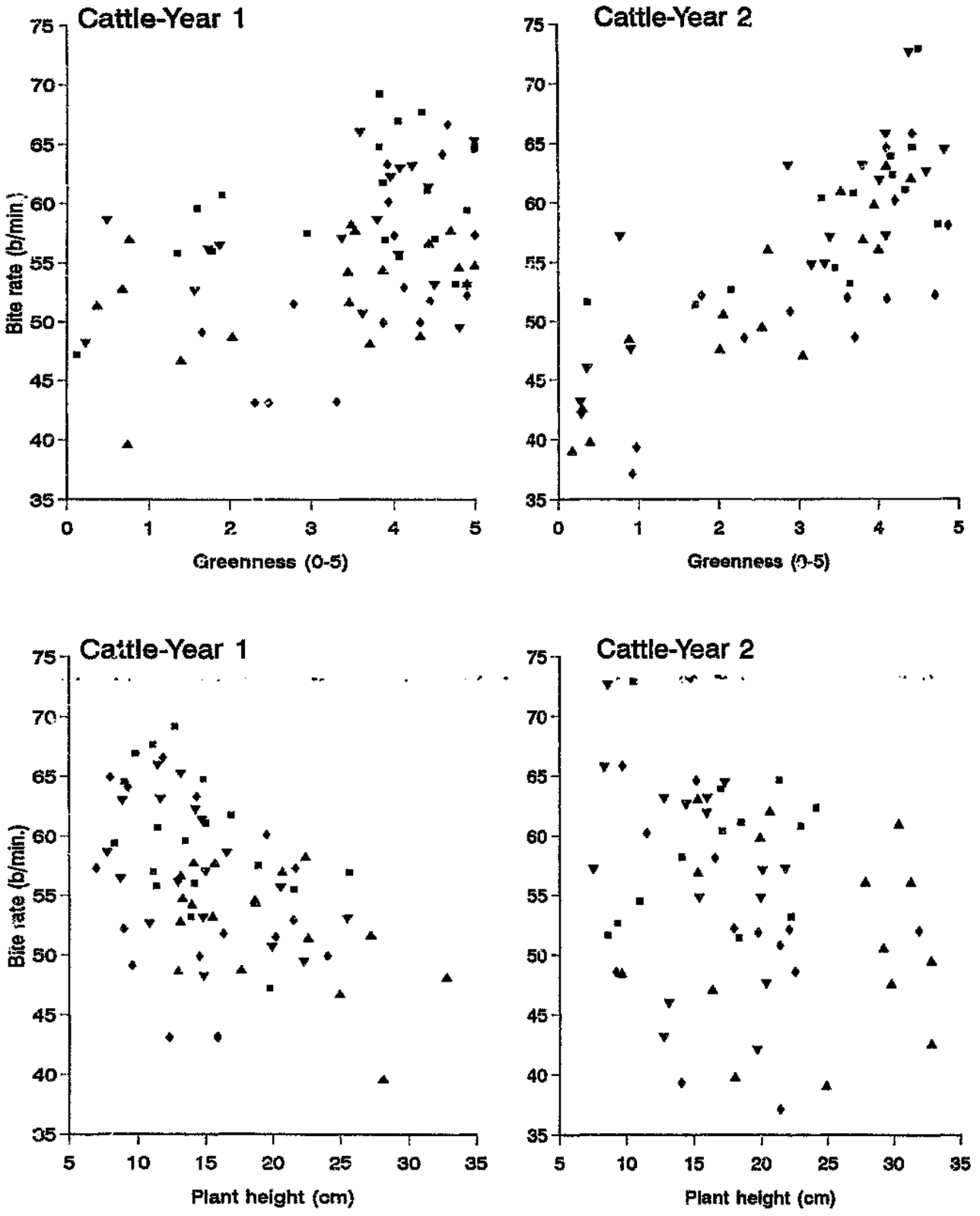

Figure 3.2 The relation between bite rate and greenness (top) and bite rate and plant height (bottom) for cattle grazing 4 sites on Dohne Sourveld in year 1 and 2 (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

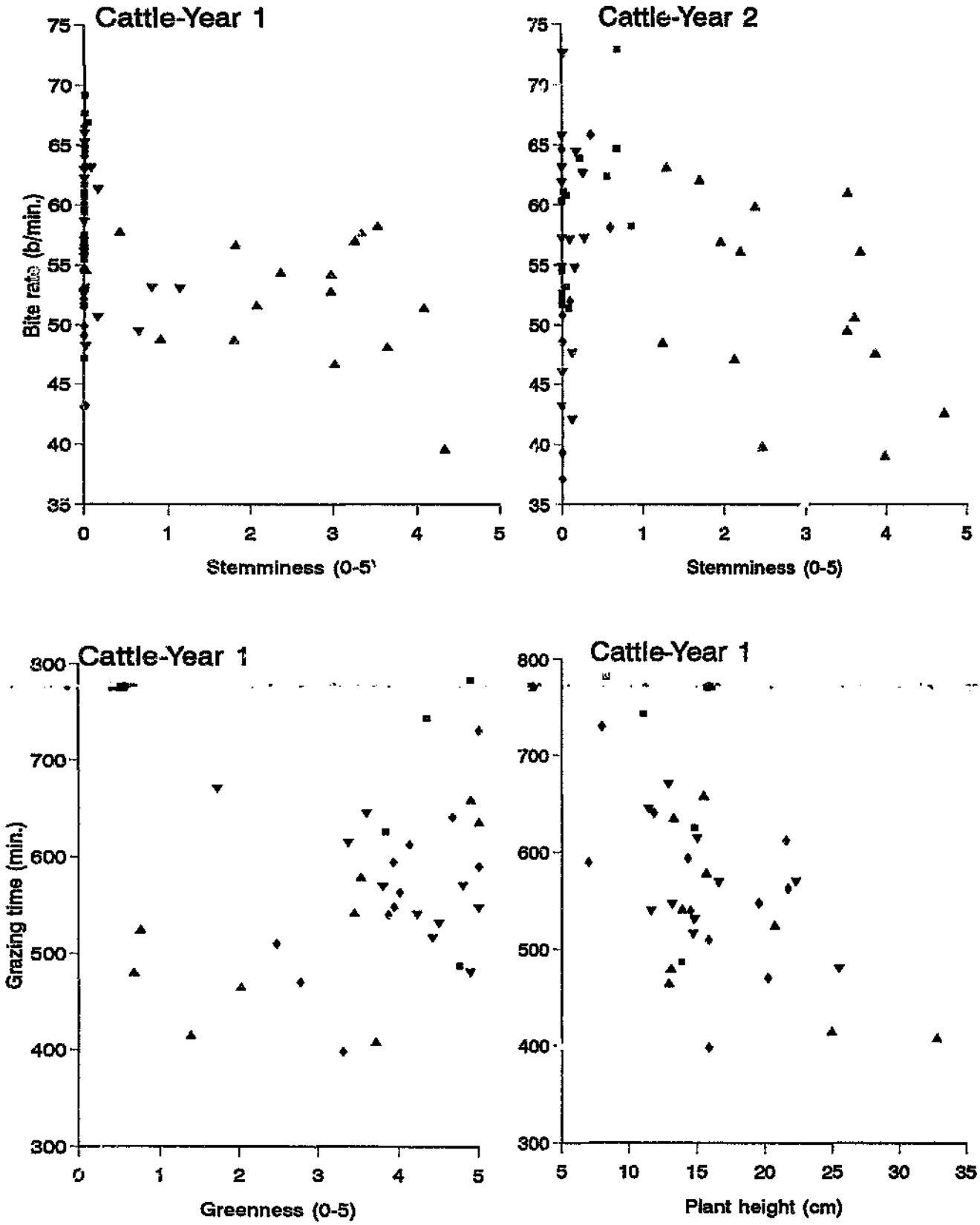

Figure 3.3 The relation between bite rate and stemminess (top) in year 1 and 2, and between grazing time and greenness (bottom) in year 1 for cattle grazing 4 sites on Dohne Sourveld (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep sned camp).

autumn and winter when greenness values were low.

Total daily grazing time was also related to sward structure; grazing time was positively correlated ($P \leq 0.05$) with greenness but negatively correlated ($P \leq 0.0001$) with plant height in year 1 (Table 3.2). A multiple linear regression model accounted for 43 % of the observed variation in grazing time in year 1 (y = 894.04 - 148.91 log height + 20.18 greenness; $r^2 = 0.43$; F = 11.95; $P \leq 0.0001$). Grazing time therefore varied from about 600 minutes per day on short, green swards to less than 400 minutes per day on taller, more senescent swards (Fig. 3.3). Grazing time was also positively correlated ($P \leq 0.05$) with greenness in year 2, but was unrelated to either plant height or herbage density (Table 3.2).

3.4.1.3 Inter-parameter correlations

As expected, the different components of ingestive behaviour in cattle were strongly inter-correlated (Table 3.4). Bite size was negatively related to bite rate ($P \leq 0.0001$) suggesting a dynamic relation between these parameters. Intake rate was strongly correlated with bite size ($P \leq 0.0001$) but not with bite rate which indicates that bite size is the major determinant of IR. Grazing time and biting rate were positively related to each other ($P \leq 0.0001$) but grazing time was negatively correlated with bite size ($P \leq 0.0001$) and IR ($P \leq 0.01$).

Table 3.4 Inter-parameter correlations for the different components of ingestive behaviour for cattle grazing the Dohne Sourveld. Data are from all camps over both year 1 and 2

	Bite rate	Intake rate	Grazing time
Bite size	-0.472***	0.902***	-0.555***
Bite rate		-0.073	0.515***
Intake rate			-0.359**

The different components of ingestive behaviour were also correlated with dietary quality (data from section 2.4), particularly in the second year (Table 3.5). Bite rate and grazing time were positively correlated with dietary CP and IVD while bite size and bite quality were inversely related. However, no relation was evident between bite quality and IR in either year.

Table 3.5 Correlation coefficients for the relation between the different components of ingestive behaviour and dietary in vitro digestibility (IVD) and crude protein (CP) content for cattle grazing Dohne Sourveld in year 1 and 2. Data are from all camps

	Bite size	Bite rate	IR	GT
Year 1:				
IVD	-0.209	0.423***	-0.05	0.388*
CP	-0.271*	0.359**	-0.137	0.274
Year 2:				
IVD	-0.451***	0.768***	-0.143	0.333*
CP	-0.511***	0.529***	-0.038	0.239

3.4.2 Sheep

3.4.2.1 Effect of species composition on ingestive behaviour in sheep

Species composition, expressed as 'camp', had a significant ($P \leq 0.05$) effect (Appendix 3.4) on both sheep bite size and biting rate, but appeared to have no effect on intake rate, expressed per unit body mass (IRM). Average bite size was lowest ($P \leq 0.05$) but, conversely, biting rate was highest ($P \leq 0.05$) in old lands compared to the other three camps (Table 3.6). Sheep appeared to compensate for the small bite sizes in the former camp by biting faster and, consequently, there were no significant differences in IRM between the different camps. Nevertheless, of the four camps, IR and IRM were, on average, lowest in old lands camp (Table 3.6).

Table 3.6 Mean bite size, bite rate, intake rate (IR) and intake rate per unit body mass (IRM) for sheep grazing four sites in the Dohne Sourveld. Within a row, means with the same superscript are not significantly different at the 5 % level

	CAMP			
	Bush	Eragrostis	Lands	Sheep shed
Bite size (g.DM)	0.0884[a]	0.0801[a]	0.0601[b]	0.0879[a]
Bite rate (bites/minute)	56.37ab	54.31[a]	60.36[b]	50.09[a]
IR (g.DM/minute)	4.91[a]	4.21[ab]	3.58[b]	4.66[a]
IRM (g.DM/minute/kg)	0.1033[a]	0.097[a]	0.0785[a]	0.0915[a]

3.4.2.2 Effect of sward structure on ingestive behaviour

At all sites, sheep bite sizes responded strongly to plant height ($P \leq 0.0001$) with the latter variable accounting for the majority of the variability in this component of ingestive behaviour (Table 3.7). In eragrostis camp there was a 5-fold increase in bite size as *T. triandra* height increased from 7 to 12 cm with bite size remaining relatively constant above this level (Fig. 3.4). Similarly, at sheep shed, bite size increased almost 4-fold as plant height increased from 6 to 9 cm (Fig. 3.4) but above this height remained relatively constant. At bush camp, bite size increased quadratically as *T. triandra* increased in height from 6 to about 12 cm but thereafter stayed fairly constant (Fig. 3.4). Bite size also increased with increasing plant height at old lands but the response was linear and, to a certain extent, less marked than in other camps with bite size showing a 4-fold increase over a nearly 6-fold increase in plant height (Fig. 3.4). The uneven distribution of data points, however, casts doubt on this relation and it is possible that bite size was approaching an asymptote at a height of about 15 cm.

Bite size was negatively correlated with greenness in all camps but, conversely, was strongly correlated with stemminess in old lands camp (Table 3.8). Bite size showed a weak positive, but non-significant, relation with herbage density in all camps.

Biting rate declined linearly ($P \leq 0.05$) with increasing sward height at all sites (Table 3.9). Biting rate was positively correlated with green[illegible]d lands camp but showed no consistent response to herbage density (Table 3.8). [illegible]ld lands camp, biting rates also declined with increasing stemminess ($P \leq 0.05$).

Sheep intake rates responded strongly to plant height at all sites (Table 3.7). In eragrostis camp the response was quadratic ($P \leq 0.0001$) with IRM increasing to a maximum at about 15 cm but thereafter tending to decline with increasing height (Fig. 3.5). The two outliers (labelled 1 and 2) were not used in the equation but are of interest; at point 1, sheep achieved high rates of intake by having exceptionally high biting rates. Point 2 represents the same block and sward structure as 3 but was sampled a day earlier when animals were very hungry in cold, wet weather. Here, sheep increased bite sizes and prehension rates to achieve almost double the rate of intake recorded a day later under normal experimental conditions.

At sheep shed camp, a non-linear Michelis-Menton type response ($P \leq 0.0001$) was evident with IRM reaching an asymptote at a height of about 12 cm for *T. leucothrix*

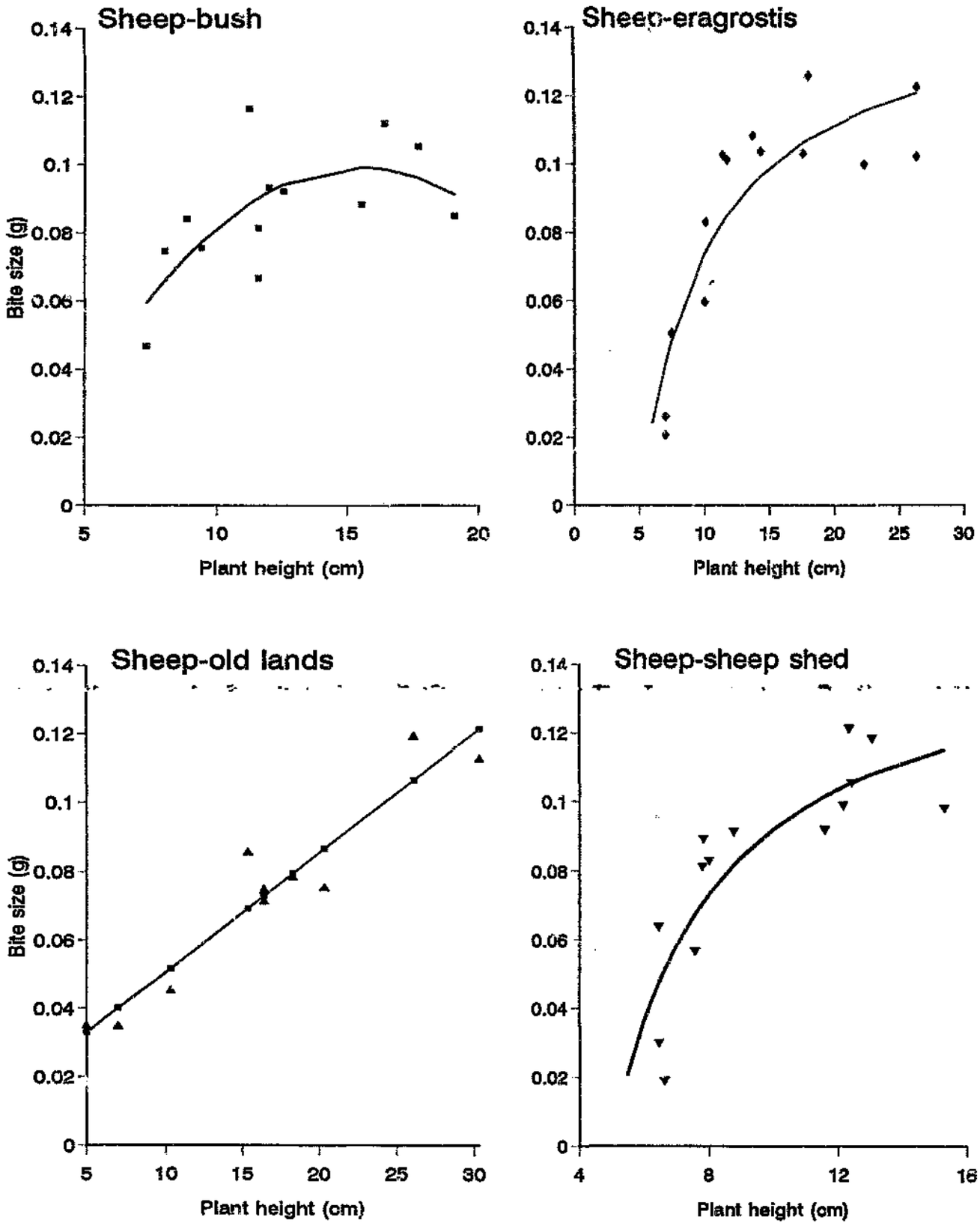

Figure 3.4 The relation between sheep bite size and plant height at four sites in the Dohne Sourveld.

Table 3.7 Models describing the relation between sheep bite size and intake rate per unit body mass, and plant height for 4 sites on the Dohne Sourveld

Camp	Equation	
Bite size		
Bush	$y = 0.04338 + 0.01845x - 0.000595x^2$	$r^2 = 0.47$; *
Eragrostis	$y = 0.1499x/(5.199+x)$	$r^2 = 0.80$; ***
Land	$y = -0.054 + 0.0474x$	$r^2 = 0.85$; ***
Shed	$y = -0.184 + 0.0474x - 0.00191x^2$	$r^2 = 0.77$; ***
Intake rate/Mass		
Bush	$y = -0418 + 0.132x - 0.0103x^2 + 0.000251x^3$	$r^2 = 0.42$;
Eragrostis	$y = -0.365 + 0.084x - 0.00456x^2 + 0.000075x^3$	$r^2 = 0.82$; ***
Land	$y = 0.0971x/(0.9544+x)$	$r^2 = 0.56$;
Shed	$y = 0.1234x/(1.53+x)$	$r^2 = 0.41$;

(Fig. 3.5). While IRM also responded strongly to plant height at old lands, the exact shape of the relation is unclear (Fig. 3.5). At points 1 and 2 animals achieved high rates of intake by selecting large bite sizes but may possibly have been grazing species other than *H. hirta*, which were not measured. If the latter points are outliers, then the relation would approximate a quadratic function with a maximum at a height of about 10 cm for *H. hirta* (curve not shown). Conversely, if these points are retained, as was done in the data analysis, then the response approximates a Michelis-Menton function with IRM reaching an asymptote at a height of about 12 cm for *H. hirta* (Fig. 3.5).

At bush camp IRM also showed a quadratic response to plant height (Fig. 3.5) but the model was not statistically significant (Table 3.7). Here, IRM increased to a maximum at a plant height of about 10 cm but declined thereafter so that intake rates were similar on both very short and very long swards. There was a large amount of variability in these data with animals achieving very different rates of intake at almost identical sward heights. For example, the points marked 1 and 2 represent the same block with an identical sward structure, grazed by the same animals at two grazings only five days apart (Appendix 1). Similarly, at point 3 intake rates were nearly 100 % higher than at 1, but plant heights were almost identical. These differences are difficult to explain but it is speculated that other factors such as the degree of hunger of the animals or the DM content of the herbage could also have affected rates of intake.

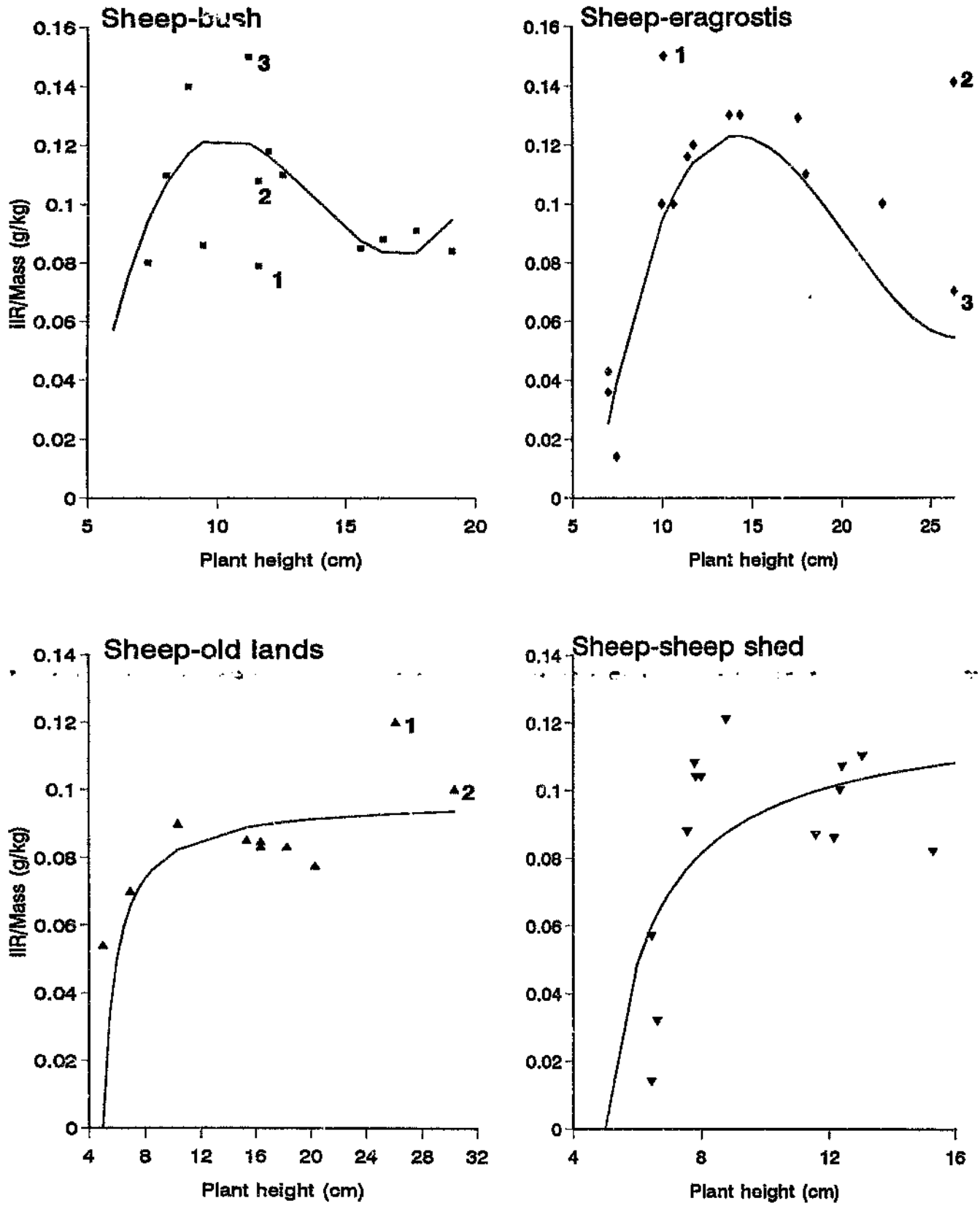

Figure 3.5 The relation between intake rate per unit body mass (IIR/Mass) and plant height for sheep grazing four sites in the Dohne Sourveld.

Table 3.8 Correlation coefficients for the relation between bite size, bite rate and intake rate per unit of body mass (IRM) and different parameters of sward structure for sheep grazing four sites in the Dohne Sourveld

Variable	Bite size	Bite rate	IRM
Bush camp			
Plant height	0.615*	-0.665*	-0.068
Herbage density	0.346	-0.089	-0.280
Greenness	-0.445	0.102	0.088
Eragrostis camp			
Plant height	0.834***	-0.589*	0.649**
Herbage density	0.478	0.048	0.598*
Greenness	-0.393	0.352	-0.283
Old lands camp			
Plant height	0.926***	-0.426	0.801**
Herbage density	0.488	-0.491	0.192
Greenness	-0.832**	0.633*	-0.527
Stemminess	0.893***	-0.671*	0.667*
Sheep shed camp			
Plant height	0.505	-0.689**	0.494
Herbage density	0.428	0.295	0.568*
Greenness	-0.490	-0.044	-0.180

Intake rate was positively correlated with herbage density in some camps but not in others. Generally, IRM showed a negative relation with greenness but was positively correlated with stemminess in old lands camp (Table 3.8).

Table 3.9 Linear regression relationships between sheep biting rates and plant height (log-transformed) at four sites in the Dohne Sourveld

Camp	Regression	r^2
Bush	y = 100.44 - 17.56 log PH	r^2= 0.44; F = 8.72; *
Eragrostis	y = 82.68 - 11.50 log PH	r^2= 0.34; F = 6.92; *
Lands	y = 74.98 - 0.970 PH	r^2= 0.68; F = 14.97; **
Sheep shed	y = 98.95 - 20.45 log PH	r^2= 0.46; F = 10.50; **

3.4.2.3 Effect of body mass on intake rate

Intake rate differed significantly ($P \leq 0.05$) between individual animals with the heaviest sheep having the fastest absolute rate of intake (Table 3.10). Conversely, when intake

rate was expressed per unit of body mass, i.e. IRM, the situation was reversed with the lightest animals consuming significantly ($P \leq 0.05$) more per kilogram of body mass than the heavier sheep.

Table 3.10 Mean intake rate (IR), intake rate per unit body mass (IRM) and average body masses of the 5 sheep used in the experiment. Within rows, means with the same superscript are not significantly different at the 5 % level

	Sheep number				
	222	240	274	429	437
IR (g/minute)	5.47[a]	4.33[b]	4.34[b]	3.82[c]	4.09[d]
IRM (g/minute/kg)	0.0875[a]	0.0945[b]	0.0941[b]	0.0985[c]	0.0964[d]
Mass (kg)	63.78	44.61	43.86	37.25	41.76

3.4.2.1 Inter-parameter correlations

Over all camps, IRM was strongly correlated with bite size ($P \leq 0.0001$) but showed no relation with biting rate (Table 3.11). Conversely, biting rate and bite size were both negatively correlated ($P \leq 0.0001$) with each other.

Table 3.11 Correlation coefficients for the relation between intake rate, intake rate per unit body mass (IRM), bite size and bite rate for sheep grazing Dohne Sourveld. Data are from all camps and all sward structures

	IRM	Bite size	Bite rate
Intake rate	0.844***	0.869***	-0.043
IRM		0.690***	0.078
Bite size			-0.437***

3.5 Discussion

Overall, the effects of species composition on ingestive behaviour in both cattle and sheep were relatively small and inconsistent. Although species composition affected biting rate, intake rate, which ultimately determines animal production, appeared to be largely unaffected by this variable. However, certain between-camp differences were

statistically significant, with intake rates at old lands being generally lower than those achieved at other camps (Tables 3.1 & 3.6). Although these differences appear small, they are likely to be of importance to the grazing animal functioning under various time-energy constraints. For example, a sheep grazing at old lands (IR = 3.58 g DM/min.) would be required to graze an extra 1.5 hours per day to achieve the same total daily DM intake as one at bush camp (IR = 4.91 g DM/min.). For cattle, a similar result would apply in year 2 but not in year 1 where the extra grazing time required would be only 23 minutes. Such differences would incur a direct cost in terms of the extra time and energy expended in grazing and would directly reduce the net energy available for growth and production. Other activities such as rumination, thermoregulation, and for wild ungulates, predator detection and avoidance, are also likely to be adversely affected by increased requirement for grazing time.

An unfortunate limitation of the present results is that intake rates were measured over relatively short periods after animals had just entered a particular block. At this stage, animals could have grazed very selectively consuming only the most palatable and accessible species present. This could have occurred even on swards dominated by unpalatable species such as *E. plana*, masking any potential effect of species composition on ingestive behaviour. Consequently, the effects of species composition on intake may only become apparent over longer time periods due to an increase in search costs associated with locating a steadily diminishing supply of preferred plants and/or a possible decrease in intake rate when animals are forced to graze species in the sward offering a low rate of DM intake. Despite this limitation, the present results do suggest that animals grazing species as diverse as *H. hirta* (old lands), *T. leucothrix* (sheep shed) and *T. triandra* (bush and eragrostis) can achieve fairly comparable rates of intake at similar sward structures.

In comparison to species composition, sward structure had a far greater effect on ingestive behaviour in both cattle and sheep. Of the sward structure variables considered, plant height had the greatest effect on ingestive behaviour in both animals. For sheep, and for cattle in year 1, bite size increased sharply over relatively small increases in plant height, as has been recorded by other workers, e.g. Allden & Whittaker 1970; Wickstrom *et al.* 1984; Hudson & Nietfeld 1985; Penning *et al.* 1991. Bite size increases with plant height as animals prehend a bigger volume of herbage

through an increase in bite depth and bite area (Black & Kenney 1984; Murson *et al.* 1989; Laca *et al.* 1992). When plant height exceeds bite depth, bite size becomes limited by the dimensions of the buccal cavity and, theoretically, should thereafter remain constant (Ungar & Noy Meir 1988; Laca *et al.* 1992). In the present study, sheep attained maximum bite size at plant heights of between 7 to 12 cm, above which bite sizes remained relatively constant. In contrast, cattle bite sizes increased with increasing plant height up to a height of about 25 cm before levelling off. Interestingly, Laca *et al.* (1992) and Gross *et al.* (1993) observed that cattle grazing artificial swards were able to increase their bite size beyond the point where it should have been restricted by buccal cavity dimensions, presumably because they could prehend large masses of herbage with their tongues and then slowly work them into their mouths as they chewed.

In contrast with other studies (Stobbs 1973b; Black & Kenney 1984; Laca *et al.* 1992) herbage density had no apparent effect on bite size in cattle while its effects in sheep were ambiguous. This possibly results from the tongue-sweeping method of grazing in the former animals which may serve to concentrate forage before ingestion (see Laca *et al.* 1992) but is more likely attributable to problems experienced with measuring herbage density in the present study. First, estimates of herbage mass were extremely variable (Appendix 1), casting suspicion on the reliability of the resultant density measurements. Second, herbage density was expressed and measured on a gross sward basis while a more useful variable might have been the green leaf density of certain target species within the sward. Despite the present results, it may therefore be assumed that bite size could be restricted by low levels of herbage density on sourveld, particularly on short, recently-burnt swards where tiller densities are low (pers. obs.).

Bite size was inversely correlated with sward greenness with bite sizes tending to be larger on more senescent swards. This occurred with both animal species although it must be emphasised that the range of greenness values encountered by sheep (3.5 - 5) was considerably narrower than that encountered by cattle (0.01 - 5). The present observations are therefore more likely a reflection of the fact that the greenest swards were also the shortest where bite size would be restricted by plant height rather than by greenness *per se*. Nevertheless, it is surprising that bite sizes did not decline on

senescent swards as animals might be expected to become more selective and reduce bite sizes as the availability and accessibility of green leaf declined. Surprisingly, stemminess appeared to have a positive effect on bite size in both cattle and sheep. Stems would be expected to reduce leaf accessibility, particularly to cattle with their relatively poor selective ability (Arnold 1962; O'Reagain & Mentis 1989). Although stemminess levels were generally low, the density of stems should have been sufficiently high at old lands to exert any potential restriction on bite size. However, plant height and stemminess were strongly intercorrelated (Table 2.7), so the effects of increased bite depth on stemmy swards may have outweighed any reduction in leaf accessibility. Surprisingly, cattle frequently consumed *H. hirta* stems rather than attempting to avoid them (pers. obs.), conceivably allowing them to maintain bite size at the expense of bite quality. Sheep possibly maintained bite sizes on stemmy swards because their small mouths allowed them to harvest leaves clustered at the base of stemmy *H. hirta* tussocks.

Biting rate was inversely correlated with plant height in both animals, in agreement with published data, e.g. Allden & Whittaker 1970; Jamieson & Hodgson 1979; Black & Kenney 1984; Burlison *et al.* 1991; Penning *et al.* 1991. This relation was particularly pronounced with sheep and possibly reflects an increase in selectivity as herbage availability increases (Smith 1961b; Hamilton *et al.* 1973; Langlands & Sanson 1976) coupled with the fact that sheep appear to have an innate difficulty in prehending longer leaves (pers. obs.). The decline in cattle biting rates with decreasing sward greenness (Fig. 3.3) conflicts with the findings of Stobbs (1974), that cattle biting rates increase on mature, senescent swards. This discrepancy is difficult to explain but probably reflects differences between the two studies in other sward structure variables. In the present study cattle presumably decreased biting rates in order to be more selective and maintain dietary quality on more senescent swards. Although sheep biting rates were also positively related to sward greenness the relationship was weak (Table 3.8). However, this probably reflects the inherent selective ability of these animals rather than an apparent indifference to maintaining dietary quality.

Biting rates were negatively related to stemminess in both cattle and sheep, as found by Ruyle *et al.* (1987) for cattle grazing *Eragrostis lehmanniana* tufts. Stemminess probably reduces biting rates through increasing the search and handling

time associated with each bite. Surprisingly, sheep biting rates appeared to be more vulnerable to stemminess than those of cattle (O'Reagain 1993, unpublished data). However, this may be because sheep appeared to continue seeking out leaf when swards were stemmy while cattle started consuming large mouthfuls of stem (pers. obs.).

Intake rate in both animals increased sharply with increasing plant height, as has been documented in other studies (Allden & Whittaker 1970; Black & Kenney 1984; Hudson & Nietfeld 1985; Hudson & Frank 1987; Penning *et al.* 1991; O'Reagain 1990). Cattle showed a curvilinear functional response, at least in year 1, with an asymptote occurring at a plant height of about 20 cm. This is in general agreement with the classic Type II functional response as described by Holling (1959). Below the asymptote, intake would be restricted by bite size and/or the search time required to find a bite (Spalinger & Hobbs 1992). Conversely, bite size is at a maximum above the asymptote with intake rate being restricted by the time required to process, i.e. chew and swallow, each bite (Spalinger & Hobbs 1992).

Sheep intake rates also showed a curvilinear response to plant height, reaching a peak at a height of about 7-12 cm. However, in some camps (Fig 3.4) the relation was quadratic with intake rates tending to decline as plant height increased above this level. This response is unexpected and represents a marked deviation from the Type II functional response documented for other grazing ungulates, e.g. Allden & Whittaker 1970; Wickstrom *et al.* 1984; Hudson & Nietfeld 1985; Hudson & Frank 1987; Laca *et al.* 1992. The present response may be attributed to the inverse relation between bite size and biting rate, and their response to plant height. In sheep, bite size generally increased with plant height to an asymptote but remained constant above this level (Fig 3.4). Conversely, biting rates showed a constant linear decline with increasing plant height with no asymptote or levelling off being evident. Consequently, once maximum bite size had been attained this variable would have remained constant while bite rates would have continued to decline as sward height increased, depressing intake rates on taller swards. Bite rates were probably reduced on these swards, first, because the lower quality encountered under these conditions necessitated increased chewing times per bite as found by Penning *et al.* (1991) and, second, because of the increased search and handling times required to locate and prehend highly dispersed items of food in these relatively low quality swards.

This highlights a shortcoming in the application of the functional response to grazers, i.e. the failure to account for the interaction between food quality and availability. While unimportant for predators where prey quality is constant and density independent, this interaction is critical for grazers where a general inverse relation between forage quality and availability exists (McNaughton 1984). The importance of this third quality dimension to the functional response has possibly been overlooked in the past either because the effects of quality were deliberately controlled, e.g. Black & Kenney 1984; Laca *et al.* 1992 or because the work was conducted under temperate (Allden & Whittaker 1970; Wickstrom *et al.* 1984; Hudson & Nietfeld 1985; Hudson & Frank 1987) or semi-arid (Short 1985) conditions where the quality:quantity dichotomy is less pronounced. It is therefore argued that a quadratic functional response is likely to be common for grazers on humid, low-quality grasslands like sourveld. Under these conditions, intake rate will be restricted by bite size when herbage availability is low but will be limited by cropping rate (biting rate) when availabilities are high due to a general decline in the quality and accessibility of herbage.

Significantly, animals on a number of occasions achieved substantially higher rates of intake than would be expected purely on the basis of sward structure, by taking bigger bites and/or biting faster. As an example, at eragrostis camp, sheep which were exceptionally hungry attained IR nearly double those achieved when relatively satiated under identical sward conditions (Section *3.4.2.2*). This confirms the assertion that the physiological status of an animal is an important determinant of foraging behaviour (Mangel & Clark 1986) which will also reflect previous nutritional history (Langlands 1968), reproductive status (Arnold 1966) and growth stage (Langlands 1968).

The increased rates of intake observed under certain conditions also suggest, in agreement with Owen-Smith (1993), that animals normally forage at rates considerably lower than their potential. If so, why do animals behave in this way? Possibly, intake can only be increased at the expense of selectivity and dietary quality. Although Greenwood and Demment (1988) noted that fasted cattle could increase intake rates without sacrificing quality, the experiment was conducted on rye-grass which is markedly different from the poor-quality, heterogeneous swards under consideration. Significantly, mastication bites were reduced in the latter study (Greenwood & Demment *loc. cit.*) possibly increasing particle size and depressing passage rates.

Alternatively, animals may not forage maximally because grazing time constraints are usually non-limiting, being significant only under extreme conditions (Owen-Smith 1993). Increased foraging rates may also be energetically inefficient or may interfere with vigilance and scanning activities leading to increased attrition by predators (Fitzgibbon 1989).

For sheep, intake was also dependent upon body mass with the largest sheep having the highest absolute rate of intake but the smallest intake per unit body mass. This is in general agreement with Kleiber's law (Kleiber 1961) but also reflects differences in growth stage with adults having only to provide for maintenance while younger sheep also have to meet the energetic requirements for growth (Langlands 1968).

A dynamic interaction between the different components of ingestive behaviour existed in both animals. Biting rate varied inversely with bite size in cattle and sheep in agreement with reports for these and other grazing ungulates (Allden & Whittaker 1970; Stobbs 1973b; Chacon & Stobbs 1976; Jamieson & Hodgson 1979; Wickstrom *et al.* 1984; Hudson & Nietfeld 1985; Spalinger *et al.* 1988; O'Reagain 1990). Animals may increase biting rates to compensate for small bite sizes and thereby maintain intake rates (Chacon & Stobbs 1976; Hodgson 1981). Although this strategy may be successful over fairly narrow limits (Allden & Whittaker 1970; O'Reagain 1990), it generally fails to maintain intake when bite sizes are restricted (Chacon *et al.* 1978; Jamieson & Hodgson 1979; Black & Kenney 1984; Wickstrom *et al.* 1984). Increased biting rates may also carry costs such as increased energy expenditure, and decreased digestive efficiency through a reduction in the number of chewing bites (Greenwood & Demment 1988). An alternative explanation is that biting rate is not under the volitional control of the animal but is indirectly determined by bite size through its effects on the ratio of cropping to chewing bites: large bites require more chewing and hence depress cropping rates through competition for jaw movements (Spalinger & Hobbs 1992; Shipley & Spalinger 1992; Gross *et al.* 1993).

Cattle also extended grazing times on shorter swards, presumably in an attempt to compensate for the effects of reduced bite size on intake (Table 3.4). However, increased grazing times are generally only partially successful in maintaining long-term intake rates and can seldom be extended beyond 13 hours (Arnold 1960; Allden 1962;

Allden & Whittaker 1970; Stobbs 1973b; Chacon *et al.* 1978; Hudson & Frank 1987). Bite size is therefore the major determinant of intake (Stobbs 1973b; Chacon *et al.* 1978; Chacon & Stobbs 1976; Hudson & Frank 1987; Greenwood & Demment 1988) with grazing animals having only limited ability to compensate for restrictions on this variable by increasing biting rates or grazing times.

An interaction between ingestive behaviour and dietary quality in cattle was also evident (Table 3.5). The inverse relation between bite size and bite quality found here and in other studies (Chacon *et al.* 1978; O'Reagain 1990) highlights the trade-off between quality and intake which may occur with patch and plant part selection in heterogeneous swards. In contrast, biting rates and grazing time were positively correlated with bite quality; high quality forages require less chewing and ruminating time (De Boever *et al.* 1990) possibly allowing more cropping bites and an extension of grazing times. Given that sward structure also had a major effect on dietary quality it may be argued that the above relations are coincidental. However, it is unlikely that ingestive behaviour is independent of dietary quality, particularly in the heterogeneous swards under consideration. Thus when high quality food items (plant species and/or plant parts) are scarce and highly dispersed the animal faces a trade-off between intake rate and diet quality but the exact extent of this trade-off will vary according to the quality of the food items, their degree of dispersion in the sward and, in particular, the 'state' (*sensu* Mangel and Clark 1982) of the foraging animal.

Present estimates of bite size and intake rate are comparable with published values. For sheep, the range of intake rates measured (1.5 to 7 g DM per minute) are directly comparable to those recorded by Allden and Whittaker (1970) of 1.0 to 7.1 g DM/minute for lambs grazing rye-grass swards of different heights. Similarly, Penning and Hooper (1985) reported intake rates of 2.2 to 6.4 g DM per minute for ewes grazing rye-grass with sward surface heights varying from 3 to 12 cm. The present results are also in accordance with those of Penning *et al.* (1991). Estimates for cattle are also comparable with those from other studies (Stobbs 1973a; Chacon *et al.* 1978; Dougherty *et al.* 1989; Greenwood & Demment 1988). For example, Greenwood and Demment (1988) reported an average bite size and intake rate respectively of 0.47 g and 26.75 g DM/minute for fasted steers on rye-grasses. Although relatively high, these figures are within the range of bite sizes (0.07 - 0.6 g) and intake rates (6 - 28 g DM/min.) recorded

in the present study. However, the *Setaria sphacelata* pastures of Chacon and Stobbs (1976) are probably closer to sourveld conditions; these authors recorded bite sizes of 0.083 to 0.322 g and intake rates of 6.6 to 20 g DM/minute which are directly comparable to present results (Fig. 3.1).

However, present measurements of ingestive behaviour are possibly higher than would be expected under normal field conditions as animals were fasted and sampling was restricted to relatively short periods of grazing (Stobbs 1974; Dougherty *et al.* 1987; Greenwood & Demment 1988). Conversely, measurements of bite size and intake rate in sheep may be underestimates as the adjustment for insensible weight loss was based on resting rather than grazing animals (Penning & Hooper 1985). Cattle bite sizes and intake rates are also likely to be underestimates given the variability in recovery rates of samples from fistulated animals (Stobbs 1973a). On the basis of the work of Stobbs (1973a) it is suggested that present estimates of bite size and intake rate in cattle underestimate actual values by about 20-30 %.

The lack of a relation between sward structure and cattle bite size and intake rates in year 2 is perplexing (Fig. 3.1). This could be attributed to experimental error in that the variability in the recovery of fistula samples exceeded differences due to sward structure, but this is unlikely as relatively precise data were obtained in year 1 with the same experimental animals. A more realistic explanation is that, due to spatial heterogeneity, animals grazed different parts or levels of the sward to those actually being measured. Despite the small experimental units used and the even grazing pressure applied, a fairly distinct grazing mosaic was beginning to emerge in some blocks by year 2 (pers. obs.). Although measurements were concentrated on the more palatable species in an attempt to avoid the problem of selectivity, it is possible that structurally distinct sub-populations within individual species arose with time through differences in the defoliation history of individual tufts. For example, within any particular species, tufts grazed early in the season would tend to be grazed again while undefoliated tufts would tend to grow out and become moribund and would probably remain ungrazed throughout the year. These differences would become more pronounced over time, creating a gradient from short, green, grazed tufts to tall, senescent, ungrazed individuals.

This emphasizes the problem associated with both the concept and measurement

of sward structure in multi-species systems selectively defoliated by grazing animals, i.e. in such a system what is the 'average' sward structure and at what level or scale should it be measured ? Even if measurements are concentrated on the palatable species, the average structure of a species is likely to be different to the subset of individuals in the species that the animal actually grazes. These differences are likely to be minimal immediately after a fire where defoliation is unselective, but are likely to become pronounced with time.

In conclusion, it is apparent that species composition in sourveld had a relatively small effect on intake rate in both cattle and sheep. Nevertheless, these differences could translate into an extra 10 % requirement in grazing time which, under certain conditions, could be of major importance for the grazing animal. Species composition may also be of importance over longer time periods when animals are forced to consume other, less accessible species or tufts. In contrast to this variable, sward structure, and in particular plant height, had a much greater effect, with intake rate increasing 3- to 6-fold in both animal species, over a 2- to 3-fold increase in plant height. Maximum intake rates were achieved at heights of 7-12 cm and 20-25 cm for cattle and sheep respectively. Sward structure can be easily manipulated through grazing management and the potential therefore exists for the grazier to manipulate this variable so as to maximise intake rates. This could be done by closely monitoring sward growth rates and grazing swards at heights where intake rates for the particular animal under consideration, are maximised. Further, by using short, intense periods of defoliation to graze the sward down, a dense, even regrowth for the following grazing period will be ensured. Contrary to current recommendations, cattle and sheep should not be grazed together due to differences in the optimum sward height for the two animals. However, it is suggested that they follow each other through the grazing rotation with camps being alternately grazed by each species.

3.6 Conclusions

3.6.1 Species composition had a relatively minor effect on the rate of dry matter intake by both cattle and sheep but could possibly affect intake over longer grazing periods than those used in the present experiment.

3.6.2 Sward structure had a far greater effect on the ingestive behaviour of cattle and sheep with plant height being the most important sward structure variable.

3.6.3 Bite size and intake rates increased with plant height in both animals. Conversely, biting rates, and for cattle, grazing time, decreased with increasing plant height.

3.6.4 Cattle intake rates increased over the range of plant heights measured and reached a maximum at a height of about 20-25 cm.

3.6.5 For sheep, there was evidence of a curvilinear functional response with intake rates being maximised at a height of about 7-10 cm. On short swards intake was restricted by bite size while above this optimum, intake was restricted by biting rate.

3.6.6 Ingestive behaviour was related to dietary quality in cattle. Bite size was negatively correlated, and biting rate and grazing time positively correlated, with dietary CP and IVD.

3.6.7 In both cattle and sheep there was a dynamic interaction between the different components of ingestive behaviour with bite size being negatively correlated with biting rate and grazing time. Intake rate was strongly correlated with bite size but not biting rate. This suggests that bite size is the overriding determinant of intake.

3.6.8 For sheep, body size was an important determinant of intake. Absolute intake rates (g/minute) increased but relative intake rates (g/minute/kg body mass) decreased with increasing body mass.

CHAPTER 4

SEQUENCE OF SPECIES SELECTION AND THE FREQUENCY AND SEVERITY OF TILLER DEFOLIATION BY CATTLE AND SHEEP ON DOHNE SOURVELD

4.1 Objectives

The specific objectives of this experiment were to:

(i) determine the sequence of species selection by cattle and sheep through a period of occupation in a camp on Dohne Sourveld;

(ii) relate this sequence to concomitant changes in dietary quality and ingestive behaviour;

(iii) compare the frequency and severity of tiller defoliation by cattle and sheep.

4.2 Introduction

Animals on rangeland commonly encounter a diversity of plant species which vary widely in their acceptability to the grazing animal. While the physical and chemical factors which determine which species are selected have frequently been investigated, e.g. Theron and Booysen (1966); O'Reagain (1993), relatively little is known about *how* they are selected. In particular, the way foods (species) are added to or excluded from the diet under conditions of changing food availability, and the relative allocation of time and energy by the animal to seeking out and consuming these different foods, are poorly understood.

This problem is of particular relevance in rotational grazing systems. Here, animals are confined at relatively high stocking densities to small, uniform camps where the relative availability of different foods (species) changes rapidly over time through the selective grazing of the more preferred species in the sward. Animals are therefore confronted with a series of foraging decisions about when to stop rejecting and start consuming species of lower acceptability when encountered. This is manifested in the form of an order or sequence of species selection over the grazing period as animals are forced to include species of lower and lower preference in their diet.

The sequence of species selection over the grazing period should also directly

affect animal production through its effects on dietary quality and intake, as the animal grazes species differing in nutritive value and potential intake rate. Conversely, if these latter variables are known for different species and if the sequence and manner of species selection is also known, then it should be possible to construct dynamic, predictive models of animal production on swards of different species composition.

Knowledge of the sequence of species selection over the grazing period is also necessary to determine the effectivity of different grazing systems and to predict their potential impact on rangeland. Many currently recommended systems assume patterns of species selection which are largely untested (O'Reagain & Turner 1992). Such systems may therefore be incapable of achieving their stated objectives and may possibly result in range degradation.

The sequence of species selection over the grazing period has been investigated for cattle (Daines 1980; Danckwerts *et al.* 1983; O'Reagain & Mentis 1989a) and for cattle and sheep grazing together (Stoltsz & Danckwerts 1990). In all cases a distinct sequence of species selection was observed; generally, preferred species and, to a lesser extent, those of intermediate acceptability are grazed first but less-preferred or avoided species are only consumed after the more-preferred species in the sward have been extensively regrazed (Daines 1980; Danckwerts *et al.* 1983; O'Reagain & Mentis 1989a; Stoltsz & Danckwerts 1990). The extent to which this sequence applies to sheep is, however, unknown and warrants investigation.

The primary objectives of the present study were therefore (i) to determine the sequence of species selection by cattle and sheep over the grazing period, and (ii) to relate this sequence to concomitant changes in dietary quality and ingestive behaviour over the same period.

Aside from the sequence of species selection, the frequency and intensity of tiller defoliation over the grazing period are also of importance as these directly affect plant growth and survival. For example, *Themeda triandra*, a desirable species, has been shown to be intolerant of frequent, severe defoliation (Danckwerts 1984). In this context, sheep are considered to be relatively detrimental to rangeland (O'Reagain & Turner 1992) as they reputedly defoliate tillers more frequently and severely than do cattle. Unfortunately, while the intensity and frequency of tiller defoliation has been investigated separately for cattle (e.g. Gammon & Roberts 1978a; Gammon & Roberts

1978b; Gillen *et al.* 1990) and for sheep (e.g. Hodgson 1966; Hodgson & Ollerenshaw 1969) no direct cattle:sheep comparison exists. The assertion that sheep defoliate tillers more frequently and severely than cattle is therefore unsubstantiated.

The secondary objectives of the study were therefore to test the hypotheses that (i) the frequency of tiller defoliation and, (ii) the severity of tiller defoliation, are greater under sheep than under cattle grazing. These hypotheses were taken to be refuted if a significant ($P \leq 0.05$) difference was not detected in the severity and intensity of tiller defoliation between the two animals.

4.3 Procedure

4.3.1 Study area

The study was conducted at the Dohne Agricultural Development Institute situated 10 km north of Stutterheim, in the Dohne Sourveld (Acocks 1988). A more detailed description of the study area and experimental conditions is given in section 2.3.1.

4.3.2 Experimental design

4.3.2.1 *General*

Data were collected at the four sites described in section 2.3.2. Briefly, these were a site which had a previous history of overgrazing (eragrostis camp), a site which had been well managed in the past (bush camp), a site which had a history of under-utilisation (sheep shed camp), and a previously cultivated land which had reverted to a secondary grassland community (old lands camp). At each site two blocks of similar sward structure were selected and grazed by either cattle or sheep. Blocks were grazed for periods of six days (five days for old lands) starting on 3 February (sheep shed), 24 February (eragrostis), 16 March (old lands) and 30 March (bush) 1992. An attempt was made to simulate a period of occupation in a rotational grazing system as this is the recommended form of grazing management in southern Africa (O'Reagain & Turner 1992).

Treatments were stocked with either 18 Dohne Merino wethers (average mass 40 kg) or 3 Bonsmara steers (average mass 400 kg). It was assumed that 6 sheep provide a similar stocking pressure in terms of metabolic mass, i.e. mass $^{0.75}$, to 1 steer (Meissner 1978). All animals had been born and raised on sourveld and were familiar

with the grass species investigated. Animals were supplemented with a salt-phosphate lick in accordance with recommendations for the area. In between experimental periods animals grazed range similar to the different study areas.

4.3.2.2 *Plant measurements*

At each site, three tussock grasses were selected, which, on the basis of previous experience (O'Reagain & Mentis 1989a; O'Reagain 1993; O'Reagain unpublished data), were taken to represent preferred, less-preferred and avoided species in terms of the preference exhibited for them by cattle and sheep. In order of decreasing preference, species chosen were *Andropogon appendiculatus*, *Tristachya leucothrix* and *Alloteropsis semialata* subsp. *eckloniana* (sheep shed camp), *A. appendiculatus*, *Themeda triandra* and *Eragrostis plana* (eragrostis camp), *T. triandra*, *T. leucothrix* and *A. semialata* (bush camp), and *Hyparrhenia hirta*, *Heteropogon contortus* and *E. plana* (old lands camp). Species nomenclature follows Gibbs Russell *et al.* (1990).

In each block, a single transect was laid out for each of the three species being investigated, with twenty-five tussocks of the species being located at regular intervals along the transect. The three transects ran parallel to each other about 2 m apart. Due to the small size of the blocks (25 x 50 m), it was assumed that grazing pressure would be equal over the whole area and that the frequency and intensity of tiller defoliation would be independent of transect position.

Plants were identified using numbered, colour-coded, wire tags inserted into bare ground about 10 cm from each tussock. In each tussock, a single ungrazed, vegetative, green tiller was selected and tagged at its base with a plastic-coated wire ring. This gave a total of 25 marked tillers of each of the three species in each block. Tillers were chosen at random from all possible locations within a tussock and varied widely in height within a species.

Immediately before a site was grazed, the height (extended) of the tallest leaf of each tiller was measured. Tillers were thereafter inspected daily at 14:00 during the grazing period and the presence and height of any defoliation recorded. The grazed edges of defoliated tillers were marked with typist's correcting fluid (Tippex) to distinguish subsequent defoliations. The latter compound appears to have no effect on tiller selection (Gammon & Roberts 1978a; Danckwerts *et al.* 1983). On each day and

at the end of the grazing period the total number of tillers which had been defoliated once, twice, three times or were undefoliated, was computed for each species. The percentage (%) of tiller removed was calculated according to the formula:

% Tiller removed = (Initial tiller height/(Initial tiller height-Final defoliation height)) x 100.

Tillers which had been only partially or unevenly defoliated were not included in this calculation. In all cases, defoliations could be directly attributed to either cattle or sheep as indigenous grazing ungulates were absent.

4.3.2.3 *Animal measurements*

Fistula samples were collected daily at 06:30 on the first five days of occupation in each camp, using two oesophageally fistulated cattle and sheep. Dietary crude protein and *in vitro* digestibility were estimated as described in section 2.3.5. Bite size, biting rates and intake rates for both cattle and sheep were measured as described in section 3.3.4.1.

4.3.3 Statistical analysis

The study was not replicated *per se* as it was considered more important to repeat the experiment at different sites rather than a number of times under identical conditions, i.e. it was assumed that greater weight could be attached to the outcome if similar results are obtained from different sites with different combinations of species.

Data for each camp (site) were analyzed separately. The sequence of species selection, i.e. the order in which species were grazed over time by cattle and sheep, was analyzed for each site using logistic regression (GENSTAT 1984). On any day in the grazing period, tillers could be either grazed or ungrazed, i.e. the data were binomially distributed. This necessitated the use of the logit link function (Sokal & Rohlf 1981, p.764) which provides the log-odds that any subject will have some characteristic relative to any other characteristic. The model was based on the total number of tillers defoliated of each species on each day of a grazing period and included terms for 'day', 'animal', and 'grass species' as well as 'day by animal' and 'grass by animal' interactions. Overall goodness of fit was based on an analysis of deviance and significance of model terms on Students t-test. For each model, sheep and a single

grass species were used as a baseline against which all other terms and interactions were compared. Baseline species were *T. triandra, H. hirta, T. leucothrix* and *T. triandra* for bush, old lands, sheep shed and eragrostis camps respectively.

In the model the term 'sequence' refers to the overall probability of tillers being defoliated with time in a camp, 'animal' refers to the probability of defoliation under cattle relative to sheep grazing and 'grass' to the overall probability of that grass species being defoliated relative to the baseline species. The 'sequence by cattle' interaction refers to the probability of a species being defoliated over time by cattle relative to sheep, while the 'animal by grass' interaction refers to the probability of cattle choosing a particular species over the baseline species, relative to sheep.

The total frequency of tiller defoliations, i.e. the number of tillers defoliated zero, once, twice or three times, of each grass species over the grazing period under cattle and sheep grazing was analyzed using loglinear analysis (SAS 1991) which primarily tests for the presence of interactions in the data (Sokal & Rohlf 1981). Grass species (S) and animal (A) were used as 'state' variables while the number of tillers in each defoliation class (F), i.e. defoliated once, twice or three times, were used as 'fate' variables (Caswell 1989, p.34). In these analyses, the null hypothesis tested was that the frequency of defoliation was independent of the species of grass and animal type, i.e. cattle or sheep. Both partial and saturated analyses were undertaken but greater significance should be attached to the former because the other factors are taken into account when an individual factor is tested. The partial analyses involved fitting a series of models containing various combinations of state-fate interactions to the data. The significance of a particular interaction is then given by the significance of the model from which it has been excluded (Caswell 1989).

Due to the relatively small sample sizes the possibility existed of significant cattle-sheep differences being obscured in the general loglinear analyses. The G-test (Sokal & Rohlf 1981) was therefore used to compare the frequency of tiller defoliation (i) for individual grasses under cattle and sheep grazing and (ii) for different grass species in the same camp under cattle and sheep grazing, respectively.

Comparison of the height of tiller defoliation and the % of tiller removed under cattle and sheep grazing was based on a factorial design using 'animal' as a treatment and grass species as a factor (GENSTAT 1984). Individual tillers were used as

replications and, consequently, the trial is pseudo-replicated (Hurlburt 1981). Where necessary, percentage data were transformed using an angular transformation.

Differences in dietary CP, IVD, bite size, bite rate and intake rate between days within a period of occupation in a camp were compared in an analysis of variance (ANOVA; SAS 1991) using individual animals as replicates.

4.4. Results

4.4.1 Sequence of species selection

In bush camp, sheep first selected *T. triandra* and *T. leucothrix*, defoliating more than 70 % of these tillers in the first two days of occupation in the camp (Fig. 4.1). Thereafter, many of these tillers were regrazed but *A. semialata* was only really utilised after day three when the majority of *T. triandra* and *T. leucothrix* tillers had been defoliated one or more times. With cattle, all three species experienced similar rates of utilisation with regrazing of tillers occurring from day three onwards. Tillers were significantly ($P \leq 0.01$) less likely to be defoliated under cattle than under sheep grazing (Table 4.1), as indicated by negative t-value (-3.33) for the cattle term in the regression model. However, the probability of tillers being defoliated with time over the grazing period was the same for both animals (sequence'cattle'= -0.14). There were significant differences both between, and within, cattle and sheep in their preferences for the different grass species. In general, animals were less likely to defoliate *A. semialata* but more likely to defoliate *T. leucothrix* than *T. triandra*. Conversely, *A. semialata* (t= 7.86) were far more likely, and *T. leucothrix*(t= -2.98) less likely, to be defoliated under cattle, than under sheep grazing (Table 4.1).

In eragrostis camp, both animals selected strongly for *A. appendiculatus* and *T. triandra* (Fig. 4.1) with many of these tillers being subsequently regrazed. *Eragrostis plana* was largely avoided and only grazed near the end of the six-day study period. Sheep were more likely to graze tillers near the end of a period of occupation than cattle (Table 4.1), indicating that they are more likely to resist grazing avoided species such as *E. plana*. There were major differences between species in the extent to which they were grazed (Table 4.1) but cattle were less selective in terms of species than sheep, as indicated by the positive, significant ($P \leq 0.01$) 'cattle' term in the regression model.

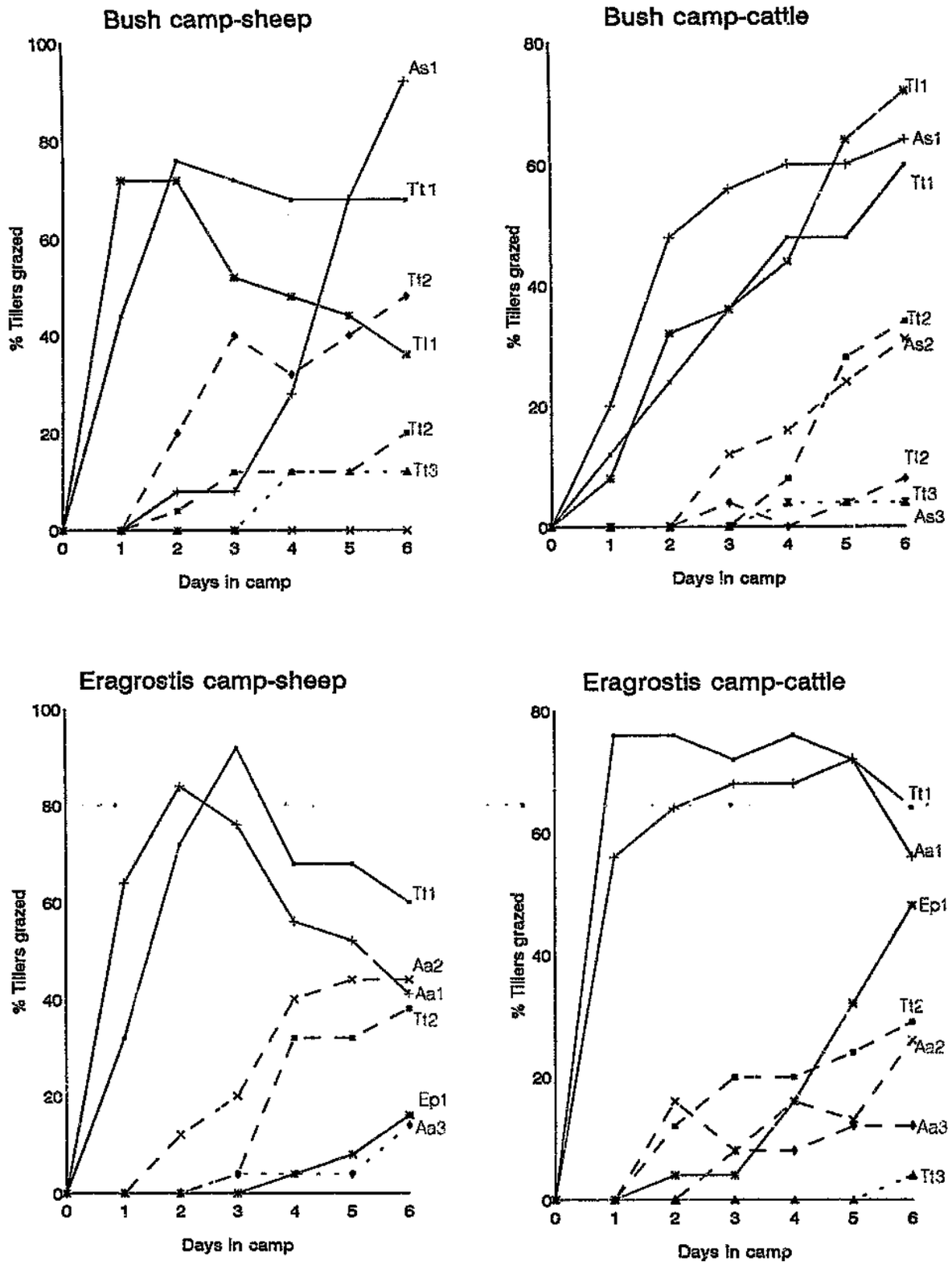

Figure 4.1(a) Percentage of tillers grazed once (solid line), twice (dashed line) or three times (dotted line) over a 6-day grazing period by cattle and sheep at bush and eragrostis camps (Aa = *A. appendiculatus*, As = *A. semialata*, Ep = *E. plana*, Hc = *H. contortus*, Hh = *H.hirta*, Tl = *T. leucothrix*, Tt = *T. triandra*).

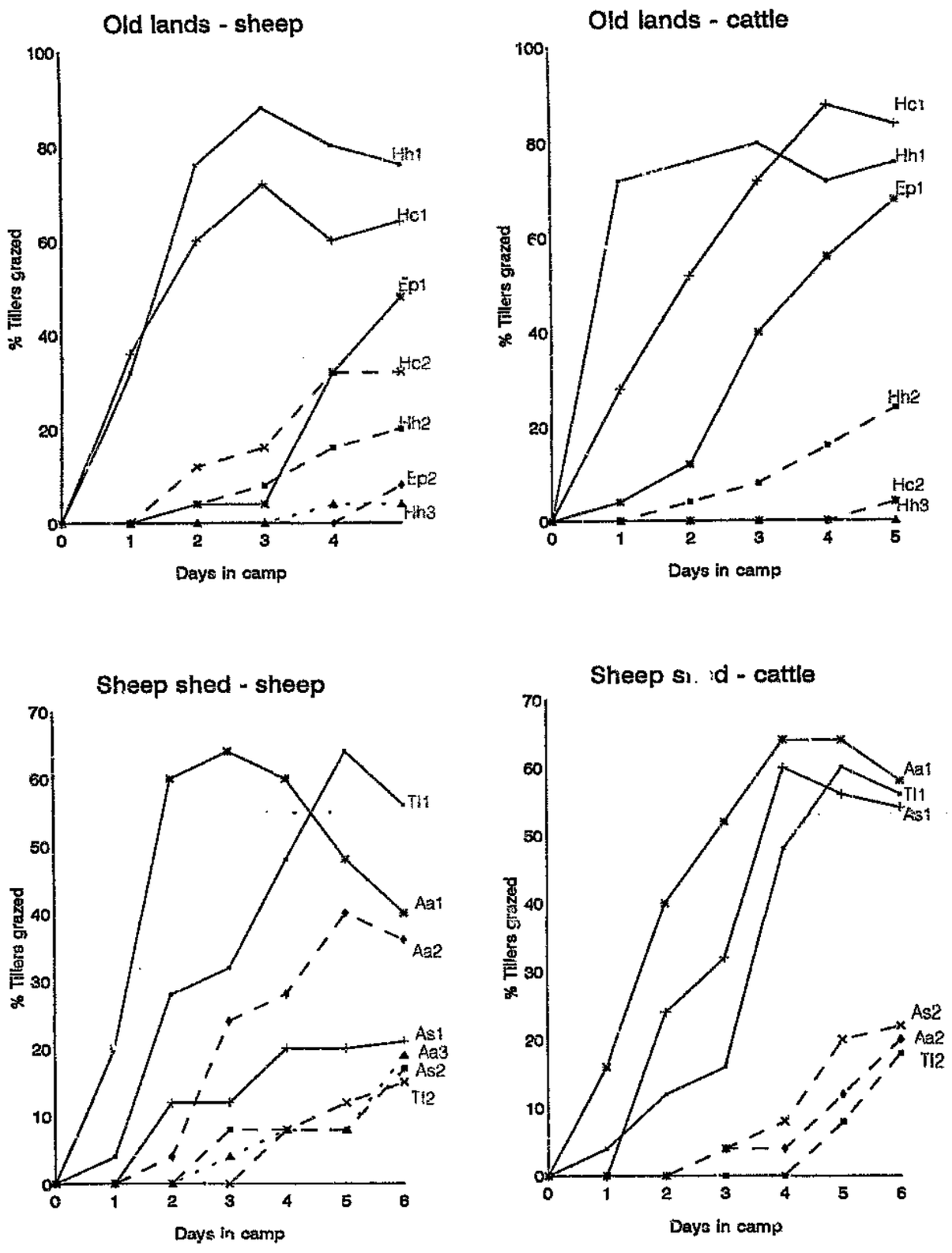

Figure 4.1 (b) **Percentage of tillers grazed once (solid line), twice (dashed line) or three times (dotted line) over a 6-day grazing period by cattle and sheep at old lands and sheep shed. Species codes as for Fig. 4a.**

Table 4.1 Model deviance ratio and t-values for model parameters for logistic regression of the sequence of species selection at four sites in the Dohne Sourveld. (Bush: species 1 = *A. semialata*, 2 = *T. leucothrix*. Eragrostis: species 1 = *A. appendiculatus*, 2 = *E. plana*. Old lands: species 1 = *H. contortus*, 2 = *E. plana*. Sheep shed: species 1 = *A. semialata*, 2 = *A. appendiculatus*). See text for details

	Camp			
	Bush	**Eragrostis**	**Old lands**	**Sheep shed**
Constant	-3.13	-4.43	-3.98	-7.20
Sequence	8.17	6.13	8.08	8.35
Animal 'cattle'	-3.33	4.18	2.58	-1.72
Grass 'species 1'	-7.95	3.17	-1.13	-5.36
Grass 'species 2'	2.77	-7.35	-8.69	4.63
Sequence 'cattle'	-0.14	-3.49	-2.69	0.73
Cattle x species 1	7.86	-3.62	-1.84	5.23
Cattle x species 2	-2.98	3.52	2.85	-0.77
Deviance ratio	49.34	262.00	76.32	33.97

[$t_{(0.05)}$ 28 df = 2.048]

[$t_{(0.01)}$ 28 df = 2.763]

At old lands sheep first grazed *H. hirta* and *H. contortus* (Fig. 4.1). Regrazing of both species then occurred with sheep defoliating *E. plana* tillers last. Cattle also selected for *H. hirta* and, to a lesser extent, for *H. contortus*, but consumed *E. plana* earlier in the grazing period than did sheep. Overall, tillers were more likely to be defoliated under cattle than under sheep grazing but conversely these tillers were more likely to be defoliated near the end of the grazing period by sheep (Table 4.1). There were vast differences in the degree of preference exhibited for the different species, but again cattle were more likely to consume *E. plana* than were sheep.

At sheep shed, sheep first selected *A. appendiculatus* followed by *T. leucothrix*. Regrazing of *A. appendiculatus* was extensive and more than 60 % of these tillers were grazed two or more times over the six-day period (Fig. 4.1). Sheep avoided *A. semialata* and grazed only a small proportion of these tillers. Cattle defoliated *A. appendiculatus* tillers in preference to those of *A. semialata* which in turn were defoliated in

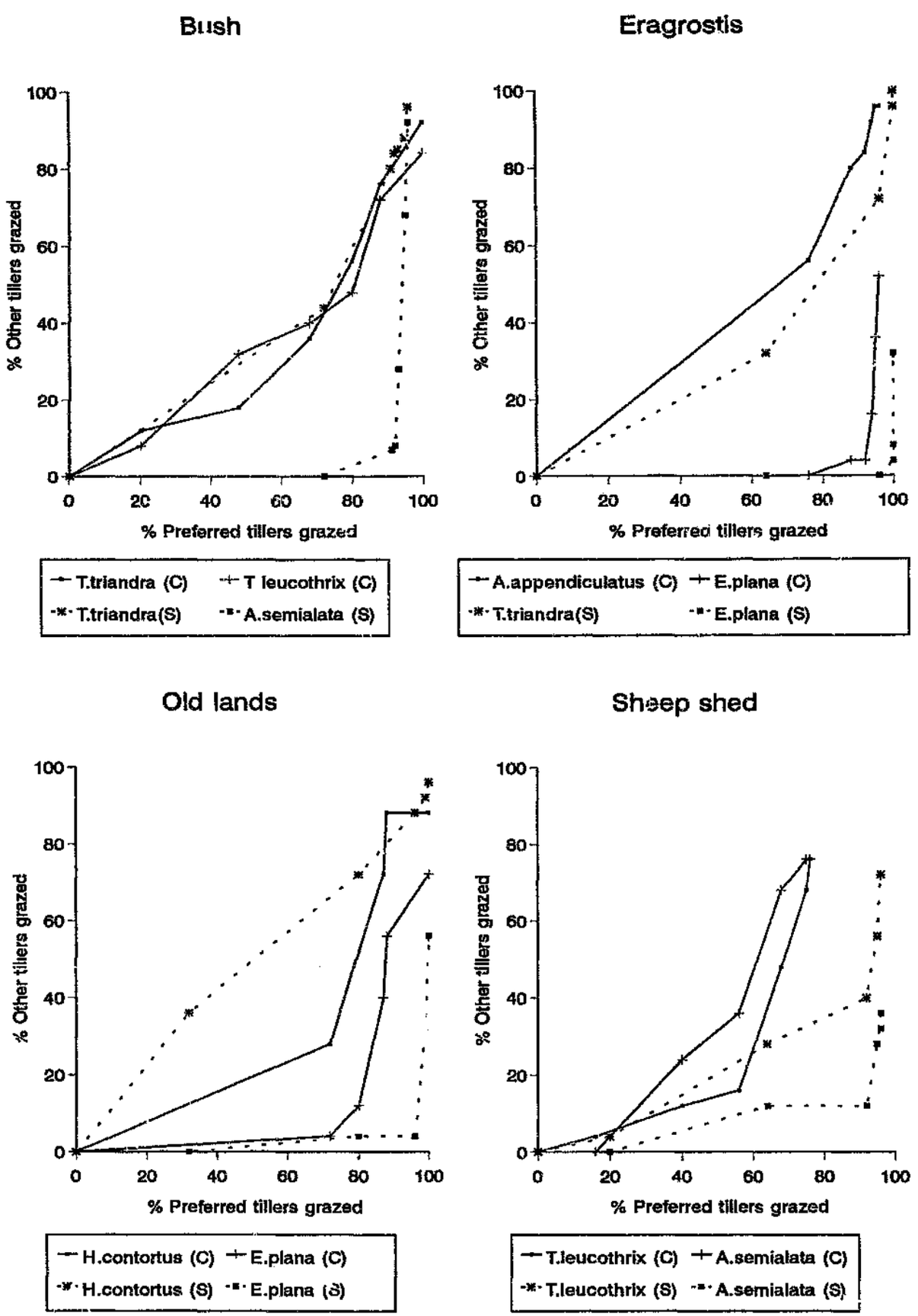

Figure 4.2 Relation between the percentage (%) of tillers of preferred species and the % of tillers of other species grazed by cattle and sheep at four sites in the Dohne sourveld.

preference to *T. leucothrix* (Fig. 4.1). Despite these differences, the three species were defoliated at roughly similar rates with regrazing of all species occurring in the latter half of the grazing period (Fig. 4.1). Overall, tillers had an equal probability of being defoliated under both cattle and sheep grazing. Differences in preference for species were highly significant with *A. semialata* and *A. appendiculatus* having a lesser and greater chance respectively, than *T. leucothrix* of being defoliated (Table 4.1).

For both cattle and sheep, the utilisation of any species was strongly dependent upon the extent of utilisation of the most-preferred species in the sward (Fig. 4.2). In most cases a two-stage response was evident. In the first stage, the degree of utilisation of the preferred species was still relatively low and ungrazed tillers of this species were available. Here, utilisation of the less-preferred species was low, or in the case of avoided species, almost non-existent. However, as the utilisation of the preferred species increased, a threshold was approached, and above this point, utilisation of less-preferred or avoided species increased dramatically (Fig. 4.2). Generally, the greater the difference in preference between the preferred and the next most-preferred species, the higher the threshold and the lower the pre-threshold utilisation of the latter species. Where species were of a similar preference ranking, the ratio of the extent of utilisation of the two species to each other was close to unity (Fig.4.2).

4.4.2 Frequency of tiller defoliation

The majority of tillers at all sites and under both cattle and sheep grazing were defoliated at least once and in some cases two or three times by the end of the grazing period (Fig. 4.3). The frequency of tiller defoliation was independent of both species and animal in all camps in the partial loglinear model but was dependent on animal type in bush camp in the saturated model (Table 4.2). On an individual species basis, the frequency of tiller defoliation was dependent on animal type in five out of twelve comparisons but the results were inconsistent (Fig. 4.3), i.e. in two cases the frequency of tiller defoliation was higher under cattle grazing while in the other three the reverse occurred. This inconsistency and the general lack of significance of the overall analysis indicates no real difference between cattle and sheep in the frequency of tiller defoliation.

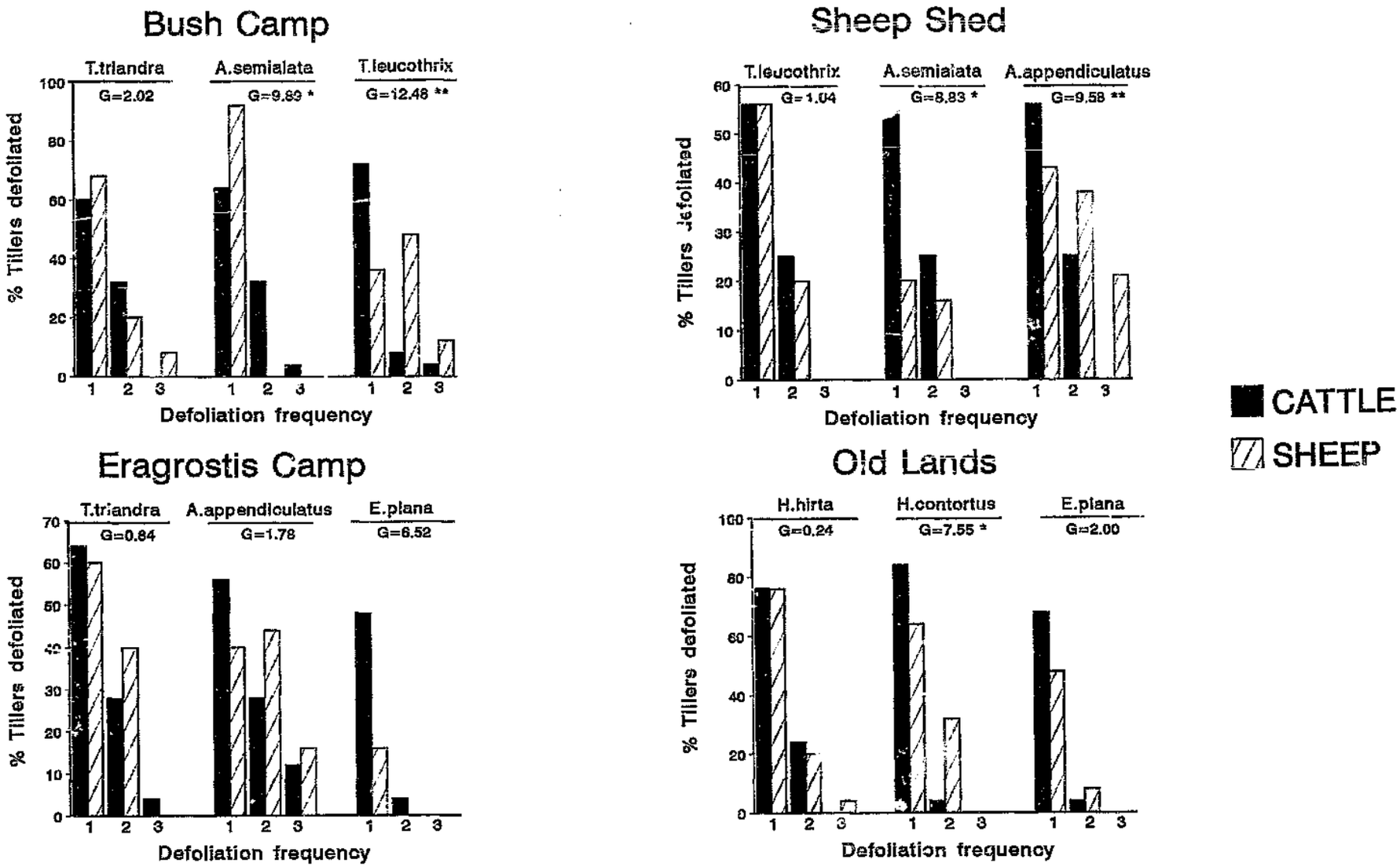

Figure 4.3 **Total percentage (%) of tillers defoliated once, twice or three times over the grazing period under cattle and sheep grazing at four sites in the Döhne Sourveld. G-value are cattle-sheep comparisons for individual species.**

Table 4.2 Probability values for partial and saturated loglinear models of the dependence of tiller defoliation (def.) frequency on grass species, animal species and an animal-grass species interaction at four different sites in the Dohne Sourveld

Model	Camp			
	Bush	Eragrostis	Old lands	Sheep shed
Partial				
Def. x species	0.349	0.835	0.201	0.215
Def. x animal	0.121	0.952	0.162	0.157
Def. x animal x species	0.095	0.999	0.183	0.293
Saturated				
Def. x species	0.096	0.238	0.207	0.293
Def. x animal	0.008**	0.389	0.062	0.141
Def. x animal x species	0.004**	0.677	0.183	0.293

The overall frequency of tiller defoliation was strongly dependent on grass species at all sites under sheep grazing (Table 4.3) highlighting the selective nature of these animals. In contrast, under cattle grazing the overall frequency of tiller defoliation was only dependent upon species at eragrostis ($P \leq 0.01$) and old lands ($P \leq 0.05$) camps.

Table 4.3 G-values for the dependence of tiller defoliation frequency on grass species under cattle and sheep grazing at four different sites in the Dohne Sourveld

Site	Animal	
	Sheep	Cattle
Bush	21.43 **	8.15
Eragrostis	61.64 ***	24.70 ***
Old lands	21.79 ***	12.64 *
Sheep shed	28.79 **	0.781

4.4.3 Severity of tiller defoliation

Sheep defoliated tillers at a significantly ($P \leq 0.05$) lower height than did cattle (Table 4.4) with this difference being consistent across all sites and all species. Mean differences in defoliation height between the two animals ranged from 1 cm for *T. triandra* (bush camp) to 3.28 cm for *A. appendiculatus* (sheep shed) (Table 4.4).

Table 4.4 Mean height (cm) of tiller defoliation by cattle (Ca) and sheep (Sh) for different grass species at four sites in the Dohne Sourveld. Statistical comparisons are for cattle versus sheep at individual sites

Site	Species			Ca vs Sh
Bush	*A. semialata*	*T. triandra*	*T. leucothrix*	
Ca	5.70	5.28	4.27	**
Sh	4.52	4.28	2.84	
Eragrostis	*A. appendiculatus*	*T. triandra*	*E. plana*	
Ca	7.26	5.03	7.50	**
Sh	4.63	3.12	5.00	
Old lands	*H. hirta*	*H. contortus*	*E. plana*	
Ca	7.42	4.06	4.96	**
Sh	4.76	2.50	3.54	
Sheep shed	*A. appendiculatus*	*A. semialata*	*T. leucothrix*	
Ca	11.25	8.58	7.62	*
Sh	7.97	8.00	5.57	

Differences in the percent of total tiller length removed were also significant ($P \leq 0.05$) with sheep consistently removing a greater percentage of the tiller than cattle (Table 4.5). This difference was also consistent across all sites and species and ranged from 0.48 % for *A. semialata* (bush camp) to 16.57 % for *H. contortus* (old lands).

Table 4.5 Mean percent tiller length removed by cattle (Ca) and sheep (Sh) for different grass species at four sites in the Dohne Sourveld. Statistical comparisons are for cattle versus sheep at each site

Site	Species			Ca vs Sh
Bush	*A. semialata*	*T. triandra*	*T. leucothrix*	
Ca	63.57	64.76	61.12	**
Sh	64.05	69.24	72.13	
Eragrostis	*A. appendiculatus*	*T. triandra*	*E. plana*	
Ca	69.07	71.43	70.36	**
Sh	79.92	80.29	77.78	
Old lands	*H. hirta*	*H. contortus*	*E. plana*	
Ca	69.91	64.91	77.33	**
Sh	73.77	81.48	81.65	
Sheep shed	*A. appendiculatus*	*A. semialata*	*T. leucothrix*	
Ca	64.06	52.11	56.65	*
Sh	73.17	61.90	71.24	

4.4.4 Changes in dietary quality and ingestive behaviour

Dietary CP declined over the grazing period for both cattle and sheep in all camps (Fig. 4.4) with the largest decline generally occurring over the first or second days of occupation (Table 4.6). However, in certain cases the decline was not constant, with dietary CP tending to level out or even increase slightly over the final days of the grazing period. Dietary IVD also showed a net decline over the grazing period (Table 4.6) but the observed trends were inconsistent (Fig. 4.4), with IVD declining fairly consistently with time in some camps but fluctuating in others.

Table 4.6 Mean *in vitro* digestibility (IVD) and crude protein (CP) content of diets selected by cattle and sheep over a 5-day period of occupation in a camp at four sites in the Dohne Sourveld. Means in the same row with the same superscript are not significantly different at the 5 % level

		Day in camp				
Variable	Camp	1	2	3	4	5
				%DM		
Cattle: IVD	Bush	45.21^{a}	40.27^{b}	41.51^{b}	38.42^{b}	38.32^{b}
	Eragrostis	53.05^{a}	51.02^{ab}	48.36^{bc}	47.70^{c}	50.62^{cab}
	Old lands	49.95^{a}	43.40^{bc}	46.03^{b}	46.01^{b}	40.95^{c}
	Sheep shed	51.31^{a}	49.25^{a}	48.17^{a}	47.89^{a}	45.50^{a}
Cattle: CP	Bush	6.17^{a}	4.61^{b}	4.74^{b}	4.03^{b}	4.35^{b}
	Eragrostis	6.07^{a}	5.57^{a}	4.79^{b}	4.84^{b}	4.25^{b}
	Old lands	6.04^{a}	4.46^{ab}	3.50^{b}	3.70^{ab}	4.22^{ab}
	Sheep shed	6.38^{a}	5.22^{ab}	4.62^{b}	4.48^{b}	5.13^{ab}
Sheep: IVD	Bush	-	45.80^{a}	44.40^{a}	47.02^{a}	46.88^{a}
	Eragrostis	58.15^{a}	55.74^{a}	53.88^{a}	50.05^{a}	54.28^{a}
	Old lands	57.27^{a}	55.15^{a}	54.28^{a}	54.2^{a}	53.54^{a}
	Sheep shed	51.52^{a}	47.66^{a}	52.70^{a}	50.88^{a}	46.95^{a}
Sheep: CP	Bush	6.49^{a}	5.13^{b}	4.67^{b}	4.85^{b}	4.62^{b}
	Eragrostis	6.54^{a}	6.06^{ab}	5.12^{bc}	4.61^{c}	4.53^{c}
	Old lands	6.96^{a}	5.64^{ab}	5.37^{ab}	4.91^{b}	4.56^{b}
	Sheep shed	5.56^{a}	4.59^{a}	4.71^{a}	4.24^{a}	3.9^{a}

Changes in ingestive behaviour over the grazing period were generally inconsistent in all camps (Fig. 4.5). For both animals, biting rates declined sharply with time in some camps but stayed fairly constant in others. For example, cattle bite rates at old lands declined from 54.54 to 47.13 bites/min. over the course of the grazing period while at sheep shed the decline was only from 54.11 to 52.76 bites/min. over the

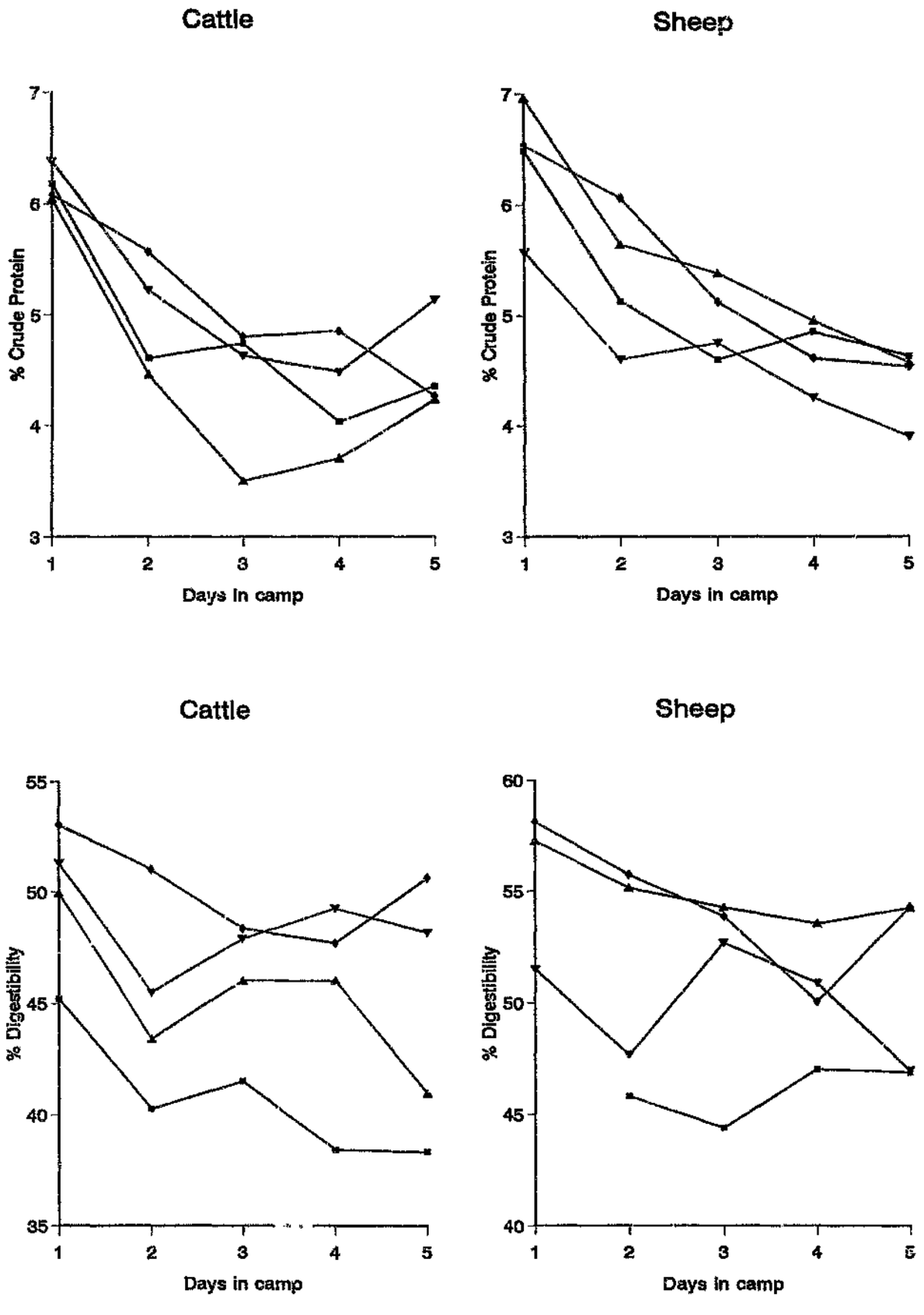

Figure 4.4 Changes in dietary crude protein (top) and *in vitro* digestibility (bottom) for cattle and sheep over the grazing period at four sites in the Dohne Sourveld (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

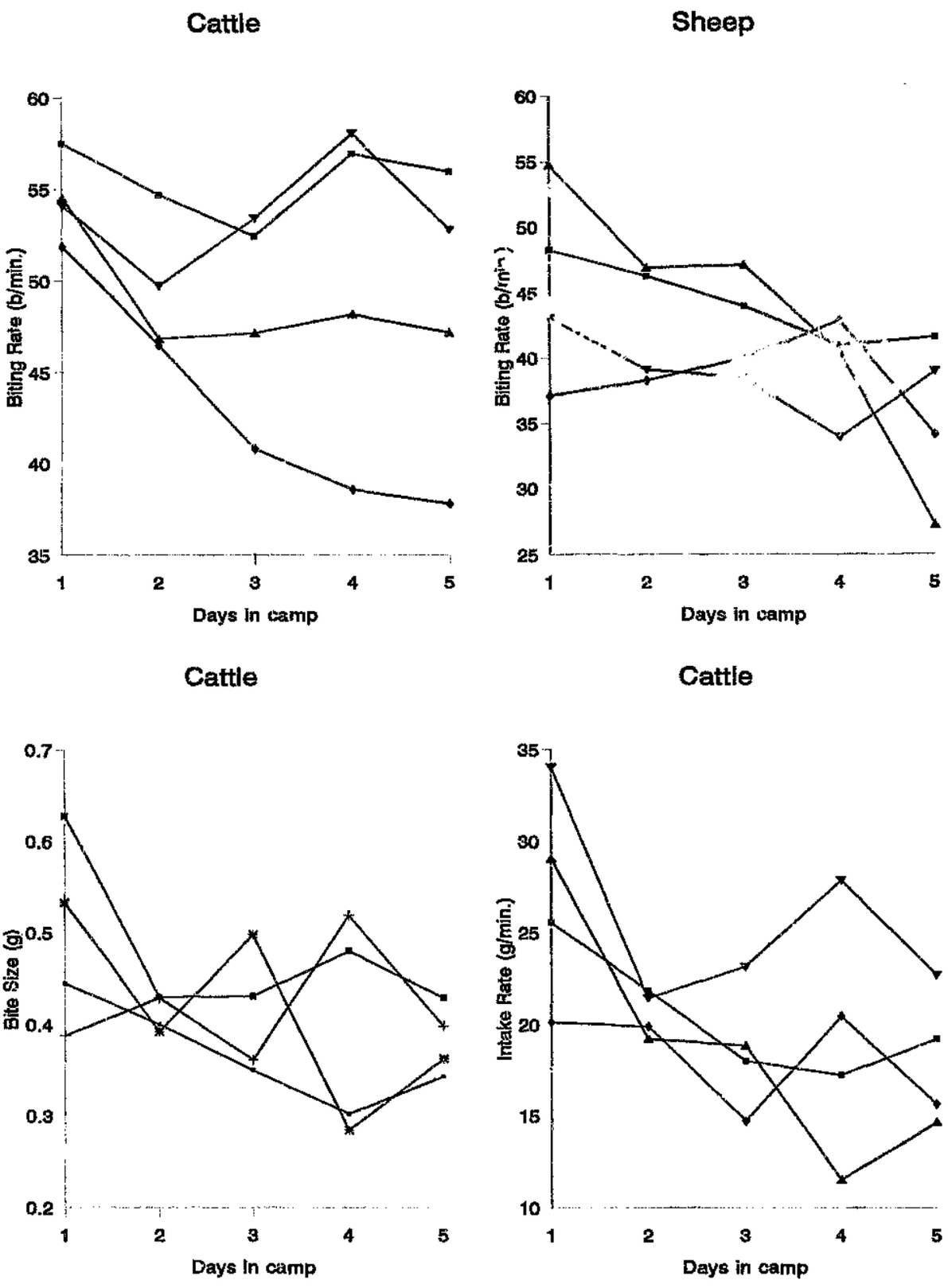

Figure 4.5 Changes in biting rate for cattle and sheep (top), and cattle bite sizes and intake rates (bottom) over the grazing period at four sites in the Dohne Sourveld (■ = bush; ♦ = eragrostis; ▲ = old lands and ▼ = sheep shed camp).

same period (Table 4.7). Cattle bite sizes and intake rates were generally highest on day 1 but tended to decline sharply on the second day. Trends for both variables were thereafter inconsistent (Fig. 4.6). Due to the inconsistent recovery rates of fistula samples with sheep, bite size and intake rate estimates for these animals were extremely variable and these data are consequently not presented.

Table 4.7 Mean bite rate for cattle and sheep, and mean bite size and intake rate for cattle over a 5-day period of occupation in a camp at four sites in the Dohne Sourveld. Means in the same row with the same superscript are not significantly different at the 5 % level

		Day in camp				
Variable	Camp	1	2	3	4	5
			bites/min			
Sheep: Bite rate	Bush	49.37^{a}	46.24^{ab}	43.73^{ab}	42.20^{ab}	41.01^{b}
	Eragrostis	37.15^{a}	38.30^{a}	40.00^{a}	42.87^{a}	34.11^{a}
	Old lands	48.30^{a}	37.46^{ab}	40.27^{a}	40.48^{a}	26.28^{b}
	Sheep shed	43.09^{a}	39.11^{a}	38.52^{a}	33.87^{a}	38.96^{a}
Cattle: Bite rate	Bush	57.50^{a}	54.45^{a}	52.42^{a}	56.88^{a}	55.92^{a}
	Eragrostis	51.87^{a}	46.46^{a}	40.76^{a}	38.54^{a}	37.76^{a}
	Old lands	54.54^{a}	46.84^{b}	47.14^{b}	48.17^{ab}	48.02^{b}
	Sheep shed	54.11^{ab}	49.73^{b}	53.41^{ab}	58.00^{a}	52.76^{ab}
			g.DM			
Cattle: Bite size	Bush	0.445^{a}	0.399^{a}	-	0.302^{a}	0.343^{a}
	Eragrostis	0.387^{a}	0.429^{a}	0.361^{a}	0.519^{a}	0.398^{a}
	Old lands	0.532^{a}	0.391^{ab}	0.498^{a}	0.283^{b}	0.362^{ab}
	Sheep shed	0.628^{a}	0.429^{a}	0.431^{a}	0.480^{a}	0.429^{a}
			g.DM/min			
Cattle: Intake rate	Bush	25.57^{a}	21.86^{a}	-	17.21^{a}	19.19^{a}
	Eragrostis	20.11^{a}	19.88^{a}	14.71^{a}	20.42^{a}	15.61^{a}
	Old lands	29.05^{a}	19.19^{b}	18.82^{b}	11.49^{b}	14.64^{b}
	Sheep shed	34.04^{a}	21.42^{a}	23.14^{a}	27.85^{a}	22.67^{a}

4.5 Discussion

The sequence or order of species selection over the grazing period could be conveniently divided into three distinct stages. In the first stage, animals selected the most-preferred species in the sward with some utilization of less-preferred species also

occurring. The second stage was initiated when about 60 % of the tillers of the preferred species had been defoliated and was characterised by regrazing of these tillers coupled with increased utilization of less-preferred species. The third and final stage commenced when 80-100 % of tillers of the preferred and less-preferred species had been defoliated at least once and grazing of previously avoided species was finally initiated. This sequence of species selection was essentially the same for both cattle and sheep although the actual categorization of species into the different preference classes varied somewhat between the two animals. For example, while sheep avoided *A. semialata*, this was a preferred species for cattle. Sheep also appeared to be more selective than cattle and tended to delay grazing avoided species until later in the grazing period than did the latter animals (Fig. 4.1).

The present results corroborate the general sequence of species selection through a grazing period first reported by Daines (1980), and later by Danckwerts *et al.* (1983), for cattle grazing Dohne Sourveld and semi-arid grassveld, respectively. Similar results have also been reported by O'Reagain and Mentis (1989a) for cattle on a secondary grassland community in northern Natal and by Stoltsz and Danckwerts (1990) for cattle and sheep grazing together on the Dohne Sourveld. The consistent feature to all these studies, is that animals generally selected previously defoliated tufts of preferred species rather than graze the undefoliated tufts of avoided species in the sward.

The general consistency of the present results with the published literature (Daines 1980; Danckwerts *et al.* 1983; O'Reagain & Mentis 1989a; Stoltsz & Danckwerts 1990) suggests that the general sequence of species selection described above, is of fairly general applicability to grazers in rotational grazing systems having relatively short periods of occupation, i.e. 1-3 weeks, in a camp. However, the extent to which this sequence operates where periods of occupation are longer, is unclear. Possibly, where periods of occupation are sufficiently long and conditions suitable for rapid growth, preferred species may regrow sufficiently quickly after defoliation to allow the animals to return to such regrowth without being forced to graze the less-preferred or avoided species in the sward.

The effect of stocking density on this sequence is also of interest. At high stocking densities animals still select preferred species first, but are forced to consume avoided species sooner than under light stocking (Daines 1980; Stoltsz & Danckwerts

1990), simply because the availability of preferred plants is depleted more rapidly. Stocking density therefore appears to affect only the 'rate' at which the sequence proceeds and not the order of selection *per se*.

A basic prediction of optimal foraging theory is that, as food availability declines, dietary breadth should be widened (Emlen 1966) with foods being added to the diet in the rank order of their utility to the animal (Pyke *et al.* 1977). Assuming that animals do forage optimally and that preference is correlated with utility, then the observed sequence of selection was in broad agreement with this prediction; both animals only consumed less-preferred species to any marked degree later in the grazing period when herbage availability had been depleted through grazing. Once a new food has been included in the diet it should always be consumed when encountered (Krebs & McCleary 1984), i.e. an all-or-nothing response. However, while an obvious step-function was evident in some situations, e.g. *E. plana* in eragrostis camp (Fig. 4.2), in others the utilization of less-preferred species was simply increased from low to high levels. This implies the existence of partial preferences with less-preferred or avoided species never being totally excluded from the diet. A number of explanations exist to explain partial preferences (Krebs & McCleary 1984) such as the need to sample a fluctuating environment (Westoby 1978) or imperfect knowledge on the part of the animal on the value and abundance of species present.

The decision to eat a lower-ranking food (species) should also depend upon the abundance of more-preferred foods and should be independent of its own abundance (Pyke *et al.* 1977). This occurred in the present study where the consumption of less-preferred species was strongly dependent upon the extent of defoliation and, therefore, the availability of more-preferred species. A threshold effect (Fig. 4.2) was evident in all camps with utilization of less-preferred species being low or non-existent when ungrazed tufts of preferred species were readily available. However, once the availability of such tufts had been depleted through grazing, utilisation of less-preferred or avoided species increased sharply.

The regrazing of tillers of preferred species when other, ungrazed species were available is unexpected. The major proportion of a tiller (>60 %) is removed in the first defoliation (O'Reagain, unpublished data) so such regrazings are likely to yield very small bites. Further, such bites are likely to be of relatively poor nutritive value as

regrazings often extend below the leaf collar (pers. obs.) into a zone comprised of tough, fibrous material of low quality. Although the more-preferred species may be of higher overall quality, it is difficult to accept that a second bite from a previously grazed tiller could be of superior value to the animal, than a fresh bite from an undefoliated, albeit slightly lower quality, species. This suggests that the regrazing of tillers is sub-optimal, particularly over the short grazing periods considered in the present study. However, over longer time periods, where tiller regrowth is possible, the high quality of such regrowth may outweigh its small potential bite size, making regrazing of preferred species an evolutionary stable strategy.

The sequence of species selection over the grazing period should also affect dietary quality and ingestive behaviour as animals consume grasses differing in nutritive value and offering different rates of intake. Overall, dietary quality declined with time in a paddock, as noted in other studies (Chacon & Stobbs 1976; Hardy 1986; O'Reagain & Mentis 1988; Olson *et al.* 1989). Assuming that species preference is partly a function of leaf quality, e.g. Field (1976), this overall trend is logical. However, on a finer scale, dietary quality might be expected to oscillate within this general downward trend as animals graze and then regraze a particular preference class, before moving on to the next, largely ungrazed, class. This appeared to have occurred in certain camps, particularly with digestibility, where the decline was inconsistent and appeared to fluctuate over time (Fig. 4.4).

Bite size might also be expected to decline and bite rate increase over the grazing period, as found on mono-specific swards (Chacon & Stobbs 1976; Jamieson & Hodgson 1979; Olson *et al.* 1989). However, changes in ingestive behaviour were inconsistent, with bite rate decreasing sharply at some sites or fluctuating in others. Similarly, cattle bite sizes showed a consistent decline at only one (bush) of the four sites studied (Fig. 4.5). Although inconclusive, these trends suggest that in multi-species swards, ingestive behaviour is not a monotonic function of time but tracks the sequence and degree of defoliation of the different species available through the grazing period.

The sequence of species selection over the grazing period is also of direct relevance to rangeland management. For example, non-selective (Acocks 1966) or high-utilisation (Booysen 1969) grazing is based on the assumption that heavy stocking

densities can be used to force animals to utilise even the most avoided species in the sward. This allegedly decreases the relative abundance of these undesirable species because they are supposedly less tolerant of grazing than the more desirable (preferred) species present in the sward (Acocks 1966; Booysen 1969; Edwards 1981). However, the results reported here, and in other studies (Daines 1980; Danckwerts *et al.* 1983; O'Reagain & Mentis 1989a), suggest that the basic concept of non-selective grazing is flawed and is, in practice, largely unattainable, even at high stocking densities. Furthermore, the resultant damage resulting to preferred species in trying to achieve such an objective is likely to outweigh any potential benefit arising from the utilisation of the less desirable species in the sward.

Danckwerts (1984) recommended that, as a rule of thumb, animals should be removed from a paddock when 80-90 % of the tufts of the preferred species had been grazed. However, the present results indicate that at this stage extensive regrazing of preferred species has already been initiated (Fig 4.1), suggesting that this management guideline (Danckwerts *loc. cit.*) could result in excessive use of these species. It is therefore suggested that if a primary management objective is to prevent excessive defoliation of preferred species, then animals be removed sooner, when about 60-70 % of these plants have received some form of defoliation.

In general, the frequency with which tillers were defoliated within a grazing period was similar under cattle and sheep grazing. While significant differences in defoliation frequency were apparent for certain grass species (Fig. 4.3), these were inconsistent, apparently reflecting differences in preference between the two animals, i.e. both cattle and sheep tended to repeatedly defoliate preferred species. Accordingly, the hypothesis that sheep defoliate tillers more frequently than cattle during a grazing period is rejected. However, given the relatively small sample sizes used, the possibility of a Type II error cannot be discounted and significant differences between cattle and sheep in tiller defoliation frequency may have been detected with larger samples. More importantly, the present study measured defoliation frequency over a relatively short period, i.e. six days, and thus did not consider defoliation of regrowth which could be of greater importance to the plant than defoliation *per se*. Consequently, the present results are inconclusive and further investigation using larger sample sizes and longer grazing periods is suggested.

The severity of tiller defoliation was, however, clearly greater under sheep than under cattle grazing; sheep always grazed tillers at a lower height, removing a greater proportion of the tiller than did cattle (Table 4.4 & 4.5). The hypothesis that the severity of tiller defoliation is greater under sheep than under cattle grazing is therefore accepted. The consistency of the above observation at all sites and across seven grass species, some of which had a very low preference ranking for sheep, suggests that this finding is robust and likely to be of wide applicability.

The species preferences exhibited by cattle and sheep were similar but not identical, with each tending to defoliate different species to different degrees. This suggests that the relative impacts of cattle and sheep on species composition in sourveld are likely to be different, simply because they graze a slightly different subset of species in the sward. Further, the relative impact of sheep on species composition might be expected to be more detrimental for two reasons. First, although the difference between the proportion of tiller removed by cattle and sheep appears relatively small (±10 %), on an average of 4-6 defoliations per season (Gammon & Roberts 1978a), the cumulative annual difference in tissue loss for an individual plant is likely to be of significance. Second, sheep appear to concentrate on a narrower spectrum of species, so that at equivalent stocking densities, preferred species are likely to experience a greater intensity of defoliation than under cattle grazing. This is corroborated by the observations of Du Toit (1967) that veld grazed by sheep had a lower basal cover, lower yield and a higher weed density than that grazed by cattle.

4.6 Conclusions

4.6.1 Within a period of grazing in a camp animals first grazed preferred species and to a limited extent, species which were less preferred. When about 60-70 % of the tillers of preferred species had been defoliated, regrazing of previously defoliated tillers of these species was initiated along with increased utilization of less-preferred species. Utilization of avoided species finally occurred only after extensive defoliation of preferred and less-preferred species in the sward.

4.6.2 Cattle and sheep had a similar sequence of species selection over the

period of grazing in a camp. However, the preference ranking of different species was not the same by the two animals. Sheep tended to be more selective, and waited longer before grazing avoided species, than did cattle.

4.6.3 The sequence of species selection was in broad agreement with the predictions of optimal foraging theory in that animals became less selective as forage availability declined while the utilization of species was directly dependent upon the degree of utilization of more-preferred species.

4.6.4 Dietary quality declined over the grazing period but the rate of decline was inconsistent. Ingestive behaviour also changed over the grazing period but no consistent trends were evident.

4.6.5 There was no difference between cattle and sheep in the frequency of tiller defoliation with both animals tending to repeatedly regraze tillers of preferred species over the period of occupation in a camp.

4.6.6 The severity of tiller defoliation was greater under sheep than cattle grazing. Sheep consistently defoliated tillers at a lower height and removed a greater proportion of tiller length than did cattle.

4.6.7 The evidence suggests that the impact of cattle and sheep on rangeland is likely to be different and that sheep have a greater potential to cause rangeland degradation than cattle.

CHAPTER 5

THE POTENTIAL INGESTION RATES OF DIFFERENT SOURVELD GRASSES

5.1 Objectives

The specific objectives of this experiment were to:

(i) determine the potential ingestion rates of different sourveld grasses by cattle and sheep;

(ii) quantify the relation between ingestion rate and plant structure for individual grass species.

5.2 Introduction

All grass species differ in their basic morphology, spatial geometry and in their leaf to stem ratio. It is thus logical to expect that species will differ substantially in bite size and the rate at which bites can be harvested, and therefore in the potential rate of DM ingestion by the grazing animal. These variables will not, however be constant for any given species but will vary according to the phenology or growth stage at which a particular grass is encountered.

Animal production is essentially the product of dietary quality and intake, less the energy expended by the animal. Therefore if the nutritive value and acceptability of a species is known and the potential rate of ingestion of that species at a particular phenological stage can be determined, then it should be possible to quantitatively predict animal production on multi-species swards like sourveld.

Quantification of the potential intake rates of different species is also of importance in modelling dietary selection; a basic tenet of optimal foraging theory is that foods should be selected on the basis of their utility to the animal, calculated as the ratio of energy content/handling costs (Emlen 1966). For the grazing animal, these handling costs arise partly from the time and energy expended in harvesting a particular food. Accordingly, the potential intake rate of a particular species should be an important determinant of its overall acceptability to the animal. This has been demonstrated for browsing ungulates (Cooper & Owen-Smith 1986) and also appears to

be important for grazers like cattle (O'Reagain & Mentis 1989b) and sheep (O'Reagain 1993).

Quantification of the potential intake rate of different grass species is, unfortunately, difficult. This is due in part to methodological problems associated with measuring short-term rates of intake in the field and, in part, to environmental and dietary heterogeneity in that animals commonly consume a number of plant species over relatively short time periods. The latter problem is particularly relevant in sourveld where swards are heterogeneous and dense, making it almost impossible to distinguish what species are being consumed, even at close range (pers. obs.).

A number of previous workers have successfully quantified the amount of herbage removed from different grass species by the grazing animal (Grunow & Van Ginkel 1965; Kruger & Edwards 1972; Danckwerts *et al.* 1983; Stoltsz & Danckwerts 1990). However, none of these studies quantified the rate at which the herbage was removed and ingested. Consequently, it is impossible to determine the actual 'profitability' or net rate of ingestion of a particular species, limiting the usefulness of such data for models of dietary selection or animal production.

5.3 Procedure

5.3.1 Study area

The experiment was conducted at the Dohne Agricultural Development Institute, situated some 10 km north of Stutterheim. A more detailed description of the general study area is provided in section 2.3.1.

5.3.2 Experimental design

The approach initially adopted was to establish monospecific plots of different grass species in the field and then to attempt to measure ingestion rates by grazing these plots with oesophageally fistulated animals (termed the 'plot' trial). This method was generally unsatisfactory (section 5.4.1) and it was subsequently discontinued. Following on the method of Murson *et al.* (1989) an attempt was made to measure ingestion rates using mature, established tussocks of each species, transplanted into pots which were then grazed by experimental animals (termed the 'pot' trial). This method was successful and the results of this experiment are presented in section 5.4.2

5.3.2.1 Plot trial

5.3.2.1.1 General procedure

Monospecific stands of *A. appendiculatus, C. dactylon, H. hirta* and *T. triandra*, measuring approximately 5 m x 5 m, were established *in situ*. Plots were established by identifying patches in the field containing a high proportion of the desired species and then coring out any other species present using a large tuft auger (15 cm internal diameter). Resultant gaps were then filled with transplanted tussocks or sods of the required species from adjacent grassveld. In all plots, contamination by other, non-target species was minimal (<5 %). The above method was chosen in preference to establishment with seed in nursery plots in order to mimic the compacted, undisturbed soil environment commonly encountered in rangeland. On occasion, plots were mown to remove excess material and condition the sward for grazing.

5.3.2.1.2 Sward structure

Immediately prior to grazing, 50 random measurements of plant height, leaf table height, greenness and stemminess were made in each plot as described in section 2.3.3.

5.3.2.1.3 Animal measurements

Plots were grazed for periods of 20 to 30 minutes using two oesophageally fistulated Bonsmara type steers (average mass 400 kg) and three fistulated Dohne merino wethers (average mass 40 kg). Animals were fasted overnight to stimulate appetite. Animals were confined to plots using portable sheep handling pens. Sheep always grazed first followed by cattle to prevent interference between animals and to facilitate measurement of ingestive behaviour. Measurements of bite size, bite rate and intake rate were made as described in section 3.3.5. Estimates of dietary crude protein and *in vitro* digestibility were made as described in section 2.3.5

5.3.2.2 Pot trial

5.3.2.2.1 General procedure

Seven grass species were chosen for the experiment. These were *Andropogon appendiculatus, Cynodon dactylon, Eragrostis plana, Heteropogon contortus, Hyparrhenia hirta, Tristachya leucothrix* and *Themeda triandra*. Cattle were also presented with

Alloteropsis semialata. (Species nomenclature follows Gibbs Russell *et al.* 1990.) Species were chosen on the basis of their general abundance in Dohne Sourveld and, therefore, their potential importance as a forage source. With the exception of *C. dactylon* which is a creeping stoloniferous species, all are tussock grasses.

Well-established tussocks or sods growing *in situ* in undisturbed (>10 years) rangeland were removed with roots intact using a steel tuft auger (internal core diameter and depth both 15 cm) and transplanted into 2.5 or 5 litre black plastic pots. Plants were established with the soil level approximately 2 cm below the lip of the pot. Where necessary, a mixture of vermiculite and sawdust was used as filling. Pots were kept in a glasshouse and maintained at or near field capacity. Nutrients were not provided except where nutrient deficiencies appeared to be restricting growth in which case plants received a single, light application of granular fertilizer (limestone ammonium nitrate:28% N).

5.3.2.2.2 Plant structure

Immediately prior to grazing plant height, leaf table height, greenness and stemminess were recorded for each pot as described in section 2.3.3.

5.3.2.2.3 Animal measurements

Four Dohne merino ewe lambs (average mass 41 kg) and one Bonsmara steer (mass 400 kg) were used in the experiment. Only one steer was used as the other experimental animal showed reluctance in grazing the pots. All animals were sourveld-raised and well-acquainted with the species in question. Animals were fasted overnight (16:00-08:00) to stimulate appetite but in the case of *E. plana*, fasting usually had to be extended until early afternoon (14:00) before animals would eat this species.

For sheep, pots were presented individually to each animal. However, for cattle, pots of similar plant structure were clamped together in groups of four using an angle-iron frame bolted to a wooden base. Cattle were therefore confronted with a 31 cm x 31 cm or 38 cm x 38 cm mini-sward, depending upon pot size. Generally, animals showed little hesitation in defoliating pots and frequently had to be forcibly restrained from grazing pots while data were being transcribed. Pots were grazed until evenly defoliated or animals lost interest. As far as possible, equal or similar numbers of pots

of each species were presented to each experimental animal.

Pots were weighed immediately before and after defoliation using a Mettler[1] electronic balance (capacity 6 kg; sensitivity 0.1 g). Bite size was calculated as mass change/number of bites, corrected for dry matter. Bites were counted manually and grazing time defined as the time between the first and last bite recorded using a stop-watch. Biting rate was calculated as total bites/grazing time while intake rate was calculated as mass change/grazing time.

5.3.3 Statistical analyses

Between-species comparisons of bite size, bite rate and intake rate were made using an analysis of variance (ANOVA; SAS 1991). For sheep, species were used as a 'treatment' while each sheep served as a replicate. As data were only available from a single steer, individual measurements were used as replicates in the analysis of cattle data. Means and standard errors are therefore derived from individual animals for sheep and from individual measurements for cattle.

Relations between ingestive behaviour and the various components of plant structure were investigated using correlation analysis (CORR; SAS 1991) and were based on individual measurements, i.e. single tufts for sheep and groups of four tufts for cattle. Linear models of bite size and intake rate against plant height were also determined for cattle using regression analysis (REG; SAS 1991). Plant height was chosen as an independent variable on the basis of results from the correlation analyses and because it can be easily and objectively measured in the field.

5.4 Results

5.4.1 Plot trial

The data obtained in this trial were, in general, unsatisfactory. This was due to the variable recovery rates of fistula extrusa, especially from the sheep, which casts doubt upon the accuracy of estimates of bite size and intake rate. Confinement of animals to the small sampling areas may also have disturbed them and, in some cases, may have affected their grazing behaviour. These data will consequently only be presented for

[1] Microscp (Pty) Ltd., PO Box 2288,Pinetown,3600.

interest in an appendix (Appendix 4). However, there are two observations from this data set which are noteworthy. Firstly, when the *T. triandra* plot was first grazed, the sward was fairly tall (mean height 31.3 cm) and stemmy with most of the green forage diluted with senescent material. While the cattle grazed this plot fairly readily, the sheep, after initially taking a few bites, refused to consume any of the material on offer. After this block had been mown, it was readily grazed by sheep on subsequent sampling occasions (Appendix 4.2).

Secondly, when the *A. appendiculatus* plot was first grazed, most of the plants present were fairly recent transplants (<2 weeks) and had also recently been exposed to a mild drought. Both cattle and sheep initially showed some interest in grazing the plot but thereafter refused to graze completely. Grazing was not affected because the animals were confined, since, as soon as the animals were moved on to an equally small, adjacent area of veld, they commenced grazing immediately. However, when moved back to the plot of *A. appendiculatus* they ceased grazing once more. This behaviour is surprising as *A. appendiculatus* is highly acceptable to both animals (Chapter 4), and on subsequent occasions they showed no hesitation in grazing this species (Appendix 4.1 & 4.2). It is speculated that the stress induced by transplanting and the subsequent drought possibly affected this species's leaf chemistry, making it unacceptable. This suggests that some induced chemical defense may operate in *A. appendiculatus*, which possibly warrants further investigation.

5.4.2 Pot trial

5.4.2.1 Sheep

Overall, *E. plana* and *H. contortus* gave the largest bite size with there being little difference in bite size between the other grasses (Table 5.1). With the exception of *T. triandra*, there was a fairly large variation in the size of bite harvested from all species (Fig. 5.1). Biting rates were highest in *H. contortus* and lowest in *E. plana*. Consequently, sheep achieved the highest rate ($P<0.05$) of DM intake from *H. contortus* while there was little difference in intake rate between the other species (Table 5.1). Overall, sheep displayed a great reluctance to graze *E. plana* and, in particular, refused to graze the taller tufts of this species with longer leaves (Appendix 4.3 & 4.4).

With the exception of *A. appendiculatus*, bite size in sheep was not correlated

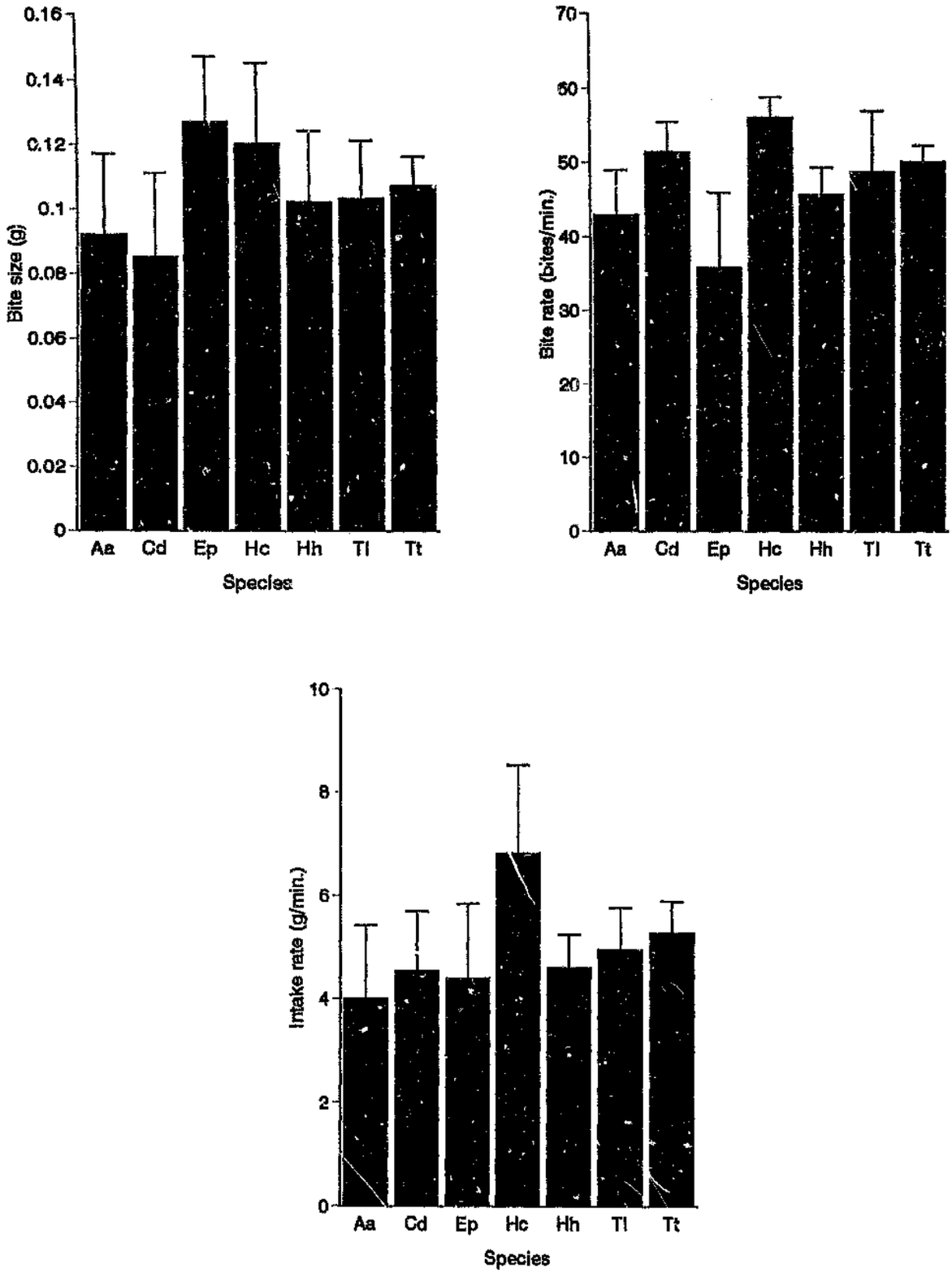

Figure 5.1 Mean (± standard error) bite size, bite rate and intake rate obtained by sheep grazing different scurvcid grasses (Aa = *A. appendiculatus*; Cd = *C. dactylon*; Ep = *E. plana*; Hc = *H. contortus*; Hh = *H. hirta*; Tl = *T. leucothrix*; Tt = *T. triandra*).

Table 5.1 Mean (±SE) bite size, bite rate and intake rate obtained by sheep from different sourveld grasses. Within a column, means with the same superscript are not significantly different ($P \leq 0.05$)

Species	Bite size (g.DM)	Bite rate (bites/min.)	Intake rate (g.DM/min.)
A. appendiculatus	0.092^{ab}	42.92^{cb}	4.01^{b}
	(0.025)	(6.05)	(1.41)
C. dactylon	0.085^{b}	51.41^{ab}	4.5^{b}
	(0.026)	(4.07)	(1.15)
E. plana	0.127^{a}	35.79^{c}	4.39^{b}
	(0.020)	(10.15)	(1.45)
H. contortus	0.120^{ab}	56.13^{a}	6.82^{a}
	(0.025)	(2.63)	(1.70)
H. hirta	0.102^{ab}	45.63^{b}	4.61^{b}
	(0.022)	(3.70)	0.630)
T. leucothrix	0.103^{ab}	48.78^{ab}	4.95^{b}
	(0.180)	(8.22)	(0.816)
T. triandra	0.107^{ab}	50.14^{ab}	5.27^{ab}
	(0.009)	(2.16)	(0.614)

with plant height in any of the seven grass species studied (Table 5.2). Bite size, bite rate and intake rate were positively correlated ($P \leq 0.01$) with the proportion of green leaf present in *T. leucothrix* and *H. hirta* (Table 5.2). These appeared to be the only species where a sufficiently wide range of greenness values were encountered to have any effect on these variables (Appendix 4.3). Similarly, bit . rate and intake rate were negatively correlated ($P \leq 0.01$) with stemminess in *H. hirta* which was the only species where the stems would have been of a density and consistency sufficient to interfere with biting rate and, consequently, DM intake (Table 5.2).

5.4.2.2 Cattle

The mean bite size obtained by cattle from *E. plana* and *T. leucothrix* was significantly ($P \leq 0.05$) larger than that obtained from any of the other grass species studied (Fig. 5.2; Table 5.3). Within the latter group of grasses there was little variation amongst species with bite sizes ranging from 0.83 g for *T. triandra* up to 1.07 g for *A. semialata*. Mean bite rate was lowest for *E. plana* (25.32 bites/min.) and highest for *T. triandra* (37.30

Table 5.2 Correlation coefficients for the relation between bite size, bite rate and intake rate in sheep and different attributes of plant structure in seven sourveld grasses

Species	Bite size	Bite rate	Intake rate
A.appendiculatus			
Plant height	0.257*	0.170	0.184
Stemminess	0.082	0.079	0.051
Greenness	0.016	0.282**	0.114
C. dactylon			
Plant height	-0.070	-0.306***	-0.225*
Stemminess	-0.083	-0.083	-0.119
Greenness	0.255**	-0.07	0.177
E. plana			
Plant height	0.192	-0.133	0.093
Stemminess	0.215	-0.073	0.076
Greenness	0.011	-0.089	0.128
H. contortus			
Plant height	-0.115	-0.039	-0.137
Stemminess	0.151	-0.196	0.042
Greenness	-0.004	-0.095	-0.037
H. hirta			
Plant height	0.196	-0.181*	-0.048
Stemminess	-0.08	-0.232**	-0.289***
Greenness	0.288***	0.409***	0.409***
T. leucothrix			
Plant height	0.267**	-0.243**	0.111
Stemminess	-	-	-
Greenness	0.262**	0.329***	0.415***
T. triandra			
Plant height	0.042	-0.259**	-0.101
Stemminess	-0.161	-0.011	-0.168
Greenness	-0.006	0.192	0.169

bites/min.) with little difference in biting rate amongst the remaining species. The mean rate of DM intake was highest for *E. plana* and *A. semialata* (32 g DM/min.) but lowest for H. *hirta* (24.30 g DM/min.) but for the remaining species (Fig. 5.2) most between-species differences were non-significant (Table 5.3)

Table 5.3 Mean (±SE) bite size, bite rate and intake rate obtained by cattle grazing different sourveld grass species. Means in the same column with the same superscript are not significantly different at the 5 % level

Species	Bite size (g.DM)	Bite rate (b/min.)	Intake rate (g.DM/min)
A. semialata	1.07^{bc}	30.39^{b}	32.13^{a}
	(0.42)	(6.21)	(13.10)
A. appendiculatus	0.96^{dc}	29.87^{b}	27.70^{ab}
	(0.44)	(5.47)	(12.25)
C. dactylon	0.94^{dc}	32.06^{b}	31.54^{ab}
	(0.42)	(13.09)	(21.72)
E. plana	1.30^{a}	25.32^{c}	32.26^{a}
	(0.60)	(4.55)	(14.62)
H. contortus	0.92^{dc}	32.12^{b}	28.96^{ab}
	(0.34)	(5.85)	(11.25)
H. hirta	0.87^{dc}	28.55^{bc}	24.30^{b}
	(0.29)	(5.25)	(8.59)
T. triandra	0.83^{d}	37.30^{a}	29.97^{ab}
	(0.28)	(8.22)	(9.39)
T. leucothrix	1.25^{ab}	25.33^{c}	30.25^{ab}
	(0.54)	(17.14)	(14.31)

There was a large degree of intra-species variation in estimates of bite size, bite rate and intake rate in all grasses (Fig. 5.2). This resulted from the wide variation in plant structure measured within each species (Appendix 4.4). On an individual species basis, a marked reluctance to graze *E. plana* was noted and on a number of occasions the animal in question refused to graze this grass. When *E. plana* was grazed, plants were frequently dislodged from pots because of the force required to break their tough leaves. On these occasions data were discarded (Appendix 4.4).

The size of bite harvested by cattle generally increased with increasing plant height for all species (Fig. 5.3). Similarly, the rate of DM intake increased in

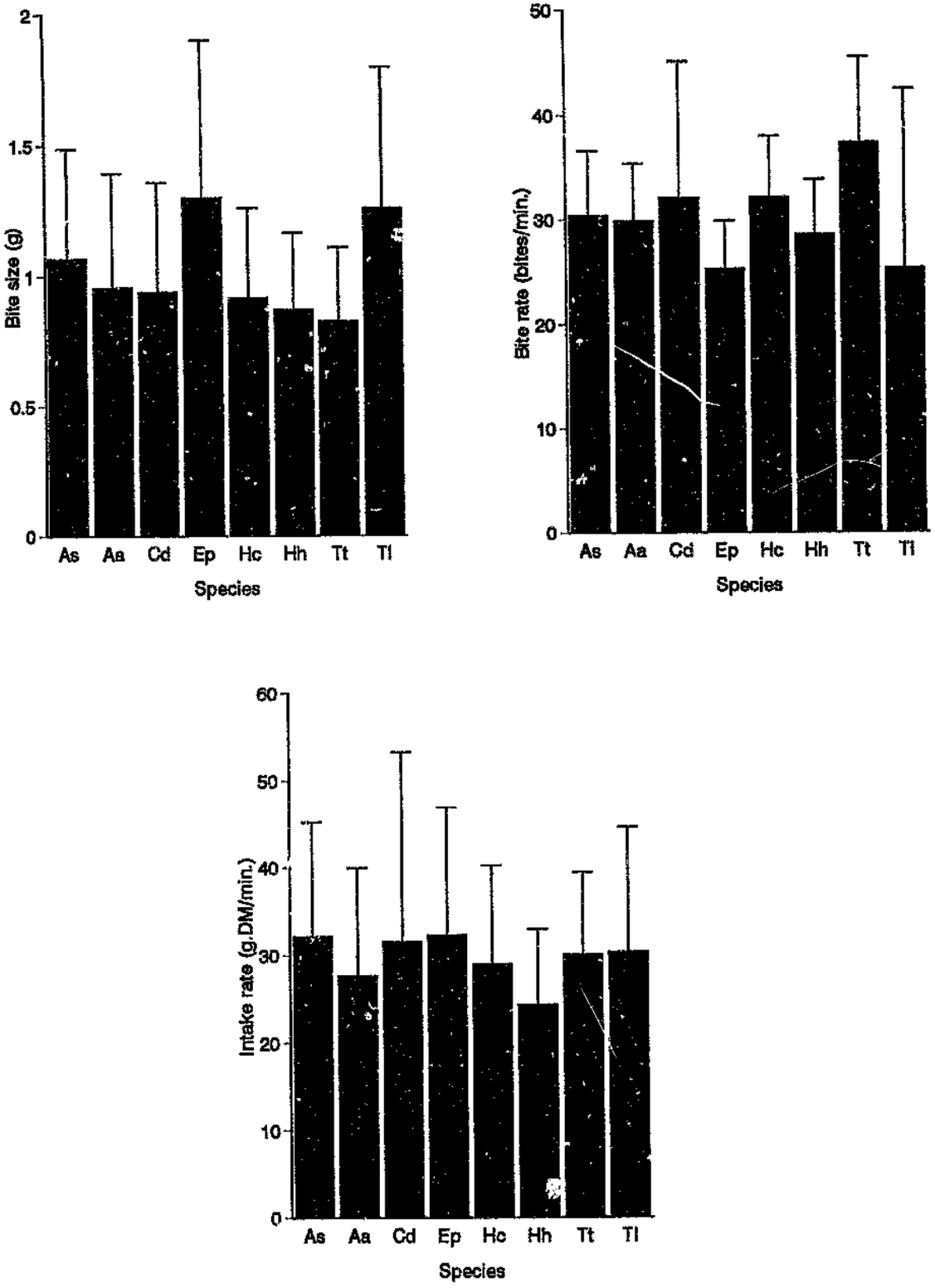

Figure 5.2 Mean (± standard error) bite size, bite rate and intake rate obtained by cattle grazing different sourveld grasses. (Species codes as for Figure 5.1. As = *A. semialata*).

Figure 5.4 The relation between the rate of dry matter intake in cattle and plant height in eight sourveld grasses. Points marked with (1) were considered outliers and not used to calculate the regression line.

Table 5.4 Correlation coefficients for the relation between bite size, bite rate and intake rate in cattle and different attributes of plant structure in eight sourveld grasses

Species	Bite size	Bite rate	Intake rate
A. semialata			
Plant height	0.754***	0.315	0.854***
Stemminess	-	-	-
Greenness	0.096	-0.149	0.002
A. appendiculatus			
Plant height	0.767***	-0.171	0.689***
Stemminess	0.497***	-0.148	0.405**
Greenness	-0.555***	0.213	-0.428**
C. dactylon			
Plant height	0.628***	0.094	0.399*
Stemminess	-0.200	0.327	0.093
Greenness	0.606***	0.055	0.370*
E. plana			
Plant height	0.507*	-0.053	0.512*
Stemminess	0.691**	0.069	0.725***
Greenness	0.431	0.153	0.500*
H. contortus			
Plant height	0.266	0.[illegible]9	0.243
Stemminess	0.474**	0.093	0.530***
Greenness	0.108	0.361*	0.218
H. hirta			
Plant height	0.631***	-0.394*	0.463**
Stemminess	0.363*	-0.199	0.271
Greenness	-0.104	0.110	-0.106
T. triandra			
Plant height	0.428*	0.170	0.522**
Stemminess	0.422*	-0.144	0.328
Greenness	-0.412*	0.171	-0.289
T. leucothrix			
Plant height	0.527**	-0.667***	0.264
Stemminess	-0.214	-0.134	-0.256
Greenness	-0.380*	0.284	-0.308

Table 5.5 Linear models describing the relation between plant height and the size of bite and rate of intake achieved by cattle grazing eight sourveld grass species

Species	Regression	r^2
	Bite size	
A. semialata	y = 0.0123 + 0.0464x	r^2= 0.57; F = 15.02; **
A. appendiculatus	y = -0.283 + 0.0547x	r^2= 0.61; F = 65.65; ***
C. dactylon	y = 0.168 + 0.0526x	r^2= 0.39; F = 18.92; ***
E. plana	y = 0.561 + 0.0205x	r^2= 0.25; F = 5.54; *
H. contortus	y = 0.0386 + 0.0608x	r^2= 0.07; F = 3.22
H. hirta	y = -0.0394 + 0.0454x	r^2= 0.40; F = 26.13; ***
T. triandra	y = 0.276 + 0.0262x	r^2= 0.18; F = 7.41; *
T. leucothrix	y = 0.135 + 0.0559x	r^2= 0.27; F = 12.37; **
	Intake rate	
A. semialata	y = -5.84 + 1.68x	r^2= 0.73; F = 30.52; ***
A. appendiculatus	y = -2.32 + 1.33x	r^2= 0.47; F = 37.18; ***
C. dactylon	y = 0.597 + 1.73x	r^2= 0.40; F = 17.36; ***
E. plana	y = 14.31 + 0.501x	r^2= 0.26; F = 5.68; *
H. contortus	y = 2.57 + 1.83x	r^2= 0.05; F = 2.65
H. hirta	y = 6.24 + 0.905x	r^2= 0.19; F = 9.17; **
T. triandra	y = 7.56 + 1.070x	r^2= 0.27; F = 12.36; **
T. leucothrix	y = 18.95 + 0.575x	r^2= 0.07; F = 2.42

conjunction with increasing plant height in seven of the eight species studied. For example, in *C. dactylon*, intake rate increased from about 10 to nearly 40 g DM/min. as plant height increased from 7 to 25 cm (Fig. 5.4). With the exception of *H. contortus* and *T. leucothrix*, plant height accounted for a significant proportion of the variability in the data for both bite size and intake rate (Table 5.5). Surprisingly, with the exception of *T. leucothrix* ($P \leq 0.0001$) and *H. hirta* ($P \leq 0.05$), bite rate did not decline with increasing plant height and, in most cases, there was no consistent relation between these variables (Table 5.4).

Bite size was negatively correlated ($P \leq 0.05$) with greenness in *A. appendiculatus*, *T. triandra* and *T. leucothrix* (Table 5.4) but this probably reflects the fact that the

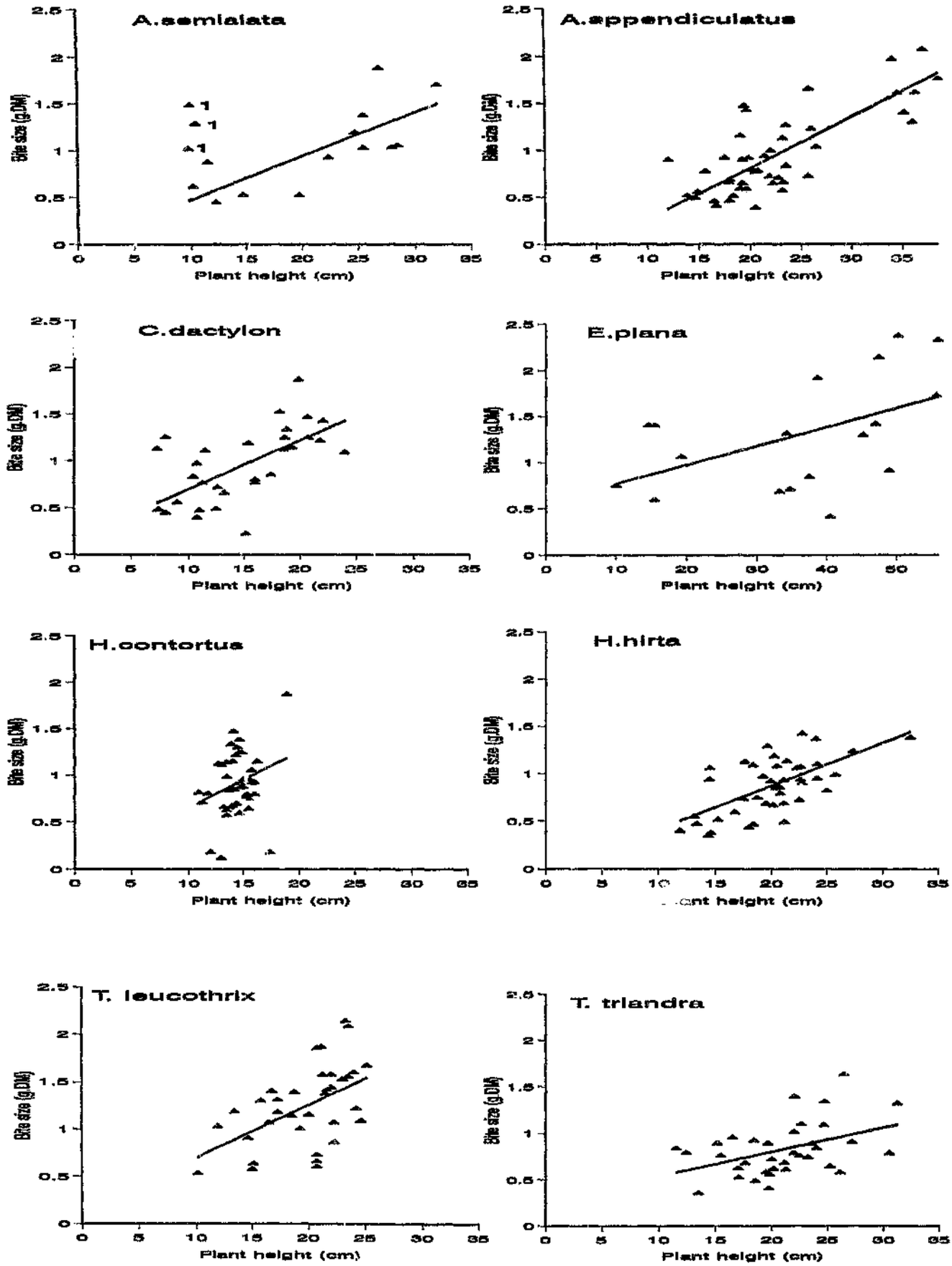

Figure 5.3 The relation between cattle bite size and plant height in eight sourveld grasses. Points marked with (1) were considered outliers and not used to calculate the regression line.

Figure 5.3 The relation between cattle bite size and plant height in eight sourveld grasses. Points marked with (1) were considered outliers and not used to calculate the regression line.

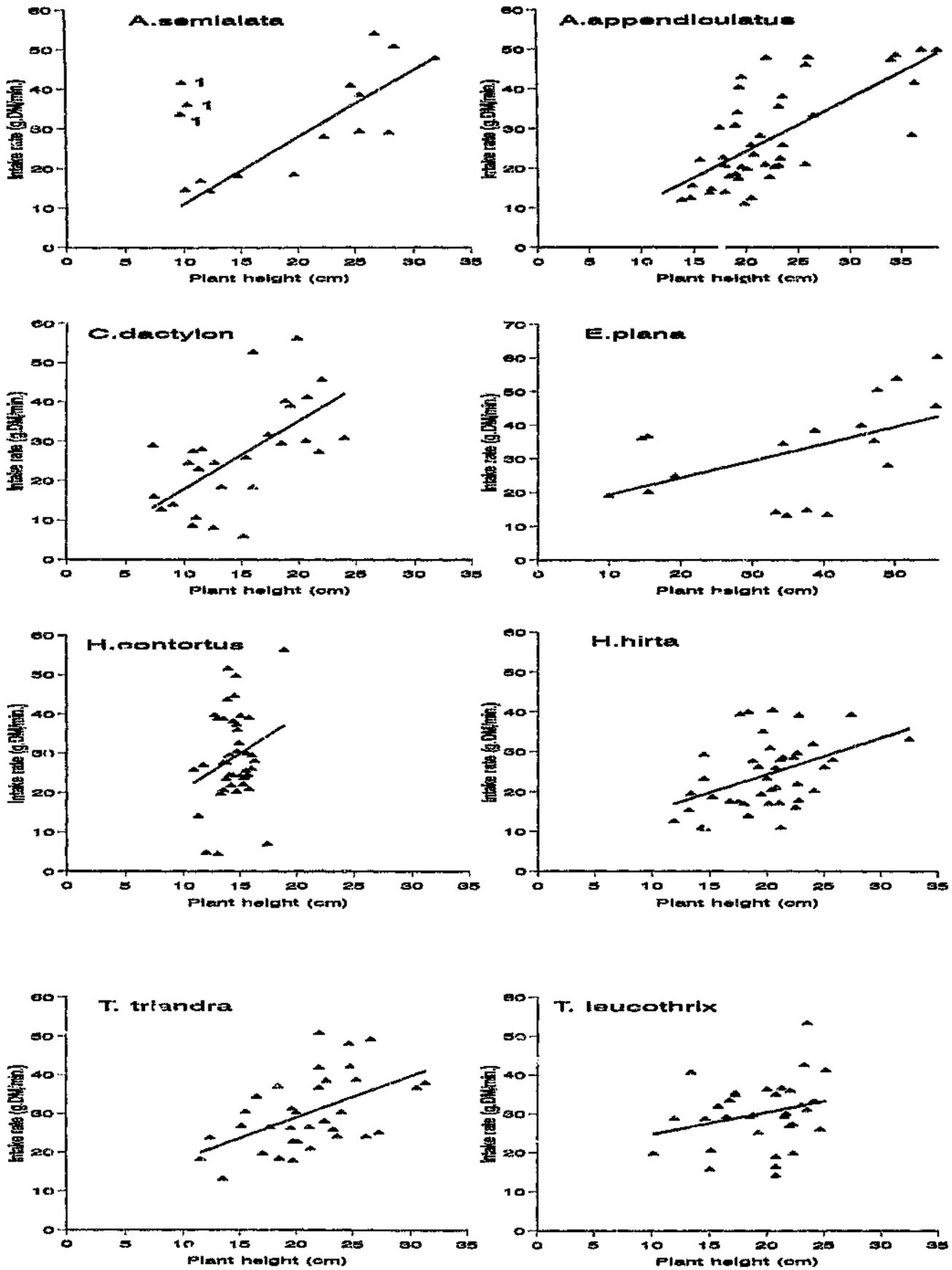

Figure 5.4 The relation between the rate of dry matter intake in cattle and plant height in eight sourveld grasses. Points marked with (1) were considered outliers and not used to calculate the regression line.

shortest plants were also generally the greenest. Bite size was also positively correlated with stemminess in different species (Table 5.4), apparently, for different reasons. In the case of *A. appendiculatus, H. contortus* and *T. triandra* this relation can be dismissed as spurious because of the low levels of stemminess actually recorded in these grasses (Appendix 4.4). Similarly, in the case of *E. plana*, the relation is also likely to be coincidental because the stemmiest plants also happened to be very tall which would have allowed the animals to harvest a very large bite (pers. obs.). However, with *H. hirta*, very large bites were harvested on stemmy tufts, because the animal in question simply prehended the whole plant and made no attempt to select the available leaf. This is identical to what cattle have frequently been observed to do in the field (pers. obs.).

5.5 Discussion

The results of the present study showed that for cattle, there was surprisingly little difference in the potential rate of DM ingestion between the eight sourveld grasses investigated. Similarly, with the exception of *H. contortus* which gave a significantly higher ($P \leq 0.05$) rate of DM intake than any of the other grasses, differences between species for sheep were also small and non-significant. These results suggest that both cattle and sheep can expect to achieve fairly similar rates of intake from all of the species considered.

Intake rate is the product of bite size and bite rate with the latter variables generally being inversely correlated (Hodgson 1981). This was evident in the present study where species with large bites tended to have low biting rates and vice versa, resulting in fairly similar rates of intake for most species (Figs 5.1 & 5.2). Thus, although cattle and sheep achieved above-average bite sizes from *E. plana*, intake rates were relatively low due to the difficulty experienced in severing and masticating its tough leaves. An obvious exception to the above was *H. contortus* which, due to its large and rapidly prehended bites, allowed sheep to achieve intake rates substantially higher than those measured on any of the other species (Fig. 5.1).

The present study therefore succeeded in its primary objective of determining the potential ingestion rates of different sourveld grasses. However, these estimates should be used with caution as first, they are mean values characterised by large

standard errors resulting from the wide range of plant structures encountered in grazing each species. Second, if it is accepted that plant structure affects intake rate, then current estimates may be biased simply because the distribution of tuft structures used in assessing each grass was unlikely to have been identical. Little biological significance should therefore be attached to absolute or between-species differences in intake rate, even when such differences are statistically significant.

The present study was only partially successful, however, in its secondary objective of quantifying the relation between ingestion rate and plant structure for individual grasses. While a direct relation between plant height and ingestion rate existed in cattle, no consistent relation could be detected with sheep. In cattle, bite size and intake rate increased with increasing leaf height in most grasses, presumably because animals were able to prehend a bigger volume of herbage through an increase in bite depth and bite area (Black & Kenney 1984; Murson *et al.* 1989; Laca *et al.* 1992). In contrast, plant height had little apparent effect on bite size and intake rate in sheep (Table 5.2). Bite size generally shows an asymptotic relation with plant height (section 3.4) so presumably the height of most of the tufts grazed by sheep exceeded the height at which bite size became restricted by this variable. This suggests that some other factor, not measured in this study, such as leaf or tiller density, was responsible for the observed variability in sheep bite sizes and intake rates.

Stemminess also affected ingestion rates but only in *H. hirta* where the culms produced were of a sufficient density and consistency to affect this variable. However, the resultant effect was markedly different between cattle and sheep. Sheep continued to select green leaf on stemmy *H. hirta* tufts, but their rate of DM intake declined due to the apparent physical restriction of stems on biting rates. Conversely, bite sizes and hence intake rates in cattle tended to increase with stemminess as they made no attempt to be selective, but harvested large masses of leaf and stem in single mouthfuls.

The present estimates of potential ingestion rates are comparable with published data, at least for sheep. For example, mean intake rates reported here (4.0-6.5 g.DM/min.) fall within the ranges recorded by Allden & Whittaker (1970), and Penning & Hooper (1985), of 1.0-7.1 g.DM/min. and 2.2-6.4 g.DM/min., respectively, for sheep on rye-grass pastures. Present results also agree with earlier, field estimates of intake

rate. For example, the mean intake rate recorded for *H. hirta* (4.3 g.DM/min.) lies within the range (1.7 - 6 g.DM/min.) recorded at old lands where sheep would also have been grazing this species (section 3.4). Sheep biting rates for this and other species (mean: 45 bites/min.) were, however, markedly lower than those recorded for animals in the field (range: 50-75 bites/min.).

Present estimates of bite size and intake rate in cattle are higher than published data for animals at pasture, e.g. Greenwood & Demment (1988) but are comparable with those of Murson *et al.* (1989) where a range of bite sizes of 0.37-0.57 g was obtained with steers grazing intact turves of rye-grass. Present estimates of ingestion rates in cattle are, however, considerably higher than previous measurements made in the field using fistulated animals (section 3.4). For example, the mean intake rate obtained for *H. hirta* (28.96 g.DM/min.) is considerably higher than the range (10 - 22 g.DM/min.) recorded over a number of sward structures at old lands camp. This discrepancy probably reflects the incomplete recovery of fistula samples and the consequent underestimation of intake rates (Stobbs 1973a). As noted with sheep, biting rates (mean: 30.11 bites/min.) were considerably lower than those recorded for cattle under field conditions (range: 35-70 bites/min.).

Despite the general consensus between pot and field estimates of ingestion rates for sheep, it is suggested that the present results overestimate potential ingestion rates of both animals for the following reasons. First, present estimates do not include the time taken to search, locate and move between tufts or feeding stations, all of which increase handling time and therefore decrease the average rate of ingestion of a particular species. The lengths of these handling time components are extremely variable and depend upon the initial density of the species, the rate at which it is being consumed and the extent to which that species has been defoliated. Second, fasted animals are likely to ingest food faster than non-fasted animals under field conditions. For example, fasted cattle (Greenwood & Demment 1988) and sheep (Newman *et al.* 1994) are recorded as having a 62 % and 57 % greater rate of DM intake, respectively, than their non-fasted counterparts. Third, the present study did not take into account the cost of discriminating between intermingled species of different acceptability which is also likely to reduce ingestion rates, particularly in cattle.

Despite these limitations, the methodology employed in the present trial was

basically successful. Realistic estimates were obtained for a number of different grass species while the logistical and methodological problems associated with trying to measure ingestion rates in the field from a number of different species were largely avoided. Although the present method may be criticised as being artificial, it is suggested that realistic estimates of ingestion rate will be achieved provided the following guidelines are adhered to. First, plants used should be of a similar structure to those growing *in situ* and should therefore be kept under comparable conditions to those in the field. Second, experimental animals should be tractable and familiar with the species in question. Third, plants should not be defoliated to a greater degree than would normally occur under field conditions. Provided these conditions are met, the method shows potential as a research tool, particularly for measurements of foraging behaviour which are intractable in the field.

In conclusion, the following recommendations on the use of the present data for modelling animal production or dietary selection are made. For sheep, it is recommended that mean ingestion rates for species be used in conjunction with the relevant standard errors to set upper and lower limits for rates of intake. For cattle, linear intake rate-plant height regressions should be used to predict ingestion rates for each species on the basis of its leaf height. In both animals, emphasis should be placed on the range of potential intakes available from a particular species rather than the absolute values.

5.6 Conclusions

5.6.1 For cattle, there was little difference between sourveld species in potential bite size and intake rate. Similarly, with the exception of *H. contortus* which had the highest potential rate of intake, there was little difference between species in bite size and intake rate for sheep.

5.6.2 In all grasses there was a large degree of within-species variation in bite size and intake rate. However, present estimates appeared realistic and, particularly for sheep, were within the range of values obtained under field conditions.

5.6.3 Bite size and intake rate in cattle increased linearly with increasing plant height in most species. However, plant height appeared to have no consistent effect on sheep bite sizes or intake rates.

5.6.4 The present methodology appeared to provide acceptable estimates of the potential bite sizes and intake rates obtainable from different sourveld grasses. However, these estimates need to be adjusted for search time and the level of satiation of the grazing animal.

CHAPTER 6

RUMINAL DEGRADATION RATES OF COMMON SOURVELD GRASSES

6.1 Objective

The specific objectives of this experiment were to:

(i) determine the rate and extent of DM and neutral detergent fibre (NDF) degradation in the rumen of certain sourveld grasses;

(ii) determine the effects of season on the rate and extent of degradation of these components.

6.2 Introduction

The sour grasslands of South Africa, termed 'sourveld', primarily comprise tropical C4 grasses which vary widely in nutritive quality and acceptability to the grazing animal (Gibbs Russell *et al.* 1990). By definition, grasses in sourveld exhibit a marked seasonal decline in quality and are generally unpalatable and of low nutritive value in the dormant season (Tainton 1981). In these grasslands, voluntary feed intake and to a lesser extent, nutritive value, are probably the major determinants of animal production. Provided herbage availability is not restricted, voluntary intake of these forages will largely depend upon the rate of DM disappearance in the rumen (Poppi *et al.* 1980a). This in turn will be dependent upon the relative proportions of cell solubles, potentially digestible cell wall and indigestible cell wall in the forage, and the rates of digestion and passage of these different components (Mertens & Ely 1982). Prediction of animal production on these multi-species swards therefore depends on accurate estimates of the nutritive value and, more importantly, the degradation characteristics of the constituent grass species.

Ruminal degradation rates are also likely to be relevant in models of dietary selection and foraging behaviour. Optimal foraging theory assumes that the utility of a food is determined by the ratio of energy content to handling costs (Emlen 1966), traditionally defined as the time and energy required to prehend and ingest a particular food. However, for ruminants, where intake is restricted by rumen capacity and outflow

rates (Roux & Meissner 1984), handling costs should also include the retention time of the forage in the rumen (Spalinger *et al.* 1986). While not a direct energetic cost to the animal, retention time nevertheless incurs an opportunity cost through a depression in forage intake. Consequently, the degradation characteristics of a species should be an important determinant of its acceptability to the animal, in conjunction with its potential rate of ingestion and nutritive value (Owen-Smith & Novellie 1982).

The nutritional quality of native grasses in South Africa have previously been investigated and published data are available on the *in vitro* and/or crude protein, crude fibre and ash content of a number of species, e.g. (Theron 1966; van Schalkwyk *et al.* 1968; Opperman *et al.* 1974; O'Reagain 1993). In particular, Oellerman (1965) documented the cellulose and protein digestibilities of *Themeda triandra* and the effect of season on these variables. However, there appears to be no published data on the rates of digestion of different species or their forage fractions in the rumen, which seriously restricts the utility of the available data for modelling.

6.3 Procedure

6.3.1 Study site

All samples were collected at the Dohne Agricultural Development Institute. A full description of the study site is given in section 2.3.1.

6.3.2 Sample collection and preparation

Eleven grass species common to the Dohne Sourveld were collected for analysis. These were *Alloteropsis semialata* (R. Br) Hitchc. subsp. *eckloniana* (Nees) Gibbs Russell, *Andropogon appendiculatus* Nees, *Cynodon dactylon* (L.) pers., *Elionurus muticus* (Spreng.) Kunth, *Eragrostis plana* Nees, *Harpochloa falx* (L.f.) Kuntze, *Hyparrhenia hirta* (L.) Stapf, *Microchloa caffra* Nees, *Themeda triandra* Forsk and *Tristachya leucothrix* Nees. Species nomenclature follows Gibbs Russel *et al.* (1990). Species were selected on the basis of a subjective assessment of their potential importance for animal production based on their general abundance, palatability and ability to produce herbage. All are perennial species and, with the exception of *Cynodon dactylon*, which is stoloniferous, all are tussock grasses. All samples were collected on sites which had been burnt the previous winter. *Hyparrhenia hirta* and *H. contortus* samples were

collected from a secondary grassland community on a previously (>10 years) cultivated site. *Cynodon dactylon* samples were collected from sites of localised nutrient deposition, e.g. around gates, within undisturbed grassland. All other species were collected from undisturbed rangeland typical of the Dohne Sourveld.

Leaf samples from all species were collected in spring (October), summer (January-March), autumn (May) and winter (August). With the exception of *E. plana* and *C. dactylon*, all samples were hand-plucked in an attempt to simulate selection by the grazing animal. *Eragrostis plana* and *C. dactylon* samples were clipped due to their tough leaves and short stature, respectively. Samples were dried in a forced air oven at 65° C for 48 hours, milled (3 mm sieve) and stored in sealed plastic bags until incubated. In some seasons, insufficient samples were collected from certain species to permit full analyses and these data are not presented.

6.3.3 Test animals and basal diet

Two, three-year-old Bonsmara steers (average mass 400 kg) each fitted with a rumen cannula (10 cm internal diameter) were used throughout. Animals were held together in stalls and fed a basal diet of approximately 20 kg of Coastcross II (*C. dactylon* x *C. nlemfluensis*) hay at 08:00 each day. Animals also received a small amount of lucerne hay (0.5-1 kg) on a daily basis. Water was freely available at all times.

6.3.4 Incubation procedure

The rate of DM disappearance in the rumen was estimated using the nylon bag technique. Bags measuring 7.5 x 10.5 cm (53 μm pore size), were double-seamed with rounded corners and all stitch-lines sealed with commercially-available epoxy. Approximately 5 g of sample was placed in each bag which was then closed with a rubber castrating-ring. Bags were placed inside a small nylon mesh bag with ballast, attached to a length of polypropylene twine and suspended in the rumen. Incubation was for 3, 9, 24, 32, 56 or 72 hours. Two grass species were generally incubated together. For each species, four bags were provided for each incubation period in each animal, i.e. a total of 56 bags per species, per season. A single milled sample of the basal ration was also included in each incubation period in each animal as a control.

Bags removed from the rumen were gently washed to remove adhering material

and then frozen. All bags from the same run were then defrosted, rinsed in a washing machine for a set cycle of 10 minutes and dried in a forced air oven at 65° C until constant mass. Bags were then reweighed and contents removed for further analysis. Residues were bulked across incubation period and animal for each species. Neutral detergent fibre (NDF) analyses were conducted on sample residues using the method of Goering and van Soest (1970).

6.3.5 Statistical analysis

Degradation data are frequently analyzed using the model of Orskov & McDonald (1979), i.e. $p = a + b[1-\exp(-ct)]$ where p = disappearance rate at time t, a = rapidly digesting fraction, b = slowly digesting fraction, c = rate constant of fraction b and t = time of incubation. However, the model seemed inappropriate for the present data as some degradation curves, e.g. *A. appendiculata* in winter, were almost linear and could not be fitted to the model. The model of Orskov and McDonald (1979) has also been criticised on the grounds that, while the constants are statistically valid, they are of little biological significance (Pienaar *et al.* 1989). Accordingly, the soluble fraction (SF) and potentially digestible fraction (PDF) of dry matter (DM) were simply assumed to be those fractions digestible at 3 and 72 hours respectively. Neutral detergent solubles (NDS) was calculated as 1-NDF, potentially digestible cell wall (PDCW) as $NDF_{(72\ hour)}$- NDS and indigestible cell wall (IDCW) as NDF-PDCW. Degradation rates of DM (k_d) and PDCW (k_c) were calculated as 1/MRT where:

$$MRT = (1/N)\ \Sigma[\tfrac{1}{2}n(t^{-}+t)]$$

and N = total mass of organic material (or NDF) that has disappeared, n = mass of organic material (or NDF) that has disappeared between t^{-} and t, and Σ signifies the sum of such quantities for successive intervals until n becomes zero, i.e. 72 hours (Graham & Williams, 1962, cited by Pienaar *et al.*, 1989). The overall degradation rate of DM (k_d) therefore includes the soluble fraction.

Differences between species and seasons in SF, PDF and k_d were analyzed using a t-test with the ANOVA procedure of SAS (SAS 1991). Bags were considered as subsamples and animals as replicates. As sample residues were bulked across animals for NDF analyses, the NDS, PDCW, IDCW and k_c data were not subjected to statistical analysis due to the lack of replication.

6.4 Results

6.4.1 Extent and rate of DM degradation in the rumen

The soluble fraction (SF), potentially digestible fraction (PDF) and degradation rate of DM (k_d) in the rumen of the different sourveld species are presented in Table 6.1. There were marked differences in the SF of the different species in all seasons, with the range in values varying from 17-27 % in spring to 7-18 % in winter (Table 6.1). *Alloteropsis semialata* had a consistently high SF while *E. plana* and, to a lesser extent, *A. appendiculatus* tended to have the lowest levels of this fraction. On average, the SF of all species declined over the growing season but the largest decrease ($P \leq 0.01$) occurred between autumn and winter (Table 6.2). There were also significant ($P \leq 0.05$) differences between species in PDF with a range in values varying from 57-81 % in spring to 32-66 % in winter. With the exception of *C. dactylon* in winter, *M. caffra* had the lowest PDF in all seasons. Season also had a major ($P \leq 0.01$) effect on PDF with this fraction declining sharply from spring (mean: 77.30 %) through to winter (mean: 55.83 %).

There were significant differences ($P \leq 0.01$) between species in the rates of DM degradation (k_d) in the rumen (Table 6.1). *Andropogon appendiculatus* and *E. plana*, as well as *H. falx* and *M. caffra* in summer, had significantly ($P \leq .05$) lower k_d than most of the other species. Conversely, *A. semialata* and *C. dactylon* tended to have the fastest k_d in most seasons. In winter, the mean rate of DM degradation of all species (Table 6.2) was significantly ($P \leq 0.05$) slower (mean:0.039 % h^{-1}) than in all other seasons (mean:0.048 % h^{-1}).

Aside from its effects on the rate and extent of digestion, season also had a marked effect on the actual shape of the degradation curve of DM in the rumen (Figure 6.1). In spring and summer degradation curves tended to be non-linear with initial rates of degradation tending to be high but then levelling off with time. Conversely, degradation curves in autumn, but particularly in winter, tended towards linearity indicating an almost constant rate of degradation with time in the rumen.

Table 6.1 The soluble fraction (SF), potentially digestible fraction (PDF) and fractional degradation rate (k_d) of different sourveld grasses in spring, summer, autumn and winter. Values in the same column with the same superscript are not significantly different at the 5 % level

Species	SPRING			SUMMER		
	SF	PDF	k_d	SF	PDF	k_d
	%DM		1/h	%DM		1/h
A. semialata	22.99^{abc}	79.28^{abc}	0.052^{cd}	25.01^{a}	75.5^{a}	0.064^{d}
A. appendiculatus	19.35^{bdc}	79.27^{abc}	0.042^{a}	18.18^{bc}	72.57^{b}	0.046^{b}
C. dactylon	23.31^{abc}	81.39^{ab}	0.054^{ecd}			
E. muticus	27.53^{a}	79.48^{abc}	0.057^{ed}			
E. plana	19.59^{bdc}	81.99^{ab}	0.043^{ab}	10.88^{d}	69.99^{b}	0.038^{a}
H. contortus	22.04^{abcd}	79.84^{abc}	0.054^{ecd}			
H. falx	24.60^{ab}	74.94^{c}	0.063^{e}	17.07^{c}	63.08^{c}	0.047^{b}
H. hirta	23.12^{abc}	82.78^{a}	0.053^{ecd}			
M. caffra	17.02^{d}	57.60^{d}	0.049^{bc}	17.07^{c}	57.51^{d}	0.044^{ab}
T. triandra	18.02^{dc}	76.86^{bc}	0.050^{cd}	20.35^{b}	76.04^{a}	0.050^{bc}
T. leucothrix	20.43^{bdc}	77.06^{bc}	0.050^{cd}	26.26^{a}	75.90^{a}	0.060^{cd}
	AUTUMN			WINTER		
A. semialata	24.13^{a}	65.35^{abc}	0.054^{fg}	18.16^{a}	58.38^{cd}	0.048^{e}
A. appendiculatus	13.32^{e}	61.01^{dc}	0.037^{a}	11.32^{cd}	58.02^{cd}	0.033^{a}
C. dactylon	18.21^{cd}	55.39^{e}	0.061^{h}	7.97^{e}	32.93^{f}	0.047^{de}
E. muticus	20.53^{b}	62.06^{bc}	0.045^{c}	14.96^{b}	54.23^{e}	0.042^{cd}
E. plana	11.90^{e}	57.21^{ed}	0.041^{b}	9.32^{ed}	61.98^{b}	0.033^{a}
H. contortus	20.71^{b}	63.72^{bc}	0.048^{cd}			
H. falx				10.87^{d}	55.12^{de}	0.037^{b}
H. hirta	22.64^{a}	68.82^{a}	0.053^{ef}	9.79^{ed}	59.13^{bc}	0.040^{bc}
M. caffra	17.99^{d}	44.96^{f}	0.059^{hg}			
T. triandra	19.91^{bc}	66.79^{ab}	0.047^{cd}	13.22^{bc}	66.53^{a}	0.042^{cd}
T. leucothrix	20.31^{b}	61.24^{dc}	0.050^{de}	11.02^{cd}	56.22^{cde}	0.041^{bc}

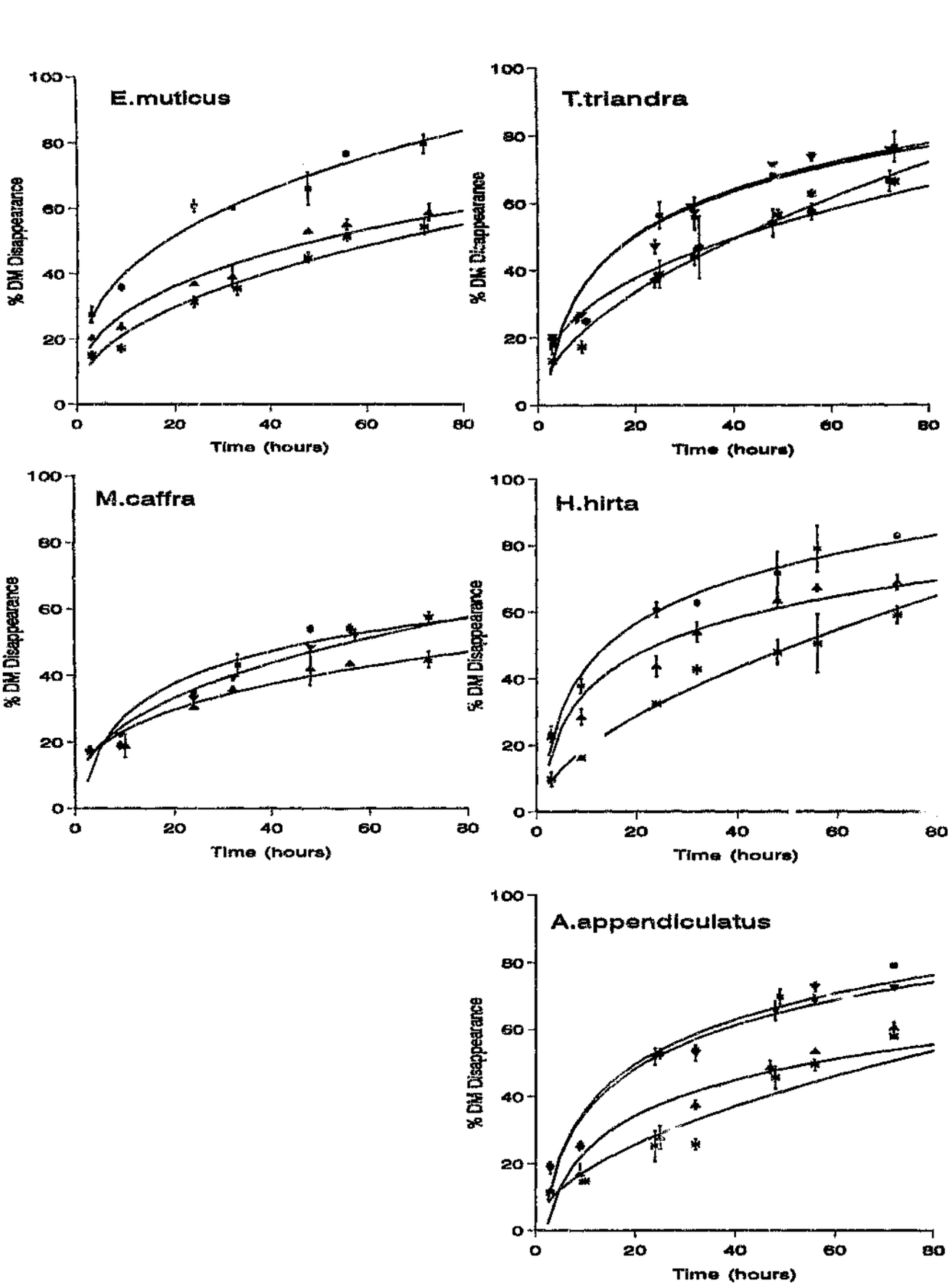

Figure 6.1 (b) Mean DM disappearance (± SE) over time of different sourveld grasses incubated in the rumen (■ = spring, ▼ = summer, ▲ = autumn, * = winter).

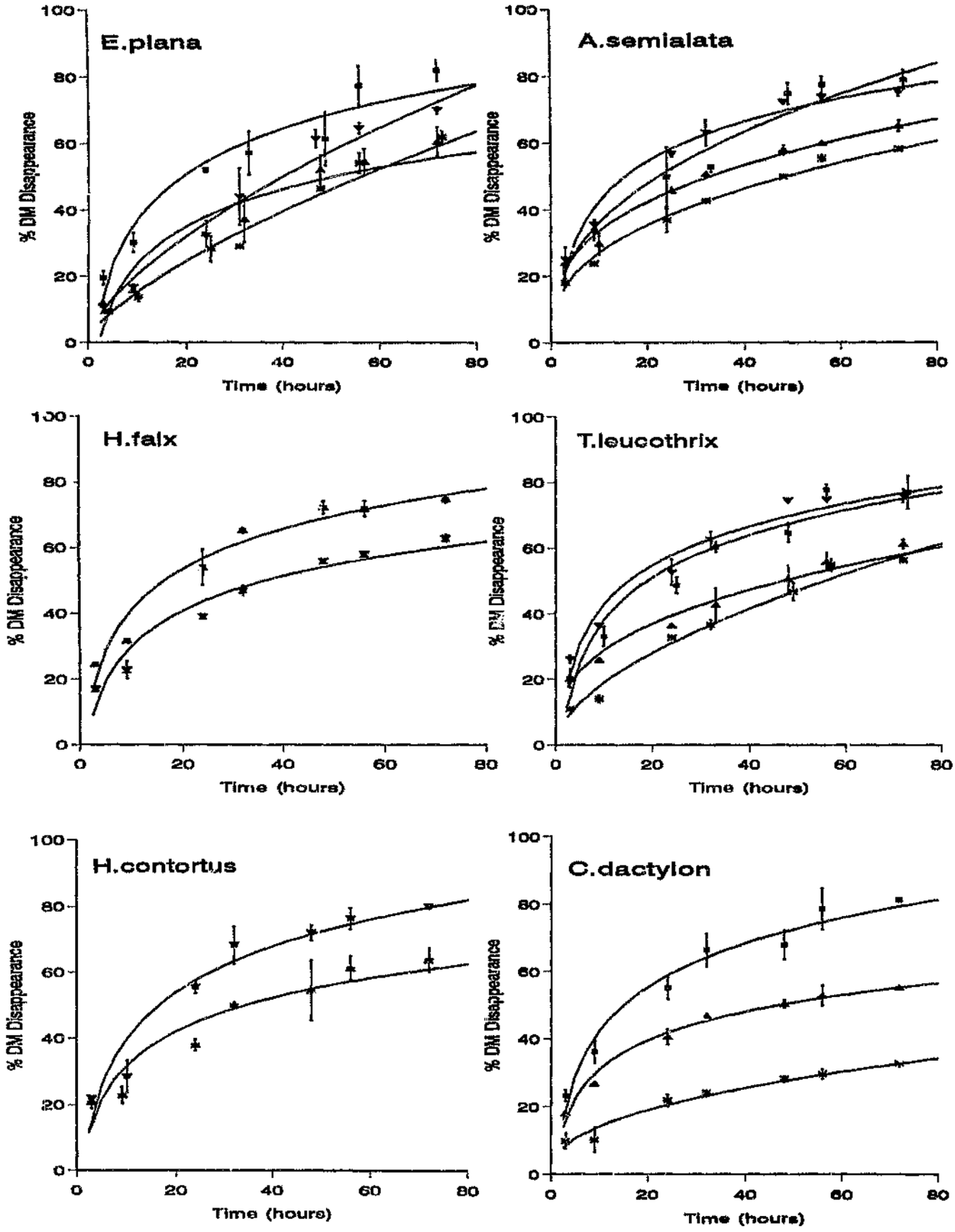

Figure 6.1 (a) Mean DM disappearance (± SE) over time of different sourveld grasses incubated in the rumen (■ = spring, ▾ = summer, ▲ = autumn, * = winter).

Table 6.2 Mean soluble fraction (SF), potentially digestible fraction (PDF) and fractional degradation rate (k_d) of sourveld grasses in spring, summer, autumn and winter. Means in the same column with the same superscript are not significantly different at the 5 % level

SEASON	SF	PDF	k_d
	% DM		1/h
Spring	21.65[a]	77.30[a]	0.05[a]
Summer	19.30[ab]	70.15[b]	0.048[a]
Autumn	18.96[b]	60.72[c]	0.048[a]
Winter	17.84[c]	55.83[c]	0.039[b]

6.4 2 Extent and rate of degradation in the rumen

The percentage of neutral detergent soluables (NDS), potentially digestible cell wall (PDCW) and indigestible cell wall (IDCW), and the degradation rates of the potentially digestible cell wall (k_c) of the different species are presented in Table 6.3. There were marked differences in NDS content between species with *E. plana, A. appendiculatus* and *C. dactylon* tending to have the lowest levels of NDS. Conversely, *T. triandra, E. muticus* and, to a lesser extent, *A. semialata*, tended to have the highest levels of this variable. Season appeared to have no effect on NDS content. There were large differences in PDCW between species in all seasons with the range in values varying by between 10 to 20 %. The content of PDCW for all species showed a marked decline from spring to winter (Table 6.3).

With the exception of spring, there were also marked differences between species in IDCW. Generally, *C. dactylon, E. plana* and *M. caffra* had the highest content of IDCW while levels were least in *T. triandra, H. hirta* and *A. semialata*. Season had a major effect on IDCW with levels in winter (mean:30.46 %) being almost double those of spring (mean:14.17 %). Degradation rates of PDCW also varied between species and were generally lowest in *E. plana, A. appendiculatus* and *M. caffra*. In terms of the effect of season rates of PDCW digestion were similar in spring and summer, lower in autumn and lowest in winter.

Table 6.3a Neutral detergent solubles (NDS), potentially digestible cell wall (PDCW), indigestible cell wall (IDCW) and PDCW degradation rate (k_c) of different sourveld grasses in spring and summer

	SPRING			
	NDS	PDCW	IDCW	k_c
Species	%DM			1/h
A. semialata	31.57	55.31	13.11	0.036
A. appendiculatus	21.60	63.25	15.15	0.033
C. dactylon	31.62	58.03	10.34	0.040
E. muticus	26.44	60.50	13.05	0.040
E. plana	26.36	62.84	10.79	0.033
H. contortus	26.61	61.63	11.75	0.042
H. falx	22.70	60.69	16.60	0.047
H. hirta	26.28	65.28	8.43	0.041
M. caffra	20.97	50.81	28.21	0.032
T. triandra	27.49	56.64	15.86	0.044
T. leucothrix	25.20	59.78	15.01	0.041
	SUMMER			
A. semialata	30.96	53.06	15.97	0.040
A. appendiculatus	24.34	57.19	18.46	0.040
C. dactylon	21.76	48.85	29.38	0.040
E. muticus				
E. plana	18.08	59.98	21.93	0.034
H. contortus				
H. falx	23.36	51.59	25.04	0.035
H. hirta				
M. caffra	23.68	48.34	27.97	0.031
T. triandra	26.58	59.57	13.84	0.040
T. leucothrix	27.40	57.67	14.92	0.041

Table 6.3b Neutral detergent solubles (NDS), potentially digestible cell wall (PDCW), indigestible cell wall (IDCW) and PDCW degradation rate (k_c) of different sourveld grasses in autumn and winter

	AUTUMN			
	NDS	PDCW	IDCW	k_c
Species	%DM			1/h
A. semialata	25.71	49.74	24.54	0.034
A. appendiculatus	23.40	51.33	25.27	0.029
C. dactylon	23.75	44.63	31.62	0.044
E. muticus	27.47	46.69	25.84	0.030
E. plana	19.42	53.47	26.61	0.030
H. contortus	26.01	48.37	25.62	0.035
H. falx				
H. hirta	25.99	53.56	20.45	0.036
M. caffra	23.33	43.93	32.74	0.027
T. triandra	26.91	51.45	21.64	0.030
T. leucothrix	24.44	49.04	26.52	0.030
	WINTER			
A. semialata	28.14	43.23	28.62	0.032
A. appendiculatus	20.83	49.72	29.44	0.027
C. dactylon	20.11	29.09	50.79	0.034
E. muticus	29.62	39.00	31.37	0.029
E. plana	22.17	52.27	25.55	0.027
H. contortus				
H. falx	20.85	48.53	30.61	0.029
H. hirta	27.77	45.80	26.42	0.029
M. caffra				
T. triandra	29.64	49.47	20.88	0.027
T. leucothrix	24.18	44.79	31.02	0.033

6.5 Discussion

The present data indicate considerable variation between the different sourveld grass species in their extent and rate of degradation achieved in the rumen. Overall, *E. plana, M. caffra* and *A. appendiculatus* had the poorest degradation characteristics in terms of the proportions of soluble and potentially digestible fractions and the rates of degradation of these components, while those of *T. triandra, H. hirta* and *A. semialata* tended to be the most favourable. *Cynodon dactylon, E. muticus, H. falx, H. contortus* and *T. leucothrix* tended to have degradation characteristics somewhat intermediate between these two groups but there were marked seasonal effects on the relative ranking of all species.

These differences in the rate and extent of degradation in the rumen appear to be partly associated with differences in leaf tensile strength between grass species. As an example, *E. plana* and *M. caffra* have tensile strengths of 9247 and 7887 (dynes m^{-1}) respectively, compared to 991 and 2819 for *T. triandra* and *H. hirta* (O'Reagain 1989; O'Reagain 1993). Leaf tensile strength is largely determined by the concentration of cellulose and the amount of sclerenchyma tissue in the leaf (Evans 1964; Wilson 1965) both of which reduce digestibility (Wilson *et al.* 1989a). Intake and degradation rates of low-strength leaves may also be greater than high-strength leaves, even though digestibilities are similar (Inoue *et al.* 1989).

Generally, the degradation characteristics of a species were also a good indication of its overall acceptability. For example, *T. triandra* and *H. hirta* are readily grazed by sheep and cattle while *E. plana* and *M. caffra* are generally avoided by both animals (Stoltsz & Danckwerts 1990; O'Reagain 1993). A noticeable exception to this trend is *E. muticus* which, despite its favourable degradation characteristics, is seldom grazed by either cattle or sheep (Stoltsz & Danckwerts 1990) possibly because of the presence of aromatic oils in this species.

However, the case of *A. appendiculatus* is more perplexing. Despite being highly acceptable (Chapter 4) and having relatively low-strength leaves (2971 dynes m^{-1}, O'Reagain 1989), the extent and rate of degradation of this species was unexpectedly low, being only marginally better than that of *E. plana*. This anomaly may be due to the presence of tannin-like substances observed in *A. appendiculatus* as well as in other sourveld grasses (Ellis 1990) which could interfere with microbial degradation of fibre

in the rumen.

However, a more likely explanation for the similarity in degradation characteristics between these species was that the rate and extent of digestion of *E. plana* was possibly overestimated in the present study, through milling. Grinding samples to a constant size may mask the effects of morphological traits on degradation (Lentz & Buxton 1992) by removing anatomical barriers to digestion. For example, milled (1 mm) rye-grass and *Phalaris tuberosa* have similar digestibilities *in vitro*, but, when cut into 10 mm sections, rye-grass is 60 % more digestible than the latter species (Grabber & Allanson 1992). Fine grinding may also artificially inflate estimates of PDCW and digestion rates (Lentz & Buxton 1992). As mastication is the major mechanism of particle breakdown (Pond *et al.* 1984; Wilson *et al.* 1989b) it is suggested that, in practice, the tough leaves of species like *E. plana* and *M. caffra* are masticated into relatively larger fragments than other species, resulting in significantly lower rates of degradation than those estimated *in sacco*.

Overall, estimates of the forage fractions of sourveld grasses are in general agreement with those reported for other tropical, C4 species. Minson (1984) reported NDS and NDF values of approximately 20 and 69 % respectively for five African *Digitaria* species, which is within the range of present results obtained in spring and summer (Table 6.3a). Similarly, potential digestibilities, i.e. 72-hour, measured here are close to those estimated *in vitro* for *D. milanjiana* (Masaoka *et al.* 1991) and *Cenchrus ciliaris* (Wilson *et al.* 1989a). However, Poppi *et al.* 1980b reported cell wall degradation rates for *Chloris gayana* and *Digitaria decumbens* (0.0208 - 0.0219) which were appreciably lower than those recorded here.

Given the paucity of information available on local rangeland grasses, individual species comparisons are difficult. The only known published work is that of Opperman *et al.* (1974); these authors (Opperman *et al.* loc. cit.) reported spring *in vitro* (48 hour) digestibilities of *E. muticus* of 62 % which are similar to those recorded for the 48 hour incubation period (59 %) in this study (Appendix 5.1).

When compared to published data on temperate C3 species, the present results emphasize the general poor degradability characteristics of C4 grasses in general and sourveld species in particular. Even in spring when sourveld grasses are most digestible, cell wall degradation rates (k_c) measured in this study were usually less than half those

for C3 species (e.g. Hoffman *et al.* 1993). For example, Lentz & Buxton (1992) reported k_c values for *Dactylis glomerata* of 0.7 to 0.9 compared to recorded values of 0.3 to 0.4 in the present study. In contrast to the present data, k_c values in C3 grasses were also markedly higher in spring than in the late season (Hoffman *et al.* 1993). Degradation rates of C3 grasses only appear to decline to those of C4 species when the former are in full bloom, e.g. Lentz & Buxton (1992).

These differences reflect the basic dichotomy in leaf anatomy between C3 and C4 species. In C3 grasses, loosely-packed mesophyll cells and widely-spaced vascular bundles (Akin 1989) allow rapid microbial degradation of the leaf substrate, while in C4 species, the typical Kranz anatomy reduces microbial access to interior mesophyll cells (Akin 1989). Interestingly, *Alloteropsis semialata* may possess either the C3 (subsp. *ecklioniana*) or C4 (subsp. *semialata*) type leaf anatomy (Ellis 1977). Although *A. semialata* from the study area has been described as having the C3-type anatomy, it does not appear to have degradation characteristics markedly different from the other species, all described as having the typical C4-type leaf anatomy (Ellis 1977). However, *A. semialata* did have significantly higher levels of cell solubles (but not NDS) in winter than other species, a possible reflection of its relatively slower rate of senescence in the dormant season (pers. obs.).

As reported, there were marked seasonal effects on degradation characteristics of all species with the potentially digestible fraction (SF, PDF, PDCW) declining, the indigestible fraction (IDCW) increasing and the degradation rate of DM decreasing from spring through to winter. These trends largely reflect seasonal changes in plant phenology and physiology with the approach of the dormant season. The sharp drop in the SF of leaves in winter is a consequence of the mass translocation of soluble components to roots and crowns in the late season (Clark 1977) and the subsequent leaf senescence in winter which occurs with the onset of low temperatures (pers. obs.).

The decline in PDF and PDCW in autumn and winter results directly from the lignification of leaf tissue with increasing maturity, e.g. Hoover (1986). In accordance with this, Oellerman (1965) reported that, although the cellulose content of *T. triandra* did not increase, the digestibility of this component decreased as plants matured. Lignin bonds to plant fibre reducing accessibility to micro-organisms (Norton 1981) and is the major determinant of the extent of herbage digestion in the rumen (Smith *et al.*

1970). In *T. triandra*, lignification initially occurs in the vascular bundles but thereafter spreads outward to surrounding tissue as leaves mature (Viljoen & Roberts 1968). Leaf silicification also increases markedly with maturity in *T. triandra* and other sourveld grasses (Theron 1966) and may further depress herbage digestibility (van Soest & Jones 1968).

The decline in degradation rates of the PDF of forages probably reflects the decrease in the SF of these species in winter. Although there appeared to be no major decline in the degradation rate of PDCW, the potential extent of degradation was markedly lower in the late season.

Present results clearly indicate that species composition has the potential to have a major impact on herbage intake, and thus animal production, in sourveld. For example, based on the present data and using the formula of Roux & Meissner (1984), a 50 kg sheep on winter sourveld should achieve a 12 % greater feed intake on *T. triandra* than on *E. plana*. When herbage digestibility is taken into account, this translates into a 22 % greater intake of digestible energy on the former species. However, the potential effects of season far outweigh any between-species differences. As an example, the potential intake of digestible energy for *T. triandra* in spring for a 50 kg sheep is more than 61 % greater than from the same species in winter. These issues and the potential animal production available from different species are explored in more detail in the following section (Chapter 7).

In conclusion, the nylon bag technique appears to be an effective method of determining the degradation characteristics of different forages in the rumen. As indicated by the generally low standard errors of digestibility estimates, the method is precise and, on the basis of the work of Pienaar *et al.* (1989), appears to yield results comparable to the more labour-intensive *in vivo* method. However, use of the present data for predictive purposes must take into account two potential problems associated with the method. Firstly, particle sizes of masticated forages may be substantially larger than ground samples, possibly lowering the rate and extent of degradation achieved *in vivo*. Secondly, the basal diet in the rumen directly affects the digestion rate of a particular forage (Lemerle 1983). Thus the rate of degradation of a forage in the grazing animal may be substantially different to that measured *in sacco* on a different basal ration.

6.6 Conclusions

6.6.1 There were marked differences in the soluble, potentially digestible and indigestible forage fractions present in the different sourveld grasses and in the rate of degradation of these species in the rumen. Overall, *T. triandra, H. hirta* and *A. semialata* had the most favourable degradation characteristics of the species considered. Conversely, *E. plana, A. appendiculatus* and *M. caffra* appeared to have the least favourable characteristics for degradation in the rumen.

6.6.2 Season had a major effect on the proportions of the different forage fractions present in the different species and in their rate of degradation in the rumen. Generally, the indigestible fraction increased while the size of the digestible fraction declined and the rate of degradation of digestible cell wall and DM decreased from spring through to winter.

6.6.3 The degradation rates and forage fractions of the present species are comparable to published values for other C4 pasture grasses but, as expected, are markedly poorer than those documented for the temperate, C3 species.

CHAPTER 7

MODELLING ANIMAL PRODUCTION ON SOURVELD

7.1 Objective

The objective of this chapter was to develop a series of simulation models based on the characteristics of (i) individual grass species and (ii) the sward as a whole, to determine the influence of such factors as sward structure, species composition and season on potential animal production on sourveld.

7.2 Introduction

In previous chapters data were presented describing the dietary quality (Chapter 2), intake (Chapter 3) and the sequence of species selection (Chapter 4) on swards of different structure and species composition on sourveld, as well as the potential digestion (Chapter 6) and ingestion (Chapter 5) rates of different sourveld grasses. Unfortunately, few of these factors operate independently and it is difficult to determine their relative importance in determining animal production when considered in isolation. The major objective of this chapter was therefore to synthesise the data presented in earlier sections into a series of simulation models in order to determine the potential influence of these factors on predicted animal production on sourveld.

To achieve this objective, two basic models were developed. In the first model, termed the **Species model**, an essentially reductionistic approach is adopted in that the properties of individual grass species, in terms of their potential ingestion and digestion rates, are used to predict animal production on sourveld. The second model, termed the **Sward model**, is aimed at a higher hierarchical level in the system and uses the dietary quality (Chapter 2) and intake (Chapter 3) measured on sites of different species composition and sward structure to predict animal production on these communities. Once these basic models were developed, they were expanded or modified to answer specific questions which were of interest.

7.3 Species models

As described above these models use the nutritive value, potential ingestion rate and degradation characteristics of individual grass species to predict animal production. The primary question addressed was:

(i) What is the potential animal production available from different sourveld grass species?

Once this question had been answered the basic model was extended to address the

Table 7.1 Definition of symbols used in chapter 7

Symbol	Parameter	Unit
A	animal age	years
ADG	animal daily gain	g
d	mean inter-tuft distance	m
Eg	energetic cost of grazing	MJ/kgW
EBG	empty body gain	kg
ER	energy retained	MJ
EVG	energy content of empty body gain	MJ/kg.EBG
GT	grazing time	min.
IVD	in vitro digestibility	%
IR	intake rate	g.DM/min.
H_{opt}	optimum sward height	cm
k_m	efficiency of energetic use for maintenance	-
k_g	efficiency of energetic use for gain	-
ME_i	intake of metabolisable energy	MJ/day
ME_m	metabolisable energy requirements for maintenance	MJ/day
MRT	mean retention time	h
PDF	potentially digestible fraction	%
SRW	standard reference weight	kg
T	model time step	days
t_w	walking speed	m/s
t_c	consumption time	tufts/s
W	animal mass	kg
VFI	voluntary feed intake	g/day
Z	mass of rumen contents	g
t_1	retention time in the rumen	h

following issues:

(ii) What is the effect of plant height on this potential production?

(iii) How does the species composition of a site affect animal production over the grazing period when animals are forced to graze other, less palatable species?

7.3.1 Species model-1

7.3.1.1 Goal

To determine the potential animal production available from different sourveld grass species at different times in the grazing season.

7.3.1.2 Model description

The model was formulated on a Quattro (4.0) spreadsheet (Quattro 1992) and predicts potential animal daily gain in mass (ADG) for cattle and sheep grazing eleven different sourveld species in spring, summer, autumn and winter. (See Table 7.1 for abbreviations.) In any given season the model assumes that diets consist entirely of leaf from a single species. Although simplistic, this assumption is based on the observation that stem generally forms a small part

(<20 %) of diets selected on sourveld (O'Reagai . 1989; O'Reagain unpublished data).

A basic plan of the model is provided in Fig. 7.1. Current animal mass, standard reference weight (SRW) and age are used as starting parameters. Standard reference weight is defined as the mass of an animal when skeletal development is complete and the empty body, i.e. minus gut contents, contains 250 g fat/kg (SCA 1990). Sheep were assumed to be 40 kg Dohne Merino wethers of 1.5 years age and 55 kg SRW while cattle were assumed to be 300 kg Bonsmara steers of 2.5 years age with a SRW of 700 kg.

Potential DM intake of different species (g.DM/day) was calculated as the product of intake rate (IR) and grazing time (GT). For convenience, grazing time was assumed constant at eight hours per day. Mean intake rates (g.DM/min.) for different species were obtained from Chapter 5 and estimated for those species for which no measurements were available (Table 7.2). Estimates were based on measured values for other species, subjectively modified according to the growth form of the species in question.

Table 7.2 Estimated intake rates (g.DM/min.) for species not assessed in the present study

Species	Cattle	Sheep
	g.DM/min.	
A. semialata	-	4
E. muticus	28	4.5
H. falx	28	3
M. caffra	15	4

Voluntary feed intake (VFI), defined as the maximum potential daily intake of DM as restricted by rumen processes, was used in the present study to quantify the upper constraint to the intake of a forage set by digestion and passage rates. VFI was calculated according to Roux and Meissner (1984) as:

$$VFI\ (g.DM/day) = 24\ [Z\ (p_1 t_1 + p_2 t_2)]$$

where p_1 and p_2 are the potentially digestible (PDF) and indigestible fractions respectively, t_1 and t_2 their mean retention times in the rumen and Z, the mass (OM) of rumen contents. Estimates of p_1, p_2, t_1 and t_2 were obtained from chapter 6 but where data were unavailable for a species in a particular season, estimates were obtained from the season immediately

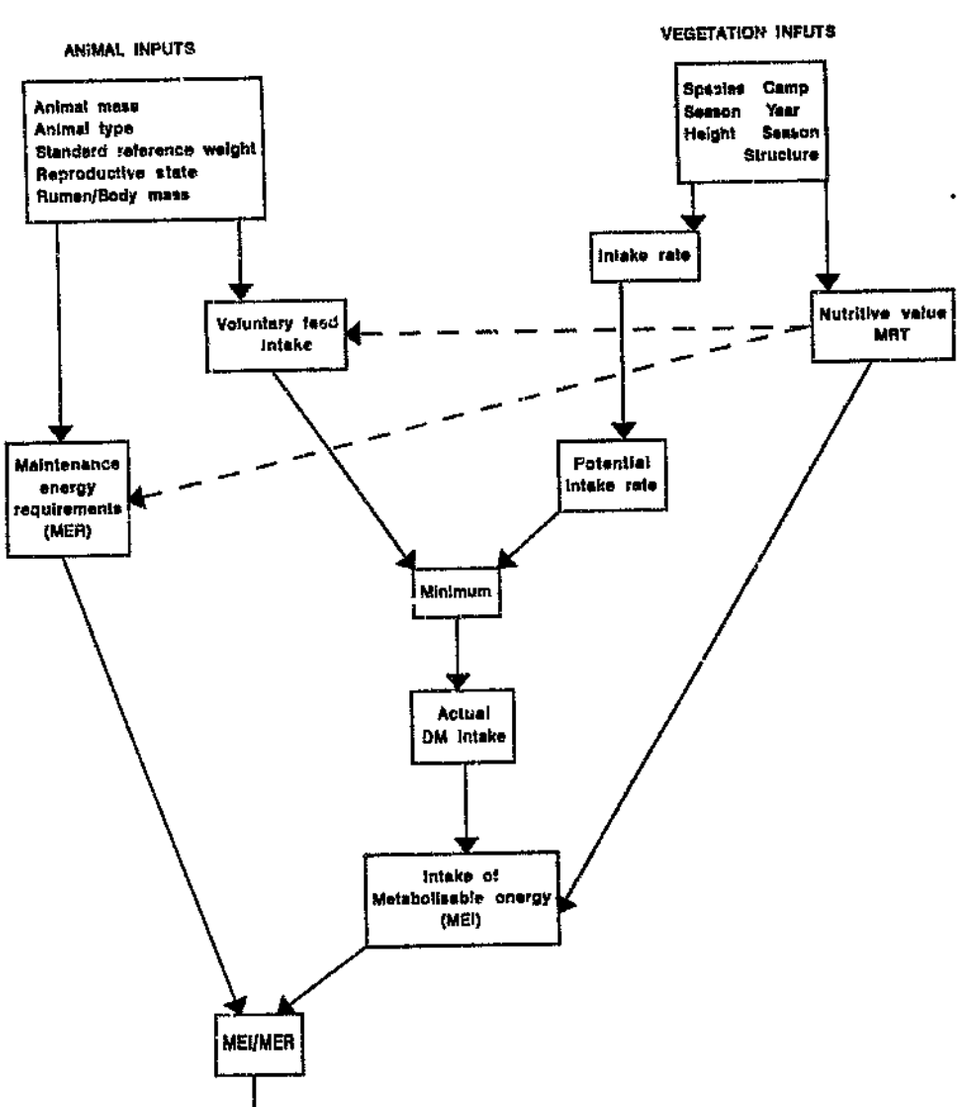

Figure 7.1 Flow diagram showing the structure of Species model-1. See text for details.

preceding the one in question.

Rumen contents (organic mass) may, theoretically, vary from about 8 to 35 g/kg of body weight depending upon dietary quality (Pienaar & Roux 1989) and environmental conditions (Baker & Hobbs 1987; Holand 1992). Unfortunately, choice of the correct ratio is problematic as there appears to be no objective means available for adjusting this ratio in relation to dietary quality. Initially, a predictive equation derived from the data of Krysl *et al.* (1987), was used but this resulted in unrealistic predictions of animal production, e.g. mass losses in spring, and the equation was discarded. A range of ratios from 15–30 g/kg was then used over a series of runs with the model and the ratio which predicted animal mass gains closest to field observations (Anon. 1994) was selected (Tables 7.3 & 7.4). For both cattle and sheep this was found to a be ratio of 20g/kg of body mass over all seasons, which is in agreement with the recommendation of Pienaar and Roux (1989) and the ratio used by Illius and Gordon (1991). While subjective, in the absence of any other quantitative relation this method appears to be the only practicable option available.

The fractional outflow rates of the indigestible fraction, i.e. $^1/t_2$, were not determined but on the basis of data published by Pienaar *et al.* (1980) were assumed to be 0.0285 for spring and summer, and 0.0238 and 0.0208 for autumn and winter respectively. The outflow rate of the PDF was assumed to be 0.012 as recommended by Pienaar and Roux (1989) from Pienaar *et al.* (1980).

Actual DM intake was taken as the minimum of VFI and the potential DM intake of each species (Fig. 7.1). Intake of digestible energy was calculated as the product of actual intake and PDF, converted to megajoules of metabolisable energy (ME_i). For present purposes the PDF was considered to be a reasonable estimate of OM digestibility.

Metabolisable energy requirements for maintenance (ME_m), in megajoules, were calculated as:

$$ME_m = K.S.\ (0.26\ W^{0.75}\ exp - (0.03A)/km + 0.09ME_i + Eg/km$$

where K = 1 for sheep and 1.4 for cattle, S = 1 for females and castrates, W = live weight, A = age in years, km = net efficiency of use of ME_m, ME_i = total ME intake and Eg = energy expended in grazing (SCA 1990). For km, fixed values of 0.70 (sheep) and 0.72 (cattle) were used as recommended by MAFF (1975, 1984) although it recognized that such values may overestimate animal production on low quality roughage. An energetic expenditure of 38.6 kJ/kg W was assumed for Eg as recommended for animals under extensive grazing (SCA 1990). Animals were assumed to be within the zone of thermoneutrality so energy expenditure for thermoregulation was considered to be negligible.

Animal daily gain (ADG) was calculated as:

$$ADG = ER/(EVG * 0.92)$$

where ER = energy retained and EVG = energy content of empty weight gain (SCA 1990), and:

$$ER = kg * (ME_i - ME_m)$$

The efficiency of use of ME for gain (*kg*) was calculated as:

$$kg = 0.063\ M/D - 0.318$$

which is the recommended equation for lower quality tropical pastures (SCA 1990) where:

$$M/D = 0.16\ OMD\% - 1.8$$

and OMD = organic matter digestibility, for present purposes taken to be the PDF or *in vitro* digestibility of the forage.

$$EVG = (6.7 + R) + (20.3 - R)/[1 + \exp(-6\ (P-0.4))]$$

where R = adjustment for rate of gain or loss and is calculated as $R = 2\ [(NE_c/NE_m)] - 1$ and NE = net energy for production (c) or maintenance (m) and:

P = current body mass/standard reference weight.

In cases where measured digestion rates were exceptionally low, i.e. *M. caffra* (autumn and winter) and *C. dactylon* (winter), *kg* was calculated as being negative. This interfered with predictions of ADG, tending to inflate them above those obtained on better quality herbage. As these results were clearly spurious, in these few cases estimates of *kg* were adjusted upwards (*kg* = .1 to .2) in order to circumvent this problem.

7.3.1.3 Sensitivity analysis

During model development it became clear that the two major inputs, in terms of their effect on predicted ADG, were VFI and the potential rate of DM intake (IR). To test the relative effects of these variables, a sensitivity analysis was conducted on the model. Accordingly, VFI was varied by 100 % by adjusting the ratio of rumen contents/body mass from 15 to 30 g/kg in 5 g intervals while IR was kept constant. Thereafter the IR was adjusted from 5 to 30 g.DM/min. and from 2 to 7 g.DM/min. for cattle and sheep respectively, while VFI was kept constant (Table 7.3 & 7.4). For simplicity, the procedure was conducted for only a single species, i.e. *A. semialata*, in spring, summer, autumn and winter. The relative effects of VFI and IR on ADG were computed as the ratio of the increase in ADG when VFI is adjusted upwards/increase in ADG due to IR being adjusted upwards. A result greater than one indicates that VFI has a relatively greater effect on ADG while a result less than one indicates the reverse (Table 7.3 & 7.4).

A number of points were clear from the sensitivity analysis. First, for both animals VFI had a greater effect on predicted ADG than did IR, although the magnitude of this effect was greater for sheep than for cattle. Second, the relative effect of VFI was noticeably more

Table 7.3 The effect of varying (i) the ratio of rumen contents to body mass and (ii) the rate of DM intake (IR), on the predicted animal daily gain (ADG), voluntary feed intake (VFI) and total potential intake (PI) of cattle at four times through the grazing season. The relative change in ADG in adjusting these two variables by 100 % is given in the last column, i.e. ADG_{VFI}/ADG_{IR}

IR g/min	PI	Rumen contents/body mass (g/kg)								RELATIVE CHANGE
		15		20		25		30		
		VFI	ADG	VFI	ADG	VFI	ADG	VFI	ADG	
		g								
SPRING										
5	2400	5507	-260	7343	-260	9178	-260	11014	-260	
10	4800	5507	256	7343	256	9178	256	11014	256	
15	7200	5507	408	7343	770	9178	770	11014	770	1.14
20	9600	5507	408	7343	800	9178	1190	11014	1279	
25	12000	5507	408	7343	800	9178	1190	11014	1578	
30	14400	5507	408	7343	800	9178	1190	11014	1578	
SUMMER										
5	2400	5481	-256	7309	-256	9136	-256	10963	-256	
10	4800	5481	186	7309	186	9136	186	10963	186	
15	7200	5481	312	7309	626	9136	626	10963	626	1.13
20	9600	5481	312	7309	646	9136	979	10963	1064	
25	12000	5481	312	7309	646	9136	979	10963	1311	
30	14400	5481	312	7309	646	9136	979	10963	1311	
AUTUMN										
5	2400	4422	-221	5896	-221	7370	-221	8844	-221	
10	4800	4422	5	5896	47	7370	47	8844	47	
15	7200	4422	5	5896	169	7370	314	8844	314	1.11
20	9600	4422	5	5896	169	7370	333	8844	497	
25	12000	4422	5	5896	169	7370	333	8844	497	
30	14400	4422	5	5896	169	7370	333	8844	497	
WINTER										
5	2400	3636	-175	4848	-175	6060	-175	7273	-175	
10	4800	3636	-88	4848	-6	6060	-6	7273	-6	
15	7200	3636	-88	4848	-3	6060	81	7273	161	1.47
20	9600	3636	-88	4848	-3	6060	81	7273	166	
25	12000	3636	-88	4848	-3	6060	81	7273	166	
30	14400	3636	-88	4848	-3	6060	81	7273	166	

pronounced in winter when herbage quality was at its lowest than in spring and summer when quality was higher. Again, this effect was more evident with sheep. Third, as would be expected, the constraint of VFI on intake increased as the season progressed, so that the relative importance of IR declined. Lastly, the measured rates of intake for *A. semialata*, and in fact for all species (Chapter 6), far exceeded potential VFI, even when the largest ratio of rumen contents to body mass was used and herbage quality was at its highest. As dietary quality is the major determinant of VFI, dietary quality is, by implication, the major determinant of animal production on sourveld.

7.3.1.4 Model output

Table 7.4 The effect of varying (i) the ratio of rumen contents to body mass and (ii) the rate of DM intake (IR), on the predicted animal daily gain (ADG), voluntary feed intake (VFI) and total potential intake (PI) of sheep at four times through the grazing season. The relative change in ADG in adjusting these two variables by 100 % is given in the last column, i.e. ADG_{VFI}/ADG_{IR}

		Rumen contents/body mass (g/kg)								
IR g/min	PI	15		20		25		30		RELATIVE CHANGE
		VFI	ADG	VFI	ADG	VFI	ADG	VFI	ADG	
					g					
SPRING										
2	960	734	10	979	58	1224	58	1469	58	
3	1440	734	10	979	62	1224	113	1469	159	
4	1920	734	10	979	62	1224	113	1469	165	1.98
5	2400	734	10	979	62	1224	113	1469	165	
6	2880	734	10	979	62	1224	113	1469	165	
7	3360	734	10	979	62	1224	113	1469	165	
SUMMER										
2	960	731	2	974	43	1218	43	1462	43	
3	1440	731	2	974	46	1218	90	1462	130	
4	1920	731	2	974	46	1218	90	1462	134	1.45
5	2400	731	2	974	46	1218	90	1462	134	
6	2880	731	2	974	46	1218	90	1462	134	
7	3360	731	2	974	46	1218	90	1462	134	
AUTUMN										
2	960	590	-26	786	-4	983	14	1179	14	
3	1440	590	-26	786	-4	983	16	1179	38	
4	1920	590	-26	786	-4	983	16	1179	38	2.69
5	2400	590	-26	786	-4	983	16	1179	38	
6	2880	590	-26	786	-4	983	16	1179	38	
7	3360	590	-26	786	-4	983	16	1179	38	
WINTER										
2	960	485	-30	646	-19	808	-8	970	2	
3	1440	485	-30	646	-19	808	-8	970	2	
4	1920	485	-30	646	-19	808	-8	970	2	59.10
5	2400	485	-30	646	-19	808	-8	970	2	
6	2880	485	-30	646	-19	808	-8	970	2	
7	3360	485	-30	646	-19	808	-8	970	2	

There were major differences in predicted animal daily gain (ADG) between the different sourveld grasses for both cattle and sheep (Figs. 7.2 & 7.3). In summer, for example, there was a 932 g/day difference between the species with the highest (*H. hirta*) and lowest (*M. caffra*) predicted ADG for cattle while differences of a similar relative magnitude were also evident for sheep. Although the magnitude of between-species differences varied with season, *H. hirta* generally gave the highest predicted ADG while *E. plana, A. appendiculatus, H. falx* and *M. caffra* gave the lowest. It is notable that the ranking of species was nearly identical for both animal species.

Microchloa caffra gave particularly low ADGs and appeared to be incapable of

T. triandra and *T. leucothrix* were generally intermediate between the best and poorest species. In this regard it is notable that, for cattle, the relative ranking of *T. triandra* increased markedly over the grazing season so that by winter it was the highest ranked of all species (Fig. 7.2). Interestingly, the predicted ADGs from *E. muticus*, an extremely unpalatable grass (Stoltsz & Danckwerts 1990), were amongst the highest predicted for both animals.

Season had a marked effect on both the relative and absolute levels of predicted ADG from all species. Generally, between-species differences were least pronounced in spring and winter when most grasses were of a fairly uniform high or low quality respectively (Figs. 7.2 & 7.3). Further, while fairly adequate animal production could be expected from most grasses in spring and summer, it was evident that nearly all species would be unable to meet basic maintenance requirements in winter. These effects were particularly pronounced for sheep with loss of body mass being predicted on some species as early as summer, and in the case of *M. caffra*, even in spring.

Levels of animal production predicted by the model are comparable with recorded values. For example, ADGs of 29-69 g and 583-525 g for sheep and cattle respectively, have been measured over spring and summer at a range of stocking rates on Dohne Sourveld (Anon. 1994). However, the relatively high cattle ADG predicted for *T. triandra* in winter (93 g/day) is most unexpected and difficult to reconcile with that predicted for sheep or the observed levels of production for cattle at this time of the year. Although *T. triandra* did have the highest recorded PDF in winter (Chapter 6) this appears to be insufficient to explain the unusually high production predicted from this species.

While predicted ADGs for sheep in autumn and winter appear low, this probably reflects the basic assumption of the model that dietary quality was the same in both animals. In practice, sheep are far more selective (Chapter 2) and could be expected to select diets of higher quality than both those of cattle and the hand-plucked samples from which the present estimates of dietary quality are derived (Chapter 7). Further, these low ADGs probably also reflect the assumption that the proportion of rumen contents to body mass, i.e. 20 g/kg remains constant over the grazing season. In reality, animals probably increase rumen pool sizes in autumn and winter (Holand 1992) in an attempt to maintain passage rates. The model was extremely sensitive to this variable (Table 7.2 & 7.3) and using a higher rumen contents:body mass ratio, i.e. 30 g/kg, markedly improved predicted animal performance, particularly in winter.

A notable feature of the model was that the estimated DM intakes, i.e. measured IR by assumed grazing time (8 hours), were always substantially greater (1.5 - 3 times) than the predicted VFI for all species. This was evident even in spring using the largest possible ratio

maintaining sheep body mass at any time in the grazing season (Fig. 7.3). Predicted ADGs for *T. triandra* and *T. leucothrix* were generally intermediate between the best and poorest species. In this regard it is notable that, for cattle, the relative ranking of *T. triandra* increased markedly over the grazing season so that by winter it was the highest ranked of all species (Fig. 7.2). Interestingly, the predicted ADGs from *E. muticus*, an extremely unpalatable grass, were amongst the highest predicted for both animals.

Season had a marked effect on both the relative and absolute levels of predicted ADG from all species. Generally, between-species differences were least pronounced in spring and winter when most grasses were of a fairly uniform hign or low quality respectively. Further, while fairly adequate animal production could be expected from most grasses in spring and summer, it was evident that nearly all species would be unable to meet basic maintenance requirements in winter. These effects were particularly pronounced for sheep with loss of body mass being predicted on some species as early as summer, and in the case of *M. caffra*, even in spring.

Levels of animal production predicted by the model are comparable with recorded values. For example, ADGs of 29-69 and 583-525 g for sheep and cattle respectively, have been measured over spring and summer at a range of stocking rates on Dohne Sourveld (Anon. 1994). However, the relatively high cattle ADG predicted for *T. triandra* in winter (93 g/day) is most unexpected and difficult to reconcile with that predicted for sheep or the observed levels of production for cattle at this time of the year. Although *T. triandra* did have the highest recorded PDF in winter (Chap. 6) this appears to be insufficient to explain the unusually high production predicted from this species.

While predicted ADGs for sheep in autumn and winter appear low, this probably reflects the basic assumption of the model that dietary quality was the same in both animals. In practice, sheep are far more selective and could be expected to select diets of higher quality than both those of cattle and the hand-plucked samples from which the present estimates of dietary quality are derived (Chapter 7). Further, these low ADGs probably also reflect the assumption that the proportion of rumen contents to body mass, i.e. 20 g/kg remains constant over the grazing season. In reality, animals probably increase rumen pool sizes in autumn and winter (Holand 1992) in an attempt to maintain passage rates. The model was extremely sensitive to this variable (Table 7.2 & 7.3) and using a higher rumen contents:body mass ratio, i.e. 30 g/kg, markedly improved predicted animal performance, particularly in winter.

A notable feature of the model was that the estimated DM intakes, i.e. measured IR by assumed grazing time (8 hours), were always substantially greater (1.5 - 3 times) than the predicted VFI for all species. This was evident even in spring using the largest possible ratio

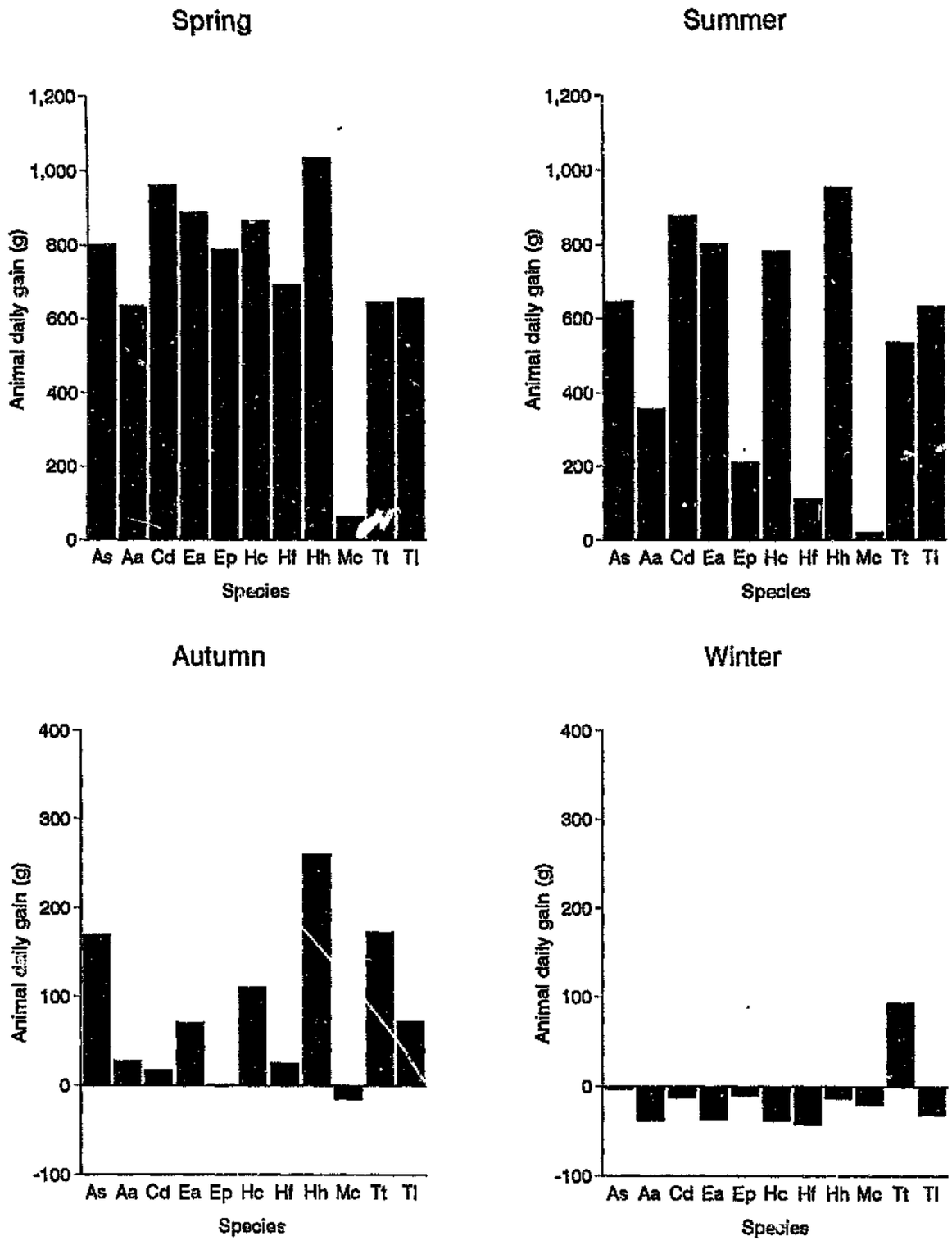

Figure 7.2 Output for Species model-1: Predicted animal daily gain (ADG) for cattle from eleven sourveld grasses in spring, summer, autumn and winter (Aa = A. appendiculatus, As = A. semialata, Cd = C. dactylon, Ea = E. muticus, Ep = E. plana, Hc = H. contortus, Hf = H. falx, Hh = H. hirta, Mc = M. caffra, Tt = T. triandra, Tl = T. leucothrix).

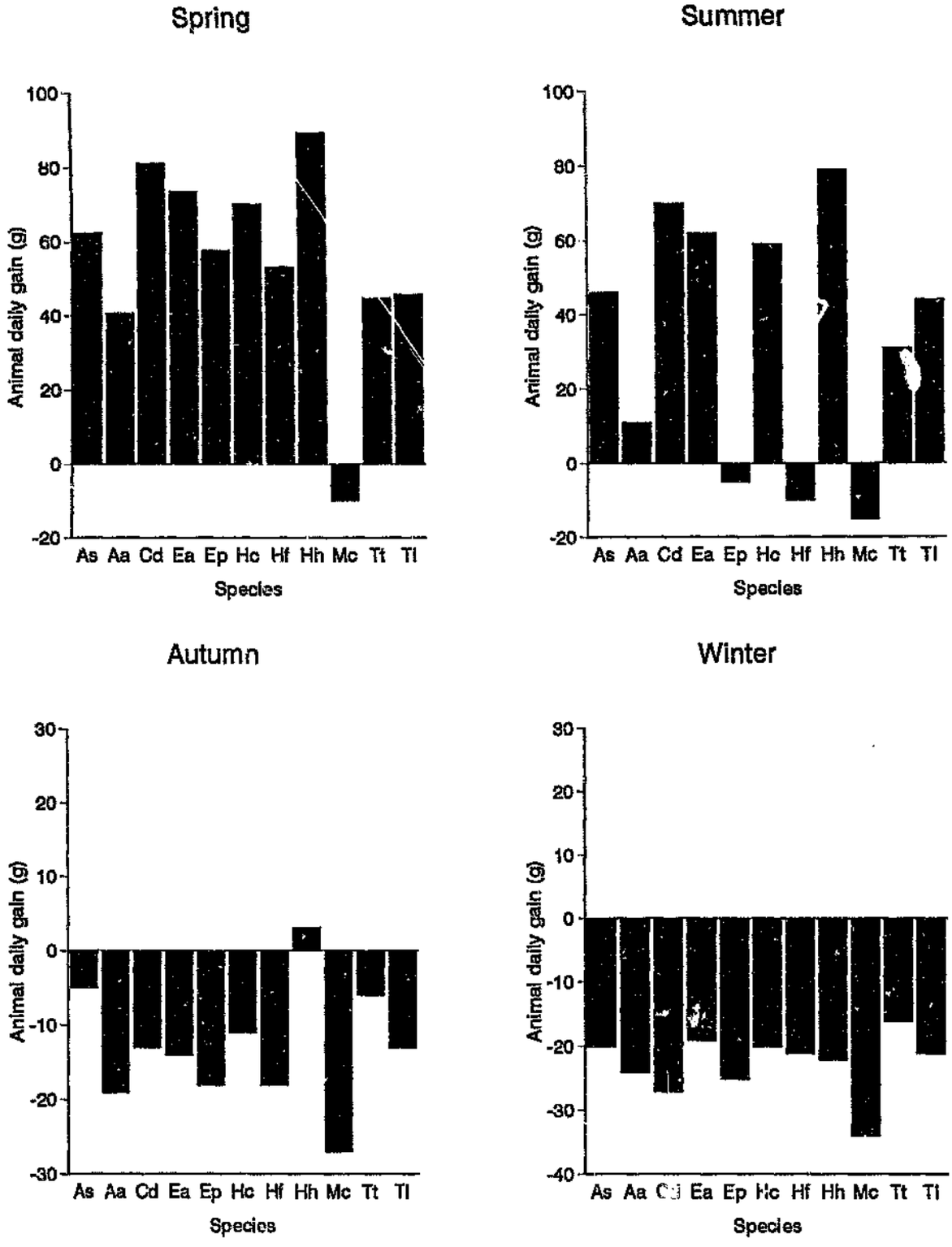

Figure 7.3 **Output for Species model-1: Predicted animal daily gain (ADG) for sheep from eleven sourveld grasses in spring, summer, autumn and winter (Species codes as for Fig. 7.2).**

of rumen contents to body mass. This suggests that dietary quality is the overriding determinant of animal production on sourveld and that, except on the shortest swards, intake is unlikely to be restricted by sward structure.

7.3.2 Species model-2

7.3.2.1 Goal

To determine the effects of plant height on potential animal production from different sourveld grasses.

7.3.2.2. Model description

The model is identical to Species model-1 but predicts ADG for cattle over a range of plant heights in spring, summer, autumn and winter. Sheep were not considered in the model as no statistically significant intake-height relations could be detected for any of the eleven grass species (Chapter 5).

Aside from the assumptions listed for Species model-1 the model also assumes that: (i) there is no interaction between plant height and forage quality, i.e. quality does not decline as height increases, (ii) the rate of DM intake is a linear function of plant height, and (iii) intake rate-plant height relations are independent of season.

Intake rate was predicted over a range of plant heights from 2 to 16 cm for each species using relations developed in chapter 5. For *T. leucothrix*, the *H. contortus* regression was used as the relation for the first species generated values which were clearly erroneous. No relation was available for *M. caffra* necessitating the use of the *regression from C. dactylon* which also has a relatively low growth habit. For all species, potential DM intake, VFI, actual intake and ADG were determined as described earlier (section 7.3.1.2).

7.3.2.3 Results

The predicted response of cattle ADG to increasing plant height is presented in Figure 7.4. Due to the general similarity of response, results from only six of the eleven species are presented. For most species, predicted ADG initially increased sharply with plant height (Fig. 7.4) reflecting the increased rate of DM intake, and hence digestible energy, with this variable. This response continued until the constraint set by VFI on DM intake was reached, at which point (H_{max}) animal production was maximized. Above this height ADG remained constant as intake was limited by passage rather than by ingestion rates. For *E. plana*, however, there was no apparent response to height as the potential DM intake of this species exceeded VFI at all

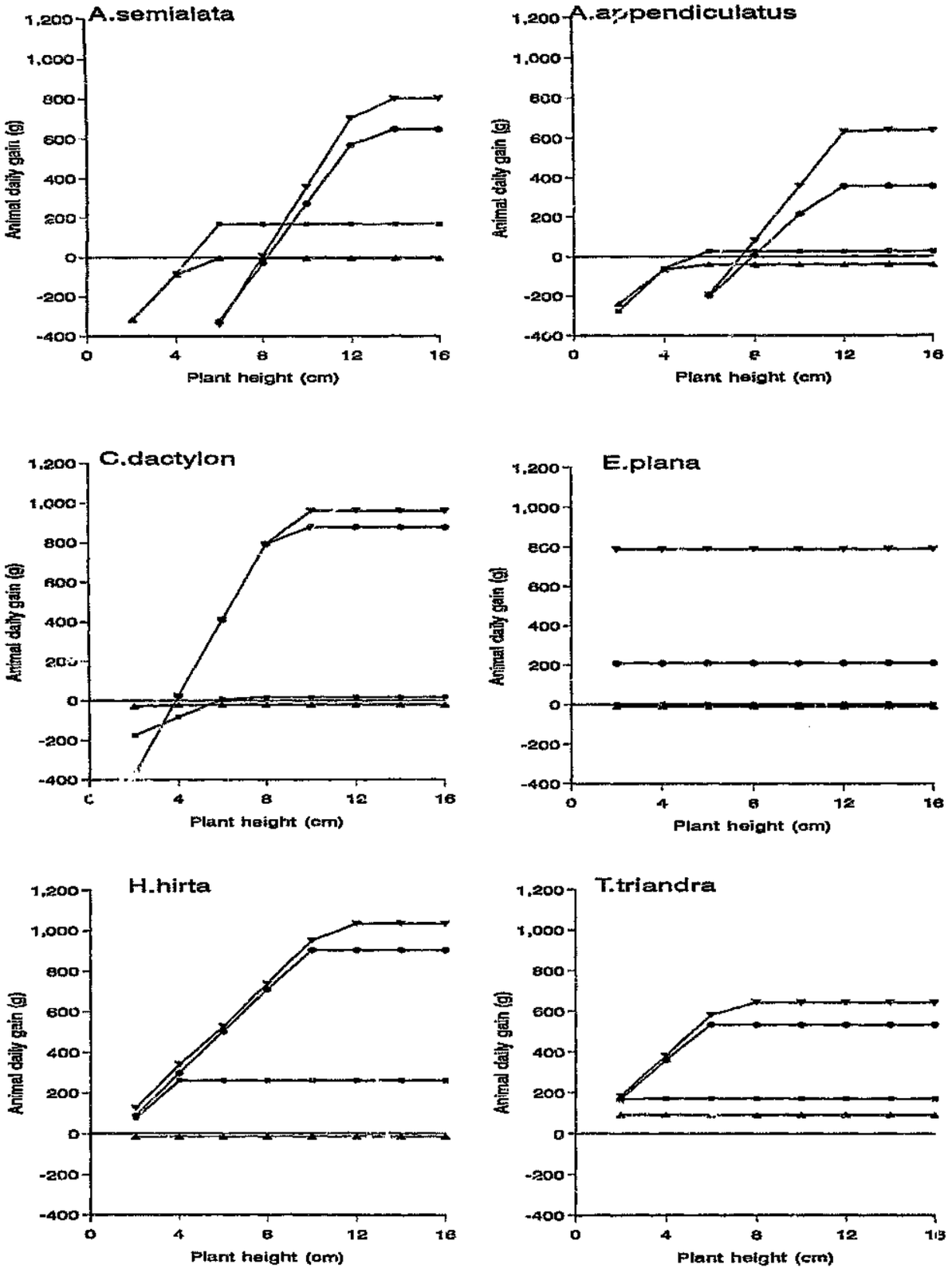

Figure 7.4 Output for Species model-2: Predicted cattle animal daily gain (ADG) with increasing plant height for six sourveld species in spring (▼), summer (♦), autumn (■) and winter (▲).

heights (Fig. 7.4).

H_{max} varied between seasons, becoming progressively lower from spring through to winter due to the concomitant decline in passage rates and the consequent lowering of the constraint set by VFI on DM intake (Fig. 7.4). For example with *A. appendiculatus*, H_{max} declined from 12 cm in spring and summer to 6 cm in autumn and 4 cm in winter. Within a season, e.g. summer, H_{max} also varied widely between species ranging from about 8 cm for *T. triandra* to 12 cm for *H. hirta*. It is noteworthy that the H_{max} values predicted here are far lower than the actual height (20-25 cm) at which cattle intake rates are maximised in the field (Chapter 3).

The model also predicts that for some species, intake would be restricted by VFI at all heights in winter and, in the case of *E. plana*, in all seasons (Fig. 7.4). However, this is extremely improbable and suggests that the ratio of rumen contents to body mass used in the model was too low and/or IR were overestimated at low heights for the species in question.

A shortcoming of the present model is that the negative relation between herbage quality and plant height is ignored. In practice, this interaction would tend to increase ADG on short swards due to the increased intake of digestible energy but, conversely, production would be depressed at heights above H_{max} due to reduced passage rates and hence VFI. In reality, animals would also compensate for reduced IR on very short swards by increasing grazing time (section 3.4). The net result of these factors would be to shift H_{max} to the left, reducing the height at which ADG was maximized.

As with Species model-1, the present model highlights the importance of herbage quality in determining animal production on sourveld. The model suggests that except when forage is of exceptionally high quality, cattle intake and hence ADG, is unlikely to be restricted by sward height on most species in this veld type.

7.3.3 Species model-3

7.3.3.1 Goal

To predict the change in animal production through a period of occupation in a paddock at sites of different species compositions.

7.3.3.2 Model description

The model predicts the change in ADG as animals consume species of different nutritional value through a period of occupation in a paddock at the four experimental sites described in section 2.3. Briefly, these sites were bush (dominated by *T. triandra* and *T. leucothrix*),

eragrostis (dominated by *E. plana*), old lands (dominated by *H. hirta)* and sheep shed camp (dominated by *T. leucothrix*).

The model was run using only data from the summer period. The model assumes that: (i) all sites have the same, arbitrarily chosen, total tuft density of 50 000 tufts/ha, (ii) there are only the three major species present at each site, with all tufts evenly distributed over the grazing area, (iii) species 1 is always consumed in preference to species 2, which in turn is always consumed in preference to species 3, (iv) only two species can be included in the diet at any given time, i.e. 1 and 2 or 2 and 3 but not 1 and 3, (v) based on the sequence of species selection described earlier (Chapter 4) animals only start consuming species 2 when 20 % of species 1 tufts have been grazed and species 3 when 70 % of species 2 tufts have been grazed i.e. species 2 and 3 are of intermediate and avoided acceptability respectively, (vi) once a tuft has been grazed it is no longer available, i.e. 'second bites' are not considered, (vii) tufts of all species are assumed to be of the same mass and yield the same rate of DM intake, and (viii) the energetic costs of search and consumption, i.e. grazing (Eg), are assumed to be constant and independent of tuft density.

The basic model layout is given in Fig. 7.5. The following starting parameters were used: paddock area (m^2), number of tufts of species 1, 2 and 3 (Table 7.4), tuft mass (g), walking speed ($m.sec^{-1}$) and the time taken to consume a single, whole tuft (sec.). Animal parameters are mass, age and SRW which were taken to be the same as in Species model-1. Estimates of the forage fractions and rumen degradation rates of different species are taken from chapter 6.

The model assumes that the animal always maximises its intake of species 1 (the most preferred species) up to the limit set by its VFI, i.e. where the actual intake of species 1 = VFI_1 then the intake of species 2 = 0. Where the intake of species 1 is less than its VFI, due perhaps to the restricted availability of the species, the animal is assumed to fill its rumen with the maximum amount possible from this species and make up the remainder of its potential intake with species 2. Here, the maximum limit on the intake of species 2 set by rumen processes is assumed to be determined by a linear combination of the respective VFIs of species 1 and 2, i.e. $Intake_2 = VFI_2 - b*VFI_1$, where $b = VFI_1/VFI_2$ and VFI_1 is also equal to the actual intake of species 1 (Fig. 7.5). The same assumptions were taken to hold for species 2 and 3.

At each site, the three most abundant grass species were chosen (Table 7.5) which in all cases collectively constituted >68 % of all recorded plants at a site. Species initially had abundances N1, N2 and N3 calculated from the species composition data for each site (Table 2.1) as: ((relative abundance of a species/sum of the relative abundances of species 1-

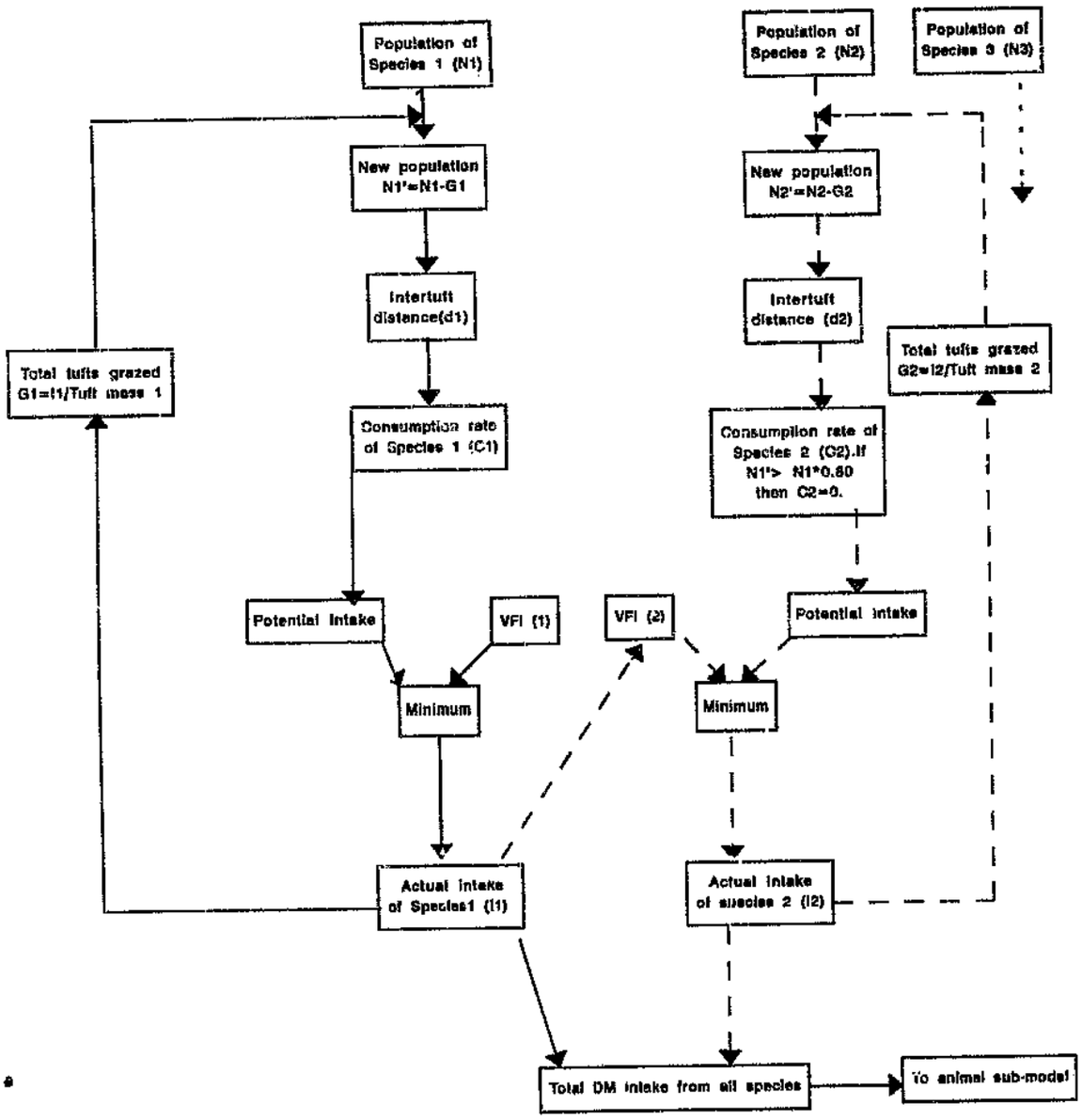

Figure 7.5 Flow diagram showing the structure of Species model-3. See text for details.

Table 7.4 Species compositions and order of preference for the four sites used in Species model-3. Absolute species abundances (thousands) are given in parentheses

Preference order	Site			
	Bush	Eragrostis	Lands	Shed
1	T. leucothrix (19500)	*T. triandra* (10500)	*H. hirta* (33500)	*A. semialata* (9500)
2	*T. triandra* (21000)	*A. appendiculatus* (13000)	*H. contortus* (9500)	*T. leucothrix* (32500)
3	*A. appendiculatus* (8500)	*E. plana* (26000)	*E. plana* (6500)	*A. appendiculatus* (7500)

3)*100)*Total tuft population, i.e. 50 000):

For each species, mean inter-tuft distance (d), derived from Pilou (1969), was calculated as:

$$d = \sqrt{\frac{total\ area}{total\ tuft\ number}}$$

As this relationship is curvi-linear (Fig. 7.6) there is initially little change in d as tuft numbers are depleted but once a certain percentage of tufts have been grazed (80 - 90 % depending upon n) d increases sharply.

A daily time step (T) was used, extending over a maximum period of occupation of 30 days. As tufts are consumed each day, the total population of ungrazed tufts declines with a corresponding increase in d (Fig. 7.5). In each time step, the total number of tufts of a particular species removed was calculated from the total amount of DM removed from that species divided by the mass of each tuft, assumed to be 5 g for all species.

Potential DM intake (g.DM/day), defined as the total amount of DM that could be removed from a species in a single day, was calculated as:

T * Tuft mass * Consumption rate

where consumption rate (tufts per second) was calculated as:

$$(T/(d/t_w + t_c))/T$$

where t_w and t_c are the walking speed and time taken to consume a tuft, respectively.

The same walking speeds and consumption rates were used for cattle and sheep. However, for sheep the total amount of DM removed per grass species was multiplied by a factor of seven based on the rough assumption that a 300 kg steer has an equivalent intake

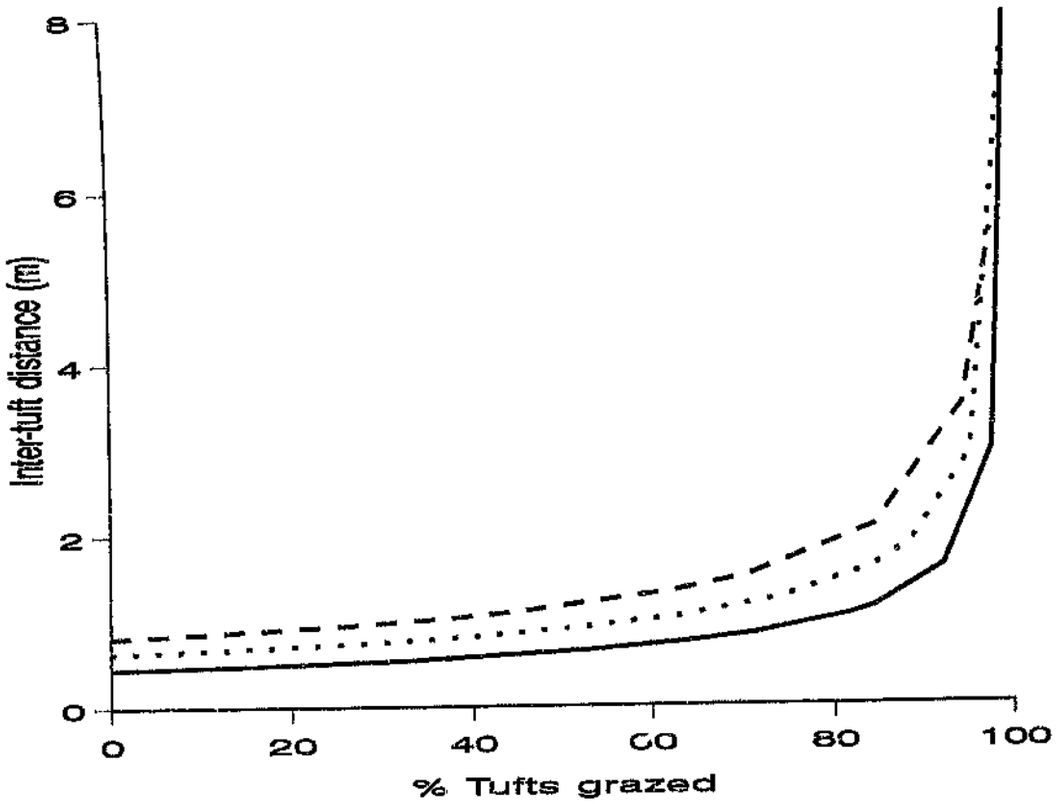

Figure 7.6 The relation between the distance between ungrazed tufts (d) and the percentage of tufts grazed at three initial population densities (_____ = 50 000, ... = 15 000 and ---- -- = 5000 tufts/ha)

(calculated at 2 % of body mass) to that of approximately seven, 40 kg sheep . Although this adjustment may be considered somewhat arbitrary, it is unlikely to change the relative shape of the curves for the different sites. Actual intake and ADG were determined as described earlier (section 7.3.1.2) with ADG being calculated from the sum of the intakes of digestible energy from all species (Fig. 7.5).

7.3.3. Results

Results are presented for cattle only due to the similarity of model output for cattle and sheep. Large differences in the rate and extent to which ADG changed over the grazing period at sites of different species composition were predicted (Fig. 7.7). These differences largely reflected the inherent nutritive value of the species present at a particular site and the changing patterns of availability and consumption of these species through the grazing period.

At all sites, a distinct three stage cycle in species selection and intake was evident through the grazing period which directly affected animal production. In the first stage, animals consumed only the most-preferred species (1) present giving some, relatively high, level of animal production. During this stage, production was stable due to the nature of the relation between tuft density and d (Fig. 7.6) which ensured that IR was initially unaffected as the abundance of species 1 was depleted through grazing. However, at some low tuft density, d increased sharply, depressing IR and reducing the total intake from this species. This necessitated the inclusion of the next ranked species (2) in the diet. In this second, transitional stage, ADG declined steadily as the amount of species 1 in the diet progressively decreased and consumption of the generally lower quality species 2 increased. This stage continued until species 1 was completely depleted through grazing and the diet consisted exclusively of species 2. In this third stage ADG usually stabilised at some second, usually lower, level. The above sequence was repeated when the animal was forced to consume the third and final species. However, in this case, ADG in stage two sometimes declined below that in stage three if the delay was too long before the third species was included in the diet, as happened at old lands camp (Fig. 7.7).

Variations of this cycle were evident at all sites. At bush camp for example, ADG was initially constant as animals consumed *T. triandra,* but thereafter declined as the availability of this species decreased, forcing animals to consume *T. leucothrix* (Fig. 7.7). Predicted ADG then stabilised before the availability of *T. leucothrix* was also depleted and animals started grazing *A. appendiculatus*, which is of marginally lower quality. At this site, ADG showed a relatively minor decline over the grazing period reflecting the relatively similar quality of the three available grasses. Similarly, at sheep shed, ADG stayed virtually constant over the first

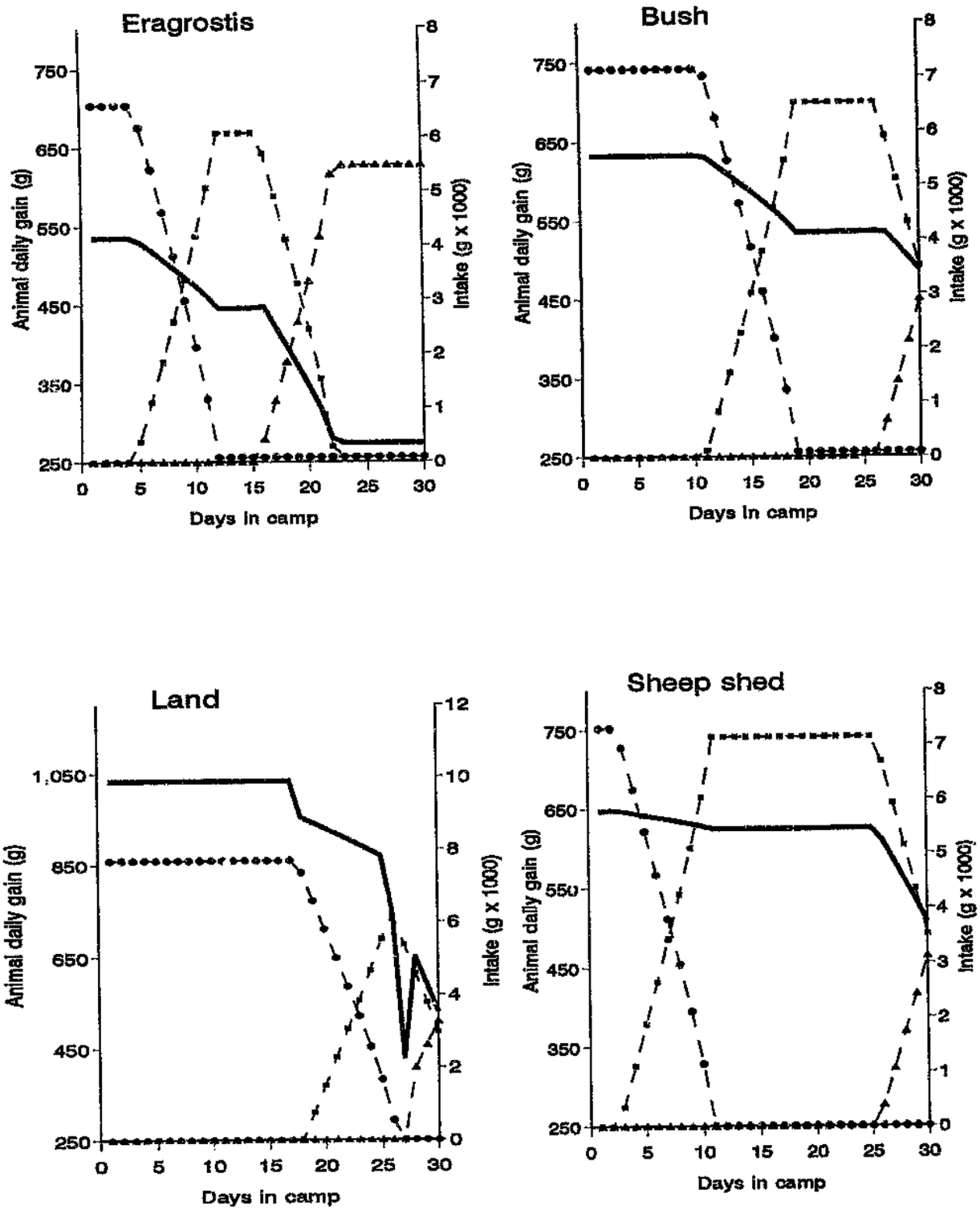

Figure 7.7 Output for Species model-3: The change in cattle ADG (solid line) and intake of three grass species over the grazing period at four sourveld sites. (▾ = species 1, ■ = species 2, ▲ = species 3).

25 days of the grazing period despite large variation in the amount of DM consumed from the different species over this time period (Fig. 7.7).

In contrast, at eragrostis camp ADG declined sharply as animals rapidly depleted the relatively small proportions of *T. triandra* and *A. appendiculatus* available and were then forced to consume *E. plana* which is of far lower quality (Fig. 7.7). At old lands camp, relatively high levels of ADG were sustained for more than half of the grazing period due to the abundance of the highly digestible *H. hirta*. However, ADG later declined sharply as the availability of this species was depleted through grazing and first *H. contortus*, and later *E. plana*, were consumed.

Overall, the model indicated that species composition is a major determinant of animal production and its rate of change over the grazing period. In this regard, the following specific factors are of importance. First, the inherent nutritive value of the species present set the limits to animal production at any particular site. Second, the relative abundance of these species determines the rate and extent of the change in production over the period of occupation in a camp. Third, the absolute species abundance (= basal cover) will determine the period over which any production can be sustained in terms of animal grazing days or stocking density.

While the model achieved its basic objective, a number of modifications are suggested which would make predictions of animal production more realistic. First, within-species variability in quality and intake should be incorporated into the model to account for the wide range of tuft structures generally encountered in the field. Second, between-species differences in bite size and intake rate should be used rather than some constant value of intake for all species. Third, the effect of grazing time on energy expenditure should be included in the model to account for the increased search times and walking distances associated with finding an ever diminishing supply of the different species in a camp. Last, the model should use the actual tuft densities measured in the field rather than assuming that similar plant populations exist at all sites. For example, on the basis of visual estimates, tuft densities at old lands camp appeared to be substantially lower than those at the other sites. Incorporation of these factors into the model would improve the accuracy of predictions, allowing a more realistic evaluation of the production potential of different sites.

7.4 Sward models

These simulation models predict production by cattle and sheep over a range of sward structures or over the grazing season at four sites of different species composition in Dohne Sourveld. As before, these models were formulated on a Quattro (4.0) spreadsheet (Quattro

1992). The models are based upon the relations between (i) dietary quality and (ii) intake in cattle and sheep, and sward structure and season developed for the four sites described in sections 2 and 3, i.e. bush, eragrostis, old lands and sheep shed camps. Questions which were addressed were:

(i) What is the effect of sward height on animal production on sites of different species composition?

(ii) What is the relative change in animal mass over the grazing season on sites of different species composition?

7.4.1 Sward model-1

7.4.1.1. Goal

To determine the effect of sward height on animal production at four sites of different species composition in Dohne Sourveld.

7.4.1.2 Model description

The model predicts ADG for cattle and sheep over a range of sward heights at four sites of different species composition. Model predictions are restricted to the growing season, i.e. swards with a mean greenness value of 2.5 - 5. Input data for the model in terms of sward structure and the dietary quality and intake available from each site were derived from chapters 2 and 3.

The model assumes that sward greenness, and hence dietary quality and MRT, decline linearly with increasing sward height as observed in chapter 2 and 3 and quantified in Appendix 6. Starting parameters for the model include sward height, greenness, dietary IVD and MRT for cattle and sheep and animal mass, age and SRW. For the purposes of the model, animals of the same breed, age, mass and SRW as described in Species model-1 were used.

In the model, sward height was varied from 3-15 cm for sheep and from 5-30 cm for cattle. The change in sward greenness with increasing height was calculated separately for each site using the relations presented in Appendix Table 6.2. Dietary *in vitro* digestibility was predicted from sward greenness for cattle and sheep at each of the four sites for the year of the burn (year 1) and the year following the burn (year 2) [Appendix Table 6.1]. MRT was also predicted from greenness for each site (Appendix Table 6.3) with the same relation being assumed to hold in both years.

Total daily potential intake was calculated as:

IR * GT

where IR = intake rate (g DM/min.) and GT = grazing time (min.). Intake rate was predicted from plant height using relations presented in Table 3.3 (cattle) and 3.7 (sheep). Cattle IR was assumed to respond to plant height in the same manner at all four sites but different relations were used for each site for sheep.

As the above relations are based upon data from fasted animals, IR should be adjusted to approximate normal levels of satiation. Newman *et al.* (1994) observed that sheep fasted for 24 hours had IRs 70 % greater than unfasted animals, while Greenwood and Demment (1988) recorded a 60 % increase in IR of cattle fasted for 36 hours. Assuming a linear relation between the length of fasting and response in both studies, this suggests that, based on the 15 hour (16:00-06:00) fasting period used in the present study, current estimates of IR should be reduced by 43 % and 25 % for sheep and cattle respectively. However, these adjustments must also take into account the possible underestimate of insensible weight loss in sheep (Penning & Hooper 1984) and the incomplete recovery of fistula extrusa in cattle (Stobbs 1973a). If both are taken to be 20 %, this translates into an effective 20 % reduction in observed intake rates in sheep while IR remain basically unchanged for cattle.

Cattle grazing time was predicted from plant height (PH) using data presented in section 3:

$$GT = 724 - 9.9*PH \quad (r^2 = 0.34;\ F = 16.77;p<0.0001)$$

For sheep, grazing time, in hours, was predicted from plant height using the equation:

$$GT = 11.2 - 0.272*PH$$

obtained by assuming a maximum grazing time of 11 hours with a sward height of 1 cm and a minimum GT of 7 hours with a sward height of 15 cm. Data from Allden and Whittaker (1971) indicate sheep grazing time of 6 and 13 hours on long and short swards, respectively.

Voluntary feed intake was calculated as:

$$VFI = (\text{Mass of rumen contents}/MRT) * 24$$

Actual intake and ADG were predicted as described for Species model-1 (section 7.3.2.1).

7.4.1.3. Results

At all sites there was an optimum sward height (H_{opt}) at which animal production was maximised (Fig. 7.8), varying from 6-9 cm for sheep to 10-12 cm for cattle. This optimum reflected the opposing relations between intake rate and height on the one hand and MRT and sward height on the other. As height increases, IR rises sharply due to the strong linear relation between bite size and plant height (Chapter 3). Conversely, VFI declines with

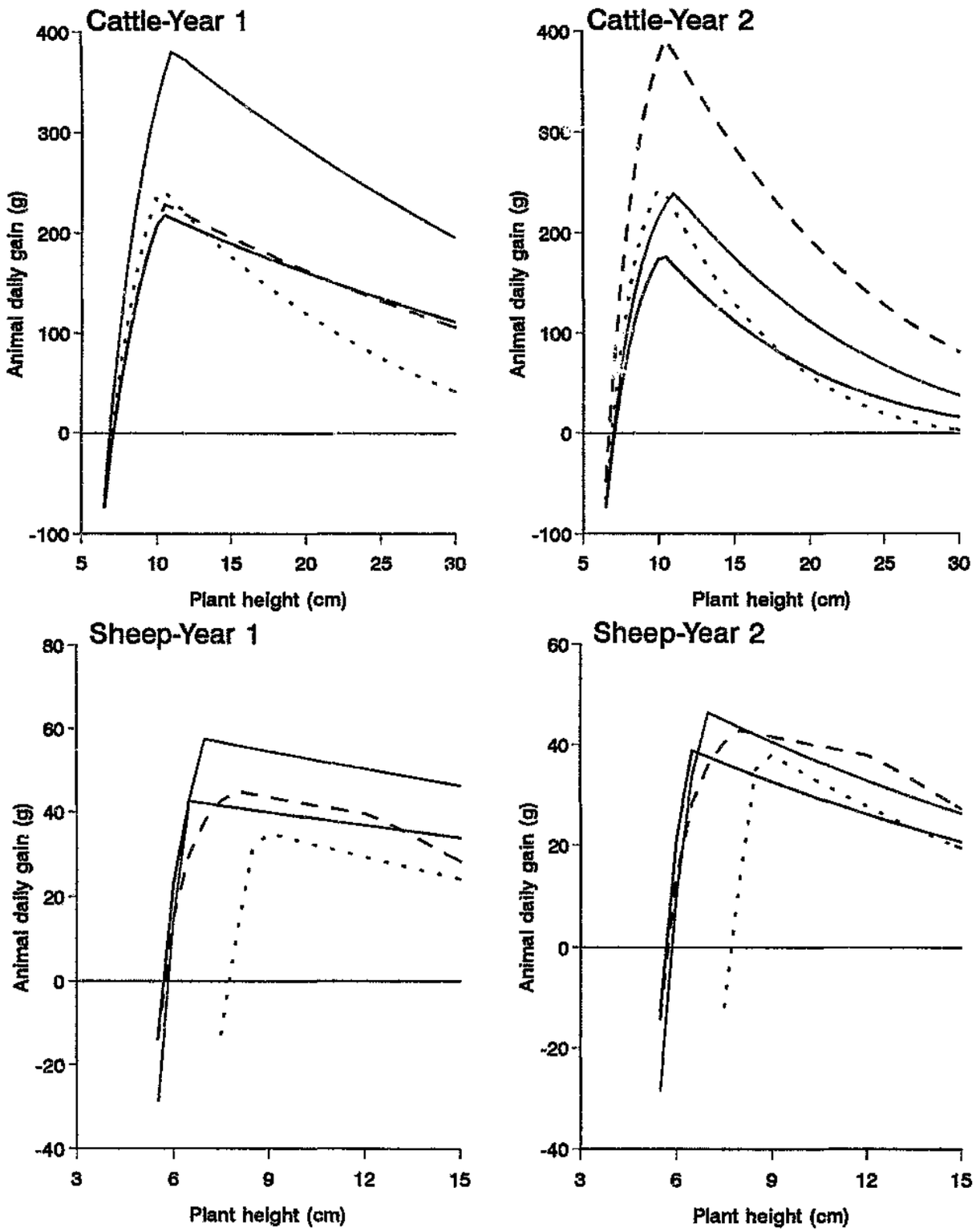

Figure 7.8 Output for Sward model-1: Predicted ADG for cattle and sheep over a range of sward heights at four sites in Dohne sourveld (_____ = bush, ... = eragrostis, -- -- = old lands and _____ = sheep shed camps).

increasing height due to the decline in herbage quality and its resultant effects on MRT. Animal production is thus optimised at the sward height where these two lines intersect. At heights below H_{opt}, production is restricted by ingestion rate while at heights above this level production is largely restricted by digestion rate. For sheep, production may also be restricted at heights above H_{opt} due to the decline in IR observed at some sites on very tall swards, e.g. eragrostis camp (section 3).

It is important to note that H_{opt} was extremely sensitive to the adjustment factor applied to IR to compensate for the effects of factors such as fasting and the incomplete recovery of fistula samples. For example, at sheep shed, adjusting cattle IR by zero, -10 %, -20 % and -40 % resulted in respective H_{opt} of 11 cm, 13.5 cm, 15 cm and 16 cm. Predicted H_{opt} for sheep was also sensitive to the adjustment factor used, changing from 6.8 cm to 10 cm at sheep shed, over the same range of adjustments to IR. Consequently, predictions of H_{opt} from the present model should not be regarded as absolute values but rather as an indication as to where these relative heights occur.

Although it was assumed that the relation between MRT and sward height was constant over the growing season, in practice, both the slope and position of this line are likely to vary, resulting in different optima through the season, as observed in Species model-2 (section 7.3.2.3). Intuitively, it may thus be expected that H_{opt} will be highest in the early season but will decline thereafter, due to the general decrease in forage quality (Chapter 2). However, even on the highest quality swards, H_{opt} should always be lower than that at which bite size is maximised, as any increase above this height only depresses forage quality, and ultimately VFI, further.

For cattle, H_{opt} was nearly identical at all sites (Fig. 7.8). However, between-site differences in predicted production were evident in both years: in year 1 predicted ADG at sheep shed was nearly 160 g higher than that for the remaining sites, largely because of the particularly low MRT of samples collected at this site. In year 2, predicted production was highest at old lands, probably due to the relatively small depression in IVD measured at this camp in the second year (Chapter 2). It is also notable that the rate of decline in ADG above H_{opt} also varied between sites due to the different nature of the relations between MRT and plant height.

In contrast to cattle, H_{opt} for sheep varied between sites tending to be lowest for bush (± 7 cm) and highest for eragrostis (± 9 cm). This probably reflects the fact that different intake rate functions were used for the four sites rather than any intrinsic difference between sites *per se*. Although predicted production was fairly similar for all sites in year 2, differences were more marked in the first year with sheep shed and eragrostis camps having

the highest and lowest predicted ADGs respectively (Fig. 7.8). As with cattle, these differences largely reflect variation in the MRT of samples collected at the different sites.

7.4.2 Sward model-2

7.4.2.1 Goal

To predict the cumulative change in body mass of cattle and sheep over the grazing season, adjusted for the differential decline in animal production over the grazing period, on swards of different species composition on sourveld.

7.4.2.2 Model description

The model predicts the cumulative change in body mass over the grazing season of cattle and sheep on sites of different species composition on sourveld. The model accounts for differences in animal production between sites by (i) predicting the potential animal production from a site based on measured values of dietary quality and intake from each site and (ii) taking into account the fact that animal production will decline at different rates over the grazing period on different sites (see Species model-3) due to differences in species composition.

The model uses a fourteen day time step (T), which is an average period of occupation in a camp in sourveld (Barnes 1989), and assumes that at the end of this period animals are moved to a new paddock of identical species composition. Animals were assumed to be 1.5 year old Dohne Merino wethers and 2.5 year old Bonsmara steers with starting body masses of 35 kg and 250 kg, and SRW of 65 and 500 kg, respectively. The model assumes that: (i) dietary quality declines but MRT increases in a constant linear fashion over the grazing season, as documented in chapter 2, (ii) sward height and therefore potential IR, remain constant over the same period (iii) dietary quality and hence animal production, in general, declines over a period of occupation in a camp, (iv) any deficiencies in dietary protein requirements are rectified through supplementation, (v) the ratio of the mass of rumen contents to body mass (20 g/kg) remains constant throughout the season, (vi) sward height is optimum for both animals, i.e. 8 cm for sheep and 12 cm for cattle, and (vii) sufficient herbage is always available for grazing when animals return to a camp.

The model starts at the beginning of the grazing season, assumed to be 1 October (day 0), and continues until the end of winter (day 350). A time step (T) of fourteen days is used with cumulative live weight gain being calculated in increments of T. Dietary IVD and MRT were predicted from days since the start of the grazing season using relations derived from

data in section 2 and presented in Appendix 6.4 & 6.5. Potential intake, actual intake and VFI were determined as described earlier (section 7.3.2.1).

Table 7.5 Predicted decline in animal daily gain for cattle and sheep through a period of occupation in a camp at different times through the grazing season

Season	CAMP			
	Bush	Eragrostis	Lands	Sheep shed
	g/day			
Cattle				
Spring	0	-3.30	-8.50	-5.00
Summer	-6.25	-9.09	-14.28	-1.78
Autumn	-2.93	-7.50	-2.33	-3.96
Winter	-2.33	-5.33	0	-1.10
Sheep				
Spring	-0.13	-0.53	-1.80	-0.52
Summer	-0.50	-1.23	-0.93	-0.26
Autumn	-0.22	-0.91	-0.27	-0.41
Winter	-0.60	-0.91	0	-0.19

At any time step T, potential animal daily gain (ADG) was predicted as described in Species model-1. The rate of change, i.e. the slope, of ADG over the grazing period at the four different sites was obtained from Species model-3. Slopes for cattle and sheep were determined by fitting a line by eye to the curves generated by this model and calculating the change in ADG per day at different times through the grazing season (Table 7.6). The zero decline in ADG at old lands camp in winter reflects the fact that because VFIs were low at this time, total intake was also lower, so animals were able to graze *H. hirta* throughout the grazing period without being forced to graze the lower quality species present in that camp.

Potential ADG was then adjusted for the expected decline in ADG over the grazing period at each site, i.e.

ADG adjusted = [(ADG potential + (ADG potential - slope * (T))/2] * T

The expected mass loss or gain over T was then calculated using this adjusted ADG as:

$$ADG * T$$

where T = length of time step in days.

7.4.2.3 Results

The model predicted a seasonal pattern of live weight gain typical of sourveld, with rapid weight gains in the first 150-200 days, followed by a levelling off or decline in mass in late season (Fig. 7.9). This trend is a direct reflection of the observed seasonal decline in dietary

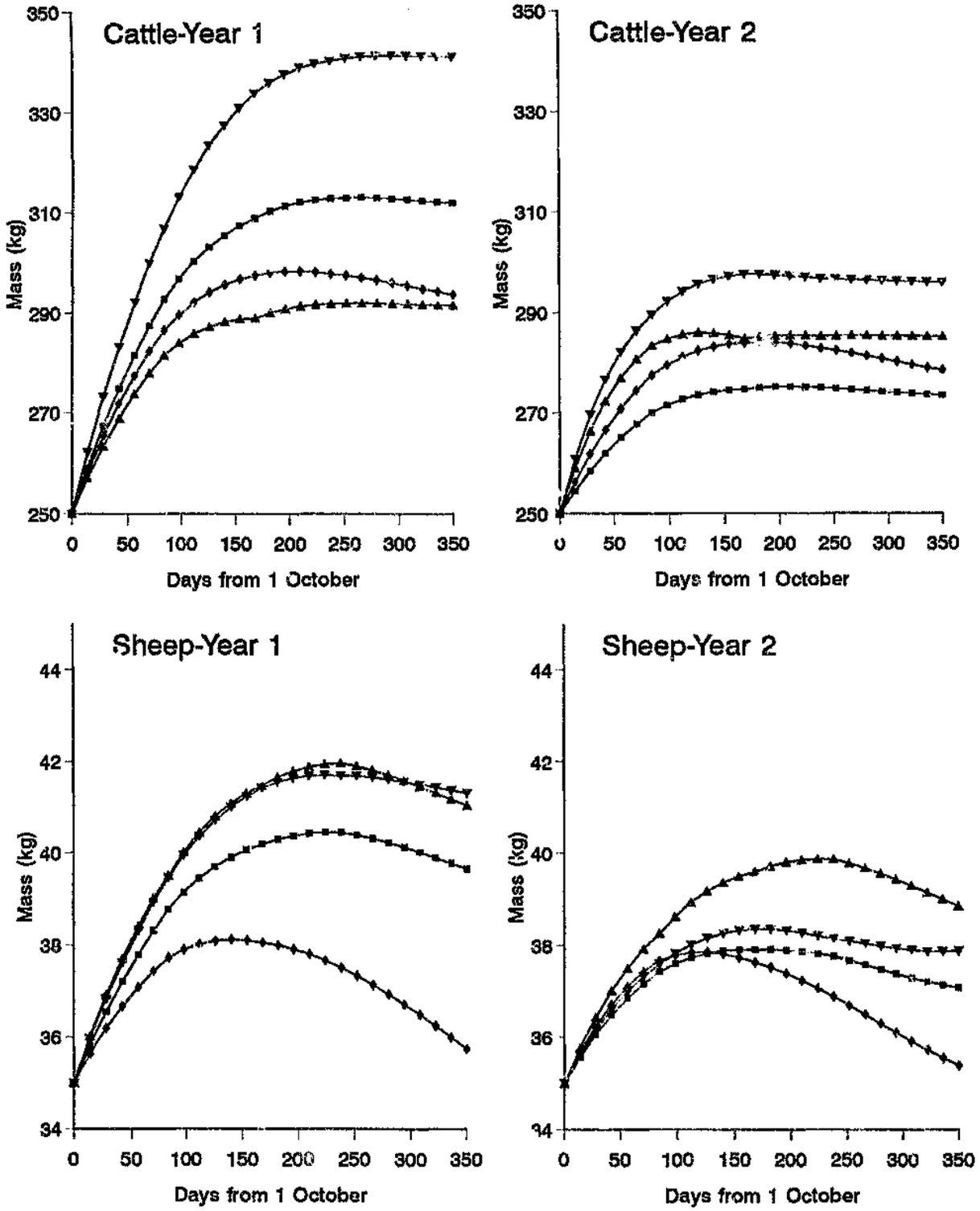

Figure 7.9 Output for Sward model-2: Cumulative change in body mass for cattle and sheep over the grazing season at four sites in Dohne sourveld (■ = bush, ♦ = eragrostis, ▲ = old lands and ▼ = sheep shed camps).

quality which is characteristic of this veld type (Chapter 2), and its resultant effects on MRT, VFI and the consequent intake of metabolisable energy. Predicted gains were within the range of recorded values for animals of similar body size on sourveld. For example, seasonal gains of 57-87 kg were measured for cattle over a number of stocking rates on this veld type (Anon. 1994) compared to predicted values of 35-90 kg (Fig. 7.9). Similarly, seasonal predicted gains for sheep of 3.5-8.5 kg are comparable to recorded gains of 2.6-6.3 kg (Anon. *loc. cit.*).

There were major differences in predicted mass gain between years with gains being markedly higher in the first than in the second year (Fig. 7.9). For example with cattle, mean predicted production was 58 and 32 kg in these two years respectively. This difference is logical and reflects the general higher nutritional quality of samples collected in the year of the burn compared to those collected in the subsequent season (Chapter 2).

There were large between-site differences in predicted gain for both animal species (Fig. 7.9). For example, with cattle, the difference between the sites with the highest and lowest predicted gain was 125 % and 80 % in the first and second year respectively, while for sheep these differences were 500 % and 680 % for the two years. Predicted gains for sheep were highest at old lands and sheep shed in year 1 but were markedly higher at old lands than at sheep shed in year 2. In both years predicted gains were lowest at eragrostis camp. Conversely, highest predicted gains for cattle were at sheep shed in both years while lowest gains were at eragostis and old lands in year 1 and at bush camp in year 2 (Fig. 7.9). While unexpected, the discrepancies in site rankings between cattle and sheep appear to reflect differences in the quality of diet selected by the two animals at the four different sites.

In the present model, predicted animal production is essentially a product of (i) the potential quality of diet available at a particular site, and (ii), the rate at which this quality declines as the animal is forced to graze other, possibly lower quality species in the sward. Thus, predicted production at sheep shed was generally high because available quality was also high while the rate of decline through the grazing period was low (Table 7.3). In contrast, predicted production at eragrostis camp was poor as the quality of diet selected there was, in general, low, while the rate of decline through the grazing period was very fast due to dominance of the low quality *E. plana* at that camp. Old lands is an interesting contrast to these two extremes; here, the rate of decline in quality over the grazing period was relatively fast, but the quality of diet selected by sheep was sufficiently high to give nearly the highest level of predicted animal production of all camps (Fig. 7.9).

The model succeeded in its basic goal of incorporating the decline in ADG through the grazing period into a basic prediction of animal production on sourveld. However, some of the basic assumptions used in the model require modification. First, the assumption that dietary

quality continues to decline (and MRT to increase) at the extreme end of the grazing season, i.e. in August and September, is simplistic as herbage quality appears to start recovering to spring levels r this stage (P.J.Zeeman pers. com.[1]). Second, Species model-3, from which the rates of change in ADG are derived, assumes that the total plant population, i.e. plant density, is the same at all sites. However this is unlikely to be the case in practice as fairly large variations in basal cover are common on rangeland which would further amplify between site differences in animal production.

7.5 Discussion

The models presented in the present chapter clearly indicate that species composition and sward structure are major determinants of animal production on sourveld. The potential importance of species composition was initially indicated by the large differences in predicted animal production between individual grass species (Fig. 7.2 & 7.3). This was confirmed by the predicted differences in production between sites of different species c. mposition using dietary quality and intake data from these sites (Figs. 7.8 & 7.9). In this regard, it is noteworthy that the small, apparently insignificant differences in dietary quality detected between different sites (Chapter 2) frequently translated into major differences in predicted animal production. These differences are likely to be of major economic relevance for the grazier. For example, the predicted difference in animal production between the best and poorest site in Sward model-2 (year 1), translates into a R187 and R24 difference in gross return per animal per year for cattle and sheep respectively (calculated at current prices of R2.50 and R3.00 per kg live weight).

Species composition appears to be an important determinant of animal production for two reasons. First, the basic nutritive value of the dominant palatable species present defines the upper limit to production which may be achieved from any area. As an example, the potential animal production from a site dominated by *H. hirta* is likely to be considerably higher than one dominated by *H. contortus*. This was apparent even in the preliminary data where in some camps the quality of diet selected in even the first few minutes of a grazing period was, on average, higher than that selected in others (Chapter 2). Second, the relative abundance and nutritive value of other, possibly unpalatable, species will determine how long this initial production can be maintained and the extent to which production will decline when animals are eventually forced to graze this second group of species. Thus in Species model-3, predicted ADG declined far faster over the grazing period at sites like eragrostis camp which

[1] Dohne A.D.I., P. Bag X15, Stutterheim, 4930.

was dominated by the low quality *E. plana*, than at other sites, where the less palatable species were less abundant and/or of higher nutritive value (Fig. 7.7).

Overall, there was considerable concordance in output between the Species- and Sward-series of models. For example, predicted production from old lands and sheep shed camps was the highest for both cattle and sheep (Sward model-1 and -2). These camps were dominated by *H. hirta* and *T. leucothrix* respectively, which both have moderate to good degradation characteristics in the rumen and a high predicted potential to support animal production (Fig. 7.2 & 7.3). Conversely, predicted production from eragrostis camp was low in all models, which is in agreement with the poor production potential of its dominant species, *E. plana*.

Despite the obvious importance of species composition, there is only limited agreement between the ranking of sites in terms of their potential to support animal production and their veld condition score. Using the accepted scoring technique for the Dohne Sourveld (Danckwerts 1987), site rankings based on veld condition score (in parenthesis) are bush (678), sheep shed (584), eragrostis (487) and old lands (424) camp. However, based on the average animal production over the grazing season for Sward model-2, site rankings in order of predicted production are sheep shed, old lands, bush and eragrostis camp. Thus, while there was some agreement on the relative value of sheep shed and eragrostis camps, based on veld condition score, the value of bush and old lands were considerably over- and under-estimated, respectively. It is therefore obvious that on sourveld the veld condition score remains an inadequate index of the potential of an area to support animal production.

Sward structure was also an important determinant of animal production, mainly through the effects of sward height and greenness on dietary quality and intake. Greenness was the major determinant of dietary quality but through its effects on MRT, also controlled VFI and ultimately, total DM intake. Sward height controlled bite size and hence the rate of herbage ingestion by the grazing animal. However, an obvious threshold effect was evident in terms of the predicted response of animal production to this variable. Below the height at which intake rate was maximized, small increases in height resulted in major increases in animal production due to the strong positive relation which exists between the first two variables (Chapter 3). However, above this point, increasing height led to no further increases in production as intake rate was then limited by mouth dimensions rather than sward height *per se*. Production would in fact decline above this height due to the decrease in sward greenness and associated declines in VFI and the energy content of ingested herbage.

The relative importance of sward height was strongly dependent upon forage quality due to the constraint set by digestion rate on intake. As quality declined, this constraint increased, restricting DM intake further and reducing the response of animal production to sward height

(Fig. 7.4). This is consistent with the observation that except on the highest quality swards, the potential rate of DM ingestion far exceeded the actual rate of digestion through the rumen. On the basis of the above it is apparent that dietary quality is the biggest single determinant of animal production on sourveld and that the relative importance of this variable increases as herbage quality declines through the grazing season.

While model outputs for cattle and sheep were generally similar, a number of differences were apparent between the two animals which are of interest. First, the optimum sward heights (during the growing season) for cattle (12 cm) and sheep (6-8 cm) were different, as would be expected for two animals functioning under markedly different physiological and anatomical constraints. For both animals, the optimum heights are marginally higher than those recommended for temperate pastures, e.g. Ernst *et. al.* (1980) but are within the range considered to be optimum by leading graziers for the Dohne Sourveld (W.G. Hartley[2], *pers. comm.*). Interestingly, for both cattle and sheep these heights are markedly lower than those at which intake rates were maximised (Chapter 3), again emphasising the overriding importance of forage quality in sourveld. Second, although the relative rankings of most sites were similar, old lands camp appeared to have a markedly higher potential for sheep than for cattle (Fig. 7.9). This is surprising as this site tended to be tall and very stemmy, and appeared unsuitable for a small, short grass grazer like sheep. However, the greater selective ability of this animal possibly allowed it to select the high-quality *H. hirta* leaves which were dispersed amongst the available material while cattle were forced to graze relatively unselectively.

It is also noteworthy that the predicted weight gains in cattle, when taken in proportion to initial body mass, were far greater than those for sheep. Thus, in Sward model-2, which is based on the actual quality of diet selected by animals in the field (section 7.4.2.2), cattle in year 1 showed an average increase in body mass of 32 % relative to only 12.5 % for sheep. This demonstrates the advantages of having a relatively large rumen:body size ratio and suggests that this factor may outweigh the greater selective ability of the latter animals in dealing with a low-quality resource like sourveld.

Lastly, it is suggested that the above models are an improvement on the model of Hardy and Mentis (1986) in that the present models incorporate the actual mechanistic processes which operate in the field, e.g. ingestion and digestion rates, rather than the coarse, higher level outcomes of such processes, e.g. total daily DM intake, as used by Hardy and Mentis (*loc. cit.*). Accordingly, the present models are likely to be relatively more flexible and have a greater ability to predict over a range of environmental conditions than that of Hardy and Mentis (1986).

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[2]'Elvadell', PO Box 232, Stutterheim, 4930.

Similarly, while the present models are relatively simplistic compared to the model developed by Owen-Smith (1991), they are an improvement, in certain respects, in that (i), they accounted for the effects of species abundance and declining food availability on search and intake rates, and (ii), they accounted for between-species differences in passage and digestion rates of cell and cell wall constituents in contrast to Owen-Smith (1991) who assumed that these were constant across all species. As observed in Chapter 6, this assumption is erroneous and possibly accounts for the fact that the differences in predicted animal production between sites of different species composition in the latter model (Owen-Smith *loc. cit.*) were relatively small compared to those predicted here. Nevertheless, the models developed in this study require modification including the development of an ability to predict herbage growth, the capacity to handle more complex species mixes in the diet, more detailed accounting of the energetic costs associated with foraging and the allometric adjustment of ingestive behaviour, e.g. bite size, in relation to changing body mass.

7.6 Conclusions

7.6.1 There were large differences between grass species in their predicted potential to support animal production. Overall, predicted ADG was greatest from *H. hirta*, and to a lesser extent from *C. dactylon*, but lowest from *A. appendiculatus*, *E. plana* and *M. caffra*.

7.6.2 Predicted ADG declined progressively through the grazing season for all species. With the exception of *T. triandra*, none of the species considered appeared capable of sustaining animal production in winter.

7.6.3 For individual grasses, predicted ADG by cattle was maximized at a height of between 8 and 12 cm, depending upon the species. However, this height became progressively lower as herbage quality declined through the grazing season.

7.6.4 Predicted ADG declined through the grazing period at all sites. The magnitude of this decline was strongly dependent upon species composition in terms of the nutritive value and the relative and absolute abundance of the species present at any site.

7.6.5 Predicted ADG was optimised at a sward height of 6 to 8 cm for sheep and about 12 cm for cattle, at all sites during the growing season. There were marked differences between sites in terms of predicted animal production.

7.6.6 Differences between sites in predicted seasonal gain were large with production at the site dominated by *T. leucothrix* (sheep shed) generally being the highest for both animals. At all sites, predicted liveweight gain was most rapid in the early season but thereafter levelled off and, in some cases, declined, in the late season.

7.6.7 On all but the shortest of swards, potential rates of DM ingestion were generally far in excess of predicted voluntary intake, i.e. rates of digestion. This suggests that in sourveld, intake is seldom likely to be restricted by the effects of sward height on intake rate *per. se.*

CHAPTER 8

REVISED FORAGE FACTORS FOR THE DOHNE SOURVELD

8.1 Objective

The objective of this section was to develop forage factors for common sourveld grasses based on measured attributes of the acceptability and the potential rates of digestion and ingestion of these species.

8.2. Introduction

The current method of determining the veld condition score of a site in the Dohne Sourveld involves multiplying the relative abundance of each species present by some forage factor. Depending upon the species, these forage factors may range from a factor of zero, e.g. *E. muticus* to a factor of ten, e.g. *T. triandra* (Danckwerts 1987). The resultant products are then summed to give the veld condition score for that particular site.

As stated previously, the current forage factors for the Dohne Sourveld are based upon subjective assessments of the palatability and potential productivity of individual grass species (Danckwerts 1987). It would, however, be an improvement if a set of factors could be derived which were rather based on some objective assessment of the relevant attributes of these species. The data and models presented in this study accordingly present an appropriate opportunity to develop a revised set of forage factors for grass species common to the Dohne Sourveld.

8.3 Procedure

Forage factors were determined separately for cattle and sheep on the assumption that these animals operate under different foraging constraints and have different species preferences. In the first step, the intake rate (Chapter 5) of each species was standardised by dividing the measured IR by the lowest recorded value for all grasses, e.g. for sheep all IR values were divided by the estimated IR for *M. caffra*. In the second step, this same procedure was repeated for the predicted VFI of all species for each of the four seasons. For each species, an overall VFI score was then calculated using the standardised scores, weighted for each season. The weighting factors used were either 1, 1, 2, 3 or 3, 3, 2, 1 for spring, summer, autumn and winter respectively.

These two weighting procedures were taken to reflect opposing theories that

either winter or summer herbage quality is of greater relative importance for animal production on sourveld. The first theory is that nutritional quality in winter is relatively more important, as the degree of mass loss at this time ultimately determines the survival or reproductive success of the animal in the following season. This theory, which will be termed winter minimisation, would presumably apply to wild animals but could be equally appropriate for breeding animals in commercial herds. The second theory is that nutritional quality in summer is relatively more important as this is when maximum animal growth occurs, and it is assumed that any potential mass loss in winter is either prevented by supplementary feeding or is made up by compensatory growth the next season or a combination of both. This could be termed summer maximisation and would approximate certain production systems on sourveld, such as an operation growing steers out to maturity.

In the third step, the standardised scores for IR and VFI were ranked from highest to lowest and each species given a score out of ten for each attribute. In the fourth step, the overall acceptability of each species was rated separately for cattle and sheep on a scale of zero to ten based on data presented in chapter 4 or on unpublished field observations.

A forage factor was finally calculated by applying different weightings to the scores for acceptability, VFI and potential IR, and determining an overall score for each species. Weightings used for sheep were 10, 1 and 2 for VFI, IR and acceptability respectively, while those for cattle were 5, 1 and 2. With both animals, any species with an acceptability score of zero automatically received a total score of 1. The weightings used for VFI and IR were derived from the sensitivity analysis presented in Tables 7.3 and 7.4 and are based on the assumption that for sheep and cattle, the rate at which herbage can be digested, i.e. its quality, is 10 and 5 times more important respectively, than the rate at which it can be ingested. For both animals, acceptability was also rated twice as high as IR on the assumption that the latter factor was of little relevance if animals would not graze a species. Forage factors were standardised to between zero and ten by dividing the sum of the weighted products of VFI, acceptability and IR by the sum of the all weighting factors for that species, i.e. 13 and 8 for sheep and cattle respectively.

Veld condition scores for the different experimental sites (see Chapter 2) were recalculated using the revised forage factors. Sites were then ranked from highest to lowest first, on the basis of the old (Danckwerts 1987) and the revised scores and

Table 8.1 Revised forage factors for different grasses in the Dohne Sourveld. Summer and winter weighted refer to the season where herbage quality was rated highest. See text for more details

Species	Previous factor[1]	Sheep			Cattle		
		Summer weighted	Winter weighted	Mean	Summer weighted	Winter weighted	Mean
A. appendiculatus	7	3.85	3.08	3.46	4.88	4.25	4.56
A. semialata	2	6.46	8.00	7.23	8.63	9.25	8.94
C. dactylon	2	6.77	4.46	5.62	6.75	4.25	5.50
E. plana	2	2.08	2.85	2.46	3.63	3.63	3.63
E. muticus	0	0.08	0.08	0.08	0.13	0.13	0.13
H. contortus	7	6.69	7.46	7.08	7.13	6.50	6.81
H. falx	4	4.23	4.23	4.23	4.00	3.38	3.69
H. hirta	4	9.69	9.69	9.69	9.13	9.13	9.13
M. caffra	0	0.08	0.08	0.08	0.13	0.13	0.13
T. leucothrix	7	6.15	6.92	6.54	6.88	6.88	6.88
T. triandra	10	6.46	9.54	8.00	7.75	9.00	8.38

[1](Danckwerts 1987)

second, on the basis of the total seasonal animal production predicted on each site using Sward model-2 (Chapter 7). These two sets of rankings were then compared to determine the degree of concordance between the two veld condition scores and the predicted animal production from each site.

8.4 Results

The revised forage factors for the different species, as well as the original factors given by Danckwerts (1987), are given in Table 8.1. The revised forage factors for *A. appendiculatus*, *T. triandra* and *T. leucothrix* are, on average, about three units lower compared to those proposed by Danckwerts (*loc. cit.*), largely due to the fact that these species were all found to be of only average quality relative to the other grass species (Chapter 6). Conversely, the forage factors for *A. semialata*, *H. hirta*, and *C. dactylon* were all markedly higher, due to the relatively high quality, and hence predicted VFI, of these three grasses. For the remaining species there was fairly good agreement between the old and the new revised forage factors (Table 8.1).

The effect of weighting herbage quality according to the strategies of summer maximisation or winter minimisation had little effect on the forage factors developed for most species (Table 8.1). However, notable exceptions were *T. triandra* and *A. semialata* which had relatively higher forage factors with winter weighting, and *C. dactylon* for which the reverse applied. These differences reflect the marked change in the relative quality rankings of these three species over the grazing season (Chapter 6). Forage factors developed for cattle and sheep were generally similar (Table 8.1) although the forage factors of *A. appendiculatus* and *E. plana* were relatively lower for sheep, largely due to the higher weighting (10 vs. 5) given to leaf quality for the latter animals. In contrast, despite its relatively high quality, the sheep forage factor for *A. semialata* was relatively low due to the low preference shown by these animals for this species (Chapter 4).

The revised veld condition scores for the four sites used in this study as well the site rankings in terms of both this attribute and predicted animal production from Sward model-2 (Chapter 7) are given in Table 8.2. Based on overall condition score, site rankings derived from the old scores were generally different from those obtained using the new forage factors. In particular, the rankings of old lands and bush camp were almost completely reversed with the former site now having the highest score and being ranked first (Table 8.2) while the latter camp was ranked second lowest of the four sites. These differences result directly from the respective increase and decrease in

Table 8.2 Site rankings based on (i) veld condition scores derived from the previous and the revised forage factors for cattle and sheep, and (ii) predicted production of cattle and sheep from these sites

Site	Site rankings				
	Previous[1] forage factor	Cattle forage factor	Production (cattle)	Sheep forage factor	Production (sheep)
Bush	1	3	3	3	3
Sheep shed	2	2	1	2	2
Eragrostis	3	4	2	4	4
Lands	4	1	4	1	1

[1]Danckwerts (1987)

the revised forage factors of *H. hirta* and *T. triandra* reported earlier. In contrast, there was little difference between the two methods in the relative rankings of sheep shed and eragrostis camps.

There was almost complete agreement between the ranking of sites obtained using the revised forage factors (Table 8.2) and predicted sheep production from these sites. This is in contrast to the old forage factors where only limited agreement between site rankings for veld condition score and predicted production occurred. Unfortunately, matching between site rankings for veld condition and predicted cattle production was only marginally better than that achieved with previous forage factors (Table 8.2). The major reason for this discrepancy between site rankings for cattle and sheep was that the revised forage factor for *H. hirta* appeared to overestimate the value of this species to cattle, at least under the conditions of the present experiment.

8.5. Discussion

The forage factors developed in this section for the Dohne Sourveld are an improvement over previous factors in that there appeared to be better agreement between the resultant veld condition scores and the predicted animal production from different sites (Table 8.2). In this regard it is interesting to compare the rankings of different communities which would be obtained using the present forage factors and those of Danckwerts (1987). Based on the latter method, well-managed *T. triandra* dominated sites (Tainton 1981) would be assessed as being in 'optimum' condition and would be ranked highest in terms of their expected potential to support animal production. Conversely, degraded sites which had suffered excessive grazing pressure and were dominated by *E. plana* or those which had been subject to extreme species selective

grazing and were dominated *E. muticus*, would be ranked the lowest. Intermediate between these extremes would come, in descending order, so called under-utilised sites (*sensu* Tainton 1981) dominated by *T. leuc rix* and *A. semialata*, followed by the secondary grassland, *H. hirta* communities.

In contrast to the above, the secondary grassland, *H. hirta* communities would be ranked highest using the new forage factors while the *Tristachya* and *Themeda* communities would be ranked lower at a level almost equal to each other. However, in agreement with conventional rankings, sites dominated by *E. plana* or *E. muticus* would be ranked lowest using the new forage factors (Table 8.2). It should be noted that despite the very high forage factor given to *H. hirta* and the resultant high ranking of sites dominated by this grass, these 'old lands' represent a relatively small fraction of the Dohne Sourveld, and are therefore not a major issue in the management of this veld type.

While the present forage factors appear to be an improvement over previous factors they nevertheless have two important shortcomings. First, in determining these factors, the persistence or ability of a species to withstand grazing pressure was not considered and the issue of sustainability, as defined by Teague and Danckwerts (1989), was therefore not addressed. However, while it is accepted that there may be a conflict between short-term production and sustainability in certain semi-arid areas (Tainton 1981), this is not likely to be a problem in sourveld partly because of the low variability of rainfall and partly because of its perennial, rather than, annual species composition. Second, the present forage factors do not take into account the forage production potential of the different species which directly determines both the short and long-term grazing capacity of a site. However, there is no evidence to show that herbage production and veld condition are related in the Dohne Sourveld (Willis 1990), suggesting that there is little difference in the herbage production potential of the constituent species of this veld type. The forage factors developed here (and in fact those of Danckwerts (1987)) should therefore be used with caution until such time as the production potential of individual grass species has been assessed and, accordingly, these factors cannot be regarded as a definitive index of the ability of a species to support animal production.

The present exercise was, nevertheless, valuable in that it highlighted the difficulties associated with assigning a forage factor to a species in terms of its potential to support animal production. In the first place, reconciling the acceptability of a species with its nutritive value is problematic. While the acceptability of most

sourveld grasses is generally correlated with leaf quality (O'Reagain & Mentis 1989b; O'Reagain 1993) there are a number of exceptions to this general rule. For example, while *E. muticus* is, theoretically, of high nutritional value (Chapter 7) it is of extremely low acceptability to both cattle and sheep (Stritsz & Danckwerts 1990). In this case it may be assumed that this species will seldom be consumed and is therefore of little practical value to the grazing animal. The case of *A. semialata* is, however, more difficult. While fairly acceptable to cattle, it is generally avoided by sheep (Chapter 4) despite the relatively high quality of its leaf material (Chapter 6). Although sheep will graze *A. semialata* (Chapter 4) when other, more acceptable herbage has been depleted, the high predicted production from this species (Chapter 7) could be negated by the increased energetic costs associated with searching for other grasses to graze before sheep finally consume this species.

A further problem is that of plant structure, with the most relevant example possibly being that of *H. hirta* for cattle. While predicted production from this species is high due to the rapid degradation rate of its leaves in the rumen (Chapter 7), the species develops a dense mass of woody, persistent stems if not defoliated in the early season. The value of such a species is therefore largely conditional upon its phenology, making it extremely difficult to allocate some average score to this species.

However, possibly the biggest problem is that of determining the relative weightings to be attached to attributes like quality, intake and acceptability in deriving a forage factor for a particular grass species. Although an attempt was made to objectively determine these weightings in the present study, a strong element of subjectivity was nevertheless unavoidable in assigning a weighting to an attribute like acceptability which is not only difficult to quantify but is also dependent upon season and the presence or absence of other, more palatable species. The weightings assigned to IR and VFI are also questionable, given that the relative importance of these attributes varied between different seasons (Tables 7.3 & 7.4).

The present exercise also highlighted potential differences between animal species in the weightings applied to the various species attributes while differences in operator objectives or the survival strategy employed by the animal, i.e. summer maximisation versus winter minimisation, were also of relevance in determining the forage factor of a particular species. Unfortunately, with a few exceptions, e.g. Teague and Danckwerts (1989), previous assessment techniques have not acknowledged these problems and have blindly assumed that a veld condition score is an absolute index, independent of both animal species and operator objectives. This assumption is clearly

erroneous and future forage factors must therefore take into account not only grazier objectives and animal type but should explicitly define the underlying assumptions about the relative importance of the different species attributes used in the determinination of these factors.

8.6 Conclusions

8.6.1 A series of new forage factors for common sourveld grasses were developed based on measured attributes of the acceptability and potential rates of ingestion and digestion of these species, weighted separately for cattle and sheep.

8.6.2 Relative to the previous system, the forage factors of *T. triandra* and *A. appendiculatus* were reduced, while those of *H. hirta, A. semialata* and *C. dactylon* increased, largely due to differences in forage quality between species.

8.6.3 With the exception of *A. semialata* and *H. contortus* which had a higher forage factor for sheep, and *E. plana* and *A. appendiculatus*, which had higher forage factor for cattle, there was little difference in species forage factor between the two animals.

8.6.4 Giving the relative winter quality of a species a greater weighting than that of its summer quality increased the forage factor of *T. triandra* and *A. semialata* but decreased that of *C. dactylon.* Changing these relative weightings also had a marked effect on the veld condition scores of different sites, particularly for sheep.

8.6.5 Use of the new forage factors markedly improved agreement between site rankings based on veld condition score and predicted animal production for sheep, but agreement between site rankings for cattle remained poor.

8.6.6 It is concluded that species forage factors must take into account grazier objectives, the type of animal involved and the underlying assumptions about the relative importance of different species attributes. Accordingly, the veld condition score of a site is not absolute, but is conditional upon these factors.

CHAPTER 9

CONCLUSIONS

9.1 Overview

In this section a brief overview of each component of the study is given. Accordingly, major findings are briefly stated, their relevance within the context of current knowledge is addressed and the influence of any shortcomings in experimental design or execution on the interpretation of results are discussed.

Species composition and, by extension, veld condition, had no clear effect on the quality of diet selected by cattle and sheep on sourveld. While this merely appears to corroborate earlier work with cattle (Mentis 1982; Hardy 1986; O'Reagain & Mentis 1990) this finding has not previously been extended to sheep. These results suggest that species composition is not a major determinant of dietary quality on sourveld. However, this finding must be treated with caution due to a limitation in experimental design. As fistula samples were always collected at the beginning of a grazing period (Chapter 2), it is likely that only the most palatable species were grazed at this stage (Chapter 4), possibly obscuring between site-differences which may only have manifested themselves later in the grazing period. Despite this, the similarity in the quality of diets selected at the four sites is noteworthy, given the marked between-site differences in species composition (Table 2.1).

In contrast to species composition, sward structure had a major effect on dietary quality in both animals, with dietary CP and IVD being strongly related to sward greenness but negatively related to sward height and herbage mass. Where swards became very stemmy, as at old lands camp, dietary quality also declined with increasing stemminess. These findings corroborate conventional grazier wisdom as well as published data from planted pastures, e.g. Hamilton *et al.* (1973). Nevertheless, this study is probably the first to explicitly quantify the effect of sward structure on dietary quality for any veld type in southern Africa. These results, and those reported above, suggest that in sourveld, sward structure is of greater importance in determining dietary quality than species composition. A disappointing aspect of the study was, however, that the sward height-dietary quality relation was not defined more precisely, as might

have been expected from pasture cutting trials, e.g. Grieve and Osbourn (1965). This aspect requires further investigation, possibly by clipping forage from single plants and relating leaf quality to plant height on an individual tuft basis.

As is characteristic of sourveld, dietary quality showed an overall decline over the grazing season and was also markedly higher in the year of the burn than in the subsequent year. However, an unexpected trend was the sharp drop in dietary quality associated with a short-term drought in mid-season, and its subsequent recovery when soil moisture levels were replenished. This trend is surprising, partly because it was not associated with any visible decline in sward greenness, and partly because moderate drought stress is generally assumed to increase herbage quality (Wilson 1981) by retarding growth and ageing. The present trend suggests that, contrary to conventional wisdom, soil moisture, possibly through its effects on the availability of soil nutrients, is an important determinant of forage quality in these mesic sour grasslands. Sheep generally selected a diet of higher quality than cattle, as would be expected from other studies, e.g. Zeeman *et al.* (1984). However, on certain occasions on very tall, rank swards the reverse occurred where cattle selected diets of higher digestibility than did sheep. Although difficult to explain, these results cannot easily be dismissed as spurious as the phenomenon was repeated at all four experimental sites under the same conditions. This discrepancy may possibly reflect the fact that by grazing at a relatively lower level within the sward (Forbes 1982 cited by Grant *et al.* 1985), sheep may inadvertently have selected lower-quality material at the base of rank swards than the cattle which tend to graze at a higher level (Forbes *loc. cit.*) where new growth is more likely to occur. If so, this suggests that cattle have both a selective, as well as a digestive, advantage in coping with tall, rank herbage.

Species composition and veld condition were also found to have no measurable effect on the rate of DM intake in cattle and sheep. While the effect of species composition on DM intake has previously been addressed for cattle on sourveld (1982; Hardy 1986) and sweetveld (Danckwerts 1984), this aspect does not appear to have been previously investigated for sheep. More importantly, the present study is probably the first in sourveld, or in fact on any veld type in southern Africa, to attempt to gain a mechanistic understanding of the process of DM intake by separating this variable into its basic components of bite size, bite rate and grazing time. Nevertheless, certain

shortcomings with the experimental methodology require consideration. First, due to variable recovery rates of fistula samples, a large component of experimental error was associated with estimates of DM intake by cattle, possibly obscuring any real between-site differences which may have existed. Second, as with dietary quality, estimates of intake rate were made at the beginning of the grazing period when animals would have grazed only the most acceptable species available. Again, this possibly obscured between-site differences in intake rate that may only have become evident over longer time periods when animals were forced to graze the less-preferred species present in the sward. Accordingly for cattle, and possibly also for sheep, these results cannot be considered as a definitive test of the effects of species composition on intake in sourveld. This aspect therefore requires further investigation using longer grazing periods and, for cattle, a more reliable method of estimating intake. Last, fasting experimental animals prior to sampling probably resulted in exaggerated estimates of intake rate, e.g. Greenwood and Demment (1988), and these consequently require adjustment to predict intake in animals at normal levels of satiation (Chapters 2 & 7).

Sward height had a major effect on intake rate in cattle and sheep but other components of sward structure such as greenness and stemminess had no clear effect on this variable. For both animals, intake rate increased two- to six- fold with increasing sward height, reaching an asymptote or maximum at a height of 10-15 cm for sheep and 20-25 cm for cattle. Given the magnitude of this effect, these results suggest that, despite the limitations of the present study, sward structure is a greater determinant of intake rate than species composition on sourveld. While the above results appear to merely corroborate the well-known effect of sward height on intake, e.g. Hodgson (1981), they nevertheless provide the first mechanistic quantification of this relation on any veld type in southern Africa. However, contrary to current theory, e.g. Laca *et al.* (1992), sward density appeared to have little effect on intake rate in cattle, while its effects on sheep intake rates were ambiguous. This is surprising but probably reflects (i) the unreliability of estimates of herbage mass and hence herbage density in the present study and (ii) the fact that herbage density was measured and expressed on a sward rather than an individual species basis. Despite this, it is suggested that, with the exception of short, post-burn regrowth, herbage density is seldom likely to restrict intake on sourveld due to the inherently dense, generally non-

stemmy nature of most swards in this veld type (pers. obs.).

Two other observations in this section were also of interest. First, at some sites a curvilinear functional response was observed for sheep which is a marked deviation from the classic asymptotic response usually documented for ungulates, e.g. Spalinger and Hobbs (1992). This indicates the existence of a third, quality dimension to the functional response that requires consideration on low-quality swards like sourveld. Second, on occasion, sheep achieved intake rates far in excess of those expected from sward structure alone. This suggests, in agreement with Owen-Smith (1993), that the observed mean values of the different parameters of foraging behaviour, in this instance intake rate, seldom reflect the upper constraints to these variables experienced by the animal. These observations emphasize the importance of other factors such as the physiological and metabolic state of the animal, as well as the trade-off between bite size and bite quality (Chapter 3) that control foraging behaviour.

Cattle and sheep both followed a definite, almost identical, sequence of species selection through the grazing period. Preferred species were defoliated first followed by less-preferred species but avoided species were generally not consumed until the majority of tillers of the preferred species had been defoliated and a considerable proportion of these tillers regrazed. While this merely corroborates previous observations for cattle (Daines 1980; Danckwerts *et al.* 1983; O'Reagain & Mentis 1989a), the present study appears to be the first to investigate and report this same sequence for sheep. Theoretically, these results are important suggesting a general order of species selection that should allow prediction of dietary selection under conditions of rapidly changing food availability. Practically, these results indicate the potential degree and extent of defoliation likely to be imposed on species of different acceptability under different grazing systems. Unfortunately, the second objective of relating the sequence of selection to changes in dietary quality and intake through the grazing period was not achieved. In retrospect, this problem is probably of greater complexity than initially believed and its successful resolution probably requires a far greater intensity of sampling through the grazing period. This, nevertheless, remains a worthwhile objective, essential for the fine scale prediction of animal performance in grazing systems or under conditions of rapidly changing herbage availability.

In general, the frequency with which individual tillers were defoliated over the

grazing period was the same under both cattle and sheep grazing. However, sheep consistently defoliated tillers at a lower height than did cattle. While the second point is simply a quantification of conventional wisdom, the study nevertheless appears to be the first published, direct comparison of the height and frequency of tiller defoliation by cattle and sheep. However, a limitation of the results was that the frequency of defoliation of tiller regrowth, considered to be a major cause of range degradation by sheep, was not addressed.

Although there were some significant between-species differences, the measured rates of DM intake from different sourveld grasses were surprisingly similar. Depending upon the species, intake rates ranged from 24 - 32 g.DM/min. for cattle and from 4 - 6.82 g.DM/min. for sheep. This suggests, in agreement with earlier results that, on sourveld, intake rate is seldom likely to be limited by species composition. Conversely, it appears unlikely that potential intake rate *per se* is an important factor in species selection on this veld type. The present results are the only known attempt to determine the potential rates of intake available from different sourveld grasses. However, considering the conditions under which the study was conducted, intake rates were probably higher than those normally achieved and consequently require adjustment for predicting intake under field conditions. Further, the range of plant heights used in the experiment tended to be skewed towards taller plants, so predictions of intake at low plant heights should be used with caution.

There were large differences in the size of the digestible and indigestible fractions present in different sourveld grasses and in their rate of degradation in the rumen. Major seasonal differences in these variables were also evident with degradation rates declining, and the indigestible fraction increasing, from spring through to winter. These trends are not unexpected. Nevertheless, the present results are the first to explicitly quantify differences in the rumen degradation rates of different sourveld species. As such, these data, in conjunction with the measured intake rates of different species, are important and have the potential to provide a basis to predict animal production over a wide variety of species compositions on sourveld. Further, present estimates of digestion and ingestion rates should enable the handling costs associated with different species to be precisely quantified, which would allow the construction and testing of an optimal foraging-based model of species selection. A possible shortcoming

in the experimental method was that milled rather than chewed samples were used which may have eliminated any potential effect of leaf toughness on particle size and hence degradation rate. Further, it was unfortunate that the effects of plant height and leaf maturity on rumen degradation rates could not be investigated. Both the above aspects deserve further study.

9.2 Synthesis

In the final stage of the study, the data collected were synthesised into a series of simulation models aimed at elucidating the effect of factors such as species composition, sward structure and season on potential animal production. The output from these models serves as an appropriate synthesis of the overall findings of the study and these are discussed below.

Dietary quality, through its effects on digestion rate, was of greater importance than the rate of DM ingestion in determining animal production on sourveld. With the exception of the shortest and/or highest quality swards, potential rates of DM intake for both cattle and sheep far exceeded potential digestion rates in the rumen. Even where intake rates were very low, it would appear that fairly moderate increases in grazing time would be sufficient to increase intake to the limits set by digestive capacity. Assuming a set ratio of rumen contents:body mass for cattle and sheep, the importance of dietary quality relative to intake rate increased as the grazing season progressed, due to the seasonal decline in herbage quality. The relative importance of dietary quality was also greater for sheep compared to cattle, as would be expected for an animal of smaller body size.

Species composition was found to have a major effect on predicted animal production, mainly due to the large differences in quality (specifically the rate and extent of digestion) between constituent grass species. This conflicts directly with the earlier finding (Chapter 2) that species composition has no apparent effect on dietary quality in sourveld. However, this discrepancy is easily resolved if it is considered that (i) fistula samples were collected when animals were probably selecting the most acceptable species at each site, (ii) recorded differences in leaf quality between the more acceptable species at the different sites were not major, e.g. *T. triandra* vs. *T. leucothrix*, and, most importantly, (iii) the digestion rates of these fistula samples were

not considered in the original data analysis (Chapter 2). In this regard it is significant that the apparently small between-site differences in quality recorded here, translated into major differences in predicted animal production over the growing season. Species composition therefore appears to be important in sourveld 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.

Species with the highest predicted potential to support animal production were not necessarily those conventionally rated the highest in terms of their forage factors, e.g. *H. hirta* (see Danckwerts 1987). Similarly, there was only partial agreement between the ranking of experimental sites based on veld condition score and that based on predicted animal production (based on measured estimates of dietary quality and intake). Significantly, the ranking of different sites, in terms of predicted animal production, varied markedly between cattle and sheep.

As expected, sward structure (specifically sward height, greenness, and to a lesser extent, stemminess) was also found to be an important determinant of animal production through its effects on dietary quality and intake. Optimum sward heights for animal production were 6 - 8 cm for sheep and 10 - 12 cm for cattle, but these varied between sites and were therefore dependent upon species composition. These optimum heights would also be expected to vary over the season, becoming progressively lower through the grazing season as the digestive constraint on intake increased. Although the relative importance of sward height and species composition is difficult to ascertain, predicted production appeared to be more sensitive to the former variable below the optimum height while species composition appeared to be more important above this optimum.

On the basis of the above, it therefore appears that, while it is simple to identify sites where animal production will be poor, e.g. those dominated by low quality and/or unpalatable species like *E. plana* or *E. muticus*, there appears to be no single optimum species composition where animal production will always be maximised on sourveld. This is due to a number of reasons. First, the optimum species composition is conditional upon the animal species and, probably, even the size and metabolic status of the animal involved. This reflects the interaction between the availability and

quality of material at a site and the particular digestive and foraging constraints under which animals of different body size must operate, e.g. Hanley (1982). Second, the optimum species composition is likely to vary between seasons with, for example, *H. hirta* swards possibly giving the highest predicted animal production in summer and *T. triandra*-dominated swards giving the highest production in winter. Lastly, the optimum species composition is also likely to be dependent upon grazier objectives in terms of whether to maximise summer mass gains, minimise winter mass loss or achieve a combination of both. In this respect, the commercial graziers' fundamental objective of maximising animal production compared to the communal graziers' objective of maximising total grazing capacity, may in fact be mutually exclusive in terms of species composition.

Similarly, while it is easy to identify sward structures where animal production will obviously be poor, e.g. very short or very rank swards, there is no optimum sward structure where animal production will always be maximised. Again, the optimum sward structure will vary between cattle and sheep and, possibly, also between different ages and classes of animals as well as being dependent upon operator objectives, e.g. maximising individual compared to total animal production. The optimum sward structure will also vary with season, with the sward height at which animal production is maximised becoming progressively lower as herbage quality declines through the grazing season. An interaction between species composition and sward structure was also evident with the optimum sward height for animal production varying with species composition (Chapter 7). Conversely, the species composition where animal production was maximised was conditional upon sward structure with predicted production being highest at certain sites on short swards while production was highest at other sites on taller swards.

The present work therefore suggests that the conventional assumption that there exists a single absolute index of the potential value of rangeland for livestock in terms of species composition, e.g. Tainton (1986), or sward structure is erroneous. Thus while it is relatively simple to define conditions on sourveld where animal production will be poor, it appears that no single, universally optimal sward structure or species composition can be identified where animal production will always be maximised. Any optimum will be conditional on the interaction between species composition and sward

structure as well as assumptions about the season in which the site is being grazed, the type and class of animal involved and the fundamental management objectives of the grazier. Attempting to define these optima without precisely specifying these factors and conditions, as has been done with conventional methods of scoring veld condition, is misleading and is unlikely to provide a reliable index of the potential of a site to support animal production.

9.3 Management recommendations

It is essential that graziers recognise the overwhelming importance of dietary quality for animal production on sourveld. However, of the factors affecting herbage quality, only species composition, sward structure and fire are under the direct or indirect control of the grazier, and therefore amenable to management.

It is obvious that a species composition with a large proportion of palatable, high-quality species should be maintained or set as an important management objective, while any increase in the abundance of low-quality and/or unpalatable species such as *E. plana* or *E. muticus* should be avoided. The present models clearly show that any increase in the latter species will result in a direct decrease in animal production (Chapter 7) and hence in financial returns to the grazier.

In contrast to current theory, it should be recognised that secondary grasslands dominated by *H. hirta* are a potentially valuable source of high-quality fodder, especially during the early growing season, and should be managed accordingly. As observed in the present study (Appendix Table 1.3), these swards can be prevented from becoming excessively stemmy through the use of fire followed by moderate grazing in October or November to remove stem apices and prevent the elongation of flowering culms (pers. obs.).

The favourable degradation characteristics of *C. dactylon* in the rumen (Chapter 6), also suggest that areas of localised 'degradation' dominated by this species (Mentis 1981; Danckwerts 1989) around gates and water points are likely to be important sources of high quality forage in sourveld. Their nutritional significance is illustrated by observations on other experiments (pers. obs.) that, when animals enter a new camp, they greedily consume all herbage in these and other sites of nutrient concentration, e.g termitaria, before starting to graze the rest of the paddock.

In terms of structure, grazing management during the growing season should aim at maintaining a green, actively-growing sward, at a height where dietary quality and intake rate are optimised. In this respect, given the strong negative relation between dietary quality and the number of 'growing days' between grazings (Chapter 2), the recommended period of absence from a paddock of sixty to ninety days (Grenfell 1991) is probably excessive, at least in terms of optimising animal production.

Similarly, in contrast to current blanket recommendations that sourveld be grazed at heights of between 10 to 15 cm, e.g. Tainton (1987), sward heights should be about 6-8 cm for sheep and 10-12 cm for cattle during the growing season. However, these optimum heights will become lower as the season progresses due to the increasing constraint of digestion on intake rate. As these heights vary for cattle and sheep it is suggested that these animals follow each other in the grazing rotation rather than being grazed together, as is usually done. Here, a leader:follower system could be applied with cattle conditioning the sward for sheep which would follow, after a short period (2-3 weeks depending on rainfall), onto the short, even regrowth. Cattle would then return to the pasture when herbage had regrown to a sufficient height for their requirements.

Fire is an obvious management tool to obtain a nutritious sward and has been used to this end for centuries. However, the magnitude and duration of this effect (Chapter 2) should be recognised and burnt areas should logically be grazed by stock with the highest nutritional requirements, e.g. young and/or lactating animals, while being kept at an optimal sward structure for as long as possible in order to maximise the duration of its effect on forage quality. Based on the experience of leading graziers in the Dohne Sourveld (W.G. Hartley pers. comm[1]; W.J. Perks pers. comm.[2]), previously burnt veld cannot be maintained at a height where animal production is maximised if the recommendation that swards be allowed to grow out to 10 - 15 cm before grazing, e.g. Trollope (1984), is adhered to.

Last, the grazing philosophy applied must reflect the seasonal availability of quality to the grazing animal. Thus, on the basis of the present study, current

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[1] 'Elvadell', PO Box 232, Stutterheim, 4930.

[2] 'Braemar', PO Box 125, Cathcart, 5310.

recommendations that sourveld be lightly grazed in the early season but heavily defoliated as quality declines in the late season 'in order to increase intake' (Daines 1976; Barnes 1989), cannot be supported. First, lenient, selective grazing early in the season will allow the less-preferred species present to grow out and become moribund and decline even further in quality and acceptability. Second, as the relative importance of quality increases through the season, animals should be allowed to be as selective as possible in order to maximise dietary quality in the late season. Therefore, in contrast to current recommendations (Barnes 1989), it is suggested that swards be kept reasonably short and uniformly grazed up until the mid-growing season (January-February) but only lightly grazed thereafter. However, swards should still be grazed down in winter with the aid of rumen-stimulating licks so as to minimise the carry-over of dead material into the next season.

9.4 Directions for future research

The present study points to a number of areas of future research that are important if better predictive and conceptual models of animal production on sourveld are to be constructed and their successful integration with management guidelines for the sustainable use of this resource is to be achieved.

First, the present study focused on the effects of species composition on individual animal production but did not attempt to address carrying capacity, which remains an important issue. While the concept of an average long-term carrying capacity for any area remains debatable, graziers nevertheless expect rangeland scientists to provide estimates of the upper and lower bounds to the potential grazing capacity of a property. The relation between species composition and carrying capacity needs to be addressed in terms of the potential of different grass species to produce grazeable herbage, the interaction between production and soil moisture and nutrients, and the production response of these species to the frequency and intensity of defoliation.

Second, while the present study determined the nutritional quality of different species, it is unclear how forage quality is affected by basic edaphic and microclimatic factors. Hence, the extent to which the present results can be extrapolated to different sourveld areas or positions on the landscape catena is obscure. The effects of

environmental factors such as soil fertility, soil moisture, soil texture, aspect and catenal position on quality therefore require investigation. This would allow basic data on species quality to be adjusted for any area in the sourveld or any site within that landscape, facilitating the prediction of forage quality at almost any spatial scale in sourveld.

Third, given the restricted availability of nutrients on most sourveld soils nutrient cycling is likely to be of major importance for herbage quality and hence animal production. It is therefore suggested that the effects of sward structure and grazing management on nutrient cycling, specifically N, be investigated. Models of N-cycling on rangeland (Holland *et al.* 1992) indicate a strong interaction between grazing intensity and the rate of N-turnover and the extent of N-immobilisation and availability to the plant. Unfortunately, aside from the work reported at Frankenwald (Roux 1969), this aspect appears to have been all but ignored on South African rangelands.

Fourth, the observation that sheep were, on occasion, capable of achieving far higher rates of intake than would be expected on the basis of sward structure alone (Chapter 3), suggests that the effect of other factors such as the physical and metabolic state of the animal on ingestive behaviour and dietary selection, need to be examined. The point of particular interest is the effect of the 'state' of the animal (*sensu* Mangel and Clark (1986)) on the degree to which dietary quality and intake are traded off against one another. While this aspect has received some attention, e.g. Greenwood and Demment (1988); Parsons *et al.* (1994), the high quality, homogeneous swards on which their work was conducted limits its relevance to the present rangeland conditions.

Fifth, predicted animal production was found to be extremely sensitive to rumen capacity in all models. In the absence of quantitative data, the interaction between this variable and dietary quality on sourveld needs to be urgently addressed.

Last, in terms of sustainability, it is vital that the effects of sward structure on species composition be investigated in terms of the tuft mortality, seed production, recruitment and, ultimately, population demography of different species. Certain sward structures, while maximising animal production, could conceivably lead to adverse changes in species composition and would not be sustainable in the long term.

Once the above issues have been addressed, existing growth models, e.g. PUTU (Fouché 1992), could be expanded and calibrated to predict the amount and quality of

herbage that may be expected under a given set of environmental conditions in sourveld. At the same time, existing animal production models will have to be expanded, or new ones developed, to predict dietary selection and ingestive behaviour in these environments, while taking into account the effect of the animals' physical and metabolic state on its foraging behaviour. Coupling these models, along with a basic model of vegetation dynamics on this veld type, should allow the response of plants and their ungulate grazers to be predicted under a wide variety of management and environmental conditions.

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APPENDIX 1

Abbreviations

ROT = block code, i.e. mean grazing frequency in weeks

DAY = days since 1 October

CP = crude protein

IVD = in vitro digestibility

MRT = mean retention time

G.TIME = daily grazing time

B.SIZE = bite size

B.RATE = bite rate

I.RATE = intake rate

HMASS = herbage mass

HDENS = herbage density

PHT = plant height

LTH = leaf table height

ST = stemminess

GR = greenness

AA = *Andropogon appendiculatus*

AS = *Alloteropsis semialata*

EP = *Eragrostis plana*

HC = *Heteropogon contortus*

HH = *Hyparrhenia hirta*

SW = 'sward'

TL = *Tristachya leucothrix*

TT = *Themeda triandra*

e.g. TTPHT = *T. triandra* plant height

APPENDIX TABLE 1.1

BUSH CAMP- YEAR 1

		CATTLE							SHEEP															
ROT	DAY	CP (%)	IVD (%)	MRT (h)	B.SIZE (g)	B.RATE (b/min)	I.RATE (g/min)	G.TIME (min.)	CP (%)	IVD (%)	MRT (h)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TTPHT (cm)	TTLTH (cm)	TTST (cm)	TTGR (0-5)	AAPHT (0-5)	AALTH (cm)	AAST (cm)	AAGR (0-5)	TLPHT (0-5)	TLLTH (cm)	TLST (cm)	TLGR (0-5)
3	23	9.69	69.99	.	0.114	64.54	7.33	.	10.56	67.65	.	67.13	684	0.00153	9.04	4.46	0.00	5.00	10.00	5.50	0.00	5.00	8.15	5.00	0.00	5.00
5	38	.	66.06	16	0.230	59.39	13.63	782	12.21	61.71	15.70	58.05	868	0.00206	8.84	4.22	0.00	4.90	12.23	6.60	0.00	5.00	10.50	7.00	1.14	4.90
8	67	9.20	56.36	17.9	0.329	56.98	18.75	.	6.43	61.44		52.27	1000	0.00163	11.14	6.12	0.00	4.50	13.00	8.00	0.00	4.90	12.00	8.00	0.64	4.80
3	95	9.39	58.09	16.9	0.126	66.90	8.44	.	8.25	58.46	16.40	64.44	685	0.00148	9.86	4.64	0.04	4.06	12.69	6.58	0.00	4.92	8.77	4.96	0.00	4.70
11	102	7.06	53.80	19.6	0.255	53.18	13.53	467	6.64	53.45	14.90	46.95	1319	0.00166	15.30	7.95	0.82	4.78	21.01	11.46	0.16	4.72	13.30	6.97	0.92	4.14
5	122	8.07	59.30	.	0.226	57.65	15.27	743	9.15	57.97	.	50.79	789	0.00138	11.10	5.80	0.00	4.35	12.98	6.90	0.00	4.39	9.14	5.28	0.00	4.26
8	137	9.18	59.49	.	0.263	61.08	16.03	.	8.88	63.87	18.60	45.70	1690	0.00235	15.03	7.16	0.00	4.41	21.74	12.56	0.04	4.74	12.49	7.00	0.00	4.56
16	144	6.99	57.49	.	0.340	55.49	18.87	.	7.65	61.86	16.60	46.95	1900	0.00174	21.58	10.90	0.00	4.07	29.84	17.40	0.10	4.16	17.73	10.74	0.20	4.03
20	177	.	59.18	16.7	0.378	58.92	21.49	.	8.20	55.12	16.70	43.05	2433	0.00182	25.67	13.34	0.00	3.90	34.82	20.14	0.06	4.18	21.71	13.24	0.10	3.94
8	186	6.68	58.15	20.3	0.248	61.73	15.26	.	7.60	56.12	18.70	54.15	1990	0.00216	16.94	9.20	0.00	3.87	24.80	14.74	0.00	4.22	13.94	7.90	0.00	4.07
5	194	7.15	55.01	19.2	0.209	59.18	14.45	.	7.50	58.92	20.80	52.88	1350	0.00206	12.74	6.54	0.00	3.84	18.56	10.06	0.00	4.21	11.09	5.74	0.00	4.06
3	205	6.21	54.20	19.6	0.161	64.75	11.66	625	6.20	54.17	17.30	66.05	916	0.00149	14.84	6.16	0.00	3.53	20.07	9.76	0.00	4.32	12.43	5.51	0.00	3.82
16	236	.	46.24	20.1	0.345	57.50	19.84	.	4.74	50.95	16.80	55.10	1849	0.00187	18.96	9.90	0.00	2.95	28.44	15.84	0.06	3.38	16.08	9.18	0.02	2.86
11	249	3.76	46.21	22.2	0.278	56.00	15.56	.	6.34	52.24	19.50	56.00	1449	0.00224	14.20	6.48	0.00	1.76	15.09	7.40	0.00	2.06	10.18	4.51	0.00	1.50
8	256	2.81	47.49	.	0.259	59.60	15.39	.	4.66	53.81	.	57.75	1619	0.00273	13.49	5.94	0.00	1.59	16.27	7.73	0.00	2.01	9.49	4.85	0.00	1.21
5	262	3.51	46.67	.	0.217	60.70	13.13	.	4.67	53.98	.	60.30	1260	0.00272	11.43	4.64	0.00	1.90	12.56	5.92	0.00	1.72	8.57	3.43	0.00	2.10
3	276	.	41.54	.	0.273	55.80	15.19	.	.	45.99	.	59.00	855	0.00185	11.37	4.61	0.00	1.34	12.90	5.48	0.00	1.15	9.91	3.53	0.00	0.47
20	310	.	38.68	22.9	0.260	47.20	12.23	.	.	.	20.90	55.00	1629	0.00189	19.80	8.63	0.00	0.12	22.89	10.52	0.06	0.40	15.67	6.66	0.00	0.01

BUSH CAMP YEAR 2 (1991-1992)

3	30	7.76	67.41	17.7	0.257	72.90	18.77	495	8.76	62.16	.	61.90	832	0.00158	10.50	5.30	0.70	4.50	14.70	7.40	0.10	4.55	9.50	5.10	0.50	4.50
5	50	8.96	63.45	.	0.257	58.20	15.02	.	8.50	66.60	16.5	56.50	1165	0.00178	14.11	6.54	0.86	4.74	19.89	9.56	0.10	4.93	12.39	5.92	0.20	4.83
8	92	8.37	53.80	.	0.285	64.65	18.51	516	7.56	55.36	.	53.11	1632	0.00159	21.39	10.24	0.56	4.42	26.91	14.10	0.24	4.60	15.91	8.48	0.16	4.59
11	106	6.50	55.25	.	0.291	62.34	18.20	.	6.72	57.96	.	60.33	2111	0.00179	24.15	11.78	0.58	4.17	34.42	18.82	0.50	4.38	18.75	9.06	0.42	4.07
3	134	5.52	49.05	.	0.414	61.12	25.34	.	5.56	53.90	.	60.97	1273	0.00168	18.52	7.60	0.02	4.33	25.60	11.78	0.06	4.55	12.78	5.38	0.00	4.48
16	141	5.12	47.57	19.5	0.482	60.81	29.36	534	5.32	49.28	.	53.84	2740	0.00257	23.02	10.28	0.06	3.66	31.66	16.10	0.24	3.99	17.04	8.00	0.20	3.44
8	142	4.79	48.05	.	0.422	63.89	26.96	.	6.60	53.10	16.3	58.24	1699	0.00209	17.02	8.12	0.22	4.15	23.38	11.04	0.00	4.55	13.21	5.77	0.04	4.32
20	179	5.13	44.55	18.6	0.364	53.20	19.40	.	5.10	37.84	.	47.90	2365	0.00209	22.27	11.30	0.06	3.64	28.93	15.46	0.16	4.08	15.97	7.74	0.04	3.80
11	219	4.02	44.65	.	0.365	60.40	22.06	.	4.97	46.63	.	62.90	1762	0.00205	17.14	8.58	0.00	3.28	23.46	12.02	0.20	3.21	11.04	5.22	0.02	3.20
8	220	8.66	47.49	.	0.291	54.50	15.87	.	4.68	50.95	.	65.90	1260	0.00218	10.98	5.88	0.00	3.45	15.00	7.48	0.02	3.57	8.15	3.84	0.00	2.95
16	239	3.56	47.07	.	0.383	51.40	19.70	474	2.48	48.10	.	57.40	1997	0.00234	18.37	8.53	0.06	1.70	25.67	12.20	0.16	2.77	14.37	6.82	0.04	1.35
3	262	3.55	42.28	.	0.303	52.66	16.29	481	5.51	51.84	.	82.27	908	0.00191	9.33	4.76	0.00	2.15	12.74	6.03	0.00	2.25	7.75	3.65	0.00	1.13
8	297	3.26	44.34	.	0.305	51.64	15.80	399	4.96	47.85	.	64.99	1000	0.00218	8.63	4.56	0.00	0.36	10.50	5.58	0.02	0.79	7.20	3.34	0.00	0.29

APPENDIX TABLE 1.2

ERAGROSTIS CAMP- YEAR 1 (1990-1991)

		CATTLE							SHEEP														
ROT	DAYS	CP (%)	IVD (%)	MRT (h)	B.SIZE (g)	B.RATE (b/min)	I.RATE (g/min)	G.TIME (min.)	CP (%)	IVD (%)	MRT (h)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TTPHT (cm)	TTLTH (cm)	TTST (cm)	TTGR (0-5)	EPPHT (0-5)	EPLTH (cm)	EPST (cm)	EPGR (0-5)	SWPHT (0-5)	SWLTH (cm)	SWST (cm)	SWGR (0-5)
3	24	.	63.04	.	0.118	57.30	6.75	590	11.43	68.06	.	65.07	312	0.00090	7.00	3.46	0.0	5.00	15.70	6.56	0.00	5.00	10.90	4.94	0.0	5.00
5	38	8.53	60.06	16.6	0.106	64.91	6.88	730	.	63.38	16.7	67.34	701	0.00175	8.00	4.00	0.0	5.00	20.26	8.57	0.00	5.00	17.50	7.93	0.1	4.90
3	42	8.89	60.65	.	.	.	.	.	10.05	63.00	.	.	312	0.00090	7.00	3.46	0.0	5.00	15.70	6.56	0.00	5.00	10.90	4.94	0.0	[illegible]
8	65	7.88	63.09	18	0.175	52.17	9.13	.	7.23	60.34	19.1	51.80	809	0.00160	9.00	5.00	0.0	4.90	25.46	10.88	0.00	4.80	25.78	10.64	0.2	4.80
3	68	8.37	54.42	16.3	0.164	64.10	10.53	.	8.94	61.64	15.9	65.38	547	0.00158	9.30	3.46	0.0	4.80	16.84	8.95	0.00	4.85	7.90	3.74	0.1	4.46
11	99	6.98	56.21	17.1	0.317	49.89	15.80	540	7.33	52.94	17.5	55.91	918	0.00156	14.56	5.90	0.0	3.87	25.16	9.10	0.14	5.00	14.14	6.06	0.1	4.28
5	121	8.15	61.00	.	0.230	66.57	15.06	640	8.53	62.29	.	67.67	1853	0.00368	11.85	5.04	0.0	4.87	19.62	[illegible]	0.02	4.94	10.13	4.10	0.1	4.78
8	136	11.75	62.42	.	0.363	51.75	18.78	.	10.35	64.18	.	52.25	1702	0.00250	18.38	6.80	0.0	4.44	29.28	15.36	0.94	4.77	17.28	9.26	0.1	4.92
16	143	9.01	61.55	.	0.561	49.91	28.00	.	9.70	63.78	.	44.61	2550	0.00226	24.08	11.28	0.0	4.32	32.10	16.82	0.90	4.10	22.72	12.66	0.1	4.59
20	171	.	59.22	21.3	0.383	52.90	19.20	612	8.27	63.32	19.6	40.34	3041	0.00299	21.56	10.16	0.0	4.13	34.04	16.74	1.86	4.72	22.76	11.88	0.1	4.45
8	185	9.21	55.10	20.3	0.282	57.28	16.19	563	9.46	57.92	20.9	52.54	2131	0.00230	21.72	9.26	0.0	4.01	28.86	14.30	2.00	3.55	17.14	9.02	0.1	4.11
5	192	8.75	54.52	21.6	0.258	60.11	15.50	546	8.37	54.69	21.3	55.36	2116	0.00262	19.56	5.08	0.0	3.94	24.50	11.78	1.44	3.80	14.58	7.46	0.2	4.30
3	200	7.75	54.26	21.3	0.271	63.25	16.76	594	9.02	60.24	18.4	61.69	1674	0.00295	14.35	5.68	0.0	3.93	22.70	10.60	1.14	3.69	11.06	5.09	0.0	4.33
16	234	.	52.00	23.4	0.531	43.20	22.92	396	5.83	54.05	23.7	51.80	2849	0.00387	15.90	7.36	0.0	3.01	31.02	12.72	1.20	3.42	12.91	6.82	0.0	3.24
11	248	4.85	43.[illegible]	23.4	0.461	51.50	23.76	470	5.32	53.83	23.6	53.70	2107	0.00258	20.24	6.12	0.0	2.76	30.54	11.32	1.76	2.51	15.70	7.82	0.0	2.80
8	254	4.53	42.72	.	0.340	43.10	14.67	510	4.96	54.94	.	52.10	1919	0.00294	15.90	6.52	0.0	2.48	24.16	10.22	2.12	2.20	11.80	6.60	0.0	3.02
5	264	3.19	50.24	.	0.251	43.10	10.83	.	4.74	58.43	.	37.10	1665	0.00340	12.25	4.90	0.0	2.31	29.82	9.32	1.73	1.92	10.07	4.93	0.0	2.59
3	296	.	44.64	.	0.340	49.10	16.72	.	4.92	.	.	57.50	1379	0.00394	9.61	3.50	0.0	1.65	20.72	7.26	0.64	0.39	8.52	3.22	0.1	0.99

ERAGROSTIS CAMP- YEAR 2 (1991-1992)

3	24	9.32	60.59	.	0.257	65.80	16.96	595	11.14	62.09	.	71.30	1334	0.00310	9.74	4.31	0.4	4.42	18.50	8.16	0.44	4.22	.	.	.	.
5	43	8.59	63.31	.	0.371	58.10	22.18	409	9.79	66.78	20.6	57.70	1610	0.00199	16.61	8.07	0.6	4.67	28.42	12.64	0.02	4.63	19.39	9.16	0.2	4.65
8	74	7.18	61.46	.	0.234	52.20	12.24	.	5.42	64.60	.	50.40	2431	0.00313	17.95	7.77	0.0	4.72	34.76	16.10	0.02	4.55	20.67	9.58	0.0	4.67
3	141	8.56	52.65	.	0.312	64.62	20.21	.	10.22	53.13	19.7	64.06	1343	0.00242	15.20	5.56	0.0	4.13	23.40	9.39	0.22	3.82	12.86	5.97	0.0	4.45
8	147	.	53.05	.	0.365	51.67	20.03	490	.	58.15	.	37.15	1865	0.00241	19.82	7.73	0.0	4.06	29.07	11.09	0.22	4.03	24.95	11.04	0.3	4.31
20	177	5.60	46.69	.	0.250	52.00	13.06	472	5.05	42.59	17.7	26.00	2976	0.00166	31.85	17.88	0.1	3.57	31.76	15.28	0.12	3.49	32.34	17.81	0.4	3.57
8	213	7.26	51.67	.	0.347	60.20	20.95	844	7.44	54.16	.	61.20	1825	0.00328	11.46	5.56	0.0	4.21	27.94	12.58	0.26	3.50	16.28	8.66	0.1	4.11
5	218	3.92	46.72	.	0.372	48.60	18.10	454	4.73	53.07	.	50.90	2426	0.00257	22.63	9.44	0.0	3.66	29.87	12.64	0.46	2.88	25.69	13.34	0.1	3.47
16	234	3.56	37.82	.	0.474	50.80	24.09	390	4.52	49.70	.	58.00	2322	0.00213	21.43	10.88	0.0	2.86	34.27	13.08	0.32	1.99	20.39	10.16	0.0	3.26
3	253	3.81	45.00	.	0.300	48.55	14.62	461	4.67	53.25	.	63.85	1462	0.00363	9.26	3.82	0.0	2.31	18.31	7.77	0.14	0.69	10.62	4.86	0.1	1.79
11	267	2.91	44.58	.	0.485	52.12	25.25	439	4.42	45.91	.	65.50	2239	0.00242	22.14	9.25	0.0	1.78	28.88	11.24	0.38	1.11	18.83	8.27	0.0	1.47
8	291	1.74	49.21	.	0.515	39.32	20.27	422	1.88	50.76	.	53.02	1714	0.00252	14.07	6.79	0.0	0.97	26.01	11.45	0.26	0.82	14.66	7.85	0.2	0.91
20	304	3.09	48.08	.	0.377	37.12	14.02	582	4.73	46.89	.	49.30	2467	0.00201	21.46	12.29	0.0	0.92	32.89	11.47	0.22	1.01	24.67	12.53	0.1	0.56

APPENDIX 1C

OLD LANDS CAMP- YEAR 1 (1990-1991)

		CATTLE							SHEEP															
ROT	DAYS	CP (%)	IVD (%)	MRT (h)	B.SIZE (g)	B.RATE (b/min)	I.RATE (g/min)	G.TIME (min.)	CP (%)	IVD (%)	MRT (h)	B.RATE (b/min)	KMASS (kg/ha)	HDENS (g/cm3)	HHPHT (cm)	HHLTH (cm)	HHST (0-5)	HHGR (0-5)	HCPHT (cm)	HCLTH (cm)	HCST (0-5)	HCGR (0-5)	SWPHT (cm)	SWLTH (cm)	SWST (0-5)	SWGR (0-5)
3	26	11.11	66.84	.	0.244	54.75	13.36	635	12.91	65.85	.	59.00	520	0.00103	13.28	5.06	0.00	5.00	8.00	5.00	0.00	5.00	14.16	6.96	0.00	4.90
3	33	12.69	64.57	.	.	.	.	.	12.97	65.00	.	.	520	0.00103	13.28	5.06	0.00	5.00	8.00	5.00	0.00	5.00	14.16	6.96	0.00	4.90
5	45	10.14	57.63	16.1	0.101	53.23	5.41	658	11.27	60.94	15.10	55.76	500	0.00059	15.53	8.44	0.00	4.90	10.00	6.00	0.00	4.90	13.40	6.71	0.06	4.80
5	68	7.91	60.66	16.2	0.147	54.61	8.02	.	7.20	63.22	15.60	50.70	900	0.00059	16.66	10.10	0.02	4.80	12.00	6.50	0.50	4.80	15.43	7.04	0.08	4.70
3	96	8.25	56.72	16.4	0.261	57.74	15.11	.	8.54	61.45	16.70	63.10	523	0.00071	14.13	7.39	0.42	4.70	10.00	6.00	0.50	4.80	13.50	6.00	0.05	4.60
11	103	7.13	53.86	16.5	0.514	48.76	23.08	.	8.39	56.20	16.50	49.33	1218	0.00124	17.68	9.82	0.90	4.32	12.26	7.14	0.80	4.62	22.00	11.00	0.15	4.70
5	123	10.06	59.85	.	0.356	56.56	20.15	.	9.69	64.90	.	58.50	1250	0.0011	13.14	6.86	1.82	4.43	10.14	6.54	0.00	4.60	13.60	6.80	0.16	4.67
5	138	9.97	53.73	.	0.350	54.36	21.31	.	9.07	62.97	.	48.98	1296	0.00140	[illegible]72	9.29	2.37	3.67	11.96	7.20	0.00	4.24	22.03	11.59	0.12	4.69
16	145	.	60.00	16.7	0.431	51.65	22.26	.	8.61	62.76	15.60	43.63	1832	0.0012.	27.23	14.71	2.06	3.46	14.56	10.23	0.04	3.63	20.65	11.19	0.10	4.27
20	176	4.77	54.58	19.7	0.374	48.14	17.99	736	10.25	42.96	18.20	37.37	3303	0.00174	32.50	18.94	3.64	3.71	17.20	10.71	0.02	4.20	25.53	13.49	0.53	4.30
8	187	5.87	53.31	19.6	0.281	58.24	16.34	.	7.45	56.56	.	50.90	2506	0.00227	22.46	11.02	3.53	3.49	16.06	9.24	0.02	4.35	22.00	11.00	0.12	3.90
5	193	8.76	59.77	.	0.409	57.71	23.82	579	7.24	62.57	16.50	52.27	1582	0.00222	15.72	7.12	3.33	3.53	12.42	6.64	0.18	3.90	19.20	8.76	0.48	3.79
3	206	6.35	44.96	.	0.421	54.23	22.87	542	6.55	59.92	16.80	52.75	1013	0.00154	13.95	6.58	2.96	3.45	12.64	6.26	0.14	3.95	18.14	7.96	0.12	3.55
16	240	3.34	52.33	20.6	0.459	46.70	21.41	415	5.23	54.95	16.20	47.90	2359	0.00161	24.96	13.06	3.02	1.39	14.71	8.95	0.00	2.48	19.41	8.76	0.30	2.36
11	248	2.63	42.66	.	0.538	39.60	21.33	.	5.91	51.51	.	45.20	2018	0.00164	25.13	12.28	4.33	0.74	18.24	10.68	0.00	2.45	22.16	10.44	0.16	3.36
8	255	2.90	46.12	.	0.295	57.00	16.84	525	3.53	50.09	.	48.80	2157	0.00260	20.74	8.31	3.26	0.76	15.27	7.86	0.04	1.70	20.08	7.70	0.26	1.74
5	261	.	42.57	.	0.333	48.70	16.39	465	.	39.68	21.20	61.70	915	0.00165	12.96	5.56	1.80	2.03	10.48	5.22	0.08	1.62	15.67	6.86	0.32	1.72
3	284	.	44.32	.	0.166	52.80	8.88	480	.	49.19	21.40	58.20	884	0.00160	13.11	5.51	2.96	0.68	11.43	5.24	0.06	2.13	17.29	7.03	0.52	0.73
20	332	3.61	37.38	.	0.354	51.40	14.83	.	5.90	40.29	.	57.50	3094	0.00363	22.64	8.52	4.06	0.37	13.26	6.06	0.00	1.10	18.02	8.96	0.18	1.26

OLD LANDS CAMP- YEAR 2 (1991-1992)

3	30	8.87	64.55	.	0.363	63.10	22.96	388	9.31	66.23	.	65.00	1259	0.00191	15.26	6.75	1.30	4.11	9.96	5.15	3.02	4.77	14.76	6.02	0.49	4.53
5	50	10.05	62.30	.	0.300	62.05	18.61	555	8.32	63.17	.	59.64	1464	0.00175	20.73	8.36	1.70	4.41	11.33	5.69	1.54	4.75	17.82	7.23	0.36	4.73
8	74	8.66	58.88	.	0.329	56.10	18.49	594	8.19	62.63	.	42.30	2707	0.00183	27.90	14.80	2.16	4.04	15.10	8.66	0.74	4.67	20.02	[illegible]39	0.26	4.62
11	119	4.90	52.83	.	0.306	60.99	18.72	490	6.52	49.80	.	53.11	2892	0.00172	30.40	15.62	3.52	3.52	17.10	8.18	0.50	3.81	25.52	9.[illegible]6	0.14	3.86
3	135	7.19	58.64	.	0.216	56.94	12.31	456	7.34	57.86	.	56.30	1246	0.00157	15.34	6.67	1.96	3.86	11.57	5.53	0.02	4.29	18.28	7.[illegible]	0.04	4.37
8	156	6.00	51.64	17.2	0.317	54.[illegible]7	19.04	.	6.15	57.22	.	47.92	1677	0.00192	19.96	9.80	2.38	3.84	12.74	6.79	0.02	4.57	17.13	7.55	0.22	4.55
16	163	6.66	46.17	18.2	0.244	56.10	13.70	487	7.35	55.41	.	38.92	4092	0.00224	31.29	18.28	3.68	2.61	18.25	11.76	0.32	3.74	22.51	11.54	0.24	4.47
20	177	4.42	44.91	.	0.355	49.50	17.60	.	5.28	40.45	14.50	35.90	2351	0.00114	32.83	20.54	3.51	2.53	17.04	11.43	0.22	3.79	28.32	14.72	0.36	4.18
8	225	4.09	47.09	.	0.381	47.10	17.98	.	4.62	56.76	.	65.40	1355	0.00182	16.43	7.44	2.12	3.01	9.81	4.20	0.00	3.49	14.45	5.11	0.10	2.52
11	226	5.43	45.92	.	0.365	50.60	18.50	567	4.11	52.61	.	48.10	2668	0.00171	29.28	15.62	3.60	2.05	14.66	7.49	0.16	2.47	23.16	10.29	0.06	2.20
16	230	2.18	45.00	.	0.299	47.90	14.26	500	4.16	52.67	.	48.10	2315	0.00128	29.84	16.00	3.86	[illegible]	15.92	8.20	0.24	2.49	20.83	8.40	0.12	2.31
3	254	2.67	49.36	.	0.303	48.47	14.70	541	3.83	51.24	.	53.10	1301	0.00261	9.86	4.96	1.24	[illegible]	9.50	3.65	0.02	2.10	15.65	5.72	0.06	1.52
8	288	3.05	46.99	.	0.349	39.82	13.91	.	2.82	50.54	.	51.43	1530	0.00184	18.06	8.33	2.46	[illegible]	10.85	5.17	0.02	0.47	14.34	6.25	0.00	0.67
16	289	1.97	46.60	.	0.256	39.05	10.03	.	1.03	45.39	.	43.12	2185	0.00187	24.62	13.12	3.96	0.77	10.66	8.17	0.30	0.75	21.45	7.74	0.08	0.48
20	318	3.87	42.68	.	0.425	42.80	16.11	483	4.61	46.88	.	41.69	4385	0.00241	32.81	18.96	4.72	0.50	21.06	12.12	0.38	1.38	26.74	13.42	0.04	1.50

APPENDIX TABLE 1.4

SHEEP SHED CAMP- YEAR 1 (1990-1991)

		CATTLE							SHEEP																
ROT	DAYS	CP (%)	IVD (%)	MRT (h)	B.SIZE (g)	B.RATE (b/min)	I.RATE (g/min)	G.TIME (min.)	CP (%)	IVD (%)	MRT (h)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TLPHT (cm)	TLLTH (cm)	(0-5)	(0-5)	AAPHT (cm)	AALTH (cm)	AAST (0-5)	AAGR (0-5)	ASPHT (cm)	ASLTH (cm)	ASST (0-5)	ASGR (0-5)
3	23	12.62	69.62	14.5	0.210	65.17	13.67	547	12.39	69.48	16.10	59.87	562	0.00068	13.16	8.24	0.00	5.00	14.00	8.00	0.00	5.00	11.00	6.00	0.00	5.00
3	32	.	69.62	.	.	.	.	.	12.15	66.00	.	.	562	0.00068	13.16	8.24	0.00	5.00	14.00	8.00	0.00	5.00	11.00	6.00	0.00	5.00
5	43	9.05	63.82	17	0.264	53.00	14.02	480	10.05	66.74	.	45.00	1154	0.00133	25.51	8.70	1.14	4.90	15.00	9.00	0.00	5.00	13.00	7.00	0.00	5.00
8	65	7.32	56.86	.	0.297	49.40	14.70	570	7.47	60.67	.	45.96	1223	0.00160	22.32	7.63	0.64	4.80	16.00	10.00	0.00	5.00	15.00	8.00	0.00	5.00
3	95	8.25	62.86	.	0.147	62.94	9.24	.	8.86	64.61	.	55.00	1063	0.00[illegible]2	8.89	5.25	0.00	4.08	14.23	8.42	0.00	4.96	11.14	6.64	0.00	4.92
11	101	5.41	60.93	17.1	0.386	53.10	20.50	551	6.11	54.91	16.30	48.84	1250	0.00153	14.82	8.19	0.50	4.50	19.49	12.77	1.96	4.76	19.05	11.18	0.00	4.86
5	120	7.58	59.54	.	0.163	63.10	10.26	540	8.03	63.06	.	51.06	940	0.00140	11.64	6.73	0.08	4.23	15.44	9.20	0.00	4.78	14.04	8.54	0.54	4.57
8	135	12.56	66.18	17.5	0.374	61.30	22.92	516	9.54	66.33	.	46.96	1191	0.00125	14.74	9.50	0.16	4.42	25.16	15.10	0.02	4.78	16.66	10.72	0.32	4.45
16	142	6.61	61.26	18.4	0.564	50.65	29.63	.	7.67	60.65	.	40.56	2000	0.00173	19.96	11.54	0.16	5.62	29.90	17.66	0.04	4.01	19.65	13.26	0.54	3.95
20	170	11.30	62.52	18.5	0.226	55.65	12.57	.	9.42	62.47	16.50	48.54	2338	0.00175	20.62	13.38	0.00	4.06	33.50	21.24	0.02	4.52	21.30	13.56	0.38	3.90
8	190	8.38	62.59	16.9	0.219	62.19	13.63	.	8.21	64.04	17.60	47.05	2295	0.00292	14.25	7.86	0.00	3.93	31.54	18.32	0.02	4.26	18.46	11.22	0.24	4.17
5	191	6.55	63.26	18	0.[illegible]20	58.58	13.67	56[illegible]	7.68	61.74	16.90	58.59	1939	0.00238	16.52	8.14	0.00	3.80	28.64	15.66	0.00	4.01	19.00	11.48	0.06	4.04
3	198	6.25	58.64	16.5	0.291	65.93	19.23	644	7.41	58.61	18.50	60.57	1507	0.00275	11.46	5.48	0.00	3.69	19.31	9.56	0.0[illegible]	3.89	15.68	9.00	0.02	3.94
16	233	4.65	47.[illegible]5	.	0.448	57.00	25.50	614	4.64	52.64	19.20	52.00	2469	0.00317	15.03	7.86	0.00	3.37	29.72	16.78	0.24	3.46	19.30	12.00	0.10	3.33
11	247	4.59	45.59	23.4	0.248	56.10	13.93	570	4.08	52.11	19.10	63.00	2388	0.00342	12.96	6.98	0.00	1.73	22.79	12.06	0.02	2.29	18.30	10.40	0.04	2.71
8	254	.	45.00	.	0.152	52.80	8.02	.	4.87	51.89	.	55.80	1867	0.00333	10.84	5.60	0.00	1.56	19.85	10.19	0.00	2.05	14.85	8.68	0.02	2.35
5	269	3.00	43.97	.	0.205	56.40	11.74	.	4.61	51.57	.	53.00	1336	0.00260	8.78	5.14	0.00	1.67	20.54	10.8[illegible]	0.00	3.00	15.38	8.52	0.00	2.[illegible]3
3	284	.	42.84	.	0.172	58.60	10.10	.	.	47.16	.	60.50	1521	0.00457	7.50	3.33	0.00	0.49	13.43	6.83	0.00	1.67	12.24	6.58	0.00	2.09
20	295	.	38.49	21.9	0.295	48.20	14.20	.	.	40.60	20.30	40.70	2673	0.00397	14.57	5.74	0.02	0.23	27.03	12.52	0.10	0.60	20.74	10.28	0.06	1.05

SHEEP SHED CAMP- YEAR 2 (1991-1992)

3	22	9.65	62.36	.	0.297	72.60	21.80	495	10.12	62.44	.	59.10	1177	0.00245	8.62	4.81	0.02	4.38	14.50	7.46	0.00	4.61	11.91	3.22	0.00	4.34
5	45	10.90	65.45	.	0.186	62.60	11.61	.	9.53	66.28	.	52.00	1384	0.00163	14.45	8.38	0.26	4.59	24.97	14.06	0.44	4.61	16.61	10.96	0.00	4.63
8	70	8.77	50.47	.	0.280	64.40	18.04	460	7.66	60.81	.	49.90	1705	0.00185	17.31	9.24	0.18	4.82	29.34	15.36	1.10	4.84	22.28	13.46	0.00	4.62
8	106	6.36	54.16	.	0.170	57.20	9.78	.	7.20	55.96	.	42.50	1967	0.00156	21.57	12.62	0.28	4.09	33.40	19.12	0.78	4.11	25.50	16.06	0.02	4.12
3	137	8.36	55.35	.	0.282	65.72	18.60	.	9.22	57.13	14.20	64.05	1268	0.00286	8.49	4.43	0.00	4.09	15.71	7.98	0.02	4.59	13.49	7.22	0.02	4.32
8	155	6.82	47.30	17.3	0.198	61.86	12.28	.	7.29	51.33	.	55.53	1597	0.00230	15.08	8.93	0.00	4.01	31.24	16.60	0.18	4.42	19.23	10.30	0.12	4.23
16	157	5.11	46.58	17.6	0.448	57.06	25.60	528	5.37	50.31	.	46.81	1871	0.00169	20.16	11.08	0.10	3.38	35.86	20.96	0.22	3.90	25.05	15.44	0.02	3.71
11	158	4.58	43.09	.	0.284	63.09	17.95	.	5.88	55.96	.	49.81	1796	0.00221	16.02	8.13	0.00	3.80	31.90	17.96	0.44	4.12	22.70	13.58	0.00	3.90
20	176	3.89	44.21	17.4	0.444	54.75	24.31	.	5.72	41.65	.	44.50	314	0.00030	19.97	10.47	0.16	3.15	35.25	19.94	0.12	4.01	23.58	14.64	0.00	3.26
8	210	4.44	46.40	.	0.254	63.10	16.03	531	5.76	48.33	.	59.30	1628	0.00234	12.79	6.95	0.00	2.86	23.24	14.66	0.16	4.02	18.69	10.83	0.02	3.11
11	211	3.90	42.40	.	0.326	54.80	20.17	506	4.28	46.11	.	52.20	1776	0.00207	15.40	8.58	0.00	3.52	32.92	19.62	0.59	3.85	20.87	12.63	0.00	3.35
16	232	4.35	41.84	.	0.455	47.60	21.67	360	3.92	46.33	.	51.70	1835	0.00219	20.42	8.37	0.12	0.99	31.44	16.31	0.42	2.67	22.39	12.87	0.02	2.56
3	250	4.19	44.21	.	0.273	57.18	15.79	515	5.52	52.23	.	62.10	1211	0.00342	7.56	3.54	0.00	0.77	12.09	5.99	0.02	2.44	10.06	5.28	0.00	2.42
11	254	2.30	46.26	.	0.392	45.97	18.63	.	2.82	47.19	.	43.34	1721	0.00265	13.16	8.50	0.00	0.36	25.01	11.68	0.06	1.13	20.39	10.77	0.00	1.32
8	265	1.69	42.57	.	0.432	43.11	18.65	431	2.40	43.51	.	55.10	1587	0.00309	12.75	5.13	0.50	0.28	19.38	8.21	0.00	0.75	15.91	7.28	0.00	0.62
20	311	2.60	44.90	.	0.497	42.06	20.92	391	4.04	33.70	.	42.89	1861	0.00195	19.70	9.56	0.12	0.29	36.17	17.76	0.30	0.[illegible]5	23.34	12.80	0.00	0.47

APPENDIX TABLE 1.5

SCALE DATA - BUSH CAMP

DATE	SHEEP I.RATE (g/min)	IRM (g/m./kg)	B.SIZE (g)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TTPHT (cm)	TTLTH (cm)	TTST (cm)	TTGR (0-5)	AAPHT (0-5)	AALTH (cm)	AAST (cm)	AAGR (0-5)	TLPHT (0-5)	TLLTH (cm)	TLST (cm)	TLGR (0-5)
13.10.92	2.85	0.080	0.047	62.96	300	0.00080	7.30	3.73	0.00	5.00	8.38	4.10	0.00	5.00	5.73	3.16	0.00	3.16
23.10.92	4.06	0.110	0.075	54.45	350	0.00078	8.00	4.47	0.00	5.00	10.95	5.71	0.00	5.00	6.57	3.49	0.08	3.49
13.11.92	5.40	0.140	0.084	64.30	450	0.00094	8.85	4.77	0.00	5.00	13.43	7.09	0.00	5.00	6.83	3.70	0.00	3.70
18.02.93	6.84	0.150	0.116	58.88	766	0.00132	11.26	5.79	0.00	3.24	12.73	6.15	0.00	3.34	.	.	.	.
25.02.93	5.55	0.110	0.092	60.29	757	0.00112	12.58	6.75	0.00	3.40	14.94	8.10	0.00	3.15	.		.	.
02.03.93	4.38	0.084	0.085	51.60	1028	0.00108	19.10	9.49	0.08	3.18	21.83	11.18	0.00	3.21	15.36	8.74	0.42	8.74
07.04.93	4.63	0.088	0.112	41.41	914	0.00099	16.44	9.23	0.00	4.00	22.60	13.51	0.06	4.07	11.91	6.60	0.00	6.60
08.04.93	4.52	0.086	0.076	59.61	745	0.00172	9.42	4.33	0.00	3.93	11.68	5.36	0.02	4.13	8.15	3.80	0.00	3.80
14.04.93	4.67	0.091	0.105	44.43	1584	0.00161	17.71	9.83	0.00	3.78	23.06	12.57	0.04	3.81	12.79	7.03	0.00	7.03
05.05.93	4.40	0.085	0.088	49.96	879	0.00113	15.58	7.77	0.00	3.33	19.37	9.80	0.02	3.74	10.83	4.82	0.00	4.82
06.05.93	5.88	0.118	0.093	63.03	742	0.00123	12.03	6.03	0.00	3.59	12.21	6.22	0.00	3.49	10.55	4.90	0.00	4.90
07.05.93	4.05	0.079	0.067	60.74	625	0.00120	11.62	5.21	0.00	3.36	11.04	5.34	0.00	3.48	9.25	3.95	0.00	3.95
11.05.93	5.54	0.108	0.081	68.10	625	0.00120	11.62	5.21	0.00	3.36	11.04	5.34	0.00	3.48	9.25	3.95	0.00	3.95

SCALE DATA - ERAGROSTIS CAMP

DATE	SHEEP I.RATE (g/min)	IRM (g/m./kg)	B.SIZE (g)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TTPHT (cm)	TTLTH (cm)	TTST (cm)	TTGR (0-5)	EPPHT (0-5)	EPLTH (cm)	EPST (cm)	EPGR (0-5)	SWPHT (0-5)	SWLTH (cm)	SWST (cm)	SWGR (0-5)
21.09.92	1.35	0.043	0.026	51.87	300	0.00087	7.00	3.46	0.00	5.00	15.70	6.58	0.00	5.00	10.90	4.94	0.00	5.00
01.10.92	1.16	0.036	0.021	56.34	350	0.00101	7.00	3.46	0.00	5.00	15.70	6.58	0.00	5.00	10.90	4.94	0.00	5.00
10.11.92	4.00	0.100	0.060	67.13	565	0.00113	10.00	5.00	0.00	5.00	14.00	7.00	0.00	5.00	13.00	6.00	0.00	5.00
27.10.92	3.98	0.100	0.065	61.60	618	0.00108	10.64	5.74	0.00	5.00	14.97	7.56	0.00	5.00	13.01	6.68	0.50	4.50
05.11.92	5.05	0.130	0.108	46.70	1255	0.00172	13.74	7.29	0.00	5.00	16.44	7.13	0.00	5.00	14.16	7.39	0.20	4.83
18.11.92	5.28	0.130	0.103	51.03	1080	0.00129	14.34	8.22	0.00	4.98	20.14	11.20	0.00	5.00	13.45	7.53	0.18	4.59
07.12.92	5.36	0.150	0.083	64.62	937	0.00199	10.12	4.71	0.00	5.00	14.88	7.15	0.00	4.98	11.32	5.29	0.42	4.07
08.01.92	5.15	0.120	0.101	50.94	910	0.00183	11.74	4.96	0.00	3.75	17.87	7.56	0.06	3.94	11.78	5.86	0.00	4.48
14.01.93	4.86	0.110	0.128	38.69	1151	0.00123	17.98	9.38	0.00	4.37	20.75	9.76	0.02	4.65	15.09	8.27	0.20	3.44
28.01.93	5.70	0.129	0.103	55.41	1940	0.00204	17.56	9.52	0.02	4.31	22.36	11.18	0.10	4.59	15.75	8.22	0.04	4.32
18.03.93	5.14	0.100	0.100	51.61	1259	0.00120	22.30	10.47	0.04	3.54	23.51	9.96	0.94	3.49	22.79	11.88	0.04	3.80
19.03.93	5.63	0.116	0.102	54.96	596	0.00128	11.42	4.65	0.00	3.73	16.75	6.58	0.33	3.47	12.73	5.40	0.02	3.20
26.03.93	3.00	0.014	0.050	59.46	370	0.00151	7.46	2.82	0.00	3.25	14.66	5.67	0.20	3.38	7.94	2.97	0.00	2.95
28.04.93	6.39	0.141	0.122	52.26	1895	0.00131	26.35	14.42	0.00	3.32	21.83	10.70	0.60	3.54	23.85	13.80	0.04	1.33
29.04.93	3.55	0.070	0.102	34.84	1895	0.00131	26.35	14.42	0.00	3.32	21.83	10.70	0.60	3.54	23.85	13.80	0.00	1.13

APPENDIX TABLE 1.6

SCALE DATA - OLD LANDS CAMP

DATE	SHEEP I.RATE (g/min)	IRM (g/m./kg)	B.SIZE (g)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	HHPHT (cm)	HHLTH (cm)	HHST (cm)	HHGR (0-5)	HCPHT (0-5)	HCLTH (cm)	HCST (cm)	HCGR (0-5)	SWPHT (0-5)	SWLTH (cm)	SWST (cm)	SWGR (0-5)
30.09.92	1.89	0.054	0.035	52.09	345	0.00115	5.00	3.00	0.00	5.00	.	.	0.00	5.00	.	.	0.00	5.00
20.10.92	2.31	0.070	0.035	66.37	345	0.00053	7.00	6.49	0.00	5.00	9.40	5.58	0.22	5.00	10.20	5.16	0.00	5.00
05.11.92	3.40	0.090	0.045	75.01	466	0.00088	10.32	5.28	0.00	5.00	8.59	4.55	0.12	5.00	11.59	5.18	0.14	4.98
09.03.93	6.00	0.120	0.119	50.34	1537	0.00137	26.07	11.24	3.37	2.82	13.12	8.11	0.50	2.72	18.48	10.47	0.72	3.00
16.03.93	5.33	0.100	0.112	47.38	2000	0.00123	30.33	16.30	2.98	2.82	13.49	7.83	0.44	3.05	19.10	11.20	0.83	3.15
15.04.93	4.33	0.083	0.075	57.89	1000	0.00122	16.42	8.22	2.12	2.96	11.02	5.37	0.06	4.21	12.23	5.18	0.10	4.05
16.04.93	4.44	0.085	0.086	51.86	945	0.00127	15.38	7.47	2.28	2.78	10.92	5.26	0.00	4.30	11.30	5.22	0.06	4.29
19.04.93	4.50	0.083	0.079	57.30	1334	0.00176	18.31	7.57	0.93	3.08	10.74	5.26	0.00	3.52	11.91	5.17	0.00	3.77
20.04.93	4.23	0.078	0.075	56.10	1517	0.00172	20.34	8.84	2.98	2.51	14.20	6.75	0.29	3.38	15.27	5.77	0.33	3.61
21.04.93	4.05	0.085	0.071	56.72	1388	0.00169	16.42	8.22	2.12	2.96	11.02	5.37	0.06	4.21	12.23	5.18	0.10	4.05

SCALE DATA - SHEEP SHED CAMP

DATE	SHEEP I.RATE (g/min)	IRM (g/m./kg)	B.SIZE (g)	B.RATE (b/min)	HMASS (kg/ha)	HDENS (g/cm3)	TLPHT (cm)	TLLTH (cm)	TLST (cm)	TLGR (0-5)	AAPHT (0-5)	AALTH (cm)	AAST (cm)	AAGR (0-5)	ASPHT (0-5)	ASLTH (cm)	ASST (cm)	ASGR (0-5)
24.09.92	1.04	0.032	0.019	55.11	250	0.00067	6.63	3.75	0.00	5.00	10.58	6.05	0.00	5.00	9.50	5.60	0.00	5.00
25.10.92	1.84	0.057	0.030	61.58	300	0.00083	6.46	3.63	0.09	4.99	10.76	5.67	0.00	4.98	9.20	5.18	0.12	4.96
30.10.92	3.41	0.088	0.057	60.17	600	0.00149	7.57	4.04	0.30	5.00	14.15	7.50	0.00	5.00	11.56	6.41	0.52	5.00
17.11.92	4.26	0.104	0.089	47.77	600	0.00140	7.83	4.27	0.20	5.00	14.98	8.29	0.02	5.00	11.96	6.45	0.41	5.00
27.01.93	.	.	0.000	48.90	1520	0.00232	12.14	6.55	0.20	4.33	20.10	10.51	0.24	4.44	16.19	8.24	0.38	4.61
08.02.93	4.23	0.087	0.092	46.04	1186	0.00209	11.59	5.67	0.22	3.59	19.28	10.04	0.10	3.76	17.09	9.02	0.98	2.71
22.03.93	4.47	0.086	0.099	45.29	1646	0.00302	12.16	5.44	0.00	3.13	20.48	10.02	0.06	3.94	15.39	8.31	0.00	4.11
24.03.93	3.23	0.014	0.064	50.67	500	0.00205	6.45	2.44	0.00	2.80	8.72	3.88	0.00	3.55	12.84	6.27	0.00	3.90
01.04.93	5.65	0.110	0.118	47.80	1664	0.00230	13.06	7.23	0.02	3.68	23.17	12.69	0.02	3.67	16.01	9.06	0.00	3.69
02.04.93	5.22	0.100	0.121	43.12	1462	0.00228	12.35	6.41	0.02	3.92	23.66	12.51	0.00	4.04	15.63	8.86	0.00	3.99
22.04.93	5.13	0.107	0.105	48.74	1436	0.00224	12.42	6.41	0.00	3.47	22.45	12.21	0.06	3.65	15.34	8.32	0.00	3.59
23.04.93	5.79	0.121	0.091	62.75	1205	0.00314	8.78	3.83	0.00	3.35	12.40	7.07	0.00	3.87	9.98	5.38	0.00	3.53
26.04.93	4.11	0.062	0.023	42.00	1545	0.00181	15.31	8.52	0.00	3.25	24.03	14.15	0.12	3.69	16.68	10.30	0.12	3.56
12.05.93	5.38	0.104	0.083	64.93	1217	0.00347	8.01	3.51	0.00	3.51	13.71	6.64	0.00	3.53	9.53	4.87	0.00	3.41
25.05.93	5.83	0.108	0.081	69.35	1374	0.00387	7.80	3.55	0.00	2.23	10.46	5.17	0.00	2.33	9.63	4.82	0.00	3.39

APPENDIX 2

Appendix Table 2.1 Proportional (%) species compositions of the different blocks used in eragrostis and sheep shed camps

Species	ERAGROSTIS						SHEEP SHED						
	Block						Block						
	3	5	8	11	16	20	3	5	8	11	16	20(i)	20(ii)
Alloteropsis semialata	1	1.5	2	4	8	7	9	8.5	16.5	12.5	12.5	20.5	14
Andropogon appendiculatus	10	25	15	26.5	21.5	15.5	12	13.5	6.5	10	7.5	8.5	14
Brachiaria serrat.									0.5	0.5			0.5
Cynodon dactylon	3.5	8	3.5	2.5									
Elionurus muticus			0.5				1	3.5	0.5		2	0.5	1
Eragrostis capensis	0.5										1		
Eragrostis chloromelas	13.5	6.5	6	4	2	2							
Eragrostis curvula	2	2	5.5	2.5	2.5	3.5	3	0.5				0.5	
Eragrostis plana	33	33	40.5	32.5	40.5	43.5	2					0.5	
Eragrostis racemosa									1				1
Harpochloa falx	2.5	1	2.5	4	3	10	5.5	3	3	7.5		4	4.5
Heteropogon contortus	1.5				2		3	5	10.5	14	9	6.5	5.5
Hyparrhenia hirta													
Microchloa caffra							2	5	8	6	12.5	12.5	6
Sporobolus africanus	7.5	8.5	5.5	6.5	0.5	2	6.5	1	0.5			1	1.5
Themeda triandra	23	10.5	16	14	17	11.5	13.5	14	9	9.5	6.5	6.5	11
Tristachya leucothrix	2	5	3	3.5	3	5	42.5	46	44	40	49	39	41
TOTAL	100	100	100	100	100	100	100	100	100	100	100	100	100

Appendix Table 2.2 Proportional (%) species compositions of the different blocks used in old lands and bush camps

Species	OLD LANDS					BUSH CAMP					
	Block					Block					
	3	5	8	11	16	3	5	8	11	16	20
Alloteropsis semialata						5	4	5.5	9	8.5	9
Andropogon appendiculatus	1.5	1	0.5	0.5	0.5	19	8	12.5	12	10.5	18
Brachiaria serrata											
Cynodon dactylon	12.5	13	15.5	7.5	5						
Elionurus muticus						2	4	1		3.5	2
Eragrostis capensis	4	2.5	1	0.5	2	1.5	2	2		1.5	0.5
Eragrostis chloromelas		5	0.5	3	2.5						
Eragrostis curvula	16.5	5.5	6.5	3							
Eragrostis plana	11	8.5	9	8	10	3	6	4	4	6.5	5
Eragrostis racemosa								1	4	1.5	2
Harpochloa falx						6.5	4	5	4.5	2	
Heteropogon contortus	7	10.5	14	15.5	19.5	1.5	2	6	7	3	1
Hyparrhenia hirta	37.5	46	45.5	52.5	50						
Microchloa caffra							2	1	1	1	0.5
Sporobolus africanus	10	8	7.5	9.5	10.5	6.5	8	8	7	4	4
Themeda triandra						21	30	25.5	30	31	36
Tristachya leucothrix						34	30	28.5	30	30.5	22
TOTAL	100	100	100	100	100	100	100	100	100	100	100

Appendix Table 2.3 Analysis of covariance of the effects of animal type (cattle or sheep), year and camp (site) on the *in vitro* digestibility and % crude protein of diets selected on Döhne sourveld

Source	df	SS	F	P
***In vitro* digestibility**				
Camp	3	123.92	1.70	0.168
Animal	1	567.06	23.31	0.0001***
Year	1	1428.22	58.70	0.0001***
Camp x Animal	3	24.55	0.34	0.799
Camp x Year	3	252.15	3.45	0.017*
Animal x Year	1	2.45	0.10	0.751
Camp x Animal x Year	3	4.29	0.06	0.981
Greenness	1	7983.04	291.11	0.0001***
Crude protein				
Camp	3	0.0000561	2.52	0.058
Animal	1	0.0000922	12.44	0.0005***
Year	1	0.0007541	101.72	0.0001***
Camp x Animal	3	0.00001616	0.73	0.5371
Camp x Year	3	0.00001768	0.79	0.4979
Animal x Year	1	0.00000051	0.07	0.7924
Camp x Animal x Year	3	0.0000248	1.11	0.3439
Greenness	1	0.003499	472.04	0.0001***

APPENDIX 3

3.1.1 Objective

To determine the relationship between air temperature, body mass and insensible weight loss (IWL) in sheep.

3.1.2 Procedure

The five sheep described in section 3.3.4 (mass range 27-60 kg) were fitted with faeces bags, weighed on a Mettler KC300 electronic scale and then allowed to stand without access to food or water for 60 minutes. Animals were then reweighed and IWL calculated as the difference in mass between successive weighings. This procedure was repeated on different occasions at different air temperatures (range 8-30.5°C).

Data were analyzed using multiple regression analysis (REG; SAS 1991) with IWL as the dependent variable and body mass and air temperature as independent variables. Individual sheep were used as replications.

3.1.3 Results

Insensible weight loss (g/kg/minute) could be accurately predicted using body mass and ambient air temperature (Table 3.1.1) according to the following equation:

IWL = -1.209 + 0.117*Temperature + 0.0331* Mass (r^2 = 0.815; SE = 0.493; P≤0.0001)

Table 3.1.1 Multiple regression analysis of the effects of body mass and air temperature on insensible weight loss in sheep

Variable	Coefficient	SE	t-value	P
Constant	-1.20	0.417	-2.89	0.007
Temperature	0.117	0.014	8.37	0.0001
Body mass	0.0331	0.011	2.80	0.0094

Appendix Table 3.2 Analysis of covariance of the effects of camp (species composition), year and camp x year interaction on bite size, bite rate and intake rate of cattle grazing Dohne sourveld

Source	df	ss	F	P
Bite size				
Camp	3	0.0173	0.88	0.455
Year	1	0.027	4.11	0.044*
Camp x Year	3	0.041	2.07	0.107
Plant height	1	0.208	31.65	0.0001***
Bite rate				
Camp	3	633.80	4.78	0.0035**
Year	1	0.116	0.00	0.959
Camp x Year	3	4.61	0.03	0.991
Plant height	1	479.04	10.85	0.0013**
Intake rate				
Camp	3	82.29	1.37	0.255
Year	1	97.26	4.86	0.0294*
Camp x Year	3	166.53	2.77	0.044*
Plant height	1	415.28	20.75	0.0001***

Appendix Table 3.3 Analysis of covariance of the effects of camp (species composition) on bite size, bite rate and the intake rate of cattle grazing the Dohne sourveld in year 1 and 2

Source	df	ss	F	P
YEAR 1				
Bite size				
Camp	3	0.0138	0.66	0.576
Plant height	1	0.262	37.96	0.0001***
Bite rate				
Camp	3	335.00	3.75	0.014*
Plant height	1	402.44	13.53	0.0005***
Intake rate				
Camp	3	9.85	0.16	0.923
Plant height	1	536.06	25.98	0.0001***
YEAR 2				
Bite size				
Camp	3	0.210	1.66	0.186
Plant height	1	0.054	12.80	0.0008***
Bite rate				
Camp	3	389.69	6.54	0.008**
Plant height	1	2335.68	117.58	0.0001***
Intake rate				
Camp	3	112.19	2.23	0.095
Plant height	1	28.05	1.67	0.201

Appendix Table 3.4 Analysis of covariance of the effects of camp (species composition) on the bite size, bite rate and intake rate per unit body mass of sheep grazing the Dohne sourveld

Source	df	SS	F	P
Bite size				
Camp	3	0.00506	3.23	0.03*
Plant height	1	0.01970	37.67	0.0001***
Bite rate				
Camp	3	587.88	4.15	0.01*
Plant height	1	1219.29	25.84	0.0001***
Intake rate/mass				
Camp	3	0.00361	1.41	0.252
Plant height	1	0.00452	5.28	0.026*

Appendix Table 3.5 Correlation coefficients for the relationship between bite size, bite rate and intake rate with plant height, herbage density and greenness in year 1 and 2 for cattle grazing 4 sites in the Dohne sourveld

Variable	Bite size		Bite rate		IIR	
Year:	1	2	1	2	1	2
Bush camp						
Plant height	0.677**	0.491	-0.474*	0.196	0.626**	0.542
Herbage density	0.206	0.636*	-0.145	-0.517	0.172	0.378
Greenness	-0.209	-0.070	0.493*	0.719**	-0.036	0.271
Eragrostis camp						
Plant height	0.785***	0.169	-0.291	-0.344	0.818***	0.001
Herbage density	0.528*	-0.300	-0.317	0.208	0.449	-0.201
Greenness	-0.486*	-0.601*	0.656**	0.791**	-0.307	-0.056
ld lands camp						
Plant height	0.416	0.134	-0.498*	-0.079	0.266	0.041
Herbage density	0.337	-0.012	0.010	0.017	0.228	-0.022
Greenness	-0.278	-0.170	0.436	0.913***	-0.075	0.553*
Sheep shed camp						
Plant height	0.534*	0.233	-0.480*	-0.390	0.420	0.104
Herbage density	-0.178	0.080	-0.184	-0.089	-0.213	-0.027
Greenness	0.201	-0.648**	0.309	0.855***	0.266	-0.236

APPENDIX 4

Appendix Table 4.1 Ingestive behaviour, *in vitro* digestibility (IVD) and crude protein (CP) content of diets selected by cattle grazing plots of different grass species. (PHT = plant height; LTH = leaf table height)

Species	Date	Bite size (g)	Bite rate (b/min.)	Intake rate (g/min.)	IVD (%)	CP (%)	PHT (cm)	LTH (cm)	Stems (0-5)	Green (0-5)	Comments
H. hirta	08.01.92	0.362	43.37	16.46	57.86	8.32	26.01	13.14	2.28	4.08	Unmown.
H. hirta	08.01.92	0.438	61.36	26.89	60.73	7.04	19.29	8.9	0.22	4.79	Mown block.
H. hirta	30.01.92	-	61.43	-	57.92	7.27	15.57	8.84	0.62	3.63	Cattle disinterested.
H. hirta	06.03.92	0.46	58.99	27.14	52.87	5.83	19.24	10.3	2.21	3.78	Mown.
H. hirta	13.05.92	0.419	47.5	18.54	45.3	4.7	15.94	7.68	1.76	2.77	Ate stalks.
T. triandra	26.11.91	0.299	39.75	11.78	54.01	6.19	31.32	16.54	3.08	3.98	Cattle grazed.
T. triandra	07.01.92	0.47	60.27	22.62	61.31	9.07	17.68	10.13	0	4.57	-
T. triandra	30.01.92	0.587	62.67	40.31	54.58	6.68	18.77	9.6	0	4.26	-
T. triandra	15.05.92	0.429	58.98	24.12	39.79	3.72	18.19	9.14	0	2.93	-
A. appendiculatus	27.11.91	0.331	47.2	15.65	58.04	9.14	35.1	20	1.08	4.76	Disinterested.
A. appendiculatus	03.01.92	0.285	54.82	15.3	59.4	8.53	30.72	16.6	0	4.85	-
C. dactylon	22.11.91	0.22	54.8	12.08	57.73	11.27	10.81	6.9	0	4.61	Ate readily.

Appendix Table 4.2 Ingestive behaviour, *in vitro* digestibility (IVD) and crude protein (CP) content of diets selected by sheep grazing plots of different grass species. (PHT = plant height; LTH = leaf table height)

Species	Date	Bite size (g)	Bite rate (b/min.)	Intake rate (g/min.)	IVD (%)	CP (%)	PHT (cm)	LTH (cm)	Stems (0-5)	Green (0-5)	Comments
H. hirta	08.01.92	0.038	36.48	1.65	63.07	7.31	19.29	8.9	0.22	4.79	Mown.
H. hirta	30.01.92	-	46.78	-	63	7.96	15.57	8.84	0.62	3.63	-
H. hirta	06.03.92	0.12	46.46	5.49	55.88	7.34	19.24	10.3	2.21	3.78	Mown.
H. hirta	13.05.92	0.068	49.82	3.33	52.13	5.49	15.94	7.68	1.76	2.77	Ate stalks.
T. triandra	26.11.91	-	34.6	-	-	-	31.32	16.54	3.08	3.98	Would not graze.
T. triandra	07.01.92	-	53.61	-	65.16	9.7	17.68	10.13	0	4.57	-
T. triandra	30.01.92	-	46.38	-	60.76	6.57	18.77	9.6	0	4.26	-
T. triandra	15.05.92	0.054	58.4	6.19	50.2	-	18.19	9.14	0	2.93	-
A. appendiculatus	27.11.91	0.038	52.21	1.66	-	-	35.1	20	1.08	4.76	Sheep disinterested.
A. appendiculatus	03.01.92	0.098	44.25	4.3	65.34	10.24	30.72	16.6	0	4.85	-
C. dactylon	22.11.91	0.067	67.6	4.47	65.66	12.41	10.81	6.9	0	4.61	Ate readily.
C. dactylon	27.11.91	0.017	63.7	2.18	58.13	11.13	10.81	6.9	0	4.61	-

Appendix Table 4.3 Mean, maximum and minimum values for sward structure variables of seven different sourveld grasses used in the pot trial for sheep

Species	Plant height (cm)	Leaf table height (cm)	Diameter (cm)	Stemminess (0-5)	Greenness (0-5)	Comments
A. appendiculatus (n=92)						
Mean	25.63	12.24	11.71	0.02	3.97	Readily grazed.
Minimum	15.00	4.00	4.00	0.00	2.50	
Maximum	44.00	20.00	22.00	1.00	5.00	
C. dactylon (n = 120)						
Mean	9.77	4.45	18.08	0.42	4.41	Readily grazed.
Minimum	3.50	1.00	5.00	0.00	3.00	
Maximum	23.00	14.00	27.00	3.00	5.00	
E. plana (n = 65)						
Mean	24.36	13.08	14.07	0.18	4.71	Extra fasting required.
Minimum	16.50	8.00	7.00	0.00	4.00	Long chewing times.
Maximum	41.00	23.00	21.00	2.00	5.00	Total refusal of longer plants.
H. contortus (n = 60)						
Mean	11.49	7.23	13.65	0.34	4.63	Fairly acceptable.
Minimum	7.60	5.00	1.00	0.00	3.00	
Maximum	41.00	35.00	23.00	5.00	5.00	
H. hirta (n = 145)						
Mean	20.09	10.26	13.97	1.11	4.25	Readily grazed.
Minimum	6.00	3.00	6.00	0.00	0.00	Animals picked out leaves on stemmy plants.
Maximum	51.00	35.00	23.00	5.00	5.00	
T. triandra (n = 143)						
Mean	17.08	8.36	14.23	0.04	4.34	Grazed very readily.
Minimum	6.00	3.00	4.00	0.00	1.00	
Maximum	31.00	19.00	21.00	1.00	5.00	
T. leucothrix (n = 127)						
Mean	17.08	7.52	11.85	0.00	3.50	Readily grazed.
Minimum	6.00	2.50	5.00	0.00	1.00	
Maximum	24.00	15.50	16.00	0.00	5.00	

Appendix Table 4.4 Mean, maximum and minimum values for sward structure variables of eight different sourveld grasses used in the pot trial for cattle

Species	Plant height (cm)	Leaf table height (cm)	Diameter (cm)	Stemminess (0-5)	Greenness (0-5)	Comments
A. semialata (n = 16)						
Mean	19.49	12.50	11.25	0.00	3.26	Not highly acceptable - plants possibly too rank?
Minimum	9.75	7.25	9.25	0.00	2.75	Animals spat out dead leaves.
Maximum	32.00	19.00	14.00	0.00	3.75	
A. appendiculatus (n=45)						
Mean	22.51	11.19	14.36	0.09	4.33	Animals grazed eagerly.
Minimum	12.03	5.50	10.00	0.00	3.13	
Maximum	38.50	22.00	17.00	1.25	5.00	
C. dactylon (n = 31)						
Mean	14.66	7.90	15.37	0.13	4.56	Some pots very lush and animals consumed these greedily
Minimum	7.25	3.13	12.00	0.00	3.63	taking very big bites.
Maximum	24.00	12.67	18.25	1.00	5.00	
E. plana (n = 18)						
Mean	35.81	16.34	14.42	1.16	3.95	Extra fasting required before animals would eat.
Minimum	10.00	8.63	11.00	0.00	3.00	Many plants pulled out.
Maximum	56.00	21.00	17.00	3.50	4.88	
H. contortus (n = 44)						
Mean	14.40	7.31	13.34	0.23	4.08	Fairly acceptable.
Minimum	10.90	5.00	11.75	0.00	3.88	
Maximum	18.88	12.63	15.50	1.50	4.88	
H. hirta (n = 42)						
Mean	20.03	9.92	11.65	0.93	4.17	Readily grazed.
Minimum	11.88	5.00	8.33	0.00	2.75	Stems consumed without hesitation giving big bites.
Maximum	32.50	14.88	13.75	3.25	5.00	
T. triandra (n = 36)						
Mean	20.93	9.36	12.61	0.60	4.20	
Minimum	11.53	3.88	9.00	0.00	2.25	Readily grazed.
Maximum	31.25	14.75	16.00	3.50	4.88	
T. leucotricha (n = 35)						
Mean	19.67	9.12	11.22	0.01	4.05	Fairly acceptable.
Minimum	10.13	4.75	8.75	0.00	2.75	Dead leaves distasteful and sometimes spat out.
Maximum	25.13	12.67	14.50	0.25	5.00	

APPENDIX 5

Appendix Table 5.1 Mean percentage dry matter disappearance (and standard deviation) in the rumen of different grasses in spring

Species	Incubation period (h)						
	3	9	24	32	48	56	72
A. semialata	22.99 (5.80)	33.97 (3.10)	49.97 (8.85)	52.37 (1.07)	74.91 (3.18)	77.76 (2.44)	79.28 (2.88)
A. appendiculatus	19.35 (1.15)	25.57 (1.08)	52.65 (1.43)	53.76 (0.94)	59.23 (14.99)	69.15 (1.14)	79.27 (0.26)
C. dactylon	23.31 (1.65)	36.21 (3.25)	55.10 (3.28)	65.98 (4.79)	67.97 (4.23)	79.40 (6.09)	81.39 (0.34)
E. muticus	27.53 (2.54)	35.82 (0.96)	60.68 (1.81)	60.10 (0.15)	65.91 (4.90)	76.55 (0.77)	79.48 (2.81)
E. plana	19.59 (1.97)	30.22 (2.92)	52.05 (0.67)	57.25 (6.42)	61.50 (7.99)	77.48 (5.76)	81.99 (3.14)
H. contortus	22.04 (0.17)	28.47 (4.76)	55.49 (1.96)	68.17 (5.56)	72.03 (1.25)	76.32 (3.15)	79.84 (0.07)
H. falx	24.60 (0.01)	31.80 (0.39)	54.04 (5.44)	65.47 (0.82)	72.46 (1.88)	72.05 (2.31)	74.94 (1.08)
H. hirta	23.12 (2.36)	37.98 (2.10)	60.75 (2.18)	62.77 (0.74)	71.58 (6.37)	79.07 (6.91)	82.78 (0.71)
M. caffra	17.02 (0.03)	19.13 (1.06)	34.92 (0.21)	43.23 (3.37)	54.17 (0.86)	54.19 (1.13)	57.60 (0.19)
T. leucothrix	20.43 (2.88)	33.08 (2.93)	48.67 (2.43)	60.38 (1.48)	64.73 (2.81)	77.80 (1.69)	77.06 (4.88)
T. triandra	18.02 (2.70)	25.63 (1.23)	56.47 (4.57)	58.81 (0.31)	68.24 (0.66)	74.52 (0.32)	76.86 (4.37)

Appendix Table 5.2 Mean percentage dry matter disappearance (and standard deviation) in the rumen of different grasses in summer

Species	Incubation period (h)						
	3	9	24	32	48	56	72
A. semialata	25.01 (0.33)	35.68 (0.52)	56.88 (0.83)	63.23 (3.84)	72.44 (0.16)	74.02 (0.90)	75.50 (1.17)
A. appendiculatus	18.48 (1.53)	24.53 (0.09)	51.85 (2.47)	52.94 (2.26)	65.65 (2.89)	72.77 (1.31)	72.57 (0.51)
C. dactylon	17.82 (0.59)	24.55 (0.20)	39.40 (0.60)	42.82 (0.60)	51.36 (1.59)	53.96 (1.58)	54.59 (0.58)
E. muticus							
E. plana	10.68 (1.61)	16.81 (0.68)	32.51 (4.41)	44.19 (8.55)	61.40 (2.60)	64.59 (1.55)	69.99 (0.97)
H. contortus							
H. falx	17.07 (0.82)	22.90 (2.66)		47.05 (1.48)	55.97 (0.57)	58.24 (0.12)	63.08 (1.07)
H. hirta							
M. caffra	17.07 (1.66)	22.18 (0.12)	33.13 (0.89)	39.30 (0.70)	48.50 (0.22)	52.29 (1.68)	57.51 (1.61)
T. leucothrix	26.26 (1.15)	36.29 (0.43)	52.60 (3.89)	63.15 (2.54)	74.45 (0.32)	74.78 (0.48)	75.90 (2.01)
T. triandra	20.35 (0.30)	26.91 (0.60)	47.14 (1.95)	57.34 (4.43)	71.43 (0.32)	73.76 (1.18)	76.04 (0.14)

Appendix Table 5.3 Mean percentage dry matter disappearance (and standard deviation) in the rumen of different grasses in autumn

Species	Incubation period (h)						
	3	9	24	32	48	56	72
A. semialata	24.13 (0.94)	29.81 (3.19)	46.00 (0.71)	50.93 (0.06)	58.08 (10.39	60.21 (0.22)	65.35 (1.60)
A. appendiculatus	13.32 (0.28)	16.99 (2.94)	29.06 (1.52)	37.22 (2.04)	50.82 (0.98)	55.64 (2.16)	61.01 (0.93)
C. dactylon	18.21 (0.45)	26.87 (0.39)	40.55 (2.26)	46.85 (0.61)	50.11 (1.11)	52.98 (2.95)	55.29 (0.02)
E. mvticus	20.53 (0.52)	23.92 (0.94)	37.04 (0.32)	41.84 (0.57)	52.90 (0.03)	56.67 (0.82)	62.06 (2.10)
E. plana	11.90 (0.17)	15.88 (0.21)	32.91 (1.37)	34.57 (3.03)	52.22 (4.33)	52.81 (1.57)	57.21 (0.33)
H. contortus	20.71 (1.85)	22.95 (2.46)	37.92 (1.70)	50.07 (0.69)	54.46 (9.14)	61.21 (3.65)	63.72 (3.59)
H. falx							
H. hirta	22.64 (0.04)	28.62 (2.32)	43.87 (3.07)	54.04 (2.87)	63.00 (1.60)	67.40 (0.96)	68.82 (2.12)
M. caffra	17.99 (0.42)	18.94 (3.35)	30.67 (0.20)	35.99 (0.61)	42.25 (5.03)	43.69 (0.43)	44.96 (2.36)
T. leucothrix	(20.31 (1.19)	26.04 (0.07)	36.44 (0.41)	46.93 (0.94)	53.75 (0.36)	57.88 (-)	61.24 (1.33)
T. triandra	19.91 (0.96)	25.10 (0.97)	37.74 (1.30)	51.41 (0.14)	56.42 (0.82)	59.40 (-)	66.79 (3.04)

Appendix Table 5.4 Mean percentage dry matter disappearance (and standard deviation) in the rumen of different grasses in winter

Species	Incubation period (h)						
	3	9	24	32	48	56	72
A. semialata	18.16 (1.15)	23.26 (1.73)	36.97 (3.46)	42.92 (0.54)	50.00 (0.21)	55.64 (0.98)	58.38 (0.51)
A. appendiculatus	11.32 (0.17)	14.38 (0.59)	25.24 (4.46)	31.60 (1.51)	45.52 (3.31)	49.41 (1.54)	58.02 (0.44)
C. dactylon	7.97 (0.38)	12.14 (0.98)	21.88 (1.70)	24.19 (0.75)	28.19 (0.82)	29.77 (1.42)	32.93 (1.01)
E. muticus	14.96 (1.14)	17.19 (1.11)	31.33 (1.63)	35.24 (1.85)	44.78 (1.46)	50.81 (1.19)	54.23 (2.37)
E. plana	9.32 (0.69)	13.67 (1.16)	28.44 (3.82)	29.19 (0.20)	46.43 (0.64)	54.17 (3.01)	61.98 (1.95)
H. contortus							
H. falx	10.88 (1.09)	16.37 (1.85)	28.50 (5.38)	32.54 (0.24)	45.18 (0.62)	49.37 (1.26)	55.13 (0.03)
H. hirta	9.79 (2.05)	16.36 (0.49)	32.54 (0.21)	42.78 (1.23)	47.92 (3.61)	50.65 (8.76)	59.13 (2.52)
M. caffra							
T. leucothrix	11.03 (0.03)	14.06 (1.07)	32.76 (0.27)	36.72 (1.29)	46.72 (2.62)	54.84 (1.86)	56.22 (0.72)
T. triandra	13.22 (0.38)	17.45 (1.73)	39.07 (4.08)	44.24 (2.46)	56.64 (1.49)	62.96 (0.93)	66.53 (0.96)

APPENDIX 6

Appendix Table 6.1 Relation between dietary *in vitro* digestibility and sward greenness for cattle (C) and sheep (S) grazing four sites on Döhne sourveld in year 1 and 2

Site	Animal	Equation	r^2
Year 1			
Bush	C	38.33 + 4.45x	r^2 = 0.84; F = 80.01; ***
	S	43.97 + 3.74x	r^2 = 0.69; F = 31.76; ***
Eragrostis	C	30.12 + 6.43x	r^2 = 0.78; F = 55.59; ***
	S	45.61 + 3.49x	r^2 = 0.50; F = 15.57; **
Lands	C	39.91 + 4.34x	r^2 = 0.7; F = 40.19; ***
	S	44.35 + 3.76x	r^2 = 0.53; F = 19.5; ***
Shed	C	36.74 + 5.90x	r^2 = 0.84; F = 74.32; ***
	S	41.45 + 4.89x	r^2 = 0.88; F = 118; ***
Year 2			
Bush	C	74.34 - 23.76x + 4.39x^2	r^2 = 0.82; F = 21.32; ***
	S	54.34 - 9.6x + 2.33x^2	r^2 = 0.51; F = 5.41; *
Eragrostis	C	62.99 - 18.02x + 3.76x^2	r^2 = 0.91; F = 50.5; ***
	S	54.55 - 7.42x + 1.96x^2	r^2 = 0.83; F = 22.57; ***
Lands	C	48.61 - 6.74x + 2.35x^2	r^2 = 0.88; F = 41.74; ***
	S	45.51 + 3.40x	r^2 = 0.49; F = 12.76; **
Shed	C	47.84 - 9.37x + 2.60x^2	r^2 = 0.76; F = 21.11; ***
	S	45.97 - 6.0x 2.06x^2	r^2 = 0.8; F = 25.03; ***

Appendix Table 6.2 Relation between sward greenness and sward height during the growing season at four sites on the Dohne sourveld

Site	Equation	r^2
Bush	4.96 - 0.047x	r^2 = 0.33; F = 4.94 *
Eragrostis	5.22 - 0.060x	r^2 = 0.45; F = 9.92; **
Old lands	5.24 - 0.037x	r^2 = 0.29; F = 4.55; *
Sheep shed	3.85 - 0.024x	r^2 = 0.04; F = 0.53

Appendix Table 6.3 Relation between mean retention time and sward greenness for cattle (C) and sheep (S) grazing four sites on the Dohne sourveld

Site	Animal	Equation	r^2
Bush	C	23.58 - 1.242x	r^2 = 0.67; F = 15.74; **
	S	21.26 - 1.04x	r^2 = 0.52; F = 11.05; **
Eragrostis	C	33.09 - 3.25x	r^2 = 0.65; F = 15.45; **
	S	32.37 - 3.13x	r^2 = 0.62; F = 13.22; **
Lands	C	22.28 - 1.05x	r^2 = 0.5; F = 6.04; *
	S	20.83 - 1.06x	r^2 = 0.49; F = 8.66; *
Shed	C	23.82 - 1.51x	r^2 = 0.79; F = 33.91; ***
	S	20.83 - 0.894x	r^2 = 0.77; F = 24.3; **

Appendix Table 6.4 Relation between dietary *in vitro* digestibility and days from start of the growing season (1 October) for cattle (C) and sheep (S) grazing four sites on Dohne sourveld in year 1 and 2

Site	Animal	Equation	r^2
Year 1			
Bush	C	69.74 - 0.0896x	r^2 = 0.88; F = 112.84; ***
	S	66.77 - 0.0577x	r^2 = 0.74; F = 41.17; ***
Eragrostis	C	66.43 - 0.0697x	r^2 = 0.68; F = 30.92; ***
	S	66.32 - 0.040x	r^2 = 0.59; F = 19.17; ***
Lands	C	66.74 - 0.082x	r^2 = 0.79; F = 53.55; ***
	S	69.46 - 0.07x	r^2 = 0.66; F = 30.41; ***
Shed	C	72.82 - 0.0955	r^2 = 0.70; F = 33.53; ***
	S	71.18 - 0.076x	r^2 = 0.68; F = 35.25; ***
Year 2			
Bush	C	60.15 - 0.064x	r^2 = 0.75; F = 33.04; ***
	S	62.60 - 0.062x	= 0.49; F = 10.83; **
Eragrostis	C	62.85 - 0 0609x	= 0.78; F = 35.76; ***
	S	66.64 - 0.0638x	r^2 = 0.83; F = 51.88; ***
Lands	C	70.10 - 0.187x + 0.000356x^2	r^2 = 0.89; F = 39.83; ***
	S	66.12 - 0.0605x	r^2 = 0.76; F = 39.83; ***
Shed	C	70.73 - 0.211x + 0.00041x^2	r^2 = 0.87; F = 44.93; ***
	S	65.66 - 0.0761x	r^2 = 0.85; F = 77.25; ***

Appendix Table 6.5 Relation between mean retention time and days from the start of the growing season (1 October) for cattle C) and sheep (S) grazing four sites on the Dohne sourveld

Site	Animal	Equation	r^2
Bush	C	15.60 + 0.02149x	r^2 = 0.66; F = 18.24; **
	S	14.17 + 0.0197x	r^2 = 0.57; F = 13.60; **
Eragrostis	C	14.52 + 0.0353x	r^2 = 0.89; F = 65.63; ***
	S	14.98 + 0.0307x	r^2 = 0.68; F = 17.4; **
Lands	C	15.28 + 0.0221x	r^2 = 0.72; F = 15.79; **
	S	13.19 + 0.0202x	r^2 = 0.[illegible]; F = 11.73; **
Shed	C	14.39 + 0.024x	r^2 = 0.69; F = 20.58; **
	S	14.84 + 0.0162x	r^2 = 0.76; F = 22.69; **

Author: O'Reagain Peter John.

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