Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author. Comparative Studies of Effects of Sward Structure on Ingestive Behaviour of Sheep and Goats Grazing Grasses and Legumes

A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy at Massey University, Palmerston North, New Zealand.

> Yaoming Gong October, 1993

# ABSTRACT

A review of the literature indicated that the ingestive behaviour and herbage intake of grazing animals are strongly influenced by characteristics of sward canopy structure. However, there is limited comparative information on the behavioural contrasts of animals grazing grasses and legumes, and little comparative information on the ingestive behaviour of sheep and goats. The projects which form the basis of this thesis concentrated on these two aspects of ingestive behaviour using an indoor crate grazing technique, in which animals were individually confined in metabolism crates, and offered prepared turves.

Three experiments were designed and were run over a period from 1989 to 1991 at the Ballantrae Research Station of the New Zealand Pastoral Agriculture Research Institute (AgResearch).

In the first experiment, five grasses and four legumes were each sampled at two stages of growth to produce a range of canopy structures. Two sub-sets of data were generated. One sub-set (restricted data set) embraced four forages (two grasses and two legumes) at two maturity stages across two experimental years (4 forages x 2 stages x 2 animal species x 2 years). This sub-set was intended to assess the effects of the variation in animal body size with increasing maturity (Chapter 4). Another sub-set (enlarged data set) involved nine forages at two maturity stages over the second experimental year. It involved an attempt to examine the effect of sward canopy structure induced by a range of forage conditions on ingestive behaviour of sheep and goats (Chapter 5).

The second experiment was designed to dissociate the effects of sward height from the confounding effects of plant growth habit and maturity stage by creating contrasting heights within a forage species, and by sampling vegetative swards only. This experiment involved four forages (two grasses and two clovers) grazed by four sheep and four goats (Chapter 6).

The third experiment tested the comparability and conformability of ingestive behaviour between indoor crate gazing and field grazing using sheep, and between oesophageal fistulated and intact sheep using a field cage grazing technique (Chapter 7).

Major conclusions may be drawn as follows:

Bite weight was strongly influenced by bite depth. There was a substantially greater response in bite depth than in bite area to variation in sward conditions. Bite depth was a major spatial component of bite volume, and hence bite weight. Bite rate declined as bite weight increased, and intake rate was determined as the combination of bite weight and bite rate.

Ingestive behaviour of the grazing animals was strongly influenced by the characteristics of the sward canopy structure. Sward height usually had a much more dominant impact than did other sward variables, and bite depth had a much greater response than did other behaviour variables. Very close positive relationships existed between sward height and bite depth, bite volume, and hence bite weight, but the relationship between sward height and bite rate was negative. There was no statistically significant relationship between bite area and either sward height or other attributes. However, there was a significant interaction between animal species (sheep vs goats) and sward categories (grasses vs legumes) in this process, as outlined below.

Chapter 5 (enlarged data set of Experiment 1) revealed that when the leguminous swards were grazed by sheep, sward bulk density had a substantially greater effect on ingestive behaviour than did sward height. In contrast, the ingestive behaviour of goats grazing legumes was influenced largely by sward height, though the effect of bulk density was substantially increased compared with that in grasses. Both animal species had a greater response in bite weight than in bite depth when grazing legumes.

Chapter 6 (Experiment 2) showed that sward height always had the most important effect in both grasses and legumes irrespective of animal species. Appreciation of the effect of bulk density on ingestive behaviour after the dominant effect of sward height was accounted for, depended very strongly upon the establishment of independent variation in sward height and bulk density over the range of test swards. Sward height had a dominant effect and bulk density had no significant effect where independent variation in height was achieved. Where the variation in sward height was confounded with bulk density, although sward height still had a dominant effect, the interactive effect of sward height and bulk density was significant in some cases, depending on the sward categories (grasses or legumes) and animal species. Animals usually had smaller bite dimensions on legumes than on grasses. However, the reduced bite depth, hence bite volume of legumes compared to grasses could be compensated for by a greater bulk density within the grazed strata, a smaller effort required to harvest herbage and less plant components slipping out of the teeth, leading to a greater bite weight.

Other differences between sheep and goats were identified as follows:

Sheep were generally capable of penetrating into swards deeply, whereas goats grazed swards from the top downwards. Sheep usually had larger bite dimensions, and hence greater bite weights than goats when grazing legumes (irrespective of maturity stages), and vegetative grasses, leading to greater bite weights on average. However, goats were able to achieve greater bite weight in relation to live weight. On reproductive grasses goats showed a greater willingness to eat, whereas sheep were selective through pushing into the swards to graze leafy components and rejected the rigid components.

When swards matured, intake rate of sheep decreased because an increase in bite weight was counterbalanced by a large fall in biting rate. Intake rate of goats increased as a result of a substantial increase in bite weight and a relatively small fall in bite rate, compared with sheep.

The variation in bite weight and bite depth between sheep and goats for a given sward may be attributed, at least partially, to the discrepancy in incisor arcade breadth between the two species. Increases in bite weight and bite dimensions with increasing maturity of animals were ascribable to increases in incisor breadth of animals with increasing maturity over time.

Experiment 3 (Chapter 7) demonstrated that the results of indoor crate grazing can be reliably extrapolated to field grazing on a short-term basis, and grazing behaviour of animals is not significantly altered by oesophageal fistulation.

Recommendations and suggestions for application to grazing management and plant selection programmes were made in practical terms.

**Key words**: canopy structure, height, bulk density, grasses, legumes, stage of maturity, ingestive behaviour, bite dimensions, bite weight, bite rate, sheep, goats, indoor crate grazing, outdoor cage grazing, fistulated sheep, intact sheep.

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# Abbreviations

The following abbreviations and symbols of statistical conventions, technical terms and names of forages were used throughout this thesis.

# Statistical conventions

Abbreviations or symbols

ns	Not statistically significant
(*)	Significant at the P<0.1 level of probability
*	Significant at the P<0.05 level of probability
**	Significant at the P<0.01 level of probability
***	Significant at the P<0.001 level of probability
s.e	Standard errors of least squares means
LSD	Least significant difference (P<0.05)
R <sup>2</sup>	Coefficient of determination: proportion of variation accounted
	for by regression
Partial R <sup>2</sup>	Proportion of variation accounted for by corresponding term
	included in the regression equation
F	Variance ratio
ANOVA	Univariate analysis of variance
MANOVA	Multivariate analysis of variance
MDF	Multivariate discriminant function analysis
MDF1	The first discriminant function
MDF2	The second discriminant function
CORR	Correlation coefficients between score and original variables
	in the discriminant function analysis
STAN	Standardized coefficients of variables in the discriminant
	function analysis

# **Technical terms**

DM	Dry matter
FM	Fresh matter
LW	Live weight
BW1	Bite weight 1 (mg FM/bite)

BW2	Bite weight 2 (mg DM/bite)
BW3	Bite weight 3 (mg DM/kgLW <sup>0.75</sup> )
BR	Bite rate (bites/min)
IR2	Intake rate 2 (mg DM/min)
IR3	Intake rate 3 (mg DM/kgLW <sup>0.75</sup> /min)
BD	Bite depth (cm)
ВА	Bite area (cm <sup>2</sup> )
BV	Bite volume (cm <sup>3</sup> )

## Forage identifiers

The forage and sward identifiers which appear in the thesis frequently are listed below. Those which only appear on few occasions will be noted where appropriate.

ry	Ryegrass
br	Browntop
ck	Cocksfoot
pg	Prairegrass
ph	Phalaris
th	Tahora white clover
kp	Kopu white clover
rc	Red clover
Veg	Vegetative stage
Rep	Reproductive stage

# Animal identifiers

sh	Sheep
go	Goats
NOF	non-fistulated animals
OF	fistulated animals

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### **CHAPTER 1**

### **GENERAL INTRODUCTION**

Grazed ecosystems are a soil-plant-animal complex, and the impact of each component is vital to understanding the complete system (Coleman *et al.*, 1989). Grazing animals and grazed swards are highly interactive during consumption of herbage (Smetham, 1990) and this interaction is described as the "plant-animal interface" (Forbes *et al.*, 1985).

Research at the plant-animal interface involves reciprocal interests: (1) study of the effects of defoliation by grazing animals upon regrowth, persistence and composition of swards, and (2) study of the effects of herbage characteristics and canopy structure on ingestive behaviour and herbage intake of grazing animals, and therefore, on animal performance (Moore & Sollenberger, 1986). Consumption influences the quantity and character of the residual herbage, and the quantity and character of the herbage on offer determines the amount and composition of pasture consumed by the grazing animal (Moore, 1983; Forbes *et al.*, 1985). To improve management of a grazing system, it is essential to understand not only the effects of grazing on sward conditions, but also the effect of sward structure on herbage intake (Penning *et al.*, 1991a).

It has been widely recognized that the production of meat, milk, fibre or offspring by domestic livestock is largely influenced by the feed intake of animals (Forbes *et al.*, 1985). Restricted nutrient intake is probably the major factor limiting production (Hodgson, 1981a) and increasing total herbage intake is one way of correcting nutrient deficiencies (Vallentine, 1990). Understanding of the impact of sward conditions on grazing behaviour of animals is vital to increasing herbage intake. However, current knowledge on this aspect is limited (Lazenby, 1981; Hodgson, 1986), many of the complex interactions between grazing animals and sward canopies are not well understood (Cosgrove, 1992), and many of the results already obtained appear to conflict (Burlison, 1987). Precise quantitative intake projections under grazing conditions are still difficult due to the numerous complex and strong interactions involved (Vallentine, 1990). Much research has focused on the influence of gross sward variables like total herbage mass or surface height on ingestive behaviour and herbage intake variables (Hodgson, 1977) like bite weight, bite rate, grazing time and daily herbage intake. However, bite dimensions, which are the behavioral characteristics causally linking sward structure and intake (Ungar *et al.*, 1991), have been investigated less frequently. As a consequence, there is limited information on the effect of sward canopy characteristics on bite dimensions, on the relationships between bite weight and bite dimensions.

It has been shown that studies of short-term ingestive behaviour can avoid the influences of some animal behavioral characteristics such as the need to spend time on resting, ruminating and socializing on estimates of intake variables (Cosgrove, 1992), and consequently can allow the study to focus on factors such as bite weight, bite rate and bite dimensions which influence the animal's ability to eat.

Ingestive behaviour and herbage intake have not been studied as much for goats or deer as they have for sheep and cattle. However, there are some special features of goats and deer that influence grazing management (Thompson & Poppi, 1990).

The project which forms the basis of this thesis was undertaken with the following objectives in mind:

- (1) to assess the effects of a wide range of structural characteristics of the sward canopy on components of ingestive behaviour and bite dimensions.
- (2) to examine the effects of animal attributes on ingestive behaviour and bite dimensions.
- (3) to compare the response patterns of ingestive behaviour and bite dimensions of sheep and goats over the same range of sward conditions.

The study was conducted within the constraints of short-term ingestive behaviour.

### **CHAPTER 2**

# LITERATURE REVIEW

#### 2.1 INTRODUCTION

The ingestive behaviour and herbage intake of grazing animals in the soil-plantanimal complex (Coleman *et al.*, 1989) are heavily influenced by a large number of factors and the control of herbage intake is apparently multifactorial. The major factors are indicated in Fig. 2.1. It is convenient to divide the factors likely to affect the herbage intake of grazing animals into four main groups: those associated with the animal, the sward, management strategy and the environment (Hodgson, 1977). In Fig. 2.1, those typed in bold denote the factors and components which were of particular interest in the present experiments.

# 2.2 SIGNIFICANCE OF THE RESEARCH ON INGESTIVE BEHAVIOUR AND HERBAGE INTAKE

The importance of level of herbage intake in determining productivity of grazing animals has been widely recognized. Within the bounds of genetic potential, production by the grazing animal is primarily a function of quantity and quality of the herbage consumed, both contributing directly to nutrient intake. Therefore, livestock production from pasture depends on the quantity of herbage harvested (intake), and the efficiency with which animals digest and use nutrients (Thompson & Poppi, 1990). Although diet quality is undoubtedly important, variation in the amount of herbage consumed has been deemed the most important factor determining level and efficiency of livestock productivity (Demment & Van Soest, 1985). Data on diet quality without information on herbage intake or ability to predict it is likely to result in a poor description of the nutritional status of range animals (Hakkila *et al.*, 1987).

Investigating ingestive behaviour of grazing livestock provides valid data in its own right and is an integral part of the development of grazing system (Forbes, 1988). The ingestive behaviour of grazing animals may be a more sensitive indicator of sward quantity and quality than direct measurements of the sward (Ruyle & Dwyer, 1985), thus monitoring animal behaviour during grazing periods may allow the grazier to Fig. 2.1 Factors Influencing Ingestive behaviour of grazing animals (after Burlison, 1987)



The bold typed factors denote those which are of particular interest in the current research.

4

identify limitations of the sward and adjust management strategies accordingly. Therefore, herbage intake prediction or measurement is a key component in assessing free-choice nutrient intake and the need for dietary enhancements, and in determining appropriate stocking rate and management practices (Vallentine, 1990).

A proper understanding of the interface between grazing animals and grazed land is crucial in achieving most efficient herbage utilization within grazing systems in order to maximize output. This is a prerequisite to identifying the scope which exists for manipulating intake (Hodgson, 1982; 1985). Identification of the factors which restrict herbage intake should suggest strategies in which limitations may be overcome and the productivity of the animal moves closer to its potential.

### 2.3 CONTROL OF HERBAGE INTAKE IN GRAZING ANIMALS

Many of the individual effects involved in the process of herbage intake control have been described in extensive reviews. However, we still lack the knowledge to predict with any certainty herbage intake from individual response factors (Hodgson, 1990). This subject has been extensively reviewed (McClymont, 1967; Arnold, 1970; Hodgson, 1977, 1985, 1986, 1990; Freer, 1981; Burlison, 1987; Poppi et al., 1987). The factors involved in control of herbage intake have been subdivided in two ways in order to explain and understand the mechanism of herbage intake control: (1) balance between facilitatory and inhibitory stimuli (McClymont, 1967), and (2) nutritional and non-nutritional determinants (Poppi et al., 1987). Both theories suggest that the control of herbage intake in the grazing animal is influenced by a wide range of variables, but that behavioural control of intake, being responsive to sward quantitative or structural characteristics, is a dominant effect (Burlison, 1987; Hodgson, 1985). The animal attempts, by adjusting components of ingestive behaviour, to achieve an adequate level of intake in the face of constraints of sward structure and composition (Burlison, 1987). This review mostly concentrates on the influence of sward quantity and arrangement (canopy structure) on herbage intake as this was the research topic, but the effects of sward quality will also be touched on briefly. In addition to pasture characteristics, some animal attributes will also be assessed.

### 2.4 INGESTIVE BEHAVIOUR OF THE GRAZING ANIMALS

### 2.4.1 Grazing activity

Grazing is a complex activity and was defined in a specific sense as the defoliation by grazing animals of rooted plants in the field (Hodgson, 1979), consisting of 'searching' (scanning, recognition, decision) and 'handling' (biting, chewing, swallowing) behaviour (Ungar & Noy-Meir, 1988).

The typical activity of a grazing animal can be described as interrupted forward movement with the head swinging from side to side in front of the forelegs (Hodgson, 1986). The horizontal movement of the head results in a mower effect, with the tops of the herbage being "trimmed" off (Vallentine, 1990). The grazing activity involves two components: feeding periods and intervals of movements between feedings. The location where an animal defoliates is referred to as the feeding location and is the area available in a half-circle in front of and to each side of the grazing animal while its front feet are stationary, and this pause is referred as feeding station interval (Ruyle & Dwyer, 1985). At intervals, the animal walks a few steps to search for desired herbage and then pauses to take bites (Ruyle & Dwyer, 1985). A bite is harvested by prehending (grasping herbage) and taking it into the mouth. The herbage is then chewed and mixed with saliva, manipulated and formed into a bolus, and then swallowed and ejected with some force into the anterior rumen (Hodgson, 1979, 1986).

#### 2.4.2 Variables of ingestive behaviour

Components of ingestive behaviour and bite dimensions will be considered under this heading.

### 2.4.2.1 Components of ingestive behaviour

Hancock (1952) first discussed the three components of daily herbage intake. In these terms, the daily herbage intake of animals (I) can be viewed as the product of three variables of ingestive behaviour: the time spent grazing (GT), the biting rate during grazing (RB) and the amount of herbage ingested per bite (IB), thus,

Two additional variables can be calculated from the terms of equation above. They are (1) the total number of grazing bites per day (B), the product of GT and RB, and (2) the rate of herbage intake (RI), the product of RB and IB. These five variables collectively describe the process of ingestive behaviour. This view of ingestive behaviour is somewhat mechanistic, and relies on the expression of continuous variables as simple means or totals (Hodgson, 1982). However, it simplifies the complex behaviour patterns of the grazing process to a simple series of quantifiable functions, and thus provides a useful basis for considering the way in which behavioural responses to variations in sward characteristics may influence herbage intake (Hodgson, 1982, 1985).

Methods and equipment used to measure ingestive behaviour have been reviewed by a number of scientists (Hodgson, 1982; Le Du & Penning, 1982; Penning, 1983; Penning *et al.*, 1984; Anderson *et al.*, 1985). Other aspects of ingestive behaviour have been reviewed by Stobbs (1975a), Hodgson (1977, 1981b, 1982, 1983, 1985, 1986, 1990), Arnold (1981), Allison (1985), Moor & Sollenberger (1986) and Forbes (1988).

In the present review, attention will be concentrated on how ingestive behaviour variables are influenced by sward and animal attributes.

#### 2.4.2.1.1 Bite weight

Bite weight (alternatively known as intake per bite, bite mass or bite size) has been measured both directly and indirectly. Direct measurement involves using oesophageal fistulates and dividing the weight of dried extrusa by the number of bites taken. Techniques for oesophageal fistulation have been detailed by Torell (1954), Hamilton *et al.* (1960), Bramley and Wait (1972), Corbett (1978) and Le Du and Penning (1982). Indirect measurement involves dividing the intake over a period of time by the corresponding number of bites taken. Generally, the former method tends to give a slightly higher estimate of bite weight than the latter (Jamieson & Hodgson, 1979a & b; Forbes, 1982) and their relative merits have been discussed by Hodgson (1982).

The importance of bite weight has long been recognized, but attempts to measure it in grazing animals have been made only relatively recently (Forbes 1982). This variable usually exerts a dominant influence upon daily herbage intake, and in most circumstances compensatory changes in biting rate and grazing time are inadequate to offset decline of bite weight resulting from sward restrictions (Hodgson, 1982). Thus, an ideal grazing sward may be defined as one where no restriction to
bite weight is imposed and on which bite weight exceeds the critical level for that species of animal (Minson, 1983).

Expression of bite weight can also be converted to a live weight or metabolic live weight basis with advantages of comparison between various livestock classes with different body sizes, e.g. mg OM (or DM)/kg LW/bite.

Bite weight varies widely with the type and stage of growth of the forage being grazed (Forbes, 1988). On temperate sown swards, the range of variation in bite weight is approximately 11-400 mg OM (0.4-2.6 mg OM/kg LW) for sheep, compared with 70-1610 mg OM (0.3-4.1 mg OM/kg LW) (Hodgson, 1986) or 50 mg -8000 mg OM (Vallentine, 1990) for cattle. Values of bite weight in cattle grazing a range of tropical swards (Stobbs, 1973a & b) have been found to range from 70 mg OM to over 590 mg OM, substantially lower than those found in temperate swards.

Individual values of bite weight may be substantially greater than mean values summarized above. In some studies (Stobbs, 1973a & b, 1974a, 1975b; Stobbs & Hutton, 1974; Chacon & Stobbs, 1976, 1977; Chacon *et al.*, 1976; Chacon *et al.*, 1978; Hendricksen & Minson, 1980), bite weight was calculated by dividing extrusa weight either by the total number of harvesting and manipulatory bites or by the number of harvesting bites plus manipulatory bites taken with head down, instead of just the harvesting bites. True bite weight was therefore underestimated (Burlison, 1987).

Bite weight is the primary animal response and is sensitive to variation in the physical characteristics of the sward canopy. It increases linearly with increasing sward height or herbage mass (or green herbage mass) in both cattle and sheep grazing temperate swards (Allden & Whittaker, 1970; Hodgson & Milne, 1978; Hodgson & Jamieson, 1981; Forbes, 1982; Black & Kenny (1984); Penning *et al.*, 1991a; Mursan *et al.*, 1989; Burlison *et al.*, 1991; Laca *et al.*, 1992a). Bite weight of sheep increased by 1 mg DM per millimetre increase in sward surface height or 0.01 mg OM/kg LW in spring; and bite weight reached a maximum at a sward height of 60 mm and then decreased as height further increased in autumn (Penning *et al.*, 1991a).

In contrast, under tropical or subtropical conditions (Stobbs, 1973a & b; Chacon & Stobbs, 1976; Hendrickson & Minson, 1980) the relationship between bite weight and sward height was negative rather than positive and variation in bite weight was attributable more to variation in sward bulk density and leaf content than to sward height. This will be considered in more detail in Section 2.5.2.2.2. However, positive

relationships between bite weight or herbage mass have been found with the tropical and subtropical swards studied by Chacon *et al.* (1978), Forbes and Coleman (1985) and Moore *et al.* (1985).

Burlison *et al.* (1991) working with a series of swards in which independent variation in surface height and bulk density was achieved, found that bite weight was positively related to both surface height (6-55 cm) and to the bulk density of the grazed stratum (range 0.1-2.0 mg DM/cm<sup>3</sup>) Similar evidence was shown by Laca *et al.* (1992a) using cattle grazing paspalum (*Paspalum dilatatum*) and lucerne (*Medicago sativa*). Surface height acted primarily upon bite depth and hence bite volume, and bulk density of the grazed stratum influenced bite weight directly. Black and Kenny (1984) also showed that both variables influence bite weight and an asymptotic relationship exists, reaching a plateau at mean sward bulk density of 4.23 mg DM/cm<sup>3</sup>. Mursan *et al.* (1989) reported that bite weight increased with sward surface height despite a two-fold reduction in bulk density of the grazed height.

# 2.4.2.1.2 Biting rate

Biting rate is usually expressed as bites per minute.

Biting rate was first measured as an indicator of sward conditions more than 40 years ago (Johnstone-Wallace & Kennedy, 1944), but only recently has it been used as a component of ingestive behaviour, combining with bite weight and grazing time to both determine and explain herbage intake (Forbes, 1982). Measurement of biting rate may be carried out by manual and automatic procedures, both techniques require an adequate definition of a "bite" (Forbes, 1982) and criteria under which measurements will be made (Hodgson, 1982).

Jamieson and Hodgson (1979a) developed a method of recording by stopwatch the time taken for an animal to make 20 consecutive bites, discarding any records where the animal lifted its head before completing 20 bites. Each bite was characterized by a short, sharp jerk of the head and the sound of the herbage being severed. This technique therefore provided a measure of the maximum biting rate for the particular sward conditions (Burlison, 1987). Jamieson (1975) (cited by Burlison, 1987) found that this technique gave values 16% higher than those derived from recording the number of bites taken over a 2-min period, because the latter record takes into account more of the normal and characteristic movements animals make during grazing, such as lifting the head while chewing large mouthfuls, walking between bites and so on. Differences between the two techniques were greatest in the morning.

Forbes (1982) and Forbes and Hodgson (1985) modified the 20-bites technique to include the time taken for herbage selection and mastication of large mouthful. Recording continued both when an animal walked with the head down while obviously selecting herbage, and when the head was lifted while chewing large mouthfuls of herbage in between bouts of biting. A close estimate of the long-term mean biting rate would have been obtained with this modified technique.

Automatic records of biting have been described by Stobbs and Cowper (1972), Chambers *et al.* (1981) and Penning (1983). In most cases bite meters were developed to record jaw movements, whereas Chambers *et al.* (1981) relied on both head and jaw movements. These procedures will not be discussed in more detail here because they are outside of the scope of the thesis.

Biting rates of 30-50 bites/min appear common in both sheep and cattle (Vallentine, 1990), however, bite rates measured in individual studies vary quite markedly. Stobbs (1974b) found that cattle bite rates were 45 to 80 per minute when grazing various tropical swards, while Hodgson and Jamieson (1981) reported rates for lactating cows of 20 to 62 bites per minute while grazing temperate ryegrass swards. Sheep have been reported to take as few as 18 bites per minute (Allden & Whittaker, 1970) and as many as 120 bites per minute (Forbes *et al.*, 1985). Penning *et al.* (1991a) showed that biting rates of lactating ewes in spring were 38 to 73 bites per minute and those of dry ewes 66 to 75 bites per minute in autumn, both varying with sward height. Burlison (1987) recorded 27 to 73 bites per minutes for sheep with almost three-fold variation between crops (herbages) and between experimental periods within crops.

Generally, there is a negative relationship between biting rate and sward height or herbage mass, on both temperate and tropical swards (Chacon & Stobbs, 1976; Hodgson & Jamieson, 1981; Forbes, 1982; Milne *et al.*, 1982; Moore *et al.*, 1985; Phillips & Leaver, 1986; Burlison, 1987; Penning *et al.*, 1991a; Mitchell, 1993). Allden and Whittaker (1970) found that bite rate in sheep increased steadily as tiller length decreased from 37 cm until an apparent maximum of 73 bites per minute was reached at a sward height of 5 cm, although it then fell sharply as tiller length fell to 4 cm. Wadsworth (quoted by Forbes *et al.*, 1985) found that declining in biting rate of sheep and lambs was not linear. Biting rate may also be negatively related to leaf content (Chacon & Stobbs, 1976; Forbes, 1982).

As herbage mass becomes very low, animals increase rate of locomotion at an exponential rate to search for bites (Laca & Demment, 1990).

An increase in biting rate, reflecting a decline in sward height or herbage mass, has been found to be accompanied by a decrease in the ratio of manipulatory to harvesting bites in sheep (Chambers *et al.*, 1981; Penning *et al.*, 1984; Penning, 1986; Penning *et al.*, 1991a; Laca *et al.*, 1992a). Penning *et al.* (1991a) found that in sheep grazing swards varying in height from 3.0-12.0 cm biting rate fell by 0.4 bites/min/mm of sward height while masticating rate increased by a similar amount as sward height increased, thus the rate of total jaw movements remained constant. As bite weight increased, a greater proportion of jaw movements were allocated to masticate and manipulate the herbage ingested and therefore, biting rate fell, but intake rate remained constant. Forbes (1988) argued that regardless of the reason for maintaining constant intake rate, this fact implies that estimates of biting rate and bite weight based on measurements of jaw movements are unreliable. It is suggested that bite meters should incorporate systems to record both head movements and jaw movements (Chambers *et al.*, 1981).

Research has suggested that biting rate may be a direct response to sward conditions rather than a compensatory mechanism for a reduced bite weight (Hodgson, 1986).

# 2.4.2.1.3 Rate of intake

The rate of intake (intake of herbage weight per unit time) is part of the mechanisms that determine daily intake (Laca & Demment, 1990) and may be calculated by dividing daily herbage intake by daily grazing time, or may be obtained by multiplying bite weight by biting rate, and thus it is a higher order variable (Laca & Demment, 1990). Ungar & Noy-Meir (1988) used the term 'instantaneous intake rate' to refer to intake rate during periods of active grazing on a time scale of seconds and minutes.

There are two kinds of assumptions involved in defining intake rate (Laca & Demment, 1990). One assumption is that the animal moves searching for bites at a constant rate, and can be chewing while searching. Each acceptable bite requires a certain time to be harvested and chewed. Prehending time is constant per bite and chewing time is constant per gram of dry matter. The other assumption is that searching and processing of previous bites take place simultaneously, contrary to the assumption that searching and eating are exclusive activities (Laca & Demment, 1990).

Rate of intake can be estimated as a daily average value or alternatively, measured directly over short periods of time (Hodgson, 1982). The latter estimation can be made using oesophageal fistulates or by calculating the difference in animal live weight before and after a certain time spent grazing after calibrating losses of faeces, urine and insensible weight (Penning & Hooper, 1985).

Rate of intake has been found to range from 22 to 80 mg OM/kg LW/min for sheep and 13 to 240 mg OM/kg LW/min for cattle on temperate sown swards (Hodgson, 1986). Allden and Whittaker (1970) reported that the maximum intake rate of hungry sheep could be as high as 190 mg DM/kg LW/min. Penning *et al.* (1991a) found that intake rate of sheep continuously grazing swards with a range of heights (30-120 mm) was 2.5-5.0 g OM/ewe/min and 1.0-3.0 g OM/ewe/min (heights 20-90 mm) in spring and autumn, respectively. Penning & Hooper (1985) found that estimations of rate of intake over short time periods were not significantly different from corresponding daily mean values.

Rate of intake is a function of bite weight and the time cost involved in searching, prehending and chewing the bite before it can be swallowed (Laca & Demment, 1990; Cosgrove, 1992). In a model of the response of intake rate to search time per bite and bite weight, Laca and Demment (1990) found that intake rate increases with bite weight in a linear relationship at low bite weights, but becomes asymptotic with further increase of the bite weight, and concluded that response of intake rate is highly sensitive to bite weight and insensitive to biting rate, unless the animal has an extremely low search efficiency and a high proportion of the herbage is not prehended. Using various sward canopy heights grazed by cattle, Cosgrove (1992) found that the variation in intake rate resulted from different bite weight and bite rate combinations. At the start of grazing, as sward height increased from 10.0 to 30.0 cm, intake rate increased as a result of an increase in bite weight and a decrease

in bite rate. But at the end of grazing when post-grazing canopy height was 5.0 cm, intake rate decreased with increasing pre-grazing canopy height as a consequence of similar bite weight, but slower bite rate. Hodgson (1981b) pointed out that bite weight and rate of intake are both sensitive to surface height, but rate of biting was less sensitive, and its magnitude in compensating for the decline of bite weight varied with the management strategy.

The rate of intake has been found to increase initially with increasing herbage mass or sward height, becoming insensitive to it beyond a certain level (Chacon & Stobbs, 1976; Hodgson, 1981b; Forbes, 1982; Penning, 1986), or the relationship may be quadratic (Penning et al., 1991a; Cosgrove, 1992). The quadratic relationship between intake rate and sward surface height seemed to be attributable to the decline in the ratio of prehension bites to masticating movements with the increase of sward height (Penning et al., 1991a). Burns (1984) (quoted by Vallentine, 1990) reported that intake rates of cattle on improved pasture appeared to be maximized at an extended plant height of around 41 cm. Burlison (1987) showed that rate of intake declines as the sward is grazed down. The trial by Penning et al. (1991a) showed that intake rate for dry ewes reached a maximum of 56 mg/kg LW/min of grazing time when grazing at a sward height of 61 mm and thereafter decreased as sward height increased. With artificial swards, Laca and Demment (1990) reported that the instantaneous intake rate increased rapidly as surface height increased to 50 cm. This response, due to deeper bite depths in taller swards, was found to be greater at low rather than at high bulk densities. The rate of intake may also be positively correlated to leaf proportion and leaf bulk density (Chacon & Stobbs, 1976). Cosgrove (1992) showed that intake rate increased quadratically with canopy height, with a predicted maximum intake rate at 28.0 cm, and the quadratic effect was caused by lower bite rate on tall canopies.

#### 2.4.2.1.4 Grazing time

The grazing animal usually divides its day into three alternative activities: grazing, ruminating and idling (Hodgson, 1990). By themselves, these activities may be of greater academic interest than of practical value but, when considered with other criteria, their balance and also deviation from the normal patterns may signal stress factors and suggest management changes (Vallentine, 1990).

Like biting rate, grazing time may be recorded manually or automatically. Unlike

biting rate, however, recording of grazing time must continue for hours, and becomes extremely laborious (Forbes, 1988). Manual records are usually made at 5-10 minutes intervals (Hodgson, 1982). Automatic recording is normally carried out continuously. The Kienzle vibracorder (Allden, 1962; Hodgson, 1982) would appear to be the most commonly used automatic recorder though some electronic apparatus has been used (Chambers *et al.*, 1981; Penning *et al.*, 1984).

In general, sheep and cattle spend approximately one third of the day actually grazing, but a great variation has been found. On temperate sown swards, grazing time has been found to range from approximately 6.5 to 13.5 hours a day for sheep and 5.8 to 10.8 hours a day for cattle (Hodgson, 1986), depending on the animal species and sward conditions. A grazing time in excess of 8-9 hours/day is likely to be indicative of limiting sward conditions (Hodgson, 1990). Burlison (1987) reported that the range of mean grazing time of sheep was less than two-fold, from 434 to 813 minutes per day, and the overall tendency was for grazing time to decline as a sward was grazed down. The results reported by Penning et al. (1991a) were 534-789 min for lactating ewes in spring and 584-660 min for dry ewes in autumn, both grazing swards of various heights. Walton (1983) calculated that a cow must graze 8 hours a day to achieve 90 kg green herbage at rate of 80 bites/min. Beef steers grazed 7.3 hours on improved pasture in West Virginia (quoted by Vallentine, 1990) whereas cows with calves on native grass range in Oklahoma occupied 9.7 hours (quoted by Vallentine, 1990), heifers on Ozark ranges 10.6 hours and cattle on Australia rangelands 10 hours (quoted by Vallentine, 1990).

Grazing animals exhibit a daily grazing cycle that is remarkably consistent and recurs each day with minimum change (Vallentine, 1990). There are usually between three and five periods of grazing during the day and the major grazing periods begin near dawn and again in the evening, ending near to sunset (Arnold, 1981). Most grazing activity occurs during daylight hours in temperate climates, though short periods of night grazing are not uncommon (Arnold, 1981). There is usually a period of ruminating activity after each grazing period, but much ruminating occurs at night (Hodgson, 1990). Freer (1981) commented that social factors and daylength may also contribute to reduction in grazing time. The trial of Penning *et al.* (1991a) suggested that grazing and ruminating time were interchangeable: as grazing time increased there was a concomitant decrease in time spent ruminating and time spent idling

remained relatively constant.

Grazing time may vary as type of sward changes. Stobbs (1974a) and Stobbs and Hutton (1974) reported that grazing times for cows were, on average, shortest on temperate swards including oats (mean value 7.7 h/day), and increasingly longer on immature tropical swards, mature tropical grasses and mature tropical legumes (mean values 9.4, 11.3 and 12.0 h/day respectively). Unfortunately, no details of canopy structure were given. Campbell *et al.* (1969) (quoted by Vallentine, 1990) concluded that sheep in temperate environments commonly graze for 8-9 hours daily on good pasture, but up to 12 hours when a pasture is overstocked or herbage is otherwise short.

As grazing time increases, more energy is used for activity and less for production, thus the minimum grazing time which results in adequate herbage intake is considered optimum (Vallentine, 1990). Grazing time depends on ease of prehension and generally varies inversely with herbage mass or sward height (Arnold, 1960, 1975; Allden & Whittaker, 1970; Forbes, 1982; Forbes & Coleman, 1985; Penning & Hooper, 1985; Phillips & Leaver, 1986; Burlison, 1987; Penning et al., 1991a). Allden and Whittacker (1970) reported that grazing time increased rapidly with a decline in herbage mass below 1000 kg DM/ha. Wadsworth (quoted by Forbes et al., 1985) found a significant quadratic relationship between grazing time and herbage mass in sheep, with short grazing times at both low and high herbage masses. A similar guadratic function was found by Hendricksen and Minson (1980) for the regression of grazing time by cattle on the yield of leaf of a tropical legume. Penning et al. (1991a) showed a fall of grazing time with an increase of sward height and predicted a minimum grazing time of 507 min at sward heights of more than 120 mm, and at this value animals would have a maximum ruminating time of 420 min. On particularly short or sparse swards, however, grazing time may start to decline because animals appear to have partly "given up" (Arnold, 1964; Chacon & Stobbs, 1976; Hendricksen & Minson, 1980; Penning et al., 1991a). This hypothesis seems to be logical, because if energy expended to harvest herbage is greater than the net energy harvested, then the best strategy to conserve energy would be to stop grazing (Stephens & Krebs, 1986; Penning et al., 1991a). Forbes (1982) found that grazing time for sheep was negatively related to the leaf content of the sward.

Extension of grazing time has been considered to be the most likely

compensatory response of the grazing animal to a decrease in bite weight (Freer, 1981), unless the sward is too short (Arnold, 1964). However, this compensation is seldom adequate to prevent a fall in daily intake (Hodgson, 1986).

#### 2.4.2.1.5 Total daily bites

The total number of harvesting bites taken in a day may be measured directly (by automatic recorder) or estimated either from the product of bite rate and grazing time, or from daily intake divided by an independently-derived estimate of bite weight.

There is some uncertainty as to the upper limit to total daily bites. On a temperate sown sward, grazing sheep may take between 10,000 and 78,000 bites per day, and grazing cows may take between 8,000 and 36,000 (Hodgson, 1986) or up to 43,000 (Zoby & Homes, 1983). Burlison (1987) reported that daily bites of sheep ranged from 16,700 to 54,000 with highly significant differences between herbages and between experimental periods within herbages, and tended to increase as a sward was grazed down. Derived values from the trial of Penning *et al.* (1991a) were 25632-51285, varying with sward height. On temperate indigenous swards, Forbes (1982) recorded total daily bites ranging from 20,000 to 49,000 for sheep and from 27,000 to 46,000 for cattle on the same plots. However, Stobbs (1973a, 1974a, 1975a) and Stobbs and Hutton (1974) stated that cows on tropical swards rarely exceed 36,000 bites per day.

The response in total daily bites to changes in sward canopy structure will obviously reflect the combined responses of bite rate and grazing time. Thus there may be a negative relationship between total daily bites and sward height or herbage mass, as in the work of Jamieson and Hodgson (1979b), or alternatively the total daily bites may increase up to a certain sward height or herbage mass and subsequently decline, as in the work of Chacon and Stobbs (1976).

#### 2.4.2.1.6 Daily herbage intake

Daily herbage intake is the net result of the ingestive behaviour variables outlined in Sections 2.4.2.1.1–2.4.2.1.5 and influences animal performance. The level of daily herbage intake is principally determined by the bite weight (2.4.2.1.1).

The daily herbage intake may be derived from the relationship:

daily intake = bite weight x biting rate x daily grazing time (Hancock, 1952),

or estimated independently using other approaches. These approaches involve three techniques:

- animal-based techniques such as those relying on the faeces output/diet digestibility relationship (Le Du & Penning, 1982);
- (2) assessments of animal performance (Baker, 1982) and
- (3) sward-based techniques (Meijs *et al.*, 1982).

The relative advantages and disadvantages of these different estimations and techniques have been discussed by the authors and other reviewers (Minson, 1983; Hodgson, 1982), and will not be further discussed here.

Burlison (1987) reported that the mean daily herbage intake of sheep varied by a factor of four, from 54.6 g OM/kg LW to 13.1 g OM/kg LW across herbages and grazing periods; the overall trend was to decline as the sward was grazed down, even though there were minor irregularities in response. The work of Penning *et al.* (1991a) showed values between 1.67-2.71 kg OM/ewe/day over the range of sward heights described.

A number of researchers have tried to establish a relationship between daily herbage intake and live weight of animals. Van Dyne *et al.* (1980) reported 1.8% and 2.4% of live weight for cattle and sheep respectively, but 2.2% of live weight for both species was reported by Skiles and Van Dyne (1983). Most estimates of intake for cattle and sheep grazing rangelands of western United States fall within the range of 40 to 90g DM/kg LW<sup>0.75</sup> or from 1 to 2.8% of body weight (Cordova *et al.*, 1978). Animals in thin body condition generally consume more herbage per unit liveweight when other factors are not limiting (Allison, 1985). In studies on Montana winter range, Adams *et al.* (1987) (quoted by Vallentine, 1990) demonstrated that large cows had a higher absolute herbage intake, but a lower intake per unit of liveweight than small cows. Leaver (1985) considered that even high-yielding cows normally consume less than 3% of live weight. Forbes and Hodgson (1985) estimated mean daily intakes of over 4% of live weight for mature, non-lactating sheep and cattle, but they considered that such values were either overestimated or a temporary phenomenon, reflecting the management used.

Positive relationships between daily herbage intake and herbage mass or sward

height have been found in numerous experiments (Arnold & Dudzinski, 1966, 1967a & b, 1969, 1978; Chacon & Stobbs, 1976; Hodgson *et al.*, 1977; Hodgson & Milne, 1978; Hendricksen & Minson, 1980; Baker *et al.*, 1981a & b; Forbes & Coleman, 1985; Forbes & Hodgson, 1985; Penning & Hooper, 1985; Burlison, 1987; Penning *et al.*, 1991a). This is apparently because of the positive relationship between sward height or herbage mass and bite weight which is a major determinant of daily herbage intake. Penning *et al.* (1991a) predicted an asymptotic relationship between sward height and daily herbage intake, in which maximum intake would be 35 g/kg LW, and animals on 60 mm height of sward would achieve 0.98 of the asymptotic value.

In addition, Arnold and Dudzinski (1969, 1978) found that daily herbage intake is associated with an increase in leaf density, and sheep grazing pastures with the same leaf length had higher daily herbage intake when the swards were denser. As in the case of bite weight, for cattle grazing swards of tropical legume (Hendricksen & Minson, 1980) or tropical grass (Chacon & Stobbs, 1976), the mass and proportion of green leaf had a strong influence on daily herbage intake.

# 2.4.2.2 Components of bite dimensions

Bite dimensions consist of bite depth, bite area and bite volume (Burlison, 1987).

Bite dimensions had not been systematically and critically investigated in grazing experiments and little was known about these measurements until Black and Kenny (1984) examined them with artificial swards. Following Black and Kenny's work, bite dimensions have been examined in more detail by a number of scientists (Burlison, 1987; Mursan *et al.*, 1989; Burlison *et al.*, 1991; Betteridge 1991; Mitchell *et al.*, 1991; Mitchell, 1993; Ungar *et al.*, 1991; Laca *et al.*, 1992a). The requirement, however, is to establish a quantitative relationship between bite weight and bulk density through the variables of bite dimensions, since by definition, bite weight may be viewed as the product of bite volume (depth x area) and bulk density of herbage within the sward horizons encompassed in a bite (Hodgson, 1985). This provides a basis for understanding the effects of plant morphology and sward structure on bite weight in terms of variation in the physical dimensions of individual bites of herbage, and in the bulk density of herbage within the volume occupied at a bite (Hodgson, 1985). Hence, bite dimensions are the behavioural characteristics causally linking sward structure and

intake (Ungar *et al.*, 1991). The interrelationships between bite dimensions and other components of ingestive behaviour and herbage intake are shown in Fig. 2.2 (Burlison, 1987; Hodgson, 1990).

This view would be helpful in explaining the positive relationship, as reviewed before, between bite weight and herbage density observed in tropical swards (Stobbs, 1973a & b; Chacon & Stobbs, 1976). However, the limitation and the extent to which it can be applied must be born in mind. The relationship between bite weight, bulk density and bite dimensions is most easily applied in the case of uniform swards in a vegetative or early reproductive stage of growth, in which animals graze largely indiscriminately from the surface strata and where individual bites can be described in terms of relatively simple dimensions (Hodgson, 1985). It requires care in more mature, taller or more complex swards in which animals discriminate actively between different plant species or morphological units and it may be necessary to consider bite dimensions in terms of individual leaves (Hodgson, 1985). In these circumstances measurements of bite area would be unrealistic because of the selective prehension.

#### 2.4.2.2.1 Bite depth

Normally, bite depth may be defined as the depth to which the open mouth of the animal is inserted into the sward (Hughes, 1988). It may be calculated from the difference between the pre-grazing sward surface height and the height of the grazed herbage after one bite has been prehended (Burlison, 1987; Ungar *et al.*, 1991). In terms of this definition, the upper limit to bite depth is the mean pre-grazing sward surface height, and the lower limit (i.e. grazed height or stubble height after grazing) is the mean height of the severed ends of the rooted herbage after a bite is prehended, regardless of whether the herbage was clamped in the animal's mouth at this height or higher up. However, this only covers the situation where the animal grazes from the sward surface down (Burlison, 1987). There are some exceptions in grazing practice. If the animal prehends extremely tall plants from the base or the side, or severs herbage from leaves which do not reach up the sward surface, the

Fig. 2.2 The components of Ingestive behaviour and bite dimensions (after Hodgson, 1990 and Burlison *et al.*, 1991).



The bold-faced boxes indicate the variables which are interested in the current research. The bold-faced arrows denote the relationships which are dealt with in the current research. upper limit to bite depth will be below the sward surface. In this case, it will be more difficult to estimate it accurately. Thus, in extreme selective grazing, bite depth as defined above may not be a meaningful statistic (Burlison, 1987).

Bite depth is not necessarily limited by the dimensions of the buccal cavity, since both sheep and cattle frequently grip long leaves or tillers from the side and tear them off before drawing them into their mouths (Hodgson, 1981a).

Grant and Hodgson (1980) and Hodgson and Forbes (1980), working with a series of contrasting temperate pastures, estimated bite depth in terms of the depth of head insertion into the sward, and found that on a perennial ryegrass (Lolium perenne) sward (surface height approximately 11 cm), both sheep and cattle concentrated their grazing in the top 5 cm of the sward, whereas for a Nardusdominant community (surface height 25-35 cm) sheep tended to graze at a depth of 10-25 cm and cattle at a depth of up to 15 cm. Burlison (1987) visually assessed bite depth, recording the insertion of depth of head as falling within one of five imaginary head depth bands, or approximately along one of the four arbitrary horizontal reference lines making the limits of the bands. She reported that sheep grazed a depth of 1.4-8.4 cm and 1.2-13.1 cm on two grazing occasions respectively, whereas cattle had a smaller maximum bite depth than sheep, even though the median value appeared to be greater overall than sheep. The bite depth measured using an improved cagedgrazing technique (Burlison, 1987; Burlison et al., 1991) was between 1.5-20.6 cm over a range of herbages. Forbes (1982), Milne et al. (1982) and Barthram and Grant (1984) measured grazed depth from several successive bites down the sward profile, instead of the depth of a single bite. However, Forbes (1982) considered that true bite depth was probably measured in his experiment because of the short grazing time allowed (15-20 min), and because of evidence from visual observation. Grazed depth in his research ranged from 0.3 to 14.4 cm at mean leaf lengths of 8.5 and 25.0 cm respectively for cattle, and from 0.3 to 11.9 cm at mean leaf lengths of 10.4 and 31.7 cm respectively for sheep. Betteridge et al. (1991) reported bite depth of cattle varied from 1.7 cm to 18.7 cm with various sward height. Laca et al. (1992) estimated that average bite depth of cattle grazing paspalum (Paspalum dilatatum) and lucerne (Medicago sativa) were 9.7 and 7.2 cm respectively. Wade (1991) found that under paddock grazing, the depth of grazing remained about one third of extended tiller height, irrespective of pregrazing height.

Barthram and Grant (1984) showed that grazing sheep seldom penetrated into the horizons containing pseudostem or dead material, even when herbage intake was severely restricted in consequence. They commented that the pseudostem acts as a barrier to bite depth and the reduction in bite depth is likely to limit bite weight and consequently also the daily herbage intake, because pseudostem is more difficult to gather and grip than leaves, and the force required to harvest pseudostem is likely to be much greater than for leaf (Hughes et al., 1991). However, Burlison et al. (1991) and Laca et al. (1992a) found that bite depth did not appear to be constrained primarily by the presence of pseudostem, even though the presence of dead leaf at the lower levels of the sward might have had some influence. Burlison et al. (1991) reported that bite depth of caged sheep ranged from 1.5-20.6 cm, and these sheep only grazed approximately half of the mean leaf depth. L'Huillier et al. (1986) found that the distribution of grass green leaf determined which strata were grazed. Sheep grazed apparently indiscriminantly at the surface of all swards with a high green leaf content in the upper strata, but the defoliation was largely concentrated in the basal 3 cm of an 18 cm tall sward which had a very high content of dead flowering stem, with green herbage only in the basal stratum.

A number of researchers have reported a positive linear relationship between surface height and bite depth (Milne *et al.*, 1982; Burlison, 1987; Mursan *et al.*, 1989; Laca & Demment, 1990; Burlison *et al.*, 1991; Betteridge *et al.*, 1991; Laca *et al.*, 1992a) and grazed height (Milne *et al.*, 1982; Wade, 1991), with bite depth being the major determinant of intake, and sward surface height being the best predictor of bite depth (Mursan *et al.*, 1989). Little change or reduction in bite depth appears to occur as bulk density increases (Laca & Demment, 1990). However, it has not been possible to determine whether the sheep responded to surface height *per se* or to some related sward attributes or their combination (Burlison *et al.*, 1991).

# 2.4.2.2.2 Bite area

Bite area is the area in a horizontal plane effectively encompassed by a typical bite (Black & Kenney, 1984; Burlison, 1987) and is particularly difficult to measure in grazing situations (Burlison & Hodgson, 1985). It may be directly measured (Burlison, 1987; Burlison *et al.*, 1991), indirectly estimated by dividing bite weight by the herbage mass per unit area when the sward height is fixed (Black & Kenney, 1984), or indirectly

estimated from the relationship between bite weight and bite area through the bulk density of the grazed stratum (Burlison, 1987), i.e.:

Bite area (cm<sup>2</sup>) =  $\frac{\text{bite weight (mg DM)}}{\text{grazed stratum bulk density (mg DM cm<sup>-3</sup>)}} \times \frac{1}{\text{bite depth (cm)}}$ 

However, whether the indirect estimation of bite area can really represent the "true" bite area depends heavily on the density and spatial arrangement of plant parts, and the value on a sparse sward can be far greater than the extent covered by the mouth dimensions (Black & Kenney, 1984).

Laca *et al.* (1993) defined "realised bite area" of cattle as the product of the area encompassed by the mouth gape and sweeps of the tongue. The probability that tillers within that area are captured and severed by the bite, can be actively adjusted by the animal by increasing the area and frequency of tongue sweeps. In hand-constructed swards, Ungar *et al.* (1991) defined bite area as the ratio of the surface area represented by the number of holes (through which leaf blades were threaded) grazed and the number of non-regraze bites. Ungar *et al.* (1991) argued that in order to avoid confusion, it is appropriate to distinguish "biting area" and "bite area". The outer perimeter of grazed plant units defines the "biting area". The area represented by only those plant units that are grazed within the biting area yields the "bite area". Biting area is only synonymous with bite area on swards of homogenous height where there is no slippage.

Little information on bite area and sward factors affecting it was available until 1984. Morris (1969) deduced (quoted by Burlison, 1987) that continuously stocked lambs tended to graze patches of herbage up to an area 16 x 16 cm<sup>2</sup> before moving to a different place in the sward, but this was an estimate of grazed area from a succession of bites rather than bite area. A conceptual model was suggested by Laca *et al.* (1992a) to describe factors controlling bite dimensions; effective bite area of a grazing animal is a result of the interaction of the height of the sward and stiffness of plant units with harvesting behaviour of the animal.

Black and Kenney (1984) first estimated bite area effectively covered by one bite using sheep grazing artificial swards. The values were between 8.6 and 33.0 cm<sup>2</sup>. Burlison (1987, experiment 1) reported that the bite area of sheep derived from the

relationships among bite weight, bulk density of the grazed stratum and bite area, varied from 3 to 358 cm<sup>2</sup>, and commented that this estimation was very crude and should be treated with a certain degree of caution. A further measurement in which "true" bite area was first measured directly (Burlison, 1987, experiment 2; Burlison *et al.*, 1991) with a caged-grazing technique showed values ranging from 9.5 to 35.5 cm<sup>2</sup> across a series of swards. The work of Betteridge *et al.* (1991) showed values of 20.1-56.4 cm<sup>2</sup> for cattle, and indirect estimates by Mursan *et al.* (1989) were 42.40-52.50 cm<sup>2</sup>. Laca *et al.* (1992a) reported that average bite area of cattle grazing paspalum and lucerne were 118 and 84 cm<sup>2</sup>, respectively.

Bite area is directly related to mouth dimensions (Burlison, 1987) within animal species, and can be viewed as the product of incisor breadth and the extent of opening of the mouth (Hughes, 1988; Burlison *et al.*, 1991), even though this relationship can be to some extent mediated by variation in grazing behaviour and depends upon the use of lips and tongue to gather herbage (Hodgson, 1983). For example, cows usually sweep an area of herbage into the mouth with the tongue, whereas sheep are capable of removing individual leaves from a plant (Hodgson, 1982). Cattle are also capable of fine resolution in removing individual components from the sward in some circumstances (Stobbs, 1973a; Hodgson & Grant, 1981). Thus, the extension of the tongue or lips together with the gape area of mouth defines the "total swept area" (Ungar *et al.*, 1991).

On very sparse swards the number of leaves and stems prehended at a bite is probably limited by the maximum bite area (Hodgson, 1985). On dense swards, Hodgson (1985) and Hughes *et al.* (1991) suggested that the number of plant units severed at a bite may be limited by the effort required to sever the herbage. It is suggested that there is a set limit to force expenditure per bite, which may be termed as summit force per bite (Hughes *et al.*, 1991), and this force may be a deciding factor (Hodgson, 1985). This force is affected by the structural strength of the herbage, (Hodgson 1985; Burlison, 1987; Hughes *et al.*, 1991) and may reflect variation in tensile strength and shear force. This issue will not be discussed further. This view predicts that, other attributes being equal, bite area will decrease with increase in the number of plant units per unit area due to the greater force required to sever the herbage. Therefore, on a dense sward, a deeper bite might result in a reduction in bite area (Hughes *et al.*, 1991).

Laca and Demment (1990) showed that bite area is reduced by increasing bulk density but increases as height increases. Burlison *et al.* (1987) ascertained positive relationships between bite area and surface height within individual grass species despite the fact that this relationship was very weak across grass species. This positive relationship suggests that sheep graze long herbage by a scooping action, with a partly horizontal movement of the head, rather than a vertical plucking action. This phenomenon conflicts with the theory of summit force per bite proposed by Hughes *et al.* (1991). Laca *et al.* (1992a) found that bite area of cattle was significantly and predictably affected by sward height and bulk density.

The amplitude and number of tongue sweeps per bite increases in a compensatory fashion as bulk density declines (Laca *et al.*, 1993). The cattle appeared to respond to declining sward density by adjusting the number and amplitude of tongue movements to gather the largest feasible bite cross-section. The larger the density the fewer tongue movements required, and the smaller the reach and bite area (Laca *et al.*, 1992a).

In addition, bite area is far less sensitive to changing sward structure than bite depth (Burlison, 1987). Mursan *et al.* (1989) found that bite area of cattle was not influenced by either sward height or density, and remained constant as sward height increased from 5 to 15 cm and as the bulk density of the grazed horizon decreased from 20.94 to 9.18 mg/cm<sup>3</sup>. Mitchell *et al.* (1991) showed that sward height had little or no effect on bite area, while bulk density had a moderate, negative effect. However, by contrast, Laca and Demment (1990) found that bite area increased quickly with increasing pasture height when bulk density was low, but only very little when bulk density was high. Laca *et al.* (1992a) noticed a slow increment in bite area with increasing sward height for cattle grazing paspalum and lucerne.

#### 2.4.2.2.3 Bite volume

Bite volume is the volume occupied in the sward by the herbage prehended at a bite. Each bite occupies a pasture volume which is assumed to be cylindrical in shape (Ungar & Noy-Meir, 1988). However, no attempt has been made to determine the true shape and dimensions of bite volume. Rather, the definition is reduced to two parameters, depth and area, the product of which is equal to the effective volume of the sward contained in a bite (Ungar *et al.*, 1991). Therefore bite volume may be derived from the product of bite area and bite depth (Burlison, 1987), being viewed as the vertical projection of bite area from the sward surface to the mean depth at which plant material was severed (Mursan *et al.*, 1989). Bite volume may also be obtained by dividing the bite weight by bulk density of the grazed stratum, as Hodgson (1981a and b) pointed out that where variation in bulk density is small, changes in bite weight must reflect changes in bite volume.

Black and Kenney (1984) reported that values of bite volume ranged 11-471 cm<sup>3</sup> for sheep, compared to 11-1083 cm<sup>3</sup> for sheep derived by Burlison (1987) which were very variable across herbages and grazing periods, 22-612 cm<sup>3</sup> for cattle observed by Betteridge *et al.* (1991), 103-388 cm<sup>3</sup> for cattle estimated by Mursan et el. (1989), and 656-1209 cm<sup>3</sup> for cattle measured by Laca *et al.* (1992a). The general trend in Burlison's experiment (1987) was that bite volume declined as the sward was grazed down. In the second experiment of Burlison's work (Burlison *et al.*, 1991) where the cage-grazing technique was used, bite volume ranged from 20 to 428 cm<sup>3</sup>. The studies of Black & Kenney (1984), Mursan *et al.* (1989), Burlison *et al.* (1991) and Betteridge *et al.* (1991) all indicated a positive relationship between bite volume and sward surface height, but a decline of bite volume as mean sward bulk density increases was only observed by Black and Kenney (1984). Mursan *et al.* (1989), Mursan *et al.* (1989) found a three-fold increase in bite volume due entirely to an increase in bite depth, whereas bite area remained constant.

# 2.4.2.3 Overall response patterns and compensatory changes in ingestive behaviour variables

The variables of ingestive behaviour have been individually reviewed so far. However, it is helpful to consider their combined effects which eventually determine daily herbage intake.

Bite weight is the primary animal response as sward conditions diminish. For example, if sward height or herbage mass declines, bite weight is the variable most directly influenced, and normally falls sharply, and consequently short-term rate of intake is negatively affected. However, animals usually tend to have a higher biting rate with declining bite weight to maintain intake rate, but the rate of increase is seldom fast enough to compensate. Therefore, an associated decline of short-term rate of intake occurs (Allden & Whittaker, 1970; Hodgson, 1981b; Penning *et al.*,

1991a). Increase in biting rate has been seen as a compensatory response by the animal to prevent the decline of intake rate, but it appears to be due primarily to a reduction in the number of manipulative jaw movements and to an increase in prehending movements with declining sward height, and consequently total jaw movements per unit time remain constant (Penning *et al.*, 1991a). The variation in biting rate should therefore be considered as a direct effect of variation in sward conditions (Hodgson, 1985).

When biting rate alone cannot fully compensate and intake rate is still low, grazing time is extended. The most readily apparent adaptive response to the decline of bite weight is the increase in grazing time which usually occurs when the rate of intake declines (Freer, 1981) and is generally considered to be a compensatory mechanism. However, the degree of compensation is again inadequate to offset the decline of intake rate and grazing time declines on particularly short swards, thus reinforcing the negative effect exerted by the depression of bite weight. Therefore, variations in daily herbage intake frequently reflect closely the observed variations in bite weight (Hodgson, 1985).

Bite weight varies to a far greater extent than either biting rate or grazing time with sward changes. Jamieson and Hodgson (1979a) found that the daily herbage intake of calves fell by 24% over a six week period as a response to reduction in herbage mass and sward height; this decline was accompanied by a 50% fall in bite weight, a 22% rise in bite rate and a 14% increase in grazing time. In the same research, a 39% fall in daily herbage intake of lambs was a net result of a 65% fall in bite weight and increases of 21% and 23% for bite rate and grazing time respectively.

# 2.4.3 Summary

Bite weight is the most important determinant of daily herbage intake. Compensatory increases in biting rate and grazing time to offset the decline of bite weight induced by sward restrictions are limited, and consequently, intake rate and daily herbage intake are depressed. Bite weight also is the most important behavioural variable of grazing animals responding to changing sward conditions.

Bite weight has been linearly and positively related to sward surface height, herbage mass and bulk density and leaf proportion. The relationships between bite weight and surface height and herbage mass have been mainly found on temperate swards, whereas those between bite weight and bulk density and leaf content have been only observed on tropical swards.

Of the components of bite dimensions, bite depth appears to be positively related to sward surface height, and to make a far greater contribution to bite volume, and hence bite weight, than does bite area. Bite depth may be restricted by barriers of pseudostem and dead material in short swards. The information on bite area and bite volume is relatively scarce. However, recent research has suggested that on sparse swards, the number of plant units prehended at a bite is likely to be restricted by the mouth area (incisor breadth x maximum open size of mouth), whereas on dense swards, the limiting factor may be the maximum force required to tear herbage off (summit force per bite).

## 2.5 SWARD ATTRIBUTES AFFECTING INGESTIVE BEHAVIOUR

In this section, attention is focused on the influences of sward attributes on ingestive behaviour. The sward factors influencing diet selection and grazing discrimination will not be considered here since these are outside of the scope of the thesis.

Ingestive behaviour and hence herbage intake are sensitive to a range of sward attributes. However, it has proved difficult under grazing conditions to isolate the independent influence of a particular sward characteristic from other structural and quality characteristics of the sward because many of them tend to change concomitantly and to associate with one another (Hodgson, 1985, 1990). But the accumulated evidence has shown that some variables exert a dominant and crucial influence in this process and are thus more important than others.

Under reasonably uniform conditions the complex of sward characteristics can be reduced to two components (Hodgson, 1990): herbage mass (quantity of sward) and surface height. The latter is one attribute of canopy structure. Quality of sward (digestibility) in some cases also has a large effect in this process. Therefore, under this heading, herbage mass will be discussed first, and then followed by consideration of a range of physical structural attributes of the sward canopy. The quality of the sward will be touched on briefly.

#### 2.5.1 Herbage mass

### 2.5.1.1 Concept

The weight of plant material above ground level can be derived in various terms, but it is best termed herbage mass (Hodgson, 1979) or biomass (Thomas, 1980) which is defined as an instantaneous measure of the total weight of herbage dry matter (DM) per unit area of ground (usually expressed in kilograms per hectare), preferably measured to ground level.

Some alternative terms, like herbage available and availability, have been used to describe the amount of herbage on offer (Arnold, 1964), or to refer to the quantity and distribution of herbage mass in space affecting intake rate through the mechanism of food-gathering (Ungar & Noy-Meir, 1988). Hodgson (1979) commented that in current usage they mean simply the herbage mass as defined above, with some arbitrary reference base, in which case the terms are unnecessary and confusing and should be avoided. Herbage yield is not an acceptable alternative either, and is better avoided altogether (Hodgson, 1979).

Herbage allowance is another term which has been commonly used to describe the amount of herbage allocated per animal per day (kg OM/animal /day) (Greenhalgh, 1966) or per unit live weight of animal at a point in time (kg OM/kg LW) (Hodgson, 1979), or per unit live weight of animal per day (OM/kg LW /day) (Sheath *et al.*, 1987).

Herbage mass indicates the amount of herbage present above ground per unit area of land. Compared to herbage mass, herbage allowance only implies a managerial decision without a clear indication of the amount of herbage and its distribution within the sward (Rodriquez Capriles, 1973). It gives a better impression of the balance between demand and supply (Hodgson, 1979) and acts effectively as a rationing process (Hodgson, 1990).

However, there has been lack of unanimity in the literature concerning the relative importance of herbage mass and herbage allowance (Greenhalgh, 1967; Hodgson & Wilkinson, 1968; Rodriquez Capriles, 1973). In a comparative study using sheep to assess the relative importance of herbage mass and herbage allowance, Hodgson and Milne (1978) concluded that herbage weight per unit area is more closely related to herbage intake than herbage weight per animal, but herbage weight per animal probably exerted an effect through its influence on the rate of change of herbage weight per unit area during a grazing period.

In this review both terms are used in accordance with the literature source, but in the experiment, only herbage mass was considered.

# 2.5.1.2 Effect of herbage mass and herbage allowance on ingestive behaviour

Herbage intake has variously been shown to be affected by variations in herbage mass (Poppi *et al.*, 1987), and by variations in herbage allowance, in cattle (Greenhalgh *et al.*, 1966; Combellas & Hodgson,1979; Le Du *et al.*, 1979) and sheep (Rattray *et al.*, 1987). The relationship between herbage intake and herbage mass has been commonly described as asymptotic (Allden, 1962; Arnold & Dudzinski,1967a), with intake declining at an increasing rate below a critical mass which has been found to vary between experiments from approximately 1,100 to 4,000 kg DM/ha for sheep and from 1,100 to 2,800 kg DM/ha for cattle, though there is marked variation in the pattern of response observed in individual studies (Allden & Whittaker,1970; Arnold & Dudzinski,1967a; Hodgson,1977). Forbes and Coleman (1987) found that herbage intake of cattle approached maximum values at approximately 5,000 kg DM/ha. It was suggested (Hodgson & Milne,1978) that other variables such as sward height, leaf/stem ratio or herbage density may modify the overall relationship between intake and herbage mass, thus leading to the variation in the critical mass that has been found.

The relationship between herbage intake and herbage mass is similar under continuous stocking and rotational grazing managements (Hodgson, 1975).

Under rotational grazing management, herbage intake has often been related to variations in the daily allowance of herbage. It has been suggested (Hodgson, 1990) that herbage intake increases at a declining rate with increasing allowance, usually reaching a plateau at a daily DM allowance equal to 10-12 per cent of the animal's body-weight for most classes of stock. The basic relationship between daily herbage allowance and herbage intake under strip- or paddock-grazing management appears to be similar to the asymptotic curve between herbage mass and herbage intake and herbage intake appears to approach the maximum only at levels of daily herbage allowance equivalent to four times the amount eaten (Hodgson, 1975). Intake only starts to decline markedly when the allowance is less than twice intake and declines rapidly when the allowance falls below 40 g OM/kg LW/day (Hodgson, 1975). This is

supported by a recent study on allowance-intake relations of cattle grazing vegetative tall fescue (Dougherty *et al.*, 1992). However, the work of Dougherty *et al.* (1992) does not support the concept that intake approaches a maximum when allowance is three to four times intake.

There seems to be general agreement that variations in herbage mass or herbage allowance exert a major influence on bite weight, and also have some effect on biting rate and grazing time (Stobbs, 1973a & b, Jamieson & Hodgson, 1979a & b). Minson (1983) concluded that animals generally have no difficulty in satisfying their appetites, provided the herbage mass is between 1,000 and 1,500 kg DM/ha, but when herbage mass falls below 1,000 kg DM/ha, bite weight will be reduced below the critical value of 300 mg OM. However, in a model describing grazing behaviour where bite weight was held constant and herbage mass was varied by increasing ground cover of a sward with constant height and density, Laca and Demment (1990) found that herbage mass in itself does not affect intake rate of cattle, but some of its components (height and density) do and this aspect will be detailed in the corresponding sections.

Jamieson and Hodgson (1979a) reported that with a reduction in herbage allowance, the intake of strip-grazed calves was depressed as a result of roughly similar reductions in bite weight, bite rate and grazing time, and they attributed this response to the increasing difficulty of prehending and ingesting herbage as swards were grazed down (Hodgson, 1975). Subsequently, Jamieson and Hodgson (1979b) found that as herbage mass was progressively reduced, both biting rate and grazing time increased , but insufficiently to offset the rapid fall in bite weight so that as a consequence, herbage intake declined for both calves and lambs respectively.

Research with sheep, cattle and goats showed that relative rate of decline of herbage intake (per Kg LW<sup>0.75</sup>) with decreasing herbage mass is also associated with the rate of disappearance of herbage mass (Collins & Nicol, 1986). The difference in herbage intake by goats, sheep and cattle was greater when the herbage mass was being slowly depleted than when it was depleted rapidly. However, the relationship between herbage mass and herbage intake depends not only on the absolute amount of herbage available, but also on the amount of effective herbage mass present. For example, when herbage mass is augmented by increasing amount of non-preferred herbage, this will result in an increase in searching time and reduce the intake rate

(Laca & Demment, 1990).

In terms of the evidence outlined above, the influences of herbage mass and herbage allowance on herbage intake of various stock classes are certainly important. However, the shapes of the general relationships between herbage mass and herbage intake, and between herbage allowance and intake found in the various studies may be modified by the structural and quality features of the herbage consumed, giving rise to a marked variation in the pattern of response ascertained in various circumstances (Hodgson, 1977). The variation between studies may reflect partly the confounding effect of concomitant changes in the quality of the herbage (Hodgson, 1977) and partly the effects imposed by the characteristics of the sward canopy structure. Additionally, response of herbage intake to variations in herbage mass depends strongly on what components (height and density) of herbage mass vary. Thus, there will undoubtedly be a need to outline the effects exerted by the canopy structure and quality of the herbage in order to understand thoroughly the relationship between herbage intake and related factors.

# 2.5.2 Sward canopy structure

#### 2.5.2.1 Concept

A sward is defined as the above- and below-ground parts of a population of herbaceous plants, characterized by a relatively short habit of growth and relatively continuous ground cover (Hodgson,1979). Sward canopy structure is defined as the distribution of, arrangement of, and interrelationships between the various components of the canopy (Thomas, 1980). The term "sward canopy structure" used in this thesis carries with it connotations of the spatial arrangement and proportions of the various components of the plant and it includes bulk density, tiller (stolon) density, surface height, stem height, depth of leaf layer, proportion of seedhead/leaf/stem and live/dead components and vertical distribution of these categories.

# 2.5.2.2 Effects of sward canopy structure on ingestive behaviour

The physical structure of the sward canopy can exert a direct effect upon the herbage intake of grazing animals, quite apart from the influence of the chemical composition and nutrient content of the herbage itself (Hodgson, 1990).

Although it is not always easy under grazing conditions to disentangle the

independent effect of an individual structural attribute on ingestive behaviour from other confounding attributes (for example, height frequently confounds density), recent studies (Black & Kenney, 1984; Burlison, 1987; Laca & Demment, 1990; Burlison *et al.*, 1991; Mitchell *et al.*,1991; Laca *et al.*, 1992a) have been able to consider the separate effects of some sward features on ingestive behaviour and herbage intake by careful control of grazed swards. Therefore, the effects of structural attributes will be reviewed on the individual basis, but their interactions will also be considered.

#### 2.5.2.2.1 Height

There are numerous interpretations as to what constitutes canopy height or sward height (Rhodes, 1981). Conventionally, sward surface height is the average height of uppermost leaves in an undisturbed sward canopy (Hodgson, 1990). Occasionally, the measurements are made of the extended height of leaves or tillers (Hodgson *et al.*, 1971; Wade, 1991). Tiller length (Allden & Whittaker, 1970) and height index (Spedding & Large, 1957) are two alternatives of the height measurement used in some previous experiments. Tiller length is the measurement from the base of a tiller to the tip of the longest leaf (Allden & Whittaker, 1970), whereas the height index relates height to the distribution of density, and is determined by a point-quadrat method (Spedding & Large, 1957). In this review, the undisturbed height is used unless an alternative is specified.

Animals respond more consistently to variations in sward height than in herbage mass, and height is more easily measured than herbage mass (Hodgson, 1990). However, variation in mass and in surface height are often closely correlated although the relationships change with seasons, and tend to influence intake in the same way (Hodgson, 1981a).

A number of detailed studies have shown that the surface height of the undisturbed sward is the primary variable influencing intake (Hodgson *et al.*, 1986; Forbes, 1988). The surface height probably is the best simple variable for predicting both animal and sward responses (Hodgson, 1981a & b) and appears to be the most useful indicator for management purposes so far (Maxwell, 1986). Management of pastures based on sward height has received a great deal of attention (Hodgson *et al.*, 1986).

Under continuous stocking management, herbage intake may also be

asymptotically related to sward height (Penning & Hooper, 1985; Penning *et al.*, 1991a). The point at which intake approaches the maximum can be regarded as the critical height. There is little point in providing taller swards than this height, because further increases will not improve intake and will result in a reduction in digestibility, ultimately counterbalancing some of the potential advantages of the increased height (Hodgson, 1990).

The critical height is important in characterizing patterns of animal response, but it has been found to vary quite substantially in various experiments. Arnold (1964) found that the maximum intake of grazing sheep was achieved at a sward height of 8 cm. Allden and Whittaker (1970) observed a rapid increase in dry matter intake by grazing sheep (lambs and yearlings) with increasing tiller length up to 15 cm, thereafter little change in intake occurred. Penning *et al.* (1991a) recommended that optimum sward surface height for continuously stocked swards grazed by sheep would be between 3-6 cm. Hodgson (1990) summarized the critical values (Table 2.1). Under continuous stocking management, herbage intake may be expected to start to decline when the surface height of the sward falls below 8-10 cm for grazing cattle and 6-7 cm for sheep.

On the other hand, a description of the stubble height remaining after grazing can also be used to assess the impact on herbage intake, particularly under rotational grazing management (Hodgson, 1990). Critical stubble heights under rotational management are similar to the critical surface heights for continuously stocked swards (Hodgson, 1990).

Variation in critical height is probably due in part to accompanying changes in other sward characteristics, particularly sward maturity, and in part to differences in the response of different stock classes (Hodgson, 1990). The associated change in maturity as sward height increases normally results in a decline in digestibility of the herbage eaten (Hodgson, 1990), and a decline in sward surface density (Forbes, 1988), both tending to limit herbage intake. Hodgson (1990) pointed out that herbage intake increases to a greater extent with sward height increase where changes in digestibility are controlled as opposed to where they are not.

Table 2.1Critical values of pre-grazing height on ryegrass dominant swards<br/>required to maintain levels of herbage intake and animal performance<br/>close to maximum (from Hodgson, 1990).

Stock classes and management	Critical value (cm)
Continuous stocking	
Ewes and lambs :	
Spring	4-5
Summer	7-8
Beef cows and calves	9-10
Weaned calves	9-10
Dairy cows	9-10
Rotational grazing	
Ewes and lambs	6-7
Cows and calves	9-10
Weaned calves	11-12
Dairy cows	9-10

Laca & Demment (1990) examined the independent effect of some confounding variables on ingestive behaviour by having consistent herbage mass, and then either varying sward height at a single level of digestibility or varying digestibility at a constant height, or obtaining the different combinations of height and digestibility in the pasture. Variation in both height and digestibility, either with no correlation or with a positive correlation, resulted in a greater change in digestible dry matter intake rate than with variation in either factor alone, but a negative correlation between height and digestibility could effectively remove the opportunity to obtain better bites than average. This negative correlation is the rule in natural grasslands, and is the result of selective grazing and plant maturation. A positive correlation is the goal of management in grazed swards, but a more infrequent situation. The authors suggested that this model can be used to explain why animals prefer to overgraze patches of low herbage mass and high quality while ignoring high mass patches of mature and rank pasture. But in the field grazing, contamination of dung/urine is also a factor affecting this selection. Variation in height at a single level of herbage mass has an important effect on digestible dry matter intake rate, particularly on swards that on average are short.

Taller swards allow a constant high digestible dry matter intake rate in absolute terms. There is a lack of response on taller swards as a result of the asymptotic response of bite dimensions to sward height (Laca & Demment, 1990).

Sward height exerts its influence on herbage intake mainly through bite weight. As noted earlier, where variation in herbage bulk density is small, the effect of sward height on bite weight must act principally on bite volume, whereas bite volume is strongly influenced by sward height through its primary effect on bite depth with deeper bites resulting in greater bite volume.

In temperate swards, bite weight and rate of herbage intake have been found to be positively and linearly or asymptotically (Allden & Whittaker, 1970; Forbes, 1982; Penning, 1986) or quadratically (Penning *et al.*, 1991a) related to sward height for various classes of stock.

The relationship between bite weight and sward height is not always positive (Hodgson, 1981a). There is less certainty in the case of rotationally-grazed swards where fluctuations in sward variables and in the associations between the variables are greater, but in this case, sward height still can be used as a first approximation to define animal responses (Barker et al. 1981b). Forbes (1988) commented that in swards with a tall flower canopy, bite weight increases initially with increasing sward surface height, until the appearance of a flower horizon, whereupon it declines. In particular, this positive relationship is not the case with tropical swards where Stobbs and his co-workers (Stobbs, 1973a & b, 1975a & b; Chacon & Stobbs, 1976) found several cases of negative rather than positive relationships between the two variables. These authors ascribed this to the low density within the top stratum in tall swards, and this effect will be discussed later this chapter. Forbes and Coleman (1987) also found that green herbage mass in warm-season grasses has more influence on bite weight and herbage intake than does sward height. Waite et al. (1950) (quoted by Rodriguez Capriles, 1973) reported a negative relationship between sward height and herbage intake for the temperate swards in which the intake of grazing cattle decreased when the sward height was increased from 10.16-12.74 cm to 22.86 cm. There was no explanation given for this fall in intake, but it is likely to have been associated with decreased digestibility rather than increased in sward height (Rodriguez Capriles, 1973), because the longest swards were also stemmy (Burlison, 1987).

When comparing results obtained by different researchers, allowance must be

made for differences in measurement techniques (Forbes, 1988), because the pattern of response to variations in sward height may also depend on the way in which height is measured (Hodgson, 1981a). If measurements are made of the extended height of leaves or tillers, the relationship may be quadratic, with intake declining on either side of an optimum extended height (Hodgson, 1981a). The increasing phase with increasing height is description of the positive linear relationships found in temperate swards, even though the declining phase may be observed on particularly long herbage as described by Waite *et al.* (1950) (quoted by Rodriquez Capriles, 1973), and intake may be maximized at an extended sward height of 40-45 cm (Hodgson *et al.*, 1977). The declining phase with increasing height is more common in tall-growing tropical swards as postulated by Stobbs (1973a & b), and probably is demonstrated most dramatically in the case of the trailing tropical legumes (Stobbs & Hutton 1974).

#### 2.5.2.2.2 Density

The bulk density of herbage within the sward refers to the herbage weight per unit volume, and normally expressed as mg DM/cm<sup>3</sup>, whereas population density is defined as number of plant units per unit area. Both terms may be used in descriptions of sward characteristics. The influence of bulk density on intake, either in the sward as a whole or within individual sward horizons, has been described by Spedding and Large (1957), Chacon and Stobbs (1976), Chacon *et al.* (1978), Hodgson (1981b). It would appear that bulk density exerts an influence upon bite weight, and thus rate of intake.

A series of studies conducted in tropical swards by Stobbs and his co-workers has shown that bulk density is one of the most important attributes in tropical swards influencing bite weight. The bulk density, or leaf bulk density or bulk density of green material (leaf and stem) all have significant positive effects on bite weight in grazing cattle (Stobbs, 1973a & b, 1975a & b; Chacon & Stobbs, 1976; Chacon *et al.*, 1978). Stobbs (1973b) demonstrated that a high density of leaf within the sward (sward leaf density) as well as a low stem content were considered to be the main factors affecting bite weight. Stobbs (1973b) interpreted this relationship as indicating that prehension of large bites is likely to be more difficult on tropical pasture than temperate swards due to low sward bulk density and higher stem component in mature swards, and that animals were selecting mainly leaf from this actively growing fraction of the sward.

Stobbs (1975b) further confirmed that swards which had the highest leaf bulk density and the highest leaf yields allowed the largest bites to be prehended. Two further experiments (Chacon & Stobbs, 1976) showed that bite weight was largely determined by bulk density of green material (leaf and stem), together with leaf yield and leaf to stem ratio, together with nutritive value of the herbage consumed (Chacon *et al.*, 1978). Unfortunately, these studies failed to separate the bulk density effect from other associated effects, such as those of leaf to stem ratio and leaf yield. It is not easy to isolate those variables from one another, particularly under natural conditions, so it is quite likely that the relationship between bulk density and bite weight was confounded.

In contrast, it has been shown in some experiments on temperate swards that bite weight and short term rate of herbage intake are not sensitive to variation in the bulk density of herbage within the grazed stratum (Hodgson, 1981b). This is not easy to understand, but it might simply reflect the dominant influence of height in circumstances where it is difficult to obtain independent variation in height and density. Mursan et al. (1989) and Betteridge et al. (1991) showed that the largest bite volume and bite weight occurred in the longest turf (15 cm) which had the lowest bulk density in the grazed stratum. But Burlison et al. (1991) found that bite weight was positively and directly related not only to height, but also to density of the grazed stratum in a series of swards in which independent variation in height and bulk density was achieved. Black and Kenney (1984) also found that the rate of intake by sheep grazing pasture in which height and density were varied independently, increased with both and was best described by herbage mass per unit area effectively covered by one bite. A functional response model recently developed by Laca and Demment (1990) showed a clear pattern of change in bite weight with different components (height and density) of herbage mass: as height increases, both bite area and depth increase so bite weight and intake rate increase steeply, but when bulk density increases alone, bite area is reduced in a compensatory fashion, with little change or reduction in bite volume which eventually counteracts the greater density of forage prehended. Thus the authors (Laca & Demment, 1990) concluded that animals can obtain larger bites from tall sparse swards than from short dense swards of the same overall herbage mass, and larger bites translate into greater intake rate, thus greater daily herbage intake. Another model developed by Laca & Demment (1990) in the same research programme indicated that although DDMIR (digestible dry matter intake rate)

responded to variation in bulk density, the response was less than half of that shown for height, since animals cannot profit as much from the increments in bulk density as from increments in sward height. Laca (1991, quoted by Ungar *et al.* (1991)) showed that increasing bulk density tended to reduce bite depth and bite area on tall swards, but there was no apparent effect at heights less than 10 cm.

In summary, some generalizations may be drawn from the evidence outlined above, even though some contradictory results are apparent and have not been fully resolved. Results from temperate swards suggest that height is the dominant sward variable and manipulation of sward height to alter herbage intake is the most ubiquitous pasture management tool the farmer uses. In tropical swards, in contrast, variations in herbage density apparently have a greater influence on herbage intake than does sward height, and particular importance is attached to parameters reflecting leaf density or leaf to stem ratio. In explaining these differences between tropical and temperate swards, it is recognized that tropical swards generally have a lower bulk density and higher stem content than temperate swards (Stobbs, 1973b, 1975a). A comparison of sward conditions in the major tropical and temperate experiments investigating bite weight in cattle (Hodgson, 1983) indicated only slight differences in most canopy structure variables, except that the bulk density of green leaf in the surface stratum of the tropical swards was on average only about half that of the temperate sown swards. This might explain the importance of the leafiness and density variables in tropical swards (Stobbs 1973a & b). However, it is uncertain whether the differences observed from the various experiments are absolute or simply artifacts of the experimental protocol (Forbes, 1988), reflect fundamental differences between temperate and tropical swards, or reflect conditions at opposite ends of a continuous spectrum of response to variations in sward structure (Hodgson, 1981a). To better understand these and other differences in response, it will be necessary to design and conduct highly controlled trials which allow a greater degree of both sward and animal manipulation than has been attempted in the past (Forbes, 1988).

# 2.5.2.2.3 Other sward attributes

Other sward characteristics may override the influences exerted by height and density under particular circumstances. A description of the distribution and proportion of various plant components within the sward canopy, and particularly their association

with short-term observations of ingestive behaviour within specified sward strata (Stobbs, 1973b) provides a means of rationalizing some of the inconsistent intake response to variations in herbage mass, sward height or density outlined earlier, and of improving the objectivity of studies on herbage intake (Hodgson, 1981a).

In pastures containing more than one plant species, the situation is further complicated. Botanical composition of the pasture can modify herbage intake through affecting selective grazing, and the extent of this effect is primarily related to stock classes. It was reported by Illius *et al.* (1992) that patch selection and herbage intake by sheep is influenced by clover content and sward height. Goats have higher forage intakes in mixed pasture containing a substantial proportion of shrubs and weeds (Lambert, 1988; McCall & Lambert, 1987).

Animals have been shown to have higher intakes when grazing legume monoculture or grass/legume mixtures compared with monocultures of grass (Thomson, 1979; 1984; Gibb & Treacher, 1983, 1984). Penning *et al.* (1991b) found that mean bite weight of sheep grazing clover was 48% higher than that of sheep grazing grass, but biting rate was similar for both swards, leading to a higher intake rate of clover than grass; however, daily grazing time was 42% greater for grass than for clover, resulting in similar daily intakes for both swards. Dougherty *et al.* (1989a) found that lucerne swards permitted cattle to prehend larger bite weights at slower rates than did tall fescue swards, leading to higher intake rates of lucerne than tall fescue (*Fescuca arundinacea* cv. Kentucky 31). Kenney and Black (1986) using artificial swards grazed by sheep showed that sheep ate subterranean clover (*Trifolium subterraneum*) four times faster than grass swards. These findings demonstrate that the animals are able to obtain greater intake rates from legumes than grasses.

The presence of thorns and spines on some species has been shown to restrict bite weight, particularly for larger animal species, with bites often being limited to individual leaves or leaf clusters. In particular, the hooked thorns of certain species tend to slow down biting rates by catching on the lips, tongues or ears of grazing animals (Vallentine, 1990).

Grazing animals not only select different plant species but also the more leafy parts of those plants (Poppi *et al.*, 1987). Therefore, the proportion of various herbage components in the pasture, particularly the amounts of leafy parts and live material, would be expected to influence the ease with which herbage is removed and this has been shown by a series of studies conducted in the tropical swards (Stobbs, 1973a & b, 1975b; Chacon & Stobbs, 1976; Chacon *et al.*, 1978).

Under some conditions, intake may be limited primarily by the rate at which green herbage, of generally good quality but low availability, can be found and prehended (Ungar & Noy-Meir, 1988). The studies on Lehmann lovegrass in Arizona (Vallentine, 1990) showed that green tiller height and amount of dead material interacted to influence cattle grazing pattern and ingestive behaviour. High selectivity for limited green material results in difficulty in harvesting enough herbage; sheep may spend 12 hours a day selecting for small green shoots from a bulk of dry pasture and have reduced intake (Arnold & Dudzinski, 1978). Under both abundant and limited biomass, searching time increased when the palatable new green growth was in short supply. The time spent grazing by cattle on intermediate wheatgrass was inversely related to the mean number of green leaves per tiller (Vallentine, 1990). This suggests that the cattle were selectively grazing green leaves and were spending more time searching for them as they become more limited.

Herbage intake is influenced by not only the amount of leafy or live material present in the pasture, but also the distribution of these various components within the pasture. Animals are presumably more likely to respond to sward conditions in the grazed stratum than to average conditions in the whole sward. It has been shown that bite weight was more closely correlated with leaf yield in the top stratum than with overall leaf yield of the whole sward (Stobbs, 1975b). Kenney and Black (1986) also showed that both intake rate and pasture availability at maximum intake rate depend greatly on the distribution of plant material within the pasture horizons. When sheep grazed artificial pastures of vegetative subterranean clover, where most plant material was in lamina at the top of the sward, intake rate was less affected by pasture height than it was in grass swards (Kenney & Black, 1986). Black and Kenney (1984) attributed most of the variation to the amount of DM that could be prehended in one bite. The relationships between bite weight and bulk density of the grazed stratum were more consistent than those observed from the whole sward (Stobbs, 1973b, 1975b). A higher proportion of total herbage is likely to be carried in the upper horizons in legume pasture than in grass pasture, and this in itself is likely to enhance intake.

Accessibility is another factor affecting herbage intake under grazing conditions.

It was suggested that to some extent herbage intake is higher on an open pasture canopy than a closed one, and this would be explained in terms of greater ease of access in open pasture (Stobbs, 1975b). The recent evidence (Hughes, 1988) suggested that lower proportion of legumes in the diets of goats relative to that on offer may be attributable to poor accessibility of legumes within the sward canopy, rather than to active avoidance.

However, Hodgson (1981b) suggested that the proportion of green material in the grazed horizon did not exert a major influence on rate of intake, particularly if bite depth is assumed to decline progressively as the horizons containing dead material are approached and penetrated. Therefore, it is unlikely that variation in leaf to stem ratio in the grazed stratum would be of any greater importance than variation in green to dead ratio (Hodgson, 1981b). But it is still possible that effects of grazing height on rate of intake may be mediated partially through the animal's response to lower horizons containing stem or dead material (Hodgson, 1981b). The apparent failure of dead material to contribute significantly to herbage intake has also been shown by a number of researchers. Fistulated cattle ate very little dead material provided some green leaf was available (Chacon & Stobbs, 1976; Hendricksen & Minson, 1980). Dead material was also rejected by sheep and goats, as a result of a low preference and inaccessibility in the base of the sward (Hughes *et al.*, 1984), but to a lesser extent by goats than sheep (Clark *et al.*, 1982).

Herbage maturity has seldom been studied as an attribute of pasture canopy structure, although attention has been concentrated on the change of digestibility as herbage matures. There is some evidence for grazing animals having difficulty in harvesting enough mature pasture (long period of regrowth) even though herbage mass is high, because grazing times on such pasture have been excessively long (Stobbs, 1973b). Therefore, pasture maturity has a large effect on ease of prehension and daily herbage intake (Stobbs, 1973b). Stobbs (1973b) also reported that animals grazing more mature swards (6 and 8 weeks regrowth) had a small bite weight despite large increases in herbage mass and bulk density. Therefore, when grazing these mature tropical pastures, much of the advantage of obtaining a high quality diet by selective grazing can be offset by a total intake limitation due to a low bite weight. It is concluded (Stobbs, 1973b) that there is an optimum stage of growth for each pasture species which allows the grazing animal to prehend large bites of herbage. Low mass and inaccessibility of herbage restrict intake at earlier or later stages of regrowth respectively. Forbes (1988) pointed out that the presence of a tall flower canopy restricts bite weight.

In summary, there have been some conflicting results from the various experiments examining the relative importance of the physical variables of sward structure on ingestive behaviour. This has been due in part to the different climate environments in which these studies have been conducted.

#### 2.5.3 Quality of sward

The quality of pasture consumed by grazing animals influences their production level. However, there has been lack of unanimity in the literature on the broadness of the definition, and on the method of assessment of sward quality. Ungar & Noy-Meir (1991) related sward quality to all physical and chemical attributes of the herbage material. It is more usual, however, to associate the quality of the pasture with the level of nutrients in the herbage (e.g. percentage of protein or fibre) and/or the digestibility. It has been generally agreed that the most important single indicator of nutritive value of the consumed diet is digestibility (Ulyatt, 1973), and this is a major nutritional factor influencing herbage intake.

Digestibility is defined as the proportion of the feed which is absorbed by the animal from the total ingested (Rodriquez Capriles, 1973). It can be measured in a number of ways. It was conventionally expressed as the proportion of dry matter (DM) or organic matter (OM) that the animal digests, namely percentage digestible DM (DDM%) or OM (DOM%), or proportion of gross energy that is digested, namely percentage digestible energy (DE%). All these estimates are usually apparent digestibility, since the denominator includes feed residues and intestinal detritus as well (Hodgson, 1990). An even better measure is the proportion of metabolizable energy (ME) contained in kilogram of DM, in terms of megajoules (MJ ME/kg DM) (Thompson & Poppi, 1990). The metabolizable energy which is available energy to the animal for maintenance and production is approximately 0.82 (0.79-0.84, assumed to be 0.82) of the digestible energy content of the feed due to the above losses (Poppi *et al.*, 1987).

The effect of digestibility on herbage intake has been primarily studied by people (Blaxter, 1962; Blaxter *et al.*, 1961; Milford, 1963; Jarrige *et al.*, 1974, quoted by Rodriquez Capriles, 1973) working with indoor-fed animals and few attempts have
been made to quantify the relationship between intake and digestibility under grazing condition until the studies by Hodgson *et al.* (1977).

In studies with housed animals, it has long been recognized that there is a positive relationship between herbage intake and digestibility (Blaxter et al., 1956) and herbage intake appears to be influenced primarily by its digestibility in the absence of specific nutrient deficiencies (Blaxter, 1962; Balch & Campling, 1962, quoted by Rodriguez Capriles, 1973). This means that plant species or parts having a high digestibility are consumed to a greater extent than those with a lower digestibility, at least to levels of digestibility between 60-70% (Blaxter et al., 1961). Beyond this level, the amount of feed intake may have little relationship to digestibility (Blaxter, 1962; Montgomery & Baungardt, 1965, quoted by Rodriguez Capriles, 1973), or may even be inversely related to it (Rodriguez Capriles, 1973). The reasons for those relationships have been discussed in detail by Balch and Campling (1969) (quoted by Rodriguez Capriles, 1973). However, other studies showed results inconsistent with the above. There have been some reports that up to levels of 80% DOM, the intake of cold stored herbage by indoor-fed sheep is still directly related to its digestibility (Osbourn et al., 1966). Conversely, a study conducted by Wilson (1977) using sheep and goats fed with a range of species of shrubs and trees showed that there was no correspondence between digestibility and organic matter intake, suggesting that estimates of digestibility may have limited use for forage evaluation.

Many studies have confirmed that the principles obtained from housed-animals also apply to the grazing situation (Hodgson, 1977). Therefore, the shape of the relationship between herbage intake and digestibility in grazing animals may be similar to that in housed animals (Minson, 1983) and generally appears to be linear (Rodriquez Capriles, 1973). But the positive relationship between diet digestibility and herbage intake appears to hold even at digestibility levels as high as 70-80% (Hodgson & Wilkinson, 1968) which is higher than the critical level (60-70%) ascertained with housed animals. The results of several experiments with grazing cattle on temperate swards demonstrate a significant and constant rate of increase in herbage intake over a wide range digestibility from 50-85% (Rodriguez Capriles 1973; Hodgson *et al.*, 1977).

The higher level of critical digestibility obtained with grazing animals than with housed ones shown above may be due more to differences in the energy demands of the animals used than to any specific differences in the eating environment. In most circumstances, the total energy expenditure of grazing animals involves the effort of searching for and prehending herbage and meeting the demands exerted by exposure to normal range of climate conditions. Therefore, it has been suggested that the energy requirements for maintenance of grazing animals are 10-20% greater than that of comparable housed ones (Young & Corbett, 1972; Hodgson, 1990).

The proposition that ruminants increase their herbage intake when digestibility goes down (Moen, 1984, quoted by Vallentine, 1990) cannot be accepted, because when herbage digestibility decreases with plant maturity the grazing animal can not compensate by eating more since the ingested material does not move through the intestinal tract fast enough (Vallentine, 1990).

As pointed out earlier, Poppi *et al.* (1987) argued that digestibility is only important in affecting the herbage intake of grazing animals and constraining their herbage intake when no restrictions are imposed by the quantity and structural characters of sward, and prehension is not a problem; namely herbage mass or allowance (Poppi *et al.*, 1987) and height are high. This argument suggests that the first priority to enhance herbage intake would be to achieve desirable structural characteristics rather than to improve digestibility. Laca and Demment (1990) demonstrated that digestible dry matter intake rate (DDMIR) of livestock responds to variation in the vertical gradient of leaf concentration, rather than to horizontal gradient through changing bite depth, and animals can obtain bites of better quality without sacrificing bite weight. The intensity of horizontal gradient has little effect on DDMIR, since horizontal variation forces the animal to trade off bite weight for bite digestibility. Therefore, all improvements in diet quality are counterbalanced by reductions in bite weight and dry matter intake rate.

# 2.5.4 Summary

Section 2.5 has shown that the attributes of the grazed sward are important in affecting the herbage intake of grazing animals. The important first point is that herbage mass, surface height and other canopy characteristics relating to the physical harvesting of herbage are the most important features limiting herbage intake, even though an argument (Laca & Demment, 1990) has arisen recently that herbage mass *per se* does not affect herbage intake so much as its components (height and density).

The commonly held view that pasture quality, described in terms of digestibility, is a major determinant of intake in these circumstances, appears to only apply in certain circumstances. Variations in digestibility may be more important when no restrictions are imposed by structural characteristics than in the case where prehension is constrained by sward structure. Therefore, when high energy intake is required by livestock at particular periods such as flushing, lactation, high growth rate, suitable pasture structure should be provided to achieve high herbage intake, then good quality of pasture would assume greater importance in affecting intake and would boost animal performance.

# 2.6 ANIMAL ATTRIBUTES AFFECTING INGESTIVE BEHAVIOUR

Although the components of ingestive behaviour may be sensitive to a range of sward attributes, they are also tempered by the attributes of the grazing animal.

Effects attributable to the animal *per se* may include animal species, breed, age, weight, body size, physiological state and nutritional status (Allden, 1962; Hodgson, 1977). These factors may affect potential nutrient intake, rumen capacity and grazing efficiency, thus altering the balance between the controls limiting herbage intake (Hodgson, 1977).

The differences in ingestive behaviour between animal species will be discussed in Section 2.7.

This section focuses on other animal attributes.

## 2.6.1 Hunger

Grazing behaviour is influenced by the internal state of the animal which is a function of the morphology of the gut and the nutritional demand of the animal as affected by its reproductive state, hunger or condition (Demment *et al.*, 1987). This section only focuses on hunger effects.

Hunger appears to affect intake, at least in the short term (Burlison, 1987). Dougherty *et al.* (1988a) regarded the hunger-satiety status of grazing animals as one of the determinants of herbage intake operating together with two others: (1) harvesting capacity of the mouth and tongue, and (2) properties of the sward. Therefore, satiety, as related to rumen fill and the amount of herbage already eaten, is an important factor in affecting ingestive behaviour, and is generally expected to reduce the herbage intake rate (Vallentine, 1990). Sidahmed *et al.* (1977) and Jung and Koong (1985) found that the rate of intake of oesophageal fistulated sheep increased when the animals had been fasted for a long period. Chacon and Stobbs (1977) fasted oesophageal fistulated cows either overnight (for sixteen hours) or for only two hours and bite weight of the longer-fasted cows was subsequently found to be higher on certain pastures. In an experiment that measured the behaviour of steers fasted for different periods, fasted animals achieved higher intakes while grazing on pasture than did non-fasted animals (Greenwood & Demment, 1988).

Owen-Smith & Novellie (1982) (quoted by Vallentine, 1990) predicted that bites per minute and per feeding station will decrease and steps between feeding stations will increase as satiety increases. Jung and Koong (1985) found that rate of intake by grazing sheep decreased as amount of feed eaten before grazing increased from 0-30% of daily intake. Cattle fasted for 3 hours had higher intake rates than unfasted animals without decreasing diet quality after fasting, but this was achieved by an increase in biting rate (Greenwood & Demment, 1981). Penning *et al.* (1991a) found that biting rate, measured in the hour immediately following fasting, was generally lower than the average measured over the whole day, and the fall in biting rate was caused by an increase in bite weight. However, the increase of biting rate after fasting was at the cost of a lower mastication rate with the implication of larger ingested particle sizes and therefore slower dry matter turnover rates in the rumen (Greenwood & Demment, 1988).

In contrast, Bond *et al.* (1976) found no increase in rate of intake by grazing steers after satiety was reduced by fasts of 12 to 48 hours. Similarly, Freeman and Hart (1989) (quoted by Vallentine, 1990) found that hay feeding prior to grazing had little effect on feeding station behaviour of steers, i.e., biting rate, bites per station, or steps per station. It was suggested that the effects of satiety or time already spent grazing may require more time to appear than provided in their study; it was also suggested that the effect of time already spent grazing may be due to fatigue rather than satiety. It seems to be a reasonable statement that fasting has an effect on ingestive behaviour, but has less influence than sward canopy structure in determining bite weight (Burlison, 1987).

#### 2.6.2 Body sizes across animal species

Body size is related allometrically to most physiological process and life history characteristics of organisms (Calder, 1984, quoted by Demment & Greenwood, 1988), and has a major effect in governing level of voluntary feed intake (Freer, 1981).

Body size and related variables (mouthpart dimensions and incisor breadth) have important consequences for herbage intake in mammalian herbivores and body size determines the ability of an animal to utilize fibrous feeds, since large animals have greater gut capacity (W) relative to energy requirements (W<sup>0.75</sup>) (Illius & Gordon, 1990b).

Illius and Gordon (1987) estimated the effect of body weight on bite weight using the relationships between body weight and incisor breadth derived for data from 32 animal species, and showed a clear effect of body size on the ability to achieve adequate herbage intake from short swards. They suggested that large animal species must experience relatively greater restriction in bite depth, and hence bite volume, on short swards than small animal species. It was assumed (Illius & Gordon, 1987) that the superiority of small animal species over large animal species in their ability to subsist on shorter swards is due to the allometric relations of bite weight and metabolic requirements to body size. It is further suggested that the scaling factor of live weight declines progressively from 0.75 on tall swards where no limitation to intake is imposed, tending to 0.36 on short swards where animals of all weights are severely restricted, and under the situation of short swards, incisor breadth is the only unrestricted bite dimension. This implies that the relative value of two alternative food patches in the sward, for example, a tall mature patch of herbage (high quantity) and a short vegetative sward (high quality) depends not only on the proportion of the sward but on the size of the animal confronted by that choice (Illius & Gordon, 1990b).

The breadth of the incisor arcade is an important determinant of the rate of herbage intake in grazing ruminants and has an important effect on diet and niche selection (Illius & Gordon, 1987). Also, incisor breadth and arcade structure are assumed to adapt as coevolved traits to grazing or browsing styles (Gordon & Illius, 1988), and the morphology of the incisor dentition is expected to determine the extent to which an animal can prehend and ingest plant food items from within the spatial array of vegetation (Illius & Gordon, 1990b). Because high quality swards tend to be

short at critical times of the year, large animal species would be selected to have wider flatter incisor arcades in order to maximize bite weight and intake rate on short swards (Illius & Gordon, 1987). Clutton-Brock and Harvey (1983) also assumed that bite weight and food intake are determined in part by incisor breadth, and scaled at 0.33 of live weight, and argued that large animals cannot tolerate sward heights that can support smaller animals, and that scramble competition between grazing species of different body sizes will lead to the exclusion of larger species from jointly preferred swards.

Clutton-Brock et al. (1987) explained differences between the habitats and diets selected by male and female red deer, and suggested that allometry theoretically acts as a mechanism for sexual segregation in dimorphic species. Gordon and Illius (1988) examined the relationship between the structure of the incisor arcade and selectivity by comparing the allometry of body size and dimensions of the incisor arcade in ruminant species with different feeding habits. It was concluded that selection has operated on the oral morphology of ruminants resulting in an incisor arcade structure which is adapted to maximize intake of forage within guality constraints. The isometric scaling of incisor breadth with body weight reported in this study (Gordon & Illius, 1988) showed that small species have a feeding apparatus which allows a greater degree of selectivity than that of large animals. This will have far-reaching effects on the digestive strategies and social behaviour of species of different body size (Hanley, 1982; Clutton-Brock & Harvey, 1983). The study by Gordon and Illius (1988) also found that species of ruminant which feed predominantly on grasses (grazers) have significantly broader and more flattened incisor arcades and appreciably wider and flatter mouths when compared at the same body size with species which browse on woody dicotyledonous plants (browsers), suggesting that browsers require a greater degree of selectivity. The authors (Gordon & Illius, 1988) commented that increased incisor breadth is likely to be a disadvantage in browsing, since it would prevent the accurate selection of particular individual parts of plant, which are of high quality, while browsers have narrower and more pointed incisor arcade, capable of greater selectivity.

Additionally, several studies have suggested that the shape of the muzzle of ungulates may be related to differences in diet (Owen-Smith, 1982; Bunnell & Gillingham, 1985, quoted by Gordon & Illius, 1988), but little information on quantitative

analysis has been available until recently (Gordon & Illius, 1988). Janis and Erhardt (1988) attempted to describe feeding selectivity across a wide range of ungulates by comparing muzzle to palatal width ratio, and also found that the ratio of first and third incisor breadths is greater in browsing than in grazing species. Variation in length or width of the lower jaw might affect bite weight, bite rate or selective ability (Hafez & Schein, 1962). "Inherent individuality" as an animal factor may also affect ingestive behaviour and intake (Hancock, 1952; Hafez & Schein, 1962).

There has also been some evidence to show that reticulo-rumen volume relative to animal size materially affects the type of herbage each ruminant species is efficient in processing (Hanley, 1982).

Hanley and Thomas (1982, quoted by Vallentine, 1990) concluded that (1) large species are more limited by time (including both ingestion and rumination) than small animals, spend less time per nutrient unit consumed, and thus can not be as selective; and (2) small body size is advantageous to livestock if herbage quantity is limiting, while large body size is advantageous if herbage quality is limiting.

# 2.6.3 Degree of maturity within a species (age, body size and mouth dimensions)

In this section, attention will be concentrated principally on comparison between animals at different stages of maturity within a species.

Evidence from various studies on the relationship between stage of maturity within a species and herbage intake seems to be equivocal (Hodgson, 1985) and conflicting. Allden and Whittaker (1970) showed that within a species, small individuals are superior to large individuals in maintaining herbage intake on short swards. These trends were accentuated when rate of intake was expressed relative to live weight. Zoby and Holmes (1983) compared the intake of cattle of three different sizes and ages under continuous-grazing management. They found that intake per unit liveweight was greater for animals of large size than small size, and the smaller animals tended to have a longer grazing time and higher bite rate, but smaller bite weight. It was concluded that younger (smaller) cattle were less sensitive than older animal to changes in sward conditions as they were better able to modify grazing behaviour to maintain intake. Illius and Gordon (1990a) predicted that young deer can tolerate shorter swards than older deer. Similar evidence was reported by Thouless

(1986, quoted by Illius & Gordon, 1990a), who showed that young red deer continue to graze short *Agrostis/Festuca* greens after larger animals have left. Conversely, Hodgson and Jamieson (1981) reported that young cattle were more sensitive to changing sward conditions than adult cattle. On the other hand, Hughes *et al.* (1984) found that age of goats and sheep had unimportant effects on composition and digestibility of diet selection.

It is argued that grazing behaviour and herbage intake are partly the expression of allometric changes in the ability and desire of the immature animal to prehend and ingest herbage (Illius, 1989). Important attributes of the grazing animal are its age, body size, and dental architecture (Taylor *et al.*, 1987). Previously, attention has been concentrated principally on either body weight or mouth dimensions or even both. However, there is no consensus view of the relative importance of the attributes which influence variation in ingestive behaviour across animals of different degrees of maturity.

As body size changes through an organism's life or through evolutionary time, a number of factors affected by body size will change in concert, and individuals of disparate sizes within a species should be ecologically quite different animals (Demment & Geenwood, 1988). To explore the implications of body size (body weight) on grazing behaviour, the interactions between ranges of body size and sward conditions were modelled by Demment and Greenwood (1988). This model showed that under a given set of conditions smaller animals always have a lower rate of energy digestion and bite weight than larger animals, and under poor nutritional conditions smaller animals approach zero energy balance. Therefore, the net rate of energy digestion and bite weight decline with body weight. This predicts that smaller body size with lower digestive capacity leads to the selection of a high quality diet, and this is the principal way in which smaller animals can compensate for their size. Conversely, requirements increase at an accelerating rate with declining body size and rumination appears to be the major compensatory mechanism as body size declines.

Illius (1989) commented that the most important determinant of voluntary food intake is body weight. In growing cattle, intake scales with about  $W^{0.70}$  at any given age between 3 and 18 months (Taylor *et al.*, 1986). Under unrestricted grazing conditions, a similar exponent of W has been found (Hodgson & Wilkinson, 1967). Maximum intake rate can be predicted in normally growing cattle by degree of maturity

in body weight which is expressed as ratio of given body weight to adult body weight, although this expression became less satisfactory and was replaced by a degree of maturity in incisor breadth after a further investigation (Taylor & Murray, 1987).

Expressing intake as an allometric function of weight must be an oversimplication unless intake is constrained by some weight-related mechanism (Illius, 1989). On the other hand, a critical component of body size is size of the buccal cavity, and in particular incisor arcade breadth (Taylor et al., 1987). Body-size scaling of incisor breadth in relation to sward resources could be important not only across adults of different species, but could also be influential in growth and survival of immature animals of both sexes within a species (Illius & Gordon, 1990a). Taylor and Murray (1987) suggested that during the growth of animals, maximum intake rate was determined more by size of buccal cavity than by body weight, and that discrepancies would be accounted for if the buccal cavity was an early maturing part of the body and therefore less affected by variation in nutrition than the body as a whole. Thus, incisor breadth is preferred to body weight as a more useful description of physiological maturity (Taylor, 1965). The morphology of the feeding apparatus can exert a marked influence on foraging efficiency and the ontogeny of the incisor arcade may impose constraints on foraging efficiency of juveniles (Illius & Gordon, 1990a). It is argued that a large mouth is an advantage in dealing with tall swards, and that, conversely, a small mouth may confer competitive advantage in relation to rate of intake (Allden & Whittaker, 1970; Schwartz & Ellis, 1981).

Taylor *et al.* (1987) examined the allometry of incisor arcade breadth in growing cattle and sheep. They found a coefficient of 0.29, showing incisor breadth to be a moderately early-maturing measure. Illius (1989) commented that immature animals, having relatively well-developed incisor breadths, would have an advantage over more mature animals in terms of their bite weight relative to weight when both graze swards which restrict intake. He obtained a coefficient of 0.46 describing the allometric relationship between bite weight and degree of maturity expressed in incisor breadth. This is the scaling factor for adult incisor breadth, which is the only unrestricted bite dimension on very short swards. Taylor and Murray (1987) showed that maximum intake rate in adult animals is a function of the square of incisor breadth. On short swards, Illius and Gordon (1987) assumed that bite weight is related to bite area, namely the square of incisor breadth, because bite depth is restricted by short swards.

In a study using red deer, Illius and Gordon (1990b) suggested that herbage intake is constrained by the allometric growth of the incisor arcade with body weight. The ontogeny of the incisor arcade and its allometry with body weight shows that growing animals experience restricted incisor breadth relative to weight during the transition from juvenile to mature dentition. Yearlings of red deer with one pair of adult incisors face the greatest limitations on sparse swards because incisor breadth in these animals is smaller relative to maintenance requirements than animals with juvenile or mature dentition (Illius & Gordon, 1990b).

Generally, grazing animals are subject to a complex interaction of sward properties, allometric changes with weight in incisor breadth, and the declining drive to acquire nutrients for growth as they mature in weight. Changes in bite weight as animals mature in weight appear to reflect both the limitations imposed by the sward on bite dimensions and allometric changes in mouth size. Depressions in intake under grazing affect animals of different degrees of maturity equally when intake is compared on the same swards (Illius, 1989).

There is also some evidence that grazing experience may affect intake. The response patterns may be unstable in young livestock with little grazing experience (Hodgson & Jamieson, 1981). Curll and Davidson (1983) found that sheep which are accustomed to swards of low herbage mass had a higher intake, due to a higher grazing time and higher estimated rate of intake, than sheep unaccustomed to those conditions.

General hypotheses about interactions between the effects of body size, mouth size and sward conditions upon ingestive behaviour and herbage intake require further critical evaluation (Hodgson, 1986).

# 2.6.4 Summary

It appears that animal species, body weight and the structure of the incisor apparatus are major attributes differentiating ingestive behaviour between animals. Within an animal species, incisor breadth is preferred to other parameters as a description of the degree of maturity which is related to variation in ingestive behaviour of individual animals of increasing age. 2.7 COMPARISON OF INGESTIVE BEHAVIOUR AND HERBAGE INTAKE BETWEEN ANIMAL SPECIES

For the sake of clarity and coherence, it is appropriate to review this heading independently after a general discussion about ingestive behaviour and about the effects of sward and animal attributes on ingestive behaviour, although some recapitulation will be involved.

The traditional domestic livestock on grazing lands in most parts of the world have been sheep, cattle and goats. Attention has also been focused recently on other species of grazing animal, such as deer, buffalo and antelopes. Extensive research has been conducted for sheep and cattle, but little information is available for goats and other species. This section will concentrate principally on general aspects of species comparison, with particular emphasis on sheep and goats where possible.

Differences in ingestive behaviour between species may exist because grazing animals exhibit considerable plasticity in grazing behaviour. This is necessary for animals that subsist on plants that vary greatly in structure (Arnold, 1985, quoted by Vallentine, 1990), and all components of ingestive behaviour and bite dimensions vary as animals attempt to achieve and maintain their intake potential (Vallentine, 1990). Comparative evaluation is difficult since animal species are seldom compared under the same grazing conditions. Thus, with some notable exceptions, evidence cited in this section comes from the research where animal species are stocked separately.

Before the comparisons are made, it would be helpful to understand the effect of the variation in mouthpart structure between the various animal species on the way in which they graze herbage, since the morphology of the jaw, teeth and other mouthparts results in differences between animal species in how the herbage is prehended.

In sheep, herbage is gathered by the lips which are thin and mobile, whereas in cattle, this function is served by the long, prehensile tongue and the lips are fleshier and less mobile (Hodgson, 1990). The large, flat muzzles of cattle allow relatively large clumps of herbage to be drawn into the mouth at one bite (Vallentine, 1990) unless the vegetation is too short (Arnold, 1981). The associated herbage consumption rate is high, but more old tissue is consumed along with the current annual growth than by grazers with narrow mouth parts (Hanley, 1982). Sheep grip herbage between the dental pad and lower incisors before it is severed, and then either tear it off by a jerk of the head (Arnold, 1981; Hodgson, 1985, 1986) backward or less commonly forward (Arnold & Dudzinski, 1978) or bite it off (Arnold, 1981). In cattle, the herbage may also be gripped between the dental pad and lower incisors (Chambers *et al.*, 1981; Hodgson, 1986) or between the tongue and lower incisors (Van Dyne *et al.*, 1980; Chambers *et al.*, 1981) or between the upper and lower molars (Ellis & Travis, 1975; Vallentine, 1990) before pulling or tearing the herbage off, often with a jerking movement. In contrast to cattle, sheep have a cleft upper lip that permits close grazing if they so choose. But cattle seldom graze closer than about 5 cm from the ground unless forced to do so (Heinemann, 1969, quoted by Vallentine, 1990).

Goats prefer to browse rather than graze (Clark *et al.*, 1982; McCall & Lambert, 1987; Hughes, 1988) and the goat's ability to browse is assisted by the presence of mobile upper lips and a very prehensile tongue (Huss, 1972, quoted by Vallentine, 1990) that permits them to eat tiny leaves of browse even from thorny species, which most other domestic livestock can not normally prehend (Martin & Huss, 1981, quoted by Vallentine, 1990). Camels are like sheep and goats in having mouth parts adapted for browsing. The mouth of deer is long and narrow, and herbage is either gripped between the molars and severed by a biting action or seized between the incisors and upper dental pad and sheared off with an upward or downward jerking action (Willms, 1978, quoted by Vallentine, 1990).

There is fairy sound evidence that different grazing livestock consume diets which are, to some extent, different in composition and quality. In term of these dissimilarities, the grazing species have been divided into three groups by Van Soest (1982, quoted by Vallentine, 1990): (1) bulk and roughage eaters, (2) concentrate selectors, and (3) intermediate feeders. These groups are mostly equivalent to those in Holecheck's classification (1988): (1) grazers, (2) browsers and (3) intermediate feeders. Cattle and Dalles sheep fall into the grazers, domestic goats and deer into the browser category, whereas domestic sheep and mountain goats were included in intermediate feeders. Because of the versatility in their diets, domestic goats can also belong to the grazers (Vallentine, 1990). No attempts will be made in this review to detail this issue which is related to diet selection and has been previously reviewed (Hodgson, 1977, 1982, 1986; Arnold, 1981; Minson, 1983; Vallentine, 1990). But the point which needs making here is that ingestive behaviour can be altered and differentiated by the influence exerted by the variation in diet preference between

species through selective grazing (Hodgson, 1990)

Differences between animals in bite weight, biting rate, grazing time and bite dimensions may all contribute to differences in intake (Hodgson, 1990). Table 2.2 summarises the range of variation in components of ingestive behaviour and bite dimensions in sheep and cattle grazing temperate sown or artificial swards. Bite weight in absolute terms on temperate sward is far greater for cattle than sheep. However, the relative magnitude is reversed when it is expressed on the basis of live weight. Jamieson and Hodgson (1979b) found that under conditions of continuous stocking lambs had a greater bite weight per kg live weight than calves. Forbes (1982) obtained a similar result for mature sheep and cattle grazing indigenous hill swards. But, overall, he found that on a live weight basis bite weights of sheep and cattle estimated using fistulates did not differ significantly; nor did they differ when sheep and cattle grazed down sown swards (Forbes & Hodgson, 1985).

Mitchell *et al.* (1991) reported that the ingestive behaviour of sheep and deer was very similar in relation to sward height and density in terms of bite weight. However, sheep had a much higher bite weight/LW<sup>0.75</sup> on short swards, but these differences declined with increasing height, increasingly so as density increased (Mitchell, 1993).

Sheep tend to have a lower biting rate than cattle and to spend more time grazing, though the differences are small and are not always consistent (Forbes, 1982). The lower biting rate is probably associated with the greater selectivity of grazing by sheep in most circumstances (Forbes, 1982), especially where the opportunity for diet selection is great. Cattle appear to maximize rate of herbage intake through faster biting, whereas sheep appear to maximize nutrient intake through selecting, which gives rise to slow biting rate. Black (1990) also pointed out that sheep that ate at a slower rate were better able to select the vegetative tillers that were in close proximity to the mature tiller than were fast eaters. Weaned calves grazing with dry and lactating cows were found to have bite rates intermediate in range to those of the adults (Hodgson & Jamieson, 1981) whereas Wadsworth (quoted by Forbes *et al.*, 1985) found that lambs had slower biting rates than ewes. Chambers *et al.* (1981) found that the ratio of manipulatory to harvesting bites was consistently greater for sheep than for cattle at any given sward height, presumably reflecting the greater use of the lips by sheep in manipulating herbage. Biting rate of mature sheep appeared

to be more sensitive to changes in sward conditions than were these variables for mature cattle (Forbes & Hodgson, 1985).

Variables	Sheep	Cattle
Bite weight		
(mg OM)	11-400	70-1610
(mg OM/kg LW)	0.4-2.6	0.3-4.1
Biting rate (bites/min)	22-94	20-66
Rate of intake		
(mg OM/kg LW per min)	22-80	13-204
Grazing time (h/day)	6.5-13.5	5.8-10.8
Total daily bites (10 <sup>3</sup> )	10-78	8-36
Bite depth (cm)	0.3-20.6	1.7-17.3
Bite area (cm <sup>2</sup> )	8.6-35.5	20.1-52.2
bite volume (cm <sup>3</sup> )	11-471	22-822

Table 2.2	Ranges of	variation	in	components	of	ingestive	behaviour	and	bite
	dimensions	in sheep	and	d cattle grazir	ng t	emperate	swards.		

Source: Hodgson (1986), Burlison (1987), Black and Kenney (1984).

Few studies have compared the grazing times of cattle and sheep grazing together, but it appears that sheep graze for 1-2 hours longer than cattle (Van Dyne *et al.*, 1980; Forbes, 1982) probably due to more selective grazing.

The herbage intake of goats was shown to be very similar to that of sheep when herbage mass was high at early stages of the progressive defoliation of a sward (Nicol *et al.*, 1987), but when the herbage mass was reduced at the same rate of allowance (DM/ha/day), the intake of goats fell more rapidly than that of sheep (Collins & Nicol, 1986). Therefore the intake of sheep was less sensitive to declining herbage mass than that of goats (Nicol *et al.*, 1987; Collins & Nicol, 1986) and this may be related to the ability of sheep to adapt to eating less preferred components of the sward with reduced herbage mass (Nicol *et al.*, 1987).

Some evidence (Collins & Nicol, 1986) with sheep, cattle and goats grazing the same residual herbage mass, but with different rate of disappearance of herbage mass (fast and slow) showed that relative rate of decline of herbage intake (per kg LW <sup>0.75</sup>) with decreasing herbage mass varied with stock classes.

Weston (1982) demonstrated that there appears to be no convincing evidence of a general difference in voluntary consumption per kg live weight between sheep, goats, cattle and buffalo.

Diurnal patterns of grazing activity (grazing, ruminating and idling) have been shown to be similar between cattle, sheep and Angora goats (Arnold, 1981; Askins & Turner, 1972).

The recent evidence suggests that goats are shallow surface grazers, defoliating pasture from the top downwards in successive layers (McCall & Lambert, 1987), whereas sheep graze closer to the ground than cattle, due to the difference in mouthpart anatomy which was reviewed at the beginning of this section. This is the case particularly in taller swards where sheep usually tend to graze further into the sward canopy than do cattle (Hodgson, 1990). However, other evidence suggested that cattle generally graze a sward from the surface down (Lane & Holmes, 1971; Stobbs, 1975b) and sheep may behave similarly (Arnold, 1964; Milne et al., 1982; Barthram & Grant, 1984). Clark et al. (unpublished, guoted by Hughes, 1988) compared the grazed depths between sheep, goats and cattle grazing a range of pregrazing sward heights encountered on farms (Table 2.3). Cattle penetrated into swards more deeply than goats on all but the shortest swards. Sheep also grazed deeper than goats on the taller swards. All three species increased the length of leaf removed with increasing pregrazing height, but bite depth for goats was significantly shallower than for sheep and cattle. Goats removed shorter portions of leaf as sward height increased. The same experiment also compared the height preference of sheep, cattle and goats when offered a range of height comparisons (Clark et al., unpublished, guoted by Hughes, 1988), and found that goats showed a stronger preference for the taller swards than sheep in terms of proportion of grazing time, bite rate and bite weight.

Herbage mass	nass Pregrazing na) height (cm)	Grazing depths (cm)			
(kg DM/ha)		Cattle	Sheep	Goats	
1,2000	5.1	2.1	1.4	1.6	
1,9000	7.8	3.5	2.5	2.6	
2,3000	11.5	5.3	4.4	4.0	
3,0000	18.4	10.0	8.2	6.0	
3,5000	23.3	12.9	12.6	9.0	

Table 2.3Pregrazing herbage mass, height and grazing depth for adult cattle,<br/>sheep and goats (quoted by Hughes, 1988).

Little information on bite area and bite volume is available for goats as detailed bite dimensions have not been previously measured. However, what little evidence there is in Table 2.2 suggests that cattle generally have larger bite area than sheep, and this is logical since cattle have greater mouth dimensions. Mitchell (1993) demonstrated that deer needed more height than sheep to maximize bite area.

However, Hodgson (1990) suggested that whatever the basic differences in diet selection, ingestive behaviour or herbage intake, different classes of livestock respond in much the same way to changes in sward conditions, with some exceptions on extremely short swards, where sheep may be able to maintain herbage intake better than cattle.

2.8 GRAZING PROCEDURES INVOLVED IN RESEARCH ON INGESTIVE BEHAVIOUR: Field grazing and indoor crated grazing

It is appropriate to end this review by noting the technical approaches which are involved in research on ingestive behaviour and herbage intake, and have helped to make substantial progress in such a difficult area. No attempt will be made to describe these technical procedures and discuss the advantages and disadvantages in more detail as these are beyond the scope of this thesis, but they are available in the literature (Leaver, 1982). This heading only involves a brief review of the grazing procedures used in this research.

Conventionally, the observation of ingestive behaviour and herbage intake under

grazing condition is made in the field on a large-plot scale. Only recently has a cratedor penned-approach been used in which animals are confined and conditions are tightly controlled (Black & Kenney, 1984; Burlison, 1987; Mursan *et al.*, 1989; Betteridge *et al.*, 1991; Mitchell *et al.*, 1991; Mitchell, 1993; Laca *et al.*, 1992a & b). Both approaches have their advantages and drawbacks (Burlison, 1987) for different research goals.

The use of crated- or penned-animals has several advantages over large-scale grazing trials. It allows observers to work close to the animals to record biting activity, and allows easy manipulation and control of the grazing process. The use of cut turf, instead of grazed plots, makes it possible to measure bite dimensions and estimate the herbage mass removed by animals during the short time grazing. Also, measurements of herbage bulk density of grazed strata can be made more directly and guite likely more accurately. It has been suggested that there is no fundamental reason to suspect that the results obtained from this technique could not be extended to the short-term responses of unrestricted animals under paddock grazing situations (Burlison et al., 1991) so long as the animals are well trained. Burlison (1987) pointed out that the effects and complications of trampling, fouling and social aggregation occurring on large-plot grazing could be also avoided by this procedure. Mursan et al. (1989) observed bite weight and bite dimensions of cattle placed in individual pens. The authors commented that this procedure proved to be extremely useful in the study of the effects of specific sward structure on intake and provided a means of identifying sward characteristics restricting bite dimensions

However, this approach cannot be used to study parameters such as daily grazing time, diurnal patten of grazing activity and intake rate over a few hours, since only short time observation is possible. Penning *et al.* (1991a) argued that it may not be acceptable to extrapolate from short-term studies of the effects of sward conditions on ingestive behaviour to free-grazing animals.

## 2.9 CONCLUSION

This review has covered the progress over the last two decades in understanding the factors influencing ingestive behaviour and herbage intake of grazing animals, how livestock respond to variation in sward conditions and how behaviour is influenced by specific animal attributes. Much of the information available so far is either quite general description due to the limited accuracy of observations obtained under uncontrolled experimental conditions, or extreme simplification under highly controlled sward conditions (artificial swards, or simple tray-grown swards) which can not represent real grazing conditions. Also, most of the studies involved use of grasses, and single animal species (sheep or cattle). The evidence obtained from these studies has allowed the development of basic principles, and has even provided clear-cut answers to some of issues involved.

However, there is now a need to move to studies under controlled experimental conditions, of a series of swards with a great contrast in canopy structure and in forage category (grasses vs legumes) grazed by more than one species simultaneously. These swards should be reasonably simplified, but must be able to practically reflect the situation encountered on farms. This will allow the relationships between sward characteristics and animal's responses to be established, under closely controlled conditions, over the wide range of swards, and a comparison of response patterns in ingestive behaviour to be made between animal species under similar grazing situations.

# CHAPTER 3

# **EXPERIMENT 1**

# **Experimental Details**

## 3.1 INTRODUCTION

This project was designed to include three experiments.

Experiment 1 involved an evaluation of responses in ingestive behaviour of sheep and goats to variation in sward structure induced by a range of grasses and legumes sampled at two stages of maturity. Experiment 2 concentrated on an assessment of effects of contrasting heights within a forage species on ingestive behaviour of sheep and goats grazing grasses and clovers. In both experiments 1 and 2, observations of grazing behaviour were made using an indoor grazing technique in which the animals were individually confined in metabolism crates and presented with prepared turves extracted from the established plots. Experiment 3 focused on comparisons between indoor and outdoor grazing using oesophageal fistulated sheep, and between fistulated and intact sheep using indoor grazing procedures.

This chapter describes details of the materials and procedures involved in Experiment 1, and explains design and construction of data sets of this experiment. The data sets generated will be used as data bases of Chapters 4 and 5.

#### 3.2 MATERIALS AND METHODS

# 3.2.1 Experimental plots

## 3.2.1.1 Natural and ecological conditions of the experimental site

The swards used in this experiment were grown on a terrace at 100 m asl, at the Ballantrae Hill Country Research Station of AgResearch Grasslands Research Center, near Woodville.

The soil is an Ashhurst silt loam/Raumati silt loam, derived from an old river terrace, and moderately well drained (J.D. Cower pers. com.). Mean annual air temperature (23 years) at 1.2 m measured 1 km from the experimental site was 12.3°C, and ranged from 7.8°C in July to 16.8°C in February. Average annual rainfall

(23 years) at the same site was 1212 mm, and was uniformly distributed seasonally (D.J. Barker pers. com.).

#### **3.2.1.2** Forages (plant species and cultivars)

A series of forages (plant species and cultivars) (Table 3.1) were utilized in this project, and they were selected to produce a range of canopy structure. These grasses, legumes and a herb varied in erectness of growth habit, leaf size and degree of steminess. A description of agronomic characteristics is given in Appendix 3.1.

	Common Name	Cultivar Name	Botanical Name	Sowing rate	Sowing date
1	Ryegrass	Grasslands Pacific	Lolium perenne	15 kg/ha	29/04/88
2	Browntop	Grasslands Muster	Agrostis capillaris syn. A.tenuis	15 kg/ha	29/04/88
3	Cocksfoot	Grasslands Kara	Dactylis glomerata	10 kg/ha	29/04/88
4	Prairie grass	Grasslands Matua	Bromus willdenowii syn. B. catharticus	30 kg/ha	29/04/88
5	Phalaris	Grasslands Maru	Phalaris aquatica	17 kg/ha	30/11/88
6	White clover	Grasslands Tahora	Trifolium repens	4 kg/ha	29/04/88
7	White clover	Grasslands Kopu	Trifolium repens	3 kg/ha	29/04/88
8	Red clover	Grasslands Pawera	Trifolium pratense	6 kg/ha	29/04/88
9	Lotus	Grasslands Goldie	Lotus corniculatus	5 kg/ha	29/04/88
10	Chicory	Grasslands Puna	Cichorium intybus	4 kg/ha	29/04/88

 Table 3.1
 Plant species and cultivars (detailed description see Appendix 3.1) utilised in experiment 1.

# 3.2.1.3 Establishment and general management of the experimental plots

Forty 6 x 10 m<sup>2</sup> plots were laid down in four rows in April, 1988 and the ten forages were sown as monoculture swards, four plots per forage, in a completely randomized design.

The terrace was ploughed and harrowed in order to level the ground. Residual turf was raked away and gravel and rocks were removed.

On 29 April 1988, forages were sown at the rates listed in Table 3.1. Seeds were mixed with sawdust to assist the sowing process, and all plots were sown by

hand in two directions to ensure an even spread. The plots were lightly raked and rolled to ensure that the seeds were properly covered by soil.

Permanent electric fences and netting fences were established around the plots.

All plots received 30 kg P and 8 kg S/ha twice annually as Longlife (phosphorus), PAPR (partially acidulated phosphate rock) and Ammo-Phos/Hycrop. Non-legume plots also received 40 kg N/ha annually in 3 instalments of Urea (spring, autumn and winter).

One month after sowing, a culture medium of rhizobium (*Rhizobium japonicum*) was watered onto *Lotus corniculatus* plots as the appropriate species was not present naturally.

During sward development, all plots became infested with weeds, and an intensive herbicide application programme was designed and carried out (Appendix 3.2).

In tall fescue plots, the weeds were so prolific and population density of tall fescue was so poor that an alternative species, phalaris (*Phalaris aquatica*), was sown to replace it. After the tall fescue plots were sprayed with Roundup, a seedbed was prepared and phalaris (Table 3.1) was sown using the same procedures as before.

All plots were satisfactorily established by mid-February 1989 (except phalaris which was at the seedling stage).

The plots were grazed, cut or irrigated, and herbicide and fertilizer were applied as necessary during the course of experimental measurements to maintain growth and purity of the sown forages.

## 3.2.2 Animals

Seven Romney female sheep and seven G4 Angora cross feral female goats, sound of foot and mouth, were obtained for this experiment. The individuals of each animal species had similar live weights, and all individuals had similar age. The animals had been selected for their tameness and willingness to eat under confined conditions. The six animals of each species which adapted most rapidly to the procedure were chosen to form the experimental group, and one was kept as a spare. The animals were 12 months old at the start of the experimental training commenced in October, 1988. At this time, the first pair of permanent incisors had come into wear (i.e. two adult incisors had erupted above the level of adjacent deciduous teeth (Bray

*et al.*, 1989)), and six permanent incisors had come into wear when the experiment was completed in the middle of 1990. Identification of individual animals was aided by large numbered ear tags.

## 3.2.2.1 Training of the animals

The animals were trained to the indoor crate-grazing environment over a period of ten weeks before the pre-experimental run (see Section 3.2.3) commenced. They were confined in a large indoor pen with slatted floor adjacent to the metabolism crates. Since there were only six crates, two groups of animals (three of each species for each group) were alternately confined in the crates on a daily basis. Animals were kept in the shed day and night during weekdays, and released at weekends and maintained in a holding paddock of permanent perennial ryegrass/white clover pastures adjacent to the shed. In the initial stage of the training, mixtures of sheepnuts and hay were supplied on regular basis, 3-4 times per day in a single container containing about 350 g hay and 150 g sheepnuts each time. Water was always accessible. Four weeks later, animals were sometimes offered fresh forage cut from adjacent paddocks or provided with turves extracted from the experimental plots to allow animals to become accustomed to the experimental swards. Daily intake ranged from 1.5 to 2.5 kg DM.

# 3.2.2.2 Animal measurements

The following animal attributes were routinely measured at approximately monthly intervals during the course of the experiment.

## 3.2.2.2.1 Body weight

The animals were weighed to the nearest 0.5 kg with an electronic scale. The day prior to weighing, the animals were mustered to the paddock where plenty of feed was available to standardize the pre-weighing condition. The animals were weighed between 9:00 - 11:00 in the morning. If the weather was wet on the weighing day or previous night, the weighing had to be delayed to an alternative fine day with the same pre-weighing preparation.

### 3.2.2.2.2 Incisor breadth and number

The incisor arcade breadth was measured to the nearest 0.1 cm as the distance between the outer edges of the right and left ramus of the permanent incisor teeth which came into wear. Dental wax was used to copy the shape of the incisor arcade and to provide a permanent record of teeth dimensions.

#### 3.2.2.2.3 Mouthpart dimensions

Various measurements of mouthpart dimensions were made using a calliper or a ruler to the nearest 0.1 cm.

Dentition width: the distance between the outer edges of the right and left dental pad on the lower jaw.

Muzzle width: the distance between the corners of the lips on either side of the muzzle, with the mouth closed.

Lip length: measured on the left side of the face, from the tip of the muzzle to the corner of the lips, with the mouth closed.

Maximum mouth opening: from the cutting edge of the incisor on the lower jaw to the dental pad on the upper jaw, with the mouth open as far as possible.

#### 3.2.3 Preparation and sampling of the swards (turves)

Variation in herbage maturity was created by allowing the plots various periods of regrowth.

After a pre-experimental run lasting a month before the experimental measurements were started, the techniques and experimental procedures were well and precisely established. The experimental measurements commenced on 20 February 1989.

The day prior to feeding, turves of the forage to be offered were extracted from the plots using a metal quadrat-cutter of size 41 x 27 cm. The locations for turf extraction were selected from the four plots of the sampled forage with regard to similarity of appearance, to minimize variation between the turves. The quadrat-cutter was hit into the ground to 7 cm depth with a rubber hammer and dug out with a spade. In the plots where plants were growing in rows engendered by the initial raking during establishment, the sampling quadrats were aligned at right angles to the rows. A typical weedy or bare patches were avoided. The cut turves were placed in deep trays with dimensions of 41 x 27 x 8.0 cm. Thirteen turves of one forage were cut each time. The six sheep and six goats each grazed one turf, and one was used to calibrate insensible moisture loss of the turf in calculation of DM percentage (see Section 3.2.6.4). The thirteen turves were immediately taken back to a chiller maintained at 5°C in the laboratory about 500 m away from the plots.

When the soil was dry, water was applied to the turves before extraction, to prevent swards drying out once in trays.

## 3.2.4 Pre-grazing measurements of the sward

The extracted turves were characterized using the following measurements prior to being grazed.

## 3.2.4.1 Sward height

Three estimates of sward height (leaf surface height, stem height and reproductive height if appropriate) were recorded to the nearest 0.5 cm. Thirty measurements for each height were estimated by inserting a needle, with minimum disturbance, into the sward to the soil surface, and measuring the depth of penetration of the needle with a ruler. The measured plant units for each height were randomly, but evenly spaced across the turf area.

Leaf surface height was estimated as the height of uppermost leaves in an undisturbed sward canopy (natural position) (Rhodes, 1981).

"Stem" height varied with forage categories:

Herbage categories	Measured "stem" height
grass	ligule of the youngest full-expanded leaf
white clover	top height of the petiole
red clover	height of youngest trifoliate leaf
chicory	top height of leaf stalk in vegetative swards

In white clover, petiole height was measured instead of that of stem or stolon because the heights of the true stem and stolon were not easy to measure due to the prostrate growth form. The stem of chicory at the vegetative stage was measured at the top of the leaf stalk, because true stem had not developed. The reproductive stage of chicory was not sampled during the experimental period due to being too high to handle with experimental facilities. Shoots of *Lotus corniculatus* bear trifoliate leaves continuously from tip to base, so it was not possible even to measure the height of the first bundle of leaflets from the ground level, and hence this attribute was not estimated for this forage.

Reproductive height was recorded as the first contact with the top of the flower in all forages, irrespective of its position relative to the leaf surface.

## 3.2.4.2 Point quadrat

The relative proportion and vertical distribution of the various herbage components within the sward profile was evaluated using an inclined (32.5°) point quadrat technique (Warren-Wilson, 1963; Grant, 1981).

All contacts and corresponding heights within 1 cm bands were recorded as the needle of the point quadrat passed through the sward, and each contact was firstly identified in terms of species categories of sown species, grass weed or broad-leaved weed. The contacts were further defined as morphological units, which fell into various categories for different herbages, for example, seedhead, stem (including flowering stalk), and leaf for grasses; seedhead, stem (including seedhead stalk, petiole and stem) and leaf for white clover; seedheads, stem (including stalk) and leaf for *Lotus corniculatus*; and leaf and stem (stalk) for chicory. Live and dead categories were also identified for each contact; brown coloured leaf was regarded as dead. For each pass of the needle, the height at which the needle reached the ground was also recorded to allow for ground zero calibration.

The point quadrat device was always sited to align along the long axis of the turf and the traverse was alternately positioned at opposite ends of the turf. If the number of the contacts had not reached fifty after four traverses (two traverses from each direction), more traverses were carried out until a minimum of fifty contacts were recorded. At least four full traverses were measured per turf even if more than fifty contacts were recorded.

On tall swards, because the needle could not reach ground level after one full traverse was passed through, the turf was divided into several profiles for measurement. In successive profiles, the needle always started from the terminating height of the previous measured profile and successive measurements from the top profile to the bottom profile within one vertical series were continued from the same end of the turf until the last profile in which the needle reached ground. In this case, all of the measurements of successive profiles within one vertical series ranging from the top profile to the bottom profile were regarded as one full traverse.

After ground zero correction, the point quadrat observations were expressed as the number of contacts per 2 cm of sward height and were set out graphically by a computer programme to illustrate the vertical distribution of the various herbage components within the sward profiles.

Turves were kept in the chiller when not being measured to minimize insensible loss of moisture. Most pre-grazing measurements were made within one day and the remainder of the measurements were completed by 10:00 am the following day, before turves were offered to animals.

The trays containing extracted turves were also placed in deep boxes (43 x 28 x 12.5 cm) before they were carried to the shed for feeding so that the loss of soil could be prevented.  $\cdot$ 

#### 3.2.5 Feeding procedures

#### 3.2.5.1 Preparation of the animals

The animals were penned in a feeding shed in the afternoon of the day when pre-grazing measurements were made. They were fasted overnight for 18 hrs (4:00 pm-10:00 am) before turves were offered for grazing in order to encourage grazing and standardize preparation. The animals were randomly classified into two groups, each of which was composed of three sheep and three goats. Since only six crates were available, one group was immediately introduced into metabolism crates (Plate 3.1) after the animals were led to the feeding shed, and the others were kept in the slatted floor pen adjacent to the metabolism crates. On the following day, the group of animals in the crates were fed sample turves, and then released from the crates. The procedure was repeated with the second group.

## 3.2.5.2 Feeding

The feeding session commenced between 10:00 - 10:30 am and was usually completed within two hours. The prepared turves were presented immediately in front of the animals with the long sides towards them, and at foot level (Plate 3.2), one turf at a time.

The turves were weighed to the nearest 0.1 g in the feeding shed, immediately before being offered and again after being grazed, with an electronic digital scale powered by a generator. Normally, the interval between the commencement and cessation of the feeding for each turf only lasted for a few minutes, so insensible loss over this interval due to transpiration examined in a turf tray set aside for the purpose of control was found to be negligible.

A count was kept of the number of harvesting bites taken by each animal as it grazed. Animals were allowed to make at least 12 bites, but normally 12-17 bites (see later), after which access was blocked, and the time elapsed between occurrence of the first and last bites was recorded using a stopwatch, to the nearest tenth of a second. Animals were not allowed to take more than 15-17 bites since more bites could result in overlapping which would affect estimation of bite area.

All grazing procedures were completed for one animal before commencing with the next. The turves were offered to sheep and goats alternately, and which of the two species was fed first was decided at random.

The experiment was run according to an unblocked factorial design (completely randomized design) where individuals of each animal species were treated as internal replications. The schedule of sampling dates of forage x stage of maturity combinations was randomly arranged where possible, however this was constrained by readiness with respect to sward conditions, such as, suitable height and a reasonable proportion of seedheads at the reproductive stage. On any feeding day, twelve turves of the same forage x stage combination were offered to all six individuals of each animal species in a random sequence. Therefore, all animals received all combinations of forage x stage in the same sequence, and each time, all individuals received the same combination of forage x stage.

In general, recorded biting activity was characterized both by the sound of herbage being severed and by the distinctive upward jerk of the head, with timing

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Plate 3.1 Animals were individually confined in the metabolism crates



Plate 3.2 Animals were offered the prepared turves.

continuing if the animal lifted its head to manipulate or masticate harvested herbage before it resumed grazing (Hodgson, 1982; Burlison, 1987). Any intervals over which animals interrupted both biting and chewing for any reason were excluded from the record of time spent grazing. However, the time for which animals were actively but unsuccessfully seeking acceptable mouthfuls of herbage to harvest with the head down nosing the herbage was included (Hodgson, 1982). Successive jerks of the head (more than one tearing action) in a compound biting action to sever one mouthful of herbage were considered as individual bites. The time spent actively chewing the harvested herbage at the completion of the last bite was excluded. In most cases, animals tended to prehend more bites than the stipulated 12 bites.

Animals sometimes grazed herbage from the side of a turf, rather than from the top. This was not representative of the way in which animals graze pasture naturally and also resulted in an underestimation of bite area. The use of the deep box-tray (Plate 3.2) to some extent overcame this problem. This shortcoming was furthermore improved by insertion of a sheet of metal with a height of 30 cm and as wide as the tray, into the deep box-tray on the side nearest the animal (Plate 3.2).

The animals grazed very readily from the turf trays and only on some occasions was it necessary to prolong the fasting time because some animals refused to graze some of the swards on offer. In this case, they had to be fasted one more day (42 hrs) to encourage their grazing. If an animal still failed to graze after further starvation, no further measurements were taken on that turf. No further estimation was made on the turves being sporadically grazed by the animals.

The overall sampling success rate was 97% for goats and 93% for sheep.

The turves were carried back to the chiller after grazing. The animals were released to the holding paddock where they were allowed to graze undisturbedly between the feeding runs.

#### 3.2.6 Post-grazing measurements of the sward

The remainder of the feeding day was used for the following post-grazing measurements. Only some of them could be completed within this day and others had to be shifted to the following day. All sward measurements taken after grazing were made on individual turves.

## 3.2.6.1 Residual height

Residual sward height after grazing was measured at severance level at thirty random positions evenly distributed across the complete grazed patches using a needle and avoiding disturbance to the sward. The mean of these measurements represented an average grazed height (or incisor height, Laca *et al.*, 1992a) and the grazed stratum of the complete sward profile was calculated by subtracting this height from the surface height of the ungrazed sward.

# 3.2.6.2 Bite area

The area of those patches which had been grazed was measured using a rectangular mesh frame (55 x 40 cm) mounted on four adjustable steel rods, and subdivided into 1 cm x 1 cm by threading stiff wires through holes. The adjustable frame was suspended above the entire turf and a piece of transparent acetate film was placed on the frame. The extent of the grazed patches was traced on the film with a whiteboard marker to give a permanent record of their shapes. The partially covered grids at the perimeter of the marked areas were approximated by visual appraisal. Estimations of grazed area were derived by summation of grid units wholly and partially covering grazed patches.

#### 3.2.6.3 Herbage mass remaining within grazed stratum

The turves were trimmed at the average grazed height using a horizon sampling technique (Rhodes, 1981) to estimate the herbage mass remaining within the grazed stratum after grazing. Horizon sampling was carried out using the equipment illustrated in Plate 3.3, which consisted of a frame which could be adjusted in height, and electric shears which rested on a frame and could be moved forward and backwards so as to cut the whole area of the turf at any specified height. The trimmed herbage was collected in a tank attached to the cutting head, by a modified vacuum cleaner connected to the tank.

The material cut from each turf at the grazing height was weighed immediately after being trimmed and re-weighed after being oven-dried at 110° C for 10 hrs. This fresh weight was viewed as the residual mass of the grazed stratum after grazing and added to the herbage removed by the animal during the grazing gave an estimation of the total fresh herbage mass within the grazed horizon.

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Plate 3.3A Horizontal sampling device.



Plate 3.3B Horizontal sampling device.

# 3.2.6.4 Calculation and calibration of DM% of the herbage of the grazed stratum

The ratio of dry and fresh weight of the trimmed herbage (Section 3.2.6.3) gave DM% of the herbage in the grazed stratum. This DM percentage varied between twelve turves due to variation in the grazed height across twelve animals (maximum range of variation was 5 units). The amount of herbage removed by each animal in DM terms could be derived using its corresponding DM percentage.

However, there was a time lag between grazing and subsequent trimming of the grazed horizon on the following day. This incurred a risk of overestimation of DM% since insensible loss of moisture over the interval between feeding and trimming (nearly 24 hours) could have reached a significant level even though turves were kept in the chiller. Hence there was a necessity to adjust this DM% in order to correct for the insensible loss of moisture.

After the feeding procedure was completed, the spare turf dug during sampling (see Section 3.2.3) was immediately trimmed at an average severance height of the twelve grazed turves approximated visually. This was assumed to represent the fresh condition of the experimental turves at the time when they were grazed by the animals, and thus was a true description of the DM percentage at that time. The material was weighed immediately after being trimmed and was re-weighed after being oven-dried with other trimmed herbages (Section 3.2.6.3). This DM percentage was consistently lower than the values obtained from the experimental turves and was used as a common value to calibrate the experimental turves. The calibration was made as follows:

Adjusted DM% = 1/2 (grazed stratum DM % of experimental turf + grazed stratum DM% of control turf)

The adjusted DM %, rather than the original calculated DM% was used as a DM% to convert fresh matters.

#### 3.2.6.5 Herbage mass below grazed height

The turf which had been trimmed at the average grazed height was then cut at ground level with electric shears. Any roots remaining on the cut herbage were removed. The cut herbage was thoroughly mixed and a standard subsampling technique (Grant, 1981) was used to take a quarter of the cut herbage before it was

washed. This subsample was dissected into sown species, dead material and miscellaneous, and the soil contamination of this subsample was simultaneously removed during this dissection. The dissected components were oven-dried at 110°C for 10 hours and weighed. The proportion of each dissected component was then obtained to establish a genuine proportion, in dry matter terms, of the sown herbage contained in this subsample. Summation of sown species mass in this subsample and the sown species mass in the remainder of the cut herbage gave an estimation of the herbage mass of the sown species distributed below the average grazed height.

Summation of the mass under the grazed height and the mass within the grazed stratum gave an estimation of total herbage mass of the ungrazed turf.

## 3.2.7 Calculation of the derived variables

The above direct measurements were used to determine the following variables.

## 3.2.7.1 Bite weight (BW)

Bite weight could be expressed in various ways.

- BW<sub>1</sub>: (fresh matter in absolute terms, mg FM/bite) = pre-grazing turf weightpost-grazing turf weight/bite number.
- BW<sub>2</sub>: (dry matter in absolute terms, mg DM/bite) = BW<sub>1</sub> x calibrated DM% of the corresponding turf.

This variable could also be scaled by the average live weight of individual animals over the experimental period for the purpose of comparison with the values reported in the literature. Either 0.75 or 1 (in accordance with the source of literature) was used as an exponent for this scaling.

$$BW_3$$
: (dry matter relative to live weight, mg DM/bite/kg LW<sup>0.75</sup>)  
=  $BW_2$ /kg LW<sup>0.75</sup>.  
or =  $BW_2$ /kg LW

# 3.2.7.2 Bite rate (BR)

Bite rate (BR) (bites/min) = bite number time spent biting (seconds) x 60

## 3.2.7.3 Intake rate (IR)

For convenience of comparison with the literature, the estimation of intake rate in dry matter terms was used.

Intake rate 2 (IR<sub>2</sub>) (mg DM/min) =  $BW_2 \times biting$  rate

Intake rate 3 (IR<sub>3</sub>) (mg DM/min/kg LW<sup>0.75</sup> or /kg LW) = BW<sub>3</sub> x biting rate

#### 3.2.7.4 Bite depth (BD)

Bite depth (BD) (cm): top surface height - grazed height.

Top surface height normally referred to leaf surface height and seedhead height of vegetative and reproductive swards, respectively. However, in the cases where the seedhead height was smaller than leaf surface height, leaf surface height was used to calculate this variable in both stages to avoid negative values for bite depth.

## 3.2.7.5 Bite area (BA)

Bite area (BA)  $(cm^2)$  = total grazed area/bite number The total grazed area was obtained from Section 3.2.6.2.

#### 3.2.7.6 Bite volume (BV)

Bite volume (BV)  $(cm^3)$  = bite area x bite depth

## 3.2.7.7 Mass bulk density

For the sake of distinction of this variable from the frequency bulk density derived from the point-quadrat measurements (Section 3.2.7.9), the bulk density in the sense of mass per unit volume is specifically referred to as mass bulk density.

This variable involved two estimations.

Mass bulk density of grazed stratum (mg DM/cm<sup>3</sup>) =

# DM remained in grazed stratum after grazing + DM removed by animal turf area x bite depth

Mass bulk density of whole profile (mg DM/cm<sup>3</sup>) = DM of herbage contained below grazed height + DM of grazed stratum turf area x sward top surface height

## 3.2.7.8 Leaf layer depth

Mean leaf layer depth was calculated for each turf as the difference between mean leaf surface height and mean stem height. This attribute was not calculated for *Lotus corniculatus* due to unavailability of stem height data (see Section 3.2.4.1).

# 3.2.7.9 Proportions and frequency bulk densities of plant components

A series of attributes could be derived from the point-quadrat measurements. However, among them, the proportions of leaf, stem and seedhead summed to unity, so it was inappropriate to use all three in representing relative proportions of these components and two of them (leaf and seedhead) were chosen. Similarly, the proportions of live material, together with proportions of dead material constitutes a binomial attribute with unity as a summation, and therefore only the proportion of live material was selected. The bulk density here referred to the number of hits per 2 cm band, and therefore was loosely termed frequency bulk density in order to distinguish it from mass bulk density (herbage mass per unit volume, see Section 3.2.7.7).

These parameters were calculated in terms of the grazed stratum and whole sward profiles, respectively.

Seedhead proportion = <u>number of seedhead hits</u> number of total hits

*Leaf frequency bulk density =	number of leaf hits height of sward profile (cm)
*Stem frequency bulk density =	number of stem hits height of sward profile (cm)
*Seedhead frequency bulk densi	ty = $\frac{\text{number of seedhead hits}}{\text{height of sward profile (cm)}}$

Live herbage proportion = <u>number of live herbage hits</u> number of total hits

\*: Since this study defined height of a unit band of sward profile as 2 cm, the above calculated values of these three variables in which the number of hits/cm band was unit had to be corrected to a basis of 2 cm band by being multiplied by 2. Also, these three variables involved grazed stratum and whole sward profiles. The distinction between the grazed stratum and whole sward profiles was made by using the corresponding height in the denominator.

## 3.3 EXPERIMENTAL DESIGN AND ORGANIZATION OF THE DATA

#### 3.3.1 Experimental design and construction of data sets

Table 3.2 gives details of the experimental design. Ten forages (species or cultivars) (Table 3.1) and two maturity stages of growth for each forage were sampled. The sampled swards were grazed by six sheep and six goats. Therefore, feeding embraced 10 forages x 2 maturity stages x 2 animal species x 6 replications for each species. However, as the reproductive stage of chicory was not sampled (Section 3.2.4.1), this forage was discarded from the data sets.

This involved 240 experimental units to measure and took six months to run. The measurements were consciously scheduled to be run over two experimental periods to avoid winter restriction. The first period was in part a preliminary period and only a small part of the experimental measurements could be completed within this period
after spending a month running pre-experimental exercises (see Section 3.2.3). Most measurements were conducted within the second period (Table 3.3). Four of nine forages (two legumes and two grasses, asterisked and bold-faced in Table 3.3) were sampled across the two periods to test between-period variation in grazing behaviour, and all nine forages were sampled within the second period to test effects of sward structure on grazing behaviour within one period. Table 3.3 illustrates the details of the experimental periods and the distribution of sampling dates for various forages at two stages. For convenience, period one and period two are referred to as years 1989 and 1990, respectively.

Factors	Levels	· Values
Forages	10	See Table 3.1
Maturity stages	2	Vegetative and reproductive
Animal species	2	Sheep and goats
Animals within species	6	6 sheep and 6 goats
Experimental periods	2	Period 1 (1989) and period 2 (1990)
Common forages across 2 periods	4	2 grasses and 2 clovers (asterisked in Table 3.3)

 Table 3.2
 Experimental design and construction of data sets.

The full experiment involved ten forages sampled at two maturity stages of growth, grazed by six sheep and six goats within one period, and four forages sampled at two stages grazed by the same animals across the two periods. However, chicory was not sampled at the reproductive stage due to being too high to handle with indoor grazing facilities, and therefore, this forage was discarded from the data set.

Forages	Vege	tative	Reproductive			
	Period 1 (1989)	Period 2 (1990)	<sup>•</sup> Period 1 (1989)	Period 2 (1990)		
1 Ryegrass*	8 Mar. 89	11 Jan. 90	18 Apr. 89	3 Apr. 90		
2 Browntop*	23 Feb. 89	8 Jan. 90	15 Mar. 89	18 Apr. 90		
3 Cocksfoot		27 Dec. 89		26 Mar. 90		
4 Prairiegrass		19 Feb. 90		29 Dec. 89		
5 Phalaris		2 Feb. 90		29 Jan. 90		
6 Tahora white clover*	20 Feb. 89	11 Dec. 89	21 Mar. 89	15 Jan. 90		
7 Kopu white clover*	3 Apr. 89	14 Dec. 89	4 Apr. 89	17 Jan. 90		
8 Red clover		6 Dec. 89		5 Feb. 90		
9 Lotus		21 Dec. 89	-	23 Jan. 90		

 Table 3.3
 Forages included in the two data subsets and distribution of the sampling dates.

Period 1: 20 February 1989 - 18 April 1989.

Period 2: 6 December 1989 - 18 April 1990.

For convenience, period 1 and period 2 are referred to as years 1989 and 1990, respectively, despite the fact that period 2 actually covered the duration from 6 December of 1989 to 18 April of 1990.

Two sub-sets of data were constructed and drawn from the full experiment as follows:

One sub-set (restricted data set) embraced four forages at two maturity stages (asterisked and bold-faced) grazed by six sheep and six goats across the two experimental periods (years) (4 forages x 2 stages x 2 animal species x 2 years). This sub-set was intended to assess the variation in ingestive behaviour across the two

years, with particular emphasis on the effects of the variation in animal body size over time with increasing maturity, and consequent changes of animal attributes (incisor breadth and liveweight) on the bite weight and bite dimensions of sheep and goats

Another sub-set (enlarged data set) involved nine forages at two maturity stages grazed by six sheep and six goats over the second experimental year. This sub-set involved an attempt to examine the effect of sward canopy structure on ingestive behaviour of sheep and goats based on a wide range of forages.

The two sub-sets formed the basis of data to be analyzed and dealt with in Chapter 4 and Chapter 5, respectively.

# 3.3.2 Alignment and correspondence of the variables between sward, animal and ingestive behaviour

In order to be able to relate the three sets of variables (sward, animal and ingestive behaviour), a computing data file was organized to consist of all observations for the three sets of variables. It was necessary, therefore, to align all direct measurements and derived calculations, and bring all variables into correspondence with years, forages, maturity stages, animal species and animal replications.

The variables in the sets of both sward and ingestive behaviour were obtained on the basis of individual experimental units (one replication of each treatment: years x forages x stages x animal species x replications of each animal species), i.e., a specific grazing by an individual animal on the sward of a particular forage at one stage within each period. However, in the set of animal attributes, some variables were derived based on the experimental unit, for instance, incisor breadth and live weight. In contrast, other variables, such as muzzle width, dentition width, lip length and maximum width, presumably were subject to greater variation since they were measured on soft tissue, so only means over each experimental period were withdrawn for each variable. Diagrams of incisor breadth and live weight against time over the experimental period were drawn, and specific values of the two variables corresponding to years, forages, maturity stages, animal species and animal replication were estimated from these diagrams. The values which were not available for some observations (for example, there was no value of reproductive height on vegetative swards), were treated as missing values in the format of the data file.

### 3.3.3 Statistical analysis

Statistical analysis of the data was conducted on the AgResearch network computer system, using SAS Procedures (SAS Institute, 1990).

All statistical calculations and analyses were carried out on the basis of the individual values of the observations, because use of means of the observations could to some extent hide the variability. Means and standard errors quoted refer to the least squares means and their standard errors (SAS Institute Inc. 1990).

### CHAPTER 4 RESTRICTED DATA SET FROM EXPERIMENT 1

### Effects of Permanent-incisor Breadth on Bite Weight and Bite Dimensions of Sheep and Goats

PROLOGUE During the examination of this thesis, it became apparent that the potential impact of sward variation on the differences in ingestive behaviour between years 1 and 2 in Experiment 1 may have been under-estimated by concentrating the analysis on animal variables. An additional section (Section 4.3.4) is therefore introduced to provide some assessment of this effect. However, the analyses of the relative contribution of incisor arcade breadth and live weight to differences in ingestive behaviour between years and between animal species are still relevant to the objectives of the thesis and are left largely unaltered. Additions are shown in bold, as here.

### 4.1 INTRODUCTION

While much research has focused on the effects of plant characteristics on ingestive behaviour (Hodgson & Jamieson, 1981; Black & Kenney, 1984; Laca et al., 1992a), scant attention has been paid to the influence of animal maturity and body size on ingestive behaviour. Incisor breadth and liveweight are related to animal maturity and body size (Taylor et al., 1987). There has been some investigation of the relationships between the structure of the incisor arcade and selectivity (Illius & Gordon, 1987; Gordon & Illius, 1988), between incisor breadth and herbage intake (Illius & Gordon, 1990a), between eating rate and incisor breadth (Taylor et al., 1987), and between herbage intake and allometric change in incisor breadth with body weight (Illius, 1989). All these studies showed that ingestive behaviour of grazing animals is closely related to incisor arcade structure. However, there has been less frequent examination of the effect of incisor breadth on bite weight and bite dimensions with increasing animal maturity for different species, or of the relative importance of live weight and incisor dimension in this process. The objective in this chapter is to provide a preliminary evaluation of the effects of incisor breadth on ingestive behaviour. In order to examine reasons for observed differences in bite variables between years and between animal species, particular emphasis was put on the effects of variation in incisor breadth within sheep and within goats over two time periods, and on the effects of differences in incisor breadth between sheep and goats within time on the bite weight and physical dimensions of the average bite in the sward.

#### 4.2 STATISTICAL ANALYSIS

The restricted data set generated in Chapter 3 (Section 3.3), and summarized in Table 4.1, was used as the database for this chapter.

In the analysis of variance of behaviour variables, the model comprised four main effects (year, animal species, forage and stage of maturity), and their interactions, and was structured according to a completely randomized design in which individuals of each animal species were treated as internal replications with repeated measures. However, since a major objective in this chapter was to screen the effects of animal variables on ingestive behaviour within animal species over time, and across animal species within time, attention was concentrated principally on assessing the variation in behaviour variables observed during the course of the experimental period (between the two years, ie. year effect), and observed between the two animal species at the same time (animal species effect). Other main effects and interactions will be dealt with more thoroughly in Chapter 5 using the enlarged data set.

Effects	Levels	Values
Years	2	1989, 1990
Animal species	2	Sheep, goats
Forages	4	Ryegrass, browntop, Tahora and Kopu white clovers
Stages of maturity	2	Vegetative, reproductive

 Table 4.1
 Structure of the restricted data set generated from Chapter 3.

An approach of data adjustment was employed after analysis of variance using original unadjusted data. The sequence and process of data analysis were as follows:

(1) An analysis of variance using original unadjusted data set was conducted first, through which substantial differences in bite variables between years and between animal species were identified.

(2) Then the relationships between animal variables (incisor breadth and live weight) and ingestive behaviour variables were assessed by comparing a set of unpartitioned regression equations of behaviour variables on animal variables in order to select a covariate which was assumed to result in the observed differences.

(3) After an appropriate covariate was determined, heterogeneity of the effects of the covariate on bite variables was examined by a series of statistical analysis in order to define appropriate subsets of the data for data adjustment.

(4) The data were then adjusted at an unpartitioned level through regression of bite variables against the chosen covariate (incisor breadth) in order to remove the concomitant confounding effects of the covariate from the background of the data set (Steel & Torrie, 1980; Draper & Smith, 1981).

(5) The regression equations which were used for adjustment of data were estimated on the subsets of data defined in two ways: (1) forages x animal species subsets (the first adjustment) which were intended to examine the effect of incisor breadth on behaviour within animal species over time (year effect), and (2) stages of maturity subsets (the second adjustment) which were intended to examine the effect of incisor breadth on behaviour across animal species within time (animal species effect). The two adjustments were conducted independently for different purposes.

(6) Analyses of variance were repeated using the two sets of adjusted data separately, these now being free of the effects of incisor breadth.

(7) The evaluation was made through comparing the analysis based on unadjusted data (effect of incisor breadth still present), and the analyses based on the two sets of adjusted data (effect of incisor breadth removed).

This data adjustment approach is quite different from the ordinary covariate analysis (Steel & Torrie, 1980) (see Section 4.4.1 for a detailed comparison between the two approaches).

### 4.3 RESULTS AND DATA ADJUSTMENT

A series of variables of the three data sets (sward, animal and ingestive behaviour) were measured or derived in the experiment (see Section 3.2.7 of Chapter 3). In this chapter, however, attention is focused on only some of them to screen the effects of animal variables on ingestive behaviour variables.

Bite weight 1 (mg fresh matter) was usually correlated with bite weight 2 (mg dry matter), and the latter was used since it was defined in DM terms and this was coincident with the expression of sward bulk density in this experiment. As attention was focused

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on bite weight and bite dimensions, the variables, bite depth, bite area, and bite volume were taken into account. Two animal variables (live weight and incisor breadth) were considered, and sward surface height and bulk densities (grazed and overall bulk density) were used to describe sward conditions.

### 4.3.1 Sward conditions

Table 4.2 describes details of sward conditions for the four forages at two maturity stages across two years.

The two grasses were taller than the two clover swards, but herbage bulk densities were greater for the two clovers than the two grasses in both grazed horizon and overall profiles except for the case of overall bulk density for browntop in 1989. Sward height was substantially increased as swards advanced in maturity, with the exception for Kopu white clover in 1989. However, in the swards of 1989, bulk densities decreased or changed little with the increase in sward maturity for ryegrass, browntop and Tahora, but increased for Kopu. In the swards of 1990, the bulk densities decreased or changed little for ryegrass and browntop, and this was also the case for the overall bulk density of the two clovers; but the bulk density of the grazed strata increased for the two clovers. Swards were consistently taller, but less dense except for Kopu white clover in 1990 than in 1989.

### 4.3.2 Animal variables

The live weight of sheep was approximately twice that of goats (Table 4.3), and incisor breadth was also greater in sheep than in goats (P<0.0001). A pooled ANOVA in which six individuals of each species were treated as an independent effect indicated that the variations across six sheep and across six goats were significant for live weight (P<0.05), but not for incisor breadth. Both live weight and incisor breadth increased substantially across the two years with increasing maturity of animals (P<0.001).

### 4.3.3 ANOVA of behaviour variables based on unadjusted data

Table 4.4 presents details of the ingestive behaviour variables of sheep and goats grazing four forages at two stages across two years. Table 4.5 gives significant levels of ANOVA based on unadjusted data for all main effects and the first-order interactions involved with the year effect.

Bite weight and all bite dimensions were significantly affected by all main effects (years, forages, maturity stages and animal species), except for an insignificant effect

Forages	Maturity	1989			1990			
i olages	stages	Surface height (cm)	Grazed bulk density (mgDM/cm <sup>3</sup> )	Overall bulk density (mgDM/cm <sup>3</sup> )	Surface height (cm)	Grazed bulk density (mgDM/cm <sup>3</sup> )	Overall bulk density (mgDM/cm <sup>3</sup> )	
Ryegrass	Vegetative	15.2	0.92	2.65	23.9	0.79	1.37	
	Reproductive	34.2	0.81	1.90	55.5	0.51	0.63	
Browntop	Vegetative	13.5	1.31	3.45	21.8	0.95	1.85	
	Reproductive	29.1	0.66	2.26	50.9	1.02	1.58	
Tahora	Vegetative	6.9	2.69	3.78	11.3	1.94	2.93	
white clover	Reproductive	8.2	1.90	3.58	18.1	2.09	2.71	
Kopu white	Vegetative	12.1	1.32	2.08	14.1	1.68	2.58	
CIOVEI	Reproductive	10.4	1.72	2.53	19.6	4.54	2.39	
	s.e.	0.9	0.6	0.1	0.9	0.6	0.1	

 Table 4.2
 Description of sward conditions for years x forages x stages

Table 4.3Changes in live weight and incisor breadth of six sheep and six goats over two<br/>experimental periods (two years). Overall ANOVA showed that the variation across<br/>six sheep and six goats within time was significant for live weight (P<0.05), but not<br/>significant for incisor breadth. Therefore, LSD tests are presented only for live<br/>weight. Means with different letters within columns differ at P<0.05.</th>

	Sh	өөр	Goa	ats
	1989	1990	1989	1990
Live weight (kg)	39.1 a	56.4 ab	17.9 b	28.1 a
Animal 1	(30.9-44.5)	(54.6-58.0)	(17.0-18.3)	(24.8-32.7)
2	41.3 a	58.4 a	22.0 a	24.3 b
	(39.2-43.)	(55.0-67.2)	(20.3-22.7)	(21.5-28.2)
3	39.7 a	58.6 a	22.5 a	29.2 a
	(37.5-43.4)	(57.0-60.0)	(19.8-24.5)	(27.3-33.7)
4	40.7 a	53.3 bc	19.4 ab	25.7 ab
	(39.0-43.8)	(48.0-58.5)	(18.0-24.0)	(23.2-31.7)
5	40.4 a	56.8 ab	19.0 ab	27.1 ab
	(38.0-44.5)	(36.0-59.8)	(17.3-24.5)	(25.3-31.3)
6	39.7 a	50.3 c	18.3 b	26.9 ab
	(37.3-43.0)	(46.1-61.7)	(16.7-23.7)	(25.5-30.0)
0.01	1.1	1.1	1.1	1.1
S.e.	40.2	56.3	26.9	26.9
s.e. <sup>2</sup>	0.6	0.6	0.6	0.6
<b>Incisor breadth (cm)</b>	1.75	2.88	1.45	2.42
Animal 1	(1.70-1.86)	(2.7-3.2)	(1.40-1.56)	(2.26-2.80)
2	1.96	3.16	1.34	2.24
	(1.90-2.06)	(3.02-3.20)	(1.30-1.44)	(2.10-2.65)
3	1.77	3.06	1.43	2.37
	(1.70-1.92)	(2.86-3.61)	(1.40-1.51)	(2.14-2.80)
4	1.67	3.11	1.45	2.47
	(1.69-1.83)	(2.94-3.50)	(1.40-1.56)	(2.26-3.00)
5	1.86	3.31	1.45	2.56
	(1.80-1.99)	(1.90-3.40)	(1.40-1.56)	(232-3.10)
6	1.75	2.86	1.44	2.44
	(1.70-1.88)	(2.60-3.45)	(1.40-1.52)	(2.22-2.95)
s.e. <sup>1</sup>	0.07	0.07	0.07	0.07
Means <sup>2</sup>	1.79	2.89	1.43	2.41
s.e. <sup>2</sup>	0.03	0.03	0.03	0.03

1. Standard errors of means of individual animals within years.

2. Means and standard errors over six individuals of each animal species within years.

3. The data in brackets are ranges of observed values for each individual animal within years.

of maturity stage on bite area (Table 4.5). Some first-order interactions were also significant (Table 4.5). However, as mentioned before, in this chapter only year effects and animal species effects were examined further.

The marked differences between the two years in bite weight and bite dimensions imply that animals had different patterns of grazing behaviour across two years, even when they were offered, on two different occasions, swards of the same forages at similar stages of maturity. It was considered that both sward changes, particularly in sward height, between the two years (Table 4.2) and development of animal maturity over the course of the experiment might have contributed to these differences.

#### 4.3.4 Sward effects on ingestive behaviour across two years

A thorough assessment of sward effects on ingestive behaviour will be made in Chapter 5 using the enlarged data set, and in this section, attention is concentrated on examining the relative contribution of sward effects to animal effects on the differences in ingestive behaviour across two years.

Swards were consistently taller despite being less dense, except for Kopu white clover, in 1990 than in 1989 (Table 4.2). Both liveweight and incisor breadth increased substantially across two years for both sheep and goats (Table 4.3). However, sward and animal variations across two years were strongly inter-correlated (Table 4.6). A simple assessment of the contribution of sward effects was made by using the regressions of bite variables (bite weight (BW) and bite depth (BD)) on sward height (H) derived from the enlarged data set of this experiment (Chapter 5) based on year 2 data set only (Chapter 3). Because there was no confounding between animal maturity and sward variation in this enlarged data set, the predicted increments of bite variables from the regressions derived from such an enlarged data set largely reflected sward effects.

Two pooled regressions over forages and animal species were derived as follows: BD (cm) = -6.2 (s.e. 0.7) + 0.65 (s.e. 0.02) H ( $R^2$  = 0.85 \*\*\*) (residual d.f = 214); BW (mg DM) = 156 (s.e 19.1) + 3.6 (s.e. 0.5) H ( $R^2$  = 0.18 \*\*\*) (residual d.f = 214).

Mean sward height difference between two years was 10.7 cm (Table 4.2), and the predicted increments in bite depth and bite weight from the above equations were 6.9 cm and 38.5 mg, accounting for all and 0.28 of observed increments across two years in the two variables, respectively.

As mentioned above, both sward effects, animal effects, and/or interactions may have been involved in resulting in the differences in ingestive behaviour between two years. The subsequent assessment will focus on the effects of animal attributes through an approach of data adjustment using a selected animal variable as covariate.

Animal sp	<b>becies</b>				Sh	өөр							G	oats			
Variab	les	Bite w (mg	eight 2 DM)	Bite ( (ci	depth m)	Bite (ci	area m²)	Bite v (cr	olume n³)	Bite w (mg	eight 2 DM)	Bite ( (c	depth m)	Bite (ci	area m²)	Bite v (cr	olume n³)
Forages	Stages	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
Ryegrass	Veg	134	209	9.1	11.9	9.8	12.5	90	149	96	156	8.0	8.5	7.4	11.9	59	100
	Rep	163	268	12.1	34.9	11.4	12.6	137	400	135	468	11.3	32.2	10.5	11.8	119	393
Browntop	Veg	238	174	6.3	8.9	7.5	11.0	49	95	148	189	6.0	7.1	7.1	9.6	44	68
	Rep	248	415	12.1	25.0	7.9	9.6	99	252	190	687	13.2	28.0	6.1	10.6	79	288
Tahora white clover	Veg	142	219	2.7	4.3	10.6	11.5	27	50	123	115	3.1	2.6	6.3	12.0	22	31
	Rep	158	379	4.8	9.1	10.0	11.7	48	109	83	240	3.7	3.9	5.1	10.1	21	38
Kopu white clover	Veg	150	303	5.1	6.3	14.8	11.2	75	72	99	159	4.7	3.4	11.3	9.3	55	31
	Rep	201	322	4.7	9.3	15.1	13.6	64	127	123	298	3.8	4.2	14.1	10.6	53	43
	s.e.	33	33	1.1	1.1	1.1	1.1	20	20	33	33	1.1	1.1	1.1	1.1	20	20

 Table 4.4
 Unadjusted values of bite weight and bite dimensions for sheep and goats grazing 4 forages x 2 maturity stages across two years.

Veg: vegetative, and Rep: reproductive.

Effects and interactions	Bite weight (mgDM)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm³)
Year	0.0001	0.0001	0.0003	0.0001
Animals <sup>1</sup>	0.0276	0.002	0.0001	0.0003
Forages	0.0001	0.0001	0.0001	0.0001
Stages	0.0001	0.0001	0.2386	0.0001
Years x animals	0.0148	0.0076	0.0911	0.2536
Years x forages	0.4887	0.0001	0.0001	0.0001
Years x stages	0.0001	0.0001	0.5845	0.0001

 Table 4.5
 Significant levels of ANOVA for main effects and the first-order interactions involved with year effect, based on unadjusted data.

1. Animals: animal species

Table 4.6	Correlation matrix of sward height, incisor breadth and liveweight, and
	bite weight and bite depth across forages and animal species.

	bite weight (mg DM)	bite depth (cm)	incisor breadth (cm)	liveweight (kg)
bite depth (cm)	0.58 ***			
incisor breadth (cm)	0.57 ***	0.51 ***		
liveweight (kg)	0.30 ***	0.28 ***	0.71 ***	
sward height (cm)	0.62 ***	0.94 ***	0.81 ***	0.27 ***

### 4.3.5 Animal factors influencing ingestive behaviour across two years

Preliminary regression analyses were carried out to examine the relationships between the animal variables (live weight and incisor breadth) and bite variables in order to determine an appropriate covariate to correct the animal effect. These regressions were fitted by 3 models, e.g. bite variables against incisor breadth (model 1), against live weight (model 2) and against both as a partial regression (model 3) (Table 4.7).

While model 1 and model 3 showed similar R<sup>2</sup> values, the R<sup>2</sup> value in model 2 was consistently lower than those in models 1 and 3. This suggests that live weight was less

Variables	Models	β <sub>1</sub> (s.e.)	β <sub>2</sub> (s.e.)	β <sub>0</sub> (s.e.)	R <sup>2</sup>	r.d.f
Bite weight	1	132.9 (14) ***		-63.0 (31) *	0.33 ***	190
(mgDivi)	2		3.2 (0.7) ***	107.2 (28) ***	0.10 ***	190
	3	168.6 (19) ***	-2.3 (0.9) *	-58.1 (30) (*)	0.35 ***	189
Bite depth	1	7.3 (0.9) ***		-5.5 (2.1) **	0.47 ***	190
(only	2		0.2 (0.04) ***	3.5 (1.7) ***	0.10 ***	190
	3	8.9 (1.3) ***	-0.1 (0.06) (*)	-5.3 (2.1) **	0.48 ***	189
Bite area	1	1.6 (0.4) ***		7.1 (0.9) ***	0.08 ***	184
(cm)	2		0.08 (0.02) ***	7.7 (0.7) ***	0.09 ***	184
	3	0.7 (0.6) ns	0.06 (0.025) *	7.0 (0.9) ***	0.10 ***	183
Bite volume (cm³)	1	85.0 (11) ***		-78.2 (23) ***	0.34 ***	184
	2		2.4 (0.5) ***	18.2 (20.6) ns	0.10 ***	184
	3	95.4 (15) ***	-0.7 (0.7) ns	-77.0 (23) **	0.35 ***	183

Table 4.7Regressions of bite weight and bite dimensions on incisor breadth, and on<br/>live weight by 3 models to define an appropriate covariate for adjustment of<br/>data.

 $\beta_1$ : regression coefficient of incisor breadth,  $\beta_2$ : regression coefficient of live weight,  $\beta_0$ : intercept. Model 1: incisor breadth is a predictor (independent variable), model 2: live weight is a predictor, model 3: partial regression with both incisor breadth and live weight as predictors. The figures in brackets are standard errors of coefficients. Significant levels following  $\beta_1$ ,  $\beta_2$  and  $\beta_0$  are t tests for them, and those following  $R^2$  are F tests for model. r.d.f: Residual degree of freedom.

suitable than incisor breadth to be individually employed as the covariate. Also, incorporation of live weight in the model (model 3) did not result in significant improvements of fit in terms of the  $R^2$  value. It was not worthwhile, therefore, to use live weight either alone or collectively with incisor breadth as a covariate. Incisor breadth was therefore chosen as the covariate for data adjustment, and subsequent analysis concentrated on this variable.

Logically, the unpartitioned regressions of bite variables on incisor breadth could be established on the overall data set, or on subsets of the data at any levels of the treatments, such as forages (4 subsets), stages (2 subsets), or animal species (2 subsets), or animal species x forages combinations (8 subsets), and so forth. Decisions on which level to use were made by assessing whether the effects of incisor breadth on bite weight and bite dimensions were heterogenous across the relevant partitions. If heterogeneity was encountered, separate regressions were estimated for each partition.

The variable, bite weight 2 (BW<sub>2</sub>) was chosen as a representative variable to describe this heterogeneity. Also, it was empirically considered that the forages x animal species interaction was an appropriate combination to work with for examining the effect of incisor breadth on ingestive behaviour within animal species over time. Therefore, a set of regression equations of bite weight 2 against incisor breadth was established for each combination of 4 forages x 2 animal species (8 equations) (details of these equations are given in Table 1 of Appendix 4.1):

Ryegrass sheep:	$BW_2 = 12 + 74$ incisor breadth;
Ryegrass goats:	$BW_2 = -214 + 213$ incisor breadth;
Browntop sheep:	$BW_2 = 116 + 64$ incisor breadth;
Browntop goats:	$BW_2 = -262 + 286$ incisor breadth;
Tahora sheep:	$BW_2 = -48 + 123$ incisor breadth;
Tahora goats:	$BW_2 = -31 + 94$ incisor breadth;
Kopu sheep:	$BW_2 = -51 + 129$ incisor breadth;
Kopu goats:	$BW_2 = -133 + 163$ incisor breadth;

The coefficients of determination (denoted by R<sup>2</sup>) of these equations were usually significant despite the fact that they were not very high (Table 1 of Appendix 4.1).

A comparison of these regression equations in terms of the intercept ( $\beta_0$ ) and slope ( $\beta_1$ ) for the contrasts between sheep and goats grazing the same forage and, between forages grazed by the same animal species was made by t tests (Table 4.8). There were significant differences in the regressions of incisor breadth on bite weight among forage x animal species combinations. On one hand (4.8a), the differences were highly significant between sheep and goats grazing ryegrass or browntop, but were not significant when Tahora or Kopu white clovers were offered. On the other hand (Table 4.8b), the differences were significant when goats grazed different forages, for example, between ryegrass and Tahora, and between browntop and Tahora. But sheep showed no regression differences across forages. The above heterogeneity of regression functions

- **Table 4.8** t tests of  $\beta_0$  and  $\beta_1$  values of the regression equations (bite weight 2 against incisor breadth) for the contrasts between sheep and goats grazing the same forage (4.8a), and between forages grazed by the same animal species (4.8b) to assess heterogeneity of these equations in describing the effects of incisor breadth on bite weight among the forage x animal species combinations.
- **4.8a:** t tests of  $\beta_0$  and  $\beta_1$  values of the regressions equations (bite weight 2 against incisor breadth) for the contrasts between sheep and goats grazing the same forages.

	β <sub>o</sub>	β1
Ryegrass, sheep vs goats	**	***
Browntop, sheep vs goats	**	***
Tahora, sheep vs goats	ns	ns
Kopu, sheep vs goats	ns	ns

**4.8b:** t tests of  $\beta_0$  and  $\beta_1$  values of the regressions equations (bite weight 2 against incisor breadth) for the contrasts between forages grazed by the same animal species

	_		βο			β <sub>1</sub>				
Animal species	Animal Forages species		Tahora	Kopu	Browntop	Tahora	Kopu			
Sheep	Ryegrass	ns	ns	ns	ns	ns	ns			
	Browntop		ns	ns		ns	ns			
	Tahora			ns			ns			
Goats	Ryegrass	ns	*	(*)	ns	**	ns			
	Browntop		*	(*)		***	*			
	Tahora			ns			ns			

 $\beta_0$ : intercept of regression equation.  $\beta_1$ : slope of the regression equation.

for incisor breadth on bite weight indicated the need to adjust for incisor breadth variation at the level of forage x animal species combinations.

Similarly, there was a heterogeneity of regression functions between the two stages of maturity (Table 3 of Appendix 4.1), and therefore the data also needed adjusting at the level of maturity stages. As outlined earlier, these two adjustments were used independently for different purposes.

The detailed procedures of the two data adjustments are given in Appendix 4.1.

# 4.3.6 ANOVA of behaviour variables based on the first adjustment of the data

Adjusted values of bite weight and bite dimensions based on the first adjustment for 2 animal species x 4 forages x 2 stages x 2 years are given in Table 4.9 (corresponding to Table 4.4 which presents unadjusted values).

Analyses of variance using this adjusted data set showed that there were no significant differences between two years in any variables (Table 4.10), in contrast to highly significant differences before the adjustment (Table 4.5).

## 4.3.7 ANOVA of behaviour variables based on the second adjustment of the data

Table 4.11 summarizes the adjusted values of the bite variables obtained from the second adjustment (compared to Table 4.4 presenting unadjusted values).

Analysis of variance using this adjusted data set indicated that there were no significant differences between sheep and goats in bite weight, bite depth or bite volume (Table 4.12), in comparison to significant differences in these variables before the adjustment (Table 4.5). However, the variation in bite area was reduced but not eliminated by this adjustment (Table 4.12).

### 4.4 DISCUSSION

### 4.4.1 Statistical approach employed in the data adjustment

In these analyses, the data were adjusted from the unpartitioned level of variance by the regression of the chosen covariate (incisor breadth) on bite variables. This was done on subsets of the data as described earlier. This approach removed the confounding variable incisor breadth (Steel & Torrie, 1980; Draper & Smith, 1981). Subsequent analysis of variance was carried out after the effect of the confounding covariate was removed. The subsequent ANOVA then partitioned that adjusted data into its model 

 Table 4.9
 Adjusted values of bite weight and bite dimensions of sheep and goats grazing 4 forages x 2 stages across two years based on the first adjustment (corresponding to Table 4.4 presenting the unadjusted values of these variables).

Animal sp	Sheep					Goats											
Variables		Bite weight 2 (mgDM)		Bite depth (cm)		Bite area (cm²)		Bite volume (cm³)		Bite weight 2 (mgDM)		Bite depth (cm)		Bite area (cm²)		Bite volume (cm³)	
Forages	Stages	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
Ryegrass	Veg	186	186	16.8	9.2	10.7	12.1	180	113	209	132	14.1	7.2	8.7	11.4	123	82
	Rep	201	199	18.5	23.4	12.1	11.4	209	270	237	287	17.5	21.1	11.5	10.0	197	257
Browntop	Veg	280	163	10.0	7.5	8.5	10.4	85	78	260	137	10.8	6.4	8.7	8.8	94	56
	Rep	290	332	16.9	17.9	9.0	8.2	150	181	361	430	19.0	19.2	7.7	8.3	149	185
Tahora white	Veg	201	168	3.9	3.1	10.6	11.5	41	38	153	96	3.1	2.6	8.9	9.6	29	24
	Rep	218	293	6.1	7.7	10.0	11.7	62	94	123	197	3.6	3.9	7.7	7.3	28	31
Kopu white clover	Veg	204	254	6.4	5.1	14.2	11.8	91	59	162	113	4.6	3.4	9.9	10.5	48	38
white clover	Rep	256	262	5.6	7.9	14.5	14.3	79	110	185	233	3.8	4.3	12.7	12.0	46	50
	s.e	34	34	1.3	1.3	1.1	1.1	22	22	34	34	1.3	1.3	1.1	1.1	22	22

Veg: vegetative, and Rep: reproductive.

Table 4.10	Comparison of the year effect on the values of bite weight and bite
	dimensions between the pre-adjustment and post-adjustment (the first
	adjustment).

Variables	Pre-adjustment				Post-adjustment		
-	1989	1990	s.e.		1989	1990	s.e.
Bite weight (mgDM)	152	288	8.2 ***		226	214	8.6 ns
Bite depth (cm)	7.6	12.5	0.3 ***		10.1	9.8	0.3 ns
Bite area (cm <sup>2</sup> )	9.7	11.2	0.3 ***		10.3	10.6	0.3 ns
Bite volume (cm <sup>3</sup> )	71	140	5 ***		105	102	6 ns

components (forages, stages, animal species, years, etc). This approach is different from the ordinary ANOVA with covariance control (conventional covariate analysis) in which regression with the confounding covariate is conducted at residual error level only (Steel & Torrie, 1980). The purpose of that analysis is to reduce the residual mean square via the concomitant variable (Steel & Torrie, 1980).

In this analysis, the unpartitioned approach was used rather than the conventional covariate analysis, because of the need to adjust all terms in the model rather than just reduce the error term. The unpartitioned adjustment completely removes the effects of the covariate from the background of the data set and then allows ANOVA to re-analyze without the effect of the covariate (Steel & Torrie, 1980). If after unpartitioned adjustment the re-analyzed ANOVA showed no significant differences between the treatments, that implies that the significant differences prior to this unpartitioned adjustment were attributable to the effects of the covariate. However, if conventional covariate analysis showed no significant differences between the treatments after error term reduction, it can be assumed that the covariate is accounting for some of the error term, and the significant differences existing before the error term reduction are due only to the amount of error accounted for by the covariate.

1990 **Animal species** 1989 Variables Bite weight 2 Bite depth Bite area Bite volume Bite weight 2 Bite depth Bite area **Bite volume** (cm<sup>3</sup>)  $(cm^3)$  $(cm^2)$ (mqDM) (cm)  $(cm^2)$ (mgDM) (cm)Forages sheep sheep goats sheep Stages sheep goats sheep goats qoats sheep qoats sheep goats goats sheep goats 9.5 8.8 8.2 Ryegrass Veq 154 139 9.0 10.4 99 79 161 140 10.8 10.9 11.4 128 93 Rep 210 244 15.3 18.6 11.8 11.3 171 198 91 369 23.0 25.6 11.2 11.0 273 323 Browntop Veq 258 191 6.8 7.0 8.1 8.5 58 64 127 173 7.8 6.7 9.4 9.1 74 61 Rep 12.9 9.8 130 325 321 17.4 22.0 8.5 7.1 154 174 235 586 21.2 8.3 218 Tahora white Veq 161 166 3.1 4.1 11.2 7.7 36 42 177 102 3.3 2.3 10.1 11.6 31 25 clover 235 12.5 10.6 234 3.6 10.0 Rep 214 10.0 6.2 104 116 297 3.5 11.1 51 34 5.5 9.8 8.9 26 Kopu Veq 161 136 5.3 15.1 12.5 80 71 260 146 5.3 3.1 53 white clover Rep 38 257 238 8.0 11.5 15.5 14.9 105 136 241 292 3.9 3.8 13.0 10.5 68 34 34 1.3 1.3 1.1 1.1 22 22 34 34 1.3 1.3 1.1 1.1 21 21 s.e.

 Table 4.11
 Adjusted values of bite weight and bite dimensions based on the second adjustment for sheep and goats grazing 4 forages x 2 stages across two years (corresponding to Table 4.4 presenting unadjusted values of these variables).

Veg: vegetative, and Rep: reproductive.

Variables	Pr	a-adiustm	ont	Pr	st-adjustr	nent
Vanables		e-aajustin				
	sheep	goats	s.e.	sheep	goats	s.e.
Bite weight (mgDM)	233	206	8 *	210	229	9 ns
Bite depth (cm)	9.0	10.4	0.3 **	9.5	10.1	0.3 ns
Bite area (cm <sup>2</sup> )	11.3	9.6	0.3 ***	10.9	10.0	0.3 *
Bite volume (cm <sup>3</sup> )	90	115	5 ***	101	106	6 ns

Table 4.12Comparison of the animal species effect on the values of bite weight and<br/>bite dimensions between the pre-adjustment and post-adjustment (the<br/>second adjustment).

# 4.4.2 Effect of incisor breadth on behaviour variables within animal species over time (the first adjustment)

Significant differences in bite weight and bite dimensions between the two years which existed in unadjusted data completely disappeared after the first adjustment (Table 4.10). This suggests that the highly significant differences in bite weight and bite dimensions displayed between the two years within sheep and within goats could be largely ascribed to variations in incisor breadth within the animal species over time.

However, the range of variation in incisor breadth within animal species (Table 4.3) over the whole period (from February 1988 to April 1990) over which the experimental measurements were run could have been contributed from two sources. Firstly, variation across individual animals within time and, secondly, the variation within individual animals over time. The first source was almost excluded by the fact that there was no significant difference in incisor breadth across either six sheep or across six goats within time. Therefore, the range of variation in incisor breadth within sheep and within goats was due mainly to increases within individual animals over time (year effect P<0.001), rather than to variation across individuals within time. This provided evidence of the consistent effects of the incisor breadth on bite weight and bite

dimensions, and substantiated the view that the variation in bite weight and bite dimensions occurring within sheep and within goats across the two years could have been brought about by the increase of incisor breadth in individual animals as they aged over the course of the experiment.

As mentioned above, the effects of sward factors and animal attributes on ingestive behaviour were confounded across two years. Further experimentation with controlled variation in sward conditions over time would be required to isolate these two sources of variation in order to clarify the effects of animal maturity on ingestive behaviour.

# 4.4.3 Effect of incisor breadth on bite parameters between animal species within time (the second adjustment)

Schwartz and Ellis (1981) considered that body size, mouthpart morphology and gut morphology and function may all make contributions to the differences in ingestive behaviour between animal species. There has been some evidence on relationships between incisor arcade structure and selection of diet niche across animal species (Gordon & Illius, 1988), and between allometric relations of bite weight and body size of animal across species (Illius & Gordon, 1987). The breadth of the incisor arcade was assumed to be an important determinant of the rate of herbage intake in grazing ruminants (Illius & Gordon, 1987). Broad and flat incisor arcades probably give rise to an advantage to grazers, whereas browsers have narrower and more pointed incisor arcade, leading to a greater and more accurate selection of plant components (Gordon & Illius, 1988). However, there is no comparable information on the relationship between incisor breadth and bite weight and bite dimensions across animal species.

In the current study, significant differences between sheep and goats in bite weight (P<0.05), bite depth (P<0.01) and bite volume (P<0.001) which were displayed before adjustment of the data set (Table 4.5) completely disappeared after the second adjustment (Table 4.12). This suggests that the difference in incisor breadth between sheep and goats could explain, at least partially, the discrepancies between the two animal species in the amount of herbage harvested per bite and in the depth to which animals inserted the mouth to sever herbage.

However, the variation in bite area was not completely eliminated by this adjustment despite a reduction (Table 4.12). This suggests that incisor arcade breadth exerts less effect on bite area than on bite depth for both sheep and goats, and hence

is not a useful attribute for predicting bite area. This was reinforced by the fact (Table 4.7) that the incisor breadth accounted for much more variation in bite depth than in bite area in the functional relationships (higher R<sup>2</sup> for bite depth than bite area), and therefore bite depth was more closely related to incisor arcade breadth than was bite area during the growth of animals. The weak functional relationship between bite area and incisor breadth was a consequence of the small and erratic variation in bite 4.3) across two years. Increasing incisor arcade breadth with increasing maturity allowed the animals to increase bite weights through increase in bite depth rather than in bite area, in agreement with the findings of Illius (pers. com.); however, in this particular case, the difference in sward height between two years has confounded with the effect of incisor breadth. The reason for much less effect on bite area compared to bite depth was unclear. This will be explored further in Chapter 8 (General Discussion), taking the information from other experiments into account.

### 4.4.4 Relative importance of incisor breadth to live weight

Although there is limited information on the relative importance of incisor breadth and live weight in affecting bite weight and bite dimensions of grazing animals, there has been previous evidence on the relationship between body size and other components of ingestive behaviour (Taylor & Murray, 1987; Taylor *et al.*, 1987; Demment & Greenwood, 1988). However, there is lack of agreement in the literature about an appropriate parameter to use to explain variations in the components of ingestive behaviour during the growth of animals.

The model developed by Demment and Greenwood (1988) showed that net rate of energy digestion per unit of time and bite weight (g DM/bite) decreased with declining body weight. Taylor and Murray (1987) used live weight to predict eating rate. Body weight was also used by several other researchers to explain the variation in ingestive behaviour with increase in maturity of animals (Allden & Whittaker, 1970; Hodgson & Jamieson, 1981). However, it was argued (Illius, 1989) that expressing intake as an allometric function of body weight must be an oversimplification unless intake is constrained by some weight-related mechanism. Taylor and Murray (1987) suggested that during the growth of animals, maximum intake rate was determined more by the size of the buccal cavity than by body weight, because buccal cavity dimensions were less affected by variation in nutrition than the body as a whole. Thus, incisor breadth was preferred to body weight as a more useful description of physiological maturity in the model developed by Taylor et al. (1987), because live weight became less satisfactory at low levels of feeding and also on high feeding levels following a period of undernutrition (Taylor et al., 1987). On the contrary, Penning et al. (1991b) reported that bite weight, intake rate and daily herbage intake were all related to mean liveweight of individual animals over the experimental period (bite weight increased by 0.7 mg/kg liveweight), and the incisor arcade breadth was not related to liveweight or any measured behaviourial variables. Unfortunately, they failed to give any possible explanation about the contrast between this result and the research where a relationship was found between incisor arcade breadth and bite variables across species (Gordon & Illius, 1988). The lack of relationship between these quantities in the work of Penning et al. (1991b) probably was because the experimental period was not long (13 July - 19 October, 1989), and the variation in incisor breadth over this period was less significant compared to the variation in liveweight, in contrast to the current data set.

The present data set was collected over a period of fifteen months (Tables 3.3) (year 1: 20 February 1989 - 18 April 1989; year 2: 6 December 1989 - 18 April, 1990). The variation in incisor breadth was highly significant across the two years (Table 4.3), but was not statistically significant within the second experimental period (see Section 5.3.1.2 of Chapter 5). This study clearly indicated that bite weight and bite dimensions of sheep and goats had far stronger functional relationships with incisor breadth than with live weight. This substantiates the view that incisor breadth exerted more consistent and more important effects on ingestive behaviour than did live weight and therefore was a more appropriate variable to explain the variation in ingestive behaviour with increasing animal maturity.

However, it was conservatively considered that the close relationship between incisor breadth and ingestive behaviour might not be necessarily a direct causative effect of incisor breadth alone; it probably is a reflection and a consequence of combined effects of increases in body size, liveweight, mouth dimensions, buccal cavity, eating ability and prehension power, enabling animals to expert a greater force to harvest herbages. All these aspects are related to an increase in incisor breadth, but incisor breadth may not be a monotonic effect. The reason for the better functional relationship for incisor breadth than other animal attributes, particularly to liveweight, might be due, in part, to less fluctuation and less sensitivity of incisor breadth to the external and nutritional effects.

### 4.5 CONCLUSIONS

- Both the sward changes and the development of animal maturity across two years could have contributed to the substantial differences in ingestive behaviour observed between two years.
- 2. For the sward effects, the increases in sward height across two years could have explained 28% of variation in bite weight and all the variation in bite depth between two years.
- 3. For the effects of animal attributes, incisor arcade breadth had a more functional relationship with bite weight and bite dimensions than did live weight, and therefore, incisor breadth was a more appropriate variable to explain the variation in the components of ingestive behaviour with increasing animal maturity.
- 4. The discrepancies between sheep and goats in bite weight, bite depth and bite volume resulted (at least in part) from the difference in incisor breadth between the two species.

### **CHAPTER 5**

### ENLARGED DATA SET FROM EXPERIMENT 1

The Effects of Sward Canopy Structure on the Components of Ingestive Behaviour and Bite Dimensions of Sheep and Goats Grazing a Wide Range of Swards

### 5.1 INTRODUCTION

Previous grazing studies using homogenous swards (Hodgson & Jamieson, 1981; Black & Kenney, 1984; Burlison *et al.*, 1991; Penning *et al.*, 1991a) have shown that bite weight is the grazing behaviour variable which has most influence on total daily herbage intake and is most sensitive to variation in sward conditions. It has been generally agreed that decrease of bite weight due to constraints of sward structure cannot usually be adequately compensated for by increasing the number of bites (Jamieson & Hodgson, 1979b; Penning, 1986; Phillips & Leaver, 1986) or time spent in grazing (Stobbs, 1973a; Hodgson, 1986). However, there is some uncertainty as to the effect of sward characteristics on bite weight and bite dimensions, and the interrelationships between bite weight and bite dimensions.

Most studies on ingestive behaviour and herbage intake have involved sheep and cattle (Black & Kenney, 1984; Mursan *et al.*, 1989; Burlison *et al.*, 1991; Laca *et al.*, 1992a). Information for goats is scant in spite of some anecdotal reports on diet selection (Clark *et al.*, 1982; 1984; Hughes *et al.*, 1984; Poppi *et al.*, 1987; Nicol *et al.*, 1987; Radcliffe & Townsend, 1988; Lambert *et al.*, 1989), particularly in New Zealand, concerning their effects on grass/clover balance in mixed pasture and on browsing preference which leads to biocontrol of gorse and other woody weeds (McCall & Lambert, 1987).

The reliability of the results obtained from observations based on large-plot grazing trials has often been questioned due to lack of general control of grazing conditions, with particular regard to the accuracy of the bite dimension measurements. But techniques employed recently in which animals were confined in crates (Burlison, 1987; Burlison *et al.*, 1991), or penned (Mursan *et al.*, 1989; Betteridge *et al.*, 1991) and allowed to graze defined swards have provided the opportunity to overcome this drawback.

In some studies, variations in canopy structure were produced in swards by pregrazing trimming (Mursan et al., 1989; Betteridge et al., 1991) or by using highly standardised tray-grown swards (Mitchell et al., 1991), or by constructing artificial swards with high uniformity (Black & Kenney, 1984; Ungar et al., 1991; Laca et al., 1992a & b). These studies examined the influences of sward structure on grazing behaviour in more mechanistic terms. Swards contrasting in plant species, and in physical maturity or stages of the growth within a species have seldom been studied. However, the key relationships generated from such simplified circumstances may not be consistently applied to swards where a great variation in canopy structure exists, because the results may be significantly influenced, complicated or mediated by interaction between the grazing animal and forage species, or by interaction between the grazing animal and plant growth stage. It is probable that the interactions may be more important and more dominant than main effects under certain circumstances. Therefore, the conclusions drawn from highly controlled swards have a limited ability to be extrapolated to real grazing situations. Also, the important principles elucidated in the above studies were mainly achieved using grasses as the grazed materials. However, the relationship established for grass pastures may not apply for legume pastures, because the two types of pastures are quite different in growth habit, which influences sward canopy structure (Kenney & Black, 1986).

The objectives of the present experiment were to contribute to the understanding and quantification of the relationships between the sward canopy characteristics and the components of ingestive behaviour and of bite dimensions of grazing livestock, and to screen response patterns of sheep in comparison with goats to variation in sward structure under identical sward conditions. This was carried out using a wide range of swards with contrasting structural characteristics, achieved by deliberately selecting a series of forages offering contrasting growth habits, and by sampling them at two maturity stages for each forage.

### 5.2 STATISTICAL ANALYSIS

### 5.2.1 Introduction

The enlarged data set generated from Chapter 3 (Section 3.3.1) summarized in Table 5.1 is used as the data base of this chapter.

After assembling one large data set with the major variables of sward, animal and ingestive behaviour, the variation in these variables between 2 animal species, among 9 forages, between 2 stages of maturity, and among their interactions was examined by analysis of variance; and the key relationships between the sward and ingestive behaviour variables were investigated by analyses of correlation and regression.

Factors and reps	Levels	Values
Animal species	2	Sheep and goats
Forages	9	see Table 3.1
Maturity stages	2	Vegetative and reproductive
Animal replications within species	6	6 sheep and 6 goats

Table 5.1	Experimental	design a	and data	structure	generated	from (	Chapter	3
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Analyses of variance included univariate analysis of variance (ANOVA), multivariate analysis of variance (MANOVA) and multiple discriminant function (MDF). Correlation analysis involved canonical analysis. Regression analysis involved multiple regression analysis.

In addition to the conventional univariate analysis of variance, multivariate analyses were used to explore the salient features of the complex data set generated. Since multivariate analyses have not been widely applied in biological research, the important principles of the method, as applied to the current study, will be outlined.

Multivariate analysis is the simultaneous analysis of two or more variables (Lindeman *et al.*, 1980) to assess treatments on the basis of all variances and covariances jointly. An important advantage over univariate analysis is that it takes all information in the data into account simultaneously, including covariance among all

variables. When covariance exists among the variables, the univariate analysis of variance is biased (Cooley & Lohnes, 1971). That is, tests on the individual means for a single variable are not independent from parallel tests on other variables and therefore such tests should not logically be applied (Kendall, 1975). A major risk under circumstances where covariances exist, is that the variable which might be analyzed univariately is an unknown mixture of all the variables with which it is correlated. In this case the interpretation of results revealed by univariate analysis needs more caution. Where a number of variables are to be analyzed in concert, multivariate analysis not only takes proper account of the correlations between the data, but also reduces the risk of type I statistical error where the treatment differences for one variable are declared significant by pure chance (Manly, 1986).

There were two reasons for use of multivariate techniques in analyzing this set of data. Firstly, it was assumed that covariances or correlations existed between two or more variables examined in either the set of sward attributes or the set of behaviour attributes (see Appendix 5.5). Secondly, it seemed that the data set involving the effects of three factors (animal species, forages and maturity stages) revealed, by univariate analysis, a very complex pattern at the levels of the main effects and their interactions, in terms of simple comparisons of each single variable concerned. Hence it was appropriate to overview the gross relationships and overall patterns at these different levels between the various treatments in terms of combinations of these variables. These multivariate techniques allowed the overall patterns of variation in the set of sward variables and in the set of behaviour variables to be screened, in their own right.

### 5.2.2 Analysis of variance

Analysis of variance was balanced with respect to treatments and external replications, but imbalanced with respect to internal replication (due to some missing values within the experimental units). The model was constructed as a completely randomized model in which 6 individuals of each animal species (i.e. 6 mini-swards, one for each animal) were treated as repeated measures. Although probability levels of P<0.05 were considered statistically significant, P-values from 0.05 to 0.1 were also reported to enable consistent interpretation of related variables.

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The model comprised three main effects (animal species, forages and maturity stages), three first order and one second order interactions. However, since nine forages were sampled at two maturity stages of growth (yielding eighteen types of swards) in the analysis of sward variables attention was only paid to main effects and the interaction of forages x stages. For the animal variables (liveweights etc.), the only sensible and logical analysis was to examine the animal species effect. In the analysis of behaviour variables, the variation was evaluated for all main effects and interactions.

The set of sward variables was examined by using ANOVA, MANOVA and MDF approaches, and the set of animal variables was analyzed by ANOVA. The set of ingestive behaviour variables was assessed by ANOVA, first in analyses involving all nine forages individually and then in analyses in which the forages were combined into two contrasting herbage categories (grass vs. legume), and afterwards by MANOVA and MDF techniques.

### 5.2.2.1 Univariate analysis of variance (ANOVA)

The conventional univariate analysis of variance (ANOVA) was used to examine the variables one by one, as a preliminary approach.

Where there were more than two levels, and the associated F-test showed significance, multiple comparisons between the levels were made. Since the number of pairs of useful comparisons in the current study was small (less than ten) (see "Results" sections), the least significant difference (LSD) (P<0.05) was used, instead of Duncans' test for such comparisons (Balaam, 1963). A protected LSD was used, i.e. comparisons were made if the F-test was significant also. LSD values were calculated in the usual way (Steel & Torrie, 1980), at P=0.05. Standard error of least squares means from overall ANOVA, and the residual degrees of freedom of overall ANOVA were used in the LSD equation.

Additionally, a t-test was conducted where the problems involved comparisons between two values (such as comparison of intercepts or slopes between two equations) using the formula (Steel & Torrie, 1980):

$$t = \frac{Y_1 - Y_2}{\sqrt{s.e_1^2 + s.e_2^2}}$$

Where  $Y_1$  and  $Y_2$  are two compared values, s.e<sub>1</sub> and s.e<sub>2</sub> are standard errors of two compared values.

# 5.2.2.2 Multivariate analysis of variance (MANOVA) and multiple discriminant function (MDF)

Since multivariate procedures have been used to only a limited extent to evaluate this kind of data, it is appropriate to precede description of results with a brief outline of the principles involved.

### 5.2.2.2.1 Some concepts underlying principles of multivariate analysis

The understanding of multivariate methods is greatly facilitated by the use of matrix algebra, because matrix algebra is the language of linear functions, upon which multivariate analysis depends (Morrison, 1976). Crucial to most multivariate techniques is the assembly of variances and covariances of the data set into a square matrix **D** of size p x p, where p is the number of variables (Morrison, 1976). Matrix **D**, called the dispersion, or variance-covariance matrix, has sample variances ( $s^2$ ) as diagonal elements and sample covariances (cov) as off-diagonal elements.

The matrix provides estimates of eigenvectors which are then used to define a series of constrained equations, which leads to an eigen problem (Morrison, 1976)( details will be presented in next section).

### 5.2.2.2.2 MANOVA and MDF

MANOVA tests the differences among the multivariate means of several treatments or populations and may be viewed as an extension of univariate analysis of variance (ANOVA) to the case in which the dependent variable is a vector rather than a scalar (Cooley & Lohnes, 1971; Lindeman *et al.*, 1980).

MANOVA considers the multivariate generalization of the analysis of variance for testing the equality of mean vectors of several populations (Morrison, 1976). It involves partitioning the matrix of total sums of squares and cross products, usually referred to as **T** (for total), in a manner that is identical to the partitioning of the sums of squares in univariate analysis of variance (Cooley & Lohnes, 1971; Lindeman *et al.*, 1980). The matrices for hypothesis and error are identified usually as **H** and **E**, respectively. It is noteworthy that the diagonal elements of **T**, **H** and **E** are the sums

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of squares for the corresponding partitions of the univariate model. In univariate analysis of variance, the optimal testing criterion is the F-test (or the sample variance ratio). Univariate hypotheses with the F statistic can be generalized to the multivariate situation merely by replacing the F-ratio sums of squares by their matrix extensions **H** and **E** (Morrison, 1976). Four test statistics have been developed, and all are related to **H** and **E** eigenvalues and eigenvectors. The four tests are: Wilks' Lamda, Pillai's Trace, Hotelling-Lawley Trace and Roy's Greatest Root. Wilks' Lambda ratio criterion is recommended the most widely (Press, 1972; Lindeman *et al.*, 1980), and it is used here. This test is analogous to the coefficient on non-determination in multiple regression, as shown below:

$$\Lambda = \frac{|\mathbf{E}|}{|\mathbf{T}|}, \text{ or } \frac{|\mathbf{E}|}{|\mathbf{H} + \mathbf{E}|}$$

The determinants of **E** and **T** (H + E) are scalar indices of multivariate generalized variance and hence the ratio is one of within-groups error "variance" to total "variance". For the univariate case, the F value and Wilks' criterion are related inversely (Morrison, 1976; Lindeman *et al.*, 1980) and in the multivariate situation, the larger the true treatment differences, the larger the denominator will be and hence the smaller the value of Wilks' criterion (Cooley & Lohnes, 1971; Lindeman *et al.*, 1980). Rao has developed an F approximation to Wilks' lamda (Cooley & Lohnes, 1971).

MANOVA and MDF were performed using the command, "MANOVA" with "Canonical" option in the GLM procedure of the SAS package (SAS Institute Inc, 1990).

. Where there are overall significant differences between treatments according to MANOVA (Rao's F from Wilks' Lambda criterion), it is most useful to determine the linear combination of the original variables which is accounting for maximum discrimination between the treatments (Cooley & Lohnes, 1971; Morrison, 1976; Lindeman *et al.*, 1980). Multiple discriminant function (MDF) is appropriate to achieve this goal (Cooley & Lohnes, 1971; Overall & Klett, 1972; Morrison, 1976; Lindeman *et al.*, 1985).

Use of MDF can gain an overview of the model effects (treatment main effects and interactions) on the variables considered jointly. It can be viewed as the discriminator of MANOVA, analogous to the least significant difference of ANOVA.

The number of discriminant functions (MDF) for a given problem is equal to the smaller of p, the number of variables (p=5 in the present study) and q-1, where q is the number of groups or treatments (in the current study, q=2 for the main effects, animal species and maturity stage; q=9 for the third main effect, forage; q=18 (9x2) for the first order interaction of forage by animal species, and so forth). To estimate these discriminant functions, the eigenvalues of  $E^{-1}H$  need to be calculated, together with their associated eigenvectors. The latter are the coefficients given to each variable in constructing the linear discriminators. The prime solving rule for establishing the discriminant functions is to maximize the ratio of amongst-groups ("hypothesis") to the within-groups ("error") sums of cross-products matrices. The ratio is termed the discriminant criterion,  $\lambda$ , and may be represented as

$$\lambda_{i} = \frac{\mathbf{v}_{i} \cdot \mathbf{H} \mathbf{v}_{i}}{\mathbf{v}_{i} \cdot \mathbf{E} \mathbf{v}_{i}}$$

where  $\lambda_j$  is the discriminant criterion for the j-th (j=1...m, where m is the number of solutions) discriminant function, H and E are the hypothesis and error sum of crossproducts matrices, respectively. Also,  $\mathbf{v}_j$  and  $\mathbf{v}_j$ ' are the eigenvector and its transpose for the j-th function. In order to achieve a finite number of solutions to the problem, constraints are imposed on the solution such that for a given discriminant function, j, premultiplying the eigenvector  $\mathbf{v}_j$  by its transpose equals unity, that is  $\mathbf{v}'_j\mathbf{v}_j = 1$ . Another restriction is that the solutions for successive functions are orthogonal (uncorrelated), that is.  $\mathbf{v}_j'\mathbf{v}_{j'} = 0$  (j≠j'). Whenever a series of equations have constraints, the solution resolves into an eigen problem (Morrison, 1976).

The solving function  $(\theta_i)$  may be written as

$$\theta_{j} = v_{j}'(E^{-1}H)v_{j} - \lambda_{j}(v_{j}'v_{j} - 1) - k_{j}v_{j}'(E^{-1}H)v_{j-1}$$

Where all terms are as defined previously and  $\lambda_i$  and  $\kappa_i$  are Lagrange multipliers for the j-th solution. Differentiation of  $\theta_i$  with respect to  $\mathbf{v}_i$  and maximisation of the resulting derivative yields for the first (and subsequent) solutions. This leads to an equation of the general form

The outcome is a typical eigen equation, as expected (Morrison, 1976). The largest eigenvalue ( $\lambda$ ) and its associated eigenvector define the linear function that gives the maximum F value for the hypothesis defined by a given H and E and hence is the best discriminator amongst the treatments viewed jointly across all variables. In fact, it is the best possible discriminator using those variables (Cooley & Lohnes, 1971). The second largest eigenvalue and its associated eigenvector (characteristic vector) define a second function providing the second largest F value and the second best discriminator amongst the treatments, and so forth. Therefore, the printout produces functions which are sequenced from the greatest to the least with regard to the extent to which they discriminate between treatments (groups). It is hoped, parsimoniously, to use only one or two discriminant solutions to account for as much of the information of the data dispersion as possible (Cooley & Lohnes, 1971), as this will facilitate interpretation. The total discriminatory power and the proportion of discriminant power due to a specific function are presented in the printout. Decision on the minimum number of solutions needed can be based on the cumulative proportion of the dispersion accounted for by successive solutions. Empirically, a satisfactory parsimonious set of discriminant functions for most practical purposes is that minimum set of functions which accounts for 70-80% of the data dispersion (Gordon, pers. com.).

The multiple discriminant functions so generated can be difficult to interpret further due to the frequently mixed scales of the original characters plus the variability in the data. Also, several solutions may be required, as determined by the cumulative proportion criterion. That is, parsimony may be weak, and the situation remains complex, despite superior discriminatory ability. A description of what a discriminant function measures must be based on the relative magnitudes of each variable in the function (Cooley & Lohnes, 1971; Lindeman *et al.*, 1980). To aid interpretation, the differences in scaling and/or variability among the set of variables can be overcome by standardising the elements of the eigenvector for the function of interest to prevent a numerically large variable from overpowering a numerically small one (Cooley & Lohnes, 1971). This is achieved by calculating standardised scores of the treatments for each discriminant function. This information may be used to determine the relative importance of the variables in contributing to discrimination between the treatments and is analogous to the use of standardised partial regression coefficients (Steel & Torrie, 1980). The original variables can be standardised value of each variable by the corresponding standardised coefficient (called "Standardised Canonical Coefficient " by SAS) in MDF printout, and the summation of the scores for all variables provide a net score of the treatment for this discriminant function. That is:

Score = 
$$a_1 X_{1n} + a_2 X_{2n} + ... + a_p X_{pn}$$

Where:

 $X_n$  denotes the standardised value of the n th observation from a data set of N observations, for each of the 1...p variables in the analysis.

 $a_1 \dots a_p$  are constants which are coefficients from "Standardised Canonical Coefficient Matrix".

The calculation of scores for each function was conducted using the program, "SCOREST" (Gordon pers. com.). Because some standardised scores may be negative, a constant was added to all scores. Both the original Z-variables and the standardised scores are scale free and have an equal variance of unity.

'The correlations between the n discriminant scores in the i th discriminant function and the original variables are often termed structure matrix (called "Between Canonical Structure" by SAS). This shows the partition - classifier association between the score and the original variables, and can be used to interpret the features of the discriminant functions. An interpretation scheme has been presented by Gordon (pers. com., see next section). One property of these correlation coefficients is that when squared across the j discriminant functions, they sum to unity for each of the p

variables in the analysis (Cooley & Lohnes, 1971; Morrison, 1976; Lindeman *et al.*, 1980). This means that if this analysis is applied where there are only two treatments, only one discriminant function is determined and all the correlation coefficients are +1 or -1. More than two experimental treatments are therefore required for a worthwhile interpretation of this set of coefficients.

### 5.2.2.2.3 A scheme of interpretation of MANOVA and MDF

In the MDF printout, structural coefficients (structural matrix) and standardised coefficients are the most useful information for the interpretation of the discriminant functions. The former set of coefficients are the correlations between the original variables and the scores. They give a general interpretation of the discriminant function by considering its association with each variable. The latter set of coefficients explains how the standardised score is calculated from standardised input. The latter set of coefficients are analogous to standardised regression coefficients, being scalefree. Their absolute magnitudes indicate the contributions of each variable to the score: i.e. their "importance", and their signs indicate positive (raise score) or negative (lower score) contribution. The levels of importance indicated in the two sets of coefficients may be harmonious. That is, the variable which is highly correlated with the score (high value of structural coefficient) usually makes strong contribution to the score (high value of the standardised coefficient), and vice versa. Signs are often harmonious also. However, this may not always be the case. That is, the variable which is highly correlated with the score sometimes may make small contribution to the Signs may be reversed as well. score, or vice versa. Therefore, a general Gordon (pers. com.) has suggested the following. interpretation is required. (1) Attention should be focused on those variables which possess relatively high values or moderate values in both sets of coefficients. Those with harmonious signs may be termed "consensual" determiners. Those with opposite signs may be termed "reversed" determiners. (2) Those variables which possess relatively high values or moderate values in one set, but very small values in another set, only receive attention in some circumstances. (3) Of course, those variables which obtain negligible values in both sets of coefficients should be ignored. And (4) for the two-levels model effects and the interaction between these two-level effects, one discriminant function could
account for 100% of dispersion, and the correlation coefficients in the "structural matrix" are +1 or -1 (Section 5.2.2.2.2); in this case, the interpretation was completely based on the standardised coefficients.

Gordon's suggestion for interpretation of the results is given in Table 5.2. The naming of the score focuses on the structure matrix (Cooley & Lohnes), using strong determiners and perhaps, strong "pseudos" (Gordon, pers. com.). Assessment of the importance of individual variables is based on the strong determiners and the standardised coefficients.

#### 5.2.3 Cluster analysis

As noted earlier, a 70-80% cumulative proportion criterion was determined as satisfactory parsimony. In the current study, two multiple discriminant functions (MDF) usually could meet this criterion.

After scores were calculated, histograms for one MDF with ascending score with respect to the levels of the treatment were drawn. Scatter plots for two MDFs using the scores of both MDF1 and MDF2 as the two axes were produced to illustrate the relative ordination of scores among the treatments. For the scatter plots of two-MDFs, a cluster analysis was carried out to determine appropriate grouping among the treatments. Because discriminant functions are the best possible combinations of the attributes for discriminating among the treatments (Cooley & Lohnes, 1971; Morrison, 1976), cluster analysis was conducted based on scores, rather than the original data. The cluster analysis was conducted using the option, "Ward Method" of the SPSS package. Squared Euclidean Distance was used as the basis of the similarity matrices (Clifford & Stephenson, 1975).

The dendrogram of the cluster analysis, which is a diagrammatic illustration of relationship based on degree of similarity (Mayr *et al.*, 1953; Clifford & Stephenson, 1975) was used to show the classification of the treatments. The number of clusters was determined by contrasting the variation within clusters to that between clusters through a series of MANOVA significance tests. Each stage of clustering defined a new set of clusters ("treatments"), which were used to define the Hypothesis criterion in each MANOVA run. The significance arising from these group analyses were used to define the truncation level. The working rule determining appropriate numbers of

Structural correlation	Standardised coefficients	Interpretation	Kind of variables	Quality
0	_	This variable algebraically "reduces the scores", but is so counteracted by other variables; result is independent of this variable	Suppressed	Neutral
+	-	Reduces; but score goes in opposite direction	Reversed	Determiner
-	-	Reduces; but score goes in opposite direction	Consensual	Determiner
0	+	Increases; score is independent	Suppressed	Neutral
+	+	Increases; score consensual increase	Consensual	Determiner
-	+	Increases; counteracted	Reversed	Determiner
0	0	No contribution; score independent	Null	Neutral
+	0	No contribution; but score positively correlated anyway, because of other variables' inter-connections with this variable	Pseudo	Neutral
$\overline{M}$	0	No contribution, score negatively correlated	Pseudo	Neutral

Table 5.2	Gordon's scheme for interpreting multivariate analyses (Gordon
	pers. com., 1993).

In the interpretation of the results, the discriminant function was named principally using "consensual" variables (and using "pseudo" variables sometimes) after taking both sets of coefficients into account. Then, the implications of the score and importance sequence of the variables were assessed by concentrating the absolute magnitudes of the standardised coefficients for determiner variables.

clusters was that the optimum number of clusters produced maximum significance (lowest probability) in the multivariate contrast of between - clusters dispersion to within - clusters dispersion (Gordon, pers. com.). The results for the present analyses are presented in Appendix 5.4, and form the bases for truncating the dendrograms.

#### 5.2.4 Analyses of correlation and regression

Overall correlation between the **set** of sward variables and the **set** of ingestive behaviour variables was examined using canonical analysis. Relationships of **individual** behaviour variables with **sets** of sward variables were established by multiple regression.

#### 5.2.4.1 Canonical analysis

Canonical correlation analysis quantifies the association between **two sets** of variables (Morrison, 1976; Johnson & Wichern, 1988). Canonical correlation analysis applies to situations in which regression techniques are appropriate and where there exists more than one dependent variable (Afifi & Clark, 1984). Therefore, it is best understood by considering it as an extension of multiple regression and correlation analysis, the difference being that it involves more than one Y variable (Afifi & Clark, 1984).

The canonical analysis defines linear functions in a set of X variables and in a set of Y variables which are maximally correlated (Morrison, 1976; Afifi & Clark, 1984). The maximizing aspect concentrates a high-dimensional relationship between two sets of variables into a few pairs of canonical variables (Johnson & Wichern, 1988).

The two sets of variables are represented by matrices X and Y: let

$$Cov(Z_x) = R_{11}; Cov(Z_y) = R_{22}; Cov(Z_x, Z_y) = R_{12} = R_{21} = R'_{12}.$$

The entire correlation matrix **R** is composed of the sub-matrices  $R_{11}$ ,  $R_{12}$ ,  $R_{21}$  and  $R_{22}$ , (Johnson & Wichern, 1988):

The basic approach involves finding one linear combination  $(U_1)$  of one set of variables (Y set), say

$$U_1 = a_1 y_1 + a_2 y_2 + \dots + a_p y_p$$
,

and a linear combination of the other set of variables (X set), say

$$V_1 = b_1 x_1 + b_2 x_2 + \dots + b_q x_q$$
.

These are solved jointly for **a** and **b** coefficients such that the correlation between  $U_1$  and  $V_1$  is maximum. That is, the sought vectors **a** and **b** should let

$$Cor(\mathbf{U}, \mathbf{V}) = \frac{\mathbf{a'} \mathbf{R}_{12} \mathbf{b}}{\sqrt{\mathbf{a'} \mathbf{R}_{11} \mathbf{a} \sqrt{\mathbf{b'} \mathbf{R}_{22} \mathbf{b}}}}$$

be as large as possible (Johnson & Wichern, 1980). At the same time, the following constraints are imposed (Cooley & Lohnes, 1971; Morrison, 1976; Lindeman *et al.*, 1980):

$$a' \mathbf{R}_{11} a = 1$$
  
 $b' \mathbf{R}_{22} b = 1$  (coefficients kept as fraction)  
 $a'_{1} \mathbf{R}_{11} a_{1'} = 0$   
 $b'_{1} \mathbf{R}_{22} b_{1'} = 0$  (independence of successive local maxima).

This leads to an eigenstructure problem which, for canonical analysis, is as follows:

$$(\mathbf{R}_{11} - \mathbf{R}_{12} \mathbf{R}_{22} - \mathbf{R}_{21} - \lambda \mathbf{I})\mathbf{b} = 0$$
 (Cooley and Lohnes, 1971)

There are successive solutions (Morrison, 1976), as in MDF.

The resulting linear combinations U and V are called the canonical scores of the Y set and X set, respectively. The resulting correlation between U and V is the canonical correlation (Afifi & Clark, 1984).

The first canonical correlation is the highest possible correlation between a linear combination of the Y set and a linear combination of the X set (Morrison, 1976; Johnson & Wichern, 1980). It is therefore the maximum linear correlation between the set of the independent variables and the set of dependent variables (Afifi & Clark, 1984). Successive solutions are independent.

The largest eigen-value  $\lambda$  is the square of the maximum correlation between  $U_1$  and  $V_1$  (i.e. its the canonical coefficient of determination). Thus  $\sqrt{\lambda_1}$  is the canonical correlation between  $U_1$  and  $V_1$  (Cooley & Lohnes, 1971; Lindeman *et al.*, 1980).

Additional interpretation of the canonical relationship between the Y set and the X set is obtained by deriving successive canonical variables  $U_1$  and  $V_1$ , and their corresponding canonical correlations. The objective is to find a second set of linear combinations which maximize the correlation among all choices which are uncorrelated with the first pair of linear combinations as discussed earlier.

The total number of canonical solutions is r, where r is equal to the minimum of p (the number of Y variables) and q (the number of X variables). In the current study, p=5 and q=7, so the maximum number of canonical correlations and their corresponding canonical solutions is 5. Each linear combination is uncorrelated with all the other linear combinations of either set except for the one corresponding linear combination in the opposite set (Cooley & Lohnes, 1971; Morrison, 1976; Lindeman *et al.*, 1980).

The first canonical correlation is at least as large as any multiple correlation between any one variable and the opposite **set** of variables. It is possible for the first canonical correlation to be very large while all the multiple correlations for predicting one of the original variables from the opposite set of canonical variables are small (Cooley & Lohnes, 1971; Morrison, 1976).

Similarly to MANOVA and MDF, a criterion of 70-80% cumulative proportion to total association was considered to provide a satisfactory parsimonious number of canonical solutions (Gordon pers. com.). This was determined based on the canonical coefficient of determination ( $R^2 = \lambda$ ).

Canonical correlation analysis was performed using a command, "Proc Cancorr" of the SAS package (SAS Institute Inc, 1990).

Both standardised and unstandardised canonical coefficients are produced. Many investigators prefer to assess the contributions of the original variables directly from the standardised coefficients (Johnson & Wichern, 1980). The interpretation of canonical correlation is usually made to assess the contributions and relative importance of the original variables directly through the standardised coefficients (Johnson & Wichern, 1988). The standardized coefficients describe the contribution of variables to the canonical score, and explain how the score of the canonical variable is calculated. The sign of the standardised coefficient indicates that the original variable would lower (negative) or raise (positive) this canonical score, and the absolute value of the standardised coefficient indicates the contribution in absolute terms made by each original variable to the score of the canonical score. In this thesis, however, the actual canonical score is not used, attention being focused only on canonical correlation itself. Therefore, we are interested only in the relative contribution of each variable as shown by the absolute value of the standardised coefficient.

The output includes the structure matrix, which is the set of correlations between the canonical scores and the original variables. Similarly to MDF, these interpretations are usually similar to those obtained by examining the standardised canonical variable coefficients (Afifi & Clark, 1984). The interpretation will be made using the same scheme as MDF (Table 5.2).

The printout also included all possible simple correlations among the input variables (simple correlations between individual variables within set, and between sets). Some of these data are presented in Appendix 5.5 as a background of comparison with canonical correlations.

The CANCORR procedure tests a series of hypotheses that each canonical correlation and all smaller canonical correlations are zero in the population. The procedure also generates, by default, a table of multivariate statistics for the null hypothesis that all canonical correlations are zero in the population. Again, Wilks' Lambda is the most common basis for this test (Lindeman *et al.*, 1980). The likelihood ratio for all canonical correlations equals Wilks' Lambda. In fact, if one set of variables is a design matrix, while the other is a data matrix, the resulting canonical analysis is MANOVA, and the two Wilks' Lambda tests are then identical (Cooley & Lohnes, 1971; Morrison, 1976).

#### 5.2.4.2 Multiple regression

Canonical analysis estimates the correlation between the two **sets** of variables, ingestive behaviour and sward conditions. However, it would facilitate understanding of the quantitative relationships if individual behaviour variables could be estimated separately against the set of sward variables. Multiple regression does this, and the relative contributions to predicting each particular behaviour variable could be identified with standardised variables. The parallel with canonical analysis is obvious, and multiple regression is, in fact, a subset of canonical analysis (Morrison, 1976).

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Multiple regression is used to examine the relationship between one dependent variable Y and a set of independent predictor variables  $X_1$  to  $X_p$ , although the X variables do not have to be independent (Afifi & Clark, 1984). The multiple regression might be performed for two goals, (1) prediction: deriving an equation to predict Y from the X variables, and (2) description: an understanding of the relationship between Y and X variables.

Multiple regression could be carried out in two ways, (1) in terms of the unstandardised regression coefficients, and (2) in terms of standardised coefficients. The former uses unstandardised predictor variables, while the latter uses standardised variables. The relationship between them is as follows:

$$\beta' = \beta \frac{\sigma_x}{\sigma_y}$$

Where  $\beta'$ : standardised coefficient;  $\beta$ : unstandardised coefficient;  $\sigma_x$ : standard deviation of x;  $\sigma_v$ : standard deviation of y<sub>i</sub>.

Standardised coefficients are the same as ones obtained if the Y and X variables were standardised prior to performing the regression analysis (Afifi & Clark, 1984). The major advantage of standardised coefficients over the unstandardised coefficients is that they are scale-free, and therefore they can be compared directly in order to determine the relative contribution of each variable to the regression. The larger the magnitude of the standardised coefficient, the more this X variable contributes to the prediction of Y. The parallel with the standardised coefficients of canonical analysis is obvious.

Multiple regression was performed using the "Proc Reg" procedure of the SAS package with "Stepwise selection" (SAS Institute Inc. 1990). In the stepwise method, variables are added one by one to the model, and the F statistic for a variable to be added must be significant at a defined entry level (by default, this entry level is 0.1500 in Proc Reg) (SAS Institute Inc. 1990). After a variable is added, however, the stepwise method looks at all the variables that do not produce a F statistic significant at the defined entry level. Only after this check is made and the necessary deletions accomplished can another variable be added to the model. The stepwise process ends when none of the variables outside the model has a F statistic significant at the defined entry level and every variable in the model is significant at the defined entry level and every variable in the model is significant at the defined entry level and every variable in the model is significant at the defined entry level and every variable in the model is significant.

Both unstandardised and standardised coefficients were generated in this analysis. Partial  $R^2$  (coefficient of determination of each variable, or alternatively, proportion of the variation accounted for by each variable), and  $R^2$  of the model (coefficient of determination of regression model, or alternatively, proportion of the variation accounted for by the regression model), were also produced.

#### 5.2.5 Transformation of data

In the analysis of point-quadrat data, some of data were analyzed in transformed scales. The variables which were based on counts were Poisson variables (Steel & Torrie, 1980), and were transformed by square root. The variables which were binomial attributes were transformed by arcsine function (Steel & Torrie, 1980). The variables which were continuous were treated as Normal, and were not transformed. Although levels of significance and standard errors of the means were analyzed in transformed scales, where appropriate the least squares means quoted in such cases were the back-transformed data.

#### 5.3 RESULTS

The results given below are sequenced as follows: univariate analysis of variance for variables of sward, animal, and ingestive behaviour, respectively (5.3.1); univariate analysis of ingestive behaviour variables by combining the nine forages into the two herbage categories, grasses vs. legumes (5.3.2); multivariate analysis of variance and multiple discriminant function analysis of sward variables and ingestive behaviour variables, respectively (5.3.3); canonical analysis between the **set** of sward variables and the **set** of ingestive behaviour variables (5.3.4.1); multiple regression analysis of **individual** behaviour variables against the **set** of sward variables (5.3.4.2).

For convenience, in this chapter when the results are presented, a brief discussion on the results is made where appropriate. After all results are presented, there is a discussion involving general issues.

#### 5.3.1 Univariate analysis of variance

#### 5.3.1.1 Descriptions of sward variables

Evaluations of sward characteristics were made by two types of measurements (1) those gross measurements involving height, mass, bulk density and so on

(Sections 3.2.4.1, 3.2.6.1, 3.2.6.3 and 3.2.6.5), and (2) point-quadrat measurements (Section 3.2.4.2). They are presented in the following two separate sections.

#### 5.3.1.1.1 Gross structural variables

Under this section, attention is concentrated on the first type of measurement. The major structural characteristics for three main effects (animal species, forage and stage) are given in Table 5.3. As indicated earlier (Section 3.2.4.1), stem height and hence leaf layer depth were not available in *Lotus corniculatus*.

Table 5.3
 Descriptions of sward variables for main effects (animal species, forages and stages), least squares means with the same letters are not significantly different (LSD P<0.05).</th>

Main effect	Level	Top surface height (cm)	Stem height (cm)	Leaf layer depth (cm)	Mass bulk density of grazed stratum (mgDW/cm <sup>3</sup> )	Mass bulk density of entire sward (mgDWcm <sup>3</sup> )	Mass in grazed stratum (gDM/m²)	Herbage mass (gDM/m²)
Animal	sheep	42.8	17.7	11.3	1.31	1.58	145	420
species	goats	43.2	17.8	11.0	1.63	1.52	110	395
	s.e. test <sub>1</sub>	0.6 ns	0.4 ns	0.4 ns	0.21 ns	0.03 ns	4.6	9.7 ns
Forages	ryegrass	55.5 c	19.9 b	11.7 c	0.65 c	1.00 ө	125 c	331 ө
	browntop	50.9 d	25.1 a	9.3 d	0.98 bc	1.72 c	170 a	593 a
	cocksfoot	60.3 b	25.7 a	11.6 c	0.71 c	0.86 e	155 ab	350 de
	prairiegrass	44.3 ө	15.0 c	17.9 b	0.58 c	0.97 е	105 cd	377 cde
	phalaris	70.4 a	26.0 a	19.3 a	0.56 c	0.85 e	173 a	441 b
	Tahora	18.1 h	11.3 e	1.9 e	2.01 ab	2.82 a	95 d	404 bcd
	Kopu	19.6 h	13.4 cd	2.1 ө	3.11 a	2.49 b	93 d	406 bcd
	redclover	36.6 f	19.1 b	2.3 ө	3.03 a	1.85 c	130 bc	410 bc
	lotus	31.6 g			1.60 bc	1.46 d	103 cd	356 cde
	s.e. test <sub>2</sub>	1.2	0.7	0.7	0.45	0.07	9.7 ••••	20.5
Stages'	vegetative	21.9	10.3	11.9	1.23	1.70	80	313
	reproductive	43.0	25.1	10.5	1.71	1.41	176	502
	s.e. test	0.4	0.4	0.4	0.21 ns	0.03	4.6	9.7

s.e.: standard error of least squares means;

test,: F test of ANOVA for the animal species;

test<sub>2</sub>: F test of ANOVA for the forages;

test<sub>3</sub>: F test of ANOVA for the maturity stages.

Stem height and hence leaf layer depth were not available in lotus (see Section 3.2.4.1 of Chapter 3).

The swards grazed respectively by sheep and goats did not differ significantly, with the exception of herbage mass within the grazed stratum (Table 5.3). However, sward features varied widely across forages (Table 5.3). As a general trend, Tahora white clover and phalaris appeared to act as the two ends of a spectrum of variation in most variables. The five grasses were much taller than the four legumes, but the bulk densities within the uppermost layer and the complete profile were generally greater for legumes than grasses. Within the legumes, red clover and lotus were taller, but less dense than Tahora and Kopu white clovers. The trend in herbage mass was not clear-cut, but the mass of browntop was much higher than others because of the greater density in the lower parts of the sward (Lucas & Thompson, 1990). Comparison of bulk density between the grazed strata and the whole profiles suggests that gradients of bulk density increased from the top to the bottom in grasses, but decreased in legumes with the exception of Tahora.

Contrasts in these variables across the two stages of maturity were also great, except for mass bulk density of the grazed stratum (Table 5.3). As the swards advanced in maturity, substantial increases in most variables and a decrease in leaf layer depth (defined as the difference between the surface height and stem height, Section 3.2.7.8) and in average mass bulk density of the complete sward occurred.

Table 5.4 gives details of sward variables for the interaction of forage by maturity. For each forage, increasing maturity from the vegetative to the reproductive phase usually brought about increases in top surface height, stem height, herbage mass (both the grazed strata and complete sward), and generally a decrease in average mass bulk density of the complete sward. Overall, the mass bulk density of the grazed stratum was not significantly affected by maturity. However, with the progression of maturity, the grazed bulk density decreased in ryegrass, cocksfoot and lotus, but increased in browntop, prairiegrass, phalaris and the three clovers. Leaf layer depth was decreased in grasses (except browntop) with maturity, but not in legumes. In vegetative swards, a comparison of bulk density generally increased (with the exception of red clover) from the top to bottom profiles. In reproductive swards, bulk density increased in grasses, but declined in legumes (except for Tahora) from top to bottom of the profiles.

Variables	Stage	Ryegrass	Browntop	Cocksfoot	Prairiegrass	Phalaris	Tahora	Kopu	Red clover	Lotus	s.e. test
Top surface height	veg LSD	24.0 d	21.8 de *	27.6 c *	32.7 b *	35.2 a *	11.3 g	14.1 f *	11.1 g *	19.7 e *	1.2
(cm)	rep	55.5 C	50.9 D	60.3 B	44.3 E	70.4 A	18.1 H	19.6 H	36.6 F	31.6 G	***
Stem height	veg LSD	7.4 d	13.0 a *	10.2 b *	9.4 bc	12.1 a *	9.7 bc	12.2 a ns	8.6 c *	-	1.0
(cm)	rep	32.4 C	37.1 B	41.1 A	20.5 D	39.9 AB	12.9 E	14.5 E	29.6 C	-	***
Leaf layer depth	veg LSD	16.7 b *	8.7 c ns	17.4 b *	23.3 a	23.1 a *	1.5 d ns	1.9 d ns	2.5 d ns	-	1.0
(cm)	rep	6.7 CD	9.8 BC	5.8 D	12.5 AB	15.5 A	2.2 E	2.2 E	2.0 E	-	***
Mass bulk density of grazed stratum (mgDM/cm <sup>3</sup> )	veg rep	0.79 0.51	0.95 1.02	0.78 0.63	0.38 0.78	0.54 0.59	1.94 2.09	1.68 4.54	2.27 3.79	1.71 1.49	0.63 ns
Mass bulk density of	veg LSD	1.37 e *	1.85 cd (*)	1.00 f *	0.85 f ns	0.88 f ns	2.93 a ns	2.58 b ns	2.09 c	1.73 d *	0.10
entire sward (mgDM/cm³)	rep	0.63 F	1.58 C	0.72 F	1.09 DE	0.81 EF	2.71 A	2.39 B	1.60 C	1.19 D	***
Mass in grazed stratum	veg LSD	82 abc *	77 bc *	98 a *	58 d *	94 ab *	65 cd *	73 cd *	66 cd *	99 a ns	13.7
(gDM/m²)	rep	169 CDE	265 A	212 BC	152 DEF	221 AR	126 EF	113 F	192 CD	108 F	***
Herbage mass (gDM/m²)	veg LSD	320 bc ns	396 a *	269 de *	278 cde	308 bcd *	322 bc	354 ab *	233 e *	337 b ns	21.0
,0,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	rep	343 F	791 A	433 DEF	475 CDE	573 BC	486 BCD	457 DE	589 B	374 EF	***

#### Table 5.4 Descriptions of sward variables for the first order interaction of forages by maturity stages of growth.

s.e. and test listed in the column of the right hand of the table refer to standard error of least squares means and F test of ANOVA for this interaction. Lower and upper cases show LSD comparisons across forages within the vegetative stage and within the reproductive stage, respectively. The symbols (\*, or ns) indicate LSD comparisons between the two maturity stages within forages.

LSD: LSD between the two stages within forage.

#### 5.3.1.1.2. Point-quadrat data

Among the selected variables from the point-quadrat measurements (Section 3.2.7.9 of Chapter 3), proportions of leaf and seedhead reflected a Poisson distribution, and the proportion of live material was binomially distributed. They were transformed by the appropriate functions (Section 5.2.5). Other variables were viewed as having a normal distribution and were not transformed. Table 5.5 presents these variables for the three main effects.

The swards grazed respectively by sheep and goats displayed a high similarity in those variables obtained from the complete sward profile, but differed markedly in those derived from the grazed stratum with the exception of the proportion of live material (Table 5.5).

Forages differed markedly in terms of the variables measured (Table 5.5). For the entire sward, average leaf proportion was higher in grasses than in legumes. Legumes generally had a higher proportion of seedheads compared to grasses in both uppermost and entire layers. The variation in leaf frequency bulk density was smaller for the whole sward profile than the grazed stratum. Within the entire profiles, on average, there was not a clear difference in leaf frequency bulk density between grasses and legumes, but within the grazed stratum it was generally higher for legumes than grasses. Leguminous swards generally had higher seedhead frequency compared to gramineous swards. "Stem" frequency (see Section 3.2.4.1 of Chapter 3 for definitions of stem for various herbage categories) was generally higher for legumes than grasses in both grazed and overall strata (the reason for this is given in Section 5.4.2 of the Discussion). Leaf frequency generally increased from the top to bottom in grasses, but not in legumes. However, stem frequency substantially increased from the top to the bottom in both grasses and legumes. Generally, variation in proportion of live material was small relative to other variables and legumes tended to contain higher percentages of live material than grasses in both the upper layers and the complete sward.

Increase in maturity also resulted in a significant decline in the percentage of leaf in both complete profile and grazed strata, substantial reductions in the leaf and stem frequencies within the complete profile, and in leaf but not stem frequency of the grazed horizon, but there was little influence on the percentage of live material in both the whole sward and the grazed horizon.

Main effect	Level	Leaf % of whole sward	Seedhead % of whole sward	Leaf frequency of whole sward (hits/2 cm)	Stem frequency of whole sward (hits/2 cm)	Seedhead frequency of whole sward (hits/2 cm)	Live % of whole sward	Leaf % of grazed stratum	Seedhead % of grazed stratum	Leaf frequency of grazed stratum (hits/2 cm)	Stem frequency of grazed stratum (hits/2 cm)	Seedhead frequency of grazed stratum (hits/2cm)	Live % of grazed stratum
Animal	Sheep	0.58	0.12	2.37	1.31	0.37	0.79	0.66	0.28	2.07	0.34	0.71	0.97
species	Goats	0.58	0.12	2.37	1.28	0.43	0.79	0.87	0.44	1.81	0.25	0.92	0.98
	S.O	0.005	0.008	0.05	0.03	0.02	0.003	0.01	0.02	0.07	0.03	0.07	0.002
	test,	ns	ns	ns	ns	ns	ns		•••	••	••	·	ns
Forages	Negrass	0.67 b	0.16 ab	2.48 b	0.77 d	0.37 d	0.77 e	0.59 cde	0.44 ab	1.46 de	0.25 c	0.71 b	0.96 bc
· ····g··	browntop	0.69 b	0.08 e	2.78 a	1.12 c	0.20 ef	0.68 f	0.83 a	0.15 c	2.27 b	0.01 d	0.35 bc	0.91 d
	cocksfoot	0.74 a	0.04 f	2.54 b	0.67 d	0.10 f	0.72 f	0.77 ab	0.17 c	2.03 c	0.01 d	0.23 c	0.95 c
	prairiegrass	0.74 a	0.14 bc	2.09 cd	0.40 ө	0.30 ed	0.78 de	0.63 cd	0.49 a	1.06 ef	0.05 d	0.46 bc	0.98 ab
	phalaris	0.67 b	0.09 de	2.04 d	0.61 d	0.19 ef	0.78 de	0.53 de	0.30 b	0.78 f	0.23 c	0.32 bc	0.98 ab
	Tahora	0.37 e	0.19 a	2.36 bc	2.78 a	0.91 a	0.81 cd	0.52 e	0.48 a	2.56 b	0.75 a	1.58 a	0.99 a
	Кори	0.42 d	0.15 ab	2.06 d	1.97 b	0.71 b	0.84 bc	0.59 cde	0.40 ab	2.08 c	0.51 b	1.16 a	1.00 a
	red clover	0.55 c	0.11 cd	3.00 a	1.94 b	0.34 d	0.85 ab	0.67 bc	0.36 ab	3.19 a	0.23 c	1.21 a	1.00 a
	lotus	0.46 d	0.13 bc	2.01 d	1.37 c	0.51 c	0.88 a	0.55 de	0.50 a	1.86 cd	0.62 ab	1.30 a	1.00 a
	S.Ø	0.01	0.01	0.11	0.06	0.04	0.006	0.02	0.05	0.15	0.05	0.15	0.004
	test <sub>2</sub>	***	***	***	***	***	***	***	***	***	***	***	***
Stages	vecetative	0.80		3 2 3	1 57		0.79	0.96		3.00	0.29		0.98
Jiages	reproductive	0.72	0.34	1.52	1.02	0.41	0.79	0.62	0.60	0.88	0.30	0.83	0.97
	S.Ø	0.01	0.006	0.05	0.03	0.01	0.003	0.01	0.02	0.07	0.03	0.05	0.002
	test	***		***	***		ns	***		***	ns		ns

 Table 5.5
 Descriptions of the point-quadrat data of swards for main effects (animal species, forages and stages).

Proportions of leaf, seedhead and live materials were transformed by the appropriate functions (see Section 5.2.5 of the text). The levels of significance and standard errors of means were analyzed in a transformed scale, but the least squares means presented in the table were obtained from the back-transformed data. These notes also refer to Table 5.6.

test,: F test of ANOVA for animal species; test,: F test of ANOVA for forages; testa: F test of ANOVA for stages of maturity. Letters indicate LSD test among forages for each variable.

The interaction of forage by stage in these variables is illustrated in Table 5.6.

	inte	action	etween	Ulayes a	inu matun	ly slayes	<b>.</b>				
Variables	Stage	Ryegrass	Browntop	Cocksfoot	Prairiegrass	Phalaris	Tahora	Kopu	Red clover	Lotus	s.e. test
Leaf % of whole sward	veg LSD	0.81 a	0.71 b	0.81 a	0.87 a	0.83 a	0.40 e ns	0.46 d ns	0.56 c ns	0.48 d	0.014
	гөр	0.53 B	0.62 A	0.67 A	0.62 A	0.55 B	0.35 D	0.38 CD	0.53 B	0.45 C	***
Leaf frequency	veg	3.68 bc	4.10 ab	3.56 c	2.82 de	2.91 d	3.00 d	2.40 ef	4.32 a	2.26 f	0.15
whole sward	rep	1.27 CD	1.46 BCD	1.52 ABC	1.35 CD	1.16 D	1.72 A	1.72 AB	1.67 AB	1.76 A	***
Stem frequency	veg	0.82 e	1.58 d	0.71 ө	0.37 f	0.58 ef	3.41 a	2.18 c	2.86 b	1.61 d	0.09
(hits/2 cm) of whole sward	rep	ns 0.73 D	0.65 D	ns 0.63 DE	ns 0.42 E	ns 0.65 D	ns 2.14 A	1.78 B	1.03 C	1.14 C	***
Live % of whole	veg	0.77 dc	0.75 d	0.70 ө	0.94 cd	0.80 bc	0.79 cd	0.84 ab	0.83 ab	0.87 a	0.009
sward	rep	ns 0.76 DE	ns 0.62 F	ns 0.73 E	ns 0.79 CD	ns 0.76 DE	ns 0.84 BC	ns 0.84 AB	ns 0.88 AB	ns 0.89 A	•••
Leaf % of grazed stratum	veg LSD	0.98 ab *	0.98 a *	1.00 a *	1.00 a *	1.00 a	0.83 c ns	0.87 c	0.92 b *	0.76 d	0.03
	гөр	0.30 CD	0.61 A	0.58 A	0.33 BC	0.21 D	0.27 CD	0.40 BC	0.45 AB	0.37 BC	***
Leaf frequency of	veg	2.38 de	3.28 c	3.27 c	1.67 e	1.67 e	4.01 b	2.91 cd	5.19 a	2.68 cd	0.2
(hits/2 cm)	rep	0.55 CD	1.27 A	0.80 BC	0.44 CD	0.28 D	1.12 AB	1.24 A	1.19 A	1.04 AB	***
Stem frequency	veg	0.09 c	0.004 c	0 c	0.02 c	0 c	0.82 a	0.47 b	0.35 b	0.84 a	0.07
(hits/2 cm)	гөр	0.42 B	0.01 C	0.02 C	0.08 C	0.46 B	0.67 A	0.55 AB	0.10 C	0.39 B	***
Live % of grazed	veg	0.96 cd	0.96 bcd	0.94 d	0.98 abc	0.97 abcd	0.99 ab	0.99 a	1.00 a	1.00 a	0.006
stratum	LSD	ns 0.96 AB	ns 0.86 C	ns 0.96 B	ns 0.98 AB	ns 0.99 AB	ns 0.99 AB	ns 0.99 AB	ns 1.00 A	ns 1.00 A	***

**Table 5.6** Descriptions of the point-quadrat data of swards for the first order interaction between forages and maturity stages.

s.e. and test listed in the column of the right hand of the table refer to standard errors and F test of ANOVA for the interaction forage by stage. veg: vegetative stage; rep: reproductive stage.

LSD: LSD between the two stages within forage, denoted by the symbols. Lowercase letters indicate LSD across forages within vegetative stage. Uppercase letters indicate LSD across forages within reproductive stage.

Four variables involving seedhead (seedhead % and seedhead frequency in both whole sward and grazed stratum) were excluded from this table because they had the same values as in the main effect, forage, which are given in Table 5.5.

This interaction was observed to exert a significant effect on each variable. With advancing maturity, legumes maintained the leaf proportion compared with grasses where leaf content fell. The graphs in Appendix 5.1 illustrate the canopy structures of swards for eighteen combinations of this interaction using these data.

#### 5.3.1.2 Descriptions of animal variables

Table 5.7 shows details of least squares mean values of animal measurements for both sheep and goats during the period of grazing the nine forages. The liveweight of sheep was twice that of goats, and the mouth dimensions also differed significantly, goats having smaller dimensions for all measurements. The variation in incisor breadth of six sheep and six goats was not significant over this experimental period (from 6 December 1989 to 18 April 1990).

		Contraction of the second s	and the second strength of the second strengt		The second se	
Animal species	Live weight (kg)	Incisor breadth (cm)	Mouth width (cm)	Dentition width (cm)	Maximum open size (cm)	Lip length (cm)
Sheep	53.2	2.87	3.3	3.2	6.5	5.7
Goats	26.2	2.37	2.3	2.6	5.5	5.3
s.e test	0.5	0.03	0.02	0.01	0.03	0.03

Table	5.7	Descriptions	of	animal	parameters.

s.e.: standard error of least squares means; test: F test of ANOVA for animal species.

### 5.3.1.3 Descriptions of ingestive behaviour variables

#### 5.3.1.3.1 Main effects (animal species, forages and maturity stages)

The main effects are shown in Table 5.8.

Average values of bite weight in absolute terms across eighteen swards (9 forages x 2 stages) were similar for the two animal species in both fresh (bite weight 1) and dry (bite weight 2) matter terms. Bite rate and intake rate 2 were significantly greater for sheep than goats. However, when they were scaled to liveweight, goats had a greater bite weight (bite weight 3) and intake rate (intake rate 3) than sheep. Sheep had a greater bite depth, bigger bite area, and consequently greater bite volume than goats.

The forage effect was found to be highly significant for all variables. Animals had the least bite weight 1 on phalaris and on prairie grass, and the greatest on Kopu. In terms of bite weight 2, phalaris still lay at the bottom of the range of variation, but browntop and cocksfoot were at the top of the range because they had higher dry

Main effects	Level	Bite weight 1 (mg FM)	Bite weight 2 (mg DM)	Bite weight 3 (mg DM/LW <sup>a75</sup> )	Bite rate (bites/min)	Intake rate 2 (mg DM/min)	Intake rate 3 (mg DM/LW <sup>ars</sup> /min)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm³)
Animal	Sheep	1120	266	13.6	27	6446	333.7	15.8	11.8	177
species	Goats	1098	279	23.8	24	5396	470.6	14.2	10.9	150
	s.e. test <sub>1</sub>	37 ns	9 ns	0.6	0.8 **	204	13.6 ***	0.4 **	0.3 *	7 **
Forages	Ryegrass	940 cd	275 bc	18.5 bc	22 cd	4810 c	333.6 ed	21.9 b	12.2 ab	250 ab
	Browntop	1098 bc	366 a	24.6 a	26 abc	6539 a	434.5 ab	17.3 c	10.2 cd	163 d
	Cocksfoot	1217 ab	327 ab	22.1 ab	18 d	4900 c	318.4 e	23.4 b	10.2 cd	221 bc
	Prairiegrass	858 d	231 cd	16.5 cd	24 bc	5081 bc	353.3 cde	17.7 c	12.4 ab	207 c
	Phalaris	856 d	221 d	15.6 d	27 abc	5247 bc	385.4 cde	30.4 a	9.4 d	284 a
	Tahora	1120 bc	238 cd	15.6 d	29 a	6497 a	413.8 bcd	4.9 e	11.3 bc	64 e
	Kopu	1343 a	271 cd	18.2 d	27 ab	6900 a	457.5 ab	5.8 de	11.2 bcd	68 e
	Red clover	1256 ab	251 cd	17.7 cd	28 ab	6207 ab	423.5 abc	6.2 de	13.7 a	81 e
	Lotus	1292 ab	269 cd	19.4 bc	27 ab	7110 a	499.5 a	7.6 d	11.8 bc	93 e
	s.e. test <sub>2</sub>	79 ***	19 ***	1.3 ***	2 ***	433 ***	28.6 ***	0.9	0.6	14 ***
Stages	Vegetative	920	191	13.2	33	6106	416.6	9.1	11.5	104
	Reproductive	1297	353	24.2	18	5736	387.7	20.9	11.2	222
	s.e. test₃	37	9 ***	0.6	1	204 ns	13.5 ns	0.4	0.3 ns	7

 Table 5.8
 Ingestive behaviour variables for main effects (animal species, forages and stages)

s.e.: standard error of least squares means. test<sub>1</sub>: F test of ANOVA between animal species; test<sub>2</sub>: F test of ANOVA across forages; test<sub>3</sub>: F test of ANOVA between stages. Least squares means with the same letters are not significantly different (LSD).

matter content than other forages. Bite rate tended to be the slowest on cocksfoot and the fastest on Tahora. Animals displayed the shallowest bite depth on Tahora and deepest on phalaris, and accordingly the smallest bite volume on Tahora and the greatest on phalaris.

Stage of maturity exercised a highly significant effect on some variables, but had little impact upon others. As swards developed in maturity, animals tended to increase bite weights substantially, but decreased biting rate greatly and, as a result, intake rates remained constant. There was also a substantially greater response across the stages of maturity in bite depth which resulted in a marked rise in bite volumes, whereas bite area was little affected.

#### 5.3.1.3.2 The first order interactions

Tables 5.9 - 5.11 summarize details of the three first order interactions.

The interaction for maturity stage by animal species (Table 5.9) was found to be significant for bite weights and intake rates, but little effect was detected for biting rate and bite dimensions. On vegetative swards, sheep tended to have greater mouthfuls of herbage than goats in both fresh and dry matter terms and intake rate 2 was greater. However, in contrast to the vegetative swards, on reproductive swards bite weight in both fresh and dry matter terms were smaller for sheep than goats, but the two animal species did not differ in intake rate 2.

When the comparisons were made across the two stages within animal species, it appeared that sheep and goats responded quite differently to increasing maturity in bite weights, bite rate and hence intake rates. Both sheep and goats tended to increase their bite weights when grazing the reproductive swards as compared to vegetative swards, but the increments for sheep were relatively small. Bite rate decreased for both species, but the fall was smaller for goats than for sheep. Consequently, as a combination of the variation in bite weight and bite rate, the intake rates decreased significantly in sheep, but slightly increased in goats.

There was a substantially greater variation across the two maturity stages in bite depth and bite volume than in bite area for the two animal species though the interactions were not significantly different, implying that magnitudes of increases were parallel between sheep and goats.

Variables	Animal		Stages	5	s.e. - test
Variables	species	Vegetative	LSD <sub>2</sub>	Reproductive	lesi
Bite weight 1	sheep	1007	*	1233	
(mgFM)	LSD,	*		(*)	
	goat	834	*	1362	53 **
Bite weight 2	sheep	207	*	323	
(mgDM)	LSD <sub>1</sub>	(*)		*	
	goat	175	*	383	13 ***
Bite weight 3	sheep	10.8	*	16.3	
(mgDM/LW <sup>0.75</sup> )	LSD1	*		*	
	goat	15.5	*	32.1	0.9 ***
Bite rate	sheep	36		19	
(bites/min)	goat	31		17	1 ns
Intake rate 2	sheep	7074	*	5819	
(mgDM/min)	LSD1	*		ns	
	goat	5139	ns	5653	288 **
Intake rate 3	sheep	375.3	•	292.1	
(mgDM/LW <sup>0.73</sup> /min)	LSD <sub>1</sub>	*		*	
	goat	457.8	ns	483.4	19.1 **
Bite depth (cm)	sheep	9.8		21.7	
	goat	8.4		20.1	0.6 ns
Bite area (cm <sup>2</sup> )	sheep	11.8		11.8	
	goat	11.3		10.6	0.4 ns
Bite volume (cm <sup>3</sup> )	sheep	116		238	
	goat	94		206	10 ns

**Table 5.9**Ingestive behaviour variables for the first order interaction of maturity<br/>stage by animal species.

s.e. and test listed in the column of the right hand of the table refer to standard errors of the least squares means and F test of ANOVA for this interaction.

LSD<sub>1</sub>: comparison between sheep and goats within stage; LSD<sub>2</sub>: comparison between the vegetative and reproductive stages within animal species.

The two animal species responded quite differently to the forages (Table 5.10) in terms of the components of intake rate (bite weights, biting rate and intake rates), but similarly in terms of bite dimensions. The two animal species tended to obtain similar bite weight in both fresh and dry matter terms on some forages, but sheep had higher bite weight than goats on Tahora and Kopu and lower bite weight on browntop and cocksfoot. The two stock classes appeared to have similar herbage intake rate 2 when grazing most forages, but it was far greater for sheep than goats on the two white clovers.

When the comparisons were made across the forages within animal species, it appeared that the forages which allowed the animals to maximize bite weights, biting rate and hence intake rates were quite different between sheep and goats. However, both sheep and goats displayed greatest bite depth on phalaris, and the smallest bite depth on legumes.

As each forage progressed from the vegetative to the reproductive stage, all behaviour variables were significantly affected (Table 5.11). Animals greatly increased their bite weights with increasing maturity on some forages in fresh matter terms, but not on others. However, the bite weights in dry matter terms were significantly greater for reproductive than vegetative stages in all forages but lotus because of higher dry matter content of the reproductive growth. Animals bit herbage faster on the vegetative swards than reproductive swards, except for lotus. Consequently, intake rate 2 changed little across the stages for most forages with the exception of ryegrass and phalaris where it declined. Amongst components of bite dimensions, bite area was constant across the stages of maturity for most forages, but apart from on white clover bite depth was increased substantially. Consequently, for most forages bite volume was substantially enlarged with advancing maturity. Forages which could allow animals to exhibit their potential in bite variables at the vegetative stages did not necessarily do so at the reproductive stages. This indicated that the sward structural characteristics which changed greatly as the forages matured exerted more influence than forage species per se on the behaviour variables, even though the forage species played an important role in affecting the ingestive behaviour.

Variables	Animal species	Ryegrass	Browntop	Cocksfoot	Prairiegrass	Phalaris	Tahora	Кори	Red clover	Lotus	s.e. test
Bite weight 1 (mgFM)	sheep LSD goats	820 e ns 1060 BCD	903 de * 1293 AB	1057 cde * 1378 A	789 ns 928 CD	917 de ns 794 D	1444 ab * 796 D	1603 a * 1083 ABCD	1348 abc ns 1164 ABC	1198 bcd ns 1386 A	112 ***
Bite	sheep	238 abc	295 ab	277 abc	214 c	235 bc	299 ab	313 a	267 abc	253 abc	27
weight 2	LSD	*	*	*	ns	ns	*	*	ns	ns	
(mgDM)	goats	312 BC	438 A	378 AB	249 CDE	206 E	177 E	229 DE	235 DE	286 CD	
Bite weight 3 (mgDM/LW <sup>0.75</sup> )	sheep LSD goats	11.7 ab * 25.4 C	14.4 a * 34.8 A	13.6 a * 30.6 AB	10.9 b * 22.1 CD	12.3 a * 19.0 DE	15.5 a ns 15.6 E	16.3 a ns 20.2 DE	14.5 a * 20.8 CD	13.2 a * 25.5 BC	1.8 ***
Bite	sheep	20 d	31 a	22 cd	27 abc	24 bcd	33 a	29 ab	30 ab	28abc	2
rate	LSD	(*)	*	*	*	*	*	ns	ns	ns	
(bites/min)	goats	25 AB	21 BC	15 C	21 BC	30 A	25 AB	25 AB	27 AB	26 AB	
Intake rate 2 (mgDM/min)	sheep LSD goats	4247 e ns 5373 ABC	6714 b ns 6363 AB	5441 bcd ns 4359 C	5184 cde ns 4978 BC	4978 de ns 5516 ABC	8919 a * 4074 D	8616 a * 5185 BC	6693 bc ns 5722 ABC	7225 ab ns 6994 A	613 ***
Intake	sheep	208.2 d	340.1 bc	273.9 bcd	266.4 bcd	257.4 cd	470.3 a	463.3 a	348.3 bc	375.7 ab	40.6
rate 3	LSD	*	*	ns	*	*	*	ns	*	*	
(mgDM/LW <sup>0,75</sup> /min)	goats	459.0 BC	528.9 AB	362.9 C	440.2 BC	513.4 AB	357.3 C	451.7 BC	498.9 B	623.3 A	
Bite	sheep	23.4 b	17.0 c	24.4 b	19.0 c	31.3 a	6.7 d	7.8 d	6.0 d	6.6 d	1.3
depth (cm)	goats	20.4 BC	17.5 CD	22.4 B	16.3 D	29.4 A	3.2 F	3.8 F	6.3 EF	8.7 E	ns
Bite	sheep	12.5 ab	10.3 bc	9.8 c	12.8 ab	10.5 bc	11.6 bc	12.4 ab	14.7 a	11.5 bc	0.8
area (cm²)	goats	11.9 ABC	10.1 BCD	10.5 ABCD	12.1 AB	8.3 D	11.0 ABC	9.9 CD	12.6 A	12.1 ABC	ns
Bite	sheep	227 b	173 c	208 bc	223 b	331 a	93 d	100 d	89 d	78 d	20
volume (cm³)	goats	247 A	178 C	232 AB	191 BC	247 AB	35 E	37 E	73 DE	109 D	ns

Table 5.10	Ingestive behaviour	variables for the	first order interaction	of forage by	animal species.
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s.e. and test listed in the column of the right hand of the table refer to standard errors of least square means and F test of ANOVA for this interaction. Lower and upper cases indicate LSD comparisons across forages within sheep and within goats, respectively. The symbols illustrate the comparisons between the two animal species within forage.

Variable	Stage	Ryegrass	Browntop	Cocksfoot	Prairiegrass	Phalaris	Tahora	Кори	Red clover	Lotus	s.e. test
Bite weight 1 (mgFM)	veg LSD rep	672 c * 1208 CD	638 c * 1558 AB	923 c * 1512 ABC	708 c (*) 1008 DE	950 bc ns 761 E	936 c 1304 BCD	1257 ab ns 1429 ABC	885 c 1627 A	1313 a ns 1270 BCD	112
Bite weight 2 (mgDM)	veg LSD rep	182 bc 368 BC	182 bc * 551 A	223 ab * 432 B	159 bc * 303 CDE	183 abc 258 E	167 bc 309 CDE	231 ab 310 CDE	144 c * 358 BCD	250 a ns 288 DE	27
Bite weight 3 (mgDM/ LW <sup>0.75</sup> )	veg LSD rep	12.4 bc 24.6 BC	13.0 bc * 36.1 A	15.6 ab 28.7 B	11.3 bc 21.8 CD	13.6 bc ns 17.7 D	10.5 bc 20.6 CD	14.8 bc 21.7 CD	9.8 c * 25.5 BC	17.5 a ns 21.2 CD	1.8 ***
Bite rate (bites /min)	veg LSD rep	33 abcd 11 D	41 a 12 D	25 e 11 D	30 cde * 18 BC	39 a * 15 CD	36 abc * 22 AB	31 bcde * 23 AB	36 ab * 20 BC	27 de ns 27 A	2
Intake rate 2 (mgDM/min)	veg LSD rep	5817 abc 3803 D	6956 ab ns 6112 ABC	5324 bc ns 4476 CD	4424 c ns 5738 BC	6924 ab 3570 E	6075 abc ns 6918 AB	7106 a ns 6694 AB	5562 bc ns 6853 AB	6761 ab ns 7458 A	612 **
Intake rate 3 (mgDM/LW <sup>0 75</sup> / min)	veg LSD rep	417.4 abcd * 249.7 E	478.4 ab ns 390.6 C	357.3 de ns 285.4 D	299.2 e (*) 407.4 BC	518.0 a * 252.8 DE	378.7 bcde ns 448.9 ABC	456.9 abcd ns 458.1 ABC	366.0 cde * 481.0 AB	477.3 abc ns 521.6 A	40.6
Bite depth (cm)	veg LSD rep	10.2 cd * 33.5 B	8.0 de * 26.5 C	13.1 bc * 33.7 B	15.0 ab * 20.3 D	17.5 a * 43.2 A	3.4 f ns 6.5 E	4.8 f ns 6.8 E	3.2 f * 9.2 E	6.5 ef ns 8.8 E	1.3
Bite area (cm²)	veg LSD rep	12.2 bc ns 12.2 ABC	10.3 cd ns 10.1 CDE	10.3 cd ns 10.1 CDE	15.5 a 9.3 E	9.4 d ns 9.4 DE	11.8 cd ns 10.9 BCDE	10.3 cd ns 12.1 ABCD	14.5 ab ns 12.8 AB	9.7 d * 13.9 A	0.9
Bite volume (cm³)	veg LSD rep	127 b * 397 A	81 c * 272 C	131 b 331 B	234 a ns 180 D	166 b 426 A	40 c ns 87 E	52 c ns 85 E	45 c 117 E	64 c * 123 DE	20

 Table 5.11
 Ingestive behaviour variables for the first order interaction of forage by maturity stage.

s.e. and test listed in the column of the right hand of the table refer to standard errors of the least square means and F test of ANOVA for this interaction. Lower and upper case letters illustrate LSD comparisons across forages within the vegetative stage, and within the reproductive stage, respectively. The symbols give LSD between the two stages within a forage. veg: vegetative; rep: reproductive.

#### 5.3.1.3.3 The second order interaction

The second order interaction between animal species, forages and stages of maturity is illustrated in Table 5.12. This higher order interaction was found to exert significant effects on some variables, but had little effects on others.

When grazing vegetative swards, sheep and goats tended to obtain similar bite weights in both fresh and dry matter terms on most of forages, but sheep had greater bite weights on Tahora and Kopu than did goats. However, when reproductive swards were presented, bite weights in both terms were larger for goats than sheep on all grasses with the exception of phalaris.

When comparisons are made along the horizontal direction in the table, representing the comparisons across two stages of each forage within animal species, it can be seen that as the forages advanced in maturity, sheep usually increased or maintained bite weight, whereas goats tended to increase bite weight on all forages but phalaris, indicating that goats grazed reproductive swards more readily. Bite rate was usually slower at the reproductive stage than the vegetative stage for both sheep and goats.

In this higher order interaction, as swards progressed from the vegetative to the reproductive stage, sheep and goats tended to have approximately parallel increases in bite depth, but remained constant in bite area when grazing each forage, leading to consistent increases of bite volume.

## 5.3.2 Univariate analysis of variance of behaviour variables by combining the nine forages into the two herbage categories (grasses vs legumes)

The above analysis in which the nine forages were assessed individually showed a relative clear-cut distinction between grass forages and legume forages. Therefore it is appropriate to examine and to compare the overall response patterns of sheep and goats to gramineous and leguminous swards at the two stages of maturity. This was achieved by combining and reparameterizing the nine forages into two herbage categories, grasses (5 forages) and legumes (4 forages), and then analyzing by ANOVA.

			Ryegra	155		Brown	lop		Coche	oot	F	Prairieg	rass		Phala	rls		Taho	ra		Кори	1	1	Red clo	ver		Lotus		S.e.
-		veg	LSD <sub>2</sub>	rep	veg	LSD	rep	veg	LSD	rep	veg	LSD;	rep	veg	LSD <sub>2</sub>	rep	veg	LSD	2 rep	veg	LSD <sub>2</sub>	rep	veg	LSD <sub>2</sub>	rep	veg	LSD <sub>2</sub>	rep	test
BW,	sh	769	ns	871	626	•	1180	956	ns	1159	630	ns	947	950	ns	885	1224	•	1663	1658	ns	1549	967	•	1730	1281	ns	1115	
	lsd,	ns		•	ns		•	ns		•	ns		ns	ns		ns	•		•	•		ns	ns		ns	ns		ns	159
	go	575	•	1545	651	•	1936	890	•	1865	786	ns	1069	951	ns	637	648	ns	944	856	•	1309	804	•	1523	1346	ns	1426	(")
BW2	sh	209	ns	268	174	•	415	227	(*)	327	145	•	282	180	•	290	219	•	379	303	ns	322	159	•	375	253	ns	253	
	lsd,	ns		•	ns		•	ns		•	ns		ns	ns		ns	(")		•	•		ns	ns		ns	ns		ns	38
	go	156	•	468	189	•	687	219	•	536	173	•	325	186	ns	227	115	•	240	159	•	298	129	•	341	248	ns	323	
DIA		40.7		40.7																				-		10.5		10.0	
BW <sub>3</sub>	sn	10.7	ns	12.7	9.1	•	19.7	11.8	ns	15.5	7.2	•	14.7	9.7	ns	14.9	11.3	-	19.7	16.0	ns	16.5	8.3	-	20.7	13.5	ns	12.9	0.0
	ISO,	14.0		26.5	10.0		50.0	10.4					•			ns	ns		ns 0.1 C	ns		•	ns 11.0		-	01.5		20.6	2.0
	go	14.2		30.5	10.9		52.0	19.4	-	41.9	15.3	-	28.8	17.5	ns	20.4	9.8	-	21.5	13.5	5	26.9	11.3		30.3	21.5		29.0	
BR	sh	28	•	12	49	•	14	30	•	14	35		20	36		11	41		25	33		25	43	•	18	26	ns	31	
	lsd,	•		ns	•		ns	•		ns	•		ns	ns		ns	•		ns	ns		ns	•		ns	ns		(")	3
	go	39	•	10	31		11	20	•	9	25		17	42		18	31		20	29	(*)	22	31		22	28	ns	24	(°)
	-																				()								
IR <sub>2</sub>	sh	5718	•	2776	8171	•	5256	6346	ns	4537	4713	ns	5656	6533	•	3423	8706	ns	9132	9776	(")	7456	7060	ns	6326	6641	ns	7810	866
	go	5917	ns	4829	5759	ns	6968	4302	ns	4416	4135	ns	5821	7313	·	3718	3444	ns	4704	4437	ns	5933	4064	•	7308	6882	ns	7106	ns
	sh	294.5	•	121.8	432.1		248.0	332.8	ns	214.9	234.5	ns	298.3	349.4	•	165.3	464.7	ns	475.8	539.9	(")	386.7	375.1	ns	321.5	355.1	ns	396.3	<b>67</b> 4
IH3	ISO,				ns			ns		ns	ns	<b>.</b>				•			ns			(*)	ns		•			-	57.4
	go	540.4		377.6	524.7	ns	533.1	381.7	ns	344.1	363.8	(*)	516.5	686.5	•	340.3	292.6	ns	421.9	374.0	(*)	529.4	356.9	•	640.6	599.5	ns	647.0	(*)
BD	sh	11.9	•	34.9	8.9		25.0	13.9	•	34.9	15.2	(")	22.8	18.2		44.5	43	03	91	63	ns	9.3	3.9	ns	9.0	6.6	ns	6.6	1.8
00	00	8.5		32.2	7 1		28.0	12.3	09	32.5	14.8	•	17.7	16.9		42.0	2.6	09	3.9	3.4	09	4.2	3.3	05	9.4	6.4	ns	11.0	ns
	90	0.0		02.2			20.0	12.0	12	02.0	14.0			10.0		42.0	2.0	15	0.0	0.4	12		0.0	110	0.1				
BA	sh	12.5	ns	12.6	11.0	ns	9.6	9.9	ns	9.8	15.7	•	9.9	10.0	ns	11.0	11.5	ns	11.7	11.2	ns	13.6	15.2	ns	14.3	9.0	•	14.1	1.2
	go	11.9	ns	11.8	9.6	ns	10.6	10.7	ns	10.4	15.3	•	8.9	8.8	ns	7.8	12.0	ns	10.1	9.3	ns	10.6	13.9	ns	11.4	10.5	(*)	13.7	ns
BV	sh	154		400	95	•	252	135	ns	320	243	•	204	183	•	479	50	ns	137	72	ns	127	47	ns	139	60	ns	96	28
	go	100	•	393	68	•	288	126	ns	338	226	•	156	148	•	345	31	ns	38	31	ns	43	44	ns	103	69	•	149	ns

Table 5.12 Ingestive behaviour variables for the second order interaction between forages, maturity stages and animal species.

s.e. and test listed in the column of the right hand of the table refer to the standard errors of the least squares means and F test of ANOVA for this interaction. sh: sheep, go: goats; veg: vegetative, rep: reproductive. LSD, and LSD<sub>2</sub> indicate comparisons between sheep and goats within the stage of maturity of each torage, and comparisons between stages of each forage within animal species, respectively. BW<sub>1</sub>: bite weight 1 (mgFM/bite); BW<sub>2</sub>: bite weight 2 (mgDM/bite); BW<sub>3</sub>: bite weight 3 (mgDM/LW<sup>a75</sup>); BR: bite rate (bites/min); IR<sub>2</sub>: intake rate 2 (mgDM/min); IR<sub>3</sub>: intake rate 3 (mgDM/LW<sup>a75</sup>/min); BD: bite depth (cm); BA: bite area (cm<sup>2</sup>); BV: bite volume (cm<sup>3</sup>). Average bite weight 1 was 21% greater on leguminous than on gramineous swards (Table 5.13), but bite weight 2 and bite weight 3 were 11% and 10% smaller. This was because dry matter content is usually higher for grasses than legumes. Animals had faster biting rates, and consequently substantially greater intake rates on legumes than grasses. Compared to legumes, animals had a far deeper penetration of the mouth into grass swards, but relatively smaller bite area. However, bite volumes were substantially larger on grasses than legumes. The interaction of herbage category by animal species (Table 5.14) showed substantial effects on the bite weights and intake rates, but had little impact on biting rate and bite dimensions. Sheep had larger average bite weights than goats on leguminous swards, but they had smaller average bite weights on gramineous swards. The two stock classes exhibited similar intake rates on grasses, but intake rates were greater for sheep than goats on legumes.

Sheep had a substantially greater fresh bite weight on legumes than on grasses, but this difference completely disappeared in dry matter terms; whereas goats had a similar fresh bite weight when grazing grasses and legumes, but in dry matter terms,

Herbage category	Bite weight 1 (mgFM)	Bite weight 2 (mgDM)	Bite weight 3 (mgDM/ LW <sup>0.75</sup> )	Bite rate (bites/ min)	Intake rate 2 (mgDM/ min)	Intake rate 3 (mgDM/ LW <sup>0.75</sup> )	Bite depth (cm)	Bite area (cm²)	Bite volume (cm <sup>3</sup> )
Grasses	994	284	19.5	24	5314	365	22.1	10.9	232.3
Legumes	1253	257	17.7	28	6679	449	6.1	12.0	76.7
s.e. test	41 ***	10 (*)	0.7 (*)	1 ***	211 ***	14.5 ***	0.6	0.3 *	8

 Table 5.13
 Comparison of ingestive behaviour variables of animals grazing the gramineous and leguminous swards

s.e. and test listed at the bottom row of the table refer to standard errors of least square means and F test of ANOVA for animal species.

bite weight was much higher on grasses than on legumes. Sheep obtained substantially greater intake rate 2 and intake rate 3 on legumes than on grasses, but these two variables did not differ significantly between grasses and legumes for goats.

The interaction of herbage category with stage of maturity exerted a significant effect on some variables, but had little impact upon others (Table 5.15). The increases in bite weight 1 and bite weight 3 with developing maturity were approximately parallel between grasses and legumes, but the increment for bite weight 2 was greater on grasses than legumes. Biting rate was reduced in both grasses and legumes as a consequence of increasing maturity. As pasture matured, animals tended to decrease intake rate 2 and intake rate 3 significantly when grazing grasses, but increased slightly when grazing legumes. In both grasses and legumes, bite depth responded much more sensitively than did bite area to the increase in maturity, leading to a substantial increase in bite volume. However, the increases across the two stages of maturity in bite depth and bite volume were greater for grasses than legumes. In grasses, bite area decreased significantly with maturity, but little variation was detected for leguminous swards.

In vegetative swards, there was little difference in bite weight 2 between grasses and legumes, but this difference was appreciable in reproductive swards. Animals did not differ significantly in bite rate when grazing vegetative swards of grasses and legumes, but they bit much faster on legumes than on grasses when grazing reproductive swards. There was no significant difference in intake rate 2 and intake rate 3 between grasses and legumes when vegetative swards were grazed, but these two variables were substantially greater on legumes than grasses when reproductive swards were grazed. Bite depth was greater in grasses than in legumes, particularly in the reproductive swards. Bite area did not differ between vegetative grasses and vegetative legumes, but on reproductive swards it was greater on legumes than on grasses. Bite volume was only one third that on grasses for both stages of legumes.

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Variables	Animal species	Grass	s.e. <sub>1</sub>	LSD₂	Legume	s.e. <sub>2</sub>	Test
Bite weight 1 (mgFM)	sheep LSD₁	897 *		*	1398		
	goat	1091	58	ns	1107	65	***
Bite weight 2 (maDM)	sheep	252		ns	283		
(	goat	317	15	*	232	17	***
Bite weight 3 (mgDM/LW <sup>0.75</sup> )	sheep LSD₁	12.6		ns	14.9 *		
( )	goat	26.4	1.0	*	20.5	1.1	***
Bite rate (bites/min)	sheep goat	25 22	1.2		30 26	1.4	ns
Intake rate 2	sheep	5309		*	7863		
(mgDM/min)	LSD₁ goat	ns 5318	296	ns	* 5494	331	***
Intake rate 3	sheep	269.1		*	414.4		
/min)	goat	460.9	20.3	ns	482.8	22.7	***
Bite depth	sheep	23.0	0.9		6.8	0.9	ne
(611)	goat	21.2	0.0		5.5	0.9	115
Bite area (cm <sup>2</sup> )	sheep	11.2 10.6	04		12.6 11 4	0.5	ns
Rito volumo	shaan	040 7	0.7		00.0	0.0	110
(cm <sup>3</sup> )	goat	246.7 215.9	11.7		90.9 63.4	12.6	ns

 Table 5.14
 Ingestive behaviour variables for the interaction between herbage category and animal species.

s.e.<sub>1</sub>: standard error of means for grasses; s.e.<sub>2</sub>: standard error of means for legumes; test listed in the column of the right hand of the table refers to F test of ANOVA for this interaction; LSD<sub>1</sub>: lsd comparison between sheep and goats within herbage category; LSD<sub>2</sub>: lsd comparison between grasses and legumes within animal species.

Variables	Stages	Grass	s.e.,	LSD <sub>2</sub>	Legume	s.e.2	Test
Bite weight 1 (mgFM)	vegetative reproductive	778 1209	58		1098 1407	65	ns
Bite weight 2 (maDM)	vegetative	186		ns	198 *		
(119211)	reproductive	383	15	*	316	17	*
Bite weight 3 (mgDM/LW <sup>0.75</sup> )	vegetative reproductive	13.2 25.8	1.0		13.2 22.3	1.1	ns
Bite rate	vegetative	33		ns	33		
(Dites/min)	reproductive	14	1.2		23	1.4	***
Intake rate 2	vegetative	5891		ns	6376		
(mguw/min)	reproductive	4736	299	*	6981	331	***
Intake rate 3	vegetative	414.1		ns	419.7		
/min)	reproductive	315.9	20.5	*	477.4	22.7	***
Bite depth (cm)	vegetative	12.8		*	4.5		
(011)	reproductive	31.4	0.8	*	7.9	0.9	***
Bite area (cm²)	vegetative	11.5		ns	11.6 ns		
()	reproductive	10.3	0.4	*	12.4	0.5	*
Bite volume (cm <sup>3</sup> )	vegetative LSD,	147.8 *		*	50.5		
· · /	reproductive	316.7	11.3	*	102.9	12.6	***

Table 5.15	Ingestive behaviour variables for the interaction between herbage category and
	maturity stage

s.e.,: standard error of means for grasses; s.e.,: standard error of means for legumes; test listed in the column of the right hand of the table refers to F test of ANOVA for this interaction;  $LSD_1$ : LSD comparison between the two stages within herbage category;  $LSD_2$ : LSD comparison between grasses and legumes within maturity stage.

The high order interaction (Table 5.16) was found to have significant effects on bite weights and bite dimensions, but little effect on bite rate and intake rates. In grasses, sheep and goats had similar bite weight 1 when grazing vegetative swards; but when grazing reproductive swards, goats had a significantly greater bite weight 1 than sheep. On legumes, sheep obtained larger bite weight 1 than goats irrespective of stages. As the swards progressed from the vegetative to the reproductive stage, both sheep and goats tended to increase bite weight 1; on legumes the two animal species had approximately parallel increases, but on grasses the magnitude of increase for sheep was substantially smaller than that in goats. Bite weight 2 reinforced the trend displayed in bite weight 1 except for the fact that goats had a similar dry matter bite weight to sheep on the reproductive swards of legumes. On legumes, bite depth and bite volume were consistently greater for sheep than goats, but bite area was only greater at the reproductive stage. For vegetative grass swards, sheep had a similar bite area to goats, but greater bite depth and consequently greater bite volume; on reproductive grass swards, the two animal species did not exhibit significant differences in bite depth and bite area, despite significantly lighter bite weights for sheep compared to goats.

# 5.3.3 Multivariate analysis of variance (MANOVA) and multiple discriminant function (MDF)

The data sets were evaluated, using MANOVA and MDF, to overview the gross response patterns of the variations in sward variables and in behaviour variables, respectively.

The calculated scores of the different treatments are presented in Appendix 5.2. The truncation probabilities for clusters are given in Appendix 5.4. Appendix 5.3 illustrates dendrograms showing cluster hierarchy of discriminant scores.

As mentioned before (Section 5.2.3), in the current study the two multiple discriminant functions usually could reach a 70-80% cumulative proportion, a suggested satisfactory parsimonious criterion in this study. In this case, for the set of sward variables, a histogram for the first discriminant function (MDF1) and a scatter plot for the combination of both the first and second discriminant functions (MDF1 and

Variables	Animal		Gra	ISS			Test			
	species	vegetative	LSD <sub>1</sub>	reproductive	s.e.,	vegetative	LSD <sub>2</sub>	reproductive	s.e. <sub>2</sub>	
Bite weight 1 (mgFM)	sheep LSD₃ goat	786 ns 771	(*) *	1008 * 1410	82	1282 (*) 914	(*) *	1514 (*) 1301	92	(*)
Bite weight 2 (mgDM)	sheep LSD <sub>3</sub> goat	187 ns 185	*	317 449	21	234 * 163	*	332 ns 301	23	*
Bite weight 3 (mgDM/LW <sup>0.75</sup> )	sheep goat	9.7 16.7		15.5 36.1	1.4	12.3 14.0		17.4 27.1	1.6	ns
Bite rate (bites/min)	sheep goat	35 31		14 13	1.7	36 30		25 22	1.9	ns
Intake rate 2 (mgDM/min)	sheep goat	6296 5485		4322 5150	419	8046 4707		7681 6281	468	ns
Intake rate 3 (mgDM/LW <sup>0 75</sup> /m in)	sheep LSD₃ goat	329 * 499	* (*)	210 422	28	434 ns 406	ns *	395 * 560	32	(*)
Bite depth (cm)	sheep LSD₃ goat	13.6 * 11.6	*	32.1 ns 30.9	0.6	5.1 * 3.9		8.5 * 7.1	0.7	(*)
Bite area (cm²)	sheep LSD₃ goat	11.8 ns 11.2	ns ns	10.6 ns 10.0	0.6	11.7 ns 11.4		13.4 11.4	0.7	(*)
Bite volume (cm³)	sheep LSD <sub>3</sub> goat	162.0 * 133.7	*	340.3 (*) 309.1	12.0	57.3 * 43.6		122.7 * 83.2	13.0	(*)

 Table 5.16
 Ingestive behaviour variables for the second order interaction between herbage category, maturity stage and animal species.

s.e.,: standard error of means for grasses; s.e.,: standard error of means for legumes; test listed in the column of the right hand of the table refers to F test of ANOVA for this interaction; LSD,: LSD comparison between the two stages within grass category; LSD,: LSD comparison between the two stages within legume category; LSD,: LSD comparison between sheep and goats within herbage category.

MDF2) are presented. For the set of ingestive behaviour variables, where appropriate two histograms for MDF1 and MDF2 separately, and a scatter plot using both MDF1 and MDF2 are presented.

#### 5.3.3.1 Set of sward variables

For univariate validity, the variables of the same data set entering into multivariate analysis should not be highly correlated (Cooley & Lohnes, 1971; Morrison, 1976). If the inter-dependence approaches a correlation of 1, the matrix also approaches reduced rank, and the solution becomes unstable (Searle, 1966; Morrison, 1976).

In univariate analysis of the sward attributes, twelve variables derived from the point-quadrat measurements and eight variables of other measurements (gross structural characteristics) entered into the analysis. In the multivariate analysis, these variables were classified into two groups: the variables of the complete sward profile (12 variables), and the variables of the grazed stratum (8 variables). Because of the above reasons, these variables were screened.

Among the twelve variables of the complete sward profile, seven variables were selected, top surface height, mass bulk density (mg DM/cm<sup>3</sup>), herbage mass (g DM/m<sup>2</sup>), leaf percentage, leaf frequency bulk density (number of leaf hits per 2 cm band), stem frequency bulk density (number of stem hits per 2 cm band) and percentage of live material. Other variables were either ignored or combined into the selected variables. Leaf layer depth was omitted because it was derived from the difference between leaf surface height and stem height, and stem height was also omitted because of missing values in some treatments (Section 3.2.7.8). The seedhead frequency bulk density (number of seedhead hits per 2 cm band) was amalgamated into stem frequency bulk density, becoming stem + seedhead frequency bulk density. Because the summation of seedhead proportion, stem proportion and leaf proportion is unity after the leaf proportion was taken into account, stem + seedhead proportion could be discarded.

Similar integration was applied to the variables of the grazed strata. Six variables were entered: mass bulk density of the grazed stratum, herbage mass in the grazed stratum, leaf percentage of the grazed stratum, leaf frequency bulk density of

the grazed stratum, stem frequency bulk density of the grazed stratum and live material percentage of the grazed stratum.

#### 5.3.3.1.1 The variables of the complete sward profile

As expected, for this set of attributes there were no significant effects of animal species or of any interactions with this main effect.

Table 5.17 illustrates details of the discriminant functions and summarizes the important statistics of the corresponding functions at levels of the main effects of forage and stage of growth and the interaction between them.

There was a highly significant difference between the two stages of maturity (Table 5.17). This function was named as "height determiner", reflecting (1) a prevailing positive contribution of the sward surface height, and (2) a moderate negative contribution of the leaf frequency bulk density to the score. The score of the reproductive stage was much higher than that of the vegetative stage (309.01 vs. 1.09). This indicates that sward height substantially increased, whereas leaf frequency bulk density substantially decreased, with advancing maturity of forages.

The forage species effect was highly significant (Table 5.17).

MDF1 (Table 5.17) was named as "height determiner", indicating that the surface height of the sward was the dominant effect, and the stem + seedhead frequency bulk density and mass bulk density also made significant negative loading to the score.

The pattern shown in Fig. 5.1A principally reflects the variation in sward height (increasing with scores), and in mass bulk density and stem + seedhead frequency bulk density (decreasing with scores). The leguminous swards were generally shorter, but denser than gramineous swards. Tahora and phalaris distributed at opposite ends of this spectrum and represented the two extremes of the variation.

MDF2 (Table 5.17) was named as "height-density determiner", reinforcing the importance of the variables reflected in MDF1 though there were opposite signs for some variables. Fig. 5.1B displays an ordination with a clear distinction between legumes and grasses. The nine forages could be classified into the three clusters (Fig. 5.1B, Fig. 1 of Appendix 5.3 and Table 1 of Appendix 5.4).

Table 5.17	Structural coefficients (correlations), standardised coefficients and summary of important statistics of the multiple discriminant functions
	(MDF) at various levels of the treatments for sward variables of entire profile.

Main effect and interaction		For	ages		Stages		Forages	x Stages	
Function	Μ	IDF1	Μ	DF2	MDF1	М	DF1	Μ	IDF2
Coefficient	correlation	standardised	correlation	standardised	standardised	correlation	standardised	correlation	standardised
Top height (cm)	0.986	3.377	0.133	4.526	4.371	0.963	6.077	0.259	-0.951
Mass bulk density (mgDM/cm³)	-0.948	-0.821	0.206	2.781	0.007	-0.222	1.738	-0.205	-1.906
mass of turf (gDM/m <sup>2</sup> )	0.020	0.129	0.151	-1.830	-0.080	0.145	-1.544	0.813	1.792
Leaf %	0.940	0.448	-0.040	1.204	0.210	-0.627	0.019	0.547	0.787
Leaf frequency bulk density (hits/2 cm band)	-0.052	-0.133	0.068	-0.755	-1.145	-0.643	-0.532	-0.659	-1.158
Stem+seedhead frequency bulk density (hits/2cm band)	-0.968	-1.212	0.214	2.241	0.211	0.120	0.461	-0.959	-1.300
Live material %	-0.582	-0.272	-0.362	-0.500	-0.149	-0.344	-0.204	-0.369	-0.393
Eigen value	24	l.174	2	.022	13.867	4	.344	2	.099
Discriminatory power	0	.832	0	.070	1	0	.596	0	.288
Significant test of the discriminant function	***			***		***			***
Cumulative discriminatory power	0.901				1	0.885			
Wilks' Lambda Test	***				***	***			

MDF1 and MDF2: discriminant functions one and two. Because there were only two levels in maturity stage, one discriminant function could account for 100% of dispersion, and all the correlation coefficients are +1 or -1. Therefore, only standardized coefficients are shown in this table for maturity stage.



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The interaction of forage with stage of maturity was also found to be highly significant (Table 5.17). As for the forage main effect, MDF1 is a "height determiner". The pattern shown in Fig. 5.2A was characterized by (1) vegetative swards of legumes and reproductive swards of grasses distributed at opposite ends of the spectrum, and (2) reproductive swards of legumes overlapped with vegetative swards of grasses. This reflects an increasing trend in height from vegetative legumes, vegetative grasses and reproductive legumes and reproductive grasses. In terms of the scores of this function, vegetative browntop (Vbr) was more similar to reproductive Tahora (Rth) and Kopu (Rkp) than to other vegetative grasses, reflecting the fact that vegetative browntop was a very short pasture compared to other vegetative grasses. The positions of reproductive swards of lotus (Rlt) and red clover (Rrc) in the ordination on the X axis reflected that they were relatively tall swards compared to other legumes, and even taller than some of vegetative grasses.

In this forage x stage interaction, MDF2 is a "mass determiner", showing a contrast between bulk densities (irrespective of mass bulk density or frequency bulk density) and herbage mass. In MDF2 (Fig. 5.2B), the general trend along the Y axis was similar to that in MDF1. This trend reflects a spectrum of increasing mass and decreasing bulk density of the whole profiles with the rise in scores from vegetative legumes to reproductive grasses. Vegetative Tahora was at one end due to the highest density (Table 5.4), and reproductive browntop was at the other end due to the high herbage mass (Table 5.4).

Classification of the eighteen forage x stage combinations into six clusters was appropriate (Fig. 5.2B, Fig. 2 of Appendix 5.3 and Table 2 of Appendix 5.4). In Fig. 5.2B, vegetative browntop fell into the cluster which was composed principally of vegetative and reproductive legumes. Reproductive red clover and lotus were separated from the other legumes, together with two other vegetative grasses, forming one cluster due to a similar MDF1 score, reflecting a similar height of these swards despite a variation in herbage mass and densities. Reproductive phalaris was isolated from the others because of the high MDF1 score reflecting extreme height.

#### 5.3.3.1.2 The variables of the grazed strata

Although this set of variables were found to be significantly affected by all main effects and their first and second order interactions, it would only be sensible to





Fig 5.2

examine them at the levels of the two main effects (forages and stages), and their interaction because the variation in this set of variables for the main effect, animal species (e.g the swards respectively grazed by sheep and goats) only represented a difference in the grazed depth between the two animal species, rather than the sward characteristics *per se*. Therefore, the animal species effect and any interactions with this effect were ignored in presenting this set of variables.

There was a highly significant difference in this set of attributes between the two stages of maturity (Table 5.18). This function was named as "mass/leaf contrast", determined as a contrast between a summation of leaf percentage and leaf frequency bulk density, and herbage mass of the grazed stratum. The score of the reproductive stage was far higher than that of the vegetative stage (97.33 vs. 0.67), as was the case for the whole sward. This showed that herbage mass of the grazed stratum substantially increased, whereas the leaf proportion and leaf frequency bulk density in the grazed stratum substantially decreased, as forages matured.

The forage effect was highly significant (Table 5.18). The MDF1 was named as "stem+seedhead frequency bulk density/mass contrast" (Table 5.18), interpreted as a contrast between a summation of stem+seedhead frequency bulk density and live material percentage, and herbage mass of this stratum. Fig. 5.3A shows a clear pattern with legumes having higher scores than grasses in MDF1, contrary to MDF1 of the entire profile (Section 5.3.3.1.1). This indicates that in the grazed stratum, the leguminous swards usually had higher stem+seedhead frequency bulk density and live material percentage than gramineous swards (the reason for this is given in section 5.4.2 of "Discussion"), whereas gramineous swards had more herbage mass than leguminous swards in the grazed stratum.
Table 5.18Structural coefficients (correlations), standardised coefficients and summary of important statistics of the multiple discriminant functions<br/>(MDF) at various levels of the treatments for sward variables of grazed stratum.

Main effect and interaction		For	age		Stage		Forage x Stage			
Function	Μ	IDF1	М	IDF2	MDF1	М	DF1	Μ	MDF2	
Coefficient	correlation	standardised	correlation	standardised	standardised	correlation	standardised	correlation	standardised	
Mass bulk density of grazed stratum (mg DM/cm³)	0.757	0.254	0.460	0.282	-0.054	0.443	0.179	-0.027	-0.046	
Herbage mass in grazed stratum (g DM/m²)	-0.848	-0.927	0.236	0.217	0.944	-0.674	-1.100	-0.604	-0.714	
Leaf % grazed stratum	-0.616	0.331	0.642	-0.065	-1.024	0.368	1.665	-0.666	-0.902	
Leaf frequency bulk density of grazed stratum (hits/2 cm band)	0.454	0.369	0.882	1.938	-1.146	-0.605	-1.501	0.587	1.304	
Stem+seedhead frequency bulk density of grazed stratum (hits/2 cm band)	0.960	1.453	-0.009	-0.306	0.380	0.634	1.368	0.378	0.071	
Live material % of grazed stratum	0.740	0.615	-0.445	-0.554	-0.193	0.335	0.453	0.781	0.853	
Eigen value	2	.738	1	.101	6.843	1.	.043	0	.759	
Discriminatory power	0	.620	0	.249	1	0	.448	0	.326	
Significant test of the discriminant function		***		***	***		***		***	
Cumulative discriminatory power	0.869				1	0.773				
Wilks' Lambda Test	***				***	***				

MDF1 and MDF2: discriminant functions one and two. Because there were only two levels in maturity stage, one discriminant function could account for 100% of dispersion, and all the correlation coefficients are +1 or -1. Therefore, only standardized coefficients are shown in this table for maturity stage.

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MDF2 was named as "leaf frequency bulk density determiner" reflecting a positive dominant effect of leaf frequency bulk density (Table 5.18). The nine forages could be classified into four clusters (Fig. 5.3B, Fig. 3 of Appendix 5.3 and Table 3 of Appendix 5.4). In Fig. 5.3B, exclusion of red clover from other legumes, and of browntop and cocksfoot from other grasses, was because of their high scores in MDF2, reflected high leaf frequency bulk density. The ordination of the scores in MDF2 (Fig. 5.3B) indicates that leaf frequency bulk densities were the lowest in phalaris and prairiegrass, but the highest in red clover, browntop, cocksfoot, Tahora and Kopu.

There was a highly significant interaction between forage and stage of maturity (Table 5.18). MDF1 was named as "stem+seedhead frequency bulk density/herbage mass contrast", indicating a contrast between a summation of leaf percentage and stem+seedhead frequency bulk density, and a summation of herbage mass and leaf frequency bulk density. The pattern of the scores in this MDF (Fig. 5.4A) was erratic, reflecting the fact that there were no clear contrasts between grasses and legumes in the grazed horizon at different stages of maturity.

MDF2 was named as "mass+leaf%/live%+leaf frequency contrast" (Table 5.18), indicating a contrast between a summation of leaf frequency bulk density and live material percentage and a summation of leaf percentage and herbage mass (Table 5.18). The eighteen treatments of this interaction could be classified into six clusters (Fig. 5.4B, Fig. 4 of Appendix 5.3 and Table 4 of Appendix 5.4). In Fig. 5.4B, the high score of vegetative red clover in MDF2 and low scores of reproductive browntop in both MDFs gave rise to separations from other forages. Vegetative red clover had high leaf frequency bulk density in the upper layer of the sward, and reproductive browntop had high herbage mass in the grazed horizon.

#### 5.3.3.2 Set of behaviour variables

Among the nine ingestive behaviour variables examined in the univariate analyses, some were the primary variables (bite weight 1, bite rate, bite depth and bite area) which were directly measured (Section 3.2.7) from the experiment, and others were the secondary (first order) variables (bite weight 3, intake rate 2, intake rate 3 and bite volume) which were algebraically derived from the direct measurements (Section 3.2.7). The four primary variables were preferred to work with in multivariate



analysis because of the following facts. (1) Logically, all the information in the secondary variables were contained in the primary variables, and the common use of the secondary variables in some studies was because of an attempt to tackle a multivariate problem by using an univariate approach. And (2) as stated before, the combination of primary and secondary variables into one dispersion matrix may result in an ill-conditioned matrix, making it impossible to solve the eigenstructure (Searle, 1966).

However, in this multivariate analysis, it is appropriate to take both bite weight 1 and bite weight 2 into account because of the following reasons. Although bite weight 2 was a secondary variable, obtained by multiplying bite weight 1 by the corresponding dry matter per cent (Section 3.2.7 of Chapter 3), there was not necessarily a parallel pattern between the two terms of bite weight across all swards due to a great variation in dry matter content across forages and across stages of maturity within forage. That is, there was not necessarily a direct causality in bite weight between fresh and dry matter terms across forages and across stages. Thus, care should be taken to define clearly what term is being referred to in assessing bite weight. Algebraically, this procedure was valid because of the fact that the overall simple correlation (r) between bite weights 1 and 2 was 0.71 (Table 1 of Appendix 5.5), leading to little risk of increasing "ill-condition" of the dispersion matrix.

In this case, there were five behaviour variables in total (four primary variables and bite weight 2) entering into the analysis. Table 5.19 gives details of the discriminant functions for the treatments at the various levels (main effects and interactions) and summarizes the important statistics of the corresponding functions.

#### 5.3.3.2.1 Main effects

There were highly significant differences between the treatments for the main effects, animal species, forage and stage of maturity (Table 5.19).

For animal species, MDF1 was named as "fresh/dry contrast" (Table 5.19), interpreted as (1) a contrast (opposite sign) between bite weight 1 and bite weight 2, and (2) bite depth also was an important attribute in making a significant loading to the score. Feature one implies that the animals tending to harvest herbage in a larger

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Table 5.19	Structural coefficients (correlations), standardised coefficients and summary of important statistics of the discriminant functions at various levels of the treatments for behavioural
	variables.

Effect and interaction	Animal species		For	ages		Stages		Forages	s x Stage	9S		Forages	x Anima	ls	Animals x Sages	Se	cond ord	er intera	action
Function	MDF1	N	IDF1	N	IDF2	MDF1	N	IDF1	Ν	IDF2	N	IDF1	м	DF2	MDF1	М	DF1	м	DF2
Coefficient	stand- ardized	corre- lation	stand- ardized	corre- lation	stand- ardized	stand- ardized	corre- lation	stand- ardized	co <b>rre-</b> lation	stand- ardized	corre- lation	stand- ardized	corre- lation	stand- ardized	stand- ardized	corre- lation	stand- ardized	corre- lation	stand- ardized
Bite weight 1 (mgFM/bite)	3.318	-0.686	-2.956	-0.151	3.374	-2.975	0.199	-2.211	-0.677	1.848	0.866	2.387	0.491	-0.119	-1.879	0.860 -	1.835	0.227	-1.192
Bite weight 2 (mgDM/bite)	-3.984	0.351	3.057	-0.731	-4.666	3.594	0.473	2.260	-0.720	-3.408	0.787	-1.444	0.565	0.767	3.653	0.896	3.045	0.310	2.292
Bite rate (bites/min)	0.661	-0.598	-0.270	0.019	-0.199	-0.558	-0.809	-0.519	0.398	0.090	0.584	0.958	-0.796	-1.066	0.807	-0.587 -	0.506	0.754	1.359
Bite depth (cm)	1.138	0.965	2.813	0.258	1.801	2.262	0.982	2.985	0.123	1.213	0.641	0.183	0.144	0.123	-0.443	0.753	1.375	-0.226	-0.823
Bite area (cm²)	0.561	-0.558	-0.131	0.033	0.304	-0.203	-0.064	-0.065	0.674	0.835	0.302	-0.051	0.711	0.277	-0.602	0.455 ·	0.126	0.795	0.158
Eigen value	0.237	1	1.069	1	.743	6.809	2	2.831	0	.626	С	.309	0	115	0.160	0.	114	0	.091
Discriminatory power	1	C	).837	C	.132	1	0	.733	0	.162	C	.540	0	201	1	0.	428	0	.341
Significant test of the discriminant function	•••		***		***	***		***		***		***		•	***		(*)		(*)
Cumulative discriminatory power	1	0.969				1	0.895				0.740				1	0.769			
Wilks' Lambda Test	***	***				***	***				***				***	(*)			

MDF1 and MDF2: multiple discriminant functions one and two. Because animal species and maturity stage are two-level effects, and degree of freedom of the interaction between animal species and stage is 1, one discriminant function could account for 100% of dispersion, and all the correlation coefficients are positive or negative one. Therefore, the correlation coefficients are not shown in this table for these effects.

fresh matter bite weight (bite weight 1) had high scores, and vice versa, whereas the animals tending to harvest herbage in a large bite weight of dry matter (bite weight 2) had low scores (because its coefficients had a negative sign), and vice versa. Feature two implies that the animals attempting deep bites obtained a high score, and vice versa. The score was much higher for sheep than goats (15.53 vs. 0.48). This indicates that when a wide range of swards (9 forages x 2 stages) were provided, sheep usually obtained a large bite weight through penetrating very deeply into swards with low dry matter content (succulent herbages). Conversely, goats usually obtained large bite weights through shallow browsing in swards with high dry matter content (less succulent herbages).

For the stage of maturity (Table 5.19), MDF1 was named as "dry+depth/fresh contrast", interpreted as (1) a contrast between bite weight 1 and a summation of bite weight 2 and bite depth, (2) bite rate also made some contribution to the scores. This implies that the stage of maturity allowing animals to have large fresh matter bites and fast bite rate had low scores, whereas the maturity stage allowing animals to have large dry matter bites and deep bites had high scores. The score for the reproductive stage was far higher than that for the vegetative stage (129.31 vs. 5.48). This indicates that on the vegetative swards, animals could usually obtain large bite weights in fresh matter terms (though not necessarily in dry matter terms), and harvest herbage at a fast rate as a consequence of less time spent manipulating and chewing the harvested herbage. On reproductive swards animals usually could obtain deep bites and large bite weights in dry matter terms, and had to spend more time manipulating and processing the harvested herbage, resulting in a slow biting rate.

For the main effect, forage, the scores were calculated for both functions (Table 1 of Appendix 5.2). The histogram and scatter plot are shown in Fig. 5.5.

The first discriminant function (MDF1) was named as "depth determiner" characterized by two aspects. The first aspect was determined as a contrast (opposite sign of the standardised coefficients, implying opposite loading to the scores of the nine forages) between a summation of bite depth and bite weight 2, and bite weight 1, even though the importance of each attribute being reflected by the absolute value of its coefficient was not equal. The second aspect emphasized that bite depth was a dominant variable of this function (high values in both sets of coefficients). The first characteristic indicates that the forages enabling animals to have deep penetration and

containing high percentage of dry matter content had high scores, and those allowing animals to harvest a great fresh matter intake per bite had low scores. The second characteristic showed that bite depth was a prevailing attribute among the five selected attributes in discriminating the nine forages, in terms of their scores.

Fig. 5.5A displays a clear pattern in terms of the scores of the nine forages in MDF1. Legumes and grasses were distributed at opposite ends of the spectrum of score variation with Tahora and phalaris placed at the two extremes. This demonstrates that on gramineous swards animals generally had a deep bite and the herbage harvested usually had a high dry matter content, whereas on leguminous swards animals usually had large fresh matter intake per bite with low dry matter content, and shallow bite depth. Animals had the deepest and shallowest bites on phalaris and on Tahora, respectively.

The second discriminant function (MDF2) was named "dry matter determiner" (Table 5.19), interpreted as (1) a contrast between bite weight 1 and bite weight 2, and (2) bite depth also had a significant loading to the score. Feature one implies that the herbages allowing animals to harvest fresh matter intake in large mouthfuls, led to high scores; conversely, those allowing animals to obtain a great bite in dry matter terms led to low scores. Feature two means that the penetration of the mouth into swards also played a significant role in discriminating among the nine forages.

In Fig. 5.5B, a general separation of legumes from the grasses with the exception of browntop was a reflection of the variation in bite depth across them, being shallow on legumes (low score) and deep on grasses (high score). Browntop obtained the lowest score in MDF2 because it allowed animals to harvest a large bite weight of dry matter (Table 5.8).

Fig. 5 of Appendix 5.3 and Table 5 of Appendix 5.4 showed that the nine forages could be classified into four clusters shown in Fig. 5.5C. Table 5.20 summarizes details of each cluster, and the associated information. The score of MDF1 decreased from cluster 1 to cluster 4, and the score of MDF2 generally decreased from cluster 1 to cluster 3, but increased from cluster 3 to cluster 4. Cluster 1 mainly reflects that phalaris allowed animals to have a extremely deep









Clusters	Components of clusters	Scor discrii func	es of minant tions	Means of variables for each cluster					
		1	2	BW1	BW2	BR	BD	BA	DM%
1	Phalaris	77.43	48.81	892 b	226 b	28 ab	29.9 a	9.5 c	25.34
	s.e.			107	30	2.7	1.8	0.7	
2	Ryegrass Cocksfoot Prairiegrass	51.63	26.81	1004 b	276 b	22 b	19.9 b	11.6 ab	27.49
	s.e.			61	17	1.5	1.0	0.4	
3	Browntop	50.77	5.90	1081 ab	359 a	28 ab	15.9 b	10.2 bc	33.21
	s.e.			109	31	2.7	1.8	0.7	
4	Tahora Kopu Red clover Lotus	2.83	12.53	1253 a	257 b	29 a	6.1 c	12.0 a	20.51
	s.e.			51	14	1.3	0.8	0.3	
	F of ANOVA			**	*	*	***	**	

Table 5.20Summary of behaviour variables for each cluster and the associated information<br/>of four clusters for main effect, forages.

s.e.: standard error of means; F of ANOVA: F test of ANOVA among clusters; means with the same letters within each variable are not significant for this variable across four clusters. DM%: ratio of BW2 to BW1 within each cluster.

BW1: bite weight 1 (mg fresh matter/bite); BW2: bite weight 2 (mg dry matter/bite); BR: bite rate (bites/min); BD: bite depth (cm); BA: bite area (cm<sup>2</sup>).

The above notes also apply for Tables 5.21 - 5.23.

penetration of the head into the swards. However, only small mouthfuls were obtained in this forage, in both fresh and dry matter terms. Because the swards of this forage were extremely tall (Table 5.4) and pseudostems and stalks were very well developed and hence very stiff and rigid at the time when they were grazed, animals selectively defoliated leafy components and left the stemmy parts ungrazed within the defined grazed strata, leading to a limited herbage intake per bite in spite of deep penetration. Animals grazed the swards of cluster 2 in a fashion characterized by a moderate bite depth, and a moderate fresh matter per mouthful with a median dry matter content. The small score of cluster 3 in MDF2 was a consequence of the fact that when grazing browntop animals could harvest very heavy bite weights in dry matter terms, although this was not necessarily very large in fresh matter terms. It is indicated in cluster 4 that penetration of the mouth when animals grazed these forages was very shallow due to proximity to soil surface, and animals achieved very large mouthfuls of fresh matter, but only moderate dry matter loading because of the succulent characteristic of these forages.

#### 5.3.3.2.2 The first order interactions

The interaction of forage by stage of maturity was highly significant (Table 5.19). MDF1 is a "bite depth determiner" (Table 5.19), interpreted as a contrast between a summation of bite depth and bite weight 2, and a summation of bite weight 1 and biting rate, and (2) a paramount determinant of bite depth. These features indicate that large bite weight 2 and deep bites led to a high score, and vice versa; on the other hand, heavy fresh matter intake per bite and fast biting rate led to a low score, and vice versa; among these, bite depth made the most significant loading to the score.

In Fig. 5.6A, vegetative swards of legumes (VL) and reproductive swards of grasses (RG) were separately distributed at the two ends of the spectrum (with the exception of vegetative browntop (Vbr)), and there was a continuum between these two extremes, being basically sequenced as VL (vegetative swards of legumes), RL (reproductive swards of legumes), VG (vegetative swards of grasses) and RG (reproductive grasses) with increasing score. On VL, animals displayed a very shallow bite depth due to proximity to the soil surface and harvested herbage at a fast rate. On RG, they exhibited a very deep bite with slower biting rate; animals also could obtain high dry matter intake per bite, even though this was not necessarily the case in fresh matter terms. Animals responded to RL and VG in an intermediate manner. They dealt with vegetative browntop in a fashion characterized by relatively shallow bites and very fast biting rate (Table 5.11), which is more similar to behaviour on legumes than other grasses. In this interaction, the discrimination is reflected first by a clear-cut distinction between legumes and grasses and within legumes.

0

20

40

Scores of forages x stages for behaviour attributes



vegetative legumes

120

br

100

60 80 1 MDF1 (depth determiner) MDF2 is a "dry matter determiner" (Table 5.19), interpreted as (1) a contrast between a summation of bite weight 1 and bite depth, and bite weight 2, and (2) a paramount determinant of bite weight 2. These features indicate that the swards allowing animals to obtain heavy fresh matter intake per bite through deep penetration gave rise to a high score, whereas the swards allowing animals to obtain heavy bites in dry matter terms gave rise to a low score; also bite weight 2 made the highest contribution to the score.

The distribution pattern of MDF2 with respect to the eighteen combinations (Fig. 5.6B) was characterized generally by a distinction between legumes (low score) and grass (high score), and by a lower score for reproductive than vegetative stages within legumes and a mixture of the two stages within grasses. The fact that animals obtained largest dry matter intake per bite (Table 5.11) when grazing reproductive swards of browntop, brought about a very low score of reproductive browntop in MDF2. For the reproductive phalaris, the high score reflected extremely deep bites and extremely low bite weight in both fresh and dry matter terms.

Division of the eighteen treatments (9 forages x 2 stages combinations) into six clusters (Fig. 5.6C) was appropriate (Fig. 5.6C, see Fig. 6 of Appendix 5.3 and Table 6 of Appendix 5.4 for clustering). Table 5.21 gives details of the information on these six clusters.

Cluster 1 comprises herbages which were handled by moderately large fresh matter intake per bite. In cluster 2, the lowest MDF2 score was a net consequence of counterbalancing from three variables: relatively shallow bite depth which led to low score, relatively great bite weight 1 which led to high score, and moderate bite weight 2 which led to low score. Cluster 3 had a moderately low MDF1 score and a moderately high MDF2 score. Exclusion of reproductive prairiegrass (cluster 4) from cluster 5 was attributable mainly to shallow bite depth, compared with other reproductive grasses of cluster 5, because some animals were keen to eat the seedheads of reproductive prairiegrass. Cluster 5 had a relatively high MDF1 score and a moderate MDF2 score. A separation of reproductive phalaris (cluster 6) from other reproductive grasses was ascribable principally to extremely deep bites, leading to the highest MDF1 score. Forage dry matter percentage increased from cluster 1 to cluster 6.

Clusters	Components of clusters	Score discrin funct	es of ninant ions	Ме	Means of variables for each cluster					
		1	2	BW1	BW2	BR	BD	BA	DM%	
1	V Tahora V Kopu V Red clover V Lotus	5.39	18.07	1098 bc	198 с	33 a	4.5 f	11.6 ab	18.03	
	s.e.			68	16	1.5	0.58	0.48		
2	R Tahora R Kopu R Red clover R Lotus V Browntop	21.54	12.98	1254 ab	290 b	27 b	7.8 e	12.0 a	23.13	
	s.e.			61	14	1.3	0.53	0.43		
3	V Ryegrass V Cocksfoot V Prairiegrass V Phalaris	37.97	26.12	813 d	187 с	32 ab	14.0 d	11.8 a	23.00	
	S.e.			68	16	1.5	0.58	0.48		
4	R Prairiegrass	65.18	18.88	1008 abc	303 b	18 c	20.3 c	9.4 c	30.06	
	s.e.			136	32	2.9	1.18	0.96		
5	R Ryegrass R Cocksfoot R Browntop	100.64	18.63	1502 a	473 a	11 d	30.6 b	10.8 abc	31.49	
	s.e.			87	21	1.9	0.76	0.62		
6	R Phalaris	137.57	47.79	822 cd	277 b	15 cd	44.7 a	9.7 bc	33.70	
	S.e.			148	35	3.2	1.3	1.1		
	F of ANOVA			***	***	***	***	(*)	<u> </u>	

Summary of behaviour variables for each cluster and the associated information of six clusters for the interaction between forage and stage. Table 5.21

V: vegetative; R: reproductive. Other notes are referred to Table 5.20.

The interaction of forage with animal species was also highly significant (Table 5.19).

MDF1 was named as "fresh matter determiner" (Table 5.19), characterized by (1) a contrast between a summation of bite weight 1 and bite rate, and bite weight 2; and (2) bite weight 1 as a dominant variable.

In Fig. 5.7A, generally, grasses had lower scores than legumes, reinforcing the indication that animals tended to obtain more herbage intake per bite in fresh matter terms and harvest herbage at a faster biting rate on legumes than grasses (Section 5.3.2). However, except for Src. Sth and Skp being distributed at the right hand of the X axis, there was no clear distinction between animal species across the continuum, corroborating the view that the two animal species did not differ significantly in overall bite weight and biting rate across a wide range of forages (Section 5.3.1.3.1). Sheep usually had larger bites than goats on some swards, whereas goats obtained larger bites than sheep on others. On the other hand, there was usually a substantial variation in the score between the two stock classes when they grazed the same forage, suggesting that sheep and goats behaved guite differently with regard to bite weight and bite rate when a particular forage was offered. The highest score was obtained when sheep grazed the three clovers, indicating that sheep were able to obtain very large bite weights of fresh matter on these swards. The lowest score was obtained when goats grazed browntop and prairiegrass and when sheep grazed ryegrass, reflecting the fact that the amount of herbage intake per bite in dry matter terms was large in these treatments, even though it was not necessarily the case in fresh matter terms.

MDF2 was named as "bite rate determiner" (Table 5.19), characterized by (1) a contrast between biting rate and bite weight 2; and (2) bite rate dominance.

The pattern of score distribution of MDF2 (Fig. 5.7B) was characterized by higher scores for grasses than legumes, contrary to MDF1. This reflected dominant contributions from biting rate and bite weight 2 which, as mentioned before, substantially differed between grasses and legumes. Again, there was no apparent distinction between sheep and goats in the distribution of score, reflecting a lack of significant difference in gross biting rate and bite weight 2 across a wide range of swards. The high scores showed that goats handled cocksfoot, browntop and ryegrass in large bites of dry matter, and consequently had slow biting rates, and this was also





• lt

10

TC.

12

\* kp

16

18

th

14

• kp ph • th 2 4 6 8 10 12 MDF1 (fresh matter determiner)

\* Pg

2

0

the case for sheep handling ryegrass. Bite weight 2 was less for goats grazing Tahora, Kopu and phalaris, and this was also the case for sheep grazing Tahora and lotus due to the low dry matter content of these herbages.

Eighteen treatments (9 forages x 2 animal species) fell into five clusters (Fig. 5.7C) according to Fig. 7 of Appendix 5.3 and Table 7 of Appendix 5.4. In Table 5.22, cluster 1 had the lowest MDF1 score and highest MDF2 score, suggesting that goats handled these two forages at a very slow biting rate, as a consequence of very heavy dry matter intake per bite, even though the fresh matter intake was not necessarily large due to the less succulent nature of these forages. Cluster 2 was the only cluster, including the treatments involving the same forage (ryegrass) grazed by both sheep and goats, with a low score for MDF1 and moderate score for MDF2. Cluster 3 indicates that grazing of goats on Tahora was characterized by low bite weight 1 which resulted in low scores for MDF1, and by fast biting rate and low bite weight 2 (Table 5.10) which resulted in low scores for MDF2, being more similar to the behaviour of sheep grazing browntop and prairiegrass than to other legumes. In cluster 4, as goats had a fast biting rate when dealing with phalaris (Table 5.10), it fell into this cluster characterized by moderate MDF1 score and the lowest MDF2 scores which was an indicator of fast bite rate. Cluster 5 indicates that sheep handled succulent clovers in very large mouthfuls, being reflected by the highest MDF1 scores. Sheep also defoliated these clovers at a fast rate, being reflected by the lowest MDF2 scores. This was also the case for goats grazing lotus (Table 5.10).

The overall separation of legumes from grasses was more clear-cut than the distinction between the animal species.

The interaction of stage of maturity by animal species was highly significant also (Table 5.19). MDF1 was named as "dry/fresh contrast", interpreted as a contrast between bite weight 1 and bite weight 2, with particular indication that bite weight 2 was a paramount discriminator. This feature shows that the treatments being characterized by high dry matter intake per bite obtained high scores, and vice versa; on the other hand, the treatments being characterized by high dry cores, and vice versa.

	forages.								
Clusters	Components of clusters	Discriminant functions		Mea	ns of va	ariable	s for ea	ach clu	ster
		1	2	BW1	BW2	BR	BD	BA	DM%
1	G Cocksfoot G Browntop	2.01	11.45	1299 ab	393 a	18 c	19.4 a	10.3 b	30.25
	S.e.			98	28	2.5	2.1	0.7	
2	S Ryegrass S Cocksfoot S Phalaris G Ryegrass G Prairiegrass	3.84	6.47	951 cd	259 bc	23 bc	22.0 a	11.4 ab	27.23
	S.e.			63	18	1.6	1.4	0.4	
3	S Browntop S Prairiegrass G Tahora	3.78	2.13	834 d	227 c	28 a	12.5 b	11.5 ab	27.22
	S.e.			81	23	2.1	1.7	0.6	
4	S Lotus G Phalaris G Kopu G Red clover G Lotus	8.26	1.68	1147 bc	244 bc	27 ab	10.1 bc	11.0 b	21.28
	S.e.			62	18	1.6	1.3	0.4	
5	S Tahora S Kopu S Red clover	13.26	2.41	1465 a	292 b	31 a	6.8 c	12.9 a	19.93
	S.e.			79	23	2.0	1.7	0.6	
÷	F of ANOVA			***	***	***	***	*	

 Table 5.22
 Summary of the behaviour variables for each cluster and the associated information of five clusters for the interaction between animal species and forages.

G: goats; S: sheep.

Other notes are referred to Table 5.20.

The trend shown in Fig. 5.8 clearly demonstrates that goats had small bite weight 1 when grazing the vegetative swards, and sheep generally had larger bite weight 1 than goats on the vegetative swards; however, on the reproductive swards, bite weight was greater for goats than sheep when it was converted into dry matter terms. The magnitude of increase in score was far smaller for sheep than goats when

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Fig. 5.9 Plot of animal x forage x stage for behaviour attributes (see Fig.8 of Appendix 5.3 and Table 8 of Appendix 5.4 for clustering)



swards progressed in maturity. This reinforces the observation that sheep showed a great reluctance to increase bite weight as sward maturity increased, whereas goats showed willingness.

The variation of score with respect to the four treatments also reinforced the view that the stage of maturity played a more influential role than the animal species in the discrimination of this interaction, because the four treatments were split well by the stage of growth, rather than by the animal species.

#### 5.3.3.2.3 The second order interaction

The second order interaction was significant at the level of P<0.1 (Table 5.19). MDF1 was named as "weight-depth determiner" (Table 5.19), considered as a contrast between a summation of bite weight 2 and bite depth, and a summation of bite weight 1 and bite rate, and bite weight 2 had a dominant loading in the score. This suggests that the treatments (combinations between the three main effects) characterized by large bite weight 2 and deep bites, obtained high scores; on the other hand, the treatments being characterized by large bite weight 1 and fast biting rate obtained low scores.

MDF2 was named as "depth determiner", considered as (1) a contrast between a summation of bite weight 1 and bite depth, and a summation of bite weight 2 and bite rate. The implications of MDF2 suggest that the treatments characterized by large bite weight 2 and fast biting rate obtained high scores, and the treatments characterized by large fresh matter intake per bite or deep bites, led to low scores.

The distribution pattern in the scatter plot Fig. 5.9 was characterized by apparent separations of grasses from legumes, and of reproductive swards from vegetative swards along the horizontal direction (MDF1). There was also a mixed zone of grasses with legumes, and reproductive swards with vegetative swards, reflecting a continuum of the variation in the grazing behaviour represented by MDF1. However, as before there was no clear distinction between animal species in this distribution pattern. Reproductive swards of grasses clumped at the right hand end of MDF1. These swards generally allowed both sheep and goats to obtain large intake per bite in dry matter terms through deep penetration of incisors into the swards. Vegetative clover swards distributed at the left hand end of MDF1. These swards usually allowed both sheep and goats to obtain large intake per bite in fresh matter

terms, and to bite at relatively fast rates, but penetrate shallowly due principally to the proximity of the incisors to the soil surface. Within grasses, vegetative swards obtained lower scores than reproductive swards, and partially overlapped with reproductive legumes in the distribution. The difference in the score between the two stages within the grasses was brought about by the disparity in bite weight 2, which was smaller for the vegetative than reproductive swards as a consequence of shallower bite depth, and of lower dry matter content for the former than the latter. Bite weight 2 was smaller in the vegetative grasses, and therefore the score should be lower for vegetative grasses than reproductive legumes, but this low score could be compensated for by deeper bite depth on the vegetative grasses, and consequently. the score was equalised. On the other hand, the lower score for reproductive legumes due to proximity of the canopy surface to the soil surface was equalised by heavier bite weight 2 than with vegetative grasses. The above two facts led to an overlap between the vegetative grasses and the reproductive legumes. Within legumes, reproductive swards were distributed at the right hand end of the vegetative stage, and this indicates that with an increase of legume maturity, the animals increased bite weight 2 through increasing bite depth.

Separation along the MDF2 axis between the levels within the three main effects was not as clear-cut as along the MDF1 axis.

Thirty six treatments (9 forages x 2 stages x 2 animal species) fell into seven clusters (Fig. 5.9) according to Fig. 8 of Appendix 5.3 and Table 8 of Appendix 5.4. In Table 5.23, the ratio of BW2 to BW1 increased from cluster 1 to cluster 7, and was reflected in the increase in MDF1 scores. Animals were unable to obtain large bites on the swards of cluster 1 because of the limitation in sward height, and they attempted to compensate for with faster bite rates. For the swards of cluster 2, animals could increase their bite weights, particularly in dry matter terms, because of greater sward heights, and were almost able to maintain their biting rate. Animals could penetrate into swards of cluster 3 relatively deep compared to the previous clusters, resulting in a slight increase in bite weight. Cluster 4 involved the same

Clusters	Components of clusters	Scor discrii func	es of minant tions	Mea	ans of va	ariable	s for ea	ch clus	ter
		1	2	BW1	BW2	BR	BD	BA	DM%
1	S V Tahora S V Red clover G V Tahora G V Kopu G V Red clover	4.07	35.20	900 bc	156 c	35 a	3.3 f	12.4 a	17.33
	s.e.			87	19	1.9	0.74	0.60	
2	S V Browntop S V Kopu S V Lotus S R Lotus G V Ryegrass G V Browntop G V Lotus G R Tahora G R Kopu	15.80	35.32	1056 bc	235 b	31 ab	6.5 e	10.9 ab	22.25
	s.e.			65	14	1.4	0.55	0.45	
3	S R Tahora S R Kopu S R Red clover S V Ryegrass S V Cocksfoot S V Phalaris S V Prairiegrass G R Red clover G R Lotus G V Phalaris G V Cocksfoot G V Prairiegrass	25.30	29.63	1152 b	257 b	27 b	12.6 d	12.3 a	22.31
	S.e.			56	12	1.2	0.48	0.39	
4	S R Prairiegrass G R Prairiegrass s.e.	45.46	23.57	1008 bc 136	303 b 30	18 c 2.9	20.3 c 1.18	9.4 c 0.95	30.06
5	S R Ryegrass S R Cocksfoot	62.23	10.83	1030 bc	303 a	13 cd	32.5 b	11.3 ab	29.42
٩	s.e.			159	35	3.4	1.36	1.09	
6	S R Browntop G R Ryegrass G R Browntop G R Cocksfoot s.e.	75.87	25.77	1714 a 106	549 a 24	10 d 2.3	29.8 b 0.91	10.6 ab 0.73	32.03
7	S R Phalaris G R Phalaris s.e.	78.35	2.12	822 c 150	277 b 33	15 cd 3.2	44.7 a 1.29	9.7 b 1.04	33.70
	F of ANOVA			***	***	***	***	**	

Table 5.23	Summary of the behaviour variables for each cluster and the associated information of seven clusters for the second order interaction

S: sheep; G: goats; V: vegetative; R: reproductive. Other notes are referred to Table 5.20.

forage (prairiegrass), with moderate scores in both functions. Cluster 5 was the only cluster involving only one animal species (sheep). In cluster 6, animals obtained maximum bite weight in both fresh and dry matter terms at the expense of slowest biting rate. Animals obtained the greatest bite depth but the smallest fresh matter intake per bite when grazing phalaris (cluster 7) despite the fact that dry matter intake per bite was moderate (highest dry matter content). The lowest score in MDF2 was a resultant of small bite weight and relatively slow bite rate, being exacerbated by the negative loading of bite depth.

### 5.3.4 Interrelationships between sward variables and ingestive behaviour variables

Because this research focuses on the influences of sward characteristics on the ingestive behaviour of the grazing animals, the set of sward attributes were regarded as influential variables and the set of behaviour attributes were regarded as response variables.

Response patterns of grazing behaviour to variation in sward structure were explored in two ways, (1) to overview the **joint correlations** (canonical correlations) between the **two sets** of variables through canonical analysis, (2) to examine the regression relationships of **individual** behaviour variables with the **set** of sward variables by multiple regression.

### 5.3.4.1 Canonical analysis between the set of sward variables and the set of behaviour variables

Multiple discriminant analysis (Section 5.3.3.2) indicated a clear contrast between gramineous and leguminous swards with respect to animal response patterns. In this section, therefore, the relationship between the **set** of animal response variables (behaviour variables) and the **set** of sward variables was examined, and then relationships for separate animal species (sheep vs. goats), separate herbage categories (grasses vs. legumes) and animal species x herbage category combinations (interaction) were explored.

All the behaviour variables (5 variables) and sward variables of the complete profiles (7 variables) which were used in MDF were entered into the canonical analysis.

### 5.3.4.1.1 Overall relationship between sward variables and behaviour variables

This section deals with the overall effect of sward variables on behaviour variables without partitioning (subdividing) at any levels of the main effects and their interactions. It gives the "general" relationship, irrespective of animal species or sward categories.

The first canonical correlation was 0.9532 (Table 5.24), higher than any simple correlation between an individual sward variable and any individual behaviour variable (Appendix 5.5). The first canonical score for the sward variables was named as "height determiner (Table 5.24). It was composed of a linear function of surface height, herbage mass, mass bulk density, and live material proportion. The largest standardised coefficient was from surface height. The coefficient of this variable was 5-6 times larger than any others, showing the importance of sward height in affecting ingestive behaviour of grazing animals.

The first canonical score for the behaviour variables was named as "depth determiner" (Table 5.24). It was largely composed of bite depth and bite weight, with the most emphasis on bite depth, its standardised coefficient being more than twice that of bite weight. This indicates that bite depth was the most important response variable and had the greatest association with the sward characteristics in combination.

## 5.3.4.1.2 Comparison between sheep and goats in responding to sward characteristics

The canonical correlations between the two sets of variables were very high for both sheep and goats (Table 5.24). There was no significant difference (t test) between the two animal species in the canonical correlation, implying that the degree of association between sward and behaviour sets was similar in the two stock classes. 

 Table 5.24
 Canonical correlation coefficients between the set of sward variables and the set of behaviour variables, standardised coefficients, structural coefficients and summary of important statistics of the first canonical score at various levels of the treatments.

Levels of treatment	Over	rall		Animal	species			Herbage category			
Variables	No parti	tioning	She	өр	Goa	ts	Gras	ses	Legu	mes	
	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation	
SWARD SET											
Top surface height (cm)	1.184	0.982	1.182	0.977	1.204	0.987	0.990	0.992	0.281	0.861	
Mass bulk density (mgDM/cm <sup>3</sup> )	0.200	-0.661	0.168	-0.700	0.200	-0.654	0.026	-0.438	-0.374	-0.460	
Herbage mass (g DM/m²)	-0.212	0.365	-0.237	0.321	-0.215	0.374	-0.039	0.534	0.199	0.563	
Leaf proportion (%)	-0.045	0.265	-0.077	0.225	-0.032	0.313	-0.147	-0.725	0.161	-0.285	
Leaf frequency bulk density (hits/2 cm)	0.028	-0.494	0.055	-0.505	0.027	-0.468	0.090	-0.804	-0.761	-0.873	
Stem+seedhead frequency bulk density (hits/2 cm)	0.001	-0.589	-0.117	-0.595	0.114	-0.591	-0.021	-0.010	0.352	-0.469	
Live material (%)	-0.159	-0.462	-0.166	-0.411	-0.121	-0.493	-0.090	-0.175	0.057	0.372	
BEHAVIOUR SET											
Bite weight 1 (mg FM/bite)	-0.314	0.125	-0.318	-0.186	-0.180	0.437	-0.304	0.482	-1.749	0.495	
Bite weight 2 (mg DM/bite)	0.355	0.468	0.241	0.195	0.307	0.662	0.404	0.585	2.057	0.698	
Bite rate (bites/min)	-0.072	-0.545	-0.083	-0.568	-0.034	-0.519	-0.119	-0.678	-0.221	-0.650	
Bite depth (cm)	0.840	0.987	0.856	0.989	0.861	0.990	0.832	0.978	0.401	0.717	
Bite area (cm <sup>2</sup> )	-0.030	-0.181	-0.002	-0.181	-0.029	-0.172	-0.080	-0.197	-0.052	0.016	
Canonical correlation	0.95	32	0.95	85	0.95	22	0.96	40	0.78	183	
Squared canonical correlation	0.90	86	0.91	87	0.90	67	0.92	93	0.62	214	
% of association	0.91	88	0.91	10	0.87	10	0.90	0.9050 0.7875			
Likelihood Ratio	0.00	01	0.00	001	0.00	01	0.00	01	0.00	001	

There was a similar general trend in the sequence of importance of sward variables between sheep and goats (both were height determiners), the first three places being occupied by sward height, herbage mass and mass bulk density for both species. However, the importance of sward height relative to herbage mass and to mass bulk density was not consistent across sheep and goats because the ratios of sward height to these two variables were quite different between the two animal species. Height/density (7.04 vs. 6.02) was higher, but height/mass (4.99 vs. 5.60) was lower for sheep than goats, indicating that, as compared to mass bulk density, sward height exerted more influence on sheep than on goats, but as compared to herbage mass, sward height had less impact upon sheep than upon goats.

The canonical score based on the set of behaviour variables gave a similar sequence of importance between sheep and goats (both were depth determiners), with predominance on bite depth (Table 5.24). However, the second important response variable was bite weight 1 for sheep, but was bite weight 2 for goats, substantiating the view that one of major differences between the two animal species in behaviour response to variation in sward characteristics was the ability to harvest large bite weight in dry matter (goats) or fresh matter (sheep) terms.

# 5.3.4.1.3 Comparison between grasses and legumes in affecting ingestive behaviour of the animals

In legumes, the first canonical score contributed 78.75% of the association (Table 5.24), but the Likelihood Ratio only showed a probability level of 0.0587 for the second canonical score, so no firm conclusion could be drawn from the second canonical variable in spite of the relatively low proportion of association accounted for by the first canonical score. In this case, only the first canonical score could be considered.

There was a significant difference (t test) between legumes and grasses in canonical correlation of the first canonical score (0.964 vs. 0.788, Table 5.24), and this suggests that the degree of association between sward characteristics and ingestive behaviour was different when animals grazed grasses and legumes.

In the set of sward variables, the sequence of importance was different between grasses and legumes (Table 5.24). The first canonical scores were named as "height determiner" and "bulk density (irrespective of mass or frequency) determiner" for grasses and legumes, respectively (Table 5.24). This showed that bulk density, with particular emphasis on leaf frequency bulk density, was the most important feature in affecting the ingestive behaviour of animals grazing leguminous swards, whereas sward height was the most important feature in gramineous swards. In addition to this, herbage mass was more influential in leguminous swards than in gramineous swards.

In the set of behaviour variables, the first canonical scores were named as "depth determiner" and " dry matter determiner" for grasses and legumes, respectively (Table 5.24). In this canonical score, bite depth was much more important than bite weight 1 and 2 for grasses (Table 5.24). In contrast, bite depth was much less important than bite weight 2 and bite weight 1 for legumes. This suggests that, when grazing grasses, animals usually adjust bite depth in response to variation in sward height and, therefore, bite depth was the most important determinant of bite weight. However, when legumes were grazed, bite depth became less important, and bite weight was the most sensitive variable to a change in bulk density of the sward. Apart from that, the importance of bite rate was much greater in legumes than in grasses.

#### 5.3.4.1.4 Comparison between sheep and goats grazing grasses and legumes

The canonical correlation was similar between sheep and goats grazing grasses, and between sheep and goats grazing legumes (Table 5.25).

The first canonical scores of the sward set were named as "height determiner" for both sheep and goats grazing grasses (Table 5.25). However, compared to other sward variables, the sward height was more important for sheep than for goats, though it was the most important variable for both sheep and goats. The secondary variables appeared to be quite different between sheep and goats. Leaf percentage and leaf frequency bulk density were more influential on sheep than on goats, whereas stem+seedhead frequency bulk density was more influential on goats than sheep. Therefore, the canonical score was composed of a linear function of surface height, leaf percentage and leaf bulk density for sheep, but a linear function of surface height, and stem+seedhead frequency bulk density for goats.

The corresponding canonical scores of the behaviour set are "bite depth determiner" for both sheep and goats. The bite depth was the most important response variable to sward characteristics in combination, and the canonical score

 Table 5.25
 Canonical correlation coefficients between sets of sward variables and behaviour variables, standardised coefficients and structural coefficients and summary of important statistics of the canonical scores at the level of interaction of herbage category (grass vs legume) with animal species.

Levels of treatment	Grasses Legumes									
Variables	She	ер	Goa	ts	She	өр	Goat	s 1	Goats 2	
	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation
SWARD SET										
Top surface height (cm)	1.024	0.989	0.866	0.992	-0.436	0.777	0.756	0.947	-0.475	0.166
Mass bulk density (mgDM/cm <sup>3</sup> )	0.103	-0.434	-0.176	-0.456	-0.811	-0.486	-0.126	-0.757	-0.307	0.537
Herbage mass (gDM/m²)	-0.084	0.534	0.141	0.516	0.623	0.587	-0.242	0.192	1.066	0.874
Leaf proportion (%)	-0.344	-0.745	0.169	-0.688	0.150	-0.316	0.228	0.029	-0.151	-0.409
Leaf frequency bulk density (hits/2 cm)	0.229	-0.806	-0.119	-0.793	-0.928	-0.853	-0.460	-0.632	-0.288	-0.503
Stem+seedhead frequency bulk density (hits/2 cm)	-0.193	-0.011	0.252	-0.123	0.504	-0.472	0.124	-0.642	0.031	0.220
Live material (%)	-0.091	0.301	-0.052	-0.298	0.190	0.382	0.039	0.444	-0.326	-0.302
BEHAVIOUR SET										
Bite weight 1 (mg FM/bite)	-0.264	0.307	-0.191	0.650	-2.141	0.321	-0.464	0.737	-2.389	-0.019
Bite weight 2 (mg DM/bite)	0.294	0.478	0.384	0.704	2.153	0.518	1.182	0.838	2.951	0.219
Bite rate (bites/min)	-0.121	-0.718	-0.058	-0.633	-0.227	-0.683	0.201	-0.383	0.278	-0.285
Bite depth (cm)	0.857	0.986	0.818	0.978	0.539	0.777	0.493	0.843	-0.662	-0.332
Bite area (cm <sup>2</sup> )	-0.054	-0.172	-0.080	-0.209	-0.063	0.032	0.111	0.113	-0.399	-0.421
Canonical correlation	0.97	32	0.96	37	0.83	40	0.84	75	0.74	52
Squared canonical correlation	0.94	71	0.92	87	0.69	56	0.71	83	0.55	53
% of association	0.93	80	0.84	80	0.76	20	0.60	40	0.2961	
Likelihood Ratio	0.00	01	0.00	01	0.00	02	0.00	01	0.00	27

All values are from the first canonical score except for legume x goats, in which the first canonical score only accounted for 0.6044 of total association, and the second canonical score also showed a highly significant level according to the Likelihood ratio, so the two canonical scores were considered for this treatment. Goats 1: the first canonical score, and Goats 2: the second canonical score.

was composed of a linear function of bite depth, bite weight 2 and bite weight 1 for both species. However, the ratios of bite depth to other behaviour variables were different between the two stock classes (Table 5.25). Bite weight 2 was more emphasized in goats than in sheep, reinforcing the view that goats were better at obtaining large mouthfuls of herbage on the swards with high dry matter content.

In the case of goats grazing legumes, the first canonical score only accounted for 0.604 of total association (Table 5.25), and the second canonical score also showed a highly significance level according to the Likelihood Ratio, so the two canonical scores were considered for this treatment (Table 5.25).

In the case of sheep grazing legumes, the first canonical score of the sward set is a "bulk density determiner" (Table 5.25), there being much more emphasis on bulk density (leaf frequency bulk density and mass bulk density) than sward height, reinforcing the pattern displayed in Table 5.24 for the leguminous swards. However, in the case of goats grazing legumes, the two canonical scores of the sward set are "height determiner" and "mass determiner". In the first canonical score, both sward height and leaf frequency bulk density were important, with more emphasis on sward height. The second canonical score emphasized herbage mass, mass bulk density and sward height, being more important for mass than bulk density and sward height (Table 5.25). The above features indicate that bulk density exerted more influence on sheep than goats; and goats' behaviour was largely influenced by sward height and herbage mass (Table 5.25). This interaction also reinforces the observation that herbage mass exerted more influence in legumes for both sheep and goats compared with that in grasses. All three corresponding canonical scores of the behaviour set in legumes are "bite weight determiners" (Table 5.25), showing that on legumes, bite weight (based on both dry and fresh matter terms) showed greater response to sward conditions than bite depth in both sheep and goats.

## 5.3.4.2 Multiple regression of individual behaviour variables against the set of sward variables

Canonical analysis showed that there were differences between sheep and goats grazing grasses and legumes in the effects of the **set** of sward attributes on the **set** of behaviour attributes. In this section, attention is concentrated on dealing with

the regression relationships between single behaviour variables and the set of sward variables involved in this interaction.

Each separate behaviour variable (bite weight 1, bite weight 2, bite rate, bite depth and bite area) was regressed in turn onto the set of sward variables at an unpartitioned level (overall), for each animal species (sheep vs. goats), each herbage category (grasses vs. legumes), and their combinations (sheep x grasses, goats x grasses, sheep x legumes and goats x legumes), using the "Stepwise" approach (Draper & Smith, 1981). The multiple regressions showed great variation in coefficients of determination (model  $\mathbb{R}^2$ ) from one behaviour variable to another.

The values of R<sup>2</sup> were low for some variables: 0.159-0.387 for bite weight 1, 0.266-0.494 for bite rate, and 0.047-0.147 for bite area. The weak functional relationships of bite rate and bite weight with sward variables were a consequence of swamping by heterogeneity and lack of independence in sward characteristics being produced by a wide range of forages and two maturity stages for each forage, which usually involved highly associated variation (Appendix 5.5). The lack of functional relationship between bite area and the set of sward variables resulted from the relative consistency of bite area over the wide range of variation across forages and stages of maturity.

Hence, the results of the relationships of bite weight 1, bite rate and bite area with sward variables will not be considered further. Tables 5.26 and 5.27 summarize the results of multiple regressions of bite weight 2 and bite depth.

The variables of leaf frequency bulk density (hits/2 cm band) and percentage of live material exerted negative effects on both bite weight 2 and bite depth (Tables 5.26 and 5.27), in contrast to the results of Stobbs (1973a & b; 1975b). This was attributable to the confounding effect of reproductive swards. Animals usually had substantially greater bite weight 2 and penetrated more deeply on the reproductive swards compared to the vegetative swards (Section 5.3.1.3), but these two sward variables were smaller in the reproductive swards than in the vegetative swards (Section 5.3.1.1). The reason for the reduction in percentage of live material with increasing stage of maturity is that, associated with appearance and development of inflorescences, there is a major reduction in the rate of tillering of grasses and hence reduced leaf density (Smetham, 1990).

 Table 5.26
 Summary of multiple regression for the different treatments, determined by Stepwise procedure.

Treatment	Intercept and independent variables	Slopes	Standard errors	Partial R <sup>2</sup>	Model R <sup>2</sup> and residual d.f	Standardised coefficients
Overall (unpartitioned)	Intercept Sward height Herbage mass	625.189 1.260 2.000	194.49 0.657 0.6	0.232 0.079	0.359	0.146 0.251
	Leaf frequency bulk density Live %	-38.126 -438.948	9.826 190.91	0.037 0.012	(r.d.f=202)	-0.292 -0.146
Sheen	Intercept	729.684	260.92			
Cheep	Herbage mass	3.000	0.7	0.243		0.336
	Leaf %	-237.932	115.19	0.042	0.321	-0.207
	Leaf frequency bulk				(r.d.f=98)	
	density	-20.314	11.74	0.017	· · · ·	-0.182
	Live %	-376.459	231.74	0.018		-0.148
Goats	Intercept	640.20	291.12			
	Sward height	3.684	0.903	0.419		0.383
	Herbage mass	2.000	0.8	0.027	0.516	0.158
	Leat frequency bulk	40.050	10.00	0.055	(r.d.t=99)	0.070
	density	-40.350	13.29	0.055		-0.273
		-503.355	200.29	0.015		-0.145
Grasses	Intercept	977.61	246.72			
	Sward height	4.180	0.86	0.290	0.447	0.406
	Herbage mass	2.000	0.8	0.128	(r.d.f=107)	0.207
	Live %	-1094.79	273.89	0.029		-0.304
Legumes	Intercept	265.61	51.24			
	Sward height	3.93	1.37	0.062	0.306	0.303
	Leaf frequency bulk				(r.d.f=93)	-0.320
	density	-37.33	12.29	0.244		
Sheep x	Intercept	850.017	267.48			
grasses	Sward height	2.509	0.997	0.075	0.396	0.329
	Herbage mass	2.000	0.9	0.249	(r.d.f=51)	0.243
	Live %	-890.785	301.44	0.075		-0.340
Goats x	Intercept	891.19	409.35			
grasses	Sward height	5.683	1.33	0.408	0.533	0.468
	Herbage mass	3.000	0.1	0.035	(r.d.f=52)	0.228
	Live %	-1060.18	447.52	0.089		-0.244
Sheep x	Intercept	266.68	87.52			
legumes	Herbage mass	2.000	0.1	0.243	0.299	0.309
•	Leaf frequency bulk				(r.d.f=45)	
	density	-34.61	18.35	0.056		-0.299
Goats x	Intercept	189,94	52.35			
legumes	Sward height	5.744	1.35	0.460	0.521	0.521
	density	-32.61	13.63	0.061	(r.u.i=45)	-0.293

Dependent variable: Bite weight 2 (mg DM/bite)

Partial  $R^2$ : coefficient of determination accounted for due to each single sward variable; Model  $R^2$ : summation of partial  $R^2$  of all variables included in the equation. Standardised coefficients are used to assess the sequence of importance of variables (see Section 5.2.4.2).

The above notes also apply for Table 5.27.

Treatment Intercept and Slopes Standard Partial Model R<sup>2</sup> and Standardised R<sup>2</sup> residual d.f Independent variables errors coefficients Overall 8.945 5.69 Intercept 0.848 (unpartitioned) 0.04 Sward height 0.855 1.207 Mass bulk density 3.908 0.74 0.014 0.891 0.266 Herbage mass -0.2 0.029 0.014 -0.300 Live % -21.11 6.01 0.007 -0.087 Sheep Intercept 14.015 7.19 Sward height 0.864 0.05 0.859 0.903 1.237 Mass bulk density 4.520 1.01 0.014 (r.d.f=98) 0.300 Herbage mass -0.2 0.04 0.017 -0.308 Live % -27.504 7.73 0.013 -0.117 Goats Intercept 7.019 8.67 0.896 1.205 Sward height 0.055 0.861 0.843 Mass bulk density 1.03 0.017 (r.d.f=99) 0.253 3.629 0.04 0.013 -0.315 Herbage mass -0.2 Live % -18.633 9.043 0.005 -0.074 Grasses Intercept -7.587 1.298 Sward height 0.737 0.026 0.898 0.905 1.000 (r.d.f=107) -0.095 Herbage mass -0.06 0.02 0.005 Stem+seedhead 0.050 0.96 0.002 frequency bulk density 1.547 Legumes Intercept 8.686 2.647 0.283 Sward height 0.119 0.054 0.317 0.374 -0.270 0.554 Mass bulk density -1.416 0.029 (r.d.f=92) Leaf frequency bulk density -0.814 0.397 0.029 -0.215 Sheep grasses Intercept -5.947 1.210 0.921 0.960 Sward height 0.921 0.690 0.028 (r.d.f=53) Goats Intercept -9.120 1.92 0.891 0.903 1.014 Sward height 0.762 0.039 grasses Herbage mass -0.09 0.04 0.008 (r.d.f=52) -0.126 Seedhead+stem 0.067 frequency bulk density 2.067 1.404 0.004 Sheep 11.07 1.007 0.323 Intercept legumes -1.775 0.379 0.323 (r.d.f=46) -0.568 Leaf frequency bulk density Goats 0.569 Intercept 2.942 1.245 0.825 (r.d.f=45)legumes Sward height 0.363 0.048 0.533 Herbage mass 0.03 0.037 -0.433 -0.1

 Table 5.27
 Summary of multiple regression for the different treatments, determined by Stepwise procedure.

Dependent variable: Bite depth (cm)

See notes of Table 5.26.

Among the two tabulated variables (Tables 5.26 and 5.27), bite depth showed much better fit than did bite weight 2, and therefore, attention is concentrated principally on bite depth, while bite weight 2 is only touched on briefly.

Bite depth was fitted very well by sward variables in most cases (Table 5.27). It is clear that sward height could account for a high proportion of the total variation in every case (partial R<sup>2</sup> of height in Table 5.27). Mass bulk density and herbage mass were also emphasized in most circumstances. The functional relationships of bite depth with respect to sward variables were stronger for grasses than legumes grazed by both sheep and goats. The importance of canopy bulk density or herbage mass relative to sward height in predicting bite depth was much greater for clovers than for grasses, reinforcing the results ascertained by canonical analysis (Section 5.3.4.1.3). Bite depths of sheep and goats were predicted by the same independent variables with the same important sequences (standardised coefficients in Table 5.27), though the ratio of the standardised coefficient of the most important variable (height) to others varied between sheep and goats. This shows that sward characteristics influenced bite depth in a similar functional way between the two animal species; however, the intercept differed by a factor of two between the two animal species. On grasses, variation in bite depth was predicted principally by sward height for sheep, whereas for goats, in addition to sward height, it was also predicted by seed + stem frequency bulk density and herbage mass (Table 5.27), reflecting the willingness of goats to eat these components.

The above information (Table 5.27) indicated that sward height was the most appropriate variable to describe and predict bite depth, and therefore it was worthwhile to investigate the relationship between them further. This was carried out based on grasses only; legumes were not considered because of the weak fits shown in Table 5.27.

Because the literature discusses a quadratic relationship between bite depth and sward height in addition to a linear relationship (Mitchell *et al.*, 1991), the regression relationship between bite depth and sward height was examined using Proc Reg (SAS Institute Inc., 1990) by including the single linear term (H) (height) only (equation 1 listed below), and by including both the linear term (H) and a quadratic term (H<sup>2</sup>) (equation 2). A sequential F-test was made between the linear and quadratic fits to determine an appropriate equation.

Although in equation 2 both linear ( $\beta_1$ ) and quadratic terms ( $\beta_2$ ) were significant, the sequential F-test (a test of a reduction of residual sum of squares) (Draper & Smith, 1981) indicated that the inclusion of a quadratic term in the equation did not

### List of regression equations between sward height and bite depth based on grasses

- 1.  $BD_{grass} = -7.965$  (s.e. 0.986) + 0.698 (s.e. 0.023)H ( $R^2 = 0.90^{""}$ ) 2.  $BD_{grass} = 0.626$ (s.e. 2.61) + 0.287 (s.e. 0.127)H + 0.005 (s.e. 0.001)H<sup>2</sup> ( $R^2 = 0.91^{""}$ ) 3.  $BD_{sheep \times grass} = -5.947$ (s.e. 1.210) + 0.690(s.e. 0.027)H ( $R^2 = 0.92^{""}$ ) 4.  $BD_{goats \times grass} = -10.210$ (s.e. 1.483) + 0.710(s.e. 0.033)H ( $R^2 = 0.90^{""}$ ) 5.  $BD_{sheep \times grass \times vegetative} = -0.547$ (s.e. 1.931) + 0.505(s.e. 0.067)H ( $R^2 = 0.67^{""}$ ) 6.  $BD_{goats \times grass \times vegetative} = -6.957$ (s.e. 2.024) + 0.610(s.e. 0.070)H ( $R^2 = 0.76^{""}$ ) 7.  $BD_{sheep \times grass \times reproductive} = -13.52$ (s.e. 4.165) + 0.822(s.e. 0.074)H ( $R^2 = 0.84^{""}$ )
- 8.  $BD_{goals x grass x reproductive} = -22.098(s.e. 5.759) + 0.937 (s.e. 0.102)H (R<sup>2</sup>=0.78<sup>**</sup>)$

significantly improve the precision of regression fit (Table 5.28). This suggests that the linear model is adequate, and on the basis of adopting the simplest adequate model (Draper & Smith, 1981) the linear model was used. This highlights the often contradicting information which different tests may give. In the case of the quadratic model, both  $\beta_1$  and  $\beta_2$  were significant as indicated by their t-test (H<sub>0</sub>:  $\beta$ =0), while the sequential F-test for inclusion of  $\beta_2$  was not significant. In cases like this, the decision should always be conservative, and in any case, the F-test is often regarded as more robust than t-test (Draper & Smith, 1981), as is evident from the large body of criticism against the LSD procedures (Steel & Torrie, 1980).

Even when t-test is used in connection with building regression model, it gives conflicting information in sequential fits (Draper & Smith, 1981). When an additional term is added each time, it may be or may not be significant. Furthermore, even though it may be significant at one stage, it can become insignificant as a consequence of another new term entering the equation (Draper & Smith, 1981). This further emphasizes that a more appropriate criterion to determine this would be the F-test which indicates the precision of the regression as a whole (Draper & Smith, 1981). This F procedure is the one reported in Table 5.28.

Table 5.28Sequential F-test of improvement of regression precision after a<br/>quadratic term was included in the equation describing the relationship<br/>between bite depth and sward height on "grasses"

Equatio	ns	Residual sum of squares	df	F value
1. Gra	isses (linear)	1526.03	109	1.0893 ns
2. Gra	sses (quadratic)	1388.14	108	

1526.03 / 109 ----- = 1.0839 = F<sub>109,108</sub> 1388.14 / 108

This linear relationship was further broken down into several subsets of "animal species x grasses" (equations 3 and 4 in the list), and of "animal species x grasses x maturity stages" (equations 5 - 8 in the list). The relationships are illustrated in Fig. 5.10.

Another objective was to test whether the subsets regression were the same or not. This requires t-tests between appropriate  $\beta$  statistics. The t-tests are appropriate for this aspect (Draper & Smith, 1981).

For equations 3 and 4, the intercepts, but not slopes, were different at P<0.05. However, this is sufficient to indicate that this functional relationship is different between sheep and goats grazing grasses.

For the vegetative grasses grazed by sheep and goats (equations 5 and 6), there was a significant difference in intercept (P<0.05), but not in slope. For the reproductive grasses grazed by sheep and goats (equations 7 and 8), the differences were not significant in either slope or intercept. This substantiates the earlier evidence that sheep usually penetrated more deeply than goats into the vegetative grasses, but not when they dealt with the tall reproductive grasses. This fact was further shown by the convergence of the regression lines between sheep and goats on the taller reproductive grasses (Fig. 5.10B). In effect, as mentioned earlier, on the tall reproductive grass pastures, sheep usually pushed into swards to graze leafy components, whereas goats severed mouthfuls of herbage from the side of the experimental turves and folded them into the mouth, leading to similar bite depths for

### Fig 5.10 Linear relationships between bite depth and sward height based on grasses

A

B

Linear relationship between bite depth and sward height for grasses, and grasses x animals



#### Linear relationships between bite depth and sward height for animals x grasses x stages


the two species on the tall reproductive grasses in spite of there being differences in bite weight.

The above differences between equations suggest that it would be more appropriate to establish this functional relationship based on the subsets than at the overall level.

## 5.4 DISCUSSION

## 5.4.1 Over-time effect of incisor breadth covariate

There was no incisor breadth covariate effect over time in this set of data, in contrast to the restricted data set (Chapter 4). In a study involving a comparison of ingestive behaviour of sheep grazing grass and clover pastures, respectively, over an experimental period of approximately 3 months (from 13 July to 19 October, 1989), Penning *et al.* (1991b) failed to find any relationship between incisor breadth and ingestive behaviour. In neither the current data set (6 December, 1989 - 18 April, 1990) nor the work of Penning *et al.* (1991b) was the length of the experimental period long enough to produce a significant over-time variation in incisor breadth. The lack of an incisor breadth effect over time provided a robust basis for the analysis approaches employed in this study: all analyses were conducted without adjustment for this factor.

## 5.4.2 Sward conditions

The close similarity in structural attributes of the complete profiles of the swards grazed by the two animal species (Sections 5.3.1.1 and 5.3.3.1.1) enabled the comparison of responses in ingestive behaviour between sheep and goats to be carried out under similar sward conditions. However, some attributes of the grazed strata differed significantly between the swards grazed by sheep and by goats (Tables 5.3 and 5.5), in contrast to the characteristics of entire swards. This was a consequence of the marked difference in bite depth between the two animal species (Section 5.3.1.3.1), rather than a reflection of sward differences *per se*.

The intention of establishing a series of swards offering a substantial range of structural variation was achieved in this experiment. The substantial variation in sward attributes across forages and stages, and the combinations between forages and stages (Sections 5.3.1.1 and 5.3.3.1) provided a great contrast in canopy structure, which allowed the animals to exhibit their grazing behaviour over a wide range of sward conditions.

In the grasses herbage bulk density was greater in the basal layers and declined towards the canopy surface, whereas the reverse was the case in the legumes (Table 5.3). This was because of the differences in growth habit between grasses and legumes. The mass is mainly concentrated in the horizontal laminae at the end of the petioles in clovers (Kenney & Black, 1986), and in the upper canopy in *Lotus corniculatus*. In grasses, however, the mass is distributed more evenly through the sward profiles (Kenney & Black, 1986), or even more in the pseudostem zone than in the leafy horizon of the sward (Table 5.3).

White clovers would normally be expected to have higher proportions of leaf compared with grasses (Waghorn & Barry, 1987). In the current experiment the opposite appears to be the case (Table 5.5), but this was a consequence of the definition of petiole as "stem" for convenience (Section 3.2.4 of Chapter 3). With increasing maturity, the leaf proportion was maintained in legumes, but decreased in grasses (Table 5.6). This reflects the fact that legumes differ from grasses in the effect of maturity on the proportions of morphological components (Ulyatt *et al.*, 1980).

The multivariate approach demonstrated that sward height was the most important variable in discriminating within a set of swards (Section 5.3.3.1). In this experiment, herbage mass and bulk density were also emphasized after sward height under certain circumstances (Section 5.3.3.1.1). This suggests that the complex of sward characteristics could be reduced to height and one or two additional components (bulk density or mass).

## 5.4.3 Ingestive behaviour

Although sheep would be expected to have greater bite weights than goats because of their greater incisor breadth (Chapter 4), overall means of bite weight in absolute terms were similar for the two species (Table 5.8). This was graphically reflected in MDF where there was no clear distinction between animal species in MDF1 (fresh matter determiner) (Fig. 5.7A and Section 5.3.3.2.2). In effect, the similar values of bite weight between the two species were a net result of greater bite weight of sheep on legumes (irrespective of stages of maturity) and vegetative grass swards, counterbalanced by lighter bite weight of sheep on reproductive grass swards (Table 5.16). The fact that sheep usually have greater bite weights than goats is consistent with the suggestion that large animals appear to meet their higher energy requirement for maintenance by having a greater bite weight rather than a higher bite rate or longer grazing time (Penning *et al.*, 1991b).

This experiment also indicated that short term bite rate was greater for sheep than goats (Table 5.8). No comparisons of grazing time were made between the two animal species, but a study involving sheep and goats fed on a chaffed lucerne hay diet (Domingue *et al.*, 1991) showed that sheep spent three hours less eating than goats. Combining this information, it may be inferred that the strategy of sheep to meet their higher energy requirement (due to large body size) is to have greater bite weight and bite rate, but shorter grazing time. Other factors may also be involved in the smaller bite weight of goats grazing legumes and this will be considered later in this section.

Goats generally had higher bite weights relative to liveweight than sheep, whether scaled to LW<sup>0.75</sup> or LW, in line with a general trend that animals of larger body size have smaller values of bite weight per unit live weight (Hodgson, 1986).

Bite depth showed a greater response than did bite area to sward variation in forage categories and stages of maturity (Fig. 5.11 A & B). Therefore, bite depth was a major spatial component of bite volume, and hence had a dominant influence on bite weight, in line with the results of Burlison (1987), Mursan *et al.* (1989) and Laca *et al.* (1992a). This was associated with a very close positive relationship between bite depth and sward height which generally is the most important sward variable influencing ingestive behaviour. A knowledge of how bite depth varies with sward structure and with animal species would enable herbage intake and diet selection to be interpreted and/or predicted and appropriate management systems to be devised for single or mixed species grazing (Hughes, 1988).

Generally, bite depths were markedly different between sheep and goats (Section 5.3.1.3; Plates 5.1 & 5.2). Deeper penetration into the sward canopy by sheep on legumes (both stages) and vegetative grasses indicated that sheep showed a greater tendency to push into the canopy (Plate 5.1), whereas goats were shallow grazers, and grazed from the top downwards successively on these swards (Plate 5.2). However, contrary to the results for vegetative and reproductive clover, and vegetative grass swards, when extremely tall stemmy reproductive grasses were offered, goats modified their behaviour and showed a willingness to deal with these rigid components, leading to similar bite dimensions to sheep (Fig. 5.10B; Fig. 5.11 A & B), though bite weight was much smaller for sheep (Table 5.16, Fig. 5.12A).











Plate 5.1 Sheep pushed into the sward canopy to graze deeply.



Plate 5.2 Goats were shallow grazers and grazed from top downwards.

Sheep had similar bite area to goats on these tall swards (Fig. 5.11B). Sheep appeared to push into tall canopies from the top down to graze leafy components, and rejected seedhead and stalk components within the defined grazed area, whereas goats preferred to prehend reproductive tillers, inflorescences and stalks as well as green leaf occurring within the defined grazed area. This may be associated with the superior fibre digesting capability of goats compared with sheep (Domingue *et al.*, 1990) and their greater efficiency in digesting the fibre fraction of the diet (McCall & Lambert, 1987). Goats had similar bite depths to sheep on these extremely tall swards (Fig. 5.10B), because they severed mouthfuls of herbage from the side of the experimental turves and folded them into the mouth. Thus the two animal species had similar bite depths and bite areas on the reproductive grasses in spite of there being differences in bite weights. This behaviour of goats was in accordance with reports of their predisposition to browsing and preferring taller vegetation (Radcliffe & Townsend, 1988).

The above contrasts between sheep and goats in bite depth on reproductive grasses indicated the existence of some exceptions to the conventional definition of bite depth. Bite depth is usually defined as the depth to which the open mouth of the animal is inserted into the sward (Hughes, 1988). Thus, bite depth is largely determined by the depth of insertion of the incisors into the sward (Illius & Gordon, 1987). It may be calculated from the difference between the pre-grazing sward surface height and the residual height of the grazed herbage (Burlison, 1987; Ungar et al., 1991). However, this appears to apply, in this study, only to those cases of legumes (both stages) and vegetative grasses where the animals grazed the herbage from the sward surface downwards. It does not cover the situation of extremely tall reproductive grasses. In fact, on the untrimmed swards, the animal's bite dimensions may respond to the upper, lower or average surface height of the patch or selected bite site (Mitchell, 1993). On these tall swards the leafy components which were selectively severed by sheep pushing into canopies did not reach to the sward surface. In this case, the difference between pre-grazing and post-grazing heights resulted in an overestimation of bite depth since the upper limit to bite depth actually was below the sward surface. Goats severed herbage from the side of the turves and folded them into the mouth. This indicates that animals can insert the mouth into swards from different angles. In this case, the bite depth estimated by the difference between pregrazing and post-grazing heights was much greater than the depth to which the long axis of the head is perpendicular to the ground. This suggests that bite depth is not necessarily limited by the dimensions of the buccal cavity when animals grip leaves

and stems on tall swards from the side and draw them into the mouth (Hodgson, 1981a). Thus, bite depth defined above (Hughes, 1988) may not be a concept applying for extremely tall and stemmy swards for either sheep or goats. In effect, animals are able to vary their methods of harvesting herbage somewhat according to the structure of the vegetation encountered (Arnold & Dudzinski, 1978). This flexibility would permit animals to grip herbages from the side when dealing with tall herbages, especially for browsers.

It has been shown (Clark *et al.*, 1982) that goats may avoid white clover, in contrast to sheep which eat white clover in proportion to that on offer. Preference of sheep for white clover would be more pronounced where availability is greater (Nicol *et al.*, 1987) because the ability of animals to express their preference for individual components of the sward is limited by both sward structure and the availability of each component (L'Huillier *et al.*, 1984). However, a recent study (Newman *et al.*, 1992) proposed that the selection for clover and grass by sheep might be related to their previous dietary background; sheep preferred the opposite species to the one they had previously grazed.

Explanations for the lower proportion of white clover in the diets of goats relative to that on offer are still unclear and difficult to interpret unless sward conditions are carefully characterized (Hughes, 1988). Hughes (1988) argued that it is too simplistic to say that goats actively reject clover in all grazing situations. However, in addition to the effect of avoidance caused by preference (Clark *et al.*, 1982; 1984), shallow grazing behaviour may help explain this phenomenon, as outlined below.

The depth of penetration at which animals position their mouths when biting ("incisor height", Laca *et al.*, 1992a) is largely determined by sward height, and hence composition of the diet is considered to be closely related to the composition of the swards where the defoliation occurs. Goats usually defoliate pastures from the top downwards in successive layers (McCall & Lambert, 1987), and hardly penetrate into the basal horizon where clover is usually more dominant than the remainder of canopies in mixed swards. Therefore, the lower proportion of white clover in the diet of goats relative to that on offer (Clark *et al.*, 1982) might partially be a consequence of poor accessibility of white clover in the upper sward canopies in addition to an active avoidance (Clark *et al.*, 1982; 1984). This suggests that it might be reasonable to argue that the intake of white clover by goats is regulated by both canopy structure (spatial distribution, accessibility and availability) and deliberate rejection, in interaction.

The smaller bite weight of goats than sheep on legumes might also be explained, at least partially, by their shallow grazing habit, in addition to body size effects. Since the swards used in the current experiment were untrimmed, they were not of a uniform height or of a vertical homogeneity. Few petioles appeared within the top strata of the canopy (Figs in Appendix 5.1). On these leguminous swards, goats harvested only those laminae present at the canopy surface, and ignored those lower in the canopy. In this case, the amount of clover mass removed per bite was largely regulated by the structure of the uppermost layer (height and mass density).

## 5.4.4 Influence of sward characteristics on ingestive behaviour

Plant species may influence intake in a variety of ways through the effects of sward structure on ease of prehension, and through differences in the rate of digestion and passage (L'Huillier *et al.*, 1986).

Compared with grasses, legumes resulted in greater bite weights of fresh matter though not necessarily of dry matter (Table 5.13), faster biting rates, and hence greater intake rate. These trends are clearly shown in MDF analysis (Fig. 5.5A), and reinforced in Fig. 5.6A. It has been shown that sheep have higher dry matter intake for legume diets than grasses (Gibb & Treacher, 1983, 1984), leading to superior growth and lactation performance (Thomson, 1984). Penning et al. (1991b) found that mean bite weight of sheep grazing clover was 48% higher than that of sheep grazing grass, but biting rate was similar for both swards. leading to a higher intake rate of clover than grass; however, daily grazing time was 42% greater for grass than for clover, resulting in similar daily intakes for both swards. Dougherty et al. (1989a) found that lucerne swards permitted cattle to prehend larger bite weights at slower rates than did tall fescue swards, leading to higher intake rates of lucerne than tall fescue. Kenney and Black (1986) using artificial swards grazed by sheep showed that sheep ate subterranean clover four times faster than grass swards. Among the above studies, Dougherty et al. (1989a) and Kenney and Black (1986) used short term measurements (1 h and 15 s, respectively), and Gibb and Treacher (1983, 1984) and Penning et al. (1991b) used relatively long term observations. These findings demonstrate that the animals are able to obtain greater intake rates from legumes than grasses.

The greater bite weights on legumes may be attributable to the following facts.

(1) There is a higher mass concentration within the grazed horizon for clover swards than grass swards (Tables 5.3 & 5.4).

- (2) Although the tensile strength was not measured in the present experiment, it appeared to be less for legumes than grasses (Penning *et al.*, 1991b), so it was much easier to sever petiole or stalk of legumes than the grass pseudostem or leaf (Kenney & Black, 1986). Because of these two facts, a smaller effort is required to obtain a full mouthful of legume than grass.
- (3) The animals removed a greater proportion of the herbage encompassed by the jaw for clover than grass (Penning *et al.*, 1991b). Animals usually harvested nearly all the laminae and petioles occurring within the area encompassed by a bite when grazing legumes. In contrast, for grasses after a bite is taken, some plant components occurring within the area encompassed by a bite slipping out of the teeth and still remained unharvested (Parsons *et al.*, 1991).

Additionally, in a study on ingestive behaviour using sheep continuously stocked on white clover or perennial ryegrass swards maintained at a sward height of 6 cm, Penning *et al.* (1991b) attributed the greater bite weight of legumes to the fact that the animals may have encompassed a greater volume of legumes at each bite by opening their mouths further or increasing their depth of biting. This was not the case in the current experiment because the swards used were much taller for grasses than legumes (Tables 5.3 & 5.4), leading to much greater bite volumes of grasses than legumes (Table 5.13). But the reduced bite volumes on legumes were sufficiently compensated for by the greater efficiency of harvesting resulting from the above three advantages.

The faster biting rate of animals on legumes was also a consequence of the flexible nature and low structural strength of the legumes (Kenney & Black, 1986). Apart from this, the lower fibre content and different morphology of the vascular bundles of clover (Kenney & Black, 1986) can lead to an increase in the rate of particle breakdown during chewing compared with grasses (Mosely & Jones, 1984), and hence reduces the time required for chewing between each mouthful (Kenney & Black, 1986). Animals on grass also spend proportionately more time ruminating than those on clover swards because of the lower rate of particle breakdown on grasses (Penning *et al.*, 1991b).

Intake rate is a measure of the combined effect of prehension, chewing and swallowing (Kenney & Black, 1986). When there are some difficulties for prehension because of the sward restrictions imposed by structural characteristics, prehension rate

usually is the limiting component of intake rate, but when prehension is not a problem, chewing and swallowing rates become limiting (Kenney & Black, 1986). Legumes allowed animals to have both larger mouthfuls of herbage and faster prehension rate, so intake rate was much greater on legumes than grasses.

As pasture matures the highly digestible leaf becomes a smaller fraction of the whole plant, and digestibility declines (Wilman & Agiegba, 1982). Therefore, daily herbage intake usually declines with increasing maturity of grazed herbage (Hodgson 1977). In the current study both sheep and goats increased their bite weights as swards advanced in maturity, in response to an approximately two-fold increase in sward height (Table 5.4). However, bite weight is only one of the components collectively influencing daily intake. Animals had to spend more time chewing and processing mouthfuls of herbage obtained from these tall and mature swards, hence bite rate followed the expected patterns of decline as bite weight increased with sward height (Hodgson, 1981b). Intake rate (mg DM/min) decreased for sheep with increasing herbage maturity, but was not significantly affected by maturity for goats, although there was a trend to increase intake rate (Table 5.9).

The decline in intake rate of sheep from 7074 mg DM/min on vegetative to 5817 mg DM/min on reproductive swards was based on an increase in bite weight from 207 mg DM to 323 mg DM and a decrease in biting rate from 36 bites/min to 19 bites/min (Table 5.9). A slightly increase in intake rate for goats from vegetative to reproductive swards (from 5139 mg DM/min to 5653 mg DM/min ) was associated with a substantially greater increase in bite weight from 175 mg DM to 383 mg DM and a decrease in bite rate from 31 bites/min to 17 bites/min (Table 5.9). This suggests the existence of countervailing or non-monotonic influences on intake rate. The benefit in bite weight of sheep from increasing sward height induced by change from vegetative to reproductive sward can be counterbalanced by a penalty of a greater time required for manipulating, chewing and processing. As bite weight increases to a high level, animals can no longer process herbage with simultaneous chew/bites but must perform exclusive (frequently head-up) chewing jaw movements to process herbage ingested during a series of bites (Laca et al., 1993). Both plant maturity and sward height, which are usually confounded in field-grown swards (Hodgson, 1990), were thought to play a role in this process, as outlined below.

The effect of maturity was considered to be associated with the particle breakdown process (Cosgrove, 1992). Because the proportion of large particles (>1.0 mm) tends to decrease and the proportion of medium particles (0.5 - 1.0 mm) to increase with maturity (Poppi *et al.*, 1981; Ulyatt *et al.*, 1982; Nelson, 1988) mature

forage requires more time and very thorough chewing to break into small particles to swallow, leading to a reduction in harvesting rate. As swards become taller, more jaw movements are associated with chewing (Laca *et al.*, 1992a), so the decline of intake rate with increasing sward height was assumed also to be attributable to the decline in the ratio of prehension bites to masticating movements (Penning *et al.*, 1991a) since manipulative jaw movements and chewing overlap to a variable extent which depends on sward height (Laca *et al.*, 1992a). However, for goats, this penalty was not sufficient to offset the benefit from greater bite weight, resulting in a greater intake rate of reproductive swards.

The reason for this difference between the two animal species was not clear; two possible explanations may be involved. Firstly, it was assumed that the particle size required to swallow was larger for goats than for sheep when coarse forages were grazed, and hence goats spent less time chewing and processing despite larger bites than sheep. There is a lack of evidence to confirm this. Domingue et al. (1991) concluded that when chaffed lucerne hay was offered the boli which were chewed during eating and then swallowed contained significantly greater percentages of small particles (passing 0.5 and 0.25 mm sieves), and smaller percentages of large particles (retained on 4.0 mm and 2.0 mm sieves) for goats than for sheep. However, Mitchell (1985) showed that in the diet of feral goats grazing coarse forages (shrubs), the size of fractions contained in boli ranged from >2 mm to >8 mm. This suggests that goats could swallow large particles of the coarse forages, although unfortunately he did not make comparisons with sheep. In the current research, the particle size of boli was not measured, but from the data of Table 5.9, it was assumed that goats were able to swallow reproductive herbages in relatively large particle sizes compared to sheep, because 19.6% greater in bite weight of goats than sheep on the reproductive swards was only accompanied by 10.5% lower bite rate.

Secondly, it was shown that the frequency of chewing during eating (number of chews/min) was greater in goats than in sheep, and hence the efficiency of chewing during eating in breaking down feed particles to <1 mm may have been greater in goats than sheep (Domingue *et al.*, 1991). The greater number of chews/min during eating in goats is a major factor explaining their greater efficiency of eating (Domingue *et al.*, 1991).

Variation in sward height influenced bite dimensions more, through its effect on bite depth, and therefore bite weight, than did variation in bulk density for both animal species, in agreement with the results of Mitchell *et al.* (1991) and Laca *et al.* (1992a). However, canonical analysis (Section 5.3.4.1) showed a great contrast in this aspect

between grasses and legumes, and between sheep and goats. The bulk density, with particular regard to leaf frequency bulk density, had a substantially greater effect on the whole set of ingestive behaviour variables than did sward height when the leguminous swards were grazed by sheep, in agreement with the results of Kenney and Black (1986). In leguminous swards, because mass is mainly distributed within the upper horizon, the effect of sward height on the herbage mass which is readily prehensible is reduced in comparison with gramineous swards (Kenney & Black, 1986), where mass is distributed more in the lower zone than in the upper horizon. This characteristic of legume swards also explains why the effect of bulk density was greater in legumes than in grasses when they were grazed by goats (Table 5.25).

However, bulk density of legumes was still less important than sward height when being grazed by goats (Tables 5.24 and 5.25). The reason for this was that as mentioned before, goats might confine their defoliation within the uppermost horizon, and ignore short petioles below this zone because of their shallow grazing and greater sensitivity to changing pasture height than sheep. This might have led to a more functional relationship of ingestive behaviour of goats with sward height than with bulk density. Consequently, in leguminous swards height can exert more effect than bulk density on goats.

For sheep, bulk density of legumes exerted an important effect not only on the whole set of behaviour variables in combination (canonical analysis), but also on variables individually (multiple regression analysis). This was substantiated in Tables 5.26 and 5.27, where bite weight and bite depth of sheep were largely determined by bulk density of legumes.

Beyond the dominant effect of sward height in grasses and the dominant effect of bulk density in legumes, the effect of herbage mass on grazing behaviour was greater in legumes than in grasses for both sheep and goats (Tables 5.24 and 5.25). This was because the dominance of bulk density over other sward variables in legumes was lower than the dominance of sward height over other sward variables in grasses (denoted by ratios of the dominant variable, bulk density or height, to others, Tables 5.24 and 5.25). This provided an opportunity for the effect of herbage mass to emerge in legumes.

In summary, the conclusions about the relative importance of alternative sward variables, with particular regard to height and density, are critically dependent on the range of values, the types of swards (grasses or legumes) and animal species adopted in specific studies.

5.4.5 Comparison of MANOVA and MDF between the set of sward variables (complete profiles) and the set of behaviour variables

There was an almost identical ordination pattern between the set of sward variables (complete profiles) and the set of behaviour variables in the distribution of scores with respect to the nine forages (Fig. 5.1A and B vs. Fig. 5.5A-C). Sward height was dominant in the discriminant functions of the sward set, and bite depth and bite weight were dominant in the discriminant functions of the behaviourial set. The high comparability in the score pattern reinforced the view that ingestive behaviour of the grazing animals was strongly influenced by the characteristics of the sward, and sward height had a dominant impact upon bite depth, and hence bite weight.

The conformable ordination of the scores with respect to the eighteen combinations of forage x stage of maturity (Fig. 5.2A and B vs. Fig. 5.6A-C) reinforced the above relationship, with more evidence that herbage mass and density (MDF2) exerted some significant effects on ingestive behaviour as well.

## 5.5 CONCLUSIONS

- On average mean bite weight over eighteen swards (9 forages x 2 stages) was similar for sheep and goats. Sheep usually obtained heavier bites than goats on both vegetative and reproductive clover swards and on vegetative grass swards, but goats had substantially heavier bites on reproductive grass pastures. Bite weight scaled to liveweight (LW or LW<sup>0.75</sup>) was greater for goats than sheep.
- 2. Generally, bite depths were markedly different between sheep and goats. Sheep showed a greater tendency to penetrate into the canopy, whereas goats were shallow grazers from the top downwards. Sheep preferred to push into the swards and to take deep bites, whereas goats restricted their defoliation within the top horizon.
- 3. When extremely tall stemmy reproductive grasses were grazed, goats modified their behaviour to deal with these rigid components by grazing from the side of the sward, resulting in similar bite dimensions to sheep. Sheep appeared to push into tall canopies from the top down to graze

leafy components, and rejected seedhead and stalk components within the grazed area, whereas goats were less selective and prehended a great mouthful of herbage including most components occurring within the defined grazed area.

- 4. Because of the greater capability of goats to handle reproductive swards the variation in intake rate in response to increasing sward maturity differed between the two animal species. When swards matured, intake rate of sheep decreased because an increase in bite weight was counterbalanced by a dramatic fall in biting rate, but that of goats increased as a result of a dramatic increase in bite weight, and a relatively small fall in bite rate, compared with sheep.
- 5. Leguminous swards usually resulted in a greater bite weight (especially on a fresh matter basis) despite a shallower bite depth compared with gramineous swards. The reduced bite depth of legumes was sufficiently compensated for by the greater efficiency of harvesting. Animals also obtained a faster bite rate on legumes than on grasses.
- 6. The taller reproductive swards led to greater bite weights, but lower bite rate than did vegetative swards.
- 7. There was substantially greater variation in bite depth than in bite area across forage categories and stages of maturity, and bite depth was a major spatial component of bite volume and hence bite weight.
- 8. Sward characteristics had a strong and substantial impact upon the ingestive behaviour components of grazing animals. Sward height generally had a much more dominant effect than did other sward characteristics, and bite depth showed a far greater response than did other behaviour components in both animal species. However, the bulk density, with particular regard to leaf frequency bulk density, had a substantially greater effect on ingestive behaviour than did sward height

when the leguminous swards were grazed by sheep. The ingestive behaviour of goats grazing legumes was still influenced principally by sward height, in spite of the fact that the effect of the bulk density was substantially increased compared with that in grasses. Herbage mass had more impact in legumes than in grasses for both sheep and goats. Bite weight was a more important response variable than bite depth for both species grazing legumes.

## **CHAPTER 6**

## **EXPERIMENT 2**

## Effects of Contrasting Sward Heights on Components of Ingestive Behaviour of Sheep and Goats Grazing Grasses and Clovers

#### 6.1 INTRODUCTION

Experiment 1 (enlarged data set) showed that in general terms height was the most important sward variable affecting ingestive behaviour, although there was some deviation from this general trend for leguminous swards grazed by sheep. Experiment 1 provided evidence on effects of sward height across forages rather than within forages, as the heights were principally contrasted between forages. Therefore, the effect of sward height was confounded with variations in other plant characteristics (e.g growth habit) across forages, and also by maturity stage within a forage. Experiment 2 was designed to separate the effect of sward height from the above effects by producing contrasting heights within forages, and by restricting sampling to the vegetative phase only. Again, the effect of this independent variation in height was evaluated using clovers and grasses to provide a contrast between the two sward categories when they were grazed by sheep and goats.

#### 6.2 MATERIALS AND METHODS

#### 6.2.1 Experimental design

Four forages comprising two grasses and two clovers (Table 6.1) were used for this experiment. Height differences within each forage were achieved by mowing plots and allowing different periods of uninterrupted regrowth. Five heights for each grass, three heights for Tahora white clover and two heights for Kopu white clover were produced (Table 6.1). Emphasis was placed on assessing influences on the components of ingestive behaviour for two main effects (animal species and height class) and their interactions, within each forage separately. The individuals of each animal species were treated as internal replications of a completely randomized design.

#### 6.2.2 Experimental procedures

Four 33 month old individuals were chosen from the pool of six animals of each species used in Experiment 1 to graze the sampled turves. Average liveweights of sheep and goats over the experimental period were 51.2 and 22.9 (s.e: 0.6) kg with 3.2 and 2.7 cm (s.e: 0.04) adult incisor arcade breadth for sheep and goats, respectively. Both species had 4-6 adult teeth per animal which contributed approximately 98% of total incisor arcade breadth.

Factors and reps	Levels	Values
Animal species	2	Sheep and goats
Forages	4	Ryegrass, cocksfoot, Tahora and Kopu white clovers *
Sward heights within a forage	5 heights within each grass, 3 heights within Tahora, 2 heights within Kopu	Ryegrass (7.8, 13.7, 16.7, 18.5, and 26.7 cm), Cocksfoot (8.0, 17.3, 22.1, 22.5 and 29.6 cm), Tahora (5.5, 5.8 and 11.0 cm), Kopu (6.8 and 13.7 cm)
Animal reps within species	4	4 sheep 4 goats

#### Table 6.1 Experimental design

\*: See Appendix 3.1 for detailed description of agronomic characteristics of these cultivars.

Experimental procedures were the same as in Experiment 1 (Chapter 3). Animals were individually housed in metabolism crates indoors and presented prepared sample turves. Animals had been trained to experimental procedures previously (Experiment 1) as well as for three weeks immediately prior to the current experiment. Measurements were taken as in Experiment 1 to characterize sward structure and state, and to determine the weight of herbage removed, bite number and time elapsed during biting. Two sets of variables (sward and ingestive behaviour) were obtained either through direct measurements or through calculations (see Section 3.2.7 of Chapter 3). Components of the functional response included bite weight on both fresh and dry matter bases, bite rate, bite depth, bite area and bite volume. Characteristics of sward structure included surface height (cm), mass within the grazed stratum (g DM/m<sup>2</sup>), mass bulk density of the grazed stratum (mg DM/cm<sup>3</sup>), herbage mass of the whole turf (g DM/m<sup>2</sup>) and overall mass bulk density (mg DM/cm<sup>3</sup>), and four others derived from the point-quadrat measurements (for details see Sections 3.2.4.2 and 3.2.7.9 of Chapter 3): leaf frequency bulk density of the grazed stratum (hits/2 cm), leaf proportion of the whole sward profiles, leaf frequency bulk density of the whole sward profiles (hits/2 cm), and stem frequency bulk density of the whole sward profiles (hits/2 cm).

Turves were extracted from the established plots of Experiment 1 (Chapter 3). Forages and height classes of each forage were offered to animals in a generally random sequence influenced by readiness of swards for grazing. At each feeding assessment, all animals received the same treatment combination (one height of one forage). During the entire experimental period, all animals received all treatment combinations, i.e. four forages with a total of 15 height treatments (Table 6.1).

The experiment was conducted between 22 May and 24 September of 1990.

#### 6.2.3 Statistical analysis

Because the objective of this experiment was to evaluate height effects within a forage on ingestive behaviour variables in an attempt to avoid confounding effects of variation across forages, it was appropriate to conduct statistical analyses within forages. However, since only two or three heights were sampled for Kopu and Tahora clovers (Table 6.1), it was more appropriate to analyze the clovers by combining the two cultivars in order to produce a wider range of height variation within white clover.

Variation in sward characteristics with increasing height was overviewed by MANOVA to examine the general patterns, whereas ingestive behaviour variables were evaluated by ANOVA, in which the model was composed of two main effects (height classes and animal species) and their interaction.



The correlations amongst sward variables, amongst bite variables, and between sward and bite variables were examined. Further, functional relationships between sward and bite variables were established by regression analysis.

Finally, a pooled analysis was conducted to examine the response patterns of the two animal species to variation in sward height across forage species (sward types). The pooled analysis involved three main effects: forage species (3: including 2 grasses separately and 2 clovers combined), height classes (5 heights for each forage species) and animal species (sheep and goats), and their interactions.

#### 6.3 RESULTS

#### 6.3.1 Sward conditions

MANOVA assessment (Table 6.2) indicated that for all three forage species, surface height and average mass bulk density of the overall sward profiles were much more important (higher standardized coefficients) than other variables, and herbage mass was also emphasized, in discriminating the variation of the set of sward attributes brought about by increases of sward height. Sward height and average bulk density were further examined and were used as bite-related variables, whereas grazed bulk density was used as a comparison with average bulk density where necessary, and leaf layer depth was also quoted in describing sward characteristics (Table 6.3).

Clover swards (Table 6.3 and Fig. 6.1 A<sub>1-3</sub>) were much denser than grass swards in both uppermost layers and whole sward profiles. The lowest densities obtained with clovers were greater than the highest bulk densities measured in the grasses. A comparison of bulk density between grazed strata and whole profiles indicated that generally, the gradients of bulk density down the vertical profiles of the canopy were opposite for grasses and clovers; increasing from the top to the bottom in the canopies of grasses, whereas decreasing in clover canopies (except for height 2 of Tahora). Because the height of petiole in clovers was measured as "stem" for convenience (see Section 3.2.4.1 of Chapter 3), the leaf layer depth (difference between surface height and "stem" height, see Section 3.2.7.8 of Chapter 3) was much smaller for clovers than grasses. Leaf layer depth increased with increasing sward height in both grasses and clovers. The proportion of leaf layer depth to surface height increased with sward height in grasses, but varied erratically in clovers. Fig 6.1 Diagrams  $(A_1 - G_3)$  of bulk density of grazed stratum, bite weight, bite rate, bite depth, bite area and bite volume against sward height for three types of sward (ryegrass, cocksfoot and clovers). Vertical bars indicate standard errors of least square means. Because standard errors based on the least squares means are the same for all means of the same line, only one bar is indicated for each line.





Table 6.2Standardized coefficients of sward variables for the discriminant functions. This<br/>MANOVA was assessed using height classes as treatments to evaluate the overall<br/>variation of the set of sward variables with increase of sward height for two grasses<br/>individually, and for two clovers combined.

Forages	Ryegrass	Cocksfoot	Clov	/ers
Variables	Standardised	Standardised	Standardised	coefficients
Vallables	function 1	function 1	function 1	function 2
Surface height (cm)	6.42	5.54	1.91	2.26
Mass of grazed horizon (g DM/m²)	-0.02	0.58	-0.01	0.39
Mass bulk density of grazed horizon (mg DM/cm³)	0.08	0.94	-0.31	0.69
Herbage mass (g DM/m²)	-2.60	-0.80	1.51	-1.09
Mass bulk density of overall profile (mg DM/cm³)	2.43	-1.87	-0.67	3.76
Leaf frequency bulk density of grazed horizon (hits/2 cm)	-0.42	-0.56	0.55	0.13
Leaf % of overall profile	0.62	1.15	0.12	-0.09
Leaf frequency bulk density of overall profile (hits/2 cm)	0.36	1.11	-0.30	-0.13
Stem frequency bulk density of overall profile (hits/2 cm)	0.16	-0.31	-1.01	-0.58
Proportion of variation accounted for by the function	0.80	0.83	0.59	0.27
Wilks' Lambda	***	***	10.84	***

<sup>1</sup> For combined clovers, because the first function only accounted for 59% of total dispersion, the second function was also taken into account, contributing 84% of total dispersion collectively.

#### 6.3.2 Ingestive behaviour variables

Tables 6.4-6.6 present details of bite variables for the interaction between sward height and animal species for each forage species. Fig. 6.1 B-G illustrate diagrams of all bite variables against sward height for ryegrass, cocksfoot and clovers separately.

Contrary to the case in Experiment 1 (Chapter 5), there was a similar pattern of response in bite weight in fresh (FM) and dry matter (DM) terms to variation in sward height (Fig. 6.1  $B_{1-3}$  and  $C_{1-3}$ ). Therefore, only bite weight based on FM is considered further.

Forages	Ryegrass					Cock	sfoot		Clovers			
Height classes	Surface height (cm)	Leaf layer depth (cm)	Grazed bulk density (mgDM cm <sup>3</sup> )	Overall bulk density (mgDM/ cm <sup>3</sup> )	Surface height (cm)	Leaf layer depth (cm)	Grazed bulk density	Overall bulk density	Surface height (cm)	Leaf layer depth (cm)	Grazed bulk density	Overall bulk density
1	7.8 ө	4.3 ө	0.47 c	0.59 c	8.0 d	4.1 d	0.47 b	0.77 a	5.5 d	0.6 e	3.52 a	2.32 a
2	13.7 d	7.9 d	0.48 c	0.50 d	17.3 c	11.3 c	0.39 c	0.40 c	5.8 d	1.1 d	1.72 b	2.12 b
3	16.7 c	11.4 c	0.63 b	0.62 c	22.1 b	14.0 b	0.45 bc	0.48 c	6.8 c	1.5 c	1.29 bc	1.11 d
4	18.4 b	12.3 b	0.78 a	0.91 a	22.2 b	14.5 b	0.58 a	0.74 a	11.0 b	1.9 b	1.53 bc	1.34 c
5	26.7 a	18.4 a	0.62 b	0.81 b	29.6 a	18.9 a	0.50 b	0.59 b	13.7 a	2.4 a	1.24 c	1.02 d
s.e. test	0.45 ***	0.30 ***	0.03	0.03	0.49 ***	0.28 ***	0.03	0.03	0.32	0.1 ***	0.16 ***	0.06

 Table 6.3
 Descriptions of sward conditions for ryegrass, cocksfoot and clovers at different heights.

For clovers, heights 1, 2 and 4 were Tahora, and heights 3 and 5 were Kopu (see Table 6.1).

## 6.3.2.1 Bite weight

Animals increased their bite weights with increasing sward height in all three forage species (Fig. 6.1  $B_{1-3}$ ). Bite weight increased more rapidly with increasing sward height in clovers than in ryegrass (91.8 mg FM/cm vs. 45.2 mg FM/cm), which in turn was greater than in cocksfoot (24.0 mg FM/cm). Bite weights obtained on the shortest clover swards (5.5 cm) were two to three times greater than those obtained on the shortest ryegrass (7.8 cm) and cocksfoot (8.0 cm) swards (Fig. 6.1  $B_{1-3}$  and Tables 6.4-6.6), respectively.

Bite weight differed significantly between sheep and goats for ryegrass (Table 6.4) and clovers (Table 6.6), but differed only at P<0.1 level for cocksfoot (Table 6.5). Compared to goats, sheep had 75% greater bite weight on clovers (Table 6.6), and 67% greater on ryegrass (Table 6.4), but only 18% greater on cocksfoot (Table 6.5). The response pattern in bite weight to variation in sward height did not differ significantly between sheep and goats (no significant interaction) grazing cocksfoot (Table 6.5 and Fig. 6.1 B<sub>2</sub>) or clovers (Table 6.6 and Fig. 6.1 B<sub>3</sub>), but differed significantly between the two animal species grazing ryegrass (Table 6.4 and Fig. 6.1 B<sub>3</sub>).

Height classes	Bite weight 1 (mg fresh matter/bite)		Bite weight 2(mg dry matter/bite)		Bite rate (bites/min)		Bite depth (cm)		Bite area (cm <sup>2</sup> )		Bite volume (cm <sup>3</sup> )		(cm³)					
	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats
Height 1 (7.8)	212 d	ns	155 c	39 d	ns	29 c	90 a	ns	107 a	4.6 d	ns	3.7 c	11.4 ab	•	9.0 b	52 c	ns	33 c
Height 2 (13.7)	625 c	*	329 bc	124 c	٠	67 bc	59 b	ns	74 b	8.6 c	•	6.2 b	12.5 a	ns	12.4 a	108 b	•	76 b
Height 3 (16.7)	706 bc	ns	559 ab	135 c	ns	112 ab	48 b	ns	59 bc	9.8 bc	•	7.4 b	11.4 ab	ns	10.8 ab	110 b	ns	80 b
Height 4 (18.5)	940 b	ns	691 a	202 b	ns	150 a	50 b	ns	40 c	10.6 b	ns	10.6 a	10.1 b	٠	6.1 c	107 b	*	65 b
Height 5 (26.7)	1454 a	*	621 ab	275 a	٠	119 ab	43 b	ns	53 bc	17.6 a	٠	11.8 a	12.6 a	*	10.1 ab	223 a	*	119 a
s.e. and test,		103 *	•		19 *	•		8 ns			0.6 ***			0.8 n	s		11 **	
Mean and test <sub>2</sub>	788	***	471	155	***	95	58	(*)	67	10.2	***	8.0	11.6	***	9.7	120	•••	75
(s.e.)	(46)		(46)	(9)		(9)	(3)		(3)	(0.3)		(0.3)	(0.4)		(0.4)	(5)		(5)

Table 6.4	Means of ingestive behaviour	variables on ryegrass for interactic	on between height and animal sp	pecies.
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Significance levels between sheep column and goats column show LSD test between sheep and goats within each height class. The lowercase letters following sheep column indicate LSD between height classes within sheep. The lowercase letters following goats column show LSD between height classes within goats. s.e and test, indicate standard errors and F test of ANOVA for each behaviour variable at the level of interaction between height and animal species. Mean and test, refer to average values of sheep and goats, and F test of ANOVA for each behaviour variable at the level of animal species effect. (s.e): standard errors of average values of sheep and goats.

The above notes also apply for Tables 6.5 and 6.6.

Height classes	Bite weight 1 (mg fresh matter/bite)		Bite weight 2(mg dry matter/bite)		Bite rate (bites/min)		Bite depth (cm)		Bite area (cm²)		Bite volume (cm³)		e (cm³)					
	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats
Height 1 (8.0)	298 c	ns	311 c	57 d	ns	64 c	66 a	ns	66 a	4.1 c	ns	4.0 c	12.5 ab	•	9.5 ab	52 c	ns	37 c
Height 2 (17.3)	765 ab	*	486 bc	143 bc	•	89 bc	54 ab	ns	42 bc	11.4 b	*	9.1 b	13.3 ab	ns	11.9 a	152 b	•	108 <b>\9</b> b
Height 3 (22.1)	643 b	ns	594 ab	141 c	ns	142 ab	50 b	ns	49 b	11.1 b	ns	10.1 b	10.9 b	ns	9.4 ab	121 b	ns	94 b
Height 4 (22.5)	905 a	ns	826 a	205 a	ns	185 a	42 bc	ns	38 bc	12.1 b	*	14.6 a	12.5 ab	*	8.6 b	152 b	ns	125 b
Height 5 (29.6)	898 ab	ns	747 a	202 ab	ns	177 a	35 c	ns	31 c	18.5 a	٠	15.6 a	14.5 a	•	10.9 ab	270 a	٠	168 a
s.e. and test <sub>1</sub>		90 ns			21 ns			7 ns			0.6 **			0.9 n	s		15 *	
Mean and test <sub>2</sub>	700	(*)	593	150	ns	131	49	ns	45	11.4	(*)	45	12.8	***	10.0	149	***	107
(s.e.)	(40)		(40)	(9)		(9)	(2)		(2)	(0.2)		(0.2)	(0.4)		(0.4)	(6)		(6)

 Table 6.5
 Means of ingestive behaviour variables on cocksfoot for interaction between height and animal species.

See Table 6.4 for notes used to interpret this table.

Height classes	Bite weight 1 (mg fresh matter/bite)		Bite weight 2(mg dry matter/bite)		(t	Bite rate (bites/min)		Bite depth (cm)		Bite area (cm <sup>2</sup> )		Bite volume (cm³)		(cm³)				
	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats	Sheep	LSD	Goats
Height 1 (5.5)	698 b	ns	480 b	125 b	ns	86 b	57 bc	ns	66 ab	2.7 c	*	1.3 d	11.5 ab	ns	8.8 a	31 c	*	11 c
Height 2 (5.8)	731 b	ns	455 b	147 b	ns	91 b	82 a	ns	74 a	2.9 c	ns	2.6 c	11.1 b	ns	9.9 a	32 c	ns	25 bc
Height 3 (6.8)	889 b	•	400 b	149 b	٠	70 b	63 ab	ns	68 ab	4.4 b	ns	3.0 bc	12.1 ab	ns	9.4 a	53 bc	٠	29 bc
Height 4 (11.0)	1051 b	ns	563 b	175 b	٠	98 ab	47 bc	ns	46 bc	6.5 a	٠	3.8 b	11.2 ab	ns	9.5 a	74 b	*	36 b
Height 5 (13.7)	1692 a	•	993 a	253 a	•	154 a	38 c	ns	35 c	7.3 a	•	6.1 a	14.7 a	ns	9.6 a	107 a	*	59 a
s.e. and test <sub>1</sub>		128 ns	6		21 ns	i		7 ns			0.4 (*)			1.1 ns			7 (*)	
Mean and test <sub>2</sub>	1012	***	578	170	***	97	57	ns	58	4.8	***	3.3	12.1	***	9.4	60	***	32
(s.e.)	(58)		(58)	(9)		(9)	(3)		(3)	(0.2)		(0.2)	(0.5)		(0.5)	(3)		(3)

 Table 6.6
 Means of ingestive behaviour variables on clovers for interaction between height and animal species.

See Table 6.4 for notes used to interpret this table.

#### 6.3.2.2 Bite rate

Bite rate (Fig. 6.1  $D_{1.3}$ ) generally declined in relation to increasing height in all three forage species. The decline was more rapid in ryegrass when swards were under 16.7 cm. In cocksfoot, this decline was slow (Fig. 6.1  $D_2$ ). In clover following an initial increase, bite rate afterwards declined with height at a relative constant rate (Fig. 6.1  $D_3$ ).

Goats had on average a 16% faster bite rate than sheep on ryegrass (Table 6.4), but a similar rate on cocksfoot and clovers (Tables 6.5-6.6). There was no significant difference in response patterns to variation in sward height between sheep and goats in cocksfoot and clover swards, but there was a slight difference in ryegrass (P<0.1) (Tables 6.4-6.6 and Fig. 6.1  $D_{1.3}$ ).

#### 6.3.2.3 Bite depth

Bite depth (Fig. 6.1  $E_{1-3}$ ) increased significantly with increasing sward height in all three forage species, and animals increased bite depth with increasing sward height at similar rate (similar slope in Fig. 6.1  $E_{1-3}$ ). On average, bite depth expressed as a proportion of sward height was 55% for the two grass species, and 47% for clover (Tables 6.4-6.6). The depths animals penetrated into swards were similar on ryegrass and on cocksfoot, but much less on clovers (Fig. 6.1  $E_{1-3}$ ).

In general, sheep penetrated more deeply than goats in all types of sward (Tables 6.4-6.6). The linear phase of increase in bite depth for sheep continued over the full range of sward heights used in this experiment, whereas a plateau appeared in ryegrass and cocksfoot for goats (Fig. 6.1  $E_{1-2}$ ). On average, sheep removed 61% of the ryegrass height, 56% of the cocksfoot height and 55% of the clover height. The corresponding values for goats were 48%, 53% and 39%, respectively. The response patterns of bite depth to variation in sward height differed significantly between animal species on the two grasses (Tables 6.4 and 6.5), but to a less extent (P<0.1) on clovers (Table 6.6).

#### 6.3.2.4 Bite area

Bite area (Fig. 6.1 F<sub>1-3</sub>) showed erratic tendencies with increasing sward height.
Bite area differed significantly (P<0.001) between sheep and goats (Tables 6.4-</li>
6.6) in each forage species. Bite areas averaged over sheep and goats were similar

across forage species (Tables 6.4-6.6) despite differences in sward height and density between the three types of sward (Table 6.3).

Responses in bite area to variation in sward height were not significantly different between the two animal species (Tables 6.4-6.6).

#### 6.3.2.5 Bite volume

Bite volume increased with increasing sward height (Fig. 6.1  $G_{1.3}$ ). However, responses differed across forage species (Fig. 6.1  $G_{1.3}$ ); as sward height increased, increases of bite volume were slower on short swards than on long swards for ryegrass and cocksfoot (or even slightly diminished when height varied from 16.7 to 18.5 cm on ryegrass, and from 17.3 to 22.1 cm on cocksfoot), but on clovers, bite volume increased continuously with increasing sward height (Fig. 6.1  $G_3$ ).

Sheep had much greater bite volumes than goats when grazing all three forage species (Tables 6.4-6.6). The rate of increase with increasing sward height was greater in sheep than in goats on ryegrass and cocksfoot (Tables 6.4-6.5), but differences were smaller (P<0.1) for the clovers (Table 6.6).

# 6.3.3 Correlation and regression relationships between sward and behaviour variables within forages

Table 6.7 shows the correlation matrices for the three sward variables and five bite variables based on three types of sward separately. Surface height was relatively independent of bulk density in cocksfoot, but was confounded to some extent by bulk density in ryegrass and clovers. With increasing sward height, bulk density increased in ryegrass (positive correlation), but decreased in clovers (negative correlation) (Table 6.3). Of the sward variables tabulated, surface height in all three types of sward was most strongly and positively correlated with bite weight, bite depth and bite volume, and highly and negatively correlated with bite rate, but generally weakly correlated with bite area. In general, there were similar correlations for the bite variables with grazed stratum bulk density and with overall bulk density. Grazed stratum bulk density and overall bulk density were both moderately (although in some cases not significantly) correlated with bite rate, bite depth and bite volume in ryegrass and

	· · · · · · · · · · · · · · · · · · ·						·	
		Surface height (cm)	Grazed bulk density (mg DM/cm <sup>3</sup> )	Overall bulk density (mg DM/cm <sup>3</sup> )	Bite weight (mg fresh matter)	Bite rate (bites /min)	Bite depth (cm)	Bite area (cm²)
Ryegrass	Grazed bulk density	0.41**						
(11=40)	Overall bulk density	0.50***	0.72***					
	Bite weight	0.74***	0.53***	0.49***				
	Bite rate	-0.67***	-0.65***	-0.46***	-0.66***			
	Bite depth	0.90***	0.48**	0.55***	0.89***	-0.68***		
	Bite area	0.04	-0.32*	-0.41***	0.20	0.03	0.08	
	Bite volume	0.79***	0.23	0.29(*)	0.85***	-0.52***	0.90***	0.49**
Cocksfoot	Grazed bulk density	0.17						
(n=40)	Overall bulk density	-0.22	0.64***					
	Bite weight	0.68***	0.29(*)	0.02				
	Bite rate	-0.76***	-0.26	0.11	-0.59***			
	Bite depth	0.94***	0.20	-0.12	0.82***	-0.72***		
	Bite area	0.06	-0.18	-0.04	0.21	0.01	0.19	
	Bite volume	0.76***	0.05	-0.13	0.74***	-0.54***	0.87***	0.61***
Clovers	Grazed bulk density	-0.45**						
(n=40)	Overall bulk density	-0.49**	0.69***					
	Bite weight	0.69***	-0.30(*)	-0.32*				
	Bite rate	-0.69***	0.25	0.35*	-0.53***			
÷	Bite depth	0.89***	-0.59***	-0.54***	0.76***	-0.56***		
	Bite area	0.32*	-0.22	-0.22	0.68***	-0.09	0.43**	
	Bite volume	0.81***	-0.51***	-0.49**	0.87***	-0.50**	0.93***	0.70***

Table 6.7Overall correlation matrices for the relationships between three sward variables and five<br/>ingestive behaviour variables based on ryegrass, cocksfoot and clovers, separately.

clovers, but not in cocksfoot where independent variation in sward height and bulk density was achieved.

The regression relationships between sward and bite variables were further examined. Generally, sward surface height was considered to provide best-fit regressions with bite variables. However, because of the correlations between surface height and bulk densities in ryegrass and clovers (Table 6.7), inclusion of terms for bulk density (D) (overall bulk density), and interaction between surface height and bulk density (HD) in the regressions of bite weight, bite rate, bite depth and bite volume on surface height (H) was expected to give some improvements of fit for these two forage species, though the improvement possibly was not always significant. A parsimonious model from these three terms (H, D and HD) was determined for the four bite variables (bite weight, bite rate, bite depth and bite volume) by the Stepwise option of Proc Reg (SAS, SAS Institute 1990). Because of the poor correlation of bulk density with bite variables (Table 6.7) in cocksfoot, where the variations in surface height and bulk density were dissociated, the four bite variables were only fitted to surface height for this species.

Unlike the other bite variables, bite area was only moderately correlated with bulk density in ryegrass, and moderately correlated with surface height in clovers (Table 6.7). Hence, bite area was regressed with only a single variable in ryegrass (bulk density) and in clovers (surface height), and no attempt was made to relate bite area to any sward variables for cocksfoot because of the weak correlations observed (Table 6.7).

Major regression equations are summarized in Tables 6.8-6.10. Among the equations shown in Tables 6.8 (ryegrass) and 6.10 (clovers), those models containing significant effects of both height and density, irrespective of independent or interaction terms, were selected (4 equations from Table 6.8 and 2 equations from Table 6.10) to show response surfaces of bite variables to variation in both height and bulk density (Figs. 6.2 and 6.3).

For ryegrass (Table 6.8), the models describing effects of sward height and bulk density on bite weight, bite rate, bite depth and bite volume were markedly different between sheep and goats. The models for sheep contained a sward height term (H) alone; but for goats, they involved both sward height and bulk density. Thus, bulk density was more important in goats than in sheep. However, sward height was still more important than bulk density for goats, because sward height contributed the majority of the model  $R^2$  values of these equations (proportion of height  $R^2$  to model  $R^2$  in Table 6.8). Therefore, for goats grazing ryegrass, height and bulk density affected bite weight, bite rate, bite depth and bite volume interactively (Fig. 6.2), rather

Fig. 6.2 Response surfaces of bite variables to sward height (H) and bulk density (D) for goats grazing ryegrass



 $BD = 4.8(s.e \ 0.8) + 0.6(s.e \ 0.07)HD - 4.6D$  $(R^2 = 0.88)$ 

 $\label{eq:BV} \begin{array}{l} \mathsf{BV} = 88.4(\text{s.e } 11.9) + 7.0(\text{s.e } 1.1) \mathsf{HD} - 141.8(\text{s.e } 29.6) \mathsf{D} \\ (\mathsf{R}^2 = 0.73) \end{array}$ 

Fig. 6.3 Response surfaces of bite variables to sward height (H) and bulk density (D) for sheep grazing clovers



 $\begin{array}{l} \text{BD=0.2(s.e~0.07)} + \text{ 0.6(s.e~0.07)H - 0.2(s.e~0.01)HD} \\ (\text{R}^2 = 0.94) \end{array}$ 



 $BV = -8.1(s.e \ 8.5) + 10.2(s.e \ 1.1)H - 1.6(s.e \ 0.8)HD$  $(R^2 = 0.89)$ 

**Table 6.8** Summary of regression equations for **ryegrass**. Among them, bite weight, bite rate, bite depth and bite volume were regressed on height (H), bulk density (D) and interaction term (HD), and parsimonious models were determined by Stepwise procedures, whereas bite area was only fitted to a single variable, bulk density (D).

Variables		Intercept and independent variables	Regression coefficients	Standard errors	Partial R <sup>2</sup> of individual term, model R <sup>2</sup> and residual d.f	Proportion of height R <sup>2</sup> to model R <sup>2</sup>
Bite weight	Sheep	Intercept	-299.9	148.8	0.77***	100%
matter)		н	63.7	8.2	(r.d.f=18)	
	Goats	Intercept	161.6	64.0	0.64***	77%
		HD	27.1	4.8	(r.d.f=18)	
Bite rate	Sheep	Intercept	97.0	11.1	0.44***	100%
(Dites/IIIII)		Н	-2.3	0.6	(r.d.f=18)	
	Goats	Intercept	96.0	8.5	0.48***	98%
		HD	-2.6	0.6	(r.d.f=18)	
Bite depth	Sheep	Intercept	-1.2	0.8	0.04***	100%
(cm)		Н	0.7	0.04	(r.d.f=18)	100 %
	Goats	Intercept	4.8	0.8		00%
		HD	0.6	0.07	0.85	30 /8
		D	-4.6	1.0	0.03 0.88*** (r.d.f=17)	
Bite area	Sheep	Intercept	12.1	1.4	0.006 ns	
		D	-0.7	2.1	(r.d.f=18)	
	Goats	Intercept	13.8	1.4	0.35**	
		D	-6.2	2.0	(r.d.f=18)	
Bite volume	Sheep	Intercept	-26.2	16.5	0.83***	100%
(0117)		Н	8.6	0.9	(r.d.f=18)	
	Goats	Intercept	88.4	11.9		
		HD	7.0	1.1	0.69	89%
		D	-141.8	29.6	0.04 0.73*** (r.d.f=17)	

- Partial  $R^2$  of individual term: proportion of variation accounted for by each term included in the equation. Model  $R^2$ : proportion of variation accounted by the model (summation of partial  $R^2$  of each term). Proportion of height partial  $R^2$  to model  $R^2$  indicates the proportion of  $R^2$  contributed by height itself to the model  $R^2$ .

- The above notes also apply for Tables 6.9 and 6.10.

than independently and additively, whereas for sheep, these four bite variables were only influenced and determined by sward height independently. The functional relationship between bite area and bulk density was very weak for both animal species, and this was particularly the case for sheep (Table 6.8).

Variables		Intercept and independent variables	Regression coefficients	Standard errors	Model R <sup>2</sup> and residual d.f
Bite weight	Sheep	Intercept	176.4	132.6	0.50***
(mg fresh matter)		Н	26.6	6.3	(r.d.f=18)
	Goats	Intercept	130.0	119.6	0.49***
		н	23.1	5.9	(r.d.f=18)
Bite rate (bites/min)	Sheep	Intercept	77.9	6.4	0.55***
		н	-1.4	0.3	(r.d.f=18)
	Goats	Intercept	73.9	5.6	0.62***
		н	-1.4	0.3	(r.d.f=18)
Bite depth	Sheep	Intercept	-0.7	0.8	0.94***
(cm)		н	0.6	0.04	(r.s.f=18)
	Goats	Intercept	0.3	1.2	0.84***
		н	0.6	0.06	(r.d.f=18)
Bite volume	Sheep	Intercept	-25.7	29.5	0.69***
(cm³)		н	8.9	1.4	(r.d.f=18)
	Goats	Intercept	-0.3	16.1	0.73***
		н	5.3	0.8	(r.d.f=18)

Table 6.9Summary of regression equations for cocksfoot. These four bite<br/>variables were only fitted to a single variable, sward height, whereas bite<br/>area was ignored due to poor correlation with height and bulk density.

See Table 6.8 for notes used to interpret this table.

In cocksfoot (Table 6.9), all four bite variables were well predicted by linear terms of height for both sheep and goats.

In clovers (Table 6.10), effects of sward height and bulk density were only markedly different between sheep and goats for bite depth and bite volume. The interaction effect between height and bulk density was more significant for sheep than for goats in determining bite depths and bite volumes, or alternatively, the effect of bulk density was more important in sheep than in goats in this process. However, sward height still had a more dominant effect than did bulk density on bite depths and bite volumes of sheep despite the significant effect of the interaction term in the models, because sward height itself contributed the majority of the model R<sup>2</sup> values (Table 6.10). Bite weight and bite rate could be reasonably predicted by a linear term of height for both sheep and goats. However, bite area showed a very weak functional relationship with sward height.

Table 6.10Summary of regression equations for clovers. Among them, bite weight, bite rate, bite<br/>depth and bite volume were regressed on height (H), bulk density (D) and interaction<br/>term (HD), and parsimonious models were determined by Stepwise procedures,<br/>whereas bite area was only fitted to a single variable, sward height (H).

Variables		Intercept and independent variables	Regression coefficients	Standard errors	Partial R <sup>2</sup> of each individual term, model R <sup>2</sup> and residual d.f	Proportion of height R <sup>2</sup> to model R <sup>2</sup>
Bite weight	Sheep	Intercept	118.7	197.5	0.58***	100%
matter)		Н	99.1	20.4	(r.d.f=18)	
	Goats	Intercept	111.4	107.0	0.55***	100%
		н	57.8	12.5	(r.d.f=18)	
Bite rate (bites/min)	Sheep	Intercept	90.4	9.3	0.45 **	100%
		Н	-3.7	0.9	(r.d.f=18)	
	Goats	Intercept	94.4	8.3	0.53***	100%
		н	-4.6	1.0	(r.d.f=18)	
Bite depth	Sheep	Intercept	0.2	0.07		
(cm)		н	0.6	0.07	0.89	95%
		HD	-0.2	0.01	0.05 0.94*** (r.d.f=17)	
	Goats	Intercept	-0.5	0.5	0.72***	100%
		н	0.5	0.06	(r.d.f=18)	
Bite area	Sheep	Intercept	9.1	1.3	0.24*	
		Н	0.3	0.1	(r.s.d=18)	
	Goats	Intercept	9.5	1.1	0.00006	
		н	-0.004	0.1	(r.d.f=18)	
Bite	Sheep	Intercept	-8.1	8.5		
(cm <sup>3</sup> )		н	10.2	1.1	0.86	97%
		HD	-1.6	0.8	0.03 0.89*** (r.d.f=17)	
	Goats	Intercept	-4.2	7.7	0.58***	100%
		н	4.5	0.9	(r.d.f=18)	

See Table 6.8 for notes used to interpret this table.
Main effects and interactions	Degree of freedom	Bite weight (mg FM)	Bite rate (bites/min)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm³)
Animal species (AS)	1	0.0001	0.5328	0.0001	0.0001	0.0001
Forage species (FS)	2	0.0014	0.0001	0.0001	0.1650	0.0001
Height classes (HC)	4	0.0001	0.0001	0.0001	0.0001	0.0001
AS * FS	2	0.0041	0.1030	0.0143	0.5821	0.1821
AS * HC	4	0.0065	0.4292	0.0001	0.0642	0.0001
FS * HC	8	0.0024	0.0001	0.0001	0.0719	0.0001
FS * HC * AS	8	0.3644	0.8090	0.0002	0.7882	0.5014

 Table 6.11
 Significance levels of the pooled analysis for the main effects and their interactions in each bite variable.

In summarizing the interrelationships between sward variables and bite variables, Fig. 6.4 illustrates the strength of the simple correlations between surface height and bulk density, and between bite variables and sward height and bulk density for each forage species. For comparative purpose, results for the two animal species are shown separately.

# 6.3.4 Comparison of response patterns of ingestive behaviour to variation in sward height across forage species (pooled analysis)

Table 6.11 gives significant levels (P=F) of the pooled analysis across three forage species for three main effects and their interactions.

On average, sheep had substantially greater bite weight and bite dimensions than goats across three forage species (Tables 6.4-6.6, 6.11). Animals usually had greater bite weights, but smaller bite dimensions on clovers than on grasses (Tables 6.4-6.6, 6.11). Taller swards usually resulted in greater bite weights and bite dimensions, but slower biting rate (Tables 6.4-6.6, 6.11).

As a consequence of the substantial effects of forage species on most bite variables, some interactions were found to have significant effects on some variables across three forage species (Tables 6.11), in contrast to the patterns within forage

Fig. 6.4. Diagrams showing the simple correlations between sward height and bulk density, and between bite variables and sward height, and bulk density for animal species x forage species.



A<sub>1</sub> Sheep x ryegrass

## A2 Goats x ryegrass



Notes : Pale arrows indicate correlations which are not significant at P<0.05 Narrow dark arrows indicate correlations significant at P<0.05 or P<0.01 Thick dark arrows indicate correlations significant at P<0.001



 $B_2$  Goats x cocksfoot



## $C_1$ Sheep x clovers



C<sub>2</sub> Goats x clovers



species (Tables 6.4-6.6). However, similar to the pattern within forage species (Tables 6.4-6.6), bite area was not affected by either forage species or its interaction with other factors.

#### 6.4 **DISCUSSION**

Attention is concentrated here principally on the current experiment, and comparison with Experiments 1 and 3 will be made in the General Discussion (Chapter 8).

#### 6.4.1 Sward conditions

MANOVA explained the greater importance of surface height and mass bulk density of the overall sward profile than of other variables. This suggests that height and bulk density are two key variables in establishing sward contrasts (Table 6.2).

This experiment was intended to isolate the effects of variation in plant growth form across various forage species, and the effects of stage of growth, from the effect of sward height. This was achieved by analyzing the data within forage species (ryegrass, cocksfoot and clovers separately), and by sampling contrasting swards within the vegetative phase. The data were combined for Tahora and Kopu white clovers, because patterns of grazing behaviour on the two clover cultivars in Experiment 1 were similar (Chapter 5). However, the association between bulk density and height, which is a common phenomenon in grazed pastures (Hodgson, 1990), still occurred in ryegrass and clover swards though not in cocksfoot (Table 6.7).

#### 6.4.2 Ingestive behaviour variables

The ranges of values for bite weight, bite rate, bite depth, area and volume for sheep were broadly similar to those quoted in, summarized in, or derived from, previous publications (Black & Kenney, 1984; Hodgson, 1986; Burlison *et al.*, 1991; Mitchell *et al.*, 1991; Laca *et al.*, 1992a; Mitchell, 1993), but there is no comparable information available for goats.

This study focused on ranges of sward height and mass bulk density for grass and clover forages over which the responses of bite weight, bite rate and bite dimensions were observed to vary linearly in most cases (Fig. 6.1). Superficially, several responses in Fig. 6.1 (bite weight of goats on ryegrass, bite weight on cocksfoot for both sheep and goats, bite rate on ryegrass for both sheep and goats) appeared to deviate from rectilineality, but no attempt was made to fit quadratic functions because of limitations of data-set size.

Generally, the absolute values of the bite variables (except for bite rate) obtained from the wide ranges of height and bulk density variation tested were substantially greater for sheep than goats within each forage species (Tables 6.4-6.6). This difference may have been attributable to the larger incisor arcade and greater liveweight of sheep.

Animals usually obtained greater bite weights, but smaller bite dimensions on clover swards than on grasses (Tables 6.4-6.6), reinforcing the results of Experiment 1 (Chapter 5).

That the interaction between animal species and sward height within forage species was only statistically significant in few cases (Tables 6.4-6.6) indicated that there were some general parallel trends of bite variables to the variation in sward height between sheep and goats when they grazed the same forage species, for example, both sheep and goats usually increased bite weight and decreased biting rate with increasing sward height.

The relative effects of sward variables in influencing ingestive behaviour were different between the two animal species, with particular regard to variation in height and density within forage species.

Ungar *et el.* (1991) suggested that increasing herbage bulk density tended to reduce both bite depth and bite area on taller swards (>10 cm), but there was no apparent effect at heights less than 10 cm (Laca, 1990, quoted by Ungar *et al.*, 1991). In the present study bulk density has no detectable negative effect on bite dimensions over the range of sward heights studied (8.0-29.6 cm) for either sheep or goats grazing cocksfoot (Tables 6.7 and 6.9), where the variation of bulk density was isolated from the variation of height (Table 6.7). However, the effect of bulk density emerged in the goats grazing ryegrass (Table 6.8, Fig. 6.2), where the two key sward variables were confounded to some extent (Table 6.7). The reasons for this will be discussed in more

detail in Section 6.4.2.4. The effect of bulk density on bite depth, and hence bite volume was also detected in sheep grazing clovers (Table 6.10 and Fig. 6.3), where an association between height and density also concealed the effects of independent variation in height (Table 6.7). This reinforced the conclusions drawn in Chapter 5 that bulk density was more significant in influencing ingestive behaviour in clover swards than in grass swards, particularly in the case of sheep.

#### 6.4.2.1 Bite depth

A very strong positive relationship between sward height and bite depth was demonstrated in this study for both sheep and goats in all three forage species (Fig. 6.1  $E_{1.3}$ ). Similar results were obtained by Milne *et al.* (1982); Wade (1991); Forbes (1982); Black & Kenney (1984); Mitchell *et al.* (1991); Burlison *et al.* (1991) and Laca *et al.* (1992a). No plateau was observed in bite depth for sheep as surface height of cocksfoot increased up to 29.6 cm, the maximum height used in this study (Fig. 6.1  $E_2$ ). There may of course be a plateau beyond this height. But there seemed to be a plateau for goats within the range between 18.5-26.7 cm for ryegrass (Fig. 6.1  $E_1$ ), and within the range of 22.5-29.6 cm for cocksfoot (Fig. 6.1  $E_2$ ). Because goats are shallower grazers (McCall & Lambert, 1987), the critical height beyond which there was no further increase in bite depth with increasing sward height was smaller for goats than for sheep.

Burlison *et al.* (1991) pointed out that some characteristics of field-grown grass swards might inhibit bite depth compared with artificial grass swards employed by Black and Kenney (1984), because the proportion of herbage length removed by sheep was greater on the artificial swards than on the field-grown swards at similar pregrazing height. In the current study, the average proportion of herbage length removed by sheep was 61% and 55% on ryegrass and cocksfoot, respectively, similar to that in artificial swards (50-60%), but the bulk density of the artificial swards was 4.23 mg DM/cm<sup>3</sup> (Black & Kenney, 1984), in comparison with less than 1.00 mg DM/cm<sup>3</sup> in the current experiment (Table 6.3). This suggests that bulk density exerted only a small negative effect on bite depth in sheep. This view is substantiated by the fact that the functional relationship between bulk density and bite depth in this study was not statistically detectable for sheep grazing grasses (Tables 6.8 and 6.9), in contrast to the results from highly controlled swards (Black & Kenney, 1984; Mitchell *et al.*, 1991). When goats grazed grasses, the effect of bulk density on bite depth was significant when the variations in height and density were confounded (in ryegrass swards, Table 6.8), but was negligible when height and density were dissociated (in cocksfoot swards, Table 6.9).

In this study sward height was found to be the most important attribute determining bite depth. Barthram and Grant (1984) found that pseudostem acted as a barrier on very short vegetative swards. Similar evidence was reported by Arias et al. (1990) and Dougherty et al. (1992). In the current study, the herbage length removed by sheep on ryegrass and cocksfoot (Tables 6.4 and 6.5) usually exceeded (on relative short swards) or was similar to (on relative tall swards) average leaf layer depth (Table 6.3). This indicates that sheep did penetrate into strata containing pseudostem on the relatively short grass swards, but if the swards were tall enough, sheep did not have to reach the pseudostem layer. The depth of herbage removed by goats were always smaller than the leaf layer depth of grass swards (Tables 6.3-6.5), and therefore goats hardly reached the pseudostem horizon when they grazed the grass swards tested in this experiment. This was considered to be attributable to their shallow grazing behaviour (Gong et al., 1993), rather than to any barrier created by the pseudostem layer. Therefore, under the conditions tested in the current study, there was no apparent vertical selectivity against pseudostem, and it was unlikely that bite depth was constrained by the presence of pseudostem. Similar results were reported by Mursan et al. (1989) who showed that cattle grazed early spring ryegrass pastures (5 and 10 cm high) to below the pseudostem level. Thus, the presence of undesirable plant parts within the vertical profile of the sward was a minor effect compared with variations in height and density, in agreement with the conclusions of Burlison et al. (1991), and Laca et al. (1992a).

#### 6.4.2.2 Bite area

The small variation in bite area over the range of sward conditions tested in this study (Fig.6.1  $F_{1-3}$ ) reinforced the results of Chapter 5, in line with those of Mursan *et al.* (1989), Hughes *et al.* (1991), and Gong *et al.* (1993).

Laca *et al.* (1992a) showed a slow increment in bite area with increasing sward height for cattle grazing paspalum (*Paspalum dilatatum*) and lucerne (*Medicago sativa*). In the current experiment, bite area varied erratically with increasing sward height for

both sheep and goats, though it was usually greater on the tallest than on the shortest swards (Fig. 6.1  $F_{1.3}$ ). A comparison of patterns of variation in bulk density (Fig. 6.1  $A_{1.3}$ ) and bite area (Fig. 6.1  $F_{1.3}$ ) indicates that the erratic variation in bite area with increasing height was a consequence of the concomitant variation in bulk density, despite a weak functional relationship between the bite area and bulk density (Tables 6.7, 6.8 and 6.10); increasing bulk density with increasing sward height usually resulted in a decrease in bite area.

Laca *et al.* (1992a) claimed that earlier modellers had assumed that bite area was independent of sward characteristics, and concluded that bite area of cattle was significantly and predictably affected by sward height and bulk density. The results of this study indicates that the effects of sward height and bulk density on bite area were not always statistically significant (Tables 6.7, 6.8 and 6.10).

The relationship between bite area and sward height was not functionally significant and predictable for either sheep or goats (Tables 6.8, 6.10). This was because the range of variation in bite area over the great range of sward heights tested (Table 6.3) was small (Tables 6.4-6.6). Similarly, Burlison et al. (1991) failed to find any relationship between bite area and sward height and density across seventeen or fourteen species of grass and cereals used, but a positive and a negative relationship with height and density, respectively, was found within the species (Burlison, 1987). In this experiment, bite area sometimes displayed an increase with increasing sward height (Fig. 6.1  $F_{1,3}$ ) despite a weak functional relationship in general (Tables 6.8 and 6.10). This suggests that taller swards enabled animals to gather and harvest a greater number of leaves into mouth (Burlison et al., 1991). It is assumed that gathering of herbage into the mouth by sheep and goats is performed with the lips and, to some extent, by a horizontal movement of the head (Burlison et al., 1991). Similarly, the amplitude of tongue sweeps by cattle is positively related to sward height; on tall swards of low density cattle attempts to obtain a bite area as large as possible, and bite area is limited by the maximum extension of tongue sweeps (Laca et al., 1992a).

It was proposed by Hodgson (1985) and Hughes *et al.* (1991) that, on dense swards, the number of plant units encompassed at a bite may be limited by the effort required to sever the herbage. This implies a set limit to the force expended per bite, termed summit force per bite (Hughes *et al.*, 1991), which may limit bite area. A negative relationship between bite area and bulk density would be expected from this theory. Although such a relationship emerged in this study (Tables 6.7 & 6.8), the correlation (Table 6.7) and regression relationships (Table 6.8) revealed were very weak and not statistically significant. In only a few cases, on the dense swards, was it observed that animals grasped bundles of herbage which they were not able to break in the first attempt, and then slipped some of the herbage to sever what remained in the reduced encompassed area. Therefore, this study suggests that although the functional relationship between sward height and bite area was not statistically significant over the range of sward conditions tested, the sward height still had more effect on bite area than did biting effort, and the force expended in biting (Hodgson, 1985) usually was not limiting or remained only a minor determinant of bite area, in agreement with Mitchell (1993).

## 6.4.2.3 Bite volume

A positive linear relationship with sward height was demonstrated in this study, supporting Black & Kenney (1984), and Burlison *et al.* (1991).

It could be inferred from the work of Black and Kenney (1984) that bite volume declined as mean sward bulk density increased. In the current study, when the relationship between bite volume and bulk density was examined by combining sheep and goats (Table 6.7), the negative correlation was negligible in ryegrass and cocksfoot, consistent with the results of Burlison *et al.* (1991), but emerged in clovers. However, when the relationship was assessed for sheep and goats separately, the effect of bulk density on bite volume appeared to be significant sometimes in the cases where variations in height and density were confounded (Tables 6.8 and 6.10, Figs. 6.2-6.3).

Variation in bite depth was the major determinant of bite volume, and the sward characteristics strongly influencing bite depth also exerted a similar effect on bite volume. This was substantiated by the fact that, in the ryegrass and clover swards (Tables 6.8 and 6.10), the terms included in the equations of bite volume were exactly the same as those included in the equations of bite depth.

#### 6.4.2.4 Bite weight

The positive relationship between bite weight and surface height in the current

study is in line with previous work (Allden & Whittaker, 1970; Hodgson, 1981a; Forbes, 1982; Black & Kenney, 1984; Burlison *et al.*, 1991; Laca *et al.*, 1992a), though there was indication of a plateau in this response for grass swards (Fig. 6.1 B<sub>1.2</sub>).

Both Burlison *et al.* (1991) with sheep and Laca *et al.* (1992a) with cattle found that the effects of sward height and density on bite weight were independent and additive. The current study demonstrated that generally, bite weight was affected primarily by sward height for both sheep and goats (Tables 6.8-6.10). However, when ryegrass was grazed by goats, bite weight was affected interactively by sward height and bulk density (Table 6.8), in agreement with Mitchell (1993). Black and Kenney (1984) and a comparison of bite weight on wheat swards with different heights (Mitchell 1993) indicated that height and density effects were interactive on shorter swards, but became increasingly independent and additive as height increased.

For a given herbage mass, the relative variation in height and density determined whether the effect of bulk density on bite weight was significant or not beyond the dominant effect of sward height, and the extent to which bulk density affected bite weight also depended on animal species (Table 6.8). Sheep obtained heavier bites on tall swards (Tables 6.8-6.10), and little effect of bulk density was detected within the range of bulk density studied (Table 6.3). This result was similar to those of Black and Kenney (1984) for sheep, and of Laca *et al.* (1992a) for cattle in which height and density varied independently at a constant herbage mass (hand-constructed swards). This was because on the tall swards, as explained above, sheep and cattle not only obtained a proportionally equivalent bite depth (Wade, 1991), but also achieved larger bite area, which resulted in heavier bites. But for goats, the effect of bulk density emerged in ryegrass (Table 6.8), and this is outlined as below.

The significant effect of bulk density apart from the dominant effect of sward height in goats grazing ryegrass (Table 6.8) was conservatively considered to be due to two facts: small mouth dimensions, and shallow grazing behaviour.

(1) Small mouth dimensions of goats provided an opportunity for the effect of bulk density to emerge, because on the dense swards the maximum area encompassed by mouth size could be a restricting factor of bite area (Hodgson, 1985). As a consequence, on the dense swards, there was a more significant functional relationship among these three variables: bulk density, bite area and bite weight. Therefore, when mouth size is small the effect of sward density may increase to a significant level, and hence become a determinant of bite weight through effects on bite area.

(2) Sheep and goats could penetrate into swards deeply to harvest herbage when grazing tall swards (Chapter 5). However, since goats were shallower grazers than sheep, the amplitude and extent of vertical penetration with increasing sward height were smaller, and therefore, the overriding effect of sward height existed to a smaller extent for goats than for sheep, leading to an emergence of the effect of bulk density for goats. However, regardless of the importance of the effect of bulk density, sward height still was a dominant variable influencing bite weight of goats grazing ryegrass.

In summary, this study suggests that both sheep and goats could obtain heavier bite weights on tall pasture, whereas bulk density within the range of values studied (Table 6.3) had little effect on bite weight in sheep irrespective of sward type (Table 6.8-6.10), but had a significant effect on goats grazing ryegrass (Table 6.8).

#### 6.4.2.5 Bite rate

It was expected that bite rate would decline in relation to increase of bite weight brought about by increases of sward height (Hodgson, 1981b; 1985; Mitchell, 1993). Such trends were obtained in the current study (Fig. 6.1  $D_{1-3}$ ). The initial increase of bite rate when clover height varied from 5.5-5.8 cm (Fig. 6.1  $D_3$ ) may have been a consequence of substantial decline in bulk density over this range (Fig. 6.1  $A_3$ ) despite a weak functional relationship between bite rate and bulk density (Tables 6.7 and 6.9).

For sheep, the bite rate was found only to be sensitive to variation in sward height, and bulk density had no significant effect (Tables 6.8-6.10). This was also the case for goats, except for ryegrass swards where the bulk density had a significant effect (Table 6.8, and Fig. 6.2 B). This was a consequence of the significant effect of bulk density on bite weight, bite depth and bite volume for goats grazing ryegrass (Table 6.8).

#### 6.5 CONCLUSIONS

This experiment extended the findings of key previous studies (Black & Kenney

1984; Laca *et al.*, 1992a) by offering animals more contrasting herbages (grasses vs. clovers), and by using two animal species simultaneously; and that of Burlison *et al.* (1991) by reducing the amount of confounding variation in sward characteristics associated with height changes.

- Bite weight, bite rate, bite depth and bite volume were generally more sensitive to variation in sward surface height than in bulk density. Animals usually increased their bite depths, bite volumes, and hence bite weights, and consequently reduced bite rates significantly in relation to increasing height of swards irrespective of forage species. Bite area generally displayed little response to variations in either height or bulk density.
- 2. Sheep and goats showed highly significant differences in absolute mean values of most bite variables, but the response patterns of bite variables to sward variation within forage species over the range of height and density studied were not always significantly different between the two animal species (Tables 6.4-6.6).
- 3. Appreciation of the effect of bulk density on ingestive behaviour apart from the dominant effect of sward height depended very strongly upon the establishment of independent variation in sward height and bulk density over the range of test swards. Sward height had a dominant effect and bulk density had no significant effect where independent variation in height was achieved. Where the variation in sward height was confounded with bulk density, although sward height still had a dominant effect, the interaction effect was significant in some cases, depending on the pastures and animal species: when ryegrass swards were grazed, bite weight, bite rate, bite depth and bite volume of goats were affected by both surface height and bulk density interactively, whereas sheep were affected only by surface height alone; in the

clovers, the effect of height was more independent in goats than in sheep in influencing bite depth and hence bite volume, because the interactive effect was more significant in sheep than in goats in this influential process.

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## Chapter 7

## **EXPERIMENT 3**

## Comparison of Ingestive Behaviour between Indoor and Outdoor Grazing Using Fistulated Sheep, and between Fistulated and Intact Sheep Using Indoor Grazing Procedures

## 7.1 INTRODUCTION

Experiments 1 and 2 were run using an indoor feeding technique. In this study, the results of indoor procedures were validated using an outdoor grazing technique in which animals were individually confined in field cages with access to experimental pasture plots. This technique was intended to provide an assessment of the extent to which the indoor observations could be extrapolated to paddock conditions.

Outdoor cage grazing involved use of oesophageal fistulated animals in order to estimate the amount of herbage removed by 12 - 15 bites on each grazing occasion. Since the first use by Torell (1954) of oesophageal fistulation, the technique has come into wide use. However, the use of fistulates raised the question as to whether fistulated animals represent, in terms of components of ingestive behaviour, the nonfistulated animals with which they are compared. This comparison has seldom been made.

Forbes and Beattie (1987) concluded from comparisons of bite rate, grazing time, faecal cuticle concentration, faecal ash, nitrogen and acid detergent fibre concentrations that fistulated and non-fistulated animals of similar history and nutritional background did not differ in grazing behaviour or diet composition. However there is no available information on comparison of bite weight and bite dimensions between fistulated and non-fistulated animals.

The objective of this experiment was to evaluate the comparabilities between indoor and outdoor grazing techniques, and between oesophageal fistulated animals and intact animals in terms of a wide range of ingestive behaviour variables. Only sheep were used in this experiment because of their availability and uncertainty about post-operative management of fistulated goats.

## 7.2 MATERIALS AND METHODS

#### 7.2.1 Experimental design

The current experiment was designed to compare two grazing environments (indoor crate grazing and outdoor cage grazing) using oesophageal fistulated sheep, and between two stock states (fistulated and intact sheep) using the indoor grazing procedure.

So as to provide an assessment of confidence in extrapolating the results obtained in Experiment 1 to field grazing, it was desirable to evaluate the grazing behaviour using some of the swards used in experiment 1. Two white clovers (Tahora and Kopu white clovers) and two grasses (ryegrass and cocksfoot) (see detailed description of these forages in Appendix 3.1), each being sampled at two stages of maturity (vegetative and reproductive) were grazed by four individuals of each stock state (fistulated and intact sheep) in indoor crates, and grazed by the same four fistulated sheep in outdoor cages.

## 7.2.2 Oesophageal fistulated animals

Five Romney wether sheep fistulated at the oesophagus and differing in age, liveweight, number of incisors, and breadth of incisor arcade (see Section 7.2.3) were obtained from the Animal Physiology Unit of Massey University.

Animals were maintained in the holding paddock of perennial ryegrass and white clover.

Two halves of a moulded rubber plug in the shape of an L were used to close the fistula (Corbett, 1978). They were easily removed for sampling. These half plugs were held together externally by slipping two or three strong elastrator rubber rings over the stem. In order to prevent loss of plugs, a polythene collar was fitted closely over the plug stem between the elastrator rings and the throat and fastened loosely around the animals' neck. A foam rubber pad over the plug stem and between the collar and the throat was also placed to prevent the collar from irritating the flesh.

Animals were accustomed in advance to being handled for sampling.

Animals had access to a lick at all times to offset the loss of salt in leakage of saliva. The fistula was cleaned daily by taking out the plug and washing it in clean water. The animal's front was also washed down with clean water, and was clipped out regularly to prevent the build up of wet wool (Bramley & Wait, 1972).

A 200 gauge 52.5 x 65 cm polythene bag was fitted around each animal's neck to collect extrusa samples of the herbage eaten when it grazed. The bag was slit down the side folds leaving 12.5-15 cm uncut at the bottom. The bag was attached, through pinning to the wool, around the animal's neck so that the bag was over the fistula (Bramley & Wait, 1972).

A circular piece of pliable sponge 5 cm in diameter and 5 cm in length was inserted into the throat immediately below the fistula to block off the lower part of the oesophagus in order to prevent the material consumed from being swallowed. A thin length of nylon cord was threaded through the centre of the circular sponge. When the circular piece of sponge was inserted into the oesophagus, the cord was looped around the animal's neck and tied, thus temporarily blocking the throat and allowing the extrusa to drop into the collection bag (Bramley & Wait, 1972).

### 7.2.3 Experimental procedures

Four of five fistulated sheep were selected in terms of willingness to eat and of tameness to handle, together with four intact sheep used in Experiment 2 (Chapter 6). Average liveweights of intact sheep and fistulated sheep over the experimental period were 57.7 and 50.3 kg (s.e: 1.9). The four intact sheep were the same age (38 months), and had all eight adult incisors present, with average breadth of 3.4 cm. The four fistulated sheep were of different ages and had two (one young sheep), four (one young sheep) and eight (two old sheep) adult incisors respectively, with 2.8 cm (s.e: 0.12) average breadth of incisor.

All animals were accustomed to the experimental procedures before the experiment was started. Intact sheep had previous confined grazing experience, so only one week re-training was required immediately prior to the current experiment. In the case of fistulates, an intensive training session lasting 10 weeks was conducted to get animals thoroughly used to both the field cages and indoor crates, and to the herbage sampling routine.

Each round of the experiment comprised twelve grazing samplings: eight indoor samplings (four each for fistulated and intact sheep), and four outdoor samplings and, since they could not be completed within one working day, they had to be run in two sub-rounds. At the start of the experiment, the eight sheep were allocated to two groups, one group for each sub-round. Each group comprised two intact sheep plus two fistulated sheep, with one old and one young fistulated sheep for each group in an attempt to balance age and live weight between groups.

The following grazing sequence was followed. In the first sub-round, two intact sheep and two fistulated sheep were fed indoors, and within the same day, the two other fistulated sheep grazed outdoors. In the second sub-round on the following day, the two other intact sheep, and the two fistulated sheep which were fed outdoors on the previous day, were fed indoors; and the two fistulated sheep which were previously fed indoors grazed outdoors. Throughout the experiment, individual fistulates were rotated between indoors and outdoors, and between sub-rounds, and individual intact sheep were rotated between rounds in an attempt to balance the effects of sequence on the desire to eat.

The swards sampled in this experiment were summer regrowths following cutting with a rotary mower at a height of approximately 5 cm. All cut herbage was removed from the sward. Two grasses and two clovers were sampled at two stages of maturity to achieve a wide range in sward canopy structure.

Indoor sampling procedures employed in this experiment were the same as in Experiment 1 (Chapter 3). Animals were restrained in metabolism crates and offered prepared turves. A series of measurements were made before grazing to characterize several aspects of sward structure, during grazing to determine the amount of herbage removed by 12-15 bites and the time spent biting, and after grazing to measure grazed area, residual height and herbage mass remaining within the grazed stratum and below the grazed stratum (see Section 3.2.6 of Chapter 3).

During outdoor grazing, each sheep was penned in a field cage (see Plate 7.1). The cage was mounted on a frame which was supported by two wheels for ease of movement. Access to the cage was through a door at the back and the sheep was not tethered in any way. Sheep stood on a wooden floor just above ground level and were constrained by solid walls surrounding the floored part of the cage. After the cage was positioned over the experimental sward, a quadrat with the same dimensions as the tray used in indoor grazing was defined in front of the cage. Narrow strips of herbage were removed from the outer edges of the quadrat to ensure that no herbage rooted outside the patches could protrude into the defined quadrats. The same measurements were taken before and after grazing on the defined patches as on the turves fed indoors in order to determine sward characteristics.

The sampling procedures of outdoor grazing were the same as the indoor grazing except for the way in which herbage weight removed by animals after a few bites was estimated (see later in this section).

In order to standardize animal preparation, the sheep used for indoor grazing were introduced to the indoor pen from 16.00 h the afternoon before grazing until sampling began the next day at 10.00 h. The two fistulated sheep which were used for outdoor grazing were penned in a shed adjacent to the field plot where outdoor quadrats were defined.

During sampling of the fistulated sheep, extrusa was collected in a polythene bag tied around the animal's neck after fitting the foam rubber plug in the oesophagus below the fistula (Plate 7.2). The bag of extrusa was removed, stored in a chiller maintained at 5° C, and subsequently weighed before and after oven-drying at 110° C for 20 hours.

Results were discarded if the foam plug was expelled during sampling or the extrusa samples were seen to be contaminated with rumen contents. If a fistulated animal did refuse to graze or sporadically grazed its particular patch (outdoor) or turf (indoor) then no further measurements were taken on that sward. Intact sheep allowed a higher sampling success rate than fistulated sheep (1.00 vs 0.90).

Sampling was always finished by 12.00 h. Turves were stored in the chiller. The remainder of the sampling day of the first subround was spent doing the set of pre-sampling sward measurements for the second sub-round. The sampling of the second sub-round was conducted on the following day. The remainder of the second sub-round sampling day, and the following two days, were required to complete the set of post-sampling sward measurements.

Two sets of variables (sward and ingestive behaviour) were obtained from the above measurements. Of the ingestive behaviour set, bite rate, bite depth, bite area and bite volume were measured or derived in a consistent procedure (see Section



Plate 7.1 A fistulated sheep was confined in the field grazing cage.



Plate 7.2 Extrusa was collected from a fistulated sheep grazing in the field cage.

3.2.7 of Chapter 3) across indoor intact sheep, indoor fistulated sheep and outdoor fistulated sheep; however, bite weight was estimated in two different ways: extrusabased estimate ( $BW_{eb}$ , both indoor and outdoor fistulated sheep) and turf-based estimate ( $BW_{tb}$ , both indoor intact sheep and indoor fistulated sheep). In the extrusabased estimate, bite weight was calculated by dividing dry matter of oven-dried extrusa by the number of bites, whereas in the turf-based estimate, bite weight was derived by dividing the difference of turf weight pre-and post-grazing by the number of bites. This was intended to check against corresponding extrusa based estimates for each turf, and to establish a recovery coefficient. The set of sward variables included surface height, stem height, herbage mass, mass bulk density of grazed stratum, and mass bulk density of complete sward profiles.

Measurements were carried out over a period from 1 November of 1990 to 29 January of 1991.

## 7.2.4 Statistical analysis

All results were subjected to analysis of variance using completely randomized designs. Ingestive behaviour variables were compared between intact and fistulated sheep within indoor grazing, and were compared between indoor crate-grazing and outdoor cage-grazing within fistulated sheep, treating individual animals as internal replications with repeated measures. Sward variables were compared between indoor sampled turves and outdoor defined quadrats to evaluate the extent to which the extracted turves could represent field grown swards in terms of structural characteristics. Least squares means and standard errors of these variables were carried out on the Proc. GLM of the SAS package (SAS Institute Inc. 1990).

## 7.3 RESULTS

## 7.3.1 Sward conditions

The turves grazed by indoor animals were not significantly different from the quadrats grazed by outdoor animals (P=0.07). Therefore, the data of sward variables presented in this chapter were based on the averaged values of indoor turves and outdoor quadrats.

Forages	Maturity stages	Surface height (cm)	Stem height (cm)	Herbage mass (gDM/m²)	Bulk density of grazed stratum (mgDM/cm³)	Bulk density of complete sward profiles (mgDM/cm³)
Ryegrass	Vegetative	12.4	5.4	230	1.29	1.90
	Reproductive	26.6	16.8	260	0.56	0.97
Cocksfoot	Vegetative	17.9	5.4	181	0.90	1.02
	Reproductive	47.8	20.9	290	0.50	0.62
Tahora	Vegetative	8.5	7.1	180	2.11	2.13
	Reproductive	19.0	13.7	265	1.40	1.10
Kopu	Vegetative	16.3	14.3	240	1.44	1.34
	Reproductive	22.6	17.9	280	1.24	1.14
s.e and test		0.5***	0.4***	14***	0.08***	0.06***

 Table 7.1
 Description of sward variables for four forages x two stages based on the averaged values of indoor turves and outdoor quadrats

'Test: F test of ANOVA for forages x stages interaction.

Table 7.1 gives the details of sward variables for forages x stages. The two grasses were taller in comparison with the two clover swards, but the mass bulk density was greater for two clovers than the two grasses in both the grazed horizon and overall profiles. Herbage mass was substantially increased as swards advanced in maturity for all forages. However, progression from the vegetative to the reproductive stage consistently decreased the bulk densities for each forage. A comparison of bulk density between the grazed strata and the complete sward profiles indicated that the gradients of bulk density greatly increased from the top to the bottom in two grasses, but decreased in two clovers.

## 7.3.2 Ingestive behaviour variables

# 7.3.2.1 Comparison between indoor intact sheep and indoor fistulated sheep

Tables 7.2 and 7.3 summarize the ingestive behaviour variables obtained for intact sheep and fistulated sheep (Table 7.2), and for stock state x forage x maturity

**Table 7.2** Comparison of ingestive behaviour variables between indoor intact sheep (indoor-N.O.F) and indoor fistulated (indoor-O.F) sheep. Bite weight refers to turf-based estimate (Bite weight<sub>tb</sub>).

Stock states	Bite weight <sub>tb</sub> (mgDM)	Bite rate (bites/min)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm <sup>3</sup> )
indoor-N.O.F	252.9	36.7	10.7	12.5	134.9
Indoor-O.F	216.4	25.3	11.0	10.9	118.3
s.e and test	19 ns	1.7***	0.5 ns	0.5 ns	7.3 ns

Test: F test of ANOVA between indoor intact sheep and indoor fistulated sheep.

stage (Table 7.3) based on indoor grazing procedures in which bite weight was derived by difference between pre- and post-grazing weighing (Bite weight<sub>tb</sub>).

On average, bite weight and bite dimensions did not differ significantly between intact and fistulated sheep based on the indoor procedures. However, bite rate was much faster for intact sheep than fistulated sheep (Table 7.2).

Table 7.4 illustrates significance levels (P=F) of the two other main effects (forage and stage) and all the first-order interactions on these behaviour variables.

Effects of forages and of stages on bite weight, bite rate, bite depth and bite volume were highly significant, but were not detected for bite area (Table 7.4).

No significant interaction effects of stock states x forages, and of stock states x stages of maturity (Table 7.4), and stock states x forages x stages (Table 7.3) were found. But the effect of interaction between forages and stages was significant.

# 7.3.2.2 Comparison between indoor fistulated and outdoor fistulated sheep

Tables 7.5 and 7.6 give comparisons of ingestive behaviour variables of the fistulated sheep between indoor and outdoor grazing conditions (Table 7.5), and details

Forag	es	Rye	egrass	Coo	ksfoot	Tahora v	vhite clover	Kopu w	hite clover	s.e
Variables	Stock	Vegetative	Reproductive	Vegetative	Reproductive	Vegetative	Reproductive	Vegetative	Reproductive	test
Bite weight <sub>tb</sub>	N.O.F	142	161	176	435	211	331	269	299	53
(mgdm)	O.F	124	126	150	405	161	263	202	302	ns
Bite rate	N.O.F	56	31	43	18	46	31	32	38	4.7
(bites/min)	O.F	32	19	31	16	46	24	22	16	ns
Bite depth	N.O.F	6.0	12.3	12.2	26.6	4.2	9.5	6.5	8.2	1.5
(cm)	O.F	5.7	14.1	11.6	30.5	3.9	8.7	6.3	7.3	ns
Bite_area	N.O.F	9.1	13.6	15.3	10.8	10.0	14.6	14.7	11.9	1.4
(cm²)	O.F	8.1	11.0	10.9	11.0	10.1	13.6	10.1	13.7	ns
Bite volume	N.O.F	54.9	168.6	198.7	285.6	94.9	96.5	42.0	137.9	20
	O.F	44.7	153.0	152.3	261.8	63.5	123.5	43.3	104.7	ns

**Table 7.3** Comparison of ingestive behaviour variables between indoor intact sheep (N.O.F) and indoor fistulated sheep (O.F) for the interaction of stock states x forages x stages. Bite weight refers to turf-based estimate (Bite weight<sub>b</sub>)

Test: F test of ANOVA for the interaction of stock states x forages x stages.

Table 7.4Significance levels of two main effects (forage and stage) and all the<br/>first-order interactions between the three main effects (stock state, forage<br/>and stage) on bite variables

Bite weight (mg DM)	Bite rate (bites/min)	Bite depth (cm)	Bite area (cm <sup>2</sup> )	Bite volume (cm <sup>3</sup> )
0.0008	0.0067	0.0001	0.2777	0.0001
0.0001	0.0001	0.0001	0.3061	0.0001
0.9690	0.1084	0.6659	0.9965	0.8186
0.8760	0.8706	0.3861	0.9979	0.6888
0.0122	0.0096	0.0001	0.0031	0.0422
	Bite weight (mg DM) 0.0008 0.0001 0.9690 0.8760 0.0122	Bite weight (mg DM)         Bite rate (bites/min)           0.0008         0.0067           0.0001         0.0001           0.9690         0.1084           0.8760         0.8706           0.0122         0.0096	Bite weight (mg DM)         Bite rate (bites/min)         Bite depth (cm)           0.0008         0.0067         0.0001           0.0001         0.0001         0.0001           0.9690         0.1084         0.6659           0.8760         0.8706         0.3861           0.0122         0.0096         0.0001	Bite weight (mg DM)Bite rate (bites/min)Bite depth (cm)Bite area (cm2)0.00080.00670.00010.27770.00010.00010.00010.30610.96900.10840.66590.99650.87600.87060.38610.99790.01220.00960.00010.0031

Stock : stock states, i.e. fistulated or intact sheep.

**Table 7.5**Comparison of ingestive behaviour variables between indoor-O.F and<br/>outdoor-O.F in which bite weight was derived from extrusa-based<br/>estimate (Bite weight<sub>eb</sub>).

Grazing conditions	Bite weight <sub>eb</sub> (mgDM)	Bite rate (bites/min)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm³)
Indoor-O.F	264.5	25.3	11.0	10.9	118.3
outdoor-O.F	255.1	32.1	11.7	10.1	118.7
s.e and test	18 ns	1.6***	0.5 ns	0.5 ns	7.0 ns

<sup>\*</sup>Test : F test of ANOVA between indoor and outdoor fistulated sheep.

Fora	ges	Rye	grass	Coc	Cocksfoot		vhite clover	Kopu wł	nite clover	s.e
Variables	Conditions	Vegetative	Reproductive	Vegetative	Reproductive	Vegetative	Reproductive	Vegetative	Reproductive	test
Bite weight <sub>eb</sub>	IN	170	165	202	390	229	265	330	365	53
(mgDM)	OUT	152	254	202	297	189	293	324	332	ns
Bite rate	IN	32	19	31	16	46	24	22	16	4.7
(Dites/min)	OUT	41	21	39	19	41	33	31	33	ns
Bite depth	IN	5.7	14.1	11.6	30.5	3.9	8.7	6.3	7.3	1.5
(cm)	OUT	5.3	15.8	10.5	29.5	3.9	7.8	6.9	13.8	ns
Bite area	IN	8.1	11.0	13.4	9.1	10.9	11.0	10.1	13.6	1.4
(cm²)	OUT	7.5	12.4	11.9	10.0	11.2	9.4	11.4	7.7	ns
Bite volume	IN	44.7	153.0	152.3	261.8	43.3	97.5	63.5	123.5	20
(cm³)	OUT	39.8	194.0	125.9	294.7	43.5	73.4	81.3	104.7	ns

Table 7.6Comparison of ingestive behaviour variables between indoor (IN) fistulated and outdoor (OUT) fistulated sheep for the<br/>interaction of grazing conditions x forages x stages. Bite weight refers to extrusa-based estimate (Bite weight<sub>eb</sub>)

Test : F test of ANOVA for grazing conditions x forages x stages.

of these variables for grazing conditions (indoor and outdoor) x forages x stages (Table 7.6), in which bite weight was derived from extrusa-based estimates (Bite weight<sub>eb</sub>).

The fistulated sheep did not exhibit any significant differences in bite weight and bite dimensions when they grazed indoor sampled turves and outdoor defined patches. However, bite rates were much slower indoors than outdoors (Table 7.5).

Table 7.7 gives significance levels of the effects (forages and stages) and all the first-order interactions on these behaviour variables.

Again, there were significant effects of forages, and of stages on bite weight, bite rate, bite depth and bite volume, but not on bite area (Table 7.7).

The effects of the interactions between grazing conditions and forages, between grazing conditions and maturity stages (Table 7.7), or between the three effects (second order interaction) (Table 7.6) on any variables were not statistically significant. But the effect of interaction between forages and stages was significant on all behaviour variables except for bite weight (Table 7.7).

Effects and interactions	Bite weight (mg DM)	Bite rate (bites/min)	Bite depth (cm)	Bite area (cm²)	Bite volume (cm <sup>3</sup> )
Forage	0.0020	0.0099	0.0001	0.7088	0.0001
Stage	0.0097	0.0001	0.0001	0.8658	0.0001
Condition x forage	0.7515	0.4135	0.1117	0.7222	0.6726
Condition x stage	0.8078	0.5865	0.2080	0.4300	0.7299
Forage x stage	0.4348	0.0652	0.0001	0.0161	0.0003

Table 7.7Significance levels of two main effects (forage and stage) and all the<br/>first-order interactions between the three main effects (grazing condition,<br/>forage and stage) on bite variables.

Condition: grazing conditions, i.e. indoor or outdoor grazing.

## 7.3.2.3 Comparison of bite weight between turfbased and extrusa-based estimates

The turf-based estimate of bite weight  $(BW_{tb})$  was used as a check against the extrusa-based estimate  $(BW_{eb})$ . The relationship between the two independent estimates was described by the following linear regression equation:

 $BW_{eb} = 88.5$  (s.e. 24.3) + 0.81 (s.e. 0.09)  $BW_{tb}$ ( $R^2 = 0.71$ , residual d.f = 30)

Both intercept and slope were significantly different from zero. Although the slope was significantly less than one, the extrusa-based estimate was greater than the turf-based estimate within the range of variation encountered.

## 7.3.2.4 Recovery coefficients of fistulated sheep

The proportional recovery of ingested herbage was derived based on indoorfistulated sheep, and it was calculated as follows:

Recovery = Bite weight<sub>eb</sub> (mg DM) Bite weight<sub>tb</sub> (mg DM)

Table 7.8 gives average recovery coefficients of indoor-fistulated sheep grazing swards of 4 forages x 2 stages.

The results indicated that when the recoveries from the current experiment were expressed in this way, the average recoveries usually exceeded unity and were variable between individual animals.

## 7.4 DISCUSSION

In this section, attention is concentrated primarily on this experiment, and briefly touches on the comparison with Experiment 1. More thorough comparison will be made in Chapter 8 (General Discussion).

The close similarity between indoor turves and outdoor quadrats in canopy

Table 7.8	Recovery coefficients based on indoor fistulated sheep on four forages
	x two stages. They were calculated by the ratios of extrusa-based
	estimates (uncorrected estimates) to turf-based estimates.

Forages	Maturity stages	Average recoveries	Ranges	S.e
Ryegrass	Vegetative	1.39	1.27-1.46	0.17
	Reproductive	1.29	0.76-1.63	0.17
Cocksfoot	Vegetative	1.39	0.94-2.22	0.17
	Reproductive	1.00	0.78-1.19	0.17
Tahora white	Vegetative	1.41	1.07-1.74	0.17
clover	Reproductive	1.13	0.91-1.37	0.17
Kopu white	Vegetative	1.69	1.24-1.91	0.17
clover	Reproductive	1.26	0.98-1.89	0.17
Average		1.32	0.76-2.22	0.06

structure shown in this experiment gave confidence that turves extracted from the plots could represent the states of swards *in situ*.

The range of sward conditions studied in the current experiment was broadly comparable with conditions covered in previous large plot grazing trials, summarized by Burlison (1987), in the cage trial of Burlison *et al.* (1991) and in artificial swards by Black and Kenney (1984).

Generally the influences exerted by the main effects and interactions on the variables of grazing behaviour were closely comparable to the corresponding effects or interactions in Experiment 1, reinforcing the trends and patterns noted in Chapter 5.

Forbes and Beattie (1987) found that bite rates did not differ significantly between fistulated and non-fistulated sheep and cattle, except on two occasions when fistulates carried Vibracorders to measure grazing times without preliminary training. They attributed this occasional difference to interference, caused by the presence of the Vibracorder. In the current study the bite rates of fistulated sheep were slower than those of intact sheep when grazing in indoor crates, and also slower than the same sheep grazing in outdoor cages (Tables 7.2 and 7.5). Although the fistulated sheep were intensively trained, they were still timid to some degree and could be disturbed by the presence of the observer. Sometimes, they hesitated to resume grazing after a mouthful was swallowed, or consciously interrupted grazing to watch the observer. It was quite likely that these interruptions resulted in overestimates of the time spent biting, and consequently underestimates of the bite rates. This phenomenon could be overcome in the field cage grazing by standing behind the cage to record the time spent biting without any disturbance, and in these conditions these sheep displayed normal bite rates, similar to indoor intact sheep (36.7 vs 32.1, P=0.085). The intact sheep were thoroughly accustomed to the procedures, and hence they were not affected by the presence of observer.

With indoor grazing, the absence of significant interactions between stock state (fistulated and intact) and the two other main effects (forage and maturity stage) indicates that fistulated sheep had similar behaviourial response patterns to intact sheep to sward variation in forage species and in plant maturity stage.

There were differences in this experiment in animal condition and background between fistulated and intact sheep because of the limitations of availability of fistulated animals (see Sections 7.2.2 and 7.2.3). However, generally the fistulated and non-fistulated sheep had no appreciable difference in ingestive behaviour despite the differences between them in management history, nutritional background and body condition. Therefore, it may be concluded on the basis of this experiment that there is no fundamental reason to suppose that ingestive behaviour of fistulated sheep will differ significantly from that of intact sheep of similar background and condition. The above conclusion is in line with the findings of Forbes and Beattie (1987), and extends their finding through investigating a wider range of ingestive behaviour variables. Because the ingestive behaviour of the fistulated animals during the actual sampling may be influenced or modified by tameness and management (Le Du & Penning, 1982; Forbes & Beattie, 1987), it is important to adhere to established procedures for the handling of fistulated animals and the collection of extrusa samples (Arnold et al, 1964; Hodgson, 1982; Forbes & Beattie, 1987), and to get animals thoroughly trained.

Both the indoor comparison between fistulated and intact sheep, and the comparison of fistulates between indoor and outdoor grazings showed that there were highly significant effects of forages, and of stage of growth on all bite variables except for bite area, in close agreement with the results of Experiment 1 (Chapter 5). In the

current experiment bite area was affected neither by stage of growth, in agreement with Experiment 1 (Table 5.8 of Chapter 5), nor by forage species, in contrast with Experiment 1 (Table 5.8). This inconsistency was because only four forages were used in the current experiment, in comparison with the nine used in Experiment 1. The wider range of forages with a great contrast in growth form produced greater variation in canopy structure, and therefore resulted in a significant effect on bite area despite the insensitivity of this variable to variation in sward structure.

Average extrusa recovery estimated in the current trial was 1.32 (s.e: 0.06), higher than the values obtained in previous work, which are summarized in Table 7.9. Each of the authors quoted obtained some recovery estimates which exceeded 1.00, and the same phenomenon occurred in the current work (Table 7.8). There was no doubt that the amount of dry matter in extrusa could be inflated by contamination of saliva dry matter, resulting in overestimates of the recovery coefficients. Burlison (1987) developed a method for correcting for saliva contamination. The methodology she used is outlined in Appendix 7.1. The corrected recovery coefficients using this method for forages x stages are summarized in Table 7.10. Average corrected recovery was 0.96 (s.e: 0.03), falling within the range of values obtained in the literature (Table 7.9). Some recoveries still exceeded unity after correction (Table 7.10). These overestimates were considered to be attributable to a small amount of herbage retained from previous feeds in the mouth or upper oesophagus (Burlison, 1987). So as to minimize this source of error it is appropriate to thoroughly wash the fistula with warm water immediately prior to grazing sampling by taking out the plug.

It has been argued that the results obtained using cage grazing are directly applicable to short term responses of unrestricted animals (Burlison *et al.*, 1991), even though there has been some criticism about the validity of extrapolation from short-term studies on ingestive behaviour to free-grazing (Penning *et al.*, 1991a). The close agreement in ingestive behaviour of fistulated sheep between indoor crate grazing and outdoor cage grazing in the present study indicates that the results of indoor crate grazing can be extended to field grazing with confidence under similar sward conditions, at least in terms of short-term behaviour. However, a thorough training of animals to indoor facilities and procedures is necessary.

Average recovery	Range of values	S.e.	Stock	Reference
• • •				
0.95	0.85-1.08		Cattle	Stobbs (1973a)
0.98		0.105	Sheep	Rodriguez Capriles (1973)
0.98		0.108	Cattle	Rodriguez Capriles (1973)
0.97		0.025	Calves	Jamieson (1975)
0.98		0.014	Calves	Jamieson and Hodgson (1979a)
0.94 (corrected)	0.60-1.12	0.012-0.132	Sheep	Burlison (1987)
1.32 (uncorrected)	0.76-1.98	0.06	Sheep	Current work
0.96 (corrected)	0.42-1.48	0.03	Sheep	Current work

 Table 7.9
 Comparison of recovery coefficients in the current trial with data withdrawn from the literature.

\* All values of previous work quoted in this table were not corrected for saliva contamination except for where it is indicated.

Forages	Maturity stages	Average recoveries	Ranges	S.e.
Ryegrass	Vegetative	1.09	1.05-1.15	0.09
, ,	Reproductive	0.94	0.42-1.21	0.09
Cocksfoot	Vegetative	0.97	0.76-1.22	0.09
	Reproductive	0.84	0.70-0.95	0.09
Tahora white	Vegetative	0.96	0.75-1.18	0.09
clover	Reproductive	0.89	0.83-0.94	0.09
Kopu white	Vegetative	1.20	0.97-1.45	0.09
clover	Reproductive	0.76	0.64-0.85	0.09
Average		0.96	0.42-1.45	0.03

 Table 7.10
 Recovery coefficients after saliva contamination was corrected.

## 7.5 CONCLUSIONS

- This experiment strongly corroborated the trends displayed and the relationships ascertained in Experiment 1 (Chapter 5) regarding the effects of the treatments (main effects and interactions) on bite variables.
- There is no conclusive evidence to indicate that fistulation at the oesophagus will significantly modify the grazing behaviour of animals, and particularly this is the case when the comparison is made between fistulated and intact animals with similar management history, nutritional background and body conditions.
- 3. It is appropriate to extrapolate the results of indoor crate grazing to field grazing, and this is reliable at least based on short-term behaviourial responses.
- Saliva contamination of extrusa samples can result in significant overestimates of recovery coefficients for the fistulated animals, and hence a correction for saliva contamination is required.

## Chapter 8

## **General Discussion and Conclusions**

This chapter considers links and relationships between the three experiments conducted in this project, and briefly discusses some aspects of experimental procedures, including the use of multivariate techniques in analyzing data. Then the focus is concentrated on a summary and a comparison (where appropriate) of the main results drawn from the three experiments. The major findings are considered within the framework of existing knowledge of animal responses to variation in sward structure. Where appropriate more emphasis is placed on sheep/goat contrasts, and on grass/legume contrasts as well, since these are the important features of this project. Finally, an account of applications and recommendations for grazing management is made in terms of the present results.

## 8.1 LINKS BETWEEN THE THREE EXPERIMENTS CONDUCTED IN THIS PROJECT

Three experiments (summarized in Table 8.1) formed the basis of this thesis, including two sub-sets of data (restricted and enlarged data sets) drawn from Experiment 1. This section briefly summarizes these experiments and explains linkages between them.

The restricted data set of Experiment 1 involved four forages grazed by two species at two maturity stages across the two experimental years (4 forages x 2 stages x 2 animal species x 2 years). It was intended to assess the effects of animal characteristics on ingestive behaviour. Analysis of this data set using a data adjustment approach showed that incisor arcade breadth had a stronger functional relationship with bite weight and bite dimensions than did liveweight over the two experimental years. It was concluded that increases in bite weight and bite dimensions with increasing maturity of animals were possibly ascribable to increases in incisor breadth of animals over the time. It was also suggested that the difference in incisor

Data sets or experiments		Experimental periods	Forages* (levels)	Maturity stages	Height levels for each forage or stage	Animal species	Animal type	Animal reps of each species	Technique
1.	Restricted data set of Experiment 1	2 (1989, 1990)	4	2 (vegetative and reproductive)	1	2 (sheep and goats	1 (NOF)	6	Indoor
2.	Enlarged data set of Experiment 1	1 (1990)	9	2 (vegetative and reproductive)	1	2 (sheep and goats)	1 (NOF)	6	Indoor
3.	Experiment 2	1 (1990)	4	1 (vegetative)	5 for grasses, 3 for Tahora, 2 for Kopu	2 (sheep and goats)	1 (NOF)	4	Indoor
4.	Experiment 3	1 (1990-1991)	4	2 (vegetative and reproductive)	1	1 (sheep)	2 (OF & NOF)	4	Indoor and outdoor

**Table 8.1** Summary and comparison of experimental designs among the three experiments.

\* Forages used in restricted data set: ryegrass, browntop, Tahora and Kopu white clovers; in enlarged data set: ryegrass, browntop, cocksfoot, prairie grass, phalaris, Tahora white clover, Kopu white clover, red clover and *Lotus corniculatus*; in Experiments 2 and 3: ryegrass, cocksfoot, Tahora and Kopu white clovers. Details of each forage are referred to Appendix 3.1 and the corresponding chapters.

NOF: non-oesophageal fistulated sheep; OF: oesophageal fistulated sheep.

breadth between sheep and goats was one of the factors resulting in the differences between the two species in bite weight, bite depth and bite volume.

The enlarged data set of Experiment 1 was used to compare and to examine grazing responses of sheep and goats to variation in sward structure induced by use of nine forages sampled at two stages of maturity for each forage over one experimental year. Following the preliminary analysis by ANOVA, the data set was assessed by means of a number of multivariate approaches. It was found that among the set of measured sward attributes sward height was the most important variable affecting grazing behaviour in general, although this applied for grasses more than legumes. Since the variation in sward height was principally created by differences between forages and between stages of maturity, it was assumed that the effect of sward height demonstrated in this data set could have been associated with and confounded with the variation in other plant characteristics (e.g. growth habit) across forages and stages of maturity.

Experiment 2 was designed to dissociate the effects of sward height from the above confounding effects by creating contrasting heights within a forage, and by sampling vegetative swards only. This data set involved four forages with height contrasts for each forage, all grazed by sheep and goats. A screening by MANOVA showed that sward height and bulk density were more important than other sward variables in discriminating the variation of the set of sward attributes. Independence of variation in sward height from other attributes, particularly bulk density, was successfully achieved in some swards, but failed in others. It was confirmed that animal responses were more sensitive to variation in sward height than in bulk density. However, the influence of bulk density on ingestive behaviour after the dominant effect of sward height was accounted for depended very strongly upon the animal species, sward types (grasses or legumes) and the establishment of independent variation in sward height and bulk density over the range of test swards.

An indoor crate grazing technique was employed in Experiments 1 and 2. In Experiment 3 an outdoor cage grazing technique was used to validate the observation of indoor procedures and to assess the comparability of the results between indoors and outdoors. Outdoor cage grazing involved the use of oesophageal fistulated animals so as to determine the amount of herbage harvested by animals over short-term grazing sessions (12-15 bites). Fistulated sheep were also compared with intact
sheep using the indoor metabolism crate grazing technique. The results showed high comparability and conformability between indoor and outdoor grazing procedures and between fistulated and intact sheep, in terms of behaviour variables observed on a short-term basis. The applicability of these results to free grazing will be considered in Section 8.2.

### 8.2 EXPERIMENTAL PROCEDURES

This research focused on short-term responses of grazing animals using an indoor crate grazing procedure, which was validated by an outdoor cage grazing technique.

Bite overlap has often been a problem hampering attempts to measure bite dimensions in grazing studies. Overlap in the vertical dimension alters the frequency distribution of residual heights of the average bite and will therefore alter the computed mean bite depth (Ungar et al., 1991). Similarly, overlap in the horizontal plane results in an underestimation of bite area. In this project, overlapping between bites was minimized by preventing further grazing once 12-15 bites were made. The chance of overlapping was very low because animals usually prefer to graze fresh places before they regraze the previously grazed area (Ungar et al., 1991). There was no evidence that bite overlap was significant enough in this study to be an important source of error. However, allowing 12-15 bites only was a compromise because a larger number of bites would probably have led to a greater accuracy of bite weight estimate.

The animals used in this project were fasted for approximately eighteen hours prior to grazing, and were then allowed to make 12-15 bites from the extracted turf (indoors) or the defined patch in the plots (outdoors). It is logical to assume that the animals would have been hungry and hence attempting to maximize bite weight and bite rate within the limitations imposed by sward conditions (Burlison, 1987). Some studies have shown that bite weight or biting rate or intake rate increase after fasting (Sidahmed et *al.*, 1977; Jung & Koong, 1985). Greenwood and Demment (1988) found that cattle fasted for 36 h had higher intake rates than unfasted animals, but that this was achieved by an increase in rate of biting. There also has been criticism (Penning, cited by Illius, pers com.) that starving animals biases estimate of intake rate, and possibly other behaviour variables. However, Dougherty et *al.* (1989a) estimated the effects of 1, 2 and 3 h fasts, using cattle grazing vegetative swards of tall fescue and

lucerne, and found that the effects of fasting were not always significant and also varied with types of swards. It was shown (Dougherty *et al.*, 1989a) that lengthening interval between meals of cattle grazing lucerne resulted in higher rates of intake during the following grazing session and had no effect on ingestive behaviour the next day. In contrast, lengthening interval between grazings on tall fescue had little immediate effect on rates of intake but depressed rates of intake during a grazing session 24 h later (Dougherty *et al.*, 1989a).

Nevertheless, the following two facts give confidence in estimates of bite variables in the current project despite the use of fasted animals. (1) The range of values for bite weight, biting rate, and intake rate from the current project broadly lay within the ranges reported in, or derived from other experiments. (2) In studies where fasting effects on bite weight and biting rate were identified, it was recognized (Burlison, 1987) that bite weight and biting rate were influenced more by sward canopy structure than by fasting. Nevertheless, it is suggested (Illius, pers com.) that in experiments examining short-term behaviour, it may be worthwhile to provide animals with sufficient swards for about thirty minutes grazing immediately prior to sampling to try to take the edge off animals' appetites and allow them to settle down to steady grazing.

Indoor crate grazing used in this project has been shown to be an efficient technique to observe short-term grazing responses. This technique is similar to those used by Burlison *et al.* (1991) (field cage grazing), and by Mursan *et al.* (1989) (indoor pen grazing). In terms of defining responses in bite weight and bite dimensions to variation in sward structure this technique has proved to be much more successful and useful than conventional, large scale grazing trials (Burlison *et al.*, 1991). Studies on a short-term basis would allow behavioural responses of animals to be related specifically to the characteristics of the swards grazed, avoiding the complication of trampling, treading and fouling (Mursan *et al.*, 1989; Burlison *et al.*, 1991). This approach can also avoid the effects exerted by daily and social behaviour activities such as ruminating, idling and socializing, and permit the observer to concentrate on the eating behaviour variables like bite weight and bite dimensions (Cosgrove, 1992). This technique enables bite dimensions to be measured more accurately and grazing activities to be observed and recorded closely.

In contrast to field cage grazing (Burlison *et al.*, 1991), indoor crate grazing in the current study involved use of extracted turves, instead of plot patches. This provided a means of characterising swards in the laboratory in more detail and under close control, and estimating the herbage mass removed over a short interval directly through weighing turves pre- and post-grazing without surgical modification of animals (Mursan *et al.*, 1989). Since insensible loss of turf weight over this short duration examined in a turf tray set aside for the purpose of control was found to be negligible (see Section 3.2.5.2 of Chapter 3) the turf technique provided confidence in the accuracy of bite weight estimation. Also, it was easier to make detailed sward measurements in the laboratory than in the field, particularly for a technique like the point-quadrat which can be hampered by wind.

The close agreement in ingestive behaviour between indoor crate grazing and outdoor cage grazing in Experiment 3 (Chapter 7) provides evidence that indoor results could be reliably extrapolated to field grazing on a short term response basis. However, there is an apparent contradiction in the literature as to the validity and certainty of extrapolating short-term responses to free grazing. Penning et al. (1991) claimed that this may not be acceptable. Fisher et al. (1987) argued that estimates of rates of intake established over short intervals are of limited value since grazing time per day is not estimated. Conversely, Hodgson (1981a) suggested that short-term rates of intake may reflect daily intake since the lengthening of grazing time rarely compensates fully for low rates of intake. Similarly, Leaver (1987) considered that the relative inflexibility of grazing time means the rate of intake is the major factor determining daily intake. On the other hand, because drastic and complex changes in the quantity and quality of ingested herbage and in grazing behaviour occur as swards are grazed down (Burlison, 1987; Dougherty et al., 1990), Dougherty et al. (1990) suggested that simulation models of grazing systems may be best served by 24 h time-steps, rather than by shorter intervals, as suggested by Elsen et al. (1988).

Apart from the differences mentioned earlier between short-term grazing and free-grazing (socializing, resting and ruminating etc.), some other contrasts involved may be of concern as follows:

In short-term grazing the confined animals are allowed to have a limited access to mini-swards. This may reduce grazing skills (Flores *et al.*, 1989), and result in different motivational states (Laca *et al.*, 1992b)

compared to the animals continuously stocked on pastures for freegrazing. Consequently, animals might graze rapidly, in anticipation of sudden removal of feed (Mitchell, 1993).

(2) Short-term biting rate tends to be overestimated, especially on swards that enable great bite weights to be achieved (Forbes, 1988). Since the intake rate declines as grazing progresses (Dougherty *et al.*, 1989b) it is thought that behaviour measured over short durations is representative of the beginning of grazing bouts (Laca *et al.*, 1992b), and hence usually is more comparable with maximum or potential intake rates under freegrazing.

Although the above differences exist, the more important traits of grazing behaviour and key relationships between responses of animals and influences of sward characteristics identified in short-term responses, would be comparable or relevant to free-grazing. It seems reasonable that the major goals of short-term grazing would be to facilitate development of principles in mechanistic terms, whereas quantitative applicability to free-grazing conditions might be of secondary importance. However, the use of naturally field-grown swards to maximize representativeness for naturally grazed pastures should provide an opportunity to increase the reliability of extrapolation of short-term results to free-grazing.

However, in using confined grazing techniques, it is crucial to get animals thoroughly trained and accustomed to experimental procedures, otherwise the results may be biased. After an intensive training programme and a preconditioning run prior to each experiment (see Sections of 3.2.2 and 3.2.3 of Chapter 3) this was achieved in the current experiments.

## 8.3 APPRAISAL OF USE OF THE MULTIVARIATE APPROACHES IN THIS PROJECT

Multivariate analysis of variance (MANOVA) and multivariate discriminant function analysis (MDF) were used in analyzing the enlarged data set of Experiment 1 (Chapter 5) to define the overall significance level of the combination of all variables considered among the treatments and to discriminate between the treatments in terms of the combinations of these variables. This is unlike univariate analysis, which examines the significance of single variables one by one among the treatments. As mentioned before (Section 5.2.1 of Chapter 5), if covariances or correlations exist between two or more variables within any set of variables, it would be worthwhile and appropriate to use multivariate analysis in order to take them into account, otherwise the results revealed by univariate analysis are biased (Cooley & Lohnes, 1971). Comparison between ANOVA and multivariate approaches will be made in this section to illustrate advantages of multivariate techniques over ANOVA.

(1) In the enlarged data set of Experiment 1 (data set of Chapter 5), there was an association between at least some of the variables within either the set of ingestive behaviour variables or the set of sward attributes (Appendix 5.5 of Chapter 5). The general presence of significant inter-correlations in these data sets indicates the need to use multivariate analysis to make allowance for them.

For example, ANOVA (Table 5.8) indicated that, on average over all swards (9 forages x 2 stages) on offer, sheep and goats did not differ significantly in bite weight in either fresh or dry matter terms. Multivariate analyses (Table 5.19) showed that the net score of sheep was much higher than that of goats. As interpreted in Section 5.3.3.2.1 of Chapter 5, this implies that when a wide range of swards were provided, sheep usually obtained a large bite weight through penetrating very deeply into swards with low dry matter content; conversely, goats usually obtained large bite weights through browsing in swards with high dry matter content. Thus, it is evident that one of the important features differentiating sheep and goats in grazing behaviour was a different response in relation to fresh or dry matter descriptions of bite weight, in contrast to that of ANOVA.

(2) The second advantage was to allow clear-cut patterns to be established with respect to the levels of experimental factors (levels of main effects or interactions) after all considered variables were jointly taken into account. This approach provided a more efficient understanding of the issues concerned in contrast to looking at variables individually.

For instance, given the interaction between animal species and forages, ANOVA (Table 5.10) only illustrated a trend of individual

variables with respect to eighteen combinations of this interaction (2 animal species x 9 forages). The MANOVA (Table 5.19 and Fig. 5.7) revealed a general pattern and showed that in terms of the combined behaviour variables these eighteen combinations fell into five clusters (Fig. 5.7C). More clear-cut patterns of variation were also demonstrated in other cases (Sections 5.3.3.2.1-5.3.3.2.3 of Chapter 5).

(3) The third advantage was to allow screening of the important sequence of a range of variables when they were jointly considered. ANOVA does not provide such a function.

For instance, responses of animals to variation in sward structure were unequal in importance, and this was clearly indicated by multivariate analyses (standardized coefficients in Table 5.19), but not by ANOVA. Bite area was a much less important variable compared to others in responding to swards on offer (Table 5.19), whereas bite depth and bite weight were much more important than others. This indicates that the depth of penetration and amount of herbage harvested per bite were more appropriate than bite area to discriminate maximally among the treatments, when considering all variables and their covariances within the data set.

From the above discussion, although the results of ANOVA are useful, they are less effective than multivariate approaches. There were autocorrelations between variables (Appendix 5.5); those variables which are highly correlated with others are not pure (Douglas, 1991) and do not give clear information because of their non-independence. Hence, results of ANOVA should be interpreted cautiously (Cooley & Lohnes, 1971).

This research demonstrates the usefulness of multivariate approaches in the analyses of data and interpretation of the results. These approaches are particularly valuable and necessary under circumstances where there is correlation or covariance among the variables.

### 8.4 SWARD CONDITIONS

Sward structure is a function of the height, bulk density, mass, botanical

composition and morphology of herbage and the distribution of the various components through the canopy profile. Some previous research involved use of either swards which were naturally grown in the field ("natural field swards"), with an inevitable heterogeneity in structure (Forbes, 1982; Milne *et al.*, 1982; Penning *et al.*, 1991a & b; Arias *et al.*, 1990; Wade, 1991; Dougherty *et al.*, 1992) or swards which were artificially constructed ("artificial mini-swards") (Black & Kenney, 1984; Kenney & Black, 1986; Ungar *et al.*, 1991; Laca *et al.*, 1992a & b). Additionally, Mitchell *et al.* (1991) used highly standardized tray-grown monoculture swards ("standardized mini-swards").

The evidence from these studies has been used to define some important principles involved in the relationships between grazed swards and grazing animals. However, each of the techniques has its advantages and drawbacks, as outlined below.

Generally, high heterogeneity, poor uniformity, and high association between attributes in natural field swards confound or mask to some extent the relationships of animal responses to particular key sward variables, but the condition of these swards would be more representative of the considerable complexity in natural pastures normally encountered by grazing animals at farm level. "Artificial mini-swards" enable a high degree of control of individual sward attributes and a level of detail in measurements that cannot be achieved in natural field swards by field techniques (Laca *et al.*, 1992a). This technique and the technique of "standardized mini-swards" (Mitchell *et al.*, 1991) allow a wide range of simultaneous and independent combinations between height and other sward attributes (such as bulk density, mass and digestibility etc.) to be achieved in a single experiment, as well as controlled introduction of other vertical and/or horizontal heterogeneity (Laca *et al.*, 1992b).

These highly controlled and simplified swards (artificial and standardized miniswards) have been proved to be very useful for defining the patterns of animal responses to particular key sward attributes, but would be less reliable in terms of the confidence and validity of extrapolation of the results to a real grazing situation. In addition, since the techniques for hand-construction of swards are extremely labourintensive, there will be a limitation to the number of replications, treatment combinations and animal species comparisons (Mitchell, 1993) unless a large working team is available. Like natural field swards, both "artificial and standardized miniswards" also tend to result in some degree of height-density autocorrelation (Laca *et al.*, 1992a & b; Mitchell, 1993).

Most of the above studies (Black & Kenney, 1984; Arias *et al.*, 1990; Burlison *et al.*, 1991; Ungar *et al.*, 1991; Mitchell *et al.*, 1991; Wade, 1991) focused on grasses. Because of the differences in agronomic characteristics and growth habit between grasses and legumes, some principles revealed for grasses may not apply to legumes, and *vice versa*. This indicates the need for comparison between grasses and legumes.

As a result of the above factors, the relationships demonstrated in these studies are limited in their contribution to a better and thorough understanding of grazing in terms of a wide range of complexity of grazing operations.

The current project was intended to achieve a compromise and a balance between "natural field swards" (Forbes, 1982; Milne et al., 1982; Wade, 1991; Penning et al., 1991a & b; Arias et al., 1991), and "artificial (Black & Kenney, 1984; Laca et al., 1992a & b) or standardized swards" (Mitchell et al., 1991). It involved use of five grasses and four legumes sampled at two stages of maturity for each forage (Experiment 1), of two grasses and two legumes sampled at various heights for each forage (Experiment 2), and of two grasses and two legumes sampled at two maturity stages for each forage (Experiment 3). All these forages were naturally grown in plots as monospecific swards and no attempt was made to standardize swards through trimming prior to being grazed. These may be called "natural mini-swards" to distinguish them from the above alternatives: "natural field swards", "artificial swards and standardized mini-swards". These swards, on one hand, could be widely encountered within the ranges used by animals at the farm level. But on the other hand, they also had a certain degree of uniformity and homogeneity in structure and a certain degree of dissociation between the key sward attributes. This offered a better opportunity to examine the responses to diverse stimuli such as forage species, stage of maturity and variation in height.

The use of a wide range of swards with contrasting growth form (see Appendix 3.1 for description of these forages), coupled with grazing by two animal species simultaneously, offered a number of advantages. Most earlier studies (Milne *et al.*, 1982; Black & Kenney, 1984; Arias *et al.*, 1990; Mitchell *et al.*, 1991; Dougherty *et al.*, 1992) focused on the relationships between swards and animals at the level of single

effects. The interactions between animal species and sward types (stage of maturity, herbage categories and height classes) dealt with in this project have allowed some important response patterns to be defined under different circumstances. These interactions covered a wide range of grazing situations, and extended the results demonstrated in the above alternatives (Milne *et al.*, 1982; Black & Kenney, 1984; Arias *et al.*, 1990; Mitchell *et al.*, 1991; Dougherty *et al.*, 1992).

Although a number of sward attributes were measured or derived in this research, multivariate analyses consistently showed sward height and bulk density to be the most important parameters defining sward variation, and influencing grazing behaviour. This indicates their value as key attributes to quantify sward characteristics and to relate to the ingestive behaviour of grazing animals. Under reasonably uniform conditions, in order to reduce the number of sward measurements and to simplify the sward description, it would probably be acceptable to reduce the complex of sward characteristics to these two key attributes.

#### 8.5 COMPONENTS OF INGESTIVE BEHAVIOUR

Values of bite variables from Experiments 1 and 3 are highly comparable, and those from Experiment 2 fell within the range of values in Experiment 1. Values for sheep broadly fitted results from previous work, but there is no comparable information available for goats.

The responses of sheep and goats to the variation in sward structure, particularly those derived from multivariate analyses, showed clear trends: some response variables were more sensitive than others, the animals usually responded in combinations of behavioural components collectively, rather than by adaptation of single variables, and a number of behavioural variables showed consistent responses across several swards. For example, biting rate, bite depth, bite volume and bite weight responded to increasing sward height irrespective of sward types and of animal species. However, each animal species and each response variable had its own traits and patterns, as outlined below.

#### 8.5.1 Bite dimensions

#### 8.5.1.1 Bite depth

All three experiments reinforced the importance of bite depth in influencing bite weight, especially in grasses, in agreement with other reports (Black & Kenney, 1984; Mursan *et al.*, 1989; Ungar *et al.*, 1991; Mitchell *et al.*, 1991; Mitchell, 1993; Laca *et al.*, 1992a). The consistency of the bite weight/bite depth relationship across experiments suggests that the great variation within the ranges of test sward characteristics used resulted in little difference between studies in the key relationships of bite variables. On tall swards, although the density of herbage in the upper horizons might be low (Stobbs 1973a & b, 1975b), and mouth dimensions may restrict the cross-sectional density of herbage prehended per bite (Burlison, 1987), large bite weights should still be readily achievable by deep penetration (Mitchell, 1993).

A positive linear relationship between bite depth and surface height held for both sheep and goats in Experiments 1 and 2. Although regression relationships were not examined in Experiment 3, the data (Tables 7.3 and 7.6) clearly indicated a similar trend. The relationship was stronger for grasses than for legumes. The slope of the height term in grasses varied from 0.505 to 0.822 for sheep, and from 0.610 to 0.937 for goats (Section 5.3.4.2, and Tables 6.8 and 6.9). Clearly the slopes from Experiment 2 (Tables 6.8 and 6.9) fell within the range of variation of Experiment 1 (Section 5.3.4.2). The results obtained from this project are broadly comparable to studies for sheep grazing ryegrass/white clover pastures (Milne *et al.*, 1982), grazing a range of grass and/or oat swards (Burlison, 1987), cattle on hand-constructed paspalum swards (Ungar *et al.*, 1991; Laca *et al.*, 1992a), and cows on natural ryegrass pastures (Wade, 1991). This suggests that the positive linear functional relationship between sward height and bite depth is relatively stable across different grazing situations.

However, the proportion of herbage length removed in relation to sward height shows a great variation across different studies (Table 8.2). This suggests that despite a general linear relationship, the rate at which bite depth increased with increasing sward height varied in different studies.

Wade (1991) found that when cattle grazed ryegrass pastures across a range of heights and two grazing regimes, grazed depth was almost consistently between 0.30 and 0.40 of the mean extended tiller height over successive grazing days,

References	Sward types	Height (cm)	Animal species	Ratios	Experimental design
1. Milne <i>et</i> a <i>l</i> . (1982)	grasses containing different proportions of white clover	5.1-11.1	Sheep	0.33	field swards
2. Wade (1991)	ryegrass	4-12.7	Cattle	0.30-0.40	field swards
3. Mursan <i>et</i> al. (1989)	ryegrass	5-15	Cattle	0.50-0.57	mini-swards
4. Burlison <i>et</i> al. (1987)	grasses and oats	5.7-55.2	Sheep	0.19-0.36	cage patches
5. Laca <i>et</i> a <i>l.</i> (1992a)	paspalum	8-30	Cattle	0.55	constructed swards
6. Laca <i>et</i> al. (1992a)	lucerne	7-25	Cattle	0.48	constructed swards
7. Hughes <i>et</i> al. (1991)	ryegrass	5-15	Sheep	0.39-0.46	mini-swards
8. Ungar <i>et</i> a <i>l</i> . (1991)	paspalum	4-10	Cattle	0.45-0.64	constructed swards
9. Mitchell (1993)	ryegrass	9-12	Sheep	0.44-0.53	mini-swards
10. Mitchell (1993)	wheatgrass	3-13	Sheep	0.70	mini-swards
11. Experiment 1 of current project	5 grasses	21.8-70.4	Sheep	0.41-0.63	mini-swards
	5 grasses	21.8-70.4	Goats	0.33-0.60	mini-swards
	4 legumes	11.1-36.6	Sheep	0.35-0.50	mini-swards
	4 legumes	11.1-36.6	Goats	0.21-0.35	mini-swards
12. Experiment 2 of current project	2 grasses	7.8-29.6	Sheep	0.50-0.66	mini-swards
	2 grasses	7.8-29.6	Goats	0.44-0.65	mini-swards
	2 legumes	5.4-13.7	Sheep	0.49-0.65	mini-swards
	2 legumes	5.4-13.7	Goats	0.24-0.45	mini-swards
13. Experiment 3 of current project	2 grasses	12.4-47.8	Sheep	0.45-0.68	mini-swards
	2 legumes	8.5-22.6	Sheep	0.33-0.50	patches

**Table 8.2**Comparisons of ratio of bite depth to sward height between the current research<br/>and the data drawn from previous work.

irrespective of pre-grazing height. A similar ratio was also derived from the work of Milne et al. (1982) using sheep grazing ryegrass/white clover pastures. In highly controlled swards (Ungar et al., 1991; Laca et al., 1992a; Mitchell, 1993), the ratio is usually higher than this, the highest proportion recorded being 0.70 (Table 8.2). This suggests that the grazed residual height increased more rapidly with increasing sward height on natural pastures (Milne et al., 1982; Wade, 1991) than on highly controlled swards (Ungar et al., 1991; Laca et al., 1992a; Mitchell, 1993). Mitchell (1993) attributed this lower proportion of herbage length removed on natural pastures to a marked accumulation of pseudostem and dead material in the basal strata. Because animals prefer leaf tissue over stem tissue (Chacon & Stobbs, 1976; Dougherty et al., 1990), the rigid pseudostem and low guality material near the basal horizon in natural field swards would make grazing more difficult and unpleasant (Cosgrove, 1992; Barthram & Grant, 1984; Mitchell, 1993), and hence animals would have to reduce depth of penetration. In contrast, highly controlled swards (Ungar et al., 1991; Laca et al., 1992a; Mitchell, 1993) are free from dead matter and display little vertical heterogeneity. This would allow animals to be able to penetrate into the canopies deeply with ease, leading to a higher proportion of herbage length being removed. In the current study the ratio of bite depth to sward height fell within the above range of variation (Table 8.2) for both sheep and goats grazing grasses, and for sheep grazing legumes. But this ratio could be lower than 0.30 sometimes when goats grazed legumes (Table 8.2). This lower ratio was a consequence of shallow grazing behaviour of goats, especially when legumes were offered (see Section 5.4.3 of Chapter 5). Also, in the present study, this ratio generally increased with increasing sward height, suggesting that the grazed residual height increases relatively slowly compared to the increase in sward height.

Pseudostem height has been established as a barrier to grazed depth of vegetative ryegrasses (Barthram & Grant, 1984; L'Huillier *et al.*, 1984) and tall fescue (Arias *et al.*, 1990; Dougherty *et al.*, 1992). Arias *et al.* (1990) concluded that animals avoided grazing the basal stratum of tall fescue where pseudostems were present, and the grazed horizon was limited to the tissue above a plane established by the tops of pseudostems, except where the pseudostem material was "immature and small" (Dougherty, 1991). In the current experiments sheep were capable of penetrating below the leaf layer and reaching the pseudostem horizon when swards were short

(Section 6.4.2.1 of Chapter 6, Tables 6.3-6.5). Sheep also pushed into the canopies below the seedhead and stalky horizon when grazing tall reproductive swards (Chapters 5 and 7) to avoid rigid components and to select leafy components. Therefore, horizons containing pseudostem and stalk appeared to have little effect on the depth to which sheep could penetrate, despite the fact that these rigid components led to a reduction in the amount of herbage harvested per bite because of selective grazing. Goats hardly reached the pseudostem horizon (Section 6.4.2.1 of Chapter 6, Tables 6.3-6.5), but this was ascribable to their shallow grazing habit, rather than to deliberate avoidance of pseudostem.

There is no such well-distinguished morphological barrier in legumes and the grazed horizon appears to be determined by the location of the fracture point when petioles or stems are severed (Dougherty *et al.*, 1990).

Experiment 2 showed that bulk density generally had only a minor effect on bite depth. In Experiment 1 (Table 5.27), the effect of bulk density on bite depth was significant in some cases, but usually was much less important than sward height. This suggests that a positive relationship between bite depth and sward height would appear to be widely held. The small negative effect of bulk density on bite depth could usually be ignored, especially in practical terms, supporting the arguments by Laca *et al.* (1992a) and Mitchell (1993).

#### 8.5.1.2 Bite area

This research clearly indicated that there was no statistically significant functional relationship between bite area and either sward height or density. This suggests that generally, the ability of animals to adjust bite area in response to variation in sward conditions is limited, in agreement with Mursan *et al.* (1989); Hughes *et al.* (1991); Burlison *et al.* (1991) and Mitchell (1993).

It was suggested that if sward conditions permit, animals use their tongue (cattle) (Laca *et al.*, 1992a) or lips (sheep and goats) (Section 6.4.2.2 of Chapter 6) to gather herbage, and also move the head in a horizontal plane (Burlison, 1987) to harvest a greater number of leaves, leading to an increase in their grazing efficiency. Hence, the gathering extent of tongue or lips together with the gape of the animals' open mouth determines the total area encompassed by a bite. This may explain why bite area appeared to increase sometimes with increasing sward height, despite an

insignificant functional relationship. However, it was considered that the size of the animal's fully open mouth has a significant constraining effect on bite area (Mitchell, 1993) since gathering with lips and tongue and horizontal movement of the head would only extend bite area to a limited degree. This further explains why there is a plateau in bite area with increasing sward height (Mitchell, 1993) and why the extent to which animals maintain bite weight by increasing bite area as sward conditions worsen is limited (Section 4.4.3 of Chapter 4, Section 5.4.3 of Chapter 5). Also, on the tall swards, the extent to which the animals could extend bite area by lips or tongue and head movement was much less than the amplitude of vertical penetration. This may explain why the proportionate variation in bite area was much smaller than that in bite depth, and also, at least partially, why there were only limited functional relationships between bite area and any sward variables (Section 6.4.2.2 of Chapter 6).

In Experiments 1 and 3, bite area decreased sometimes (Tables 5.11 & 5.12; Tables 7.3 & 7.6) with increasing forage maturity, especially in grasses. This might be associated with rigidity and toughness of tillers, which increase with plant maturity (Hodgson, 1990). Demment *et al.* (1992) showed that on swards with tough reproductive stem in the basal layers, bite area was related to leaf layer depth rather than to surface height, suggesting an apparent effect of tiller flexibility on bite area. Hughes *et al.* (1991) found that peak bite force increased with sward surface height, and bite area was limited by peak bite force on 5 and 10 cm swards. This suggests that when animals encounter rigid tillers they have difficulty gathering and harvesting herbage because of peak limitation to bite force, and hence bite area is constrained.

Although there was no statistically significant functional relationship to be found between bite area and bulk density in the current study, animals still reduced bite area to some extent as bulk density increased under certain circumstances (Tables in Appendix 5.5 and Table 6.7). This might also have been a consequence of reductions in the extent of mouth opening and in the extent of gathering by lips and head movement because of the limitation to bite force (Hodgson, 1985; Hughes *et al.*, 1991).

As tiller structural strength and bulk density increase, although animals are likely to attempt to increase biting effort so as to maintain bite weight, they have to reduce bite area at a rate which prevents biting effort increasing excessively (Mitchell, 1993). Optimal foraging theory (Stephens & Krebs, 1986) suggests that animals would seek to optimize energy intake relative to energy expended in the process of grazing, and would cease grazing when energy costs equal or exceed energy intake.

The much smaller response in bite area than in bite depth to variation in sward characteristics was reinforced in all three experiments. This is in agreement with the observations of Mursan *et al.* (1989), and Hughes *et al.* (1991). Therefore, bite depth was a major spatial component of bite volume and the relationships of bite volume with sward characteristics largely reflected those of bite depth.

A far lower sensitivity of bite area than bite depth may also explain, at least partially, why increasing incisor arcade breadth with increasing maturity of animals allowed both sheep and goats to increase bite weights through increases in bite depth, rather than bite area (Chapter 4). Logically, increases in incisor arcade breadth would be expected to exert more effect on bite area than on bite depth. The explanation for this apparent contradiction may be outlined as below.

Because proportional variation in bite depth with changes in sward conditions is much greater than that in bite area, the most efficient way to increase bite volume, and hence bite weight would be to take deeper bites, rather than to encompass greater area. Therefore, any increases in harvesting ability with increases of animal maturity should reflect the capability for taking deep bites. Similarly, any variation in canopy characteristics leading to increases in bite weight should operate through influence on bite depth more than on bite area, particularly when sward height does not impose significant restriction to penetration. Increase in incisor breadth with increasing maturity enables animals to expert greater force to sever herbage deeper, despite a relatively small increase in cross-sectional area encompassed by a bite. On tall swards, animals with greater incisor breadth do encompass a larger bite area, but they must also sever herbage more deeply, than animals with small mouths. Consequently, the greater an animal's incisor breadth, the taller the herbage it should require to maximize bite area (Mitchell, 1993) and bite depth. This supports the argument (Illius & Gordon, 1987) that large animals must experience relatively greater restriction in bite depth on short swards than small animals, and small animals can subsist on short swards better than large animals.

However, as outlined in Chapter 4, it should be borne in mind that increase in bite depth with increasing incisor breadth (Chapter 4) might not necessarily be a direct causative effect of incisor breadth *per se*, but rather a result of combined effects of

increases in body size, body weight, buccal cavity, mouth dimensions, eating ability and prehension power. All these properties are related to an increase in incisor breadth, but incisor breadth may not be a monotonic effect. The reason for stronger functional relationship for incisor breadth than liveweight with ingestive behaviour might be due partially to the smaller fluctuation and less sensitivity of incisor breadth to external and nutritional effects.

### 8.5.2 Bite weight and bite rate

Experiment 2 demonstrated a positive relationship between bite weight and sward height, and this relationship also held in most cases in Experiment 1 (Table 5.26). Fig. 8.1 illustrates the linear relationships between bite weight and sward height among the three experiments. A t-test showed that both intercept and slope of equation 1 were different at a level of P<0.01 from all the other equations derived from grasses (equations 2-5), which were similar. Also, equation 6 was significantly different from equation 8 (intercept, P<0.05, slope, P<0.01), but not significantly different from the others (equations 7, 9 and 10). The reason for this variation is given in the next paragraph. This positive linear relationship is largely because bite depth, which is a major determinant of bite weight, as noted before, was strongly affected by sward height.

However, there may be a poor functional relationship between bite weight and sward height when large differences in quality between herbage components lead to selective grazing in the vertical plane. This occurred in Experiment 1 of the current study when reproductive swards were grazed by sheep (equations 1 and 6 in Fig. 8.1), where the values of  $R^2$  were low. On both reproductive grasses and legumes of Experiment 1, although sheep penetrated into these tall swards very deeply, they selected leafy components and left stems or stalks and seedheads ungrazed (Section 5.4.3 of Chapter 5). This led to a difference between the linear relationships obtained from this experiment and others (Fig. 8.1). On these reproductive swards, the increases in bite weights of sheep with increasing sward height were significantly slower than on other swards (Fig. 8.1). A poor relationship between bite weight and sward height was particularly the case on tall tropical swards (Stobbs, 1974b; Chacon & Stobbs, 1976).

**Fig 8.1** Comparisons of linear relationships between bite weight (BW) and sward height (H) among the three experiments for the two species grazing grasses and legumes



The selective grazing resulting from tall reproductive swards suggests that the conceptual model that bite weight may be viewed as the product of bite depth, bite area and bulk density of the grazed strata (Hodgson, 1985) may only apply in the case of uniform swards in a vegetative or early reproductive stage of growth. In these swards animals graze largely indiscriminantly from the surface strata and significant slippage of plant components from the mouth during prehension does not occur. With more mature and taller swards, where a greater heterogeneity in sward structure and herbage quality exists in the vertical plane, there is a limitation in using this model. In this case, there is a need for more care and caution in an attempt to describe individual bites in terms of these components, substantiating the suggestion by Hodgson (1985).

Compared with sward height, bulk density of grasses generally shows less important effects on bite weight, and hence poorer functional relationships with bite weight (Tables 5.26, 6.7 - 6.10). This was largely because, as outlined earlier, both bite depth and bite area were weakly affected by bulk density.

There was a reciprocal response of bite weight and bite rate to variation in sward height. The positive relationship between bite weight and sward height was usually accompanied by a negative relationship between biting rate and sward height (Fig. 6.1  $D_1$ - $D_3$ ). This trend is in common with other studies (Chacon *et al.*, 1978; Hodgson, 1981a; Forbes, 1982; Dougherty *et al.*, 1988b; Penning *et al.*, 1991a; Mitchell, 1993; Illius *et al.*, 1992).

Intake rate is the instantaneous combination of bite weight and bite rate and will be dependent on the moderating effects of sward conditions on both bite weight and bite rate. The degree to which animals increase bite rate to maximize intake rate is limited because of the minimum number of jaw movements required to manipulate and process herbage for any sized bite (Demment *et al.*, 1992; Laca *et al.*, 1993). The findings from previous work showed that bite weight is the primary animal response variable and the major determinant of intake rate, and hence daily intake (Hodgson & Jamieson, 1981; Penning *et al.*, 1991a); biting rate and grazing time are negatively related to intake, and tend to increase as bite weight declines; however, the compensatory extent of biting rate and grazing time are limited and usually not sufficient to offset the decline in bite weight, and hence unlikely to maintain the level

of intake when bite weight declines sharply (Stobbs, 1973a; Hodgson, 1986). This appears to apply, in this study, only to vegetative swards.

When pastures are both mature and tall, intake rate may be penalized if animals spend more time manipulating and chewing large mouthfuls of mature herbage (Tables This indicates the existence of counteracting or non-monotonic 5.9 and 7.6). influences on intake rate. More mature herbage such as that from lower sward horizons (Cosgrove, 1992) requires more time for manipulating and processing from harvesting to swallowing (Ulyatt et al., 1982; Illius, 1986; Nelson, 1988; Dougherty et al., 1988b). In addition to the effects of maturity, a large mouthful of longer herbage also involves more manipulative jaw movements to draw all of the ingested material into the mouth (Burlison, 1987), as well as more chewing to reduce particle size before swallowing (Kenney & Black, 1984), leading to an increase in ratio of jaw movements of manipulating and chewing to prehension bites as swards became taller (Laca et al., 1992a). Consequently, the substantial increase in bite weight obtained from the more mature and taller pasture led to a greater fall in biting rate, and this fall could not be compensated for by the benefit from the increase in bite weight. This was particularly the case for sheep. Because goats have greater efficiency of chewing than sheep during eating in breaking down feed particles (Domingue *et al.*, 1991), and can swallow relatively large particles of coarse forages (Mitchell, 1985), the decline in bite rate occurred to a lesser extent than in sheep, despite a much greater increase in bite weight on mature and tall swards. Consequently, the fall in bite rate was not sufficient to penalize intake rate.

## 8.6 EFFECTS OF SWARD STRUCTURE ON GRAZING BEHAVIOUR OF ANIMALS

This study demonstrated that in general sward height is the most important variable influencing ingestive behaviour, and bulk density has much less important effects than sward height in this process, in line with the results obtained from other temperate pastures (Allden & Whittaker, 1970; Forbes, 1982; Mitchell *et al.*, 1991; Penning *et al.*, 1991a). However, the relative importance of the effects of bulk density and sward height varied, depending on pasture type and animal species, as outlined below.

In Experiment 1, bulk density was more important than sward height in influencing the combined set of behaviour variables when legumes were grazed by

sheep, as revealed by Canonical analysis (Chapter 5). This was also the case in determining individual behaviour variables (bite weight, bite depth) of sheep grazing legumes, as determined by multiple regression (Tables 5.26 and 5.27).

In Experiment 2, sward height always had a dominant effect, but bulk density had a statistically detectable effect on bite depth and hence bite volume when sheep grazed clover swards varying in height.

The reason for this difference between two experiments in the magnitude of the effects of bulk density on sheep grazing, and in the relative importance of bulk density and sward height, is unclear and can only be surmised as follows.

Experiment 2 involved use of swards varying in height created by sampling different heights within forage species, in contrast to Experiment 1 which involved use of swards varying in height created across forages and across stages of maturity. Thus, sward height was less confounded with other sward describers in Experiment 2 than in Experiment 1. This may have led to the greater expression of a sward height effect in Experiment 2 than in Experiment 1. Consequently, sward height was always more important than bulk density in Experiment 2. However, Kenney and Black (1986) used artificial leguminous swards involving different combinations of height and density, and still found that bulk density was more important than sward height in affecting sheep grazing. This apparent difference between Experiment 2 and Kenney and Black's work may reflect differences in nature and structure between artificial swards and field-grown swards. The former were of uniform height, and varied independently in height and density. The latter were heterogeneous in length of petioles and usually showed an association between height and density (Fig. 6.4C, and C<sub>2</sub>). Further experimentation would be required to clarify this issue. Nevertheless, both Experiments 1 and 2 confirmed that bulk density was more important in legumes than in grasses, especially for sheep grazing. The reasons for the greater effect of bulk density in legumes than in grasses have been given in Sections 5.4.2 and 5.4.4 of Chapter 5. In summary, herbage bulk density in grasses usually increases steadily from the top to the bottom of the sward profiles. Conversely, in legumes, the concentration of mass is greater within the upper strata than in lower strata, so sward height only affects readily prehensible material to a limited extent in legumes compared to grasses (Kenney & Black, 1986), leading to a less important effect of sward height in legumes than in grasses. Consequently, the effect of bulk density was more significant in legumes than in grasses.

All three experiments reinforced the observation that legumes usually resulted in smaller bite dimensions, but greater bite weights, especially when this parameter was on a fresh matter basis, and faster biting rate (not always attaining significance) than on grasses. In a study of sheep grazing pairs of swards varying in proportion of two botanical components, perennial ryegrass and white clover, and varying in sward surface height, Illius *et al.* (1992) reported that animals bit less deeply into a high clover content sward when the alternative sward was low in clover content, and *vice versa*, but maximum bite weight and intake rate were not achievable at low clover content despite a deep penetration. These differences between two types of swards were attributable to a number of factors, as discussed in Section 5.4.4 of Chapter 5. In summary, the reduced bite depth induced by legumes can be sufficiently compensated for by a higher density of material in the grazed stratum, a smaller effort required to harvest herbage and less plant components slipped out of the teeth.

Experiment 1, where nine forages were sampled at two maturity stages of growth, demonstrated that although both herbage categories (grasses and legumes) and maturity stages (vegetative and reproductive stages) had substantial impacts upon the ingestive behaviour of grazing animals, the variation induced by herbage categories was greater than the variation induced by stage of maturity. Burlison (1987) detected a significant effect of crop in a field trial where twelve crops were used, but failed to find any effect of crop in an accompanying cage trial where only five of the crops were used. She attributed the lack of a crop effect in the cage trial to a number of reasons: the overriding effect of hunger resulting from sixteen hours fasting, diet digestibility effects and a narrower range of crops in comparison with the field trial (Burlison, 1987). Herbage digestibility per se, which was not measured in the current project, was not considered to have a direct effect on ingestive behaviour in a short-term trial unless it was associated with other related properties, e.g. structural strength. Experiments 2 and 3 of the current project involved use of four forages and still showed a strong effect of forages (Tables 6.11, 7.4 and 7.7). This suggests that selection of pasture herbages, with particular regard to grasses vs legumes, together with management of stage of growth, are crucial issues in improving level of herbage intake in a farming operation.

# 8.7 SUMMARY OF COMPARISON OF INGESTIVE BEHAVIOUR BETWEEN SHEEP AND GOATS

A number of differences in ingestive behaviour and in patterns of response to variation in sward structure between sheep and goats have been identified in this project. They can be summarized as follows:

- (1) Sheep usually had greater bite weights and larger bite dimensions than goats when grazing legumes, irrespective of maturity stages, and vegetative grass swards.
- (2) Goats showed a greater willingness than sheep to graze reproductive swards, especially reproductive grasses. With increasing maturity of pastures, intake rate of sheep decreased as a consequence of a combination of an increase in bite weight and a greater fall in bite rate; but intake rate of goats increased as a consequence of a combination of a substantially greater increase in bite weight and a smaller decline in bite rate than sheep. This may be associated with goats' greater chewing efficiency during eating compared with sheep (Domingue *et al.*, 1991), and their capability to swallow large particles of coarse forages (Mitchell, 1985).
- (3) Generally, sheep showed a greater tendency to penetrate into the sward canopy, whereas goats were shallow grazers from the top downwards. Consequently, sheep pushed into the swards and to take deep bites, whereas goats restricted their defoliation to the top horizon.
- (4) However, when extremely tall stemmy swards of the reproductive grasses were grazed, goats modified their behaviour to deal with the rigid components, in contrast to sheep. Sheep appeared to penetrate into canopies below the seedhead horizon (Section 5.4.3 of Chapter 5) to select leafy components, and rejected rigid stalk, pseudostem and seedheads. However, in contrast to the above general case, goats severed mouthfuls of herbage from the side of the experimental turves rather than prehending within the top strata, and folded them into the mouth, being willing to prehend reproductive tillers, seedheads and stalks as well as green leaves. This led to a much greater bite weight for goats than sheep, and to a similar bite depth for goats and sheep.

(5) Bulk density of legumes usually was more important in affecting sheep than goats. This was associated with a contrast between the two animal species in the depth of penetration when leguminous swards were grazed. Since the swards used in the current research were not trimmed, they displayed a heterogeneity in length of petioles. Goats grazed from the top of the sward canopy downwards, so they could only harvest the petioles which had entered the uppermost layer, and ignored those below this horizon. In contrast, sheep pushed further into lower horizons where bulk density was greater than in the uppermost layer where goats defoliated. As a result, the importance of the effect of bulk density was lower for goats than for sheep.

Schwartz & Ellis (1981) attributed the differences in grazing behaviour between animal species to body size, mouthpart morphology and gut morphology and function. The restricted data set of Experiment 1 (Chapter 4) demonstrated that the variation in bite weight and bite depth between sheep and goats for a given sward may be partially attributed to the discrepancy in incisor arcade breadth between the two species. Broad and flat incisor arcades probably lead to an advantage to grazers, whereas browsers have narrower and more pointed incisor arcades, capable of greater selectivity (Gordon & Illius, 1988). Measurements (Table 5.7) and visual appraisal of teeth impression recorded in dental wax (Chapter 3) indicated that the incisor arcades of sheep were broader and less "pointed" than those of goats, disadvantaging the sheep in dealing with tall reproductive swards, but creating advantage in grazing vegetative grasses and both stages of clovers.

There may be some complementarity in ingestive behaviour between various grazing animal species. Collins (1989) considered "complementarity" as a situation in which mixed species improve their nutritional status as a consequence of grazing together. However, in the sense of a broad concept, it would be more sensible to regard the following case as "complementarity" as well. That is, mixed species can lead to greater overall output of productivity in economic terms and better performances of pasture in ecological terms, even though the nutritional status may be slightly reduced for either species, so long as this penalty can be more than offset by the matched improvement of the co-grazer.

Competition may exist among ungulates, particularly if they have not evolved together (Ellis & Travis, 1975). "Competition", in the sense of grazing, is rivalry for feed and space (Radcliffe & Townsend, 1988). An animal is described as competitive when it improves its nutritional status on mixing at the expense of the co-grazer (Collins, 1989). However, grazing animals tend to reduce competition by exploiting the environment in different ways (Ellis & Travis, 1975; Schwartz & Ellis, 1981), reducing competition and leading to complementarity because of variation across animal species in anatomical, physiological, behavioural and epidemiological characteristics (Lambert & Guerin, 1989). Collins (1989) considered that it may be possible to explain the 10-20% improvement in productivity of mixed grazing systems by the difference in grazing behaviour between species.

Some differences in ingestive behaviour between sheep and goats have been identified in this research, as discussed above. Complementarity can be achieved if sward conditions are carefully characterized because, as revealed in this study, the relativity of ingestive behaviour responses between the two species alters as sward conditions change. There has also been extensive information on the differences in diet selection in relation to choice and discrimination of plant species (Clark et al., 1982; 1984; L'Huillier et al., 1986; Nicol et al., 1987; Lambert & Clark, 1987; Radcliffe & Francis, 1988), efficiency of grazing, botanical composition and seasonal energy requirements (Lambert & Guerin, 1989) between animal species. These differences are thought to lead to differences in habitat selection, grazing succession and social system (Schwartz & Ellis, 1981). Integrated information on the differences in ingestive behaviour and diet composition between sheep and goats, and other species as well, would provide more evidence on the extent of competition or complementarity between grazing animals. This information is important for making managerial decisions regarding the use of herbage resources to the best possible advantage. This aspect will be considered in the next section.

#### 8.8 APPLICATION AND RECOMMENDATION

There is an apparent contrast between sheep and goats in their modes of grazing grasses and legumes, and vegetative and reproductive swards. This knowledge is essential to design appropriate grazing management systems for the two

species alone or mixed. The applications of these findings are considered here in practical terms.

The relative importance of sward height and bulk density effects in determining ingestive behaviour of sheep and goats grazing grasses and legumes suggests that optimal sward characteristics allowing animals to obtain high levels of herbage intake should be characterized as tall for grasses, and dense for legumes if they are grazed by sheep, but tall for both grasses and legumes if they are grazed by goats.

Goats are shallow grazers and more sensitive to changing sward height than sheep. Thus, it would be advisable that goats should be stocked less intensively and be left greater post-grazing heights than with sheep grazing. Adoption of short rotation length, for instance, should be considered when high goat production is a managerial goal.

Consumption of white clover by goats is assumed to be influenced partly by avoidance behaviour (Clark *et al.*, 1982; 1984), and partly by the vertical distribution and the availability of white clover relative to other sward components (Section 5.4.3 of Chapter 5). Thus, substantial concentration in the grazed horizon and good accessibility would be desirable to promote the intake of white clover by goats.

The greater capability of goats to deal with reproductive swards gives them advantages over sheep and suggests that for greatest biological efficiency goats could be used to utilize low quality roughages and to clean up overgrown rank and/or stemmy pastures, confirming the previous suggestion by Radcliffe and Francis (1988), and by Domingue *et al.* (1991). But rank pastures should be avoided for sheep.

Goats graze downwards successively and sheep can push into canopies to approach or to penetrate into pseudostem horizons. This is similar to the evidence previously reported that the intake of sheep is less sensitive to declining herbage mass than that of goats since sheep are more ready to adapt to eating less preferred components of the sward with reduced herbage availability (Nicol *et al.*, 1987). This suggests that in an integrated grazing system involving the separate grazing of sheep and goats on the same pasture at different times, for functional efficiency goats should be stocked ahead of sheep, especially on tall pastures. When goats are moved sheep may still obtain satisfactory intake on residual pastures.

Sheep and goats are complementary to the extent that they select different diets (Nicol *et al.*, 1987; Clark *et al.*, 1982; 1984; Lambert & Clark, 1987) and display

different ingestive behaviour when grazing the same pasture. Goats readily graze coarse forages, and harvest seedheads, which are usually rejected by sheep. There have also been some anecdotal reports of goats browsing gorse and thistles (Clark et al., 1982; Lambert & Clark, 1987), grazing on the steeper banks between tracks (Clark et al., 1984; Lambert & Clark, 1987) and eating woody vegetation, bark (Radcliffe & Townsend, 1988) and seedheads (Clark et al., 1984). These characteristics of goat grazing would lead to benefits, in terms of pasture appearance and animal performance, accruing from a concurrent mixed grazing of goats, sheep and other stock classes, and give rise to flexibility in grazing systems. Where dietary complementarity is not possible, concurrent mixed grazing would be less appropriate. This is because under such a case, more competition between the two species for sward components exists (Nicol et al., 1987), especially for green nutritious herbage which is needed by both species for rapid growth (Radcliffe & Francis, 1988). Consequently, the two species become essentially competitive rather than complementary (Hughes et al., 1984).

Goats are often stocked on predominantly perennial ryegrass/white clover pastures in intensive managed systems (Radcliffe & Francis, 1988). This project showed that browntop, cocksfoot, prairie grass, phalaris, lotus and red clover all were readily eaten by goats, and this suggests that the choice of feeds for goats can be flexible and diverse. This suggestion, together with the information on the effects of different pasture species or cultivars on goat production, can provide information to assist in selection of new pasture species or cultivars for on-farm use.

As higher levels of herbage intake were achieved from legume diets than from grass diets, animals requiring high nutritional intake should be stocked on pastures containing legumes.

The results demonstrated in this study have also indicated a serious challenge for plant breeders. Generally, introduction of plant species or cultivars into a pasture should be assessed in terms of their likely contribution to herbage intake. Released cultivars should include some characteristics which would be expected to stimulate a high level of herbage intake by grazing animals. In more intensively managed pastures where improving herbage intake is a major goal, then tall and erect growth would be preferred attributes for both grasses and legumes. Further, foliage density is also an important characteristic for legumes.

## 8.9 CONCLUSIONS

Major conclusions arising from this research project may be summarized as follows:

- There is a consistent positive relationship between bite weight and bite depth. Bite depth is a major spatial component of bite volume, and hence bite weight. This leads to a simple way to predict bite weight from the relationship between bite depth and the most closely related sward attributes.
- There is a negative relationship between bite weight and bite rate. Intake rate will be dependent on the moderating effects of sward conditions on both bite weight and bite rate.
- 3. Sward height usually has the most important and positive effect on bite weight through operating on bite depth and hence bite volume, especially for grasses. The effect of bulk density on ingestive behaviour is usually more important in legumes than in grasses.
- 4. Animals have different responses in ingestive behaviour to grasses and legumes.
- 5. Sheep and goats have different ingestive behaviour and response patterns to sward conditions, but not always, when they are offered a wide range of swards. These differences provide further evidence on competition and complementarity between stock classes for integrated management at the farm level.
- 6. Incisor arcade breadth is a more appropriate attribute than live weight to explain the variation in bite weight and bite dimensions with increasing maturity of animals over time, and also to explain, at least partially, the differences in ingestive behaviour between the two animal species.

- 7. Ingestive behaviour of animals is not significantly altered by fistulation at the oesophagus, and the responses of grazing animals observed indoors can be extrapolated to the field grazing with confidence on a short-term basis.
- In addition to the conventional perennial ryegrass/white clover pastures, the choice of forages for introduction to sheep and goats' pastures can be flexible and diverse.

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## **Appendices**

#### **APPENDIX 3.1**

## Description of Agronomic Characteristics of Forages Used in Experiment 1

The following information is taken from a booklet, "The Grasslands Range of Cultivars", edited by AgResearch Grasslands Research Center of New Zealand in 1992.

'Grasslands Pacific' perennial ryegrass (*Lolium perenne*) is bred from selections within Ruanui and incorporating genes from Spain and Italy. It is a long-lived perennial grass with a capacity of producing many hairless tillers. This cultivar has shown good persistence through the dry season, good autumn-winter growth and good tolerance to crown rust, but high endophyte levels causing ryegrass stagger.

'Grasslands Muster' Browntop (*Agrostis capillaris* syn. *A. tenuis*) is bred from collections made on hill country pastures of New Zealand. One of its major characteristics is a fine tiller with a narrow and high ligule. It has been selected and improved in leafiness, preference, disease-resistance, seasonal distribution of production and adaptation to close grazing. It performs very well in low fertility and/or acid soils in summer-moist climates. Therefore, it is a desirable and suitable species for low input and organic farming.

'Grasslands Kara' Cocksfoot (*Dactylis glomerata*) is bred from crossing Apanui with a Portuguese cocksfoot giving greater cool-season activity and a wider spread of seasonal production. It is a tall erect plant and has excellent seedling vigour better suited to rotational grazing systems with dairying and cattle, and used as a component of pasture mixture for quality summer feed. It is rust free and does not cause livestock health problems.

'Grasslands Matua' Prairie grass (*Bromus willdenowii* syn. *B. catharticus*) is a perennial with good winter growth, but also productive in other seasons if grazed and given adequate fertilizer. It's seasonal growth pattern complements ryegrass pasture. It requires free-draining soil with medium to high fertility. It is best suited to rotational grazing under dryland and irrigated systems. It is also well suited to silage and hay and

palatable at all stages of growth. It does not produce animal health problem such as stagger.

'Grasslands Maru' Phalaris (*Phalaris aquatica*) can grow vigorously in the cooler part of the year, and tends to be dormant in hotter weather, so it is most suited for regions too dry for ryegrass, and best used in mixtures with other grasses. It is very persistent once established and will withstand hard grazing. It is more acceptable to stock than other commercially available lines. It is resistant to insects such as grass grub and black beetle, but strong regrowth from pure swards can produce phalaris staggers. It is also suitable for erosion control.

'Grasslands Tahora' white clover (*Trifolium repens*) was bred from collections made on New Zealand hill country farms. It is small-leaved, densely stoloned low-growing clover. It is more persistent in hill country, and suited to continuous grazing management. It is best used as a permanent sheep pasture. It is more persistent under grazing and in and other low input environments than other available white clovers. It recovers well after drought.

'Grasslands Kopu' white clover (*Trifolium repens*) is a tall, large-leaved white clover combining the long growing season of Pitau with the high summer growth of Ladino clover. It can grow actively in warmer climates, is nematode-tolerant, and best suited to rotational grazing.

'Grasslands Pawera' red clover (*Trifolium pratense*) is late-flowering tetraploid red clover and more persistent than diploid varieties. It has high production in late summer and early autumn.

'Grasslands Goldie' birdsfoot trefoil (*Lotus corniculatus*) is a weakly rhizomatous non-bloating tap-rooted legume which is suited to dry, acid, low-fertility soils. It is more productive in summer.

'Grasslands Puna' Chicory (*Cichorium intybus*) is a persistent tap-rooted leafy herb producing high-quality summer forage, giving excellent animal production. It can be used as an alternative to forage brassica crops if sown as pure stand under high fertiliser. It contains a high concentration of most important minerals, can be used in pasture mixes, and is suited to free draining soil and rotational grazing.

### **APPENDIX 3.2**

# Application of Herbicide During the Courses of Plot Establishment and Experimental Measurements

The weeds which appeared in the plots mainly were Toad rush (*Juncus bufonius*), Sweet vernal (*Anthoxanthum odoratum*), Annual poa (*Poa annua*), Yorkshire fog (*Holcus lanatus*), Scotch Thistle (*Cirsium vulgare*), Duckweed (*Lemna minor*), Mouse-eared Chickweed (*Cerastium fontanum*), Dock (*Rumex ottusifolius*) and Dandelion (*Taraxacum officinale*). The herbicides used in various categories of forages are listed as follows:

Grasses	Legumes and Chicory			
2.4-D, Dicamba, Tribunil,	Alloxal, Fusilaide, 2.4-DB, Ethofumesate			
(Tramat), Versitil, Nortron,	Combine, Kerb, MCPB, Asulox, Atrazine,			
Tordon 50-D	Gallant			

Application of herbicides followed the recommended rates by New Zealand Agrichemical Mannual (1984).

Grass weeds were also present in the grass plots to a varying extent, but could not be selectively sprayed out. Each plot was sprayed by a LPG gas sprayer with herbicide plus 5 litres water and each plot was covered twice, half in each direction.

#### **APPENDIX 4.1**

#### Adjustment of Data

The data were adjusted at an unpartitioned level of the data set through regression of bite variables against the chosen covariate (incisor breadth) in order to remove the concomitant confounding effects of the covariate from the background of the data set (Steel & Torrie, 1980). The data were adjusted in two ways: (1) forages x animal species combination (the first adjustment), and (2) stages of maturity (the second adjustment). The two adjustments were conducted independently for different objectives.

#### 1. The First Adjustment

Table 1 of Appendix 4.1 summarizes regression equations of behaviour variables against incisor breadth by forages x animal species combinations, which were used for the first adjustment of data.

The original data were adjusted by the following formulae (Steel & Torrie 1980):

 $\hat{\mathbf{Y}}_{j} = \mathbf{Y}_{j} - \beta_{j} (\mathbf{X}_{j} - \mathbf{X}_{j});$ 

where  $\hat{Y}_{j}$ : adjusted value of ingestive variable, i.e bite weight 2, bite depth, bite area and bite volume;

Y; observed value of the corresponding variable;

 $\beta_i$ : regression coefficient by forage and animal species, and

is available from Table 1 of this Appendix.

X<sub>i</sub>: observed incisor breadth;

X<sub>j</sub>: mean of incisor breadth of sheep and goats grazing four forages (Table 2 of Appendix 4.1).

Thus, if we use notation of index  $Y_{ijklm}$  to describe a particular

situation of a variable, where i: year, j: forages, k: stage, I:animal species and m: replication of each animal species, then the formula above can be specified as follow:

 $\hat{Y}_{,j,L} = Y_{,j,L} - \beta_{,j,L} (X_{,j,L} - X_{,j,L});$ 

For example, adjustment of bite weight 2 (bw<sub>2</sub>) involved the following calculations in which the  $\beta_{.j.L}$  and  $\overline{X}_{.j.L}$  were from Tables 1 and 2 of this Appendix, respectively.

Ryegrass and sheep,  $Abw_2 = bw_2 - 74.4$  (incbreadth - 2.45);

Ryegrass and goats,  $Abw_2 = bw_2 - 212.6$  (incbreadth - 2.02);

Browntop and sheep,  $Abw_2 = bw_2 - 63.8$  (incbreadth - 2.40);

Browntop and goats,  $Abw_2 = bw_2 - 285.6$  (incbreadth - 1.98); Tahora and sheep,  $Abw_2 = bw_2 - 122.8$  (incbreadth - 2.22); Tahora and goats,  $Abw_2 = bw_2 - 94.3$  (incbreadth - 1.81); Kopu and sheep,  $Abw_2 = bw_2 - 129.0$  (incbreadth - 2.29); Kopu and goats,  $Abw_2 = bw_2 - 162.5$  (incbreadth - 1.87). where,  $Abw_2$ : adjusted bite weight 2;  $bw_2$ : observed bite weight 2

where,  $Abw_2$ : adjusted bite weight 2;  $bw_2$ : observed bite weight 2; incbreadth: observed incisor breadth.

Therefore, 24 calculations (2 years x 2 stages x 6 individuals of each animal species) of each adjusted variable (bite weight 2, bite depth, bite area and bite volume) were generated for each combination of forage x animal species. All ingestive behaviour variables were adjusted in this way and adjusted values constituted a new data set on which analysis of variance was re-conducted.

#### 2. The Second Adjustment

The equation for this adjustment was specified as follows:

 $\hat{\mathbf{Y}} = \mathbf{Y}_{..k.} - \beta_{..k.} (\mathbf{X}_{..k.} - \mathbf{X}_{..k.});$ 

Where the regression coefficients ( $\beta_{.k.}$ ) were from Table 3 of this Appendix. Average means of incisor breadth of the animals over the period during which they grazed vegetative and reproductive swards were 2.03 cm (s.e. = 0.002) and 2.23 cm (s.e. = 0.002), respectively.

Adjustment of bite weight 2 (Abw<sub>2</sub>) included the following calculations:

Vegetative stage: $Abw_2 = bw_2 - 66.9$  (incbreadth - 2.03);Reproductive stage: $Abw_2 = bw_2 - 155.1$  (incbreadth - 2.23);

In this case, 96 adjusted values (2 years x 4 forages x 2 animal species x 6 individuals of each animal species) of each variable were generated for each maturity stage of growth. A new data set was constructed using all adjusted values of the four bite variables. An analysis of variance was re-analyzed based on this adjusted data set.

	_		Sheep			Goats		1.4+
Variable	Forages	β <sub>0</sub> (s.e.)	β <sub>1</sub> (s.e.)	R²	β <sub>0</sub> (s.e.)	β <sub>1</sub> (s.e.)	R²	r.a.r
Bite weight (mgDM)	ryegrass	11.6 (54) ns	74.4 (21) **	0.36	-214 (67)	212.6 (32) ***	0.67 ***	22
	browntop	115.7 (99) ns	63.8 (40) ns	0.29 **	-262 (100)	285.6 (48)	0.61 ***	22
	Tahora	-48.4 (81) ns	122.8 (35) **	0.35 **	-30.8 (55) ns	94.3 (29) **	0.32	22
	Kopu	-51.4 (96) ns	129.0 (41) **	0.31 **	-133 (70) (*)	162.5 (37) **	0.47 ***	22
Bite depth (cm)	ryegrass	-13.0 (5) *	12.3 (2) ***	0.60	-10.9 (5) **	12.9 (2) ***	0.58	22
	browntop	-3.8 (3) ns	7.1 (1)	0.59	-5.6 (5) ns	9.7 (1.7)	0.63 **	22
	Tahora	-0.5 (2) ns	2.6 (1)	0.30 **	3.4 (1)	-0.06 (0.6) ns	0.35 **	22
	Кори	-1 (2) ns	3.1 (1) **	0.39 **	4.5 (2) *	-0.2 (1) ns	0.37 **	22
Bite area (cm²)	ryegrass	8.4 (2)	1.3 (0.8) ns	0.12 ns	6.1 (2)	2.1 (0.9)	0.19 *	21
	browntop	5.4 (2) **	1.6 (0.7) *	0.18 *	3.2 (1.5) *	2.6 (0.8) **	0.37 **	21
	Tahora	10.8 (3.6) **	0.08 (1.6) ns	0.11 ns	-2.6 (2) ns	6.0 (1)	0.53	22
	Kopu	17 (3) ***	-1.4 (1) ns	0.12 ns	18.0 (2) ***	-3.6 (1)	0.32	22
Bite volume (cm³)	tyegrass	152.4 (62)	140.6 (25)	0.61	-157 (88) (*)	160 (43) **	0.49 **	20
	browntop	-64.8 (45) ns	77.0 (19) ***	0.58 **	-113 (45) *	117 (29) ***	0.52 **	20
	Tahora	-3.6 (38) ns	28 (17) ns	0.12 ns	-0.8 (12) ns	15.9 (6) *	0.23	22
	Кори	3.0 (37) ns	36.0 (15) *	0.20 *	79 (22) **	-0.2 (12) ns	0.29 *	22

Table 1 of Appendix 4.1:

Regressions of bite weight and bite dimensions against incisor breadth for animal species x forages combinations to obtain coefficients to be used in the data adjustment

The coefficients in column  $\beta_t$  were used in the data adjustment (see this appendix). The data which are listed in other columns show the relevant statistics of the regression equations. r.d.f: Residual degree of freedom, applied to both sheep and goats. The figures in brackets are the standard errors of coefficients. Significant levels following  $\beta_t$  and  $\beta_0$  are t tests for them, and those following  $R^2$  are F tests for model.

Forages	Sheep	Goats	N*
Ryegrass	2.44	2.02	24
Browntop	2.40	1.98	24
Tahora	2.22	1.81	24
Кори	2.29	1.87	24
s.e.	0.04	0.04	

 Table 2 of Appendix 4.1:
 Average incisor breadth of sheep and goats grazing four forages. These values were used in the data adjustment

N\*: number of observations (2 years x 2 stages x 6 reps)

#### Table 3 of Appendix 4.1:

Regressions of bite weight and bite dimensions against incisor breadth for the subsets of maturity stages of growth to obtain coefficients to be used in the second adjustment

	Vegetative			Re	1.(*		
Variable	$\beta_0$ (s.e.)	β <sub>1</sub> (s.e.)	R²	$\beta_0$ (s.e.)	β <sub>1</sub> (s.e.)	R²	r.d.f
Bite weight (mg DM)	30.0 (28) ns	66.9 (13) ***	0.28	-71.4 (47) ns	155.1 (20)	0.38	94
Bite depth (cm)	2.9 (1.1)	1.6 (0.5)	0.42	-9.9 (2.8) ***	10.4 (1.2)	0.45	94
Bite area (cm²)	y 5.8 (1.2) ***	2.2 (0.6)	0.13	8.1 (1.3) ***	1.2 (0.6) *	0.15 *	94
Bite volume (cm³)	2.8 (14) ns	30.1 (7) ***	0.38 **	-105 (38) **	112 (17) ***	0.39 ***	94

The coefficients in column  $\beta_1$  were used in the data adjustment. The data which are listed in other columns show the relevant statistics of the regression equations. Significant levels following  $\beta_1$ ,  $\beta_2$  and  $\beta_0$  are t tests for them, and those following  $R^2$  are F tests for model.

r.d.f: Residual degree of freedom, applied to both sheep and goats. Figures in brackets are the standard errors of coefficients.

The t tests indicated that both  $\beta_0$  and  $\beta_1$  of the above equations were significantly different between the two stages of maturity, and therefore, heterogeneity in the effect of incisor breadth on bite weight existed between the stages of maturity. This indicated the need to adjust for incisor breadth variation at the level of the maturity stage effect (the second adjustment). This adjustment was independent of the first adjustment for different purpose.

## Appendix 5.1

# Graphs illustrating the canopy structures of swards for 9 forages x 2 stages using point-quadrat data

## Key to graphs



Seedheads Leaves

Stems (including petioles, stalks)



Weeds

Brown and dead materials







2. Reproductive Ryegrass



3. Vegetative Browntop



4. Reproductive Browntop



11. Vegetative Tahora white clover



## Key to graphs



#### Seedheads

Leaves

Stems (including petioles, stalks)

Weeds

Brown and dead materials



13. Vegetative Kopu white clover



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14. Reproductive Kopu white clover



15. Vegetative Red clover



17. Vegetative Lotus corniculatus



16. Reproductive Red clover



18. Reproductive Lotus corniculatus

## Appendix 5.2

Tables presenting scores of multiple discriminant functions at different levels of treatments for three data sets (entire profiles of sward set, grazed strata of sward set and behaviour set)

Forages	Entire profiles of sward set		Grazed strata of sward set		Behaviour set	
Discriminant functions	MDF1	MDF2	MDF1	MDF2	MDF1	MDF2
Browntop	165.80	64.76	0.44	25.13	50.79	5.90
Cocksfoot	219.58	88.91	5.79	17.38	58.37	28.43
Kopu	32.88	1.91	30.42	12.39	1.28	12.09
Lotus	96.64	0.32	30.67	7.91	7.33	14.20
Phalaris	259.34	131.72	5.60	1.00	77.43	48.81
Prairiegrass	194.55	50.24	11.18	0.90	45.73	25.70
Red clover	79.64	16.66	26.44	28.48	1.86	14.34
Ryegrass	190.73	70.41	14.12	6.99	54.80	26.30
Tahora	1.01	24.89	36.75	17.27	0.86	9.50

Table 1 of Appendix 5.2Forages

MDF1 and MDF2: multiple discriminant functions 1 and 2. This note also applies to other tables of this appendix.

MDF1 and MDF2 were named as follows, respectively: "height" and "heightdensity" determiners for entire profiles of sward set; "stem bulk density/mass contrast" and "leaf bulk density" determiners for grazed strata of sward set; and "depth" and "dry matter" determiners for behaviour set.

## Table 2 of Appendix 5.2Forage x stage

Forages	Entire p of swa	profiles rd set	Grazed strata of sward set		Behaviour set	
Discriminant functions	MDF1	MDF2	MDF1	MDF2	MDF1	MDF2
Browntop						
Reproductive Vegetative	205.74 48.11	80.28 45.37	0.53 13.49	0.95 29.77	95.91 22.19	2.89 15.75
Cocksfoot						
Reproductive Vegetative	263.61 73.71	63.95 68.89	8.93 11.73	15.23 28.94	102.94 38.00	22.74 20.51
Kopu						
Reproductive Vegetative	52.44 24.75	33.23 30.05	27.80 19.64	27.65 31.83	17.41 7.08	11.96 15.54
Lotus						
Reproductive Vegetative	130.88 41.69	51.71 48.49	27.64 20.77	27.83 30.83	23.50 13.25	16.38 15.24
Phalaris						
Reproductive Vegetative	319.90 115.30	57.29 71.16	3.61 24.72	18.82 18.89	137.57 41.77	47.79 29.88
Prairiegrass						
Reproductive Vegetative	171.44 100.95	72.90 77.56	13.49 27.90	20.70 21.65	65.20 39.94	18.88 30.65
Red clover						
Reproductive Vegetative	128.82 1.06	60.82 14.19	19.44 4.46	22.24 45.81	25.24 0.69	12.42 23.04
Rvegrass						
Reproductive Vegetative	240.36 54.64	56.04 64.28	16.08 20.44	20.36 23.60	103.06 29.17	25.26 22.42
Tahora						
Reproductive Vegetative	50.50 19.40	20.32 1.04	27.02 15.31	28.94 38.52	19.33 2.70	8.42 18.49

MDF1 and MDF2 were named as follows, respectively: "height" and "mass" determiners for entire profiles of sward set; "stem+seedhead bulk density/herbage mass contrast" and "mass+leaf%/live+leaf density contrast" determiners for grazed strata of sward set; and "depth" and "dry matter" determiners for behaviour set.

## Table 3 of Appendix 5.2

Forage x animal species, and forage x stage x animal species for behaviour set.

Forages	Behavi	our set	Behaviour set			
			Reproc	luctive	Veget	ative
Discriminant functions	MDF1	MDF2	MDF1	MDF2	MDF1	MDF2
Browntop						
Sheep	3.59	4.22	69.96	27.48	15.39	39.61
Goals	0.87	10.51	79.00	32.83	17.90	35.22
Cocksfoot						
Sheep	5.72	6.39	62.65	11.99	26.82	28.81
Goats	3.81	12.41	76.06	21.97	26.58	25.12
Кори						
Sheep	15.11	2.87	23.30	32.65	13.06	36.28
Goats	6.56	1.43	17.84	34.73	6.87	31.88
Lotus						
Sheep	9.31	1.48	16.57	36.57	15.52	31.41
Goats	10.13	3.28	26.94	31.95	13.16	31.67
Dhalaria						
Sheen	6.96	5 86	70.20	0 00	25 60	25 38
Goats	8.83	1 76	79.20	3.35	23.67	29.50
	0.00		//.00	0.00	20.07	20.00
Prairiegrass						
Sheep	4.49	3.12	46.92	21.38	22.56	28.09
Goats	2.99	6.35	44.00	25.77	24.82	23.53
Red clover						
Sheep	12.99	1.95	26.40	31.56	1.07	34.66
Goats	8.83	2.01	25.90	32.59	2.99	32.14
Rveorass						
Sheep	2.97	7.89	61.80	9.68	24.98	30.38
Goats	4.51	6.85	73.59	20.81	15.41	36.81
Tahora						
Sheep	13.84	0.56	26.92	35.96	6.06	36.91
Goats	3.19	0.92	17.26	32.52	3.37	32.42

MDF1 and MDF2 were named as follows, respectively: "fresh matter" and "bite rate" determiners for forage x animal species; and "weight-depth" and "depth" determiners for the second order interaction.

#### Appendix 5.3

Dendrograms showing cluster hierarchy of discriminant scores for different sets of attributes at different levels of treatments (Abbreviations used below: V: vegetative; R: reproductive; S: sheep; G: goats)

Fig. 1: Sward attributes of complete profiles for forages (corresponding to Table 1 of Appendix 5.4 and to Fig. 5.1B of scattergram in Thesis text).



Fig. 2: Sward attributes of complete profiles for forage x stage (corresponding to Table 2 of Appendix 5.4 and to Fig. 5.2B of scattergram in Thesis text).







Fig. 4: Sward attributes of complete profiles for forage x stage (corresponding to Table 4 of Appendix 5.4 and to Fig. 5.4B of scattergram in Thesis text).



Fig. 5: Behaviour attributes for forages (corresponding to Table 5 of Appendix 5.4 and to Fig. 5.5C of scattergram in Thesis text).



Fig. 6: Behaviour attributes for forage x stage (corresponding to Table 6 of Appendix 5.4 and to Fig. 5.6C of scattergram in Thesis text).



Fig. 7: Behaviour attributes for animal species x forage (corresponding to Table 7 of Appendix 5.4 and to Fig. 5.7C of scattergram in Thesis text).



Fig. 8: Behaviour attributes for animal species x forage x stage (corresponding to Table 8 of Appendix 5.4 and to Fig. 5.9 of scattergram in Thesis text).



## Appendix 5.4

## Tables presenting truncation probabilities for clusters

Appropriate number of clusters were determined by the lowest probability.

Table 1 of Appendix 5.4	Sward	attributes	of	complete	profiles	for	forage
	(corresp	conding to	Fig.	1 of Appe	endix 5.3	and	to Fig.
	5.1B of	Thesis tex	t).				

No. of clusters	F values	Probabilities
6	15.84 (12,2)	0.0611
5	15.05 (10,4)	0.0121
4	19.10 (8,6)	0.0019
<u>3</u>	12.95 (6,8)	0.0016
2	10.57 (4,10)	0.0017
1	15.66 (2,6)	0.0049

The two numbers in brackets are degrees of freedom of numerator and denominator, respectively. The double underlined number is the optimal number of truncation for cluster hierarchy. These notes also apply for all tables of this appendix.

## Table 2 of Appendix 5.4

Sward attributes of complete profiles for forage x stages (corresponding to Fig. 2 of Appendix 5.3 and to Fig. 5.2B of Thesis text).

No. of clusters	F values	Probabilities
10	27.04 (18,14)	0.601 x 10 <sup>-5</sup>
9	26.53 (16,16)	0.289 x 10 <sup>-5</sup>
8	27.23 (14,18)	0.141 x 10 <sup>-5</sup>
7	28.85 (12,20)	0.707 x 10 <sup>-6</sup>
<u>6</u>	26.48 (10,22)	0.632 x 10 <sup>-6</sup>
5	21.35 (8,14)	0.115 x 10 <sup>-5</sup>
4	19.70 (6,16)	0.191 x 10 <sup>.5</sup>
3	20.07 (4,28)	0.363 x 10 <sup>-5</sup>
2	17.32 (5,25)	0.265 x 10 <sup>-3</sup>

# Table 3 of Appendix 5.4

Sward attributes of grazed strata for forage (corresponding to Fig. 3 of Appendix 5.3 and to Fig. 5.3B of Thesis text).

F values	Probabilities
23.10 (10,4)	0.652 x 10 <sup>-2</sup>
13.15 (8,6)	0.380 x 10 <sup>-2</sup>
16.56 (6,8)	0.774 x 10 <sup>-3</sup>
12.87 (4,10)	0.900 x 10 <sup>-3</sup>
40.76 (2,6)	0.726 x 10 <sup>-3</sup>
	F values 23.10 (10,4) 13.15 (8,6) 16.56 (6,8) 12.87 (4,10) 40.76 (2,6)

## Table 4 of Appendix 5.4

Sward attributes of grazed strata for forage x stage (corresponding to Fig. 4 of Appendix 5.3 and to Fig. 5.4B of Thesis text).

No. of clusters	F values	Probabilities
9	28.43 (16,16)	0.241 x 10 <sup>.5</sup>
8	22.64 (14,18)	0.242 x 10 <sup>-5</sup>
7	18.90 (12,20)	0.273 x 10 <sup>-5</sup>
<u>6</u>	17.50 (10,22)	0.272 x 10 <sup>-5</sup>
5	7.51 (6,26)	0.208 x 10 <sup>-3</sup>
4	11.45 (6,26)	0.232 x 10 <sup>-4</sup>
3	9.73 (4,28)	0.128 x 10 <sup>-3</sup>
2	8.94 (2,15)	0.308 x 10 <sup>-2</sup>

Table	5 of	Appendix	5.4
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Behaviour attributes for main effect, forages (corresponding to Fig. 5 of Appendix 5.3 and to Fig. 5.5C of Thesis text).

No. of Clusters	F values	Probabilities
6	105.94 (18,14)	0.4404 x 10 <sup>-6</sup>
5	80.21 (16,16)	0.2715 x 10 <sup>-6</sup>
<u>4</u>	66.00 (14,18)	0.1786 x 10 <sup>-6</sup>
3	45.26 (12,20)	0.2154 x 10 <sup>-6</sup>
2	32.49 (10,22)	0.3363 x 10 <sup>-6</sup>

## Table 6 of Appendix 5.4

Behaviour attributes for interaction between forages and stages (corresponding to Fig. 6 of Appendix 5.3 and to Fig. 5.6C of Thesis text).

No. of Clusters	F values	Probabilities
9	105.94 (18,14)	0.440 x 10 <sup>-6</sup>
8	80.21 (16,16)	0.272 x 10 <sup>-6</sup>
7	60.00 (14,18)	0.215 x 10 <sup>-6</sup>
<u>6</u>	50.26 (12,20)	0.179 x 10 <sup>-6</sup>
5	32.49 (10,22)	0.336 x 10 <sup>-6</sup>
4	21.08 (8,24)	0.121 x 10 <sup>-5</sup>
3	21.72 (6,26)	0.127 x 10 <sup>-5</sup>
2	18.31 (4,28)	0.553 x 10 <sup>-5</sup>
1	39.21 (2,15)	0.157 x 10 <sup>-5</sup>

#### Table 7 of Appendix 5.4

Behaviour attributes for interaction between forage and animal species (corresponding to Fig. 7 of Appendix 5.3 and to Fig. 5.7C of Thesis text).

F values	Probabilities
30.75 (18,14)	0.438 x 10 <sup>-5</sup>
23.04 (16,16)	0.428 x 10 <sup>-5</sup>
18.99 (14,18)	0.422 x 10 <sup>-5</sup>
19.05 (12,20)	0.265 x 10 <sup>-5</sup>
19.04 (10,22)	0.182 x 10 <sup>-5</sup>
20.99 (8,24)	0.138 x 10 <sup>-5</sup>
14.80 (6,26)	0.675 x 10 <sup>-5</sup>
14.56 (4,28)	0.165 x 10 <sup>-4</sup>
21.27 (2,15)	0.125 x 10 <sup>-3</sup>
	F values 30.75 (18,14) 23.04 (16,16) 18.99 (14,18) 19.05 (12,20) 19.04 (10,22) 20.99 (8,24) 14.80 (6,26) 14.56 (4,28) 21.27 (2,15)

# Table 8 of Appendix 5.4

Behaviour attributes for the second order interaction (corresponding to Fig. 8 of Appendix 5.3 and Fig. 5.9 of Thesis text).

No. of clusters	F values	Probabilities
8	108.82 (16,52)	0.392 x 10 <sup>-10</sup>
<u>7</u>	110.14 (14,54)	0.337 x 10 <sup>-10</sup>
6	82.52 (12,56)	0.626 x 10 <sup>-10</sup>
5	58.04 (10,58)	0.189 x 19 <sup>-9</sup>
4	50.94 (8,60)	0.409 x 10 <sup>-9</sup>
3	48.88 (6,62)	0.926 x 10 <sup>-9</sup>
2	43.98 (4,64)	0.538 x 10 <sup>-8</sup>
1	82.37 (2,33)	0.515 x 10 <sup>-7</sup>

#### Appendix 5.5 Tables presenting correlation matrices showing simple correlations between seven sward variables and five ingestive behaviour variables for animal species x herbage categories.

#### Table 1 of Appendix 5.5 Unpartitioned (overall) correlations

	Surface height (cm)	Overall bulk density (mg DM/cm <sup>3</sup> )	Herbage mass (g DM/m²)	Leaf%	Leaf frequency bulk density (hits/2 cm)	Stem+seedhead frequency bulk density (hits/2 cm)	Live%	Bite weight 1 (mg FM/bite)	Bite weight 2 (mg DM/bite)	Bite rate (bites/min)	Bite depth (cm)
Overall bulk density	-0.68										" <u>_</u> ,
Herbage mass	0.44	0.21									
Leaf %	0.26	-0.57	-0.19								
Leaf frequency bulk density	-0.54	0.14	-0.48	0.45							
Stem+seedhead frequency bulk density	-0.63	0.78	-0.07	-0.76	-0.14						
Live%	-0.34	0.24	-0.16	-0.38	-0.07	0.33					
Bite weight 1	0.15	0.07	0.31	-0.29	-0.37	0.08	0.08				
Bite weight 2	0.46	-0.14	0.48	-0.13	-0.49	-0.14	-0.22	0.71			
Bite rate	-0.53	0.28	-0.33	0.14	0.53	0.20	0.18	-0.40	-0.57		
Bite depth	0.93	-0.64	0.30	0.26	-0.45	-0.56	-0.48	0.12	0.42	-0.47	
Bite area	-0.16	0.01	-0.15	-0.01	0.09	0.09	0.16	0.15	0.07	0.05	-0.15

### Table 2 of Appendix 5.5Sheep x grasses

	Surface height (cm)	Overall bulk density (mg DM/cm <sup>3</sup> )	Herbage mass (g DM/m <sup>2</sup> )	Leaf%	Leaf bulk frequency density (hits/2 cm)	stem+seedhead frequency bulk density (hits/2 cm)	Live%	Bite weight 1 (mg FM/bite)	Bite weight 2 (mg DM/bite)	Bite rate (bites/min)	Bite depth (cm)
Overall bulk density	-0.47										
Herbage mass	0.52	0.44									
Leaf %	-0.70	0.10	-0.46								
Leaf frequency bulk density	-0.83	0.41	-0.46	0.72							
Stem+seedhead frequency bulk density	-0.06	0.50	0.19	-0.49	0.16						
Live%	0.05	-0.25	-0.25	-0.08	-0.08	-0.04					
Bite weight 1	0.29	-0.06	0.29	-0.17	-0.26	-0.02	-0.30				
Bite weight 2	0.44	0.03	0.50	-0.37	-0.40	0.08	-0.39	0.82			
Bite rate	-0.67	0.31	-0.40	0.56	0.63	0.06	0.17	-0.42	-0.55		
Bite depth	0.96	-0.48	0.46	-0.68	-0.76	-0.05	0.03	0.31	0.43	-0.64	
Bite area	-0.14	-0.01	-0.14	0.23	0.12	-0.13	0.08	0.20	0.12	-0.03	-0.12

## Table 3 of Appendix 5.5Goats x grasses

	Surface height (cm)	Overall bulk density (mg DM/cm <sup>3</sup> )	Herbage mass (g DM/m <sup>2</sup> )	Leaf%	Leaf frequency bulk density (hits/2 cm)	Stem+seedhead frequency bulk density (hits/2 cm)	Live%	Bite weight 1 (mg FM/bite)	Bite weight 2 (mg DM/bite)	Bite rate (bites/min)	Bite depth (cm)
Overall bulk density	-0.50										
Herbage mass	0.49	0.44									
Leaf %	-0.66	-0.01	-0.59								
Leaf frequency bulk density	-0.82	0.40	-0.47	0.68							
Stem+seedhead frequency bulk density	-0.12	0.54	0.19	-0.45	0.26						
Live%	-0 24	-0.11	-0 38	0.24	0 19	-0.09					
Bite weight 1	0.24	-0.11	-0.50	0.24	0.13	-0.05	0.00				
Bite weight 2	0.59	-0.24	0.40	-0.41	-0.52	0.02	-0.32				
Bite rate	0.64	-0.11	0.55	-0.54	-0.59	0.10	-0.44	0.89			
	-0.59	0.29	-0.34	0.52	0.55	-0.01	0.37	-0.69	-0.72		
Bite depth	0.94	-0.53	0.39	-0.59	-0.73	-0.08	0.20	0.54	0.57	-0.53	
Bite area	-0.22	-0.11	-0.30	0.22	0.09	-0.08	-0.10	0.08	0.05	-0.02	-0.17

## Table 4 of Appendix 5.5Sheep x legumes

	Surface height (cm)	Overall bulk density (mg DM/cm³)	Herbage mass (g DM/m²)	Leaf%	Leaf frequency bulk density (hits/2 cm)	Stem+seedhead frequency bulk density (hits/2 cm)	Live%	Bite weight 1 (mg FM/bite)	Bite weight 2 (mg DM/bite)	Bite rate (bites/min)	Bite depth (cm)
Overall bulk density	-0.54		· · · · · · · · · · · · · · · · · · ·		······································				- •		
Herbage mass	0.74	0.11									
Leaf %	0.15	-0.39	-0.17								
Leaf frequency bulk density	-0.62	0.11	-0.62	0.48							
Stem+seedhead frequency bulk density	-0.72	0.50	-0.42	-0.49	0.48						
Live%	0.44	-0.39	0.21	0.40	-0.18	-0.58					
Bite weight 1	0.22	0.18	0.42	-0.22	-0.36	-0.14	0.07				
Bite weight 2	0.35	0.07	0.49	-0.26	-0.49	-0.22	0.14	0.91			
Bite rate	-0.48	0.34	-0.33	0.08	0.51	0.42	-0.27	-0.33	-0.43		
Bite depth	0.48	-0.20	0.47	-0.28	-0.57	-0.25	0.23	0.59	0.65	-0.44	
Bite area	0.15	-0.16	0.04	0.10	0.12	-0.02	0.24	0.19	0.21	0.04	0.12

Table 5 of Appendix 5.	5 Goat	s x legumes									<u></u>
	Surface height (cm)	Overall bulk density (mg DM/cm <sup>3</sup> )	Herbage mass (g DM/m²)	Leaf%	Leaf frequency bulk density (hits/2 cm)	Stem+seedhead frequency bulk density (hits/2 cm)	Live%	Bite weight 1 (mg FM/bite)	Bite weight 2 (mg DM/bite)	Bite rate (bites/min)	Bite depth (cm)
Overall bulk density	-0.62										
Herbage mass	0.42	0.40									
Leaf %	0.13	-0.22	-0.08								
Leaf frequency bulk density	-0.54	0.18	-0.40	0.61							
Stem+seedhead frequency bulk density	-0.60	0.63	0.01	-0.46	0.26						
Live%	-0.34	-0.37	-0.01	-0.03	-0.30	-0.28					
Bite weight 1	0.57	-0.49	0.12	0.03	-0.42	-0.44	0.40				
Bite weight 2	0.68	-0.45	0.29	-0.08	-0.57	-0.42	0.37	0.94			
Bite rate	-0.27	0.10	-0.22	0.32	0.48	-0.001	-0.34	-0.59	-0.68		
Bite depth	0.64	-0.67	-0.09	0.11	-0.32	-0.51	0.34	0.43	0.48	-0.13	
Bite area	0.03	-0.22	-0.27	0.07	0.08	-0.01	0.15	-0.09	-0.08	0.11	0.06

#### **APPENDIX 7.1**

#### Correction of recovery for saliva contamination

The methodology for correction for saliva contamination was developed by Burlison (1987) from a knowledge of the fresh weight and dry weight of extrusa samples. The method is based on relationships among the following four variables: (1) fresh weight of the complete extrusa (liquid saliva + fresh herbage); (2) dry weight of the complete extrusa (DM of saliva + DM herbage), and hence DM% of complete extrusa (ratio of the above two measurements); (3) DM% of the herbage as grazed; and (4) DM% of the saliva.

The first variable was sampled or measured during the trial. The second variable was measured from oven-drying of the fresh extrusa. The third one was assumed equal to DM% of herbage in the grazed stratum of the swards. Burlison (1987) found the DM content of saliva to be 0.0116 g DM/g saliva (s.e. 0.00034) by oven-drying saliva samples collected from each of three fistulated sheep.

First of all, it was necessary to know the fresh weight of the herbage fraction of the extrusa.

Some abbreviations are defined as follows to derive the appropriate equation to calculate this variable:

- Let (1) ExtrFM = fresh weight of extrusa (sampled)
  - (2) HerbFM = fresh weight of herbage fraction in extrusa (to be calculated)
  - (3) SalvFM = fresh weight of saliva in extrusa (derived)
  - (4) ExtrDM = dry weight of extrusa (oven-drying (1))
  - (5) HerbDM = dry weight of herbage fraction in extrusa ((2) x (8))
  - (6) SalvDM = dry weight of saliva in extrusa ((3) x (9))
  - DM%<sub>Extr</sub> = dry matter percentage of complete extrusa (ratio of 4 to 1)
  - (8) DM%<sub>Herb</sub> = dry matter percentage of herbage in extrusa (assumed to be equal to DM% of grazed stratum of swards, see Section 3.2.6.3 of Chapter 3).
  - DM%<sub>Satv</sub> = dry matter percentage of saliva in extrusa (obtained by Burlison: 1.116%)

Then: HerbDM + SalvDM = ExtrDM Or: (HerbFM x DM%<sub>Herb</sub>) + (SalvFM x DM%<sub>Salv</sub>) = (ExtrFM xDM%<sub>Extr</sub>) Substituting: ExtrFM - HerbFM for SalvFM: (HerbFM x DM%<sub>Herb</sub>) + (ExtrFM - HerbFM) x DM%<sub>Salv</sub> = (ExtrFM x DM%<sub>Extr</sub>) Expanding: (HerbFM x DM%<sub>Herb</sub>) + (ExtrFM x DM%<sub>Salv</sub> - HerbFM x DM%<sub>Salv</sub>) = (ExtrFM x DM%<sub>Extr</sub>)

Rearranging: (HerbFM x DM%<sub>Herb</sub>) - HerbFM x DM%<sub>Salv</sub>)  $\approx$  (ExtrFM x DM%<sub>Extr</sub>) - (ExtrFM x DM%<sub>Salv</sub>)

Factorizing: HerbFM ( DM%<sub>Herb</sub> - DM%<sub>Salv</sub>) = (ExtrFM x DM%<sub>Extr</sub>) - (ExtrFM x DM%<sub>Salv</sub>)

Therefore:

$$HerbFM = \frac{(ExtrFM \times DM\%_{Extr}) - (ExtrFM \times DM\%_{Salv})}{(DM\%_{Herb} - DM\%_{Salv})}$$

The calculated HerbFM value was then multiplied by DM%<sub>Herb</sub> to estimate the HerbDM, which was then divided by number of bites to obtain corrected extrusabased bite weight. The corrected proportional recovery for saliva contamination is as follows:

Corrected recovery = <u>corrected extrusa-based bite weight</u> turf-based bite weight

The corrected recoveries obtained from the above equation are summarized in Table 7.10.