The Effects of Sward Height, Bulk Density and Tiller Structure on the Ingestive Behaviour of Red Deer and Romney Sheep

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ABSTRACT

The ingestive behaviour of Red deer and/or Romney sheep was examined in relation to two major components of sward structure, height (HT) and bulk density (DEN), by measuring the depth, area and rate of biting on a series of artificial swards.

HT and DEN effects were examined in a series of four short-term indoor grazing experiments using two novel mini-sward techniques, developed to minimise confounding of HT with DEN and other differences in tiller structure. The first experiment used the deep, leafy horizon of tall vegetative sorghum swards, whereas the next three experiments used seedling wheat swards. A fifth experiment using both ryegrass and wheat swards built upon the previous four experiments (examining HT and DEN effects), by measuring the bite dimensions of sheep in relation to changes in tiller structure down the sward profile.

Wheat seedlings grew on seed reserves and achieved a high degree of separation of HT and DEN variation, enabling the description and conceptualisation of how bite parameters respond to independent HT and/or DEN variation. However, when compared to natural grass swards these seedling swards, with 100% green matter and low shear strength, resulted in large bite volumes and high bite rates.

Bite depth increased rapidly and linearly with increasing HT, and at a slightly greater rate the sparser the sward, although on very short swards (<3-4 cm) bite depth was insensitive to even large changes in DEN. High levels of dead matter had no influence upon the bite depth of sheep grazing ryegrass swards. Similarly, the tops of the pseudostems had little if any influence upon the bite depth of deer or sheep grazing wheat or ryegrass swards. However, sheep avoided penetrating the tough rigid pseudostem at the base of ryegrass swards when leaf-like immature pseudostem was available in the overlying strata. Bite depth averaged 70% of HT on the sorghum and seedling wheat swards, appreciably deeper than that typical for natural grass swards.

As the HT of wheat swards increased from minimum grazable levels, bite area increased rapidly as increasing tiller length enabled greater horizontal displacement of tillers. However, the rate of

increase soon declined and bite area plateaued as mouth dimensions rather than HT (tiller length) constrained the area of herbage which animals could efficiently prehend per bite. As DEN increased, animals reduced bite area so that HT became less of a constraint; consequently, bite area plateaued at lower maxima on shorter swards.

The rate of increase in bite area was low relative to the rate of decline in DEN (or tiller shear strength), probably in part reflecting the way mouth dimensions limit the ability of animals to adjust bite area upwards as DEN or tiller strength decline to low levels. Further, there was evidence that the forces required to sever a bite differed considerably across sward treatments.

The potential influences of bite depth, HT and mouth dimensions upon the efficiency of tiller capture per bite, were examined in simple models. These indicated that by penetrating to around 40-50% of HT, as is commonly the case, animals appear to optimise grazing efficiency in terms of the number, length and quality of tillers captured, per unit of grazing effort.

Bite weight increased linearly in relation to HT and DEN, but HT had the dominant influence, because bite volume increased with HT but declined with DEN. However, bite weight still increased rapidly with DEN, because the rate of reduction in bite volume was much lower than the rate of increase in DEN.

Bite rate declined linearly in relation to increasing HT and DEN, primarily because of their influence upon bite weight. However, bite rate was slightly more sensitive to increases in bite weight due to HT than DEN, evidently because bites of dense herbage required less gathering, while bites of long herbage required extra jaw movements to draw them into the mouth and/or reduce particle size.

Rate of intake increased at a declining rate with HT. The effects of HT and DEN were interactive on short swards but became largely independent and additive as HT increased.

Deer and sheep grazed the sorghum and wheat swards representing a very wide range of HT and DEN variation to a similar depth. However, sheep were able to graze 1 cm swards, whereas the minimum HT grazed by deer was 2 cm. Further, not only did sheep have larger mouths in relation to body size, they also appeared to be superior at prehending short swards compared to deer. However, the bite area of deer increased more rapidly with HT, and to higher peak levels in line with their larger mouth dimensions. Reflecting these differences, bite weight per kg $LW^{1.0}$ was much higher for sheep than deer on short swards, but the proportional difference declined with increasing HT. Practical implications are that deer would require more HT than sheep to obtain equivalent intakes.

The results are considered in relation to evidence on the foraging strategy of free grazing ruminants.

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ABBREVIATIONS

AHD	Actual horizontal displacement (cm)
BA	Bite area (cm^2)
BD	Bite depth (cm)
BR	Bite rate (bites min^{-1})
BV	Bite volume (cm^3)
BW	Bite weight (mg DM)
DEN	Herbage bulk density (mg DM cm^{-3})
DHI	Daily herbage intake (mg DM day^{-1})
dwt	Dry weight (mg)
fwt	Fresh weight (mg)
ha	Hectare (10 000 m^2)
HM	Herbage mass (mg DM cm^{-2})
HT	Sward height (cm)
IAW	Incisor arcade width (cm)
IHT	Incisor height (cm)
LC	Tiller length captured (cm)
LL	Tiller length lost (cm)
LW	Liveweight (kg)
MLC	Mean tiller length captured (cm)
N	Newtons (kg x m sec^{-2})
PBA	Maximum potential bite area for a given bite depth and height (cm^2)
PHD	Potential horizontal displacement of tiller (cm)
RHT	Height of grazed residual (cm)
RI	Rate of intake (mg DM min-1)
t	Tonne (1000 kg)
T	Treatment (eg. T1 = treatment one)
TPHD	Total potential horizontal displacement of tillers (cm)

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CHAPTER 1

INTRODUCTION

Much of the world's agricultural lands can only be practically and economically utilized through grazing animals, and grazing lands provide most of the feed eaten by livestock, as well as the cheapest forms of animal production (Morley 1981). Restricted nutrient intake is probably the major factor limiting production of grazing animals globally (Hodgson 1982a; Black 1990). Of the limits to nutrient intake, daily herbage intake is the most variable (Hodgson 1982a), and is especially important under conditions of low to moderate herbage availability (Penning 1986), reflecting the difficulty grazing animals have in ingesting sufficient herbage per day (Vallentine 1990).

There are few fully functional models dealing with the control of herbage intake in grazing animals. This largely reflects the variability of pasture composition and growth, and the difficulties of relating herbage intake to sward characteristics (Christian 1981). Those models which do exist tend to utilize untested assumptions regarding ingestive behaviour and diet selection (Illius & Gordon 1987; Ungar & Noy-Meir 1988). Illius & Gordon (1990a) concluded that it was inappropriate to define optimal grazing strategies for mammalian herbivores because of the current lack of knowledge of selective and ingestive behavioural processes.

The mass and structure of the sward affect daily herbage intake, height being particularly important on sown temperate swards, and bulk density and proportion of leaf being more important under tropical sward conditions (Hodgson 1982a). In the many previous studies of ingestive behaviour and herbage intake, sward structural variables have typically been confounded and/or results conflicting (Burlison 1987). Although Black & Kenney (1984) successfully separated out the effects of sward height and bulk density upon bite weight and bite rate, they did not measure in any detail the spatial dimensions of the bite which reveal the actual mechanism of bite weight adjustment as sward structure changes.

The principal aim of the experiments in this thesis was to understand the individual and relative effects of sward height and bulk density upon ingestive behaviour, by independent manipulation of these sward variables. Of particular interest were the spatial bite dimensions, over the range of variation likely to restrict daily herbage intake. Observations were made on Red deer, a less well understood, comparatively new agricultural species (defined as an adaptable intermediate feeder (Hofmann 1985)) in comparison with sheep (defined as a selective grazer (Hofmann 1985)). Sheep formed a basis of reference because of the existing volume of literature about this species. The likely modification of height and bulk density effects on ingestive behaviour by variations in other sward structural characteristics including leaf:pseudostem ratio, pseudostem height, tiller shear strength and dead matter content were also examined.

CHAPTER 2

THESIS OUTLINE AND STRUCTURE

2.1 Thesis structure

This thesis is based upon five related ingestive behaviour studies, reported in the form of four separate papers (Chapters 5-8) prepared for publication in scientific journals. Chapter 3 contains a collection of plates illustrating experimental techniques. Chapter 4 contains the general literature review, with more specific and detailed reference to literature occurring in the discussion sections in Chapters 5 through 9. Chapter 9 contains the general discussion and concluding summary.

2.2 The structure of the chapters describing the five ingestive behaviour studies

1) **Chapter 5** (Paper 1) examined the comparative ingestive behaviour of deer and sheep grazing swards 3-21 cm high x 0.19-0.75 mg DM cm^{-3} (bulk density) by utilising the upper 26 cm deep leafy horizon of tall vegetative sorghum swards (Plates 1 & 8). All swards were trimmed to the same height, and grazable height was determined by passing rods through the sward at 3 to 21 cm below the trimmed surface to form an impenetrable grid. This paper is based on that published in 1991 in The Proceedings of the New Zealand Society of Animal Production 51, 159-165.

2) **Chapter 6** (Paper 2) included measurement of the comparative ingestive behaviour of deer and sheep over an extremely wide range of bulk density variation in two studies using a seedling wheat sward technique (Plates 2, 3 & 9). The high energy reserve of wheat resulted in tillers of similar size regardless of the sowing density. In the first study height was restricted to 3-7 cm largely to avoid confounding height and bulk density

variation with changes in tiller size. Via modification of the sward growing technique, a second study enabled the height range to be extended to 4-13 cm, with bulk densities of 0.63-3.25 mg DM cm^{-3} (Plates 5 & 10). This chapter was based on a paper submitted to the Journal of Applied Ecology.

3) **Chapter 7** (Paper 3): Further development of the wheat sward technique enabled the production of 1-8 cm x 0.65-2.90 mg DM cm^{-3} leafy swards with reduced variation in leaf depth in relation to height variation. This enabled bite dimensions to be measured over what the previous studies had indicated would be the most critical and dynamic range of heights. This chapter was also based on a paper submitted to the Journal of Applied Ecology.

4) **Chapter 8** (Paper 4) utilised five different sward types to examine the effects of changes in leaf:pseudostem ratio (Plate 7), pseudostem height, dead matter content (Plate 6), their proximity in the sward, and tiller shear strength on the bite depth and bite area of sheep. This chapter was based on a paper submitted to the New Zealand Journal of Agricultural Research.

Results are presented in the text as fitted regression lines. Treatment means and standard errors of bite parameters are listed in Appendices 3-5.

CHAPTER 3

ILLUSTRATIONS OF EXPERIMENTAL CONDITIONS

3.1 Experimental techniques

Sward techniques developed by previous researchers were too time consuming (Black & Kenney 1984) or confounded treatment variation with considerable differences in tiller structure (Burlison 1987) and were thus inappropriate (see Chapters 5, 6 & 9). Consequently, much of the first year's research was spent developing two new sward preparation techniques; these were grid based (Plates 1, 7, 8) and wheat seedling (Plates 2, 3, 4, 5, 9 & 10) sward techniques used in Chapters 5 & 8, and Chapters 6-8, respectively. Experimental Red deer and Romney sheep were selected from initial pools of 15 weaner hinds and 20 ewe lambs, and were trained over a period of several months (Plate 8). In general, the same individual animals were used for each of the five experiments. Their ages increased from approximately 12 to 36 months over the experimental period.

Plate 1 : A partially grazed 15 cm sorghum sward (Chapter 5) illustrates how the same sward surface could be presented to the grazing animal at heights of 3-21 cm, simply by moving the sward up or down relative to an impenetrable grid of rods. A number of tropical grasses, erect temperate grasses and gramineous forage crops were evaluated for suitability. *Sorghum bicolor* (cv. Jumbo) was selected as it produced the most uniform and deepest pseudostem-free leafy horizon. The illustrated sward was a prototype grown in winter; experimental swards were virtually free from dead matter within the grazed stratum.

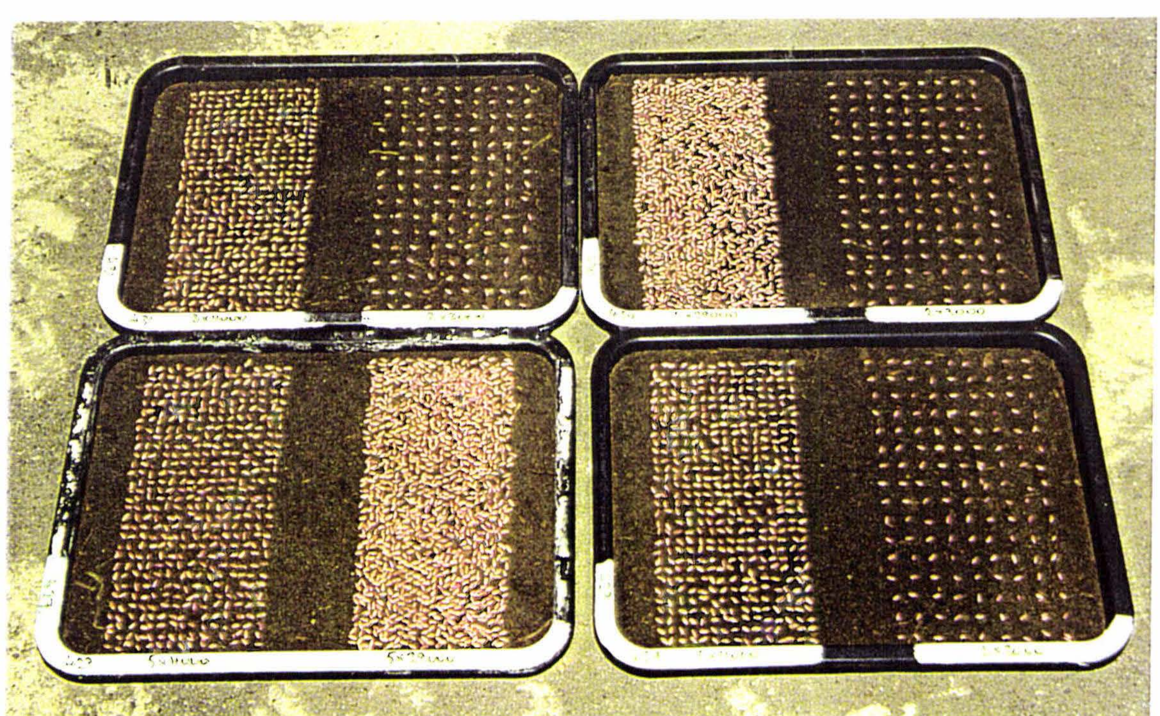

Plate 2 : Wheat seeds (Chapters 6 & 7) were sown evenly onto level potting mix, pressed down and covered gently with sand. When grown, the three sowing densities illustrated were equivalent to 2.90, 1.30 and 0.33 mg DM cm^{-3}.

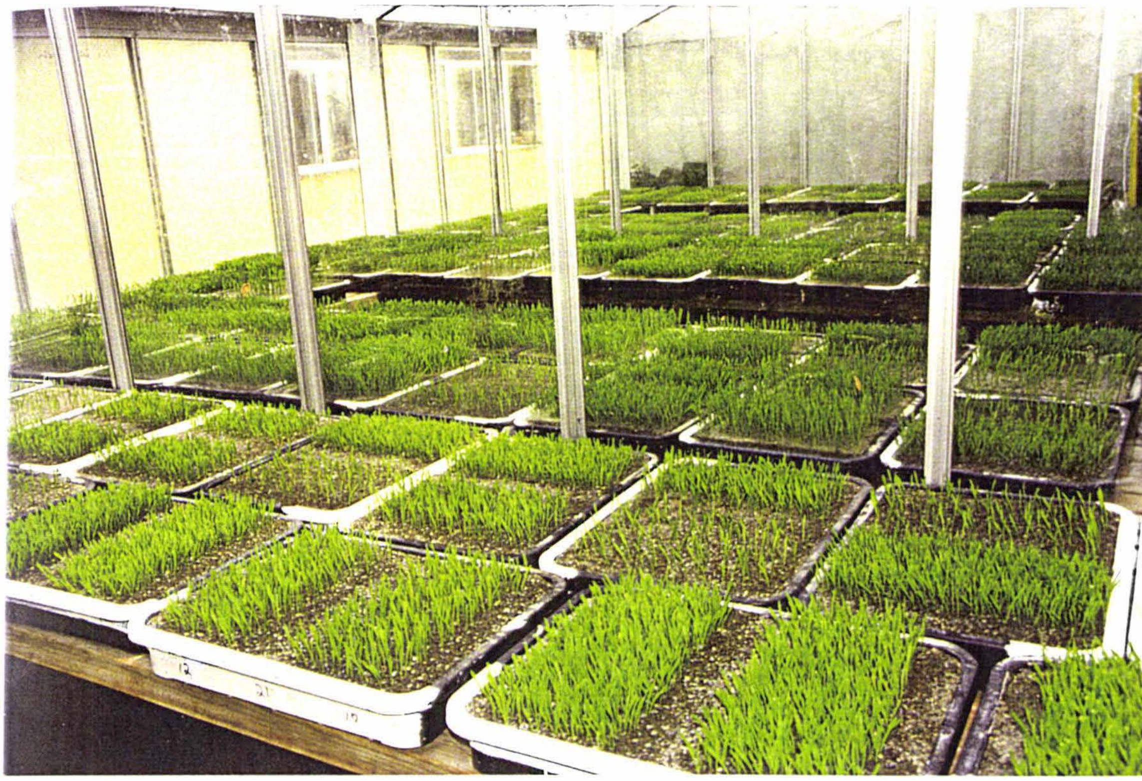

Plate 3 : Five-day old wheat swards (Chapters 6 & 7) growing vigorously in a series of temperature regulated glasshouses. Many grain species and cultivars were evaluated for uniformity of germination, tiller size and structure, and severing characteristics (their inherent tendency to sever below where they were actually gripped); these included oats, barley, rye, triticale and many wheat cultivars. Based on these criteria *Triticum aestivum* (cv. Rongotea) was selected.

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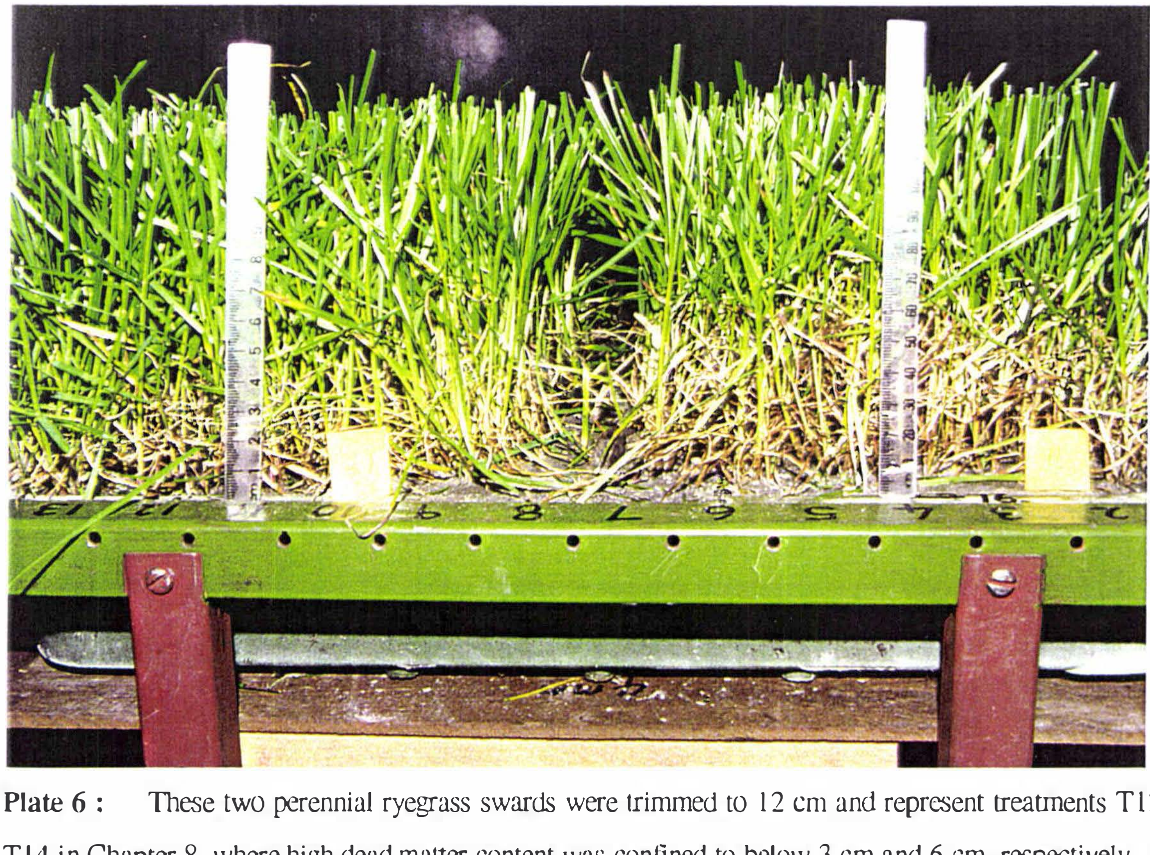

Plate 6 : These two perennial ryegrass swards were trimmed to 12 cm and represent treatments T12 and T14 in Chapter 8, where high dead matter content was confined to below 3 cm and 6 cm, respectively. They were used to examine the effects of dead matter on the bite dimensions of sheep.

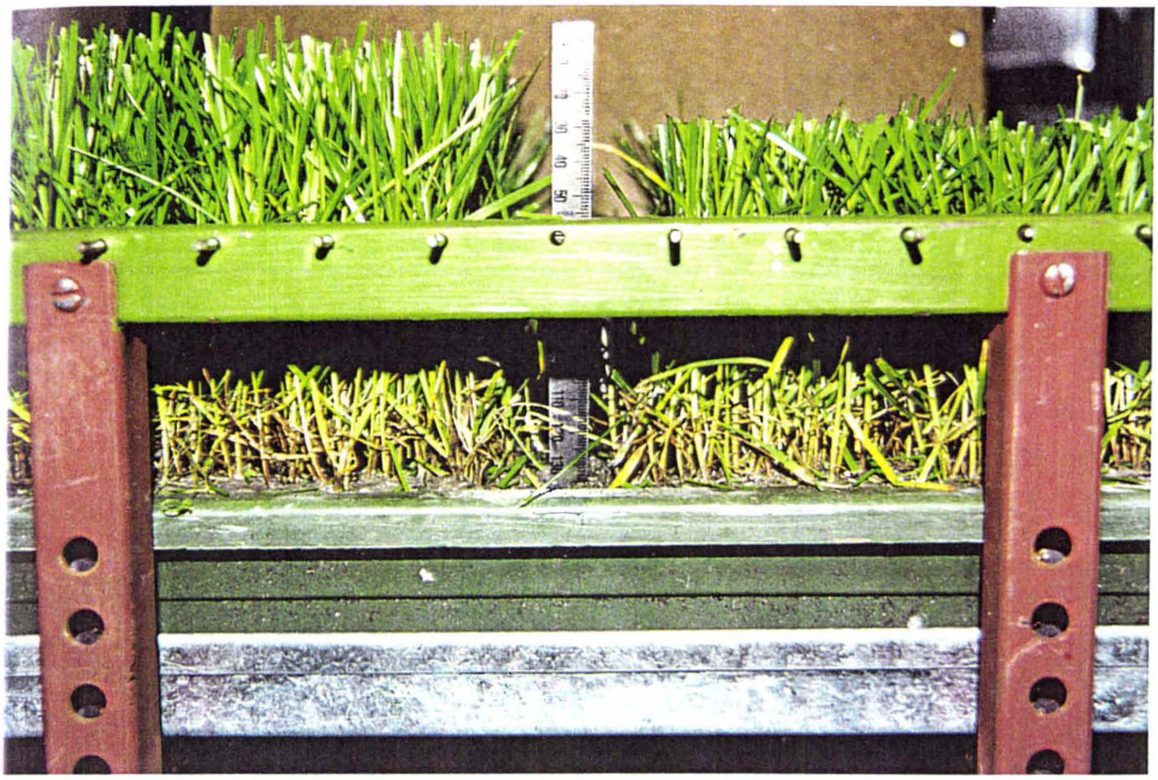

Plate 7 : The effect of increasing pseudostem content upon the bite dimensions of sheep were examined by trimming these swards to 13, 10, 7 or 4 cm above ground level and passing rods through the sward at 3 or 6 cm below the trimmed surface (Treatments T1-T7 in Chapter 8; T5 & T2 are depicted from left to right).

Plate 8 : Training a young hind (about 7 months old) to graze experimental swards using a 15 cm prototype grid-based sorghum sward (Chapter 5).

Plate 9 : A sheep grazing a 5 cm x 2.90 mg DM cm^{-3} wheat sward (Chapter 6). Note how the upper lip is curled back when gathering herbage for another bite, and how herbage from the previous bite is still visible on the tongue.

Plate 10 : A mature hind about to close its jaws on a mouthful of wheat tillers. One can see how longer herbage such as this needs to be drawn into the mouth after being severed.

CHAPTER 4

GENERAL LITERATURE REVIEW

This chapter provides a general review of the literature. More detailed references to items of literature are made in the chapters relating to specific experiments.

4.1 Introduction

When herbage availability is high, physical constraints such as particle size, digestibility, rate of passage and rumen size (Chacon & Stobbs 1976; Freer 1981; Minson 1982; Armstrong *et al.* 1986; McLeod & Smith 1989) may largely restrict herbage intake in the grazing animal. However, the long feeding times under grazing (4-14 hours, Arnold 1981) compared to stall feeding (1.5-2.8 hours, McLeod & Smith 1989) reflect the behavioural constraints or difficulty which grazing animals face in prehending and ingesting sufficient herbage per day (Hodgson 1990a; Vallentine 1990). Behavioural constraints become increasingly important when herbage mass (HM) (Johnston-Wallace & Kennedy 1944; Hodgson 1990a) or particularly herbage accessibility (Allden & Whittaker 1970; Chacon & Stobbs 1976; Black & Kenney 1984) become restrictive. As herbage availability declines animals cannot maintain the weight of herbage ingested per bite (BW) (Hodgson 1985; Penning 1986; Dougherty *et al.* 1988) but may be able to compensate to a limited degree by increasing bite rate (BR) and/or grazing time. However, eventually daily herbage intake (DHI) will also decline (Arnold 1960b; Penning 1986; Chacon & Stobbs 1976; Jamieson & Hodgson 1979b).

As listed in Burlison (1987), many earlier studies have described sward conditions simply in terms of HM or height (HT) and, in some cases digestibility. Such measures tend to overlook differences in sward canopy structure which may alter the ingestive process and consequently DHI in relation to HM (Chacon *et al.* 1978; Freer 1981; Hodgson 1985). As well as ignoring differences in tiller structure, either down through the sward profile or between swards (Stobbs 1973b; Baker *et al.* 1981; Barthram & Grant 1984; Wade 1991; Cosgrove 1992), such measurements do not account for the effects of HT and bulk density (DEN). HT and DEN appear to have dominant roles in determining BW, but to different degrees under different circumstances, such as temperate (Black & Kenney 1984) vs tropical (Chacon & Stobbs 1976) sward conditions (Hodgson 1982a).

Early studies highlighting the importance of HT or DEN variation include that of Allden & Whittaker (1970), who removed strips of herbage in temperate grass swards to show that the rate of intake (RI) of sheep was not strictly associated with HM. In a second experiment they demonstrated how BW increased linearly up to 40 cm HT, although simultaneous reductions in BR (and initially grazing time) maintained a constant RI for heights greater than 7 cm. Penning (1986) obtained similar results for continuously stocked sheep on 3-12 cm ryegrass pastures.

Stobbs (1973b) and Chacon & Stobbs (1976) took stratified cuts of herbage down through the profile of tropical grass swards and described large differences in tiller structure and herbage quality from the top to the base. They suggested that BW was much more closely related to the DEN and proportion of leaf than HT.

In general, ingestive behaviour appears to be particularly sensitive to HT on temperate swards (Allden & Whittaker 1970; Jamieson & Hodgson 1979b; Hodgson 1981; Black & Kenney 1984; Penning 1986; Mursan *et al.* 1989; Hodgson 1990a, b; Hughes *et al.* 1991), but more closely related to DEN and proportion of leaf on tropical swards (Stobbs 1973 a, b; Chacon & Stobbs 1976; Chacon *et al.* 1978; Hendricksen & Minson 1980). However, HT and DEN tend to be negatively correlated within and between swards (Hodgson 1981; 1990a) and confounded with other changes in tiller structure. Consequently, it is very difficult to disentangle the separate effects and relative importance of HT and DEN, two "major variables" (Burlison *et al.* 1991) influencing BW and DHI.

Black & Kenney (1984) and Burlison *et al.* (1991) attempted to describe the individual effects of a wide range of HT and DEN variation on the ingestive behaviour of sheep. Black & Kenney

(1984) painstakingly hand-threaded tillers through hardboard sheets with different hole densities to avoid confounding tiller size and DEN variation (0.17-4.23 mg DM cm^{-3}), as well as to achieve a similar tiller structure at the sward surface regardless of the HT (1-22 cm). These swards lacked some of the natural changes in tiller structure down the sward profile such as a pseudostem zone of proportionally similar depth in relation to HT (swards of less than 18 cm were all leaf to the base). Further differences in tiller rigidity, breaking strength and weight per unit length were not measured along the length of tillers. However, these limitations were probably of minor significance and the experiment provided a large step forward in terms of understanding the individual effects of HT and DEN variation on ingestive behaviour. Black & Kenney (1984) found that RI was several fold higher on tall sparse swards than short dense swards when HM was less than 1000 kg DM/ha, indicating the critical importance of HT on low herbage mass swards. They found RI was only related to HT or DEN when the other factor was constant, and that the best predictor of RI was the mass of herbage sheep could encompass with an individual bite. The effects of HT and DEN on BW and RI appeared to be interactive up to about 6 cm HT and then became largely independent and additive.

Burlison (1987) used 17 grass and oat swards grown under different sowing and trimming regimes to generate a wide range of largely independent HT and DEN variation (5.7-55.2 cm and 0.12-2.04 mg DM cm^{-3}). However, many of these swards would have differed markedly in tiller structure. BW was only highly correlated with HT when the very tallest swards were included in the data set, possibly because treatment differences in tiller structure prevented a very close relationship between HT and BD. The effects of HT and DEN on BW appeared to be independent and additive.

The work of Black & Kenney (1984) showed that BD declined with increasing DEN on tall swards. They did not however, fully describe how animals alter the depth of penetration or the horizontal area of herbage prehended per bite, which reflect the actual prehensile adjustments made by the animal in relation to changing sward conditions (i.e. the mechanism of BW adjustment).

Burlison (1987) gave indications of how BA and particularly BD were affected by HT and DEN, but did not establish clear relationships between these variables, presumably because of confounding variation in tiller structure between treatments.

Ingestive behaviour has also been reviewed recently by Gordon & Lascano (1993) and Hodgson, Clark & Mitchell (1994). Further, near the completion of this current project, Demment and his colleagues published a series of papers (Laca *et al.* 1992a, b, 1993) showing the spatial bite dimensions and BW of large steers in relation to changing sward HT and DEN; consideration of this work is deferred to the discussion sections of individual experiments and the general discussion.

4.2 Ingestive behaviour

4.2.1 The grazing process

The grazing process may involve patch selection followed by bite selection within the patch, when for example animals are grazing shrub communities (Ungar & Noy-Meir 1988). However, on uniform leafy swards the direction of travel is likely to be "erratic" and the "ingestion of herbage almost continuous" (Hodgson 1990a). During grazing the animal moves forward with the head moving from side to side in a horizontal plane and selects in the vertical plane, using mobile lips in sheep, or prehensile and protractile tongue in cattle to gather the herbage (Arnold 1960a, 1981; Hodgson 1986). Herbage is gripped between the incisors and dental pad and severed by jerking the head. Alternatively, leaves may be "nibbled" from tall lucerne or tropical swards (Arnold 1981).

4.2.2 The spatial dimensions of the bite

Models of ingestive behaviour have generally assumed that animals graze to the same very short residual as HT increases, up to a point (determined by mouth dimensions) above which bite depth (BD) remains constant (Ungar & Noy-Meir 1988; Laca *et al.* 1992b). Further, bite area (BA) was assumed to be constant (Ungar & Noy-Meir 1988), or to be proportional to incisor arcade width and to increase with HT in a simple mechanistic manner (Illius & Gordon 1987).

However, the empirical evidence does not necessarily support these assumptions. For example, sheep grazing grass/oat swards penetrated to about half the depth of the leafy horizon (Burlison 1987), while cows removed 30-40% of current extended tiller height, regardless of leaf depth and grazing management (Wade 1991). In contrast, sheep continuously stocked on short swards appeared reluctant to penetrate the pseudostem zone, even when leaf depth was only 1.6 cm (Barthram 1981; Barthram & Grant 1984). Thus animals appear to adjust BD in relation to HT, although depth of leaf (Hodgson 1986) or pseudostem height may become increasingly important on some short temperate swards (Barthram 1981; Hodgson 1986). Similarly, leaf:stem ratio may determine BD and depth of grazed stratum on tall tropical swards (Stobbs 1973b).

Although BA appeared to be positively related to HT (Betteridge *et al.* 1991) within plant species (Burlison *et al.* 1991), other studies have suggested that BA was insensitive to HT (Mursan *et al.* 1989; Hughes *et al.* 1991) and negatively related to DEN (Wade *et al.* 1989; Burlison *et al.* 1991; Hughes *et al.* 1991).

Based on the constant rate of head acceleration observed by Chambers *et al.* (1981) for sheep and cattle grazing a range of sward conditions, Hodgson (1985) suggested that animals may regulate BA in an attempt to maintain or limit the biting effort necessary to sever a bite as DEN and/or tiller strength changes. When examined experimentally with a force plate meter (Hughes *et al.* 1991), sheep did reduce BA as DEN increased but also appeared to adjust biting effort in relation to the size of bite they could achieve.

It has been suggested that animals might constrain BD in an attempt to limit biting effort, because DEN and tiller strength are likely to increase deeper in the sward (Burlison *et al.* 1991; Cosgrove 1992). Further, shallower bites should result in the ingestion of shorter fragments of higher quality herbage, which may optimally balance BW and BR (by reducing chewing) in terms of maximising RI (Kenney & Black 1984; McLeod & Smith 1989; Cosgrove 1992).

4.2.3 Bite weight

Bite weight (BW) is the bite parameter most sensitive to sward conditions (Jamieson & Hodgson 1979b; Hodgson 1985), increasing 20-fold in relation to a 2-fold reduction in BR as HM increased from 0.04 to 7.61 t DM ha^{-1} (Black & Kenney 1984). Black & Kenney (1984) showed that BW was very sensitive to both HT and DEN, and was highly predictable, only when both these parameters were known. Other sward structural characteristics which apparently influence BW are dead matter content (Stobbs 1974; Black *et al.* 1989) and pseudostem height or leaf depth (Arias *et al.* 1990; Dougherty 1991), particularly on short continuously stocked swards (Barthram & Grant 1984). However, on vegetative ryegrass turfs dug from pasture, then trimmed and regrown to alter leaf:pseudostem ratio and/or pseudostem height, such variables had little if any effect upon BW and BD of sheep (Hughes *et al.* 1991), suggesting that the qualitative differences between the same herbage components may alter their effect in different experiments. On tropical swards BW is also sensitive to leaf:stem ratio and the distribution of leaf (Stobbs 1973a, b; Chacon & Stobbs 1976; Hendricksen & Minson 1980).

Although the experimental evidence (Allden & Whittaker 1970; Jamieson & Hodgson 1979b; Hodgson 1981, 1985; Collins & Nicoll 1986) is inconclusive, when scaled to body size the proportionally larger mouths of smaller animals (Clutton-Brock *et al.* 1987), and their relatively deeper bites at any given HT (Illius & Gordon 1987), should in theory give smaller animals the BW advantage on shorter swards. In comparison, the scaling of gut capacity and metabolic rate to body size suggest large animals should be better able than smaller grazers to process tall swards which yield larger bites of lower quality herbage (Jarman 1974; Demment & Van Soest 1985; Illius & Gordon 1987, 1990a; Demment & Greenwood 1988). The above, body size related differences are thought to lead to the seasonal habitat segregation of grazers, such as sexually dimorphic Red deer (Staines *et al.* 1982; Clutton-Brock *et al.* 1987) and different sized animals such as Red deer and sheep (Osborne 1984).

In most studies on temperate swards BW increased with HT for both sheep and cattle, and usually in a close to linear manner (Allden & Whittaker 1970; Jamieson & Hodgson 1979b; Hodgson 1981; Forbes & Hodgson 1985a; Penning 1986), indicating that BD increased with HT. Black & Kenney (1984) achieved similar results, except on the very high density ryegrass swards where BW increased linearly, only up to a peak of 6.5 cm.

Studies with both tropical grasses (Stobbs 1973a, b; Chacon & Stobbs 1976; Chacon *et al.* 1978; Ludlow *et al.* 1982) and tropical legumes (Hendricksen & Minson 1980) have generally indicated that BW was more closely related to the DEN, distribution and proportion of leaf, than to HT. In some of these trials where sward structure was manipulated with plant growth regulators, fertiliser and/or different periods of regrowth, BW actually declined with increasing HT (Stobbs 1973a, b; Ludlow *et al.* 1982). However, these weak or even negative HT effects upon BW may well reflect the declining DEN and/or quality of grazable components (near the surface of swards), which were associated with the increases in HT (Stobbs 1973a, b; Ludlow *et al.* 1982). Similarly, RI and presumably also BW were more closely related to DEN than HT on pure clover swards where most of the lamina were concentrated at the top of the sward (Kenney & Black 1986).

4.2.4 Bite rate

When grazing, an animal's bite rate (BR) will be largely determined by the average search time (scanning, recognition, decision) and handling time (biting, manipulating, chewing, swallowing) (Ungar & Noy-Meir 1988) per bite. The diversity of the food source will determine whether animals are selecting patches and sites within patches (as when grazing heterogeneous shrub communities), or simply bite-sites (as within uniform managed swards) (Ungar & Noy-Meir 1988). On managed temperate pastures, handling time is likely to be the more important with respect to limiting BR (Hodgson 1990a; Cosgrove 1992).

BR varies widely (for example 22-94 bites min^{-1} in sheep (Hodgson 1986)), but the rate of total jaw movements appears to be reasonably constant with the ratio of ingestive to manipulative movements changing as HT, DEN or HM change (Black & Kenney 1984; Penning 1986; Penning *et al.* 1991a). However, animals can increase the rate of total jaw movements when hungry, with most of the increase being in terms of BR so that RI is increased, although at the expense of increased particle size (Greenwood & Demment 1988).

Black & Kenney (1984) found BR was closely related to BW, with ingestive bites increasing from 20 to 80% of the constant number of total jaw movements as BW decreased from 200 to 10 mg DM. As a consequence, sheep were able to maintain RI until BW fell below approximately 100 mg DM. Similarly, as the BW of sheep declined with decreasing HT, increases in BR were adequate to maintain RI until sward HT declined to below about 8 cm (Allden & Whittaker 1970).

Thus BR appears to vary predictably in relation to BW, when for example sheep are grazing vegetative ryegrass swards of different heights (Allden & Whittaker 1970; Black & Kenney 1984; Penning *et al.* 1991a). However, BR can differ appreciably in relation to BW, within the upper compared to lower sward strata (Dougherty *et al.* 1990; Cosgrove 1992), on clover compared to grass (Penning *et al.* 1991b), on long compared to short herbage or in relation to herbage maturity (Spalinger *et al.* 1988; Gong *et al.* 1993; Gong 1994). Further, at least in cattle, BR can be insensitive to changes in BW over a certain range (Hodgson 1981; Moore & Sollenberger 1986; Greenwood 1990; Demment *et al.* 1992), probably in part because of the overlap in function of chewing and manipulative jaw movements enabling animals to simultaneously manipulate and chew most of the herbage accumulating in the mouth, provided bites are not too large (Demment *et al.* 1992). Similarly, the BR of reindeer foraging on Alaskan tundra appeared unrelated to BW, but was related to the availability of and opportunity for selection of palatable vascular plants (Trudell & White 1981). Thus while BR may change in relation to BW (Dougherty *et al.* 1988), as suggested by Hodgson (1985), BR may also be a direct consequence of sward conditions.

4.2.5 Rate of intake and daily herbage intake

Although measurements of ingestive behaviour may be impractical in the determination of daily herbage intake (DHI) (Vallentine 1990), they are very useful in terms of understanding and conceptualising how grazing animals respond to sward conditions (Holmes 1982; Demment *et al.* 1992). Consequently, such measurements are an integral part of the development of grazing systems (Forbes 1988).

Penning & Hooper (1985) found that short term rate of intake (RI) measurements were not significantly different from those based on daily averages (ie. proportional to DHI). However, other studies suggest short term measurements may over-estimate the average daily RI (or BR and therefore probably also RI) (Jamieson & Hodgson 1979a; Forbes 1982; Bazely 1988; Illius 1989). Further BR and RI may change within (Stobbs 1974; Jamieson & Hodgson 1979a; Dougherty *et al.* 1987, 1992) or between bouts (Stobbs 1974; Phillips & Leaver 1986; Forbes 1988). Ideally measurements of ingestive behaviour should be long enough to include search time (Forbes & Hodgson 1985a) and be taken several times a day covering at least the major grazing periods (Hodgson 1982b). Although RI and DHI estimates may not always be directly proportional in relation to time, their response trends to increasing HM frequently appear similar, with both showing a rapid, but often declining rate of increase which levels off and plateaus (Allden & Whittaker 1970; Hodgson 1977; Black & Kenney 1984; Penning 1986; Laca & Demment 1991).

In general, RI is likely to be positively related to both HT and DEN in temperate sward conditions (Burlison *et al.* 1991; Hughes *et al.* 1991). At low to moderate HM the influence of HT appears to be dominant (Black & Kenney 1984). For example, the RI of sheep on hand-constructed ryegrass swards peaked at 6.5 cm on high DEN swards with a HM of 2.7 t DM ha^{-1}, but at 10.5 cm on medium DEN swards despite their much lower HM of 1.1 t DM ha^{-1} (Black & Kenney 1984). Increases in BW on taller swards were counterbalanced by reductions in BR so that RI did not increase. Similarly, on natural ryegrass pastures RI and DHI plateaued at heights above 6 cm, due to reductions in BR, or BR and grazing time respectively (Penning 1986). Further, herbage quality and leaf density declined above 6 cm pasture HT (Penning *et al.* 1991a). In contrast, on tropical grass swards RI appears to be more sensitive to the DEN and proportion of leaf, than to HT (Chacon & Stobbs 1976). Similarly, lamina DEN appears to be more important than HT in determining RI on leguminous swards, both temperate (Kenney & Black 1986) and tropical (Hendricksen & Minson 1980).

The need to optimally balance the maintenance of ideal sward conditions (Hodgson & Maxwell 1981; Parsons & Johnson 1986; Grant *et al.* 1987) with the differing intake requirements of various stock classes has led to the definition of target sward heights for continuously stocked swards (Le Du *et al.* 1981; Wright & Russell 1986; Hodgson 1990a; Penning *et al.* 1991a) or target residual heights for rotationally grazed swards (Baker *et al.* 1981; Hodgson 1990a). These target heights differ somewhat with seasonal changes in tiller density and structure, and animal requirements (Hodgson & Maxwell 1984; Hodgson 1990a). Optimum heights for continuously stocked perennial ryegrass swards have been defined as 3-6 cm for sheep (Penning 1986; Hodgson & Maxwell 1984; Maxwell & Treacher 1987; Orr *et al.* 1990; Penning *et al.* 1991a) and 7-10 cm for cattle (Le Du *et al.* 1979, 1981; Wright & Whyte 1989). In comparison, recent work with weaner stags demonstrated increased LW gains during spring (59%) and winter (107%) on 10 cm compared to 5 cm ryegrass/white clover swards (Ataja *et al.* 1989, 1992).

Hodgson (1981) found that the effect of changing HT on the RI of calves or lambs was greater under rotational grazing than continuous stocking. The marked changes in structure of the grazed stratum under rotational grazing appears to alter the relationship between HT and ingestive behaviour compared to continuous stocking (Jamieson & Hodgson 1979a, b; Penning *et al.* 1989; Hodgson 1990a) where, regardless of HT, animals are likely to be eating predominantly green leaf (Barthram 1981; Clark 1993). The availability of green leaf is probably a major determinant of DHI on both temperate and tropical swards (Arnold & Dudzinski 1967b; Stobbs 1974; L'Huillier *et al.* 1986; Sheath *et al.* 1987; Penning *et al.* 1989). Clover content of temperate swards can also influence liveweight gain and presumably DHI (Askin *et al.* 1987; Rattray *et al.* 1987; Sheath *et al.* 1987).

However, there may be little difference between grazing methods in terms of DHI (Allden & Whittaker 1970; Le Du *et al.* 1981), reflecting the fact that the differences in frequency and intensity of defoliation may not be large, and tend to balance out (Wade & Baker 1979; Chapman & Clark 1984; Wade 1991). Stocking rate is a much more important determinant of DHI (Morley 1981; Hodgson 1989), as it alters the herbage available per animal. As stocking rate is raised, both efficiency of conversion of ingested herbage into animal product and per animal production fall, although animal production per ha increases, because of the even greater increase in the efficiency of utilisation of herbage growth (Hodgson 1990a). Stocking rate will be a major determinant of ingestive behaviour in any given sward situation as it will largely determine the structure of the sward and/or the rate and direction of change, with HT declining as stocking rate increases (Grant *et al.* 1987; Hodgson 1990a). It is noteworthy however that within normally practised levels, stocking rate may have little direct effect upon herbage production or upon herbage quality (Hodgson & Wade 1978; Hodgson & Maxwell 1981; Grant *et al.* 1987).

4.3 Diet selection

Although not examined specifically in this study, diet selection is inevitably part of all ingestive behaviour trials. Even if animals are grazing monocultures (ie. not selecting different plant species) they still ingest herbage with a different composition to that of the whole sward (Burlison 1987; Bazely 1988). The composition of the grazed stratum may reflect the active selection of legume over grass (Milne *et al.* 1982; Laidlaw 1983; Moore & Sollenberger 1986; Armstrong *et al.* 1993), leaf from stem or pseudostem (Arnold 1960a; Hendricksen & Minson 1980; Arnold 1981; Laidlaw 1983; L'Huillier *et al.* 1986; Ruyle *et al.* 1987; Edwards *et al.* 1993; Flores *et al.* 1993), or short frequently grazed areas over rank infrequently grazed areas (Bakker *et al.* 1983; Gibb 1991). Similarly, by adjusting BD, animals may select the upper leafy horizon and avoid lower horizons containing dead matter and rigid pseudostem material (Barthram & Grant 1984; L'Huillier *et al.* 1984; Dougherty 1991; Clark 1993), particularly when such swards are infected with endophyte (Edwards *et al.* 1993). Further, sheep select for urine patches (Keogh 1973), whereas to varying degrees both sheep and cattle avoid dung (Hamilton *et al.* 1976; Hodgson *et al.* 1987).

BR (Jamieson & Hodgson 1979b; Hodgson 1986; Ruyle *et al.* 1987) and probably also BV (Arnold 1981; Trudell & White 1981; Hodgson 1986; Black *et al.* 1989; Dougherty *et al.* 1990) may be adjusted to enable selection of palatable components within the grazed stratum. The need for adjustment of bite dimensions is likely on tropical grass or legume swards where the quality of large components is highly differentiated (Chacon *et al.* 1978; Hendricksen & Minson 1980), or reproductive temperate swards where the quality of stem and leaf are very different (Arnold 1960a; L'Huillier *et al.* 1986; Flores *et al.* 1993).

Animals are sensitive to the ease and rate at which they can eat herbage (Kenney & Black 1984; Black *et al.* 1989; Colebrook *et al.* 1987, 1990) and may select for taller or denser herbage (Black & Kenney 1984; Arnold 1987; Bazely 1988, 1990; Illius & Gordon 1990a; Distel *et al.* 1991; Griggs *et al.* 1991b; Demment *et al.* 1993), sward characteristics which tend to increase RI (Black & Kenney 1984). The selectivity of animals is also likely to vary in relation to hunger (Arnold 1981), the quality (Schwartz & Ellis 1981) and availability of the feed source (Hamilton *et al.* 1973; Penning *et al.* 1986; Moore & Sollenberger 1986), particularly in relation to the availability of other preferred foods, as well as the size and distribution (Clark & Harris 1985) of food patches (Crawley 1983). Further, the need for constant sampling in heterogeneous environments is likely to limit the ability of grazing ruminants to optimise any particular intake goals (Crawley 1983; Illius *et al.* 1992).

Alternatively selection may be passive (Arnold 1981; Dougherty *et al.* 1988), with the grazed stratum simply representing herbage at the surface (Hodgson 1986) being most easily and efficiently prehended. At high intensities of grazing the diet may in part reflect differences in the growth rate of plant species rather than preference by the animal (Parsons *et al.* 1991). In many swards, selection for different plant species, types or associations (Arnold 1981, 1987) may reflect gross chemical or surface properties of the plant which are detectable to the animal principally via touch, taste and smell (Arnold 1966, 1981; Arnold *et al.* 1980). However, many nutritionally important compounds are not detectable to the animal and therefore do not influence diet selection (Arnold 1981).

Differences occur between animal species regarding mouth and incisor structure (Gordon & Illius 1988), flexibility and manoeuvrability of the lips, and use of the tongue (Vallentine 1990). These factors affect the way an animal grazes and may set different limits on how close to the ground it can graze (Dudzinski & Arnold 1973) and its ability to be selective (Vallentine 1990), possibly explaining some of the apparent sheep/cattle differences in diet selection. Species differences in ingestive behaviour and diet selection may result in some advantages being achieved through mixed grazing (Nolan & Connolly 1989; Lambert & Guerin 1989).

4.4 Animal factors affecting herbage intake and ingestive behaviour

The balance between metabolic, physical and behavioural constraints to DHI may change in relation to the species, age, nutritional or physiological status of an animal due to differences in potential nutrient intake, rumen size and grazing efficiency (Hodgson 1977).

Differences in animal size due to species (Bell 1971; Jarman 1974), sex (Staines *et al.* 1982) or age (Illius & Gordon 1990b) may affect the likely fitness of an animal within a particular sward environment due to the allometric relationships between BW, metabolic rate and body size (Illius & Gordon 1987, 1990a; Taylor *et al.* 1987). Further, an animal's grazing habits and dentition (Gordon & Illius 1988; Illius & Gordon 1990a) can also affect its fitness in different plant communities. Because dentition matures more rapidly than body weight (Taylor *et al.* 1987; Illius 1989) (and faster in deer (Challies 1978; Tisdall *et al.* 1985) than sheep (Bray *et al.* 1989)), light immature animals might be expected to have an advantage over mature animals in terms of BW scaled to LW (Illius 1989). This would clearly be advantageous as their energy demands are much higher due to the requirements of growth, as well as maintenance. Illius & Gordon (1990b) however, suggested that the gradual replacement of juvenile with adult incisors may place the young animal at a disadvantage in terms of incisor width and body size during this transition stage.

Thin (Arnold 1981; Weston 1982) or hungry (Jung & Koong 1985; Dougherty *et al.* 1988; Greenwood & Demment 1988; Greenwood 1990) animals will tend to have a higher RI and/or DHI than fat or non-fasted animals respectively. Further, DHI tends to increase greatly during lactation, slightly during early pregnancy and decline in late pregnancy (Arnold & Dudzinski 1967a; Freer 1981; Weston 1982). Hot weather or high humidity can depress DHI whereas cold conditions tend to increase it (Weston 1982). Herd size, breed, social status and distribution of urine and dung may all affect how animals move about and utilise their food resource (Keogh 1973; Forbes 1982; Forbes & Hodgson 1985b; Hodgson *et al.* 1987; Taylor 1987). Similarly, previous grazing experience may markedly affect diet selection and grazing efficiency, particularly when animals go to more complex or less favourable feeding conditions (Arnold & Maller 1977; Curll & Davidson 1983; Flores *et al.* 1989a, b).

Differences occur between animal species in the way they select or utilise herbage. For example, lambs ate more clover and less grass than calves (Hughes *et al.* 1984). Cows tend to graze evenly at the sward surface (Forbes 1982; Forbes & Hodgson 1985a; Hodgson *et al.* 1991), removing herbage in layers (Wade 1991), compared to sheep which can be deeper, more selective (Jamieson & Hodgson 1979b; Forbes 1982; Hodgson *et al.* 1991) and patchier grazers (Morris 1969; Forbes & Hodgson 1985a). Exceptions will occur of course, for example in some circumstances sheep can be less selective than cattle (Schwartz & Ellis 1981). Similarly, goats differ from sheep in taking shallow bites, selecting browse if available (Hughes 1988) and grazing seed heads, stem and leaf from the top of reproductive swards (Gong *et al.* 1993), whereas sheep will penetrate the upper layer to access leafy material at the base of the sward (L'Huillier *et al.* 1984, 1986; Gong *et al.* 1993).

4.4.1 Red deer and sheep

Sheep (*Ovis aries*) are defined as "selective grazers" and are "efficient grass and roughage eaters", while Red deer (*Cervus elaphus* L.) are "intermediate feeders" equally able to browse woody vegetation or graze pastures (Kay & Staines 1981; Hofmann 1985). As seasonally adaptable, versatile opportunists, Red deer tend to exploit the best source of nutrients available (Kay & Staines 1981; Hofmann 1985).

Lactating hinds were observed to graze predominantly from the upper sward horizons of indigenous hill and improved ryegrass pastures (Loudon *et al.* 1984), suggesting perhaps that in this respect deer may be more like cattle and goats than sheep (Forbes 1982; Gong *et al.* 1993). Given the opportunity, Red deer may range wider and graze less intensively than domestic stock, grazing selectively, possibly so as to minimise the fibre content of their diet (Kay & Staines 1981; Hofmann 1985). When their ranges overlap in New Zealand, Red deer appear to be out competed by Sika deer (*Cervus nippon*), a less selective species with a morphophysiological classification closer to that of domestic sheep (Hoffman 1985; Davidson & Fraser 1991; Lentle & Saxton 1992). However, Red deer are able to utilise poorer quality forage compared to many small deer which are concentrate selectors (Hofmann 1985). When compared to sheep on the same pasture, Red deer covered larger areas and grazed for longer (Colquhoun 1971 cited in Kay & Staines 1981). Red deer have been observed to graze short swards more evenly than domestic stock (Hofmann 1985). Harbord (1988) suggested that Red deer reject soiled pasture earlier than sheep or cattle.

While sheep show some degree of selection for legumes and weeds (Laidlaw 1983; Clark & Harris 1985), Red deer are noted for their tendency to seek out a varied diet (Kay & Staines 1981). On improved pastures, if given a choice, Red deer actively select weeds and legumes and avoid grasses, especially perennial ryegrass (Hunt & Hay 1989). The hinds in particular, have a clear preference for red clover over ryegrass (Hunt & Hay 1988, 1990) and achieve higher liveweight gains and lactation performance due to increased intakes on red clover compared to ryegrass/white clover pastures (Niezen *et al.* 1991; Semiadi *et al.* 1992). The increased intake (Niezen *et al.* 1991) may reflect the structure and high quality of the whole red clover sward, ie. both behavioural and physical constraints to intake may be reduced on red clover compared to ryegrass.

In contrast to cattle, but like goats, both deer and sheep have a cleft upper lip enabling them to graze close to ground level (Vallentine 1990). Both species have major periods of grazing at dawn or dusk, but only deer usually graze for significant periods at night, increasingly so if disturbed by man (Arnold 1981; Kay & Staines 1981; Lentle & Saxton 1992).

Compared to sheep, Red deer on average eat more per kg LW, have higher metabolic rates and need 30-40% more energy per kg $LW^{0.75}$ for maintenance (Kay 1981, 1985; Kay & Staines 1981; Milne & Reid 1989). Further, deer are much larger than sheep at maturity, suggesting that deer would be at a comparative disadvantage to sheep on short, low herbage mass swards (Osborne 1984; Clutton-Brock *et al.* 1987; Illius & Gordon 1987; Milne & Reid 1989). Deer might be expected to have an advantage on taller swards of lower quality (Jarman 1974; Staines *et al.* 1982; Demment & Van Soest 1985; Demment & Greenwood 1988), although selection by man and the relatively large rumino-reticulum of sheep appears to have resulted in sheep having more generalist feeding habits and better fibre digestion than expected based on body size (Schwartz & Ellis 1981). Being smaller than stags, hinds may be more tolerant of short or low HM swards, so that stags may choose to graze lower quality plant communities with higher herbage availability (Staines *et al.* 1982; Clutton-Brock *et al.* 1987).

New Zealand studies show better digestion of fibre in Red deer compared to sheep (Fennessy *et al.* 1980; Domingue *et al.* 1990). However in agreement with the morphological classification of ruminant feeding types (Hofmann 1985), studies in the UK suggest the reverse (Milne *et al.* 1978; Kay 1981; Kay & Staines 1981). Kay (1981) suggests that when comparing the digestive function of Red deer, sheep and cattle, it is the similarities rather than the differences which are significant.

Changes in day length regulate seasonal adjustments in metabolic rate and appetite (Tucker *et al.* 1984; Klein 1985; Loudon 1985; Suttie & Simpson 1985), resulting in an increase in voluntary intake from winter to summer. This seasonal adjustment tends to be greater in wild animals, particularly cervids such as Red deer, compared to domesticated animals such as sheep (Kay 1979; Loudon 1985; Milne & Reid 1989). In one recent study sheep showed no seasonal change in voluntary intake whereas castrated Red deer had very low voluntary intake and rumen pool sizes in winter but a much higher voluntary intake in summer (Domingue *et al.* 1990, 1991). This depression of intake is much more marked for stags than hinds (Suttie & Simpson 1985). Metabolic rather than physical constraints appear to be largely responsible for the low winter intakes of deer (Kay 1985), although there is considerable evidence that behavioural constraints can also be an important factor (Staines *et al.* 1982; Fennessy & Milligan 1987; Ataja *et al.* 1989; Barry *et al.* 1991). Despite such differences, the productivity per ha of deer may be similar to that of sheep and cattle (Coop & Lamming 1976; Drew 1976; Milne & Reid 1989).

4.5 Conclusion

BW is frequently the key variable in determining RI and even DHI, and in turn HT and DEN are key sward variables influencing BW. Although we can often predict BW and intake in relation to HT or HM given a specific set of sward conditions, we have only limited understanding as to how animals actually adjust BW to changes in HT, DEN, and other aspects of sward structure. Despite the broad range of largely independent HT and DEN variation covered in the study of Burlison (1987), differences in tiller structure across treatments evidently confounded their influence upon bite dimensions.

The use of highly uniform swards with minimal variation in tiller structure between treatments appears necessary to understand the separate effects of HT and DEN. Once the influence of these two key components upon bite dimensions is more clearly understood a better foundation will exist from which to interpret the modifying influence of other sward structural variables, ultimately leading to the more reliable prediction of ingestive behaviour and intake based upon sward structure.

CHAPTER 5

THE EFFECT OF VARYING LEAFY SWARD HEIGHT AND BULK DENSITY ON THE INGESTIVE BEHAVIOUR OF YOUNG RED DEER AND ROMNEY SHEEP

5.1 ABSTRACT

The effect of varying the height and bulk density of the leafy zone of the sward on the ingestive behaviour of seven 11 month old Red deer hinds and seven 14 month old Romney ewes was examined. Deer and sheep, confined to metabolism crates were randomly allocated 21 sward height x density combinations consisting of 7 heights (3-21 cm) x 3 bulk densities (0.19-0.75 mg DM cm^{-3}). The *Sorghum bicolor* swards were grown in 42 x 30 cm trays and had a deep, pseudostem free leafy zone. The required height of leaf was made accessible to animals by raising or lowering each sward relative to a horizontal grid of fine rods forming 3 cm x 3 cm squares below which animals could not graze. The two lower bulk densities were engineered by snipping out alternate rows, or rows and columns of plants. After grazing for 20 or more bites, the following were measured or calculated: bite depth, bite weight, grazed stratum bulk density, bite volume and bite area.

The ingestive behaviour of deer and sheep was very similar in relation to height (HT) and bulk density (DEN). As HT increased by 600% from 3 to 21 cm, bite depth averaged 73% of HT and increased by 425% from 2.4 to 12.6 cm. DEN effects upon bite depth were interactive with the much more dominant effects of HT; with animals taking slightly deeper or much deeper bites the sparser or taller the sward, respectively. The effect of DEN on bite depth was negligible at 3 cm HT, but bite depth was 4 cm shallower at 21 cm HT on the most compared to the least dense swards. Bite area declined on average as DEN increased, but appeared to be largely unaffected by

HT. Bite weight increased by 420% (28.4-147.6 mg DM) on average as HT increased by 600% (3 to 21 cm), but by only 92% (63.6-122.0 mg DM) as DEN increased by almost 300% (0.19-0.75 mg DM cm^{-3}). This reflects the way that bite volume increased in relation to HT but decreased in relation to bulk density. Thus height was the major determinant of bite volume and bite weight via its influence on bite depth.

The study suggested that Red deer, a relatively new agricultural species, responds in a similar manner to sheep to a wide range of HT and DEN variation.

Key words ingestive behaviour; bite dimensions; sward height; bulk density; Red deer; Romney sheep

5.2 INTRODUCTION

A major factor limiting production of grazing animals is restricted nutrient intake (Hodgson 1982a). Nutrient intake is restricted by 3 factors: diet digestibility and metabolisability, and herbage intake. Depending on sward conditions, herbage intake may vary fourfold (Hodgson 1982a) thus emphasising the need to understand what parameters within the sward determine intake.

Daily herbage intake appears to be closely correlated with bite weight (Hodgson 1985; Penning 1986). The evidence to date suggests that the major determinants of bite weight are sward surface height (Black & Kenney 1984; Burlison *et al.* 1991; Mursan *et al.* 1989) and bulk density (Black & Kenney 1984; Burlison *et al.* 1991).

Burlison *et al.* (1991) measured the bite parameters of sheep over a wide range of sward heights and bulk densities using 9 different grass swards and 8 oat swards. A disadvantage with using such swards is that variation in height and bulk density is often confounded with considerable differences in leaf size, spatial arrangement, age and strength, stem height and leaf to stem ratio, degree of dead matter and acceptability to the animal. Black & Kenney (1984) fed sheep uniform, leafy ryegrass swards, constructed by threading tillers through holes in hardboard sheets to achieve a wide range of heights and bulk densities, a technique that is too time consuming to be ideal for animal species comparisons.

The current study aimed to describe largely unconfounded height and bulk densities effects on ingestive behaviour of deer vs. sheep. Red deer were selected as little is known about their ingestive behaviour. Sheep were used as most current evidence relates to them.

5.3 MATERIALS AND METHODS

5.3.1 Design

Twenty-one sward height x density combinations, involving 7 sward heights (HT) (3, 6, 9, 12, 15, 18 & 21 cm) and 3 bulk densities (DEN) (0.19, 0.38 & 0.75 mg DM cm^{-3}) were offered to 7 deer and 7 sheep. Each animal was offered 1 sward per day for 3 days in each of 2 weeks. In total each animal species was offered 2 randomly allocated sets of the 21 HTxDEN combinations.

5.3.2 Animals

Eleven month old Red deer hinds weighed 51 to 56 kg (incisor widths, 3.2 to 3.3 cm). Fourteen month old Romney ewes weighed 41 to 46 kg (incisor widths, 3.5 to 3.6 cm). Animals were trained to the experimental procedures and swards over 8 weeks. While taking measurements, allowances (of good quality meadow hay and grain) were reduced to 60% of *ad libitum* intakes.

5.3.3 Swards

Seeds (*Sorghum bicolor*) were sown in 18 columns by 12 rows, 25 mm apart, in 42 x 30 cm seedling trays. From each of the 2 sets of 60 trays, sown one week apart, 46 trays were selected by eye for uniformity. Swards were trimmed to a uniform surface height 26 cm above stem height. Once trimmed, 14 swards were left at 100% density (0.75 mg DM cm^{-3}) 14 thinned to 50% density (0.38 mg DM cm^{-3}) by removing alternate rows of plants, and 14 to 25% density (0.19 mg DM

cm^{-3}) by removing alternate rows and columns.

5.3.4 Measurement procedure

Two swards of equal density were weighed to the nearest 0.1 g. One sward was positioned in a feeding frame so that the prescribed height of leaves protruded above the surface of the frame which was level with the floor of the animal crates. A false bottom to the sward was formed by passing thin (3 mm) stainless steel rods at 3 cm intervals through the sward at the frame surface height; forming an impenetrable horizontal grid (Plate 1).

Animals were allowed to graze until 20 or more bites were taken. The depth below the trimmed sward surface of all visibly grazed leaves was measured with a ruler. Grazed and ungrazed swards (used to determine insensible weight losses) were reweighed.

5.3.5 Ungrazed sward descriptions

Leaf number, weight, angle and bulk density, per stratum (0-3 cm down to 18-21 cm) were measured for the tallest, shortest and a medium sward from each set, to describe sward variability within and between sets. Further, shear strength (using an Instron machine and Warner-Bratzler attachment) and leaf width of 10 typical plants were measured for each leaf, at the stratum mid-points.

5.3.6 Calculation of bite parameters

The more direct measurements of bite weight (BW) and bite depth (BD) were used to calculate bite volume (BV), bite area (BA) and grazed stratum bulk density indirectly as follows.

N = number of bites taken by animal

bi = bulk density in the ith strata (i = 0-3, 3-6, 6-9, 9-12, 12-15, 15-18 & 18-21 cm)

n = total number of severed leaves measured

d = depth at which each leaf was severed (cm)

si = number of leaves severed in the ith strata

WL= insensible weight losses of ungrazed sward (g)

W1= pre-grazed weight of sward (g)

W2= post-grazed weight of sward (g)

bite weight = [(W1-W2)-WL]/N

bite depth=($\sum$d)/n

grazed stratum bulk density =$\sum$sibi/n

bite volume=bite weight/grazed stratum bulk density

bite area=bite volume/bite depth

5.3.7 Statistical analyses

Bite parameters (and ungrazed sward data) were analysed by analysis of variance. Wherever HT, DEN or their interaction were significant, coefficients for the best fit regression equations were determined by fitting HT, DEN, HT^2, DEN^2 or HTxDEN as covariates, with data averaged across days, animals and species for each HT by DEN treatment level (for more detail see Section 6.3.6).

5.4 RESULTS

5.4.1 Ungrazed sward description

There were no differences between swards except for leaf density differences of up to 16% in the 6-9 cm and 9-12 cm stratum ($P<0.05$). Factors increasing ($P<0.05$) from the top to lowest stratum were leaf density (97%), leaf shear strength (50%) and the DEN of individual strata (96%); whereas leaf width decreased by 83% (Table 5.1). However, the DEN of a 21 cm sward was only 59% (47% on fwt basis) greater than that of a 3 cm sward.

Table 5.1 Mean leaf parameters measured from 6 ungrazed swards†. Means with the same letters are not significantly different at P<0.05.

Stratum from top (cm)	Leaf density* (leaf # 9cm^{-2})	Leaf width (mm)	Leaf shear strength (N leaf^{-1})	Leaf angle (degrees)	Leaf dry weight (mg 3cm^{-1} strata)	Bulk density of strata (mg DM cm^{-3})	Bulk density of sward (mg DM cm
0-3	2.23 a	12.6 a	34 a	70	6.85	0.56 a	0.56
3-6	2.61 b	12.5 a	38 ab	71	7.60	0.73 b	0.65
6-9	2.94 c	12.3 a	43 abc	76	7.41	0.80 b	0.70
9-12	3.31 d	11.0 a	48 c	76	7.73	0.94 b	0.76
12-15	3.81 e	10.0 a	48 bc	78	7.37	1.04 cd	0.81
15-18	4.25 f	8.6 b	49 c	80	6.76	1.06 d	0.86
18-21	4.40 f	6.9 c	51 c	77	6.78	1.10 d	0.89
overall mean	3.36	10.3	44	75.4	7.21	0.89	-
S.E.M.	0.03	0.2	1	0.2	0.11	0.01	-

† all 6 swards had all plants present, ie 100% relative bulk density.
\+ sward depth is from the surface to the bottom of the respective strata.
* number of leaves in each 3x3 cm square of grid.

5.4.2 General relationships between bite parameters and sward height and bulk density

In total 21 of the 84 sward records were discarded from the analyses because animals had eaten hesitantly or erratically.

Apart from a small difference in BV (P=0.056) the ingestive behaviour of deer and sheep was similar (P>0.100), consequently their results were combined.

HT was strongly correlated with BD, BW and BV in that order (Table 5.2), while it had a negative or nil effect upon BA (Table 5.2; Fig. 5.1b). In contrast DEN had a negative effect upon all bite parameters except BW. The interactive effects of HT and DEN were significant in determining all the bite parameter equations except BV (Table 5.3), and all equations were slightly curvilinear with the exception of bite area.

Table 5.2 Correlation matrix showing the relationship between sward parameters and bite parameters of deer and sheep combined.

	Height	Bulk density	Herbage mass	Bite depth	Bite area	Bite volume
Bulk density	0.00					
Herbage mass	0.69 ***	0.62 **				
Bite depth	0.96 ***	-0.16	0.52 *			
Bite area	-0.46 *	-0.73 ***	-0.63 **	-0.37		
Bite volume	0.70 ***	-0.61 **	0.07	0.83 ***	0.12	
Bite weight	0.80 ***	0.48 *	0.95 ***	0.68 ***	-0.61 **	0.29

*=P<0.05; **=P<0.01; ***=P<0.001.

Because small increases in DEN were confounded with increases in HT, grazed stratum bulk density was auto-correlated with HT. Consequently, it was more valid to relate the bite parameters to the independent, manipulated DEN levels (see Section 5.4.3), which were very highly correlated with grazed stratum bulk density (r = 0.98; P<0.001).

On average, for every 100% increase in HT or DEN, BD increased by 71% or decreased by 10% respectively, clearly indicating the dominant role of HT in determining BD (Table 5.3; Fig. 5.1a). The BD/HT ratio averaged 73% but declined with HT (P<0.05) from approximately 80% for the 3 - 9 cm swards to 60% for the 18 and 21 cm swards. BA did not change with HT for the highest density (Fig. 5.1b). As HT increased, the rate of increase of BV declined, reflecting both the non-linearity of BD and the decline in BA with increasing HT (Table 5.3; Fig. 5.1c).

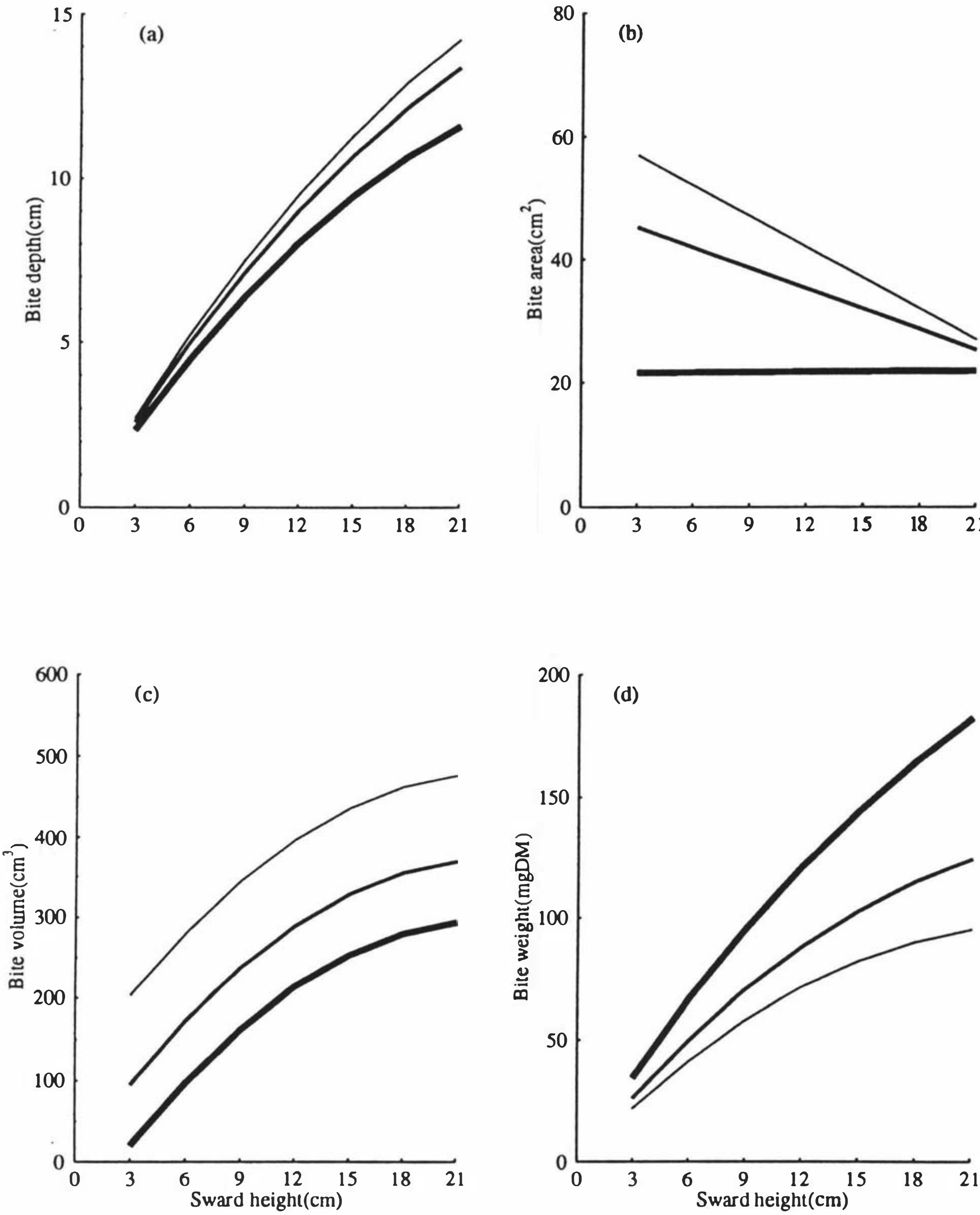

Fig 5.1 The effects of changes in sward height (3, 6, 9, 12, 15, 18 & 21 cm) and DEN (0.19, 0.38 & 0.75 mg DM cm^{-3})(fine through heavy lines respectively) on the bite depth (a), bite area (b), bite volume (c) and bite weight (d) of deer and sheep (combined). These figures are based on regression equations 1,2,3 and 5 (Table 5.3).

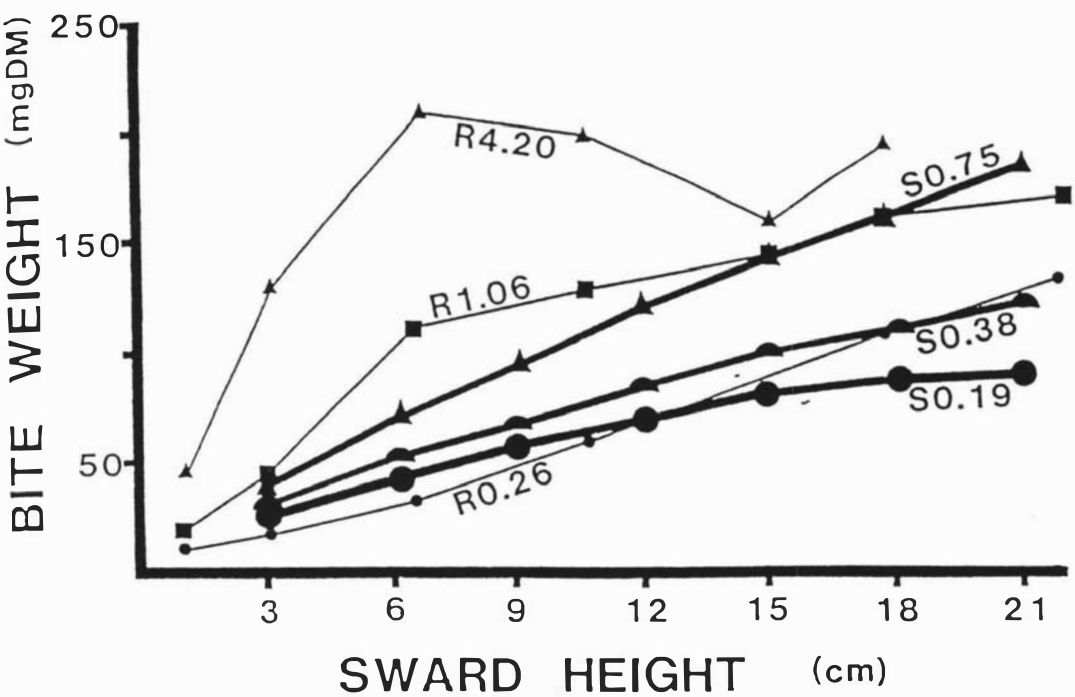

Fig. 5.2 Bite weight in relation to leafy sward height and DEN of young deer and sheep (combined) on sorghum swards (S) (0.19, 0.38 & 0.75 mg DM cm^{-3}) compared with the bite weight of sheep on hand-constructed ryegrass pastures (R) (0.26, 1.06 & 4.20 mg DM cm^{-3}) (Black & Kenney 1984).

Table 5.3 Regression equations for bite parameters of Red deer and Romney sheep (combined) in relation to sward height (3-21 cm) and bulk density (0.18-0.75 mg DM cm^{-3}) variation. Equations 1, 2, 3 & 5 are used in Fig. 5.1.

1) Bite depth = 0.993 (±0.106) HT-0.013 (±0.004) HT^2-0.223 (±0.042) HTxDEN $r^2 = 0.98$***
residual d.f. = 17

2) Bite area = -2.2 (±0.3) HT-71.8 (±9.1) DEN+3.0 (±0.7) HTxDEN+75.4 (±4.8) $r^2 = 0.88$***
residual d.f. = 17

3) Bite volume = 31.5 (±5.6) HT-0.7 (±0.2) HT^2-949.3 (±213.9) DEN+665.1 (±219.5) DEN^2 +268.0 (±50.4) $r^2 = 0.94$***
residual d.f. = 16

4) Bite weight = 7.02 (±1.89) HT-0.18 (±0.08) HT^2+8.96 (±0.76) HTxDEN $r^2 = 0.96$***
residual d.f. = 17

5) Bite weight (unconfounded)= 6.42 (±1.93) HT-0.16 (±0.07) HT^2+7.39 (±0.77) HTxDEN $r^2 = 0.95$***
residual d.f. = 17

5.4.3 Bite weight corrected for confounded increases in bulk density with height

As HT increased from 3 to 21 cm, the grazed stratum bulk density also increased by 0.23 mg DM cm^{-3}, due to the increases in bulk density associated with increases in HT (Table 5.1). The effect of these confounding increases in bulk density on BW in relation to HT was estimated by multiplying the DEN coefficient (102.8) of the best fit simple linear equation for BW ($r^2 = 0.87$; $P<0.001$) by the confounded increase in grazed stratum bulk density (0.23 mg DM cm^{-3}). This gave an estimate of the total error in BW (due to confounding) incremented over the entire HT range (23.6 mg). By calculating the mean grazed stratum bulk density for each HT it was possible to determine the correction to be applied to the mean BW values at each HT (proportion of the total error which should be subtracted from the mean BW values for each HT) to estimate the true unconfounded BW in relation to HT. As a check, the mean BW for each HT was calculated assuming a constant DEN of 0.56 mg DM cm^{-3} for all strata and adding on the appropriate correction factors. When compared with the mean measured BW values, the estimates were within

9 to 11% of the original mean values. As confounded and unconfounded BW had similar variables and coefficients, only unconfounded BW was considered further (Table 5.3; Fig. 5.1d).

On average BW was more than twice as sensitive to HT as to DEN given proportional increases in both.

5.5 DISCUSSION

5.5.1 Sward Factors

Despite the almost 100% higher bulk density of 18-21cm vs 0-3 cm strata, the DEN of a 21cm sward was only 59% higher than that of a 3 cm sward, with differences in DEN between other sward heights being smaller still (Table 5.1). Unconfounded BW was calculated to minimise the influence upon BW estimates of these increases in bulk density down the profile, which were auto-correlated with changes in HT.

However, the direct influence upon BD and BA of these changes in DEN and other structural variables down the sward profile warrant further consideration. For example, the almost 100% increase in leaf density and up to 50% increase in leaf shear strength down the sward profile (Table 5.1), indicate that the force required to sever a bite could be up to three fold higher near the base of tall vs short swards (of equivalent DEN). Further, swards 12 cm or less in HT were composed almost entirely of broad soft lamina. As the grid was lowered to achieve heights greater than 12cm, swards began to contain a basal horizon of narrower, more rigid leaves since leaves narrowed as they approached their point of attachment to the sheath. The rigidity of leaves in this horizon increased towards the grid , while the depth of this horizon as well as the average rigidity of leaves contained in it also increased as HT was increased by lowering the grid.

5.5.2 Deer and sheep

The ingestive behaviour of deer and sheep was not statistically different at P<0.05 in relation to the wide range of HT and DEN variation. However, the BV of sheep was 12% larger than for deer (P=0.056); a difference indicated in BA and BW (10-11%; P<0.12) but not BD. These trends may have reflected the 9% greater incisor arcade widths of the 14 month old sheep compared to the 11 month old deer.

5.5.3 Bite depth

The BD of deer and sheep increased rapidly and in a close to linear manner with increasing HT, trends similar to the linear response evident for sheep and cattle grazing a range of gramineous plant species (Burlison 1987; Laca *et al.* 1992b; Gong *et al.* 1993).

On sorghum swards, however, BD decreased (P<0.05) from approximately 80% to 60% of HT as HT exceeded 12-15 cm, as reflected in the slightly curvilinear response (Fig 5.1a). In view of these factors, ie. the typically linear BD response, the changes in sorghum leaf structure (Section 5.5.1; Table 5.1) and corresponding reduction in BD/HT ratio, it is probable that the marked increases in leaf rigidity in the base of the taller swards did limit grazing penetration. Flores *et al.* (1993) found that a lower horizon of tough, rigid, stem limited the penetration of cattle to the surface horizon of leaf. In contrast, Demment *et al.* (1992) found that a lower horizon of very high density leaf did not restrict BD of cattle in a leafy sward, strongly suggesting that the comparatively small confounded increases in DEN with increasing HT on sorghum swards would have had little or no effect upon the BD/HT ratio or linearity. That the BD/HT ratio only declined by 10% on average for every 100% increase in manipulated sorghum DEN also supports such a conclusion.

Bites were very deep on grid-based sorghum swards compared to those of sheep (≤46% of height) grazing ryegrass pasture (Bathram & Grant 1984) and turfs (Hughes *et al.* 1991). These deep bites would have increased BW in relation to HT and may have also altered BA. The limited

BD data in the study of Black & Kenney (1984) indicated that, as for sorghum, hand-constructed ryegrass swards were grazed more deeply than equivalent turfs or pasture, suggesting that the grid technique itself did not necessarily encourage very deep bites. The high quality and very deep leafy profile of sorghum and hand-constructed ryegrass swards may have contributed to such deep bites.

As for deer and sheep in the current experiment, studies with sheep grazing ryegrass turfs (Hughes *et al.* 1991) or hand-constructed swards (Black & Kenney 1994) demonstrated a negative effect of DEN upon BD. In agreement with recent work using cattle (Laca *et al.* 1992b), the degree to which increases in DEN reduced the BD of deer and sheep was dependent upon HT. For example at 3 cm HT, four-fold changes in DEN had very little effect upon BD, whereas at 21cm HT, BD increased from 10 cm on the most dense, to 14 cm on the least dense sorghum swards. HT and DEN tend to be strongly correlated during pasture growth (Hodgson 1990a), so that tall pastures will probably be grazed more deeply than expected (based on HT alone) if extrapolating from shorter pastures. However, the BD/HT ratio on natural pasture should be much shallower (Milne *et al.* 1982; Bathram & Grant 1984; Wade 1991) than in the current study, suggesting that the HT up to which even large changes in DEN will have an insignificant effect on BD, may in practice be considerably greater than indicated from Fig 5.1a. Further, plots of the means indicated that DEN effects on BD were in fact negligible up to at least 6 cm HT, whereas the fitted regression equation has tended to over-accentuate the DEN effects for these shorter heights (Fig 5.1a). Similarly, even large changes in DEN had no effect upon the BD of cattle grazing leafy paspalum at heights of up to 10 cm (Ungar *et al.* 1991) or 15 cm (Laca *et al.* 1992b).

5.5.4 Bite area

The BA of cattle and sheep remained constant as HT increased from 5 to 15 cm (Mursan *et al.* 1989; Hughes *et al.* 1991). These trends are similar to those on the 0.75 mg DM cm^{-3} sorghum swards, where BA was also reasonably stable across all heights. In contrast, on 0.38mg DM cm^{-3}

swards and especially 0.19 mg DM cm^{-3} swards, BA was very large on short swards but declined with increasing HT (Fig. 5.1b).

The low leaf density and slight clumping or grouping together of leaves from each plant resulted in inter-leaf and/or inter-leaf group distance exceeding mouth dimensions on shorter, lower DEN swards. This would have accentuated BA estimates on such swards to beyond the actual area encompassed by the animal's mouth (Black & Kenney 1984). As HT increased, both the leaf density in the grazed strata as well as the distance animals could displace tillers horizontally (due to increased tiller length (Burlison *et al.* 1991)) increased, steadily reducing the degree to which average inter-leaf distance exceeded actual BA. Although not apparent from the regression used in Fig. 5.1b, a plot of the means showed that BA also plateaued for 0.38 mg DM cm^{-3} swards taller than 9-12 cm, indicating that (as for 0.75mg DM cm^{-3} swards) inter-leaf distance no longer exceeded mouth dimensions for taller swards of that DEN.

Further, on short, low density swards, animals frequently returned to a grazed region to nip off a single leaf and such bites were not counted. Thus, true bite number was underestimated, and therefore BA, BV and BW overestimated for short, lower density swards. It is suggested that BA on the denser, spatially uniform 0.75 mg DM cm^{-3} swards would more closely reflect the actual area of herbage prehended per bite in relation to changing HT.

Evidently, the increase in leaf shear strength and DEN with increasing HT was insufficient to reduce BA even on 0.75 mg DM cm^{-3} swards, suggesting that the animal's ability to gather leaves into the mouth may have been limiting, rather than biting effort. As indicated by Hodgson (1985), biting effort may be more important at higher levels of DEN and tiller strength.

5.5.5 Bite weight

Trends for BW on the sorghum swards most closely resembled those for the low DEN (0.26 mg

DM cm^{-3}) ryegrass swards of Black & Kenney (1984) (Fig. 5.2). Even at the highest DEN of 0.75 mg DM cm^{-3}, sorghum swards did not show the very rapid increase in BW up to around 6 cm HT evident for ryegrass swards with a DEN of 1.06 mg DM cm^{-3} or more. These differences may largely reflect the comparatively low densities of the sorghum swards.

The slope for BW (Fig. 5.1d) increased at a declining rate as sorghum swards became taller, probably reflecting the limiting effects of the increasing rigidity of leaves near the base of taller swards on BD, rather than a true HT effect. The studies of Burlison (1987), Hughes *et al.* (1991) and Laca *et al.* (1992b) demonstrate a linear relationship between BW and HT.

Despite an increase in BV with declining DEN (Fig. 5.1c), Figure 5.1d shows that this increase was too small to maintain BW (Fig. 5.1d); which declined by approximately 30% on average for every 100% decrease in DEN. The antagonistic effects of DEN (negative) and grazed stratum bulk density (positive) on BV help explain why, firstly, large changes in DEN must occur to markedly alter the slope of BW in relation to HT (Fig. 5.1d; Fig. 5.2) and, secondly, why HT frequently has a dominant role in determining BW (Laca *et al.* 1992b; Gong *et al.* 1993).

5.6 CONCLUSIONS

BD is largely determined by HT, although marked increases in tiller rigidity appear to measurably reduce BD in relation to HT, as do large increases in DEN on all but short swards.

The large increases in leaf rigidity and moderate increases in leaf strength, had very little effect upon BA on these low to moderate DEN sorghum swards, suggesting that under such conditions an animal's ability to gather herbage into the mouth may be a more important constraint upon BA, than biting effort.

Reflecting the negative effect of DEN on BV, an increase in HT on average caused more than twice the increase in BW than did a proportional change in DEN. Thus not only did HT very largely determine BD, but it was also the major determinant of BW.

The study indicated that the bite dimensions of young Red deer and sheep are likely to be similar over a wide range of sward heights and bulk densities, at least when grazing a leafy gramineous, monoculture.

CHAPTER 6

THE INGESTIVE BEHAVIOUR OF RED DEER AND ROMNEY SHEEP. I) IN RELATION TO HEIGHT AND HERBAGE BULK DENSITY IN ARTIFICIAL SWARDS

6.1 SUMMARY

(1) The independent effects of sward height (HT) and bulk density (DEN) on the comparative bite parameters and rates of intake of young Red deer hinds and Romney ewes were examined in two experiments using seedling wheat swards which simulated a leafy grass-like monoculture of low shear strength. Experiment 1 examined a very wide range of bulk densities (0.33-4.00 mg DM cm^{-3}) over a limited range of heights (3-7 cm), while experiment 2 covered an extended range of heights (4-13 cm) over a narrower range of bulk densities (0.63-3.25 mg DM cm^{-3}).

(2) The influence of HT was greater than that of DEN in determining all bite parameters although bite area became less sensitive to HT on taller swards.

(3) As swards became taller, bite depth, bite volume and bite weight increased and bite rate decreased linearly, while over the greater range of heights covered in experiment 2 bite area and rate of intake increased at a declining rate. As swards became more dense all bite parameters declined in a linear or close to linear manner except bite weight and rate of intake, which both increased.

(4) Bite depth increased rapidly in relation to HT, but only declined slightly in response to large increases in DEN. Consequently, bite depth was very largely determined by HT at all levels of DEN.

(5) On short swards, bite area was constrained by HT. As DEN declined, bite area increased more rapidly with increasing HT and, in experiment 2, peaked at higher levels on taller swards. Consequently the rate of reduction in bite weight as DEN declined was counteracted to some

degree by animals increasing bite volume.

(6) Incisor arcade width alone was not a good predictor of bite area on short swards, or when DEN varied widely.

(7) The bite depths of deer and sheep were similar. However, reflecting the trends for bite area, the bite weights of deer and sheep were similar on short swards, but increased faster for deer in relation to increasing HT.

(8) On a per kg LW basis, sheep achieved approximately 40% higher bite weights and rates of intake on average compared to deer, although the relative difference between deer and sheep declined with increasing HT. Implications were that sheep would out-compete deer on simple gramineous swards, and that deer would need appreciably taller swards, higher residuals or lower stocking rates than sheep to achieve equivalent intakes.

6.2 INTRODUCTION

The key determinant of daily herbage intake and consequent animal performance in the grazing ruminant is likely to be the weight of material ingested per bite (bite weight) (Hodgson 1985), particularly when herbage mass is low to moderate (Penning 1986). The two major structural variables determining herbage mass and probably bite weight are height (HT) and bulk density (DEN) (Black & Kenney 1984; Burlison *et al.* 1991; Chapter 5; Laca *et al.* 1992b). The HT and DEN of the sward affect bite weight through their influence upon bite depth and bite area, and also the density of the grazed stratum. Consequently, understanding how bite depth and bite area change in relation to HT and DEN, reveals the mechanisms of bite weight adjustment by the grazing animal, knowledge critical for predicting bite weight and consequent intake in relation to sward conditions.

Many studies have examined the effects of HT and/or DEN on bite weight and/or rate of intake; only a few (Mursan *et al.* 1989; Burlison *et al.* 1991; Hughes *et al.* 1991) have measured the spatial dimensions of the bite, bite depth and area. Yet in these cases HT and DEN were autocorrelated

(Hodgson 1990a), and/or confounded with other sward structural variables such as tiller size, spatial arrangement, breaking strength, leaf:stem ratio, stem height or proportion of dead matter.

In recent studies with deer and sheep (Chapter 5) and particularly cattle (Laca *et al.* (1992b) it has been possible to isolate to a greater degree the effects of HT and DEN on bite dimensions. Laca *et al.* (1992a, b) used hand-constructed swards similar to those of Black & Kenney (1984) and made detailed measurements of bite depth and bite area for 750 kg cattle on 8-30 cm grass or 7-25 cm lucerne swards. Chapter 5 utilised 3-21 cm sorghum swards representing a comparatively narrow range of low to moderate DEN variation (0.19-0.75 mg DM cm^{-3}) for a deer vs sheep comparison of changes in bite dimensions and bite weight. However, HT variation was still confounded with considerable changes in leaf structure and arrangement, and it was not possible to precisely describe bite area variation.

In this study novel seedling sward techniques which kept HT and DEN variation largely independent and unconfounded were utilised to generate large numbers of uniform swards in two separate experiments. The first experiment (E1) extends the previous comparison of deer and sheep (Chapter 5) over a much wider range of DEN variation for the two different ruminant species. However, limitations with the sward technique restricted HT to a range of 3-7 cm. The second experiment (E2) covered an extended HT range of up to 13 cm, by using a modified sward growth technique and reducing the range of DEN variation.

6.3 METHODS

6.3.1 Design

Experiment 1: Fifteen sward combinations (five tiller densities x three heights) allocated in a balanced, incomplete block design were offered to four deer and four sheep. Each animal was fed three swards per day in order of increasing DEN, and a total of 96 swards were fed over two consecutive days in each of two consecutive weeks. The tiller densities were 3250, 6500, 13 000, 29 000 and 40 000 tillers m^{-2} and heights were 3, 5, and 7 cm.

Experiment 2: Four months after experiment 1 (E1), sixteen sward combinations (4 heights x 4 densities) allocated in a balanced block design were offered to the same four deer and four sheep. A total of 128 swards were fed as for E1, but at a rate of four swards per animal per day in order of increasing herbage mass. The heights were 4, 7, 10 and 13 cm and tiller densities were 3250, 6500, 13 000 and 29 000 tillers m^{-2}.

6.3.2 Animals

Experiment 1: In late autumn the ingestive behaviour of four 19 month old hinds weighing 75-85 kg with total incisor arcade widths of 41-47 mm (adult incisors 36-40 mm) was compared with that of four 22 month old ewes. Sheep weighed 47-52 kg and total incisor arcade widths were 35-37 mm (adult incisors 28-30 mm). Both species had only four adult teeth per animal, and these contributed approximately 85% of total arcade width and appeared to form the effective prehending edge. The deer and sheep had been selected for their quietness and willingness to eat. Animals were housed in metabolism crates indoors and had been trained to experimental procedures previously (Chapter 5), as well as for three weeks immediately prior to the current experiment. A range of the experimental swards were offered on several occasions. Animals were fed hay and grain *ad libitum* except on measurement days and the 2 preceding days when allowances were reduced to 60% of their *ad libitum* intakes.

Experiment 2: In early spring, four months after experiment 1 (E1), the same four hinds weighed 70-78 kg and each had a full complement of incisors, with arcade widths of 42-50 mm. The sheep weighed 38-47 kg and had only six adult incisors with arcade widths of 33-38 mm. Remaining milk (juvenile) teeth in sheep appeared to be well below the effective cutting edge of the adult incisors. Animals were retrained to experimental swards and procedures, and fed hay and grain as in E1.

6.3.3 Swards

Experiment 1: Two replicates of wheat seedling swards (with 48 trays per replicate) were sown one week apart, over two days per week. Seeds were sown onto a firm, level 60% peat, 40% sand medium in 42 x 30 cm seed trays using hard board templates with holes drilled so as to achieve uniform seed spacing at the required density (Plate 2). Once sown, seeds were covered in 1.5 cm of sand. This produced a uniform rectangle of pasture (38 x 28 cm). Swards were grown in a glasshouse under regulated temperature conditions so as to reach 7-10 cm when fed (Plate 3). Once the wheat seedlings had grown to about 1 cm above the sand surface, a cement solution was squirted gently onto the sand. This allowed tillers to grow up through the coleoptile but prevented the seedling plants from pulling out during grazing. Swards were trimmed uniformly to the required HT just before grazing (Plate 4).

Experiment 2: Two replicates of wheat swards, with 64 trays in each, were prepared as for experiment 1, except the growing times and procedures differed slightly.

6.3.4 Measurements

Experiments 1 and 2: Swards were presented to animals at foot level on a moveable trolley (Plates 9 & 10). Animals were allowed to graze for at least 20 bites and until they paused or began regrazing areas of the sward. Time spent with the head down grazing undisturbed pasture was recorded using a stopwatch. The grazed height of 60 leaves in E1 and 40 leaves in E2 was measured with a ruler along at least three transects evenly spaced across the grazed region of the sward. Transects were defined by positioning a ruler on edge, on the sward surface, across the width of the tray. The grazed leaf closest to the transect ruler was measured to the nearest millimetre with no more than one leaf per centimetre interval being measured. The rectangular area of the sward from which leaves had been grazed was measured with a ruler. All remaining ungrazed leaves within this rectangular area were then counted. The above direct measurements were used to determine bite rate (BR), bite depth (BD), the number of grazed leaves, bite area (BA), bite volume (BV), bite weight (BW) and short term rate of intake (RI) as follows:

N= number of bites taken by animal

T = time spent grazing (seconds)

d = sward height minus grazed residual height of each measured leaf

D= number of grazed leaves measured for residual height

n = number of grazed leaves

a = total rectangular area of sward from which leaves had been grazed

U= number of ungrazed leaves in rectangular area of sward which had been grazed

L = total number of leaves in sward

W= average leaf weight per cm of length

A = total area of the sward

Bite depth $=(\sum d)/D$

Number of grazed leaves = (a L/A) - U

Bite area = (n A/L)/N (ie. area per bite)

Bite volume = bite area x bite depth

Bite weight = (bite depth x number of grazed leaves x W)/N

Bite rate = N/T

Rate of intake = bite weight x bite rate

The very short term grazing measurements used here gave high BR and RI estimates when compared with longer term measurements under grazing (Jamieson & Hodgson 1979a; Forbes & Hodgson 1985a; Bazely 1988) but the relative changes in BR in relation to BW, HT or herbage mass would still be valid.

6.3.5 Sward description

Experiment 1: Fifteen tillers, 7-10 cm in height, were trimmed to a height of 7 cm from each of a 3250 and a 29 000 tiller m^{-2} sward. The fresh weight of each tiller was measured to determine density effects on tiller size.

Ten tillers, 7-10 cm in height, were cut into stratum sections (0-2, 2-3, 3-5 and 5-7 cm) and the fresh weight and dry weight per unit length were measured. Thus bulk density could be calculated for each HT x DEN combination.

To detect leaf strength differences between height strata, shear strength was measured at the stratum mid-points of 3 samples of 5 tillers each, from a 29 000 tiller m^{-2} sward using an Instron machine and Warner-Bratzler shear attachment.

Experiment 2: Twenty tillers were trimmed to a height of 13 cm from one sward of each of the four tiller densities. The fresh weight and dry weight of each tiller were measured to determine density differences in tiller size. Stratum bulk density differences were determined from the fresh weight per unit length of 10 tillers each cut into strata (0-4, 4-7, 7-10 & 10-13 cm), from each of the 4 density levels. Shear strength measurements were made at stratum mid-points for 20 fresh, two-tiller samples, for each of the four DEN levels.

6.3.6 Statistical analysis

Experiments 1 and 2: An initial analysis of variance for each bite parameter tested the effects of weeks and days within weeks for E1 or days for E2, plus species, animals within species, DEN and HT. First order interactions, DEN x HT, DEN x species and HT x species were also tested in the model. Species differences (and first order interactions) were tested against animals nested within species. Wherever DEN, HT or their interaction were significant, the coefficients for the best fit regression equations were determined by reanalysing with DEN, HT or DEN x HT terms fitted as covariates, with data averaged over weeks, days, and animals, and species where species effects were not significant. DEN^2 and HT^2 terms were also included when significant. Regression equations were compared across experiments by analysis of covariance.

6.4 RESULTS

6.4.1 Sward structure

Experiment 1: Swards were ready to graze when the tallest tillers reached 10 cm. At this stage 93% of tillers had reached 7 to 10 cm (n = 150) and 99% had emerged. No correction was made for the 7% of tillers not reaching 7 cm.

There was no difference in the fresh weight of 15 tillers trimmed to 7 cm from a 3250 tiller m^{-2} sward (72.0 ± 1.8 mg) and a 29 000 tiller m^{-2} sward (69.7 ± 1.9 mg). Consequently, tiller size was assumed equal for all sowing densities.

Tillers consisted of rolled leaf or pseudostem up to 1.0-2.0 cm, about the first 1 cm of which was encased in the coleoptile. Above the pseudostem was the first and tallest leaf, and the second leaf which typically reached a height of 4-8 cm.

Based on the 10 tillers cut into sections, 0-2, 2-3, 3-5 and 5-7 cm, there was no significant difference in fresh weight (10.0 ± 0.4 mg cm^{-1}) between strata. Bulking the 10 tillers for each stratum gave a DM % ranging from 9.6-10.3% and a dry weight ranging from 0.96-1.04 mg cm^{-1}. Consequently, an average tiller dry weight of 1.0 mg cm^{-1} was assumed for all treatments, so that the 5 tiller densities (3250 to 40 000 tillers m^{-2}) equated to bulk densities (DEN) of 0.33, 0.65, 1.30, 2.90 and 4.00 mg DM cm^{-3}.

Measurements at stratum mid-points of 15 tillers showed that shear strength did not differ between 0-2 cm (3.4 ± 0.3 N $tiller^{-1}$) and 2-3 cm (3.3 ± 0.2 N $tiller^{-1}$) strata, but was lower for 3-5 cm (2.2 ± 0.2 N $tiller^{-1}$) and especially 5-7 cm (1.3 ± 0.1 N $tiller^{-1}$) strata. All the above measurements excluded the coleoptile as this was seldom a grazed component.

Experiment 2: Tiller dry weight per unit length decreased from 1.95 ± 0.05 to 1.12 ± 0.04 mg cm^{-1} as sowing rate increased from 3250-29 000 seeds m^{-2}. Sward bulk densities (DEN) calculated from the four corresponding sowing rates and tiller weights equated to 0.63, 1.01, 1.74 and 3.25 mg DM cm^{-3} respectively.

Measurements of stratum bulk densities showed that the largest difference between strata within any of the four density levels was 14% and most differences were considerably smaller. As such small differences in stratum bulk density would produce negligible effects on the spatial dimensions of the bite (Chapters 5 & 7), they were ignored and the average bulk density based on whole tillers (0-13 cm) was assumed for each stratum and sward height.

Shear strength within strata did not differ across DEN levels except for two small differences of 6 and 7% ($P<0.05$). Averaged across DEN levels, shear strength changed little from the base to the top of the sward, being 4.5 ± 0.1, 5.1 ± 0.1, 4.9 ± 0.1 and 4.6 ± 0.1 N $tiller^{-1}$ for the 0-4, 4-7, 7-10 and 10-13 cm strata respectively.

6.4.2 Sward height by bulk density effects on bite parameters

All treatments were readily grazed, except for a few of the 3 cm swards in E1 where DEN was below 1.30 mg DM cm^{-3}. The range of sward and bite parameters for E1 and E2 are described in Table 6.1.

In both experiments HT was extremely well correlated with BD, and strongly so with BV and BR, while DEN was strongly and negatively correlated with BA (Table 6.2). BW and RI were strongly correlated with herbage mass in both experiments, and with DEN in E1, but with HT in E2. Trends were similar for both E1 and E2 although significant differences did exist between experiments for all bite parameters, except BR, and the BA of sheep. These differences are addressed in the discussion. Separate regression equations are presented for deer and sheep for all bite parameters except BD ($P>0.59$), reflecting significant effects of species, species by HT and/or

Table 6.1. The range and mean values of sward variables and bite parameters for deer and sheep in experiments 1 and 2.

			Experiment 1		Experiment 2	
Parameter	Units	Deer/sheep	Range	Mean	Range	Mean
Height	cm	-	3 - 7	-	4 - 13	-
Bulk density	mg DM cm^{-3}	-	0.33 - 4.00	-	0.63 - 3.25	-
Herbage mass	mg DM cm^{-2}	-	0.99 - 28.00	-	2.54 - 42.22	-
Density	tillers m^{-2}	-	3250 - 40000	-	3250 - 29000	-
Bite depth	cm	D	1.5 - 5.7	3.4	2.3 - 10.8	6.1
		S	1.5 - 5.8	3.5	2.3 - 10.4	6.1
Bite area	cm^2	D	9.4 - 23.6	16.4	12.8 - 30.2	20.4
		S	10.1 - 21.8	15.8	11.3 - 27.5	18.4
Bite volume	cm^3	D	17.4 - 119.8	59.8	29.2 - 324.5	135.9
		S	15.1 - 126.9	55.6	33.3 - 285.4	117.5
Bite weight	mg DM	D	6.4 - 365.6	96.0	25.2 - 521.4	191.9
		S	10.2 - 312.5	88.4	27.9 - 332.9	161.7
Bite rate	bites $min.^{1}$	D	46.2 - 109.2	75.0	32.6 - 85.0	61.7
		S	35.4 - 82.8	65.4	38.6 - 78.8	56.8
Rate of intake	mg DM $min.^{-1}$	D	450 - 19716	6466	2067 - 17075	9780
		S	612 - 19590	5432	2208 - 12858	8049
Bite depth/height ratio	%	D	50.2 - 80.9	66.6	57.8 - 82.7	69.8
		S	49.5 - 83.0	66.5	57.9 - 79.9	69.7

species by DEN interactions (Table 6.3). Species differences in BA were only significant at P=0.115 in E2. The effects of HT and DEN were interactive for all bite parameters except RI (in E2 only) for which they were additive and independent. Equations were non-linear for BA and RI in E2. For the sake of simplicity and ease of comparison the RI equations from E2 are also presented in a simplified form (Table 6.3) without a DEN^2 term and with little loss of predictive accuracy. The DEN^2 terms reflected a slightly faster rate of increase in RI between the lower two or three DEN levels, which was more marked for deer than sheep. Similar DEN^2

Table 6.2. Correlation matrix indicating the general relationships between sward variables (height and bulk density) and bite parameters of deer and sheep combined, in experiments 1 and 2.

	Height	Bulk density	Herbage mass	Bite depth	Bite area	Bite volume	Bite weight	Bite rate
Experiment 1								
Bulk density	0.00							
Herbage mass	0.38	0.88***						
Bite depth	0.99***	-0.08	0.29					
Bite area	0.59*	-0.75**	-0.47⁺	0.65**				
Bite volume	0.93***	-0.31	0.03	0.96***	0.82***			
Bite weight	0.57*	0.74**	0.97***	0.49⁺	-0.26	0.24		
Bite rate	-0.77***	-0.50⁺	-0.77***	-0.73**	-0.09	-0.55*	-0.84***	
Rate of intake	0.54*	0.77***	0.96***	0.47⁺	-0.29	0.22	-0.99***	-0.80***
Experiment 2								
Bulk density	0.00							
Herbage mass	0.52**	0.79***						
Bite depth	0.99***	-0.10	0.42*					
Bite area	0.42*	-0.75***	-0.47**	0.51**				
Bite volume	0.84***	-0.41*	0.02	0.89***	0.82***			
Bite weight	0.81***	0.48**	0.86***	0.75***	-0.01	0.46**		
Bite rate	-0.81***	-0.47*	-0.80***	-0.75***	0.05	-0.45**	-0.93***	
Rate of intake	0.74***	0.51*	0.75***	0.69***	0.08	0.48***	0.93***	-0.81***

* = P≤0.05; ** = P≤0.01; *** = P≤0.001; ⁺ = 0.05<P<0.10

trends were evident for BA, BV and BW in both experiments, but did little to improve the fit. Further these DEN^2 terms were sometimes only marginally significant and/or would have necessitated the inclusion of a frequently non-significant DEN term, and in some cases the trends were not consistent across different heights. For the above reasons DEN^2 terms were included in Table 6.3 only for RI and even here, the reduced equation omitting DEN^2 showed little loss of precision. The HT^2 terms for BA and RI represented substantial effects and these were not removed.

In both experiments BD increased rapidly and linearly with HT, but declined slightly with DEN, increasingly so as HT increased, reflecting both the much greater influence of HT (Table 6.4), as well as the interactive effects of HT and DEN (Table 6.3, Fig. 6.1a (i, ii)), upon BD. Plots of the means indicated that DEN effects on BD were negligible for swards shorter than 3-4cm. The effects of HT and DEN on BA were interactive such that the lower the bulk density the greater the rate of increase in BA with HT. Further, BA increased at a declining rate as swards became taller (Fig. 6.1b (iii, iv)) in E2, although not in E1 (Fig. 6.1b (i, ii)) which covered only a limited range of shorter sward heights. At the lowest DEN in E2, BA increased by an average 66% ($P<0.001$) between 4 and 13 cm, yet at 3.25 mg DM cm^{-3}, BA was almost constant. Similar trends were evident for E1. Both HT and DEN had on average a similar influence upon BA in E2 but, reflecting the lower average height, in E1 the influence of HT was relatively greater (Table 6.4).

BW increased rapidly with DEN and in particular HT, their effects being interactive (Figs. 6.1d (i, ii, iii, iv); Table 6.3). The dominant role of HT (Table 6.4) is exemplified by the more than 100% larger bite weight of sheep for example, on 10 cm x 0.63 mg DM cm^{-3} vs 4 cm x 1.74 mg DM cm^{-3} swards despite a 10% higher herbage mass on the shorter 4 cm sward.

Bite rate declined as DEN or particularly HT (Table 6.4) increased, their effects being interactive (Figs. 6.1e (i, ii, iii, iv); Table 6.3) so that an increase in DEN caused a slightly greater reduction in BR, the taller the sward. BR was most strongly correlated with BW, and was much more strongly correlated with HT than DEN (Table 6.2). BR was evidently overestimated for 13 cm E2 swards (see Section 6.5.6), so BR and RI trends were derived from 4-10 cm data.

As for BW, RI increased rapidly in relation to DEN and particularly HT (Table 6.4), their effects being interactive in E1 but independent and additive in E2 (Figs. 6.1f (i, ii, iii, iv); Table 6.3). The HT^2 terms for the E2 equations reflected the declining rate of increase in RI as HT increased.

6.4.3 Species differences in bite parameters

On average the BW of deer was 10% larger than that of sheep in E1 (97.2 ± 2.0 vs 88.7 ± 1.9 mg DM; $P=0.020$) and 17% larger in E2 (190.0 ± 6.5 vs 162.3 ± 6.1 mg DM; $P=0.021$). These

Table 6.3. Regression equations for bite parameters of Red deer and Romney sheep in relation to sward height and bulk density variation in: A) Experiment 1 (0.33-4.00 mg DM cm $^{-3}$ x 3-7 cm) or in B) Experiment 2 (4-13 cm x 0.63-3.25 mg DM cm^{-3})

Bite parameter	Animal species	Sward variable coefficient (± S.E.M.)						Statistics		
		HT	HT^2	DEN	DEN^2	HTxDEN	Intercept	r^2	P	residual d.f.
A) Experiment 1:										
Bite depth	D+S	0.901 (0.011)				-0.017 (0.002)	-0.904 (0.053)	0.99	***	27
Bite area	D	1.80 (0.21)				-0.25 (0.04)	9.70 (1.00)	0.88	***	12
	S	1.14 (0.24)				-0.31 (0.05)	13.05 (1.17)	0.79	***	12
Bite volume	D	21.0 (0.7)				-1.3 (0.1)	-32.6 (3.3)	0.99	***	12
	S	18.8 (0.7)				-1.6 (0.1)	-23.1 (3.2)	0.99	***	12
Bite weight	D	12.7 (2.6)				9.5 (0.5)	-53.0 (12.5)	0.98	***	12
	S	10.2 (2.2)				8.0 (0.5)	-35.5 (10.7)	0.97	***	12
Bite rate	D	-2.8 (1.0)				-0.6 (0.2)	93.5 (4.8)	0.67	***	12
	S	-2.4 (0.6)				-0.4 (0.1)	81.2 (2.9)	0.78	***	12
Rate of intake	D	657 (176)				561 (36)	-1773 (859)	0.97	***	12
	S	490 (179)				440 (37)	0	0.94	***	12
B) Experiment 2:										
Bite depth	D+S	0.897 (0.011)				-0.035 (0.003)	-1.009 (0.086)	0.99	***	29
Bite area	D	3.25 (0.87)	-0.09 (0.04)			-0.47 (0.05)	6.72 (3.32)	0.92	***	12
	S	2.33 (0.73)	-0.07 (0.03)			-0.46 (0.04)	11.12 (2.80)	0.92	***	12
Bite volume	D	30.4 (1.6)				-4.3 (0.5)	-61.6 (12.3)	0.97	***	13
	S	24.4 (1.4)				-4.3 (0.4)	-29.2 (11.2)	0.96	***	13
Bite weight	D	19.6 (2.3)				7.5 (0.7)	-79.9 (18.1)	0.97	***	13
	S	17.5 (2.1)		24.4 (9.8)		2.6 (1.1)	-63.6 (19.0)	0.98	***	12
Bite rate•	D	-3.4 (0.6)				-1.0 (0.2)	102.2 (4.0)	0.93	***	9
	S	-2.9 (0.4)				-0.8 (0.1)	90.2 (2.9)	0.95	***	9
Rate of intake•	D	3813 (959)	-194 (58)	5898 (1702)	-1083 (421)		-13526 (3315)	0.95	***	7
	S	2542 (598)	-127 (30)	3467 (1061)	-480 (262)		-7823 (2067)	0.97	***	7
Rate of intake•	D*	3814 (1252)	-194 (64)	1582 (377)			-10430 (4031)	0.90	***	8
	S*	2542 (680)	-127 (31)	1555 (205)			-6452 (2189)	0.95	***	8

• These equations are based on a reduced data set excluding 13 cm swards (see rate of intake section discussion).

* As described in the results section these are simplified versions which exclude D^2 terms from the E2 rate of intake equations. These simplified equations are not used for Fig. 6.1.

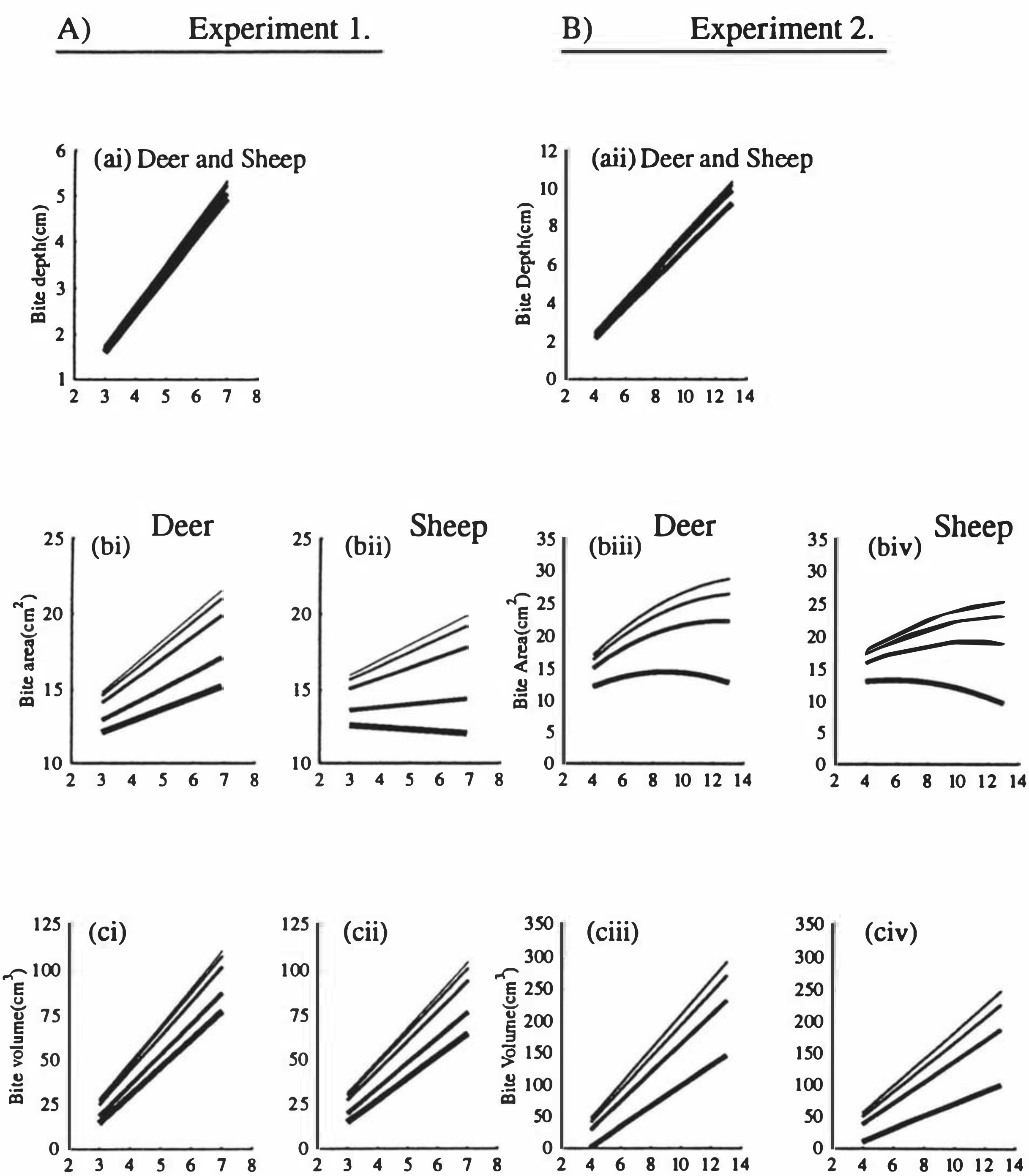

Fig 6.1 The effects of independent changes in sward height and bulk density (fine through heavy lines represent sparse through dense swards respectively) in A) Experiment 1 (3-7 cm x 0.33-4.00 mg DM cm^{-3}) and B) Experiment 2 (4-13 cm x 0.63-3.25 mg DM cm^{-3}) on the combined (deer and sheep) bite depth (ai-aiv) or separate (deer or sheep) bite areas (bi-biv) and bite volumes (ci-civ). These figures are based on regression equations in Table 6.3.

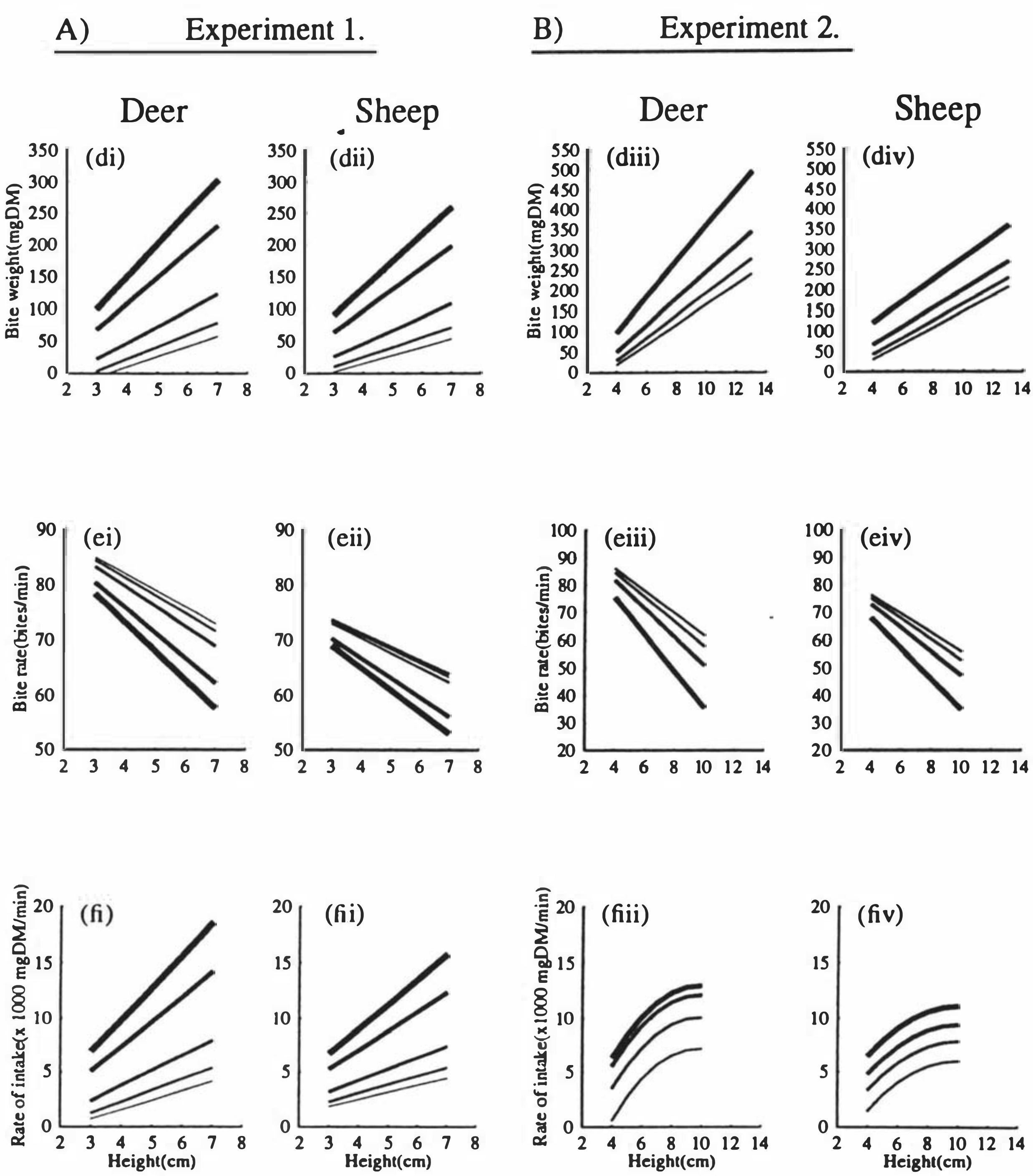

Fig 6.1(cont.) The effects of independent changes in sward height and bulk density (fine through heavy lines represent sparse through dense swards respectively) in A) Experiment 1 (3-7 cm x 0.33-4.00 mg DM cm^{-3}) and B) Experiment 2 (4-13 cm x 0.63-3.25 mg DM cm^{-3}) on the separate (deer or sheep) bite weights (di-div), bite rates (ei-eiv) and rates of intake (fi-fiv). These figures are based on regression equations in Table 6.3.

Table 6.4. The relative changes in sward height or bulk density required to change each bite parameter by a given amount assuming the animal was grazing a medium height x bulk density (equivalent to grazed stratum bulk density) sward defined as 7.5 cm x 1.5 mg DM cm^{-3}. (Averages are taken across animal species and experimental sward variation). Note how the influence of height relative to that of bulk density is reduced in E2, because it includes a taller, less restrictive range of heights on average compared to E1.

Bite dimension	Experiment	Necessary % change in		- to change bite parameter by -	Ratio %HT : %DEN
		Sward height	Bulk density		
Bite depth	1	15	845	1 cm	1:57
	2	16	249	1 cm	1:16
Bite area	1	14	40	1 cm^2	1:3
	2	19	17	1 cm^2	1:1
Bite weight	1	48	159	100 mg DM	1:3
	2	49	116	100 mg DM	1:2
Bite rate	1	36	298	10 bites min^{-1}	1:8
	2	37	98	10 bites min^{-1}	1:3
Rate of intake	1	9	27	1000 mg DM min^{-1}	1:3
	2	14	38	1000 mg DM min^{-1}	1:3

differences reflected the way the BW of deer increased 21% and 49% faster ($P<0.048$) in relation to increasing HT in E1 and E2 respectively. Differences in BW were on average negligible on short swards, but deer achieved 14% and 32% larger ($P<0.004$) bite weights at 7 cm and 13 cm HT in E1 and E2 respectively. Deer also achieved slightly larger bite weights than sheep ($P<0.049$) on the highest DEN swards in each experiment, although the slopes only differed significantly in E1 ($P<0.070$). These DEN trends appeared to reflect deer having slightly larger bite areas and very slightly deeper bite depths at higher DEN levels, compared to sheep; although no bite parameters other than BW differed significantly between species in relation to DEN.

Despite these differences in BW and BV, the BD of deer and sheep was otherwise very similar over the entire HT and DEN range in both experiments (Table 6.1), indicating that BA was the dominant source of disparity between deer and sheep. In E1, sheep achieved larger bite areas at 3 cm HT (14.6 ± 0.5 vs 13.0 ± 0.4 cm2; P=0.064). These differences were most marked at lower densities, and on average species differences in BW were negligible on short swards. However, as HT increased above 3 cm, deer increased their BA more rapidly (P<0.032) than sheep, and achieved larger bite areas by 7 cm HT (18.7 ± 0.5 vs 16.9 ± 0.5; P=0.046). Very similar trends were evident in E2, with BA showing no increase between 7 cm and 13 cm HT for sheep (18.8 ±1.4. vs 19.4 ±1.4; P=0.764) compared to an 18% increase indicated for deer (20.4 ± 1.5 vs 24.1 ± 1.5; P=0.127). When scaled to incisor arcade width, the BA of sheep exceeded that of deer by more than 21% on average (P<0.015) in both experiments, although differences tended to decline, becoming non-significant above approximately 7 cm HT.

BR trends were broadly similar across species in both experiments, except that deer had a 16% (P<0.066) and 12% (P<0.036) higher BR across treatments in El and E2 respectively. Although the slopes did not differ significantly, there was a tendency for species differences in BR to decline and become non-significant on taller swards, as species differences in BW increased.

The RI of deer was 22% (6659 ± 371 vs 5441 ± 343 mg DM min^{-1}; P<0.053) and 18% (8234 ± 350 vs 6968 ± 328 mg DM min^{-1}; P<0.039) higher than that of sheep on average in E1 and E2 respectively. As for BW, the least square means for both experiments indicated negligible differences in RI between species on 3 or 4 cm swards, but the RI of deer was approximately 25% higher at 7 cm HT in El (P=0.073) and 10 cm HT in E2 (P=0.044).

6.5 DISCUSSION

6.5.1 Sward parameters

In E1 tillers were virtually touching at the highest DEN, but were about 1.5 cm apart at the lowest. By restricting the range of HT variation to 3-7 cm, E1 swards kept HT and DEN independent as well as largely unconfounded with other structural variables such as leaf strength, size, age, spatial arrangement, proportion of dead matter and apparent acceptability to the animal.

E2 covered an extended range of heights up to 13 cm, where RI was expected to become increasingly restricted by chewing and swallowing rates (Kenney & Black 1986), rather than spatial bite dimensions which severely limit RI on shorter swards (Chapter 7). Although DEN differences in E2 were confounded with limited differences in tiller size, the narrower range of densities examined (5-fold compared to 12-fold in E1) kept this to a level where tillers were otherwise similar in age, shear strength and structure and it was considered unlikely that this altered the DEN effect on bite dimensions.

Swards were grown to a uniform height (in their respective experiments) before being trimmed to the HT required for feeding. Consequently, as HT declined the proportion of tiller length consisting of pseudostem increased markedly in both experiments. The use of shorter swards in either experiment was avoided as this would have necessitated trimming off the entire leafy strata from most tillers. However, animals still penetrated into the pseudostem zone during their initial grazing of a particular site and, if allowed to regraze, sheep for example grazed tillers down to a very short 0.5 cm residual. Thus the transition from leaf to pseudostem did not appear to present an obvious barrier to penetration of these seedling swards.

Wheat swards appear to have provided a good model for describing the independent effects of HT and DEN on bite dimensions, although very short swards (< 3 cm) close to minimum grazable heights were not measured and, BD may have been reduced slightly on the shorter swards which had relatively tall pseudostems and shallow leafy horizons.

6.5.2 Bite depth

BD increased rapidly and linearly with HT. DEN had only a small negative effect on swards taller than 3-4 cm, and this was best explained in terms of a HTxDEN interaction, reflecting the increasing effect of DEN with increasing HT. The stronger HTxDEN interaction in E2 compared to E1 swards (-0.035 vs -0.017; $P<0.001$) was in line with the increased rigidity of the thicker, more mature tillers in E2. However, the HTxDEN coefficients for the BD of deer (-0.029) and sheep (-0.039) in later experiments (Chapter 7) using swards of a similar age to those in E1 were more similar to those for E2 than E1. This suggests that the low coefficient for E1 may simply reflect error associated with the narrow range of short sward heights used.

When compared to sorghum swards (Chapter 5), the negative effect of DEN in both of the current experiments was small. For example, at a height of 13 cm, a 1 mg DM cm^{-3} increase in DEN caused BD to decline by 4.1 cm in Chapter 5, compared to only 0.5 cm in E2. Similarly, extrapolation up to 18 cm HT using the E2 BD equation (Table 6.3) and assuming DEN levels of 4.23 and 0.47 mg DM cm^{-3} (equivalent to those used by Black & Kenney 1984) indicated the DEN effect on the BD of sheep grazing hand-constructed ryegrass swards was more than twice as large as that on E2 wheat swards.

Both the sorghum (Chapter 5) and ryegrass (Black & Kenney 1984) comparisons suggest that the fragile seedling wheat tillers were easy to penetrate, and that tiller rigidity and strength may interact with DEN to alter BD. However, the DEN effect of hand-constructed paspalum swards on the BD of large steers (Laca *et al.* 1992b) was similar to that evident for the E2 wheat swards (respective coefficients for the HTxDEN terms were -0.030 vs -0.035). Logically, the large tillers of paspalum swards would be more rigid than seedling wheat or ryegrass tillers, and more similar to sorghum. Perhaps the small DEN effect upon BD evident for paspalum swards can be explained if the BD of large, powerful animals such as cattle is less affected by tiller density and rigidity at any given HT than for smaller animals such as sheep. In support of this suggestion, DEN had no effect on BD below 15 cm HT for cattle grazing hand-constructed paspalum swards (Laca *et al.* 1992b), compared to only 3-4 cm HT in E2, despite similar ranges in DEN.

Although the interactive effects of tiller strength and rigidity with DEN need further clarification, in general the effects of DEN on BD can probably be ignored as only large differences in DEN appreciably alter BD. Further, BD appears to be relatively insensitive to DEN within the critical range of heights likely to restrict daily herbage intake.

6.5.3 Bite area

The use of very uniform sward conditions in both the current study and that of Laca *et al.* (1992b) with cattle, clearly demonstrate that BA increases with HT, although at a slower or declining rate as DEN or HT increase, respectively.

BA trends for E1 and E2 were similar although, as for BD, the stronger HTxDEN terms for E2 equations (-0.47 vs -0.25 for deer, and -0.46 vs -0.31 for sheep; $P<0.069$) correlate with the greater strength and rigidity of the older E2 swards, characteristics which can make the ...nsion and severing of tillers more difficult (Ungar *et al.* 1991; Laca *et al.* 1992b). There was no difference in curvilinearity between E1 and E2, suggesting that E1 represented the close to linear section of the BA response to increasing HT on shorter swards.

Declining BA with increasing DEN was also demonstrated in earlier studies (Hughes *et al.* 1991; Chapter 5) and indicated, although non-significant, in Burlison *et al.* (1991). These trends appear to support the concept that BA is influenced by the effort required to sever a bite (Hodgson 1985). In the current study however, even on taller swards where differences in BA due to DEN were close to maximal, the rate of increase in BA was much lower than the rate of decline in DEN, indicating that animals have only a limited ability to maintain BW, by increasing BA, as DEN declines. On hand-constructed paspalum or lucerne swards (Laca *et al.* 1992b), the rate of change in the BA of cattle per unit change in DEN was greater as indicated by the three fold higher HTxDEN coefficient (-1.43). Grazing with the tongue (cattle), probably enables greater increases in BA as DEN declines and may also be more sensitive to increasing DEN than gathering with the mouth only (sheep and deer). Differences between coefficients may also in part reflect experimental sward differences in tiller strength or rigidity, which can alter BA in relation to DEN (Demment *et al.* 1992; Chapter 8).

The BA of sheep was greater than or at least equal to that of deer on the shortest swards in E1 and E2 respectively, but was smaller on taller swards, because above 3-5 cm HT the BA of sheep increased more slowly with increasing HT, to smaller maxima BA, at lower optimum heights. This suggests that deer could utilise or needed longer swards than sheep in terms of maximising BA. Alternatively sheep required less HT in terms of maximising BA, and could achieve larger or at least equivalent bite areas on very short swards despite the approximately 30% wider incisor arcades (IAW) of deer in E1 and E2. When scaled to IAW, sheep achieved almost 50% larger bite areas than deer at 3-4 cm HT, although differences declined with HT and became non-significant at around 7-10 cm HT. This implies that sheep were superior at prehending short herbage, being able to gather and prehend more tillers per bite in relation to mouth width. This data suggests that IAW is not necessarily an accurate predictor of BA across animal species, or within a species where swards are short or DEN differs widely. Further, the current trials as well as those for cattle (Ungar *et al.* 1991; Laca *et al.* 1992b), suggest that any assumptions of a constant BA in relation to changing sward HT (Ungar & Noy-Meir 1988) or DEN (Illius & Gordon 1987) may be somewhat simplistic, if short swards (relative to animal body size) or large differences in DEN are involved.

6.5.4 Bite weight

Despite the 67% heavier live weights of deer, sheep achieved similar bite weights on short swards in both E1 and E2. However, deer were able to increase their bite weights more rapidly ($P<0.048$) than sheep as swards became taller. Thus deer achieved 14% and 32% larger ($P<0.004$) bite weights on 7 cm and 13 cm swards in E1 and E2 respectively. Yet, when scaled to LW, the BW of sheep was approximately 50% larger ($P<0.039$) on average across E1 and E2. Such trends are in line with the field studies of Osbourne (1984), where sheep were able to competitively exclude feral deer from preferred swards in the Scottish Highlands. However, in the current study the relative disadvantage of deer tended to decline as HT increased, due to both the faster increase in the BW of deer with HT as well as the much larger bite weights of both species on taller swards. For example in E1 the BW of sheep (scaled to LW) declined from being 88% greater at 3 cm HT ($P<0.066$) to only 45% greater across 7 cm swards ($P<0.100$). Similar trends were evident for E2.

By assuming that sheep need a BW of about 80 mg DM to maximise daily herbage intake (Penning 1986), a crude estimate of the increasing importance of HT as DEN declines (or conversely the increasing importance of DEN as HT declines) can be determined from Fig. 6.1d (iv) and the E2 BW equation for sheep in Table 6.3. To maintain a BW of 80 mg DM as DEN declined from 3.25, 1.74 or 1.01 down to 0.63 mg DM cm^{-3} required heights of 2.5, 4.6, 5.9 and 6.7 cm, respectively; only a 4.2 cm (150%) change in HT to compensate for a large 2.62 mg DM cm^{-3} (416%) change in DEN. Similarly, the influence of HT on BW was clearly dominant over that of DEN on 3-21 cm sorghum (Chapter 5), 8-30 cm paspalum, 7-25 cm lucerne (Laca *et al.* 1992b), and a range of grass swards (Gong *et al.* 1993).

In agreement with the studies of Burlison *et al.* (1991), Hughes *et al.* (1991), Penning *et al.* (1991a) and Laca *et al.* (1992b), BW on wheat swards increased linearly with HT, up to 7 or 13 cm, in E1 or E2 even at the highest DEN of 4.00 or 3.25 mg DM cm^{-3}, respectively. In contrast,

. increased with HT above 6.5 cm on the very dense 4.23 mg DM cm^{-3} hand- ...ted ryegrass swards of Black & Kenney (1984). Because BA (Fig. 1b (ii, iv); Fig. 2 in Laca . *al.* 1992b) is unlikely to decline rapidly enough or sufficiently (in relation to increasing HT) to account for the lack of further increase in BW on the hand-constructed ryegrass swards, it is probable that BD was markedly restricted at this very high DEN. Thus contrary to earlier discussion (see Section 6.5.2) and most published data, this suggests that under some circumstances, very high DEN can override the usual close to linear relationship between BD and HT. This is discussed further in Chapter 9.

6.5.5 Bite rate

With the exclusion of the tallest swards from the E2 data set (see Section 6.5.6), BR trends did not differ across experiments. BR declined linearly in relation to increasing HT, and at a slightly greater rate the higher the density, trends apparently reciprocal to those for BW (Allden & Whittaker 1970; Penning 1986). In agreement with Demment *et al.* (1992), the regression of BR on BW indicated that variations in BR were largely due to differences in BW. However, the regressions of BR on BW were improved (P<0.089) by the inclusion of a HT term in 3 out of 4 cases, suggesting the influence of some direct sward effects upon BR (Hodgson 1985).

Broadly similar BR trends in relation to HT and DEN were also evident on moderate-high density hand-constructed ryegrass swards (Black & Kenney 1984), up to heights of about 6.5 cm, above which BR plateaued or declined more slowly. However, on these ryegrass swards BR was much lower than for comparable seedling wheat swards, particularly those from E1. These differences probably reflect the fragile nature of the seedling wheat tillers when compared to ryegrass. Such differences appear similar to the contrasts observed between pure clover vs ryegrass swards, where the high RI on clover was associated with an increased ease in chewing and swallowing clover (Kenney & Black 1986), relative to ryegrass.

6.5.6 Rate of intake

Plots of treatment means for E2 showed that RI increased rapidly up to 7 cm HT, but much more gradually between 7 and 10 cm, trends consistent across DEN levels (except the lowest DEN level in the case of sheep) and animal species. However, between 10 and 13 cm HT, RI again increased rapidly as a result of a much lower rate of decline in BR above 10 cm. BR is sensitive to the rate of accumulation of herbage in the animal's mouth (Demment *et al.* 1992) and as for BW, was more sensitive to herbage length than DEN (Table 6.4; Section 9.5). On tall or high herbage mass swards animals perform a lot more exclusive chewing bites during which they may raise their head away from the sward (Demment *et al.* 1992; Laca *et al.* 1992a). This behaviour is necessary to process the large amounts of herbage which rapidly accumulate in the mouth and cannot be processed by simultaneous manipulative-chewing jaw movements (Laca *et al.* 1992b; Demment *et al.* 1992; Section 9.5). Further, ingestion of long herbage can involve extra jaw movements simply to draw it into the mouth (Burlison 1987; Gong 1994).

Head-up, exclusive chewing bites were observed on the tallest E2 swards, but this time was discounted at the time as animals (particularly the deer) also lifted their heads if disturbed and pausing from eating. However, as recognised by Forbes & Hodgson (1985a), this head-up chewing behaviour should have been included in BR estimates and would have considerably reduced the RI estimates for the tallest wheat swards in E2. For the above reasons BR and RI results in E2 were derived from 4-10 cm sward data and excluded data for 13 cm HT. Based on the reduced data set, indications were that RI would have plateaued at around 10 cm HT for both species, results very similar to those for sheep on 1-8 cm swards (Chapter 7). Further, the very short-term BR measurements used in E1 and E2 would have over-estimated BR and consequently RI for all treatments, although not to any great degree (Jamieson & Hodgson, 1979a).

In comparison with the wheat swards experiments, the RI of sheep peaked at heights of only 6.5 cm and 10.5 cm for the 4.23 and 1.06 mg DM cm^{-3} hand-constructed ryegrass swards of Black & Kenney (1984). Similarly, the RI of sheep peaked at about 6 cm HT on ryegrass pastures (Penning 1986). Despite the probable over-estimation of RI on wheat swards and their low DM content (10%), they clearly enabled very high rates of DM intake. This was probably because these immature, all green, low shear strength swards were easy to prehend (Laca *et al.* 1992b) and sever, and in particular, like clover, to chew and swallow (Kenney & Black 1986).

Comparisons across experiments indicated that RI differed in terms of DEN effects ($P<0.065$) possibly reflecting, as previously suggested, differences in herbage maturity.

The increasingly greater BW and RI (scaled to LW) of sheep relative to deer as HT declined, suggested that sheep needed less HT than deer to achieve high rates of intake. These trends are in line with the theory that small animals should be relatively better off on short swards compared to large animals (Clutton-Brock *et al.* 1987, Illius & Gordon 1987). Not only is a short sward relatively less limiting to the BD of a small animal but small animals also have larger mouths relative to body weight (Illius & Gordon 1987) and should therefore be able to achieve larger bites in relation to their body size (Illius 1989).

In practical terms, both experiments suggest that under continuous stocking, sheep could be run at relatively higher stocking rates than deer, because the sheep could obtain equivalent intake rates and, when limited by grazing time, daily intakes on the resultant shorter pastures. In both E1 and E2 for example, the RI of sheep was on average approximately 40% greater ($P<0.038$) than that of deer, when scaled to LW. Under rotational grazing deer should require taller initial and/or residual heights than sheep to achieve equivalent rates of intake. Similarly, other studies for sheep (Allden & Whittaker 1970) and deer (Staines *et al.* 1982; Clutton-Brock *et al.* 1987) have indicated that small animals may have an advantage under restrictive sward conditions.

6.6 CONCLUSIONS

HT and DEN clearly influenced all bite parameters. However, given proportional increases in HT and DEN, HT generally has the greater influence on BW, because BD and BA increase with HT, but decline with DEN. Yet BW still increases rapidly with DEN, because the rate of reduction in BV (BD and BA) is much lower than the rate of increase in DEN.

While BD is very sensitive to HT, DEN appears to have comparatively little influence upon BD on most leafy vegetative swards. As for BD, BA declines more with DEN as HT increases. BA also increases with HT on short swards, evidently reflecting the degree of horizontal displacement of herbage (when gathering herbage into the mouth) made possible by increasing tiller length. Consequently, on short swards, restricted BA as well as the more obviously constrained BD will effectively limit BW.

Despite the narrower IAW of sheep, their BW did not decline as rapidly with decreasing HT, and was at least equal to that of deer on the 3 or 4 cm swards in El and E2, respectively. Reflecting these trends for BW and in particular the differences in body size, the relative difference between sheep and deer in terms of their BW or RI scaled to LW or $LW^{0.75}$ increased as HT declined, in line with expectations that small animals are at an advantage on short swards. In practical terms these trends suggest that sheep would obtain equivalent herbage intakes to deer on appreciably shorter swards, lower allowances or at higher stocking rates, and that sheep are likely to out-compete deer on managed temperate gramineous pastures.

Allowing for animal size differences the bite dimensions of deer and sheep grazing wheat swards show a high degree of similarity with those for cattle on leafy paspalum swards (Laca *et al.* 1992b), suggesting that the observed trends may be quite broadly applicable across a range of different sized animals, on a relative basis at least. However, in terms of predicting ingestive behaviour and herbage intake, these 100% green, fragile seedling swards probably represent conditions near the end of the spectrum allowing maximisation of BV and BR for a gramineous type sward. For a normal range of grass swards, the positive effects of HT on BD and BA would probably be smaller than those observed on these wheat swards and the negative effects of HT and DEN on BR larger, thus reducing BW and RI responses.

CHAPTER 7

THE INGESTIVE BEHAVIOUR OF RED DEER AND ROMNEY SHEEP. II. INFLUENCE OF HEIGHT AND BULK DENSITY IN ARTIFICIAL SWARDS MANAGED TO CONTROL PSEUDOSTEM HEIGHT

7.1 SUMMARY

(1) The bite parameters of Romney sheep and Red deer were measured on 1-8 cm x 0.65 - 2.90 mg DM cm^{-3} leafy grass-like swards which had been trimmed and regrown so as to reduce variation in leaf depth and pseudostem height across treatments.

(2) Bite depths, bite areas and bite rates were deep, large and high respectively on these young, leafy seedling swards, when compared to bite dimensions on natural grass swards.

(3) On short swards, bite area increased rapidly at a declining rate with increasing sward height (HT), up to a point where mouth dimensions rather than HT appeared to constrain bite area. Bite area approximately doubled on average as sward height increased from 1 to 5 cm. Further, the higher the DEN, the slower the rate of increase with HT, so that BA peaked at a height of 5-6 cm on dense compared to ≥ 8 cm on sparse swards.

(4) Only sheep managed to graze 1 cm swards, 2 cm HT being the shortest swards grazed by deer. The bite rate of sheep increased as HT declined down to 2 cm, while that of deer peaked at 3 cm HT.

(5) The LW of deer was 104% higher than that of sheep, while their incisor widths were only 31% greater. Yet sheep achieved a 79% higher RI (scaled to LW) across 2-8 cm swards, heights typical for managed temperate pastures. Thus sheep were better adapted to grazing short swards than deer. The relative RI kg $LW^{-1.0}$ difference between species declined slightly as HT increased.

(6) The concept of bite depth remaining a constant proportion of HT, as HT changes, is

discussed in relation to the current experiment where bites became relatively deeper as HT increased from minimum grazable levels.

(7) A simple model examines the relative influence of HT, bite depth and mouth dimensions upon tiller prehension (bite area) and demonstrates how penetration to greater than 30% of HT is necessary for animals to achieve large bite areas on short swards.

7.2 INTRODUCTION

As intake per bite or bite weight declines with declining herbage mass it becomes increasingly difficult for the grazing ruminant to maintain daily herbage intake by increasing bite rate and/or grazing time (Allden & Whittaker 1970; Chacon & Stobbs 1976; Hodgson 1985). Consequently, on low to moderate herbage mass swards, bite weight is likely to be the principal determinant of daily herbage intake (Hodgson 1985; Penning 1986). While height (HT) appears to have a dominant role in determining bite weight on temperate swards (Hughes *et al.* 1991; Laca *et al.* 1992b; Chapter 5) the influence of bulk density (DEN) is still important, particularly in the case of some tropical swards (Chacon & Stobbs 1976).

Although somewhat simplistic compared to natural pastures (Burlison 1987), techniques using hand-constructed ryegrass swards (Black & Kenney 1984; Laca *et al.* 1992a, b) and seedling wheat swards (Chapter 6) have made it possible to measure the simultaneous yet independent effects of changing HT and DEN on bite parameters. Using 1 or 2 sheep, Black & Kenney (1984) measured bite weight, bite rate and rate of intake on 1 to 22 cm swards over a wide range of bulk densities, but only made limited measurements or indirect estimates of bite depth and bite area respectively. Both Laca *et al.* (1992b) with cattle on 8-30 cm paspalum swards and Chapter 6 with deer and sheep on 3-13 cm wheat swards measured bite depth, bite area, bite volume and bite weight over a wide range of sward bulk densities, and showed that both spatial dimensions of the bite were sensitive to the interactive effects of HT and DEN.

Using an improved sward technique compared to that in Chapter 6, which reduced relative inter-treatment differences in pseudostem height, the aim of the current experiment was to describe the bite parameters of sheep and deer, over a restricted range of sward heights, for which the most dynamic changes in bite dimensions should be observed as HT increases from minimum grazable levels. Limitations in access to facilities dictated that sheep and deer were used in separate experiments.

7.3 METHODS

7.3.1 Design

Fifteen sward treatments (5 heights x 3 densities) were fed to four sheep and four deer. Each animal received all 15 treatments, at 7-8 treatments per day on two consecutive days. Treatment allocation was balanced over days and animals, with each animal receiving treatment swards in order of increasing herbage mass on any one day. Sheep were fed in late spring 1990, and deer in late winter 1991 when facilities became available. Sward heights were 1, 2, 3, 5 and 8 cm, and tiller densities 6500, 13 000 and 29 000 tillers m^{-2}.

7.3.2 Animals

The four 27 month old Romney ewes weighed 38-47 kg and had total incisor widths of 34-39 mm (adult incisors 34-37 mm). The four 33 month old Red deer hinds weighed 82-93 kg and had incisor arcade widths (IAW) of 46-47 mm. Sheep had 6 adult teeth per animal which contributed 95% or more of total incisor widths. Deer had all 8 adult incisors. Animals had been selected for their willingness to eat and were housed in metabolism crates. These animals were familiar with the experimental procedures (Chapter 6), but were also retrained for 2-3 weeks. They were fed hay and grain *ad libitum* except on measurement days when allowances were reduced to 60% (details in Chapter 6).

7.3.3 Swards

For both sheep and deer respectively, two replicates of seedling wheat swards with 30 trays per replicate were sown one day apart. As detailed in Chapter 6 seeds were spaced and sown using perforated hardboard sheets into seed trays and grown until tillers reached 8-11 cm (Plates 2 & 3).

To achieve similar proportions of pseudostem and leaf across all sward heights, 1 and 2 cm swards were trimmed to a residual height of 0.5 cm, and 3 cm swards to 1.0 cm 2 days before grazing. This allowed these short swards to regrow with a much higher proportion of expanded green leaf than if trimmed to height when 8-11 cm high, as for 5 and 8 cm swards.

7.3.4 Grazing measurements

Animals were presented with swards at foot level on a moveable trolley and allowed to take at least 20 bites (Plates 9 & 10). Time spent grazing, number of bites taken, area of leaves grazed and the residual height of 40 grazed leaves were determined. These direct measurements were used to determine bite depth (BD), the number of grazed leaves, bite area (BA), bite volume (BV), bite weight (BW), bite rate (BR) and short term rate of intake (RI). Measurements, calculations and statistical procedures are detailed in Chapter 6.

7.3.5 Sward description

Previous work had shown that tillers could reach 10 cm in height without resulting in density differences in tiller size, due to the large energy reserve of wheat seeds (Chapter 6). Consequently, tiller variation due to density was ignored.

The fresh weight and dry weight per unit length of three 10-tiller samples from each of a 1-2 or 3 cm sward cut into 1 cm strata, or 5-8 cm sward cut into 2 cm strata, were measured. Thus bulk density could be calculated for each sward height x density combination. Pseudostem heights measured for 30 tillers were representative of the 1-2, 3 and 5-8 cm swards.

7.4 RESULTS

7.4.1 Sward structure

Swards were free of dead material, and ready to feed when the tallest tillers reached 11 cm. Previous work had indicated that by this stage about 90% of tillers would have reached 8 cm (Chapter 6). No correction was made for any tillers not reaching 8 cm.

Pseudostem heights were 0.60 ± 0.01, 1.01 ± 0.01 and 1.8 ± 0.01 cm for 1-2, 3 and 5-8 cm swards respectively.

Tillers consisted of pseudostem (0.5-2.0 cm), the first 0.25-1.0 cm of which was encased in coleoptile. Above the pseudostem was the first and tallest leaf, and the second leaf which typically reached a height of 4-8 cm. Averaged over all swards, the total tiller dry weight per unit length was 1.00 ± 0.04 mg DM cm^{-1}. As in Chapter 6 the value of 1.00 mg DM cm^{-1} was used in the calculation of all sward bulk densities regardless of sward height.

7.4.2 Sward height by density effects on bite parameters

Treatments covered in this trial ranged from short, low density swards which animals could barely graze, through to HT x DEN combinations allowing extremely high rates of intake (Table 7.1). Only sheep managed to graze 1 cm swards.

The relationships between HT and DEN, and the bite parameters are described graphically (Fig. 7.1), by correlation (Table 7.2), in regression equations (Table 7.3) and in the following text.

Over the 7-fold increase, HT was extremely well correlated with BD, and also with BV due to the strong positive correlation of HT with BA (Table 7.2). Further, HT was strongly correlated with RI and BW. By comparison, over the 3.5 fold increase, DEN was not well correlated with any bite parameters. BW and RI were even better correlated with herbage mass than HT.

The interactive effects of HT and DEN were significant in the regressions for all bite parameters (Table 7.3). For BA and RI the HT^2 terms reflected a declining rate of increase with HT. DEN^2

Table 7.1. The mean and range of sward variables and bite parameters for deer and sheep.

Parameter	Units	Sheep/deer	Mean	Range
Height	cm	-	-	1-8
Bulk density	mg DM cm^{-3}	-	-	0.65-2.90
Herbage mass	mg DM cm^{-2}	-	-	0.65-23.2
Tiller density	tillers m^{-2}	-	-	6500-29000
Bite depth	cm	S	2.8	0.6-6.7
		D	3.0	0.8-6.5
Bite area	cm^2	S	16.1	8.8-23.2
		D	20.4	11.4-31.8
Bite volume	cm^3	S	53.5	5.6-152.0
		D	70.3	8.6-205.5
Bite weight	mg DM	S	71.1	2.8-266.2
		D	84.2	3.1-299.3
Bite rate	bites $min.^{-1}$	S	72.9	41.5-88.7
		D	76.2	52.6-93.1
Rate of intake	mg DM $min.^{-1}$	S	4395	173-11070
		D	5714	204-15846
BD/HT ratio	%	S	70.4	58.3-83.4
		D	68.7	57.1-80.1

terms were indicated for BA, BV, BW and RI, but did very little to improve the fit and were left out of the equations for the reasons given in Chapter 6.

As HT increased from minimum grazable levels, BD increased very rapidly and linearly, increasing (P<0.001) from about 60 to 80% of HT. Plots of the means indicated that BD was insensitive to DEN on very short swards (<3-4cm HT), but declined slightly as DEN increased on taller swards(Fig. 7.1a (i, ii); Table 7.3).

Table 7.2. Correlation matrix indicating general relationships between sward variables and bite parameters of deer and sheep combined.

	Height	Bulk density	Herbage mass	Bite depth	Bite area	Bite volume	Bite weight	Bite rate
Bulk density	0.00							
Herbage mass	0.68***	0.66***						
Bite depth	0.99***	-0.01	0.61***					
Bite area	0.77***	-0.33+	0.20	0.77***				
Bite volume	0.94***	-0.16	0.43*	0.96***	0.87***			
Bite weight	0.85***	0.45*	0.95***	0.81***	0.42*	0.67***		
Bite rate	-0.68***	-0.17	-0.68***	-0.68***	-0.25	-0.58**	-0.77***	
Rate of intake	0.85***	0.46*	0.90***	0.81***	0.50**	0.70***	0.96***	-0.66***

*** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$, + = $0.05 < P < 0.10$

BA increased with HT at a declining rate the taller the sward, but at a considerably lower rate on dense compared to sparse swards (Fig. 7.1b (i, ii); Table 7.3). However, even on the most dense swards BA increased ($P<0.001$) by up to 90% as HT increased from minimum grazable levels. The declining influence of HT on BA (when averaged across species and DEN levels) meant that for every 1 cm increase in HT between 1-2, 2-3, 3-5 and 5-8 cm, BA increased by approximately 5, 4, 1.8 and 0.7 cm^2 respectively.

BV increased in a linear or close to linear manner with HT but, as for BD and BA, at a lower rate the higher the DEN (Fig. 1c (i, ii); Table 7.3). In contrast to BV, and reflecting the direct positive influence of DEN on BW, the denser the sward the more rapid the increase in BW (Fig. 7.1d (i, ii); Table 7.3) with increasing HT.

. BR increased with HT up to 2-3 cm but then declined linearly ($P<0.001$) at a slightly higher rate the higher the DEN, declining by about 5 bites min^{-1} per cm increase in HT on average. Only the portion where BR declined linearly in relation to HT is described by the equations in Table 7.3, and by Fig. 7.1e (i, ii). BR declined linearly in relation to DEN although trends were much less consistent on 1-2 cm swards. HT effects were dominant (Chapter 6).

Table 7.3 Regression equations for bite parameters of Romney sheep and Red deer in relation to sward height (1-8 cm) and bulk density (0.65-2.90 mg DM cm^{-3}). Criteria for including variables are described in Chapter 6.

Bite parameter	Animal species	Sward variable coefficient (± S.E.M.)				Statistics		
		HT	HT^2	HTxDEN	Intercept	r^2	P	residual d.f.
Bite depth	S	0.875 (0.016)		-0.039 (0.006)	-0.266 (0.054)	0.99	***	12
	D	0.863 (0.027)		-0.029 (0.011)	-0.433 (0.099)	0.99	***	10
Bite area	S	4.81 (0.44)	-0.29 (0.05)	-0.33 (0.05)	5.88 (0.77)	0.97	***	11
	D	6.52 (1.15)	-0.36 (0.11)	-0.76 (0.09)	6.41 (2.41)	0.96	***	8
Bite volume	S	22.6 (0.7)		-2.4 (0.3)	-17.7 (2.4)	0.98	***	12
	D	31.0 (1.3)		-4.3 (0.5)	-32.8 (5.3)	0.99	***	9
Bite weight	S	9.8 (1.1)		9.0 (0.4)	-21.3 (3.4)	0.99	***	12
	D	15.9 (1.8)		8.9 (0.7)	-45.6 (7.3)	0.99	***	9
Bite rate[1]	S	-3.2 (0.5)		-1.3 (0.2)	96.2 (2.5)	0.97	***	9
	D	-4.7 (0.7)		-0.6 (0.2)	105.0 (3.5)	0.94	***	6
Rate of intake	S	1587 (485)	-105 (51)	346 (59)	-1600 (853)	0.94	***	11
	D	1928 (476)	-103 (46)	477 (36)	-3338 (1001)	0.99	***	8

[1] The bite rate equations describe the linear part of the response for heights of 2-8cm and 3-8cm, in sheep and deer respectively (see results Section 7.4.2).

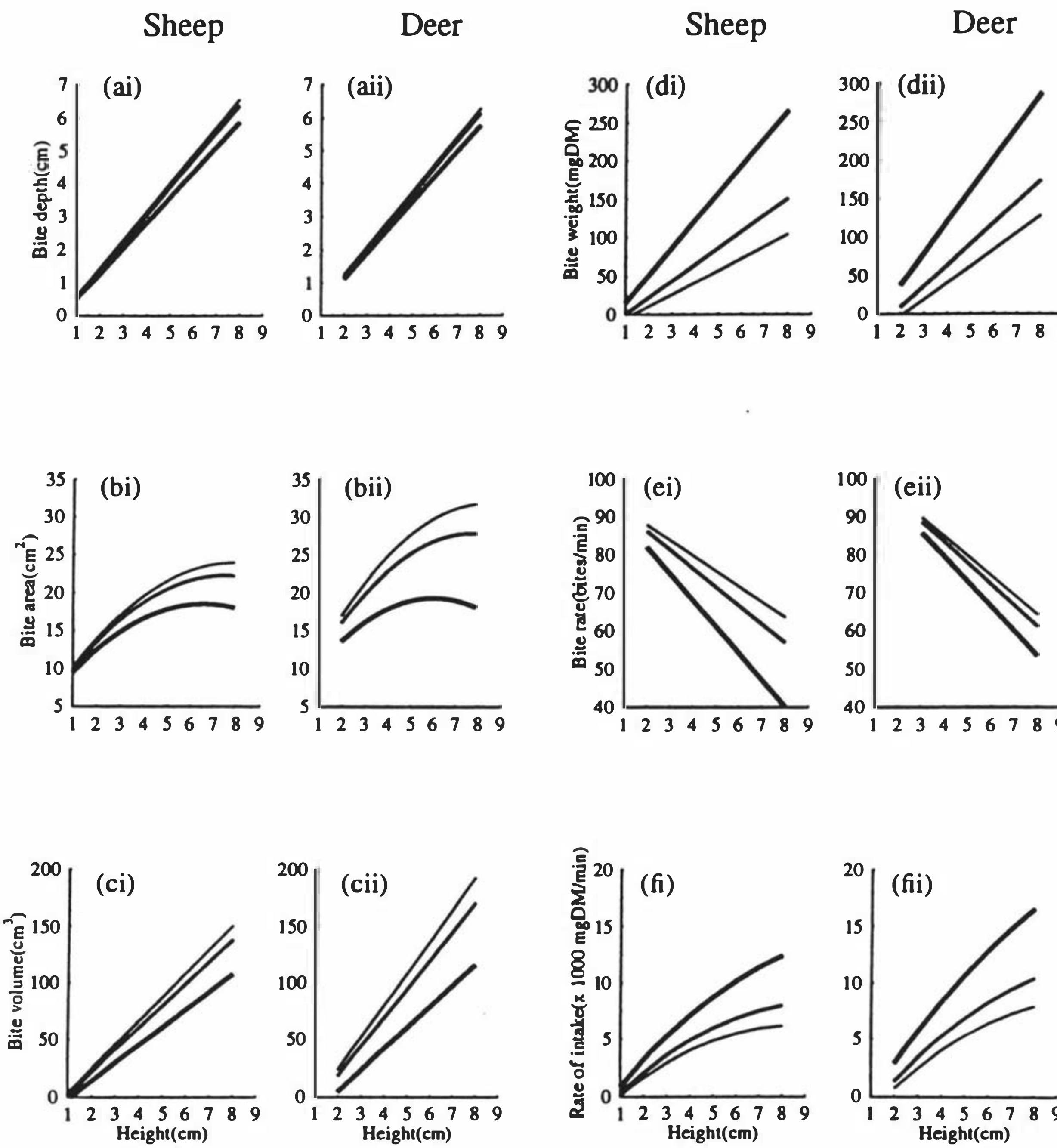

Fig 7.1. The effects of independent changes in sward height (1, 2, 3, 5 & 8 cm) and bulk density (0.65, 1.30 & 2.90 mg DM cm^{-3})(fine through heavy lines respectively) on the bite depths (ai & aii), bite areas (bi & bii), bite volumes (ci & cii), bite weights (di & dii), bite rates (ei & eii) and rates of intake (fi & fii) of sheep or deer. These figures are based on regression equations in Table 7.3.

RI increased rapidly with HT, at a declining or lower rate the taller or sparser the sward respectively (Fig. 7.1f (i, ii); Table 7.3). Increases in RI in relation to DEN were close to linear and less marked than for increases in relation to HT on short swards.

7.4.3 Species differences in bite parameters

Results from 1 cm swards were highly variable for deer as they would not or could not readily prehend such very short tillers, so these results were excluded from analysis. Sheep had notably less difficulty with 1 cm swards, and these data were included for analysis.

The BD of sheep was 5% greater (P=0.046), while the BA of deer was 19% larger (21.1± 0.7 vs 17.7 ± 0.7 cm^2; P=0.017) on average, with species differences in BA increasing slightly as HT increased.

BW was similar for deer and sheep overall (90.9 ± 3.9 vs 87.6 ± 4.0 mg DM; P=0.567), reflecting the deeper bites of sheep and larger bite areas of deer. However, similar to the trends in Chapter 6, the L.S.M. values indicated that by 8 cm HT the bite volumes and bite weights of deer were 15-21% higher (P<0.057) than those of sheep, although species differences in slope were not significant.

The BR of sheep increased with HT up to 2 cm (P<0.001) compared to 3 cm for deer (P<0.049) and then declined at a similar rate, although the BR of deer was 10% higher (P<0.096) on average between 3 and 8 cm. Largely reflecting these differences in BR, RI was on average 18% higher for deer between 3 and 8 cm HT (7667 ± 513 vs 6495 ± 523 mg DM min^{-1}), with a difference of 32% (P<0.056) at 8 cm HT.

7.5 DISCUSSION

7.5.1 Sward techniques

It was considered inappropriate to confound variation in sward height to the extent of comparing taller leafy swards with shorter, all-pseudostem swards when trying to measure the independent effects of HT and DEN on ingestive behaviour. Previous studies of ingestive behaviour using wheat seedling swards (Chapter 6) excluded sward heights less than 3 cm where BD, BA and BW were becoming very restricted, as such short swards necessitated trimming off all the leafy strata. In the current trial, trimming and regrowth procedures enabled the inclusion of leafy-surfaced swards, ranging in HT from 1 cm (which was barely grazable) to 8 cm, facilitating the description of bite dimensions over the range of heights where the most dynamic changes in BA (Chapter 6), BR and RI (Black & Kenney 1984) were to be expected. Although leaf depth was not proportionally constant across all heights, it exceeded 60% of HT on all but 1 cm swards, for which it was only 0.4 cm deep. Further, the young pseudostems were not a lot more rigid than leaf and were penetrated during grazing, although bite depths on short swards of equivalent HT and DEN, but with proportionally much taller pseudostems (Chapter 6) were slightly shallower ($\leq$15%; $P<0.05$) than those in the current experiment. Experimental differences in BD/HT became negligible on taller swards as differences in pseudostem height declined.

With respect to DEN variation, the treatments encompassed a wider range than that likely to occur in managed temperate pastures of similar heights; the effects of even wider DEN variation having been described in Chapter 6.

7.5.2 Sheep - deer differences

As sheep and deer were fed 9 months apart, in late spring and late winter respectively, species differences may have been confounded with day or seasonal effects (Kay 1979; Barry *et al.* 1991). This implies less reliable species comparisons than in earlier experiments (Chapter 6). Further, sheep were shorn just prior to their experimental period, another factor which might have altered their appetite (Arnold 1981).

The slightly deeper bites of sheep may simply be measurement error associated with the separate experiments as no differences in BD occurred in earlier experiments (Chapters 5 & 6). Alternatively the difference in BD might reflect an increased hunger drive in spring compared to winter grazing.

On the other hand, the BA area of deer exceeded that of sheep to an even greater degree compared to earlier experiments (Chapter 6), in line with the increased (ca. 60%) species differences in LW and body size in the current study. The greater similarity between species for BW and RI compared to earlier wheat sward experiments largely reflects the antagonistic effects of the species differences in BD and BA upon BV.

When BA was scaled to incisor arcade width (IAW), the BA of sheep was marginally greater (10%; $P<0.115$), a similar but smaller species difference to those in Chapter 6. This trend, plus the ability of sheep to successfully prehend 1 cm swards, and their slower rate of decline in BA with reducing HT (indicated in Chapter 6), all suggest that sheep were not only allometrically superior, but also behaviourally superior at prehending short swards compared to deer. The BR of sheep increased with HT up to 2 cm before declining with further increases in HT, while the BR of deer increased up to 3 cm, again indicative that deer needed more HT than sheep to graze with equivalent ease. The slightly higher BR of deer above 3 cm HT is in agreement with earlier studies (Chapter 6).

For both sheep and deer the regressions of BR on BW were significantly improved ($P<0.051$) by the inclusion of a BA term. It is plausible to suggest that an increase in gathering required to enlarge BA as DEN declines may in part offset the positive effect of declining DEN upon BR, via reducing BW (i.e. reduced processing time). This may in part explain the corresponding increased DEN effects on BA and reduced DEN effects on BR indicated for deer compared to sheep in Fig. 7.1(bi & bii) vs (ei & eii).

On 2 cm swards (which appeared to be the shortest the deer could graze) the BW kg $LW^{-1.0}$ of sheep was 167% greater than that of deer. However, the faster ($P<0.048$) increase in the BW kg $LW^{-1.0}$ of deer with increasing HT plus the larger bite weights of both species on taller swards, resulted in the BW kg $LW^{-1.0}$ of sheep being only 79% greater ($P=0.007$) relative to that of deer on the 8 cm swards. Very similar trends were evident for RI kg $LW^{-1.0}$, although species differences were slightly smaller, being 56% higher ($P<0.007$) for sheep at 8 cm HT and 79% higher ($P=0.001$) on average across 2-8 cm swards; heights typical for managed temperate pastures. These species differences are in line with earlier experiments in Chapter 6, although when scaled to LW they are more marked than in Chapter 6, because of the considerably greater differences in species LW within the current study. Such trends support the concept that the RI of smaller animals is not as restricted by short or low herbage mass swards (Allden & Whittaker 1970; Illius & Gordon 1987). They also suggest that the larger deer had the potential to slightly reduce their disadvantage relative to the smaller sheep as HT increased. Larger animals (eg. cattle) may also graze more deeply than smaller animals (sheep), further reducing any differences in RI kg $LW^{-1.0}$ (I.J. Gordon pers. com.; Betteridge *et al.* 1994)). However, such differences in BD were not evident in the current series of trials, possibly reflecting the rather small differences in animal size between sheep and deer (I.J. Gordon pers. com.).

Extrapolation to heights greater than 8 cm indicated that the RI of sheep would have reached a plateau at around 10 cm HT, several centimetres shorter than for the ca. 100% heavier deer, although a plateau at 10 cm HT is in close agreement with the results for both species in Chapter 6.

7.5.3 The spatial dimensions of the bite

7.5.3.1 Bite depth in relation to height

In the current experiment the BD/HT ratio increased with increasing HT at a rapidly declining rate, as indicated in other studies involving short, high quality artificial swards (Ungar *et al.* 1991; Chapter 6). Presumably animals are under greater pressure to take proportionally deeper bites within the range where HT is severely restricting BW. As HT continues to increase, leaving a taller residual becomes less important in terms of restricting BW but should increase the ease and efficiency of biting as well as the quality of herbage ingested. On natural swards, where herbage quality declines more markedly down the sward profile, leaf depth may be the more important constraint on BD (Hodgson 1985). The above trends suggest that penetration will become a relatively constant proportion of HT as HT increases.

Both Wade (1991) and Laca *et al.* (1992b) suggested that grazing cattle may typically remove a reasonably constant proportion of sward HT. Very short-term studies with vegetative gramineous swards indicate BD/HT ratios of approximately 50-60% for cattle (Mursan *et al.* 1989; Laca *et al.* 1991a,1992b) and 40-50% for sheep (Hughes *et al.* 1991; Gong *et al.* 1993; Gong 1994; Chapter 8). In comparison, field studies appear to indicate slightly shallower ratios of at most 40-50% for cattle (Wade 1991; Betteridge *et al.* 1994) or 40% for sheep (Betteridge *et al.* 1994). The slightly deeper BD/HT ratios indicated in these short-term trials using mini-swards may reflect the way that animals can tend to graze more aggressively at the beginning of a feeding bout (Dougherty *et al.* 1987; Taylor *et al.* 1987) during which they can remove a greater proportion of sward HT (Dougherty *et al.* 1989c). These differences do not appear to be due to differences in measurement techniques, which were taken into account when estimating the above ratios (Section 9.2.4).

However, in other examples the BD/HT ratio differs considerably, either within experiments (Milne *et al.* 1982; Burlison *et al.* 1991), in relation to HT or leaf depth across short swards (Barthram & Grant 1984), or in relation to plant maturity or plant species morphology (Gong 1994). Further, as indicated above, BD may be slightly deeper in very short-term experiments compared to longer studies. There is a need to further clarify this potentially useful tool in relation to pasture and experimental conditions.

7.5.3.2 Bite area as affected by sward height and bite depth

On the basis that tillers flex at their base (Laca et al. 1993), it is possible to examine the relative impact of changes in HT and BD on the horizontal distance tillers can be displaced before they will be lost from the grazing animal's mouth. In simple terms, BA has two components, firstly breadth which reflects incisor arcade width (IAW), and secondly the potential horizontal displacement (PHD) of tillers that can occur as the jaws close, without the tillers pulling out of the mouth. Breadth should be constant, but the PHD will be sensitive to HT and depth of penetration or incisor height (Laca *et al.* (1992b). Incisor height was not measured, but closely approximates residual height (RHT, which equals HT-BD) which was measured and is substituted for incisor height in this case. HT sets an ultimate limit on the PHD because tillers cannot be displaced horizontally by more than their own length without totally escaping from the edge of the animal's mouth (Fig. 7.2). Also, the deeper an animal bites, the greater the PHD (and therefore area) of tillers it should be able to prehend before losing those tillers near the front and rear edges of the bite. With reference to Figure 7.2, a BD/HT ratio of 29% (vertical axis) allows both the upper and lower prehending surfaces of the animal's mouth to displace tillers horizontally towards the centre of the bite by the equivalent of up to 70% of HT (horizontal axis) before the outer-most tillers must escape the mouth. Assuming that tillers are displaced equidistant (towards the centre line of the bite) by both the upper and lower jaws, a total PHD (TPHD) equivalent to 140% of HT should result. As BD declines below 29% of HT, the PHD of tillers prehended declines rapidly and at an ever increasing rate (Fig. 7.2). Increases in the BD/HT ratio above 29% of HT only increase the PHD slightly because the angle of escape is more than 45° from the vertical and most of the increase in tiller displacement is vertical (Fig. 7.2)

Although reductions in the BD/HT ratio will have an increasingly large influence on the PHD, particularly those to less than 29% of HT, on average PHD would be more sensitive to proportionally equivalent reductions in HT. For example, halving the BD or BD/HT ratio from 50 to 25% (of HT) only reduces the PHD by 11% (from 87 to 66%; Fig. 7.2), but halving the HT also halves the PHD, ie. HT is more important than BD.

Based on Figure 7.2 it is possible to estimate the potential BA by multiplying the breadth (IAW) and total potential horizontal displacement (TPHD) of the bite (Equation 7.1).

$$Potential\,BA = IAW\,x\,RHT\,x\,2TAN\left[COS^{-1}\left(\frac{RHT}{HT}\right)\right] \qquad \text{Equation 7.1}$$

where RHT=HT-BD (RHT=grazed residual height)

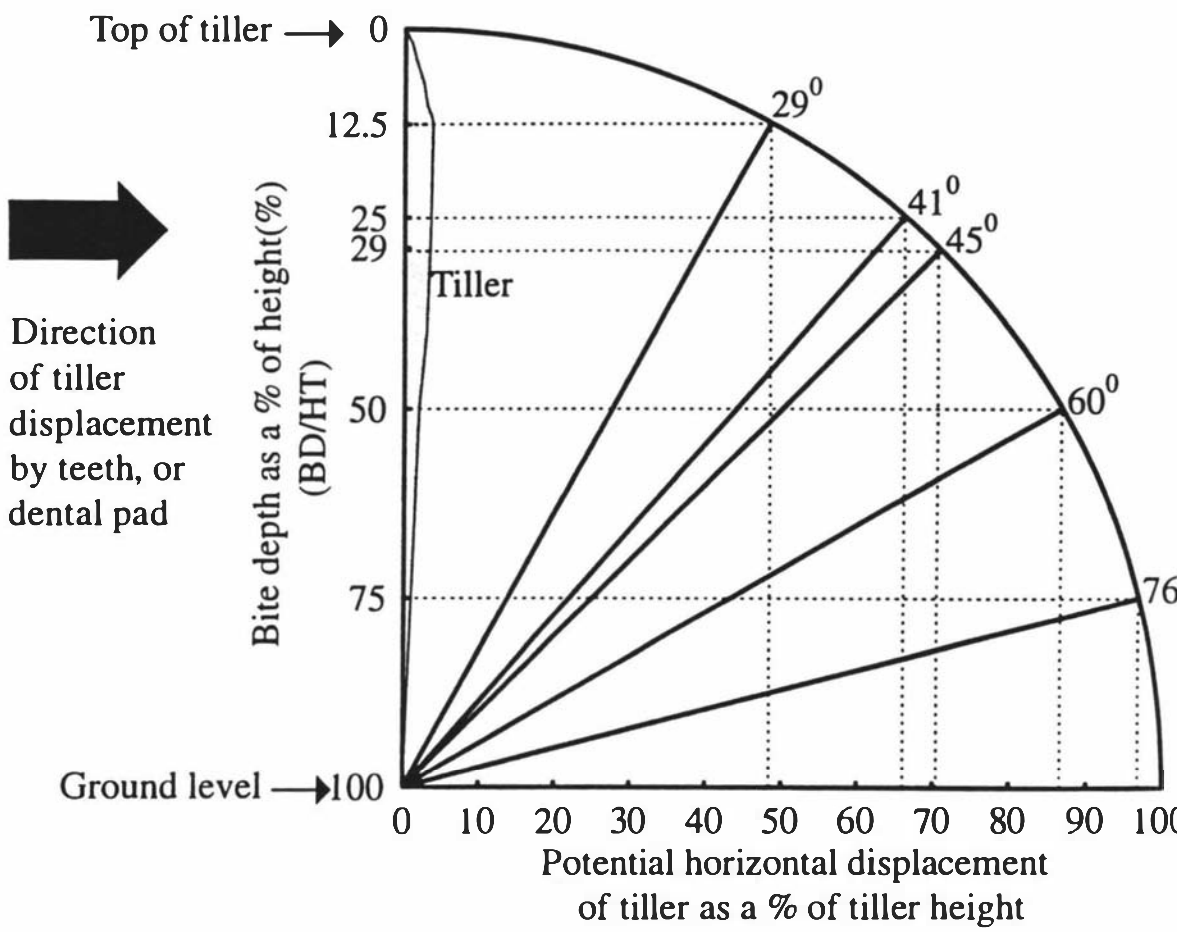

Fig 7.2 The potential influence of bite depth and height upon bite area.

Increasing bite depth and especially height affect bite area by increasing the potential horizontal distance which tillers can be displaced towards the centre of the bite by the teeth or dental pad. The deeper the bite (y axis) and in particular, the taller the herbage, the further the tiller can be displaced horizontally (x axis) before the end of the tiller must pull out of the animal's mouth.

As HT increases from zero, both the potential BA (TPHD x IAW; Equation 7.1) and the actual BA (actual horizontal displacement of tillers x IAW) of sheep increase rapidly (Fig. 7.1b (i)). Because increasing HT enables the TPHD to increase linearly (Fig. 7.2), the potential BA will also continue to increase linearly as swards become taller. However, on dense (2.9 mg DM cm^{-3}) wheat swards for example, the measured BA of sheep (Fig. 7.1b (i)), and consequently the actual horizontal displacement of tillers (BA/IAW), levelled off at around 18 cm^2 and 5 cm (18 cm^2 /3.6 cm = BA/IAW) respectively. That the actual horizontal displacement levelled off at around 5 cm, corresponds closely with the 5 cm maximum gape (distance between teeth and dental pad when mouth is open) measured for sheep by Burlison (1987). Just as the maximum extension of the tongue in cattle limits BA on tall swards (Laca *et al.* 1992b), so too the maximum gape of simple (tongue not used to prehend herbage) grazers such as sheep, appears to largely constrain BA as HT increases. The importance of gape in restricting BA ties in with the observations on wheat swards, where only slight gathering via horizontal movement of the head occurred during herbage prehension. However, sheep were observed to purse back their lips during prehension and manipulate the herbage with rapid movements of their jaws and lips (Hodgson 1990a), in a way which may have extended their gape slightly. By slightly increasing the degree of horizontal head movement or the extension of their lips, sheep would have been able to achieve modest increases in BA as DEN declined, as illustrated in Fig. 7.1b (i).

Thus for simple grazers such as sheep and deer, it would appear that as swards become taller, initially HT, but subsequently maximum gape are the principal constraints upon BA. For example the BA or TPHD of a sheep grazing with a BD/HT ratio of 30% would be restricted up to a HT of at least 3.5 cm (Equation 7.1), at which point the TPHD is equal to the maximum gape of 5 cm. Above 3.5 cm HT, the 5 cm gape as opposed to the TPHD should largely restrict BA. As HT continues to increase the TPHD increases very rapidly so that the BD/HT ratio becomes increasingly less important in terms of restricting BA, because even very shallow bites (<30% of HT) would still enable the TPHD to exceed the 5 cm gape. This suggests that BD will only constrain BA on short pastures, such as continuously stocked swards where HT is restricted and pseudostem height also restricts BD.

In practice however, the sward heights at which the gape will restrict BA and PHD, appear to be somewhat greater than those calculated from Equation 7.1. For example, even on dense (2.9 mg DM cm^{-3}) wheat swards (Fig. 7.1b(i)), where gathering with the lips and horizontal movement of the head should be minimal, and thus BA more directly constrained by gape, the BA of sheep increased rapidly up to about 5 cm HT (Fig. 7.1b(i)). This is approximately 2 cm taller than would be expected based on the measured BD and Equation 7.1, which indicates that BA should approximate the gape of sheep at around 3 cm HT. Such a discrepancy is not surprising in that a reasonable length of even the outer tillers must be gripped within the animal's mouth to enable them to be severed and to be of any benefit to the animal, and is therefore unavailable for displacement. Animals took small nibbling bites on very short swards, suggesting that they reduce their gape as declining HT starts to reduce the efficiency of capture of outer tillers. This would make sense in that maximising BA or the number of tillers severed per bite is not as important as optimising the sum length of tillers captured per bite (Section 9.3.5), in relation to the cost of gathering and severing those tillers. Therefore animals are likely to increase BA with HT at a rate which is below the potential maximum (TPHD), but which enables them to grip and even more especially sever reasonable lengths from all tillers, even those near the front and rear edges of the bite.

Thus in terms of achieving a large BA on short swards where tiller length is limited, animals should penetrate to considerably in excess of 30% of HT. BD/HT ratios in field studies frequently fall in the 40-50% range (Wade 1991; Betteridge *et al.* 1994; Gong 1994) and may reflect some of the above constraints, as animals are no doubt sensitive to the efficiency with which they can prehend tillers.

As well as slightly wider incisor arcades, the longer jawed deer probably had a wider maximum gape than sheep, enabling them to continue to increase BA with increasing HT, up to greater maxima at greater optimum heights (Chapter 6). However, gape measurements were not attempted for deer or sheep in this study. The small mouth (relative to body size) of large grazers such as cattle, suggests a much greater need for them to use their tongue compared to small animals, such as sheep. The extended sweep due to the tongue would help large animals to compensate for their relatively more restricted BA (compared to small 'simple' grazers) and BD (Illius & Gordon 1987), although large grazers may also bite deeper than small grazers (Betteridge *et al.* 1994; I.J. Gordon pers. com.).

7.5.4 Bite rate, bite weight and rate of intake

On ryegrass pastures the BR of sheep increased with HT between 3.7 and 5.0 cm and subsequently declined up to 36.7 cm (Allden & Whittaker 1970). Qualitatively, very similar trends were observed in the current study except that the absolute BR was higher, and the point of inflection was at a lower HT. The low strength of wheat tillers (Chapters 6 & 8), and the short-term BR measurements (Jamieson & Hodgson 1979a) would be expected to lead to high BR values in the wheat sward experiments. Conversely, a shallower BD/HT ratio on the natural swards (Barthram & Grant 1984; Burlison *et al.* 1991; Wade 1991) may have contributed to the higher point of inflection in Allden & Whittakers' study.

Although BW will increase with HT up to high values (Black & Kenney 1984; Burlison *et al.* 1991; Laca *et al.* 1992b; Chapter 5) the range of practically useful heights on well managed temperate pastures tends to be quite narrow (3-10 cm, depending upon the season, the animal species and it's physiological state), as swards need to be kept short enough to maintain a high efficiency of utilisation and keep them vegetative and dense (Wright & Whyte 1989; Hodgson 1990a; Penning *et al.* 1991a), yet tall enough so as not to restrict BD, BA and consequent BW and daily herbage intake unnecessarily. Such pastures are within the HT range covered in the current study and in Chapter 6, suggesting that on managed temperate swards the bite weights of sheep and cattle are likely to be limited via restriction of BD, or BD and BA respectively. On short natural swards however, BD and in some cases BA are likely to be even more restricted than on the wheat swards of the same HT, because the BD/HT ratio is likely to be appreciably lower (Milne *et al.* 1982; Barthram & Grant 1984; Burlison *et al.* 1991; Hughes *et al.* 1991; Wade 1991).

7.5.5 Generalised response

Currently available data for sheep or cattle grazing vegetative grass-dominant swards suggests that the grazing herbivore is likely to remove about 40% of sward height from each grazing horizon (Wade 1991; Betteridge *et al.* 1994), although, for short-term trials using mini-swards, slightly deeper BD/HT ratios may be more usual. The ratio is also likely to increase slightly as animal size increases (Betteridge *et al.* 1994; I. J. Gordon pers. com.), and, on reproductive compared to vegetative swards (Gong *et al.* 1993; Gong 1994). Although BA increases with HT on short swards, it is less sensitive to HT when DEN is high. Thus BA should be reasonably stable on dense (>2.5 mg DM cm^{-3}) swards provided they are not very short (<3-4 cm for sheep). BA increases more rapidly with increasing HT and up to greater heights as DEN declines. However, sparse swards are usually sufficiently tall (>8-10 cm for sheep) for BA to again be reasonably stable. BA is likely to be up to 100% larger on tall, sparse (<0.7 mg DM cm^{-3}) swards compared to dense (>2.5 mg DM cm^{-3}) swards of any HT, provided tiller rigidity and strength are reasonably similar (Chapter 8). BR, the other determinant of short term RI, is likely to decline as swards become denser and especially as they become taller, largely as a direct result of increasing BW. However, the overlap in function of manipulative and chewing jaw measurements may render BR in cattle largely unresponsive to increases in BW up to 1.5-2.0 g DM (Demment *et al.* 1992). As for BA, BR appears to be sensitive to the length, strength and qualitative state of the herbage, so that large changes in these factors may considerably alter BR in relation to BW (Hodgson 1985; Spalinger *et al.* 1988; Gong *et al.* 1993; Gong 1994).

7.6 CONCLUSIONS

The seedling sward techniques employed in the current trials were even more successful in terms of separating HT and DEN variation than was the case for some hand-constructed swards, which tended to change in DEN down the sward profile (Laca *et al.* 1992a; Demment *et al.* 1992). This high degree of control resulted in very young, low shear strength, all green swards with little vertical and no horizontal heterogeneity, compared to natural swards. These sward conditions encouraged deep penetration, large bite areas and high bite rates compared to natural grass swards, resulting in very high rates of intake lying between those typical for pure ryegrass (Black & Kenney 1984) and the much higher values for pure clover (Kenney & Black 1986). Thus, while not suited to direct quantitative prediction of ingestive behaviour and daily herbage intake under field conditions, results from the wheat sward trials enable a good conceptual understanding of how the depth of biting, area of tillers prehended and rate of biting actually respond to independent variation in HT and DEN.

Relative to deer, the shorter minimum grazable HT of sheep, their lower point of inflection for BR, and increasingly large BW and RI per kg LW as HT declined, all point towards sheep being better adapted to grazing short swards.

As HT increases from minimum grazable levels, BA increases rapidly (as increases in BD and especially tiller length allow greater horizontal displacement of tillers), up to a level where mouth dimensions largely constrain further increases.

CHAPTER 8

THE BITE DIMENSIONS OF SHEEP GRAZING SWARDS DIFFERING IN LEAF:PSEUDOSTEM RATIO, DEAD MATTER CONTENT AND/OR TILLER SHEAR STRENGTH

8.1 ABSTRACT

The bite depth (BD) and bite area (BA) of four Romney sheep were measured over a range of 14 ryegrass (*Lolium perenne*) or seedling wheat (*Triticum aestivum*) swards varying in leaf:pseudostem ratio, dead matter content, and/or tiller shear strength. Sheep were housed indoors in metabolism crates and fed uniform swards which had been grown in seed trays.

BD declined slightly but significantly ($P<0.001$) as the percentage of pseudostem and the rigidity of tillers in the grazed stratum increased; BA however, did not change significantly. Similarly, BD as a proportion of height declined close to the ground, where tillers approached their point of attachment to the substrate. The willingness of sheep to penetrate the basal strata of the sward containing large amounts of tough pseudostem appeared to decline when better quality herbage was available in the overlying strata. In contrast, BD and BA were unaffected by the proximity of strata containing high levels of dry dead matter. The increases in BA on low shear strength wheat compared to ryegrass swards were small in relation to the differences in tiller shear strength. This indicated that the force required to sever a bite differed across sward types, and that sheep had only limited ability to increase BA as bulk density declined.

Keywords sheep; bite depth; bite area; leaf:pseudostem ratio; dead matter content; tiller shear strength; ryegrass; wheat seedlings

8.2 INTRODUCTION

Restricted bite weight may depress daily herbage intake when grazing time and/or bite rate cannot be increased sufficiently to compensate (Hodgson 1985). Bite weight is largely determined by sward height and bulk density (Black & Kenney 1984) via their influence upon the depth and area of the bite, and also the bulk density of the grazed stratum (Laca *et al.* 1991b, 1992b; Chapters 5 & 6). However it is evident that other sward structural variables influence bite depth (BD) and bite area (BA), the determinants of bite volume. Such factors may include distribution of leaf (L'Huillier *et al.* 1986), leaf/stem ratio (Chacon & Stobbs 1976), dead matter content (Clark & Harris 1985) and pseudostem height (Barthram & Grant 1984).

BD and BA were highly predictable in relation to height and bulk density variation on uniform wheat swards (Chapters 6 & 7) or paspalum swards (Laca *et al.* 1992b) grazed by deer and sheep or by cattle respectively. However, this was not the case for 9 grass swards grazed by sheep (Burlison 1987), indicating in the latter case that between-sward differences in tiller structure or stratum composition such as those mentioned above were confounding the effects of height and bulk density. The aim of this study was to examine how differences in leaf:pseudostem ratio, dead matter content, tiller shear strength, and/or proximity to the ground surface, pseudostem zone or high levels of dead matter, might affect the spatial bite dimensions (BD and BA) of sheep.

8.3 MATERIALS AND METHODS

8.3.1 Sward treatments and experimental design

Each of four sheep was fed 14 swards representing 14 different treatments. Treatments consisted of different 3 cm deep strata, or combinations of these 3 cm deep strata from 5 different sward types (Fig. 8.1 & Table 8.1). Treatments (T1-T14) differed in leaf:pseudostem ratio, dead matter content, tiller shear strength and/or the position of pseudostem and/or dead matter in the sward. Seven treatments using type 1 swards were fed on day 1 and seven treatments from sward types 2-5 were fed on a subsequent day 2 weeks later (Fig. 8.1). Swards were fed in a randomised order and between-day differences ascertained by feeding one replicate of T10 on each day. Type 1-4 swards were endophyte-free perennial ryegrass (cv. `Grasslands Nui') sown evenly by hand at 1500 seeds m^{-2}; type 5 swards were wheat sown at 1300 seeds m^{-2}. Seeds were sown at an even depth in seed trays to produce swards of similar surface area (29 x 19 cm). Trays were rotated and outer edges shaded slightly to reduce edge effects on plant growth.

8.3.1.1 Type 1 swards

Perennial ryegrass was grown to a surface height of 15 cm and trimmed back to 13 cm; the upper 6 cm was all leaf and the lower 7 cm contained an increasing proportion of pseudostem. The lowest 1 cm was not utilised (see Fig. 8.1). Differences within and between the upper 6 cm leafy and lower 6 cm pseudostem zones were used to form four 3 cm deep strata (treatments T1-T4; Fig. 8.1; Table 8.1) differing in rigidity of leaf (T1 vs T2) or pseudostem (T3 vs T4), degree of leaf expansion (T1 vs T2) and/or leaf:pseudostem ratio (T1-T2 vs T3-T4), to examine the effects on bite dimensions. The lower, upper and middle pairs of these 3 cm strata were also combined to form three 6 cm deep treatments (T5-T7; Fig. 8.1; Table 8.1) to examine how bite dimensions (BD in particular) might differ on 6 cm swards of all leaf (T5) vs all pseudostem (T7) vs 3 cm of leaf subtended by 3 cm of pseudostem (T6).

Treatments 1-7 were uniformly trimmed at the upper surface of the strata or stratum to be fed (see Fig. 8.1) and suspended in a feeding frame (Chapter 5; Plate 7) so that only the prescribed 3 cm or 6 cm to be grazed protruded above the frame surface which was level with the floor of the sheep metabolism crates. Thin steel rods were passed through the base of the strata (T1-T4) or pair of strata (T5-T7) at frame surface height, forming an impenetrable grid of 3 x 3 cm squares.

8.3.1.2 Type 2 swards

Perennial ryegrass swards were grown to 10 cm and trimmed back to 6 cm repeatedly until they developed a high dead matter content between 0 and 6 cm. They were then allowed to regrow to in excess of 13 cm. This produced an upper zone of green matter and a lower 6 cm zone with a high dead matter content. These swards were trimmed to 9 or 12 cm (T13 & T14; Fig. 8.1; Table 8.1; Plate 6) to examine how the proximity of large amounts of dead matter in the two lower strata (0-6 cm) would affect bite dimensions, particularly BD.

8.3.1.3 Type 3 swards

These were similar to type 2 swards but provided a comparison by having most of the dead matter restricted to the lower 3 cm (T11 & T12; Fig. 8.1; Table 8.1; Plate 6), to test whether this encouraged a deeper BD compared to type 2 swards (ie. T13 & T14).

8.3.1.4 Type 4 swards

These were produced from trays of established perennial ryegrass. Swards were trimmed to a height of 3 cm, removed from the trays, the lower 3 cm of potting mix and roots trimmed off and placed back in the trays with the upper surface of the potting mix now 3 cm below the edge of the trays. Trays were filled with sand so that the tips of the tillers just broke the surface, with as uniform a distribution as possible. As for other sward types the sand surface was covered with a cement solution (Chapter 6) to anchor the tillers. Tillers were allowed to regrow rapidly indoors to 8-10 cm and trimmed to produce 3 or 6 cm swards (T8-T9; Fig. 8.1; Table 8.1) that were soft green leaf to ground level, to see how a lack of pseudostem and dead matter at the base of the sward would affect bite dimensions, especially BD.

8.3.1.5 Type 5 swards

Wheat seedling swards (Chapter 6) were grown to 10 cm and trimmed back to 6 cm (T10; Fig. 8.1; Table 8.1) to provide a low shear strength comparison with the various 6 cm ryegrass swards. This treatment was fed on both days to determine any day effects.

8.3.2 Animals

The bite dimensions of four 31 month old ewes weighing 34, 57, 58 and 62 kg but of similar frame size were measured. The 34 kg sheep had previously suffered from facial eczema but grazed readily. All sheep had 8 adult incisors (although the fourth incisors were only partially erupted) and arcade widths were 36-38 mm. All sheep were familiar with being housed indoors in metabolism crates and grazing swards presented on a moveable feeding frame (Chapter 5). Sheep were fed an *ad libitum* ration of hay and grain, although on measurement days new rations were withheld until after experimental feeding was complete.

8.3.3 Feeding and measurement procedure

Immediately before being grazed, the outline of the surface area of each sward was traced onto uniform plastic sheeting overlying a perspex sheet suspended above the sward surface. Swards were then presented to animals at foot level on a moveable trolley. Animals were allowed to graze for at least 20 bites and until they paused or began regrazing areas of the sward. The height of 40 grazed leaves was measured with a ruler. Measurements were spaced evenly across the entire grazed region of the sward, and were never closer than 1 cm. The grazed area of the sward was traced inside the ungrazed outline on the plastic sheet. The area of plastic representing grazed sward was cut out and weighed to determine the total area grazed. The above direct measurements were used to determine BD and BA as follows:

N = number of bites taken by animal

d = sward height minus residual height of each measured leaf

a = total area of sward from which leaves had been grazed

Bite depth = $(\sum d)/40$

Bite area = a/N

Three type 1 swards were cut into 3 cm deep strata from which fresh and dry weight stratum bulk densities were determined. The lack of inter-sward variation indicated one sward per type was adequate provided any irregular swards were discarded. Consequently on day 2, only one sward of each of types 2-5 were described (as for type 1 swards). For each sward type the proportional composition of each stratum was determined from a 20 tiller sample cut into 3 cm strata and dissected into live leaf or pseudostem, and dead matter.

Differences in tiller shear strength were measured at the stratum mid-points of 5 samples of 10 tillers each, for each sward type, using a Warner-Bratzler shear attachment.

8.3.4 Statistical analysis

An analysis of variance tested BD and BA for treatment and animal effects and calculated least square means; separate analyses of variance tested for treatment effects within either 3 cm or 6 cm swards. T11-T14 were analysed for the effects of sward type, height, animal and sward type x height interactions. Day effects were ignored as BD and BA results were the same for T10 swards on both days.

8.4 RESULTS AND DISCUSSION

8.4.1 Bite depth and leaf:pseudostem ratio

A comparison of the four 3 cm deep strata differing in leaf:pseudostem ratio showed a small but significant (P<0.001) decline in BD from 2.6 cm on the 100% green leaf TI to 2.1 cm on T4 containing 75% of up to 3 months old rigid pseudostem (Fig. 8.1; Table 8.1). When these 3 cm strata were paired into 6 cm treatments (T5-T7), swards were grazed to within approximately 1 cm of the grid on the predominantly leaf T5 and the 3 cm leaf/3 cm pseudostem T6, but the sheep left a taller 2.3 cm residual (P<0.001; Fig. 8.1; Table 8.1) on the predominantly pseudostem T7. The increase in bulk density was evidently not the cause of changing BD since it increased by equal amounts between T5 and T6, and T6 and T7 (Table 8.1). Further, Chapters 5-7, as well as studies by Ungar *et al* (1991) and Laca *et al.* (1992b) indicate that BD is relatively insensitive to changes in bulk density at these heights.

As animals jerk their head to sever a mouthful of herbage, tillers can slip a little between the prehending surfaces of the animals mouth so that tillers are severed slightly above where they were initially gripped (Ungar *et al.* 1991). As tiller strength increases down the sward profile, the degree to which tillers slip is likely to increase and leave slightly taller residuals (Ungar *et al.* 1991), giving the impression that BD is declining due to restricted penetration. Increased slipping might explain the small but significant increase in residual height (height-BD) (0.4 - 0.9 cm, P<0.001; Fig. 8.1) over T1-T4. Assuming that slipping was the sole cause of increasing residual height, the increase in residual height between T2-T3 (0.2 cm), and T3-T4 (0.2 cm) should closely approximate the increases in residual height across corresponding strata when combined to form the 6 cm treatments (see Fig. 8.1) T5-T6 and T6-T7, respectively. In fact in these cases the increments were 0.3 cm and 1.1 cm respectively. Clearly slipping does not appear adequate to account for the much larger difference in residual height between T6-T7 (1.1 cm) compared to T3-T4 (0.2 cm), suggesting that real changes in penetration occurred.

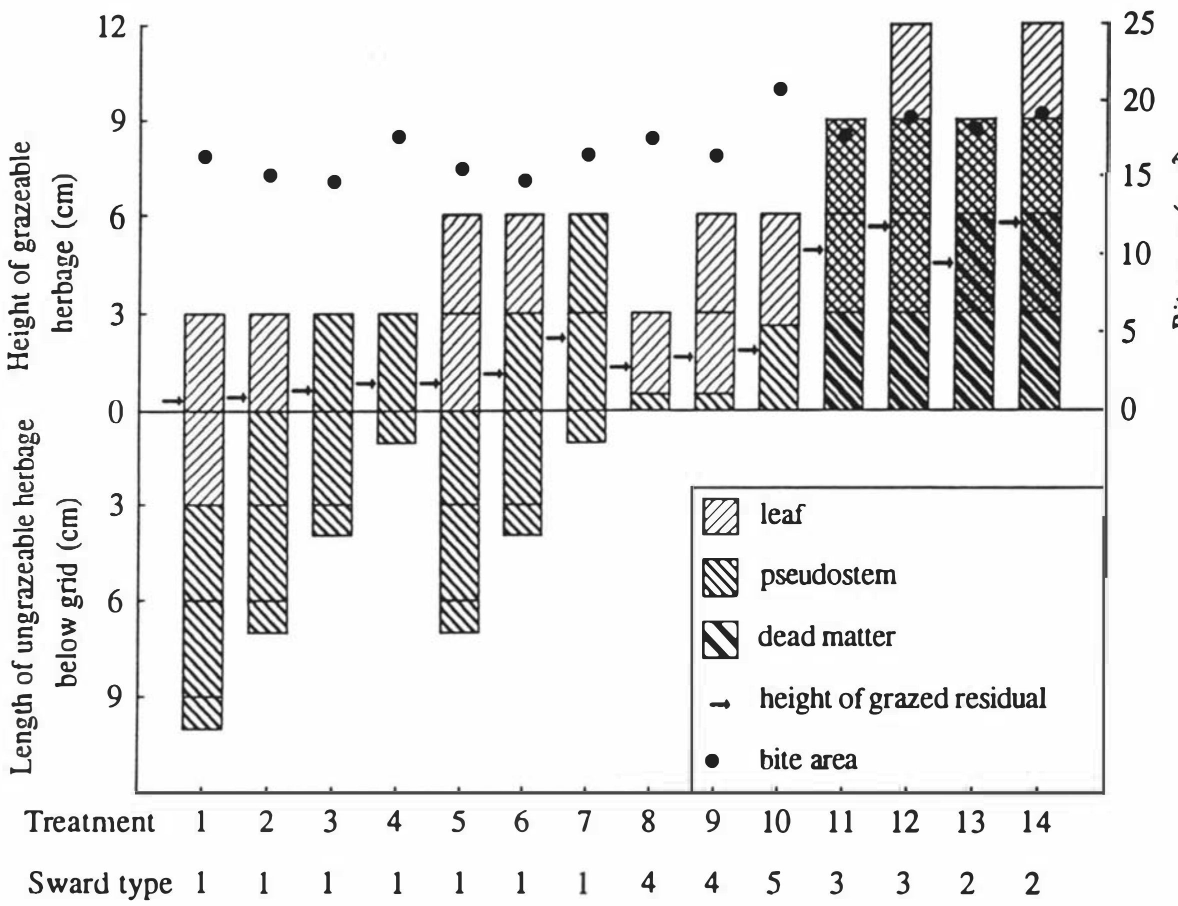

Fig. 8.1 Treatments T1-T14 are 3 cm strata or combinations of 3 cm strata from sward types 1-5 used to examine the spatial bite dimensions (bite depth and bite area) of sheep in relation to sward differences in leaf:pseudostem ratio, dead matter content, tiller shear strength, proximity to the ground, pseudostem zone or dead matter (detailed in Table 8.1). Major herbage components in each strata and mean bite depths (height of grazed residual) and bite areas are denoted as in the key (for SEM of bite dimensions, see Table 8.1). Only the upper 3 cm of T1-T4 or upper 6 cm of T5-T7 were available for grazing, with the lower remaining strata (below zero on the Y axis) beneath an impenetrable grid of rods. For T8-T14, the entire sward down to ground level (zero on the Y axis) was available for grazing.

Table 8.1. Sward variables and spatial bite dimensions from 14 sward treatments, differing in leaf pseudostem ratio, degree of dead matter, tiller shear strength and/or pseudostem height. All 14 treatments are 3 cm deep strata or combinations of these strata, from 1 of 5 different sward types.

Treatment	Sward type	Height or depth of treatment (cm)	Strata utilised (cm)	Treatment or stratum bulk density (mg DM cm^{-3})	%DM	Pseudostem height (cm)	Tiller density #/10 cm^2	% green leaf (% DM)	% green pseudostem (% DM)	% dead matter* (% DM)	Shear strength at strata mid-point (N tiller^{-1})	Bite depth (cm) Mean	± SE	Bite area (cm^2) Mean	± SE	BD/ height (%)
T1	1	3	9-12	0.36	12.5	6.2	10.3	100	0	0	6.2	2.6	0.0	16.3	1.3	87
T2	1	3	6-9	0.59	11.7		10.3	83	5	12	6.8	2.5	0.0	15.1	1.5	83
T3	1	3	3-6	0.86	10.6		10.3	37	42	21	6.6	2.3	0.0	14.7	1.0	77
T4	1	3	0-3	1.14	9.6		10.3	11	75	14	7.9	2.1	0.0	17.6	0.3	70
T5+	1	6	6-12	0.48	-		10.3	91	3	6	-	5.1	0.1	15.5	1.0	85
T6+	1	6	3-9	0.73	-		10.3	60	24	16	-	4.8	0.1	14.7	0.5	80
T7+	1	6	0-6	1.00	-		10.3	24	58	18	-	3.7	0.1	16.5	1.6	62
T8	4	3	0-3	0.30‡	11.4	0.5		86	14	0	4.0	1.6	0.1	17.5	1.3	53
	4	-	3-6	0.20‡	12.7			100	0	0	3.5					
T9	4	6	0-6	0.25‡	-			93	7	0	-	4.3	0.1	16.3	0.5	72
T10	5	6	0-6	1.3	-	2.6	13	49	51	0	-	4.1	0.1	20.8	1.0	68
	5	6	3-6	1.3	10.0		13	95	5	0	2.2					
	5	6	0-3	1.2	9.5		13	2	98	0	2.5					
T11	3	9	0-9	1.08	-	8-9†	9.8	31	53	16	-	4.0	0.2	17.7	0.6	44
T12	3	12	0-12	0.98	-		9.8	48	40	12	-	6.3	0.3	18.9	1.0	53
	3	-	9-12	0.64	12.8		9.8	100	0	0	-					
	3	-	6-9	0.87	12.4		9.8	56	44	0	6.4					
	3	-	3-6	1.11	11.0		9.8	38	48	14	6.8					
	3	-	0-3	1.27	9.0		9.8	0	65	35	8.0					
T13	2	9	0-9	1.69	-	8-9†	10.8	31	35	34	-	4.4	0.2	18.1	0.8	49
T14	2	12	0-12	1.39	-		10.8	48	26	26	-	6.2	0.3	19.1	1.8	52
	2	-	9-12	0.49	15.5		10.8	100	0	0	-					
	2	-	6-9	0.72	14.6		10.8	70	30	0	8.0					
	2	-	3-6	1.61	15.3		10.8	23	25	52	13.2					
	2	-	0-3	2.74	13.1		10.8	0	50	50	13.6					

* The % DM of green vs dead matter was approximately 12% vs 83% respectively, so that multiplying the % dead matter by 0.14 and leaving the % green matter unchanged would give the approximate proportions of each on a fresh weight basis.

+ These three 6 cm deep treatments are pair combinations of the above 3 cm treatments (strata).

† These pseudostem heights are adjusted estimates as they were actually measured one week before being grazed.

‡ These are approximate as tiller spacing was less uniform both within and between swards compared to other treatments.

Most of the difference in the BD of cattle was associated with real changes in depth of penetration or incisor height (Laca *et al.* 1992b). Thus with T7, it appears that sheep only slightly penetrated the lowest 3 cm strata (equivalent to T4) containing the tougher, more rigid pseudostem fraction. This suggests that although sheep may readily penetrate strata containing flexible green pseudostem (equivalent to T3, lower half of T6 and upper half of T7) they avoid penetrating lower strata containing tough rigid pseudostem (lower half of T7), when this subtends immature, leaf-like pseudostem above (upper half of T7). However, sheep did graze this tough rigid basal zone (T4) almost as deeply as higher strata containing pseudostem (T3) when there was no choice (Fig. 8.1; Table 8.1). This sort of selective grazing may, if on a horizontal plane, be one reason for sward mosaics forming under less intense grazing pressure (Wright & Whyte 1989; Gibb 1991).

The results for T5-T7 appear similar to those for sheep grazing ryegrass pastures (Barthram & Grant 1984; Clark 1993) or cattle grazing tall fescue (Arias *et al.* 1990), where animals apparently adjusted BD so as not to penetrate the pseudostem zone. In the case of the ryegrass swards continuously stocked by sheep (Barthram & Grant 1984; Clark 1993), this zone probably contained quite mature (Hodgson 1990a) and therefore rigid pseudostem material. In apparent contrast, Flores *et al.* (1993) found that pseudostem height of paspalum swards had no effect upon the BD of cattle. However, when lower horizons contained stem material, BD was restricted if stem height was greater than the residual height to which animals usually penetrated on leafy, stem-free swards. Presumably, the different result for pseudostem and stem reflected differences in tiller rigidity and/or strength; as was probably the case for the T7 vs T5 and T6 comparison although these contrasts involved pseudostem and/or leaf material. Similarly, qualitative differences in the pseudostem of tall fescue (Arias *et al.* 1990) and paspalum swards (Flores *et al.* 1993) may explain the apparent experimental contrasts in penetration by cattle. However, Demment *et al.* (1992) suggested that the pseudostem height of tall fescue (Arias *et al.* 1990) may have been below the normal zone of penetration. Results for sheep on ryegrass/white clover (Milne *et al.* 1982) and ryegrass or timothy swards (Burlison *et al.* 1991) support this conclusion.

Based on the current experiment and the available literature it would appear that in many instances the upper strata containing pseudostem do not limit BD, because such strata are below the normal zone of penetration and/or (unlike true stem material) are not sufficiently different from leaf, in terms of maturity and structural strength, to restrict BD. Pseudostem probably does have considerable influence on very short swards (Barthram & Grant 1984) where animals may be under greater pressure to maximise BD (Chapter 7; Section 9.2.3), the depth of stratum containing leaf and immature pseudostem is shallow, and the tough mature pseudostem at the base of the sward is also close to the sward surface.

For both 3 and 6 cm swards in T8 and T9 the small amounts of pseudostem which regrew above the sand (Table 8.1) were so young and soft as to be indistinguishable from leaf. Cementing at the base did not prevent small amounts of the sand around some tillers being dislodged and ingested by sheep during grazing. Sheep were observed to quickly reduce penetration after several initially deep bites, thus minimising further ingestion of sand which they appeared to find very unpleasant. Based on the few groups of very closely grazed tillers (approximately 0.7 cm residual height) and the above observations, sheep would have grazed T8 and possibly T9 more closely (Fig. 8.1) had the sand not contaminated the tillers. Sheep grazed 3 cm ryegrass leaves protruding through smooth hardboard sheets to board level (Black & Kenney 1984), which is much deeper than on comparable natural ryegrass/white clover swards (Milne *et al.* 1982; Barthram & Grant 1984), suggesting that certain characteristics of natural swards inhibit penetration near the base of the sward.

The young tillers of the 6 cm wheat swards (T10), anchored with sand and cement, were easily displaced yet BD was 7-10 mm shallower (Table 8.1; $P<0.001$) than on ryegrass 6 cm all leaf (T5) or leaf/pseudostem swards (T6) with a grid base. Similarly, BD was shallower on T10 compared to much more mature and rigid 6 cm wheat swards with equivalent structure to and fed with the same grid technique as T5 and T6 (Mitchell, Hodgson & Clark unpubl. data). Tillers passing through the

3 x 3 cm grids could be displaced by up to 4.2 cm along the diagonal of the grid in the horizontal plane at grid level, equivalent to ground level. This probably made it easier for animals to penetrate close to the very base of the sward (ie. grid level), as well as more efficiently capture the herbage initially encompassed by the bite, compared to the young seedling wheat tillers (T10) which were firmly anchored at their base. Firmly anchored tillers near the front or rear edge of the bite will tend to slide out of the mouth as the jaws close, leaving taller residuals compared to grid based swards. In other words, both penetration and the efficient capture of tillers probably become more difficult close to the ground, near the fulcrum or point at which tillers are firmly anchored to the ground and become most rigid (Sections 9.2.3 & 9.3.5).

Based on pre- and post-grazing measurements both Wade (1991) and Betteridge *et al.* (1993) suggested that sheep and/or cows grazing grass dominant pastures representing a range of heights and management conditions removed a fairly constant proportion of sward height. In contrast, the BD/height ratio varied widely (44-87%) in the current experiment (Table 8.1). However, this variation largely reflected the very deep bites on grid based swards (62-87%) for reasons described above. BD/height ratios on the more natural ground based T11-T14 swards were in fact shallower and less variable at 44-53%. Results similar to the 41-52% of height removed by sheep across a range of 22-35 cm untrimmed vegetative turfs representing 5 different grass species (Gong 1994) or the 39-46% of height removed by sheep grazing trimmed 5-15 cm ryegrass turves differing in tiller structure (Hughes *et al.* 1991).

8.4.2 Bite area and leaf:pseudostem ratio

BA was similar across 3 cm (T1-T4) or 6 cm (T5-T7) stratum treatments respectively (Fig. 8.1; Table 8.1). Even the marked decline in the leaf:pseudostem ratio between T1 and T4 did not significantly alter BA, possibly because the increases in tiller shear-strength down the sward profile were not particularly large (≤27%, Table 8.1). However, on the 3 cm treatment containing the lowest leaf:pseudostem ratio (T4), sheep were observed making particularly vigorous head jerks when compared to severing bites on the higher strata or taller swards, suggesting that biting effort was greater in this case. It is possible that the clumping of tillers around individual plants, which became quite marked in the lowest strata (T4), led to an overestimation of the true area encompassed per bite in the lower stratum (ie T4 and possibly T7).

BA on the 6 cm low shear-strength wheat swards (T10) was 15-41% larger ($P<0.06$) than on any 3, 6 or 9 cm ryegrass swards (Fig. 8.1; Table 8.1 and excluding T8 and T9, where tiller strengths and densities were very low and bite dimensions suspect due to sand contamination). Similarly, the BA of steers was larger on oat swards of equivalent sward bulk density but of lower tensile strength compared to paspalum swards (Demment *et al.* 1992). In the current trial however, estimates of the forces required to sever a bite (BA x tillers cm^{-2} x tiller shear strength) were up to about 3 fold higher on ryegrass compared to wheat swards, ie. much larger than the differences in BA. This suggests that while animals may reduce BA as bulk density or tiller strength increases, the force required to sever the bite is likely to increase considerably. The delicate and slightly brittle nature of the seedling wheat tillers possibly made them comparatively easy to gather and prehend (Laca *et al.* 1991a, 1993) during grazing. Further, the much lower shear strength of wheat tillers (Table 8.1) probably reduced their tendency to slip out of the mouth rather than sever (Demment *et al.* 1992), and may have encouraged sheep to increase BA on wheat compared to ryegrass, although BA was as large on 12 cm T14 ryegrass swards. The greater BA on 12 cm and some 9 cm swards compared to most 6 cm and 3 cm ryegrass swards is in line with the observation that BA increases with height (Betteridge *et al.* 1991; Laca *et al.* 1992b; Chapters 6 & 7).

8.4.3 Bite depth and bite area in relation to dead matter content

In apparent contrast to the generally held view that sheep avoid dead matter in the sward (Arnold 1981; Black *et al.* 1989), BD on T11-T14 (Fig. 8.1) was related to height ($P<0.001$) and was unaffected by the proximity of dead matter regardless of the height. In fact BD was slightly deeper ($P<0.05$) on the 9 cm treatment with the high dead matter content up to 6 cm (T13) vs 3 cm (T11). Despite the reasonably high pseudostem content up to about 9 cm in T11-T14, the BD/height ratios ranged from 44 to 53%, very comparable to the results of Hughes *et al.* (1991) and Gong (1994) for sheep on a range of grass turfs, and appreciably deeper than the 19 to 32% for sheep on 5.7 to 22.1 cm ryegrass swards (Burlison *et al.* 1991). Thus neither dead matter, nor pseudostem height and content, had any obvious influence upon BD. It is noteworthy that the sheep were used to eating hay, and the standing dead matter in the swards was predominantly dry during the latter stages of sward growth and showed only minor signs of decay. Further, animals may learn to eat rapidly and be less selective when given brief and infrequent access to feed during short-term indoor studies (Section 9.1.3.3). Animals also tend to eat faster and may therefore be less selective at the beginning of a feeding bout (Dougherty *et al.* 1987, 1989c; Taylor *et al.* 1987; Arias *et al.* 1990).

BA did not differ across any of these four treatments (T11-T14), confirming the observation that sheep did not appear to be selecting green components within the grazed horizon (L'Huillier *et al.* 1986). BA values (18-19 cm^2) were very similar to those for sheep grazing 5-15 cm ryegrass turfs in Hughes *et al.* (1991).

8.5 CONCLUSIONS

BD as a proportion of height declined close to the ground, where tillers approached their point of attachment to the substrate and tiller rigidity increased. BD also declined slightly as the leaf:pseudostem ratio declined down through the sward profile, although the increasing strength and rigidity of tillers probably had as much influence as did the increasing proportion of pseudostem. However, the degree to which actual penetration became more restricted when animals grazed lower strata, as opposed to residuals becoming taller due to increased slipping of tillers between the prehending surfaces of the animals mouth during severing, is unclear. The willingness of sheep to penetrate the lower, more rigid pseudostem zone near the base of the sward appeared to be strongly influenced by the availability of other more palatable herbage in the overlying strata.

A high level of dry dead matter in the sward had no effect upon BD or BA. Similarly, flexible green pseudostem at or near the sward surface did not appear to restrict BD, again indicating the probable importance of qualitative factors in determining bite dimensions. BA was larger on wheat swards than comparable ryegrass swards, probably reflecting the low shear-strength of the wheat seedling tillers. However, differences in BA were small in relation to differences in tiller strength, indicating that the force required to sever the two types of herbage differed considerably.

Sheep can graze very close to ground level, but the ingestion of small amounts of undesirable matter such as sand, can cause a marked reduction in the depth of subsequent bites.

CHAPTER 9

GENERAL DISCUSSION

In this chapter the experimental techniques used in these trials are discussed first (Section 9.1). Next, key results, trends and concepts arising from the five trials and other relevant work are drawn together, compared and discussed; practical implications are alluded to and suggestions for future work made (Section 9.2 - 9.7). Emphasis is upon the spatial bite dimensions, as these closely reflect the grazing animal's response to sward conditions and the actual mechanisms of BW adjustment.

9.1 Techniques

9.1.1 Mini-swards

Mini-sward trials using seedling wheat swards (Chapters 6 & 7), the grid technique (Sorghum swards in Chapter 5) or hand-constructed swards (Black & Kenney 1984; Laca *et al.* 1991b; Laca *et al.* 1992a, b) stand apart from other short-term or field studies in terms of achieving independent variation in HT and DEN, largely unconfounded with other structural variation.

The grid technique (Plates 1 & 8) can only encompass a limited range of DEN variation before marked clumping of tillers occurs. Further, HT and DEN are likely to be autocorrelated if all swards are trimmed to a single uniform HT, and HT is adjusted by moving the grid up or down relative to the sward surface, because of the naturally occurring changes in DEN down the sward profile. The grid itself may not be recognised as the ground, because animals can see through it, even though it blocks penetration. The grid also alters the way tillers behave when being grazed, because it allows them to move about horizontally at ground (grid) level, by an amount dependent upon grid size. These characteristics probably affect BD and BA by increasing the ease of penetration and efficiency of prehension respectively, near the base of the sward (the grid). To correct for differences in microclimate, tall sorghum swards needed constant attention (shifting and rotation) during growth; this was very labour intensive but necessary even in well set-up glasshouses to ensure uniformity of tiller structure across trays.

Hand-constructed swards allow the widest range of HT x DEN combinations in a single experiment, as well as the controlled introduction of other vertical and horizontal heterogeneity; but they are extremely labour intensive. Unless quite a large team of people is available this will limit replication, numbers of treatment combinations and animal species comparisons. Like natural and grid-based swards they tend to change in DEN down the sward profile (Laca *et al.* 1992a), which is likely to result in some degree of HT-DEN autocorrelation. When short they also appear to be grazed more deeply than comparable natural swards (compare Black & Kenney 1984 with Milne *et al.* 1982).

In comparison, seedling wheat swards (Chapters 6 & 7) can be produced in very large numbers with only one or two people and, given good temperature regulation, can produce very uniform swards within very short, predictable growth periods (Plate 3). Production, grazing and measurements involve about 0.4 compared to 11 man hours per sward for wheat and hand-constructed swards (Laca *et al.* 1992a) respectively. Despite having a more natural ground level or base than hand-constructed swards, wheat swards also appear to result in deeper grazing penetration than occurs on natural swards. Tillers of young seedling wheat swards, as with the youngest leaf on mature grass plants, tended to pull out or sever below where they were actually gripped by the animal, leading to the potential overestimation of BD. However, selection of plant variety, temperature control during the final stages of growth and care during measurement procedures helped to minimise this problem.

The problem of tillers severing too low was much less marked on the older 4-13 cm wheat swards (Chapter 6; Plate 5), yet the BD/HT ratio trends were similar to those for younger swards (3-7 cm and 1-8 cm swards; Chapters 6 & 7 respectively) suggesting that any measurement errors on younger swards were not large. The delicate nature and low shear strength of wheat tillers also resulted in larger bite areas and higher bite rates than on comparable ryegrass swards (Chapters 6-8).

9.1.2 The use of trimmed swards

In an attempt to precisely define HT and to save time in measurements, researchers frequently use trimmed swards to evaluate height effects on bite dimensions (Plates 4, 5, 6 & 7). A trimmed sward presents the animal with a relatively simple surface (Plates 8, 9 & 10) compared with that of many natural swards. It could be argued that such differences might affect bite dimensions, as they can affect patch and possibly even bite site selection (Bazely 1988; 1990; Illius & Gordon 1990a; Demment *et al.* 1992). On an untrimmed sward, the animal's bite dimensions may respond to the upper, lower or average surface height of the patch or selected bite site. When steers grazed heterogeneous paspalum swards constructed from alternating 10 and 20 cm tall, 400 or 100 cm^2 patches, they appeared to respond primarily to the taller patches (Demment *et al.* 1992). Penetration was deeper and slightly shallower than expected on tall and short patches respectively, although both BD and incisor height were on average close to the values (about 1 cm deeper) achieved on swards with a single uniform 15 cm HT (Demment *et al.* 1992). Further, on average BD did not differ across a range of shorter heterogeneous paspalum swards averaging 6 cm HT (alternating 4 & 8 cm patches) or 10 cm HT (alternating 6.7 & 13.3 cm patches) when compared to BD at a uniform 6 or 10 cm HT (Ungar *et al.* 1991). These results suggest that BD will be approximately proportional to average surface height and, in view of the potential time savings, appear to lend support to the continued practice of trimming swards for some experimental purposes.

Further, as DEN declines and animals attempt to prehend larger areas of herbage (Section 9.2.2.1), residual height should increase near the outer edges of the bite, and thus BD should decline. However, on sorghum and wheat swards BD actually increased as DEN decreased, clearly indicating that incisor height also decreased (ie. penetration increased). In future work however, it appears that precise definition of the real constraints on BD will ideally include measurement of not only BD itself, but also incisor height and biting effort, as performed by Laca *et al.* (1992b).

9.1.2.1 Number of grazed horizons

The tendency for sheep and deer to regraze an area (take bites from the second horizon) of the wheat swards before removing all of the available ungrazed surface horizon was a very rare event on short swards but was observed more frequently for heights greater than about 8 cm. When it began, regrazing was largely avoided by shifting the grazed area slightly away from the animal's muzzle. Regrazed areas were excluded from measurements as much as possible. This raises the possibility that, unlike cattle (Wade 1991; Demment *et al.* 1992), sheep and deer may not remove the surface horizon before grazing the next horizon down. However, recent studies with sheep, goats, deer and cattle (I.J. Gordon pers. comm.) lend support to Wade's findings . Of course, the high quality of the whole sward profile, the small size of mini-swards, their rapid depletion and the intense short-term nature of the experimental procedures may have modified their behaviour in comparison with field conditions.

9.1.3 Animal factors

During grazing measurements in Chapters 5-7 animals were offered only two-thirds of the hay and grain ration they normally consumed each day. This was to ensure an adequate feeding drive (Dougherty *et al.* 1987), so as to overcome any reluctance to eat some of the low herbage mass swards being offered. Reduced rations were unnecessary in the sheep only trial in Chapter 8, as sward conditions were not as restrictive and, compared to deer, sheep were more consistent in terms of their willingness to graze even low herbage mass swards.

9.1.3.1 The effects of hunger and fasting on ingestive behaviour

Reducing the ration in the experiments in Chapters 5-7 may have had a similar effect to fasting animals for a few hours prior to offering them experimental swards. Fasting does not usually alter diet quality (Sidahmed *et al.* 1977; Jung & Koong 1985; Greenwood & Demment 1988), suggesting (as above) that the depth of the grazed horizon is not markedly altered. Also, when measured, BW (and presumably BV) are in many instances not affected by fasting. For example, fasting cattle for up to 36 hours increased their bite rates on ryegrass (Greenwood & Demment 1988) and lucerne (Dougherty *et al.* 1989a) swards, but had little or no influence upon their bite weights. Similarly, fasting slightly increased the BW of cattle on only two out of eight pasture types (Chacon & Stobbs 1977) or the tallest of five ryegrass pastures (Greenwood 1990).

Similarly, when steers were fed to 0, 30, 60 and 90% of their daily maintenance ratio of lucerne pellets, any differences in hunger had no effect upon BD, BA or BR when subsequently grazing hand-constructed paspalum swards (Griggs *et al.* 1991b; Demment *et al.* 1992).

Based upon the above discussion it would appear likely that reducing the daily hay ration had little if any effect upon the spatial bite dimensions of animals grazing wheat swards.

9.1.3.2 Length of grazing period and background diet

Although difficult to separate from the effects of fasting (Greenwood & Demment 1988), animals appear to graze faster at the beginning of a grazing bout (Chacon & Stobbs 1977; Dougherty *et al.* 1989c), presumably due to a greater hunger drive, low physical satiety (Dougherty *et al.* 1987) and perhaps also reduced fatigue. This would suggest that short-term studies may overestimate RI, because access to experimental swards is often restricted and intermittent.

For example Penning *et al.* (1991a) suggested that sheep withheld from pasture for even one hour took larger bites at the recommencement of grazing, when compared to daily averages. Also when cattle were corralled overnight and allowed to graze for 0, 45, 60, 90 or 120 minutes before grazing treatment plots for one hour, their RI during that hour tended to decline the longer the pre-measurement grazing period (Dougherty *et al.* 1989c). Differences in RI were primarily due to BR however, and BW did not decline significantly, although the depth of the grazed horizon was up to 37% deeper (P<0.010) for animals which had no pre-measurement grazing. Further, given that the RI of cattle may decline after considerably less than one hour of feeding (Taylor *et al.* 1987), Dougherty's study may have underestimated the treatment differences when compared to the much shorter measurement intervals commonly used in short-term indoor studies. For example steers were held overnight and then allowed to graze pasture for 0, 2 or 4 hours (Griggs *et al.* 1991a). When subsequently grazing small hand-constructed paspalum swards their bite weights decreased the longer the pre-measurement grazing interval, although in this case the increase in BW was due to BA, and BD was unaffected.

These examples suggest some likelihood of BW and/or BR being overestimated by short-term studies. On the other hand, when the steers used in Grigg's study were stall fed on a maintenance ration of hay, their bite dimensions on hand-constructed paspalum swards most closely resembled those after 4 hours of grazing pasture in the above mentioned study (Griggs *et al.* 1991a; Demment *et al.* 1992). Thus contrary to the preceding discussion, this similarity appears to support the extrapolation from short-term mini-sward studies to field conditions (Demment *et al.* 1992). Further, the reduction in BW of steers as pre-measurement grazing time increased from 0 to 4 hours (Griggs *et al.* 1991a), and the lack of any effect of hunger due to altering their pelleted ration from 0 to 90% of previous mean daily intake (Griggs *et al.* 1991b) suggests an interaction between background diet and hunger level (Demment *et al.* 1992). Ingestive behaviour may be more sensitive to hunger when the background diet is similar to the experimental swards.

The effects of length of grazing and background diet upon animal status and consequent ingestive behaviour clearly require further clarification. However, short-term mini-sward studies are usually employed with the aim of studying specific sward and bite variables which cannot readily be isolated or measured in the field, rather than for direct extrapolation to field conditions. For this purpose they appear to be effective and, for want of less artificial but practical alternatives, they appear to be justified. However, any direct application of the results of short-term studies will need to be tempered with the knowledge that they may not represent the average ingestive behaviour of free grazing animals under equivalent sward conditions in the field.

9.1.3.3 Experience and learning

On entry to a new strip of herbage, calves on a low herbage allowance learned to graze faster (by increasing both BW and BR) when compared to those on a high allowance (Jamieson & Hodgson 1979a). Similarly, restricting the grazing time of cattle grazing five different ryegrass pastures, or retarding the beginning of grazing relative to cohorts, led to increased rates of intake and/or bite weights even on the shortest swards (Greenwood 1990).

Although not examined experimentally, animals used in the current (and other) short-term indoor studies would appear to be in an environment where they might learn to graze rapidly. Despite being keen to feed, their grazing time on swards was restricted, and they were able to observe cohorts grazing when they could not; factors which increased the RI of cattle (Greenwood 1990). These conditions prevailed over a period of several hours on any one measurement day, during which animals experienced only brief and infrequent exposure to experimental swards, and had no access to any alternative food source. Under these conditions the animals appeared to graze aggressively, with some individuals rushing to the front of their crate and straining forward in an attempt to reach a sward.

Both the experimental conditions and the observed grazing behaviour would appear to be conducive to high rates of intake. However, as discussed previously (Section 9.1.3.2), steers stall fed on hay had bite weights most similar to those of steers after four hours of grazing (Demment *et al.* 1992). Experience and learning are factors which in the context of short-term mini-sward studies require further clarification. However, as indicated by Demment they appear unlikely to override the general ingestive response of animals to sward conditions.

9.1.4 Conclusions

1. The grid technique probably alters how tillers respond when prehended close to the base of the sward (ie. the grid), and possibly also the animal's perception of sward depth. Hand-constructed swards largely overcome these problems and allow maximal variation of HT and DEN, as well as the controlled introduction of other sward structural variables. In comparison seedling wheat swards are much less labour intensive, but tiller structure is largely constrained by the HT and DEN of the swards being used.

2. Short-term mini-sward studies are a useful and efficient means of separating out and understanding the influence of some sward factors upon ingestive behaviour, although they may not represent the average ingestive behaviour of free grazing animals under equivalent sward conditions.

9.2 Bite depth

9.2.1 Bite depth on wheat and sorghum swards

Deer and sheep grazed to a similar depth in relation to changing sward HT, although sheep were capable of grazing 1 cm swards, in contrast to the minimum 2 cm HT grazed by deer (Chapters 5-7).

As indicated by the high BD/HT ratios, height of the ungrazed residual increased much more slowly than did sward surface height (HT), so that the depth to which animals actually penetrated the wheat swards was very largely determined by the changes in HT. In comparison, on some natural pastures residual height increases rapidly with increasing HT because animals remove a much lower proportion of the available herbage length (Milne *et al.* 1982; Wade 1991). The very deep bites on wheat swards (about 70% of HT; Chapters 6 & 7) imply either that such swards were easy to penetrate or that animals reduce BD on natural swards (commonly 40-50% of HT; Section 9.2.4) because of the changes in tiller structure in the lower sward horizons (see Section 9.2.5). Compared to natural swards, which tend to increase very markedly in maturity and dead matter content (Forbes 1982) and DEN (Hodgson 1990a) in the lower sward horizons, wheat swards were green, free from dead matter and showed little vertical heterogeneity in DEN right down to ground level, or in tiller strength within the basal strata where they were severed (Chapter 6; Plate 4).

Another minor contributing factor is that low breaking strength wheat tillers would have less tendency to slip past the prehending surfaces of the animal's mouth during severing, and are therefore likely to leave slightly shorter residuals, resulting in deeper apparent bites than tillers of greater strength (Ungar *et al.* 1991; pers. obs.). Further, the tendency of wheat tillers to sever below where they were gripped would also lead to an overestimation of true BD. Care was taken to avoid including such tillers in the measurements but some would inevitably have been measured and therefore caused a degree of overestimation of BD. In many instances such tillers were easily distinguishable because they had pulled out of the coleoptile, severed at ground level or severed appreciably closer to the ground than other closely adjacent grazed tillers.

In contrast to normal ground-based swards, the BD/HT ratio actually declined ($P<0.05$) with HT on the grid-based sorghum swards (Plate 8), being approximately 80% on shorter swards but declining to around 60% by 18 cm HT (Chapter 5). This may in part reflect attempts by the animals' to optimise BD on short swards. However, in comparison with ground-based swards, animals could not only see through the grid (to varying degrees dependent upon the HT and DEN), but they could also much more readily penetrate to the base of short grid-based swards as tillers were leafy and could move about in the horizontal plane, right down to the grid itself. The mobility of tillers within the grid probably made it possible to prehend, and sever very close to the grid, many of the tillers that were initially near the outer edges of the bite (Section 9.3.5). In a ground-based sward, such tillers would have left a taller residual, because their bases were fixed and could not move towards the centre of the bite as the jaws close. Further, close to the base of taller sorghum swards, there were marked increases in leaf strength and especially rigidity, which probably discouraged very deep penetration, and increased slipping during severing, causing the BD/HT ratio to decline as HT increased.

9.2.2 Height and bulk density effects

The wheat sward trials for deer and sheep (Chapters 6 & 7) indicated that BD increases linearly with HT, in general agreement with other studies for sheep grazing a range of grass or oat swards (Milne *et al.* 1982; Burlison 1987), cattle on hand-constructed paspalum swards (Laca *et al.* 1992b), or cows on natural ryegrass pastures (Wade 1991). Similarly Gong (1994) found the BD of sheep increased linearly with HT on grass swards, although BD increased slightly faster in relation to HT for taller reproductive swards, where sheep penetrated deeply to obtain leaf, compared to shorter vegetative swards. Exceptions may occur however, with BD increasing at a declining rate in relation to HT for deer and sheep on sorghum swards (Chapter 5), probably reflecting the marked increases in tiller rigidity near the base of taller swards, as described above. Even more marked curvilinearity for BD in relation to HT is implied from the BW trends (see Chapter 6) of sheep on very dense hand-constructed ryegrass swards (Black & Kenney 1984). As for the sorghum swards, such differences might be associated with an increase in tiller rigidity, strength or density down the sward profile, although no such trends were evident at lower DEN levels.

Based on the above evidence, it would appear that a linear relationship between BD and HT is the norm, although an increase in slope as swards change from vegetative to reproductive is likely

(Gong 1994).

9.2.2.1 Bite depth and bulk density

The small reductions in BD in response to large increases in DEN observed for the wheat swards, the ryegrass swards of Black & Kenney (1984) and the paspalum swards of Laca *et al.* (1992b) suggest that in practical terms DEN effects on BD can usually be ignored, particularly as DEN has a negligible influence at heights likely to restrict daily herbage intake on improved temperate pastures. Also tillers in sparse natural swards may be clumped (Hodgson 1985), increasing DEN at the bite site. There is no obvious explanation for the much larger DEN effects on BD (see Chapter 6) evident for grid-based sorghum swards (Chapter 5), although again this may be related to the special characteristics of those swards (Section 9.2.1). Also, the narrow range of comparatively low DEN swards examined leaves more room for error when extrapolating the effects up to higher DEN levels.

In contrast to the wheat sward experiments with deer and sheep, where BD was insensitive to DEN only up to heights of 3-4 cm (Chapters 6 & 7), Ungar *et al.* (1991) and Laca *et al.* (1992b) found that the BD of cattle on hand-constructed paspalum swards did not decline with increasing DEN at heights below 10 or 15 cm, respectively. It seems plausible that penetration of short swards by larger, stronger animals is less inhibited by increases in DEN, particularly as the larger the animal, the more restricted its BW as HT declines, and the greater its need to bite deeply on short swards, even when DEN is high.

9.2.3 Bite depth on short swards

In the wheat sward experiments (Chapters 6 & 7) the BD/HT ratio increased at a rapidly declining rate, as HT increased from minimum grazable levels. This implies a reasonably constant ratio on slightly taller swards, as suggested by Hodgson (1985) and Wade (1991). Similar trends were evident for cattle grazing 4-10 cm hand-constructed paspalum swards (Ungar *et al.* 1991). Because a minimum number of jaw movements per bite is required to manipulate herbage (Laca *et al.* 1993), the ability of animals to increase BR as BW declines is limited (Chapter 6). Consequently, a severely restricted BD will depress RI (via BW), presumably putting pressure on animals to rapidly increase BD as HT increases, thus in part explaining the increasing BD/HT ratio on short swards. Similar trends were observed for sheep grazing a range of natural ryegrass pastures (Barthram & Grant 1984) although in this case changing leaf depth (Hodgson 1985) as opposed to HT itself was probably the main constraint upon BD. Of course another contributing factor is that animals do not normally graze to ground level, so that the BD/HT ratio would necessarily decline due to relatively taller residuals as height declines to minimum grazable levels. On medium to tall swards, BD and consequently BW tend to be much less restricted and, as argued by Laca *et al.* (1992b), animals may remove the surface horizon of high quality leaf which is likely to represent a fairly constant proportion of the available HT (see below).

Other factors which should also have a relatively greater impact upon residual height as HT declines to low levels, and therefore reduce the BD/HT ratio, include the semi-circular shape of the incisors, which will tend to leave taller residuals near the sides of the bite. Similarly, if animals do not sufficiently reduce their gape (Chapter 7) as HT declines within the range where BA is restricted, this would also leave relatively taller residuals near the front and rear edges of the bite (Section 9.3.5).

9.2.4 Bite depth as a proportion of height

RI and daily herbage intake are largely constrained by BW on short, low herbage mass swards, and BW is in turn very largely constrained by BD (Chapters 5 & 6; Gong *et al.* 1993). Yet with the possible exception of some high quality experimental swards (Black & Kenney 1984; Chapters 6 & 7), animals do not appear to optimise BW by maximising BD even on very short swards (Barthram

& Grant 1984). Rather, animals commonly remove a fairly constant proportion of HT (Hodgson 1985; Wade 1991; Laca *et al.* 1992b; Betteridge *et al* 1994). In doing so animals may be maximising nutrient intake by severing shallow bites of high quality herbage from the surface horizon (Laca *et al.* 1992b). The ingested herbage will be less mature and of higher leaf content compared to the average of the whole sward. Being shorter, the ingested herbage should require less manipulative jaw movements per bite (Hodgson 1985) and less chewing before swallowing (Kenney & Black 1984). In comparison, deeper bites involving longer lengths of herbage would tend to be of lower average quality, and on taller swards are likely to require extra jaw movements to draw them into the mouth (Burlison 1987; Gong 1994). This is likely to reduce the efficiency of chewing and the rate of bolus formation (Dougherty *et al.* 1989b), reducing BR in relation to BW and thus reducing RI. These factors can also reduce the rates of particle size reduction and rates of passage in the rumen (McLeod & Smith 1989; McLeod *et al.* 1990). Thus, despite increasing BW, taking deeper bites may not help optimise daily herbage intake.

As argued in Section 9.1.3.2 animals may take deeper, larger bites at the beginning of grazing when hunger drive is high and rumen fill is low (Dougherty *et al.* 1987, 1989c). Certainly a number of very short-term indoor studies using vegetative gramineous mini-swards indicate deep bites, with cattle and sheep removing around 50-60% and 40-50% of HT respectively in a single grazed horizon (see Section 7.5.3.1). In these studies animals are usually in a hungry state, have only brief (<1-2 minutes) and infrequent access to swards over a period of up to several hours of experimental feeding; factors which might encourage high rates of intake and large bites (Section 9.1.3.3). Such studies include cattle and sheep grazing trimmed, all-leaf, hand-constructed paspalum swards, through to trimmed or untrimmed turves dug from pasture, representing a range of grass species (Mursan *et al.* 1989; Hughes *et al.* 1991; Laca *et al.* 1991a,1992b; Gong *et al.* 1993, Gong 1994; Chapter 8). In comparison, when free grazing in field trials, cattle and sheep removed at most an estimated 40-50% (Wade 1991; Betteridge *et al.* 1994) *or* 40% (Betteridge *et al.* 1994) of HT, respectively (see below).

With the exception of Wade's and Betteridge's studies, the slightly greater BD/HT ratios indicated for very short-term experiments do not appear to be attributable to differences in sward measurement techniques. Researchers such as Barthram (1981), Milne *et al.* (1982), Burlison *et al.* (1991) and Gong *et al.* (1993) used inclined point quadrats, rulers or the HFRO sward stick which should all give reasonably similar estimates of mean sward height, comparable to those made on trimmed swards (Section 9.1.2).

Wade (1991) and Betteridge *et al* (1994) however, measured the extended height of the tallest ungrazed and shortest grazed components on marked tillers, resulting in bite depth/extended height ratios of 45, 52 and 45% for cows, cows and sheep, respectively. Such measurements would alter BD/HT estimates compared to mean BD and HT measurements. By extending the leaves and measuring only the longest ungrazed leaf, HT is probably at least slightly overestimated compared to true mean surface height, while measuring only the shortest grazed component will underestimate mean residual height, further increasing the overestimation of BD. In comparison, when Wade measured the tallest grazed component his ratio fell from 45% to around 35%. This suggests that if based upon mean BD and HT values, the BD/HT ratios in Wade's and Betteridge's studies would have been about 40, 47 and 40% at most for cows, cows and sheep respectively; i.e. at least 5% lower than the values quoted in their studies.

Short-term trials with mini-swards can in some cases result in very high BD/HT ratios (eg. wheat swards in Chapters 6 & 7; Section 9.2.1) and, as discussed elsewhere, this may in part reflect the high quality of these swards. However, BD/HT ratios of around 50% are more usual for mini-swards, even when using turves dug from pasture (Mursan *et al.* 1989; Gong 1994). This would suggest that differences in herbage quality do not necessarily explain the slightly shallower BD/HT ratios evident for many of the field studies.

There are however exceptions to this pattern of shallower bites in longer term studies using larger areas of herbage. For example, the horizon removed by tethered cattle grazing for one hour on tall fescue swards was up to 53% of HT (Dougherty *et al.* 1989c). However, when grazing very similar swards at double the allowance, the cattle removed around 30% of HT, perhaps suggesting that at the lower allowance the cattle removed two horizons each representing 30% of remaining sward HT. Further, sheep grazing for 30 minute periods on small outdoor or cage plots of ryegrass removed 20-30% of HT (Milne *et al.* 1982; Burlison *et al.* 1991). Evidently, there is a need to further clarify and confirm the consistency of BD/HT ratios across agriculturally important sward conditions and animal species, as well as in relation to different experimental techniques. There is also a need to better understand the sward factors affecting BD.

9.2.5 Effects of pseudostem and dead matter content

Based on grazed stubble heights, sheep grazed only slightly deeper into 3 cm swards of pure leaf than into swards of almost pure pseudostem, and even these small differences may reflect tillers of different strength slipping to different degrees in the mouth before severing, as opposed to real differences in penetration (Chapter 8). However, the willingness of sheep to penetrate the tough pseudostem near the base of the sward declined markedly when leaf-like, immature pseudostem was available in the overlying strata. In contrast however, sheep penetrated deeply into the horizon containing tender leaf like pseudostem when it subtended good quality leafy herbage (Chapter 8; Plate 7), a result which appears to be consistent with the findings of Wade (1991). Wade found that as cows grazed 23-35 cm (extended tiller height) ryegrass pastures down to a 10 cm residual over a period of 5 days, BD remained a similar proportion of remaining sward height regardless of whether cows were grazing the upper, 90% leaf horizon on day 1, or a lower, 80% pseudostem horizon on day 5. Similarly, deer and sheep readily penetrated to below pseudostem height on seedling wheat swards (Chapters 6 & 7), as did cattle on 5 and 10 cm early spring ryegrass turves (Mursan *et al.* 1989). Further, cattle grazing hand-constructed paspalum swards containing a horizon of pseudostems (Flores *et al.* 1993), penetrated to below pseudostem HT, to the same depth as when grazing equivalent swards of pure leaf. In contrast, when paspalum swards were constructed so as to contain a horizon of rigid reproductive stem material, this restricted the BD of cattle to above stem height (Laca *et al.* 1993; Flores *et al.* 1993). Alternatively in studies with sheep, both Milne *et al.* (1982) and Burlison *et al.* (1991) found that pseudostem height was typically well below the bottom of at least the first (upper most) grazed stratum.

The above studies suggest that in some instances the upper strata containing pseudostem will not limit BD, because such strata are below the initial zone of penetration or, unlike stem material, are not sufficiently different from the overlying leaf (in terms of maturity or structural strength) to restrict BD.

In contrast, Barthram & Grant (1984) suggested that the BD of sheep on short, continuously stocked swards was restricted by even the upper portions of the pseudostem horizon. On such swards, the leaf whorls tend to be close together, perhaps forming a barrier to penetration in themselves, so that the transition from leaf to tough pseudostem occurs over a short vertical distance. This may reduce the animal's ability to selectively remove the upper horizon of immature pseudostem compared to more elongate (greater inter-ligule distance) rotationally grazed swards. Close proximity to the ground, where tillers approach the point of attachment to the substrate, also appears to reduce penetration per unit of sward HT (Chapter 8; Section 9.2.3), although in many instances it will be difficult to separate this effect from the increasing toughness of the pseudostems close to ground level.

As for Barthram & Grant (1984), Arias *et al.* (1990) suggested that cattle grazing endophyte free tall fescue restricted BD to horizons above those containing pseudostem, except (and in agreement with Chapter 8) where the pseudostem material was "young and small" (Dougherty 1991). In another short-term outdoor study cows actually ceased grazing tall fescue swards at 1-2 cm above the tops of the pseudostems (Dougherty *et al.* 1992).

Sheep may also avoid dead matter near the base of the sward (Barthram & Grant 1984; Clark & Harris 1985; Rattray *et al.* 1987), which can occur at very high levels under continuous stocking (Hodgson 1990a; Penning *et al.* 1991a) and can considerably reduce diet digestibility and intake (Rattray *et al.* 1987). However, in the current short-term indoor trial (Chapter 8; Plate 6), dead leaf matter had no effect on the BD of sheep on 9 or 12 cm ryegrass mini-swards, despite their containing up to 34% dead matter (Chapter 8), which is above the 15-20% considered likely to reduce animal production (Rattray *et al.* 1987). Had the dead matter constituted entire senescent tillers as apposed to dead lamina only, selection for green matter may have occurred, as in Black *et al.* (1989). Similarly, lamina in a more advanced state of decay may have resulted in its avoidance. Alternatively, had these same swards been grazed in the field, the prolonged and continuous access (as opposed to brief and infrequent access during mini-sward trials) to pasture might have resulted in sheep being more selective. However, even reasonably high levels of dead matter appeared to have "no direct influence" upon the RI of strip grazed calves (Hodgson 1981).

There is a need to further clarify the factors affecting the palatability of the lower sward horizons, however it would seem probable that the maturity and rigidity of pseudostem material, and the degree of decay and morphological composition of dead matter, will be at least as important in influencing BD as are the relative amounts of pseudostem or dead matter present in or near the grazed stratum.

9.2.6 Conclusions

1. The BD of deer and sheep is similar when grazing vertically and horizontally homogeneous, monospecific gramineous swards, although sheep can graze slightly shorter swards than deer.

2. BD increases rapidly and linearly with HT, but declines slightly with increasing DEN on all but short swards. In practice however, DEN can probably be ignored as a determinant of BD on

improved, temperate, gramineous pastures, its influence being negligible at heights likely to restrict daily herbage intake.

3. Studies frequently indicate that animals remove a fairly constant proportion of HT, although the exact proportion can differ quite widely in relation to sward and experimental conditions, and appears to be reduced on some short swards due to restricted leaf depth or HT.

4. The difference in qualitative state or toughness between the leaf and pseudostem horizons, as well as the degree of opportunity for selection, appears to strongly influence the willingness of animals to penetrate below the leafy horizon.

9.3 Bite area

9.3.1 Bite area and height

The wheat sward experiments showed clearly that the BA of deer and sheep increases with HT at a declining or lower rate the greater the HT or DEN respectively. Large steers on paspalum or lucerne swards (Laca *et al.* 1992b) showed a qualitatively very similar response to increasing HT and DEN. The similarity between these two studies suggests that similar trends may apply across a wide range of different sized animal species and include species which prehend herbage with or without the use of their tongue.

The lack of a clear HT effect on BA in many previous studies may be the result of swards being too tall, or of confounded differences in tiller DEN, strength or rigidity which can cause animals to alter BA in relation to HT, as well as of the limited ability of animals to adjust BA in relation to sward conditions (Chapters 6-8; Sections 9.33 & 9.3.3.1).

9.3.1.1 Bite area in relation to bulk density on wheat swards

Throughout the wheat sward trials (Chapters 6 & 7), there were indications that BA did not increase in a strictly linear fashion in relation to declining DEN, over the entire range of DEN. The rate of increase was in some cases lower between the two lowest DEN levels. This may have reflected the limiting effects of mouth dimensions upon BA as discussed above. These trends were also evident for BV, BW and RI. However, the extent of curvilinearity was small, usually occurring only between two low densities, below those typical of real temperate pastures. Further, these trends were not particularly consistent across animal species or experiments and were generally more apparent on tall swards, probably reflecting the greater sensitivity of BA to DEN on these swards. Frequently DEN^2 terms were only marginally significant, and in all cases would have required the inclusion of a linear DEN term which was often non-significant. For these reasons, and for the sake of simplicity and ease of comparison the DEN^2 terms were in general excluded from the regression equations.

9.3.2 Deer-sheep differences

Compared to deer, sheep were able to prehend slightly shorter swards, required less HT to maximise BA and, when BA was scaled to incisor arcade width (IAW), achieved increasingly larger bite areas as HT declined (Chapters 6 & 7). Figure 9.1 shows how sheep achieved larger bite areas (scaled to IAW) compared to deer on short swards, but also how BA plateaued at lower heights for sheep than deer so that species differences in BA were reduced on taller swards.

For an animal to avoid losing even the tips of the outer-most tillers encompassed by its fully opened mouth during grazing, foliage height would need to be at least greater than half the span (gape) of the animal's fully open mouth (Fig. 7.2). Therefore, the wider an animal's fully opened mouth, the taller the foliage, and on short swards the deeper the bite it should require to maximise BA (Chapter 7). Assuming that the larger, longer jawed deer had a wider gape than sheep

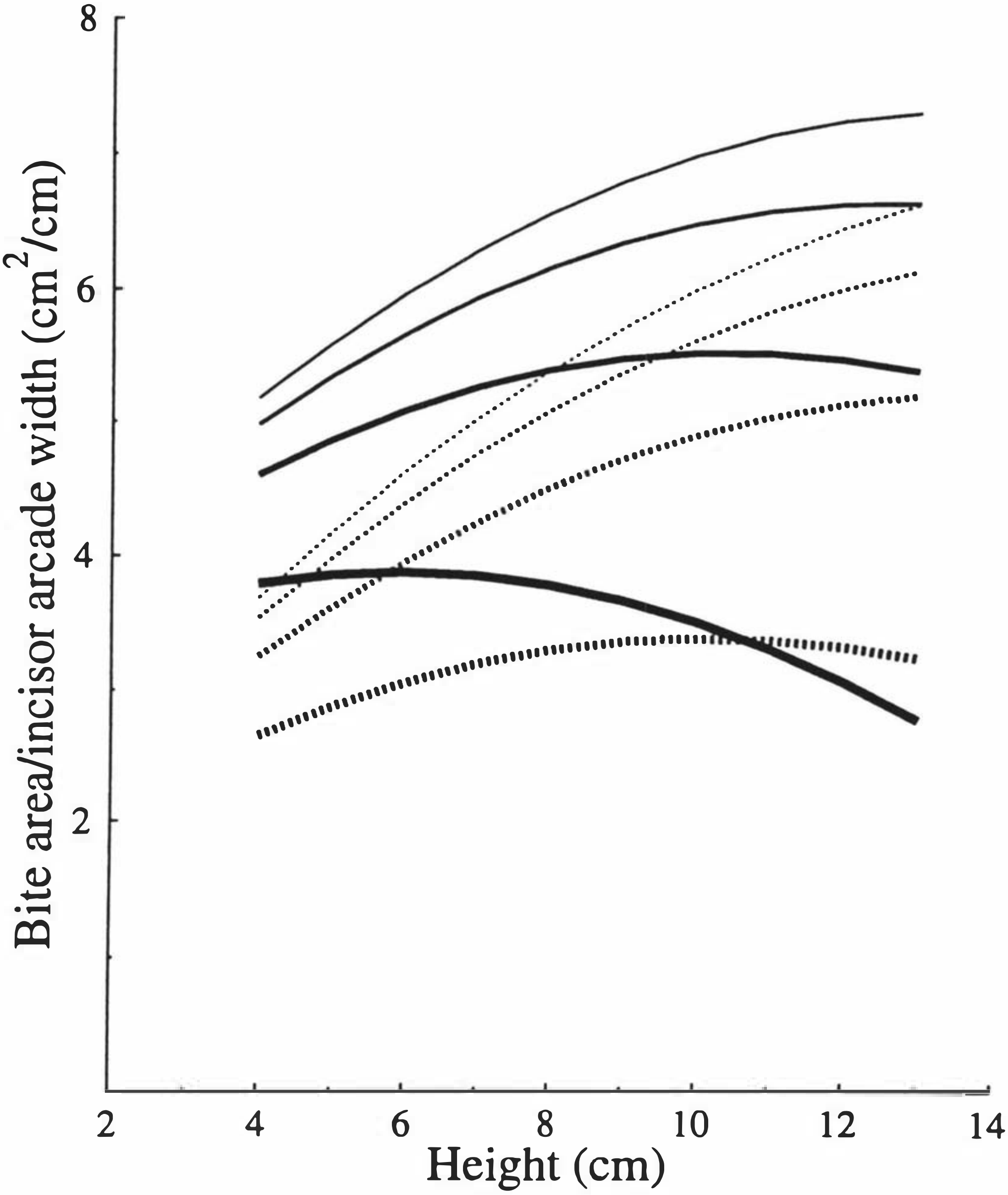

Fig 9.1 The bite area (scaled to incisor arcade width) of sheep (solid lines) and deer (dotted lines) when grazing 4-13cm, sparse through dense (0.63, 1.01, 1.74 or 3.25 mgDMcm^{-3}; fine through thick lines respectively) wheat swards. Sheep achieved larger bite areas (scaled) on short swards than deer, although as HT continued to increase, deer were able to reduce these differences.

(Plates 9 & 10), it would be reasonable to expect that deer would need a greater HT than sheep (Illius & Gordon 1987) to maximise BA, as was indicated (Fig. 9.1) in the wheat sward experiments (Chapter 6).

A slightly deeper BD might be considered a possible explanation for the larger BA of sheep on short swards, although (see Section 9.3.3 and Fig. 7.2) there was no consistent evidence from the grazing measurements that such a difference occurred. The tendency for young wheat tillers to pull out or sever below where they were gripped may have masked small species differences in BD. However there were no species differences in BD evident on more mature 4-13 cm wheat (Chapter 6; Plate 5) or sorghum swards (Chapter 5; Plates 1 & 8), which seldom severed below where they were gripped. Only on young 1-8 cm wheat swards (Chapter 7) did sheep have a slightly deeper BD (5%; $P<0.05$) than deer, and this may have reflected the fact that sheep were recently shorn (Arnold 1981), seasonal physiological differences (Kay 1979; Loudon 1985), or simply measurement bias associated with the different experimental periods for the two species.

Another possible explanation for the species differences in BA might be that sheep had a superior mouth morphology (Gordon & Illius 1988; Illius & Gordon 1990a) compared to deer. Broad and flat incisor arcades are probably an advantage to grazing animals, whereas pointed arcades may be more suited to browsing (Gordon & Illius 1988). However, jaw measurements by Gordon & Illius (1988) indicated that the incisor arcades of sheep have more curvature than those of Red deer. In the current series of trials, visual appraisal of teeth impressions left in dental bite wax confirmed that the incisor arcades of deer were in fact broader and flatter in relation to total width than those of sheep. As flat incisors should leave a slightly shorter average residual than curved incisors, slightly deeper penetration by sheep might have been masked in the BD measurements. However, such small differences could not account for the considerable differences in BA/IAW, especially given the deep bites on the wheat swards (Chapter 7; Section 9.3.3).

Thus in terms of optimising BW, it may be concluded that sheep did in fact have a superior prehending technique, and this appeared to be associated with very rapid gathering and positioning movements of tillers performed by sheep with their mouth and lips. In comparison, deer bit off the herbage in what appeared to be a relatively more simple series of prehending movements, although further observations of slow motion video recordings are required to clarify the extent of such differences, as the recordings made in this study covered only a limited range of sward conditions.

Grazing experience might have contributed to the observed species differences (Arnold & Maller 1977; Curll & Davidson 1983; Flores *et al.* 1989a, b). On average, deer were maintained on higher herbage mass swards than sheep, although both species experienced a wide range of sward conditions over time, largely in relation to seasonal availability. Species differences in the seasonallity of intake (Kay 1979; Milne & Reid 1989; Domingue *et al.* 1991) may also be a potential source of confounding. However, the similarity of trends across the wheat sward experiments, which were carried out in different seasons, suggests any such effects were minor relative to those of sward conditions.

9.3.3 Bite depth and sward height constraints on bite area

Allden and Whittaker (1970) suggested that the ease of herbage prehension was related to tiller length. In an attempt to consider these sorts of constraints upon herbage prehension, in Chapter 7 (Section 7.5.3.2 & Fig. 7.2) it was argued how HT and BD limit the potential horizontal distance (PHD) that tillers near the front or rear edges of the bite (relative to the dental pad and teeth respectively when open) can be displaced towards the centre of the bite before being lost from the mouth.

By multiplying the Total PHD (TPHD (ie. PHD of both jaws)) by the IAW of the animal (Equation 7.1), it was possible to estimate the maximum potential BA that the grazing animal could achieve at any given HT and BD. In Table 9.1 these potential BA estimates are compared with actual BA results measured from the wheat swards used in Chapter 7. The discrepancies between the TPHD and the "actual horizontal distance" (AHD = BA/IAW) that tillers were displaced were small on very short swards (Table 9.1), where the TPHDs allowed by HT and BD constraints were less than or similar to the maximum gape for sheep of about 5 cm (Burlison 1987). However, the TPHD continued to increase linearly with increasing HT, while the actual horizontal displacement appeared to approach an asymptote similar to the 5 cm gape measured by Burlison (Table 9.1).

For the BA of a sheep to markedly exceed the gape x IAW dimensions (5 cm x 3.6 cm = 18 cm^2; Chapter 7), the animal would need to perform a gathering action via considerable horizontal displacement of the head during tiller prehension. However, observation of video recordings suggested that horizontal head displacement was not a major component of tiller prehension on wheat swards, although sheep extended their lips (Plate 9), and performed rapid gathering movements with their lips and mouth when prehending a mouthful of herbage. These observations support the concept that gape will be a major constraint on BA, as gathering with the lips and head in this manner would only extend BA to a limited degree.

The constraining influence of maximum gape would thus explain why BA rapidly reaches an upper limit as HT increases (Chapters 6 & 7). Close-up video recordings of cattle grazing paspalum swards, (Laca *et al.* 1992b) reveal similar constraints on BA. For cattle, the degree of tongue extension increased as HT increased, and maximum tongue extension was associated with BA ultimately reaching a plateau (Laca *et al.* 1991a; 1992b). The gape of sheep also appeared to be sensitive to HT to some degree, with animals taking small nibbling bites on very short swards. Whether or not sheep precisely adjust their gape up or down in relation to the constraints of HT on PHD is unknown, but is considered likely (Chapter 7; Section 9.3.5). As Laca *et al.* (1992b) did for cattle, it may be possible to determine this from further detailed observation of video recordings, although sheep jaw movements are very rapid. Similar BA vs potential BA trends were indicated for deer (Plate 10) but the lack of any gape measurements preclude any comparison with PHD.

Table 9.1 The maximum potential bite area (PBA) and maximum total potential horizontal displacement of tillers (TPHD), which sheep should be able to achieve based on BD and HT constraints (Fig. 7.2; Sections 7.5.3.2 & 9.3.3) compared with the actual bite areas (BA) and actual horizontal displacement of tillers (AHD) respectively, of sheep grazing 2-8 cm wheat swards of 2.9 mg DM cm^{-3} (Chapter 7).

HT (cm)	BD (cm)	RHT (HT-BD) (cm)	TPHD (cm)	PBA (TPHD x IAW) (cm^2)	BA (cm^2)	BA/PBA (%)	AHD (BA/IAW) (cm)
2	1.3	0.7	3.7	13.3	12.4	93	3.4
3	2.1	0.9	5.7	20.3	14.8	73	4.1
5	3.8	1.2	9.7	34.5	17.8	52	4.9
8	6.2	1.8	15.6	55.0	18.1	32	5.0

Note 1: BA results slightly exceeded PBA on 1 cm swards, because as HT declined to such low levels there was a tendency for the short fragile tillers (which were anchored immovably in the cement base) to shear off without actually being prehended, as the animal's mouth (lips) displaced them. Consequently, results for 1 cm swards were some what suspect and are not presented in Table 9.1.

Note 2: A comparison of the TPHD (PBA/IAW) and AHD (BA/IAW) suggests that, as HT increases, the 5 cm maximum gape of sheep (Burlison 1987) becomes a major constraint upon BA. This is evident from the rapidly increasing discrepancy between TPHD and AHD as the TPHD exceeds the maximum gape. (PBA is calculated from measured HT, BD, RHT (residual height) and IAW (incisor arcade width))values using Equation 7.1.

As argued in Chapter 7, in many grazing situations BD probably does not constrain BA, as according to Fig. 7.2 it need only be around 30% of HT to allow a large TPHD in relation to HT. However, in reality, BD/HT ratios would have to be considerably greater than 30% (probably closer to 40-50%), because a reasonable proportion of available tiller length must be inside the animal's mouth to enable it to gather and grip the herbage during severing (Unger *et al.* 1991), and to be of any benefit to the animal. This issue is considered further in Section 9.3.5.

Similarly, HT only constrains BA over a limited range up to a maximum, largely constrained by mouth dimensions, which is quickly reached because the TPHD increases very rapidly with HT (Table 9.1).

9.3.3.1 Influence of gape limitations on bite area responses to changes in bulk density

The constraints of gape would also help explain why animals have only a limited ability to maintain BW by increasing BA as DEN declines. In the wheat sward trials, BA peaked at or close to IAW x gape dimensions on high DEN swards (Fig 7.1b (i)), where animals did not need large bite areas to achieve large bite weights. On lower DEN swards, sheep increased BA beyond this level, however, the changes in BA were not large in relation to the changes in DEN. For example, despite a change in DEN of 346% on 1-8 cm wheat swards (Chapter 7), at the lowest DEN (0.65 mg DM cm^{-3}) the BA of sheep peaked at 24 cm^2, only 33% above the 18 cm^2 gape x IAW dimensions achieved at the highest DEN (2.9 mg DM cm^{-3}). Even at 24 cm^2, BA was still less than half the potential BA (Table 9.1), again indicative of gape having a dominant influence on BA.

Cattle reduced the number of tongue sweeps per bite as DEN increased (Laca *et al.* 1992b), thus explaining why BA declined. That BA was similar to the maximum mouth dimensions (gape x IAW) on high DEN wheat swards (Chapter 7) suggests that sheep slightly increased the amplitude of gathering movements with the lips or head as DEN declined, compared to behaviour on high DEN swards.

9.3.3.2 Body size and prehension technique

Once HT has increased to the point where gape is restricting PHD, the use of the tongue to gather tillers over a larger area would begin to give an advantage over simpler grazing techniques and would help explain why the BA of cattle could increase with HT up to around 30 cm (Laca *et al.* 1992b). Logically, gathering with the tongue becomes more important as animal size increases, because mouth size decreases in relation to body size. Using the tongue, rather than extending gathering ability solely by moving the whole head, would presumably be much more efficient (increasingly so as animal size increases) because, compared to the head, the tongue is a light, highly mobile and prehensile body part.

9.3.4 Bulk density, tiller strength and biting effort

It has been postulated that animals might adjust BA to maintain or limit the effort required to sever a bite (Hodgson 1985; Hughes *et al.* 1991). The BA of sheep did not change significantly on 3 or 6 cm ryegrass swards, despite large changes in leaf:pseudostem ratio in the zone of severance, perhaps in part because the differences in tiller strength across treatments were not especially large (Chapter 8). However, the BA of cattle was on average about 20% greater on wild oat swards than on paspalum swards with 120% greater tensile strength (Demment *et al.* 1992). Similarly, the BA of sheep was approximately 35% greater on wheat swards compared to ryegrass swards which were the same height but had about a 110% higher shear strength per unit area, based on calculations of Newtons tiller^{-1} x tillers cm^{-2} (Chapter 8).

Just as in response to large changes in tiller strength, BA only declined slightly in relation to large increases in DEN on the wheat swards (Chapter 6; Section 9.3.3.1). Similarly, the rate of change in BA was proportionally much lower than that of DEN for cattle on paspalum swards (Laca *et al.* 1992b). Thus it appears that the rate of reduction in BA is frequently much lower than the rate of increase in DEN or tiller strength, implying that animals are also adjusting biting effort. However, this is not necessarily the case, as such a discrepancy may largely reflect the biting effort of the animal having two main components of force: firstly, the force to accelerate the mass of its own head (head resistance), which should be reasonably constant; and secondly, the force to sever the herbage (herbage resistance), which should increase in direct proportion to any increases in DEN or tiller strength. Head resistance probably forms a substantial component of biting effort, so that any adjustment of biting effort and/or BA necessary to cope with an increase in herbage resistance will be relatively much smaller than the change in herbage resistance alone. Further, the momentum generated by overcoming head resistance may be sufficient to sever a range of tiller densities without any adjustment in BA or increase in head acceleration by the animal. Consequently, it is suggested that animals will adjust BA in relation to total biting effort rather than herbage resistance itself, and this may largely explain why relatively small changes in BA are adequate to sever bites from much denser or stronger herbage, regardless of whether or not animals increase head acceleration or try to maintain it.

Hughes *et al.* (1991) found that sheep would increase "bite force" (measured with a force plate meter and therefore probably equivalent to herbage resistance) provided BW increased. However, as head acceleration was not measured, it is unclear as to whether or not head acceleration and consequently biting effort actually increased.

Mouth and/or tongue dimensions appear to limit the animal's ability to adjust BA upwards (Section 9.3.3.1). When DEN declines to the point where inter-tiller or inter-clump spacing actually exceeds mouth dimensions (IAW x PHD), apparent increases in BA may simply reflect biases in estimating the area actually encompassed per bite (Black & Kenney 1984).

9.3.4.1 Sward height, bulk density and biting effort

On very short swards, BA is constrained by HT and is therefore relatively insensitive to variations in DEN. However, as HT increases, there is greater scope for adjustment of BA to limit biting effort as DEN or tiller strength increase. This may in part explain why Hughes *et al.* (1991) detected significant changes in biting force for sheep in relation to increasing DEN across short ryegrass swards, but significant changes in BA (implied from changes in BV) in relation to increasing DEN across taller swards. Further, as HT increases, BW increases due to increased BD, so that animals can more readily afford to reduce BA, which is in fact what they appear to do as HT continues to increase on dense swards (Laca *et al.* 1992b; Chapters 6 & 7).

Demment *et al.* (1992) suggests animals may be sensitive to the visual or apparent density of the sward. If so, this would help them to more accurately adjust BA at the bite site in less homogeneous swards, and thus more readily maintain biting effort.

9.3.5 The efficiency of tiller capture

The discussion in Chapter 7 provided a rationale for the determination of BA based on the potential influence of HT, BD, gape and IAW upon the area of tillers captured per bite. This described how the area or number of tillers captured per bite is largely determined by the length of tillers and the maximum gape of the animal, with BD becoming important when tiller length is short. It may be postulated, however, that in terms of optimising BW, animals are probably not only trying to optimise the total number of tillers severed per bite (related to BA) but also the average length severed (related to BD). In this section attention will be concentrated upon the effects of variation in the height of the sward (HT) and the depth of penetration (≈BD) and the gape of the jaw (Section 9.3.3) upon the mean and sum of the lengths captured (ie. gripped between the jaws when closed) from those tillers initially encompassed by the jaws when fully open (ie. at maximum gape).

At any given HT, the length captured (LC) from tillers anchored at the centre of the bite should closely approximate BD. However, the length captured from tillers, as their point of attachment moves horizontally at right angles away from the bite centre and towards the front or rear perimeters of the bite (relative to upper and lower jaw) will decline by an amount dependent upon tiller length (HT), their distance from the bite centre (DC) and the height of the prehending surfaces of the teeth and dental pad above the ground. This latter is incisor height (IHT; Demment *et al.* 1992)) which approximates HT-BD or residual height (RHT). These relationships are described in Equation 9.1 below.

Equation 9.1 assumes that the initially open upper and lower jaws move equal distances to close at the centre of the bite, as this should maximise the mean and the sum of lengths captured, and consequently BW. It assumes the jaws travel in a straight horizontal line when closing rather than a slight arc around the pivotal point of the jaw and skull. Similarly, it makes no allowance for the curvature of the incisor array and the consequent transverse curvature of the bite. Finally, it makes no allowance for the lengths of tillers necessarily gripped in and above the prehending surfaces in order to ensure efficient gripping and severance (Ungar *et al* 1991). Severed length is likely to be several percentage points shorter than captured length due to the slipping of tillers as the head is jerked (Chapter 8). However, these approximations are unlikely to invalidate the subsequent discussion and conclusions in this section.

$$MLC \quad (mean\ length\ captured) = \frac{1}{n}\left[\sum_{DC=\frac{1}{2}gape}^{DC=0} LC\right] \qquad \textit{Equation } 9.1$$

$$where \quad LC = HT - LL \quad and \quad LL = \frac{IHT}{Sin\left[Tan^{-1}\left(\frac{IHT}{DC}\right)\right]}$$

n = number of tillers encompassed by fully open mouth (≈tiller density x gape x IAW)

LC = length of tiller above closed prehending surfaces of mouth (cm)

LL = length of tiller below closed prehending surfaces of mouth (cm)

HT = sward surface height (cm) (HT=LC+LL)

IHT = height of prehending surfaces of mouth above ground (cm) (≈HT-BD)

DC = horizontal distance (cm) directly 90° in front of, or behind, the bite centre line (line along which closed jaws capture herbage) to a point directly (vertically) above the point of attachment of each tiller within the area encompassed by the bite (≈ gape x IAW).

Animals grazing the high quality swards in this series of studies removed around 70% of HT (Chapters 5-7). Such deep bites reflect some degree of overestimation of BD, as well as the unique characteristics of these seedling or grid based swards (Section 9.2.1). However, in short-term or field studies utilising more natural swards, BD is commonly around 40-50% of HT (Chapters 7 & 8; Section 9.2.4). For the current purpose of examining the effects of penetration (≈BD), HT and gape upon tiller capture, we will assume an animal with a 5 cm maximum gape, penetrating to 12.5% -75% of HT, at sward heights of 2.5 cm, 5 cm and 10 cm (ie. 0.5, 1.0 and 2.0 times maximum gape). Calculations of mean LC (MLC) are based upon a constant bite area and number of tillers initially encompassed by the animal's fully open mouth (ie. area initially encompassed is assumed to be ≈ maximum gape x IAW, regardless of sward conditions), but take into account the effects of the above variables on the subsequent loss of length from all but central tillers as the jaws close (Fig. 9.2). Consequently, the sum LC is simply the product of MLC and the constant number of tillers initially encompassed in any bite, where LC for a varying proportion of tillers towards the front and rear peripheries of the bite is zero (ie. MLC is directly proportional to and effectively synonymous with sum LC). Similarly, assuming for the time being negligible changes in DEN down the sward profile, BW will be the product of the sum LC and tiller weight per unit length (ie. BW can be inferred from MLC).

Figures 9.2 and 9.3 illustrate, diagrammatically, the capture or loss of peripheral tillers and changes in MLC with variation in HT and BD. The results shown are derived from Equation 9.1. When HT is 2.5 cm or less (ie. HT ≤ 0.5 gape), the outer most tillers will always escape capture as the jaws close, regardless of BD, although increasing proportions of total length will be captured from more central tillers as BD increases (Fig. 9.2). The MLC increases in a close to linear manner, from 3 to 37% of HT, as penetration increases from 12.5 to 75% of HT, respectively (Fig. 9.3). The total loss of outer tillers suggests that, in these circumstances, greater grazing efficiency would be achieved by animals reducing their gape. In fact, in Chapter 7 it was shown that the HT at which animals achieved a given BA was taller than expected, when compared to potential bite area estimates. This suggests that animals did in fact reduce

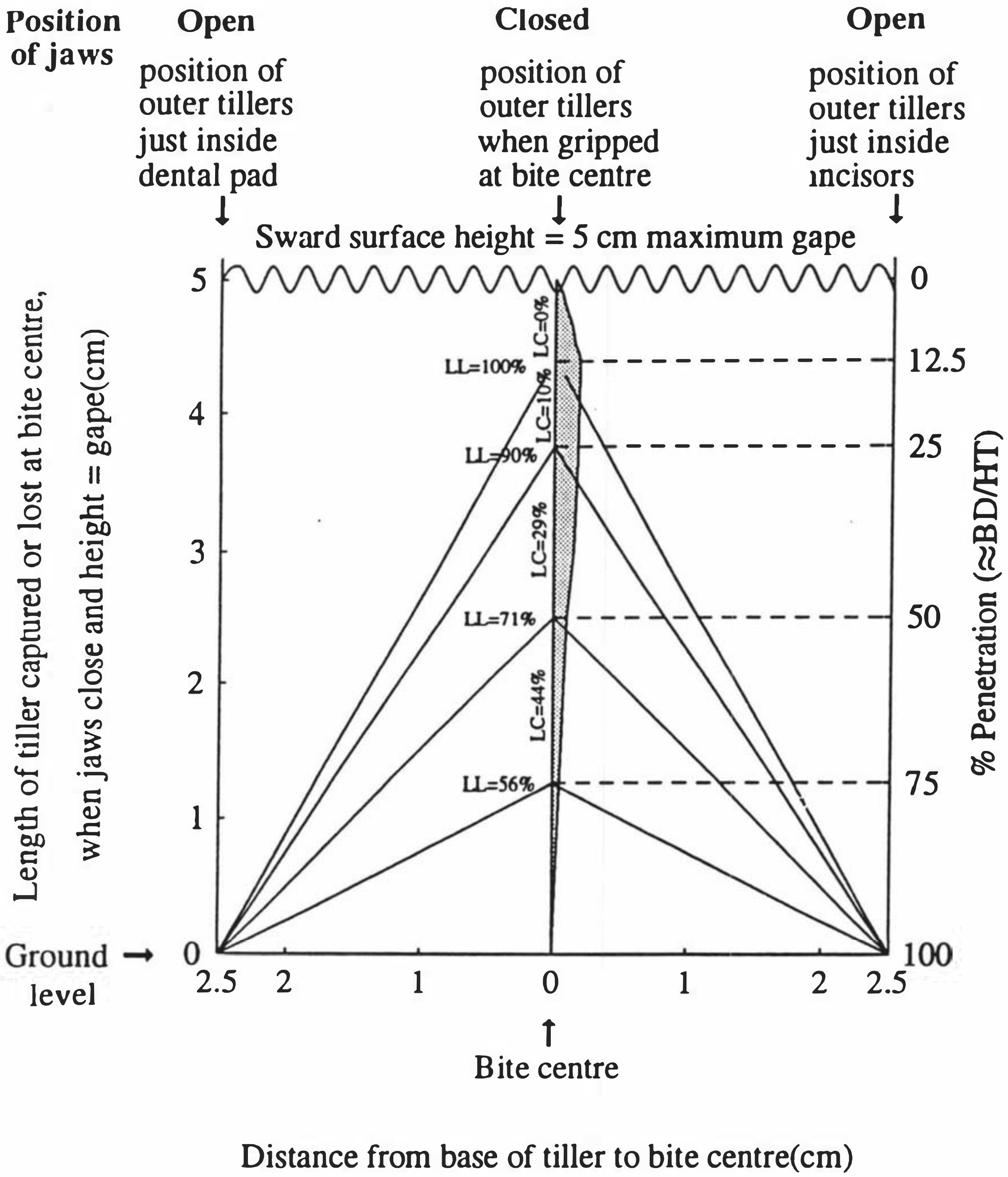

Fig. 9.2 The lengths captured (LC) or lost (LL) from tillers which were initially at either the front or rear edges of the bite (relative to the dental pad and teeth, respectively), after being displaced to and gripped at the centre of the bite, between the closed jaws of an animal with a 5 cm maximum gape, when penetrating to 12.5, 25, 50 or 75% of height on a 5 cm sward (ie. height = 1.0 gape).

Note: The length captured (LC = HT-LL) and lost (LL = HT-LC) from tillers at different distances from the bite centre are presented in Table 1 in the appendix, and were calculated using Equation 9.1. For an animal of any given gape, the shorter the sward or shallower the bite, the greater the proportion of tiller length on average that is lost in diagonal displacement towards the centre of the bite, and therefore escapes capture.

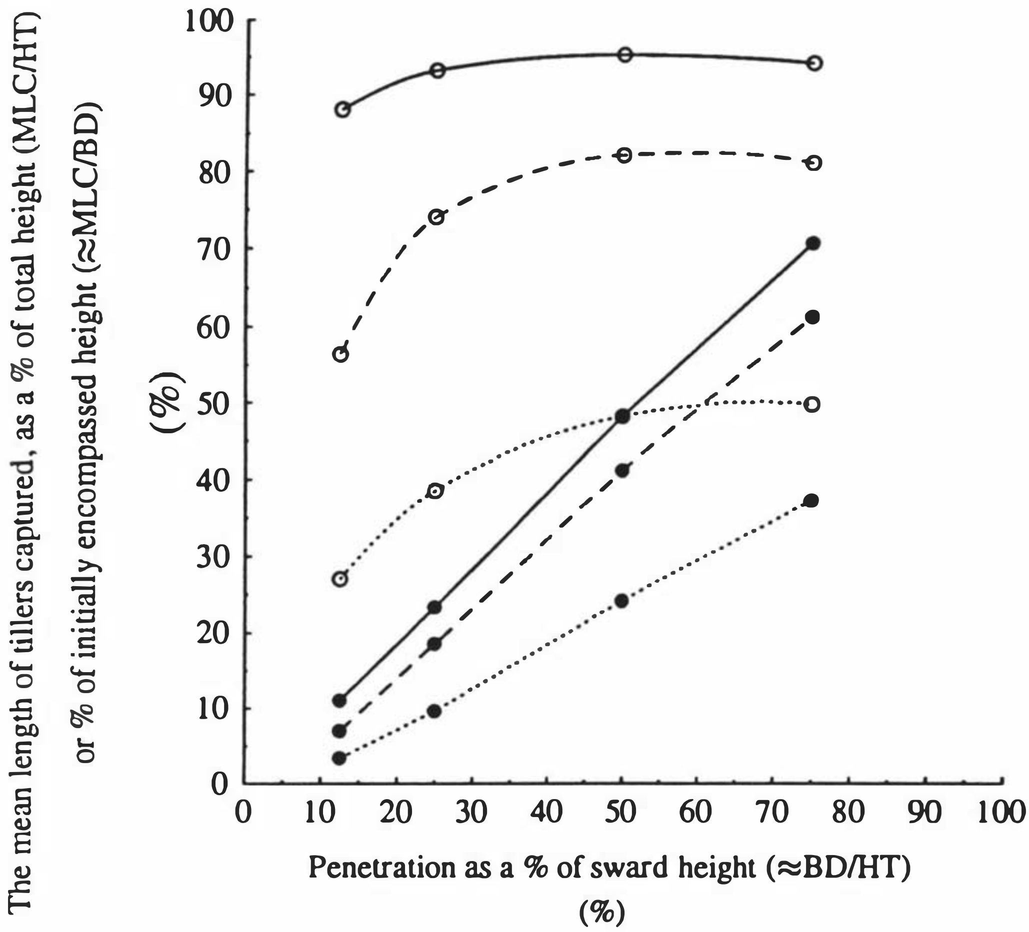

Fig. 9.3 The effect of depth of penetration (≈BD) and sward height upon the percentage of a) total length (•; ie.MLC/HT x 100) or b) length initially encompassed inside open mouth (o; ie. MLC/BD x 100), subsequently captured when the jaws are closed, by an animal with a 5 cm maximum gape, penetrating to 12.5-75% of height, at sward heights of 2.5 cm (.........=0.5 gape), 5 cm (-----= 1.0 gape) or 10 cm (———= 2.0 gape)

Note: These values are calculated using Equation 9.1, assuming a tiller density resulting in 5 tillers evenly spaced from the front or rear edge to the centre of the bite. Some of these values are shown in tabular form in Table 1 of the appendix.

their gape on short restrictive swards, and thus achieved improvements in the average length captured in relation to the time and energy expended per bite.

At less restrictive heights, for example when HT equals gape, penetration to 12.5-75% of HT captures 0-44% of HT from the outer tillers (Fig. 9.2), while the MLC approximates 7-61% of HT, respectively (Fig. 9.3). At HT = 1.0 gape, %MLC (ie. MLC/HT x 100) is on average about 70% greater compared to when HT was equal to 0.5 gape. In contrast %MLC increases by only about 20%, as HT increases from 1.0 gape to 2.0 gape (Fig. 9.3). Thus a change in HT will have much greater impact upon MLC or BW at a HT of around 0.5. gape compared to heights in excess of 1.0 gape. Similarly, increasing penetration from 25 to 50% of HT increases the MLC by between 109% (HT = 2.0 gape) and 140% (HT = 0.5 gape), whereas increasing penetration from 50 to 75% of HT only increases MLC by about 50%. In other words, a proportionately much greater gain can be achieved by increasing penetration up to 50% of HT than by an equivalent increase above this level

The mean length captured when the jaws close, as a proportion of the length initially encompassed in the open mouth and above incisor height (ie. ≈ MLC/BD x 100) also increases rapidly, at a progressively declining rate as penetration increases up to around 40-50% of HT, and declines slightly above this level (Fig. 9.3). Further, this effect declines with increasing HT, becoming negligible above about 25% penetration as HT approaches 2.0 gape. For heights approaching 1.0 gape or less, however, Figure 9.3 indicates that by penetrating to about 40-50% of HT, animals should maximise the efficiency of capture of the herbage they initially selected or tried to prehend.

In conclusion, by penetrating to around 40-50% of HT as animals frequently do (Section 9.2.4), they appear to be optimising grazing efficiency in terms of: i) the number (area) of tillers captured per bite on shorter swards (Fig. 7.2; Sections 7.5.3.2 & 9.3.3), ii) the proportional gain in MLC per unit of penetration, as well as iii) the efficiency of capture of herbage initially encompassed or selected (ie.≈MLC/BD x 100); while minimising the negative effects of declining quality in the lower horizons of the sward. This captured herbage comes from the higher quality upper half of the sward, while utilising the poorer quality herbage in the lower half of the sward to achieve the necessary horizontal displacement of non central tillers towards the bite centre (see Appendix 2). The normal increase in herbage strength and rigidity, and decline in quality down the profile of natural swards, would be expected to considerably reduce the gains in harvesting efficiency to be made from deep penetration within the lower horizons (Laca *et al.* 1992b; Demment *et al.* 1992). Thus the observed patterns of variation in BD and BA with changing sward height appear logical in terms of the optimisation of bite dimensions, diet quality and rate of capture of nutrients relative to grazing effort.

9.3.6 Conclusions

1. Sheep appear to be superior at prehending short swards compared to deer, as indicated by their larger bite areas (scaled to IAW), as well as their ability to prehend slightly shorter swards. However, the BA of deer peaked at greater sward heights than for sheep, so that differences were reduced on taller swards.

2. As HT increased from minimum grazable levels, BA increased at a declining rate. BA increased as increasing tiller length enabled greater horizontal displacement of reasonable lengths of tillers by the animal's mouth, up to a point where it was largely constrained by mouth dimensions (gape).

3. As DEN increased, animals increased BW and therefore may have increased biting effort. However, they did reduce BA, presumably because this made tiller prehension a simpler and faster process and, on swards of high tiller strength prevented biting effort increasing excessively. The result of such adjustments was that, as DEN increased, BA increased more slowly in relation to

increasing HT and, peaked at lower levels on shorter swards.

4. By penetrating to around 40-50% of sward height, animals appear to be optimising grazing efficiency in terms of the number (area), length and quality of tillers captured, per unit of grazing effort.

9.4 Bite Weight

9.4.1 Height and bulk density effects

This series of trials demonstrated the mechanism (Chapters 5 & 6) by which tall, sparse swards allow much higher bite weights than short, dense swards of equivalent herbage mass; principally because both spatial components of BV decline with increasing DEN but increase with increasing HT. For example, in the study involving 1-8 cm wheat swards (Chapter 7), BV declined on average by approximately 4 cm^3 per mg DM cm^{-3} increase in DEN, but increased by 20 cm^3 per cm increase in HT. On average across the range of heights and bulk densities measured, BW increased at approximately twice the rate in relation to an increase in HT compared to proportionately equivalent increases in DEN.

HT appears to be the principle determinant of BW in many studies representing a wide range of heights and different types of grass swards (Black & Kenney 1984; Laca *et al.* 1992b; Gong *et al.* 1993; Chapters 5-8). This is probably because animals grazed relatively indiscriminately at the sward surface resulting in a reasonably close relationship between HT and BD (Chapters 5-8; Section 9.2.4). Despite the reductions in DEN on taller swards, large bite weights should be readily achievable, as bite dimensions should be relatively unrestricted by the sward itself, provided herbage quality does not decline down the sward profile. On some tall swards the density of herbage at the surface might be sufficiently low (Stobbs 1973a, b; 1975) that mouth-dimensions may severely restrict the area of herbage prehended per bite, although by taking deep bites in such cases, animals should still achieve large bite weights (Burlison 1987).

However, HT may be a poor indicator of potential BW when large differences in quality between herbage components necessitate more selective grazing in the vertical or horizontal planes, and thus reduce BV. This is likely on tall tropical swards, particularly when reproductive or as they are grazed down (Stobbs 1974; Chacon & Stobbs 1976; Chacon *et al.* 1978). It may be largely the size, degree of differentiation in quality and average distance between plant components which separates swards into HT responsive (typically temperate) and DEN responsive (typically tropical) categories.

The relative adjustments in HT or DEN necessary to maintain a given BW, as DEN or HT change, reveal their relative impact upon BW. To achieve a BW of about 80 mg DM, which enabled lactating ewes to maximise daily herbage intake (Penning 1986), sheep grazing the 1-8 cm wheat swards (Chapter 7) would have required 2.8, 4.7 or 6.4 cm HT when DEN was 2.90, 1.30 or 0.65 mg DM cm^{-3} respectively. Thus, a very large 2.25 mg DM cm^{-3} decline (346% change) in DEN, was compensated for by only a 3.6 cm increase (129% change) in HT. Alternatively, a very large increase in DEN is necessary to compensate for a reasonably small decline in HT on moderately short swards. From a slightly different perspective these results show how DEN becomes much less important as HT increases only slightly on short swards, but is critically important in allowing animals to achieve an adequate BW and intake as HT falls to low levels, where daily herbage intake becomes restricted. In line with this and earlier discussion, Dougherty *et al.* (1992) found that DEN was an important determinant of intake in cattle on low herbage mass tall fescue swards.

Compared to sheep grazing 1-22 cm hand-constructed ryegrass swards (Black & Kenney 1984), BW values on wheat swards were similar on short swards but increased faster with HT, probably reflecting larger bite areas (Chapter 8), as well as deeper BD/HT ratios on the taller wheat swards. Bite weights in these two studies were much higher than for sheep on 5-15 cm ryegrass turves dug from pasture (Hughes *et al.* 1991), probably reflecting deeper bites on these high quality, artificial swards (Chapter 7; Section 9.2.1) and also larger bite areas in the case of wheat swards, (Chapter 8).

There is insufficient detail in the sward data to compare BW for sheep grazing natural ryegrass pastures from Jamieson & Hodgson (1979b), Penning (1986) or Penning *et al.* (1989; 1991a) with results from the wheat swards. BV estimates based on BW, HT and average sward DEN values from Penning *et al.* (1991a) are clearly in error, probably reflecting the much lower density of the grazed stratum compared to the average sward DEN (Burlison 1987). For example a BW of 45 mg DM on a 9 cm x 9.0 mg DM cm^{-3} sward indicates a BV of 5 cm^3 which is ridiculously low compared to values of 51, 62 and 158 cm^3 on 10-11 cm swards from the studies of Burlison *et al.* (1991), Hughes *et al.* (1991), and Chapter 6 respectively. The very high mean sward DEN in Penning's study reflected the very high levels of dead matter (45%) which probably (Barthram & Grant 1984; Hodgson 1990a; Clark 1993) would have occurred predominantly below the grazed stratum.

The effects of HT and DEN on BW have proved to be independent and additive in most studies (Hodgson 1990b; Burlison *et al.* 1991; Laca *et al.* 1992b). However in some studies involving short swards the effects appear to be interactive (Black & Kenney 1984; Chapters 6 & 7). DEN has a much larger (negative) effect upon BV on tall compared to short swards. Consequently, on tall swards the positive effects of increases in DEN upon BW tend to be diluted by the concomitant reductions in BV, and this may explain why they appear as additive to those of HT. In contrast, on short swards BV is relatively less sensitive to DEN and the direct positive effects of DEN upon BW appear to be multiplicative (interactive) with those of HT. For example, the BW trends of sheep on 1-8 cm (Chapter 7) and 4-13 cm (Chapter 6) wheat swards appear broadly similar to those on 1-22 cm hand-constructed ryegrass swards (Black & Kenney 1984). BW is markedly interactive on 1-8 cm wheat and short ryegrass swards, but increasingly additive on 4-13 cm wheat and taller ryegrass swards.

Further, the stronger the effect of DEN upon BD or BA, the stronger the negative HTxDEN interaction evident for BV and consequently the weaker their positive interactive effects for BW. On the fragile seedling wheat swards the effects of DEN upon BV appear to be lower (Section 9.3.4) compared to other swards so that the effects of HT and DEN on BW are probably more strongly interactive than usual and may remain interactive to greater heights than on other swards. Similar trends appear to hold for RI (Black & Kenney 1984; Chapter 7), although the negatively interactive effects of HT and DEN upon BR appear to further dilute any positively interactive effects present for BW. This appears to largely restrict any interactive effects upon RI to even lower sward heights than evident for BW.

9.4.2 Deer-sheep differences

Figure 9.4 shows how the BW kg $LW^{-1.0}$ difference between deer and sheep on 1-8 cm wheat swards tends to increase slightly in absolute terms with increasing sward HT. However, the relative difference (BW kg $LW^{-1.0}$ of sheep/BW kg $LW^{-1.0}$ of deer) between sheep and deer actually declines slightly with increasing HT, because of the rapid rate of increase in the bite weights of both species as well as the deers' faster rate of increase in BW with increasing HT (Chapters 6 & 7).

The differences shown in Fig. 9.4 may be smaller than in practice, because the deer were comparatively light (82-93 kg), yet had IAWs of 46-47 mm compared to the 43 mm quoted by Gordon & Illius (1988) for 150 kg (presumably male) Red deer. The different seasons and experiments in which deer and sheep were fed (Chapter 7) may also have affected apparent deer-sheep differences. Variation in age (Kay & Staines 1981; Fennessy & Milligan 1987), season and related physiology (Kay 1979; Loudon 1985; Suttie & Simpson 1985) will markedly alter the relative requirements of deer and sheep over time (Fenessey *et al.* 1981; Harbord 1984; Milne & Reid 1989).

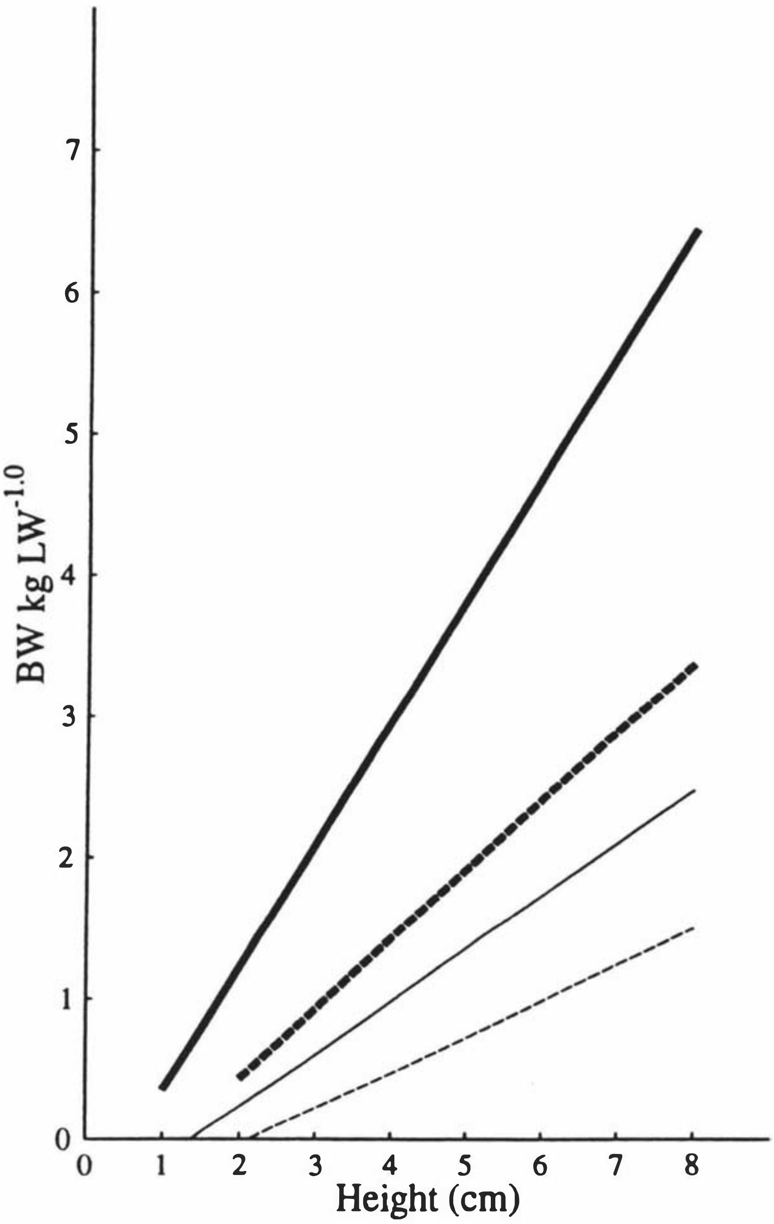

Fig 9.4 The BW kgLW$^{-1.0}$ of Red deer (dotted lines) and Romney sheep (solid lines) on sparse (0.65 mgDM cm^{-3} = fine lines) or dense (2.9 mg DM cm^{-3} = thick lines) 1-8 cm wheat seedling swards.

9.4.3 Conclusions

1. Tall sparse swards enable larger bite weights than short dense swards of equal herbage mass, because BV (both BD and BA) increases with HT but declines with DEN.

2. As HT declines to low levels, the importance of DEN increases greatly in terms of enabling animals to achieve an adequate BW. However, BW is much more sensitive to HT on short swards than DEN, with only small increases in HT resulting in proportionally very large increases in BW. DEN is much less likely to be critical on taller swards, where animals can more readily compensate by increasing BV.

3. The BW kg $LW^{-1.0}$ of sheep was much larger than that of deer on short swards where daily herbage intake might be restricted, however the relative difference between species declined steadily as HT increased.

9.5 Bite rate

The BR of deer tended to be slightly higher than that of sheep and this may reflect a reduction in gathering per bite by deer, as indicated by their smaller BA (scaled to IAW).

The limited degree to which deer and sheep were able to increase BR in relation to huge reductions in BW reflect the minimum number of jaw movements and resultant high time cost of each bite (Laca *et al.* 1993; Chapter 6), and explain the importance (in terms of RI and daily herbage intake) of animals being able to achieve an adequate intake per bite.

In general, BR trends for sheep in relation to HT appear similar across sward types, with BR increasing with HT on very short swards and then declining again with further increases in HT (Allden & Whittaker 1970; Penning *et al.* 1991a; Chapter 7). However, large between-sward differences in tiller strength and depth of grazed stratum appear to result in differences in absolute

BR and points of inflection at equivalent HT and DEN (Chapter 6).

As in many studies involving sheep or cattle (Allden & Whittaker 1970; Stobbs 1973a; Chacon & Stobbs 1976; Jamieson & Hodgson 1979b; Hodgson 1981; Penning *et al.* 1989, 1991a), on wheat swards BR increased as BW declined. Further, on wheat swards BR was in general more strongly correlated with BW than any other sward or bite parameter. In contrast however, in a number of studies including cattle (Hodgson 1982; Dougherty *et al.* 1988; Arias *et al.* 1990) BR appears to be unrelated to BW. Recent work by Demment *et al.* (1992) showed that the BW of cattle could increase up to 1.5 g DM without altering BR, because animals were able to process the increase in herbage per bite without increasing total jaw movements or altering time per bite, by increasing the overlap in function of manipulative and chewing jaw movements. Such overlap might well explain the insensitivity of BR to changing BW in the study of Arias *et al.* (1990) as bite weight did not exceed 1.5 g DM.

In some cases the increased chewing required to process more fibrous tissue (Spalinger *et al.* 1988; McLeod & Smith 1989), such as mature herbage from reproductive swards (Gong 1994) or that from lower horizons of vegetative swards (Cosgrove 1992) may reduce BR in relation to BW. Similarly the need to be more selective or the increasing difficulties of prehension as HT (Chapter 7) or leaf depth (Allden & Whittaker 1970; Penning *et al.* 1991a) approach minimum grazable levels may reduce both BR and BW.

Whether or not sheep, like cattle, can maintain BR over a range of bite weights by increasing the overlap in function of jaw movements is unknown, although there seems to be little evidence for it from the current series of studies (Chapters 6 & 7) or from the literature (Allden &Whittaker 1970; Black & Kenney 1984; Penning *et al.* 1991a). Sheep gather herbage with their mouth rather than their tongue and this probably explains in part the higher ratio of manipulative jaw:severing head movements in sheep compared to cattle (Chambers *et al.* 1981). Whether or not such differences result in the BR of sheep being more sensitive to changing sward conditions than that of cattle

(Forbes & Hodgson 1985a; Hodgson *et al.* 1991) requires further investigation.

On wheat swards (Chapters 6 & 7) BW was more sensitive to HT than DEN and, reflecting its sensitivity to BW, so too was BR. Further, BR was slightly more sensitive to changes in BW due to HT, than to equivalent changes in BW due to DEN. As herbage length increases, it probably requires more chewing simply to reduce the greater average particle size before swallowing (Kenney & Black 1984). On taller swards, taking bites of long foliage involves more manipulative jaw movements (Hodgson 1985) simply to draw it into the mouth (Burlison 1987; Gong *et al.* 1993, Gong 1994). This is also likely to reduce the efficiency of chewing, as much of the herbage remains temporarily outside the animal's mouth (Dougherty *et al.* 1989b).

While increasing DEN negatively affects BR by increasing BW, it also enables animals to reduce BA (Demment *et al.* 1992; Chapters 6 & 7; Sections 9.3.3.1 & 9.3.4). The regression of BR on BW was significantly improved by the inclusion of a BA term ($P<0.056$) in 4 out of 6 cases (and marginally so in a fifth case, ($P<0.101$)) for deer and sheep in the three wheat sward studies. Thus large increases in DEN probably make tiller prehension a simpler and faster process, by reducing the number or magnitude of gathering movements per bite (Laca *et al.* 1992b). Consequently the negative (increasing BW) and smaller positive (decreasing BA) effects on BR would tend to reduce the negative DEN effect on BR, relative to that of HT, which increases both BW and BA. Similarly, Moore & Sollenberger (1986) found that as the percentage of legume (joint vetch) increased within the upper sward horizon, BR declined due to increased manipulative jaw movements prior to each bite.

Thus, while a close negative relationship between BW and BR might in general be expected (Illius 1986; Dougherty *et al.* 1988) this may not always occur because of the variable overlap in function of manipulative and chewing jaw movements (at least in cattle) or the direct influence of sward conditions upon BR (Hodgson 1985; Chapter 7).

9.5.1 Conclusions

1. The BR and BW of deer and sheep increase as HT increases for a centimetre or more above minimum grazable levels, above which their BR declines with further increases in HT and BW.

2. BR was sensitive to HT and DEN, very largely because of their effects upon BW. However, BR was more sensitive to changes in BW due to HT than DEN, apparently reflecting a reduction in BA with increasing DEN and/or the greater number of manipulative jaw movements required to process tillers as their length increased.

9.6 Rate of intake, and practical implications

9.6.1 Height and bulk density effects on rate of intake

In the discussion of BW, the dominant role of HT compared to that of DEN has been emphasised. However, their influence on RI will be dependent upon the moderating effects of sward conditions on BR. Potentially there is the moderating influence of reductions in herbage quality upon BR, which are likely to be associated with increases in HT or maturity (Dougherty *et al.* 1988; Gong *et al.* 1993, Gong 1994). Secondly there is the apparently greater direct negative influence of herbage length (compared to that of DEN) upon BR. In terms of RI, both of these factors appear likely to moderate the greater effects of HT upon BW compared to that of DEN.

9.6.2 Sward type affects rate of intake

Although the hand-constructed swards of Black & Kenney (1984) were composed of the two youngest leaves per tiller from vegetative annual ryegrass pastures, sheep achieved much higher RI levels on wheat swards (Chapters 6 & 7). This difference largely reflected higher bite rates, but also larger bite weights on the taller wheat swards. Differences in RI were small only on shorter swards due to higher bite weights on the ryegrass, probably because of very deep bites close to board level

(Black & Kenney 1984). The high rates of intake on wheat, even when compared to the high quality ryegrass swards, suggests that wheat tillers may represent conditions allowing close to maximal intake rates for a gramineous type sward. Such high rates of intake were probably due to the ease of prehending, severing and, in particular, chewing and swallowing the fragile seedling wheat tillers (Chapters 6-8).

Despite the high rates of intake on wheat swards, the estimated maximum RI levels were still far below those achievable on pure clover swards (Kenney & Black 1986). Clovers tend to concentrate very high densities of herbage in the surface horizon, due to the horizontal alignment of laminae at the tops of the petioles, presumably increasing the efficiency of prehension of lamina in particular. It may be that these factors, as well as the flexible nature and low structural strength of the petioles, encourage or enable large bite areas and high bite rates in relation to DEN on some legume swards (Gong *et al.* 1993, Gong 1994; pers. obs.; Penning *et al.* 1991b).

9.6.3 Overestimation of rate of intake

As BW increases to high levels, animals must perform an increasing number of exclusive chewing jaw movements to process the large amounts of herbage which rapidly accumulate in the mouth during a series of bites (Laca *et al.* 1993; Demment *et al.* 1992; pers. obs.). While chewing these large mouthfuls they are likely to raise their heads away from the sward. As observed for cattle (Laca *et al.* 1993) and sheep (Forbes & Hodgson 1985a) on higher herbage mass swards, deer and sheep on the tallest swards in the 4-13 cm wheat sward experiment (Chapter 6) raised their heads from the sward while chewing mouthfuls of long, rapidly ingested herbage. This time was not counted as grazing time, because animals would also raise their heads if disturbed when grazing any treatment, momentarily pausing from eating. The effects of not including head-up chewing were evident in data from the tallest swards, with BR almost plateauing above 10 cm HT. This resulted in RI, which had almost levelled off between 7 and 10 cm, increasing more rapidly again above

10 cm HT (Fig. 9.5).

In view of the fact that BW appeared to very largely determine BR, it was somewhat surprising that with the exception of the lowest DEN for sheep (Fig. 9.5), RI appeared to level out at much the same height for all DEN levels, for both deer and sheep. However at 13 cm HT, large compensatory increases in BV were possible as DEN declined, such that a 222% increase in DEN (from 1.01 to 3.25 mg DM cm^{-3}) only increased the BW of sheep by 61% (from 216 to 348 mg DM). Further, as described in Section 9.5, BR was considerably more sensitive to herbage length than DEN. Also the low structural strength of wheat swards may have reduced the effect of DEN on BR relative to that of HT (Chapter 6) when compared to swards with greater tiller strength.

Further, although not evident from the plots of the regression equations, the plots of the mean RI values gave some indication that RI might have plateaued at slightly greater heights on low compared to high DEN swards. This being the case, rates of intake for lower DEN swards would tend to converge upwards, towards those which had already plateaued for higher DEN swards, as observed for sheep grazing hand-constructed ryegrass swards (Black & Kenney 1984).

The short term nature of all BR measurements in Chapters 6 & 7 would also have resulted in some degree of overestimation of RI, even for lower herbage mass swards (Forbes & Hodgson 1985a; Forbes 1988). However, the degree of overestimation probably was not large (Jamieson & Hodgson 1979a; Illius 1986, 1989) and probably would have declined slightly as BW declined (Forbes 1988), given that small bites are faster to process than large bites (Demment *et al.* 1992). Further, to increase the likelihood that all animals would eat all the sward treatments, including those of low HM, animals were put on a reduced ration while sward measurements occurred (Chapter 6). It is possible that this and other behavioural factors may have increased RI relative to normal daily intakes (Sections 9.1.3.1-9.1.3.3).

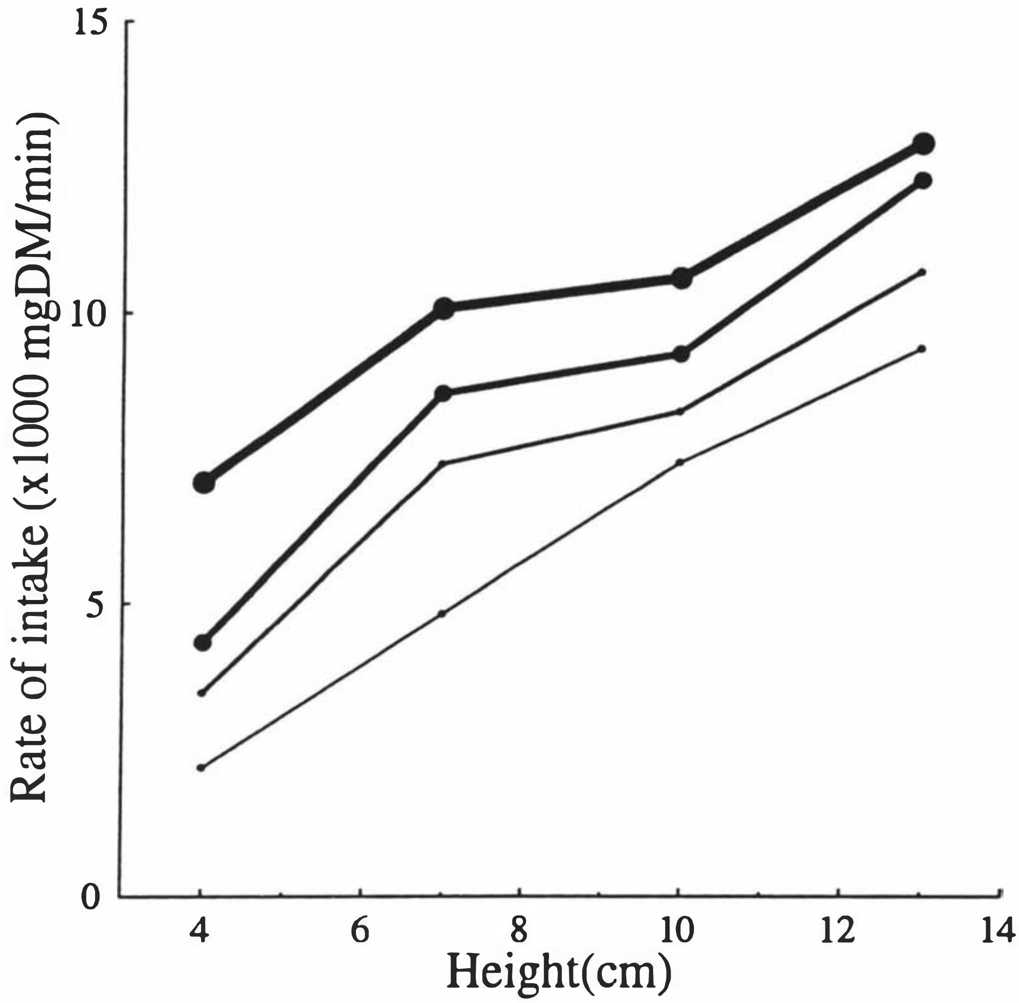

Fig. 9.5 The effects of sward height (4-13cm) and bulk density(0.63, 1.01, 1.74, 3.25 mgDMcm^{-3}; fine through heavy lines respectively) upon the mean rate of intake of sheep.

9.6.4 Scaling to metabolic requirements

Seasonal variation aside, there are substantial differences in the mean fasting metabolic rate of adult animals, and it is somewhat dubious to compare requirements across animal species unless such values are established by direct experimentation (Kay 1985). Indications are that the metabolic rate per unit $LW^{0.75}$ of Red deer is similar to that of cattle, but some 30-40% higher than that of sheep (Simpson *et al.* 1978; Kay 1981; 1985). Comparisons of sheep and cattle use $LW^{0.9}$ (Minson & Whiteman 1989) suggesting that sheep/deer comparisons should perhaps use a similar scaling value or even $LW^{1.0}$.

9.6.5 Practical Implications

9.6.5.1 Sward height requirements for deer and sheep

Mouth size and sward height become greater relative to LW as animal size declines (Illius & Gordon 1987) suggesting that smaller animals should achieve larger bite weights in relation to body size (Illius 1989). Such constraints may encourage large wild herbivores to move to less preferred habitats containing tall herbage of lower quality ahead of smaller herbivores (Bell 1971). In line with these concepts, the BW and RI (scaled to LW or $LW^{0.75}$) of sheep became increasingly large relative to that of deer as HT declined. Figure 9.4 for example suggests that deer required approximately 75% more HT than sheep to obtain an equivalent BW kg $LW^{-1.0}$ on dense wheat swards. Further, there were indications that mature deer required taller swards than sheep to achieve peak rates of intake (Chapter 7). Similarly, field studies of Red deer and sheep in the Scottish highlands suggest that intense grazing by sheep on Agrostis-Festuca swards reduced their use by the larger hinds (Osborne 1984). Further, hind grazing (Charles *et al.* 1977) or a combination of sheep and hind grazing (Osborne 1984) on these swards appeared to have a pronounced effect on their use by the much larger stags, even to the point where stags actually avoided such swards (Osborne 1984). A study of weaner stag performance on set stocked ryegrass pastures (Ataja *et al.* 1989, 1992) also indicated that deer might require greater sward heights than sheep (Hodgson 1990a; Penning *et al.* 1991a) to obtain equivalent or maximal intakes.

In practical terms the trends suggest that deer should be grazed less intensively on taller swards or to higher residuals than sheep, and that in this regard herbage quality, density and productivity (Bircham & Hodgson 1983; Hodgson & Maxwell 1984), may be more difficult to maintain under deer grazing. However, the critical sward heights for deer production require more precise definition and those for ewe/lamb production can be as high as 7-8 cm for summer swards (Hodgson *et al.* 1986; Hodgson 1990a). Further, there are many factors, such as differences in diet selection (Hughes *et al.* 1984; Hunt & Hay 1990; Gong *et al.* 1993) and seasonal changes in intake and metabolic rate (Kay 1979, 1981, 1985; Fennessy *et al.* 1981; Loudon 1985) which might markedly alter the relationship between sward conditions, intake rate and body size for different animal species, so that much of the empirical evidence is equivocal (Jamieson & Hodgson 1979b; Baker *et al.* 1981; Hodgson 1981; Forbes & Hodgson 1985a).

9.6.5.2 Mixed grazing

Gwynne & Bell (1968) suggested that the differences in diet selection related to the successive occupation of habitat by zebra, wildebeest and Thompsons gazelle on the Serengeti plains indicated a facilitative rather than competitive relationship between these species. Fully domesticated animals are unlikely to experience such consistent selection, natural or otherwise, for co-adaptation. However, in a review of 14 mixed grazing studies (Lambert & Guerin 1989), production was apparently increased in 12 cases for at least one of the animal species. Similarly, Gordon (1988) reported increased fecundity in Red deer that were preferentially grazing areas with more green grass, as a result of previous use by cattle. However, in other comparisons with sheep and cattle, there has been little evidence of either increased herbage productivity or utilisation efficiency under mixed grazing (Hodgson *et al.* 1987).

While the current series of short term trials cannot seriously address the complementarity of deer and sheep, the results as they stand do suggest that in any combination of the two species in a grazing rotation deer should be placed in front. Deer probably need taller swards than sheep because of their larger size (Illius & Gordon 1987), their poorer ability to prehend short swards (Chapters 6 & 7) and possibly also their 30-40% higher energy requirements per unit $LW^{0.75}$ (Kay 1985). Also deer may make relatively better use of the extra height as indicated by their faster rate of increase in BW with HT (Chapters 6 & 7). Further, Clutton-Brock *et al.* (1987) states "the tendency for sheep to graze swards to a level at which they will not support cattle or other large grazing animals is well known" and in areas where sheep are present available herbage is reduced and little used by Red deer (Osborne 1984). Even on species rich indigenous pastures, sheep appear to competitively exclude deer to a large degree (Osborne 1984). Thus despite the marked preference of Red deer for legumes and herbs over grass (Hunt & Hay 1990), the likelihood of complementarity on relatively simple improved pastures would seem small (Lambert & Guerin 1989). Disease considerations alone probably preclude any reversal of species grazing order, or simultaneous continuous grazing.

9.6.5.3 Implications of sward structure for plant breeding and management

Bite dimensions and consequent ingestive behaviour respond to both HT and DEN over wide limits (Black & Kenney 1984; Laca *et al.* 1992b; Chapters 5-7) and, in some situations, potential intake benefits might be achievable by increasing either of these sward parameters. As either HT or DEN increase or decline, the other factor becomes increasingly unimportant or important, in absolute terms, with regards to the animal's ability to achieve an adequate BW and RI. However, only on short pastures are increases in erectness or DEN likely to have a significant impact upon potential BW. Quality factors aside, DEN can be critically important in ensuring an adequate BW on short swards, although the influence of HT is still much greater relative to that of DEN.

Firstly, with naturally short, prostrate plant species, even small increases in HT or erectness should be of benefit in terms of BW (Section 9.4.1) by increasing the depth of the grazable strata as well as the ease of tiller prehension, particularly where multi-purpose pastures have to cater for large grazing animals. The negative effects on BW of the small concomitant reductions in DEN as HT increases, should be easily outweighed by the positive effects of HT on BV, on swards short enough to restrict daily herbage intake. The HT above which little benefit will be obtained will of course depend upon the type of animals being catered for and the type of plants being used.

While increasing HT may increase RI within the surface horizon, the effects on daily herbage intake may be less marked under strip-grazing, because RI within the lower sward stratum may be reduced as pregrazing canopy height increases (Cosgrove 1992). Similarly, Wade (1991) suggested that intake was affected by current sward HT as well as pregrazing sward HT. Allowing HT to increase will tend to reduce tillering activity, and increased build up of dead matter becomes more likely (Hodgson & Maxwell 1984; Hodgson 1990a). However, at any given HT, reductions in pseudostem height would increase leaf depth. Potentially this would enable higher rates of intake within the surface horizon of short, continuously stocked swards and possibly also in the lower horizons of rotationally grazed pastures, while perhaps minimising the reductions in herbage DEN, quality or sward vigour associated with simple increases in HT.

The constraining influence of HT on the BA and especially the BD of animals grazing very short swards implies that benefits may arise from increases in DEN, on short continuously stocked swards for example. On slightly taller pastures, where gape as opposed to HT limits BA, DEN is unlikely to limit BW because animals can usually take deeper bites and more readily adjust BA in relation to DEN. Increases in DEN without loss of quality, would of course be beneficial in terms of increasing the potential carrying capacity of the land.

Although tiller strength and rigidity influence the ease of prehension (Laca *et al.* 1991a; 1992b; Ungar *et al.* 1991; Chapter 8), the resultant differences in BA between fragile wheat and tougher ryegrass leaf or pseudostem swards were not large (Chapter 8), and their major impact may be upon post-ingestive processes such as chewing during eating and rumination, and rate of passage (Inoue *et al.* 1989; McLeod & Smith 1989). However, the need for continued work in this area is indicated from our incomplete understanding of BA/biting effort trade-offs (Chapters 6 & 8; Section 9.3.4), the predictability of BD/HT ratios (Chapters 7 & 8; Section 9.2.4), variation in RI across swards of similar HT and DEN (Chapter 6; Section 9.6.2) and the considerable differences in ingestive behaviour on grass and clover or legumes (Kenney & Black 1986; Moore & Sollenberger 1986; Penning *et al.* 1991b; Gong *et al.* 1993).

9.6.5.4 Conclusions

1. Deer need taller swards than sheep to achieve equivalent intakes.

2. Any grazing rotation with deer and sheep should place deer in front. If both species were continuously stocked simultaneously on improved pasture, sheep are likely to out compete deer because of their superior grazing ability and allometry as sward height falls to low levels.

3. Reductions in pseudostem height may be beneficial on some short pastures by increasing the average depth of the grazed horizons (as small increases in BD, when BD is restricted, can enable proportionally large increases in BW) while minimising reductions in herbage quality associated with simply increasing HT.

9.7 Generalised response

Modelling was not an objective of this study. Rather the aim was to more clearly establish the relationships between bite parameters and some of the major sward variables, from which a more realistic model of grazing behaviour might be formulated. Based on current studies of ingestive behaviour, a generalised response for the grazing herbivore is attempted here, although probably with greatest applicability to sheep on vegetative, ryegrass-dominant swards.

BD should increase in a close to linear fashion with HT (Chapters 5 & 6) and is likely to be around 40% or slightly more of current sward height in field or short-term mini-sward studies (Chapters 7 & 8; Section 9.2.4). The BD/HT ratio will decline slightly with large increases in DEN on medium to tall swards (Chapters 6 & 7) but, on short swards and for practical purposes, the influence of DEN upon BD can usually be ignored (Chapter 6). BD/HT may also increase slightly as animal size increases (I.J. Gordon pers. com.; Betteridge *et al.* 1994) and on reproductive compared to vegetative pastures (Gong 1994). On the other hand the ratio may become very low on short swards where shallow leaf depth and/or close proximity to some unpalatable component or even the ground itself restricts BD (Barthram & Grant 1984).

Although BA increases with HT on short swards, it is less sensitive to HT when DEN is high (Chapters 6 & 7). Thus BA should be reasonably stable on dense (>2.5 mg DM cm^{-3}) swards provided they are not very short (<3-4 cm for sheep) or tall (>10-12 cm for sheep), because BA is constrained by HT on short swards, but declines with increasing HT on tall dense swards (an improbable combination). BA increases more rapidly with increasing HT and up to greater heights as DEN declines. However, sparse swards are usually sufficiently tall (>8-10 cm for sheep) for BA to again be reasonably stable. BA can be up to 100% larger on tall sparse (<0.7 mg DM cm^{-3}) swards compared to dense (>2.5 mg DM cm^{-3}) swards of any HT, provided tiller rigidity and strength are reasonably similar. Large differences in tiller strength (say >100%) are likely to significantly alter BA although only to a relatively much smaller degree. The most likely circumstances under which considerable differences in BA will occur, are probably when dense swards of any HT are compared with moderately tall to tall sparse swards. In practice, when grazing perennial ryegrass swards the BA of sheep is likely to be in the vicinity of 12-20 cm^2 (Burlison *et al.* 1991; Hughes *et al.* 1991; Gong *et al.* 1993, Gong 1994; Chapter 8).

BW will increase in a close to linear manner with HT or DEN (Burlison *et al* 1991; Chapters 5-7) at a rate dependent upon the BD/HT ratio and the modifying influence of HT, DEN and tiller strength upon BA. Further, because of the negative interactive effects of HT and DEN on BV, the influence of HT and DEN on BW are likely to be interactive on very short swards, but become increasingly independent and additive as HT increases (Black & Kenney 1984; Burlison *et al* 1991; Laca *et al* 1992b; Chapters 6 & 7).

Typically, BR will decline as HT or DEN increase, largely as a direct result of increasing BW, although BR is likely to increase with increasing HT (and BW) for a centimetre or so above the animals' minimum grazable HT, before it declines (Chapter 7). Further, the ingestion of long herbage is likely to reduce BR by requiring extra manipulative jaw movements to draw the herbage into the mouth (Hodgson 1985; Gong *et al.* 1993, Gong 1994) , which probably also reduces the efficiency of chewing (Dougherty *et al.* 1989b). BR also appears to differ in relation to large differences in herbage strength or maturity (Spalinger *et al.* 1988; Gong *et al.* 1993, Gong 1994; Chapter 6) and the consequent ease of harvesting and processing it in the mouth (Kenney & Black 1984, 1986). In cattle the overlap in function of chewing and manipulative jaw movements may largely prevent any change in BR as BW increases up to 1.5 g DM (Demment *et al.* 1992).

RI increases at a gradually declining rate with HT (and also DEN) up to a level where decreasing BR counter balances further increases in BW. The effects of HT and DEN may be largely independent and additive, although there are indications that they are interactive on short and possibly again on tall swards (Black & Kenney 1984). This requires further investigation.

A knowledge of both HT and DEN are required to predict BW and RI when HT and DEN are varied artificially over a wide range (Laca *et al.* 1992b). However, the correlation between HT and DEN on natural swards is likely to enable reasonable prediction of BW, RI and especially daily herbage intake (given the animals' ability to adjust grazing time) based on HT alone (Orr *et al.*1990; Penning *et al.* 1991a; Parker & McCutcheon 1992; Morris *et al.* 1993), provided pasture management and plant growth habit are similar. Under rotational grazing, rapid depletion of herbage and consequent changes in sward structure can occur (Ungar *et al.* 1992) so that "development of models to correctly predict intake curves on the basis of initial sward structure will require more research on the mechanisms by which BW decreases within and between horizons" (Demment *et al.* 1992).

9.8 Concluding summary

This series of trials clarifies many aspects of how sward HT, DEN and vertical changes in tiller structure on gramineous type swards affect the depth, area and rate of biting of the grazing herbivores, Red deer and Romney sheep. The potential importance of both HT, BD and mouth dimensions in determining the horizontal area and average length of herbage which animals are able to prehend is illustrated and discussed. The inter-relationships between HT, mouth size and animal size, and bite dimensions (Illius & Gordon 1987) are considered.

All bite parameters were influenced by both HT and DEN. However, the influence of HT was dominant relative to that of DEN over the range of 1-21 cm vegetative leafy swards examined, although on taller swards DEN would have had the greater influence upon BA and possibly RI.

The trials indicated that sheep could graze shorter swards and attain peak bite rates at lower sward heights than deer. Sheep could also prehend larger bite areas (scaled to IAW) on short swards, indicating that sheep were not only allometrically better adapted, but possibly also behaviourally superior at grazing short swards relative to deer. The lower LW, larger mouth in relation to LW and apparently superior prehending behaviour of sheep enabled them to achieve higher rates of intake (scaled to LW or $LW^{0.75}$) than deer, particularly on short swards, although the relative (proportional) difference between sheep and deer declined as HT increased.

With the possible exception of very short swards where the BD/HT ratio may increase slightly as

HT or leaf depth increases, many studies indicate a reasonably constant BD/HT ratio across a given set of sward conditions. However, this potentially useful tool requires further confirmation across both animal species and plant morphologies, and in short term vs field experiments. Within limits BA appears to be reasonably constant in practice, so that a constant BD/HT ratio should make BW (which is otherwise difficult to measure) relatively simple to estimate from sward conditions.

Studies using ryegrass dairy pastures (Wade 1991) and hand-constructed paspalum swards (Demment *et al.* 1992) both indicate that cattle tend to graze swards down in layers of predictable depth, a phenomenon which may hold for a range of grazing herbivores (I.J. Gordon pers. comm.). In terms of predicting daily herbage intake, it would be useful to firmly establish under which conditions different animal species do actually graze off single horizons and how stable this behaviour is across the range of normally encountered sward conditions, particularly as HT increases. For animal species which do have a predictable and stable BD/HT ratio, BA and pattern of regrazing, useful estimates of allowance and daily herbage intake may be derived from measurements/predictions of the area grazed per animal per day (Wade 1991) in relation to known sward conditions, although this would not reveal BR and grazing time.

With the exception of short, continuously stocked swards, most indications are that the upper horizons containing pseudostem have little influence on bite dimensions as this portion of the pseudostem tends to be below at least the uppermost grazed stratum, or is too similar to leaf to limit penetration (Wade 1991; Demment *et al.* 1992; Chapter 7). However, there is still the need to further clarify how ingestive behaviour is modified by pseudostem or stem height as well as commonly occurring quantitative and qualitative differences in leaf:pseudostem ratio, dead matter content, tiller rigidity, and tiller breaking strength under both rotational and continuous stocking. How these factors affect depth of penetration and BR on temperate grass swards will be important, because BD is the most likely factor to limit BW while differences in BR can have an important influence upon RI. In comparison, the influence of these factors upon BA probably assumes greater importance on some tropical grass swards where the heterogeneity and density of plant components reach greater extremes.

Constant DEN, similar tiller morphology, shear strength and apparent acceptability to the animal down through the sward profile, and lack of dead matter near the base, were unique characteristics of wheat swards enabling a high degree of separation of HT and DEN variation across a wide range and large number of treatment combinations. These same features effectively reduced or removed some of the characteristics normally associated with natural sward conditions which affect ingestive behaviour; with the result that both spatial (BD and BA) and temporal (BR) bite dimensions were larger and higher respectively, when compared with published data for natural grass dominant swards. Consequently, although wheat swards were very useful in terms of separating, measuring and conceptualising the effects of HT and DEN on the mechanisms controlling bite dimensions and ingestive behaviour, their unique qualities effectively limit their direct applicability in terms of extrapolation to field grazing conditions.

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APPENDIX 1:

Table 1. The effect of penetration (≈BD), sward height and tiller density upon the lengths captured from individual tillers (LC), or the mean length of tillers captured per bite (MLC; which is proportional to sum of lengths captured or bite weight), by an animal with a 5 cm maximum gape when penetrating to 25%, 50% or 75% of height on 2.5 cm or 5 cm tall swards.

HT	BD	BD/HT	IHT (≈HT-BD)	%DC	DC	LL# (HT-LC)	LC (HT-LL)	MLC+	LC/BD x100	MLC+ /BD x100	LC/HT x100	MLC /HT x100
(cm)	(cm)	(%)	(cm)	(%)	(cm)	(cm)	(cm)	(cm)	(%)	(%)	(%)	(%)
5	1.25	25	3.75	100	2.5	4.51	0.49		39.4		9.9	
"	"	"		75	1.875	4.19	0.81		64.6		16.1	
"	"	"		50	1.25	3.95	1.05	0.93_5	83.8	74.2_5	20.9	18.5_5
"	"	"		25	0.625	3.80	1.20	0.87_3	95.9	69.3_3	24.0	17.3_3
"	"	"		0	0	3.75	1.25		100.0		25.0	
5	2.5	50	2.5	100	2.5	3.54	1.46		58.6		29.3	
"	"	"		75	1.875	3.13	1.87		75.0		37.5	
"	"	"		50	1.25	2.80	2.20	2.04_5	88.2	81.9_5	44.1	41.0_5
"	"	"		25	0.625	2.58	2.42	1.96_3	96.9	78.7_3	48.5	39.4_3
"	"	"		0	0	2.50	2.50		100.0		50.0	
5	3.75	75	1.25	100	2.5	2.80	2.20		58.8		44.1	
"	"	"		75	1.875	2.25	2.75		73.2		54.9	
"	"	"		50	1.25	1.77	3.23	3.03_5	86.2	81.0_5	64.6	60.7_5
"	"	"		25	0.625	1.40	3.60	2.92_3	96.1	78.0_3	72.0	58.4_3
"	"	"		0	0	1.25	3.75		100.0		75.0	
2.5	0.625	25	1.875	100	2.5	3.13	-0.62		0		0	
"	"	"		75	1.875	2.65	-0.15		0		0	
"	"	"		50	1.25	2.25	0.25	0.24_5	39.4	38.5_5	9.9	9.6_5
"	"	"		25	0.625	1.98	0.52	0.23_3	83.8	35.8_3	20.9	9.0_3
"	"	"		0	0	1.87	0.63		100.0		25.0	
2.5	1.25	50	1.25	100	2.5	2.80	-0.30		0		0	
"	"	"		75	1.875	2.25	0.25		19.7		9.9	
"	"	"		50	1.25	1.77	0.73	0.60_5	58.6	48.1_5	29.3	24.1_5
"	"	"		25	0.625	1.40	1.10	0.54_3	88.2	43.4_3	44.1	21.7_3
"	"	"		0	0	1.25	1.25		100.0		50.0	
2.5	1.875	75	0.625	100	2.5	2.58	-0.08		0		0	
"	"	"		75	1.875	1.98	0.52		27.9		20.9	
"	"	"		50	1.25	1.40	1.10	0.93_5	58.8	49.5_5	44.1	37.1_5
"	"	"		25	0.625	0.88	1.62	0.81_3	86.2	43.5_3	64.6	32.6_3
"	"	"		0	0	0.63	1.87		100.0		75.0	

+ So as to illustrate the impact of tiller density upon MLC, these values are calculated for two densities, giving an average of either 3 or 5 (subscripts) tillers evenly spaced from either the extreme front or rear edge to the centre of the bite.

LL should closely approximate true residual length of each grazed tiller

Note: When the animal's upper and lower jaws meet at the centre of the bite, the angles to which tillers are displaced and the length of each tiller severed (Figs. 9.2 & 9.3) will depend upon the animal's depth of penetration into the sward (≈BD), the horizontal distance between the prehending surfaces of the animal's open jaws (gape), and the length of tillers (HT) as well as their horizontal distance from the centre line (where jaws meet when closed) of the bite (DC), the average of which can be altered slightly by tiller density. Calculations of length lost (LL) and length captured (LC) from tillers are derived from Equation 9.1 assuming an animal with a 5 cm maximum gape grazing swards of 5 cm or 2.5 cm HT and penetrating (≈BD) to 25, 50 or 75% of HT. The influence of these factors upon the efficiency of tiller capture are described in terms of the MLC/HT x100 or the MLC/BD x100.

APPENDIX 2:

Aid to visualising the effects of bite depth and height on the efficiency of tiller capture

Penetration (≈BD) to around 50% of HT should be efficient because it positions the high quality upper half of available herbage length above the level of the incisors, while utilising the poorer quality lower half to efficiently achieve the necessary horizontal displacement of non central tillers towards the bite centre. In doing so, the angles of captured non central tillers, even those near the periphery (even of short swards), are likely to be reasonably small. The smaller the angle, the more efficient the displacement and capture of herbage initially above the open incisors from non central tillers, because small angles achieve very substantial horizontal displacement of tillers with relatively little change in their vertical position relative to the animal's incisors. In effect, the shallower the bite (increasingly so the taller the sward), the smaller the angle of displacement, and the higher the ratio of horizontal displacement to vertical displacement (Fig. 7.2). In comparison, very deep bites initially encompass long lengths of tillers, but more of this length (from non central tillers) is subsequently dragged out of the mouth as the jaws close. This is because the deeper the bite (increasingly so the shorter the sward), the greater the angle of displacement, so that displacement becomes increasingly vertical (ie. tiller length is pulled from the mouth as it closes), especially as the angle exceeds 45° (Fig. 7.2). Further the deeper the bite, the more rigid tillers become (as they increase in maturity and approach the point of attachment) and the sharper the angle of displacement, suggesting that animals will also experience greater resistance across the teeth and dental pad as they close their jaws to prehend the bite, as well as during preliminary gathering jaw movements. Further, resistance during severing will probably also be increased.

APPENDICES 3-5

Data files for Chapters 5-7, presenting means
and standard errors of bite parameters for sheep and deer
for specified sward characteristics.

Abbreviations used in the tables:

DEN	Bulk density (mg DM cm^{-3})
HT	Surface height (cm)
SPP	Species: 1 = Deer 2 = Sheep
FREQ	Number of records
M	Mean
S	Standard error of mean
BW	Bite weight (mg DM)
BD	Bite depth (cm)
BA	Bite area (cm^{-2})
BV	Bite volume (cm^{-3})
GSBD	Grazed stratum bulk density (mg DM cm^{-3})

APPENDIX 3 (CHAPTER 5 DATA)

OB	BULK DEN	HGHT	SPE	FRE	MBW	MBN	MBA	MBV	MGSBD	SBW	SNWC	SBN	SBA	SBV	SGSBD
1	0.188	3	1	2	19.154	2.300	59.3460	136.498	0.140325	4.7096	4.7096	0.000	14.5922	33.5621	0.0000000
2	0.188	3	2	1	30.789	2.540	86.3840	219.415	0.140325						
3	0.188	6	1	2	37.262	4.500	51.7653	232.944	0.159945	8.4788	8.4788	0.000	11.7582	52.9119	0.0000668
4	0.188	6	2	1	27.200	4.500	38.1365	171.614	0.158495						
5	0.188	9	1	2	68.560	7.450	53.4028	397.078	0.172667	1.5595	1.5595	0.250	3.0887	9.6602	0.0002730
6	0.188	9	2	2	67.440	7.850	49.8496	388.565	0.173638	7.4400	7.4400	0.350	7.8720	44.3479	0.0006700
7	0.188	12	1	2	74.800	9.650	41.8414	404.757	0.184683	8.2017	8.2017	0.350	2.2130	41.8700	0.0011588
8	0.188	12	2	2	68.767	8.950	42.4890	379.563	0.181096	3.0962	3.0962	0.550	1.2967	11.7636	0.0025446
9	0.188	15	1	1	91.436	11.300	42.1167	475.918	0.192126						
10	0.188	15	2	1	91.032	12.400	37.3317	462.913	0.196650						
11	0.188	18	1	1	83.019	13.900	29.3594	408.095	0.203430						
12	0.188	18	2	2	89.159	13.050	34.3915	447.999	0.198984	13.0782	13.0782	0.150	5.3950	65.2460	0.0002128
13	0.188	21	1	1	84.416	14.900	27.4082	408.383	0.206707						
14	0.188	21	2	1	96.181	13.500	35.6682	481.521	0.199745						
15	0.375	3	1	1	31.863	2.500	45.4128	113.532	0.280650						
16	0.375	3	2	2	21.472	2.500	39.3546	97.886	0.280650	2.4098	2.4098	0.100	5.0088	8.5867	0.0000000
17	0.375	6	1	1	58.286	4.800	37.6961	180.941	0.322125						
18	0.375	6	2	2	57.733	4.500	41.5967	184.130	0.313962	4.7672	4.7672	0.400	7.6380	17.7324	0.0043450
19	0.375	9	1	2	85.255	6.830	36.6666	249.261	0.341654	6.1639	6.1639	0.670	1.7466	12.6239	0.0074254
20	0.375	9	2	2	67.432	7.250	27.1129	197.665	0.339787	13.1460	13.1460	0.950	1.1542	34.1251	0.0078458
21	0.375	12	1	2	96.046	7.950	34.1112	272.345	0.351836	14.4805	14.4805	0.650	1.7656	36.3677	0.0061874
22	0.375	12	2	1	117.288	10.570	29.6633	313.541	0.374075						
23	0.375	15	1	1	88.315	6.000	31.2499	249.999	0.353262						
24	0.375	15	2	2	114.342	10.700	26.7426	302.696	0.376904	18.5091	16.5091	0.700	6.9295	54.0256	0.0064797
25	0.375	18	2	2	114.187	10.250	30.2751	304.933	0.374468	4.1672	4.1672	1.350	3.9902	0.0261	0.0137660
26	0.375	21	1	2	150.776	13.800	26.7619	370.934	0.405680	22.2405	22.2405	0.800	2.0241	49.3425	0.0059935
27	0.750	3	1	2	21.602	1.895	20.0429	38.450	0.561699	5.9494	5.9494	0.105	4.4644	10.5646	0.0003986
28	0.750	3	2	2	43.560	2.275	34.3273	77.606	0.561300	1.5600	1.5600	0.225	2.1734	2.7793	0.0000000
29	0.750	6	1	2	47.012	4.650	15.8429	73.973	0.634321	18.6235	18.6235	0.050	6.0658	28.9962	0.0031011
30	0.750	6	2	2	86.771	5.400	24.9574	135.728	0.641244	34.1060	34.1060	0.100	9.5779	54.2165	0.0046622
31	0.750	9	1	2	71.122	5.950	20.1390	107.948	0.661858	2.7163	2.7163	1.650	7.1994	9.6071	0.0337409
32	0.750	9	2	2	106.842	6.500	25.7031	159.697	0.669546	1.4911	1.4911	1.300	5.6716	3.4512	0.0236064
33	0.750	12	1	1	113.324	8.200	19.5701	160.475	0.706181						
34	0.750	12	2	2	124.625	7.450	24.3587	179.229	0.695234	4.1059	4.1059	0.850	2.6398	1.0381	0.0188820
35	0.750	15	1	1	193.600	10.600	24.2247	256.782	0.753946						
36	0.750	15	2	1	180.195	9.500	25.8829	245.888	0.732834						
37	0.750	18	1	1	168.539	11.600	19.3896	224.919	0.749330						
38	0.750	18	2	1	195.617	8.640	31.6208	273.204	0.716011						
39	0.750	21	1	1	163.226	13.300	15.3181	203.731	0.801183						
40	0.750	21	2	2	217.013	10.720	26.6630	286.386	0.757650	29.7543	29.7543	0.180	3.1018	38.0501	0.0032323

APPENDIX 4 (Chapter 6, Experiment 1 data)

Means (M) and standard errors (SE) of bite parameters (BD, BA, BV, BW, BR & RI) from Experiment 1 (E1) of Chapter 6. (Spp 1 ≈ deer & Spp 2 ≈ sheep).

HT	DEN	SPP	FREQ	MBD	MBA	MBV	MBW	MBR	MRI	SEMBD	SEBA	SEBV	SEBW	SEBR	SERI
3	0.325	1	4	1.78864	14.0069	25.355	8.240	1.35083	11.409	0.07243	1.62712	3.98380	1.2947	0.07952	2.5019
3	0.325	2	3	1.71968	19.3556	33.295	10.821	1.19964	13.061	0.04527	0.33845	1.19947	0.3898	0.10648	1.6007
3	0.650	1	3	1.72111	14.3889	24.762	16.095	1.38907	22.323	0.05856	0.85480	1.63968	1.0658	0.02002	1.2467
3	0.650	2	3	1.80354	15.3729	27.708	18.010	1.27489	23.004	0.06509	0.13812	0.75518	0.4909	0.04704	1.4391
3	1.300	1	3	1.72611	13.9111	24.075	31.298	1.55844	47.888	0.07079	1.18559	2.60042	3.3806	0.14103	1.5290
3	1.300	2	4	1.69250	13.7493	23.277	30.260	1.20687	36.631	0.02429	0.70674	1.26159	1.6401	0.03980	2.7815
3	2.900	1	2	1.57000	13.2651	20.838	60.430	1.27536	76.880	0.06333	0.18311	1.12756	3.2692	0.05792	0.6672
3	2.900	2	3	1.67500	12.0022	20.088	58.254	1.16441	67.979	0.01418	0.57356	0.79680	2.3107	0.05876	5.4666
3	4.000	1	3	1.76222	10.9502	19.252	77.007	1.26820	97.330	0.04736	0.94957	1.50403	6.0161	0.03333	5.5081
3	4.000	2	3	1.60611	12.7037	20.497	81.989	1.10780	94.066	0.07558	1.44978	2.76374	11.0549	0.15248	22.8320
5	0.325	1	2	3.51138	20.2616	71.237	23.152	1.09361	25.415	0.12138	0.74571	5.07783	1.6503	0.05790	3.1453
5	0.325	2	4	3.65220	19.4944	71.134	23.119	1.15075	26.620	0.06795	0.77386	2.61100	0.8486	0.04539	1.5110
5	0.650	1	3	3.49626	18.5837	65.086	42.306	1.37037	57.595	0.02325	2.48893	9.18164	5.9681	0.08173	7.1393
5	0.650	2	3	3.45500	17.1230	59.481	38.663	1.13864	44.991	0.17264	1.04578	6.29985	4.0949	0.15720	9.4221
5	1.300	1	2	3.51250	18.7907	65.854	85.610	1.35517	116.236	0.09417	1.58018	3.78085	4.9151	0.04483	10.4985
5	1.300	2	3	3.46444	17.4807	60.257	78.534	1.10640	86.784	0.12498	1.46992	3.56572	4.6354	0.13848	11.7717
5	2.900	1	4	3.35292	14.7812	49.428	143.342	1.16741	167.474	0.10277	0.48914	0.84432	2.4485	0.02750	6.2971
5	2.900	2	3	3.46000	14.0577	48.638	141.049	1.13307	159.919	0.03521	0.13916	0.61705	1.7894	0.06732	10.4269
5	4.000	1	3	3.30278	13.9995	46.096	184.384	1.21723	224.161	0.15710	0.63817	1.74033	6.9613	0.05809	10.7799
5	4.000	2	3	3.21556	12.2089	39.007	156.029	0.99315	156.126	0.11128	1.13076	2.17417	8.6967	0.06745	19.4925
7	0.325	1	3	5.42486	20.0900	109.103	35.459	1.26815	44.546	0.13100	0.54155	5.39363	1.7529	0.12203	2.3047
7	0.325	2	3	5.30916	21.0684	111.991	36.397	0.95758	34.383	0.25755	0.61662	7.55315	2.4548	0.09683	1.3876
7	0.650	1	4	5.21917	20.3871	106.193	69.026	1.18347	81.548	0.08729	0.88795	3.19604	2.0774	0.03192	1.7682
7	0.650	2	3	5.41889	17.9943	97.567	63.418	1.02625	65.608	0.10259	0.53057	4.12957	2.6842	0.10936	9.2199
7	1.300	1	3	5.15722	20.9782	108.172	140.624	1.15091	159.342	0.05664	0.36665	1.79303	2.3309	0.03091	2.3997
7	1.300	2	2	5.43584	17.2313	93.665	121.765	1.14461	139.460	0.04584	0.02770	0.63920	0.8310	0.10539	13.7842
7	2.900	1	2	5.08500	15.6626	79.616	230.887	1.05357	242.671	0.03333	0.84278	3.76351	10.9142	0.05357	0.8701
7	2.900	2	4	5.18375	14.7122	76.161	220.867	0.91911	202.825	0.13930	0.25549	0.82715	2.3987	0.09160	19.7874
7	4.000	1	3	4.91111	16.2871	80.128	320.514	0.92082	289.855	0.23481	0.75862	6.32245	25.2898	0.13083	23.9551
7	4.000	2	3	4.70611	13.5099	63.616	254.463	0.85856	224.730	0.15889	1.40852	7.33172	29.3269	0.13720	57.1231

APPENDIX 4 continued (Chapter 6, Experiment 2 data)

Means (M) and standard errors (SE) of bite parameters (BD, BA, BV, BW, BR & RI) from Experiment 2 (E2) in Chapter 6. (Spp 1 = deer & Spp 2 = sheep).

HT	DEN	SPP	FREQ	MMBD	MBA	MBV	MBW	MBR	MRI	SEMBD	SEBA	SEBV	SEBW	SEBR	SERI
4	0.634	1	4	2.3944	16.6620	39.750	25.226	82.8158	2067.53	0.07419	1.08479	2.1582	1.3697	6.12861	91.9
4	0.634	2	4	2.4363	17.9963	43.892	27.855	78.8173	2208.10	0.06049	0.76981	2.4627	1.5629	3.89251	213.5
4	1.014	1	3	2.4650	16.2753	40.095	40.646	85.0000	3457.47	0.04589	0.31040	0.4422	0.4483	2.88675	155.1
4	1.014	2	4	2.4613	18.0539	44.451	45.062	76.7502	3480.04	0.05817	1.49947	3.9287	3.9827	2.96728	399.0
4	1.742	1	4	2.4200	13.8651	33.420	58.208	82.0383	4781.35	0.06987	0.72582	0.9666	1.6836	3.81153	304.9
4	1.742	2	4	2.3163	14.3760	33.265	58.199	74.6307	4335.57	0.05097	0.48303	1.0238	2.0290	1.87608	104.7
4	3.248	1	4	2.3138	12.7944	29.207	94.886	75.0372	7096.79	0.11380	1.24243	1.5861	5.1529	2.01909	266.4
4	3.248	2	4	2.3763	14.2453	33.874	110.059	64.5949	7076.07	0.03441	0.55134	1.5728	5.1037	3.74141	357.5
7	0.634	1	4	5.0006	23.4619	117.188	74.371	83.8659	6262.23	0.12862	1.11960	5.6306	3.5733	2.91407	495.0
7	0.634	2	4	5.0631	22.8493	115.753	73.460	65.7665	4829.72	0.03412	0.79691	4.7149	2.9922	3.83689	328.3
7	1.014	1	4	4.8144	24.8630	119.857	121.504	76.5813	9336.12	0.08751	2.35002	12.1398	12.3066	6.03397	1239.3
7	1.014	2	4	5.1800	21.2158	109.791	111.300	66.3577	7391.48	0.07170	1.74690	8.6855	8.8048	3.64379	696.9
7	1.742	1	2	4.7888	20.2295	96.837	168.662	61.5789	10383.11	0.12375	0.29950	1.0692	1.8622	1.57895	151.6
7	1.742	2	4	4.9350	17.0960	84.551	147.263	58.1029	8621.37	0.11820	0.92882	6.0416	10.5227	2.98210	974.2
7	3.248	1	4	4.4588	14.0669	62.342	202.534	56.7188	11608.60	0.41711	0.51151	5.1740	16.8091	3.28125	1454.2
7	3.248	2	4	4.4756	14.1034	62.710	203.729	49.4730	10065.38	0.15166	0.98991	2.3233	7.5480	1.46569	370.8
10	0.634	1	4	7.5819	26.1113	197.654	125.564	61.5333	7698.98	0.20740	1.57540	12.8536	8.1573	2.30359	430.2
10	0.634	2	4	7.8088	25.0900	196.043	124.415	59.4917	7419.41	0.09247	0.79754	7.7480	4.9171	2.72311	537.2
10	1.014	1	4	7.7656	27.5658	213.919	216.857	54.5970	11876.00	0.11169	0.86531	5.8499	5.9303	4.55308	1160.7
10	1.014	2	4	7.3469	23.1766	171.231	173.583	49.0927	8315.68	0.17762	1.99152	18.8934	19.1529	4.39494	445.1
10	1.742	1	4	7.4000	19.1968	141.507	246.465	49.4389	12048.34	0.10521	2.09667	13.6605	23.7927	3.24043	891.6
10	1.742	2	4	7.3200	16.4688	121.187	211.046	44.7647	9291.96	0.25914	0.90248	10.3070	17.9516	3.31051	418.2
10	3.248	1	3	6.6875	14.1578	94.658	307.524	40.0366	12200.87	0.49124	0.86850	8.8922	28.8887	2.46626	754.9
10	3.248	2	4	6.5806	12.6738	83.501	271.277	40.4138	10578.17	0.15169	1.23441	8.5582	27.8038	4.67841	431.6
13	0.634	1	3	10.7600	30.1719	324.457	205.910	58.6473	12046.27	0.17863	1.04911	9.8790	6.2695	2.76166	324.8
13	0.634	2	4	10.3881	27.4742	285.442	181.149	51.7053	9388.30	0.03434	1.46982	15.5206	9.8498	1.71370	679.5
13	1.014	1	4	10.1444	29.1841	295.153	299.208	48.3851	14419.22	0.18950	3.30530	30.9745	31.4000	2.46009	1575.6
13	1.014	2	4	10.3894	21.9223	228.066	231.149	46.4479	10693.56	0.14245	1.30254	15.4647	15.7209	1.51435	614.7
13	1.742	1	4	9.7294	21.3839	207.846	362.008	39.0703	14127.00	0.33991	0.21539	5.4186	9.4376	2.55589	884.6
13	1.742	2	4	9.6244	16.8929	163.221	284.285	43.2013	12230.17	0.25458	1.36074	16.6880	29.0657	1.17370	1087.2
13	3.248	1	3	9.6558	16.6901	160.479	521.361	32.5857	17075.34	0.22613	1.61243	12.4883	40.5718	1.35897	1940.4
13	3.248	2	3	9.0917	11.2800	102.481	332.938	38.5882	12858.45	0.14632	0.70696	5.9500	19.3301	0.55101	844.5

APPENDIX 5 (Chapter 7 data)

Means (M) and standard errors (SE) of bite parameters (BD, BA, BV, BW, BR & RI) from Chapter 7 (Spp 1 ≈ sheep & Spp 2 ≈ deer).

HT	DEN	SPP	FREQ	MBD	MBA	MBV	MBW	MBR	MRI	SEMBD	SEBA	SEBV	SEBW	SEBR	SERI
1	0.65	1	4	0.58300	11.0809	6.474	2.835	60.6092	173.31	0.02921	0.58079	0.5023	0.2515	4.67613	23.63
1	0.65	2	.	.	.	.	.	.	.	.	.	.	.	.	.
1	1.30	1	4	0.64338	8.8374	5.665	6.220	83.7797	527.91	0.02526	0.44112	0.2409	0.5281	9.45188	92.38
1	1.30	2	.	.	.	.	.	.	.	.	.	.	.	.	.
1	2.90	1	4	0.59680	9.5042	5.610	12.822	79.6793	1024.37	0.04491	0.78175	0.4386	0.5513	3.81975	78.89
2	0.65	1	4	1.31779	15.0449	19.828	10.744	87.5021	941.45	0.05161	1.09898	1.6485	0.5854	2.53339	66.60
2	0.65	2	4	1.21424	16.5570	20.007	7.318	82.1010	601.06	0.05068	1.56086	1.6219	0.3385	2.62252	34.09
2	1.30	1	4	1.31299	12.4338	16.340	19.014	86.7017	1645.20	0.05353	0.27057	0.8458	0.6593	4.28791	77.56
2	1.30	2	4	1.18876	15.4981	18.408	15.945	86.4375	1377.18	0.01140	1.76508	2.0496	1.5350	2.93395	138.71
2	2.90	1	3	1.32000	12.0723	15.989	42.224	81.5803	3470.47	0.04537	0.83822	1.5357	3.8997	4.89148	493.02
2	2.90	2	4	1.29813	13.3505	17.379	36.966	83.4355	3088.92	0.04739	0.85500	1.5309	3.4118	1.45456	311.84
3	0.65	1	4	2.07516	16.8656	35.109	21.097	88.6983	1863.80	0.06197	0.87013	2.6454	1.5341	3.76754	122.31
3	0.65	2	4	1.86448	22.2513	41.672	19.055	93.0714	1778.25	0.04484	1.52406	3.8849	0.6033	3.32456	116.62
3	1.30	1	3	2.16583	16.6308	36.085	42.702	79.8783	3430.63	0.04144	1.07295	2.8411	3.5301	5.65816	472.15
3	1.30	2	4	2.05563	19.8620	41.032	41.575	85.6550	3538.90	0.08321	1.03190	3.6017	4.6554	3.11564	339.93
3	2.90	1	4	2.12313	15.3927	32.641	86.759	76.3054	6641.44	0.05762	1.08141	2.3496	5.4591	4.59095	658.57
3	2.90	2	4	1.71438	17.3490	29.690	68.035	87.3366	5946.33	0.03309	0.60934	0.6205	1.1585	2.26514	230.26
5	0.65	1	4	4.02124	21.9002	87.608	52.379	70.4018	3654.97	0.25730	1.20757	5.1501	3.1899	4.52129	176.20
5	0.65	2	4	3.71625	29.5737	109.940	59.195	74.4643	4403.90	0.13186	1.23779	6.2319	3.8862	2.11037	292.46
5	1.30	1	4	3.99223	20.4984	81.775	94.398	75.3230	7096.23	0.06430	1.04090	3.9634	3.5663	5.20383	482.73
5	1.30	2	4	3.57500	23.9599	85.742	96.765	77.1895	7496.33	0.11775	0.69166	4.3124	4.5904	4.40072	685.92
5	2.90	1	4	3.46500	16.8421	58.395	150.821	60.2138	8947.62	0.11667	1.01058	4.2877	12.3553	3.81523	304.52
5	2.90	2	4	3.34813	16.9641	56.791	145.044	75.4079	10948.30	0.06225	0.99193	3.3992	7.6214	2.86420	751.60
8	0.65	1	4	6.67250	22.8050	152.007	94.029	64.2018	6018.77	0.05935	1.47128	9.0749	6.2542	4.09176	510.30
8	0.65	2	4	6.46214	31.8443	205.457	113.428	69.2353	7925.23	0.13202	2.00403	11.9709	6.7381	5.92075	1033.79
8	1.30	1	4	6.20125	23.2486	143.666	163.510	57.5833	9411.28	0.21963	1.24598	6.4225	12.2544	1.58334	731.50
8	1.30	2	4	6.19087	26.4482	163.715	188.565	58.8204	11120.81	0.17582	1.51428	10.3216	10.2142	4.68763	1169.75
8	2.90	1	4	5.84938	18.1015	105.632	266.203	41.5497	11070.24	0.13815	0.95288	4.2652	4.4615	2.51549	752.09

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