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The effect of varying leafy sward height and bulk density on the ingestive behaviour of young deer and sheep

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ABSTRACT

The effect of varying the height and bulk density of the leafy zone of the sward on the ingestive behaviour of six 11 month old Red deer hinds and seven 14 month old Romney ewe hoggets 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, stem 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 at least 20 bites, bite depth, bite weight, grazed stratum bulk density, bite volume and bite area were calculated.

The ingestive behaviour of deer and sheep was very similar in relation to height and bulk density. The positive effect of height on bite depth was on average 11 times as large as the negative effect of bulk density. Height had little or no effect upon bite area, while bulk density had a moderate, negative effect. On average a 100% increase in height or bulk density respectively resulted in a 64% vs. only 21% increase in bite weight; reflecting the fact that bite volume increased in relation to H (39%) but decreased in relation to bulk density (18%). Thus height was the major determinant of bite volume and bite weight via its influence on bite depth.

Keywords Ingestive behaviour, bite dimensions, sward height, bulk density, Red deer, Romney sheep.

INTRODUCTION

A major factor limiting production of grazing animals is restricted nutrient intake (Hodgson, 1981). Nutrient intake is restricted by 3 factors: diet digestibility and metabolisability, and herbage intake. Depending on sward conditions, herbage intake may vary fivefold (Hodgson and Grant, 1981) 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, 1982; Penning, 1985). The evidence to date suggests that the major determinants of bite weight are sward surface height (Black and Kenney, 1984; Burlison *et al.*, 1991 and Mursan *et al.*, 1989) and bulk density (Black and 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 14 different grass and 3 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 and 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 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 them.

MATERIALS AND METHODS

Design

Twenty-one sward, height x density combinations,

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involving 7 sward heights (H) (3, 6, 9, 12, 15, 18, 21 cm) and 3 bulk densities (D) (0.19, 0.38 and 0.75mg 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 H x D combinations.

Animals

Eleven month old Red deer hinds weighed 51 to 56 kg (incisor widths, 3.2 to 3.3 cm). Fourteen month old Romney ewe hoggets 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 were reduced to 60% of *ad libitum* intakes.

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 26cm above stem height. Once trimmed, 14 swards were left at 100% density (D0.75), 14 thinned to 50% density (D0.38) by removing alternate rows of plants, and 14 to 25% density (D0.19) by removing alternate rows and columns.

Measurement Procedure

Two swards of equal density were weighed to the nearest 0.1 gm. 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.

Animals were allowed to graze until at least 20 bites were taken. The depth of all visibly grazed leaves below a rod set at sward surface height, was measured with a ruler. Grazed and ungrazed swards (used to determine insensible weight losses) were reweighed.

Ungrazed Sward Descriptions

Leaf number, weight, angle and bulk density, per stratum (0-3 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, leaf shear strength (using an Instron machine and Warner-Bratzler attachment) and width were measured at the stratum mid-points of 10 typical plants.

Calculation of Bite Parameters

The more direct measurements of bite weight and bite depth were used to calculate bite volume, bite area 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)

$$\textit{bite weight} = \frac{[(W1 - W2) - WL]}{N}$$

$$\textit{bite depth} = \frac{\sum d}{n}$$

$$\textit{grazed stratum bulk density} = \sum \left(\frac{si\,bi}{n}\right)$$

$$\textit{bite volume} = \frac{\textit{bite weight}}{\textit{grazed stratum bulk density}}$$

$$\textit{bite area} = \frac{\textit{bite volume}}{\textit{bite depth}}$$

Statistical Analyses

Bite parameters (and ungrazed sward data) were analysed by analysis of variance. Wherever H, D or their interaction were significant, coefficients for the best fit regression equations were determined by re-analysing with H, D, H^2, D^2 or H x D terms fitted as co-variates.

TABLE 1 Mean leaf parameters measured from 6 ungrazed swards*. Means with different letters are significantly different at $P<0.05$.

Stratum from top (cm)	Leaf density (leaf #/9 cm^2)	Leaf width (mm)	Leaf shear strength (N/leaf)	Leaf angle (degrees)	Leaf dry weight (mg/3 cm strata)	Bulk density of sward+ (mg DM/cm^3)
0-3	2.23 a	12.6 a	3.38 a	70	6.85	0.56
3-6	2.61 b	12.5 a	3.82 ab	71	7.60	0.65
6-9	2.94 c	12.3 a	4.29 abc	76	7.41	0.70
9-12	3.31 d	11.0 a	4.79 c	76	7.73	0.76
12-15	3.81 e	10.0 a	4.78 bc	78	7.37	0.81
15-18	4.25 f	8.6 b	4.92 c	80	6.76	0.86
18-21	4.40 f	6.9 c	5.14 c	77	6.78	0.89

* 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.

RESULTS

Ungrazed Sward Description

There were no differences between swards except for leaf density differences of up to 16% in the 6-9cm and 9-12cm stratum ($P<0.05$). Factors increasing ($P<0.05$) from the top to lowest stratum were leaf density (96%) and leaf shear strength (52%); where as leaf width decreased by 83% (Table 1). However, the bulk density of a 21cm sward was only 59% (47% on fresh weight basis) greater than that of a 3 cm sward.

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.

The ingestive behaviour of deer and sheep was similar in relation to H and D, consequently their results were combined.

Leaf height was strongly correlated with bite depth, bite weight and bite volume in that order (Table2), while it had a negative or nil effect upon bite area (Table 2 and Fig. 2). In contrast D had a negative effect upon all bite parameters except bite weight. The interactive effects of H and D were significant in determining all the bite parameter equations (equations 1-5) and all equations were slightly curvilinear with the exception of bite area.

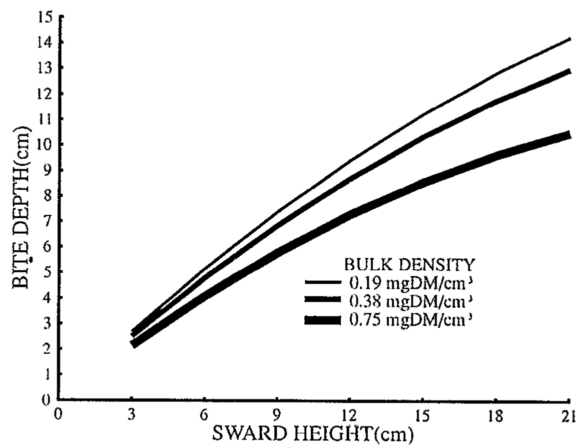

FIG 1 Bite depth of young deer and sheep (combined) in relation to leafy sward height and bulk density.

Because of the small confounded changes in bulk density with H, grazed stratum bulk density was auto-correlated with H. Consequently, it was more valid to relate the bite parameters to the independent, manipulated bulk density levels (D0.19-D0.75); which were very highly correlated with grazed stratum bulk density ($r = 0.98$, $P<0.001$).

On average, for every 100% increase in H or D, bite depth increased by 77% or decreased by 7%

TABLE 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

* $P<0.05$
** $P<0.01$
*** $P<0.001$

respectively, clearly indicating the dominant role of H in determining bite depth (equation 1, Fig.1). The bite depth/height ratio declined with H ($P<0.05$) from approximately 0.78 for the 3 - 9 cm swards to 0.63 for the 18 and 21 cm swards.

Bite area did not change with H for the highest density (Fig. 2). Bite area was the most variable of the bite parameters in relation to H or D as indicated by its lower r^2 and r values (equation 2 and Table 2, respectively).

As H increased the rate of increase of bite volume declined reflecting both the non-linearity of bite depth and the decline in bite area with increasing H (equation 3 and Fig. 3).

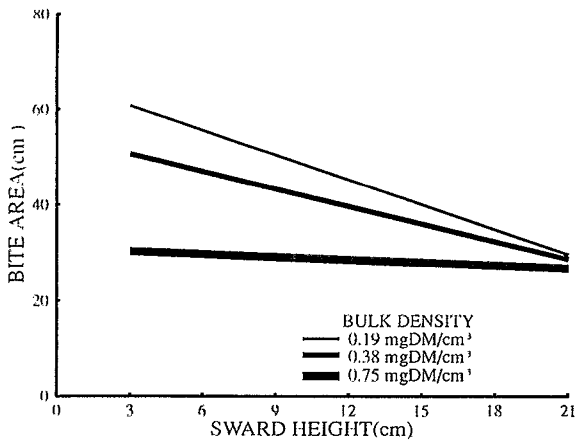

FIG 2 Bite area of young deer and sheep (combined) in relation to leafy sward height and bulk density.

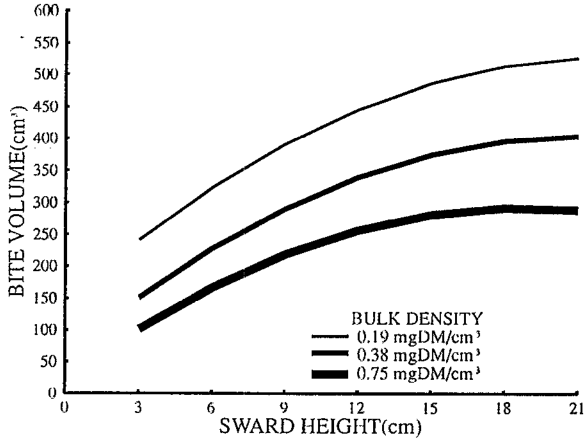

FIG 3 Bite volume of young deer and sheep (combined) in relation to leafy sward height and bulk density.

Bite Weight Corrected for Confounded Increases in Bulk Density with Height

As H increased from 3 to 21 cm, the grazed stratum bulk density also increased by 0.23 mg DM/cm^3. The confounding effect of H and D on bite weight was estimated by multiplying the D coefficient (102.788) of the best fit simple linear equation (r^2=0.87, $P<0.001$) by the confounded increase in grazed stratum bulk density (0.23 mg DM/cm^3) to give an estimate of the total error in bite weight incremented over the entire height range (23.6 mg). By calculating the mean grazed stratum bulk density for each height it was possible to determine the correction to be applied to the mean bite weight values (proportion of the total error which should be subtracted from the mean bite weight values) at each height to estimate the true unconfounded bite weight. Mean bite weight for each height was calculated using a constant bulk density of 0.56 mg DM/cm^3 for all stratum and adding on the appropriate correction factors. When compared with the mean measured bite weight values, the estimates were within 9 to 11% of the original mean values. As unconfounded bite weight (equation 5) and bite weight (equation 4) had similar variables and coefficients, only unconfounded bite weight was considered further (equation 5 and Fig. 4).

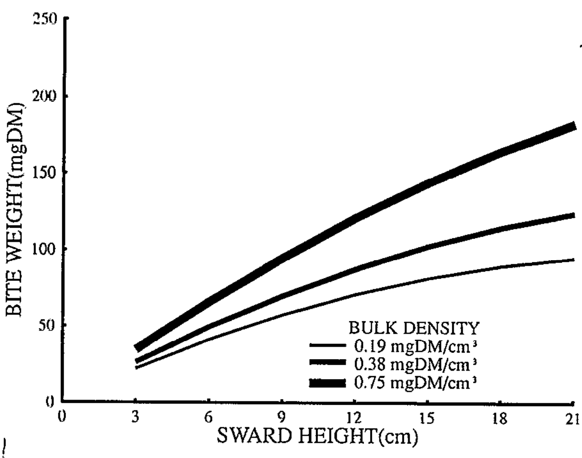

FIG 4 Bite weight of young deer and sheep (combined) in relation to leafy sward height and bulk density.

On average bite weight increased by 64% and 21% for every 100% increase in H and D respectively; a ratio of 3:1.

1) *Bite depth* $= 0.989(\pm 0.111)H - 0.012\ (\pm 0.004)\ H^2 - 0.317\ (\pm 0.099)H \times D - 0.103$
$r^2 = 0.96^{***}$ *residual d.f. = 39*

2) *Bite area* $= -2.234(\pm 0.478)H - 62.140(\pm 11.997)D + 2.715(\pm 0.838)H \times D + 77.565$
$r^2 = 0.78^{***}$ *residual d.f. = 39*

3) *Bite volume* $= 35.997(\pm 5.754)H - 0.763(\pm 0.224)H^2 - 798.881(\pm 231.595)D + 617.048 (\pm 216.676)D^2 - 9.641(\pm 5.139)H \times D + 273$
$r^2 = 0.91^{***}$ *residual d.f. = 39*

4) *Bite weight* $= 6.519(\pm 2.035)H - 0.170(\pm 0.079)H^2 + 9.282(\pm 1.816)H \times D + 0$
$r^2 = 0.92^{***}$ *residual d.f. = 39*

5) *Bite weight (unconfounded)* $= 6.420(\pm 1.932)H - 0.156(\pm 0.073)H^2 + 7.387(\pm 0.770)H \times D + 0$
$r^2 = 0.95^{***}$ *residual d.f. = 17*

DISCUSSION

The leafy region of the sward had a low density (circa. 934 to 3738 leaves/m^2) of large (2.4mg DM/cm) erect leaves. Yet bite weight in relation to H and D was comparable to bite weight on the ryegrass swards of Black and Kenney (1984) indicating that leaf size was not a major factor affecting bite weight (Fig. 5).

The response of deer and sheep to the wide range of H and D variation was very similar. However, the bite volume of sheep was 12% larger than for deer (P= 0.0564); a difference reflected in bite area and bite weight (10-11%; NS) but not bite depth. These trends may have reflected the 9% larger incisor arcade widths of sheep.

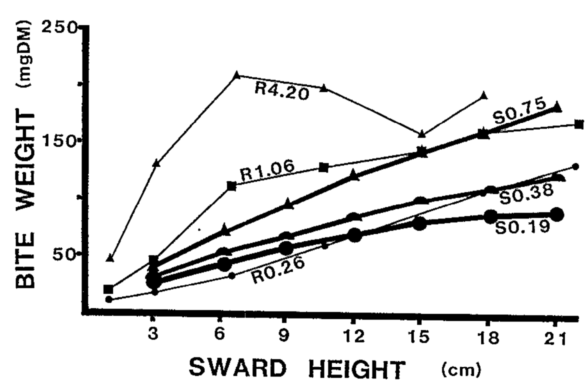

FIG 5 Bite weight in relation to leafy sward height and bulk density, of young deer and sheep (combined) on sorgum swards (S) (0.19, 0.38, 0.75 mg DM/cm^3) compared with sheep on artificial ryegrass pastures (R) (0.26, 1.06, 4.20 mg DM/cm^3) (Black and Kenney 1984).

Bite Depth

Previous work has demonstrated a strong relationship between H and bite depth (Mursan *et al.*, 1989, Burlison *et al.*, 1991), yet only the current experiment and that of Black and Kenney (1984) using very controlled sward conditions have been able to measure the smaller negative effect of D on bite depth.

Sheep frequently penetrated to about half the depth of the leafy zone of the natural grass swards (Burlison, 1987); similar to the bite depth/height ratio for the tall dense, sorgum (55-65%) or artificial ryegrass swards (circa. 50-60%, Black and Kenney, 1984). This may indicate, animals adjusting their bite depth in relation to the depth of the leafy, pseudo-stem free zone of the sward, as suggested by Barthram (1981). In contrast, although the bite depth/height ratio for cattle was similar, at 50-57% on 5 and 10 cm early spring ryegrass pastures, they grazed both heights to below the pseudo-stem level (Mursan *et al.*, 1989).

It is uncertain whether the bite depth/height ratio declines with increasing H alone on leafy swards, as increasing H was confounded with increases in leaf rigidity and shear strength. Further, Milne *et al.* (1982) found that the bite depth/height ratio of sheep on ryegrass white clover swards increased with height; possibly reflecting either selection by the sheep for white clover, or the proportionally deeper stem-free leafy zone with increasing height.

Presumably the small confounded increases in D with H had little effect on the bite depth/height ratio which declined only 7% on average for every 100% increase in manipulated D.

Bite Area

Burlison *et al.* (1991) found no relationship between bite area and H or D, yet Mursan *et al.* (1989) found that the bite area of cattle remained constant as H increased from 5 to 15cm; trends similar to those on D0.75 swards; where bite area was circa. 30 cm^2 for all heights. This is close to the maximum described for sheep (33.0 or 35.5 cm^2) by Black and Kenney, (1984) or Burlison *et al.* (1991), respectively.

In contrast with the D0.75 swards, on D0.38 and especially D0.19 swards, bite area was very large on short swards but declined with increasing H (Fig. 2). When eating short, low density swards animals tended to rapidly nip off the sparse, soft leaves; an action that was less distinct than the obvious head jerks associated with grazing denser and/or taller swards where leaf density and/or strength were greater respectively. Also 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 probably underestimated, and therefore bite area, bite volume and bite weight overestimated for short low density swards.

Further, the greater the penetration of the leafy zone, the greater the tendency for leaves to become clustered as they converged on the stem of each plant. Thus, gaps were formed between groups of leaves in the lower stratum of lower density swards (by the removal of rows or rows and columns of plants), but not for D0.75 swards. This probably reduced bite area on taller, low density swards.

Consequently, we suggest that bite area trends for the two lower density swards may reflect an overestimation of bite area on shorter swards combined with bite area being limited by clumping near the base of taller swards. By comparison bite area on the denser, spatially uniform D0.75 swards would more closely reflect bite area in relation to H.

Evidently, the increase in leaf shear strength and density with increasing H was insufficient to reduce bite area even on D0.75 swards; suggesting that the animals ability to gather leaves into the mouth rather than biting effort (Hodgson, 1985) was limiting.

Bite Weight

Trends for bite weight on the sorgum swards most closely resembled those for the low density (0.26 mg DM/cm^3) ryegrass swards (Fig. 5); but did not show the very rapid increase in bite weight up to 6 cm evident for ryegrass swards with a bulk density of 1.06 mg DM/cm^3 or more. These differences may reflect the low densities of the sorgum swards as well as the large bite areas achieved at 3cm. Further, bite weight kept increasing with H up to 21 cm or 22 cm for all bulk density levels except on the very dense ryegrass sward (4.2 mg DM/cm^3) where bite weight peaked at a height of only 6cm. This indicates that for low to moderate bulk densities, animals can keep increasing bite weight up to high levels of H (probably via bite depth); while at extremely high levels of D, maximum bite weight can be reached on short swards, presumably due to restricted bite depth (Fig. 5).

The slope for bite weight (Fig. 4) began to plateau on taller sorgum swards probably reflecting in part the increasing rigidity of leaves near the base of taller swards limiting bite depth rather than being purely an effect of H.

A strong correlation between herbage mass and bite weight was evident in the current experiment ($r = 0.95$, $P>0.001$) and that of Black and Kenney (1984); but not for the 14 grass swards examined by Burlison *et al.* (1991). This indicates the need to clarify the interactive effects of other sward variables along with those of H and D.

Despite an increase in bite volume with declining bulk density (Fig. 3), Figure 4 shows that this increase was too small to maintain bite weight; which declined by 21% on average for every 100% decrease in bulk density. The antagonistic effect of bulk density on bite volume and grazed stratum bulk density help explain why firstly, large changes in D must occur to markedly alter the slope of bite weight in relation to H (Figs. 4 and 5), and secondly why H had the dominant role in determining bite weight.

CONCLUSION

On average bite volume increased twice as much with H (via bite depth) as it did decrease with a proportional increase in D (via bite depth and bite area). Reflecting this negative effect of D on bite volume, an increase in H had on average 3 times as much affect on the resultant bite weight as did a proportional change in D. Thus for these low to moderate bulk density swards, H almost entirely determined bite depth and largely determined bite volume and bite weight.

The study demonstrated that red deer, a relatively new agricultural species, responded in a similar manner to sheep to a wide range of leafy sward heights and bulk densities. Further it adds to the findings of key previous studies such as Black and Kenney (1984) by describing a wider range of bite parameters; and that of Burlison *et al.* (1991) by reducing the amount of confounding variation associated with H and D variation.

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