
VOLUME 62 2002

The influence of sward structure on peak bite force and bite weight in sheep

T.P. HUGHES, A.R. SYKES, D.P. POPPI AND J. HODGSON[1]

Animal and Veterinary Sciences Group, Lincoln University, New Zealand.

ABSTRACT

An upper limit to the force animals exert to sever a bite maybe important in maintaining grazing momentum. Structural strength of accessible pasture components would then determine bite dimensions and weight.

Pure perennial ryegrass turfs (surface area $0.1m^2$ x 0.1m soil depth), were manipulated by clipping to produce 3 pasture heights (5, 10 and 15cm) x 3 sward structures (varying in leaf to pseudostem ratio and bulk density). Six sheep grazed 4 turfs fixed to a force plate of each height and bulk density. Mean peak bite force, bite weight, bite depth, bite area, bite volume and grazed stratum bulk density were calculated.

Peak bite force increased with sward surface height but significantly so only between 10 and 15cm. Sward structure had no effect except on the 5cm sward treatment with the highest grazed stratum bulk density. Bite depth and bite weight increased with pasture height and were not influenced by sward structure at a constant height. Bite area was similar at all sward heights, but decreased as grazed stratum bulk density increased. On short swards, proximity to the ground restricted bite depth and bite weight rather than peak bite force. Low bite weights per newton bite force may constrain bite depth and weight rather than absolute peak bite force.

Keywords Sheep, turfs, intake rate, bite weight, bite dimensions, perennial ryegrass, peak bite force.

INTRODUCTION

To maintain grazing momentum it is conceivable that an upper limit has evolved for force that an animal species exerts in prehension (peak bite force). Such a mechanism would avoid grazing fatigue from the exertion of variable bite forces and maintain a grazing rhythm, a consistent rate of jaw movement/minute of grazing time (harvesting plus mastication bites), regularly observed when sheep graze temperate pastures (Penning *et al.*, 1991). Bite dimensions of the grazing animal would in turn depend on the tensile strength of the pasture components within the horizon being grazed so that bite force was constrained below the upper limit. If shear forces predominate in prehension then evolution has served large grazing ruminants badly as scissor-like matching incisors would be far more effective as the grazing process would require only the positioning of the head and not the extensive subsequent movement, consistent with tensile breaking. In addition the biomechanical properties of grass make it well suited to severing by tensile force alone (Vincent, 1982; 1983). Teeth may function as an edge over which to crease or bend leaves. Tensile strength of ryegrass leaf was significantly reduced when it was bent at the tip of the beak by grazing geese (Bignall, 1984). Shear strength of ingested plant material and/or its' volume may determine the ratio of mastication to prehending bites. Bite area, the area of the undisturbed pasture covered by a bite, of sheep grazing temperate pastures where variation in height and density were not confounded, decreased with increasing bulk density of leaf (Black and Kenney, 1984; Burlison and Hodgson, 1985) and pasture height (Burlison and Hodgson, 1985). In such circumstances peak bite force may constrain bite area as plant cross sectional area increases with bulk density and the tensile strength of leaves and associated pseudostem could be expected to increase with pasture height. Provided prehension relies predominantly on tensile fracture, force to sever a bite depends on the tensile strength/unit cross sectional area of the plant components within the bite area. A proportion of the 2 to 3 fold greater intake rates of clover to ryegrass (Kenney and Black, 1985) may also be related to the lower tensile strength of the legume. In the current study sheep grazed a series of turfs fixed to a force plate

[1] Department of Agronomy, Massey University, Palmerston North, New Zealand.

so that the relationships between the force to sever individual bites, bite dimensions, bite weight and intake rate could be studied. Pasture treatments were designed to vary the tensile strength of the pasture surface by altering the leaf to pseudostem ratios at 3 pasture heights.

MATERIALS AND METHODS

Six healthy Scottish black-face hoggets, sound of foot and mouth and of similar age and live weight (63.6 ; 2.1kg) were selected from a pool of eight animals and trained for at least 5 days to graze turfs indoors. In early summer, eight weeks prior to the start of the trial, 216 ryegrass (*Lolium perenne*) turfs (area 0.1m2, soil depth, 0.10m), 72 at each of three heights (5, 10 and 15cm, measured with a HFRO sward stick) were carefully cut from a silage aftermath using a grid guide and wedged into polystyrene boxes and packed with soil, as necessary, to produce an even ground surface. All harvested turfs received 2 dressings of nitrogen (equivalent to 60kgN/ha), one immediately after harvesting and the other 3 weeks prior to grazing. The 72 turfs at each height were divided randomly into 3 groups of 24. One group was maintained at the harvested height by regular clipping (M), the second cut 5cm below the harvested height and allowed to regrow to the harvested height (G), while the third was permitted to grow 5cm beyond the harvested height and cut back to the desired height just prior to grazing (C). A rectangular grid (60 x 40cm) mounted on adjusTable tripod legs was positioned at the desired height above the soil surface of the turf when trimming or cutting was required. Stiff wires were then threaded through guide holes at 2cm intervals from one side of the grid to the other causing a minimal disturbance to the pasture so that material above the wire could be removed by clippers and a vacuum. All turfs were stored in a green house and trimmed and watered as required. Spare turfs of each height and pasture treatment were prepared and used to train animals and familiarize staff with the force measuring equipment for 2 weeks prior to the trial. The six sheep were blocked hierarchically into two groups of three, of similar mean liveweight. Pasture treatments consisted of a 3 x 3 (height x clipping) factorial replicated four times to each of the two blocks of three sheep throughout six days. Each of the six days were split into 6 equal periods and the sheep were fed within their block in the same sequence within each period to minimize confounding due to time of grazing, time since last grazing and level of satiety on grazing behaviour. Animals were not fasted pregrazing as a maintenance quality pelleted ration and chaffed hay were available *ad libitum* at all times.

Measurements

Prior to grazing, the boxed turfs were fixed to a standard Kistler force plate (Kistler 2581, Kistler Instrumente Ag, Eulachstr. 22, Postfach 304 Ch-8408 Winterhur, Schweiz) by an overlapping top plate that encroached 2cm in from the perimeter of the turf and was fixed down tightly with wing nuts. Technical specifications of the force plate have been described in detail by Scott (1985) and Webb and Clark (1981). A computer integrated the resultant forces at 0.002s intervals during grazing in both horizontal (*x* and *y* direction) and vertical axes (*z* direction). An algorithm which identified genuine bites, (where at least two successive records showed resultant forces of greater than one newton) eliminated the vast number of records between bites. Smoothed peak force (1/3{ f_{xyz}peak + f_{xyz}peak-1 + f_{xyz}peak+1}) for each identified bite was calculated.
Prior to grazing all turfs were trimmed as uniformly and close to the desired height as possible using the tripod grid described above and weighed to the nearest 0.1g. A second similar turf was also immediately weighed and the time noted so that insensible weight loss (Wins) during the grazing period could be calculated. Grazing commenced during the trial period at 0800h and was generally completed by 1800h. Turfs were grazed in two 10 second grazing bouts (run 1 and 2) as the computer was incapable of handling more than 10 seconds of data at a time. Prehending bites (BN) were recorded by two observers independently and checked against a video record of the grazing.

At the completion of grazing, the turf was detached from the force plate, reweighed (W_2) and the elapsed time since first weighing (W_1) noted. The paired ungrazed turf was also weighed again. Grazed stratum bulk density (GSBD) was calculated by setting the grid at the mean grazed height, (the mean height of 40 grazed plant units (H_2)) and removing all grass above this height with cutters and a vacuum system. Grazed

TABLE 1 Mean bite depth (BD), bite area (BA), bite weight (BW), intake rate (IR), and bite weight/N peak bite force (gDM/N) of sheep grazing ryegrass pasture turfs of three pasture heights and clipping treatments. Means without a letter or with the same letter are not significantly different.

	Height			Pasture treatment			
	5	10	15	C	G	M	S.E.D.
Pasture height (cm)	56.4	102.2	146.3	104.1	98.8	102.1	1.39
Bite depth (cm)	2.1^{a}	3.9^{b}	6.9^{c}	4.2	4.5	4.2	0.019 ***
Bite area (cm^2)	18.6	18.5	17.2	16.5^{a}	19.3^{b}	18.5^{b}	0.86 **
Bite weight (gDM)	0.088^{a}	0.095^{a}	0.179^{b}	0.124	0.113	0.126	0.007 ***
Intake rate (gDM/min)	6.7^{a}	7.1^{a}	12.6^{b}	9.1	8.2	9.1	0.58 ***
Bite weight/N (gDM/N)	0.012^{a}	0.013^{ab}	0.015b	0.013	0.013	0.014	0.001 **

(df = 129)

stratum bulk density was the difference between the original turf weight pre grazing (W_1) and the weight of the turf trimmed to the grazed height (W_3), (corrected for insensible weight losses), divided by the turf surface area and the mean bite depth. An ungrazed representative sample of the pasture removed from the grazed stratum was kept for DM determination. Mean bite weight and dimensions were then calculated as described by Mursan *et al.*, (1989) where :-

Fresh bite weight (FBW) g = $(W_1 - W_2 + Wins)/(BN)$
(BN = number of prehending bites)
Bite weight (BW) gDM = FBW * (DM% in grazed stratum)
intake rate (IR) gDM/min = BW * BN * 60/GT
(where GT was grazing time in seconds)
Bite depth (BD) cm = $(H^1 - H_2)$
Grazed stratum bulk = $((W_1 - W_3 + Wins)/(BD)*TA))*DM*1000$
density (GSBD) mgDM/cm^3
(Where TA = Turf area, 1000 cm^2)
Bite volume (BV) cm^3 = BW * 1000/GSBD
Bite area (BA) cm^2 = BV/BD

Statistical Analyses

Periods, animal group and animals were blocked, and day, run and height*structure considered initially as treatments. As there were no significant differences between runs in mean impulse (i.e. the integration of force x time for each bite), mean maximum bite force and the standard deviations of individual mean maximum forces, the force data for the two runs were combined. On day 3 sward height and bite volume, and on day 5 GSBD, were significantly higher than on the other 5 days of the trial. Data were not adjusted for these unexplainable day effects.

RESULTS AND DISCUSSION

To date while bite weight has been related to pasture structure in many studies (Allden and Whittaker, 1970), bite dimensions have not been widely measured (Black and Kenney, 1984; Burlison, 1985). The current trial is unique in that in addition to the great degree of experimental control which allowed dimensions of the

TABLE 2 Mean grazed stratum bulk density (GSBD), bite volume (BV), and peak bite force (PBF) for sheep grazing ryegrass turfs of three heights and clipping preparations. Means without a letter or with the same letter are not significantly different.

	Height x	pasture treatment interactions			
		Height	Pasture treatment		
		C	G	M	SED
Grazed stratum bulk density (mgDM/cm^3)	5	3.28^{d}	1.92^{b}	2.51^{c}	0.095^{***}
	10	1.68^{b}	1.17^{a}	1.43^{a}	
	15	1.85^{b}	1.41^{a}	1.70^{b}	
Bite Volume (cm^3)	5	34.9^{a}	41.3^{a}	37.9^{a}	7.59 ***
	10	62.0^{b}	75.6^{b}	68.7^{b}	
	15	95.4^{c}	136.7^{c}	115.0^{d}	
Peak bite force (N)	5	10.7^{b}	6.4^{a}	7.5^{a}	1.04 ***
	10	8.0^{a}	6.9^{a}	7.7^{a}	
	15	13.1^{c}	14.1^{c}	14.0^{c}	

(df = 129)

average bite to be calculated, the force exerted to sever each grazing bite was also measured. Swards of the desired surface height (H) and a range of grazed stratum bulk densities (GSBD) were produced. Considerable variation (180%)in GSBD (an indirect indicator of sward bulk density), was achieved among pasture treatments and heights, but within a height such differences among pasture treatments were smaller (70, 44 and 36% for 5, 10 and 15cm swards respectively (Table 1 and 2). Variations in sward height were not independent of GSBD (Table 3) as they were in the trials of Black and Kenney (1984) and Burlison *et al.*, (1991). Independent effects of height or density on intake parameters and bite dimensions could not therefore be measured. However the primary objective of producing sward variation in height and bulk density to study the effect of structural strength of accessible pasture components on bite force and bite dimensions was achieved. Pasture treatments produced swards with considerable variation in leaf size, spatial arrangement of leaf, pseudostem height and leaf to pseudostem ratio.

Bite Force

There was a significant height x pasture treatment interaction for peak bite force (Table 2). Pasture treatment had no effect on mean peak bite force (PBF) with the exception of 5cm C swards. While PBF increased with pasture height only the 82% increase between 10 and 15cm swards was significant. Although mean PBF on 5cm C pasture treatments was significantly higher than all other 5 and 10cm swards it was significantly lower than the mean for 15cm swards (13.7N). A higher GSBD on the 5cm C pasture treatments when compared to all other swards may have enabled the sheep to prehend more plant material within the bite catchment thus increasing the PBF. Sward height, grazed stratum bulk density and the number of bites on the force plate during grazing (FBN), while highly significant variables, explained very little of the variation in PBF (equation 1).

TABLE 3 Correlation matrix showing the relationship between sward and intake parameters for sheep grazing ryegrass turfs where GSBD, is grazed statum bulk density (gDM/cm³); BD, is bite depth (cm); BA, bite increase (cm²); BV, bite volume (cm³); BW, bite weight (gDM) and PBF, peak bite force (N).

	Height	GSBD	BD	BA	BV	BW	FRC
GSBD	-0.39 ***						
BD	0.88 ***	-0.38 ***					
BA	-0.09	-0.22 ***	-0.23 ***				
BV	0.77 ***	-0.47 ***	0.79 ***	0.33 ***			
BW	0.67 ***	0.12	0.67 ***	0.11	0.70 ***		
FRC	0.48 ***	-0.02	0.48 ***	0.02	0.45 ***	0.53 ***	
PM	0.63 ***	0.14	0.73 ***	-0.44 ***	0.39 ***	0.79 ***	0.47 ***

(PM is pasture mass, kgDM/ha, within the grazed horizon)
(df for comparison = 176)

(1) PBF=6.8(±1.1) H - 0.69(±0.13) FBN + 1.23(±0.48) GSBD + 6.15 (±2.2)

r^2 = 0.34***, residual df = 173

Peak bite force was significantly correlated with BW (Table 3) which suggests sheep were prepared to exert greater force where sward conditions ensured a larger bite. Mean bite weights/N PBF increased with pasture height but were not effected by pasture treatment (Table 1). No other published estimates of PBF could be found for comparison purposes, however PBF was in the range predicted (5 - 40n) from tensile strength of ryegrass leaf (Burlison, 1987) and plant units severed/bite, provided grazing involved predominantly tensile forces. As sward height decreased, the parallel decline in bite weight could not be explained by a reduction in bite dimensions to maintain PBF below a summit value as originally proposed.

Bite Dimensions

Bite weight is the product of bite volume (BV) and GSBD of plant material severed. Bite volume in turn is the product of bite depth (BD) and bite area (BA). On short swards Illius and Gordon (1987) suggested, from their model, that bite depth was the major constraint to intake. Bite depth in the current trial was positively correlated with pasture height and negatively correlated with GSBD. Fitting a PBF term in the best fit linear regression reduced the variation accounted for in equation 2, possibly because H and PBF were positively and significantly correlated (Table 3).

(2) BD = 5.23 (±0.18) H - 2.12 (±1.07) GSBD - 7.05 (±1.82) (r± = 0.79*** residual df = 173)

Burlison *et al.* (1991) reported a positive relationship between BD and H but found none with GSBD, unlike Black and Kenney (1984) and the current trial where BD declined as GSBD increased. The concept of a summit PBF could not explain why sheep grazing the 10cm swards did not increase BD as bite forces were some 80% below those on 15cm swards (Table 2). Proximity to soil and dead material may be sufficient deterrent. Bite area was not significantly correlated with H (Table 3) but negatively and significantly correlated with GSBD. As GSBD of pasture treatments increased BA decreased (Table 1) as previously reported by Black and Kenney (1984). The variation in BA for all heights and pasture treatments (16.5 - 19.3cm² Table 1) in the current trial is considerably smaller than that recorded by Black and Kenney (1984) and Burlison *et al.* (1991), of 8.6 - 33.0 and 9 - 35.5cm² respectively. In the current trial the range of sward GSBD (1.17 - 3.28mgDM/cm³) was narrower but higher than that of Burlison *et al.* (1991) (0.44 - 2.04mgDM/

cm^3) and only represented a small portion of the range of Black and Kenney (1984) (0.46 - 4.23mgDM/cm3). Bite area was not constrained by peak bite force on the 5 and 10cm swards (Table 1) which suggests sheep had difficulty gathering and prehending plant material. There was a significant height x pasture treatment interaction for bite volume (BV) confined solely to the 15cm swards. Bite volume increased with pasture height. On 15cm swards bite volume increased as GSBD decreased, largely a reflection of pasture treatment effects on BA, as the other component of BV, BD was not effected.

Bite Weight

Bite weight was positively correlated with BV but not GSBD (Table 3), and increased with H (Table 1). However GSBD was a significant term in the best fit regression between BW and sward variables (equation 3). The positive coefficients for both height and GSBD indicates their effect on BW is additive as reported by Black and Kenney (1984) and Burlison *et al*., (1991).

(3) $BW = 0.013 (\pm 0.001) H + 0.024 (\pm 0.003) GSBD - 0.059 (\pm 0.011)$
($r^2 = 0.61^{***}$ residual df = 173)

On the sward treatment with the lowest GSBD (treatment G, Table 2), there was a tendency for both bite depth and bite area to increase, thus maintaining BW and a constant PBF peculiar to that sward height.

CONCLUSIONS

Bite weight at low pasture heights was not constrained by peak bite force, but rather the animals ability to gather and prehend pasture and to increase bite depth as suggested by Illius and Gordon (1987). On the 15cm swards sheep maintained a similar peak bite force but adjusted bite dimension, primarily bite volume dependent on sward bulk density. On the taller swards sheep exerted greater peak bite forces provided bite weight increased. Low bite weights/N bite force may constrain bite weight rather than peak bite force and partially determine bite dimensions. Pasture height was the best single predictor of bite weight.

ACKNOWLEDGEMENTS

The trial work in this paper was performed at the Scottish Farm Building Research centre in Aberdeen, Scotland, while the major author was on sabbatical leave at Hill Farming Research Organization in Edinburgh.

REFERENCES

Allden, W.G.; Whittaker, I.A.McD. (1970). The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* **21**: 755-766.

Bignall, M.R. (1984). Interactions during grazing with the bill of the Barnacle goose and grass. *Thesis. Ph.D.* University of Reading, United Kingdom.

Black, J.L.; Kenney, P.A. (1984). Factors affecting diet selection by sheep. II. Effects of height and density of pasture. *Australian Journal of Agricultural Research* **35**: 565-78.

Burlison, A.J. (1987). Sward canopy structure and ingestive behaviour in grazing animals. *Thesis. Ph.D.* University of Edinburgh, United Kingdom.

Burlison, A.J.; Hodgson, J. (1985). The influence of sward structure on the mechanics of the grazing process in sheep. *Animal Production* **40**: 530-582.

Burlison, A.J.; Hodgson, J.; Illius, A.W. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass and Forage Science* **46**: 29-38.

Illius, A.W.; Gordon, I.J. (1987). The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**: 989-1000.

Kenney, P.A.; Black, J.L. (1985). Effects of simulated sward structure on the rate of intake of subterranean clover by sheep. *Proceedings of the Australian Society of Animal Production* **16**: 251-254.

Mursan, A.; Hughes, T.P.; Nicol, A.M.; Suguira, T. (1989). The influence of sward height on the mechanics of grazing in steers and bulls. *Proceedings of the New Zealand Society of Animal Production* **49**: 233-236.

Penning, P.D.; Parsons, A.J.; Orr, R.J.; Treacher, T.T. 1991. Intake and behaviour responses of sheep to changes in sward characteristics under continuous stocking. *Grass and Forage Science* **46**: 15-28.

Scott, G.B. (1985). Designing floors for animal's feet. *Farm Building Progress* **82**: 27-32.

Vincent, J.F.V. (1982). The mechanical design of grass. *Journal of Material Science* **17**: 856-860.

Vincent, J.F.V. (1983). The influence of water content on the stiffness and fracture properties of grass leaves. *Grass and Forage Science* **38**: 107-114.

Webb, N.G.; Clark, M. (1981). Livestock foot-floor interactions measured by force and pressure plate. *Farm Building Progress* **66**: 23-66.