Final Report 4170

Optimising sward structure and herbage yield for the performance of dairy cows at pasture.

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Contents

Summary

- **The basic unit of intake is the bite.** The total daily intake of grazed grass is determined by the number of bites taken and the weight of the average bite. In this project the focus was on sward structure (architecture) and its effects on bite volume and weight. There were two objectives. The first was to determine the plant growth mechanism responsible for variations in sward structure. The investigation was carried out at The Queen's University in Belfast and involved microscopic study of leaves from plants grown under controlled conditions. The second objective, to determine how bite volume and mass was affected by differences in sward structure was a field study using fistulated cows and was done at Moorepark.

- The grass plant is almost entirely composed of leaf and an understanding of the growth of the individual leaf is of central importance in understanding how sward structure is controlled. The growth of a leaf results from cell division and cell enlargement in a short section at the base of the leaf. In the present study the light environment of the developing leaf on an intact tiller was altered by vertical incision of the tiller's sheath tube and the effects on the kinematics of cell processes were measured. The measured differences in leaf morphology and rate of development were the indirect result of treatment effects on the location and size of the zone of cell expansion and possibly also on the rate of cell multiplication. The results suggest that these zones exercise central control over sward structure by controlling individual leaf morphology and, through their effect on the rate of leaf development, on leaf appearance and tiller production rates also. An ability to control the zones of cell activity would have considerable practical significance.

- Bite mass is the dominant factor determining short-term intake rates. Bite mass is the product of bite volume and the bulk density of the herbage in the bite volume. The grazing animal may adjust bite volume by varying the depth and/or the area of bite. Quantification of the inter-relationships between these bite parameters and bite mass has been hampered by the difficulty of measuring bite characteristics under natural field conditions. The first objective of this part of the project was to develop a field technique for measurement of bite mass and bite dimensions. The technique employed pre- and post-grazing measurements on labelled tillers. The second objective was to determine the effect of sward structure, specifically sward density, on bite characteristics using the technique. The third objective was to compare the bite characteristics of a range of grass varieties.

- There were four experiments. In the first experiment a range of sward bulk densities was obtained by varying the management of the swards in the weeks prior to the experiment but the pre-treatments resulted also in a range of sward heights and the height effect on bite mass dominated the results. In the second experiment a range of sward bulk densities was obtained by manual removal of tillers from the swards immediately before grazing and there was a significant effect on bite mass. In the third and fourth experiments six grass varieties were sown to give a range of bulk densities. There were two diploid perennials (Glen and Aberelan), two tetraploids (Twins and Green Isle), a hybrid Italian/Perennial ryegrass (Polly) and an Italian ryegrass (Multimo). Bite mass was least in the Italian and in the hybrid which were the least dense varieties (Tables 1 and 2). In the subsurface bites the trends were similar(Table 3).

- General relationships between bite mass, bite dimensions, sward height and density were established. Bite mass increased as both height and density increased. However, the height effect was clearly more important than the density effect. The relative importance of bulk density increased as the height of the sward decreased. Bite volume increased as height increased but tended to decrease as density increased. This explained the relatively smaller effect of density compared to height. The trends in volume reflected parallel trends in bite depth and area. The six grass varieties differed in bulk density but not in height. In surface bites the bite bulk density was less in the Italian variety (Multimo), in the Italian/Perennial Ryegrass hybrid (Polly) and in the diploid Aberelan than in the two tetraploids (Green Isle and Twins) and the diploid Glen. Varietal differences in bulk density were due to differences in both tiller number and individual tiller weight. The results indicate that, insofar as higher bite mass is related to higher bulk density, breeding for tiller density or for heavy tillers represent alternative routes to increased bite mass. In sub-surface bites the order of bite bulk density was maintained in all varieties except Green Isle. Green Isle fell to an intermediate density and this suggests that, in this variety, the herbage tended to be concentrated in the upper horizons of the profile.

Introduction

Milk yield per cow has become more important than yield per hectare since the introduction of milk quota limitations on production from dairy farms. It is a recognised feature of the milk production system typically practised in Ireland that annual milk yield per cow is restricted by more than 10% of the animal's potential. With the introduction in recent years of cows bred for greater milk yield the restriction assumes greater importance.

Milk yield is directly related to feed intake. In Ireland, grazed grass is the main source of feed during each lactation so that the identification of the factors that control intake rate when the cow is grazing is critical. The basic unit of intake is the bite. The total daily intake of grazed grass is determined by the number of bites taken and the weight of the average bite. Typically the bite has a volume of approximately one litre and weighs approximately one gram (dry weight). In this project the focus was on sward structure (architecture) and its effects on bite volume and weight. There were two objectives. The first was to determine the plant growth mechanism responsible for variations in sward structure. The second objective was to determine how bite volume and mass was affected by differences in sward structure.

The project was funded by the Walsh Fellowship Programme and was a joint venture between Teagasc, Moorepark and The Queen's University, Belfast. Work was done at both locations. The investigation of the mechanisms of sward structure formation was mainly done in Belfast. The investigation involved microscopic study of leaves from plants grown under controlled conditions. The study of the effects of structure on bite characteristics was a field study using fistulated cows and was done at Moorepark. Throughout, attention was restricted to Perennial Ryegrass in the vegetative condition.

3. The Control of Sward Structure

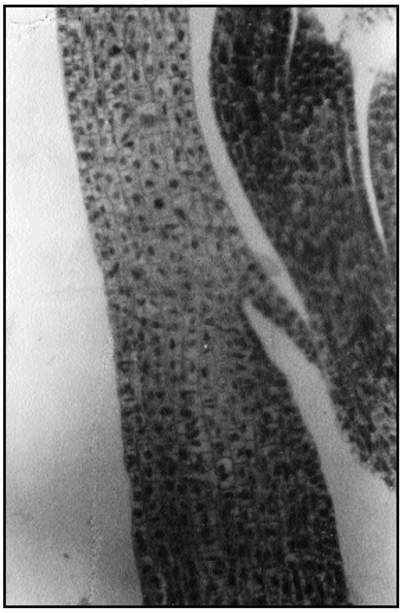
3.1 Sward structure and tiller growth

The features of a sward that make up its structure are tiller density, the vertical separation between, and the depths of the upper leaf lamina and lower leaf sheath layers, the length and width of the laminae and the number of laminae on a tiller. The vegetative grass tiller is almost entirely composed of leaf. The lower part of each leaf forms a rolled tube (the sheath tube) and the upper part forms a flat blade (the lamina). A small membrane called the ligule marks the separation between sheath and lamina (Fig.2) Picture 1.

The stem, which produces the leaves, is very small and is located at soil level. Successive leaves grow at the stem apex and each new leaf appears through the tube of the next older leaf. The tube of sheaths form the "stalk" of a tiller on which the leaf blades are carried (Fig.1). A new tiller bud is formed in association with each new leaf but the initiation of growth in the tiller bud is delayed until the leaf has completed its growth. Typically, in Perennial Ryegrass there are three live laminae on each tiller. From the relative constancy of this number it has been deduced that leaf initiation and death is co-ordinated. As new tiller-bud formation is also co-ordinated with leaf initiation it is obvious that an understanding of the growth of the individual leaf is of central importance in understanding how sward structure is controlled.

3.2 Leaf growth and cellular processes

The growth of a leaf results from cell division and cell enlargement in a short section at the base of the leaf - at the join between the leaf and the stem (Fig.2). Extension of the leaf depends first on enlargement of lamina cells and later on sheath cells. When the lamina is fully emerged from the tube, cell enlargement ceases throughout the leaf.



PICTURE 1: Longituidinal Section of a developing leaf showing early ligule development (Lamina and sheath cells) (x150)

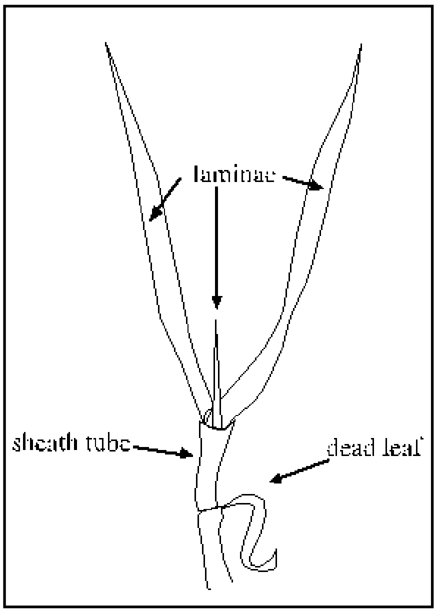


FIG 1: TILLER

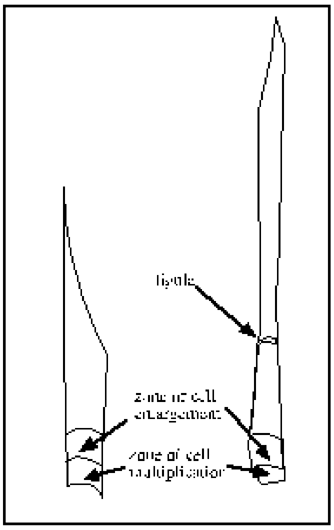


FIG 2: LEAF CELL ZONES

3.3 Experiment

The results of several studies have suggested that exposure of the leaf tip to light is important in controlling the dynamics of cell multiplication and growth at the leaf base. In the present study the light environment of the developing leaf on an intact tiller was altered by vertical incision of the tiller's sheath tube and the effects on the kinematics of cell processes were measured. The method employed allowed all conducting tissue of the sheath and lamina material above the incision to remain intact so that normal supply of photosynthate was not affected. There were three treatment incision depths - 0, 0.3 and 0.7 of the sheath tube length. By destructive dissection at five consecutive occasions, the temporal pattern of blade and sheath development, of the spatial distribution of cell elongation within the leaf and of the rates of cell elongation were measured on a leaf in each treatment. The first dissections were done on the day the treatments were imposed and at 3, 6 12 and 24 days subsequently.

The experimental leaf was the youngest developing leaf which was just above the shoot apex at the start of the experiment. At each harvest the experimental leaf was cut from the apex. The length of lamina and sheath of the leaf was recorded and an impression of the epidermal cells on the adaxial surface was made using dental impression wax. Length of cells in cell columns near the stomata rows on the impression were measured at 1mm intervals from the base of the leaf for the first 10 mm of the leaf length, at 2 mm for the next 10 mm and every 5 mm for the next 20 mm. The remainder of the leaf was divided into five divisions and cell length was measured at each division. The distance of the ligule from the base of the leaf was also measured. Total cell number for each section of leaf between adjacent measurement locations was calculated by dividing the length of the section by the mean cell length of the two adjacent locations.

3.4 Experimental results

Incision treatments reduced the period of leaf development and final length of both lamina and sheath. Treatment effects were evident at three days after treatment when the average leaf length was 71, 46 and 39mm in the control, moderate and severe treatments, respectively. Effects on rates of cell division and cell elongation from the exposure of the tip to light were operating from the earliest stages. In all treatments cell division effectively terminated at or before day 12. On day 12 the development of the leaf in the severe treatment was complete. Between days 12 and 24 leaf length increased in both of the other treatments - due to cell elongation only and in the sheath only. The development of the leaf in the moderate treatment was complete at day 24 but development in the control was not complete as part of the lamina remained within the sheath at the end of the experiment.

Relative elemental growth rate (REGR) in all treatments was concentrated towards the leaf base as expected (Figure 3). The length of the zone was reduced and the peak REGR was displaced towards the leaf base by incision. The peak value of REGR was increased from 0.05 mm mm-1 hr-1 to 0.09 mm mm-1 hr-1 in response to severe incision which suggests that incision caused an increase in the metabolic activity of the lower part of the zone and may have compensated partly for the decrease in the length of the zone. The treatment effects on elongation rate was more evident in the distribution of cell elongation rate (CER) (Figure 4). CER was maintained at greater than 0.005 mm hr-1 across 25 mm from 5mm to 30 mm from the leaf base in the control. In the severe incision treatment the length of the zone was reduced to 5mm.

The reduction in the length of the elongation zone and the reduced rate of cell production observed in response to incision explained the reduction in leaf growth. The displacement of the zone of elongation towards the leaf base and the increased REGR in the basal end of the zone by incision explained the earlier development of the sheath in the severe incision treatment. Displacement of the zone towards the leaf base would result in the earlier entry of sheath cells into the elongation zone. The greater REGR on entry would lead to an enhanced rate of elongation immediately on entry. The reduction of the rate of cell division by incision would be expected to reduce the rate at which sheath cells approach the zone of elongation. The results indicate that the effect of the reduced rate of cell division on the movement of cells towards the elongation zone was more than offset by the zone shift towards the base. Mature cell length in the sheath was approximately 2.5 times the mature length of lamina cells. This reflects the slower rate of passage of cells through the zone as the result of the cessation of production of new cells at the leaf base.

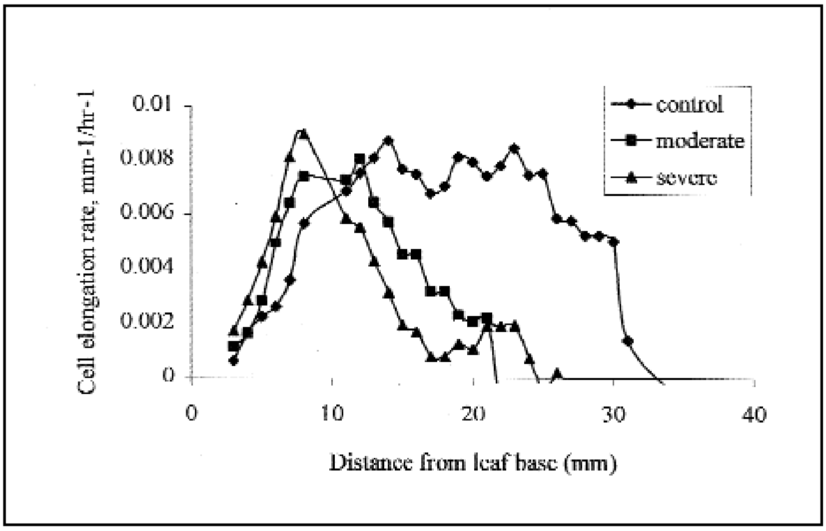


Figure 3 : Relative elemental growth rate (REGR)

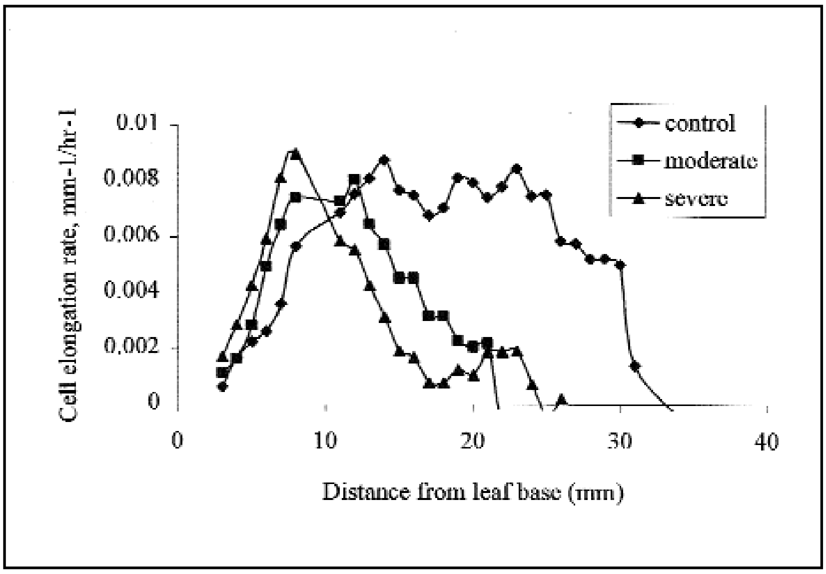


Figure 4 : Spatial distribution of epidermal cell elongation rates (CER) in the elongation zone

A ligule was not discernible in any treatment until the harvest on day 12 but it may be assumed that the ligule existed from before treatments were imposed. Other research has found that ligule cells in Tall Fescue were already formed when the leaf was in the earliest stage of development. Therefore in this study no effect of treatment on the time of initiation of the ligule would be expected. It has been suggested that the leaf tip emergence above the sheath tube coincides with cessation of cell division. In the present experiment the leaf tip was emerged in all treatments at day 3. Although cell division continued until day 12, the rate was decreasing rapidly and the results indicated that the decline in cell division rate may have coincided with leaf tip emergence. The exposure of the leaf tip in the severe treatment occurred earliest and the results indicate that the decline in cell division began earlier. This is significant in regard to the suggested co-ordination of adjacent leaves on the grass tiller. Detailed studies of leaf development have indicated that there is synchronisation between three consecutive leaves. The termination of cell division in a leaf is coincident with initiation of sheath development in the next younger leaf and the initiation of the primordium of the youngest leaf.

The rate of leaf extension is controlled by the rate of cell multiplication and by the rate of enlargement within the zone of cell enlargement. It is also controlled by the length of the zone which determines the duration of cell expansion and the final size of cells. The data suggest that cell dynamics at the leaf base, through their effects on leaf extension rate, may be the basic control of the rate of leaf appearance, of leaf structure and the rate at which new tillers are laid down.

3.5 Field survey of tiller morphology

Comparative analysis of the morphology of tillers collected from field trials showed that morphological responses to different growth conditions could be interpreted in terms of the model of leaf growth described above. For example, a 50% reduction in radiation receipt at the sward surface resulted in a reduction in the number of leaves per tiller from 3.0 to 2.7, an increase in total tiller lamina length from 270mm to 291mm and a shift from a positive to a negative tillering rate. These responses would be predicted by the model. As radiation receipt was reduced, the zone of rapid cell elongation would shift away from the leaf base and it would increase in length. The increase in zone length would lead to an increase in cell size on exit from the zone and to a consequent increase in leaf extension rate and final leaf length. The shift of the zone away from the leaf base would delay the initiation of sheath development, prolong the period of leaf development and, as a result, delay the initiation of new leaves and tillers.

Conclusions

The measured differences in leaf morphology and rate of development were the indirect result of treatment effects on the location and size of the zone of cell expansion and possibly also on the rate of cell multiplication. The results suggest that these zones exercise central control over sward structure by controlling individual leaf morphology and, through their effect on the rate of leaf development, on leaf appearance and tiller production rates also. An ability to control the zones of cell activity would have considerable practical significance. Apart from the demonstrated effects on morphology, digestibility may be affected by changes in cell size and the proportions of cell wall to cell content. In this experiment the zonation was manipulated by altering the light environment of the developing leaf within the sheath tube. The possibility of manipulation by breeding needs to be examined.

4. Sward structure and bite size

Bite mass is the dominant factor determining short-term intake rates. Bite mass is the product of bite volume and the bulk density of the herbage in the bite volume. The grazing animal may adjust bite volume by varying the depth and/or the area of bite. Quantification of the inter-relationships between these bite parameters and bite mass has been hampered by the difficulty of measuring bite characteristics under natural field conditions.

The first objective of this part of the project was to develop a field technique for measurement of bite mass and bite dimensions. The second objective was to determine the effect of sward structure, specifically sward density, on bite characteristics using the technique. The third objective was to compare the bite characteristics of a range of grass varieties. The technique was used in four experiments. There were two bulk density and two grass variety experiments. In each case one of the experiments was carried out in summer and the other in autumn.

4.1 Development of a field method of bite measurement

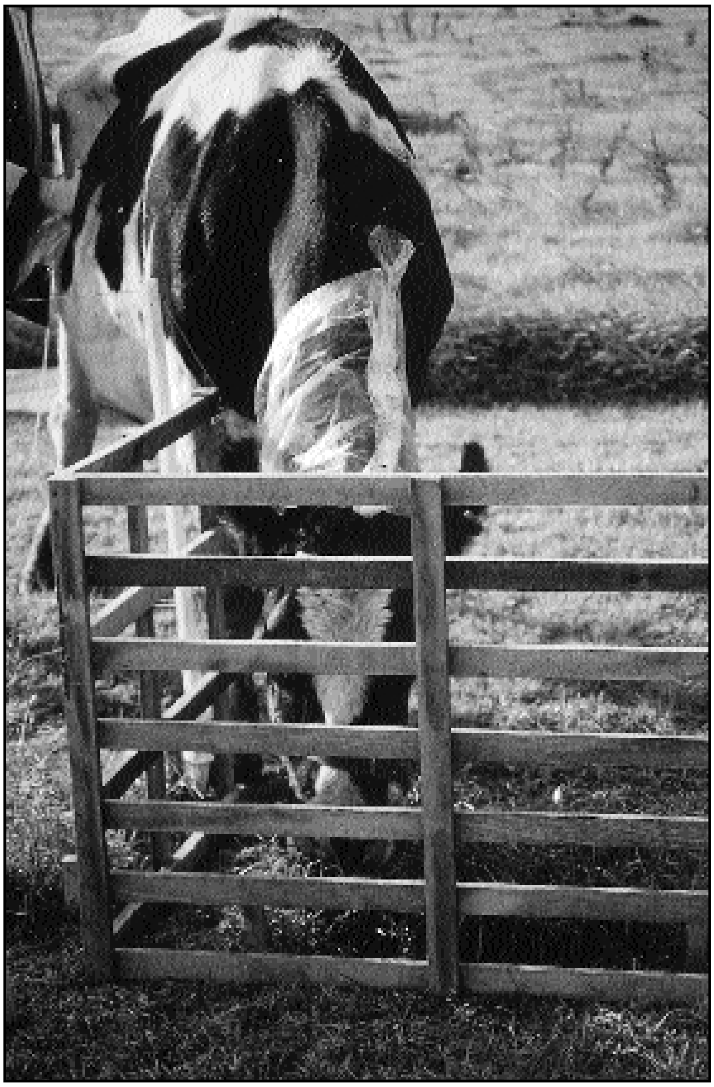
The technique employed pre- and post-grazing measurements on labelled tillers. Sixty four tillers were labelled in 60cm X 60cm plots and the height of each tiller was measured. The labelled tillers were distributed evenly within the plot on a grid. The herbage surrounding the plot was removed by cutting and a light fence was placed around three sides of the plot (Picture 2). A fistulated cow was allowed to remove approximately 25 bites from the plot (Picture 3).

The height removed from each labelled tiller was recorded after grazing. Tillers were classified into height classes and the distribution of weight along the length of tiller was determined for each class using tillers selected from the sward adjacent to the grazing plots before cutting. The amount of herbage removed from a tiller of each class was calculated from the depth removed and the weight per unit length of the section removed.

Sward bulk density and tiller density was also measured in the area surrounding the grazing plot before cutting. The total mass removed was calculated by summing the product of the mean weight removed from a tiller of each class and the number of tillers of that class in the plot area. Bite mass was calculated by dividing the total removed and the number of bites taken. The area of a single bite was estimated by determining the area of the plot occupied by grazed tillers. This was done by placing a grid over the plot after grazing and directly observing the presence or absence of grazed tillers in one centimetre square cells. The herbage recovered from the fistulated cow was used to calculate bite mass independently of the sward measurements. In the study of the bite characteristics of grass varieties the technique was extended to measure the characteristics of bites taken from the sub-surface remaining after the first grazing.

The technique was reasonably successful. The treatments means of the sward estimate of bite mass in the 4 experiments are compared in Figure 5 with the bite mass obtained from the fistulated cows.

PICTURE 2 : A microplot of sward prepared for grazing



PICTURE 3 : The grazing of the microplot sward by a fistulated cow.

4.2 *Effect of herbage density on bite mass*

In the first experiment a range of sward bulk densities was obtained by varying the management of the swards in the weeks prior to the experiment (Table 1). The pre-treatments however, resulted also in a range of sward heights and the height effect on bite mass dominated the results (Table 2). The most clear demonstration of a bulk density effect was obtained in the second experiment where bulk density was the only sward variable. A range of sward bulk densities was obtained by manual removal of tillers from the swards immediately before grazing (Table 1). There was a significant effect on bite mass. In the third and fourth experiments six grass varieties were sown to give a range of bulk densities (Table 1). There were two diploid perennials (Glen and Aberelan), two tetraploids (Twins and Green Isle), a hybrid Italian/Perennial ryegrass (Polly) and an Italian ryegrass (Multimo). Bite mass was least in the Italian and in the hybrid which were the least dense varieties (Tables 1 and 2). In the subsurface bites the trends were similar (Table 3).

Table 1: The morphology of microplot swards before grazing

		Sward			Herbage		
	Treatment	**Bd $g\ mm^{-3}$**	**Tillers m^{-2}**	**Height mm**	**Mass $kgha^{-1}$**	**Leaf fraction**	**Tiller Mass $mg\ mm^{-1}$**
1	High density	0.0021	7581	152	2259	0.53	0.196
	Moderate high density	0.0018	7852	186	2943	0.49	0.202
	Moderate low density	0.0015	7025	222	3064	0.53	0.196
	Low density	0.0022	6312	123	1990	0.58	0.256
2	High density	0.0015	5788	177	2467	0.72	0.241
	Moderate high density	0.0011	5350	171	1649	0.68	0.180
	Moderate low density	0.0011	5275	160	1659	0.71	0.197
	Low density	0.0010	4058	133	1564	0.72	0.290
3	Glen	0.0020	8516	210	4536	0.6	0.254
	Aberelan	0.0017	5592	230	4262	0.5	0.331
	Twins	0.0017	5250	200	4508	0.57	0.429
	Green isle	0.0017	3642	200	4206	0.48	0.577
	Polly	0.0014	4466	240	4291	0.47	0.400
	Multimo	0.0008	1958	210	2255	0.51	0.548
4	Glen	0.0018	7158	170	3432	0.71	0.282
	Aberelan	0.0016	4941	180	3299	0.68	0.371
	Twins	0.0016	4675	190	3137	0.61	0.353
	Green Isle	0.0018	3083	180	3511	0.65	0.633
	Polly	0.0015	3241	170	2809	0.7	0.510
	Multimo	0.0014	2258	190	3163	0.63	0.737

Table 2: The bite dimensions and bite mass of microplot swards

	Treatment	Animal Based Bite Mass g dm	Sward Based Bite Mass g dm	Bite Depth mm	Bite Area mm^2	Bite Density g cm^{-3}	Bite Volume mm^3
1	High density	1.1	1.3	114	5900	0.0017	650
	Moderate high density	1.3	1.8	128	5700	0.0018	710
	Moderate low density	1.5	1.0	159	5200	0.0019	799
	Low density	0.6	0.9	129	6200	0.0008	754
2	High density	1.2	1.3	133	6700	0.0013	918
	Moderate high density	1.0	1.1	124	6000	0.0013	749
	Moderate low density	1.0	1.2	121	5900	0.0014	725
	Low density	0.9	0.7	104	5900	0.0015	610
3	Glen	1.4	1.2	113	8830	0.0014	996
	Aberelan	1.4	1.1	125	10010	0.0011	1260
	Twins	1.4	1.6	124	7550	0.0014	995
	Green isle	1.6	1.7	129	10020	0.0012	1325
	Polly	1.3	1.4	145	8640	0.0010	1259
	Multimo	1.3	0.8	162	9950	0.0008	1627
4	Glen	0.9	0.7	100	8600	0.0010	860
	Aberelan	1.1	1.1	122	6600	0.0011	1016
	Twins	1.0	0.8	113	7700	0.0011	882
	Green isle	1.1	0.8	119	7400	0.0012	889
	Polly	0.9	0.6	139	7400	0.0009	1031
	Multimo	0.7	1.0	183	7100	0.0005	1312

Table 3: The bite dimensions and bite mass of sub-surface bites

	Treatment	Animal Based Bite Mass g dm	Sward Based Bite Mass g dm	Bite Depth mm	Bite Area mm^2	Bite Density g cm^{-3}	Bite Volume cm^3	Sub-Surface Height mm
3	Glen	1.1	0.7	58	8610	0.002558	430	144
	Aberelan	1	0.9	73	9560	0.001605	623	122
	Twins	1	0.8	70	8370	0.002188	457	112
	Green Isle	0.9	0.6	71	9650	0.001978	455	131
	Polly	1	0.9	82	7240	0.002174	460	117
	Multimo	0.5	0.2	75	7240	0.000767	652	85
4	Glen	0.8	0.3	65	6300	0.0019	421	108
	Aberelan	0.8	0.5	75	5000	0.001914	418	106
	Twins	0.8	0.4	63	5000	0.002564	312	88
	Green Isle	0.6	0.3	71	5200	0.001626	369	98
	Polly	0.7	0.3	87	5100	0.001532	457	95
	Multimo	0.5	0.4	84	6400	0.001121	446	88

The data of all four experiments, including the subsurface bite data of experiments 3 and 4, have been compiled (Fig.6) to illustrate the general relationships found between bite mass, bite dimensions, sward height and density. Figure 6a shows that bite mass increased as both height and density increased. However, the height effect was clearly more important than the density effect. There was an indication that the relative importance of bulk density increased as the height of the sward decreased. The explanation for the relatively smaller effect of density is illustrated by Figure 6b.

Bite volume increased as height increased but tended to decrease as density increased. Figures 6c and 6d show that the trends in volume reflected parallel trends in bite depth and area. The trends illustrated in Figures 6a,6b and 6c indicate that one general model may be applied to all four experiments. The subsurface data was coherent with the surface data. In Figure 6d the subsurface data was not coherent. The sub-surface bite area could not be estimated by a grid survey of the plot area after the second (sub-surface)grazing because it was not possible to distinguish between tillers grazed only at the first(surface) grazing and tillers grazed twice (surface and sub-surface grazing). In the case of the sub-surface bites, area was estimated from the proportion of labelled tillers grazed and the sub-surface bite area may be overestimated.

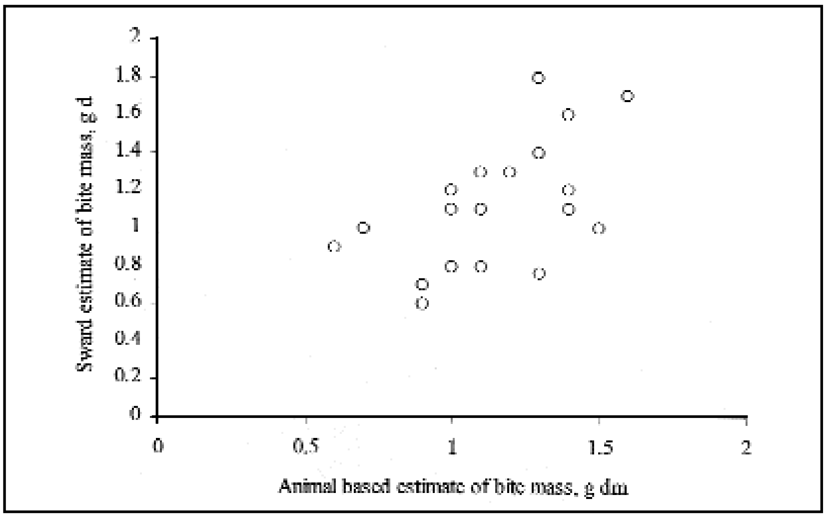


Figure 5 : Comparison of sward and animal estimates of bite mass

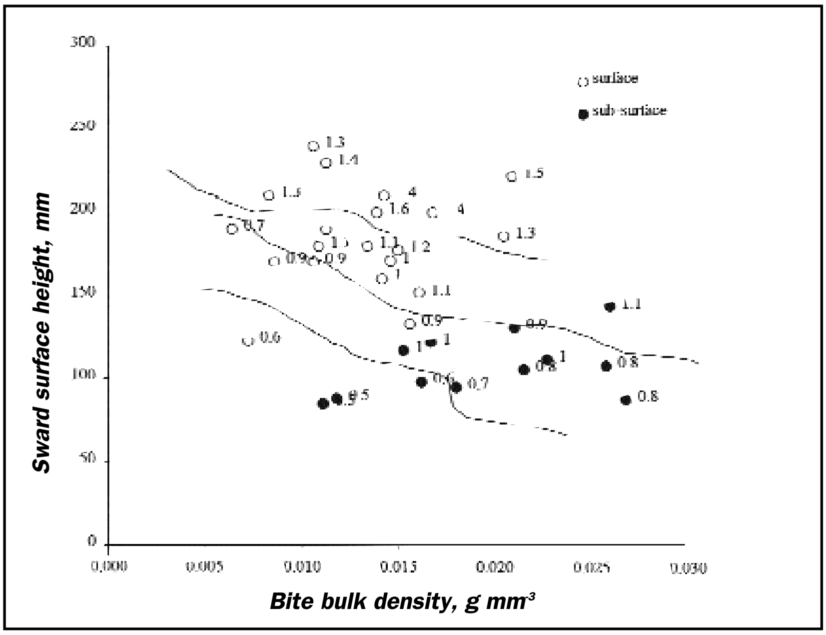


Figure 6a : Bulk density, sward height and bite mass

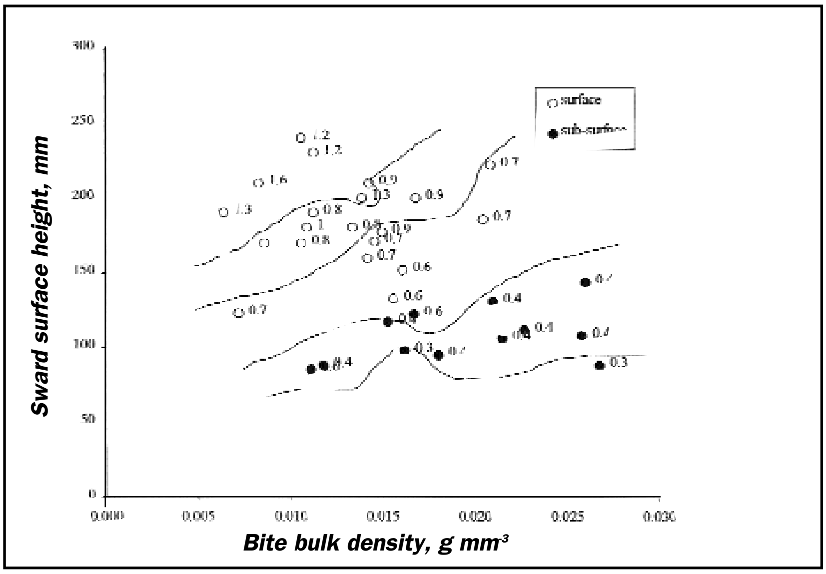


Figure 6b : Bulk density, sward height and bite volume

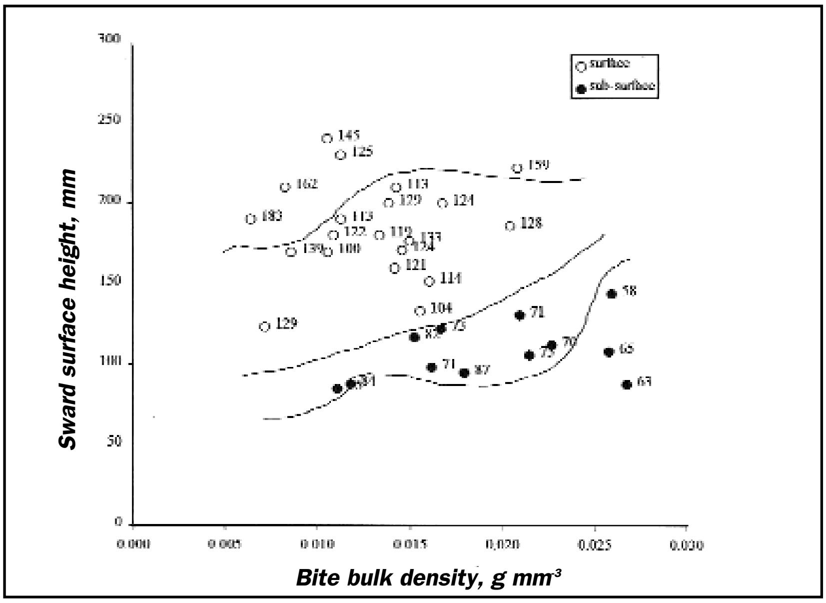


Figure 6c : Bulk density, sward height and bite depth

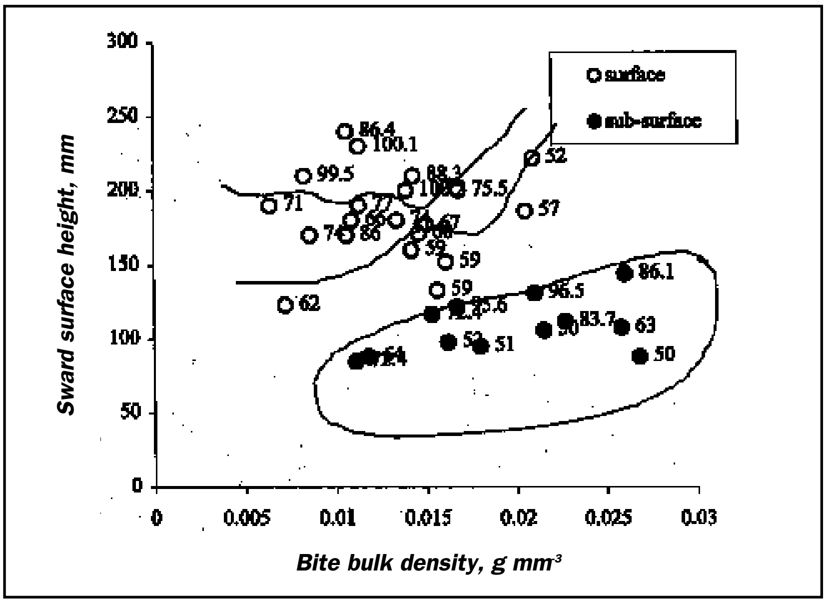


Figure 6d: Bulk density, sward height and bite area.

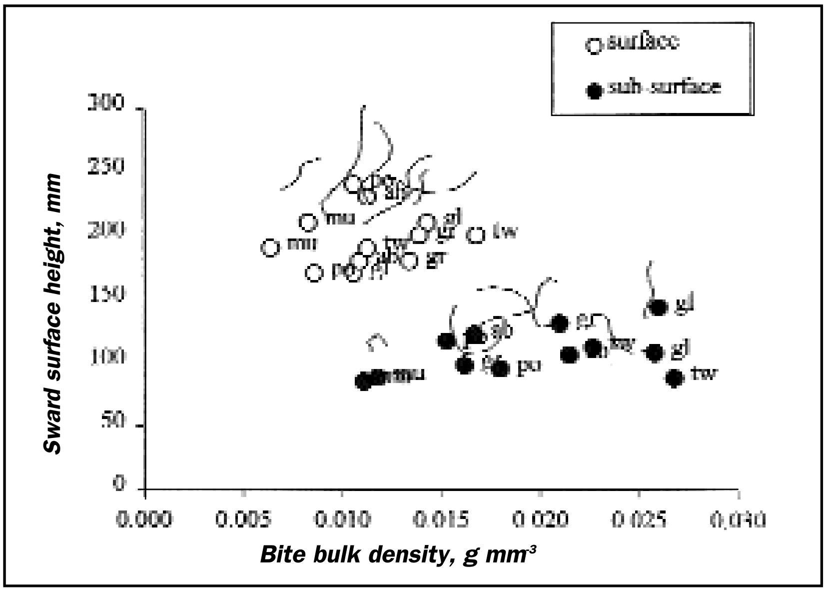


Figure 7: Bulk density, sward height and grass variety.

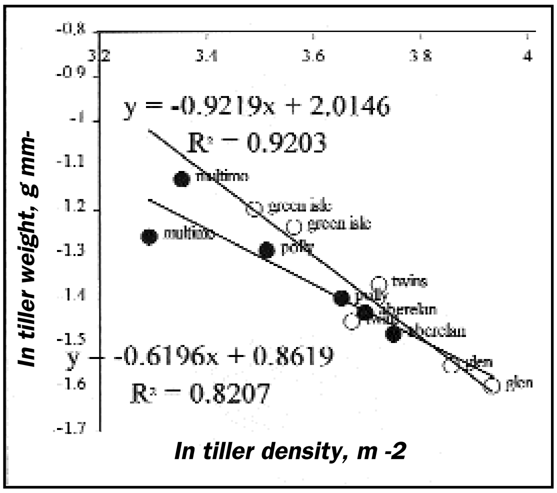


Figure 8: Tiller density and tiller weight per mm

The distribution of grass varieties in the data set is illustrated in Figure 7. The varieties differed in bulk density but not in height. This reflected the basis on which the selection was made. There was a general consistency between the two experiments in the varietal trends. In the surface bites the bite bulk density was less in the Italian variety (Multimo), in the Italian/Perennial Ryegrass hybrid (Polly) and in the diploid Aberelan than in the two tetraploids (Green Isle and Twins) and the diploid Glen. This distribution of bulk density in the upper horizon from which the bites were taken reflected trends in the sward average bulk density (Table 1). Varietal differences in bulk density were due to differences in both tiller number and individual tiller weight. There was an inverse relationship between tiller weight and tiller number. Similar bulk densities in Glen and Green Isle were the result of high tiller numbers in the former and to high tiller weights in the latter (Table 1). The results indicate that, insofar as higher bite mass is related to higher bulk density, breeding for tiller density or for heavy tillers represent alternative routes to increased bite mass.

The inverse relationship between tiller number and tiller weight was curvilinear. The relationship was linear after both variables were log-transformed (Fig. 8). Separate relationships were found for the three higher and three lower bite density varieties. The relationships shown may form the basis of selection of varieties for desirable grazing characteristics.

In the sub-surface bites the order of bite bulk density was maintained in all varieties except Green Isle. Green Isle fell to an intermediate density and this suggests that, in this variety, the herbage tended to be concentrated in the upper horizons of the profile.

4.4. Conclusions

- The selection of plant material for certain physiological traits (e.g. characteristics of the leaf growth zone) will allow the control of sward structure.
- Sward surface height is the primary determinant of bite mass. Sward density is of secondary importance in taller swards but it increases in importance as sward height decreases.
- Density is relatively less important than height because bite volume increases as height increases but decreases as density increases.
- Bite depth and area both contribute to differences in bite volume.
- Varietal difference in density affect bite mass. Higher density in a variety may be achieved by increasing tiller number or tiller weight.
- Varietal differences in profile distribution of herbage mass may affect the rate at which bite mass decreases as a sward is grazed down.
- Varietal structural differences effect instantaneous intake and may therefore have the potential to effect daily intake.

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