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HERBAGE QUALITY AND PHYSICAL BREAKDOWN IN THE FOREGUT OF SHEEP

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SUMMARY

The physical breakdown of white clover and perennial ryegrass in the foregut was studied in 6 mature wether sheep. Animals were fed once daily and total rumen contents were serially sampled over 24 hours. Disappearance of dry matter from the rumen was 10 times faster during the 3 hours following ingestion, when 60% of the DM intake disappeared, than during the between-meal periods. The proportion of DM intake lost as particles was greater for clover (57%) than for grass (49%) during this period. Changes in the particle size spectrum showed that most breakdown occurred during the eating period and that the total amount of small particle material in the rumen remained relatively constant. The results indicated significant differences in the processing of clover and grass in the foregut which appeared to be associated with anatomical characteristics of the plants.

INTRODUCTION

Differences in the nutritive value of herbage grasses and clovers for animal production have been attributed to variation in voluntary intake, site of digestion and other factors (e.g. Miles et al., 1969; Ulyatt and McRae, 1974; Rattray and Joyce, 1969; Moseley and Jones, 1979a). However, the nutritive value of a forage depends primarily on the extent, rate and mode of processing as it is eaten and passed through the reticulo-rumen. This initial and rate-limiting step in ruminant digestion is governed by the physical comminution of feed particles to a size capable of passage through the reticulo-omasal orifice to the hind-gut (Balch and Campling, 1962). Although the processes involved in this breakdown are known, their relative contributions, or the way in which these may change with different feeds, are not well understood. Several recent publications, particularly those concerned with modelling rumen function (e.g. Baldwin, et al., 1977) have stressed the importance of physical breakdown to herbage digestion in the ruminant and highlighted the relative lack of information on this subject. In the present work a comparison was made of the physical and chemical disintegration of two forages chosen for their diversity in nutritive value. Detailed measurements of their physical breakdown over the
foregut were carried out and an attempt was made to investigate the relationships between measured differences and plant characteristics.

MATERIALS AND METHODS

FEEDS

Perennial ryegrass (var. S23) and white clover (var. Sabeda) were cut with an Allen Autoscythe and collected fresh into hessian bags, frozen rapidly and stored at −20°C. Both crops were from pure sown one-year-old leys which contained less than 10% weeds or unsown species. Prior to feeding the crops were thawed and dried overnight in a forced-draught oven at 40°C to approximately 85% dry matter and chopped to a staple length of 30 mm.

ANIMALS

Six 2-year old Clun Forest wether sheep were prepared with large removable rumen fistulas (Moseley and Jones, 1979b) and housed indoors in individual pens over slatted floors. The animals were maintained on a dried grass diet with free access to water and were treated for intestinal parasites.

EXPERIMENTAL

The sheep were randomly assigned to two groups and fed either 600 g/d of perennial ryegrass or white clover in two consecutive crossover periods. Food was offered once daily at 0900 hours for a period of 15 days which comprised 9 days prefeeding and 6 days during which a representative sample of rumen contents was obtained once daily from each sheep at 3, 6, 9, 12, 18 or 24 hours post feeding. During the sampling sequence, total rumen contents were removed, weighed and subsampled before returning them to the animal.

Total rumen contents and particle fractions were analysed for dry matter (DM) by heating to constant weight at 100°C in a forced-draught oven and for organic matter by subtraction after ashing overnight at 450°C in a muffle furnace. Particle size distribution analysis was carried out on whole rumen contents by the technique of Jones and Moseley (1977), using the range of sieve sizes shown in Table 1. The two smallest fractions were separated by washing the initial sieving residue through individual sieves.

Total microbial DM in rumen contents was measured using the DAPA method described by Ling and Buttery (1978).
TABLE 1: SIEVE SIZES USED IN PARTICLE SIZE SEPARATION

<table>
<thead>
<tr>
<th>Sieve No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture mm</td>
<td>4.00</td>
<td>2.00</td>
<td>1.18</td>
<td>0.60</td>
<td>0.42</td>
<td>0.30</td>
<td>0.15</td>
<td>0.10</td>
<td>0.05</td>
</tr>
</tbody>
</table>

RESULTS

The total weight of wet rumen contents declined with time and was significantly lowered by 20% for both feeds between 3 and 24 hours post-feeding (Table 2). Grass fed animals had a higher weight of wet rumen contents than clover fed, but a lower DM proportion which resulted in a similar rumen DM content for both feeds. The proportion of DM in rumen contents and the proportion of particulate and organic matter in the DM also declined significantly between 3 and 24 hours, but there were no significant differences in the rates of decline between feeds. While there were no consistent significant differences in the proportion of particulate matter in rumen contents the grass fed animals showed a higher organic matter proportion than the clover fed.

TABLE 2: CHANGE IN THE TOTAL WEIGHT; DRY MATTER %; ORGANIC MATTER %; AND PARTICULATE MATTER % IN RUMEN CONTENTS OF SHEEP WITH TIME

<table>
<thead>
<tr>
<th>Diet</th>
<th>3</th>
<th>6</th>
<th>Time After Feeding (h)</th>
<th>9</th>
<th>12</th>
<th>18</th>
<th>24</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet Weight g</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clover</td>
<td>4950</td>
<td>5090</td>
<td>4950</td>
<td>4580</td>
<td>4760</td>
<td>3980</td>
<td>4720</td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>5510</td>
<td>5680</td>
<td>5050</td>
<td>5170</td>
<td>4830</td>
<td>4340</td>
<td>5100</td>
<td></td>
</tr>
<tr>
<td>SED</td>
<td>245</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>DM%</td>
<td>9.04</td>
<td>8.51</td>
<td>8.15</td>
<td>7.47</td>
<td>6.53</td>
<td>5.58</td>
<td>7.55</td>
<td></td>
</tr>
<tr>
<td>Clover</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>8.18</td>
<td>7.86</td>
<td>8.32</td>
<td>6.82</td>
<td>5.97</td>
<td>5.24</td>
<td>7.07</td>
<td></td>
</tr>
<tr>
<td>SED</td>
<td>0.427</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.145</td>
<td></td>
</tr>
<tr>
<td>OM%</td>
<td>84.4</td>
<td>84.9</td>
<td>85.3</td>
<td>83.1</td>
<td>80.2</td>
<td>77.2</td>
<td>82.5</td>
<td></td>
</tr>
<tr>
<td>Clover</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>86.2</td>
<td>86.8</td>
<td>87.5</td>
<td>84.4</td>
<td>83.1</td>
<td>80.7</td>
<td>84.7</td>
<td></td>
</tr>
<tr>
<td>SED</td>
<td>1.44</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.59</td>
<td></td>
</tr>
<tr>
<td>Particulate %</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clover</td>
<td>52.3</td>
<td>48.7</td>
<td>44.4</td>
<td>39.3</td>
<td>38.7</td>
<td>39.3</td>
<td>43.8</td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>54.6</td>
<td>50.0</td>
<td>44.8</td>
<td>43.3</td>
<td>38.8</td>
<td>31.0</td>
<td>43.8</td>
<td></td>
</tr>
<tr>
<td>SED</td>
<td>3.36</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.37</td>
<td></td>
</tr>
</tbody>
</table>
The decline with time of the total rumen DM components is shown in Fig. 1 where the 0 hour data has been calculated from the rumen contents at 24 hours and the feed input. The disappearance of total DM from the rumen was similar for both feeds with 59% of the daily intake being lost over the first 3 hours and the remainder disappearing at a slower, constant rate over the following 21 hours. The disappearance of particulate matter, however, was more rapid over the first 3 hrs for the clover diet (57% of particulate intake) compared with the grass diet (49% of particulate intake). Of the remaining non-particulate DM between 31% and 41% was accounted for by microbial dry matter, with a slightly higher proportion in the rumen contents of grass fed compared to clover fed sheep. The clover fed animals therefore showed a slower net rate of loss of non-particulate material over the first 3 hours compared with the grass fed.

The size distribution of particulate material in the rumen is given in Fig. 2 as the percentage of total particulate material retained on the 9 sieve fractions described in Table 1. The sequence of histograms for both diets shows a decrease with time of the 4 mm fraction and a reciprocal increase of the 0.15 mm fraction with little
change in the proportional contribution of the intermediate fractions. However, the rate of disappearance of the large particle fraction was significantly greater for the clover diet (43%) over the first 3 hours compared to the grass diet (21%), and the final particle size distribution at 24 hours also showed a smaller proportion of large (4 mm) particles. When the particle distribution was converted to total dry weight of each fraction in the rumen (Fig. 3), it was seen that the disappearance of the largest fraction showed an exponential trend, with 71% and 57% of the total weight of 4 mm particles disappearing during the first 3 hours for clover and grass diets respectively. The rate of loss of large particles from 3 to 24 hours then followed a linear trend for both diets. The 0.15 mm fraction, however, did not show any significant change with time and remained fairly constant for both feeds, although there was a slightly higher total amount of the small particle material in the rumen contents of clover fed animals compared to the grass fed.

**Fig. 2:** Particle size spectrum of whole rumen contents as % of total retained per sieve
DISCUSSION

Since the intakes of both feeds were restricted well below ad libitum it would follow that the daily rate of passage of digesta through the rumen would also be well below its maximum. In the present experiment it appeared that the rate and pattern of net outflow of DM from the rumen was similar for both feeds. For clover and grass the rate of net DM outflow during the first 3 hours after feeding was ten times greater than during the between meal periods and accounted for 60% of the ingested dry matter. This compares with a reported elevation in flow rate of DM from the rumen of cattle during eating of 2-3 times the between meal flow rate (Balch, 1958). This was shown to be correlated with increased reticular and omasal activity, contractions of the reticulo-omasal orifice and jaw movements. Reid et al. (1979), also recorded a higher rate of DM loss from the rumen of lucerne fed sheep during eating which was 3½ times greater than the between-meal period and accounted for the disappearance of 43% of the DM intake within 5 hours feeding. This rapid rate of outflow from the rumen during eating could have important implications with regard to the
passage of undigested plant material. While the recorded loss of DM during the first 3 hours in this experiment was equivalent to 75% of the mean rumen DM pool, at higher intakes this would be expected to increase. Thus it seems inevitable that with the higher-intake forages a greater proportion of the undigested food must pass rapidly through the rumen and into the intestines for digestion.

DM can only be lost from the rumen by passage of particulate, soluble or microbial matter through the reticul- omasal orifice or by the absorption of solutes through the rumen wall. In the present work there appeared to be differences in the way in which clover and grass DM components disappeared from the rumen, since the loss of particulate DM during the first 3 hours was significantly greater for the clover diet than the grass. This would suggest either a faster rate of breakdown and passage of clover particles and/or a faster rate of conversion of particulate to soluble material. The lower net loss of soluble DM with the clover feed over this period might indicate a build-up of soluble DM from the breakdown of particulate material but may also be the result of an increased contribution from salivary or endogenous sources. It is, however, unlikely that this apparently lower rate of loss of soluble material would occur under ad libitum conditions, when a relatively higher flow rate out of the rumen would be expected.

Figs. 2 and 3 showed that there was little change in the proportion or absolute weight of the intermediate sized particles in the rumen and that their contribution to the total amount of particulate material was small. This might suggest a number of possibilities: that the particle breakdown proceeded rapidly through these stages, that the majority of material became broken down immediately to the smaller size, that there was a more rapid movement of these particle sizes out of the rumen or that there was a retention of the smaller particle size in the rumen. At present it is not known which of these processes might occur, although information is being sought on this aspect of digestion.

Troelson and Campbell (1968) showed that with grasses virtually no material greater than 0.5 mm passed into the omasum of sheep while for alfalfa the size limit appeared to be 1 mm. Similarly Reid et al. (1977) showed that in lucerne-fed wether sheep less than 1% of material greater than 1 mm appeared in the abomasum, while Poppi et al. (1980) claimed that for grasses and legumes only 1-3% of the material passing out of the reticul- rumen was greater than 1.18 mm. This concept of a critical particle size, which can pass out
FIG. 4: Change in the proportion of rumen particles above and below 1.18 mm.

of the rumen, may be usefully applied to the present results. If it is accepted that particles above 1.18 mm cannot pass from the rumen while those below can, then the proportional change in particles which can or cannot pass out of the rumen is shown in Fig. 4. It is clear that the proportional reduction of large particles and the reciprocal increase of small particles in the rumen of clover-fed sheep followed an exponential fashion while that of grass-fed were almost linear. Furthermore, the time taken to reach the crossover point was only 3½ hours with clover but 12 hours with grass. Fig. 5 however, shows that despite the very rapid reduction of the total weight of large particle material from the rumen of both clover-and grass-fed animals there was very little change in the total weight of small particle material present in the rumen. This indicates a very rapid flow of small particles out of the rumen during the eating phase which was significantly higher for the clover feed than for the grass.

This significantly higher rate of breakdown and passage of particulate material with clover compared to grass during the ingestion period helps to explain the reported differences in nutritive value of these herbages (e.g. Rattray and Joyce, 1969; Ulyatt, 1971). While the faster rate of particle breakdown would lead to a greater DM intake (Campling, 1979), the higher rate of passage associated with eating clover may lead to a higher rate of flow of undigested plant residues and solutes to the hind-gut (McRae and Ulyatt, 1974), thus improving the efficiency of utilisation of nutrients.

The physical breakdown of herbage is accomplished by a combination of processes including chewing during eating and ruma-
tion, microbial fermentation and muscular detrition by the reticulorumen walls. In the present work the maximum rate of breakdown was recorded during the eating period and, according to Pearce (1967) and Reid et al. (1979), very little rumination takes place during this time. Furthermore, the time interval was too short for any significant degree of microbial digestion of structural components to occur (Bailey, 1965). Reid et al. (1979) also showed that chewing during eating alone caused a 50\% reduction in the large particle fraction of a lucerne feed when fed to sheep. It therefore appears that the particle breakdown observed here was primarily due to the process of chewing during eating. Consequently, the nutritive quality of these herbages would depend greatly on their ability to resist the shearing forces imposed by chewing. Preliminary microscopic examination of rumen particles has shown (G. Moseley, unpublished) that such anatomical features as vascular tissue, epidermal cells and cuticular material were the most durable and that variation in these features appeared to be related to differences in the rate of breakdown.

Further investigation of those factors which are responsible for maintaining the structural integrity of herbages during digestion could lead to a better understanding of which plant components are important in determining nutritive quality, particularly voluntary intake. This may then lead to the development of selection criteria for breeding improved herbage varieties and also of techniques for the prediction of nutritive quality.

**Fig. 5:** Change in the total weight of rumen particles above and below 1.18 mm.
ACKNOWLEDGEMENTS

My thanks are due to Mr J. R. Jones for technical assistance throughout the experimental work, and to Dr J. R. Ling for the microbial analyses.

REFERENCES