British Journal of Nutrition (1986), **56**, 463–476

The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep

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(*Received 16 July 1985 – Accepted 29 April 1986*)

1. The characteristics of digestion, passage and rumen fill of three hays: early- and late-cut perennial ryegrass (*Lolium perenne* cv. Endura) and white clover hay (*Trifolium repens* cv. Blanca and Pronitro) were studied using six rumen-cannulated sheep fed at a restricted level of intake (18 g dry matter (DM)/kg live weight (LW) per d), in a two 3 × 3 Latin square design.

2. Voluntary intake of the same diets was measured using a further six non-cannulated sheep in a similar design.

3. Rate of digestion of the three hays was measured using dacron bags and the rates of digestion of DM and neutral-detergent fibre (NDF) for clover hay were significantly ($P < 0.05$ and $P < 0.001$ respectively) faster than those for the two grass hays whose rates did not differ. Rates of passage, determined using chromium-mordanted hay, did not differ between treatments.

4. Rumen pool sizes of DM, organic matter and fibre were generally greatest for the late-cut grass hay and lowest for the clover hay, while voluntary intake was highest ($P < 0.001$) for the clover hay (36·6 g DM/kg LW per d) and lowest for the late-cut grass hay (24·7 g/kg LW per d).

5. The net rate of removal of indigestible fibre from the rumen appeared to vary within the day, with maximal disappearance occurring during eating, followed by a lag phase between 5 and 10 h after feeding, with a second increase in rate between 10 and 24 h post-feeding.

The use of forages as diets for ruminants is associated with prolonged retention times within the digestive tract (Warner, 1981). The degree of distension and fill of the reticulo-rumen can therefore be an important factor limiting the voluntary intake of forage diets (Balch & Campling, 1969). However, the exact mechanism by which such diets can control intake through their effect on the extent of fill of the digestive organs is not clear.

The extent of rumen fill is governed by factors which affect digestion in and passage from the rumen. A high content of structural carbohydrates which are fermented more slowly than other substrates (Van Soest, 1975) will lead to a higher degree of rumen fill, and Osbourn *et al.* (1974) found that intake of forages by sheep was highly correlated with the cell-wall (CW) content of the diet. However, such a relation would not be expected to hold for diets with characteristically low CW contents, where metabolic satiety is likely to exert a dominant effect on intake (Conrad, 1966).

The objectives of the experiments reported here were to study the removal of digesta from the rumen and the voluntary intake by sheep offered forages of contrasting digestibility and dietary fibre content. Grass hay, cut at two levels of maturity, provided diets of high and low digestibility with corresponding low and high CW contents, although both were considered to be within the range where physical limitation of intake was expected to dominate. In addition, the influence of forage species was investigated, with a white clover (*Trifolium repens*) hay intermediate in digestibility between the two grass hays, but with a lower CW fraction. Expt 1 examined the removal of digesta, in particular the CW fraction, from the rumen, with sheep fed on the three diets at a restricted level of intake, while the voluntary intakes of the three diets were measured in Expt 2.

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MATERIALS AND METHODS

Expt 1

Animals. Six yearling, Scottish half-bred, wether sheep, weighing between 49 and 60 kg, were used. Each had been fitted with a rumen cannula of 80 mm in diameter (Moseley & Jones, 1979) 5 months before the start of the experiment. The animals were housed in individual pens with mesh flooring and had free access to water and a mineral block. Feed was offered once daily at 09.00 hours.

Feeds. Three hays were prepared: two were from the primary growth of a single sward of perennial ryegrass (*Lolium perenne* cv. Endura) cut at two stages of maturity, on 25 May and 19 June 1981 (treatments EC and LC respectively). The third was harvested from a sward of white clover (cv. Blanca and Pronitro) hay cut on 21 June 1981 (treatment CL). Before feeding, the hays were chopped to a length of 30–50 mm.

Experimental procedure. The experiment consisted of three periods, during each of which the sheep were fed on one of the three experimental diets. The periods were of 30 d duration, and each was divided into a 9 d initial period during which the animals were adapted to their new diets, and 20 d during which the experimental measurements were carried out. Rumen emptying took place over a period of 14 d. Dacron bag and behaviour study measurements also took place during this time, but there was always one full day after a rumen emptying before further experimental observations were made. Animals were weighed on two consecutive days at the beginning of each period, and the mean live weights were used to calculate the individual intakes based on a level of 18 g hay dry matter (DM)/kg live weight (LW).

Rumen contents. Estimates of the total weight of rumen digesta were made by manually emptying the rumen, weighing, mixing and subsampling the contents and returning the remainder to the rumen, the whole process taking less than 20 min per animal. Four subsamples, each approximately 3% of the total weight of digesta, were taken, using a hollow cylinder 90 mm in diameter, to remove a representative core of digesta. Three of the subsamples were oven-dried at 100° for 24 h for determination of DM and ash content, while the fourth was freeze-dried for subsequent fibre analysis. Measurements were made at intervals of 5, 7, 10 and 24 h after feed was offered to the animal. There was an interval of 4 d between sampling from each sheep. This interval was found to be necessary to overcome the effects of emptying on the repeatability of the measurements, particularly with the prefeeding samples (Aitchison, 1985).

Rates of digestion. Dacron bags, containing weighed quantities (approximately 5 g DM) of the chopped hay on offer to each animal, were used to estimate *in situ* rates of digestion of the hay in the rumen. The bags used measured 150 × 60 mm, with pore size of 100 mesh. Pairs of bags were soaked in water for 10 min; one pair of bags was used for determination of '0 h wash' values for each animal and the remaining pairs of bags were inserted into the rumen immediately before feeding and incubated for 3, 6, 9, 12, 24 or 48 h. As soon as the bags were removed from the rumen, they were washed thoroughly under running tap-water until the water leaving the bag became clear. Disappearance of DM was measured as the loss in weight of the bag contents after freeze-drying, and the residues were analysed for neutral-detergent fibre (NDF) content to determine the loss of fibre.

The fractional rates of digestion were estimated by fitting the values for percentage disappearance of DM or NDF with time to the equation:

$$y = a + b(1 - e^{-k_d t}), \quad t > t_0$$

(Ørskov & McDonald, 1979), where y is DM or NDF disappearance from the bag, a is loss at time $t = 0$, b is potentially degradable insoluble material, k_d is fractional rate of digestion of DM or NDF, t is time of incubation and t_0 is lag time.

In fitting the equation to estimates of DM disappearance from the bags, the estimates of a and b were constrained so that their total did not exceed 100%. For NDF disappearance the sum $(a+b)$ was constrained such that it was equal to the amount of indigestible NDF (INDF) present in the total NDF of the diet. Estimates of the initial lag period (t_0) were obtained from $t = -1/k \log_e((b-a-y_0)/b)$ where y_0 is the value obtained for the disappearance of NDF from the '0 h wash' values.

Rates of passage. The flow of undigested feed residues through the digestive tract was measured using feed mordanted with sodium dichromate as an indigestible marker. For particulate markers, difficulties are often encountered in obtaining representative samples of rumen digesta which may result in less reliable estimates of rumen-outflow rates. These problems can be overcome by sampling from the faeces. In this experiment, digesta samples were taken from the rumen and were used to support the identification of the rumen outflow rate constant obtained from mathematical analysis of the faecal excretion values. The mordanting procedure of Uden *et al.* (1980) was followed, using samples of the chopped hay on offer to the animals. Portions (40–50 g DM) of the mordanted hay were placed into the rumen immediately before feeding. Samples (15–20 g DM) of rumen digesta and of faeces were taken at intervals over a period of 7 d. Four samples were taken on the 1st day, and then three on each of the following 6 d. These samples were dried at 100°, and analysed for concentration of Cr.

Using the rumen values, rate constants were calculated by regression of the logarithmic values of the decrease in Cr concentration *v.* time.

For the faecal values in five of the eighteen sets of values, the model of Blaxter *et al.* (1956) could not be fitted. This was either due to non-convergence to a solution with acceptable estimates of rate constants or due to systematically underestimating or overestimating parts of the excretion curve. Thus, the model of Dhanoa *et al.* (1985) was used. This was of the form:

$$y = Ae^{-k_1 t}\, e^{-Be^{-(k_2-k_1)t}},$$

where y is Cr concentration, A and B are constants, k_1 and k_2 are rate constants and t is time of sampling, which contains an exponential term and a double-exponential term derived by considering digesta flow as a multi-component exponential process.

The estimates of k_1 and k_2 derived from the faecal values were then compared with the estimates calculated from the decline of Cr concentration in the rumen to determine which rate constant applied to the rate of removal from the rumen.

Digestibility. Total faecal production during a 7 d period was collected, as described by Cammell (1977). Total daily production was stored frozen, until after completion of the collection, when the bulk sample for each sheep was weighed, thoroughly mixed and subsampled for determination of oven DM, ash, NDF and acid-detergent fibre (ADF) contents.

Rumen fluid sampling. Rumen fluid samples were obtained on days 6 and 7 of the faecal collection, using a vacuum fluid extractor. Sample volume was restricted to 20 ml and samples were taken immediately before feeding, and on seven further occasions during each 24 h period. The pH of the sample was measured immediately following collection and then acidified with 10 M-sulphuric acid, and stored at 4° until required for analysis of volatile fatty acid (VFA) concentration.

Behaviour study. Visual observations of eating behaviour were made once every 3 min on each of the six animals over 24 h, once in each period. Three categories were used to classify the animal's behaviour: chewing during eating (E), ruminating (R) and idling (I).

Expt 2

The objective of this experiment was to measure the voluntary intakes of the three hays which were used in Expt 1.

Animals. A further six yearling, Scottish half-bred, wether sheep (non-fistulated), weighing between 50 and 58 kg, were used. They were housed in individual metabolism crates throughout the experment, and had free access to water and mineral blocks.

Feeds and experimental procedure. The experiment consisted of three periods, and the sheep were fed on one of the three treatment hays during each period. Animals were weighed on two consecutive days at the beginning and end of each period.

Animals were adapted to their new diets at the start of each period until intake was stable for seven consecutive days. Voluntary intake was then measured over a period of 10 d, during which time refusals were collected daily. Hay was offered each morning at 09.30 hours, at an amount 10–15% in excess of the previous day's consumption. Samples of feed offered to and refused by the animals were taken and stored for subsequent analysis.

Chemical analysis

DM contents of feeds, faeces and digesta samples were determined by drying samples to constant weight in a forced-draught oven at 100° (24 h). Ash was measured by igniting samples in a muffle furnace at 550° (16 h) and total nitrogen of feed and faeces and water-soluble carbohydrate (WSCHO) content of the feed were determined as described by Siddons *et al.* (1984). NDF and ADF analyses were carried out on freeze-dried samples according to the method of Goering & Van Soest (1970) whilst indigestible ADF (IADF) content of rumen digesta was measured using the method described by Penning & Johnson (1983).

Indigestible NDF was measured as the amount of NDF remaining after a 96 h in vitro digestion. Samples (0·5 g) were weighed into boiling tubes and incubated at 39° for 96 h with rumen fluid and a phosphate bicarbonate buffer (McDougall, 1948) at pH 6·9. The solid residue after 96 h was then refluxed for 1 h with 50 ml neutral-detergent solution and the NDF residue isolated as for conventional NDF analysis.

The concentrations of total VFA in the samples of rumen fluid were determined on centrifuged samples (2 ml) of the acidified extract by gas–liquid chromatography, using a Hewlett–Packard model 5700A gas liquid chromatograph, employing a column fitted with Chromosorb 101 at 160°.

In vitro digestibility of the feeds was determined by the two-stage procedure of Tilley & Terry (1963), comprising a 48 h digestion in the presence of rumen inoculum, followed by digestion with pepsin in acid solution.

The concentrations of Cr in faeces and digesta samples were measured by atomic absorption spectrometry. Samples were prepared for analysis by ashing at 550° overnight, and the Cr was extracted by wet digestion as described by Christian & Coup (1954).

Statistical analysis. The design of each experiment was constructed using two 3 × 3 Latin squares, balanced for the residual effects of treatments not estimated in the analysis of variance. The limitations of this design should be recognized (Kempthorne, 1952) but it was chosen to accommodate the small number of fistulated sheep available for this work. Animals were allocated at random to the six sequences of the treatments EC, LC and CL. The statistical package GENSTAT was used to perform analysis of variance in which animal, period and treatment effects were estimated leaving eight residual error degrees of freedom. The maximum likelihood program MLP (Ross, 1980) was used in the estimation of rates of digestion and rates of passage: this program estimates non-linear parameters using direct iterative methods.

Table 1. *Chemical composition (g/kg dry matter (DM)) of the three hay diets used: perennial ryegrass* (Lolium perenne) *cut early (EC) or late (LC) in the season, and white clover* (Trifolium repens; *CL*)

Treatment...	EC	LC	CL
In vitro DOMD (g/g)	0·676	0·558	0·650
Organic matter	897	916	874
Nitrogen	24	17	40
Water-soluble carbohydrates	129	79	55
Neutral-detergent fibre (NDF)	545	652	294
Acid-detergent fibre (ADF)	307	404	288
Lignin	19	48	35
Indigestible NDF*	85	194	91
Indigestible ADF†	25	79	62
DM (g/g fresh weight)	0·870	0·875	0·865

DOMD, digestible organic matter in the DM.
* Determined as the NDF residue after a 96 h in vitro digestion.
† Determined as the ADF residue after a 7 d cellulase (*EC* 3·2·1·4) digestion.

RESULTS

Expt 1

Diet composition. The composition of the hays fed to the animals is shown in Table 1. The grass hays were cut at two levels of maturity which resulted in a difference in in vitro digestible organic matter (OM) in DM (DOMD) of 0·12. This decrease in digestibility with increasing maturity was associated with a reduction in the N and WSCHO contents, and a corresponding increase in fibre as measured by the NDF, ADF, INDF and IADF fractions. Despite its lower digestibility, the clover hay had a higher N content than the EC hay, but lower WSCHO values. Total NDF and ADF values were lower than either of the two grass hays, but the indigestible components INDF and IADF were intermediate beween the corresponding values for the two grass hays.

Rates of digestion and passage. The fractional rates of digestion of DM and NDF from the dacron bags estimated using the method of Ørskov & McDonald (1979) are shown in Table 2. The rates of digestion of both DM and NDF were significantly ($P < 0·05$ and $P < 0·001$ respectively) higher for the clover hay, with no significant differences between the early- and late-cut grass hays.

Rumen fluid analysis. Feeding resulted in a rapid decrease in pH for all diets, although this decline was most marked for diet CL and least for diet LC. Minimum values of 6·3–6·4 were obtained on all diets approximately 9 h after feeding. Rapid increases in VFA concentration (Fig. 1) were observed directly after feeding for all diets, and these concentrations remained elevated throughout the subsequent samplings. Highest concentrations of VFA were observed with diet CL and lowest with diet LC. No marked treatment differences in the molar proportions of the VFA were recorded.

Estimates of the fractional rates of passage from the rumen obtained from analysis of the decline in rumen Cr concentration were 0·0400, 0·0403 and 0·0393 (SEM 0·00216)/h for treatments EC, LC and CL respectively. However, there was a high random variability in concentration between samples, presumably due to sampling problems. This resulted in a large error associated with the prediction for individual animals and hence the values obtained from faecal excretion curves were chosen as being more accurate. In order to assign k_1 or k_2 from the faecal curves to rumen outflow, the mean rate constants from the

Table 2. *Expt 1. Fractional rates of digestion (/h) of dry matter (DM) and neutral–detergent fibre (NDF), estimates of the NDF lag-time* (t_0, *h) and fractional rates of passage (/h) from the rumen* (k_p) *in sheep offered diets of early (EC)- or late (LC)-cut perennial ryegrass* (Lolium perenne) *or white clover* (Trifolium repens, *CL) hay*

(Mean values for six sheep per treatment)

	Treatment				Statistical significance of difference	
	EC	LC	CL	SEM	EC *v.* LC	Grasses *v.* CL
DM	0·0361	0·0264	0·0506	0·00638	NS	*
NDF	0·0295	0·0268	0·0480	0·00284	NS	***
NDF t_0	2·96	3·32	4·35	0·928	NS	NS
k_p	0·0332	0·0354	0·0298	0·00288	NS	NS

NS, not significant.
* $P < 0·05$, *** $P < 0·001$.

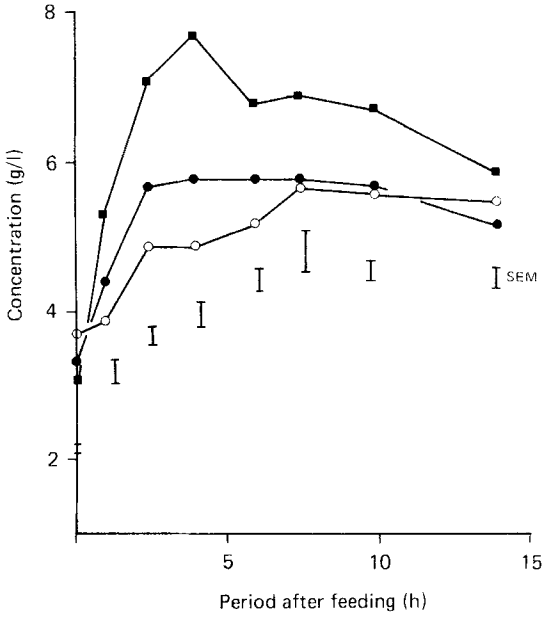

Fig. 1. Expt 1. Changes in total volatile fatty acid (VFA) concentration (g/l) with time-period (h) after feeding for sheep offered perennial ryegrass (*Lolium perenne*) hay cut early (●) or late (○), or white clover (*Trifolium repens*) hay (■).

rumen data were compared with the rate constants k_1 and k_2 estimated from the faecal excretion values. This showed a mean bias of +0·00703/h (SE of difference (SED) 0·00157) for k_1, and a mean bias of −0·1314 (SED 0·0321) for k_2. The values for k_1 were therefore assigned to rumen outflow. These values for k_1, termed k_p, are shown in Table 2. There were no significant differences between treatments.

Digestibility. The apparent digestibilities of DM, OM, NDF and ADF (Table 3) all showed significant ($P < 0·001$) treatment effects and in all cases values for diet EC were highest and those for diet LC were lowest.

Table 3. *Expt 1. Apparent in vivo digestibility coefficients of dry matter (DM), organic matter (OM), neutral–detergent fibre (NDF) and acid–detergent fibre (ADF) in sheep offered early (EC)- or late (LC)-cut perennial ryegrass* (Lolium perenne) *or white clover* (Trifolium repens, *CL) hay at* 18 *g DM/kg live weight once daily*

(Mean values for six sheep per treatment)

	Treatment				Statistical significance of difference	
	EC	LC	CL	SEM	EC *v.* LC	Grasses *v.* CL
DM	0·805	0·675	0·766	0·008 53	***	*
OM	0·813	0·680	0·796	0·008 19	***	***
NDF	0·880	0·728	0·839	0·0129	***	NS
ADF	0·851	0·709	0·812	0·007 60	***	**

NS, not significant.
* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

Rumen pool size. Table 4 shows the mean weights of wet digesta, DM and OM in the rumen for the three treatments at the four sampling times after feeding: 5, 7, 10 and 24 h; also shown are the mean weights for each treatment, and the mean daily intakes of DM and OM.

There were large and significant differences ($P < 0·001$) in mean rumen pool sizes between treatments, except for the wet weights of rumen contents between diets EC and LC, where the differences were not significant. In almost all instances, the highest digesta pool sizes were those of sheep fed on diet LC and the lowest those fed on diet CL.

Within each treatment, considerable differences in digesta pool sizes were found between the measurements taken before and after feeding. The rumen DM contents immediately before feeding were 0·52, 0·74 and 0·45 of the daily DM intake for animals fed on diets EC, LC and CL respectively.

Mean daily fibre intakes, and the rumen fibre contents at the same sampling times are shown in Table 5. Significant differences in pool sizes were again observed between treatments ($P < 0·001$), except between diets EC and LC for digestible NDF, and between the two grass diets and the clover diet for IADF. Pool sizes were generally highest for dietary treatment LC, particularly for the indigestible fractions. Significant differences within dietary treatments were seen between measurements at 5 h and 24 h after feeding for all the fibre fractions. However, the pool sizes of the digestible NDF remaining in the rumen at the 24 h sampling time were only 0·05, 0·12 and 0·04 of the daily intake for diets EC, LC and CL respectively, whereas the corresponding values for the indigestible NDF remaining before the next day's feeding were 1·85, 1·74 and 1·36. A similar effect was also seen with the fractions digestible ADF and IADF.

For all the digesta components shown in Tables 4 and 5, excluding the wet weights of digesta, there were no significant differences between the rumen pool sizes at the 5 h and at the 7 h sampling times. Measurements at 10 h after feeding were significantly lower than the 5 h values, except for digestible ADF and the indigestible fractions INDF and IADF, where samples taken at 5, 7, and 10 h did not differ significantly within treatments.

Eating (E) and ruminating (R) behaviour. The length of time taken to eat each diet did not differ significantly between treatments (Table 6). However, there were significant differences ($P < 0·001$) in R times and consequently the period of time spent idling. The total periods of time spent both E and R were significantly different from each other

Table 4. *Expt 1. Mean rumen pool size* (g) *at four sampling times after feeding, treatment means* (g) *and intake* (g/d) *of total wet weight of digesta, dry matter* (*DM*) *and organic matter* (*OM*) *of sheep offered diets EC, LC and CL at 18 g DM/kg live weight once daily*

(Mean values for six sheep per treatment)

Period after feeding (h)	Treatment			SEM	Statistical significance of difference	
	EC	LC	CL		EC *v.* LC	Grasses *v.* CL
			Wet weight of digesta			
5	12795	13168	11557	402·8	NS	*
7	13162	12265	11432	340·9	NS	*
10	12518	12682	10212	354·1	NS	***
24	9560	11073	7993	363·4	*	***
Mean	12009	12297	10298	263·2	NS	***
			DM			
5	1073	1251	1097	42·1	*	NS
7	1067	1190	977	48·0	NS	*
10	967	1167	833	53·7	*	**
24	516	754	449	26·5	***	***
Mean	906	1090	839	26·2	***	**
Intake	995	1014	996	6·5		
			OM			
5	918	1109	908	37·7	*	NS
7	903	1057	797	44·1	*	*
10	823	982	663	56·8	NS	**
24	415	644	336	26·7	***	***
Mean	765	948	676	27·8	**	***
Intake	892	929	871	5·8		

EC, early cut perennial ryegrass (*Lolium perenne*) hay; LC, late cut perennial ryegrass hay; CL white clover (*Trifolium repens*) hay; NS, not significant.
* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

($P < 0·001$), as was (E+R)/kg DM intake. Diet CL required the least chewing time and diet LC the longest. However, when expressed in terms of total CW (as NDF) intake, then diet CL required significantly ($P < 0·01$) longer than either of the two grass hays on a per kg NDF intake basis. There was no significant difference between the two levels of digestibility of grass hays of (E+R) required per kg NDF intake.

The pattern of E and R behaviour throughout the 24 h period is shown in Fig. 2. One animal on diet LC was slow to eat up its feed, and accounts for all the E observed between 6 and 10 h after feeding. For all diets, a peak in rumination activity shortly after the end of feeding was followed by a lull at approximately 17.00–18.00 hours. R occupied a greater proportion of the time during the second half of the feeding cycle than in the first 12 h after feeding.

Expt 2

Mean daily intakes of the three diets at *ad lib.* feeding levels are given in Table 7. Intake of DM and OM (g/d) was highest for animals eating diet CL, and lowest for animals eating diet LC ($P < 0·001$). These relations were also significant when the daily DM intake was expressed as g/kg LW. However, daily intake of NDF was significantly lower ($P < 0·001$) for diet CL, both in terms of g/d and g/kg LW, than for either of the two grass–hay diets. Intake of NDF (g/d) was higher ($P < 0·01$) for sheep eating diet EC than LC, but this

Table 5. *Expt 1. Mean rumen pool sizes (g) at four sampling times after feeding, treatment means (g) and intake (g/d) of fibre measured as dNDF, dADF, INDF and IADF of sheep offered diets EC, LC and CL at 18 g dry matter/kg live weight once daily*

(Mean values for six sheep per treatment)

Period after feeding (h)	Treatment			SEM	Statistical significance of difference	
	EC	LC	CL		EC *v.* LC	Grasses *v.* CL
			dNDF†			
5	324	292	179	21·5	NS	**
7	299	294	157	15·0	NS	***
10	238	237	99	17·1	NS	***
24	22	52	7	8·7	NS	NS
Mean	221	219	111	13·4	NS	***
Intake	448	442	192	4·3		
			dADF‡			
5	264	333	226	11·0	**	**
7	253	315	205	15·5	**	**
10	214	298	138	17·9	**	***
24	75	168	48	6·1	***	***
Mean	201	278	154	8·6	***	***
Intake	280	330	225	2·5		
			INDF			
5	207	454	188	11·2	***	***
7	218	439	188	21·8	***	***
10	211	448	171	25·3	***	***
24	174	381	137	17·3	***	***
Mean	202	431	171	13·5	***	***
Intake	94	219	101	2·7		
			IADF			
5	48	135	105	4·2	***	NS
7	53	128	100	5·7	***	NS
10	49	123	85	7·7	***	NS
24	32	95	58	5·5	***	NS
Mean	46	120	87	3·6	***	NS
Intake	25	80	62	1·1		

NDF, neutral–detergent fibre; ADF, acid–detergent fibre; dNDF, digestible NDF; dADF, digestible ADF; INDF, indigestible NDF; IADF, indigestible ADF; NS, not significant; EC, early-cut perennial ryegrass (*Lolium perenne*) hay; LC, late-cut perennial ryegrass hay; CL, white clover (*Trifolium repens*) hay.

** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$.

† Calculated as NDF − INDF.

‡ Calculated as ADF − IADF.

difference was not significant when expressed in g/kg LW. ADF intakes of all diets did not differ significantly between treatments.

DISCUSSION

Measurements both in vivo and in vitro have shown that plant characteristics are one of the main determinants of digestion rates (Mertens & Ely, 1982) and thus the experimental diets were chosen to provide a range of digestibilities and NDF contents (Table 1). The three diets were offered to the fistulated animals in Expt 1 at a restricted level to enable

Table 6. *Expt 1. Mean time (min/d) spent eating (E), ruminating (R) and idling (I) by sheep offered diets EC, LC and CL once daily*

(Mean values for six sheep per treatment)

	Treatment				Statistical significance of difference	
	EC	LC	CL	SEM	EC *v.* LC	Grasses *v.* CL
E	118	185	105	21·9	NS	NS
R	422	554	278	9·8	***	***
I	900	702	1058	26·1	***	***
E+R	540	739	382	26·1	***	***
(E+R)/kg DM intake	545	729	386	25·7	***	***
(E+R)/kg NDF intake	999	1118	1313	52·1	NS	**

EC, early-cut perennial ryegrass (*Lolium perenne*) hay; LC, late-cut perennial ryegrass hay; CL, white clover (*Trifolium repens*) hay; DM, dry matter; NDF, neutral–detergent fibre; NS, not significant.
** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$.

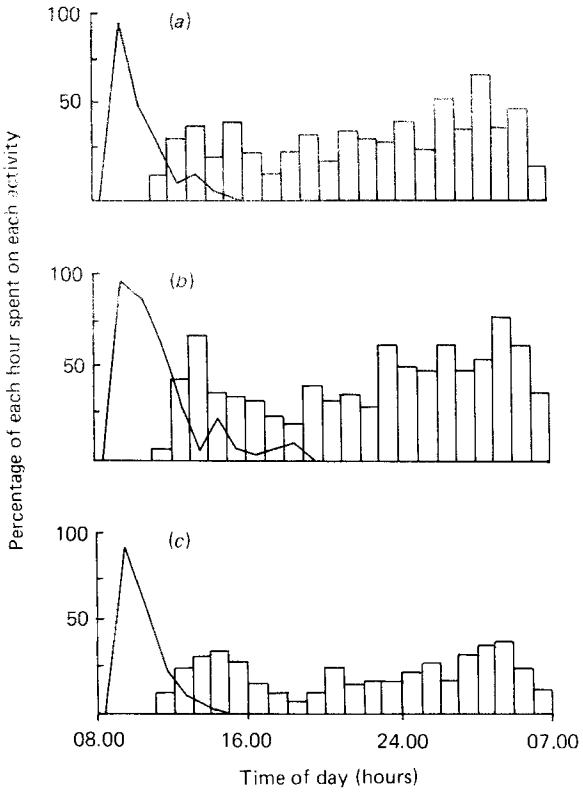

Fig. 2. Expt 1. Daily pattern of eating (—) and ruminating (□) for sheep offered hay once daily at 09.00 hours as (*a*) early-cut perennial ryegrass (*Lolium perenne*), (*b*) late-cut perennial ryegrass, and (*c*) white clover (*Trifolium repens*).

Table 7. *Expt 2. Mean daily voluntary intakes of dry matter (DM), organic matter (OM) and fibre of sheep eating early (EC)- or late (LC)-cut perennial ryegrass* (Lolium perenne) *and white clover* (Trifolium repens; *CL*) *hay (kg/d)*

(Mean values for six sheep per treatment)

	Treatment				Statistical significance of difference	
Intake	EC	LC	CL	SEM	EC *v.* LC	Grasses *v.* CL
DM	1·79	1·38	2·05	0·0406	***	***
OM	1·60	1·26	1·78	0·0369	***	***
NDF	0·963	0·883	0·587	0·0195	**	***
ADF	0·461	0·462	0·501	0·0258	NS	NS
DM (g/kg live wt per d)	31·3	24·7	36·6	0·615	***	***
NDF (g/kg live wt per d)	16·9	15·8	10·5	0·340	NS	***

NDF, neutral-detergent fibre; ADF, acid-detergent fibre; NS, not significant.
** $P < 0·01$, *** $P < 0·001$.

treatment differences to be assessed at the same level of DM intake. The level of restriction was chosen such that each day's intake would be consumed within one meal, thus permitting the fate of this material to be followed in detail over the following 19 h period.

The dacron bag and Cr-mordant measurements permitted between-treatment comparison of rates of digestion and rates of passage on a daily basis (Table 2), while the rumen emptying values (Tables 4 and 5) enabled study of the net removal of digesta from the rumen within the day. Both DM and NDF daily digestion rates decreased with an increase in the proportion of CW in the diet, although differences between the two grass hays were not significant (Table 2). Similar results have been reported both in vitro (Smith *et al.* 1971, 1972; Mertens, 1973) and in vivo (Robles *et al.* 1981) in comparisons of rates of digestion of the neutral detergent fraction of forages differing in CW content. On the other hand, fractional rates of passage of Cr-mordanted hay out of the rumen, estimated from interpretation of faecal excretion curves, did not differ significantly between treatments (Table 2).

Measurements of the net removal of digesta from the rumen have generally concluded that the rate of removal is an exponential process (e.g. Bailey, 1967; Alexander *et al.* 1969). In the present experiment, the rate of removal, as measured by total emptying of DM from the rumen, appeared to be enhanced during the 5 h feeding period. A quantity of DM equivalent to 44, 50 and 35% of the daily DM intake was lost from the rumen by 5 h after feeding for diets EC, LC and CL respectively, compared with a loss during the next 5 h equivalent to only 10, 7 and 24% of the DM present in the rumen at 5 h after feeding. Closer inspection of the findings of Bailey (1967), Alexander *et al.* (1969) and Moseley & Jones (1984) indicates that this may be observed in their results as well: during the initial period after feeding, fractional removal rates appeared to be higher than those during the remainder of the 24 h period.

In the present experiment this rapid loss appears to be due to increases in both digestion and passage. During the period 0–5 h after feeding, 231, 169 and 280 g of the non-CW fraction were lost from the rumen for diets EC, LC and CL respectively, in agreement with the observation that the highest VFA concentration was measured on the clover diet between 0 and 5 h after feeding (Fig. 1). This rapid digestion of the readily-fermentable

carbohydrates in the rumen is in agreement with other reported observations, both with fresh and conserved forages (MacRae & Armstrong, 1969; Ulyatt & MacRae, 1974). During the same period the relative losses of INDF were greater than the losses of total NDF (65, 67 and 50% of INDF intake compared with 38, 52 and 24% of NDF intake for diets EC, LC and CL respectively) and this suggests that during eating the outflow from the rumen contains a high proportion of the residues from the previous day's feed. This possibility is supported by evidence relating to particle size: for example, Reid *et al.* (1979) showed that only 13% of the rumen digesta particles prefeeding were large enough to be retained on a 1 mm sieve. As particles that pass through a 1 mm sieve are generally considered to be those small enough to pass out of the rumen easily (Poppi *et al.* 1980), it follows that the probability of passage of the particles present in the rumen prefeeding would be very high. Since the frequency of reticulum contractions increases during E (Balch, 1971; Ulyatt *et al.* 1984) compared with R or resting, it is worth noting that the proportion of NDF lost during the 5 h period may be related to the length of time taken to consume the diet and, therefore, the length of time of enhanced reticulum contraction frequency. The diet that took the longest to eat (LC) also lost the greatest percentage of both DM and NDF (50 and 52 respectively), whereas the diet that was eaten in the shortest time (CL) only lost an amount equivalent to 24% of its NDF intake. The higher loss of total DM in this case (35%) probably occurred as a result of the high non-CW fraction of the diet.

It may also be observed in many of the studies on the removal of digesta from the rumen with intermittent feeding (e.g. Bailey, 1967; Alexander *et al.* 1969; Moseley & Jones, 1984) that the rapid loss of digesta immediately after feeding is followed by a lag phase during which removal from the rumen is slower than either earlier or later in the feeding cycle. This characteristic was also encountered particularly with the indigestible fractions of the diets in the present experiment. It was most evident for the INDF and IADF of the two grass hay diets EC and LC, for which there were almost no changes in rumen contents during the period 5–10 h after feeding. A decrease of this nature in the rate of passage may be due to the large load of digesta present in the intestines at the end of feeding, stimulating a negative feedback mechanism on reticulo-rumen activity (Phillipson & Ash, 1965). In addition, the large particle size of the newly ingested digesta may have limited its passage from the rumen. Reid *et al.* (1979) found that 48% of the digesta at the end of feeding was retained on a 1 mm sieve for a chaffed lucerne (*Medicago sativa*) diet, while 31% was retained on a 4 mm sieve. This latter fraction would tend to make up the floating raft of larger particles within the rumen (Evans *et al.* 1973), and these particles would have a very low probability of escape from the rumen by passage because of their situation in the rumen and their large size (Poppi *et al.* 1981; McBride *et al.* 1984).

The rate of removal of indigestible fibre increased slightly between 15 and 24 h after feeding and this coincided with a greater proportion of time being spent on rumination during the second half of the 24 h period (Fig. 2). Rumination has been shown to increase the frequency of recticulum contractions (Poppi *et al.* 1981). A similar daily pattern of rumination was also observed, for sheep fed once daily, by Ulyatt *et al.* (1984).

The effect of this variation in rate of removal of digesta during the day resulted in considerable differences in digesta pool sizes of all constituents between the start and finish of eating (Tables 4 and 5). Mean values for the wet weights of the digesta ranged between 8·0 and 13·2 kg, with dry weights of between 449 and 1251 g. Ulyatt *et al.* (1984) compared pool sizes in the rumen of sheep fed hourly with those fed once daily on lucerne hay; rumen DM pool sizes on hourly feeding were 579 g DM, while those fed once daily had pool sizes ranging from 440 g DM before feeding to 1163 g DM at 4 h after feeding, all animals being fed approximately 950 g DM daily. Variations in rumen pool size were also seen with the

fibre fraction: in the present experiment NDF amounts varied from 144 to 747 g, while Ulyatt *et al.* (1984) found fibre (cellulose + hemicellulose + lignin) contents ranging from 251 to 612 g on once-daily feeding, compared with 327 g on hourly feeding.

The mean pool size of digesta was smallest for diet CL and largest for diet LC, both in terms of DM and NDF (Table 5). These differences, obtained at restricted levels of feeding, are reflected in the voluntary intakes obtained from Expt 2: DM intake of diet CL was the highest, and that of diet LC the lowest. The voluntary DM intake of diet LC was only 36% higher than the level of intake imposed on Expt 1, whereas the corresponding intakes of diets EC and CL were 79 and 196% higher respectively. NDF intake at *ad lib.* levels, however, was lowest for diet CL, but did not differ significantly between the two grass hays, when expressed in g/kg LW (Table 7). These relatively constant amounts of NDF intake of the grass hay diets are in agreement with the observations by Mertens (1973) and Osbourn *et al.* (1974), that the CW fraction is the major component of forage diets that influences intake. The same relation does not apply for the clover diet. The reason for the lower NDF intake of the clover diet is unclear, but could be a result of the influence of the large non-CW fraction of the diet on rumen fill, as a consequence of the high intake of INDF compared with diet EC, or as a result of metabolic factors rather than rumen fill being the major satiety signal (Baumgardt, 1970).

These results thus support the hypothesis that degree of rumen fill is involved in the control of voluntary intake, particularly with the grass hays, while additional factors appeared to be involved in limiting the intake of the clover hay. They also suggest that in animals fed once daily there is a lag in passage of digesta out of the rumen shortly after the end of feeding, with an increase in rate during the second half of the daily feeding cycle.

E.M.A. was in receipt of an AFRC Postgraduate Scholarship during this work and this help is gratefully acknowledged. The authors would also like to record their appreciation to Miss Julia Marsh, Mr A. R. Austin, Mr R. F. Barnes and his staff, Dr E. Owen, and to Dr J. M. Cobby. The Grassland Research Institute was financed by the Agricultural & Food Research Council and this work was commissioned in part by the Ministry of Agriculture, Fisheries and Food.

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Printed in Great Britain