The partial digestion and ruminal volatile fatty acid concentrations in wethers fed high- and low-fibre diets*

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Twenty Dohne merino wethers with an average mass of 52 kg, were used to study the effect of varying the fibre content of the diet on differences in ruminal concentrations of volatile fatty acids (VFA) and the partial digestion of these diets. Dietary carbohydrate was provided as either structural (HF treatment) or readily fermentable (LF treatment), while energy and nitrogen intakes remained constant. The wethers were fitted with simple 'T' cannulae in the rumen, abomasum and ileum. The diets were fed at half-hourly intervals. ^{51}Cr-EDTA and ^{103}RuP were infused intraruminally for 14 days and spot samples were withdrawn from the various cannulae over the last four days, in order to determine digesta flow and apparent digestion of the diets in the different gastrointestinal compartments. Changing the form of dietary carbohydrate had no effect on organic matter (OM) or nitrogen (N) digestion. Quantitatively more starch ($p \leq 0.05$) was digested in the rumen (186 ± 24.6 g.day^{-1}) and small intestine (35.6 ± i2.6 g.day^{-1}) of the LF than the HF wethers, whereas more fibre ($p \leq 0.05$) was digested in the rumen (84.2 ± 10g.day^{-1}) and small intestine (7.4 ± 5.1 g.day^{-1}) of the HF than the LF wethers. Ruminal fermentation was significantly affected by altering the fibre : concentrate ratio in the diet. The molar proportions of the VFA differed significantly ($p \leq 0.05$) between the two treatments. The ruminal proportions of acetate, propionate and butyrate (mmol.mol^{-1}) were 0.721, 0.208 and 0.071 ± 0.01, respectively, in the HF group and 0.645, 0.226 and 0.112 ± 0.01, respectively, in the LF group. As a result the acetate : propionate ratio was lower ($p \leq 0.05$) in the LF compared to the HF wethers (2.86 and 3.48 ± 0.07, respectively). The main differences between the two treatments appeared to be an increased supply of glucogenic precursors (viz. glucose and propionate) to the host when the LF rather than the HF diet was fed.

Twintig Dohne merino hammels met 'n gemiddelde massa van 52 kg is gebruik om die verskil in ruminale konsentrasies van vlugtige vetsure (VVS) en die parsiële vertering van diëte te bepaal. Die dieet koolhidrate is as struktureel (HF behandeling) of maklik fermenteerbaar (LF behandeling) aangebied, terwyl energie en stikstofinnames konstant gebly het. Enkelvoudige 'T'-kannulas is in die rumen, abomasum en ileum, van die hammels ingesit. Die diëte is halfuurliks gevoer. ^{51}Cr-EDTA en ^{103}RuP is vir 14 dae intra-ruminaal geïnfuseer en monsters is oor die laaste vier dae vanuit die verskeie kannulas geneem om digestavloei en die oënskynlike vertering van die diëte binne die verskillende spysverteringskompartemente te bepaal. Die vormverandering van dieetkoolhidrate het nie 'n effek op die vertering van die organiese material (OM) of stikstof (N) gehad nie. Kwantitatief is meer ($p \leq 0.05$) stysel in die rumen (186 ± 24.6 g.dag^{-1}) en dunderm 35.6 ± 2.6 g.dag^{-1}) van die LF as die HF hammels verteer, terwyl meer ($p \leq 0.05$) vesel (84.2 ± 10 g.dag^{-1}) in die rumen en dunderm (7.4 ± 5.1 g.dag^{-1}) van die HF as die LF hammels verteer is. Ruminale fermentering is betekenisvol verander deur die dieetvesel : konsentraat-verhouding te verander. Die molêre verhoudings van die VVS het verskil tussen die twee behandelings. Die ruminale verhoudings van asetaat, propionaat en butyraat was 0.721, 0.208 en 0.071 ± 0.01, onderskeidelik, in die HF behandeling en 0.645, 0.226 en 0.112 ± 0.01, onderskeidelik, in die LF behandeling. As gevolg hiervan was die asetaat : propionaat-verhouding laer ($p \leq 0.05$) in die LF in vergelyling met die HF behandelde hammels (2.86 en 3.48 ± 0.07, onderskeidelik). Die belangrikste verskil ($p \leq 0.05$) tussen die twee behandelings lyk asof dit die groter voorsiening van glukogeniese voorlopers (glukose and propionate) aan die gasheer is wanneer die LF eerder as die HF dieet gevoer is.

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Introduction

Ruminants use dietary digestible energy (DE) more efficiently for production when this energy is provided as readily fermentable (soluble) carbohydrate (RFC; Black, 1983). Many hypotheses have been proposed to explain the differences in the efficiency of utilisation of roughage and concentrate diets with special attention being given to individual nutrients (Gill *et al.*, 1984; Black *et al.*, 1987a,b). When roughages are fed, little starch escapes rumen fermentation and only small amounts pass through to the small intestine. However, the fermentation of starch to VFA is an inefficient process for utilising feed energy and represents a loss to the nutritional economy of the animal.

Although there have been many studies to assess the effect of concentrate in the diet on partial digestion, the results are conflicting. Nicholson & Sutton (1969) and Chase & Hibberd (1989) reported that fibre digestion was depressed by a high amount of readily fermentable carbohydrates in the rumen. Soeparno *et al.* (1983) also showed that increasing the CP content of diets increased ruminal OM digestion. It may well be that differences in growth rate and efficiency result from changes in the efficiency of digestion, specifically when nitrogen and ME intakes are not balanced.

The results of a previous growth study (Linington *et al.*, 1996), utilising the same diets, showed that lambs fed high-fibre diets use the ME available less efficiently for growth than lambs fed low-fibre diets when fed at isonitrogenous and isoenergetic levels. The aim of this study was to determine the partial digestion of high- and low-fibre diets, to determine whether differences in energetic efficiency may be explained in terms of differences in the end products of digestion.

Methods

Animals

Twenty mature Dohne Merino wethers (body mass = 52 to 58 kg) were fistulated and had cannulae fitted in the dorsal sac of the rumen, the abomasum and the terminal ileum at least two months before experimentation. The animals were housed indoors in metabolic cages under artificial lighting and had free access to water. The diets were fed at equal energy and nitrogen intakes and were identical to those described by Linington *et al.* (1996), i.e. a high- (HF) and low-fibre (LF) diet. The sheep were inoculated and vaccinated against enterotoxaemia, blue-tongue and internal parasites. The wethers were randomly divided into two equal groups which were adapted to the HF diet (group HF) or the LF diet (group LF).

Experimental procedure

The voluntary intake of the HF sheep was determined over a two-week period. Thereafter, to ensure consistent intake, the HF sheep were fed at 90% of their *ad libitum* intake. The amount of the LF diet equal to 90% of the *ad libitum* ME intake of the HF diet was calculated and this amount offered daily to the LF sheep. The ration was fed in equal portions at half-hourly intervals. Feed refusals were determined daily. Two sheep, one from each diet, experienced problems with their cannulae and data from these sheep were omitted from the analyses. Live mass was determined before and after each trial.

Infusions

In order to estimate flow at the abomasum and ileum, ^{51}Cr-EDTA and ^{103}Ru-phenanthroline (^{103}Ru-P) (Pelindaba, S.A.) were infused into the rumen as liquid and particulate markers, respectively, according to the dual label method of Faichney (1975). The sheep were fitted with faeces bags and a priming dose of the radioactive markers (0.25 MBq ^{51}Cr-EDTA and 0.15 MBq ^{103}Ru-P) was given as a pulse dose into the rumen. This was followed by a continuous infusion (36 ml.h^{-1}) of ^{51}Cr-EDTA (2.23 MBq.d^{-1}, Downes & McDonald, 1964) and ^{103}Ru-P (1.15 MBq.d^{-1}, Tan *et al.*, 1971).

Sampling

After allowing 10 days for marker concentration in the rumen to reach equilibrium, spot samples were taken from the rumen, abomasum and ileum over the next four days of infusion. Samples were taken every 6 h, with the sampling times staggered from each other by 2 h each day. The pH of each ruminal sample was measured. Each spot ruminal, abomasal and ileal sample was divided in two. One half was frozen immediately, while the other half was divided into liquid- and solids-rich fractions (Faichney, 1980b). Nine millilitres of the liquid phase was preserved with 1 ml 10% m/v NaOH for VFA analysis. The unfractionated and fractionated samples were pooled for each sheep by combining equal aliquots after each collection. An aliquot (10%) of the faeces voided at each sampling time was taken, bulked, and stored frozen.

Analytical procedures

Radioactive concentrations of ^{51}Cr and ^{103}Ru in all digesta samples (whole and fractionated) and faeces were determined using a gamma-radiation spectrometer (LKB, Sweden), after first suspending the samples in a gel. The remaining unfractionated samples were freeze-dried and stored for further analysis. Dry matter (DM), organic matter (OM), crude fibre (CF) and nitrogen (N) content were determined according to standard methods (A.O.A.C., 1990). Starch was measured according to the method of MacRae & Armstrong (1968). Acid detergent fibre (ADF) was determined according to the method of Goering & van Soest (1972). Volatile fatty acids (VFA) concentrations were estimated via gas chromatography (Suzuki & Lund, 1980).

Calculations

The quantity and composition of true digesta flowing at the abomasum and ileum was calculated by reference to ^{51}Cr-EDTA as the liquid phase marker and ^{103}Ru-phenanthroline (Ru-P) as the particulate markers (Faichney, 1975). True digesta were reconstituted according to marker concentrations in unfractionated and fractionated digesta. Apparent digestibilities of the dietary components in the rumen, small intestine and large intestine were calculated from the difference in flow of these components between compartments.

Statistics

pH values were converted to log values for statistical calculation. The statistical significance of differences between diets was calculated using the Statgraphics 6.0 (Manugistics, Inc., Maryland, USA) personal package in which the two-sample test with pooled variance provided a *t*-statistic for unpaired samples with unequal variances.

Results

Intake

No feed refusals occurred. DM intake was 1.36 and 1.13 kg.day^{-1} for the HF and LF diets, respectively. The gross energy (GE) intake of the HF fed group was 24.27 MJ.day^{-1}, 19% greater than that of the LF group. The digestible energy (DE) intake was 16.3 and 15.2 ± 0.57 MJ.day^{-1} for the HF and LF groups, respectively. The nitrogen and theoretical ME intakes of both diets were similar (ca. 141 g N.day^{-1} and 13

MJ ME.day^{-1}, respectively) and the ME intake was 0.82 and 0.86 of the DE intake for the HF and LF groups, respectively.

Digesta flow

The cannula for sampling postruminal flow was inserted in the abomasum since duodenal cannulae may affect digesta flow (Egan & Doyle, 1984). The flow of digesta past the different sites is depicted in Table 1 and was significantly higher in the HF compared to the LF group probably since the DM intake of the HF fed sheep was 20% higher than that of LF fed sheep. When expressed as kg flow per 100 g of OM intake, flow at the ileum and faecal output differed significantly ($p \leq 0.05$) between diets.

It is clear that, although some of the differences in flow resulted from the higher intake (Otchere *et al.*, 1974), there were also differences in digestion and flow kinetics in the gastrointestinal tract (GIT) between groups.

Partial digestion of nutrients

Organic matter

The intake, flow and digestion rates of OM in the GIT are shown in Table 2. The flow of OM was similar to DM flow and tended to be higher in the HF than the LF group. OM faecal output was 45.5% higher in the HF compared to the LF group ($p \leq 0.05$). The apparent digestion of OM in the rumen and small intestine did not differ between groups. Although intake and flow of OM was greater in the HF than LF group, the amount of OM disappearing from the large intestine was 69.3% greater in the LF than the HF group. This resulted in the OM digestibility coefficient in the large intestine being significantly ($p \leq 0.05$) greater in the LF than in the HF group. Relatively small amounts of the total OM digestion occurred in the large intestine, about 9% and 5% in the case of the LF and HF groups, respectively. However, the amount digested per day was similar. Thus these results were to contrary to those of Chase & Hibberd (1989), who reported a depression of OM digestibility owing to a higher starch intake but similar to results obtained by Poore *et al.* (1993).

Acid detergent fibre

The intake, flow and digestion rate of acid detergent fibre (ADF) in the HF and LF fed sheep are given in Table 3. ADF intake of the HF diet was double that of the LF diet (330 vs. 165 g.day^{-1}). As a result, the flow along the tract as well as

Table 1 Digesta flow at various sites of the gastrointestinal tract (kg.day^{-1}; n = 9 per group; mean ± s.e m.)

Site	HF	LF	s.e.m.	p
Abomasum				
kg.day^{-1}	18.7	15.84	± 0.81	0.05
kg. 100 g OM intake^{-1}	1.51	1.51	± 0.025	NS
Ileum				
kg.day^{-1}	5.32	3.30	± 0.23	0.05
kg.100 g OM intake^{-1}	0.433	0.314	± 0.014	0.05
Faecal output[d]				
kg.day^{-1}	1.11	0.79	± 0.07	0.05
kg.100 g OM intake^{-1}	0.094	0.071	± 0.002	0.05

[d] Calculated from total faeces excreted

s.e.m. = standard error of the mean; NS = non-significant

Table 2 The intake, flow and apparent digestion of organic matter in the gastrointestinal tract on a dry matter basis (n = 9 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Intake (g/day)	1236	1048		
Total flow (g/day)				
At abomasum	638	585	± 92	NS
At ileum	412	327	± 35	NS
Faecal output	367	250	± 23	0.05
Apparent digestion (g/day)				
In rumen	597	462	± 81	NS
In small intestine	225	258	± 30	NS
In large intestine	45.9	76.3	± 5	0.05
In total tract	868	797	± 55	NS
Site of digestion (% of total)				
Rumen	68.8	58.0	± 9.3	NS
Small intestine	26.0	32.4	± 4.1	NS
Large intestine	5.2	9.6	± 0.6	0.05
Digestibility coefficients (%)				
In rumen	48.4	44.1	± 6.9	NS
In small intestine	35.4	44.1	± 5.0	NS
In large intestine	10.9	23.3	± 1.4	0.05
Total tract	70.3	76.1	± 4.5	NS

s.e.m. = standard error of the mean; NS = not significant.

Table 3 The intake, flow and apparent digestion of acid detergent fibre (ADF) in the gastrointestinal tract on a dry matter basis (n = 9 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Intake (g/day)	328.2	164.6		
Total flow (g/day)				
At abomasum	200	121	± 25.2	0.05
At ileum	163	89.9	± 10.7	0.05
Faecal output	152	86.0	± 9.4	0.05
Apparent digestion (g/day)				
In rumen	127.3	43.1	± 14.5	0.05
In small intestine	37.6	31.7	± 4.1	NS
In large intestine	11.2	3.9	± 0.6	0.05
In total tract	176.1	78.7	± 10.9	0.05
Site of digestion (% of total)				
Rumen	72.3	54.7	± 9.4	0.05
Small intestine	21.4	40.3	± 4.5	0.05
Large intestine	6.4	4.9	± 0.5	NS
Digestibility coefficients (%)				
In rumen	38.8	26.1	± 5.0	0.05
In small intestine	18.7	26.1	± 2.9	NS
In large intestine	6.9	4.4	± 2.1	NS
Total tract	53.7	47.8	± 3.4	NS

s.e.m. = standard error of the mean; NS = not significant.

faecal output was significantly greater for the HF compared to LF group. However, the difference in flow at the abomasum (36%) was lower than the difference in intake. Similarly, the apparent digestion of ADF was significantly greater in the HF than the LF group, except in the small intestine where equivalent amounts of ADF disappeared. The smaller difference in abomasal flow derived from the significantly ($p \leq 0.05$) lower ADF digestibility in the rumen of the LF group. As a result, the rumen played a less important ($p \leq 0.05$) role than that of the small intestine in this group.

Fibre digestion in this portion of the gastrointestinal tract probably results from bacteria derived either from the large intestine (retrograde colonisation) or viable organisms passing through the tract. If the digestion in the small intestine of the LF fed sheep is expressed as a percentage of intake, it contributed only 19.3% to fibre digestion. Although this is greater than the 11.5% in the HF fed group, it is clear from the small intestine digestibility coefficients of 18.7% and 26.1% for the HF and LF diets respectively, that it is not significant. Total tract ADF digestibility was higher in the HF than in the LF group but the difference was not significant.

Starch

The intake, flow and apparent digestion of starch is depicted in Table 4. Starch intake of the LF group was more than double that of the HF group (415 vs. 189 g.day^{-1}). As a result, flow and apparent digestion of starch was significantly ($p \leq 0.05$) greater for the LF than the HF group. These differences were proportional to the difference in intake, except for faecal output, which was 85% lower in the HF in than the LF group, considerably more than the decrease in intake. This appears to be the result of a lower starch digestibility in the large intestine in the LF group. About 80% of starch, irrespective of intake, was digested in the rumen. This agrees with results of Tucker *et al.* (1966), Waldo (1973), Poore *et al.* (1993) and Murphy *et al.* (1994b), who also showed that ruminal fermentation of maize starch depends on the method of processing.

There was no effect of diet on site of digestion. The digestibility coefficients of the various compartments were lower for the LF than the HF diet. This however, was only significant in the large intestine. The low digestibility of starch in this compartment on the LF group is probably due to a combination of a faster flow rate i.e. decreased digestion, and a deficiency of enzymes i.e. the capacity of the large intestine to digest starch might have been exceeded.

Nitrogen

The intake, flow and apparent digestion of N is shown in Table 5. Intake and flow through the gastrointestinal tract was similar for both diets. The amount of nitrogen disappearing from the various regions of the gastrointestinal tract was similar for both diets. It is interesting to note that the difference between the two groups in the amount disappearing from the rumen was 3.5 g and from the small intestine 3.8 g. Thus the amount disappearing from the tract anterior to the large intestine was similar for both groups, i.e. 23.5 and 23.8 ± 3.1g N per day for the HF and LF diets, respectively.

There was a net loss of N from the rumen on both diets (HF: 7.7 and LF: 4.2 ± 0.9 g.day^{-1}). Our results agree with Siddons *et al.* (1985), who reported a net loss of N from the rumen of sheep fed on high N diets. About 77% and 87% of N bypassed the rumen and was available for digestion in the

Table 4 The intake, flow and apparent digestion of starch in the gastrointestinal tract on a dry matter basis (n = 9 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Intake (g/day)	189.1	415.2		
Total flow (g/day)				
At abomasum	38.8	88.6	± 8.0	0.05
At ileum	7.3	21.5	± 2.1	0.05
Faecal output	1.4	9.3	± 0.2	0.05
Apparent digestion (g/day)				
In rumen	150.3	326.6	± 27.4	0.05
In small intestine	31.5	67.1	± 3.6	0.05
In large intestine	5.9	12.2	± 0.8	0.05
In total tract	187.7	405.9	± 13.3	0.05
Site of digestion (% of total)				
Rumen	80.1	80.5	± 11.8	NS
Small intestine	16.8	16.5	± 2.3	NS
Large intestine	3.1	3.0	± 0.3	NS
Digestibility coefficients (%)				
In rumen	79.4	78.7	± 6.93	NS
In small intestine	81.2	75.7	± 5.24	NS
In large intestine	80.8	56.8	± 4.96	0.05
Total tract	99.3	97.8	± 6.29	NS

s.e.m. = standard error of the mean; NS = not significant.

Table 5 Nitrogen intake, flow and apparent digestion in the gastrointestinal tract on a dry matter basis (n = 9 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Intake (g/day)	33.2	32.5		
Total flow (g/day)				
At abomasum	25.5	28.3	± 4.0	NS
At ileum	9.7	8.7	± 0.9	NS
Faecal output	7.7	7.6	± 0.5	NS
Apparent digestion (g/day)				
In rumen	7.7	4.2	± 0.9	NS
In small intestine	15.8	19.6	± 2.2	NS
In large intestine	2.0	1.1	± 0.1	0.05
In total tract	25.5	24.9	± 1.6	NS
Site of digestion (% of total)				
Rumen	30.0	16.9	± 3.3	0.05
Small intestine	62.0	78.7	± 8.6	NS
Large intestine	7.8	4.4	± 0.44	0.05
Digestibility coefficients (%)				
In rumen	23.2	12.9	± 2.0	0.05
In small intestine	62.0	69.3	± 4.6	NS
In large intestine	20.6	12.6	± 1.9	0.05
Total tract	76.8	76.6	± 3.8	NS

s.e.m. = standard error of the mean; NS = not significant.

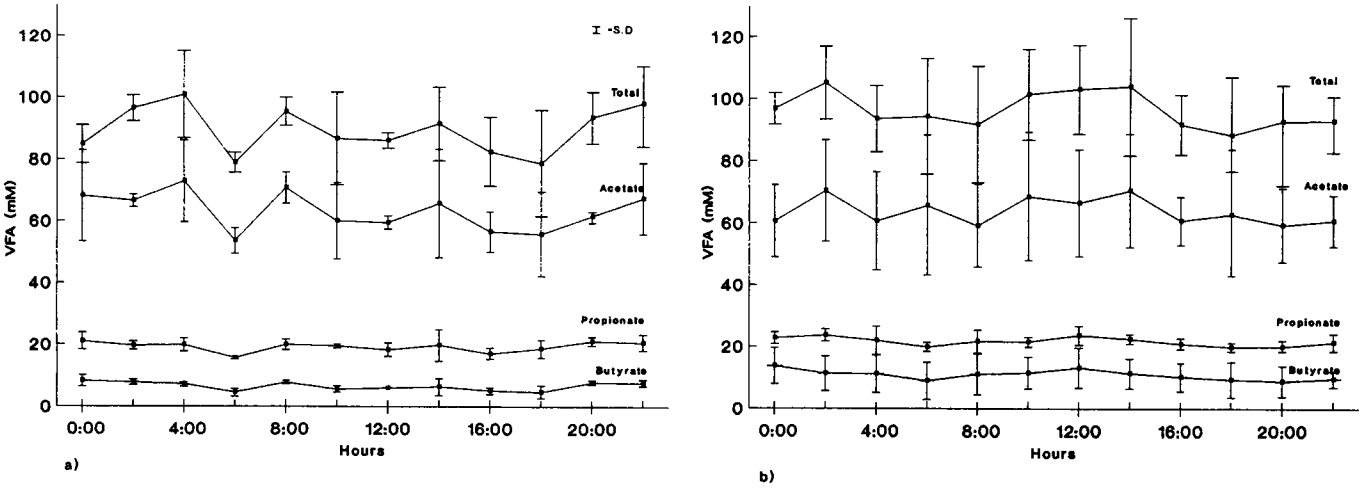

Figure 1 The ruminal VFA concentrations in (a) the LF and (b) the HF wethers over a 24-h period (n = 9 per group; mean ± standard deviation).

small intestine in the HF and LF groups, respectively. The digestibility of N in the rumen was significantly ($p \leq 0.05$) greater in the HF than in the LF group. The small intestine was the major site of digestion and there was no significant difference between diets in N digestibility in the small intestine. Total tract digestibility was similar for both diets.

pH and volatile fatty acid concentrations in the rumen

The VFA concentration patterns over a 24-h period are shown in Figure 1. There were no significant differences between concentrations over a 24-h period. The slight fluctuations in total concentration appeared to have resulted from fluctuations in acetate concentration. One result of frequent feeding is nutritional steady state in the rumen (Sutton *et al.*, 1986), which is reflected in this data. The importance of establishing that the feeding regime produced constant ruminal VFA concentrations, was to ensure that data obtained in further experiments was representative of normal ruminal conditions. Consequently results may be extrapolated to daily values.

The ruminal pH levels and concentrations of VFA are shown in Table 6. pH was lower in the rumen of the LF than the HF group but this difference was not significant. Total VFA concentrations were between 94–96 mM and did not differ significantly between the two groups. The molar proportion of acetate in the LF group was lower ($p \leq 0.05$) than in the HF diet, whereas the proportions of propionate ($p \leq 0.05$) and butyrate ($p \leq 0.05$) were significantly higher in the LF than in the HF group. As a result, the ruminal acetate : propionate ratio was significantly lower ($p \leq 0.05$) on the LF diet (2.86 vs. 3.48 ± 0.07) compared to the HF diet. The non-glucogenic ratio (NGR) is a measure of the proportion of propionate compared to the non-glucogenic VFA. The NGR is significantly lower on the LF compared to the HF diet (3.85 and 4.15 ± 0.1, respectively). The difference is less than the acetate : propionate ratio owing to the higher butyrate concentration in the LF than in the HF group.

Table 6 The concentrations and proportions of volatile fatty acids and pH in the rumen (n = 9 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	$p \leq$
pH	5.72	5.57	± 0.27	NS
Total VFA (mM)	93.87	95.73	± 7.04	NS
Molar VFA Proportions: (mmol/100 mmol)				
Acetate	0.721	0.645	± 0.01	0.05
Propionate	0.208	0.226	± 0.01	0.05
Butyrate	0.071	0.112	± 0.01	NS
A: P ratio	3.48	2.86	± 0.07	0.05
NGR	4.15	3.85	± 0.1	0.05

s.e.m. = standard error of the mean; NS = not significant; NGR = non-glucogenic ratio.

The results reported here agree with those of Sutton *et al.* (1986) and MacLeod *et al.* (1994). The total products of rumen fermentation were not affected by meal frequency but there was a definite response in terms of the end products of fermentation to decreased dietary fibre.

Discussion

The double marker technique for estimating flow in animals (Faichney, 1980b) allows for deviations from the ideal in particular the imperfect association of marker with phase, provided that there is a continuous, constant and equal inflow and outflow in the system. The use of Ru-P as a marker has however been questioned. Egan & Doyle (1984) suggested that ^{103}Ru-P should not be used as a particulate marker with roughage diets, but that it would be acceptable when highly digestible or finely ground diets are fed.

Denny *et al.* (1979) used ^{103}Ru-P successfully with sheep fed roughage diets, contrary to Egan & Doyle (1984) and Pienaar *et al.* (1980) who obtained poor results when feeding coarsely chopped roughages. According to Faichney (1980a; 1982), errors only accumulate if conditions deviate greatly from steady-state.

In this study, ^{103}Ru-P was an acceptable particulate phase marker since these diets were milled, were of reasonable digestibility and were fed at half-hourly intervals. Although less than 10% of samples were reconstituted, the double marker method provided the assurance that the composition

of the digesta samples reflected the true composition of digesta flowing past the cannulae (Faichney, 1993).

Changing the form of carbohydrate from structural to readily fermentable did not affect the digestion of OM in the rumen, small intestine or total tract. These results do not agree with the findings of Nicholson & Sutton (1969) and Chase & Hibberd (1989). These authors found that, although total OM digestibility was not influenced by maize supplementation, hay OM and fibre digestibilities were suppressed by maize addition. However, Ben-Ghedalia & Solomon (1987) and Poore *et al.* (1993) reported that increasing barley or starch intake did not affect OM digestion. Few of these diets were fed at isoenergetic and isonitrogenous levels and it is possible that the altered energy : nitrogen ratio could have influenced ruminal OM digestion. Our data show that the form of carbohydrate does not affect ruminal OM digestion, provided that the diets are isonitrogenous and iso-energetic.

Nicholson & Sutton (1969) and Chase & Hibberd (1989) reported that fibre digestion was also depressed by a high amount of readily fermentable carbohydrates in the rumen. The data presented here support the hypothesis that ruminal fibre digestion is suppressed when low-fibre diets are fed. However, there was no effect on digestion in the total tract, similar to the results of Poore *et al.* (1993). These results differ from those of Chase & Hibberd (1989), who reported that ruminal depression of fibre digestion in the presence of readily fermentable carbohydrates was accompanied by decreased ruminal OM digestibility.

Goetsch *et al.* (1987) suggested that when diets are ground and pelleted, there would be less frequent rumination and more time for bacterial attachment to the fibre. This would thereby increase fibre digestion of a low-fibre diet comparable to that of a high-fibre diet. In this study, although the diets were milled and pelleted, there was still reduced ruminal fibre digestion. This is most probably due to a shift in the microbial population resulting in fewer and less active cellulolytic bacteria than in roughage fed animals (Hiltner & Dehority, 1983). Furthermore, microbial efficiency is greater in the rumen of sheep fed forage diets than those fed concentrate diets (Martin *et al.*, 1994; Poore *et al.*, 1993), as a result of a faster ruminal digestion rate, a higher pH and a longer retention time for solids. The greater cellulolytic activity in the rumen of roughage-fed animals might expose more cellulose to microbial attack.

The digestibility coefficients of starch in the rumen were similar for both diets. Approximately 80% of starch entering the rumen was fermented. This represented 11% and 28% of the GE intake for the HF and LF diets, respectively. Waldo (1973) estimated ruminal fermentation of maize starch to be 78 ± 12% and showed that the proportion of starch fermented in the rumen is more dependent on the method of processing than on intake (Poore *et al.*, 1993; Murphy *et al.*, 1994b). In the present study, the maize was milled and the ruminal digestibility coefficients would thus appear to be reasonable.

A higher starch intake may affect the heat increment of feeding (HIF) produced by the rumen. Arieli (1986) investigated the heat increment of glucose fermentation (H_f) *in vitro*. His results showed that adding glucose to rumen inoculum caused a dose-dependent increase in the HIF. Although in the present study it is likely that a large quantity of starch was incorporated into bacterial polysaccharides, total heat produced from starch fermentation would still have been greater on the LF than on the HF diet.

It is possible that the capacity of the small intestine to digest starch may have been exceeded in the LF group of sheep (Owens *et al.*, 1986). This phenomenon has been previously reported (Ørskov *et al.*, 1969; Russell & Chow, 1993). The results of Ben-Ghedalia & Solomon (1987) showed that glucose digestibility in the small intestine increased with a higher barley intake, whereas Russell & Chow (1993) found a decreased starch digestibility. The response to increased starch bypass would seem to depend on prior exposure, since sheep seem to be able to adapt to increased starch intake. Janes *et al.* (1985a,b) reported an increase in both the activity and the concentrations of the enzymes necessary to digest and absorb starch in the intestinal mucosa in response to the feeding of starch. In the present study, *ca* 26.5 g more starch was digested daily in the small intestine of the LF compared to the HF fed sheep, thereby supplying the animal with *ca* 29 g more glucose and 0.62 MJ more energy per day.

The amount of nitrogen disappearing from the rumen was greater in the HF than in the LF sheep. It is possible that the greater cellulolytic activity and the longer ruminal retention time exposed more protein to microbial attack. These results are similar to those of Murphy *et al.* (1994a,c) and Meyer *et al.* (1986), who found that flow of nitrogen to the small intestine increased with increased starch intake. These results support the principle that energy availability is a major determinant of microbial growth in the rumen (Sudweeks *et al.*, 1981; Herrera-Saldana *et al.*, 1990).

Most of the protein reaching the abomasum is of microbial origin. Ben-Ghedalia & Solomon (1988) fed various combinations of roughage and barley and concluded that most of the nitrogen reaching the small intestine was of microbial origin, irrespective of the roughage : concentrate ratio. In the present study, the digestibility of nitrogen in the small intestine ranged between 62–70%. The digestibility of microbial nitrogen in the small intestine has been found to be 80%. This suggests that the dietary nitrogen not degraded in the rumen must have been of a very low quality. Since there was no significant dietary effect on the digestibility of N in the small intestine, it is therefore reasonable to assume that the CP composition reaching the small intestine was unaffected by diet. The amount of nitrogen apparently digested in the small intestine is a good indication of the protein available to the host (Cotta & Hespell, 1986), and was similar for both diets in the present study.

Another factor affecting N digestion is the ratio of energy to N in the diet (Murphy *et al.*, 1994c). Soeparno *et al.* (1983) reported that increasing the CP content of diets increased OM digestion in the rumen, as well as the supply of CP to the small intestine. In the present study, the energy and protein intakes were similar for both diets in order to ensure that there was no effect of either protein or energy level on digestion. This may well have contributed to the similar digestion of the two diets in the small intestine.

The total concentration of VFA in the rumen did not differ between diets, however molar proportions of the individual acids were different. The VFA patterns were similar to those expected (Dijkstra, 1994; Dijkstra *et al.*, 1993; McAllan *et*

al., 1994). The frequent feeding regime produced concentrations and fluctuations (Figure 1) as reported by other authors e.g. Sutton *et al.* (1986) & MacLeod *et al.* (1994) who demonstrated that frequent feeding smoothed the cyclic pattern of VFA supply, and affected VFA pattern and concentration only slightly. Other authors (Froetschel *et al.*, 1983; Holzer *et al.*, 1986) found ruminal VFA concentrations to be higher for roughage than for concentrate diets while the molar proportions did not differ between diets, and concluded that this unexpected pattern may have been due to either the frequency of feeding or to the fact that the diets were isoenergetic and isonitrogenous. In the present study, the feeding frequency was higher (half-hourly as opposed to two hourly intervals) and the ME and N intakes were similar. The reason for these differences is not clear, however these do not appear to be due to feeding frequency or the equal energy and N intakes. Feeding frequency has been shown to have no effect on VFA patterns (MacLeod *et al.*, 1994) whereas feeding diets isoenergetically as well as isonitrogenously but changing the fibre content caused the molar proportions of VFA to shift from a high acetate type fermentation pattern on the high-fibre diet to a high propionate type of fermentation pattern on the low-fibre diet Abdul-Razzaq *et al.*, 1988).

The VFA concentrations in the rumen have been shown to be proportional to their production rates in sheep fed a high-fibre diet (van der Walt & Briel, 1976). However, MacLeod *et al.* (1984) reported that this held true only for hay diets and not for diets containing concentrates. Dijkstra (1994) suggested that the ruminal VFA proportions in the rumen do not represent the proportions in which they are produced since the individual VFA absorption rates vary with changes in pH or VFA concentration (Dijkstra *et al.*, 1993). Thus the VFA proportions in Table 6 only indicate a range in ruminal fermentation pattern and not necessarily a change in production rates.

The data from the digestion study showed that changing the type of carbohydrate in the diet (from structural to readily fermentable) did not have a major effect on the digestion and partial digestion of substrates. There was no significant difference in total tract digestibility of OM, ADF, starch or nitrogen, or total ruminal VFA concentrations between diets. The results from the partial digestion study contradict the results of some other authors (Lee *et al.*, 1986; Asplund, 1987) who found that increased starch intake decreased OM and fibre digestion. Goetsch *et al.* (1987) suggested that ground maize creates a more segmented ruminal fermentation pattern by initially increasing starch breakdown and decreasing fibre digestion. A possible explanation for the conflicting results might lie in the physical treatment given to the diets, i.e. the milling and pelleting of the diet (Murphy *et al.*, 1994 a,b,c). Changing the form of the carbohydrate however, caused fibre digestion in the rumen of sheep fed the LF diet to be lower. This was not accompanied by lower ruminal OM digestibility when compared to the HF diet, or lower digestibility of starch and nitrogen in the large intestine. There were no effects on small intestine digestibility of nutrients. However, N disappearing from the rumen of the HF group was higher than in the LF group. Whether this N was lost as ammonia and then converted to urea by the liver and incorporated into amino acids or excreted in the urine is not known.

The most significant finding of the partial digestion study was the change in the ruminal fermentation pattern. Although ruminant nutritionists have often concentrated on the VFA as the major factors in changing the efficiency of ME utilisation, the quantity of digestible carbohydrates fermented in the rumen and absorbed from the small intestine may also have important effects on ruminant energy balance. The improved efficiency of ME utilisation observed on the LF diet in the growth study may have resulted from the by-pass glucose digested in the small intestine and the altered VFA pattern in the rumen.

It may be concluded, therefore, that changing the form of carbohydrate had little effect on lower tract digestion but did alter the pattern of rumen fermentation. Since the total VFA concentration in the rumen did not differ between diets, it appears that the differences in the efficiency of nutrient utilisation do not lie in the fermentation or digestion of the diets, but possibly in the partitioning of the absorbed end products between various metabolic processes.

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