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Ammonia treatment of wheat straw. 1. Voluntary intake, chewing behaviour, rumen pool size and turnover and partition of digestion along the gastro-intestinal tract of sheep

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Abstract

The impact of ammonia treatment of wheat straw on intake and digestion and passage kinetics was studied with 6 wether sheep. Ammoniated wheat straw (AWS) was compared with untreated wheat straw (UWS) and untreated wheat straw supplemented with urea (SWS). Ammonia treatment increased intake and whole tract digestion without affecting rumen pool size and rate of passage significantly. The increased cell wall intake due to ammonia treatment could for 91 % be attributed to a higher rumen degradation of cell walls. No significant effects of ammonia treatment on concentration, molar composition or rate of absorption of volatile fatty acids were observed. The rate of passage in the hindgut and the contribution of the hindgut to whole tract digestion were not significantly affected by ammonia treatment. Rumination and eating time and daily number of rumen contractions did not differ between rations, but AWS showed a lower rumination time per kg NDF ingested than the control rations. Whole tract digestion and rumen degradation of hemicellulose increased more due to ammonia treatment than those of cellulose. The effects of ammonia treatment could not be attributed to N supplementation, since no effect of urea supplementation on any parameter, except rumen ammonia-N concentration was observed.

Keywords; wheat straw, ammonia treatment, site of digestion, rumination, rumen degradation, rumen passage, hindgut passage

Introduction

In small-scale farming systems in densely populated areas in the tropics the productivity of the ruminant livestock depends to a large extent on fibrous crop residues like rice and wheat straw. These crop residues are generally characterized by a low intake and digestibility. Improvement of the nutritional quality of fibrous crop residues may be achieved through selection and breeding of varieties with a relatively

good straw quality (Capper, 1988), supplementation with deficient nutrients and alkaline treatment (Sundstøl & Owen, 1984). Alkaline treatment of straw with ammonia or NaOH as the reagent, improves microbial digestion of the cell wall fraction through disruption of ester bonds between hemicellulose and lignin (Mason et al., 1990; Morrisson, 1983; Chesson et al., 1983).

The extent of microbial digestion in the reticulo-rumen is determined by the rate and potential extent of degradation of digesta and the retention time of particles in the reticulo-rumen. Retention time in the reticulo-rumen is related to particle size distribution (Poppi et al., 1980; Egan & Doyle, 1984) and functional specific gravity of particles (Sutherland, 1987). The contribution of microbial degradation to particle size reduction is limited and reduction of particle size is therefore mainly determined by chewing during eating and rumination (Ulyatt et al., 1986).

Particle size reduction is, however, probably not the main rate limiting step for passage of particles from the reticulo-rumen (Ulyatt et al., 1986). Passage of particles is higher during eating than during resting and rumination (Girard, 1990), which could be related to the higher frequency of rumen contractions during eating (Ulyatt et al., 1986). Okine et al. (1990) observed, that the duration of individual rumen contractions rather than frequency of rumen contractions was positively related to geometric mean particle size of faeces, indicating an increased probability of passage of larger particles with increased duration of rumen contractions.

Increased intake is often associated with increased rate of passage of particles, but ruminants with higher intake may also increase the rumen load of particles either by increasing the total rumen load or by increasing the DM content of the rumen digesta (Owens & Goetsch, 1986, Bosch et al., 1992).

Increased particle passage from the rumen may result in a lower degradation, particularly due to a reduced duration of microbial degradation. This may, however, in part be compensated by a higher hindgut fermentation, since more potential degradable material becomes available for microbial degradation in the caecum and colon (Demeyer, 1991).

The nutritive value of low quality feeds is in addition to voluntary intake and digestion related to proportions of individual volatile fatty acids produced and the amount of amino acids that become available for absorption from the small intestine. Propionic acid is a precursor for gluconeogenesis, while acetate and butyrate can only be utilized for energetic purposes and fat synthesis. In case of limited propionate production amino acids could be utilized for gluconeogenesis. The amount of amino acids that come available for absorption in the small intestine depends, in case of low quality feeds largely on the quantity of microbial protein synthesized in the rumen (Hvelplund, 1989).

The experiment reported here had as objective to study the implications of ammonia treatment of wheat straw on parameters as

- voluntary intake, digestion and site of digestion
- eating and rumination behaviour
- rumen pool size
- rumen degradation and rumen and hindgut passage.

The effect of ammonia treatment on amino acid and N digestion is reported elsewhere (Oosting et al., 1993).

Materials and methods

Six sheep (wethers) with an average live weight of 44 kg were fitted with a rumen cannula (Bar Diamond Inc. 3 inch diameter) in the dorsal rumen sac, a silastic infusion tube (3 mm internal diameter) in the abomasum and with T-shape hard pvc cannulas (12 mm internal diameter) in the proximal duodenum and terminal ileum. The experiment started 2.5 months after surgery, after the animals had well recovered.

During the experiment the animals were kept in metabolic cages and received equal portions of their ration at 04.00, 08.00, 12.00, 16.00, 20.00 and 24.00 h. Water and a mineral lick containing NaCl, Fe, Mg, Mn and Co were freely available.

The animals were randomly allotted into three groups of two sheep each. Group one was fed untreated wheat straw ad libitum supplemented with pelleted sugar beet pulp (UWS). Group two was fed the same ration with an infusate into the rumen of an urea solution (60 ml/h; concentration of 5.4 g urea-N/l; 7.9 g N daily) (SWS) and group three was fed ammoniated wheat straw ad libitum also with a supplement of pelleted sugar beet pulp (AWS).

The untreated and ammoniated wheat straws were offered in a quantity of 1.8 kg daily, thus allowing selection. The sugar beet pulp was supplied at a level of 240 g product daily. The composition of the feeds is given in Table 1.

The wheat straw was ammoniated in the late summer of 1989 by injecting 40 kg of anhydrous ammonia into stacks of 900 kg baled straw, totally covered with two layers of polythene sheets of 0.15 mm thickness. During injection, tubes were inserted in the bottom of the stacks to let the air out. After injection these tubes were removed. The stacks were opened after 35 days.

Before the onset of the experiment the animals were well adapted to the straw rations and the whole experimental routine. Before the start of the experiment untreated straw was fed during 5 weeks. Subsequently, the experiment consisted of a two week adaptation period and a seven week experimental period, in which the various measurements were conducted as indicated in Table 2.

In experimental weeks 1 and 6, the turnover rates of the liquid and particulate phases in the reticulo-rumen were estimated with Co-EDTA and Cr-NDF (Udén et al., 1980), respectively. On Monday at 08.00 h, 3.4 g Co-EDTA (0.51 g Co) and 10 g Cr-

Table 1. Composition (g/kg) of untreated wheat straw (UWS), ammoniated wheat straw (AWS) and pelleted sugar-beet pulp (SBP).

	UWS	AWS	SBP
DM	887	843	886
Ash (DM)	84	85	105
N (DM)	6	18	13
NDF (DM)	785	751	425
Hemicellulose (DM)	285	250	151
Cellulose (DM)	425	437	237
Lignin (DM)	75	64	37

Table 2. Time chart of activities over the experimental period.

	Experimental week[1]						
	1111111	2222222	3333333	4444444	5555555	6666666	7777777
in sacco degradation	** *				** *		
rumen NH_3/VFA/pH	*					*	
eating/rumination	******					******	
rumen passage	******	*				******	*
rumen contractions	******					******	
hindgut passage		***			***		
flow small intestine			****	****			
intake and digestion			******	******			
rumen evacuation							***

[1] Days within week Sunday to Saturday.

NDF (0.43 g Cr, particle size 0.2-1.0 mm) were introduced into the ventral rumen sac. Subsequently, rumen fluid samples were collected at 09.00, 10.00, 11.00, 12.00, 14.00, 16.00, 18.00, 20.00, 22.00 h on Monday and at 0.00, 2.00, 4.00, 6.00, 8.00, 12.00, 16.00 and 20.00 h on Tuesday. Co was determined with an atomic absorption spectrophotometer (Varian SpectraA 300; 240.7 nm) after wet destruction.

Total collection of faecal excreta was done from Tuesday 08.00 h to Thursday 0.00 h every 4 hours, from Thursday 0.00 h till Saturday 08.00 h every 8 hours and from Saturday 08.00 h till Sunday 20.00 h every 12 hours. After subsampling, faeces were dried and Co and Cr were measured after wet destruction by atomic absorption spectrophotometry at wavelengths of 240.7 and 357.9 nm, respectively.

The dilution rate of the liquid phase marker (Co) was estimated directly in the rumen fluid ($k_{l\text{-rumen}}$) and from the faecal excretion pattern ($k_{l\text{-faeces}}$, adapted from Grovum & Williams, 1973). The fractional passage of the particulate phase marker (Cr) from the reticulo-rumen was derived from the descending part of the faecal excretion curve (k_p, adapted from Grovum & Williams, 1973). The reticulo-rumen liquid volume was estimated by extrapolation of the Co dilution curve obtained from direct sampling of rumen fluid to $t = 0$.

The pH, ammonia and volatile fatty acid (VFA) concentrations in the rumen fluid were measured in samples taken on Monday, hourly from 09.00 till 12.00 h, and two hourly from Monday 12.00 h till Tuesday 08.00 h in experimental weeks 1 and 6. The ammonia concentration was measured by the indophenol method (Scheiner, 1976). The extinction of the blue colour was measured at 634.8 nm with a Hitachi U 2000 spectrophotometer. VFA concentrations were determined by gas liquid chromatography (Packard 419, glass column filled with chromosorb 101, carrier gas N_2 saturated with formic acid, 190 °C with isocapronic acid as an internal standard).

The kinetics of fermentative degradation of untreated and ammoniated wheat

straw were studied in sacco starting on Friday before experimental weeks 1 and 6. Three grams of wheat straw or ammoniated wheat straw (ground to pass a 1 mm sieve) were weighed into dacron bags (size 70 × 120 mm; pore size 40 μm). The bags were incubated over 0.5, 6, 12, 24, 36, 48 and 72 h periods. Each straw was incubated in the rumen of a sheep consuming the same experimental straw. For the estimation of the truly undegradable fraction, the straws were incubated at the end of the experiment for 240 hours. After removal from the rumen and washing with tap water till the effluent was clear, the bags were dried at 70 °C during 24 hours, after which the residue was analyzed for DM, ash and NDF. The degradation parameters were estimated according to the following model (Robinson et al., 1986):

$$f_t = f_r + f_d \cdot e^{-kd \cdot (t-t')} \quad (1)$$

in which f_t represents the residual fraction of a feed component at time = t, f_d the potentially degradable fraction, f_r the truly undegradable fraction, k_d the fractional rate of degradation and t' the lag-time before microbial digestion starts. Fitting of the model was done by the non-linear regression option of the statistical program DBSTAT (Brouwer, 1989).

Rumen contractions and eating and rumination activity were measured in weeks 1 and 6. Rumen contractions were recorded with an open tip catheter connected to a pressure transducer. Specifications were as described by Bosch et al. (1988). Chewing activity was measured by a switch attached with a halter to the lower jaw of the animals.

In experimental weeks 2 and 5, the passage of liquid and particles from the hindgut was measured by administering into the ileum about 50 g of an aquous solution/suspension containing 4.0 % Cr-NDF (4.3 % Cr), 1.5 % Carboxy Methyl Cellulose, 0.9 % NaCl and 1.3 % Co-EDTA (14.9 % Co) at 20.00 h on Wednesday. Subsequently, total faecal excreta were collected at the moment of defaecation on Thursday and Friday from 06.00 till 18.00 h and analyzed for Co and Cr as described earlier. The rate of passage of the markers was estimated from the model:

$$C_t = C_0 \cdot e^{-k \cdot t} \quad (2)$$

in which C_t is the concentration of the marker in the faeces at time = t and k is either the rate constant of passage of Cr (k_p) or of Co (k_l).

In the 3rd and 4th week of the experiment the flow of nutrients in the duodenum and ileum was assessed based on a continuous infusion of about 20 mg Co and 20 mg Cr per hour into the abomasum, starting one day prior to sampling. The infusate had the following composition: 0.75 % Cr-NDF (4.3 % Cr), 0.26 % Co-EDTA (14.9 % Co), 0.9 % NaCl, 1.5 % Carboxy Methyl Cellulose and 96.6 % water. Hourly samples (about 10 g) of duodenal and ileal digesta were collected from Monday till Friday from 08.00 till 20.00 h. The samples were freeze dried, ground, sieved through a 1 mm screen and pooled per sheep per week and cannula, and subsequently analyzed for dry matter (DM), ash, Co and Cr, neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL). Duodenal and ileal collection was

done simultaneously. Duodenal or ileal flow of a constituent was estimated from its concentration relative to the concentration of the markers. Correction of the ileal flow for withdrawal of digesta in the duodenum was considered not necessary because the concentration of a constituent relative to the concentration of markers in ileal digesta is not affected by duodenal sampling.

Digestion was measured by daily collection and subsampling of residual feed and total collection of faeces over six days in weeks 3 and 4. Faecal excretion was not corrected for duodenal and ileal sampling, which was done during four of the six days of faecal collection. The average DM withdrawal over the faecal collection period by duodenal and ileal sampling was approximately 10 g/d. Since part of the withdrawn DM would be degraded in the large intestine, the actual underestimation of faecal DM excretion was less than 10 g/d.

During the 7th week of the experiment total rumen evacuations were conducted in such a schedule, that of all animals total rumen contents were measured and a proportional sample for analyses of DM, ash, NDF, ADF and ADL and sieve analysis was taken at 1, 2 and 3 hours after feeding. Analyses were done in samples pooled per animal. Wet sieve analysis of rumen samples of approximately 50 g was done on a Fritsch Analysette 3 over a sieve of 1.25 mm. After sieving the material retained on the sieve was quantitatively collected and dried at 103 °C.

Prior to the experiment described above an intake and digestion experiment was conducted with all six sheep fed untreated wheat straw. The experimental period lasted six days with an adaptation period of two weeks. During this experiment one dacron bag with untreated wheat straw was incubated in the rumen of each sheep for 48 hours. The procedure was equal to the procedure described before. Sugar beet pulp was incubated for 48 hours in duplicate in the rumen of two spare sheep fed untreated wheat straw.

DM and ash were determined by drying at 103 °C and ashing at 550 °C, respectively. N was determined by the Kjeldahl method with K_2SO_4 and $CuSO_4$ as catalysts. NDF, ADF and ADL were determined according to Goering & Van Soest (1970). Hemicellulose was calculated as NDF - ADF and cellulose as ADF - ADL.

Statistical analysis was done on means per animal (average of two repeated measurements) by the program DBSTAT (Brouwer, 1989). The model was: Y_{ij} = mean + $treatment_i$ + $error_{ij}$, with total degrees of freedom (d.f.) 6. To test the significance of contrasts: L1 : $-1 \cdot UWS - 1 \cdot SWS + 2 \cdot AWS$ and L2 : $-1 \cdot UWS + 1 \cdot SWS$, the treatment sum of square was subdivided in the sum of square of each contrast with d.f. = 1. The d.f. of the error term was 3. (Snedecor & Cochran, 1967). The level of significance of a contrast was indicated in the tables for $p < 0.25$ (§), $p < 0.10$ (†), $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

For testing of differences between parameters the difference per animal was calculated and analyzed by the full model. Whether the overall mean difference or the difference within rations differed significantly from zero was tested by Student's t-test (Snedecor & Cochran, 1967).

Results

Voluntary intake, digestion and site of digestion

For calculation of the organic matter digestibility (OMD) of straw the OMD of sugar beet pulp was assumed 850 g/kg. The in sacco OMD of sugar beet pulp after 48 h incubation in the rumen of two sheep fed untreated wheat straw was 948 g/kg. Intake (I) of DM, OM and digestible organic matter (DOM) of the whole ration as well as of the straw component of the ration were significantly increased by ammonia treatment (Table 3). DMD and OMD of the whole ration tended to increase due to ammonia treatment, while DMD and OMD of the straw component of the rations were significantly higher for AWS than for UWS and SWS. Urea infusion had no effect on intake and digestion of DM and OM. Ammoniation of wheat straw had more effect on intake than on digestibility of wheat straw. Ammoniation of wheat straw increased OMI of straw by 87 %, OMD of straw by 43 %, while DOMI of straw increased by 180 %.

Assuming maintenance requirements of 26 g DOMI/kg$^{0.75}$/d for sheep (ARC, 1980) the rations UWS, SWS and AWS could cover 70, 75 and 133 % of the maintenance requirements, respectively.

Intake and digestion of cell wall components of whole rations were higher for AWS than for UWS and SWS (Table 4), though the effects of ammonia treatment on digestion of cellulose and lignin were not significant ($p > 0.05$). Hemicellulose

Table 3. Intake and digestion of DM and OM, DOMI and average weight of the animals.

		UWS	SWS	AWS	Significance of contrast		SEM
					L1	L2	
Intake (g/kg$^{0.75}$/d)							
DM	– whole ration	36.0	39.2	59.0	*	ns	3.27
	– straw	23.3	26.6	46.8	*	ns	3.34
OM	– whole ration	32.6	35.6	53.6	*	ns	2.98
	– straw	21.3	24.4	42.7	*	ns	3.05
Digestibility (g/kg)							
DM	– whole ration	544	519	611	†	ns	24.7
	– straw	372	360	548	*	ns	21.9
OM	– whole ration	569	545	641	†	ns	27.1
	– straw	416	403	587	*	ns	23.1
DOMI (g/kg$^{0.75}$/d)							
	– whole ration	18.3	19.4	34.5	**	ns	1.48
	– straw	8.3	9.4	24.8	**	ns	1.63
Average weight of the animals (kg)		43.1	43.3	45.5	§	ns	1.05

ns: not significant, §: $p < 0.25$, †: $p < 0.10$, *: $p < 0.05$, **: $p < 0.01$. L1: contrast $-1 \cdot$ UWS $- 1 \cdot$ SWS $+ 2 \cdot$ AWS. L2: contrast $-1 \cdot$ UWS $+ 1 \cdot$ SWS.

Table 4. Intake (I) and digestion (D) of cell wall components of whole rations.

		UWS	SWS	AWS	Significance of contrast		SEM
					L1	L2	
NDF							
I	($g/kg^{0.75}/d$)	24.3	27.2	40.7	*	ns	2.77
D	(g/kg)	572	544	695	*	ns	29.3
Hemicellulose							
I	($g/kg^{0.75}/d$)	7.7	9.3	13.4	*	ns	1.04
D	(g/kg)	540	523	749	**	ns	29.3
Cellulose							
I	($g/kg^{0.75}/d$)	14.5	15.6	23.5	*	ns	1.54
D	(g/kg)	656	618	730	†	ns	24.4
Lignin							
I	($g/kg^{0.75}/d$)	2.2	2.4	3.5	*	ns	0.23
D	(g/kg)	112	141	243	§	ns	58.7

ns: not significant, §: $p < 0.25$, †: $p < 0.10$, *: $p < 0.05$, **: $p < 0.01$. L1: contrast $-1 \cdot$ UWS $- 1 \cdot$ SWS $+ 2 \cdot$ AWS. L2: contrast $-1 \cdot$ UWS $+ 1 \cdot$ SWS.

digestion increased more due to ammonia treatment than cellulose digestion (41 % and 15 %, respectively). Urea infusion had no significant effect on intake and digestion of cell wall components.

Selective consumption of straw was not observed for AWS. In UWS and SWS a positive selection of cellulose occurred. The cellulose content of the straw part of UWS and SWS offered was 425 g/kg and of the straw consumed 486 g/kg ($p < 0.05$). Insignificant differences existed between the NDF and hemicellulose contents of the straw part of UWS and SWS offered and consumed. In the straw offered NDF was 785 g/kg and hemicellulose 286 g/kg, while in the straw consumed NDF was 817 g/kg and hemicellulose 264 g/kg. The animals probably selected for leaves, which contain more cellulose and less hemicellulose than stems (Wales et al., 1990).

The ratio of Co to Cr in the marker mixture infused for estimation of flows of digesta in the duodenum and ileum was 1.16. In the duodenal samples this ratio was 1.17 (SEM 0.04) and in ileal samples 1.14 (SEM 0.04), indicating, that representative samples of duodenal and ileal digesta with respect to fluid and particulate phases were obtained.

Based on estimates of flows of nutrients at various sites of the digestive tract, the contribution of digestion in a particular site of the digestive tract to whole tract digestion was calculated. Estimates of this partial digestion in the rumen, small intestine and large intestine are presented in Table 5. No significant differences emerged between rations in respect of the contributions of various sites of the digestive tract to whole tract digestion. Partial digestion in the rumen was significantly lower and partial digestion in the large intestine significantly higher for OM than for cell wall components. The contribution of the small intestine to whole tract digestion of OM and cell wall components was low and did over and within rations not differ signifi-

Table 5. Partial digestion in various sites of the digestive tract (% of whole tract digestion).

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
OM						
– rumen	75.8	79.9	81.8	ns	ns	3.64
– small intestine	1.4	–1.5	6.0	§	ns	2.87
– large intestine	22.8	21.6	12.2	§	ns	5.74
NDF						
– rumen	94.1	92.6	96.3	ns	ns	5.43
– small intestine	–5.1	–2.0	–1.3	ns	ns	1.79
– large intestine	10.9	9.4	5.0	ns	ns	6.93
Hemicellulose						
– rumen	92.6	92.4	97.6	ns	ns	4.24
– small intestine	–5.0	–1.6	–0.4	§	§	1.50
– large intestine	12.4	7.6	2.8	ns	ns	5.55
Cellulose						
– rumen	86.1	86.6	90.0	ns	ns	3.88
– small intestine	0.1	–0.2	1.0	ns	ns	2.32
– large intestine	13.8	13.6	9.1	ns	ns	4.50

ns: not significant, §: $p < 0.25$. L1: contrast $-1 \cdot UWS - 1 \cdot SWS + 2 \cdot AWS$. L2: contrast $-1 \cdot UWS + 1 \cdot SWS$.

cantly from zero. The apparent digestion of lignin occurred in the rumen, where on average 383 g/kg lignin intake was degraded. In the small and large intestines a negative digestion of lignin was observed of respectively 94 and 115 g/kg lignin intake. The latter values did not differ significantly from zero.

The flows of potentially degradable NDF (NDF_d) at various sites of the digestive tract are given in Table 6. Assuming an f_r of sugar beet pulp of 100 g/kg NDF and of straw NDF equal to $f_r/(f_r + f_d)$ (see Table 9) the intake of truly undegradable NDF (NDF_r) could be estimated. In a steady state situation, the amount of NDF_r entering a digestion compartment is equal to the amount flowing out of that compartment. The flows of NDF_d at the various sites of the digestive tract could therefore be calculated as the difference between the total NDF flow minus intake of NDF_r.

No significant differences emerged between rations with regard to intake of NDF_r and flows of NDF_d in duodenum, ileum or faeces. Faecal excretion of NDF_d was slightly underestimated due to withdrawal of digesta from duodenum and ileum. NDF withdrawal from duodenum and ileum was approximately 5 g/d averaged over the faecal collection period.

Whole tract degradation of NDF_d was over rations 805 g/kg NDF_d ingested. The average degradation of NDF_d in the rumen was 758 g/kg NDF_d ingested and in the large intestine 241 g/kg NDF_d entering the small large intestine. The latter value would be slightly lower, if a correction was made for the underestimation of faecal NDF_d excretion.

Table 6. Flows of truly non-degradable NDF (NDF_r) and potentially degradable NDF (NDF_d) and degradation of NDF_d in various sites of the digestive tract.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
Intake (g/d)						
– NDF_r	123	140	111	ns	ns	17.6
– NDF_d	287	319	596	**	ns	35.6
Duodenal flow (g/d)						
– NDF_d	70	90	123	§	ns	15.8
Ileal flow (g/d)						
– NDF_d	81	96	130	§	ns	18.9
Faecal excretion (g/d)						
– NDF_d	57	70	103	§	ns	16.5
Degradation of NDF_d (g/kg flow)						
– whole tract	809	781	824	ns	ns	30.0
– rumen	758	723	793	§	ns	28.7
– large intestine	317	205	200	ns	ns	90.8

ns; not significant, §: $p < 0.25$, **: $p < 0.01$. L1: contrast $-1 \cdot UWS - 1 \cdot SWS + 2 \cdot AWS$.
L2; contrast $-1 \cdot UWS + 1 \cdot SWS$.

The degradation of NDF_d in a digestion compartment can be described by $k_d/(k_d + k_p)$ (Aitchisson et al., 1986). The k_p of Cr-NDF in the large intestine was on average 10.7 %/h (Table 10). Assuming that this was also the k_p of NDF_d in the large intestine, the k_d of NDF_d was over rations estimated as 4.8 %/h (s.e. of estimate 1.95, no significant differences between rations).

Passage of NDF from the rumen could be calculated as duodenal NDF flow/rumen NDF pool ($k_{p,eff}$, see Table 11). On the assumption, that the $k_{p,eff}$ of NDF_d was equal to the $k_{p,eff}$ of NDF, the estimated k_d of NDF_d was 5.3, 4.2 and 6.1 %/h (SEM 0.99) for UWS, SWS and AWS, respectively. These estimates did not differ significantly between rations, but differed significantly from the values given in Table 9.

Eating and rumination behaviour

An overview of the results obtained from measurements of ingestion and rumination characteristics and of rumen contractions is given in Table 7.

No significant differences were observed in total daily chewing time, eating time and rumination time between the rations. However, per kg NDFI less time was spent chewing ($p < 0.05$), ruminating ($p < 0.001$) and eating ($p < 0.25$) for AWS relative to UWS and SWS. The number of chews per minute eating or rumination was not different between rations as was the number of boli per minute rumination. The frequency of chewing during eating was higher than during rumination.

No differences were observed in rumen contractions between the rations, neither

Table 7. Daily chewing time (CT), eating time (ET) and rumination time (RT), related chewing characteristics and number and frequency of rumen contractions.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
CT (min/day)	735	826	816	ns	ns	59.8
ET (min/day)	210	233	209	ns	ns	36.0
RT (min/day)	526	593	604	ns	ns	59.9
CT (min/kg NDFI)	1813	1815	1148	*	ns	122.3
ET (min/kg NDFI)	534	519	292	§	ns	108.7
RT (min/kg NDFI)	1279	1297	856	***	ns	34.9
Frequency of chewing (chews/min)						
– during eating	117	104	114	ns	ns	18.5
– during rumination	93	89	97	ns	ns	3.6
rumination boli (per minute RT)	0.92	1.04	1.06	ns	§	0.053
Rumen contractions						
– total daily	2790	2733	2771	ns	ns	116.0
– frequency (number/min)						
• eating	2.8	2.8	2.7	ns	ns	0.13
• rumination	1.7	2.0	1.8	ns	ns	0.12
• resting	1.9	1.5	1.8	ns	ns	0.19

ns: not significant, §: $p < 0.25$, *: $p < 0.05$, ***: $p < 0.001$. L1: contrast $-1 \cdot$ UWS $- 1 \cdot$ SWS $+ 2 \cdot$ AWS. L2: contrast $-1 \cdot$ UWS $+ 1 \cdot$ SWS.

in total daily number, nor in frequency during eating, rumination or resting. Over rations the frequency of rumen contractions was higher during eating than during resting and rumination ($p < 0.05$).

Rumen pool size

Table 8 presents the rumen pool sizes for the three rations tested. The within ration variation was high and consequently no significant differences between rations could be observed. In line with the lower chewing activity per kg NDF ingested, a significantly higher proportion of large particles was found in the rumen DM of sheep fed with ammoniated wheat straw. The DM contents of rumen digesta were 122, 126 and 111 g/kg (SEM 4.1) for UWS, SWS and AWS, respectively. The DM content was lower for AWS than for UWS/SWS ($p < 0.05$).

Rumen degradation and rumen and hindgut passage

Degradation characteristics of OM and NDF as determined by dacron bag incubations are presented in Table 9. Ammonia treatment increased the potentially degrada-

Table 8. Rumen pool size and distribution of particle size.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
Total pool size						
– (g)	6394	7348	9430	§	ns	1481.8
– (% of weight)	15.4	17.7	21.2	ns	ns	2.94
DM (g)	775	917	1054	ns	ns	182.3
OM (g)	737	877	996	ns	ns	175.0
NDF (g)	529	617	628	ns	ns	129.8
Hemicellulose (g)	210	244	217	ns	ns	50.2
Cellulose (g)	266	306	341	ns	ns	63.6
Lignin (g)	52	67	70	ns	ns	16.5
Particles > 1.25 mm (% of DM)	14.9	15.8	21.0	*	ns	1.21

ns: not significant, §: $p < 0.25$, *: $p < 0.05$. L1: contrast –1 · UWS – 1 · SWS + 2 · AWS. L2: contrast –1 · UWS + 1 · SWS.

ble part of OM and NDF significantly and reduced the truly undegradable part significantly. However, no significant effect of ammonia treatment on the rate of degradation was observed. Differences in degradation between untreated wheat straw incubated in the rumen of sheep fed UWS or SWS were not observed.

No significant differences in fractional outflow rates as measured by markers from the rumen or hindgut were found between rations (Table 10). Over rations estimates of $k_{l\text{-rumen}}$ were higher than estimates of $k_{l\text{-faeces}}$ ($p < 0.05$). In contrast to the rumen,

Table 9. Truly undegradable fraction (f_r), potentially degradable fraction (f_d), rate of degradation (k_d) and lag-time (t') of straw OM and NDF.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
OM						
f_r (%)	33.3	33.3	17.3	***	ns	0.25
f_d (%)	51.6	52.0	66.7	***	ns	0.52
k_d (%/h)	1.85	1.92	2.23	§	ns	0.192
t' (h)	3.4	4.2	2.8	§	ns	0.53
NDF						
f_r (%)	34.1	34.1	15.6	***	ns	0.23
f_d (%)	61.7	62.0	79.4	***	ns	0.50
k_d (%/h)	1.98	2.07	2.55	§	ns	0.211
t' (h)	3.7	4.1	2.5	§	ns	0.71

ns: not significant, §: $p < 0.25$, ***: $p < 0.001$. L1: contrast –1 · UWS – 1 · SWS + 2 · AWS. L2: contrast –1 · UWS + 1 · SWS.

Table 10. Fractional rate of passage of the liquid (k_l) and particulate (k_p) phase to the lower gut and from the hindgut and rumen liquid volume.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
Reticulo-rumen						
$k_{l,rumen}$ (%/h)	6.3	5.7	7.2	ns	ns	0.82
$k_{l,faeces}$ (%/h)	4.3	4.0	3.9	ns	ns	0.42
k_p (%/h)	2.7	2.4	2.8	ns	ns	0.46
Hindgut						
k_l (%/h)	10.2	9.2	10.4	ns	§	0.44
k_p (%/h)	11.5	10.5	10.2	§	†	0.30
Rumen liquid volume						
direct (l)	5.6	6.3	8.8	§	ns	1.21
CoEDTA (l)	4.8	6.5	7.2	ns	ns	0.98

ns: not significant, §: $p < 0.25$, †: $p < 0.10$. L1: contrast $-1 \cdot$ UWS $- 1 \cdot$ SWS $+ 2 \cdot$ AWS.
L2: contrast $-1 \cdot$ UWS $+ 1 \cdot$ SWS.

in the hindgut k_l and k_p did not differ. The faecal excretion pattern of Cr and Co administered into the ileum could nicely be described by the first order model. R^2 values for these excretion curves, but also for dilution curves of Co in the rumen and faecal excretion curves of Co and Cr administered into the rumen were all higher than 0.97.

Rumen liquid volumes as derived from direct measurements (rumen evacuations) and rumen Co-EDTA dilution are also given in Table 10. No significant differences were found between both methods of estimation.

Table 11 presents the rumen turnover (k_{cl} (%/h) = intake/rumen pool size), the effective passage ($k_{p,eff}$ (%/h) = duodenal flow/rumen pool size) and the effective degradation ($k_{d,eff}$ (%/h) = (intake – duodenal flow)/rumen pool size) for cell wall components.

The k_{cl} increased with ammoniation, but the increase was only significant for hemicellulose. The $k_{p,eff}$ did not differ between rations. Over rations, hemicellulose had a significantly lower $k_{p,eff}$ than cellulose, while lignin had a significantly higher $k_{p,eff}$ than the other cell wall components.

The $k_{d,eff}$ of cell wall components was higher for AWS than for UWS and SWS, which was significant for NDF and hemicellulose. The $k_{d,eff}$ of hemicellulose was significantly lower than that of cellulose for UWS and SWS, but not for AWS.

In Table 12, the average daily rumen pH, ammonia-N concentration and concentration, profile and rate of absorption of VFA's are presented. The diurnal variation in these parameters was low. The VFA production was calculated from the apparently rumen degraded OMI (ARDOMI = OMI – OM flow in the duodenum) by assuming a molecular weight of glucose in polymerized carbohydrates of 162 g/mole and a VFA production of 100/(0.5 · (proportion of HAC + proportion of HPr) + proportion of HBu) per mole glucose (Czerkawski, 1986). The turnover was estimated as

Table 11. Rumen clearance (k_{cl} = intake/rumen pool/24, %/h), effective rumen passage ($k_{p,eff}$ = duodenal flow/rumen pool/24, %/h) and effective rumen degradation ($k_{d,eff}$ = (intake – duodenal flow)/rumen pool/24, %/h).

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
NDF						
k_{cl}	3.4	3.2	4.8	†	ns	0.45
$k_{p,eff.}$	1.5	1.6	1.6	ns	ns	0.19
$k_{d,eff}$	1.9	1.6	3.1	*	ns	0.28
Hemicellulose						
k_{cl}	2.7	2.7	4.6	*	ns	0.34
$k_{p,eff.}$	1.4	1.3	1.2	ns	ns	0.16
$k_{d,eff}$	1.3	1.3	3.3	**	ns	0.19
Cellulose						
k_{cl}	4.1	3.6	5.1	§	ns	0.51
$k_{p,eff.}$	1.8	1.7	1.7	ns	ns	0.18
$k_{d,eff}$	2.3	2.0	3.4	†	ns	0.35
Lignin						
k_{cl}	3.1	2.5	3.8	ns	ns	0.59
$k_{p,eff.}$	2.5	1.9	2.5	ns	ns	0.51
$k_{d,eff}$	0.7	0.6	1.3	†	ns	0.19

ns: not significant, §: $p < 0.25$, †: $p < 0.10$, * $p < 0.05$, ** $p < 0.01$. L1: contrast –1 · UWS – 1 · SWS + 2 · AWS. L2: contrast –1 · UWS + 1 · SWS.

the hourly VFA production/VFA pool in the reticulo-rumen, whereas the rate of absorption of VFA was derived from VFA turnover - $k_{l\text{-rumen}}$.

No differences between rations were observed in average daily pH, VFA concentration and profile of VFA, non-glucogenic/glucogenic ratio (NGR) and VFA turnover and absorption rate of VFA, except for the contrast UWS versus SWS in case of molar proportion of HPr in the VFA pool and consequently NGR. UWS showed a significantly lower ammonia N concentration than SWS and AWS. Over rations, absorption of VFA's contributed for 72 % to the rumen turnover of VFA's.

Discussion

Intake, digestion and site of digestion

Voluntary intake and digestion of wheat straw increased due to ammonia treatment. The increase in straw OMI in the present experiment was higher than that observed by Silva et al. (1989) for barley straw in sheep and by Dias-da-Silva & Sundstøl (1986) for wheat straw in sheep. In these experiments, however, the intake of untreated straw was higher than that in the present experiment. The increase in OMD of wheat straw due to ammoniation was comparable with that found by Dias-da-Silva &

Table 12. Rumen concentration of VFA and NH_3-N, pH and rate of turnover and rate of absorption of VFA's in the rumen.

	UWS	SWS	AWS	Significance of contrast		SEM
				L1	L2	
pH[1]	6.81	6.84	6.84	ns	ns	0.097
NH_3-N[1] (mg/l)	42.6	225.4	175.2	†	**	12.28
VFA[1] (mmol/l)	107.1	91.9	111.6	ns	ns	15.94
Profile (mol/100 mol)						
HAc	70.7	73.0	70.7	ns	ns	1.18
HPr	19.1	17.3	18.3	ns	*	0.29
HBu	9.7	9.3	10.0	ns	ns	0.74
HVa	0.5	0.4	1.0	ns	ns	0.27
NGR[2]	4.6	5.2	4.8	ns	*	0.12
VFA turnover[3] (%/h)	21.8	22.3	23.7	ns	ns	6.25
VFA absorption[4] (%/h)	15.5	16.6	16.5	ns	ns	6.01

ns; not significant, †; $p < 0.10$, *: $p < 0.05$, ** $p < 0.01$. L1: contrast –1 · UWS – 1 · SWS + 2 · AWS, L2: contrast –1 · UWS + 1 · SWS.
[1] daily average. [2] Non-glucogenic/glucogenic-ratio; (HAc+2 · HBu+HVa)/(HPr+HVa). [3] VFA production/VFA pool/24. VFA production = ARDOMI/162 · (100/(0.5 · (proportion HAc + proportion HPr) + proportion HBu). [4] VFA turnover – $k_{1\text{-rumen}}$.

Sundstøl (1986). The effect of ammonia treatment on intake was higher than the effect on digestibility.

The effect of ammonia treatment on intake and digestion of straws is attributed to cleavage of ester linkages between hemicellulose and lignin (Morrisson, 1983; Chesson et al., 1983; Mason et al., 1990). After treatment generally an increased digestibility of hemicellulose is observed, but also cellulose digestion may increase, sometimes as much as that of hemicellulose (Lindberg et al., 1984), probably due to enhanced microbial activity (Chesson et al., 1983). In the present experiment, in vivo digestion and effective rumen degradation of hemicellulose increased more after ammonia treatment than those of cellulose. A higher effective rumen degradation could either be attributed to a higher potentially degradable fraction and/or to an increased rate of degradation of the potentially degradable fraction.

The effect of sugar beet pulp supplementation on intake and digestion of untreated wheat straw is summarized in Table 13. OMI and OMD of UWS without sugar beet pulp supplementation were measured in the experiment conducted prior to the main experiment. Results for UWS and SWS from the main experiment were combined and compared with results for the same sheep in the earlier experiment.

Supplementation of UWS/SWS with 11.3 g OM/$kg^{0.75}$/d from sugar beet pulp reduced straw OMI with 8.9 g/$kg^{0.75}$/d. Both in vivo and in sacco OMD of UWS decreased due to sugar beet pulp supplementation. If it was assumed, that the truly undegradable and the soluble fractions and the lag time of UWS were not affected by sugar beet pulp supplementation, for UWS incubated in the rumen of sheep fed unsup-

Table 13. Intake and digestion parameters of UWS supplemented (+) or unsupplemented (–) with sugar beet pulp (between brackets SEM). Data for the four sheep fed UWS or SWS during the main experiment.

Supplementation	–		+	
OMI (g/kg$^{0.75}$/d)				
sugar beet pulp	0		11.3	
UWS/SWS	31.7[b]	(0.20)	22.8[a]	(1.99)
OMD (g/kg)				
in vivo	499[b]	(16.5)	410[a]	(17.3)
in sacco (48 h)	497[b]	(6.3)	457[a]	(9.0)

Different superscripts per row indicate significant differences ($p < 0.05$).

plemented UWS the rate of degradation of OM could be calculated from the OM disappearance after 48 h. The derived estimate was 2.52 %/h compared to the value of 1.88 %/h for UWS incubated in the rumen of sheep fed UWS/SWS supplemented with sugar beet pulp. This reduction in rate of degradation of OM could, at least partly explain the reduction in intake of OM from UWS due to sugar beet pulp supplementation. The pH in the rumen of sheep fed UWS/SWS supplemented with sugar beet pulp was 6.8 with almost no diurnal variation. It is therefore unlikely, that the effect of sugar beet pulp on intake and digestion of wheat straw could be attributed to a decreased pH.

In contrast to the results given above, Silva et al. (1989) observed positive effects of sugar beet pulp supplementation on intake and digestion of untreated or ammoniated barley straw fed to sheep and cattle. In the present experiment, however, the supplementation level was higher than in the experiment of Silva et al. (1989).

No effects of urea supplementation on intake, in vivo and in sacco digestion and site of digestion were observed. This indicates, that N was not limiting microbial activity, although the ammonia-N concentration in the rumen of sheep fed UWS was close to the level of 50 mg/l required for maximal microbial growth in vitro as found by Satter and Slyter (1974) and lower than the required value of about 80 mg/l as reported by Oosting et al. (1989) for maximal in vitro degradation of low quality roughages. Hence, other nutrients may have been more limiting than N. The efficiency of microbial protein synthesis was low in the present experiment (Oosting et al., 1993) probably caused by limiting availability of true protein, branched chain VFA's and/or sulphur.

The contribution of the rumen to OM digestion was on average 79 %. For untreated and alkali treated straws reported values for partial rumen OM digestion vary from 54 to 80 %.(Demeyer, 1981; Zorrilla-Rios et al., 1991). Supplementation with easily rumen degradable concentrates as sugar beet pulp may give higher contributions of rumen digestion to total OMD.

The contribution of digestion in the small intestine to whole tract OMD was low and ileal flows of NDF, hemicellulose and lignin seemed even higher, though not significantly, than the duodenal flows of these cell wall components. Over and with-

in rations differences between apparent small intestinal crude protein (N · 6.25) and non cell wall-OM disappearance were not significant. Apparent crude protein disappearance in the small intestine was 29, 34 and 53 g/day for UWS, SWS and AWS, respectively, (Oosting et al., 1993), while apparent small intestinal disappearance of non cell wall-OM was 16, 0 and 44 g/day for UWS, SWS and AWS, respectively.

The contribution of digestion in the hindgut to whole tract digestion was lower (insignificantly) for AWS than for UWS and SWS, which is confirming the suggestion by Demeyer (1991), that the importance of hindgut fermentation is increasing with decreasing quality of feeds. The partial digestion of cell wall components in the large intestine was in line with literature data summarized by Demeyer (1981). Since only 200-300 g/kg potentially degradable NDF entering the large intestine was degraded in the hindgut, the conclusion seems justified, that retention time in the hindgut was more limiting the extent of hindgut fermentation than availability of potentially degradable material.

The contribution of the large intestine to whole tract digestion was higher for OM than for NDF. This could be attributed to the fact, that the digesta entering the large intestine contained a high proportion of non-cell-wall OM (average over rations 36%), with a higher apparent digestion in the large intestine (over rations 390 g/kg) than NDF (over rations 109 g/kg).

Eating and rumination behaviour

No differences were observed in eating and rumination time between rations. The rumination time was approximately 9-10 hours, about equal to the maximum daily time spent ruminating as suggested by Bosch et al. (1992) and Welch (1982). It is likely, that this maximum rumination time was required for the low quality roughages as fed in the present experiment. However, for sheep consuming low quality roughages rumination time per day was found to vary between experiments from 6 to 12 hours, though within experiments rumination time was fairly constant (Bae et al., 1979; Hogan et al., 1989; Gherardi & Black, 1989; Wales et al., 1990).

Assuming a constant efficiency of rumination (min. rumination/g NDF) and a fixed criticle particle size for escape from the rumen (Kennedy & Poppi, 1984), eating time will be restricted by maximum time for rumination. However, Gherardi & Black (1989) and Faichney (1986) suggested, that rumination efficiency may increase with higher intake of the same feed and the average size of particles leaving the rumen may also increase with increasing NDF content of the ingested feed (Bosch et al., 1992) or increasing rumen fill (Okine et al., 1990). Thus, it is unlikely, that maximum rumination time alone determines eating time and consequently intake.

The efficiency of rumination and eating (the reciprocal of time spent eating or ruminating per kg cell wall intake) was higher for AWS than for SWS and UWS. A higher efficiency of rumination and eating could mean a lower resistance to particle comminution, but could also result in a higher average particle size in the rumen. A reduced resistance to particle size comminution due to ammonia treatment was observed by Oosting & Van Bruchem (unpublished) in cattle. Doyle (1984) reported a

lower power consumption required for grinding of alkali treated rice straw than for untreated rice straw. Although particle size reduction per minute rumination time could have been more for AWS than for UWS/SWS in the present experiment, a higher proportion of rumen DM was retained on a 1.25 mm sieve in case of AWS.

No differences were found between rations in frequency of chewing during eating or rumination. More chews were recorded per minute eating than per minute rumination, which could be indicative of a higher efficiency of particle size reduction per minute chewing than per minute rumination.

The number of daily rumen contractions was not significantly different between rations and also no differences in frequency of rumen contractions during eating, rumination and resting were found. During eating the frequency of rumen contractions was higher than during rumination or resting, which could explain why passage of particles is higher during eating than during rumination (Girard, 1990), although Okine et al. (1990) observed, that duration of individual rumen contractions rather than frequency of rumen contractions determined rate of passage.

Rumen pool size

The rumen pool size is determined by the quantity of feed entering the rumen and the quantity disappearing from the rumen through passage or degradation. NDF intake was significantly higher for AWS than for the other rations, while the rumen NDF pool was not significantly different between rations. The higher NDF intake of AWS compared with UWS/SWS was predominantly determined by increased rumen degradation and only to a small extent by increased passage of feed particles. Of the increased NDF intake due to ammonia treatment of 270 g/d, 91 % disappeared from the rumen due to higher rumen degradation and only 9 % due to a higher passage of NDF.

Rumen degradation and rumen and hindgut passage

In sacco studies by Adebowale et al. (1989) and Ørskov et al. (1989) showed that ammoniation of straw increased the potentially degradable fraction. The rate constant of degradation was only slightly, if at all affected in these experiments. Also in the present experiment no significant increase due to ammoniation was observed with regard to the in sacco rate constant of degradation of the potentially degradable fraction. The potentially degradable fraction increased, however, due to ammonia treatment, which resulted in an increased in sacco $k_{d,eff}$ of NDF ($k_d \cdot f_d/(f_d + f_r)$) of 61 %. A similar increase (77 %) in $k_{d,eff}$ estimated from NDF intake, duodenal NDF flow and rumen NDF pool was found.

The estimate of k_d of NDF_d from in sacco analysis was over rations 2.2 %/h (for straw), while the in vivo estimate based on intake and duodenal flow of NDF_d was 5.2 %/h. The discrepancy between the two estimates may partly be attributed to the fact, that the in vivo estimate is the overall k_d of the rumen pool of NDF_d, which consisted of straw and, probably a small proportion, of sugar beet pulp with a higher k_d than for straw. Another reason for overestimation of the in vivo k_d is, that it was ba-

sed on the assumption, that the effective passage of NDF_d was equal to the effective passage of NDF. This is only true, if the ratio NDF_d/NDF_r was equal in the large and small particle pool in the rumen and if the k_p of small particle NDF_r was equal to the k_p of small particle NDF_d. However, Tamminga et al. (1989) reported a lower k_p for NDF_d than for NDF_r and Oosting et al. (unpublished) observed a higher NDF_d/NDF_r ratio in large particles than in small particles in the rumen of cattle fed straw based rations. Both observations indicate, that the $k_{p,eff}$ of NDF_d is lower than the $k_{p,eff}$ of NDF, which would result in lower estimates of k_d.

Although the extent of overestimation of the in vivo k_d in the present experiment is unknown, the large deviation between the in sacco and in vivo k_d in the present experiment seems to confirm the conclusion of Aitchisson et al. (1986), that k_d derived from in sacco analysis underestimates in vivo k_d.

Although the accuracy of estimates of k_d of NDF_d in the large intestine was relatively low, the average over rations of 4.8 %/h was comparable to the estimate of 5.2 %/h for k_d in the rumen. The first order degradation model generally applied for analysis of degradation kinetics implies, that k_d is not affected by the extent to which the NDF_d was degraded. Hence, the comparable values for k_d of NDF_d in the rumen and in the large intestine indicate, that microbial degradation is of similar effectiveness in both degradation compartments.

Rumen passage of Cr-NDF and of rumen cell wall pools did not reveal significant differences between rations. Effective passage measured from actual flow of NDF was lower than when measured from Cr-NDF. Excretion curves based on Cr-NDF only describe the passage characteristics of a pool of small and indigestible particles with a high functional specific gravity. Due to entrapment of fermentation gasses in rumen particles, the functional specific gravity of rumen particles will be lower than of Cr-NDF, which may partly explain the difference in passage characteristics (Sutherland, 1987).

The effective passage of cellulose was slightly, but significantly higher than the effective passage of hemicellulose. Lignin had a higher effective passage than other cell wall components. Particles with a relatively high lignin content have probably a relatively high functional specific gravity, which may explain the relatively high effective passage. Why cellulose had a higher effective passage than hemicellulose is unknown. It could probably be associated with the fact, that leaves have a higher cellulose/hemicellulose ratio than stems (Wales et al., 1990). Leaves will probably be broken down to small particles more easily than stems.

The underestimation of $k_{l\text{-rumen}}$ by $k_{l\text{-faeces}}$ was also observed by Bosch et al. (1992). This can be attributed to the fact, that the faecal excretion pattern is the result of passage through at least two mixing compartments i.e. the rumen and the hindgut. The flow rate out of a series of mixing compartments is lower than that out of one (Van 't Riet, 1988).

The retention time in the hindgut was over rations 10.0 h for Co-EDTA and 9.3 h for Cr-NDF. These observations were well in line with results from other experiments. Warner (1981) concluded, that in ruminants hardly any separation of fluid and particulate markers occurs post-abomasum. Retention time in the large intestine increased with decreasing intake level from 5 to 11 h in sheep fed lucerne chaff

(Grovum & Williams, 1977). Caton et al. (1988) observed retention times in the large intestine of approximately 5 h for sheep fed a mixture of prairie hay and oat straw either with or without supplementary cottonseed meal.

Despite the higher DOMI for animals fed AWS and consequently a higher rumen VFA production, no drastic differences were observed between rations in pH and concentration and molar proportions of VFAs in the rumen. Also the rate of absorption of VFA was not significantly different between rations. The higher rumen fluid volume and the higher rate of fluid passage of animals fed AWS, although both not significantly, could probably explain the absence of differences in VFA concentration and consequently in rumen pH between the rations. In the present experiment no differences between rations were found in VFA composition. Murphy et al. (1982) related molar proportions of VFA to substrate composition, which in the present experiment, was not markedly altered by ammonia treatment. The proportion of total VFA production, that disappeared from the rumen through absorption (average 72 %) was in line with values for sheep fed roughages with an OMD of 500-600 g/kg (Ketelaars & Tolkamp, 1991) and with the estimate of 70 % for dairy cows at a maintenance level of intake (Tamminga & Van Vuuren, 1988).

It can be concluded, that the most important effects of ammonia treatment of wheat straw were an increased voluntary intake and increased degradation in the rumen. Effects on rumen pool size and rates of rumen passage and degradation were not significant. Ammonia treatment reduced the time spent ruminating per kg NDF ingested. The increased intake and digestion due to ammoniation of wheat straw did not affect the pattern of rumen fermentation end products and the relative importance of hindgut fermentation.

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