Effect of fibre level, particle size and adaptation period on digestibility and rate of passage as measured at the ileum and in the faeces in the adult rabbit

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The use of specific methods other than gravimetric ones to analyse fibre permitted a more precise study of the degradation of cell wall (CW) in the digestive tract. Digesta flow and rate of passage measurements have not been assessed previously in rabbits to investigate fibre digestion and fibre effects simultaneously in the proximal and in the distal segments of the tract. The effect of the level of dietary fibre on ileal and overall digestibility and rate of passage were studied by comparing semi-purified diets containing only one source of CW (dehydrated lucerne (*Medicago sativa*) meal) given to adult female rabbits. The effect of fibre particle size and adaptation period were also investigated. Measurements of fibre composition using both colorimetric and gas-liquid chromatographic techniques, showed that large amounts of (CW) were degraded in the caecocolic segments. Increasing dietary fibre level reduced the rate of passage but fibre degradation was increased, at the same time a lower digestive efficiency for energy in the small intestine was found. A small quantity of CW was apparently degraded before the caecum, assuming that the water-soluble fraction of CW was essentially implicated. Grinding lucerne meal through a 1 mm instead of a 3 mm screen did not improve CW digestibility in spite of a longer rate of passage in the caeco-colic segments. Adaptation to a high-fibre diet resulted in an higher digestive volume for colon and caecum, related to an improved degradation of CW. Furthermore, digestive efficiency in the small intestine appeared higher for rabbits adapted to a high-fibre diet than that for rabbits initially fed on a low-fibre diet.

Fibre: Digestion: Rate of passage: Rabbit

Nutritional effects of dietary fibre in simple-stomached animals generally have been studied in the whole digestive tract of non herbivorous species (e.g. pigs and rats), using faecal digestibility or rate of passage measurements. More recently, there have been some reports on the effects of fibre on digestion in the small intestine of the pig (Fadel *et al.* 1989; Laplace *et al.* 1989), but there are no known comparable studies in herbivorous simple-stomached animals (e.g. horse and rabbit). Furthermore, little information is presently available about fibre degradation using precise analytical methods rather than gravimetric methods (Longland *et al.* 1989; Longstaff & McNab, 1989).

Evidence for the effect of fibre composition on digestive phenomena was obtained in several studies (Graham *et al.* 1986; Gidenne, 1987), but no consistent results were obtained on the effect of the level of cell wall (CW) on diet digestion because mixed diets including various fibre sources were used. Also, frequently the particle sizes of CW were not considered in spite of their role in digestive processes and motility of the tract. In addition, particle size has a particular effect on caeco-colic motility of the rabbit (Bouyssou *et al.* 1988), and fine particles are delayed in the colon and are brought back to the caecum during the hard faeces excretion phase, as shown by Björnhag (1972).

Table 1. *Composition (g/kg diet) of the experimental diets*

	Diet...	Low-fibre	High-fibre	High-fibre finely ground
Ingredients (g/kg diet)				
Dehydrated lucerne (*Medicago sativa*) meal		485	765	765
Purified maize starch		390	166	166
Fish-meal concentrate		100	48	48
Minerals and vitamins		25	21	21
Type of grinding		3 mm	3 mm	1 mm
Chemical composition (g/kg dry matter)				
Organic matter		912	889	887
Minerals		88	111	113
Starch		353	158	161
Crude protein (nitrogen × 6·25)		176	182	179
Gross energy (MJ/kg)		17·64	17·54	17·33
NDF		236	357	356

NDF, neutral-detergent fibre.

The purpose of the present study was to provide further information on the effect of fibre level and particle size on digestion in the rabbit small intestine and caeco-colic segment, using a single source of CW in the diets (dehydrated lucerne (*Medicago sativa*) meal) to prevent associative effects between the composition and the level of the fibre source. In addition, we also investigated the effect of adaptation to a fibrous diet with growing rabbits on digestive volume and CW degradation.

MATERIALS AND METHODS
Diets and animals

Three diets were formulated and given *ad lib.* in a pelleted form throughout the entire experiment. All diets contained dehydrated lucerne meal (LM) as the only source of CW (Table 1), fish-concentrate meal and purified maize starch to obtain a similar digestible protein:digestible energy value for the low-fibre (L) and high-fibre (H) diets. Diet F differed from diet H in that the LM was milled through a 1 mm instead of a 3 mm screen. Before pelleting, each diet was divided into two batches, one being supplemented (9·5 g/kg) with ytterbium-labelled lucerne CW (Ellis & Beever, 1985). Yb was used in order to perform rate of passage studies and digesta flow measurements at the ileum as described previously by Gidenne & Ruckebusch (1989). Labelling of the particulate phase with Yb was sufficient for ileal flow measurements, as shown by Gidenne (1988). Particle sizes in feeds were determined on four samples of pellets by wet sieving (Table 2).

The experiments were carried out with two groups of eighteen weaned (4 weeks old) Californian female rabbits. In each group ten animals were used for digestive volume measurements, and eight animals were used for digestibility measurements and fitted (at 8 weeks old) with a T-shaped glass cannula (Gidenne *et al.* 1988) about 50 mm before the ileo-caecal junction in order to perform ileal flow and rate of passage measurements. All animals were housed in individual cages under a 12 h–12 h light–dark schedule.

Adaptation time and digestive volume measurements

First, diets L and H were given for an adaptation period (PO; food intake was assessed twice weekly), from 4 to 11 weeks of age, to the two groups of rabbits (*n* 18). Then, ten animals from each group were slaughtered by stunning narcosis at about 10.00 hours in

Table 2. *Class of particle size (g/kg dry matter) in the experimental diets**

(Mean values and standard deviations)

Diet ... Particle size (mm)	Low-fibre		High-fibre		High-fibre, finely ground		Statistical significance of difference:
	Mean	SD	Mean	SD	Mean	SD	P
> 1	6[a]	2	15[b]	2	—	—	< 0·01
0·5–1	58[a]	5	103[b]	6	83[c]	9	< 0·01
0·3–0·5	73[a]	4	105[b]	6	107[c]	5	< 0·01
< 0·3	863[a]	4	771[b]	1	810[c]	6	< 0·01

[a,b,c] Mean values with different superscript letters in the same line were significantly different ($P < 0.05$).
* For details, see Table 1 and p. 134.

order to measure digesta contents and fresh organ weights for the stomach, caecum and proximal colon. The total digestive tract was removed by severing at the base of the skull. Organs were weighed and then emptied by gentle squeezing. Then they were rinsed clear of contents with water and dried with paper towels.

Digestibility and rate of passage measurements

Five rabbits from each group of eight (L or H) were used, from 11 weeks of age, in three periods of digestibility measurements. Animals were chosen according to similar intake and live weight. The same rabbits were used during the three periods, except one animal in each group was replaced after the first period. Groups of rabbits were defined according to dietary treatment: rabbits were initially fed on diets L or H in PO, then, in the first period rabbits were fed on the same diets as in PO (group LL and HH), in the second period rabbits received diet F (groups LF and HF), and in the third period rabbits received diets H or L (groups LH and HL).

Apparent faecal digestibility coefficients (FDC) were calculated, after 7 d of adaptation, from total collection of faeces during 7 d. Faeces were pooled individually in plastic bags and stored at −18° for further analyses. Ileal digesta were collected from the cannula. Six collections (1 h each) were made over a period of 3 d, such that they covered a 24 h period: 01.00, 05.00, 09.00, 13.00, 17.00 and 21.00 hours. In order to calculate the digestibility coefficient at the ileum (IDC), the total intake (including diet plus soft faeces intake) was determined. Thus, soft faeces excretion was measured in each period and individually for each rabbit wearing a plastic collar during 24 h (Gidenne & Lebas, 1987).

Rate of passage measurements of Yb-labelled lucerne CW were performed using the same rabbits after digestibility assessment, at the ileum and in the whole tract (Gidenne & Ruckebusch, 1989). Total faecal collection was fractionated during 56 h by means of an automatic faecal sampler adapted for use in the metabolism cages. During digestibility and rate of passage measurements food intake was assessed every day.

Chemical analyses

Dry matter (DM) was determined on duplicate samples by heating at 105° for 24 h, and all results were calculated on a dry weight basis. Analyses were performed on duplicate freeze dried samples of feeds, soft and hard faeces and ileal digesta. Organic matter (OM) was determined by ashing at 550° for 5 h. Nitrogen was measured by a Kjeldhal procedure and converted to crude protein using the factor 6·25. Starch was hydrolysed enzymatically and the resultant glucose was measured by using the hexokinase (*EC* 2.7.1.1)–glucose-6-

phosphate dehydrogenase (NAD) (*EC* 1.1.1.49) system (Böehringer Mannheim). Gross energy was measured by an adiabatic bomb calorimeter. Neutral-detergent fibre (NDF) was determined according to Van Soest & Wine (1967) using an amylase (*EC* 3.2.1.1) and protease (*EC* 3.4.24.4) treatment (Giger *et al.* 1979). Water-insoluble non-starch polysaccharides (NSP) in feeds were isolated using amylase and pronase (*EC* 3.4.21.4, 3.4.24.4; from *Streptomyces griseus*) treatments (Carré *et al.* 1984). The water-soluble NSP of feeds were isolated from supernatant fractions resulting from amylase and pronase treatments using extensive dialysis against water at 4° (dialysis tubes with 3500 molecular weight cut-off; spectra/Por 3; Poly-labo, Strasbourg). Water soluble and insoluble NSP of faeces were measured as neutral and acidic sugars in residues obtained after amylase and pronase treatments, freezer drying of suspensions, reflux in ethanol–water (80:20, v/v) and centrifugation. Starch contamination was assessed on the insoluble NSP fraction and was less than 2 and 6 g/kg (NSP dry matter basis) respectively for feed and faeces samples. Neutral sugars of NSP were measured by gas-liquid chromatography analysis of their alditol acetate derivatives (Blakeney *et al.* 1983). Uronic acids were determined colorimetrically by the *m*-phenyphenol method (Blumenkrantz & Asboe-Hansen, 1973). Yb was determined by atomic absorption spectrometry.

Calculations and statistics

Mean retention time (MRT) values for the whole tract were obtained after a continuous infusion of Yb had been stopped; the following equation was used: $\mathrm{MRT} = T_1 + \Sigma A_i(T_{i+1} - T_i)$. MRT between ileum and rectum was obtained after single dose administration of Yb, the following equation was used: $\mathrm{MRT} = \Sigma(M_i T_i)$. T_1 was the time elapsed between the end of feeding labelled diet (TO) and the defaecation for which A first became less than unity, A_i was the marker concentration as a proportion of the equilibrium concentration, T_i was the time elapsed between TO and the *i*th defaecation and M_i was the quantity of marker excreted in the *i*th defaecation (Faichney, 1975).

Analysis of variance was conducted with GLM procedure of Statistical Analysis System (1985) using a split-plot design for determining diet and adaptation period effect.

RESULTS

As dehydrated LM was the only source of CW in the diet, its NSP composition was deduced from Table 3. Water-soluble NSP represented 120 g/kg total NSP. They originated mainly from pectic substances, as water-soluble uronic acids.

Effect of level of dietary CW (HH v. LL groups)

From 4 to 11 weeks of age (PO), voluntary food intake of the rabbits increased (+38%) as the digestible energy (DE) content of the diets fell: 10·6 and 9·03 MJ/kg respectively for diets L and H. Then, daily weight gain was similar and feed:gain ratio was higher for diet H (Table 4). Increasing the proportion of LM resulted in a significant increase in the empty weight of the stomach and caecum and also in their digesta content (Table 4).

Diet H resulted in a lower FDC of OM, energy and crude protein (Table 5). FDC of starch was almost complete whatever the diet. CW digestion was improved with increasing level of CW in the diet. This result was consistent with two different methods of analysis: NDF (method of Van Soest & Wine, 1967) or determination of total (water-soluble and water-insoluble) NSP by gas-liquid chromatography (Table 6). This increase in CW digestion was mainly due to better digestibility of xylose and glucose units. Xylose, a typical hemicellulose unit, appeared as the least-degraded neutral sugar (15–30%). Cellulose digestibility was estimated by analysis of non-starch glucose: FDC was about 25–38%.

Table 3. *Composition of non-starch polysaccharides (NSP) of experimental diets (g/kg diet)**

Diet...	Low-fibre		High-fibre		High-fibre, finely ground	
	Insoluble	Soluble + insoluble	Insoluble	Soluble + insoluble	Insoluble	Soluble + insoluble
Rhamnose	1·8	3·1	2·8	4·4	2·8	4·2
Arabinose	7·5	10·6	11·4	16·0	11·3	15·8
Xylose	28·4	28·4	43·9	45·1	43·6	44·4
Mannose	5·9	5·9	9·9	10·8	9·9	10·9
Galactose	4·7	7·3	7·6	11·4	7·6	11·1
Glucose	104·5	104·5	161·8	161·8	160·7	160·7
Uronic acids	29·2	48·3	46·1	72·2	45·8	67·9
Total NSP	182·0	208·1	283·5	321·7	281·7	315·0

* For details, see Table 1 and p. 134.

Table 4. *Characteristics of growth, digesta contents and visceral organ weights of rabbits, after the adaptation period to the experimental diets**

	Diet...	Low-fibre	High-fibre	SED	Statistical significance of difference: P
Growth					
Initial wt (g) (4 weeks of age)		667	707	32·4	0·404
Slaughter wt (g) (11 weeks of age)		2033	2194	85·5	0·202
Daily wt gain (g)		27·9	30·4	1·4	0·227
Daily feed (g)		89	123	4·3	0·001
Feed:wt gain		3·2	4·1	0·1	0·001
Organ wt (g)					
Stomach		15·3	17·4	0·6	0·035
Caecum		25·8	29·9	1·4	0·051
Proximal colon		13·5	14·5	0·4	0·122
Digesta contents (g)					
Stomach		51·8	68·8	4·2	0·018
Caecum		88·1	107·8	4·1	0·004
Proximal colon		10·2	13·0	0·8	0·142
Faecal dry matter (g/kg)		674	533	15	0·001

SED, standard error of the difference, (16 df, except for faecal dry matter, 8 df).
* For details of diets and procedures, see Table 1 and p. 134.

Arabinose, galactose and uronic acids, which are the typical monomers of pectic substances in lucerne, were the most digested CW components (65–80%). About half the digested pectic substances could be accounted for by water-soluble NSP, but values of concentrations (Table 1) showed that even water-insoluble pectic substances were more digested than xylose or glucose units. Thus, mean faecal digestibility of total pectin components (sum of arabinose, rhamnose, galactose and uronic acids) reached 72%, without significant changes for diet or group effect. As the NDF residue did not include the highly digested fraction of CW, i.e. pectic substances and water-soluble CW, digestibility values were always lower than those for total NSP.

Table 5. *Ileal and overall digestibilities of dietary components of experimental diets fed to rabbits**

(Values are means for five rabbits, except in period 1, where four rabbits were used)

Diet of adaptation (during PO)...	Low	High	Low	High	Low	High			Statistical signifiance of effect of:		
Diet received in experimental period...	Low	High	Fine	Fine	High	Low	SED[1]	SED[2]	Adaptation	Diet	Interaction
Period no....	1		2		3						
Ileal digestibility											
Organic matter	0·448	0·354	0·325	0·317	0·282	0·534	0·019	0·017	0·006	0·001	0·004
Gross energy	0·420	0·316	0·304	0·288	0·270	0·526	0·020	0·021	0·032	0·001	0·054
Crude protein (nitrogen × 6·25)	0·650	0·585	0·542	0·535	0·454	0·626	0·030	0·029	0·262	0·004	0·072
Starch	0·926	0·956	0·958	0·971	0·936	0·968	0·013	0·014	0·025	0·332	0·462
Neutral-detergent fibre (NDF)	−0·056	0·065	0·070	−0·028	−0·006	0·014	0·035	0·035	0·712	0·552	0·082
Overall digestibility											
Organic matter	0·714	0·603	0·577	0·607	0·587	0·711	0·008	0·009	0·061	0·001	0·103
Gross energy	0·684	0·578	0·555	0·587	0·557	0·682	0·010	0·011	0·071	0·001	0·249
Crude protein	0·721	0·654	0·608	0·645	0·652	0·729	0·016	0·017	0·310	0·001	0·456
Starch	0·995	0·993	0·991	0·994	0·994	0·996	0·001	0·001	0·232	0·004	0·056
Neutral-detergent fibre (NDF)	0·211	0·284	0·216	0·279	0·248	0·224	0·015	0·016	0·011	0·026	0·253

SED[1], standard error of differences between means for rabbits adapted to different diets in PO (8 + 14 df); SED[2], standard error of differences between means for rabbits adapted to the same diet in PO (14 df); PO, adaptation period.

* For details of diets and procedures, see Table 1 and pp. 134–135.

Table 6. *Ileal and overall digestibilities of non-starchy polysaccharides (NSP) (soluble + insoluble) of experimental diets*

(Values are means for five rabbits (except in period 1, where four rabbits were used) for overall digestibilities, and two rabbits for ileal digestibilities)

Diet of adaptation (during PO)...	Low	High	Low	High	Low	High			Statistical significance		
Diet received during period...	Low	High	Fine	Fine	High	Low	SED¹	SED²	Adaptation	Diet	Interaction
Period no. ...	1		2		3						
Ileal digestibility											
Arabinose	0·240	0·321	0·176	0·142	0·196	0·412	0·021	0·028	0·007	0·004	0·018
Xylose	−0·236	0·072	−0·018	−0·022	−0·038	−0·091	0·043	0·053	0·077	0·029	0·304
Galactose	−0·248	0·084	0·003	−0·003	−0·111	−0·044	0·067	0·063	0·004	0·345	0·187
Glucose	−0·233	0·103	0·033	0·023	−0·043	−0·059	0·021	0·021	0·004	0·002	0·024
Uronic acids	0·254	0·383	0·278	0·202	0·252	0·339	0·023	0·022	0·070	0·063	0·024
Total NSP	−0·077	0·174	0·088	0·063	0·035	0·071	0·015	0·020	0·002	0·004	0·007
Overall digestibility											
Arabinose	0·783	0·813	0·770	0·756	0·768	0·734	0·014	0·015	0·483	0·181	0·019
Xylose	0·145	0·286	0·195	0·259	0·228	0·153	0·022	0·021	0·034	0·001	0·287
Galactose	0·659	0·666	0·614	0·629	0·643	0·619	0·024	0·024	0·957	0·427	0·376
Glucose	0·241	0·376	0·307	0·379	0·334	0·255	0·012	0·019	0·001	0·001	0·096
Uronic acids	0·742	0·758	0·712	0·745	0·708	0·750	0·013	0·013	0·057	0·480	0·421
Total NSP	0·384	0·488	0·420	0·485	0·446	0·400	0·011	0·015	0·001	0·001	0·102

SED¹, standard error of differences between means for rabbits adapted to the same diet in PO, 14 df for overall digestibilities, 4 df for ileal digestibilities; SED², standard error of differences between means for rabbits adapted to different diets in PO, 22 df for overall digestibilities, 8 df for ileal digestibilities; PO, adaptation period.

Table 7. *Intake and mean retention time (MRT; h) of cell wall material between the ileum and rectum and in the whole tract of rabbits*

(Values are means for five rabbits, except in period 1, where four rabbits were used)

| Diet of adaptation (during PO)... | Low | High | Low | High | Low | High | | | Statistical significance | | |
| Diet received during period... | Low | High | Fine | Fine | High | Low | | | | | |
Period no....	1		2		3		SED[1]	SED[2]	Adaptation	Diet	Interaction
Diet intake (g/kg live weight)	40·0	46·5	44·1	51·4	45·8	38·5	0·028	0·030	0·284	0·036	0·182
MRT: mouth–ileum (hours)	7·9	7·6	6·0	7·2	6·3	7·0	0·007	0·007	0·599	0·399	0·204
MRT: ileum–rectum	12·1	6·5	9·6	8·8	7·9	13·3	0·005	0·004	0·255	0·001	0·220
MRT: mouth–rectum	20·1	14·1	15·5	15·9	14·2	20·4	0·008	0·007	0·781	0·001	0·697

SED[1], standard error of differences between means for rabbits adapted to the same diet in PO (14 df); SED[2], standard error of differences between means for rabbits adapted to different diets in PO (8 + 14 df); PO, adaptation period.

Measurements of digesta flow at the terminal ileum allowed IDC to be estimated and compared with those values obtained in the whole tract for the same rabbits. Values for OM or energy were similar and varied from 35 to 45 % according to the level of CW (Table 5). As ileal digestibility was related to the extent of digestion in the whole tract, it was better to compare the proportions of nutrients digested before the caecum to estimate digestive efficiency in the small intestine. Thus, 60 % of the digested OM was apparently digested before the caecum, and a slight reduction in group LL compared to group HH was found: 58·7 and 62·7 % respectively. The amount of crude protein flowing at the ileum remained low and similar (13 g/d) for the two groups; the digestible fraction of crude protein was almost entirely digested in the small intestine (90 %), even for diet H which contained mainly protein from lucerne. Starch was incompletely degraded before the caecum. Increasing its proportion in the diet (diet L) significantly increased the quantity of starch reaching the caecum, but it remained very low: 3·2 *v.* 1·0 g/d for diets L and H respectively.

CW estimated by the NDF method (insoluble CW except pectic components) appeared to be undegraded before the caecum, with no effect of the level of LM. Values obtained for total NSP (water-soluble and insoluble CW) showed a low level of CW degradation (0–17 %) in the small intestine (Table 6). Xylose and glucose remained undegraded. Neutral and acidic sugars of pectic substances were apparently hydrolysed at an extent of 20–40 % of the intake, and about 50 % of digestible pectin disappeared before the caecum.

MRT for the particulate phase of the diet (Table 7) measured in the whole tract (MRTt) was greatly reduced for rabbits receiving diet H (14 h) compared with that for those fed on diet L (20 h). This effect originated mainly from a reduction in ileo–rectal transit time: 12 and 6 h for groups LL and HH respectively. Thus, the MRT in the stomach and small intestine was not significantly modified by the effect of fibre level.

Effect of fibre particle size

As expected, the pellets of diet F (Table 2) contained no large particles (size > 1 mm) and a lower proportion of particles over 0·3 mm compared with diet H. The granulometric profile of diet F was intermediate between those of diets L and H.

At the same level of dietary fibre, grinding LM through a 1 mm screen did not significantly influence ileal or faecal digestibilities of dietary constituents, except for the IDC of uronic acids which was reduced significantly (Table 6) for rabbits of group HF compared with that for group HH.

Total MRT was increased after grinding LM (+1·8 h). This effect was mainly due to a longer transit time in the distal part of the tract, without significant changes in diet intake (Table 7) between diets H and F.

Effect of adaptation to dietary fibre level

The effect of adaptation was significant ($P < 0·1$) for faecal digestibility of OM and energy for rabbits fed on diet H during growth, which seemed to digest high-fibre diets (diets F or H) more efficiently. This effect was not due to changes in starch or crude protein digestion, but lower fibre degradation was observed, as shown by NDF or total NSP digestibility coefficients, for rabbits receiving diets L during PO. Lower cellulose (non-starch glucose) and xylose FDC were measured for animals adapted to diet L. Adaptation to diet H significantly improved the efficiency of the digestion of pectic components of LM, whereas there was no effect of fibre level on FDC.

The effect of adaptation to fibre level also modified some variables of digestion in the small intestine. Rabbits initially fed on diet L (high starch level) had a lower IDC for starch irrespective of the diet they were fed later. In addition, rabbits of group HL had

significantly higher IDC values (OM and energy) than those of group LL. Highly digestible components of NSP were also affected by PO: rabbits adapted to diet H had higher IDC for uronic acids, galactose and arabinose in diets L and H.

The effect of adaptation to the level of LM was not significant for MRT values in the whole tract or in the ileo-rectal segment.

DISCUSSION

The increase in the empty weight of the stomach and caecum of rabbits fed on diet H during growth (4–11 weeks of age) suggests physical adaptation of the digestive tract to the increase in diet intake (bulking effect of increasing proportions of LM). Such an effect was not observed previously in rabbits by Lebas *et al.* (1982), probably because the adaptation period was too short (4 weeks). However, the bulking effect of fibre on the development of digestive organs has been reported for other non-herbivorous simple-stomached species, i.e. the pig (Kass *et al.* 1980; Pond *et al.* 1988) and the rat (Rémesy & Demigne, 1989). The increase in fresh digesta contents for all organs could be a result of a higher diet intake by rabbits fed on diet H, but the higher water-holding capacity of the high-fibre diet would also contribute, as shown by the lower DM content of faeces.

The decrease in the faecal digestibility of OM and energy with increasing dietary proportions of LM was in general agreement with results obtained with simple-stomached animals. This was mainly due to the dilution effect of CW because of their low DE content. Simultaneous measurement of rate of passage (MRT) allows us to show another effect of CW, which seemed to act in addition to the first one. Thus, our results and previous findings in the pig (Kuan *et al.* 1983; Ravindran *et al.* 1984; Roth & Kirchgessner, 1985) indicated that high dietary fibre level reduced MRT in the whole tract, reducing the time available for enzyme degradation.

Very few studies have attempted to measure rate of passage in different digestive segments, especially in simple-stomached herbivorous animals. Our findings suggest that the effect of fibre level on variations in the rate of passage originated mainly from variations in MRT between ileum and rectum. Any changes in the rate of passage in the small intestine were related to the LM level, and small variations in the efficiency of digestion in this segment were observed for digestible constituents. Starch was almost entirely digested before the caecum, as has been found in pigs (Darcy *et al.* 1981; Graham *et al.* 1986). High amounts of protein were digested before the caecum irrespective of diet. Protein from LM (700 *v*. 400 g/kg protein respectively in diets H and L) was digested to a lesser extent than that from fish-concentrate meal. It would be expected that the origin of protein added to an eventual fibre effect (decreasing small intestine MRT) would induce variations in the efficiency of the digestion, but proportions of the digestible crude protein apparently absorbed before the caecum were similar for each diet.

Degradation of CW was reduced for diet L, the low-fibre high-starch diet, as shown by two different methods of CW analysis: gravimetric method (Van Soest & Wine, 1967) or colorimetric and gas-liquid chromatographic analysis of sugars from fibre polysaccharides. Changes in CW faecal digestibility seemed to be due mainly to the water-insoluble fraction of polysaccharides: glucose and xylose were better digested in diet H, and they were absent from the water-soluble CW of LM. Digestion of pectic material remained very high for all the diets. Water-soluble pectic substances represent 40 % of total pectin in LM. Considering that water-soluble pectic substances were entirely degraded, 55 % of water-insoluble pectic substances would be degraded without differences related to the level of CW. This absence of variation in degradation of pectic materials could be explained by their faster degradation rate compared with those of other CW polysaccharides (Chesson & Monro, 1982). However, Chabeauti & Noblet (1989) reported in pig trials that there were no

changes in NDF digestion but a decrease in digestion of pectic material with increasing levels of wheat bran. Kuan *et al.* (1983) observed no significant variations in CW degradation when pigs were fed on diets containing high *v.* low LM content. Our results obtained with adult rabbits were confirmed by a trial conducted on growing rabbits with the same diet. A positive effect of increasing dietary LM content on NDF digestibility was also observed and it was related to higher caecal volatile fatty acid concentrations (Gidenne & Scalabrini, 1990).

Two main nutritional factors are susceptible to change: caecal fermentation and therefore, fibre degradation. First, the amount of rapidly fermentable nutrients (protein, available carbohydrates) which would be able to reach fermentative compartments (caecum and proximal colon for rabbit) must be considered because of their ability to modify caecal pH and flora. Second, the turnover rate (inverse of rate of passage) of digesta contents in these digestive segments must also be considered. Measurements of digesta flow performed at the ileum gave some evidence for a small effect of the first factor. The amounts of starch reaching the caecum were different between groups HH and LL, but they remained at a very low level (< 2.5 g/d). Similarly, ileal flow of protein did not differ relative to fibre level. On the other hand, the lower turnover rate (higher MRT) measured in the caecum and proximal colon for rabbits fed on diet L could be related to the lower CW degradation. Our findings suggest that CW hydrolysis would be reduced if the removal of digesta (equivalent to the inverse of MRT) was too low to provide a sufficient supply of readily fermentable substrate and fibre polysaccharides. In addition, it is generally assumed that positive correlation between digestive volume and fibre degradation would exist. Effectively, our findings suggested that an enlargement in digestive organs of the distal part of the tract (caecum and colon of rabbits adapted to diet H) would contribute to a higher fibre degradation.

IDC of NDF residues (water-insoluble CW, except pectic substances) were similar between diets and were not significantly different from zero. This was in agreement with the general idea of fibre indigestibility in the proximal part of the gastrointestinal (GI) tract. However, the IDC of CW obtained with a more specific method showed that large amounts of arabinose and uronic acids disappeared before the caecum, whereas xylose and glucose units (75 % of dietary water-insoluble CW) were almost totally recovered at the ileum (over 90 %). CW degradation *before* the posterior part of the GI tract was also reported in ileostomized man (Sandberg *et al.* 1981) and in pigs with an ileo-rectal shunt (Laplace *et al.* 1989; Chabeauti & Noblet, 1990) or with a T-shaped cannula (Millard & Chesson, 1984). Cellulolytic activity was also found in the small intestine of pigs (Chesson *et al.* 1985). Our findings obtained with rabbits suggest that the fibre fraction which was susceptible to hydrolysis to a relatively large extent in the small intestine would probably be mainly water-soluble pectic components.

It is generally assumed that particle size does affect susceptibility of fibre to bacterial degradation but the findings of earlier studies in the rabbit are inconsistent. Laplace & Lebas (1977) found an increase in DM digestibility when the same diet was subject to regrinding, whereas Lebas *et al.* (1986) reported no significant effect of a fine grinding of the raw material on the digestibility of the dietary constituents. Our results showed that for the same level of CW, reduction in particle size did not improve CW digestibility in spite of a longer retention time in the caeco-colic segments. This contradicts the proposal, essentially based on results obtained with ruminants, that fibre degradation is improved by improved contact between bacterial enzymes and CW. A possible explanation for results obtained with the rabbit was that anti-peristaltic movements of the proximal colon would be enhanced by fine grinding (Bouyssou *et al.* 1988) contributing to the higher MRT of fine particles (size < 0.3 mm), water-soluble constituents and bacteria. Thus, the turnover rate

of caecal contents was decreased and, as suggested previously, this would impair CW degradation. This effect would balance the effect of reducing fibre particle size which was supposed to increase CW degradation. This absence of effect of particle size on CW degradation obtained in herbivorous simple-stomached species was also found in pigs (Ehle *et al.* 1982) and rats (Nyman & Asp, 1985) when using coarse or fine wheat bran.

In conclusion, dietary fibre level affects digestive efficiency in the small intestine, without variations in the rate of passage. Our study has also shown that the digestive tract of the rabbit adapts to the fibre content of the diet with changes in the rate of passage and digestibility. Further experiments will be conducted using different sources of CW, in order to confirm these preliminary conclusions with LM. However, it will be useful to employ our experimental model for studying in vivo enzymic and fermentative digestion.

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