Dietary fibre fermentation in the rat intestinal tract: effect of adaptation period, protein and fibre levels, and particle size

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1. The fermentative breakdown of one resistant type of dietary fibre (wheat bran) and one easily-fermented fibre (low-methoxyl pectin) was studied with respect to the length of the adaptation period and fibre level in the diet. The breakdown of the resistant fibre was also studied regarding the protein level in the diet and particle size of the fibre.

2. Prolongation of the adaptation period from 4 to 18 d decreased the faecal dry weight considerably. The excretion of dietary fibre however, was similar, whereas a decrease in faecal nitrogen excretion could be seen.

3. A level of dietary protein of less than 50 g/kg impaired the fermentation of wheat-bran fibre, whereas a level higher than 100 g protein/kg did not further increase the degree of fermentation of the fibre.

4. The particle size did not change the fermentability of the fibre, equal amounts of the main components of coarse and milled bran being excreted in faeces.

5. Two different levels of wheat-bran fibre (48 and 96 g/kg) in the diet did not influence the fibre breakdown. Similar results were obtained with two levels of fibre from low-methoxyl pectin (42 and 84 g/kg), but a tendency towards a decreased percentage of faecal excretion of uronic acids was seen at the lower level of low-methoxyl pectin.

The extent of dietary fibre fermentation in the intestinal tract varies between different types of fibre, and is dependent on the solubility and the chemical structure of the fibre (Cummings, 1982). Dietary fibre rich in lignin and cellulose, such as wheat bran, is resistant to micro-organisms in the intestinal tract, whereas hemicellulosic and pectic substances are completely fermented (Cummings *et al.* 1979; Dintzis *et al.* 1979; Gramstorff Fetzer *et al.* 1979; Bertrand *et al.* 1981; Nyman & Asp, 1982). Fermentation is the main factor determining the bulking capacity of dietary fibre. The low bulking capacity of fermented fibre is due to increased bacterial mass (Stephen & Cummings, 1980). In contrast, the increase in faecal dry matter produced by wheat bran is mainly due to unfermented fibre. The capacity of the unfermented fibre to bind water is also of importance with regard to faecal bulking capacity. Dietary fibre with a high water-binding capacity in vitro has a poor bulking capacity due to the extensive fermentation of this kind of fibre (Stephen & Cummings, 1979).

The fermentability of a certain dietary fibre can also be expected to be influenced by a number of other factors such as particle size of the fibre, and also by non-fibrous components in the diet, e.g. the protein content. Heller *et al.* (1980) found that the fermentation of cellulose was more pronounced with fine bran than with coarse bran in man, while Ehle *et al.* (1982) showed that coarse bran in pigs was more susceptible to microfloral action. The importance of particle size has been further established by Brodribb & Groves (1978), who found a significantly higher wet weight of faeces with coarse bran than with finely-ground bran in man. Adaptation of the intestinal microflora is another factor that might affect fibre degradation, especially for an easily-fermented type of fibre. In a previous investigation (Nyman & Asp, 1982) it was shown that the variability between rats given pectins was considerable, which could be due to the rats being in different phases of adaptation. One could therefore expect that a longer adaptation period to the diet would decrease this variation. Cunningham *et al.* (1962), however, did not find any increase in fermentability when pigs were given a resistant dietary fibre (Solkafloc) for 14 weeks

compared with 1 week. In human studies, Cummings (1982) found the same resistance to bacterial action of wheat-bran fibre after 6 weeks compared with 3 weeks. Ehle (1980) did not observe any long-term adaptation of the faecal microflora to fibre in humans and pigs. The amount of fibre in the diet can also be expected to affect fibre breakdown. Keys *et al.* (1970) demonstrated that fibre digestibility decreased with increasing fibre level.

The present study was undertaken to provide information on whether factors such as adaptation time to the diet, level of protein or fibre in the diet, and particle size could change the fermentability of the fibre. A resistant dietary fibre (wheat bran) and an easily-fermented fibre (low-methoxyl pectin) were investigated in balance experiments with rats. This rat model appears to be useful in predicting dietary fibre breakdown in man.

MATERIALS AND METHODS

Dietary fibre preparations

Two batches of wheat bran (Kungsörnen, Sweden and Dunn Clinical Nutrition Unit, Cambridge; England): one batch of enzyme-treated, concentrated and dephytinized wheat bran, referred to as processed bran (Fiberform; Tricum AB, Höganäs, Sweden); and one low-methoxyl pectin (Copenhagen Pectin Factory Ltd, Denmark) were used. The dietary fibre preparations were milled to a particle size of less than 0·4 mm, except where the effect of particle size was studied.

Diets

The diets contained (g/kg): dietary fibre 42–100, casein as the source of protein 0–200, sucrose 100, maize oil 50, mineral mixture 48 and vitamin mixture including choline chloride 10 (for details of vitamin and mineral mixtures, see Nyman & Asp, 1982). Maize starch was added to adjust dry matter content. A basal diet with no added fibre and with 100 g casein/kg was also included as a control. The diets were mixed without heat-treatment and given as powders.

Protein level. Casein at 0, 50, 100, 150 and 200 g/kg was used when investigating effects of the protein level. Wheat bran (49 g fibre/kg) was used as the source of fibre in these experiments. When evaluating the effects of adaptation time, fibre level and particle size, a protein level of 100 g/kg was used.

Adaptation time. Processed wheat-bran fibre (100 g/kg) or low-methoxyl pectin (84 g/kg) were used and given to rats for short (4 d) and long (18 d) adaptation periods.

Dietary fibre level. Dietary fibre was added in the following concentrations (g/kg): wheat bran 48 or 96, low-methoxyl pectin 42 or 84.

Particle size. Milled and coarse (particle size 0·4–1·4 mm) processed wheat-bran fibres were investigated.

Balance experiments

Male Sprague–Dawley rats (80 g) were divided into groups of five and placed individually in metabolism cages (Nyman & Asp, 1982). The food intake was restricted to 10 g dry weight/d. Water was provided *ad lib.* After a 4 d adaptation period, feed residues and faeces were collected during a 5 d balance period. The weight of the rats at the beginning of the balance period was about 90 g. Faeces were removed every day and frozen at −20°. The faeces were lyophilized, weighed, milled and stored at −20° until analysed.

A longer adaptation period of 18 d was also used for processed wheat bran and low-methoxyl pectin. The experimental diet was then provided *ad lib.* to rats weighing 40 g, during the first 14 d. Groups with short adaptation periods were given standard pellets during the additional period. The experimental diet (10 g dry weight/d) was then given for another 4 d to the different groups, followed by a 5 d balance period, when feed residues

and faeces were collected. The weight of these rats at the beginning of the balance period was about 100 g.

Analyses

Fibre analyses. Dietary fibre content was measured gravimetrically after digestion with physiological enzymes using the method of Asp *et al.* (1983). Dietary fibre residues were corrected for protein (nitrogen × 6·25) and ash associated with the fibre.

Dietary fibre composition in feed and in faeces was measured by gas–liquid chromatography (GLC) of neutral sugars as their alditol acetates (Sawardeker *et al.* 1965; Theander & Åman, 1979). Allose was used as internal standard. The hydrolysis was performed in 12 M-sulphuric acid for 2 h and then diluted and reflux boiled for 6 h. Uronic acids were measured with a decarboxylation method (Bylund & Donetzhuber, 1968; Theander & Åman, 1979). All dietary fibre constituents were expressed as their polymer weight.

N determination. N in food and faeces was determined by using the Kjeldahl method. Crude protein was calculated as N × 6·25.

Calculation. All dietary fibre constituents excreted in faeces were corrected for the basal excretion, i.e. typical 'dietary fibre' saccharides excreted in faeces, when the rats were given a basal diet with no added fibre (Nyman & Asp, 1982). The sum of basal excretion of 'dietary fibre' monomers was about 120 mg/5 d. The glucan values were also corrected for the free glucose found in faeces (less than 10 mg/5 d).

Statistical evaluation. The materials in Table 1 were analysed by Dunnett's method for comparing several groups with one control group (Winer, 1971). Table 4 was analysed by a one-way analysis of variance design followed by the Newman-Keul's procedure for multiple comparisons (Winer, 1971). Other statistical evaluations were made by Student's *t* test.

RESULTS AND DISCUSSION

Faecal dry weights

The faecal dry weights obtained with milled and coarse processed wheat bran were similar (Table 1). On the other hand, faecal dry weight obtained with processed wheat bran after a long adaptation period was significantly ($P < 0·01$) lower than that after a short one. The faecal dietary fibre excretion, however, was similar after long and short adaptation periods, whereas protein excretion ($P < 0·001$) (and probably also fat excretion) was lower after the long adaptation period. Thus the longer adaptation period led to less faecal protein and fat losses, whereas dietary fibre fermentation was unaffected. A prolonged adaptation with low-methoxyl pectin (84 g/kg) also caused a lower mean faecal dry weight. However, since there was a considerable variation between rats, especially when the short adaptation period was used, the decrease was not significant. The decrease in faecal dry weight with the long adaptation period (0·8 g/5 d) seemed to be due to a decreased excretion of dietary fibre (not significant), protein ($P < 0·01$) and probably fat.

The particle size had no pronounced effects on faecal dry weights. Any conclusions on faecal wet weights in relation to particle size cannot be drawn since the rat faeces dry between collections. Other studies have shown an importance of particle size for faecal wet weights (Brodribb & Groves, 1978; Heller *et al.* 1980; Van Dokkum *et al.* 1983). Results on the effect of particle size on faecal dry weights are more ambiguous (Heller *et al.* 1980; Ehle *et al.* 1982; Van Dokkum *et al.* 1983). However, according to Heller *et al.* (1980), faecal dry weights were significantly higher in humans given a coarse-bran diet than in humans given a fine-bran diet.

Table 1. *Dietary fibre intake and faecal dry weights*
(Mean values and standard deviations)

	Casein in diet (g/kg)	Period of adaptation	Dietary fibre intake (g/5 d)		Faecal dry wt (g/5 d)				
					Total		Mean increment	Fibre residue†	Protein increment
			Mean	SD	Mean	SD			
Basal diet (no fibre)	100	—	—	—	1·4	0·4	—	—	—
Low-methoxyl pectin (g/kg diet)									
42	100	S	2·1	0·0	2·5**	0·5	1·1	0·5	0·4
84	100	S	4·0	0·2	3·4***	1·1	2·0	1·3	0·5
84	100	L	4·0	0·3	2·6**	0·5	1·2	1·0	0·2
Wheat bran (g/kg diet)									
48	100	S	2·1	0·0	3·2***	0·3	1·8	1·5	0·3
96	100	S	4·4	0·3	5·1***	0·4	3·7	2·9	0·4
49	0	S	1·6	0·2	3·0***	0·2	1·6	1·3	0·1
49	50	S	2·0	0·4	3·6***	0·9	2·2	1·4	0·3
49	100	S	2·5	0·0	3·6***	0·4	2·2	1·6	0·3
49	150	S	2·4	0·1	3·9***	0·6	2·5	1·6	0·5
49	200	S	2·4	0·0	3·5***	0·5	2·1	1·6	0·5
Processed wheat bran (Fiberform) (g/kg diet)									
100	100	S	5·0	0·0	6·2***	0·3	4·8	3·6	0·5
100	100	L	5·0	0·0	5·3***	0·3	3·9	3·6	0·3
100‡	100	S	5·0	0·1	6·4***	0·5	5·0	3·6	0·6

S, short (4 d) adaptation period; L, long (18 d) adaptation period.
Significantly different from the basal diet group (Dunnett's method): $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.
† Including basal excretion of dietary fibre (approximately 120 mg/5 d) and free glucose (approximately 10 mg/5 d).
‡ Coarse particle size (0·4–1·4 mm).

Table 2. *Composition and faecal recovery of dietary fibre with the processed wheat bran*
(Pooled samples from five rats)

	Composition of dietary fibre (g/kg dry matter)	Faecal excretion					
		mg/5 d			% of intake		
		Short adaptation	Long adaptation	Short adaptation–coarse	Short adaptation	Long adaptation	Short adaptation–coarse
Rhamnose	—	6	10	7	—	—	—
Arabinose	158	660	630	675	69	68	70
Xylose	251	710	680	660	46	44	43
Mannose	7	47	50	44	109	105	105
Galactose	13	63	94	55	80	84	70
Glucose	198	790	840	840	65	69	70
Uronic acids	26	160	190	110	100	119	69
Lignin	157	1080	970	1140	112	101	118
Total	810	3520	3460	3530	71	69	71

Table 3. *Composition and faecal recovery of low-methoxyl pectin dietary fibre*
(Mean values and standard deviations)

	Composition of dietary fibre (g/kg dry matter)	Dietary fibre (g/kg)...	Faecal excretion									
			mg/5 d						% of intake			
			Short adaptation 42		Short adaptation 84		Long adaptation 84		Short adaptation 42		Short adaptation 84		Long adaptation 84	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rhamnose	7		2†		17†		0†		—		—		—	
Arabinose	2		42†		13†		15†		—		—		—	
Xylose	1		9†		6†		7†		—		—		—	
Mannose	1		8†		7†		5†		—		—		—	
Galactose	3		7†		31†		16†		—		—		—	
Glucose	4		16†		73†		40†		—		—		—	
Uronic acids	873		320	170	1020	650	750	430	22 NS	14	27	18	21 NS	14

NS, not significant compared with reference group, i.e. short adaptation, 84 g fibre/kg.
† Pooled samples from five rats.

Fermentation of dietary fibre components

In the present study, faecal polysaccharides were determined without any previous fractionation and it can be questioned whether the saccharides detected represent dietary fibre residues, bacterial cell-wall polysaccharides or endogenous polysaccharides. However, there is evidence that most of the saccharides excreted in faeces originate from the fibre. When rats were given a starch-based diet, with no added fibre, a very low level of saccharides was detected in faeces (Nyman & Asp, 1982). Of course it cannot be excluded that the excretion of saccharides will increase with fibre in the diet. Guar gum, however, which may stimulate the microbial activity in the large intestine through its considerable fermentability, did not significantly increase the excretion of faecal saccharides compared with a fibre-free diet (Nyman & Asp, 1982). In addition, no saccharides other than those present in the fibre could be detected in considerable amounts in faeces (Nyman & Asp, 1982) and the pentoses, arabinose and xylose, which are the main components in wheat bran, are very rare in bacterial saccharides (Kenne & Lindberg, 1983). Thus, by far, most of the saccharides excreted in faeces are fibre saccharides.

Adaptation period. The faecal recovery of the main dietary fibre constituents with processed wheat bran was very similar after both adaptation periods (Table 2). The mean excretion in faeces was 69 and 68% for arabinose, 46 and 44% for xylose and 65 and 69% for glucose, with the short and long adaptation periods respectively. In the case of low-methoxyl pectin there was a small decrease in the mean excretion of uronic acids with a long adaptation period, but no significant differences were detected (Table 3). When a short adaptation period was used 27% were excreted compared with 21% with a prolonged period.

Thus the adaptation period had no pronounced effects on the extent of fermentation on a resistant type of dietary fibre, or on an easily-fermented one. However, the variation between different rats with an easily-fermented type of fibre seemed to decrease with a longer adaptation period.

Table 4. *Faecal recovery of wheat bran dietary fibre with different levels of protein in the diet (0, 50, 100, 150 and 200 g/kg)*
(Mean values with standard deviations)

	Composition of dietary fibre (g/kg dry matter)	Dietary protein (g/kg)...	Faecal excretion																	
			mg/5 d										% of intake†							
			0		50		100		150		200		0		50		100		150		200	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rhamnose	—		5	4	4	4	5	4	10	5	1	2	—	—	—	—	—	—	—	—	—	—
Arabinose	99		210	29	240	61	270	22	290	35	270	31	65	8	59	7	57	5	60	6	55	6
Xylose	143		340	37	300	74	320	17	380	65	320	76	73[b]	5	50[a]	3	45[a]	2	54[a]	8	45[a]	11
Mannose	4		7	2	7	4	9	1	17	6	9	3	62	14	49	21	50	7	55	59	48	18
Galactose	10		3	4	19	11	15	6	19	8	7	5	9	9	46	26	29	13	38	15	19	10
Glucose	131		270	40	310	100	330	30	380	37	340	41	64	7	56	8	51	5	59	4	53	6
Uronic acids	5		5‡		1‡		10‡		5‡		6‡		29‡		6‡		56‡		20‡		24‡	
Total	392		840	99	880	240	960	48	1100	130	950	150	65[b]	5	54	5	49[a]	2	57	6	49[a]	8

[a, b] Mean values with different superscript letters in the same line are significantly different ($P < 0{\cdot}01$).
† Statistical analyses of the material were performed with one-way analysis of variance followed by the Newman-Keul's method (see p. 637).
‡ Pooled samples from five rats.

Table 5. *Faecal recovery of wheat bran dietary fibre, with two different levels of fibre in the diet (48 and 96 g/kg)*

(Mean values and standard deviations)

	Composition of dietary fibre (g/kg dry matter)	Dietary fibre (g/kg)...	Faecal excretion							
			mg/5 d				% of intake			
			48		96		48		96	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
Rhamnose	—		15	6	15	3	—	—	—	—
Arabinose	133		290	32	620	28	63	6	63	3
Xylose	183		300	18	640	45	47	2	48	2
Mannose	3		17	4	27	7	140	35	99	26
Galactose	11		28	3	45	5	5	4	21	5
Glucose	169		420	34	910	44	60*	7	68	3
Uronic acids	31		80†		80†		47†		33†	
Klason lignin	67		250	28	470	73	110	12	96	18
Total	597		1400	30	2810	140	61	2	61	3

* $P < 0{\cdot}05$, (Student's t test).
† Pooled samples from five rats.

Similar fermentability of the fibre after different lengths of the feeding time have also been reported by other authors. Cunningham *et al.* (1962) found the same cellulose digestibility (Solkafloc) in pigs after 1 and 14 weeks. Furthermore, no long-term adaptation of the faecal microflora to the fibre has been observed in man or pigs (Ehle, 1980).

Protein level. The fermentation of the total fibre was most extensive at a protein level of 100 g/kg, followed by 200, 50, 150 and 0 g/kg respectively (Table 4). The main dietary fibre constituents showed a similar trend. One-way analysis followed by multiple comparisons (Newman-Keul's test) showed that the excretion of total fibre at protein levels of 100 and 200 g/kg was significantly ($P < 0{\cdot}01$) lower compared with a protein level of 0 g/kg. No significant differences between arabinose values or between glucose values, were obtained. The faecal excretion of xylose following the wheat-bran diet with no added protein was significantly ($P < 0{\cdot}01$) higher than after the other diets. Thus, protein (N) seemed to be a limiting factor for dietary fibre fermentation at dietary protein levels lower than 50 g/kg. However, a level of protein higher than 100 g/kg, used routinely, did not increase the fermentability of the fibre further (Nyman & Asp, 1982; Björck *et al.* 1984).

Fibre level. The extent of fermentation of wheat-bran fibre was similar when given at two different levels (48 and 96 g/kg) (Table 5). In both experiments 61% of the total fibre was recovered in faeces. Of the arabinose 63% was excreted in faeces and the corresponding value for xylose was 48%. The percentage excretion of glucose-based fibre, however, was reduced ($P < 0{\cdot}05$) when the level of ingested fibre decreased.

The fermentability of low-methoxyl pectin did not change significantly when the level of fibre was reduced (Table 3). However, there was a tendency towards a decreased faecal excretion of uronic acids as well as a decreased variation between rats at the lower level.

Thus, the fermentability of both resistant and easily-fermented types of fibre seems to be independent of the fibre level given, at least at the concentrations used in the present study. This suggests that certain chemical bonds in the polysaccharides are resistant to bacterial fermentation. This is further supported by the fact that the adaptation time seems to be rather unimportant.

The results obtained in the present study are in agreement with other studies (Kies *et al.* 1984; Nyman *et al.* 1985), reporting similar resistance of cellulose given at different levels. Moreover, Garrison *et al.* (1978) could not detect any significant effects on the fibre breakdown in rats given increasing levels of fibre from bagasse. In contrast, Frank *et al.* (1983) found a decreased digestibility of maize-cob fibre in pigs with increasing dietary fibre levels. Similar results were obtained by Keys *et al.* (1970). However, since quite different fibre levels were tested in the different investigations, it is difficult to compare them. Another complicating factor is the different methodologies used when measuring dietary fibre.

Particle size. Very similar amounts of the main components in coarse and milled-processed bran were excreted in faeces (Table 2). The faecal recovery with milled and coarse bran, was 69 and 70% for arabinose, 46 and 43% for xylose and 65 and 70% for glucose respectively.

It is generally assumed that the particle size *per se* does affect the susceptibility to bacterial degradation of the fibre (Cummings, 1982), but earlier studies are not consistent. Heller *et al.* (1980) found a decrease (not significant) in the susceptibility to bacterial fermentation in man given coarse bran compared with fine bran, whereas Ehle *et al.* (1982) reported a slight increase in the fermentation of cellulose in pigs given coarse bran. They interpreted this as an effect of the longer transit time. Our results are in agreement with Björck *et al.* (1984) who found the same dietary fibre content in faeces from rats given extruded (i.e. a process that increases the surface area of particles) and unprocessed whole-grain wheat flour.

CONCLUSIONS

In conclusion, a 4 d adaptation to the diet and a protein level of 100 g/kg seem adequate when evaluating the fermentability of dietary fibre in rats. This kind of balance experiment has also been shown to correlate well with balance experiments in man (M. Nyman, N.-G. Asp, J. Cummings and H. Wiggins, unpublished results) where apple, cabbage, carrot, guar gum and bran were found to be fermented to similar extents in man and in rats.

The particle size *per se* did not affect faecal dry weight or the fermentability of the fibre. Neither was the fermentation affected by the level of fibre in the diet. Prolongation of the adaptation period decreased faecal dry weight, due to a decreased excretion of protein and probably also fat, but the fermentation of the fibre was practically unchanged.

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