Gastrointestinal implications in the rat of wheat bran, oat bran and pea fibre

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The gastrointestinal (GI) effects of three different dietary fibre (DF) sources: wheat bran (WB), oat bran (OB) and pea fibre (PF), were compared with a low-fibre diet in a 4-week trial with rats (initial body-weight 210 g). The DF sources varied widely in chemical composition, solubility and water-holding properties, and particle size. The DF sources were mixed into diets to comprise the same amount of non-starch polysaccharides (NSP; 135 g/kg dry matter (DM)). Compared with the control diet, all fibre-containing diets reduced apparent digestibility of DM, energy, and protein significantly but to different extents. The ranking order of faecal DM bulking followed that of NSP recovery in the faeces: WB > OB > PF > control. The elongating effect of the diets on the GI tract was most pronounced in the rats fed on the OB diet. The mean transit time (MTT) of the OB diet was similar to that of the control diet (approximately 37 h), which was significantly slower than the MTT of the WB and PF diets (approximately 23 h). The study confirms that no simple cause and effect relationship exists between chemical composition, physical properties, and physiological effects of dietary fibre and their effects along the GI tract.

Dietary fibre: Non-starch polysaccharides: Apparent digestibility: Faecal bulking: Rat

The benefits associated with an increase in the consumption of dietary fibre (DF) or complex plant carbohydrates relate primarily to their effects on gastrointestinal (GI) function. Diets rich in this group of plant substances affect many processes along the entire alimentary tract from ingestion to excretion (Heaton, 1980; Southgate, 1990). The physiological and nutritional implications will depend on the level of complex carbohydrates present, the chemical and structural compositions of the plant poly-saccharides, as well as on their physical properties (Selvendran *et al.* 1987). Water solubility, particle size, water-holding capacity (WHC) and cation-exchange capacity are but some of the factors relating to the effects of DF in the GI tract (Institute of Food Technologists, 1989).

To elucidate the present knowledge of the effects of complex plant carbohydrates much work has been done on purified sources like soluble gums such as pectins, guar gum, etc. and on insoluble substrates like purified cellulose. These studies have led to the current emphasis of a partitioning of DF into a soluble and insoluble fraction for the purpose of predicting the physiological effects of DF along the entire GI tract. Soluble DF has its major impact in the small intestine through reduction of the rate of glucose absorption (Jenkins *et al.* 1981; Anderson, 1988) and through reduction of plasma cholesterol (Kritchevsky, 1988), whereas insoluble DF exerts its beneficial effects primarily through its

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diluting effect of digesta content, thus decreasing digesta transit time (Eastwood & Brydon, 1985) and increasing faecal bulk (Cummings, 1986).

The rat experiment described here was conducted to study the GI implications of some DF sources which are presently used to increase the DF level of common foodstuffs. The variables studied included digestibility, transit time, faecal bulking and the development of the GI tract.

The DF sources were chosen to represent available DF sources with different chemical composition and physical properties. The DF sources included: wheat bran (WB), which for a long time was almost synonymous with DF; oat bran (OB), which has been studied extensively lately in relation to its possible hypocholesterolaemic effects; pea fibre (PF), which belongs to the more recently developed DF sources.

A brief account of part of the present work has been published (Hansen, 1990).

MATERIALS AND METHODS
Animals and diets

Seventy-two male Wistar rats, weighing approximately 210 g, were randomly allocated to one of four dietary treatments.

The diets comprised three DF diets mixed to contain approximately the same amounts of total DF (130 g/kg dry matter (DM)) and a low-DF control diet. All diets were adjusted to about 200 g protein/kg by addition of casein. The fibre sources: WB, OB, and PF were added to the low-DF control diet at the expense of a nitrogen-free mixture and casein (Table 1). The white wheat flour ('Falke Mel') was produced by Valsemøllen A/S, Esbjerg, Denmark and the WB was obtained from the Research Mill at the Carlsberg Research Laboratory, Copenhagen, Denmark (Bach Knudsen & Hansen, 1991). The OB ('Mothers Oat') was provided by Quaker Oats, Chicago, USA, and the PF product (Nutrio P-Fibre 150C) was provided by Danisco, Copenhagen, Denmark.

Study protocol

Eighteen rats were adapted to one of the four dietary treatments for 14 d. Six rats in each group were killed and their GI tract excised as described later (p. 453). The remaining rats were fed for two consecutive 8 d balance periods after which another six rats per diet were killed. Finally, measurements of the rate of passage of digesta were carried out on the remaining six rats per diet as described later (pp. 453–454).

Each rat was kept individually throughout the study in metabolism cages and placed at ambient temperatures of 24° and at a relative humidity between 55 and 70%. A 12 h (06.00–18.00 hours) light–dark cycle was operated.

The body-weight of each animal was recorded between 07.30 and 08.30 hours at the beginning of the study and at the beginning and end of each of the two consecutive balance periods.

Feeding scheme

Throughout the study food intake was registered each day and limited to an amount that ensured that the difference in food intake between the least-eating and most-eating animal in each dietary group did not exceed 1·5 g. Water was available at all times.

Faecal collection

Faecal material from twelve rats per diet was collected every day during the 16 d balance period. The faecal material from each animal was pooled for 8 d at a time and kept in the freezer at −18° until subsequent dry weight measurement and further analysis.

Table 1. *Composition of control (C), wheat bran (WB), oat bran (OB), and pea fibre (PF) diets (g/kg dry matter (DM))*

Diet...	C	WB	OB	PF
Ingredients				
White wheat flour	300	300	—	300
Nitrogen-free mixture*	480	265	214	248
Casein†	164	107	—	128
Wheat bran	—	272	—	—
Oat bran	—	—	730	—
Pea fibre	—	—	—	268
Mineral mixture†	40	40	40	40
Vitamin mixture‡	16	16	16	16
Analysis				
DM	889	901	910	912
Gross energy (MJ/kg)	18·3	18·5	18·9	17·9
Crude protein (N × 6·25)	216	196	193	205
Fat	13	27	73	12
NSP: Total	21	130	133	144
Soluble NSP	12	28	87	63
Insoluble NSP	9	102	46	81
Klason lignins	12	36	17	10
Constituent sugars of NSP fraction (g/kg DM)				
Rhamnose	tr	tr	tr	1
Arabinose	4	26	13	58
Xylose	5	51	19	13
Mannose	3	4	3	2
Galactose	1	5	3	11
Glucose	6	35	86	31
Uronic acids	2	9	9	28

NSP, non-starch-polysaccharides; tr, trace.
* Contained (g/kg): raw maize starch 850, sucrose 95, soya-bean oil 55.
† Including 10 g methionine/kg.
‡ For details, see Eggum (1973).

Sampling of GI tissue

Length and wet weight of the GI tract were measured and recorded in six rats per diet after the 14 d adaptation period, and in another six rats per diet after a further 16 d. The rats were killed in random order between 09.00 and 11.00 hours over a 2 d period. The animals were anaesthetized by intramuscular injection of Immobilon, the abdomen opened and the GI tract excised. The total length of the GI tract was measured with minimal stretching. The length of the small intestine and of the colon–rectum was recorded individually. The total weight of the full GI tract was recorded before the digesta contents of the gut segments were squeezed out gently. The contents of the stomach, the caecum and the colon–rectum were weighed, as was the empty GI tract.

Rate of passage of digesta

The rate of passage of digesta through the digestive tract was estimated in six rats per diet after a total of 30 d on their experimental diets. Glass beads (50 μm for chromatography columns) were used as markers, and administered orally as a repeated pulse dose. The

experimental diets were mixed with 40 g marker/kg, and a total of 34·6 g diet was divided into three equal portions and administered at 08.30, 11.30 and 14.30 hours after a previous fast of 18 h. Faecal collection included twelve samplings at 0, 6, 9, 12, 15, 24, 30, 36, 48, 60, 72, and 96 h after the first feeding. During the collection period each rat was fed 17 g DM/d of their respective diets.

The accumulation of glass beads recovered in the faecal samples as well as percentage recovery were calculated. The time for 15, 50, and 85% of the markers to be recovered in the faecal excretion was extrapolated from the curves of the cumulative recovery of markers against time-interval (h) after feeding. Mean transit time (MTT) was defined as the time-interval for 50% of the markers to be excreted in the faeces.

Chemical analysis and physical properties

DM in diets and faecal material was determined by oven-drying at 105° for 20 h. N and energy were determined on duplicate samples by a modified Kjeldahl method (KjellFoss 16200 Autoanalyser; Foss Electric A/S, Denmark), and by bomb calorimetry (IKA-C 400; Janke and Kundel, Germany) respectively. Crude protein was calculated as $N \times 6·25$. Fat was determined after acid-hydrolysis and extraction with diethyl ether (Stoldt, 1952). DF was defined and measured as the sum of non-starch polysaccharides (NSP). The neutral-sugar constituents of NSP were determined as alditol acetates by gas–liquid chromatography after the principles of Englyst et al. (1982), Theander & Åman (1979), and Theander & Westerlund (1986). The uronic acids were determined by colorimetric measurements according to Englyst et al. (1982). Klason lignins in the diets were determined gravimetrically as the residue resistant to 12 M-sulphuric acid (Theander & Westerlund, 1986).

Solubility properties of the DF sources were determined in the chemical analysis of the NSP thus defined and measured at pH 7·0 (Englyst et al. 1982). The average size and distribution of the fibre particles were measured using a Jel sieve (J. Engelsmann, AS, Germany) and a total sieving period of 15 min. WHC, defined as the weight of water retained by 1 g dry material under the conditions of soaking and centrifugation used, was determined in the diets according to the method by Robertson & Eastwood (1981).

The determination of glass beads in each faecal sample was determined as described by Raczynski et al. (1982).

Statistical analysis

Results are presented as mean values and standard deviations. The results from each balance period were tested statistically in an analysis of variance test using a General Linear Model (GLM) procedure. If no significant differences were found between balance periods, the results from the two periods were pooled. When significant overall differences were found, pairwise comparisons between dietary groups were done in a Least Square Means (LSMeans) test and the results indicated in the Tables. All statistical tests were performed on a computerized statistical software package (SAS, 6.03 version, SAS Institute Inc., Cary, NC, USA). All tests were considered significant at a 5% level ($P < 0·05$).

RESULTS

Diets

The chemical analyses revealed that all four diets contained similar amounts of energy (ranging from 17·9 to 18·9 MJ/kg DM) and crude protein (193–216 g/kg DM; Table 1). The relatively high fat content of OB caused a higher amount of fat (73 g/kg DM) in the OB diet compared with the other diets, but all diets were still to be considered low-fat diets.

Table 2. *Body-weight, feed intake, body-weight gain, total faecal output and normalized faecal output of rats fed on control (C), wheat-bran (WB), oat-bran (OB), and pea-fibre (PF) diets**

(Means and standard deviations for twelve rats per diet)

Diet...	C		WB		OB		PF	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Body-wt (g)†	271·3[b]	8·2	275·5[b]	14·8	288·4[a]	15·1	282·1[a]	9·7
Feed intake (g DM/d)	17·8[c]	1·3	19·8[a]	1·5	19·1[b]	0·9	18·1[c]	0·8
Body-wt gain (g/d)	3·3[a]	0·9	2·8[ab]	0·5	3·2[a]	0·5	2·5[b]	0·6
Faecal output (g DM/d)	0·56[d]	0·08	2·89[a]	0·29	1·83[b]	0·19	1·10[c]	0·16
Normalized faecal output	3·14[d]	0·25	14·57[a]	0·95	9·59[b]	0·84	6·08[c]	1·03

[a,b,c,d] Mean values with different superscript letters were significantly different ($P < 0.05$).
* For details of diets, see p. 452 and Table 1.
† Body-weight at the beginning of the first balance period.

Total NSP varied from 21 g/kg DM in the low-DF control diet to 130 g/kg DM in the WB diet, 133 g/kg DM in the OB diet and 144 g/kg DM in the PF diet (Table 1). The composition of the NSP in the diets reflected the composition of the DF sources used: arabinose, xylose and glucose were the predominant NSP sugar monomers in the WB diet comprising 200, 390, and 270 g/kg total NSP respectively. Glucose was by far the dominant NSP constituent in OB diet, comprising about 650 g/kg total NSP, while arabinose and xylose contributed 100 and 140 g/kg total NSP respectively. The NSP constituents of the PF diet were distinctively different from the cereal brans: arabinose was the single major NSP constituent comprising 400 g/kg total NSP while glucose and uronic acids each contributed 200 g/kg total NSP.

The content of Klason lignins in the diets varied from (g/kg DM) 10 in the PF diet, 12 in the control diet, 17 in the OB diet, to 36 in the WB diet.

While the content of total NSP in the WB, OB, and PF diets was similar, their solubility properties differed considerably. The soluble:insoluble NSP constituents of the four diets were: control diet 57:43, WB diet 22:78, OB diet 65:35, and PF diet 44:56 (Table 1).

The mean particle sizes of the NSP sources were in decreasing order (μm): PF 1380, WB 945, and OB 680. WHC of the same NSP sources were (g water/g DM): PF 2·3, WB 1·5, OB 5·8.

Feed intake, body-weight gain and faecal output

All the experimental diets were well accepted by the animals and, with the feeding scheme used, the food intake in each balance period varied little. The average daily feed intake during the balance periods ranged from 17·8 g DM/rat per d in the rats on the control diet to 19·8 g DM/rat per d in the rats fed on the WB diet (Table 2).

The average body-weight gain of the rats in the four groups differed significantly ($P < 0.05$) with the highest daily weight gain in the control and OB groups (about 3·3 g/rat) and the smallest weight gain in the WB and the PF groups (about 2·7 g/rat) (Table 2).

Faecal DM output increased significantly when NSP were included in the diets compared with the control group (Table 2). The highest daily faecal DM output was measured in the WB group (2·89 g), followed by the OB (1·83 g) and PF (1·10 g) groups. If faecal output was normalized (calculated as g faecal DM/g dry food intake × 100) as suggested by Johnson

Table 3. *Apparent digestibility of dry matter (DM), energy, protein, and non-starch polysaccharides (NSP) in control (C), wheat-bran (WB), oat-bran (OB), and pea-fibre (PF) diets**

(Means and standard deviations for twelve rats per diet)

Diet...	C		WB		OB		PF	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DM	0·969[a]	0·002	0·854[d]	0·010	0·904[c]	0·008	0·940[b]	0·010
Energy	0·972[a]	0·002	0·855[d]	0·010	0·902[c]	0·008	0·938[b]	0·009
Protein (nitrogen × 6·25)	0·946[a]	0·002	0·865[b]	0·007	0·835[c]	0·018	0·872[b]	0·012
NSP: Total	0·860[b]	0·009	0·491[c]	0·020	0·931[a]	0·008	0·930[a]	0·051
Soluble	0·947[a]	0·013	0·729[b]	0·107	0·975[a]	0·004	0·948[a]	0·134
Insoluble	0·714[c]	0·048	0·423[d]	0·057	0·848[b]	0·020	0·926[a]	0·062

[a,b,c,d] Mean values with different superscript letters were significantly different ($P < 0.05$).
* For details of diets, see p. 452 and Table 1.

et al. (1990), the values would be 14·57 for the WB group, 9·59 for the OB group, 6·08 for the PF group, and 3·14 for the control group (Table 2).

Apparent digestibility of nutrients

All digestibility values reported were defined and calculated as apparent digestibility. Apparent digestibility values of DM, energy and protein were high (0·95–0·97) in the control group, and reduced significantly in the diets including DF (Table 3). The reduction in apparent digestibility of DM was similar to that of energy and was in decreasing order: PF (0·94), OB (0·90), and WB (0·86). Apparent digestibility of protein was similar (0·87) in the WB and PF groups which was significantly higher than in the OB group (0·84).

Apparent digestibility or fermentation of total NSP was significantly higher (0·93) in the OB and PF groups than in the control group (0·86) and in the WB group (0·49). Apparent digestibility of the soluble part of the NSP varied between 0·73 in the WB group and 0·98 in the other three groups. The same values for the insoluble NSP varied from 0·42 for the WB group to 0·93 in the PF group (Table 3).

Length and weight of GI tract

The lengths of the total GI tract differed significantly. The longest GI tract was measured in the rats fed on the OB diet (1470 mm), followed in decreasing order by the rats fed on the WB diet (1380 mm), PF diet (1350 mm), and the control diet (1300 mm) (Table 4). Compared with the rats in the control group, the elongating effect of all three NSP-enriched diets on the GI tract was significant in the lowest segments (colon–rectum), whereas the elongating effect on the small intestine was only observed in the OB group.

The differences in weight of the full and empty GI tract between the dietary groups followed the same order as that of the length. The average weight of the empty GI tract was about 15 g in the three NSP-enriched dietary groups compared with the significantly lower value of 11 g in the control group (Table 4). The content of all GI segments weighed significantly more in the rats fed on the NSP-enriched diets than in the control group.

Rate of passage of digesta

The total recovery of markers after 96 h from initial intake ranged from 96 % in the OB and control diets to 105 % in the WB and PF diets. The cumulative recovery of markers

Table 4. *Length of total gastrointestinal (GI) tract, small intestine, and colon–rectum segments and wet weight of full and empty GI tract, stomach and caecal contents, and colon–rectum contents in rats fed on control (C), wheat-bran (WB), oat-bran (OB), and pea-fibre (PF) diets**

(Means and standard deviations for twelve rats per diet)

Diet...	C		WB		OB		PF	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Length (mm) of								
Total GI tract	1300[b]	7·3	1380[b]	7·4	1470[a]	12·8	1350[ab]	15·4
Small intestine	1110[b]	6·6	1140[b]	8·6	1280[a]	12·3	1140[b]	15·6
Colon–rectum	153[c]	1·4	179[ab]	1·5	191[a]	1·5	172[b]	2·9
Weight (g) of								
Full GI tract	17·1[b]	4·7	24·9[a]	3·9	25·9[a]	3·2	25·3[a]	4·2
Empty GI tract	11·3[c]	1·2	14·7[b]	1·8	16·5[a]	1·8	15·0[a]	1·4
Stomach contents	0·7[c]	0·6	2·9[a]	1·9	1·9[ab]	1·1	1·7[bc]	1·4
Caecal contents	2·2[b]	0·6	3·5[a]	0·9	3·9[a]	0·9	3·7[a]	1·0
Colon–rectum contents	0·6[b]	0·5	1·7[a]	1·0	1·0[a]	0·5	1·2[a]	0·7

[a, b, c, d] Mean values with different superscript letters were significantly different ($P < 0.05$).

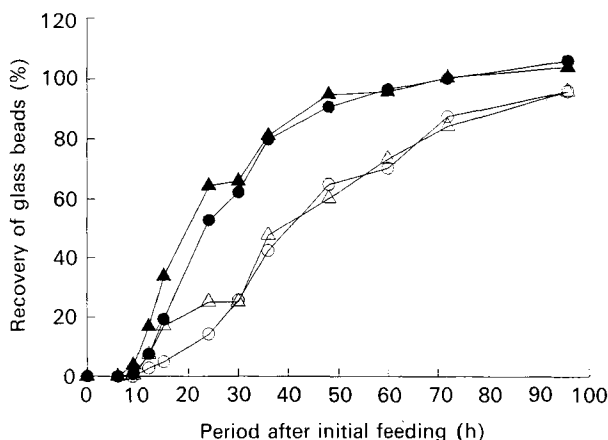* For details of diets, see p. 452 and Table 1.

Fig. 1. Faecal recovery of markers in rats fed on a control diet (○), wheat-bran diet (●), oat-bran diet (△), or pea-fibre diet (▲). Each value is the mean of six rats on each diet. For details of diets, see p. 452 and Table 1. For details of procedures, see pp. 452–453.

collected at different time-intervals after initial feeding and calculated as percentage of administered markers is shown in Fig. 1, which shows a distinctly different pattern of marker passage rate through the GI tract between the diets: the recovery of glass beads from the rats on the WB and PF diets occurred at a significantly faster rate than that of the rats fed on the OB and control diets.

The time-intervals (h) for 15, 50, and 85 % of the glass beads recovered in the faeces are shown in Table 5. For the rats fed on the WB and PF diets 50 % of the markers was

Table 5. *Rate of passage (h) for 15, 50, and 85 % of the markers excreted in the faeces of rats fed on control (C), wheat-bran (WB), oat-bran (OB), and pea-fibre (PF) diets*

(Means and standard deviations for six rats per diet)

Diet...	C		WB		OB		PF	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Excretion rate of markers (%)								
15	22·4[a]	9·9	14·8[b]	1·9	16·0[ab]	7·5	11·5[b]	1·8
50	38·3[a]	8·1	24·8[b]	4·7	36·5[a]	7·2	21·5[b]	6·5
85	65·5[a]	7·3	48·8[b]	10·4	66·5[a]	6·5	40·2[b]	9·7

[a,b,c,d] Mean values with different superscript letters were significantly different ($P < 0.05$).

recovered in the faeces after approximately 23 h. The recovery of 50 % of the markers from the rats in the OB and control diets lasted 14 h more (approximately 37 h). For the WB and PF diets 85 % of the markers were recovered after about 2 d, but only after a further 20 h from the rats on the OB and control diets.

DISCUSSION

With the inclusion of WB, OB, and PF as the main sources of NSP in the diets we obtained three isofibrous diets with quite different chemical composition and physical properties.

The chemical composition of WB, which comprised cell wall material mainly from the outer layers of the wheat grain, revealed the presence of mainly insoluble cellulose and arabino-xylans (Selvendran, 1984). In contrast to the WB, the major fraction of the NSP in the white wheat flour, which was used as a bulk component of the control diet, the WB and the PF diet, was mainly soluble arabino-xylans, the dominant NSP in the wheat endosperm cell walls (Nyman *et al.* 1983). The dominant glucose monomer in the OB diet had its origin in the soluble fraction of the oat β-glucans (Bach Knudsen *et al.* 1990), but also a considerable amount of arabino-xylans derived from cell walls was found in the OB diet. The cell-wall polysaccharides predominating in the PF diet were derived from pectic arabinans and minor amounts of cellulose and xyloglucans (Selvendran, 1984). The PF in the present study was derived from the cotyledon cell walls and, thus, contained less cellulose and insoluble NSP than PF including hull fractions which have been used in other rat studies (Goodlad & Mathers, 1990).

In recent work by Larsen *et al.* (1991) the authors found only very small differences in the apparent digestibility of macronutrients between groups of rats fed on daily amounts of DM ranging from 5 to 13 g. Increasing amounts of NSP (1·6–102·8 g/kg DM) from whole peas did not affect NSP digestibility when determined in rats (Goodlad & Mathers, 1990). The apparent digestibility values in the present study were, therefore, believed not to be affected significantly by the small differences in daily food intake between dietary groups (Table 2), and it was trusted that the effects brought about were mainly due to the presence of NSP.

The results demonstrated how different NSP sources even when fed at the same levels were digested to very different degrees. In contrast to pigs where a considerable degradation of NSP and particularly soluble NSP may occur in the terminal ileum (Graham & Åman, 1987; Bach Knudsen & Hansen, 1991), virtually all NSP may be degraded microbially in

the large intestine of the rat (Nyman & Asp, 1985; Goodlad & Mathers, 1990). The results from the present study confirmed that the degradation of soluble NSP was much higher (between 0·73 and 0·98) than the degradation of the insoluble fraction (between 0·42 and 0·93; Table 3). Degradation of the insoluble NSP fraction differed significantly, with a much lower degradation of insoluble wheat bran NSP compared with the insoluble fraction of OB and PF. This is probably due to the tight association between the cellulose and arabino-xylan strands and the presence of lignified tissues in wheat bran (Robertson et al. 1990; Bach Knudsen & Hansen, 1991). Particle size of DF is generally assumed to be a determinant for the susceptibility to bacterial degradation of the DF in man (Nyman & Asp, 1985). However, rat studies using similar techniques as in the present study have failed to show any marked effect of particle size (Nyman & Asp, 1985; Mongeau & Brassard, 1985). In our study the two diets with the largest particle sizes for NSP (the WB and PF diets) gave similar transit times but their constituent NSP were degraded to different extents (Table 3). In contrast, the NSP of the PF and OB diets were degraded to similar extents (Table 3) in spite of their different particle sizes and significantly different transit times. We, therefore, conclude from our study that along with chemical composition, physical structure, and particle size of the NSP, retention time of the digesta in the GI tract is another important determinant for NSP degradability.

The relatively low digestibility of NSP of the WB diet resulted in the highest faecal bulking value (Table 2). Even if faecal bulking values were 'normalized' as suggested by Johnson et al. (1990) to compensate for any differences in food intake, the ranking order of the faecal output (i.e. WB > OB > PF > control) would be no different. In concert with the conclusions drawn in a recent human study by Forsum et al. (1990) who studied the composition of wet faecal material rather than the faecal DM as in our rat study, we found that the ability of DF sources to increase faecal output primarily was correlated to the apparent digestibility of the DF source.

One of the important aspects of an increase in DF intake is the effect on the apparent digestibility of other dietary constituents. The present study showed that the same level of DF intake reduced apparent digestibility of energy, DM and protein significantly, but that the reductions differed significantly between diets. The reduction of apparent digestibility of protein was more pronounced in the case of OB than for WB or PF. This may partly be explained by the fact that the OB in this diet was the only protein source, contrary to the other diets where casein was added (Table 1). Proteins associated with cell-wall materials may have a negative effect on protein digestibility as discussed by Donangelo & Eggum (1985) and Gallaher & Schneeman (1986). Further, in the case of OB and PF, faecal protein may comprise considerable amounts of bacterial protein (Mason, 1984; Cummings, 1986), the synthesis of which is enhanced with increased substrate flow to the bacterial fermentation chamber (Remesy & Demigne, 1989).

In the present study no attempts were made to measure the effects of NSP on apparent digestibility of fats as measurements of such low concentrations present in the diets were likely to be blurred by excretions of endogenous fatty acids. Neither was digestibility of starch determined, as we have previously shown (Larsen et al. 1991) that the raw maize starch present in the N-free mixture was undetectable in rat faeces.

The reduction in the apparent digestibility of DM and energy in the high-DF diets differed significantly between diets, but were all in the range expected when compared with other studies (Nyman & Asp, 1985). The current trend to increase the consumption of DF has led to a need for an agreement for the determination of energy value of particular DF sources. If the apparent digestible energy values are calculated for the NSP in the present study (i.e. heat of combustion multiplied by digestibility), the energy values (kJ/g) are: WB 8·4, OB 16·0, PF 16·0. However, if partial digestible energy values are used, as recommended

in a recent workshop (Livesey, 1989), account is taken for the extra losses of protein and fat into faecal material which will inevitably follow an increase in DF intake. Using the equation: $17.2 \times 0.7 \, \alpha$ kJ/g, where α is the apparent digestibility of the unavailable carbohydrates (Livesey, 1990), the partial digestible energy values for the NSP in the present DF sources would be (kJ/g NSP): WB 5.9, OB 11.2, PF 11.2. The values for OB and PF are, thus, similar to those calculated in the same way for a highly purified guar gum (10.1 kJ/g; Davies et al. 1987). The value for WB would only be slightly lower than that calculated for a sugar-beet fibre (Johnson et al. 1990).

Digestibility of NSP and other nutrients also depends on the time of retention in the GI tract. In spite of slight differences in the methodology used, the MTT of approximately 25 h for the WB diet was remarkably close to the results of other rat studies (Table 5; Otsuka et al. 1989). The increased rate of passage of digesta of the PF diet may be partly explained by the shorter GI tract in the rats fed on this diet, while for the rats fed on the more indigestible WB diet, the increased rate of passage of digesta may be explained by the increase in motility of the intestine due to the sheer physical presence of bulk material. The significantly increased digesta MTT observed in the OB group may be related to the longer colon–rectum segments, which is the part of the entire GI tract with the longest residential time (Clemens & Stevens, 1980).

Transit time through the GI tract also depends on the length of the entire gut. Measurements confirmed that intake of the cereal-bran diets caused a significant extension of especially the colon–rectum segments (Table 4). This observed hypertrophy of gut tissues after intake of fibrous diets has been confirmed in earlier rat studies (Goodlad & Mathers, 1990). Statistical analysis performed on the data for total length and length of the GI tract segments showed no significant differences between the rats killed after a 14 d adaptation period and rats killed after a further two 8 d adaptation periods. We take this as an indication that a period of 14 d for rats at a size of 250 g is sufficient for the adaptation in GI size to take place. The question of appropriate adaptation time in DF studies has been raised in animal as well as human studies. Based on the present findings of the wide variations in the GI responses to the high-DF diets we feel that more attention should be drawn to the adaptation variable.

Conclusion

The results from the present study confirm that no simple cause and effect relationship exists between chemical composition, physical properties, and physiological effects of NSP along the GI tract. It is suggested from the present study that more notice should be taken of the stage of development of the GI tract and that further knowledge about long-term GI adaptation is needed.

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