Gastrointestinal implications in pigs of wheat and oat fractions

1. Digestibility and bulking properties of polysaccharides and other major constituents

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The present work was undertaken to study the gastrointestinal effects of wheat and oat dietary fibre (DF) using 40–50 kg pigs cannulated in the terminal ileum. The variables studied were: chemical characteristics of the DF, ileal and faecal digestibility of nutrients and bulking properties of polysaccharides and other major constituents. The wheat products studied included refined wheat flour and wheat fractions rich in the following botanical components: aleurone, pericarp/testa and bran. The oat products used were rolled oats and oat bran. The products varied considerably in DF content (g/kg dry matter) and composition; non-starch polysaccharides (NSP) and Klason lignin content ranged from 34 and 1 g/kg respectively in wheat flour, to 465 and 92 g/kg in pericarp/testa. The main NSPs in the wheat were arabinoxylans (AX) (64–69 %) and cellulose (15–31 %) and in oats mixed linked $\beta(1 \rightarrow 3; 1 \rightarrow 4)$-D-glucans ($\beta$-glucans; 46–63 %) and AX (28–32 %). The lowest content of soluble NSP was found in the lignified wheat fractions (bran and pericarp/testa) and the highest in oat bran. Eight diets were produced using the wheat and oat products and studied in two series of experiments using wheat flour as the DF-depleted control. The diets in Expt 1 were based on wheat flour and three iso-DF enriched diets prepared by adding DF from the fractions rich in wheat aleurone, pericarp/testa or bran. In Expt 2, oat bran was added to wheat flour to achieve the same DF intake level as in Expt 1. This series also included diets based on rolled oats and rolled oats plus oat bran. Starch was almost completely digested in the small intestine (0·97–1·00). However, there was a tendency to a slightly lower digestibility of oat starch compared with wheat starch. The recovery of wheat NSP in ileal digesta was 82–104 % compared with 64–66 % for oats. The low recovery of NSP in oat diets was primarily due to the low recovery of β-glucans (25–36 %). In the large intestine NSP and starch residues were extensively degraded. For the DF-depleted control diets or diets based on oats, 8–17 % NSP survived breakdown while in the diets enriched with aleurone, pericarp/testa or bran fractions, NSP recovery was 33, 50 and 38 % respectively. Fermentative breakdown of carbohydrates in the large intestine was estimated to contribute between 10 and 24 % of the energy for maintenance. Energy derived from the inflow of organic acids from the ileum contributed an additional 1–4 % of maintenance energy. In wheat endosperm, AX were broken down to a greater extent than cellulose, while the breakdown of AX in pericarp/testa was similar to that of cellulose. This difference in NSP breakdown can be explained by structural differences in the two types of cell walls. The breakdown of oat AX was lower than that of wheat flour. Wheat DF increased faecal bulk primarily by virtue of its physical presence and its water-holding capacity, while the oat DF stimulated faecal output through an increase in microbial biomass (Bach Knudsen *et al.* 1991). The result was a higher excretion of protein and fat. The higher fat excretion with the oat diets was probably due to a higher bile acid excretion caused by the more extensive fermentation of carbohydrates and the lower lumen pH.

Polysaccharides: Dietary fibre: Digestibility: Pig

Wheat and oat bran have been used in many investigations of the gastrointestinal (GI) tract and metabolic implications of dietary fibre (DF) in man and simple-stomached animals

(Anderson & Chen, 1979; Stephen & Cummings, 1980; Kirby *et al.* 1981; Wisker *et al.* 1985; Chen & Anderson, 1986). Although the non-starch polysaccharides (NSP) content of both are referred to as DF the physiological effects of wheat and oat bran are markedly different (Wyman *et al.* 1976; Anderson & Chen, 1979; Chen & Anderson, 1986). Wheat bran has a high proportion of insoluble lignified cell walls (Selvendran, 1984) and behaves more or less like a particulate marker in the GI tract with little or no effect on digestion and absorption in the small intestine. In the large intestine, wheat bran is resistant to microbial degradation (Southgate *et al.* 1976; Stephen & Cummings, 1980; Nyman & Asp, 1982; Donangelo & Eggum, 1985). Consequently, wheat bran due to its physical presence, is one of the most effective DF sources in increasing faecal bulk and in decreasing mouth-to-anus transit time (Cummings *et al.* 1978; Spiller *et al.* 1986).

In contrast to wheat bran, oat bran and oat products derived from oat endosperm have a high proportion of soluble DF in the form of mixed linked $\beta(1\rightarrow3;1\rightarrow4)$-D-glucans ($\beta$-glucans) (Aspinall & Carpenter, 1984). Soluble DF may increase the viscosity of the intralumen contents of the GI tract so delaying stomach emptying, increasing the mouth-to-caecum transit time and reducing the rate of absorption in the small intestine (Jenkins *et al.* 1978; Holt *et al.* 1979). This in turn has consequences for carbohydrate and lipid metabolism (Anderson & Chen, 1979; Chen & Anderson, 1986). Oat bran has been demonstrated to provide a significant hypocholesterolaemic effect (Chen & Andersen, 1986). In the large intestine oat bran, like other sources of soluble DF, is assumed to be readily fermented by colonic micro-organisms and has therefore only marginal effects on faecal bulk and mouth-to-anus transit time (Cummings *et al.* 1978).

While the metabolic consequences of wheat and oat bran are relatively well documented, much less is known about the GI implications of the various types of cell-wall materials (CWM). The main botanical constituents of wheat bran are pericarp/testa and aleurone tissues (Bacic & Stone, 1981*a*). The former has thick lignified cell walls whereas the aleurone cells are larger and have a high content of protein and lipids and thick and unlignified cell walls (Bacic & Stone, 1981*a*). The main polysaccharide constituents of isolated pericarp/testa cell walls are arabinoxylans (AX) (660 g/kg) and cellulose (320 g/kg) while in aleurone it is AX (650 g/kg) and β-glucans (310 g/kg) (Ring & Selvendran, 1980; Bacic & Stone, 1981*b*; Selvendran, 1984). Virtually all the grain lignin is associated with the pericarp/testa cell walls (Selvendran, 1984). Oat bran consists botanically of aleurone, subaleurone and various parts of endosperm tissues (Wood, 1986). The main polysaccharide constituents of oat bran are β-glucans (800 g/kg) and AX (200 g/kg) while only trace levels of cellulose are found (Aspinall & Carpenter, 1984).

The aim of the present investigation was to study the GI implications of various types of CWM derived from wheat and oats using a low DF control diet based on wheat flour and various experimental diets with DF derived from wheat or oats. The present paper deals with the digestion and bulking properties of polysaccharides and other major constituents in the GI tract of pigs. The effects of these treatments on microbial activity in the various segments of the GI tract are reported in an accompanying paper (Bach Knudsen *et al.* 1991).

EXPERIMENTAL

Raw material for diets

The wheat fractions – white flour, aleurone, pericarp/testa and bran – were produced at the research mill of the Carlsberg Research Laboratory, Copenhagen. Fractions rich in pericarp/testa or aleurone were prepared in the following way: the pericarp/testa was removed by abrasive stone milling (Schule GmbH, Hamburg) and further separated by sifting into fine (<500 μm) and coarse (500–850 μm) fractions. The yields of the fine and

Table 1. *Composition of experimental diets (g/kg dry matter)*

	Expt 1				Expt 2			
Diet...	WF1	WFA	WFPT	WFWB	WF2	WFOB	RO	ROOB
Ingredients								
Wheat flour	794	675	744	740	794	705	—	—
Wheat aleurone	—	174	—	—	—	—	—	—
Wheat pericarp/testa	—	—	72	—	—	—	—	—
Wheat bran	—	—	—	82	—	—	—	—
Rolled oats	—	—	—	—	—	—	892	794
Oat bran	—	—	—	—	—	154	—	151
Casein	122	79	105	100	122	66	70	21
Soya-bean oil	46	39	43	42	46	41	—	—
Vitamin/mineral mixture*	34	29	32	32	34	30	34	30
Chromic oxide (marker)	4	4	4	4	4	4	4	4
Composition of diet								
Protein (nitrogen × 6·25)	195	169	182	182	195	169	191	164
HCl-fat	60	61	57	62	57	70	66	73
LMW-sugars	11	12	11	10	11	11	12	13
Fructans	10	12	11	12	10	10	1	1
Starch	654	648	628	629	652	659	600	593
NSP	30	48	54	54	34	47	80	96
S-NSP	nm	nm	nm	nm	20	28	42	52
I-NSP	nm	nm	nm	nm	14	19	38	44
β-Glucans	3	5	4	4	3	12	38	47
Klason lignin	4	7	8	8	9	10	13	13
Dietary fibre	34	55	62	62	43	57	93	109

LMW-sugars, low-molecular weight sugars; HCl-fat, hydrochloric acid-fat; NSP, non-starch polysaccharides; S-NSP, soluble non-starch polysaccharides; I-NSP, insoluble non-starch polysaccharides; dietary fibre, NSP + Klason lignin; nm, not measured; WF1, WF2, wheat flour; WFA, wheat flour + aleurone; WFPT, wheat flour + pericarp/testa; WFWB, wheat flour + wheat bran; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran.

* For composition, see Eggum *et al.* (1982).

coarse fractions were 5·8 and 0·4% respectively. Microscopic inspections and chemical analysis indicated that the coarse fraction primarily consisted of the pericarp tissues while the fine fraction was more difficult to define. In this experiment, however, the two fractions were mixed 1:1 (w/w) and referred to as pericarp/testa. A fraction rich in aleurone was obtained by further decortication to yield 6·7% of the remaining kernels. Low extracted white flour (53%) and bran were produced in a process involving disk and conventional roller milling techniques. For the purpose of the present study the wheat fractions are referred to as wheat flour, aleurone, pericarp/testa and wheat bran. The oat products used were commercially available rolled oats (OTA A/S, Nakskov, Denmark) and Morthers Oat Bran (The Quaker Oats Company, Barrington, USA).

Experimental diets

The experimental diets were prepared from: wheat flour (WF), wheat flour + aleurone (WFA), wheat flour + pericarp/testa (WFPT), wheat flour + wheat bran (WFWB), wheat flour + oat bran (WFOB), rolled oats (RO) and rolled oats + oat bran (ROOB) (Table 1). The diets were tested in two series of experiments, using diet WF as the low-DF control diet (diets WF1 and WF2, Table 1). The low-DF control provided 54 g DF/d in the balance period; diet WFA, WFPT, WFWB and WFOB 95–102 g DF/d; diet RO 130 g DF/d; and diet ROOB 173 g DF/d. Appropriate adjustment for protein content was made by

adjusting the casein content. Chromic oxide marker was added to each diet (4 g marker/kg dry matter).

Animals and feeding

Pigs (40–50 kg), cannulated at the end of the small intestine, were used. Surgery was performed at 30–35 kg and a 'T' cannula was placed in the ileum approximately 150 mm anterior to the ileo-caecal junction. A total of thirty-two cannulated pigs, sixteen pigs in each series, were used. In each series the sixteen pigs were divided into four groups (one group per diet) with one littermate from each herd in each group. The animals were fed three times daily at 07.00, 15.00 and 23.00 hours with 1·5–1·8 kg/d of diet adjusted to give the same amount of net energy per day (1·8 Feeding Units, pigs (FU_p); 1 FU_p = 7·7 MJ net energy; Just, 1975) (body-weight (BW) 40 kg) and with increases of 0·02 FU_p/d. The feed was thoroughly mixed with water before feeding. After a 7 d adaptation period, faeces were collected quantitatively on days 7–11 and ileal digesta on days 12–14. Ileal digesta were collected for a total period of 12 h; on day 12 at 9.00–11.00 hours and 13.00–15.00 hours, on day 13 at 8.00–10.00 hours and 12.00–14.00 hours and on day 14 at 7.00–9.00 hours and 11.00–13.00 hours. The whole procedure was repeated with the same pig on days 15–28.

Faeces were collected twice daily, frozen and stored at −20°. At the end of the experiment the faeces was mixed before sampling for analysis. The dry matter content of faecal material was determined on fresh faecal material taken immediately after the pigs were transferred from the balance cage to the pen. The ileal digesta were collected on ice, frozen immediately after collection, stored at −20° and mixed thoroughly before samples were taken for analysis.

Analytical methods

Nitrogen, Cr_2O_3 and organic acid determinations were performed on wet materials, all other analyses were carried out on freeze-dried materials. Dry matter contents of feed, ileal digesta and faeces were determined by drying at 105° for 5 h. All the following analyses were made in duplicate. Protein (nitrogen × 6·25) was determined by the Kjeldahl method using a Kjell-Foss 16200 autoanalyser, and energy was measured in a IKA calorimeter C 400 (Janke & Kunthel KG IKA-werk, Germany). Ash was analysed according to the Association of Official Analytical Chemists (1975), while fat (hydrochloric acid–fat) was extracted with diethyl ether after acid-hydrolysis (Stoldt, 1957). Cr_2O_3 was determined using the method of Schürch *et al.* (1950).

Low molecular weight (LMW) sugars, glucose, fructose and sucrose, and fructans were extracted with acetate buffer (0·1 M, 65°, pH 5·0), and the glucose and fructose residues before and after hydrolysis (0·037 M-sulphuric acid, 80°, 70 min) were quantified with specific enzymes (Larsson & Bengtsson, 1983). Fructans were calculated as the total of fructose in hydrolysate less free fructose and fructose deriving from sucrose. Fructose residues were converted to polysaccharides by the factor 0·92. Starch was analysed by the enzymic method of Bach Knudsen *et al.* (1987), and total β-glucans by the fluorometric method of Jørgensen & Aastrup (1987). Total NSP and their constituent sugars were determined as alditol acetates by gas–liquid chromatography (GLC) for neutral sugars, and by a decarboxylation method for uronic acids using a modification of the Theander & Åman (1979), Theander & Westerlund (1986) and Englyst *et al.* (1982) procedures. Starch was quantitatively removed by incubation (100°, 60 min; 60°, 16 h) with a thermostable α-amylase (*EC* 3.2.1.1; Termamyl®; Novo A/S, Denmark) and with amyloglucosidase (*EC* 3.2.1.3; Boehringer Mannheim GmbH, Mannheim, Germany). The polysaccharides in the starch-free residue were allowed to swell in the presence of sulphuric acid (12 M, 30°, 60 min), hydrolysed with 0·41 M-H_2SO_4 (125°, 60 min), reduced with potassium boro-hydride to alcohols and acetylated using 1-methylimidazole to catalyse the reaction; allose

was used as internal standard. In Expt 2 this method was modified and hydrolysis of NSP constituent sugars was performed with 1 M-H_2SO_4 (100°, 2 h) (Englyst *et al.* 1982). Soluble NSP (S-NSP) in the starch-free residue was extracted from all raw materials, and from diets, ileal digesta and faeces from Expt 2, using a phosphate buffer at neutral pH (0·2 M, 100°, pH 7·0) (Englyst *et al.* 1982) and the neutral and acidic sugars in insoluble NSP (I-NSP) analysed as described previously. Content of cellulose was calculated as:

$$\text{cellulose} = \text{NSP}_{\text{glucose}} - \beta\text{-glucans}, \quad (1)$$

arabinoxylans (AX) as:

$$\text{AX} = (\text{arabinose} + \text{xylose} + \text{uronic acids}), \quad (2)$$

and S-NSP as:

$$\text{S-NSP} = \text{Total-NSP} - \text{I-NSP}. \quad (3)$$

Klason lignin was measured gravimetrically as the residue resistant to 12 M-H_2SO_4 (Theander & Westerlund, 1986). Klason lignin in faecal materials was corrected for N.

Total short-chain fatty acids (SCFA) were estimated by titration of 200 ml distillates derived from either 12·5 g wet faeces or 25·0 g ileal digesta with 0·1 M-sodium hydroxide. The titrated distillates were evaporated almost to dryness at 80° in an oven with air circulation and transferred with a small amount of water to a 20 ml glass-stoppered test tube. After evaporation to dryness, 10 ml ethyl ether were added followed by 0·5 ml 4 M-HCl. This was followed by 30 min phase separation under which the test tube was vigorously shaken three to four times. Drying agent was added and the ethyl layer transferred to a small vial. Separation of the individual SCFA was performed by GLC. Total lactic acid (LA) was determined by means of specific enzymes in a coupled enzymic reaction with NAD^+ (Gawehn, 1984; Noll, 1984). The reaction between L-lactic acid, D-lactic acid and NAD^+ is catalysed by the enzymes L-lactate dehydrogenase (*EC* 1.1.1.27; Boehringer Mannheim GmbH) and D(−)-lactate dehydrogenase (*EC* 1.1.1.28; Boehringer Mannheim GmbH). The amount of NADH formed during the oxidation of NAD^+ was stoichiometric with the amount of lactic acid in the sample.

Calculation and statistical analyses

The content of polysaccharide residues was calculated as anhydro-sugars, and all digestibilities and flow measurements were calculated relative to the Cr_2O_3 content. When calculating starch digestibility it was assumed that the free glucose in ileum digesta derives from starch. The digestion of nutrients and the net disappearance of energy in the large intestine were calculated on the basis of the daily flow at the ileum, and the faecal content of the specific nutrients: energy, LMW-sugars, starch, NSP, N, fat, lactic acid, acetic acid, propionic acid and butyric acid and calculated as:

$$\Delta X_{\text{LI}} = (\text{ileum}_{\text{flow}} - \text{faeces}_{\text{flow}}) \quad (4)$$

where ΔX_{LI} is the net disappearance of the various nutrients in the large intestine. When converting the non-carbohydrate sources into energy values the following factors were used: N 145·6 kJ/g; fat 37·7 kJ/g; lactic acid 1368 kJ/mol; acetic acid 875 kJ/mol; propionic acid 1528 kJ/mol and butyric acid 2185 kJ/mol.

The results from Expts 1 and 2 were initially examined by a two-way analysis of variance (ANOVA) model, as outlined by Snedecor & Cochran (1973):

$$X_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \epsilon_{ijk}, \quad (5)$$

where X_{ijk} is the dependent variable (i.e. NSP constituent sugar values, etc.); μ is the overall mean; α_i is the effect of diet; β_j is the effect of period and ϵ_{ijk} is a normally distributed

random variable. However, because no period effect was identified this effect was omitted from the model and included in the estimate of error (e_{ijk}).

RESULTS

Chemical composition of raw materials

The refined wheat flour was nearly pure endosperm tissue as judged from the high starch content (g/kg dry matter) of 829 g/kg and the low content of NSP and Klason lignin of 34 and 1 g/kg respectively (Table 2).

Pericarp/testa was the most lignified CWM and the fraction with the highest absolute (140 g/kg) and relative content of cellulose. In this fraction the cellulose content represented 31 % and the AX content 64 % of total NSP. The starch present (160 g/kg) was due to contamination with endospermic tissues. The aleurone fraction was more heavily contaminated with endosperm tissues and to a minor degree with pericarp/testa CWM as judged from the high level of starch (514 g/kg) and the relatively high Klason lignin content of 26 g/kg. Compared with pericarp/testa, the relative content of cellulose of NSP in the aleurone fraction was reduced to 28 %, while AX accounted for 68 % of NSP; similar to that of pericarp/testa.

The NSP and in particular the cellulose content of wheat bran was lower than that of pericarp/testa, while Klason lignin only was slightly lower. The high content of fat and LMW-sugars indicated high levels of germ in the bran fraction.

β-Glucans were the main NSP constituent of oats with absolute and relative values of 42 g/kg and 46 % in rolled oats and 98 g/kg and 63 % in oat bran. In these two products AX made up 32 and 28 %. Higher levels of protein and fat were a common feature of the oat products.

The variation of NSP composition and in particular the content of β-glucans had great impact on the solubility of wheat and oat DF (Table 2). In the fractions with the highest proportion of lignified CWM (pericarp/testa and wheat bran), S-NSP was only 11–15 % of total NSP, while in oat bran, 60 % was soluble. The relatively high solubility in wheat flour, however, was due to soluble AX.

Digestibility of polysaccharides and LMW-sugars

Starch in Expt 1 was almost completely digested before the end of the small intestine (0·99–1·00) (Table 3). In Expt 2 the starch digestibility was in general lower with the lowest values found for the oat diets of 0·97 (Table 4). Even more marked differences between the two cereals were seen for NSP. For wheat, the recovery of NSP was 82–105 % (not-significant) compared with 64–66 % ($P < 0·05$) for oats. The low recovery of NSP in the oat diets was primarily due to the low recovery of β-glucans of 25–36 %. Comparative values for the recovery of cellulose and AX in all diets were cellulose 56–123 % and AX 88–110 %. Partition of total NSP into soluble and insoluble fractions further indicated that wheat flour AX undergoes modifications during passage through the small intestine (Fig. 1). For diet WF2 recovery of S-NSP was 106 % and that of I-NSP was 53 %, while in diets RO and ROOB recovery of S-NSP was 38–43 % and that of I-NSP was 93–96 %.

At the end of the small intestine there was a recovery of 7–52 % of LMW-sugars (not significant) and 5–29 % of fructans (not significant).

Extensive breakdown of NSP and starch residues took place in the large intestine (Tables 3 and 4). For the non-lignified CWM derived from wheat flour (diets WF1 and WF2) and oat (diets WFOB, RO and ROOB) only 8–17 % survived breakdown during passage of the entire gut. CWM of aleurone and in particular pericarp/testa was more resistant to microbial degradation. For the latter CWM the recovery of NSP increased to 33 and 50 %

Table 2. *Chemical composition of wheat and oat fractions for diets (g/kg dry matter)*

	Wheat fractions					
	Flour	Aleurone	Pericarp/ testa	Bran	Rolled oats	Oat bran
Protein (nitrogen × 6·25)	103	157	110	151	139	250
HCl-fat	21	54	5	65	75	102
LMW-sugars						
Glucose	<1	2	4	4	<1	<1
Fructose	<1	<1	2	2	<1	<1
Sucrose	12	33	26	43	12	18
Total sugars	13	36	33	48	12	18
Fructans	16	19	15	27	1	2
Starch	829	514	160	168	646	424
NSP						
Cellulose	5	39	144	98	14	8
β-Glucans	4 (4)*	9 (8)	9 (11)	14 (12)	42 (38)	98 (77)
AX	22 (11)	118 (25)	296 (36)	287 (46)	29 (8)	43 (11)
Arabinose	8 (4)	41 (6)	123 (10)	94 (11)	11 (4)	15 (4)
Xylose	13 (6)	66 (14)	143 (18)	168 (26)	13 (2)	21 (4)
Uronic acid	1 (<1)	11 (5)	28 (8)	25 (9)	5 (2)	7 (3)
Total NSP	34 (17)	174 (38)	465 (52)	414 (63)	91 (47)	155 (91)
Klason lignin	1	26	92	86	15	30
Dietary fibre	35	200	557	500	106	185

HCl-fat, hydrochloric acid-fat; LMW-sugars, low-molecular weight sugars; NSP, non-starch polysaccharides; AX, arabinoxylans.

* Values in parentheses are soluble-NSP.

for diets WFA and WFPT respectively. When wheat bran was added to the diet the recovery was 38%, i.e. significantly lower than that for diet WFPT and slightly, but non-significantly, higher than that for diet WFA.

For all NSP constituents other than β-glucans, the recovery in faeces followed the same trend as for total NSP. While only trace levels of β-glucans survived breakdown irrespective of source, lignification played an important role in reducing the breakdown of cellulose (recovery 17–76%) and AX (recovery 10–50%). Similarly the recovery of S-NSP of the diets in Expt 2 was only 2% while 17–23% of I-NSP was recovered in faeces (Fig. 1).

Digestibility of energy, protein and fat

The wheat-flour diets were highly digestible with energy digestibilities at the terminal ileum and in faeces of 0·91–0·92 and 0·97 (Table 5). The lower ileal digestibility in Expt 2 was primarily due to the lower digestibility of starch and protein. Increasing the daily DF intake from 54–57 g/d (diets WF1 and WF2) to 95–102 g/d by the various wheat fractions reduced energy digestibility at the terminal ileum by 0·04 (0·03–0·05). Given the same amount of DF in the form of oat bran had a less detrimental effect (−0·02), while raising the DF intake further to 130 g/d (diet RO) and 173 g/d (diet ROOB) resulted in an additional reduction of energy digestibility by the end of the ileum to 0·82 and 0·80 respectively.

Digestibility of energy was on average 0·06 higher in faeces than at the terminal ileum when feeding the diets based on wheat flour or with added fibre from either the wheat fractions or oat bran. With diets RO and ROOB the difference between the two values was approximately 0·11.

Table 3. *Recovery at ileum and in faeces (% intake) of polysaccharides when feeding diets composed of various fractions of wheat*

Diet*...	WF1	WFA	WFPT	WFWB	SEM
Ileum					
Starch	1	1	1	1	0·3
NSP	97	104	104	90	8·3
Cellulose	121	117	123	95	15·1
β-Glucans	12[b]	23[b]	22[b]	36[a]	4·2
AX	110	109	110	97	8·6
Arabinose	110	106	112	95	8·5
Xylose	111	112	112	98	10·6
Uronic acid	101	102	96	108	7·7
Faeces					
Starch	Trace	Trace	Trace	Trace	
NSP	17[c]	33[b]	50[a]	38[b]	2·5
Cellulose	40[c]	53[b]	76[a]	56[b]	5·7
β-Glucans	Trace	Trace	Trace	Trace	
AX	15[c]	32[b]	50[a]	38[b]	2·4
Arabinose	15[c]	37[b]	56[a]	44[b]	3·1
Xylose	10[c]	23[b]	42[a]	28[b]	2·2
Uronic acid	54[b]	68[ab]	73[a]	78[a]	5·3

NSP, non-starch polysaccharides; AX, arabinoxylans; WF1, wheat flour; WFA, wheat flour + aleurone; WFPT, wheat flour + pericarp/testa; WFWB, wheat flour + wheat bran.

* For details, see Table 1.

[a, b, c] Values in the same horizontal row with different superscript letters were significantly different ($P < 0·05$).

Table 4. *Recovery at ileum and in faeces (% intake) of polysaccharides when feeding wheat and oat fractions*

Diet*...	WF2	WFOB	RO	ROOB	SEM
Ileum					
Starch	2[ab]	1[b]	3[a]	3[a]	0·4
NSP	82	64	64	66	4·8
Cellulose	80	56	62	70	10·6
β-Glucans	21	25	27	36	6·1
AX	88	89	106	108	5·4
Arabinose	95	93	107	109	5·4
Xylose	88[ab]	86[b]	108[a]	107[a]	5·8
Uronic acid	100	93	98	112	5·6
Faeces					
Starch	Trace	Trace	0·3	0·3	—
NSP	13	9	10	8	1·3
Cellulose	37[a]	17[b]	22[b]	17[b]	4·4
β-Glucans	Trace	Trace	Trace	Trace	—
AX	10[b]	10[b]	18[a]	16[a]	1·4
Arabinose	11	10	14	12	1·4
Xylose	8[b]	7[b]	14[a]	12[a]	1·4
Uronic acid	32	37	39	41	4·0

NSP, non-starch polysaccharides; AX, arabinoxylans; WF2, wheat flour; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran.

* For details, see Table 1.

[a, b] Values in the same horizontal row with different superscript letters were significantly different ($P < 0·05$).

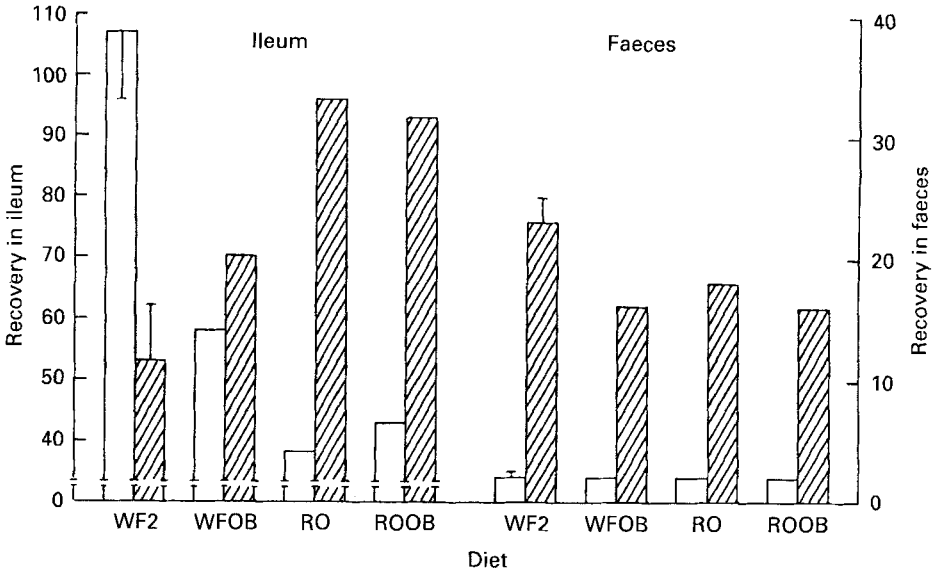

Fig. 1. Recovery at the ileum and in the faeces (% intake) of soluble non-starch polysaccharides (□) and insoluble non-starch polysaccharides (▨). Values are means with their standard errors represented by vertical bars. WF2, wheat flour; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran. For details of diets, see Table 1.

Table 5. *Apparent ileal (I) and faecal (F) digestibilities of dietary constituents when provided in diets composed of various wheat and oat fractions*

	Apparent digestibility					
	Energy		Protein		HCl-fat	
Diet*	I	F	I	F	I	F
Expt 1						
WF1	0·92[a]	0·97[a]	0·92[a]	0·97[a]	0·92[a]	0·92[a]
WFA	0·89[b]	0·95[b]	0·90[b]	0·94[b]	0·88[ab]	0·88[a]
WFPT	0·89[b]	0·93[bc]	0·90[b]	0·93[b]	0·90[a]	0·87[a]
WFWB	0·87[b]	0·94[bc]	0·91[ab]	0·94[b]	0·86[b]	0·87[a]
Expt 2						
WF2	0·91[ab]	0·97[a]	0·91[ab]	0·97[a]	0·88[ab]	0·91[a]
WFOB	0·89[b]	0·96[ab]	0·88[b]	0·94[b]	0·86[b]	0·87[a]
RO	0·82[c]	0·92[c]	0·84[c]	0·90[c]	0·69[c]	0·75[b]
ROOB	0·80[c]	0·91[c]	0·77[c]	0·84[d]	0·68[c]	0·74[b]
SEM	0·009	0·005	0·010	0·007	0·016	0·017

WF1, WF2, wheat flour; WFA, wheat flour + aleurone; WFPT, wheat flour + pericarp/testa; WFWB, wheat flour + wheat bran; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran.

* For details, see Table 1.

[a, b, c, d] Values in the same vertical column with different superscript letters were significantly different ($P < 0·05$).

The digestibility of protein at the terminal ileum and in faeces paralleled that of energy. When feeding wheat-flour diets, ileal and faecal digestibilities of protein were 0·91–0·92 and 0·97, respectively. Addition of the high-fibre wheat fractions and oat bran reduced ileal digestibility to 0·88–0·91 and faecal digestibility to 0·93–0·94. A further reduction due to DF

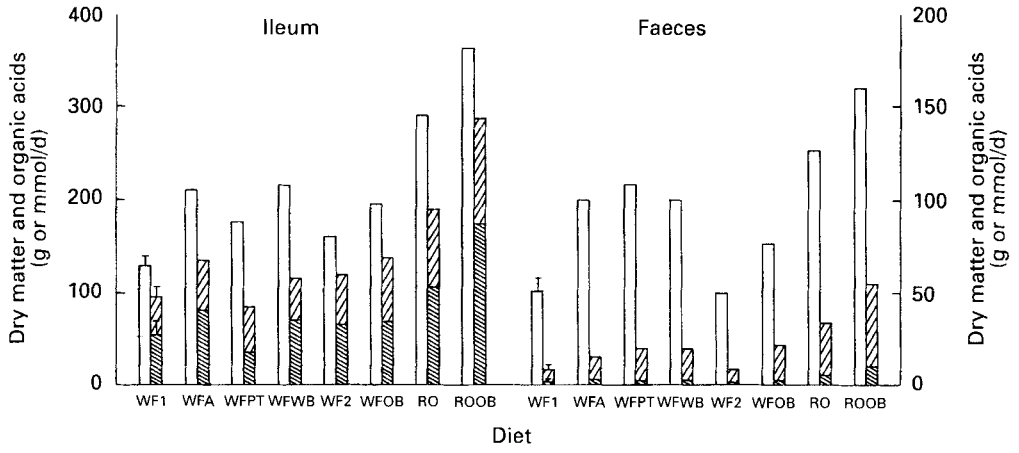

Fig. 2. Daily flow (g dry matter or mmol/d) at the ileum and in the faeces of dry matter (□), lactic acid (▨) and short-chain fatty acids (▨). Values are means with their standard errors represented by vertical bars. WF1, WF2, wheat flour; WFA, wheat flour + aleurone; WFPT, wheat flour + pericarp/testa; WFWB, wheat flour + wheat bran; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran. For details of diets, see Table 1.

levels was seen with diets RO and ROOB. For these diets ileal digestibility was 0·84 and 0·77 and faecal digestibility 0·90 and 0·84. For fat the effect of the addition of wheat or oat fibres to the wheat-flour diets were less significant and only the ileal digestibility of diets WFWB and WFOB were significantly lower than that of wheat flour. In contrast the diets based on oat fibre alone had significantly lower ileal and faecal digestibilities. For these two diets ileal digestibility was 0·68–0·69 and faecal digestibility 0·74–0·75.

Organic acids

The concentrations of organic acids (LA and SCFA) were reasonably constant in ileal digesta with values in the range LA 23–57 mmol/l and SCFA 31–45 mmol/l, and with a ratio between the two acids of LA:SCFA 0·55 and SCFA:LA 0·45.The daily flow of organic acids calculated on the basis of the flow of marker and concentrations of organic acids in digesta was 96–137 mmol/d for the wheat-flour diets and the iso-DF diets. This value increased to 189 mmol/d for diet RO and further to 286 mmol/d for diet ROOB (Fig. 2). The flow of organic acids was primarily determined (r 0·95, $P < 0·001$) by the flow of dry matter.

The amount of organic acids excreted in faeces was only 7–23% of that passing the ileum, with SCFA accounting for more than 82% of the organic acids.

Digestion of nutrients in the large intestine

The total amount of energy absorbed from the large intestine varied from 1133 kJ/d for diet WFPT to 3533 kJ/d for diet ROOB. The amount of energy, before and after correction for the net disappearance of N, fat and organic acids was highly correlated to the overall digestion of plant carbohydrates within the large intestine (Fig. 3). The lowest value (average) was obtained with diet WF1 (45 g/d) and the highest with diet ROOB (120 g/d), with even greater variations among the individual pigs (24–157 g/d) (Fig. 3). In addition to the digestion of carbohydrates, 1·1–3·7 g N/d and −3·3–7·0 g fat/d disappeared within this GI compartment. The amount of energy disappearing in the large intestine in the form of N and fat varied from 41 kJ/d for diet WFPT to 825 kJ/d for diet ROOB and in the form of organic acids from 77 to 278 kJ/d respectively for the diets.

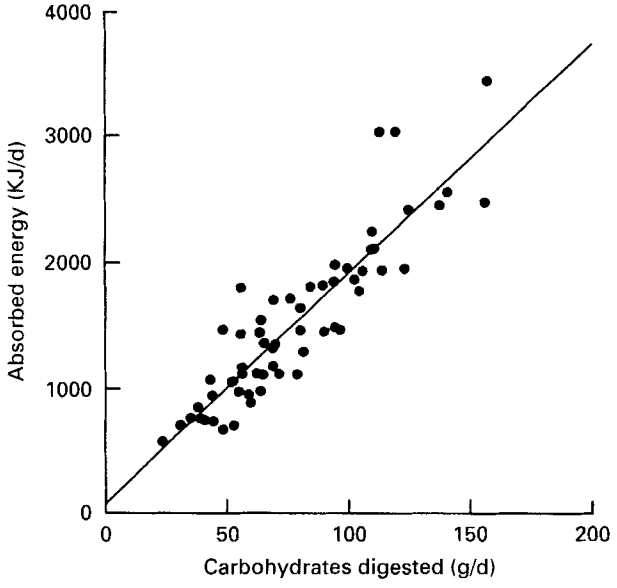

Fig. 3. The correlation between energy absorbed (kJ/d) and the amount of carbohydrate digested (g/d) in the large intestine. Absorbed energy is corrected for the energy value of the net disappearance of nitrogen, fat and organic acids. The relationship between digested carbohydrates (X) and absorbed energy (Y) can be expressed as: $Y = 74{\cdot}4 + 18{\cdot}4X$ (R^2 0·812).

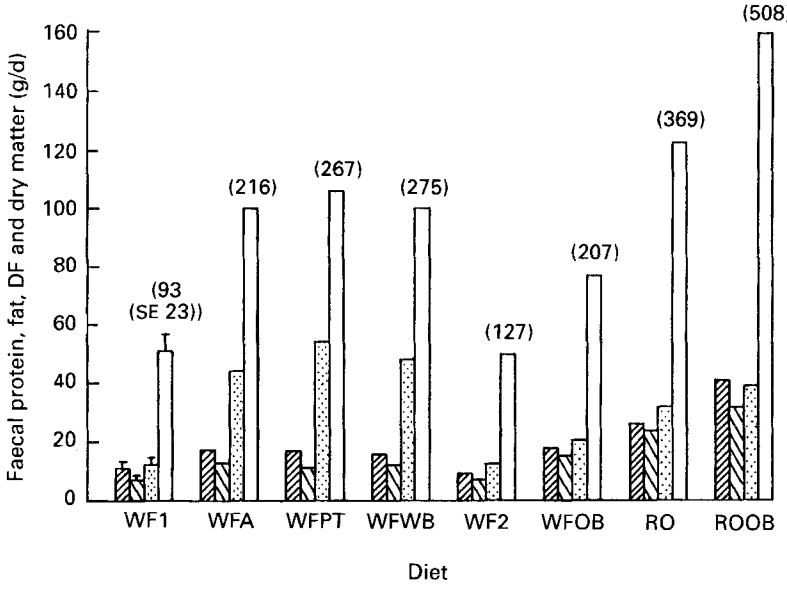

Fig. 4. Faecal excretion of protein (▨), fat (▧), dietary fibre (▩) and dry matter (□). Faecal wet weight (g/d) is given in parentheses. Values are means with their standard errors represented by vertical bars. WF1, WF2, wheat flour; WFA, wheat flour + aleurone; WFPT, wheat flour + pericarp/testa; WFWB, wheat flour + wheat bran; WFOB, wheat flour + oat bran; RO, rolled oats; ROOB, rolled oats + oat bran. For details of diets see Table 1.

Bulking properties

Increasing the DF intake in Expt 1 by the addition of fibre-rich wheat fractions caused an increment in faecal bulk from 93 to 216–275 g/d and in dry matter from 51 to 110–104 g/d (Fig. 4). The most important factor was the undigested DF which increased from 32 to 42 g/d, while the increases in protein and fat were more marginal. In Expt 2 faecal bulk increased from 127 (diet WF2) to 508 g/d (diet ROOB) and dry matter from 50 to 160 g/d for the two diets respectively, with much less of the increase 8–26 (g/d) caused by the DF residues. In contrast protein and fat increased from 9 and 7 g/d respectively in diet WF2 to 41 and 32 g/d respectively in diet ROOB.

DISCUSSION

The results from the present pig experiment are consistent with the current physiological knowledge concerning digestion of cereal polysaccharides in various segments of the digestive tract in simple-stomached species. In spite of the lower starch digestibility in Expt 2 it can be concluded that starch was almost completely digested at the end of the small intestine. The recovery of wheat NSP at this site was nearly complete (82–104%) while there was a substantial loss in the small intestine of oat NSP. Similar results were obtained in other studies with pigs (Millard & Chesson, 1984; Graham *et al.* 1986*a*). When feeding a diet based on cereal grains (wheat:barley:oats; 1:1:1) to pigs, 80% of NSP was recovered in ileal digesta while NSP recovery was raised to 89% when one-third of a basal diet was substituted with wheat-bran (Graham *et al.* 1986*a*). The recovery of NSP at the end of the small intestine in man seems to be slightly higher because of a lower colonization of micro-organisms in the lower portion of the small intestine. In man (ileostomy patients) Sandberg *et al.* (1981) recovered 80% of NSP in wheat bran at the terminal ileum while total recovery of NSP (95–115%) was obtained by Englyst & Cummings (1985) when studying rolled oats, white bread and cornflakes. The NSP recovery in the latter study was higher than that found for a similar diet in the present study (rolled oats) or when feeding other soluble DF sources in the form of pectins (Sandberg *et al.* 1983) to man, or sugarbeet pulp and swede (*Brassica napus* L.) to pigs (Millard & Chesson, 1984; Graham *et al.* 1986*a*). For these diets NSP recovery was 70% in man and 56–66% in pigs.

There was a substantial loss of β-glucans in the small intestine as only between 12 and 36% escaped digestion here. Similar results were obtained by Graham *et al.* (1986*b*), who found that 74% of barley β-glucans were recovered at the duodenum and 30% at the terminal ileum. It is most likely that the high solubility of β-glucans makes this an easily degradable substrate for the bacteria permanently colonizing this part of the GI tract in pigs. Recent studies (Bach Knudsen *et al.* 1990) have shown that oat β-glucans were primarily broken down in the distal segment of the small intestine where microbial activity may reach considerable levels (Bach Knudsen *et al.* 1991). The relatively high microbial activity in the lower portion of the small intestine was probably also responsible for the modifications of wheat endosperm NSP which takes place during the passage of this part of the GI tract. At the terminal ileum recovery of S-NSP was 106% compared with 53% for I-NSP. The reason might be breakage of bridges between diferulic acid and AX found in wheat endosperm (Neukom *et al.* 1964; Markwalder & Neukom, 1976).

Assuming an efficiency of 75% for converting carbohydrates into organic acids (Mason, 1980) the present results suggest that the net absorption of energy derived from fermentative breakdown of carbohydrates in the large intestine corresponded to 10–24% of the metabolizable energy required for maintenance (ME_m (kJ) = 4060 + 210 $BW^{0.75}$; Eggum *et al.* 1982). Although the present diets had significantly lower DF contents than conventional pig diets (Graham *et al.* 1986*a*) these estimates are within the same order of

magnitude as found by Mason (1980) on the basis of results obtained with a cereal-based diet (Mason & Just, 1976). In the study of Mason & Just (1976) the energy released by fermentation in the large intestine corresponded to 18% of metabolizable energy for maintenance (ME_m). More extreme estimates for energy contribution from large intestinal fermentation (33–44% of ME_m; Mason, 1980) can be calculated when the amount of fermentable substrates entering the large intestine are raised by including either α-amylase resistant starch from ungelatinized potatoes (Mason & Just, 1976) or CWM from hay (Keys & DeBarthe, 1974). For comparison, estimates in vitro (Imoto & Namioka, 1978) indicate that the SCFA produced in the large intestine accounts for 11·6% and 9·6% of ME_m with low- and high-carbohydrate diets respectively. In addition the net balance of organic acids ($Ileum_{flow} - faeces_{flow}$), which certainly derive from carbohydrate fermentation in the lower portion of the small intestine, account for an additional 1–4% of ME_m.

Although the aleurone and pericarp/testa fractions prepared by the current dry milling process did not represent completely pure fractions, the results allow conclusions to be drawn about the breakdown of the main cell wall polysaccharides from various parts of the wheat grain. The order of NSP breakdown was endosperm > aleurone > pericarp/testa. Hence NSP in primary unlignified cell walls from endosperm and aleurone were much more extensively broken down than NSP in the secondary lignified cell walls from pericarp/testa. This supports the results of Cheng *et al.* (1987), who found a significantly higher SCFA concentration in caecal fluid and in plasma from the portal vein and a higher faecal bacterial mass in rats fed on pure aleurone cells compared with pericarp/testa. Moreover, the results are in accordance with earlier studies at this Institute with milling fractions from barley fed to rats (Bach Knudsen & Eggum, 1984; Bach Knudsen *et al.* 1984). In those studies fractions rich in aleurone cells stimulated microbial activity in the caecum and colon in contrast to husk-rich fractions (secondary lignified CWM) which reduced microbial activity relative to whole-grain barley.

The general order of breakdown of the main cell wall polysaccharides in wheat are AX > cellulose in endosperm and AX similar to cellulose in pericarp/testa. These differences in the relative breakdown can be explained by the manner in which the polysaccharides are organized and linked to other macromolecules within the two types of cell walls. In pericarp/testa (lignified cell walls) the cellulose microfibrils are dispersed in AX polysaccharides and lignin, while in endosperm and aleurone cell walls lignin is not present (Mares & Stone, 1973; Bacic & Stone, 1981*a*, *b*; Selvendran, 1984). The AX present in pericarp/testa are acidic with linkages to other macromolecules (e.g. lignin or proteins, or both) while in endosperm neutral AX are found. Moreover, approximately one-third of endosperm AX are soluble in water in contrast to the acid AX from pericarp/testa which are insoluble in water (Ring & Selvendran, 1980; Selvendran, 1983). Thus the structural features of the two types of cell walls explain, first, the higher breakdown of cellulose and AX in endosperm relative to pericarp/testa. Second, the organization of the polysaccharides and their crosslinkages to other macromolecules makes the pericarp/testa cell walls much more rigid than those of endosperm. Therefore, during microbial fermentation cellulose and AX sugar monomers are released from the cell walls of pericarp/testa with approximately the same rate, while the more loose organization of endosperm cell walls allows AX polysaccharides to be released with a higher rate than that of cellulose.

A further demonstration of the importance of the chemical composition and organization of CWM for digestibility is seen when comparing the digestibility of oat AX with the analogous polysaccharide deriving from wheat flour. The digestibility of the former AX polysaccharide is lower than of the latter, probably because of its lower solubility.

When discussing the GI implications of various DF sources the digestibility of the polysaccharides and the other major constituents are important factors to consider. In

keeping with other studies (Stephen & Cummings, 1980; Spiller *et al.* 1986), lignified DF sources (wheat bran and pericarp/testa) are only degraded to a small extent resulting in an increase in faecal dry matter and bulk by virtue of its physical presence and water-holding capacity. In the colon these DF sources caused a dilution of the contents. In contrast oat DF and to some extent cell walls from wheat aleurone were degraded in the large intestine. This stimulation of microbial activity leads to an increased microbial biomass in faecal material and a softer faeces. The same was found with cell walls from other soluble DF sources: cabbage, pectins and carrots (Stephen & Cummings, 1980; Nyman & Asp, 1982). The increased microbial activity (Bach Knudsen *et al.* 1991) associated with the higher fermentation of carbohydrates might have significant implications for the N metabolism in the large intestine. Certainly the higher faecal loss of N is associated with the higher excretion of microbial biomass. One can only speculate to what extent the higher fat excretion is due to a higher faecal bile acid excretion caused by the fermentation of carbohydrates and following lower luminal pH (Bach Knudsen *et al.* 1991). In a study with rolled oats given to man, faecal fat excretion increased by 47% and faecal bile acids by 35% (Judd & Truswell, 1981) compared with the control group.

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