The digestion of fibre by pigs

1. The effects of amount and type of fibre on apparent digestibility, nitrogen balance and rate of passage

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1. The effects of the amount and the type of dietary fibre on the apparent digestibility (AD) by growing pigs of neutral-detergent fibre (NDF) and NDF components, on nitrogen balance and on the rate of passage of digesta were studied using a semi-purified basal diet and fibre in the forms of soya-bean hulls, lupin (*Lupinus* sp.) hulls, pea (*Pisum sativum*) hulls, wheat bran, maize hulls, maize cobs, oat hulls and lucerne (*Medicago sativa*) stems.

2. Both the amount and the type of dietary fibre significantly influenced the AD of dietary dry matter, N and energy. The AD of NDF and of NDF components was markedly affected by the type and the amount of fibre in the diet. The proportion of NDF digested ranged from 0·016 to 0·905, of cellulose from 0·026 to 0·931 and of hemicellulose from 0·010 to 0·999.

3. N retention by the pigs ranged from 12·9 to 25·8 g/d and with some fibres there was a tendency towards increased N retention with increasing intakes of NDF.

4. Rate of passage of digesta, expressed as the 50 and 95% excretion times of stained feed particles, ranged from 22·2 to 85·1 h and 40·0 to 117·1 h respectively. Large individual variations in rate of passage occurred but, in general, the rate of passage tended to increase with increasing intakes of NDF. No strong associations between the rate of passage of digesta and apparent digestibility of NDF components were observed.

5. The results suggest that the extent of fibre digestibility depends predominantly on the origin of the fibre and to a lesser extent on the amount of fibre in the diet.

In many studies on the utilization of dietary fibre by pigs, the digestibility of fibre itself and its effect on the digestibility of other dietary components have been assessed using crude fibre as the component representing dietary fibre. However, depending on the relative contents of cellulose, hemicellulose, pectins and lignin, crude fibre almost always represents only part of the real fibre intake of the animal (Van Soest & McQueen, 1973). Thus, depending on the source and, hence, chemical composition of the fibre used, measurements based on crude fibre may lead to inaccurate estimations of the apparent digestibility (AD) of dietary fibre. Misleading information might also be obtained when purified celluloses are used as a source of dietary fibre, because they differ considerably from natural cellulosic materials in their physical and biological properties (Van Soest, 1978) and they may be more resistant than normal celluloses to microbial digestion in the large intestine of pigs. Other factors known to affect the digestibility of fibre by pigs include variability among individual animals (King & Taverner, 1975), restricted or *ad lib.* feeding, adaptation, age and live weight of the animal (Cunningham *et al.* 1962; Henry & Etienne, 1969; Gargallo & Zimmerman, 1981), level of fibre in the diet (Farrell & Johnson, 1972; Gargallo & Zimmerman, 1980, 1981) and presence in the diet of components such as sugars (Skipitaris *et al.* 1957), fats (Kennelly & Aherne, 1980*b*) and antibiotics (Friend *et al.* 1963; Gargallo & Zimmerman, 1980).

In the work reported here the effects of varying intakes of fibre from different sources on the AD by pigs of neutral-detergent fibre (NDF) and NDF constituents were studied.

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The suggestion by Keys *et al.* (1969) that pigs appear to be able to digest hemicellulose to a greater extent than cellulose led us to choose fibres with cellulose:hemicellulose values extending over a wide range. In order to eliminate any interference in the digestibility measurements caused by the presence in the diet of fibre from a source other than the test one, a basal diet composed of semi-purified components was used. Because the NDF content in the fibre sources varied widely, in order to determine the AD of NDF and NDF constituents at equal levels of intake by the pigs, diets were formulated to contain equal amounts of NDF rather than equal amounts of dry matter (DM) from each fibre source. The effect of the level of intake and the type of fibre on the AD of other dietary components was also determined.

If the level of fibre intake and the type of fibre in the diet should affect the AD of dietary components, this might be associated with differences in rate of passage of food through the alimentary tract. Therefore, rate of passage of the diets containing the different types of fibres at varying levels were determined concurrently with the AD determinations. Because of the difficulties associated with identifying and counting stained feed particles the effectiveness of using as a marker polyethylene beads, which can be easily recovered and counted, was assessed with some of the fibre sources.

MATERIALS AND METHODS

Animals

The animals used in these experiments were entire male pigs of the Large White breed and of an initial mean body-weight of 45 (SE 2) kg. They were maintained in metabolism cages equipped with movable sides, a feeding trough and a tray beneath for collection of food spillages. A metal tray at the back of each cage enabled faeces collection to be made and plastic sheets were used to direct urine into collection buckets during balance studies. The temperature of the room in which the pigs were housed was approximately 21°. The animals remained here for 30 d of which 20 d were used for adaptation and 10 d for the collection of faeces and urine. Because measurements of the rate of passage of digesta were made at the same time as the AD measurements, faeces were collected every 4 h until no more stained particles, used for the determination of the rate of passage, could be detected in the faeces. Thereafter, collection of faeces was made at 08.00 and 20.00 hours. Samples were stored at −15° until needed. Urine was collected in hydrochloric acid (100 ml/l), bulked over the collection period and stored at −15°. Following the collection period, the pigs were slaughtered.

Diets and feeding

Diets containing four concentrations of NDF from each of eight sources of fibre were used. The NDF contents of these diets, expressed relative to the DM contributed by the basal diet and that contributed by the NDF portion of each fibre, were 75, 150, 225 and 300 g/kg dry matter. The materials used to provide these levels of NDF in the diet were soya-bean hulls, lupin (*Lupinus* sp.) hulls, pea (*Pisum sativum*) hulls, wheat bran, maize hulls, maize cobs, oat hulls and lucerne (*Medicago sativa*) stems, all of which were hammer-milled through a 3 mm screen. There were, therefore, thirty-two treatments and, as three pigs were allocated to each treatment, a total of ninety-six pigs were involved. The daily allocations of feed per pig of the diets containing 75, 150, 225 and 300 g NDF/kg consisted of 856 g of basal diet DM and amounts of each fibre source that would provide 69, 151, 249 or 367 g NDF respectively. Each day's feed allowance was given in two equal meals at 08.00 and 16.00 hours and was mixed with sufficient water to form a gruel. All pigs were provided with additional water except those given the highest amount of NDF.

Table 1. *Chemical composition of fibrous materials (g/kg DM)*

Source of fibre	Nitrogen	CF	EE	NFE	Ash	NDF	ADF	Cell	Hemic	Lignin	GE (kJ/g DM)
Soya-bean hulls	16	411	13	432	44	704	474	452	230	21	19·4
Lupin (*Lupinus* sp.) hulls	4	599	9	338	26	848	625	586	223	28	17·4
Pea (*Pisum sativum*) hulls	9	455	8	457	24	625	555	510	70	45	19·3
Wheat bran	22	170	40	594	58	470	116	81	354	34	21·5
Maize hulls	6	212	11	732	8	863	207	187	656	19	19·1
Maize cobs	6	387	6	533	38	813	421	358	392	44	21·6
Oat hulls	1	370	5	563	54	872	389	348	483	22	18·2
Lucerne (*Medicago sativa*) stems	24	365	18	395	73	493	382	277	111	92	21·6

CF, crude fibre; EE, diethyl ether extract; NFE, N-free extract; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; Cell, cellulose; Hemic, hemicellulose; GE, gross energy; DM, dry matter.

Table 2. *Mineral composition of fibrous materials (mg/kg DM)*

Source of fibre	Calcium	Phosphorus	Magnesium	Sodium	Potassium	Zinc
Soya-bean hulls	5100	900	2300	ND	17600	47
Lupin (*Lupinus* sp.) hulls	3300	< 500	600	< 500	3500	34
Pea (*Pisum sativum*) hulls	4200	800	3200	< 500	8600	31
Wheat bran	700	11800	2700	< 500	15500	66
Maize hulls	< 500	700	< 500	ND	3800	10
Maize cobs	< 500	1300	< 500	< 500	13900	66
Oat hulls	< 500	600	600	< 500	7000	6
Lucerne (*Medicago sativa*) stems	4600	2400	1300	2300	18200	27

ND, not detectable; DM, dry matter.

Table 3. *Ingredients (g/kg DM) in the basal diet and its chemical composition*

Ingredient	
Casein	177·0
Starch	522·0
Sucrose	165·0
Maize oil	44·0
Dicalcium phosphate	65·4
Potassium carbonate	8·8
Magnesium carbonate ($3MgCO_3 . Mg(OH)_2 . 3H_2O$)	3·2
Sodium chloride	5·0
Choline chloride	2·3
Premix*	7·3
Chemical composition	
Nitrogen	27
Diethyl ether extract	48
Ash	72
GE (kJ/g DM)	18·7

DM, dry matter; GE, gross energy.

* The premix contributed vitamins and trace minerals (mg/kg air-dry diet) as follows: vitamin A 1, vitamin D 0·01, vitamin E 2·9, vitamin K 1·5, thiamin 2·9, riboflavin 4·9, pyridoxin 4·9, cobalamine 0·02, pantothenic acid 19·7, nicotinic acid 2·4, niacin 24·1, Fe 76·6 as $FeSO_4 . 7H_2O$, Mn 43·8 as $MnSO_4 . H_2O$, Zn 98·6 as $ZnSO_4 . 7H_2O$, Cu 7·7 as $CuSO_4 . 5H_2O$, I 4·4 as KI.

The diets varied considerably in chemical composition but on the assumption that all ingredients of the semi-synthetic basal diet were almost completely digestible, the feeding regimen adopted aimed at maximum utilization of the nutrients in the fibre while fulfilling the requirements of the pigs for essential nutrients. The compositions of the fibre sources, the basal diet and the composite diets are presented in Tables 1–4.

Experimental design

In a preliminary experiment, the AD of the chemical components in the basal diet was determined using twelve pigs. Following this, each of the eight fibre sources was included at four levels in diets given to four groups of pigs at a time, in eight successive experiments. In each experiment the pigs were randomly assigned to the four treatments. The choice of the fibre to be tested was also made at random.

Since the pigs were of the same breed, of similar live body-weights and were kept under

Table 4. *Calculated chemical composition (g/kg DM) of diets containing varying levels of neutral-detergent fibre from eight sources of fibre*

Dietary NDF level (g/kg DM)	Source of fibre	Chemical component											
		Nitrogen	EE	Ash	NFE	CF	NDF	ADF	Cell	Hemic	Lignin	GE	DMI
75	Soya-bean hulls	23	45	69	681	42	73	49	47	24	2	18·8	955
	Lupin (*Lupinus* sp.) hulls	25	45	68	677	52	74	54	51	20	2	18·6	938
	Pea (*Pisum sativum*) hulls	25	44	67	680	52	72	64	59	8	5	18·8	967
	Wheat bran	26	47	70	693	24	69	17	12	52	5	19·1	1004
	Maize hulls	25	45	67	711	18	74	18	16	56	2	18·7	936
	Maize cobs	25	44	69	694	35	74	38	32	36	4	19·0	941
	Oat hulls	25	45	71	696	32	74	33	30	41	2	18·6	936
	Lucerne (*Medicago sativa*) stems	27	44	72	665	52	70	54	39	16	13	19·1	997
150	Soya-bean hulls	25	41	67	654	82	141	95	91	46	4	18·8	1070
	Lupin hulls	23	42	64	645	103	145	108	101	38	5	18·5	1034
	Pea hulls	23	39	62	654	100	138	122	112	16	10	18·8	1098
	Wheat bran	26	46	68	679	46	128	32	22	96	9	19·5	1177
	Maize hulls	23	42	61	714	36	147	35	32	112	3	18·8	1031
	Maize cobs	23	41	66	678	69	145	75	64	70	8	19·2	1042
	Oat hulls	23	41	69	685	62	147	65	59	82	4	18·6	1029
	Lucerne stems	26	40	72	628	96	130	101	73	29	24	19·5	1162
255	Soya-bean hulls	24	38	64	628	120	206	138	132	68	6	18·9	1209
	Lupin hulls	21	38	60	615	153	216	159	149	57	7	18·4	1149
	Pea hulls	21	56	37	629	144	198	176	162	22	14	18·9	1254
	Wheat bran	25	45	67	665	65	180	44	31	136	13	19·8	1384
	Maize hulls	22	39	56	716	53	217	52	47	165	5	18·8	1144
	Maize cobs	22	37	63	663	102	214	111	94	103	12	19·5	1162
	Oat hulls	21	38	68	672	92	218	97	87	212	5	18·6	1141
	Lucerne stems	26	37	73	593	135	183	141	103	42	34	19·8	1360
300	Soya-bean hulls	23	35	62	603	156	266	179	171	87	8	18·9	1377
	Lupin hulls	20	35	57	585	201	285	210	196	75	9	18·3	1288
	Pea hulls	20	32	53	606	185	254	226	207	29	18	18·9	1443
	Wheat bran	25	44	65	655	81	224	55	39	169	16	20·0	1636
	Maize hulls	20	36	51	717	70	236	69	62	167	6	18·8	1281
	Maize cobs	20	34	60	649	133	281	145	123	136	15	19·7	1307
	Oat hulls	19	34	66	661	122	287	128	115	159	7	18·5	1277
	Lucerne stems	26	34	73	563	170	229	177	129	52	43	20·0	1600

DM, dry matter; EE, diethyl ether extract; NFE, N-free extract; CF, crude fibre; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; Cell, cellulose; Hemic, hemicellulose; GE, gross energy (kJ/g DM); DMI, dry matter intake (g/d).

similar environmental conditions, it was assumed that any added variance due to time effects would be randomly distributed among the treatments.

Analytical methods

The gross energy of the fibre sources and basal diet, and freeze-dried samples of faeces and urine, were determined in a ballistic bomb calorimeter. The proximate composition of the feeds and freeze-dried faecal samples together with total nitrogen in the urine were determined according to standard procedures (Association of Official Agricultural Chemists, 1975). Acid-detergent fibre (ADF), NDF, lignin and cellulose were measured using the techniques of Goering & Van Soest (1970) but incorporating a 2 h refluxing time for NDF and ADF as proposed by King & Taverner (1975). Hemicellulose was calculated as the difference between NDF and ADF. Individual mineral concentrations were determined using the technique of Hilliard & Smith (1979).

Particle size and rate of passage measurements

Particle size of the fibre sources was determined using a modified form of the method outlined by the American Society of Agricultural Engineers (1967) for measuring the modulus of fineness. Six tared sieves with aperture sizes of 1·000, 0·711, 0·500, 0·353, 0·252 and 0·124 mm and fitted with a pan and a cover were used. A known amount of sample (50 g) was placed on the largest sieve and 'nested' sieves were shaken mechanically for 10 min, disassembled and their undersides gently brushed. They were then reassembled and shaken for two additional 10 min periods, each time having the brushing procedure repeated. At the end of the third shaking period, each sieve was weighed and the residue remaining on each sieve was expressed as a percentage of the original sample weight.

The method used to study the rate of passage of digesta was a slightly modified form of the method used by Castle & Castle (1956). Stained particles from each fibre source, that would pass through a 1·0 mm but not a 0·7 mm sieve, were used as the reference marker. For comparison, white plastic beads (polyethylene pellets GA7260; Hoechst, Australia), 3 mm in diameter, were used as a second marker. Stained particles and plastic beads were included in the diets at the rate of 10 and 30 g/kg fibrous material respectively. The method of staining the particles was the same as that used by Castle & Castle (1956), with the exception that boiling of the particles in sulphuric acid (12·5 ml/l) took place after the particles had been stained. It was assumed that this would prevent decolourization of the particles in the acidic environment of the pig's stomach. Both markers were mixed into the morning feed.

Statistical analysis

Analysis of variance of the results identified the fibre source in the diet (FS) and the level of NDF content with orthogonal (NDF), linear (NDF_L) and quadratic (NDF_Q) effects. The sums of squares for the interaction between the fibre source and the NDF content were also split into linear ($FS \times NDF_L$) and quadratic ($FS \times NDF_Q$) terms. Significance in each main effect and the interactions were tested by comparison of the mean squares for FS, NDF, NDF_L, NDF_Q, $FS \times NDF_L$ and $FS \times NDF_Q$ with the error mean square. These statistical procedures were used as outlined by Snedecor & Cochran (1973).

RESULTS

Digestibility of DM, NDF and NDF components

Tables 5 and 6 show the apparent digestibility values of DM, NDF, cellulose and hemicellulose. Highly significant ($P < 0·001$) responses of level of NDF intake and NDF

Table 5. *Digestibility of dry matter (DM) and neutral-detergent fibre (NDF) by the pigs on each treatment*

(Mean values with their standard errors for thirty-two groups of three pigs each except for zero NDF in the diet, where there was one group of twelve pigs)

	Dietary NDF level (g/kg DM)					Statistical significance of effects					
								NDF†		FS × NDF†	
Source of fibre	0	75	150	225	300	SEM	FS	L	Q	L	Q
				Dry mattter							
Basal	0·941	—	—	—	—	0·001	—	—		—	
Soya-bean hulls	—	0·925	0·907	0·875	0·860						
Lupin (*Lupinus* sp.) hulls	—	0·923	0·910	0·880	0·865						
Pea (*Pisum sativum*) hulls	—	0·891	0·825	0·722	0·602						
Wheat bran	—	0·898	0·865	0·827	0·789						
Maize hulls	—	0·887	0·848	0·812	0·711	0·008	***	***	**	***	***
Maize cobs	—	0·871	0·808	0·757	0·690						
Oat hulls	—	0·884	0·819	0·741	0·674						
Lucerne (*Medicago sativa*) stems	—	0·868	0·809	0·757	0·703						
				Neutral-detergent fibre							
Soya-bean hulls	—	0·783	0·826	0·783	0·809						
Lupin hulls	—	0·905	0·843	0·795	0·820						
Pea hulls	—	0·661	0·469	0·197	0·029						
Wheat bran	—	0·504	0·480	0·519	0·499						
Maize hulls	—	0·327	0·416	0·443	0·278	0·031	***	***	NS	***	***
Maize cobs	—	0·232	0·104	0·209	0·181						
Oat hulls	—	0·198	0·213	0·145	0·160						
Lucerne stems	—	0·244	0·175	0·200	0·201						

FS, main effect of fibre source; L, linear; Q, quadratic; NS, not significant.
$^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.
† Main effect of level of NDF in diet.

Table 6. *Digestibility of cellulose and hemicellulose by the pigs on each treatment*

(Mean values with their standard errors for thirty-two groups of three pigs each)

Source of fibre	Dietary NDF level (g/kg DM)				Statistical significance of effects					
							NDF†		FS × NDF†	
	75	150	225	300	SEM	FS	L	Q	L	Q
Cellulose										
Soya-bean hulls	0·799	0·842	0·778	0·762	0·036	***	***	NS	***	***
Lupin (*Lupinus* sp.) hulls	0·931	0·856	0·807	0·815						
Pea (*Pisum sativum*) hulls	0·727	0·522	0·249	0·026						
Wheat bran	0·192	0·216	0·161	0·185						
Maize hulls	0·299	0·408	0·423	0·190						
Maize cobs	0·266	0·178	0·241	0·195						
Oat hulls	0·217	0·235	0·134	0·136						
Lucerne (*Medicago sativa*) stems	0·316	0·199	0·266	0·216						
Hemicellulose										
Soya-bean hulls	0·847	0·889	0·866	0·948	0·032	***	***	**	***	***
Lupin hulls	0·865	0·882	0·842	0·890						
Pea hulls	0·999	0·999	0·784	0·240						
Wheat bran	0·599	0·560	0·636	0·603						
Maize hulls	0·343	0·425	0·451	0·309						
Maize cobs	0·315	0·021	0·202	0·196						
Oat hulls	0·249	0·285	0·211	0·212						
Lucerne stems	0·174	0·154	0·179	0·154						

FS, main effect of fibre source; NDF, neutral-detergent fibre; DM, dry matter; L, linear; Q, quadratic; NS, not significant.
$^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$. † Main effect of level of NDF in diet.

source occurred for dietary DM AD. These responses were decreased curvilinearly with significant linear ($P < 0{\cdot}001$) and quadratic ($P < 0{\cdot}01$) effects as the amount of NDF intake by the pigs increased. A highly significant ($P < 0{\cdot}001$) interaction with significant ($P < 0{\cdot}001$) linear and quadratic effects was observed between NDF intake and NDF source, indicating that both the slopes and the shapes of the regression lines differed widely among different types of fibre.

Variation in the level of NDF intake and the source of NDF in the diet had a highly significant ($P < 0{\cdot}001$) effect on the AD of NDF, cellulose and hemicellulose. High NDF intakes were associated with lower NDF, cellulose and hemicellulose digestibilities, the depressive influence of NDF intake being linear ($P < 0{\cdot}001$) although, in the case of hemicellulose, there was some evidence of curvilinearity ($P < 0{\cdot}01$). There was a highly significant ($P < 0{\cdot}001$) NDF intake × NDF source interaction with significant ($P < 0{\cdot}001$) linear and quadratic components. This demonstrates that the decline in the AD of NDF, cellulose and hemicellulose with higher levels of NDF intake was related to the source of NDF in the diet.

Inspection of the values for the individual sources of NDF showed that the most striking reductions in the AD of dietary components with higher NDF intakes occurred in the diets containing pea hulls. Moreover, the faeces from animals on these diets contained more ADF than NDF. According to Van Soest (1975), such results can occur in fibrous materials with high contents of tannin compounds which are dissolved by neutral detergent (Van Soest & Robertson, 1980). Although a higher ADF than NDF content in the faeces would suggest 1·00 AD of hemicellulose, the value of 0·999 was adopted to facilitate processing of the results.

Digestibility and retention of N

Mean values for the AD of N and N retention by the pigs in each treatment are given in Table 7.

Both the level of NDF intake and the type of fibre in the diet had a significant ($P < 0{\cdot}001$) effect on AD of N and of N retention. Over all types of fibre, N digestibility decreased, whereas N retention increased with the level of NDF intake by the pigs ($P < 0{\cdot}001$). There was a large linear component to these effects ($P < 0{\cdot}001$) but there was some curvilinearity ($P < 0{\cdot}001$ or $P < 0{\cdot}05$) indicating a disproportional change in these response criteria for each increase in NDF intake. Both the linear and the quadratic effects differed widely among sources of NDF (NDF intake × NDF source interaction).

Digestibility and metabolizability of energy

Mean values for the coefficients of the AD and metabolizability of energy are given in Table 8.

There was a highly significant ($P < 0{\cdot}001$) effect of level of NDF intake by the pigs and source of NDF in the diet on the AD and metabolizability of dietary energy. There was a linear ($P < 0{\cdot}001$) decrease in both these response criteria with the level of NDF intake, although there was strong evidence of curvilinearity ($P < 0{\cdot}001$). The linear and the quadratic components of the interaction between level of NDF intake and NDF source were highly significant ($P < 0{\cdot}001$), indicating that the extent and the rate of decrease in AD and metabolizability of energy with level of NDF intake was related to the source of NDF in the diet.

Particle size

Table 9 shows the proportional distribution of the particles from each fibre source. If, on the basis of the results obtained, an arbitrary classification of the fibre particles into small, medium and large should be made, then those ascribed to the small size would include oat

Table 7. *Digestibility of nitrogen and N retention (g/d) by the pigs on each treatment*

(Mean values with their standard errors for thirty-two groups of three pigs each except for zero NDF in the diet, where there was one group of twelve pigs)

Source of fibre	Dietary NDF level (g/kg DM)					Statistical significance of effects					
								NDF†		FS × NDF†	
	0	75	150	225	300	SEM	FS	L	Q	L	Q
				Nitrogen							
Basal	0·970	—	—	—	—	0·001	—	—		—	
Soya-bean hulls	—	0·930	0·886	0·829	0·803	0·007	***	***	***	***	***
Lupin (*Lupinus* sp.) hulls	—	0·919	0·907	0·860	0·814						
Pea (*Pisum sativum*) hulls	—	0·896	0·817	0·748	0·653						
Wheat bran	—	0·934	0·918	0·885	0·789						
Maize hulls	—	0·947	0·913	0·880	0·837						
Maize cobs	—	0·923	0·890	0·881	0·841						
Oat hulls	—	0·955	0·941	0·926	0·907						
Lucerne (*Medicago sativa*) stems	—	0·906	0·868	0·844	0·758						
				Nitrogen retention							
Basal	13·9	—	—	—	—	0·480	—	—		—	
Soya-bean hulls	—	14·2	18·2	17·8	20·4	0·866	***	***	*	***	***
Lupin hulls	—	14·2	14·8	14·1	15·7						
Pea hulls	—	13·1	15·9	16·1	13·5						
Wheat bran	—	15·8	17·3	21·0	19·2						
Maize hulls	—	13·2	16·2	15·8	14·0						
Maize cobs	—	12·8	14·3	13·5	15·8						
Oat hulls	—	13·4	15·7	14·8	15·0						
Lucerne stems	—	13·8	16·2	16·3	20·8						

FS, main effect of fibre source; NDF, neutral-detergent fibre; DM, dry matter; L, linear; Q, quadratic.
$^{*}P < 0{\cdot}05$, $^{***}P < 0{\cdot}001$. † Main effect of level of NDF in diet.

Table 8. *Digestibility and metabolizability of gross energy by the pigs on each treatment*

(Mean values with their standard errors for thirty-two groups of three pigs each except for zero NDF in the diet, where there was one group of twelve pigs)

	Dietary NDF level (g/kg DM)					Statistical significance of effects					
								NDF†		FS × NDF†	
Source of fibre	0	75	150	225	300	SEM	FS	L	Q	L	Q
				Digestibility of gross energy							
Basal	0·981	—	—	—	—	0·001	—	—		—	
Soya-bean hulls	—	0·951	0·931	0·896	0·874						
Lupin (*Lupinus* sp.) hulls	—	0·957	0·941	0·907	0·880						
Pea (*Pisum sativum*) hulls	—	0·922	0·856	0·747	0·626						
Wheat bran	—	0·922	0·885	0·842	0·786						
Maize hulls	—	0·920	0·871	0·823	0·731	0·007	***	***	***	***	***
Maize cobs	—	0·902	0·829	0·783	0·691						
Oat hulls	—	0·914	0·859	0·773	0·697						
Lucerne (*Medicago sativa*) stems	—	0·898	0·832	0·765	0·698						
				Metabolizability of gross energy							
Basal	0·949	—	—	—	—	0·002	—	—		—	
Soya-bean hulls	—	0·919	0·912	0·873	0·827						
Lupin hulls	—	0·932	0·916	0·886	0·862						
Pea hulls	—	0·894	0·837	0·731	0·610						
Wheat bran	—	0·889	0·851	0·810	0·751						
Maize hulls	—	0·888	0·848	0·799	0·706	0·009	***	***	***	***	**
Maize cobs	—	0·866	0·803	0·755	0·664						
Oat hulls	—	0·883	0·835	0·750	0·675						
Lucerne stems	—	0·861	0·795	0·730	0·664						

FS, main effect of fibre source; NDF, neutral-detergent fibre; DM, dry matter; L, linear; Q, quadratic.
$^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$. † Main effect of level of NDF in diet.

Table 9. *Fibre particles retained on sieves of different apertures and expressed as proportions of the total sample*
(Mean values with their standard errors for three estimations)

	Sieve aperture (mm)													
	> 1·000		> 0·711		> 0·500		> 0·353		> 0·252		> 0·124		< 0·124	
Source of fibre	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Soya-bean hulls	0·015	0·00	0·191	0·001	0·307	0·003	0·175	0·001	0·135	0·001	0·124	0·001	0·053	0·001
Lupin (*Lupinus* sp.) hulls	0·120	0·001	0·386	0·001	0·222	0·003	0·128	0·001	0·092	0·001	0·039	0·001	0·010	0·001
Pea (*Pisum sativum*) hulls	0·076	0·001	0·239	0·003	0·342	0·001	0·192	0·001	0·104	0·001	0·034	0·001	0·013	0·001
Wheat bran	0·085	0·002	0·298	0·003	0·359	0·005	0·169	0·005	0·059	0·001	0·012	0·002	0·018	0·001
Maize hulls	0·102	0·004	0·193	0·002	0·306	0·005	0·193	0·003	0·111	0·001	0·042	0·002	0·053	0·002
Maize cobs	0·161	0·001	0·189	0·002	0·180	0·002	0·133	0·001	0·120	0·001	0·111	0·002	0·106	0·003
Oat hulls	0·001	0·001	0·012	0·001	0·118	0·001	0·359	0·009	0·313	0·005	0·160	0·001	0·037	0·001
Lucerne (*Medicago sativa*) stems	0·014	0·001	0·116	0·001	0·204	0·001	0·146	0·001	0·156	0·001	0·221	0·001	0·143	0·001

Table 10. *Times (h) taken for 50 and 95% of the stained particles and the polyethylene beads to be excreted by the pigs on each treatment*

(Mean values with their standard errors for three pigs)

	Dietary NDF level (g/kg DM)							
	75		150		225		300	
Source of fibre	Mean	SE	Mean	SE	Mean	SE	Mean	SE
	Excretion times of 50% of the particles							
Soya-bean hulls	82·6	10·37	68·2	8·39	56·7	0·66	62·6	5·31
Lupin (*Lupinus* sp.) hulls	71·5	10·34	75·1	7·07	66·5	2·74	70·1	6·79
Pea (*Pisum sativum*) hulls	59·8	0·73	58·5	10·36	33·3	2·05	50·9	14·28
Wheat bran	45·6	3·45	48·1	3·96	40·4	7·87	22·2	4·91
Maize hulls	66·7	5·07	74·1	12·50	57·4	7·26	43·6	5·48
Maize cobs	58·0	11·47	40·1	2·31	34·8	2·40	31·0	2·08
Oat hulls	74·0	0·71	85·1	16·82	51·0	6·01	55·6	2·80
Lucerne (*Medicago sativa*) stems	43·7	5·42	39·3	8·75	31·7	1·69	28·8	2·38
	Excretion times of 95% of the particles							
Soya-bean hulls	99·3	13·30	87·2	10·48	80·9	1·56	82·3	4·59
Lupin hulls	110·5	14·25	104·0	8·04	98·1	6·31	90·6	7·53
Pea hulls	77·1	1·48	82·9	17·00	48·1	5·31	58·6	14·37
Wheat bran	60·4	1·12	66·8	3·48	56·0	3·23	40·0	4·48
Maize hulls	82·8	3·79	98·5	15·66	74·3	8·41	54·2	2·36
Maize cobs	71·9	10·44	58·7	1·39	53·7	2·24	47·5	5·29
Oat hulls	80·9	1·41	117·1	14·89	70·0	6·95	77·4	2·15
Lucerne stems	63·8	6·99	57·6	7·67	53·1	1·56	44·0	5·29
	Excretion times of 50% of the polyethylene beads							
Lupin hulls	78·6	14·02	74·5	8·44	66·4	3·19	82·7	9·21
Wheat bran	51·4	2·48	48·3	5·92	43·7	7·25	30·9	1·92
Maize cobs	60·1	10·71	48·4	0·28	38·7	6·47	31·9	3·01
Lucerne stems	42·0	7·84	39·8	9·41	39·1	6·92	28·4	2·22
	Excretion times of 95% of the polyethylene beads							
Lupin hulls	102·1	13·21	111·5	13·68	94·6	6·83	103·6	12·02
Wheat bran	62·3	1·31	62·4	3·36	65·7	7·94	53·1	4·32
Maize cobs	70·0	9·34	61·7	2·09	57·8	1·01	54·0	8·99
Lucerne stems	64·8	7·20	55·9	12·06	63·8	8·66	42·9	5·61

NDF, neutral-detergent fibre; DM, dry matter.

hulls and lucerne stems. Those ascribed to the medium size would include soya-bean hulls, maize hulls, maize cobs and pea hulls and the category large would comprise lupin hulls and wheat bran.

Rates of excretion of stained feed particles and polyethylene beads

The mean values for the excretion times of 50 and 95% of the stained fibre particles and polyethylene beads are given in Table 10.

Wide variation in the rate of excretion of stained particles and polyethylene beads was observed among replicated pigs on each treatment. Hence, only the means with their standard errors for each treatment are presented in Table 10. Generally, the diets that contained soya-bean hulls, lupin hulls and oat hulls had longer excretion times of stained particles than the rest of the diets. Also, there was a close agreement between the respective excretion times of stained fibre particles and polyethylene beads.

DISCUSSION

The AD of DM, N and energy of the diets decreased linearly with increasing levels of NDF intake and this is in accord with earlier literature reports (DeGoey & Ewan, 1975; Kornegay, 1978; Kennelly & Aherne, 1980*a*, *b*). The AD of NDF, cellulose and hemicellulose, however, was affected to a lesser extent by the increased intakes of NDF. Apparently, increasing the level of fibre in the diet has a far more depressive effect on the AD of the non-fibre components of the diet than on the digestibility of its own components. The depressive effect of increased intakes of NDF on the AD of DM, N and energy might have been the result of one or more of the following factors: (*a*) faster rate of passage of food through the alimentary tract (Gargallo & Zimmerman, 1981); (*b*) increased excretion of metabolic (Whiting & Bezeau, 1957*a*) and microbial (Mason & Palmer, 1973) N; (*c*) low availability of N and other nutrients in fibre (Forbes & Hamilton, 1952; Pals & Ewan, 1978); (*d*) increased excretion of N and other nutrients bound or physically entrapped in the bulk of the bolus of the fibrous digesta (Bailey *et al.* 1974; Eastwood & Kay, 1979).

While the source of fibre is an important factor in determining the AD of the fibre itself and its individual components (Baird *et al.* 1970), wide controversy exists about the effects of the level of fibre in the diet on its AD. Addition of purified cellulose to standard commercial pig diets to increase the crude fibre level of the diet resulted in a lower AD of crude fibre in high-fibre diets compared with low-fibre diets when these diets were fed *ad lib.* (Cunningham *et al.* 1962) at restricted levels (Farrell & Johnson, 1972) or at maintenance levels (Gargallo & Zimmerman, 1980). When intake of the diets used by Cunningham *et al.* (1962) was reduced to maintenance levels, AD of crude fibre in the high- and low-fibre diets was equal but significantly greater than the AD of fibre in the same diets when fed *ad lib.* Although these reports suggest that the effect of crude fibre *per se* is more likely to be exerted through the actual amount of fibre intake rather than the proportion of fibre in the diet, the significance of these reports is not clear. In experiments reported by Keys *et al.* (1970), cell wall and cellulose digestibilities by pigs given restricted amounts of a basal fibre-free diet, in which 200, 400 or 600 g/kg was substituted by orchard grass (*Dactylis glomerata*) hay, were not significantly different, and neither were there differences in the AD of cell wall in rats given the same diets on a restricted or *ad lib.* basis. Similarly, no changes were observed in the AD of cellulose by pigs when ground lucerne was substituted for the basal diet in amounts varying from 0 to 1000 g/kg (Farrell, 1973). Increased intakes of fibre in the present study significantly reduced the AD by the pigs of NDF and cellulose in the diets containing pea hulls, maize cobs and lucerne stems and the AD of hemicellulose in the diets containing pea hulls, maize cobs and soya-bean hulls. However, with the exception of pea hulls, there was no indication of a consistent effect of the level of intake on the AD of NDF components in these diets. In general, there appears to be a close agreement between the results obtained in the present study and those reported by Keys *et al.* (1970) and Farrell (1973), with respect to the effect of the extent of dilution of the diet with fibrous ingredients on the AD of NDF and its components.

From the reports of Forbes & Hamilton (1952) and Keys & DeBarthe (1974), who gave pigs fibre from purified and natural sources and obtained cellulose AD ranging from 0·210 to 0·921, it can be concluded that the source of fibre is an important factor in determining the extent of its AD. Also, Baird *et al.* (1969) showed that pigs digested from 0·205 to 0·665 of the crude fibre from different sources. The results of the present study, where the mean AD values of NDF from natural fibres ranged from 0·181 to 0·840, clearly illustrate the importance of the source of fibre as a factor determining its AD. Kornegay (1978) reported that the digestion coefficient of cell wall from soya-bean hulls, calculated by difference from a basal ration containing either none or 150 and 300 g soya-bean hulls/kg and fed to growing pigs, was 0·540. This value is considerably lower than that reported here and it

is probably due to the relatively high level of feeding (110 g/kg metabolic body size) adopted.

The AD of cellulose, except for wheat bran, followed the same trend as that of NDF. The wide range in the AD of cellulose from the different sources of fibre used in the present study may be related to the extent of lignification, mineralization, crystallinity, size of the cellulose chain or particle size of the fibre, or both (Cowling & Brown, 1969). It is possible that in the case of maize hulls, maize cobs and oat hulls, the low AD of cellulose was in part due to the low N content in these fibres. It is reasonable to assume that the fermentation by bacteria in the caecum and the large intestines of pigs, like the bacteria in the rumen, requires adequate N for optimum performance. On the assumption, however, that casein was completely digestible in the small intestines of the pigs in the present study, the bacteria in the lower parts of the alimentary tract receiving maize hulls, maize cobs and oat hulls would not be supplied with sufficient amounts of N and, hence, would not be able to digest much fibre.

In all fibre sources, except in lucerne stems, the AD of hemicellulose in the present study appeared to be higher than that of cellulose, thus confirming the results previously reported by Keys *et al.* (1970). However, since both starch and N of fibre origin can lead to inflated estimates of NDF digestibility, caution should be exercised in interpreting the results obtained when materials with high contents of these components are examined. The lower AD of hemicellulose than of cellulose in lucerne stems may be related to particularly strong chemical and physical bonds between hemicellulose and lignin, which formed almost equal amounts of the DM in this fibre. Lower hemicellulose AD than cellulose AD by pigs given diets containing high levels of a lucerne hay was also reported by Keys & DeBarthe (1974).

The remarkable decrease in the AD of all dietary components with increasing intakes of the diets containing pea hulls can only be explained by the presence in pea hulls of a substance toxic to the digestive enzymes and the microflora of the alimentary tract. The nature of the antinutritive substance(s) in pea hulls is largely unknown but Lindgren (1975) reported that, when a variety of field peas with low tannin content was substituted for one with high tannin content, the digestion coefficients of N and organic matter dropped by five digestibility units. Tannin compounds can affect digestibility in a number of ways: through the formation of stable tannin–protein and tannin–cellulose complexes, by enzyme inhibition, by microbial inhibition and through reactions with endogenous proteins of the intestinal mucosa (McLeod, 1974). Thus it appears that the pea hulls used in the present studies may have contained high levels of tannin which resulted in marked decreases in the digestibility of the major dietary components.

In examining the factors influencing the AD of dietary protein, the role of the factors influencing the excretion of metabolic N in the faeces cannot be overlooked. Whiting & Bezeau (1957*a*, *b*) reported that the type and amount of dietary fibre considerably affects the metabolic N excretion in pigs whether expressed as a proportion of DM intake or faecal DM output. On the other hand, Mason & Palmer (1973) believed that it was not the amount but the extent of fermentation of dietary DM which resulted in the production of more bacterial cells and hence more bacterial residues appearing in the faeces, thus increasing the amount of faecal N. Thus, according to Mason & Palmer (1973), fibre sources that undergo extensive degradation in the large intestine of the pig will decrease the AD of N to a larger extent than fibre sources less susceptible to microbial attack provided they are fed at similar levels. While the reduction in the AD of N caused by the inclusion in the diet of soya-bean hulls, lupin hulls and wheat bran appears to confirm this view, the reduction caused by the inclusion in the diet of the less-digestible lucerne stems, as compared with the former fibres, suggests that factors other than digestibility of fibre, i.e. N content of the fibre, and perhaps volume, are also important.

There was a tendency for increased N retention with increased levels of NDF intake

particularly in the diets containing soya-bean hulls, wheat bran, maize hulls and lucerne stems. As these fibres, except maize hulls, contained more N on a percentage basis than the rest of the fibres, there appears to be a relation between N intake and N retention with more N being retained when the intake of N is raised. In addition to the increased N intake, presumably more energy was available for the synthesis of new tissue at the higher levels of NDF intake, as increased N retention can be achieved only if the intake of energy is adequate too (Fuller & Crofts, 1977). Our results are in agreement with those of Pals & Ewan (1978), who also reported increased N retentions when increasing levels of wheat bran were added to a basal ration for pigs.

Castle & Castle (1957) reported that fast passage of digesta through the alimentary tract of pigs was associated with a high feed consumption while small differences in the fibre content of the diet do not seem to affect rate of passage (Cole *et al.* 1967*a*, *b*). In the present study, a trend towards a fast rate of passage of digesta with increasing intakes of NDF and, hence, DM intake was apparent although not very consistent. Large variations within groups of pigs given the same diet were observed in the present study, as they were in that of King & Taverner (1975). Differences in gastrointestinal responses among individual pigs within the same treatment may have been, partly, the reason for this wide variability.

The rate of passage of digesta may be related to physical characteristics of the feed, such as particle size of the feed, water absorption and retention capacity, bulk of feed and body-weight of the pig. The fibres used in the present study had been hammer-milled through the same size screen; nevertheless, some variation in the mean particle sizes occurred. Similarly, the water-holding capacity and the volumes per unit weight of these fibres were variable (G. Stanogias, unpublished results) and this might have contributed also to the differences in the rates of excretion among the different fibres. The excretion times of the polyethylene beads compared with those obtained with the stained food particles were almost the same. This finding is very important because of the obvious advantages in using plastic beads in terms of time required for staining and particularly counting stained food particles. In addition, problems such as decolourization and breakage into invisible or hardly visible particles are largely eliminated by using polyethylene beads.

Unless the point where the limit by other nutritional factors, such as lignification and lack of other essential nutrients, is reached, the length of time digesta remains in the alimentary tract of the animal, where it is exposed to digestive enzymes and microbial degradation, largely influences the extent to which food is digested (Kass *et al.* 1980; Gargallo & Zimmerman, 1981). In the present study, while the high AD of all dietary components in the diets containing soya-bean and lupin hulls might have been related to the extended time digesta from these diets remained in the alimentary tract of the pigs, transit time did not appear to influence the AD of the fibre components in the diets containing oat hulls. This suggests that the AD of fibre and its components might depend on either the length of time the fibre remains exposed to enzymic and microbial action in the intestines or the chemical and physical characteristics of the fibre.

The results of the present study clearly show that the AD of DM, N, energy and possibly other non-fibrous dietary components, are inversely related to the proportion of fibre in the diet or, conversely, to the amount of fibre intake. However, it is not clear from the available results to what extent this was due to a direct decrease in the AD of these components or due to an increased excretion in the faeces of microbial and endogenous material. To the contrary, the level of fibre in the diet, under the conditions described, did not appear to influence considerably the AD of its own components.

The fibre components from the leguminous seeds were more digestible than those from the cereal grains, which suggests that there is a relation between the source of fibre (and hence its chemical composition and physical properties) and the AD of its components by

growing pigs. However, the strong influence of factors associated with interactions between the total diet, the individual fibres and the individual NDF constituents make it difficult, if not impossible, to find a generally applicable cause-and-effect relation between dietary fibre and AD of dietary components. In addition to the major NDF constituents, namely cellulose, hemicellulose and lignin, other costituents, such as tannins and pectins, may also affect the AD of a particular fibre through their physical and chemical properties. However, the contribution to the variation of the AD of dietary components by such substances was not investigated in the present study.

Finally, the present results emphasize strongly the need for caution when comparisons among experiments in which different levels and sources of dietary fibre are used.

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