The influence of dietary fibre source and level on the development of the gastrointestinal tract, digestibility and energy metabolism in broiler chickens

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The present study was undertaken to provide detailed information about the effect of fibre source (pea fibre, wheat bran or oat bran) at inclusion levels of 0, 187 and 375 g/kg diet on the development of the digestive tract, nutrient digestibility and energy and protein metabolism in broiler chickens. Heat production was measured using open-air-circuit respiration chambers. Diets with increasing levels of pea fibre decreased the DM in droppings and increased excreta output (2·5-fold) relative to DM intake. Adaptation to increased dietary fibre levels included increases in the size of the digestive system, with pea fibre exerting a stronger impact than wheat bran or oat bran. The length of the intestine, and particularly the length and weight of the caecum, increased with the fibre level. The digestibility of all nutrients also decreased with increasing fibre level. The decrease in the digestibility in relation to NSP for the three fibre sources was bigger for oat bran (0·0020 per g dietary NSP) than for pea fibre and wheat bran (0·0014 and 0·0016 per g dietary NSP) indicating that the cell walls in oat bran (aleurone and subaleurone) had a significant negative effect on the digestibility of cellular nutrients, i.e. protein and fat. The degradation of the NSP constituents was far lower in chickens than found in other animal species such as pigs and rats, thus supporting the view that chickens do not ferment fibre polymers to a great extent. Excretion of organic acids (mainly lactic acid and acetic acid) accounted for up to 2% of metabolizable energy (ME) intake with the highest excretion for the high-fibre diets. H_2 excretion was related to the amount of NSP degraded and indicated higher microbial fermentation with increasing fibre levels. The chickens' feed intake responded to a great extent to dietary ME concentration but expressed in terms of metabolic body size ($W^{0.75}$) ME intake was depressed at the high fibre levels. Dietary NSP was able to explain between 86% (oat bran) and 96% (pea fibre) of the variation in ME concentration. The amount of energy available from fermentation of NSP appears to reach a maximum of 42 kJ/d independent of fibre source and level. Expressed in relation to ME intake the NSP fermentation contributed 3–4%. With increasing fibre intake the partitioning of retained energy between body protein and body fat changed in favour of protein.

Gutfill: Heat increment: Non-starch polysaccharides: Fermentation

The feed ingredients used in poultry diets are mostly of vegetable origin. Plant materials are rich sources of carbohydrates, i.e. low-molecular-weight sugars, starch and NSP, the latter being resistant to digestive enzymes. However, the NSP fraction can, to a certain degree, be broken down by the microbial flora permanently colonizing the gastrointestinal (GI) tract. The end-products of the microbial degradation are various gases (H_2, CO_2, CH_4), lactic acid and short-chain fatty acids (SCFA). The SCFA produced are rapidly absorbed

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from the gut lumen (Rechkemmer *et al.* 1988) and, in pigs, provide a significant amount of the metabolizable energy (ME). In the chicken, the caecum appears to be the main environment for microbial degradation of dietary fibre (DF), protein and uric acid, and for absorption of the fermentation products (Thomas & Skadhauge, 1988). Compared with pigs and rats, microbial degradation of DF in the caecum and colon of poultry appears to be low (Carré & Leclercq, 1985; Longstaff & McNab, 1989) although some higher values have been reported (Petterson & Åman, 1989). Petterson & Åman (1989) reported, also, that faecal digestibility of insoluble pentosans was not different from values found in the middle and last thirds of the small intestine, suggesting DF degradation in the crop and gizzard and a poor fermentation of insoluble pentosans in caecum and colon. Other experiments found that the soluble NSP, especially, was digested to a significant extent whereas the insoluble NSP fraction remained almost completely undigested (Carré *et al.* 1990; Annison, 1991). The ME value of released cell-wall monosaccharides (e.g. arabinose, xylose) *per se* is low (Schutte *et al.* 1991, 1992), but when they are fermented to SCFA the energy can be utilized to a certain extent (Savory, 1992*b*). As in other animal species (Anugwa *et al.* 1989; Hansen *et al.* 1992; Zhao *et al.* 1995), DF affects the length and weight of the GI tract (Savory & Gentle, 1976; Moss, 1989; Savory, 1992*a*). There is also a strong indication that the differences in weight of visceral organs are highly related to differences in fasting heat production in animals caused by different nutritional treatments (Koong *et al.* 1985; Ferrell & Koong, 1986).

The present study was undertaken to provide detailed information on the effects of different DF sources and levels on development of the GI tract, digestibility and energy metabolism in broiler chickens.

MATERIALS AND METHODS

Experimental design

The study involved three DF sources: pea fibre, wheat bran and oat bran, which were used in three successive experiments at three inclusion levels, i.e. 0, 187 and 375 g/kg diet. Each experiment was carried out in two blocks of twenty-four chickens from 12 d of age which were of either 5 or 4 weeks duration. A balance period was carried out every week.

At 4 d before completion of the experiment Cr_2O_3 (2·5 g/kg diet) was added to all diets as an indigestible marker. After completion of the experiment the animals were killed by dislocation of the neck. The content of the GI tract was removed and weighed and the weights of the digesta-free empty body (EBW) and GI tract of each chick were recorded. Digesta content of the last 100 mm of the small intestine was collected for estimation of ileal digestibility.

Animals and housing

The experimental animals of broiler type (Ross 208), all males, were obtained from a commercial hatchery. From hatching to 12 d of age the chickens were kept at 30° and fed on a starter diet containing 241 g protein and 12·70 MJ ME/kg. They were placed in pairs in metabolism cages in an air-conditioned room. The temperature was 26° in the first week and 22° after that. The relative humidity was adjusted to 0·60 and a 24 h light regimen was maintained.

Heat production was estimated from calculations of gas exchange using two open-air-circuit respiration chambers as described by Chwalibog *et al.* (1979). The gas exchange was measured over periods of 24 h on four chickens in each chamber. The volume of the outgoing air from the two chambers was measured continuously from the differential pressure over both sides of an orifice (Hartmann & Braun, Germany) and converted to

Table 1. *Chemical composition of the dietary fibre sources*

Fibre source...	Pea fibre	Wheat bran	Oat bran	Barley
Chemical composition (g/kg DM)				
Ash	26	51	28	18
Protein (N × 6·25)	99	177	201	149
HCl-fat	12	61	90	36
Starch	338	204	528	581
NSP				
S-NSP	194	43	75	50
I-NSP	220	318	53	124
Total NSP	414	361	128	174
Cellulose	104	76	11	36
Constituent sugars of the NCP residues (g/kg DM)				
Rhamnose	11	tr	1	tr
Arabinose	218	85	143	28
Xylose	29	155	18	56
Mannose	3	3	3	4
Galactose	39	8	3	4
Glucose	7	33	75	47
Uronic acids	43	16	3	6

HCl-fat, hydrochloric acid-fat; S-NSP, soluble non-starch polysaccharides; I-NSP, insoluble non-starch polysaccharides; NCP, non-cellulose polysaccharides; tr, trace.

standard temperature and pressure for dry air. A paramagnetic O_2 analyser (Magnos 4G, Hartmann & Braun, Germany), an infra-red analyser for measuring CO_2 (Uras 3, Hartmann & Braun, Germany) and an electrochemical analyser for measuring H_2 (Exhaled Hydrogen Monitor (81 HP), GMI Ltd, Renfrew, Scotland) were used to determine the concentrations of O_2, CO_2 and H_2 in aliquot samples of the out-going and in-going air. The concentrations of O_2, CO_2 and H_2, temperature, relative humidity, and rate of flow from each chamber were recorded automatically on-line every second minute, so that the composition of the gas from each chamber was measured fifteen times per h.

Diets and feeding

The diets, given in meal form, comprised two inclusion levels of each DF source and a low-DF control diet containing barley. The chemical compositions of the DF sources are given in Table 1. All diets were adjusted to about the same digestible protein level by addition of fish meal, casein and methionine (Table 2). The pea-fibre product (Nutrio P-Fibre 150C) was provided by Danisco A/S, Brabrand, Denmark, oat bran was obtained from HavneMøllerne, Vejle, Denmark and wheat bran and barley were purchased commercially.

Experimental procedure

The chickens had free access to feed and water throughout the experiment. Each experiment consisted of two blocks that were partitioned into either five or four 1-week periods with 2 d between during which no collection of excreta took place. Weekly feed consumption was recorded, and the droppings were collected daily from each cage of two birds and stored at −18° for analysis. A 24 h respiration trial was inserted on the third day of each balance period of 5 d. As only two respiration units with a capacity of four birds each were available, the eight birds from one of the DF levels started their balance period at intervals of 2 d.

Table 2. *Ingredients and chemical composition of the experimental diets*

Fibre source...	Control	Pea fibre		Wheat bran		Oat bran	
Fibre level...	Low	Medium	High	Medium	High	Medium	High
Ingredients (g/kg)							
Fibre source	—	187	375	187	375	187	375
Barley	241	373	504	373	504	373	504
Wheat starch	563	281	—	281	—	281	—
Fish meal	93	69	46	69	46	69	46
Casein	40	30	20	30	20	30	20
Soyabean oil	30	30	30	30	30	30	30
Methionine	2	2	1	2	1	2	1
Calcium carbonate	—	2	2	2	2	2	2
Dicalcium phosphate	11	13	15	13	15	13	15
Monocalcium phosphate	13	6	—	6	—	6	—
NaCl	3	3	3	3	3	3	3
Mineral and vitamin mixture*	4	4	4	4	4	4	4
Chemical composition (g/kg DM)							
Ash	62	43	47	52	56	47	47
Protein (N × 6·25)	157	153	160	171	184	189	211
HCl-fat	62	65	63	60	71	74	89
Starch	680	422	544	554	419	595	507
NSP							
S-NSP	13	60	100	36	36	39	50
I-NSP	32	89	151	96	168	52	78
Total NSP	45	149	251	132	203	91	127
Gross energy (MJ/kg DM)	18·90	18·85	18·91	19·09	19·50	19·41	19·81

HCl-fat, hydrochloric acid-fat; S-NSP, soluble non-starch polysaccharides; I-NSP, insoluble non-starch polysaccharides.

* Supplied (per kg diet): retinol acetate 5504 μg, cholecalciferol 70 μg, DL-α-tocopherol acetate 42 mg, thiamin 1·4 mg, riboflavin 7·4 mg, pyridoxine 4·2 mg, D-pantothenic acid 13·5 mg, niacin 42 mg, betaine anhydrate 473 mg, pteroylmonoglutamic acid 1·4 mg, biotin 0·11 mg, cyanocobalamin 0·03 mg, avoparcin 21 mg, butylhydroxytoluene 140 mg, $FeSO_4.7H_2O$ 116 mg, ZnO 112 mg, Mn_3O_4 140 mg, $CuSO_4.5H_2O$ 21 mg, KI 560 mg, Na_2SeO_3 413 μg.

Analytical methods

All analyses were carried out on freeze-dried materials except the diets which were analysed on an air-dry basis. DM content of feed and droppings was determined by oven-drying at 105° for 20 h. All the following analyses were made in duplicate: protein (N × 6·25) by a modified Kjeldahl method (KjellFoss 16200 Autoanalyser; Foss Electric A/S, Denmark) and energy by bomb calorimetry using a LECO Ac 300 automated calorimeter system 789-500 (LECO, St. Joseph, Michigan, USA). Ash was analysed according to the Association of Official Analytical Chemists (1975) while fat was extracted with diethyl ether after acid hydrolysis (Stoldt, 1952). Cr_2O_3 was determined using the method of Schürch *et al.* (1950). C was measured as described by Neergaard *et al.* (1969). Starch was analysed by the enzymic method reported by Bach Knudsen *et al.* (1993). Total NSP and their constituent sugars in diet and droppings were determined as alditol acetates by GLC, and uronic acids by a colorimetric method using a modification of the Uppsala and Englyst procedures as described by Bach Knudsen *et al.* (1993). Soluble NSP (S-NSP) in the starch-free residue was extracted using a phosphate buffer at neutral pH (0·2 M, 100°, 60 min, pH 7·0) and the neutral and acid sugars in the insoluble NSP analysed by GLC and colorimetry. Cellulose was estimated as the difference in NSP-glucose obtained for total NSP and that obtained

after hydrolysing starch-free residues directly with 1 M-H_2SO_4. SCFA and lactate were measured by a modification of the capillary GC method (Richardson *et al.* 1989) as described by Jensen *et al.* (1995).

Calculations and statistical analyses

All calculations of gas exchange were carried out on the means of four chickens as kept in the respiration chambers while the other data were calculated on the basis of two chickens as kept in the same cage. The average daily heat production was calculated according to Brouwer (1965). The carbon–nitrogen (CN) balance method was used to calculate heat production (Christensen *et al.* 1988). All calculations of gas exchange were carried out on the mean of the two 24 h respiration measurements. ANOVA was done using the general linear models procedure (Statistical Analysis Systems Institute, 1987) on means from all periods with the DF level as main effect and adjusting for the block effect. When appropriate the effect over time was tested using the regression procedure. Differences between means were compared by the least squares means test (Statistical Analysis Systems Institute, 1987) when significant effects were obtained.

RESULTS

Body weight, food intake and amount of excreta

Body-weight gain did not differ significantly ($P > 0{\cdot}05$) between the medium and high DF levels for any of the three DF sources tested (Table 3). The chickens fed on the low-DF control diets had a significantly lower feed intake and consequently lower daily gain than the chickens fed on the other two DF levels. The feed:gain ratio was always highest for the high-DF levels. The chickens fed on the medium-DF level of oat bran had the highest growth rate and the lowest feed conversion ratio.

The amount of wet excreta relative to DM intake was approximately 0·5 for the low-DF control diet, approximately 1·0 for the medium-DF level, while it was approximately 2·5-fold higher for the high-pea-fibre diet. This group also had the lowest DM content of excreta. The amount of excreta for the high-DF level of the other two DF sources was about 0·5-fold higher relative to DM intake.

Length and weight of gastrointestinal tract

The empty body weights of chickens fed on the high-DF diets tended to be lower than for chickens fed on the medium-DF diets. However, chickens on both the medium and the high-DF levels were significantly ($P < 0{\cdot}05$) heavier than chickens fed on the low-DF diets (Table 4). Digesta in the GI tract (gutfill) was linearly related to the DF level with the DF from pea exerting a significantly greater influence than the other two DF sources.

The empty-body weights of chickens fed on the control diets were in general lower than for the other chickens, making direct comparisons between the other groups difficult. Both the weight and length of the GI tract increased with increasing DF level; in particular the caecum increased considerably.

Digestibility

Ileal and faecal digestibility of DM followed the same pattern, being negatively related to the intake of DF (Table 5). Digestibility of organic matter (OM) was estimated from differences between DM and ash in food and droppings, neglecting the small amount of OM in urine. With inclusion of the DF sources the OM digestibility decreased: with pea fibre from 0·87 to 0·58; with wheat bran from 0·88 to 0·65; and with oat bran from 0·88 to 0·70. Relating the decrease in OM digestibility to dietary NSP levels the digestibility

Table 3. *Effect of dietary fibre source and level on growth rate, feed utilization and amount of excreta in chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
n	16	16	16	16	16	16	16	16	16
Initial wt (g)	275	276	276	236	239	236	242	242	242
Final wt (g)	1311[b]	1650[a]	1622[a]	1410[b]	1865[a]	1785[a]	1401[b]	2197[a]	2126[a]
Wt gain (g/d)	29·5[b]	38·7[a]	37·8[a]	32·4[b]	45·6[a]	43·0[a]	32·4[b]	54·3[a]	52·1[a]
Food:gain ratio	2·32[b]	2·44[b]	2·76[a]	2·30[b]	2·20[b]	2·49[a]	2·27[a]	2·03[b]	2·23[a]
DM intake (g/d)	65[b]	86[a]	94[a]	68[c]	96[b]	101[a]	66[b]	101[a]	111[a]
Excreta (g/d)	36[c]	95[b]	233[a]	37[c]	91[b]	148[a]	38[c]	91[b]	143[a]
Excreta DM (g/kg)	285[a]	267[b]	184[c]	267	277	270	253	246	252

[a,b,c] Values in the same row within treatments with different superscript letters were significantly different ($P < 0·05$).
* For details of diets and procedures, see Tables 1 and 2 and pp. 380–381.

Table 4. *Effect of dietary fibre source and level on body weight, gutfill, and weight and length of the gastrointestinal tract in chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
EBW (g)	1279[b]	1586[a]	1526[a]	1376[b]	1816[a]	1713[a]	1368[b]	2141[a]	2061[a]
Relative EBW	100[b]	124[a]	119[a]	100[b]	132[a]	124[a]	100[b]	157[a]	151[a]
Gutfill (g/kg BW)	24[c]	40[b]	58[a]	24[b]	27[b]	41[a]	23[b]	26[b]	31[a]
GI tract wt (g/kg EBW)									
Gizzard	23·1[a]	17·4[b]	19·7[b]	20·4	19·2	21·5	19·7[a]	15·1[b]	16·1[ab]
Small intestine	21·9[c]	23·9[bc]	29·7[a]	25·3[a]	23·4[b]	25·8[a]	22·9[b]	22·6[b]	25·5[a]
Caecum	3·3[b]	3·4[b]	4·1[a]	3·3[c]	3·7[b]	4·3[a]	3·0[b]	3·1[b]	4·2[a]
Colon	1·1[c]	1·9[b]	2·6[a]	1·0[c]	1·3[b]	1·7[a]	1·1[c]	1·3[b]	1·7[a]
Total GI tract	49·4[b]	46·6[b]	56·1[a]	50·0[ab]	47·7[b]	53·3[a]	46·6[a]	42·1[b]	47·5[a]
GI tract length (m/kg EBW)									
Small intestine	1·108	0·969	0·981	1·014[a]	0·804[b]	0·928[a]	0·994[a]	0·794[b]	0·848[b]
Caecum	0·108	0·109	0·118	0·097[b]	0·091[b]	0·105[a]	0·098[a]	0·082[b]	0·096[a]
Colon	0·047	0·047	0·048	0·046	0·044	0·046	0·046[a]	0·035[b]	0·039[b]

BW, body weight; EBW, empty-body weight; GI, gastrointestinal.
[a,b,c] Values in the same row within treatments with different superscript letters were significantly different ($P < 0·05$).
* For details of diets and procedures, see Tables 1 and 2 and pp. 380–381.

Table 5. *Effect of dietary fibre source and level on digestibility and metabolizability of feed by chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
Ileal digestibility†									
DM	0·85[a]	0·76[b]	0·60[c]	0·85[a]	0·72[b]	0·60[c]	0·86[a]	0·80[b]	0·67[c]
Faecal digestibility									
DM	0·85[a]	0·71[b]	0·56[c]	0·86[a]	0·75[b]	0·63[c]	0·86[a]	0·79[b]	0·68[c]
Organic matter	0·87[a]	0·73[b]	0·58[c]	0·88[a]	0·76[b]	0·65[c]	0·88[a]	0·81[b]	0·70[c]
Starch	0·97[a]	0·95[b]	0·92[c]	0·98	0·97	0·97	0·97[a]	0·97[a]	0·94[b]
NSP									
Arabinose	0·30[a]	0·10[b]	0·13[b]	0·29[a]	0·11[a]	0·18[b]	0·31	0·32	0·21
Xylose	0·17[a]	0·03[b]	0·14[a]	0·11	0·03	0·09	0·21	0·24	0·13
Mannose	0·52[a]	0·04[b]	0·00[b]	0·60[a]	0·22[b]	0·17[b]	0·37[a]	0·34[a]	0·11[b]
Galactose	0·36[a]	0·11[b]	0·15[b]	0·46[a]	0·15[b]	0·11[b]	0·41[a]	0·31[a]	0·12[b]
Glucose	0·31[a]	0·07[c]	0·18[b]	0·42[a]	0·34[b]	0·24[c]	0·41	0·42	0·32
Uronic acids	0·39[a]	−0·07[c]	0·02[b]	0·55[a]	0·27[b]	0·11[c]	0·55[a]	0·41[b]	0·29[c]
Total NSP	0·28[a]	0·06[c]	0·12[b]	0·33[a]	0·19[b]	0·16[c]	0·33	0·35	0·25
Metabolizability (ME/GE)	0·87[a]	0·74[b]	0·59[c]	0·87[a]	0·76[b]	0·65[c]	0·88[a]	0·80[b]	0·69[c]

ME, metabolizable energy; GE, gross energy.

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

* For details of diets and procedures see Tables 1 and 2 and pp. 380–383.

† Determined at slaughter from the Cr_2O_3 marker.

Table 6. *Effect of dietary fibre source and level on faecal concentration and daily excretion of lactic acid, short-chain fatty acids, carbon dioxide and hydrogen in chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
Lactic acid (mmol/kg)	—†	22·6	24·4	$18·5^{a}$	$10·8^{ab}$	$5·4^{b}$	$22·7^{b}$	$27·5^{b}$	$65·4^{a}$
Acetic acid (mmol/kg)	—	$46·3^{b}$	$58·8^{a}$	$17·9^{ab}$	$16·8^{b}$	$20·3^{a}$	$22·7^{b}$	$30·6^{a}$	$30·9^{a}$
Propionic acid (mmol/kg)	—	tr	tr	tr	tr	tr	tr	tr	tr
Butyric acid (mmol/kg)	—	$2·2^{a}$	$1·4^{b}$	$2·6^{ab}$	$1·8^{b}$	$3·0^{a}$	$3·2^{b}$	$5·9^{a}$	$5·7^{a}$
Lactic acid (mmol/d)	—	$2·4^{b}$	$6·3^{a}$	0·6	1·1	1·0	$1·0^{b}$	$2·8^{b}$	$9·7^{a}$
Acetic acid (mmol/d)	—	$4·3^{b}$	$12·9^{a}$	$0·6^{c}$	$1·6^{b}$	$3·1^{a}$	$0·8^{c}$	$2·8^{b}$	$4·4^{a}$
Butyric acid (mmol/d)	—	0·2	0·3	$0·1^{b}$	$0·2^{b}$	$0·5^{a}$	$0·1^{c}$	$0·6^{b}$	$0·9^{a}$
CO_2 (litres/d)	$31·6^{b}$	$35·6^{a}$	$31·8^{b}$	$31·3^{b}$	$38·2^{a}$	$35·5^{a}$	$28·4^{c}$	$39·9^{a}$	$38·0^{b}$
H_2 (ml/d)	11^{c}	31^{b}	56^{a}	40^{c}	129^{b}	198^{a}	33^{c}	131^{b}	186^{a}
CO_2 (litres/d per kg $W^{0·75}$)	$42·4^{a}$	$39·8^{b}$	$35·4^{c}$	$42·9^{a}$	$41·4^{a}$	$38·0^{c}$	$37·8^{b}$	$39·4^{a}$	$35·6^{c}$
H_2 (ml/d per kg $W^{0·75}$)	16^{c}	35^{b}	62^{a}	64^{c}	148^{b}	209^{a}	52^{c}	133^{b}	169^{a}

$W^{0·75}$, metabolic body weight; tr, trace amount.

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

* For details of diets and procedures, see Tables 1 and 2 and pp. 380–383.

† Samples were lost.

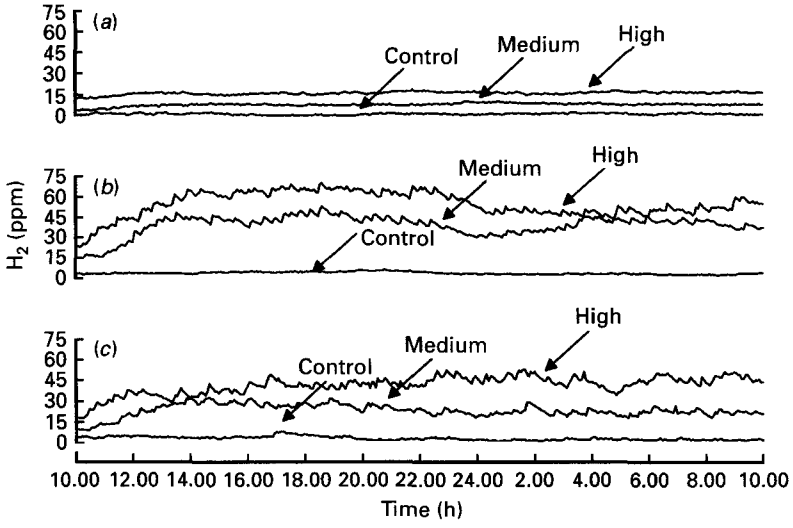

Fig. 1. Diurnal variation in hydrogen concentration in the out-going air from respiration chambers housing chickens (n 4 per chamber) fed on diets containing different levels of (a) pea fibre, (b) wheat bran and (c) oat bran. For details of diets and procedures see Tables 1 and 2 and pp. 380–383.

decreased to the same extent with pea fibre and wheat bran (0·0014 and 0·0016 per g dietary NSP) while the decrease with the oat-bran diets was higher (0·0020 per g dietary NSP). The major NSP residues arabinose, xylose and glucose appeared to be digested well in most of the diets. The highest digestibility of the total NSP fraction was generally found for the control diet, while the total amount of NSP degraded daily on average increased from 1 g (control) to 2·8 g (pea fibre), 2·9 g (wheat bran) and 3·5 g (oat bran).

Lactic acid, short-chain fatty acids, carbon dioxide and hydrogen

The dominant organic acids in the droppings were lactic and acetic acids (Table 6). Their concentration and daily amount excreted generally increased with a higher DF level. Of the SCFA there were measurable quantities only of acetic and butyric acids while propionic acid and other SCFA were present in trace amounts or below the detection limit.

Microbial fermentation does not only yield organic acids but also H_2. As seen in Table 6 the higher DF levels significantly increased the H_2 production for all DF sources indicating increased microbial activity. The concentration of H_2 in the out-going air from the respiration chamber is shown in Fig. 1. No systematic diurnal variation seemed to occur. CH_4 was detected occasionally during the growth period but the concentration was below the sensitivity of the instrument.

Nitrogen and energy balance

Daily N retention was calculated from the N balance values while fat and energy retention included the C balances obtained from the respiration measurements (Table 7). The chickens given the more fibrous diets retained more N but the gross utilization of N intake decreased compared with the low-DF control diet. The retained fat:N ratio decreased with increasing DF level in the diet indicating leaner chickens at the high DF levels.

There was no significant difference in ME intake between the control diet and the pea-fibre diets whereas in the wheat-bran and oat-bran experiments the chickens fed on the control diet had a lower ME intake. In all three experiments there were no significant differences in ME intake between medium- and high-DF levels, facilitating comparisons.

Table 7. *Effect of dietary fibre source and level on nitrogen and energy balances in chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
N intake (g/d)	1·58[c]	2·11[b]	2·40[a]	1·72[c]	2·61[b]	2·98[a]	1·71[c]	3·05[b]	3·73[a]
Retained N (g/d)	0·99[b]	1·26[a]	1·31[a]	1·14[b]	1·59[a]	1·70[a]	1·14[b]	1·93[a]	2·05[a]
Retained N/N intake	0·63[a]	0·60[b]	0·55[c]	0·67[a]	0·61[b]	0·57[c]	0·67[a]	0·64[b]	0·55[c]
Retained fat (g/d)	6·68[a]	7·16[a]	4·67[b]	7·98[b]	9·76[a]	7·50[b]	9·21[b]	12·60[a]	11·47[ab]
GE intake (kJ/d)	1236[b]	1627[a]	1775[a]	1279[b]	1824[a]	1969[a]	1245[c]	1966[b]	2191[a]
ME intake (kJ/d)	1069	1195	1034	1112[b]	1386[a]	1280[a]	1090[b]	1573[a]	1510[a]
RE (kJ/d)	414	472	382	487[b]	625[a]	552[a]	535[b]	790[a]	762[a]
HP (kJ/d)	655[b]	722[a]	653[b]	625[b]	761[a]	728[a]	554[c]	784[a]	748[b]

GE, gross energy; ME, metabolizable energy; RE, retained energy; HP, heat production.

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

* For details of diets and procedures, see Tables 1 and 2 and pp. 380–383.

Table 8. *Effect of dietary fibre source and level on energy utilization and amount of energy derived from NSP degradation in chickens**

Fibre source...	Control	Pea fibre		Control	Wheat bran		Control	Oat bran	
Fibre level...	Low	Medium	High	Low	Medium	High	Low	Medium	High
ME (MJ/kg DM)	16·52^{a}	13·87^{b}	11·06^{c}	16·37^{a}	14·50^{a}	12·69^{b}	16·57^{a}	15·53^{a}	13·65^{b}
HP (MJ/kg DM)	10·05^{a}	8·30^{b}	7·24^{c}	9·30^{a}	8·01^{a}	7·35^{b}	8·46^{a}	7·86^{a}	6·81^{b}
RE (MJ/kg DM)	6·47^{a}	5·57^{b}	3·82^{c}	7·07^{a}	6·49^{b}	5·35^{b}	8·11^{a}	7·67^{a}	6·84^{b}
HP/ME	0·61^{ab}	0·60^{b}	0·65^{a}	0·57	0·55	0·58	0·51	0·51	0·50
RE/ME	0·39^{ab}	0·40^{a}	0·35^{b}	0·43	0·45	0·42	0·49	0·49	0·50
RE-fat/RE	0·64^{a}	0·59^{a}	0·40^{b}	0·63^{a}	0·61^{a}	0·52^{b}	0·67	0·62	0·59
RE-protein/RE	0·36^{b}	0·41^{b}	0·60^{a}	0·37^{b}	0·39^{b}	0·48^{a}	0·33	0·38	0·41
ME (kJ/kg $W^{0·75}$)	1446^{a}	1359^{b}	1126^{b}	1515^{a}	1501^{a}	1350^{b}	1463^{ab}	1534^{a}	1410^{b}
HP (kJ/kg $W^{0·75}$)	882^{a}	802^{b}	733^{c}	860^{a}	825^{ab}	782^{b}	746^{ab}	778^{a}	704^{b}
RE (kJ/kg $W^{0·75}$)	566^{a}	557^{a}	393^{b}	656^{a}	676^{a}	568^{b}	716	756	706
Digested NSP (g/d)	0·9^{b}	0·8^{b}	3·5^{a}	1·0^{c}	2·5^{b}	3·5^{a}	1·0^{b}	3·3^{a}	3·5^{a}
Partially digested NSP† (kJ/d)	11^{b}	10^{b}	42^{a}	13^{c}	30^{b}	42^{a}	12^{b}	40^{a}	43^{a}
Partially digested NSP/ME	0·010^{b}	0·008^{b}	0·040^{a}	0·011^{c}	0·022^{b}	0·033^{a}	0·011^{b}	0·026^{a}	0·028^{a}
Partially digested NSP/HP	0·017^{b}	0·014^{b}	0·063^{a}	0·020^{c}	0·040^{b}	0·057^{a}	0·022^{b}	0·051^{a}	0·057^{a}

ME, metabolizable energy; HP, heat production; RE, retained energy; RE-fat, retained energy in fat; RE-protein, retained energy in protein; $W^{0·75}$, metabolic body weight.

^{a,b,c} Values in the same row within treatments with different superscript letters were significantly different ($P < 0·05$).

* For details of diets and procedures, see Tables 1 and 2 and pp. 380–383.

† Partially digested NSP = 17·2 × 0·7 g digested NSP, kJ (Livesey, 1990).

Energy utilization

Because of the lower metabolizability of the fibrous diets the content of ME per kg DM dropped from an average for the control diets of 16·49 MJ/kg DM to 11·06, 12·69 and 13·65 MJ/kg DM at the highest inclusion level for pea fibre, wheat bran and oat bran respectively (Table 8). The relationship between ME and dietary NSP is shown with regression equations below. Standard errors of coefficients and constants are shown in parentheses next to the corresponding mean. The proportion of variation accounted for by the regression is in parentheses after each equation.

Pea fibre (df 53): ME (MJ/kg DM)
$$= 17{\cdot}670\ (\text{SE}\ 0{\cdot}121) - 0{\cdot}023\ (\text{SE}\ 0{\cdot}001)\ \text{g NSP/kg DM}\ (0{\cdot}96).$$
Wheat bran (df 53): ME (MJ/kg DM)
$$= 17{\cdot}422\ (\text{SE}\ 0{\cdot}138) - 0{\cdot}022\ (\text{SE}\ 0{\cdot}001)\ \text{g NSP/kg DM}\ (0{\cdot}91).$$
Oat bran (df 53): ME (MJ/kg DM)
$$= 18{\cdot}358\ (\text{SE}\ 0{\cdot}189) - 0{\cdot}034\ (\text{SE}\ 0{\cdot}002)\ \text{g NSP/kg DM}\ (0{\cdot}86).$$

With inclusion of wheat bran and oat bran in the diet the decreases in heat production and retained energy expressed per kg DM intake were similar leaving heat production and retained energy relative to ME unaffected. The relative heat production increased significantly with pea-fibre inclusion leaving somewhat less energy to be retained. With increasing DF level from all three DF sources more energy was being retained as protein and consequently less energy retained as fat.

DISCUSSION

Body weight, food intake and amount of excreta

The DM intake and consequently the growth rate of chickens fed on the low-DF control diets were in all cases lowest (Table 3). The reason for this is presumably a low palatability caused in part by the high concentration of wheat starch (Table 2) and the meal form of the diets.

The amount of excreta was not only related to the DM intake but also to the digestibility of the diets. In particular the high-DF diets caused a significant increase in the excreta output. It was only the pea fibre that had any significant influence on DM in excreta, presumably due to the high pectin content of pea fibre (Hansen *et al.* 1992). This agrees with results obtained with pigs where pea fibre increased the digesta flow 5–6-fold compared with a low-fibre diet (Jørgensen *et al.* 1996).

Length and weight of gastrointestinal tract

All chickens in the present experiment had free access to feed and water until slaughter. The high DF levels linearly increased the amount of gutfill by 0·17 g/kg body weight for each g NSP given as pea fibre and 0·10 and 0·09 g/kg body weight when given as wheat bran and oat bran respectively. This is much less than found in experiments with pigs fed on similar diets (Jørgensen *et al.* 1996) but the results demonstrate that gutfill may contribute significantly to live weight depending on diet composition. The strong influence of pea fibre on gutfill is in agreement with the higher excreta output and the lower DM content. These findings, however, are in contrast to results obtained on rats with similar DF sources (Hansen *et al.* 1992), as these authors found a 2-fold higher faecal output from rats fed on a wheat-bran diet compared with rats fed on a pea-fibre diet.

Measurements in the present study confirm that intake of high-DF diets causes a significant expansion of the GI tract with an increased length as well. A similar hypertrophy

of gut tissues, especially the size and length of the caecum, has been confirmed in other studies with birds (Savory & Gentle, 1976; Moss, 1989; Savory, 1992*b*), and with other animal species such as the rat (Goodlad & Mathers, 1990; Hansen *et al.* 1992; Zhao *et al.* 1995) and the pig (Jørgensen *et al.* 1996). These changes will have an impact on energy metabolism as visceral organs have a high rate of energy expenditure relative to their size (Ferrell & Koong, 1986; Pekas & Wray, 1991).

Digestibility

The different DF sources varied in NSP content (Table 1), which was highest for pea fibre (414 g NSP/kg DM) and lowest for oat bran (128 g NSP/kg DM). This caused a variation in the total NSP content from the low- (control 62 g NSP/kg DM) to the high-DF diets (251, 203 and 127 g NSP/kg DM for the diets based on pea fibre, wheat bran and oat bran respectively). The estimation of the degradation in the hindgut by taking the differences between the ileal and faecal digestibility should be approached with caution. First, the faecal digestibility is based on average values from all periods. Although no period effect could be identified the measured DM digestibility tended to decrease with time because of a higher contribution of nitrogenous matter from the urine. The utilization of dietary protein (retained N/intake protein) decreased with time and consequently more nitrogenous matter was excreted in the urine. Second, faecal digestibility is measured by total collection, while ileal digestibility is estimated by use of the insoluble Cr_2O_3 marker which could cause some systematic differences. In spite of these shortcomings, however, it can be concluded that the degradation of nutrients in the hindgut of broiler chickens is very limited and far lower than that found for pigs and rats fed on similar diets. Provided the reduction in OM digestibility of the high-DF diets can be attributed solely to the differences in NSP the decreases in digestibility per g NSP were higher for oat bran than for pea fibre and wheat bran. Comparing the results obtained for pea fibre with similar diets given to either pigs or rats the decrease in digestibility is 3-fold higher (Zhao *et al.* 1995; Jørgensen *et al.* 1996) which clearly proves the much lower ability of chickens to digest fibrous materials. Other factors affecting the difference in OM digestibility, however, are indigestible starch, protein and fat and endogenous matter. It is well established that the digestibility of other constituents is influenced by the DF level as plant cell walls hinder the access of the digestive enzymes to the cell content (Bach Knudsen *et al.* 1993). DF has been found to cause increased mucus secretion in the digestive tract. This could, as discussed by Satchithanandam *et al.* (1990), result in a more rapid transit and impaired nutrient absorption.

The low or negative digestibilities found for some polysaccharide constituents (Table 5) are presumably due to contamination with endogenous or microbial matter leading to an underestimation of the DF digestion (Carré & Leclercq, 1985). Similar findings have been reported by Graham *et al.* (1986) when feeding wheat bran and sugarbeet pulp to pigs. Degradation of NSP constituents of pea fibre showed a similar pattern (arabinose > uronic acids) to that obtained with adult cockerels given the hull fraction of peas (Longstaff & McNab, 1989). The low degradation of uronic acids in all fibre sources is similar to results from adult cockerels given enzyme-treated wheat and wheat fractions (Steenfeldt *et al.* 1995) but in contrast to findings from experiments with pigs (Graham *et al.* 1986; Jørgensen *et al.* 1996) and supports the view that chickens have a very low capacity to ferment these polymers.

It is well established that viscosity has a negative effect on digestibility in chickens as an increased digesta viscosity (Pettersson & Åman, 1989; Bedford *et al.* 1991; Choct & Annison, 1992) may inhibit nutrient digestion simply by impeding the diffusion of digestive enzymes and their substrate and products. This is presumably the cause of the significant

decrease in DM content of the droppings from chickens fed on the pea-fibre diet. Furthermore NSP comprise a large proportion of the endosperm cell walls, which physically limit access of digestive enzymes to the nutrients within the cell.

Lactic acid, short-chain fatty acids, carbon dioxide and hydrogen

The concentration of lactic acid and SCFA in droppings was in the same range as found in ileal digesta from pigs (Just *et al.* 1983; Bach Knudsen *et al.* 1991; Jørgensen *et al.* 1996) demonstrating significant microbial activity. In terms of energy the excreted amounts of lactic acid and SCFA contributed 20 kJ/d with pea fibre, 4 kJ/d with wheat bran and 17 kJ/d with oat bran at the high DF level. When relating this excreted energy to intake of ME it accounts for up to 2% for chickens fed on the highest inclusion level of pea fibre. The loss of energy from H_2 production can hardly influence the energy expenditure because it is equivalent to less than 0·2% of ME intake. However, the measurement of H_2 production can be used to indicate and quantify the microbial fermentation within the GI tract (Lewitt & Donaldson, 1970; Wolever *et al.* 1986). The correlation (r) between H_2 production and fermented NSP was high (pea fibre, 0·86; wheat bran, 0·81; oat bran, 0·80). This indicates a close relation between NSP fermentation and H_2 production even if, as discussed recently by Livesey (1994), the interpretation should be made with caution. In spite of a possible difference in H_2 production between the three experiments the much lower H_2 production in the pea-fibre experiment correlates well with the lower NSP degradation of this DF source (Table 5). In the experiments with wheat bran and oat bran it can be estimated that up to 2·9 and 3·5 g NSP daily were fermented corresponding to the much higher H_2 production (wheat bran: 198 ml H_2 and oat bran: 186 ml H_2). No measurable amounts of CH_4 could be detected, indicating lack of methanogenic bacteria. In a study using pigs (Jensen & Jørgensen, 1994) the CH_4 production increased along the colon and the highest concentration was detected at rectum level. Compared with pigs, birds have a much shorter colon and a faster transit time of digesta. Consequently the potential for CH_4 production is limited. The relatively high concentration of organic acids in droppings can be related to an increased thickness of the unstirred water layer and by that impaired diffusion in the digesta with the lower DM content (Ikema *et al.* 1990; Satchithanandam *et al.* 1990; van der Klis *et al.* 1993).

Energy metabolism

There were no significant differences in daily ME intake between the medium- and high-DF diets for any of the three DF sources (Table 7). When expressed in terms of metabolic body size (kg $W^{0·75}$) the intakes were reduced for wheat bran and oat bran (Table 8). The DF content in the high-DF diets is rather high for practical conditions but the results agree with those of MacLeod (1990) and Jørgensen *et al.* (1990) that the broiler chicken to a great extent regulates voluntary feed intake. In all three experiments fat retention reached maximum at the medium-DF level whereas N (protein) retention was highest at the high-DF levels. Increasing DF levels changed the relation between fat and protein towards leaner birds, confirming the susceptibility of the growing fowl's body composition to dietary influence (MacLeod, 1990).

The higher inclusion of DF decreased, for all DF sources, the ME content of the diet (Table 8). Regression equations show that a close relationship existed between the ME concentration and DF (NSP) from all three DF sources. The dietary NSP accounted for 86–96% of the variation in ME which confirms the view that DF is a very good predictor of the ME content of broiler diets (Carré *et al.* 1990; Annison, 1991). The partially digestible energy available from the fermentation of NSP can be calculated taking into account the extra losses of protein and fat into faeces material which inevitably follow an

increase in DF intake (Livesey, 1990). The amount of energy derived from NSP fermentation was highest for the high-DF diets (pea fibre: 42 kJ/d, wheat bran: 42 kJ/d and oat bran: 43 kJ/d). These values are remarkably similar and appear to be independent of the NSP intake indicating an upper capacity for DF fermentation under these feeding conditions. Expressing the NSP fermentation relative to either ME intake or total heat production the contributions were 3–4% and 6% respectively, for the high-DF diets. It can be concluded that by means of DF degradation the microflora may benefit the host bird by supplying extra energy. When energy is deficient the benefit from DF digestion seems to be even greater (Moss, 1989; Muramatsu *et al.* 1991).

It was only when feeding pea fibre that the energy expenditure (heat production) increased significantly relative to ME. When the absorption of SCFA is limited and dietary protein and fat do not vary to a great extent as in the present study, the composition of absorbed nutrients is relatively uniform across treatments. This explains the limited effect on diet-induced thermogenesis when feeding the wheat-bran and oat-bran diets. The reasons for the different effect when feeding the pea-fibre diets could be several. The pea fibre exerted a stronger impact on the GI hypertrophy and there is a strong indication that differences in weight of visceral organs are highly related to differences in energy expenditure (Koong *et al.* 1985; Ferrell & Koong, 1986; Yen *et al.* 1989). The physico-chemical properties of NSP from pea fibre (0·47 in the form of S-NSP) leading to lower luminal DM could also contribute to increased energy expenditure due to increased bulk of digesta. In contrast to the findings with pea fibre there was no increase in heat production relative to ME when using oat bran in the diet. Although the fibre concentration of the oat bran was not as high as for the other two DF sources the study confirms results reported by Sibbald *et al.* (1990) that utilization of oats by poultry is relatively high.

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