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Digestion by pigs of non-starch polysaccharides in wheat and raw peas (*Pisum sativum*) fed in mixed diets

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The digestion by pigs of non-starch polysaccharides (NSP) in wheat and raw peas (*Pisum sativum*) fed in mixed diets was measured. In the four experimental diets, wheat was included at a constant 500 g/kg whilst peas contributed 0–300 g/kg and these were the only dietary sources of NSP. Separate estimates of digestibility for wheat and peas were obtained by using a multiple linear regression technique which also tested the possibility that the presence of peas might influence the digestibility of wheat NSP. There was little evidence of the latter and it was found that the digestibility of peas NSP (0·84) was considerably greater than that of wheat (0·65). The non-cellulosic polysaccharides (NCP) had twofold greater digestibilities than had cellulose for both foods with essentially all the peas NCP being digested. Faecal α, ε-diaminopimelic acid concentration increased with feeding of peas, suggesting stimulation of bacterial biomass production in the large intestine using the readily fermented peas NSP. All three major volatile fatty acids produced by large intestinal fermentation were detected in jugular blood and increased significantly with increasing peas inclusion rate in the diet.

Non-starch polysaccharides: Peas: Wheat: Pig

Mature dry peas (*Pisum sativum*) are a rich source of oligosaccharides and polysaccharides, the latter including starches which are relatively slowly digested by pancreatic α-amylase (*EC* 3.2.1.1) (Longstaff & McNab, 1987) even after cooking (Würsch *et al.* 1986) and the cell-wall polysaccharides (non-starch polysaccharides; NSP) which contribute to the dietary fibre complex. NSP, oligosaccharides and that fraction of starch which is not digested by α-amylase provide the majority of organic matter which flows to, and is fermented in, the large bowel (LB) (Cummings & Englyst, 1987). In a previous study (Goodlad & Mathers, 1990) in which raw peas were incorporated into semi-purified diets offered to rats, starch and oligosaccharides were not detected in faeces and it was assumed that these carbohydrate fractions were completely digested or fermented, or both. In addition, the apparent digestibility of peas NSP was high (0·79) at all levels of dietary inclusion (100–500 g peas/kg). In adult cockerels, coefficients of digestion for starch and NSP from ground raw peas were considerably lower at 0·88–0·92 and 0·31–0·44 respectively (Longstaff & McNab, 1987). There is no comparable information for peas carbohydrate digestion by pigs which, because of their relatively larger LB and longer transit times, might be expected to be more effective in digesting those carbohydrate fractions which escape digestion in the small intestine.

The present study was designed to measure the digestibility of NSP and its constituent monosaccharides in raw peas fed to pigs. The peas were incorporated at graded levels into wheat-based diets such that wheat and peas provided the only complex carbohydrates and the contribution made by wheat remained constant. A multiple linear regression (MLR)

* For reprints.

procedure was used to derive separate estimates of apparent digestibility for peas and wheat and to ascertain whether there was any interaction between these two foods in the extent of NSP digestion. Concentrations of volatile fatty acids (VFA) in jugular blood were measured as an indication of the potential for LB fermentation to influence metabolite supply to post-hepatic tissues (Pomare *et al.* 1985).

MATERIALS AND METHODS

Animals and housing

Twenty castrate male pigs (the progeny of Large White boars on F1 sows which were crosses between Large White, Duroc and Landrace animals), mean initial weight 29·9 (SE 0·91) kg were selected from the commercial herd at Cockle Park Farm (University of Newcastle upon Tyne) and housed in individual metabolism cages which allowed separation and complete collection of urine and faeces.

Diets and feeding

Four experimental diets, each containing 500 g milled wheat/kg and graded concentrations (0–300 g/kg) of milled raw peas (*Pisum sativum* var. Sentinel), were formulated to be of similar nitrogen and energy contents, as shown in Table 1, with peas included at the expense of sucrose and fish meal. Wheat and peas were the only dietary sources of complex carbohydrates.

For the first 5 d whilst in metabolism cages, the pigs were fed on a complete commercial diet (Customix; Varley Feeds, Darlington). Over the next 3 d the pigs were gradually accustomed to the appropriate experimental diet by mixing it with the commercial diet in the proportions 1:3, 1:1 and 3:1 (w/w) on days 6, 7 and 8 respectively so that by day 9 of the study and, thereafter, each animal received the appropriate experimental diet only. Each animal was offered daily an amount (kg) of air-dry food equivalent to 0·1 of the animal's metabolic body-weight, i.e. (body-weight)$^{0.75}$. The ration was offered in two equal meals mixed into a slurry with 1 litre water at 09.00 and 16.00 hours daily. Access to the meal was permitted for 45 min after which any uneaten food was removed, oven-dried and weighed. Drinking water was available *ad lib.*

Experimental protocol

After 7 d on the full experimental diet, the animals were weighed and a 7 d balance study carried out during which food intake was measured and all faeces and urine produced were collected. Faeces were collected daily and stored at −20° until required for analysis. Urine was collected into buckets containing 20 ml aqueous sulphuric acid (500 ml/l). The daily output from each animal was measured and a subsample (50 ml/l) stored at 4°. The pigs were reweighed at the end of the 7 d balance period and 10 ml blood collected by jugular puncture into heparinized tubes and held on ice until storage at −20°.

Analytical methods

Before analysis, frozen faeces from each animal were allowed to thaw, then bulked, mixed in a commercial dough mixer and a subsample taken for freeze-drying and subsequent milling. Diets and faeces were analysed for N by a Kjeldahl procedure and for gross energy using a Gallenkamp ballistic bomb calorimeter. For the latter analysis, urine was first freeze-dried. Determinations of NSP on diets and faeces were carried out by the method of Englyst & Cummings (1984), and resistant starch was measured by omitting the dimethyl sulphoxide (DMSO) addition step. Oligosaccharides in the diets and faeces, α, ϵ-diaminopimelic acid (DAPA) in faeces and blood volatile fatty acids (VFA) were

Table 1. *Formulation (g/kg) and analysed composition (g/kg dry matter (DM)) of the diets*

Constituent	Diet 1	2	3	4
Peas	0	100	200	300
Wheat	500	500	500	500
Fish meal	205	170	135	100
Sucrose	245	170	95	20
Maize oil	0	10	20	30
Vitamin and mineral premix*	50	50	50	50
Analysed composition (g/kg DM)				
Gross energy (MJ/kg DM)	18·0	18·9	17·6	19·5
Nitrogen	28·1	28·4	27·5	28·5
Total non-starch polysaccharides	44·2	59·7	73·1	89·7
Cellulose	7·7	14·0	17·8	21·9
Non-cellulosic polysaccharides	36·4	45·7	55·3	67·6
Arabinose	9·5	13·6	18·1	23·1
Xylose	16·7	18·6	22·0	24·6
Mannose†	0·3	0·4	0·5	0·6
Galactose	0·9	2·1	2·6	3·5
Glucose	16·2	22·1	27·9	37·6
Uronic acids	1·4	4·1	4·9	5·7
Resistant starch	11	14	31	54
Total oligosaccharides	0	5·1	7·5	9·5
Raffinose	0	1·5	1·5	2·2
Stachyose	0	2·2	2·6	3·4
Verbascose	0	1·5	3·4	4·0

* Supplied by Unilever Research, Colworth House, Bedford.
† Calculated from analysed composition of wheat and peas.

determined as described by Goodlad & Mathers (1990). Blood glucose was assayed using a Yellow Springs Instruments (Yellow Springs, Ohio 45387, USA) model 23A glucose analyser.

Experimental design and statistical analysis

The experiment was designed as a single factor study with four treatments (diets) and five replicates (pigs) per diet. Values were examined by one-way analysis of variance and orthogonal polymonials were used to describe responses to peas inclusion in the diets. Results are presented as means for each diet with their standard errors based on the between-animals within-diets variation with 16 df. Separate estimates of apparent digestibility of wheat and of peas polysaccharides were obtained by an MLR technique outlined by Key & Mathers (1990); a similar approach was adopted by Van Dokkum *et al.* (1983) to obtain estimates of the digestibility of fibre in breads added to a basal diet. In the present study, two MLR models were used:

$$\text{MLR model 1: } Y = \alpha_1 X_1 + \alpha_2 X_2 + \alpha_3 X_1 X_3,$$

where Y was output of NSP in the faeces, X_1 and X_2 were intakes of NSP from wheat and peas respectively, X_3 has the value of 0 or 1 when peas were absent from or present in the diet respectively, α_1 and α_2 are the coefficients of indigestibilities for NSP in wheat and peas respectively and α_3 is the additional effect of presence of peas on wheat NSP indigestibility. Where α_3 is non-significant, a simpler model is appropriate:

$$\text{MLR model 2: } Y = \beta_1 X_1 + \beta_2 X_2,$$

where β_1 and β_2 are the coefficients of indigestibility for wheat and peas NSP respectively. Computations were carried out using the Statgraphics package (STSC Inc., Rocksville, Maryland, USA). Apparent digestibilities were calculated by subtracting the appropriate coefficients of indigestibility from unity.

RESULTS

Diet composition

Gross energy (GE) and N contents of the diets were similar as intended, whilst the concentration of NSP increased twofold as the proportion of peas in the diet increased. Where wheat was the only complex carbohydrate source (diet 1), glucose and xylose were the major NSP constituent sugars with smaller contributions from arabinose and uronic acids. As the peas inclusion rate increased, arabinose, uronic acids and galactose made relatively greater contributions whilst mannose was quantitatively unimportant in all diets. The concentration of starch resistant to α-amylase in vitro without previous treatment with DMSO (resistant starch) increased fivefold from the lowest to highest peas inclusion rate. The oligosaccharides raffinose, stachyose and verbascose were not detected in diet 1 (zero peas) but contributed nearly 10 g/kg to the highest peas-containing diet (Table 1).

Animal well-being and growth

Two pigs scoured after being transferred to the metabolism cages and were replaced by two others. All animals consumed all the allocated food during the experimental period and there was no evidence of any adverse effect of the diets. The slightly lower dry matter (DM) intakes for animals on the higher-peas diets were due to the slightly lower DM concentration in these diets and to slightly smaller pigs being randomly allocated to these diets. Growth rates were high and food conversion ratios were low and similar for all diets. There were no significant effects of diet on any measure of N metabolism (Table 2).

Faecal DM and GE

Output of wet faeces and of faecal DM tended to increase whilst apparent DM digestibility decreased with increasing dietary peas inclusion rate, but none of these dietary effects was statistically significant ($P > 0{\cdot}05$; Table 3). There was a significant ($P < 0{\cdot}01$) linear increase in the GE content of faecal DM as peas inclusion rate increased which resulted in a linear increase ($P < 0{\cdot}05$) in faecal GE output and a linear ($P < 0{\cdot}05$) decrease in apparent GE digestibility. Urinary GE output was not significantly ($P > 0{\cdot}05$) affected by diet (Table 3) as would be expected from the lack of effect on urinary N output (Table 2).

Apparent digestibility of NSP

Including peas in the diet resulted in significant linear increases in the apparent digestibilities of dietary NSP, of non-cellulosic polysaccharides (NCP) and of the NSP constituent sugars arabinose, galactose and uronic acids, and non-significant increases for the other constituents cellulose, xylose, mannose and glucose (Table 4). For galactose and uronic acids, apparent digestibility was considerably higher and similar with the three peas-containing diets compared with the basal (zero peas) diet. It should be noted that the analysed contents of galactose and uronic acids in the diets (Table 1) did not show the expected regular increase with increasing peas inclusion rate. Any errors in diet analysis will tend to reduce the linearity in response in digestibility to increasing dietary peas content and may account for the deviations in linearity observed for galactose and uronic acids. Cellulose was less well digested than NCP in all diets but especially in the basal (zero peas)

Table 2. *Dry matter (DM) intake, growth performance and nitrogen metabolism in pigs given wheat-based diets containing graded amounts of raw peas* (Pisum sativum *var. Sentinel*)†

(Means for five pigs per diet)

	Peas in diet (g/kg)				SE of mean	Statistical significance of linear effect of dietary peas inclusion rate
	0	100	200	300		
DM intake (kg/7 d)	9·02	9·06	8·72	8·75	0·111	*
Growth rate (kg/7 d)	5·10	5·05	4·91	5·32	0·539	NS
FCR	1·80	1·88	1·88	1·71	0·182	NS
N intake (g/7 d)	253	257	239	249	3·2	NS
Faecal N output (g/7 d)	31	33	35	34	3·3	NS
Urinary N output (g/7 d)	100	103	94	100	7·4	NS
N retention (g/7 d)	122	121	110	115	6·7	NS
Apparent BV	0·55	0·54	0·54	0·54	0·033	NS

NS, not significant; FCR, food conversion ratio (DM intake ÷ live-weight gain); BV, biological value (N retention ÷ N apparently absorbed).
* $P < 0·05$.
† For details of diets, see Table 1.

Table 3. *Outputs and digestibilities of dry matter (DM) and gross energy by pigs fed on wheat-based diets containing graded levels of raw peas* (Pisum sativum *var. Sentinel*)†

(Means for five pigs per diet)

	Peas in diet (g/kg)				SE of mean	Statistical significance of linear effect of dietary peas inclusion rate
	0	100	200	300		
Faecal output (g/7 d)	2402	2597	2818	2895	191·8	NS
Faecal DM (g/kg wet wt)	336	354	317	330	20·9	NS
Faecal DM output (g/7 d)	873	884	935	946	75·6	NS
Apparent DM digestibility	0·90	0·90	0·89	0·89	0·008	NS
GE intake (MJ/7 d)	162	171	153	170	2·1	NS
Faecal GE (MJ/kg DM)	17·8	18·7	19·6	20·8	0·68	**
Faecal GE output (MJ/7 d)	15·5	16·5	18·2	19·4	1·22	*
Apparent GE digestibility	0·90	0·90	0·88	0·88	0·007	*
Urinary GE output (MJ/7 d)	5·3	5·3	4·9	4·9	0·27	NS

GE, gross energy; NS, not significant.
* $P < 0·05$, ** $P < 0·01$.
† For details of diets, see Table 1.

diet. Estimates of apparent digestibility for mannose were associated with relatively high SE, probably because of the difficulty in measuring the small concentrations present in diets and faeces.

Since wheat and peas were the only significant sources of NSP in the diets, use of MLR

Table 4. *Apparent digestibilities of non-starch polysaccharides and constituents in pigs fed on wheat-based diets containing graded levels of raw peas (*Pisum sativum *var. Sentinel)*†

(Means for five pigs per diet)

	Peas in diet (g/kg)				SE of mean	Statistical significance of linear effect of dietary peas inclusion rate
	0	100	200	300		
Total NSP	0·65	0·70	0·71	0·75	0·022	*
NCP	0·72	0·77	0·79	0·82	0·013	***
Cellulose	0·34	0·48	0·47	0·54	0·064	NS
Arabinose	0·60	0·73	0·78	0·87	0·019	***
Xylose	0·76	0·78	0·78	0·80	0·018	NS
Mannose	0·46	0·61	0·55	0·57	0·100	NS
Galactose‡	0·33	0·71	0·74	0·79	0·022	***
Glucose	0·60	0·64	0·61	0·68	0·040	NS
Uronic acids‡	0·65	0·87	0·85	0·86	0·019	***

NSP, non-starch polysaccharides; NCP, non-cellulosic polysaccharides; NS, not significant.
* $P < 0·05$, *** $P < 0·001$.
† For details of diets, see Table 1.
‡ Responses for galactose and uronic acids contained significant non-linear components.

procedures allowed the derivation of separate estimates of digestibility for two foods. In addition, MLR model 1 tested the possibility that the presence of peas in the diet could influence the apparent digestibility of NSP (or its constituents) in wheat with the extent of this influence estimated as the parameter, α_3 (Table 5). The latter was very small and not statistically significant for total NSP, NCP and most individual constituents of NSP, with the exceptions of galactose and uronic acids where highly significant ($P < 0·001$) negative values for α_3 were obtained. These negative α_3 values indicate that the estimated digestibility of wheat galactose and uronic acids were greater when peas were present in the diet. Apparent digestibilities for wheat NSP (and its constituents) estimated by MLR models 1 and 2 were similar and, as expected, close to those for the basal (zero peas) diet. Peas NSP were considerably more digestible than that of wheat with apparent digestibility of the NCP fraction not significantly different from unity. For both foods, the cellulose fraction had the lowest digestibility. Both MLR models provided very satisfactory descriptions of the relationship between intake and output of NSP and its constituents in these mixed diets, with R^2 greater than 0·92 for all components except mannose (R^2 0·86). Oligosaccharides were not detected in faeces from pigs given the 300 g peas/kg diet; other diet groups were not examined.

Consequences of large intestinal fermentation

As an index of large bowel (LB) bacterial biomass production, faecal DAPA was measured (Table 6). Faecal DAPA when expressed either as a proportion of faecal DM or crude protein, increased in a significant ($P < 0·05$) linear fashion with increasing peas inclusion rate. Similar increases were observed in faecal DAPA output but were not statistically significant given the relatively large between-animal variation. Part of this variation was due to differences in food intake (food provided was based on a fixed proportion of body-weight daily) and when this was removed by expressing DAPA output per kg food DM intake, a highly significant ($P < 0·01$) linear increase with increasing peas consumption became apparent (Table 6).

Blood glucose concentrations were consistently lower for pigs fed on peas than for those given the basal (zero peas) diet but this was not statistically significant (Table 7). All three

Table 5. *Apparent digestibilities, estimated by multiple linear regression (MLR)*, for non-starch polysaccharides (NSP) of wheat and raw peas* (Pisum sativum *var. Sentinel*) *when fed in mixed diets to growing pigs*

(Estimates were derived using individual values for all twenty pigs; mean values with their standard errors)

	Wheat		Peas		α_3		
	Mean	SE	Mean	SE	Mean	SE	R^2
MLR model 1							
NSP	0·65	0·034	0·85	0·080	0·001	0·061	0·97
NCP	0·72	0·081	1·01	0·080	−0·003	0·035	0·98
Cellulose	0·34	0·124	0·53	0·052	−0·074	0·191	0·94
Arabinose	0·60	0·027	1·05	0·056	0·010	0·052	0·98
Xylose	0·76	0·021	1·07	0·263	0·008	0·040	0·97
Mannose	0·44	0·109	0·44	0·384	−0·194	0·199	0·86
Galactose	0·27	0·055	0·90	0·046	−0·321	0·078	0·97
Glucose	0·60	0·070	0·72	0·120	0·021	0·142	0·94
Uronic acids	0·66	0·044	0·83	0·051	−0·215	0·053	0·96
MLR model 2							
NSP	0·65	0·027	0·84	0·046			0·97
NCP	0·72	0·015	1·02	0·046			0·98
Cellulose	0·37	0·092	0·54	0·044			0·94
Arabinose	0·60	0·022	1·04	0·032			0·98
Xylose	0·76	0·017	1·03	0·150			0·97
Mannose	0·50	0·091	0·72	0·241			0·86
Galactose	0·43	0·054	1·02	0·048			0·95
Glucose	0·59	0·059	0·71	0·068			0·94
Uronic acids	0·81	0·033	0·94	0·060			0·92

α_3, Additional effect of presence of peas on indigestibility of NSP fraction in wheat; NCP, non-cellulosic polysaccharides.
* For details of MLR models 1 and 2, see pp. 261–262.

Table 6. *Faecal concentration and output of α, ε-diaminopimelic acid (DAPA) in pigs fed on wheat-based diets containing graded levels of raw peas* (Pisum sativum *var. Sentinel*)†

(Means for five pigs per diet)

	Peas in diet (g/kg)				SE of mean	Statistical significance of linear effect of dietary peas inclusion rate
	0	100	200	300		
Faecal DAPA (mg/g DM)	1·3	1·3	1·6	1·7	0·13	*
Faecal DAPA (g/16 g faecal N)	0·57	0·49	0·68	0·75	0·063	*
Faecal DAPA output (g/7 d)	1·2	1·1	1·5	1·6	0·20	NS
Faecal DAPA output (g/kg DM intake)	0·12	0·10	0·16	0·18	0·016	**

NS, not significant; DM, dry matter.
* $P < 0·05$, ** $P < 0·01$.
† For details of diets, see Table 1.

Table 7. *Concentrations of glucose (mM) and of volatile fatty acids (μM) in peripheral blood from pigs fed on wheat-based diets containing graded levels of raw peas* (Pisum sativum *var. Sentinel*)†

(Means for five pigs per diet)

	Peas in diet (g/kg)				SE of mean	Statistical significance of linear effect of dietary peas inclusion rate
	0	100	200	300		
Glucose	4·7	4·1	4·0	4·1	0·28	NS
Acetate	291	302	385	409	34·8	*
Propionate	17	14	27	25	3·8	*
Butyrate	9	10	13	24	4·3	*
Total VFA	317	326	425	459	39·3	**

VFA, volatile fatty acids; NS, not significant.
* $P < 0·05$, ** $P < 0·01$.
† For details of diets, see pp. 260–261.

major VFA (acetate, propionate and butyrate) produced by LB fermentation could be detected in peripheral blood, with acetate accounting for 0·89–0·93 of the total on a molar basis. Increasing peas in the diet resulted in linear increases in blood concentration of each VFA, with butyrate showing the largest proportional increase (2·5-fold).

DISCUSSION

Although there is now no doubt that plant cell wall polysaccharides in many foods can be extensively digested by omnivorous animals including man (Cummings, 1981), and that this occurs largely by fermentation within the LB, the factors which influence the extent of fermentation of NSP for a given food in a particular animal are poorly understood. There is no clear evidence of between-species differences in the rate of degradation, but it is probable that the time available for fermentation (transit time, TT) will have a major influence on NSP digestibility (Stephen *et al.* 1987). The shorter TT in the chicken LB compared with that in the rat may explain the less extensive fermentation of peas NSP by cockerels (Longstaff & McNab, 1987) than by rats (Goodlad & Mathers, 1990). TT in the pig LB is considerably longer (1–5 d; Luckey *et al.* 1979; Mroz *et al.* 1986) than that in the rat (0·5–1 d; Goodlad & Mathers, 1990; Mathers *et al.* 1990) so it might be expected that pigs would ferment NSP more effectively than would rats. This was examined in the present study.

Faecal composition

Whilst there were no significant effects of diet on faecal output of wet or dry matter, both tended to increase when feeding peas. Faeces from pigs fed on peas tended to have lower DM content but had significantly ($P < 0·05$) greater concentrations of energy and of DAPA in that DM. The higher faecal concentration and output of DAPA suggests strongly, but does not prove, that there was greater bacterial biomass production with the peas-containing diets. The possibility that diet may alter the DAPA concentration in bacterial cells (Czerkawski, 1976) means that it is not possible to assume constant proportionality between faecal DAPA outputs and faecal bacterial biomass.

The increased faecal energy density for pigs fed on peas was unexpected and suggests a higher concentration of lipid was present. This extra lipid may have been derived from several sources including unabsorbed dietary fat, endogenous lipid and lipid synthesized by

LB bacteria. Additional maize oil was added to the peas-containing diets (Table 1) but this is a highly digestible product and is unlikely to affect faecal fat concentrations in the amounts used. More likely is the possibility that peas reduced the ileal absorption of bile salts and other steroids and increased their output in faeces. Several dietary fibre sources including pectin and guar gum have this effect (Kay & Truswell, 1977; Miettinen & Tarpila, 1977; Shutler *et al.* 1987) and the blood-cholesterol-lowering properties of legume-rich diets (Mathur *et al.* 1968; Shutler *et al.* 1989) may be due, in part, to this steroid-binding property. Gut anaerobic bacteria are relatively rich in lipid (100–200 g/kg DM; Czerkawski, 1976) and if feeding peas resulted in greater bacterial biomass production as suggested by the DAPA results, a greater concentration of bacterial lipid in faeces would also be expected, resulting in the observed increase in faecal energy density.

Digestion of NSP

Including peas in the diet increased dietary NSP concentration by up to twofold and was associated with marked increases in the apparent digestibility of whole-diet NSP which suggested that the peas NSP were considerably more digestible than those of wheat (Table 4). The use of MLR procedures allowed calculation of separate estimates of apparent digestibility for wheat and for peas NSP and also tested the possibility that the presence of one dietary component (peas) could influence the apparent digestibility of the other (wheat), i.e. MLR model 1 tested for associative effects (Mitchell, 1964). For NSP and its major components, there was little evidence of any associative effect between wheat and peas (Table 5). The observation that α_3 was significant and negative for galactose and uronic acids implies that the digestibility of these components in wheat was increased by having peas in the diet. Whilst this possibility is of some interest, it is unlikely to be of nutritional significance given the small contribution made by these components to the total NSP fraction. The simpler MLR model 2 provided a very good description of the relationships between NSP (and each of its components) output in faeces and intake from wheat and peas.

The apparent digestibility of wheat NSP (0·65) was similar to those (0·61 and 0·65) reported for barley (Fadel *et al.* 1988), higher than that (0·48) observed for a basal mixed-cereal diet based on wheat, barley and oats (Graham *et al.* 1986) and midway between estimates of 0·52 and 0·78 reported for another basal diet containing wheat, barley and soya-bean meal (Longland & Low, 1989). All these estimates were obtained in pigs. In contrast, poultry appear to digest wheat NSP less effectively with coefficients of digestibility of 0·30–0·46 reported by Longstaff & McNab (1986) whilst rats digested 0·56 of the NSP in wholemeal bread (Key & Mathers, 1990).

Table 8 gives a comparison of estimates of the apparent digestibility of raw peas NSP and its constituent sugars for chickens (Longstaff & McNab, 1987), rats (Goodlad & Mathers, 1990) and pigs (present study). The major between-species difference is the markedly lower digestibility by poultry. It is possible that this difference is due, in part, to the experimental protocol used by Longstaff & McNab (1987) who starved their birds for 48 h before tube-feeding a single meal of peas. Starvation for 24 or 48 h greatly reduced the weight of rat caecal contents and the concentrations of VFA in that organ (Illman *et al.* 1986) and may reduce the LB capacity for NSP fermentation in the immediate re-feeding period. However, other work has shown very poor digestibility of NSP from white lupin (*Lupinus albus* L.) cotyledon by adult cockerels (Carré & Leclercq, 1985) so that the relatively low digestibility of peas NSP observed by Longstaff & McNab (1987) may illustrate a true species effect.

Apparent digestibilities of NSP and of NCP were slightly greater by pigs than by rats but the rats seemed to digest cellulose better than did the pigs. It is not clear to what extent these differences are real between-species differences or confounded by possible differences in the

Table 8. *Comparison of the apparent digestibility of raw peas non-starch polysaccharides (NSP) and its constituent sugars by chickens, rats and pigs*

Source ...	Longstaff & McNab (1987)	Goodlad & Mathers (1990)	Present study
Species ...	Chickens*	Rats	Pigs
NSP	0·38†	0·79	0·84
NCP	—	0·90	1·02
Cellulose	—	0·68	0·54
Arabinose	0·32	0·99	1·04
Xylose	0·11	0·58	1·03
Mannose	0·48	0·84	0·72
Galactose	0·52	0·89	1·02
Glucose	0·47	0·74	0·71
Uronic acids	—	0·78	0·94

NCP, non-cellulosic polysaccharides.
* Mean for two experiments.
† Does not include uronic acids.

susceptibility to fermentation of the two peas samples. We are not aware of any systematic study of the digestion of NSP from different pea varieties. Although different varieties of wheat appeared to differ in NSP digestibility by poultry, none of the varietal differences was statistically significant (Longstaff & McNab, 1986).

Consequences of large intestinal fermentation

Clearly pigs are able to digest most of the cell wall material in raw peas. Whilst the intestinal site of digestion of these carbohydrates was not examined in the present study and it is recognized that a portion of this material may be digested before the end of the ileum (Millard & Chesson, 1984; Graham *et al.* 1986; Fadel *et al.* 1988), it is reasonable to assume that the majority of this carbohydrate was fermented in the LB, with VFA as the major energy-containing end-products. These VFA are readily absorbed (McNeil *et al.* 1978; Ruppin *et al.* 1980) and passed via the portal vein to the liver. Stimulation of LB fermentation by feeding lactose to weaned pigs has been shown to raise portal VFA concentrations (Giusi-Perier *et al.* 1989). Including peas in semi-purified diets for rats resulted in higher concentrations of acetate, propionate and butyrate in portal blood but only acetate was detected in peripheral blood and increased with increasing peas consumption (Goodlad & Mathers, 1990). This efficient removal of the C_3 and C_4 VFA was expected given the relatively high activities of liver propionyl- and butyryl-CoA synthetases (*EC* 6.2.1.17 and *EC* 6.2.1.2 respectively) (Aas, 1971; Ash & Baird, 1973). Whilst acetate was the major VFA in jugular blood in the present study, propionate and butyrate were also detected and all three VFA increased with increasing dietary peas inclusion rate. Propionate and butyrate were also detected in blood collected from the ear vein of pregnant sows and increased (significantly so for propionate) when additional oat hulls were eaten (Mroz *et al.* 1986). Taken together, the results of these two studies suggest that the pig liver may not be as efficient as that of the rat in removing absorbed VFA so raising the possibility that these metabolites will reach peripheral tissues where their fate and effects are uncertain.

The non-significant reduction in blood glucose concentration in peas-fed pigs may be a consequence of a reduced rate of glucose absorption from the slowly digested pea starch (Fleming & Vose, 1979; Snow & O'Dea, 1981; Longstaff & McNab, 1987) compared with the sucrose which it replaced in the diet and is in line with reports of better glucose tolerance with legume-containing diets (Simpson *et al.* 1981; Tappy *et al.* 1986).

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