

Differential effects of feeding fermentable carbohydrate to growing pigs on performance, gut size and slaughter characteristics

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Abstract

Thirty-five gilts grown between 18 and 55 kg live weight were used to examine the effects of feeding fermentable carbohydrate on voluntary food intake, performance, carcass characteristics, and large intestinal growth. Five diets were used. The first diet contained steam-flaked sorghum and a supplement based on animal protein sources and 40 g/kg soya-bean meal (diet SAP). Using this diet as a base, three other diets contained either (i) guar gum, a source of soluble non-starch polysaccharide (NSP) (diet SAP + S-NSP), (ii) NoveloseTM, a source of resistant starch (RS) (diet SAP + RS), and (iii) a combination of both S-NSP and RS (diet SAP + S-NSP + RS). The final diet (diet WBL) was based on wheat, barley and Australian sweet lupins. Diets (i), (ii) and (iii) were formulated such that the concentrations of soluble NSP, oligosaccharide and RS were similar to those contained in diet WBL. There was no relationship ($P > 0.05$) between voluntary food intake and indices of hind-gut fermentation, although pigs given diets SAP + S-NSP and SAP + S-NSP + RS took longer to reach the slaughter weight of 55 kg ($P < 0.001$) and converted food less efficiently than pigs given other diets ($P < 0.001$). An increased intake of S-NSP ($R^2 = 0.842$, $P < 0.05$) and S-NSP + RS ($R^2 = 0.805$, $P < 0.05$) was positively correlated to an increased (empty) weight of the large intestine. A significant negative relationship ($R^2 = 0.78$, $P < 0.05$) existed between the daily intake of S-NSP + RS and dressing proportion, such that each gram increase caused a 0.25 g/kg decrease in the dressing proportion of pigs. No such relationships existed between the daily intake of soluble NSP, insoluble NSP, or RS ($P > 0.05$) with dressing proportion. These data suggest that the sources of fermentable carbohydrate used in this study, i.e. soluble NSP and RS, may not significantly depress voluntary food intake but can affect performance and have a significant effect on large intestinal growth and dressing proportion.

Keywords: carbohydrates, carcass composition, food intake, large intestine, pigs.

Introduction

Microbial fermentation of a wide range of endogenous (e.g. sloughed cells) and exogenous (e.g. food components) materials occurs in the large intestine of the pig with the production of volatile fatty acids (VFA), lactate, gases and bacterial biomass. Components of food digested in the large intestine by the microflora are non-starch polysaccharides (NSP), resistant starch (RS), and oligosaccharides (e.g. raffinose series from legumes), collectively called 'dietary fibre' (Annisson, 1993; Annison and Topping, 1994). Diets given to

growing/finishing pigs in Western Australia are based predominately on wheat, barley and Australian sweet lupins (*Lupinus angustifolius*) and can contain high levels of dietary fibre. Although the overall (faecal) digestibility of such a diet may be high (0.80 to 0.85), it has been estimated that proportionally 0.47 of the total digested energy in lupins disappears in the large intestine (Taverner and Curic, 1983). Hence the level of productive energy provided to the pig by such a diet is lower because carbohydrate fermented to VFA is used less efficiently as an energy source than glucose absorbed in the small intestine (Müller *et al.*, 1989).

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In addition, the high concentration of dietary fibre in such a diet, and in particular soluble NSP, may limit production due to a reduction in voluntary food

intake and decreased dressing proportion. There is general agreement amongst researchers and food industry personnel that a high inclusion level of lupins in diets depresses voluntary food intake (PRDC Lupin Working Group, 1994), although evidence in support of this is largely anecdotal. Certainly, increased rates of hind-gut fermentation with diets containing lupins cause an increase in VFA production which, in turn, is correlated to large intestinal weight (Siba *et al.*, 1996). How this may then influence food intake, however, is currently unknown (Van Barneveld *et al.*, 1995b).

Our intention in this experiment was to examine the effects of microbial fermentation in the large intestine on voluntary food intake, live-weight gain, and large intestinal growth in pigs given diets containing dietary fibre. Furthermore, we were interested in the effects of dietary fibre on dressing proportion, since King (1990) estimated that the dressing proportion of finishing pigs decreased by 8 to 14 g/kg for each 100 g/kg increment in dietary lupin-seed meal. Our hypothesis, i.e. increased hind-gut fermentation causes reduced voluntary food intake, was difficult to test in the absence of purified sources of carbohydrate from the foods of interest, such as oligosaccharide from lupins. Given this, we tested whether a high rate of fermentation *per se* affected these measurements by adding 'model' sources of dietary fibre to diets based on steam-flaked sorghum, a cereal that is inherently low in soluble NSP and RS (Pluske *et al.*, 1996b). These diets were then compared with a standard commercial diet based on wheat, barley and Australian sweet lupins.

Material and methods

Animals, housing and management

The experiment was conducted at the Medina Research Centre, Medina, Western Australia, using a total of 35 female pigs (Large White × Landrace) initially weighing 18.3 (s.e. 0.40) kg that originated from Wandalup Farms, Mandurah, WA. After transportation, pigs were weighed, tagged, and then randomly allocated to individual pens on the basis of live weight, treatment, and pen position within the animal house. Pigs were kept in individual pens having a floor area of 1.6 m² that had metal sides and fully slatted, plastic-coated floors. Each pen was equipped with a single nipple drinker and food trough. All pigs were offered their diets on an *ad libitum* basis, and weekly food refusals were recorded. The experiment was conducted between April and July 1996. The Animal Ethics Experimentation Committee of Agriculture Western Australia, in accordance with the National Health and Medical Research Council of Australia Guidelines, approved the conduct of this experiment.

Experimental design and diets

The experiment was a completely randomized design with five treatments consisting of seven pigs per treatment. An individual pig was considered the experimental unit. The first diet contained steam-flaked sorghum and a protein supplement based on animal protein sources and 40 g/kg soya-bean meal (diet SAP). Using diet SAP as a base, and substituting for sorghum, three other diets were formulated which contained either (i) a source of soluble NSP in the form of guar gum [Guar NP 3500; Germantown (Australia) Company, Botany, NSW., Australia] (diet SAP + S-NSP), (ii) a source of retrograde (high-amylose) resistant starch (RS) from maize (Novelose™, National Starch and Chemical Company, Bridgewater, NJ, USA) (diet SAP + RS), and (iii) a combination of both S-NSP and RS (diet SAP + S-NSP + RS). The final diet (diet WBL) was based on wheat, barley and Australian sweet lupins (cv. Gungurru), and was typical of a commercial grower diet used in Western Australia (see Table 1 for composition of all diets). Prior to mixing all ingredients, the steam-flaked sorghum was comminuted through a conventional hammer mill containing an 8-mm screen.

The levels of S-NSP and RS chosen were similar to those of soluble NSP plus oligosaccharide, and RS, from the levels of these carbohydrate fractions contained in diet WBL (see Table 2 for concentrations). Therefore, guar gum was added to the diet at a rate of 50 g/kg to approximate the concentration of soluble NSP plus oligosaccharide contained in a wheat-barley-lupin-based diet (based on chemical analysis of NSP and the work of Evans *et al.*, 1993). Novelose™, the source of RS, was added to the diets at a rate of 80 g/kg to approximate the concentration of RS found in diet WBL. In diet SAP + S-NSP + RS, these ingredients were added at inclusion level of 50 g/kg and 70 g/kg, respectively, such that diet SAP + S-NSP + RS approximated diet WBL in its composition of soluble NSP plus oligosaccharide, and RS.

Measurements

Average daily gain and voluntary food intake were recorded for each pig on a weekly basis until pigs reached their target slaughter weight of about 55 kg. When pigs neared this weight, they were sent to a commercial abattoir (Watsonia, Spearwood, WA) and killed by electrical stunning and exsanguination. After 45 to 60 min, the entire gastrointestinal tracts were recovered into plastic bags, put on ice, and then transported to a necropsy room. The large intestine was identified and excised from the small intestine at the ileo-caecal junction. The caecum and colon were then separated and weighed full, the contents emptied, washed and blotted dry, and then each was

Table 1 Composition of diets (g/kg of air-dry diet)

Ingredient	Diet†				WBL
	SAP	SAP + S-NSP	SAP + RS	SAP + S-NSP + RS	
Steam-flaked sorghum	805.95	749.49	708.82	684.39	
Guar gum		50		50	
Resistant starch			80	70	
Wheat					200
Barley					476.96
Lupins					250
Canola oil	10	10	14.55	10	11.7
L-lysine HCl	2.26	1.15	1.05	1.86	1.57
DL-methionine	0.26			0.25	0.51
Olaquinox	0.5	0.5	0.5	0.5	0.5
Choline chloride, 50%	0.4	0.4	0.4	0.4	0.4
Dibasic calcium phosphate		22.08			7.34
Limesand					7.49
Salt	1	1	1	1	1
Vitamin/mineral premix‡	1	1	1	1	1
Blood meal	20	20	20	20	
Fish meal	18.68	48.36	39.79	21.01	30
Meat and bone meal	99.96	36.02	92.89	99.59	11.53
Soya-bean meal	40	60	40	40	
Calculated analysis					
Digestible energy (MJ/kg)	13.9	13.9	14.0	13.7	13.5
Total lysine (g/kg)	9.6	9.0	9.3	9.1	9.3
Methionine + cysteine (g/kg)	5.3	5.0	5.1	4.9	5.8
Threonine (g/kg)	6.2	6.1	6.3	5.9	6.1
Calcium (g/kg)	12.0	12.0	12.0	12.0	11.0
Av. Phosphorus (g/kg)	7.0	8.0	6.0	6.0	6.0
Proximate analysis (g/kg)					
Dry matter	892	897	898	888	903
Crude protein	190	188	192	173	181
Fat	46	50	50	40	39
Ash	61	60	61	61	46
Acid-detergent fibre	43	40	43	39	78
Neutral-detergent fibre	182	154	159	142	196

† See text for details of diets fed.

‡ Provided the following nutrients (per tonne air-dry diet): Vitamins: retinol 1.5 g, cholecalciferol 0.0325 g, α -tocopherol 10 g, phytolmenaquinone 2.2 g, riboflavin 2 g, pyridoxine 0.8 g, cyanocobalamin 10 mg, Ca-pantothenate 7 g, nicotinic acid 10 g; minerals: Co (CoSO₄) 0.1 g, I (KI) 0.3 g, Fe (FeSO₄) 60 g, Mn (MnO) 30 g, Zn (ZnO) 100 g, Cu (CuSO₄) 5 g, Se (selenium selenite) 66.7 mg.

re-weighed. Given that the time from slaughter to processing of the gastrointestinal tract varied from 90 to 240 min, collection of digesta for determination of fermentative indices, such as VFA levels and pH, was not undertaken.

Chemical analysis

Proximate analysis of diets for dry matter, crude protein, ether extract and ash was performed according to Association of Official Analytical Chemists (1988) methods. Analysis of neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) was performed according to Van Soest *et al.* (1991). Methodology for the measurement of resistant starch

in vitro is described in the publication by Pluske *et al.* (1996b). NSP were analysed according to the technique of Theander and Westerlund (1992).

Statistical analyses

Data were subjected to one-way analysis of variance for treatment effects using the statistical package SuperAnova® (Abacus Concepts Inc., Berkeley, CA). Pair-wise comparisons between treatment means were made using Fisher's protected least significant difference (LSD) procedure (Maindonald, 1992). Statistical significance was accepted at $P < 0.05$. Simple linear regression analysis was conducted also using SuperAnova®.

Table 2 Levels of soluble non-starch polysaccharides (S-NSP), insoluble non-starch polysaccharides (I-NSP), total non-starch polysaccharides (T-NSP) and resistant starch (RS) in diets given to pigs (g/kg dry matter)[†]

Diet	NSP component			RS [‡]
	S-NSP	I-NSP	T-NSP	
SAP	8	33	41	101
SAP + S-NSP	58	34	92	94
SAP + RS	8	30	38	124
SAP + S-NSP + RS	55	29	84	117
WBL	53§	122	176	126

[†] Calculated from individual ingredients and then summed.

[‡] Estimated RS *in vitro* according to method described in Pluske *et al.* (1996b).

§ Includes oligosaccharides of lupins from the stachyose, raffinose and verbascose series (after Evans *et al.*, 1993).

Results

Performance data

There was no difference in slaughter weight between any of the treatment groups, although pigs given diets SAP, SAP + RS and WBL took fewer days to reach the target slaughter weight of 55 kg than pigs given all other diets ($P < 0.001$; Table 3). Pigs given diet SAP grew fastest at 923 g/day, but this was not significantly different from pigs given diets SAP + RS (874 g/day) and WBL (834 g/day; $P > 0.05$). Despite pigs on SAP growing 89 g/day faster than those receiving diet WBL, the difference was not statistically significant ($P > 0.05$). Pigs given diets SAP + S-NSP and SAP + S-NSP + RS grew more slowly than pigs given the remaining diets ($P < 0.001$). Pigs on all treatment groups consumed similar amounts of food ($P > 0.05$), however pigs

given diets SAP, SAP + RS and WBL converted food more efficiently than pigs given diets containing S-NSP and S-NSP + RS ($P < 0.001$; Table 3).

Carcass data

Carcass weights were similar ($P > 0.05$) between treatments (Table 4). Pigs given diets SAP, SAP + S-NSP and SAP + RS had, on average, a 40 g/kg higher ($P < 0.01$) dressing proportion than pigs on all other diets. Nevertheless, pigs given diet WBL had less backfat (10.1 mm, $P > 0.05$), attracted a higher price (AUD \$2.56/kg, $P = 0.068$), and had a higher net return per pig (AUD \$96.70, $P > 0.05$), than their counterparts given any of the other diets (Table 4).

A significant negative relationship ($R^2 = 0.775$, $P < 0.05$) existed between the daily intake of soluble NSP + RS and dressing proportion, such that each gram increase caused a 0.25 g/kg decrease in the dressing proportion of pigs (Figure 1). No such relationship existed between the daily intake of soluble NSP ($R^2 = 0.437$, $P > 0.05$), or the daily intake of RS ($R^2 = 0.075$, $P > 0.05$), with dressing proportion. Similarly, the daily intakes of insoluble NSP and total NSP were not related to dressing proportion ($P > 0.05$).

Slaughter data

When expressed as a proportion of pig live weight at slaughter, pigs given diet WBL had heavier empty caeca compared with pigs on all other diets (Table 5). The colon and large intestine of pigs given diets SAP and SAP + RS, whether 'full' (i.e. containing digesta) or 'empty' (minus digesta), were lighter than in pigs on all other diets ($P < 0.001$; Table 5).

Daily intake of NSP and RS

Pigs given diets SAP and SAP + RS consumed the least amount of soluble NSP ($P < 0.001$) and soluble

Table 3 Performance data and time taken to reach slaughter from time of allocation

Diet [†]	LW§ at start (kg)	LW at slaughter (kg)	Time to slaughter (days)	Average daily gain (g)	VFI§ (kg/day)	FCR§
SAP	18.4	58.0	43 ^a	923 ^a	2.26	2.46 ^a
SAP + S-NSP	18.4	57.6	56 ^b	708 ^b	2.07	2.96 ^b
SAP + RS	18.3	55.9	43 ^a	874 ^a	2.20	2.53 ^a
SAP + S-NSP + RS	18.3	55.9	59 ^b	646 ^b	2.03	3.16 ^b
WBL	18.3	56.9	47 ^a	834 ^a	2.22	2.69 ^a
s.e.d. [‡]	0.58	1.94	3.7	74.1	0.136	0.164
Significance			***	***		***

^{a,b} Within columns, means not having the same superscript differ ($P < 0.05$).

[†] See text for details of feeding treatments.

[‡] Standard error of difference between treatment means.

§ LW: live weight; VFI: voluntary food intake; FCR: food conversion ratio (g food : g live-weight gain).

Table 4 Carcass data for pigs at slaughter

Diet†	Hot weight (kg)	Dressing (g/kg)‡	P ₂ , mm	\$/kg (AUD)	Value per pig \$ (AUD)
SAP	40.2	694 ^a	12.1	2.06	81.40
SAP + S-NSP	39.7	690 ^{ab}	11.7	2.34	92.40
SAP + RS	39.2	701 ^a	13.7	1.77	69.20
SAP + S-NSP + RS	37.4	669 ^{bc}	11.3	2.37	88.60
WBL	37.8	663 ^c	10.1	2.56	96.70
s.e.d.‡	1.86	15.2	1.69	0.371	13.74
Significance		**			

^{a,b,c} Within columns, means not having the same superscript differ ($P < 0.05$).

† See text for details of feeding treatments.

‡ Standard error of difference between treatment means.

§ Dressing proportion: hot carcass weight after slaughter/live weight measured 24 h prior to slaughter.

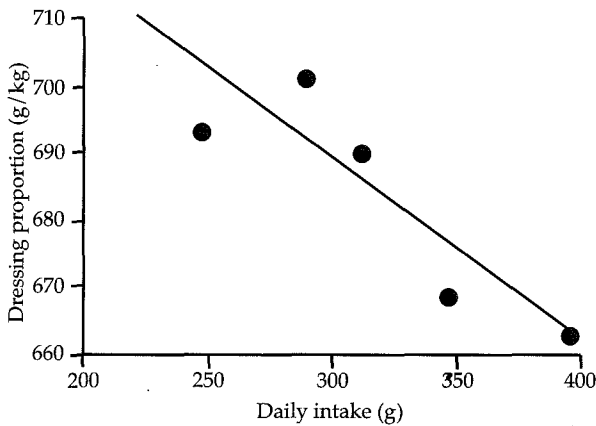


Figure 1 Relationship between the daily intake (g) of soluble non-starch polysaccharide plus resistant starch and the dressing proportion of pigs killed at approximately 55 kg live weight ($y = 764 + 0.25x$, $R^2 = 0.78$, $P = 0.048$).

NSP plus RS ($P < 0.001$; Table 6). Pigs given diet WBL consumed similar quantities of soluble NSP to pigs on diets SAP + S-NSP and SAP + S-NSP + RS, but consumed the highest amount of soluble NSP plus RS ($P < 0.001$; Table 6).

The relationship between the daily intakes of soluble NSP and soluble NSP plus RS to the empty weight of the large intestine (caecum + colon) is depicted in Figure 2. Increased intakes of soluble NSP and soluble NSP plus RS were positively correlated to an increased (empty) weight of the large intestine. There was no relationship between the daily intake of RS ($R^2 = 0.194$, $P > 0.05$), the daily intake of insoluble NSP ($R^2 = 0.004$, $P > 0.05$), or the daily intake of total NSP ($R^2 = 0.711$, $P = 0.072$), to the weight of the large intestine.

Discussion

In this experiment, we hypothesized that increased fermentation of fermentable carbohydrate in the

Table 5 Weights of the caecum, colon, and large intestine (i.e. caecum + colon), in pigs at slaughter

Diet†	Full caecum‡	Empty caecum‡	Full colon‡	Empty colon‡	Full large intestine‡	Empty large intestine‡
SAP	7.5	1.9 ^a	40.9 ^a	16.0 ^a	48.4 ^a	17.9 ^a
SAP + S-NSP	8.0	2.1 ^a	52.2 ^b	19.3 ^b	60.6 ^b	21.4 ^b
SAP + RS	5.7	1.9 ^a	39.6 ^a	15.4 ^a	44.1 ^a	17.3 ^a
SAP + S-NSP + RS	8.3	2.1 ^a	53.1 ^b	20.8 ^b	61.1 ^b	23.1 ^{bc}
WBL	11.3	2.9 ^b	55.0 ^b	20.6 ^b	66.3 ^b	23.5 ^c
s.e.d.‡	2.55	0.32	4.82	1.11	5.64	1.22
Significance		***	***	***	***	***

^{a,b,c} Within columns, means not having the same superscript differ ($P < 0.05$).

† See text for details of feeding treatments.

‡ Standard error of difference between treatment means.

§ All values expressed as proportion of liveweight at slaughter (g/kg).

Table 6 Daily intakes of soluble NSP, RS, and soluble NSP plus RS, of pigs given different diets

Diet†	Daily intake (g) of:		
	S-NSP	RS‡	S-NSP + RS
SAP	19.2 ^a	228.1 ^{ac}	247.3 ^a
SAP + S-NSP	120.5 ^b	194.0 ^a	314.5 ^{bc}
SAP + RS	18.0 ^a	273.0 ^b	291.1 ^{ab}
SAP + S-NSP + RS	112.1 ^b	236.3 ^c	348.4 ^c
WBL	117.8 ^b	280.4 ^b	398.2 ^d
s.e.d.§	6.25	15.36	21.06
Significance	***	***	***

a,b,c,d Within columns, means not having the same superscript differ ($P < 0.05$).

† See text for details of feeding treatments.

‡ Estimated RS *in vitro* according to method described in Pluske *et al.* (1996b).

§ Standard error of difference between treatment means.

large intestine of pigs would reduce voluntary food intake. Overall, the results of this study do not support this hypothesis and show that increased fermentation in the large intestine had no negative effect on food consumption. Nevertheless, and despite this lack of statistical significance ($P > 0.05$)

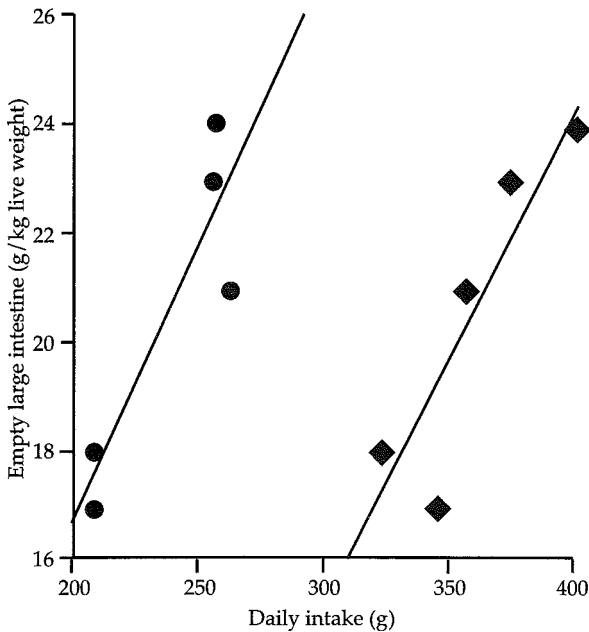


Figure 2 Relationship between the daily intakes of soluble non-starch polysaccharide (NSP) (●) and soluble NSP plus resistant starch (◆) and the empty weight of the large intestine (caecum + colon), when expressed as g/kg of pig live weight at slaughter (for soluble NSP intake, $y = 16.6 + 0.05x$, $R^2 = 0.84$, $P = 0.028$; for soluble NSP + RS intake, $y = 5.4 + 0.05x$, $R^2 = 0.80$, $P = 0.039$).

between treatment groups, pigs given diets SAP + S-NSP and SAP + S-NSP + RS ate between proportionally 0.06 and 0.1 less food than pigs given all other diets ($P > 0.05$), suggesting that the addition of a soluble NSP, either alone or in combination with a source of resistant starch, had a depressive effect on food consumption. Similar results have been observed in growing rats (Davies *et al.*, 1991). Furthermore, these data suggest that the NSP used as a 'model' source of soluble NSP, i.e. guar gum, behaved differently *in vivo* from the 'native' soluble NSP (and perhaps oligosaccharide) found in diet WBL. For example, pigs given diets SAP + S-NSP and SAP + S-NSP + RS consumed, on average, proportionally 0.92 of the food ($P > 0.05$), grew proportionately at 0.81 of the rate ($P < 0.001$) and converted food at proportionately 0.88 of the level ($P < 0.001$), of pigs given diet WBL. This was despite the daily intake of soluble NSP in pigs given diet SAP + S-NSP being proportionally 0.79 ($P < 0.001$) that of pigs given WBL and the daily intake of soluble NSP and RS in pigs given diet SAP + S-NSP + RS being proportionally 0.80 of the value for WBL ($P < 0.001$).

Guar gum is composed predominately of galactose and mannose as a galactomannan (Brunsgaard *et al.*, 1995), consisting of a linear chain of (1 → 4)- β -mannopyranosyl units with α -D-galactopyranosyl units attached by (1 → 6) linkages (M. Choct, personal communication). Consequently, guar gum most likely behaves differently *in vivo* in the luminal environment from the soluble NSP contained in diet WBL. For example, the major soluble sugars found in the hulls of Australian sweet lupins (cv. Gungurru) are xylose, uronic acids and mannose, while those found in the cotyledons are galactose, arabinose and uronic acid residues (Evans *et al.*, 1993). Moreover, the predominant soluble NSP in wheat and barley are arabinoxylan and β -glucan, respectively (Annison and Choct, 1994). In this regard, differences between foodstuffs in NSP composition (and associated molecular structure) are likely to be important determinants of their physiological effects (Annison *et al.*, 1996). These may include the extent of glucose absorption across the small intestinal mucosa (Rainbird *et al.*, 1984), and the ileal digestibility of macronutrients such as starch (LeClere *et al.*, 1993), protein (Graham *et al.*, 1986), fat (Bakker *et al.*, 1995) and amino acids (Van Barneveld *et al.*, 1995a). Most of these effects relate to the viscous-forming (viscosity) properties of NSP in the small intestine (Annison *et al.*, 1996). In addition, Davies *et al.* (1991) hypothesized that guar gum elevates energy expenditure commensurate with an inherent putative thermogenic effect, a factor that may also cause differences in performance between diets.

Diet WBL had a higher concentration of insoluble NSP (I-NSP) than diets SAP + S-NSP and SAP + S-NSP + RS (Table 2). No attempt was made to balance the I-NSP concentration between diets, mainly because of difficulties associated with formulating diets to the same nutrient specifications and ingredient profile. Moreover, there is conflicting evidence in the literature as to the effects of I-NSP, such as cellulose, on food intake. In this respect, it was decided to balance the S-NSP concentration of diets as closely as possible such that any differences in food intake could be attributed to the S-NSP source alone. Nevertheless, pigs given diet WBL consumed, on average, 272 g/day of I-NSP compared with 58 to 73 g/day for pigs given all other diets (data not shown). Interestingly, pigs given diet WBL also consumed more S-NSP + RS than pigs given diets SAP + S-NSP and SAP + S-NSP + RS (Table 6), yet performed better. The four- to five-fold increase in intake of I-NSP by pigs given WBL most likely expedited the movement of digesta through the gastrointestinal tract, since foodstuffs containing higher concentrations of I-NSP have a shorter mouth-to-anus transit time than diets containing soluble polysaccharides (Potkins *et al.*, 1991). This mechanism may have reduced the residence time of soluble NSP in the small intestine, and hence reduced the anti-nutritive properties of S-NSP on digestion and absorption. Alternatively, production of VFA from microbial fermentation in the large intestine may have provided additional energy for maintenance and growth. These mechanisms may serve as explanations as to why pigs given diet WBL were able to consume more I-NSP and S-NSP + RS, yet grow better than pigs given diets SAP + S-NSP and SAP + S-NSP + RS.

Possible interactions between soluble NSP and RS should also be considered. Three major types of RS are likely to appear in diets for pigs: RS 1, which refers to physically inaccessible starch locked within the matrix of plant cells, e.g. as in partly milled grains and seeds and in legumes; RS 2, which is native (ungelatinized) granular starch found in foods containing uncooked starch (e.g. in bananas); and RS 3, which is an indigestible starch fraction which forms after the two major polymeric forms of starch, amylose and amylopectin, recrystallize when cooled after cooking in which form they are highly resistant to enzymatic digestion in the small intestine (Englyst and Kingman, 1990; Muir *et al.*, 1993). The biological significance of RS in pig production, particularly with respect to their ability to form viscous solutions and (potentially) influence nutrient digestibility, is largely unknown. Brown (1993) reported that high-amylose corn starches, such as that used in this study, may resemble soluble NSP with respect to forming viscous solutions given their physicochemical

properties, although this seemingly occurs only when gelatinized fully. Given that the source of RS used in this study was retrograded RS, and there was uncertainty associated with the degree of gelatinization that occurred during the steam flaking of sorghum, full gelatinization of starch may not have occurred. Nevertheless, there is evidence in humans that, along with increases in faecal weight, nitrogen excretion is increased with feeding of RS (Scheppach *et al.*, 1988; Cummings *et al.*, 1996). In addition, Phillips *et al.* (1995) and Cummings *et al.* (1996) reported a significant increase in the amount of NSP in the faeces given a diet containing RS, suggesting an interaction between the two carbohydrate sources.

Pigs also appear capable of digesting a considerable portion of the RS prior to its entry into the caecum, further dismissing the notion that RS has marked anti-nutritional properties in the small intestine. Govers *et al.* (1997), for example, offered diets containing RS (a mixture of RS 1 and RS 2) to growing pigs having an ileal cannula and reported that proportionally 0.375 of the RS disappeared prior to the ileum. This shows that the pig is capable of digesting a large amount of RS in the small intestine. In contrast, Englyst *et al.* (1996) gave breakfast supplements based on different forms of RS (e.g. high-amylose maize starch, banana flour) to human ileostomy subjects and reported mean starch recoveries in the ileostomy effluent of 1.004 (range 0.91 to 1.06). This suggests that there are considerable between-species differences in the capacity to digest RS in the small intestine, and that the pig is more efficient at digesting RS than humans. A likely reason for this is the larger small intestine in the pig that allows more time for digestion of starch with pancreatic α -amylase.

In this experiment, the amount of guar gum added reflected the contribution of soluble NSP plus oligosaccharides from diet WBL. This was done on the basis that oligosaccharides, such as those of the raffinose, stachyose and verbascose series found in lupins, should be considered as part of dietary fibre because they act similarly to NSP, i.e. they are not hydrolysed by endogenous α -galactosidase in the small intestine but are cleaved by microbially derived glycanases in the large intestine (Annison, 1993). Nevertheless, and using young pigs ranging from 11 to 24 kg, Gdala *et al.* (1997) reported ileal digestibilities of oligosaccharides in lupins ranging from 0.407 to 0.929, suggesting considerable hydrolysis of lupins seed oligosaccharides prior to entry into the large intestine. Using growing pigs, Van Barneveld *et al.* (1996) reported a 0.5 MJ digestible energy (DE) increase in the value of Australian sweet lupins following the ethanol

extraction of oligosaccharides from dehulled lupins, suggesting that levels are of a magnitude to influence energy availability to the pig. Furthermore, and again using ethanol-extracted dehulled lupins, Van Barneveld *et al.* (1997) reported significant enhancements in apparent ileal amino acid digestibility when oligosaccharides were removed. Collectively, these data suggest that oligosaccharides do have anti-nutritive properties and alter nutrient digestion in the small intestine of the pig, although the precise mechanism(s) of how this occurs are unknown. Given their low molecular weight, oligosaccharides are likely to have much smaller effects on viscosity than would polysaccharides such as guar gum. One suggestion is that the presence of α -galactosides causes an increase in osmolarity in the small intestine that, in turn, may interfere with nutrient absorption (Wiggins, 1984).

The apparent (faecal) digestibility and retention of dry matter, the degree of NSP fermentation, and the subsequent amount of energy available to the pig for productive purposes, depends largely on the source of dietary fibre (Stanogias and Pearce, 1985; Noblet and Henry, 1991). When formulating least-cost diets for pigs, one assumes that when a range of ingredients are combined in a compound food, they will behave in an additive fashion. However, some evidence suggests that when high levels of ingredients containing soluble NSP are included in diets, this may not be the case (Hansen *et al.*, 1991; Bakker *et al.*, 1995). For example, Hansen *et al.* (1991) used digestibility coefficients of protein, energy, starch and dietary fibre in individual foodstuffs to predict the digestibility of food mixtures. For all significant differences between calculated and measured values, the measured digestibility coefficient was lower than the calculated value, suggesting that combinations of ingredients with high levels of soluble NSP may result in a further reduction in nutrient digestibility. Furthermore, and when different sources of fibre are combined in mixed diets, it appears that the properties of the resulting combination of fibre does not necessarily reflect those of the individual constituents (Laplace *et al.*, 1989), an effect proposed by R. J. Van Barneveld (personal communication) to reflect changed digesta viscosity rather than any changes in microbial activity.

It was not possible to measure the rate and extent of fermentation in this experiment because processing of the gastrointestinal tracts often occurred up to 4 h following slaughter. We used the size of the large intestine (caecum + colon), expressed as a proportion of pig live weight prior to slaughter, as an indicator of fermentation in the hind-gut. Support for the use of this measurement is found in Figure 2, where the

daily intake of soluble NSP and soluble NSP plus RS was linearly correlated to the weight of the large intestine. VFA produced in the large intestine, and predominately butyrate, can be trophic to the colonic mucosa lining the large intestine. Mucosal hypertrophy will occur if the rate of epithelial proliferation relative to that of cell loss is increased. Diets rich in complex carbohydrates (NSP and resistant starch) have been observed to cause large-intestinal hypertrophy in rats (e.g., Wyatt *et al.*, 1988; Goodlad and Mathers, 1990; Larsen *et al.*, 1994) and pigs (e.g., Pond and Varel, 1989; Jin *et al.*, 1994; Pluske *et al.*, 1996a; Topping *et al.*, 1997). In the present study we also observed increased colonic and large intestinal (caecum + colon) growth in response to an increased level of fermentable substrate entering the large bowel, however we did not distinguish between growth of the mucosa and that of the underlying muscle layers. Several groups have suggested (Brown, 1979; Wyatt *et al.*, 1988) that when viscous fibres, such as guar gum, are given, the increased 'work' needed to propel the digesta along the large intestine may lead to muscular hypertrophy, thus increasing their weight. This effect can seemingly occur independent of the VFA concentration in the large intestine (Wyatt *et al.*, 1988). In addition, Wyatt *et al.* (1988) suggested that viscous fibres might increase intestinal mucosal weight by causing hypertrophy of the mucosal cells through the physical suppression of intestinal water absorption due to the sequestration of water by the viscous polysaccharides.

We observed a negative correlation between the daily intake of soluble NSP plus RS and dressing proportion (Figure 1). These data are in accordance with those of King (1990) who estimated that dressing proportion of growing/finishing pigs decreased by 8 to 14 g/kg for each 100 g/kg increment in dietary lupin-seed meal. The existence of such a relationship has commercial significance because it shows that pigs given a typical 'commercial' diet have a lower dressing proportion than those given a diet that is extensively digested and absorbed in the small intestine (e.g. a diet based on sorghum/animal protein/soya-bean meal).

Despite having a higher dressing proportion, pigs given diets SAP and SAP + RS were fatter and attracted less money than pigs given diet WBL (Table 4). Pigs given diet WBL attracted the highest price in the grading schedule used by the processor, suggesting that diet formulation on a DE basis was accurate. In contrast, formulating a sorghum/animal protein/soya-bean meal diet (diet SAP) based on DE underestimated the amount of energy that was available to the pig, and consequently the extra energy was deposited as fat. Most of the variation in

the digestibility of energy is associated with the presence and the type of fibre contained in the diet (Noblet and Henry, 1991), with highly-digestible fibre sources being associated with higher digestibility coefficients (Chabeauti and Noblet, 1990). Consequently, and relative to net energy (NE), diets containing fibre are overestimated when expressed on a DE basis.

In conclusion, the overall results of this study do not support the hypothesis that increased fermentation in the large intestine causes reduced voluntary food intake. However, we have demonstrated that increased dietary intake of soluble NSP and RS is associated with increased large intestinal weights and a decreased dressing proportion, findings that are both of significant commercial importance. Furthermore, we have shown that 'model' sources of soluble NSP and RS are not necessarily representative, neither do they behave the same *in vivo*, when compared with native sources of these carbohydrate fractions.

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