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Original research article

Pattern of non-starch polysaccharide digestion along the gut of the pig: Contribution to available energy

David J. Cadogan [a,*], Mingan Choct [b]

[a] Feedworks Pty Ltd, Lancefield 3435, Australia
[b] School of Environmental and Rural Science, University of New England, Armidale 2351, Australia

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ABSTRACT

We investigated the pattern of non-starch polysaccharide (NSP) digestion along the gut of pigs fed two different wheats, which were offered with or without xylanase supplementation. The two wheats used were pre-characterised before the experiment on the basis of low and normal feed intake of young pigs. Wheat type significantly influenced feed intake and growth rate in the first 7 days, however, by day 14 the only significant effect of wheat type was on growth rate. Xylanase supplementation increased the growth performance of pigs fed the poor quality wheat to a level similar to those fed the normal wheat. It also increased the daily gain of pigs fed the normal wheat. Wheat type had no significant effect on the digestibility of dry matter (DM), energy, free sugars or the different fractions of NSP in the duodenum, ileum or in the faeces. The duodenal gross energy digestibility values for the low and high performance diets were −27.4 and −47.5%, respectively, and xylanase supplementation significantly increased the digestibility of energy back to positive levels. Dry matter digestibility values followed a similar pattern. In the duodenum, xylanase increased ($P < 0.05$) the digestibility values of both soluble and insoluble NSP, whereas in the ileum, xylanase had a significant effect only on the digestibility of the soluble NSP fraction. Xylanase did not affect free sugar digestibility. The reduction in soluble NSP level coincided with a marked reduction in the amount of fucose, a prominent component of mucosal polysaccharides. This suggests that soluble NSP substantially increase endogenous losses. The absence of differences in the digestibility of the measured NSP between the two wheat samples suggests that the structures of the NSP, rather than just their amount and solubility, are important for the anti-nutritional properties of NSP in pig diets.

1. Introduction

Wheat is one of the most variable in composition among cereal grains (Choct et al., 1999a). These differences are exacerbated by the environmental conditions under which the grains are grown (Longstaff and MacNab, 1986). A review by van Barneveld (1997) using past data for more than 70 cultivars of wheat found differences of up to 3.7 MJ/kg dry matter (DM) in digestible energy (DE) content. The highest DE reported in Australia was at 17.0 MJ/kg DM (Kopinski, 1997), and the lowest was 13.8 MJ/kg DM (King, 1976). Batterham et al. (1980) found that the hemicellulose (mainly arabinoxylan) component of wheat correlated closely with the DE value in wheat. The relationship between DE and more specific components of wheat NSP has been variable (van Barneveld, 1997), although Zijlstra et al., 1988 found a strong correlation between xylose level and DE content in wheat.

The majority of research on wheat in pigs has evaluated the variation in energy content (Kopinski, 1997; van Barneveld, 1997) and devised methods to improve the digestibility of cereal grains (Wiseman, 1997). However, faecal DM digestibility and DE content of cereals are poorly related to pig growth performance compared to ileal DM digestibility measurements (van Barneveld et al., 2001; Cadogan et al., 2003). It appears that growth, feed intake and health of pigs are affected by wheat type but not by the energy and protein levels of wheat (Cadogan et al., 1999; Choct et al., 1999b;

* Corresponding author.
E-mail address: david.cadogan@feedworks.com.au (D.J. Cadogan).
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Simmins et al., 2001; Caine et al., 1997). The majority of variation in pig growth performance produced by different wheats has been attributed to the content of non-starch carbohydrates (NSC), which includes NSP and free sugars, such as mono- and oligosaccharides up to 10 sugar units, present in feed ingredients (Cadogan, 1999). This observation is strongly supported by the significantly enhanced growth performance of pigs fed diets based on low quality wheats supplemented with xylanase (Choct et al., 1999b; Partridge et al., 1999; Simmins et al., 2001).

There have been many studies investigating the effect of NSP on human health and animal performance but their detailed modes of action in pig diets are largely speculative (Choct and Cadogan, 2001; Partridge, 2001). Numerous studies (Bach Knudsen and Hansen, 1991; Yin et al., 2000; van Barneveld et al., 2001; Bartelt et al., 2002; Pederson et al., 2012) have reported the digestion pattern of wheat NSP fractions at the ileal level. There is, however, limited information on the digestion of NSP from different wheat types and of the modifying effects of exogenous xylanase on wheat fibre in the small intestine of the pig. The hypothesis is that NSP fractions of pre-characterised high and normal feed intake wheats behave differently in the various sections of the gastrointestinal tract (GI tract) of the pig. It is expected that xylanase supplementation will eliminate the differences between the two wheats.

2. Materials and methods

2.1. Pig husbandry and bioassay

The animal protocol was approved by the Ethics Committee of Rivalea Australia Pty Ltd (formerly QAF Meat Industries), and followed principles established by the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council: Canberra, 1997). Sixty male pigs used in the experiments were from Large White × Landrace cross dams crossed with a synthetic terminal sire (Primegro Genetics, Corowa, NSW Australia). The pigs were weaned at 25 days of age and then put into individual cages with wire floors and sides and offered a commercial nursery diet for three days until the experiment commenced. The temperature was kept at a constant 28 °C. Water and feed were available ad libitum. Pigs were selected with a live weight range of 6.5 to 7.5 kg. After three days, pigs were re-weighed and randomly allocated to treatment groups of equal mean weight (12 pigs per treatment). Each pen had an area of 0.5 × 0.9 × 0.5 m and was equipped with a conventional dry feeder and a single drinking nipple. The drinking water was medicated with Apralan (Elanco Animal Health, Greenfield, IN, USA) to reduce potential of *Escherichia. coli* scours on a daily basis throughout each experiment.

Weight gain and feed intake of each individual pig were taken on a weekly basis (0 to 7, 7 to 14, and 14 to 21 days). From these measurements daily feed intake, feed conversion ratio (FCR) and rate of gain values were calculated on an individual pig basis.

2.2. Wheat pre-charactisation and experimental diets

Ten newly harvested wheats were sourced from the eastern and central Riverina districts of New South Wales, as well as the north eastern, central north and Wimmera regions of Victoria, Australia. From this ten, two wheats were selected, one low quality and one normal quality, based on feed intake of young pigs. Briefly, the low quality one was a Currawong cultivar (Wheat 1), and produced 23% (90 g/d) and 26% (83 g/d) lower feed intake and daily gain, respectively, compared with a Whistler cultivar (Wheat 2), which represented the average performance expected of the genotype of pigs used in the study. The total NSP contents of both Wheat 1 and Wheat 2 were similar at 9.49 and 9.75%, respectively, however wheat 1 contained a higher level of soluble NSP (1.67% versus 0.99%) but a lower level of insoluble NSP (11.39% versus 9.75%) compared with wheat 2. The protein and starch content of wheat 1 was 12.56 and 55.0%, respectively, with crude protein and starch in wheat 2 was measured at 11.81 and 58.9%.

Both wheats were hammer-milled through a 3.2 mm screen. A basal diet containing 70% wheat was formulated to have a DE of 14.5 MJ/kg and an available lysine content of 0.90 g/MJ DE for both wheats (Table 1). The dietary essential amino acid contents were formulated to 115% of requirements, which had been predetermined for the pig genotype within Rivalea Australia Pty Ltd. The 15% excess was based on the differences in the protein contents of the wheats in order to maintain an adequate level of protein in all diets. A commercially produced xylanase from *Thermomyces* spp. (Ronozyme WX; DSM Nutritional Products, Wagga Wagga, NSW, Australia), was added to the experimental diets at 0 or 300 mg/kg. An alkane digestibility marker, hexatriacontane ($C_{36}H_{74}$), was added to the diets at a level of 150 mg/kg.

2.3. Measurements

After 21 days, 8 randomly selected pigs were slaughtered, and digesta samples were obtained from the first 80 cm of the small intestine (duodenum and upper jejunum), from the terminal ileum and from the rectum. These were frozen immediately; freeze-dried after 4 days and stored for digesta (alkene) marker and nutrient analyses. Gross energy (GE) was analysed by complete combustion in a DDS CP500 isoperibol calorimeter (Digital Datasystems, Johannesburg). Free sugars, soluble and insoluble NSP were measured using the alditol acetate method of Englyst and Hudson, 1987. Dry matter (DM) was determined gravimetrically following drying at 105°C for 24 h. The alkane marker, hexatriacontane ($C_{36}H_{74}$), was determined as follows: from (100 to 500 mg) freeze-dried samples, an appropriate amount (50 to 200 mg) of internal standard ($C_{34}H_{70}$ in dodecane) was added. The samples were then subjected to 1.5 M ethanolic KOH in a heating-block at 90°C for 1 h with stirring. After cooling, the alkanes were extracted in n-hexane several times, filtered, purified and

Table 1
Ingredients and analyzed composition of the basal diet, as-fed basis.

Ingredient, g/kg	Amount	Analysis composition, g/kg	Amount
Wheat (11.0% CP)	700.0	DE, MJ/kg	14.5
Meatmeal (55% CP)	44.0	NE, MJ/kg	10.4
Fishmeal (67% CP)	100.0	Available lysine, g/(MJ · kg)	0.9
Bloodmeal	23.0	Crude protein	22.0
Skim milk powder	50.0	Fat	5.4
Whey powder	50.0	Ash	5.3
Water	10.0	Lysine	14.3
Tallow	12.0	Methionine	4.6
Salt	2.0	Methionine + Cysteine	7.9
Lysine HCl	1.8	Threonine	9.2
Threonine	1.0	Isoleucine	8.2
Tryptophan	0.3	Tryptophan	2.6
Endox[1]	0.2		
Premix[2]	2.7		
Zinc Oxide	3.0		

[1] Anti-oxidant.
[2] Premix provided the following levels of vitamins, trace minerals and medication per tonne of mixed feed; vitamin A 10 MIU, vitamin D_3 1.5 MIU, vitamin E 40 g, niacin 10 g, Ca-D-panthothenate 5 g, riboflavin 2.5 g, pyridoxine 2.5 g, cyanocobalamin 20 mg, biotin 50 mg, selenium 0.3 g, copper 20 g, iron 100 g, manganese 50 g, zinc 60 g, iodine 0.5 g, betaine 100 g, endox 100 g, anti-microbial (Lincospectin) 100 g.

quantified by gas chromatography. Dry matter and energy digestibility were calculated using the alkane ($C_{36}H_{74}$) marker in both the diets and gut contents. The two pre-characterised wheats were analysed for various fractions of NSP.

2.4. Digestibility calculation

The digestibility coefficient (DC) of nutrients or energy was calculated using the following equation:

$$DC = 1 - [(\text{Faecal nutrient \%}/\text{Faecal marker \%})/(\text{Diet nutrient \%}/\text{Diet marker \%})].$$

2.5. Statistical analyses

Multifactorial analyses of variance were carried out to determine statistical significance for the performance and digestibility data generated from each experiment. The Fisher's Least Significant Difference (LSD) procedure was carried out to provide multiple comparisons to ascertain significant differences between treatment means. The software package used was Statistica v. 4.5, supplied by Tulsa, OK, USA.

3. Results

3.1. Performance

At day 7, wheat type significantly affected ($P < 0.05$) feed intake and growth rate, but not FCR. Xylanase supplementation did not affect feed intake, weight gain or FCR. At day 14, wheat type did not affect feed intake, but significantly influenced ($P < 0.05$) growth rate, and tended to ($P < 0.08$) affect FCR. There was no wheat type × xylanase interaction either at day 7 or at day 14 (Table 2).

3.2. Non-starch polysaccharide digestibility along the gut

Duodenum: wheat type had no significant effect on the digestibility of energy, free sugars or the different NSP fractions in the duodenum (Table 3). Xylanase supplementation improved ($P < 0.008$) the duodenal digestibility of soluble NSP ($P = 0.008$), insoluble NSP ($P = 0.024$) and total NSP ($P = 0.012$). There was a tendency for xylanase to increase duodenal digestibility for energy ($P = 0.071$) and DM ($P < 0.082$). Both wheat-based diets, without added xylanase, had negative digestibility values for energy and soluble NSP in the duodenum. The digestibility values for insoluble and total NSP of Wheat 2 were also negative in the absence of the enzyme.

All treatments showed that there was a negative digestibility value for free sugars in the duodenum. There was a trend ($P = 0.069$) for an interaction between wheat type and xylanase supplementation on free sugar digestibility. The enzyme improved the digestibility of the free sugars of Wheat 1, however, it had a negative effect on the free sugar digestibility of Wheat 2.

Ileum: the ileal digestibility results showed that wheat type had no significant impact on energy, free sugars or NSP digestion (Table 3). Xylanase supplementation increased the digestibility of DM ($P < 0.036$), energy ($P = 0.045$) and soluble NSP ($P < 0.001$). An interaction between wheat type and enzyme supplementation for soluble NSP digestibility tended to exist ($P = 0.115$) where the enzyme increased the digestibility of soluble NSP in Wheat 2 but not in Wheat 1. Xylanase had no significant effect on the digestibility of free sugars or insoluble NSP at the distal ileum.

Total tract: there was no significant effect of wheat or xylanase supplementation on the faecal digestibility of energy, free sugars and fractions of NSP. Xylanase supplementation, however, numerically reduced the faecal digestibility of insoluble NSP by 21.2 and 17.7%, respectively, for Wheat 1 and Wheat 2 ($P = 0.093$). Although the free sugar digestibility was above 99%, there was a strong trend for an interaction between enzyme addition and wheat type on free sugar digestion ($P = 0.066$). The enzyme improved free sugar digestibility in Wheat 1 but reduced the digestibility for Wheat 2.

3.3. Fucose content along the GI tract

Mucin polysaccharides are rich in fucose (Lien et al., 1997). Fucose was measured as an indicator of endogenous losses via mucus secretion in this experiment. There was no effect of wheat

Table 2
Effects of wheat type and xylanase supplementation on the growth performance of male pigs from d 0 to 7 and d 0 to 14, commencing at 7.8 kg live weight.

Item	Enzyme, 300 g/t	Live weight, kg	Daily gain, g	Feed intake, g	FCR, g/g
d 0 to 7					
Wheat 1	−	9.51	240^{b}	244^{b}	1.11
Wheat 1	+	9.81	272^{ab}	253^{b}	0.96
Wheat 2	−	9.77	277^{ab}	265^{ab}	1.01
Wheat 2	+	10.21	332^{a}	296^{a}	0.91
SEM		0.130	12.67	8.93	0.045
Two way analysis					
Wheat (W)		0.029	0.029	0.050	0.164
Enzyme (E)		0.261	0.261	0.119	0.903
W × E		0.663	0.663	0.865	0.391
d 0 to 14					
Wheat 1	−	12.12	306^{b}	346	1.13^{a}
Wheat 1	+	12.52	330^{b}	343	1.04^{ab}
Wheat 2	−	12.46	331^{b}	353	1.07^{ab}
Wheat 2	+	13.13	375^{a}	385	1.02^{b}
SEM		0.169	9.27	9.41	0.019
Two way analysis					
Wheat (W)		0.013	0.013	0.237	0.081
Enzyme (E)		0.119	0.119	0.992	0.050
W × E		0.794	0.794	0.795	0.991

SEM = standard error of means.
[a,b]Treatment means followed by the same superscript letter are not significantly different ($P < 0.05$).

Table 3
The digestibility (%) of energy, free sugars and non-starch polysaccharide (NSP) of high and low performance wheat based diets, with and without xylanase supplementation.

Item	Enzyme	DM	GE	Free sugar	Soluble NSP	Insoluble NSP
Duodenum						
Wheat 1	–	−19.4	−27.4	−58.3	−8.8^{bc}	7.3^{ab}
Wheat 1	+	5.1	16.4	−10.6	24.7^{ab}	17.4^{a}
Wheat 2	–	−37.0	−47.5	−10.0	−33.0^{c}	−18.7^{b}
Wheat 2	+	7.7	4.5	−24.9	35.7^{a}	22.3^{a}
P-value (ANOVA)	Wheat (W)	NS	NS	NS	NS	NS
	Enzyme (E)	0.082	0.071	NS	0.008	0.024
	W × E	NS	NS	0.069	NS	0.162
Ileum						
Wheat 1	–	64.6^{ab}	66.2^{b}	72.9	6.9^{b}	22.3
Wheat 1	+	73.7^{a}	73.6^{a}	69.4	50.9^{a}	19.7
Wheat 2	–	61.9^{b}	66.7^{b}	79.7	−9.0^{b}	10.9
Wheat 2	+	70.0^{ab}	70.4^{ab}	74.1	59.3^{a}	13.0
P-value (ANOVA)	Wheat (W)	NS	NS	NS	NS	NS
	Enzyme (E)	0.036	0.045	NS	< 0.001	NS
	W × E	NS	NS	NS	NS	NS
Faeces						
Wheat 1	–	84.4	83.2	99.2	87.8	37.2
Wheat 1	+	85.0	83.9	99.4	88.3	29.3
Wheat 2	–	84.5	83.4	99.6	88.3	37.8
Wheat 2	+	84.6	83.6	99.3	89.0	31.1
P-value (ANOVA)	Wheat (W)	NS	NS	NS	NS	NS
	Enzyme (E)	NS	NS	NS	NS	0.093
	W × E	NS	NS	0.066	NS	NS

DM = dry matter; GE = gross energy; NS = not significant.
[a,b,c]Means values on the same column not sharing a superscript are significantly different ($P < 0.05$).

type on fucose level throughout the gut. The fucose content was very high in the duodenum without xylanase supplementation, but low in the ileum and very low in the faeces. Xylanase supplementation markedly ($P < 0.01$) decreased fucose level in the duodenum for both wheats and in the ileum for Wheat 2. There was no difference in fucose level in the faeces regardless of wheat type or enzyme supplementation (Fig. 1).

4. Discussion

The two wheats used in this study produced significantly different daily gains for the 14-day trial period and different feed intakes for the first seven days with pigs fed Wheat 1 being markedly lighter and eating significantly less than those fed Wheat 2.

The influence of wheat type on weaner growth rate is well known (Cadogan et al., 2003). In the current study, the effect of wheat type on growth performance was significant at day 7 of the experiment and then started to diminish over time, although there remained a strong trend for wheat type to influence growth rate after 21 days (day 7 of the experimental period). It is possible that older pigs deal with the anti-nutritive effect of NSP better than younger ones due to their better developed guts, and perhaps due to a more stable gut microflora in older pigs. Xylanase supplementation significantly improved FCR at day 14 of the experiment through a reduction in feed intake and an increase in weight gain, although such an effect on FCR was not apparent up until day 7 of the experiment. Interestingly, xylanase supplementation increased the daily gain of pigs fed Wheat 2 further without having a significant effect on feed intake, but only had minimal influence on weight gain of pigs fed Wheat 1. This was unexpected because poorer quality wheat samples usually respond better to xylanase

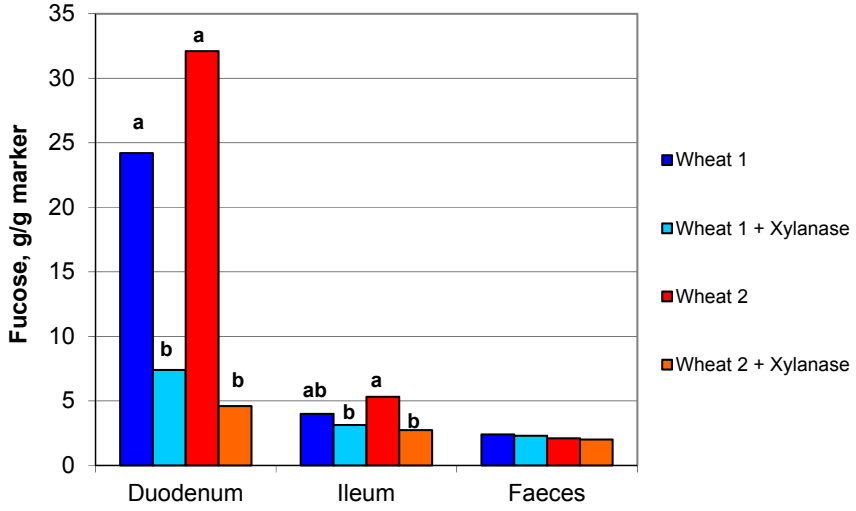

Fig. 1. Effect of wheat type and xylanase supplementation on gastrointestinal tract fucose level. [a,b]Treatment means followed by the same letter are not significantly different (LSD; $P < 0.05$).

supplementation than better quality samples (Cadogan et al., 2000). It is generally conceded that the NSP level of wheat contributes to the differences between wheat samples in terms of their nutritive value in young pigs (Choct et al., 1999b). Wheat 1, the low feed intake cultivar (Currawong) had higher levels of soluble and insoluble NSP and free sugars compared with Wheat 2, a normal Australian Standard White wheat cultivar (Whistler). Wheat 1, compared to Wheat 2 also contained a lower amount of starch (55.0% vs. 58.9%) and a higher amount of phytin phosphorus (0.28% vs. 0.22%). It is, thus, not likely to be the content of NSP or other nutrients per se that led to the different responses of the two wheats to xylanase supplementation. It is thought that there were significant differences in the cell wall architecture of the two wheats that elicited contrasting responses to xylanase supplementation. This argument is supported by our findings on the detailed composition of the NSP fractions and their pattern of degradation along the gut of weaner pigs. For instance, the duodenal digestibility values for free sugars, soluble NSP and insoluble NSP were −58.3, −8.8 and 7.3%, respectively for Wheat 1 without xylanase, whereas they were −10.0, −33.0 and −18.7%, respectively for Wheat 2 without xylanase. These figures show two things: firstly, in Wheat 1, much of the soluble NSP was degraded into low molecular weight carbohydrates in the stomach, yielding a large amount of free sugars in the duodenum, making the digestibility value highly negative. But in Wheat 2, a much smaller amount of free sugars and a markedly higher level of soluble NSP entered the duodenum, compared with Wheat 1, making their digestibility values less negative; secondly, the site for degradation of soluble NSP and solubilisation of insoluble NSP differed between the two wheats, where these occurred earlier in the digestive tract for Wheat 1 and for Wheat 2. The manifestation of these differences probably meant that digesta transit rates also differed between the two wheats, where the NSP in Wheat 1 were affected in the gut, moving the resulting digesta more quickly through the small intestine. The opposite seems to be true in the case of Wheat 2 as shown by the digestibility values for duodenal soluble and insoluble NSP. The highly negative values simply mean that the NSP were accumulated in the duodenum relative to the amounts present in the respective diets.

The different behaviours of the two wheats in terms of NSP digestibility may be related to the fact that NSP undergo changes within the gastrointestinal tract, especially under acidic conditions of the stomach (van der Meulen et al., 2001). In some cases, ester linkages may be cleaved, reducing originally soluble NSP into smaller fragments, including free sugars, and solubilizing some originally insoluble NSP (Choct and Cadogan, 2001). It appears that Wheat 1 was more susceptible to such changes in the stomach than Wheat 2. Increased amounts of osmotically active free sugars and viscosity-producing arabinoxylans in the stomach may be one of the factors that reduced feed intake of pigs fed Wheat 1. Indeed, soluble NSP have been shown to increase the viscosity of stomach contents in monogastric animals (Ellis et al., 1996). The pig has a sieving mechanism in the stomach in which large particles fall to the bottom of the stomach and undergo prolonged physical and chemical breakdown, and solubilised digesta flows into the duodenum (Ellis et al., 1996). An increase in digesta viscosity may reduce the sieving ability of the stomach and allow larger particles to stay suspended thereby reducing stomach digestion and flow of nutrients into the duodenum. The increase in particle size entering the duodenum would reduce diet digestibility. Furthermore, it is possible that the larger particle size may have diluted the digestible marker (as described above) and caused a temporary accumulation of particular dietary components. How the two wheats differed so much in their susceptibility stomach degradation is worthy of further investigation from their cell wall architecture.

The ability of the enzyme to effectively depolymerise the NSP is clearly demonstrated in Table 3. In addition to the negative digestibility values for the NSP, the dry matter and energy digestibility values in the duodenum of pigs fed the control diets were also negative. For example, the duodenal energy digestibility values of diets based on Wheat 1 and Wheat 2 were −27.4 and −47.5%, respectively, and were increased the to positive values by xylanase supplementation. The DM digestibility followed a similar pattern. The negative digestibility values for NSP residues, as observed in the duodenum and ileum, have been recorded in the past (Pettersson et al., 1997). The values are mostly a reflection of the fact wheat NSP are not absorbed in the proximal GI tract and are consequently enriched relative to the content found in the diet, when calculated per gram of dried digesta. Negative DM and energy digestibility values, however, have not been reported in past literature, and at first the results seem confusing. The best explanation for the negative energy digestibility values is that endogenous secretions diluted the dietary nutrients and the digestibility marker. The results indicated that endogenous protein, fat and carbohydrate secretions from the mucosa, pancreas, and bile duct were substantially increased from non-hydrolysed soluble and insoluble NSP. The effect of NSP on endogenous secretions in rats, pigs and poultry is well documented (Ikegami et al., 1990; Schulze, 1994; Angkanaporn et al., 1994; D nicke et al., 2000). It appears that NSP, in particular, the soluble fraction, interact with the mucosal surface, perhaps leading to modification of peptide hormones in the gut. When the molecular structure of NSP are broken down by exogenous enzymes, their ability to increase secretions seems to be reduced (D nicke et al., 2000). The negative digestibility of energy calculated in the duodenum does not necessarily suggest that net energy is lower for the control diets. The majority of endogenous secretions are re-absorbed in the small intestine, therefore absolute differences in net energy would be more accurate when measured at the terminal ileum. The presence of xylanase negated the negative effects on energy and soluble NSP digestibility and the results also showed that there is significant hydrolisation of soluble NSP by the enzyme, especially xylose and arabinose, in the proximal gastrointestinal tract.

Xylanase supplementation significantly increased ileal DM digestibility by 10 and 5.7%, respectively, for Wheats 1 and 2. There was, however, no significant difference between wheat type or enzyme supplementation on the faecal DM digestibility. Digestible energy was found to be unrelated to growth performance of young pigs offered diets containing different wheat types (Cadogan et al., 1999), even though there was a 45% difference in feed intake and growth rate. Nortey et al. (2008) observed a 2.2 and 2.8% increase in ileal and faecal dry matter digestibility, respectively, however growth performance was not reported. These observations highlight the limitations of faecal DM and gross energy digestibility measurements, and caution must be placed on the relationships between the DE of grains and pig growth performance.

The negative digestibility value for energy raises questions about an excessive endogenous loss in the duodenum and its impact on voluntary feed intake. Effects of NSP on endogenous secretions have been clearly demonstrated in broiler chickens (Angkanaporn et al., 1994; Selle et al., 2003). It is proposed that NSP, especially the soluble fraction, places an increased pressure on pancreatic and mucosal secretions, which may lead to negative feedback on feed intake, perhaps through increased cholecystokinin (CCK) and gastric inhibitory polypeptide (GIP) production. Cholecystokinin and GIP are both involved in negative feedback mechanisms on pig satiety and thus feed intake in the pig (Ellis et al., 1996). The current study showed a high level of fucose present in the duodenum and ileum (Fig. 1), which was a markedly reduced by xylanase supplementation. It is known that mucin

carbohydrates contain a considerable amount of fucose, with up to 74% of fucose in the ileal digesta of pigs arising from mucin (Lien et al., 1997). Turch et al. (1993) found that the fucose concentration in mucin was significantly affected by diet and age. In the current study, the elevated fucose level in the ileum suggests the extent of endogenous losses induced by the two wheats. Endogenous losses lead to loss of energy efficiency for maintenance and growth, and this effect is exacerbated as the pig gets older (Snyder and Walker, 1987).

5. Conclusion

The effect of wheat type on pig performance is manifested through massive variation in feed intake in young pigs. The NSP in wheat play a key role, but it is not just the content of NSP that affects feed intake, it appears that the cell wall architecture of wheat is important to determining where in the GI tract NSP are solubilised or degraded to low molecular weight carbohydrates and their subsequent effects on the movement of digesta. The use of an efficacious xylanase can alleviate most of the negative effects of NSP on feed intake.

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References

Angkanaporn K, Choct M, Bryden WL, Annison EF, Annison G. Effects of wheat pentosans on endogenous amino acid losses in chickens. J Sci Fd Ag 1994;66:399–404.
Bach Knudsen KE, Hansen I. Gastrointestinal implications in pigs of wheat and oat fractions. 1. Digestibility and bulking properties of polysaccharides and other major constituents. Br J Nutr 1991;65:217–32.
Bartelt J, Jadamus A, Wiese F, Swiech E, Buraczewska L, Simon O. Apparent preceacal digestibility of nutrients and level of endogenous nitrogen in digesta of the small intestine of growing pigs as affected by various digesta viscosities. Arch Anim Nutr 2002;56:93–107.
Batterham ES, Lewis CE, Low RF, McMillan CJ. Digestible energy content of cereals and wheat by-products for growing pigs. Anim Prod 1980;31:259–71.
Cadogan DJ. Agronomic and physico-chemical factors of wheat affecting nutrient availability and performance of pigs. (MSc thesis). Armidale, NSW, Australia: University of New England; 1999.
Cadogan DJ, Choct M, Campbell RG, Kershaw S. Effects of new season wheats on the growth performance of young male pigs. In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 1999. p. 40.
Cadogan DJ, Partridge GG, Simmins PH. Effect of xlyanase addition in feed containing either pre-characterised wheat or wheat by-products on the performance of growing pigs. In: Proceedings of the British society of animal science nutrition society, Scarborough, UK; 2000. p. 21.
Cadogan DJ, Choct M, Campbell RG. Effects of storage time and xylanase supplementation of new season wheats on the performance of young male pigs. Can J Anim Sci 2003;83:105–12.
Caine WR, Suaer WC, Tamminga S, Verstegen MWA, Schulze H. Apparent ileal digestibilities of amino acids in newly weaned pigs fed diets with protease-treated soybean meal. J Anim Sci 1997;75:2962–9.
Choct M, Cadogan DJ. How effective are supplemental enzymes in pig diets? In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 2001. p. 240–53.
Choct M, Hughes RJ, Annison G. Apparent metabolisable energy and chemical composition of Australian wheat in relation to environmental factors. Aust J Ag Res 1999a;50:447–51.
Choct M, Cadogan DJ, Campbell RG, Kershaw S. Enzymes can eliminate the difference in the nutritive value of wheats for pigs. In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 1999b. p. 39.
D nicke S, Jeroch H, Simon O. Endogenous N-losses in broilers estimated by a [15N]-isotope dilution technique: effect of dietary fat type and xylanase addition. Arch Anim Nutr 2000;53:75–97.
Ellis PR, Rayment P, Wang Q. A physio-chemical perspective of plant polysaccharides in relation to glucose absorption, insulin secretion and the entroinsular axis. Proc Nutr Soc 1996;55:881–98.
Englyst HN, Hudson GJ. Colorimetric method for routine measurement of dietary fibre as non-starch polysaccharides. A comparison with gas-liquid chromatography. Food Chem 1987;24:63–76.
Ikegami S, Tsuchuhashi F, Harada H, Tsuchuhashi N, Nishide E, Innami S. Effect of viscous indigestible polysaccharides on pancreatic-biliary secretion and digestive organs in rats. J Nutr 1990;120:353–60.
King RH. The feeding value for different classes of wheat for grower finisher pigs. Aust J Exp Ag Anim Husb 1976;16:668–71.
Kopinski J. Characteristics of cereal grains affecting energy value. Final Report DAQ35P. Canberra, ACT, Australia: Pig Research and Development Corporation; 1997.
Lien KA, Sauer WC, Fenton M. Mucin output in ileal digesta of pigs fed a protein-free diet. Ernahrungswiss 1997;36:182–90.
Longstaff M, MacNab JM. Influence of site and variety on starch, hemicellulose and cellulose composition of wheats and their digestibilities by adult cockerels. Br Poult Sci 1986;27:435–49.
Nortey TN, Patience JF, Sands JS, Trottier NL, Zijlstra RT. Effects of xylanase supplementation on the apparent digestibility and digestible content of energy, amino acids, phosphorus, and calcium in wheat and wheat by-products from dry milling fed to grower pigs. J Amin Sci 2008;86:3450–64.
Partridge GG. The role and efficacy of carbohydrates enzymes in pig nutrition. In: Bedford MR, Partridge GG, editors. Enzymes for farm animals. UK: CAB International; 2001. p. 161–98.
Partridge GG, Simmins PH, Cadogan DJ. Influence of xylanase addition to diets containing wheat co-products and nutritionally defined wheat on growing pig performance. In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 1999. p. 37.
Pederson NR, Azem E, Broz J, Guggenbuhl P, Le DM, Fojan P, et al. The degradation of arabinoxylan-rich cell walls in digesta obtained from piglets fed wheat-based diets varies depending on digesta collection site, type of cereal and source of exogenous xylanase. J Amin Sci 2012;90:149–51.
Pettersson D, Mullertz A, Ohmann A. Ileal carbohydrate digestion in broiler and humans. In: Corbett JL, Choct M, Nolan JV, Rowe JB, editors. Recent advances in animal nutrition. Armidale, NSW, Australia: University of New England; 1997. p. 17–20.
Schulze H. Endogenous ileal nitrogen losses in pigs- dietary factors. (PhD thesis). Wageningen, The Netherlands: Wageningen Agricultural University; 1994.
Selle PH, Cadogan DJ, Bryden WL. Influence of phytate and phytase on growth performance of weaner pigs offered phosphorus-adequate, wheat-based diets. Aust J Ag Res 2003;54:322–30.
Simmins PH, Pluske JR, Mullan BP. Effect of xylanase in diets containing pre-characterised wheat varieties on the performance of weaner pigs. In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 2001. p. 260.
Snyder JD, Walker WA. Structure and function of intestinal mucin: developmental aspects. Allergy Appl Immunol 1987;82:351–6.
Turch D, Feste AS, Lifschitz CH. Age and diet affect the composition of porcine mucins. Pediatr Res 1993;33:564–7.
van Barneveld RJ. Characteristics of feed grains that influence their nutritive value and subsequent utilisation by pigs. In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 1997. p. 193–207.
van Barneveld RJ, Ru YJ, Hughes RJ, Flinn PC, Black JL. Comparative digestion of energy from grains fed to pigs, poultry and ruminants: can the efficiency of pig production be improved? In: Cranwell PD, editor. Manipulating pig production VII. Werribee, VIC, Australia: Australasian Pig Science Association; 2001. p. 222–34.
van der Meulen J, Inborr J, Bakker JG. Effects of sell degrading enzymes on carbohydrate fractions and metabolites in stomach and ileum of pigs fed wheat bran based diets. Arch Anim Nutr 2001;54:101–15.
Wiseman J. Assigning energy values to ingredients for pigs. In: Feed ingredients Asia '97, Singapore; 1997. p. 1–12.
Yin YL, McEvoy JDG, Schulze H, Hennig U, Souffrant WB, McCracken KJ. Apparent digestibility (ileal and overall) of nutrients and endogenous nitrogen losses in growing fed wheat (var. Soissons) or its by-products without or with xylanase supplementation. Livest Prod Sci 2000;62:119–32.
Zijlstra RT, de Lange CFM, Patience JF. Nutritional value of wheat for growing pig: chemical composition and digestible energy content. Can J Anim Sci 1988;79:187–94.