Wheat carbohydrate constituents and voluntary feed intake in pigs

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Summary

The large variation in the nutrient composition of wheat is well documented, but certain types of wheat cause substantial decreases in voluntary feed intake that are unrelated to energy and protein composition. The potential negative influence on feed intake is higher in new season grains, and the effect declines over time (after 6 to 10 months). The variation in feed intake is largely related to the non–starch carbohydrate (NSC) fraction of wheat, and the restriction on feed intake and growth are mostly alleviated in the presence of a xylanase with affinity for both soluble and insoluble non–starch polysaccharides (NSP). Exogenous enzymes that have preference to hydrolyse insoluble wheat NSP can improve the intake of some wheats, but these enzymes can solublise anti–nutritional NSC of 'poor wheats' and produce a further decline in feed intake. Data presented in this paper demonstrate that the soluble fraction of wheat NSC has the most potential to restrict nutrient intake. The present results strongly suggest that the majority of the anti–nutritional effects of soluble NSP occur in the small intestine.

Keywords: wheat, non–starch carbohydrate, xylanase, feed intake, pigs

Introduction

Wheat is one of the cereal grains most variable in composition (Choct *et al.* 1999a). This variation is exacerbated by various environmental conditions (Longstaff and McNab 1986) rather than cultivar, especially with the extreme climates in Australia. 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 17.0 MJ/kg DM (Kopinski 1997), and the lowest was 13.8 MJ/kg DM (King 1976). Batterham *et al.* (1980) found the hemicellulose (mainly arabinoxylan) component of wheat to be negatively correlated with the DE of wheat. The relationship between DE and more specific components of wheat NSP has been variable (van Barneveld 1997), although Zijlstra *et al.* (1998) found a strong negative correlation between xylose and DE content of wheat. The protein digestibility coefficients have been reported to vary from 0.69 to 0.84 (van Barneveld 1997).

Most research on wheat in pigs has focussed on evaluating the variation in DE (Kopinski 1997; van Barneveld 1997) and designing methods to improve the digestibility of cereal grains (Wiseman 1997). However, faecal DM digestibility and DE values of cereals are poorly related to pig growth performance compared to ileal DM digestibility measurements (Cadogan 1999; van Barneveld *et al.* 2001). It appears that growth and voluntary feed intake of pigs are affected by wheat type, but are unrelated to energy and protein levels (Cadogan *et al.* 1999; Choct *et al.* 1999b; Simmins *et al.* 2001; Caine *et al.* 2002). The majority of the variation in pig growth performance produced by different wheats has been attributed to the content of the non–starch carbohydrates (NSC) (Cadogan 1999). The NSC include non–starch polysaccharides (NSP) and free sugars such as mono– and oligosaccharides present in feed ingredients. Although there have been many studies investigating the effect of NSP on human health and animal performance, proposed modes of NSP action in pig diets are largely speculative (Partridge 2001; Choct and Cadogan 2001).

This paper reviews findings related to the performance of pigs fed wheat–based diets and presents recent data on wheat carbohydrates that affect feed intake in pigs.

Variation in performance of pigs fed different wheats

The effects of viscous, low apparent metabolizable energy (AME) wheats on broiler chicken performance have been extensively researched and reported (Choct 1991; Choct and Annison 1992). Viscosity has not been regarded as the causative factor for impaired feed intake in weaner pigs fed wheat–based diets, despite evidence that certain wheats can significantly reduce growth performance of pigs between 6 and 60 kg live weight (Partridge 2001). The first study showing the influence of wheat type on pig voluntary feed intake was by Schultze *et al.* (1997), who reported a 15% difference in voluntary feed intake between wheat varieties grown in the same field. Investigating the effects of 10 different wheat types on pig growth (Table 1), Cadogan (1999) demonstrated that young pigs fed diets based on wheats of various cultivars differed by 47% in voluntary feed intake and 48% in daily weight gain (Table 1). Wheat type had no significant influence on the feed conversion ratio (FCR). The level of NSC was negatively correlated to feed intake ($r = -0.56$: $P = 0.002$) and daily gain ($r = -0.57$: $P = 0.006$) produced by the 10 different wheats. No other physico–chemical analyses, including DM digestibility and DE, were directly related to the large variation in growth and feed intake. Additional evidence that the variation in the quality of wheats is related to the NSC content comes from the finding that degradation *in vivo* of the main component of the NSC, arabinoxylan, by a microbial xylanase largely eliminated the difference between the wheats (Table 2). Thus, xylanase supplementation of the low quality wheats increased feed intake by 42.8% and weight gain by 50.6% in weaner pigs (Choct *et al.* 1999b). The problem of reduced feed intake does not seem to be alleviated when pigs get older. Cadogan *et al.* (2000) demonstrated that wheats that caused large differences in feed intake in weaner pigs remained problematic in grower pigs.

Another dimension to the effect of wheat type on feed intake is the phenomenon that a gradual improvement in feed intake of pigs offered various wheats occurs when the grains are stored for a period of time. This is generally known as the 'new season grain phenomenon' in poultry. The following section will discuss the implications of this phenomenon in pig production.

Use of new season wheats in pig diets

Most wheats have been reported to undergo post–harvest changes within the first three to four months of

Table 1 Effects of new season wheats on the performance of young male pigs offered diets for 21 days commencing at 7.5 kg liveweight (Cadogan *et al.* 1999).

Wheat cultivar	Final W (kg)	Daily gain (g)	Feed intake (g/d)	FCR (g:g)	DM digestibility (%)
Currawong	12.41	233^{a}	271^{a}	1.18	86.4^{abc}
Dollarbird	14.63	341^{b}	388^{b}	1.15	85.0^{cde}
Finley Rosella	15.48	376^{bc}	432^{bc}	1.14	84.7^{cde}
Wimmera Rosella	16.66	433^{c}	476^{c}	1.10	84.2^{cde}
Cocamba	15.78	396^{bc}	438^{bc}	1.11	85.8^{abcd}
Parsons Rosella	15.95	399^{bc}	445^{bc}	1.13	83.3^{e}
Matong	16.15	419^{c}	486^{c}	1.16	84.2^{de}
Triller	16.39	438^{c}	502^{c}	1.15	85.3^{abcd}
Janz	15.73	394^{bc}	432^{bc}	1.09	86.4^{ab}
Lawson	16.45	447^{c}	514^{c}	1.14	86.8^{a}
Significance[1]	***	***	***	NS	***

[1] NS not significant, ****P*<0.001
[a b c d e] Means within columns with different superscripts are significantly different (*P*<0.05)

Table 2 Effects of wheats characterised as high, medium and low feed intake types on grower pig performance commencing at 27 kg liveweight (Cadogan *et al.* 2000).

Intake type	Final W (kg)	Daily gain (g)	Feed intake (kg/d)	FCR (g:g)
Wheat — high	61.9	960^{a}	1.77^{a}	1.84
Wheat — medium	60.2	918^{ab}	1.62^{ab}	1.80
Wheat — low	58.3	878^{b}	1.58^{b}	1.76
SED	0.65	12.4	0.033	0.021
Significance	NS	*	*	NS

[1] NS not significant, **P*<0.05
[a b] Means within columns with different superscripts are significantly different (*P*<0.05)

storage under conventional conditions (Choct and Hughes 1997). The change is usually manifest as a marked increase in the AME value of the grain and in feed efficiency of broilers fed the stored wheats. It is believed that the post–harvest change in the nutritive value of grains for poultry is probably due, in part, to the activation of the endogenous glycanases in the grain, leading to partial depolymerisation of the viscous NSP. However, questions may arise as to how any enzyme could act on the substrate under moisture levels as low as 10–15% post–harvest. It is therefore postulated that the moisture level of grains can be high immediately after harvest (Svihus *et al.* 1995).

In addition, Choct and Hughes (1999) suggested that non–enzymic scission of NSP may also occur in cereals, increasing the AME value over time. This occurs when cell wall hydroxyl radicals are produced under mildly acidic conditions, which are able to cleave polysaccharides (Miller 1986; Fry 1998). The generation of hydroxyl radicals in cereal grains may be influenced by soil nutrients and growing conditions (Choct and Hughes 1999).

The new season wheat phenomenon was observed in pigs by Cadogan (1999) who reported that after 10 months of storage the differences between the varieties remained although feed intake and daily gain were, on average, 11.3% and 9.8% higher, respectively, than in samples immediately post–harvest. Similar effects on the storage of wheat (6 months) were observed in broiler chicks; feed intake and body weight gain

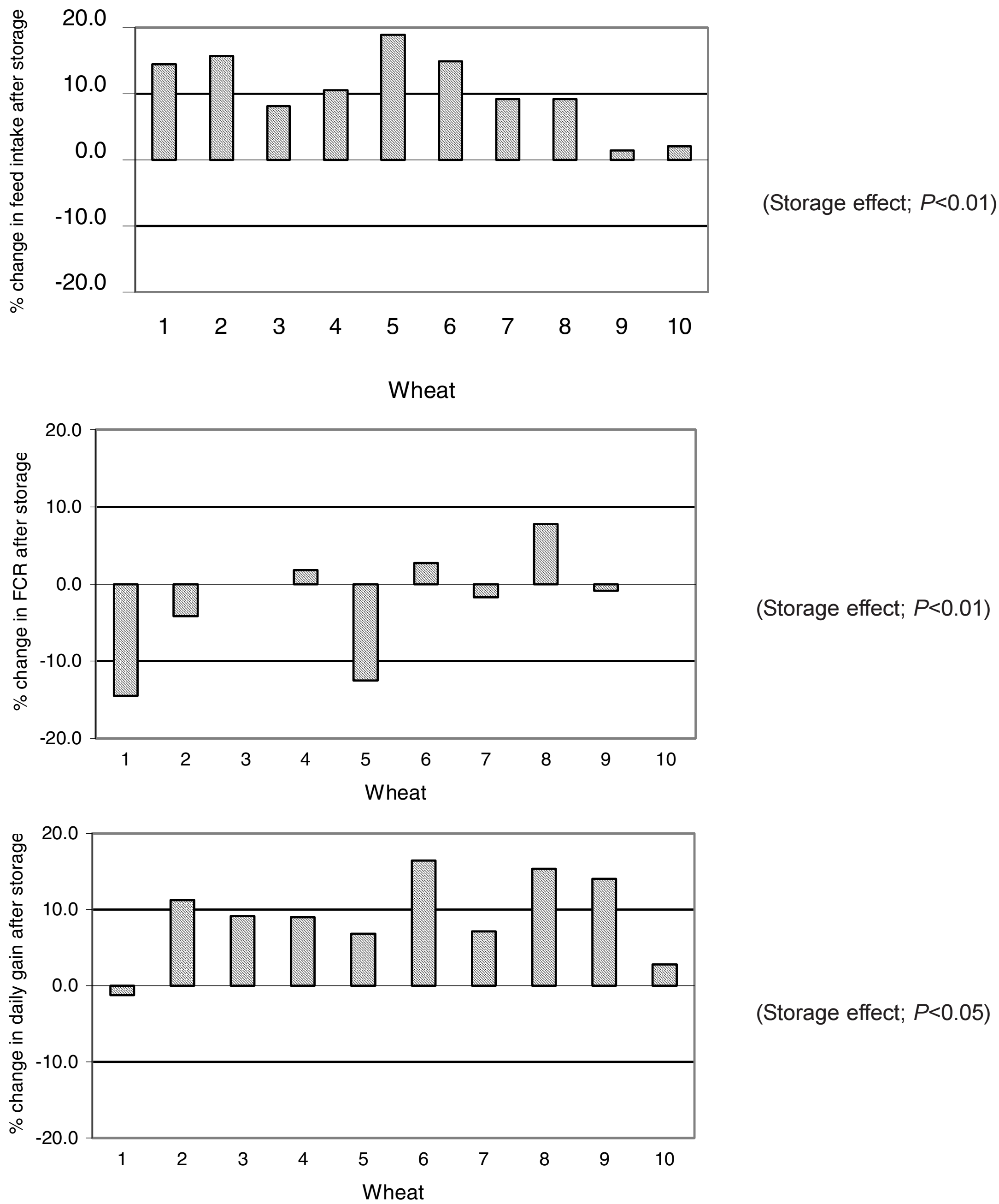

Figure 1 Changes in feed intake, weight gain and feed efficiency in pigs fed different wheats 10 months after harvest (Cadogan 1999).

increased by 16.1% and 22.7%, respectively (Scott and Pierce 2001). The marked increase in voluntary feed intake on every tested wheat stored for 10 months, assuming there were no outside influences of environmental, seasonal, or disease status, suggests that over time the endogenous enzymes in wheat may act upon the NSP in a similar manner to exogenous enzymes, leading to increased feed consumption in pigs. The hydrolysis of anti–nutritional factors such as NSP and phytic acid would similarly reduce the negative effects of NSP on growth performance. Figure 1 shows feed intake, weight gain and feed efficiency of weaner pigs fed 10 different wheats before and after 10 months of storage (Cadogan 1999).

Although most FCR results were similar between new season and 10–month old wheats, the storage of three wheats reduced the efficiency of growth, whereas one wheat showed an improved FCR. In poultry, the storage of wheat generally improved FCR, although storage of some wheats had a negative effect on FCR (Choct and Hughes 1999; Scott and Pierce 2001). Similar findings were reported for weaner pigs by Kim *et al.* (2001) who observed a net reduction in wheat DE following 6 months of storage.

Digestion of non–starch carbohydrate and its effects on feed intake

The physiochemical properties of NSC are highly complex and therefore their effect on the physiology and microflora of the gut in pigs is multifaceted. In regard to their actions on feed intake in pigs, it is believed that NSC affect the passage rate of digesta by the viscous nature of their soluble components, increase the water–holding capacity of digesta by their bulking effect, change the gut microflora by selective provision of various substrates, and possibly influence satiety through changes in gut physiology such as the osmotic pressure and hormonal secretion (Partridge 2001; Choct and Cadogan 2001).

Observations by Cadogan (1999) indicate that both soluble and insoluble NSP have negative effects on feed intake by young pigs, and hence on their growth rate. This is clearly suggested by the interaction between the enzyme type and wheat quality on feed intake. As shown in Table 3, an enzyme that only solubilizes the insoluble NSP worked well in good quality wheat (cv. Lawson), but had a negative effect on the poor quality wheats (cv. Currawong and Dollarbird). It was hypothesised that the native soluble NSP and the soluble NSP released through exogenous enzyme hydrolysis from the Currawong and Dollarbird wheats contained anti–nutritional properties that restricted feed intake. Thus it appears that when the level of anti–nutritional soluble NSP is low in the gut, it is beneficial to break down the insoluble cell walls to release entrapped nutrients, but when the background level of anti–nutritional NSP is high, such as in the case of Currawong and Dollarbird wheats, the release of soluble NSP, hence the increase in gut viscosity, overwhelms the benefit of breaking down the cell walls. Further support of this hypothesis comes from the data presented in Table 4, where an enzyme capable of opening up the cell walls as well as breaking down the both the native and

Table 3 Effects wheat type and supplementation of an enzyme with affinity for insoluble NSP on the performance of male pigs from 35 to 56 days of age commencing at 9.0 liveweight (Cadogan *et al.* 1999).

Wheat variety	Xylanase	Final W (kg)	Daily gain (g)	Daily intake (g)	FCR (g:g)
Currawong	–	14.01	309[ab]	389[a]	1.30
Currawong	+	13.62	253[a]	323[a]	1.28
Dollarbird	–	16.76	435[c]	537[b]	1.24
Dollarbird	+	15.44	345[b]	442[a]	1.29
Rosella	–	17.70	476[c]	551[b]	1.16
Rosella	+	18.06	478[c]	583[b]	1.21
Triller	–	19.29	562[d]	691[c]	1.23
Triller	+	20.23	596[de]	730[c]	1.22
Lawson	–	19.34	567[d]	691[c]	1.21
Lawson	+	20.65	630[e]	733[c]	1.15
SEM		*0.306*	*14.2*	*17.4*	*0.013*
P values	Wheat (W)	<0.001	<0.001	<0.001	0.521
	Enzyme (E)	0.681	0.584	0.695	0.875
	W x E	0.036	0.035	0.214	0.511

[a b c d e] Treatment means followed by the same superscript letter are not significantly different released soluble NSP improved the feed intake of pigs fed various wheats.

An earlier study by Dunshea *et al.* (1997) showed an interaction between enzyme supplementation and weaning age. The xylanase used in the study exhibited stronger affinity for insoluble wheat NSP and was relatively inefficient at hydrolysing soluble NSP. The study showed that the enzyme negatively affected the growth of 14–day old pigs, but it significantly improved the growth performance of pigs 28 days old. Although not stated by the authors, the results suggest that the enzyme may have been hydrolysing insoluble NSP, and releasing entrapped nutrients and soluble NSP. The action of the enzyme significantly improved the growth of older pigs, more capable of extracting nutrients from the hydrolysed insoluble NSP and relatively unaffected by the increase in viscosity caused by released, relatively neutral, soluble NSP. The early–weaned pigs could be more susceptible to any type of soluble NSP, due to their less developed GIT. Thus when the enzyme acted on the insoluble NSP, the released soluble NSP may have negatively affected feed intake, negating the benefits of released nutrients and improved digestibility. The hydrolysis of NSP may have also released other another anti–nutrient, phytic acid, further limiting growth performance of the early–weaned pig (Cadogan and Selle 2000).

In an attempt to gather more information on how NSC influences voluntary feed intake, an experiment was designed to measure the digestibility of the free sugars and soluble and insoluble NSP of wheats along the GIT of young male pigs. This was achieved by using wheats pre–characterised as low and high intake types, with and without the addition of a xylanase with affinity for soluble and insoluble NSP. The growth assay showed wheat type produced a significant difference in feed intake and growth rate during the first 7 days but by day 14 the only significant effect of wheat type was on growth rate (Table 5). The significant influence of wheat type on pig growth was similar to that observed in the pre–characterisation experiment. Xylanase supplementation of the lower quality wheat (wheat 1) increased growth performance up to a similar level of the high quality wheat control (wheat 2). Choct *et al.* (1999b) and Cadogan *et al.* (2000) reported similar findings. In the current study, however, xylanase supplementation significantly increased the daily gain of pigs offered the higher quality wheat. This was unexpected. The difference between the xylanase supplemented diets suggests that the NSP present in the wheat were restricting growth of the higher performance wheat, whereas additional factors in wheat 1 affected its quality. These additional factors in wheat 1 were later analysed to be lower starch levels (55.0% compared to 58.9%) and a higher level of phytin phosphorus (0.28%) compared to wheat 2. Selle *et al.* (2003) have described the potential anti–nutritional effects of phytate on nutrient availability in weaner pigs.

Overall, wheat type had no significant effect on the digestibility of DM, energy, free sugars or the different fractions of NSP (Table 6) in the duodenum, ileum or the GIT (faeces). Energy digestibilities in the duodenum of diets based on low and high intake wheats were –27.4% and –47.5% respectively and were increased to positive values by xylanase supplementation. 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 that wheat NSP are not absorbed in the proximal GIT and are consequently enriched relative to the content found in the diet when calculated per gram of dried digesta. Negative DM and

Table 4 Effect of wheat type and supplementation of a xylanase with affinity for both soluble and insoluble NSP on the performance of male pigs offered diets for 21 days commencing at 7.3 kg live weight (Choct *et al.* 1999b).

Wheat variety		Xylanase	Final W (kg)	Daily gain (g)	Daily intake (g)	FCR
Currawong		–	12.10^{a}	230^{a}	318^{a}	1.38
Currawong		+	17.10^{b}	466^{b}	556^{b}	1.23
Cocamba		–	16.26^{b}	425^{b}	540^{b}	1.27
Cocamba		+	16.72^{b}	445^{b}	521^{b}	1.20
Lawson		–	16.96^{b}	460^{b}	525^{b}	1.14
Lawson		+	17.31^{b}	479^{b}	570^{b}	1.20
SEM			*0.296*	*13.9*	*13.4*	*0.02*
P values	Wheat (W)		<0.001	<0.001	<0.001	0.074
	Enzyme (E)		<0.001	<0.001	<0.001	0.121
	W x E		<0.001	<0.001	<0.001	0.206

[a b]Means within a column with the same superscript letters are not significantly different (P>0.05)

energy digestibility values, however, have not been reported elsewhere and at first the results seem confusing. The explanation for the negative energy digestibility values is that endogenous secretions diluted the duodenal digesta and the alkane digestibility marker. In other words, the amount of endogenous compounds secreted into the duodenal lumen outweighed absorbed dietary nutrients by 19.4 and 37% for wheats 1 and 2 respectively. The results indicated that endogenous protein, fat and carbohydrate secretions from the mucosa, pancreas, and bile duct were substantially increased due to the presence of large amounts of (soluble) NSP in the diet. Low (1990) reported increases in pancreatic juice from 115 to 390% and bile from 26 to 32% by the addition of wheat NSP. The effect of NSP on endogenous secretions in rats, pigs and poultry is well documented (Low 1990; Ikegami *et al.* 1990; Schultze *et al.* 1994; Angkanaporn *et al.* 1994; Danicke *et al.* 2000). It appears that NSP, in particular the soluble fraction, interact with the mucosal surface, perhaps leading to modulation of peptide hormones in the gut. When exogenous enzymes break down the molecular structure of NSP the ability of NSP to increase secretions seems to be reduced (Danicke *et al.* 2000). The majority of endogenous secretions are re–absorbed in the small intestine, therefore absolute differences in energy and protein digestibility 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 a significant hydrolysis of soluble NSP by the enzyme, especially arabinoxylans, in the GIT.

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 diets in the faecal DM digestibility values. DM digestibility 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. These observations highlight the limitations of measuring DM and energy digestibility at the faecal level.

It is thought that NSP undergo changes within the GIT, especially under acidic conditions of the stomach (van der Meulen *et al.* 2001). In some cases, ester linkages may be cleaved, solubilizing some originally insoluble NSP (Choct and Cadogan 2001). Therefore it is possible that more soluble NSP were generated (especially for wheat 2) in the stomach and by microbes in the ileum. This would be manifest as negative digestibility values for soluble NSP in the duodenum and ileum. As there would be no enzyme present to hydrolyse the soluble NSP, the soluble NSP structure remains intact until it is fermented in the caecum and colon. The increased solubility of arabinoxylan may be

Table 5 Effects of wheat type and xylanase supplementation on the growth performance of male pigs for the 0 to 7 and 0 to 14 day periods commencing at 7.8 kg live weight (Cadogan, unpublished data).

		Enzyme (300 g/t)	Liveweight (kg)	Daily gain (g)	Feed intake (g)	FCR (g/g)
0 to 7 day period						
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*
P values	Wheat (W)			0.029	0.050	0.164
	Enzyme (E)			0.261	0.119	0.903
	W x E			0.663	0.865	0.391
0 to 14 day period						
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*
P values	Wheat (W)			0.013	0.237	0.081
	Enzyme (E)			0.119	0.992	0.050
	W x E			0.794	0.795	0.991

[a b]Means within a column with the same superscript letter are not significantly different (P<0.05)

one of the factors reducing pig feed intake and growth performance.

The growth performance and NSC digestibility from this study strongly suggests soluble NSP are the main constraint on feed intake. On the other hand, insoluble NSP through its water–holding capacity (WHC) and bulking effects (Kyriazakis and Emmans 1995; Aulrich and Flachowsky 2001) may also influence feed intake. If insoluble NSP were added to the diet rather than being part of the grain encapsulating nutrients they perhaps would have little influence on feed intake. In a recent study, when millrun (1 part wheat pollard, 2 parts wheat bran) was added at graded levels up to 50% in weaner diets, there was no noticeable effect on feed intake compared with a barley diet (l'Arson, unpublished data). In another study, Xylanase A which has affinity for both soluble and insoluble NSP and Xylanase B with an affinity for insoluble NSP were included either singly or in combination in a millrun–based weaner diet. Voluntary feed intake and growth rate were significantly increased when Xylanases A and B were combined, but they had no influence on feed intake when added singly (Table 7).

As shown in Table 8, addition of Xylanase B or the combination of Xylanases A and B markedly improved DM digestibility at the faecal level. The failure of Xylanase A to improve DM digestibility indicates that the constraint on the nutritive value of millrun for pigs is related to its insoluble NSP content. Thus Xylanase B, an enzyme with a strong affinity for

Table 6 The digestibility[1] (%) of DM, gross energy, free sugars and NSP of high and low performance wheat based diets with and without xylanase supplementation (Cadogan, unpublished data).

		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 values	Wheat (W)		NS	NS	NS	NS	NS
	Enzyme (E)		0.082	0.071	NS	0.008	0.024
	W x 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 values	Wheat (W)		NS	NS	NS	NS	NS
	Enzyme (E)		0.036	0.045	NS	<0.001	NS
	W x 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 values	Wheat (W)		NS	NS	NS	NS	NS
	Enzyme (E)		NS	NS	NS	NS	0.093
	W x E		NS	NS	0.066	NS	NS

[a b] Treatment means within columns followed by the same superscript letter are not significantly different (P>0.05)
[1] Digestiblity values were determined from concentrations of an alkane marker ($C_{36}H_{72}$) in digesta obtained by slaughter following consumption by the pigs of experimental diets with added known amounts of the alkane

insoluble arabinoxylans, depolymerised the polymers and resulted in better digestibility of the NSP. Aulrich and Flachowshky (1998) found NSP degrading enzymes (xylanase and β–glucanase) increased the digestibility of protein and mineral by 17% and 40%, respectively, as well as reducing the WHC of a wheat bran based diet. The authors claimed that it was due to the activities of the enzymes to break down the cell walls to release these nutrients. In the current study, although Xylanase B led to more insoluble NSP being digested at the faecal level, the apparent increase in DM digestibility did not translate into better growth. It is believed that the soluble NSP was not depolymerised by Xylanase B as this enzyme did not have affinity for soluble substrates, leaving the anti–nutritive effect of soluble NSP on feed intake unhindered. The addition of Xylanases A and B to the diet, on the other hand, not only effectively degraded insoluble NSP, but also hydrolysed the soluble NSP to remove their anti–nutritive effect on feed intake in the millrun–based diet. This was manifest as increased DM digestibility and improved weight gain. These findings highlight the negative properties of soluble NSP on young pig performance.

The significant reduction in ileal soluble NSP, in the presence of xylanase, can substantially improve pig growth performance, as demonstrated in a later study (Cadogan and Choct, unpublished data), but insoluble carbohydrate can create a physical barrier towards exogenous and endogenous enzymic digestion. The results from the above growth and digestibility studies also demonstrate that insoluble wheat NSP can act as a reservoir of soluble NSP. In the absence of exogenous enzymes, these originally insoluble NSP are solubilized by a combination of stomach acid hydrolysis of ester linkages (Choct and Cadogan 2001; van der Meulen *et al.* 2001) and microbial actions, releasing soluble NSP along the small intestine and providing substrates for fermentation in the large intestine. In the current study, the solubilization of NSP in the small intestine was shown by the negative digestibility value of soluble NSP in the duodenum and ileum, which in real terms shows that there is a net increase of soluble NSC in the intestine.

The growth depressing effects of soluble NSP from wheat, whether naturally occurring or released from insoluble fibre, have been well documented (Vahouny *et al.* 1982; Low 1989; Choct 1997). The current findings suggest the solubility of the NSP in the stomach of the pig depends on the wheat type, with some wheats having cell wall structures that are more prone to stomach acid. Once solubilized, the NSP exacerbate their effect on reducing digesta transit rate (Rainbird 1986), leading to a decrease in feed intake. Further evidence that soluble NSP negatively influences the small intestine is the high level of fucose in the duodenum and ileum and the subsequent reduction in the presence of xylanase (Figure 2). This strongly suggests that intact soluble NSP significantly increase small intestinal mucin production, but has little effect in the hindgut. Mucin carbohydrate contains a considerable amount of fucose and galactose. Up to 74 and 76% of the respective neutral sugars in the ileal digesta from pigs can be attributed to mucin (Lien *et al.* 1997). Turch *et al.* (1993) found that the fucose concentration in mucin was significantly affected by diet and age, whereas no changes were recorded in the levels of galactose. These findings suggest that the duodenal and ileal fucose levels can indicate the degree by which anti–nutritional NSP affect overall endogenous secretions in the small intestine (e.g. protein, carbohydrate and minerals). Along with mucin proteins, the gut secretes some 20 hormones or regulatory peptides (Unväs–Moberg 1992), some of which enhance nutrient absorption and others depress that it. Feed components that have effects on endogenous protein secretion ought to have an effect on hormonal secretions, such as glucagon–like peptide–1, which in turn may have a negative feedback on feed intake (Gunn *et al.* 1997).

Several observations also suggested that the negative influences of NSP are produced in the large

Table 7 Effects of supplementing Xylanase A and Xylanase B on the growth performance of male pigs fed diets containing a high level of millrun between 32 and 53 days of age (Cadogan and Choct, unpublished data).

Xylanase A (300 mg/kg)	Xylanase B (400 mg/kg)	Liveweight at 21 days (kg)	Daily gain (g)	Feed intake (g)	FCR (g/g)
–	–	17.60[ab]	461[ab]	599	1.30
+	–	17.12[b]	427[b]	577	1.35
–	+	17.75[ab]	462[ab]	594	1.29
+	+	18.77[a]	512[a]	670	1.31
SEM		*0.295*	*11.86*	*17.72*	*0.021*
P values	Xylanase A	NS	NS	NS	NS
	Xylanase B	0.055	0.040	0.111	NS
	A x B	0.201	0.122	0.216	NS

[a b] Treatment means within columns with the same superscript letter are not significantly different (P>0.05)

intestine. For example, results from the millrun experiment showed the combination of Xylanase A and Xylanase B produced the lowest gain in DM digestibility in the large intestine of 7.7%, whereas the control, individual Xylanase A and individual Xylanase B supplemented diets recorded substantially larger intestinal DM digestibility increases of 11.2, 13.9 and 12.2%, respectively. This indicates that the increase in hindgut digestibility of DM leads to higher rates of microbial fermentation. An increase in hindgut fermentation may irritate the bowel by producing higher levels of methane, ammonia and various VFA. Pluske *et al.* (2001) showed an increase in dietary fibre intake, and hence raised levels of large intestinal fermentation, could reduce dry matter intake. The suggested reason for the negative relationship between dietary fibre level and feed intake was a negative feedback mechanism through the gut hormone glucagon–like peptide 1 in the presence of increased VFA production (Tappenden *et al.* 1996).

The current evidence, however, strongly suggests that the majority of the negative influence on nutrient intake of soluble anti–nutritional NSC is occurring in the small intestine. It is postulated that the negative effects of soluble NSP in the small intestine include reduced digesta rate of flow (Rainbird *et al.* 1986; Aulrich and Flachowsky 2001), increased WHC (Kyriazakis and Emmans 1995; Aulrich and Flachowsky 2001), elevated endogenous secretions (de Lange *et al.* 1989; Nyachoti *et al.* 1997) and enhanced growth of certain microflora in the small intestine (Chesson 1994).

The results also demonstrate that improvements in DM and NSP digestibility at the faecal level does not necessarily relate to an increase in pig growth

Table 8 The digestibility[1] (%) of DM, free sugars and NSP in millrun based diets supplemented with two different xylanase activities (Cadogan and Choct, unpublished data).

Xylanase A		Xylanase B	DM	Free sugar	Soluble NSP	Insoluble NSP
			Duodenum			
–		–	13.9[ab]	20.3	–81.2	–23.6
+		–	–8.3[b]	12.0	–61.0	–13.6
–		+	6.6[ab]	48.4	–34.6	–12.3
+		+	26.4[a]	11.6	–15.3	–11.5
P values	Xylanase A		NS	NS	NS	NS
	Xylanase B		0.191	NS	0.126	NS
	A x B		0.016	NS	NS	NS
			Ileum			
–		–	59.9[a]	75.9	–59.3[a]	10.4
+		–	59.3[b]	67.0	–25.1[ab]	7.1
–		+	62.4[ab]	69.6	–53.9[a]	21.7
+		+	66.7[a]	73.2	–1.7[b]	30.0
P values	Xylanase A		NS	NS	0.014	NS
	Xylanase B		0.022	NS	NS	0.138
	A x B		0.244	NS	NS	NS
			Faeces			
–		–	71.1[b]	99.1	77.0	31.0[b]
+		–	73.2[ab]	99.1	79.1	36.8[ab]
–		+	74.6[a]	99.3	80.3	41.0[a]
+		+	74.4[a]	99.2	79.7	42.0[a]
P values	Xylanase A		NS	NS	NS	0.132
	Xylanase B		0.007	0.233	0.104	<0.001
	A x B		0.337	NS	NS	0.302

[a b] Treatment means within columns followed by the same superscript letter are not significantly different (P>0.05)
[1] Digestiblity values were determined from concentrations of an alkane marker ($C_{36}H_{72}$) in digesta obtained by slaughter following consumption by the pigs of experimental diets with added known amounts of the alkane

performance. This demonstrates the importance to confirm findings from digestibility experiments with a growth study before any commercial implications are drawn from an experiment.

Conclusion

The information reported in this paper demonstrates the strong influence that different wheat types potentially have on the voluntary feed intake of young pigs fed nutrient–adequate diets. The NSC fraction in wheat is one, if not the main, factor limiting feed intake, and the anti–nutritional effects of wheat NSP can be alleviated by supplementation of xylanases with affinities for both soluble and insoluble NSP. New information presented on the pattern of NSC digestion along the GIT showed that the soluble fraction of NSC caused the majority of the restriction on nutrient intake. Insoluble wheat carbohydrates can also limit voluntary feed intake, although current evidence suggests this portion of wheat fibre can act as a reservoir of soluble NSP which is released in the stomach and along the small intestine by physio–chemical factors and microbial action. The presence of modern, commercial feed xylanases in wheat–based diets can produce highly consistent pig growth performance that matches or is superior to that with other cereal grains.

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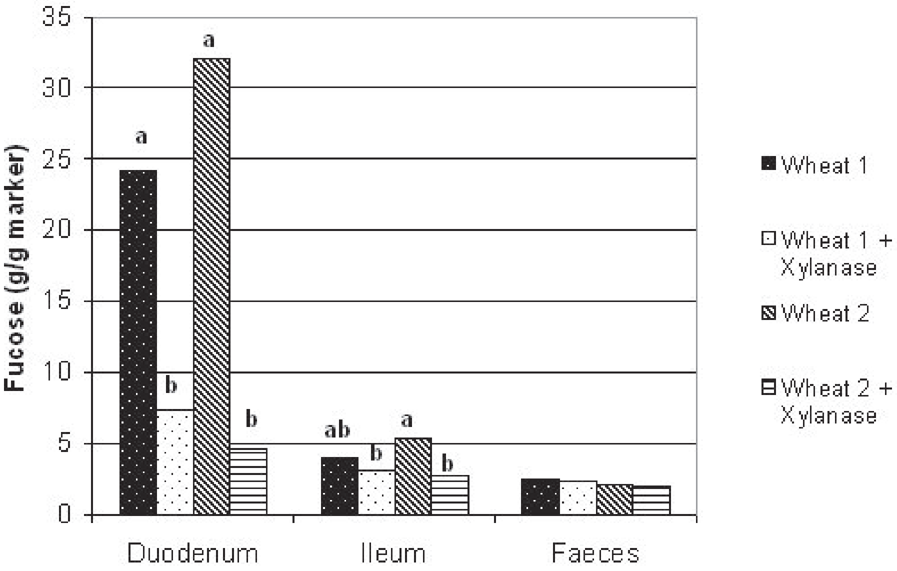
Figure 2 Effect of wheat type and xylanase supplementation on GIT fucose level (Cadogan unpublished data).



[a b]Treatment means with the same superscript letter is not significantly different (LSD; P>0.05)

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