Growth performance, nutrient utilization, and digesta characteristics in broiler chickens fed corn or wheat diets without or with supplemental xylanase[1]

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ABSTRACT Efficacy of supplemental xylanase on growth performance, nutrient utilization, and digesta characteristics in broiler chickens fed corn- or wheat-based diets was investigated. In experiment 1, 192 male broilers (8 birds/pen; n = 6) were fed 4 diets (corn or wheat without or with 1,250 xylanase units/kg) in 2 phases (starter, d 0–21 and grower, d 22–42). There was no interaction ($P > 0.05$) between diet and xylanase on performance (d 0–42). Wheat diets resulted ($P < 0.01$) in better performance than corn diets, whereas xylanase-fed birds had improved ($P < 0.01$) BW gain (2,457 vs. 2,275 g) and feed per gain (1.677 vs. 1.762) relative to birds not fed xylanase. In experiment 2, TiO_2 (0.3%) was added in starter diets used in experiment 1, allocated to 13-d-old broiler chicks (n = 6) housed in cages (6 birds/cage) and fed up to d 21. Excreta samples were obtained from d 17 to 20 and birds were euthanized on d 21 for digesta. Corn diets had a greater concentration (10.7 vs. 9.8%) of insoluble nonstarch polysaccharides (NSP) than wheat diets, which in turn had more than twice the concentration of soluble NSP. There was an interaction ($P < 0.03$) between diet type and xylanase on jejunal digesta viscosity but not ($P > 0.10$) on apparent ileal digestibilities of nutrients, cecal volatile fatty acids, and AME_n. In this context, diet type influenced ($P < 0.05$) cecal volatile fatty acids and retention of nutrients and fiber but did not affect ($P = 0.45$) AME_n. In contrast, xylanase-fed birds showed higher ($P < 0.05$) ceca digesta acetic acid, apparent ileal digestibilities of nutrients, and retention of components. As a result, birds fed xylanase had higher AME_n (3,059 vs. 2,995 kcal/kg; $P < 0.01$) compared with birds not fed xylanase. Although wheat diets had superior growth performance, the AME_n was similar in both diets. Xylanase improved growth performance and AME_n independent of diet type, suggesting hydrolysis of both soluble and insoluble NSP.

Key words: broiler, nutrient utilization and retention, growth performance, xylanase, phytase, volatile fatty acid

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INTRODUCTION

Corn is by far the most commonly used cereal grain in the diets for intensively reared poultry. One reason for the widespread use of corn is the perception of consistent and high nutritional value (Slominski, 2011). It has been demonstrated that the chemical composition and nutritional value of corn is variable (Cowieson, 2005) and could be improved by supplemental enzymes (Cowieson et al., 2010; Romero et al., 2011; Gehring et al., 2012). However, the magnitude of supplemental enzymes response is generally lower than could be expected for diets based on viscous grains such as wheat, rye, and barley (Adeola and Cowieson, 2011; Slominski, 2011). Presumably, the reason for the lower magnitude of supplemental enzymes in corn-based diets is the lower concentration of antinutritive high molecular weight soluble nonstarch polysaccharides (**NSP**) (Bedford and Schulze, 1998). Studies have shown that corn-based dried distillers grains with solubles (**cDDGS**) can be successfully included in broiler diets to levels of up to 20% as long as accurate nutrient profiles specific to the cDDGS batch/source are applied, and diets are formulated on a digestible amino acid basis (Loar et al., 2010; Masa'deh et al., 2011; Shim et al., 2011). However, incorporation of cDDGS in corn-based diets could increase the concentrations of NSP, in particular soluble pentosans that can increase intestinal viscosity (Loar et al., 2010). Supplemental xylanase can hydrolyze the NSP in cDDGS and consequently improve utili-

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zation of dietary components commensurate to benefits seen in wheat-based diets. For example, supplemental xylanase increased the digestibility of hemicelluloses and energy in broiler chickens fed corn-based diets with 20% DDGS (Liu et al., 2011). There are, however, only limited reports comparing the efficacy of xylanases in broilers fed corn-based diets with cDDGS and wheat-based diets to document the magnitude of the response.

The efficacy of fiber degrading carbohydrases in enhancing nutrients and energy utilization in poultry is well documented and has been largely associated with reduction of intestinal viscosity through depolymerization of soluble NSP (Bedford and Schulze, 1998; Adeola and Cowieson, 2011; Slominski, 2011). However, the mechanism through which xylanases improves nutrient utilization in low-NSP wheat (Persia et al., 2002) and corn-based diets (Nian et al., 2011; O'Neill et al., 2011; Romero et al., 2011) is unclear. It has been suggested that carbohydrases release fermentable oligosaccharides in the process of NSP depolymerization, which are fermented to volatile fatty acids (**VFA**) in the ceca in such concentrations that they trigger a neuro-hormonal response through peptide YY, which results in (gastroparesia or ileal brake) delayed gastric emptying and duodenal transit rates (Cuche et al., 2000; Park et al., 2013) with the consequence of enhanced diet digestion and nutrient absorption in the small intestines (O'Neill et al., 2012a; Singh et al., 2012). Peptide YY is a neuropeptide released in the enteroendocrine cells located predominantly in the distal ileum and colon and its release has been shown to be stimulated by presence of VFA in the intestinal lumen (Cuche and Malbert, 1999; Cuche et al., 2000). Courtin et al. (2008) showed that the inclusion of wheat oligosaccharides isolated from xylanase-treated wheat bran improved feed to gain in corn-fed birds to the same extent as the inclusion of the same xylanase in the ration. There are apparently few studies where the in situ generation of oligosaccharides has been monitored in chickens fed diets containing xylanases (Kiarie et al., 2013). However, supplemental xylanases not only increased nutrient digestibility but also concentration of cecal VFA linked to increased flow of xylo-oligomers into the ceca (Choct et al., 1996, 1999). Microbial metabolites such as VFA have been suggested as apparent indicators of exogenous enzymes induced in situ generation of fermentative oligosaccharides (Kiarie et al., 2013) and could be measured to link effects of xylanase on nutrient digestibility and retention.

The present investigation hypothesized that xylanase will improve growth performance of broilers fed corn- and wheat-based diets linked to reduced jejunal digesta viscosity, enhanced ceca VFA, and dietary AME_n. Thus the objectives of the investigation were (i) to evaluate the effects of xylanase supplementation on performance of broiler chickens (experiment 1), and (ii) to evaluate the effects of xylanase on jejunal viscosity, nutrient digestion, AME, and cecal digesta VFA concentration (experiment 2).

MATERIALS AND METHODS

The experimental procedures were approved by the Massey University Animal Ethics Committee and complied with the New Zealand Code of Practice for the Care and Use of Animals for Scientific Purposes.

Experiment 1—Growth Performance

Diets. Two basal diets (Table 1), one based on corn and the other based on wheat, were formulated to meet or exceed the recommended requirements for nutrients, except AME (~5% less), for broilers (NRC, 1994). The basal diets contained phytase (Axtra PHY, a *Buttiauxella* spp. phytase expressed in *Trichoderma reesei*) at 500 phytase units (**FTU**)/kg of final feed. Each basal diet was split in 2 portions; one portion was the control and the other portion was supplemented with xylanase at 1,250 xylanase units/kg. The xylanase product is a mono-component preparation of endo-1,4-β-xylanase produced by a strain of *T. reesei*. One unit of xylanase was defined as the quantity of the enzyme that liberated 1 μmol of xylose equivalent per min. The enzymes along with the assay procedures were supplied by Danisco Animal Nutrition (Danisco UK Ltd., Marlborough, Wiltshire, UK). Diets were fed as mash.

Birds, Management, Feeding, and Performance Measurements. Male broiler (Ross × Ross 308) chicks were obtained at 1 d old from a commercial hatchery. The chicks were individually weighed and allocated to 24 brooder cages (8 chicks per cage) so that the average bird weight per cage was similar. The 4 dietary treatments were then randomly assigned to 6 cages each. On d 12, the birds were transferred to grower cages. The space allocation per bird in brooder and grower cages was 530 and 640 cm^2, respectively. The brooder and grower cages were housed in environmentally controlled rooms. The temperature was maintained at 31°C during the first week and then gradually reduced to 24°C by the end of third week. The birds received 20 h of fluorescent illumination and were allowed free access to the diets and water. A 2-phase feeding program (starter and finisher; Table 1) was used. The starter and finisher diets were offered from d 0 to 21 and 22 to 42, respectively. Body weights and feed intake were recorded at weekly intervals throughout the 42-d experimental period. Mortality was recorded daily. Feed conversion ratios were calculated by dividing total feed intake by weight gain of live plus dead birds.

Experiment 2—Digesta Characteristics, Nutrient Digestibility, and Total Tract Retention

Diets. The experiment used starter phase diets used in experiment 1 except that titanium dioxide (0.3%) was added to all diets as an indigestible digesta marker at the expense of either corn or wheat.

Table 1. Composition of basal diets (% as fed)[1]

	Starter, d 0–21[2]		Finisher, d 22–42	
Item	Corn	Wheat	Corn	Wheat
Ingredient, %, as fed				
Corn	57.4	—	58.5	—
Corn DDGS[3]	11.0	—	15.0	—
Wheat	—	60.2	—	63.3
Wheat bran	—	9.00	—	13.0
Soybean meal, 45%	26.5	22.3	19.0	14.0
Tallow	1.75	4.85	3.20	5.95
Vitamin-mineral premix[4]	0.33	0.33	0.33	0.33
Sodium bicarbonate	0.20	0.22	0.20	0.29
Salt	0.38	0.38	0.34	0.35
Monocalcium phosphate	0.35	0.37	0.13	0.20
Limestone	1.70	1.69	1.70	1.65
L-Lys-HCl	0.14	0.25	0.20	0.34
DL-Met	0.19	0.23	0.13	0.19
L-Thr	0.10	0.19	0.09	0.22
Calculated analysis				
ME, kcal/kg	2,976	2,908	3,090	2,994
CP, %	21.0	21.1	18.6	18.2
Calcium, %	0.81	0.80	0.75	0.73
Available P, %	0.25	0.25	0.21	0.21
Digestible Lys, %	1.01	0.99	0.90	0.87
Digestible Met, %	0.47	0.47	0.39	0.39
Digestible Met + Cys, %	0.76	0.76	0.65	0.65
Digestible Thr, %	0.74	0.74	0.64	0.66
Digestible Trp, %	0.19	0.21	0.16	0.17

[1]All diets were top-dressed with Phytase (Axtra PHY, a *Buttiauxella* spp. phytase expressed in *Trichoderma reesei*) to supply 500 phytase units/kg of final feed.

[2]Titanium dioxide (0.3%) was added to all diets as an indigestible digesta marker at the expense of either corn or wheat for experiment 2.

[3]Analyzed chemical composition (% as is): DM (87.8), CP (29.1), starch (4.4), NDF (30.8), fat (9.6), ash (3.8), soluble nonstarch polysaccharides (NSP, 1.3), insoluble NSP (24.1), and total NSP (25.4).

[4]Supplied per kilogram of diet: antioxidant (ethoxyquin), 100 mg; biotin, 0.2 mg; calcium pantothenate, 12.8 mg; cholecalciferol, 60 μg; cyanocobalamin, 0.017 mg; folic acid, 5.2 mg; menadione, 4 mg; niacin, 35 mg; pyridoxine, 10 mg; *trans*-retinol, 3.33 mg; riboflavin, 12 mg; thiamine, 3.0 mg; DL-α-tocopheryl acetate, 60 mg; choline chloride, 638 mg; Co, 0.3 mg; Cu, 3.0 mg; Fe, 25 mg; I, 1 mg; Mn, 125 mg; Mo, 0.5 mg; Se, 200 μg; Zn, 60 mg.

Birds, Management, and Sample Collections. Male broiler chicks (Ross × Ross 308) were obtained at 1 d old from a commercial hatchery. The trial was conducted from 13 to 21 d of age. Prior to the introduction to cages (from d 0 to 12), the birds were reared in floor pens and fed a common starter wheat-corn-soybean meal-based diet (CP, 22.2%; Ca, 1.1%; and total P, 0.5%) with no added enzymes. On d 13, the birds were individually weighed and allocated to 24 cages (6 birds per cage) so that the average bird weight per cage was similar. The 4 dietary treatments (Table 1; starter phase only) were then randomly assigned to 6 replicate cages. The cages were housed in environmentally controlled rooms. The temperature was maintained at 26°C on d 13 and then gradually reduced to 24°C by d 21. The birds received 20 h of fluorescent illumination daily and were allowed free access to the diets and water throughout the experimental period.

From d 17 to 20 posthatching, feed intake and total excreta output were measured quantitatively per cage over 4 consecutive days for the determination of nutrient retention and AME. On d 21, all birds were euthanized by intracardial injection of sodium pentobarbitone and contents of the lower half of the ileum were expressed by gentle flushing with distilled water. Digesta from birds within a cage were pooled, resulting in 6 samples per dietary treatment, and frozen immediately after collection. Jejunal and cecal digesta from 4 birds per cage were used for viscosity and short-chain fatty acid (VFA and lactic acid) measurements, respectively.

Laboratory Analysis

The viscosity of the jejunal digesta samples was read immediately upon collection. Briefly, within 30 min of collection, 1 g of thoroughly mixed digesta sample was vortex mixed and centrifuged at 22,640 × *g* for 15 min. The supernatant was then separated to carry out digesta viscosity measurements. Viscosity was measured using a Rheometer (Anton Paar Physica MCR 301 Rheometer, Anton Paar GmbH, Graz, Austria) fitted with a plate-plate geometry and a gap of 2 mm appropriate for small volumes of centrifuged digesta. The supernatant was loaded onto the rheometer platform using a micropipette attached with a tapered tip. Flow curves for each sample were obtained by shearing the samples at an increasing shear rate up to 1,400 s^{-1} within 240

s. The temperature of the sample was maintained at 60°C during the measurements. The shear rate-stress data were fitted to a Newtonian model, using the built-in software provided with the instrument. This method is a similar setup to that used by the Brookfield viscometer, but the accuracy was greater. The results are presented as solution viscosity (mPa·s).

The samples of excreta and ileal digesta were freeze-dried and along with samples of the diets ground to pass through a 0.5-mm sieve and stored in airtight plastic containers at −4°C until chemical analyses. All samples were analyzed for DM, nitrogen, gross energy (**GE**), fat, and titanium. Samples of diets and excreta were also analyzed for calcium, phosphorus, neutral detergent fiber (**NDF**), and acid detergent fiber (**ADF**). Dry matter determination was carried out according to standard procedures (AOAC International, 2005, method 930.15). Nitrogen was determined by the combustion method (AOAC International, 2005, method 968.06) using a CNS-2000 carbon, nitrogen, and sulfur analyzer (Leco Corporation, St. Joseph, MI). The CP values were derived from multiplying the assayed nitrogen values by a factor of 6.25. Gross energy was determined using an adiabatic bomb calorimeter (Gallenkamp, London, UK), standardized with benzoic acid. Fibertec System M (Tecator, Höganäs, Sweden) was used for determination of NDF and ADF. Titanium content was measured on a UV spectrophotometer following the method of Short et al. (1996). Fat content was determined following Soxhlet extraction procedure. Briefly, fat in samples were dissolved by repeatedly washing with petroleum-ether by refluxing in a Soxtec apparatus (Soxtec System HT 1043 Extraction Unit, Höganäs, Sweden). The solubilized fat was then collected in the distillation flask and the increase in weight of the flask represented the dissolved fat. The samples were wet acid digested with nitric and perchloric acid mixture (AOAC International, 2005; method 990.08), and concentrations of calcium and phosphorus were determined at specific wavelengths for each element (calcium, 393.3 nm; phosphorus, 185.9 nm) by inductively coupled plasma-optical emission spectroscopy using a Thermo Jarrell Ash IRIS instrument (Thermo Jarrell Ash Corporation, Franklin, MA). The instrument was calibrated against standards (Junsei Chemical Co., Ltd., Tokyo, Japan) of known concentration. The basal diets were further analyzed for the starch and nonstarch polysaccharides (**NSP**) levels. Briefly, total starch was determined by a modified version of Englyst (Englyst et al., 2000), which involved initial heat dispersion together with heat stable amylase followed by treatment with alkali to disperse any retrograded type III resistant starch. A pH 4.5 buffered aliquot was treated with amyloglucosidase to release glucose, which was quantified by high performance anion exchange chromatography with pulsed amperometric detection. The NSP was determined by the method of Englyst (Englyst et al., 1994), whereby starch was completely dispersed and then hydrolysed enzymatically. The NSP was isolated by precipitation in 80% ethanol then hydrolysed by sulfuric acid and the released component sugars measured by gas chromatography as their alditol acetate derivatives. Xylanase activity in feed was measured using a modified method based on the Megazyme xylanase assay kit (Megazyme International Ireland Ltd., Bray, Ireland).

The cecal samples were thawed on ice for short-chain fatty acid assay. D- and L-Lactic acids were measured using a Megazyme assay kit (K-DLATE, Megazyme International Ireland Ltd., Wicklow, Ireland), as per procedures described by Noll (1988) and Gawehn (1988), respectively. Volatile fatty acids were determined with gas chromatography as per procedures outlined by Cottyn and Boucque (1968). The sample was deproteinized using metaphosphoric acid. The supernatant was injected directly into gas chromatography (Carlo Erba 5380, capillary column Alltech ATTM-1000, 15 m × 0.53 mm ID, 1.00 um film) with hydrogen as the carrier gas, flame ionization detector, and iso-caproic acid as an internal standard.

Calculations and Statistical Analysis

The AME values of the diets were calculated using the following formula, with appropriate corrections for differences in moisture content.

$$\text{AME, kcal/kg of diet} = \frac{(\text{feed intake} \times \text{GE}_{\text{diet}}) - (\text{excreta output} \times \text{GE}_{\text{excreta}})}{\text{feed intake}},$$

where GE is given in kilocalories per kilogram, and feed intake and excreta output in kilograms per day.

Nitrogen-corrected AME were determined by correction for zero nitrogen retention by simple multiplication with 8.22 kcal per gram nitrogen retained in the body as described by Hill and Anderson (1958).

The apparent ileal digestibility of DM, nutrients (CP and fat), and GE was calculated by the following formula using the titanium marker ratio in the diet and ileal digesta:

$$\text{apparent ileal digestibility, \%} = \left[\frac{(\text{NT/Ti})_{\text{diet}} - (\text{NT/Ti})_{\text{ileal digesta}}}{(\text{NT/Ti})_{\text{diet}}}\right] \times 100,$$

where $(\text{NT/Ti})_{\text{diet}}$ = ratio of component and titanium in the diet, and $(\text{NT/Ti})_{\text{ileal digesta}}$ = ratio of component and titanium in ileal digesta. Component can be DM, CP, fat, or GE.

Apparent total tract retention of DM, fat, CP, calcium, phosphorus, NDF, and ADF were calculated as follows:

$$\text{retention, \%} = \left[\frac{(\text{feed intake} \times \text{component}_{\text{diet}}) - (\text{excreta output} \times \text{component}_{\text{excreta}})}{(\text{feed intake} \times \text{component}_{\text{diet}})}\right] \times 100.$$

Component can be DM, fat, CP, calcium, phosphorus, NDF, or ADF. Feed intake and excreta output are given in kilograms per day and components as a percentage.

Data were analyzed as a completely randomized design with 2 × 2 factorial treatment arrangements using the GLM procedures of SAS (SAS Inst. Inc., Cary, NC). The model included the main effects of diet type, xylanase, and associated 2-way interactions. Treatment effects were determined with orthogonal contrasts for a 2 × 2 factorial arrangement. The cage was the experimental unit for all the response criteria. Differences were considered significant at $P \leq 0.05$.

RESULTS

The assayed xylanase activities in xylanase-treated diets in starter phase were 1,571 and 1,676 U/kg in corn- and wheat-based diets, respectively. The corresponding values for finisher phase were 1,741 and 1,458 U/kg for corn- and wheat-based diets, respectively.

Experiment 1—Growth Performance

In the starter phase (d 0–21), there was no interaction ($P > 0.05$) between diet type and supplemental xylanase on growth performance (Table 2). However, main effects were observed in the starter phase in which case birds fed wheat diets grew faster, consumed more feed, and had better feed per gain ($P < 0.01$) than birds fed corn diets, whereas birds receiving supplemental xylanase showed improvements in these parameters (except feed intake) relative to the control. An interaction ($P < 0.01$) was observed between diet type and supplemental xylanase on BW gain and feed per gain in the finisher phase (d 22–42; Table 2) in which case supplemental xylanase improved BW gain and feed per gain in wheat and not in corn diets (Table 2). There was no interaction ($P > 0.05$) between diet type and supplemental xylanase on growth performance over the entire experiment (d 0–42), but main effects on growth performance were significant ($P < 0.05$) for diet type and supplemental xylanase (except on feed intake). Birds fed diets with xylanase showed improved ($P < 0.01$) BW gain (2,457 vs. 2,275 g) and feed per gain (1.677 vs. 1.762) relative to birds fed diets without xylanase. The diet type effect was such that BW gain and feed per gain were greater ($P < 0.01$) in wheat diets compared with corn diets.

Experiment 2—Digesta Characteristics, Nutrient Digestibility, and Retention

Wheat diets were determined to contain more than twice the concentration of soluble NSP (Table 3), and the concentrations of soluble arabinose and xylose in wheat diets were 7.25 and 5.35 times the concentration in corn diets. The corn diets had greater concentration of insoluble NSP (10.7 vs. 9.75%) compared with wheat diets (Table 3).

Table 2. Influence of xylanase supplementation on the performance of male broilers fed corn- or wheat-based diets (0–42 d posthatching), experiment1[1]

		BW gain, g/bird			Feed intake, g/bird			Feed per gain,[2] g/g		
Item	Xylanase	d 0–21	d 22–42	d 0–42	d 0–21	d 22–42	d 0–42	d 0–21	d 22–42	d 0–42
Diet										
Corn	−	655	1,458^{c}	2,113	979	2,759	3,738	1.494	1.964^{a}	1.810
	+	709	1,501^{c}	2,210	985	2,766	3,751	1.425	1.920^{a}	1.753
Wheat	−	731	1,707^{b}	2,438	1,026	3,030	4,056	1.422	1.853^{b}	1.715
	+	782	1,922^{a}	2,704	1,061	3,174	4,235	1.369	1.703^{c}	1.601
SEM		18.0	38.4	47.4	26.6	95.9	117	0.023	0.022	0.017
Main effect, diet										
Diet										
Corn		682^{b}	1,479^{b}	2,162^{b}	982^{b}	2,763^{b}	3,745^{b}	1.460^{a}	1.942^{a}	1.781^{a}
Wheat		757^{a}	1,815^{a}	2,571^{a}	1,044^{a}	3,102^{a}	4,145^{a}	1.396^{b}	1.778^{b}	1.659^{b}
SEM		12.7	27.8	33.5	18.8	67.8	82.5	0.016	0.016	0.012
Xylanase										
−		693^{b}	1,582^{b}	2,275^{b}	1,003	2,894	3,897	1.458^{a}	1.908^{a}	1.762^{a}
+		746^{a}	1,712^{a}	2,457^{a}	1,023	2,970	3,993	1.397^{b}	1.811^{b}	1.677^{b}
SEM		12.7	27.18	33.5	18.8	67.8	82.5	0.016	0.016	0.012
Probability										
Diet		<0.01	<0.01	<0.01	0.03	<0.01	<0.01	0.01	<0.01	<0.01
Xylanase		<0.01	<0.01	<0.01	0.45	0.44	0.42	0.02	<0.01	<0.01
Diet × xylanase		0.92	0.04	0.09	0.60	0.48	0.49	0.74	0.03	0.11

[a–c]Means assigned different letters within a factor of analysis (diet, xylanase, and their interactions) are significantly different, $P < 0.05$.

[1]Each mean represents values from 6 replicates (8 birds/replicate).

[2]Corrected for mortality.

Table 3. Analyzed chemical composition of basal diets, experiment 2 (% as fed)[1]

Item	Corn	Wheat
DM, %	89.4	90.7
Gross energy, kcal/kg	3,965	4,056
CP, %	21.7	21.7
Fat, %	3.89	4.67
Neutral detergent fiber, %	13.6	13.4
Acid detergent fiber, %	4.11	4.35
Starch, %	38.5	37.4
Calcium, %	0.65	0.69
Phosphorus, %	0.56	0.54
Nonstarch polysaccharide, %		
Soluble		
Rhamnose	0.16	0.14
Arabinose	0.08	0.58
Xylose	0.17	0.91
Mannose	0.24	0.20
Galactose	0.20	0.28
Glucose	0.66	1.46
Uronic acid	0.33	0.36
Total soluble	1.83	3.94
Insoluble		
Rhamnose	0.02	0.05
Arabinose	2.43	2.31
Xylose	2.52	2.95
Mannose	0.12	nd[2]
Galactose	1.69	1.20
Glucose	3.22	2.50
Uronic acid	0.66	0.73
Total insoluble	10.7	9.75
Total nonstarch polysaccharides	12.5	13.7

[1]Samples analyzed in duplicates.

[2]nd, not detected.

There was an interaction ($P = 0.01$) between diet type and supplemental xylanase on jejunal digesta viscosity such that greater reduction of viscosity due to supplemental xylanase was observed in birds fed wheat diets (5.22 to 2.22 mPa·s) than in corn diets (3.72 to 2.37 mPa·s; Table 4). There were no interactions ($P > 0.05$) between diet type and xylanase on VFA and lactic acid concentrations in the cecal digesta (Table 4). However, cecal digesta from birds fed wheat diets had higher ($P < 0.05$) concentrations of acetic and butyric acids than that from birds fed corn diets. In contrast, corn diets resulted in higher ($P < 0.01$) cecal concentration of propionic, valeric, and iso-varelic acids relative to wheat diets. The main effects of xylanase was such that cecal digesta of birds fed xylanase had higher ($P = 0.01$) concentration of acetic acid (73.5 vs. 47.7 mM/L) compared with birds fed nonsupplemented diets.

There was no interaction ($P > 0.10$) between diet type and supplemental xylanase on the apparent ileal digestibility of DM, fat, CP, and GE (Table 5). Compared with the control, birds fed diets with supplemental xylanase had higher ileal digestibility of fat (87.3 vs. 82.8%, $P < 0.01$), CP (82.9 vs. 79.4%, $P < 0.01$), and GE (74.4 vs. 72.5%, $P < 0.05$). Birds fed wheat diets exhibited higher ileal digestibility of fat ($P = 0.01$) and CP ($P < 0.05$) than those fed corn diets. The feed intake during the 4 d collection of the excreta was not influenced ($P > 0.05$) by the dietary treatments. The feed intake for the corn fed birds was 297 and 294 g/bird for the control and xylanase-fed birds, respectively, and the corresponding values for the birds fed wheat diets were 295 and 304 g/bird, respectively. Data on the apparent total tract retention for DM, fat, calcium, phosphorus, NDF, and ADF, and AME_n are shown in Table 5. Interaction ($P < 0.05$) between diet type and supplemental xylanase was observed only for fat, which was due to supplemental xylanase having greater improvement of fat retention in birds fed wheat (8.8 percentage units over the respective control) than those fed corn (4.2 percentage units over the respective control) diets. Birds fed corn diets retained more ($P < 0.05$) DM, phosphorus, NDF, and ADF than those fed wheat diets; however, the AME_n was not different ($P = 0.45$) between corn and wheat diets. The main effect of xylanase was found to be significant, with birds fed diets

Table 4. Influence of xylanase supplementation on jejunal digesta viscosity and cecal digesta short-chain fatty acids concentrations in 21-d-old broiler chickens fed corn or wheat diets, experiment 2

			Short-chain fatty acid concentration, mM/L					
Item	Xylanase	Jejunal viscosity, mPa·s	Acetic	Propionic	Butyric	Valeric	Iso-valeric	Lactic
Diet								
Corn	−	3.72[b]	38.5	7.76	23.4	1.80	1.43	0.31
	+	2.37[c]	56.5	9.38	26.5	2.14	1.53	0.40
Wheat	−	5.22[a]	56.8	4.94	36.5	1.15	0.89	0.50
	+	2.22[c]	90.5	5.46	34.4	1.17	0.87	0.42
SEM		0.29	8.51	1.03	3.14	0.19	0.17	0.07
Main effect, diet								
Corn		3.04[b]	47.5[b]	8.57[a]	24.9[b]	1.97[a]	1.48[a]	0.36
Wheat		3.72[a]	73.7[a]	5.20[b]	35.5[a]	1.16[b]	0.88[b]	0.46
SEM		0.20	6.02	0.73	2.22	0.14	0.12	0.05
Main effect, xylanase								
−		4.47[a]	47.7[b]	6.35	30.0	1.47	1.16	0.41
+		2.29[b]	73.5[a]	7.42	30.4	1.65	1.20	0.41
SEM		0.20	6.02	0.727	2.22	0.14	0.12	0.05
Probability								
Diet		0.03	0.01	0.01	0.01	<0.01	0.01	0.13
Xylanase		<0.01	0.01	0.31	0.89	0.36	0.81	0.99
Diet × xylanase		<0.01	0.37	0.60	0.42	0.42	0.74	0.21

[a–c]Means assigned different letters within a factor of analysis (diet, xylanase, and their interactions) are significantly different, $P < 0.05$. n = 6.

with supplemental xylanase having greater retention ($P < 0.05$) of DM (71.9 vs. 70.0%), fat (87.9 vs. 82.6%), phosphorus (56.1 vs. 53.0%), NDF (32.3 vs. 27.9%), and ADF (16.6 vs. 9.57%) than those fed diets without xylanase. As a result, birds receiving diets with supplemental xylanase derived more dietary AME_n (3,059 vs. 2,995 kcal/kg; $P < 0.01$) compared with those fed diets without xylanase.

DISCUSSION

The BW gain, feed intake, and feed per gain of birds fed wheat diets were better than those fed corn diets. This observation was unexpected because it is well recognized that feed ingredients such as wheat that are rich in water-soluble and viscous NSP result in poor broiler growth performance relative to nonviscous cereals such as corn (Marquardt et al., 1994; Jia et al., 2009; Rodriguez et al., 2012). An accepted paradigm is that increased intestinal digesta viscosity due to soluble NSP is the key mechanism for poor growth and feed utilization in broilers fed wheat-based diets (Bedford and Schulze, 1998). Indeed, the present data showed that wheat diets contained more than double the concentration of soluble NSP relative to corn diets, which may be implicated in the higher jejunal digesta viscosity observed in birds fed wheat diets. Whereas concentration of soluble fiber and attendant deleterious effects of elevated intestinal viscosity are important considerations in poultry feed formulations, the present data suggest that concentration of insoluble NSP might also be relevant, particularly in younger birds. Insoluble NSP can affect gut transit time and gut motility, and may also hinder the ability of endogenous enzymes to gain access to their respective substrates, all of which collectively impair nutrient utilization and bird productivity (Bedford and Schulze, 1998). It is no coincidence that corn diets had slightly higher concentration of insoluble NSP and exhibited poor growth performance. It is generally held that corn-based diets have less fibrous components that can affect nutrient digestion (Slominski, 2011). However, with the poultry industry increasingly using cereal co-products such as cDDGS to manage feed costs, it is important to consider that a characteristic of cereal co-products is high concentrations of insoluble NSP, particularly arabinoxylans. For example, the concentration of insoluble arabinoxylans has been reported to be 4.7% in corn and 12% in cDDGS (Bach Knudsen, 2011). As observed in the present study, even modest inclusion of cDDGS in corn-based diets could result in poor broiler performance relative to wheat-based diets.

The benefits of exogenous xylanases (endo-1,4-β-xylanase) in wheat-based diets for poultry is well documented and has been extensively reviewed (Bedford and Schulze, 1998; Adeola and Cowieson, 2011; Slominski, 2011). The positive effect of supplemental xylanase was observed on growth performance throughout the entire experiment (experiment 1) and nutrient utilization (experiment 2). The interaction between diet type and supplemental xylanase was evident only in the finisher phase, wherein xylanase had more pronounced effects on growth performance in wheat diets, perhaps mediated via reduction of intestinal digesta viscosity. The lack of interactive effects in the starter phase suggests that young birds are particularly sensitive to both soluble and insoluble NSP and could benefit from supplemental xylanases irrespective of the cereal type. Although viscosity per se is unlikely to be a major problem, the use of xylanase may have beneficial effects in corn diets for young birds, perhaps through improvements in nutrient digestibility. This effect is probably mediated through changes in the cell wall architecture achieved by hydrolysis of structurally important arabinoxylans, which may release encapsulated nutrients. This might explain why xylanase improved energy and nutrients utilization in both wheat- and corn-based diets. Indeed, there is evidence that diets based on low-NSP wheat still respond well to enzyme addition (Persia et al., 2002), suggesting there is a mechanism other than viscosity reduction. Previous evaluation of xylanase in corn diets fed to broilers suggested the mechanism may be a result of an increase in feed use efficiency driven primarily through a significant increase in BW gain with a marginal effect on feed intake (O'Neill et al., 2011; O'Neill et al., 2012b). Cowieson et al. (2010) found a significant xylanase improvement in feed per gain with no effect on feed intake in broiler fed corn diets and a substantial increase in BW gain. This was accompanied by a significant improvement in ileal nutrient digestibility, supporting the mechanism of increased feed use efficiency, which has also been observed by others (Zanella et al., 1999).

The anaerobic fermentation of material entering the ceca produces mainly VFA in largely conservative molar proportions of acetic acid > butyric acid > propionic acid (Svihus et al., 2013). Wheat diets resulted in increased ceca concentrations of acetic and butyric acids, whereas corn diets exhibited higher concentrations of propionic, valeric, and isovaleric acids. Hübener et al. (2002) observed similar cereal grain-dependent cecal fermentation patterns in broilers fed corn or wheat/rye-based diets. The concentration of VFA in the hindgut is indicative of microbial diversity and activity as influenced by available substrates (Kiarie et al., 2007; Kiarie et al., 2013). The NSP composition of feed ingredients can bring about significant changes to the microbial ecology of the gut (Apajalahti, et al., 2004). For example, (Rodriguez et al., 2012) observed the number of *Escherichia coli* and *Lactobacilli* to be higher in the digesta of broilers fed wheat and barley versus those fed corn diets. These bacteria are predominantly acetic and butyric acid producers (Guilloteau et al., 2010) and might explain the higher concentrations of these 2 acids in the ceca digesta of wheat-fed birds. Supplemental xylanase increased ceca concentration of acetic acid as has been previously observed (Choct et al., 1996). Bacteria in the gut derive most of their carbon and energy from luminal compounds (dietary, endogenous, or

Table 5. Influence of xylanase supplementation on the apparent ileal digestibility and total tract retention of nutrients, fiber, and energy in 21-d-old broiler chickens fed corn or wheat, experiment 2

		Ileal digestibility, %				Retention, % of intake						
Item	Xylanase	DM	Fat	CP	Gross energy	DM	Fat	Calcium	Phosphorus	NDF[1]	ADF[1]	AME_n, kcal/kg
Grain												
Corn	−	71.0	81.0	78.5	73.2	70.8	83.7[b]	52.5	58.0	31.7	11.9	3,005
	+	71.3	86.2	82.6	74.1	72.4	87.2[a]	54.1	60.0	36.2	19.4	3,061
Wheat	−	69.7	84.6	80.2	71.8	69.3	81.4[c]	48.0	48.1	24.0	7.23	2,985
	+	72.6	88.4	83.2	74.7	71.3	88.6[a]	51.4	52.2	28.4	13.9	3,057
SEM		0.966	1.087	0.514	0.839	0.375	0.771	1.872	0.461	1.022	2.29	16.18
Main effect, diet												
Corn		71.2	83.6[b]	80.6[b]	73.6	71.6[a]	85.5	53.3	59.0[a]	33.9[a]	15.7[a]	3,033
Wheat		71.1	86.5[a]	81.7[a]	73.3	70.3[b]	85.0	49.7	50.1[b]	26.2[b]	10.6[b]	3,026
SEM		0.68	0.77	0.36	0.59	0.27	0.55	1.32	0.98	0.72	1.62	11.44
Main effect, xylanase												
−		70.4	82.8[b]	79.4[b]	72.5[b]	70.0[b]	82.6[b]	50.3	53.0[b]	27.9[b]	9.57[b]	2,995[b]
+		71.9	87.3[a]	82.9[a]	74.4[a]	71.9[a]	87.9[a]	52.8	56.1[a]	32.3[a]	16.6[a]	3,059[a]
SEM		0.68	0.77	0.36	0.59	0.27	0.55	1.32	0.98	0.72	1.62	11.44
Probability												
Diet		0.97	0.01	0.05	0.65	0.01	0.59	0.07	<0.01	<0.01	0.04	0.45
Xylanase		0.12	<0.01	<0.01	0.04	<0.01	<0.01	0.19	0.04	<0.01	0.01	<0.01
Diet × xylanase		0.19	0.52	0.23	0.25	0.62	0.03	0.63	0.46	0.95	0.86	0.63

[a–c]Means assigned different letters within a factor of analysis (diet, xylanase, and their interactions) are significantly different, $P < 0.05$. n = 6.

[1]NDF, neutral detergent fiber; ADF, acid detergent fiber.

both), which are either resistant to attack by digestive fluids or absorbed so slowly by the host that bacteria can successfully compete for them. It is inevitable that the use of any additive that influences the digestibility of the diet will change the selection pressures on the resident microbiota, which in turn will moderate the efficiency with which the host utilizes its feed (Bedford and Cowieson, 2011; Kiarie et al., 2013). It has been demonstrated that supplementation of poultry diets with exogenous enzymes can effect changes to the composition and metabolic potential of gut microflora (Choct et al., 1996; Hübener et al., 2002). This may be achieved by improving the absorption of nutrients in the proximal gut, which results in a reduction in the quantity of nutrients in the terminal ileum and ceca that are available as substrates for bacteria (Apajalahti et al., 2004). Additionally, supplemental xylanase not only increased nutrient digestibility but also was shown to increase concentration cecal VFA concentration linked to increased flow of fermentable xylo-oligomers into the ceca (Choct et al., 1996, 1999). There are apparently few studies where the in situ generation of oligosaccharides has been monitored in chickens fed diets containing xylanases; however, partial hydrolysis and rupturing of NSP-containing cell walls have been associated with reduced recovery of NSP when feedstuffs were incubated with fiber-degrading enzymes (Kiarie et al., 2013).

Ileal nutrient digestibility data showed diet types differences with wheat diets showing superiority in fat and CP digestibilities. In contrast, birds fed corn-based diets retained more DM, phosphorus, and fiber relative to wheat-based diets. However, these differences did not contribute to gross efficiencies of feed use by birds, as the 2 diet types did not exhibit differences in AME_n. These observations suggested that the superior growth performance (experiment 1) in birds fed wheat diets relative to birds fed corn diets could not be explained by nutrient digestibility and retention (experiment 2). Perhaps better growth performance in birds fed wheat diets might have been due to improved gut health and function mediated through microbial activity. For example, butyric acid has been associated with stimulation of the digestive enzyme secretions, modification of intestinal luminal microbiota, improvement of the epithelial integrity and defense systems, tissue development, and repair and downregulation of bacteria virulence (Guilloteau et al., 2010). Although these mechanisms were not evaluated in the present study, the high concentrations of acetic and butyric acids seen in birds fed wheat-based diets could partly explain superior growth performance relative to the corn diets. Improvements in growth performance with supplemental xylanase can be attributed to increase in nutrient digestibility and retention as has been reported elsewhere (e.g., Cowieson et al., 2010; Nian et al., 2011; Romero et al., 2011). It is well accepted that xylanase is effective in diets based on viscous cereals through the mechanism of gut viscosity reduction. However, the mechanism in corn-based diets is unclear. Volatile fatty acids are rapidly absorbed, metabolized, or both in the hindgut. Annison et al. (1968) estimated that ceca VFA could provide up to 11% of the ME for mature chickens; however, subsequent work estimated the amount of energy from ceca fermentation to approximate 3 to 5% of the total energy needs of the chicken (Jørgensen et al., 1996; Jamroz et al., 2002). This has led to the suggestions that energy derived from microbial fermentation in the chicken is small in quantity and inefficient as a metabolic fuel (Choct et al., 1996). However, there is evidence that VFA can induce other physiological responses that may play a role in the overall dietary nutrients digestion and absorption and gut health (Cherbut, 2003; Guilloteau et al., 2010; Liou, 2013). The implication is that VFA-trigger neuro-hormonal response through peptide YY resulting in (gastroparesia or ileal brake) delayed gastric emptying and duodenal transit rates (Cuche et al., 2000; Park et al., 2013) with consequence of enhanced diet digestion and nutrient absorption in the small intestines (O'Neill et al., 2012a; Singh et al., 2012). Indeed, intra-colonic infusions of VFA have been shown to inhibit colonic motility in mammals, linked to peptide YY (Cherbut et al., 1998; Cuche et al., 2000). In chickens, intraluminal infusion of fatty acids precipitated regulation of gastrointestinal motility via inhibition of gastric electrical activity, the increase in the number of duodenal anti-peristaltic spike bursts, and the elongation of the migrating myoelectric complex (Martinez et al., 1995). These observations suggested that the participation of intraluminal fatty acids in the regulation of gastrointestinal motility is a phenomenon present along the phylogenetic scale with similar characteristics among different species.

Furthermore, Courtin et al. (2008) showed that the inclusion of wheat oligosaccharides isolated from xylanase-treated wheat bran improved feed per gain in corn-fed birds to the same extent as the inclusion of the same xylanase in the ration. It is suggested that the xylanases provides oligosaccharides via depolymerization of NSP, which are fermented to VFA in the ceca in such concentrations that they trigger an neuro-hormonal response that results in delayed gastric emptying (Goodlad et al., 1987) and duodenal transit rates (Park et al., 2013). Taken together, the foregoing describes possible explanations of fundamental mechanisms that may underlie situations in which xylanase may increase nutrient utilization in diets based on nonviscous and viscous cereals. An understanding of these mechanisms may provide an opportunity to develop strategies for optimizing use of xylanases across diet types.

Different diet types resulted in differences in growth performance that could not be explained by nutrient utilization and AME_n. However, observed differences between wheat and corn diets on ceca VFA suggest differential impact on microbial profiles that could explain effects of diet types on growth performance. Xylanase was efficacious across different diet types on growth performance. These benefits were related to the break-

down of both soluble and insoluble arabinoxylan fractions in corn- and wheat-based diets linked to better nutrient digestibility and retention and ceca fermentation.

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