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The impact of xylanase and body weight, and their interaction, on the utilization of dietary components in swine

by

Sarah A. Weiland

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Animal Science

Program of Study Committee:
John F. Patience, Major Professor
Cheryl L. Morris
Jason W. Ross

Iowa State University

Ames, Iowa

2017

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DEDICATION

To my parents, Dave and Jane Weiland. Your unending love, support, and encouragement have allowed me to pursue this unexpected, wonderful career. I will never be able to thank you enough.

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ABSTRACT

The increased use of corn co-products in swine diets has prompted interest in the ability of carbohydrase enzymes, such as xylanase, to assist the pig in fiber degradation. It has been proposed that, by breaking down arabinoxylans, xylanase enzymes can mitigate the negative effects of fiber on digestive efficiency. However, previous studies with xylanase in corn-based diets in swine have produced inconsistent results. A digestibility study was conducted in order to better understand how the enzyme impacts diet utilization in the pig by measuring the impact of xylanase on energy and nutrient digestibility in the small and large intestines and across the total tract. Thirty-two gilts (32.6 ± 0.47) were surgically fit with T-cannulae at the terminal ileum, housed individually, and assigned to 1 of 4 dietary treatments in a complete randomized design. Diets were arranged in a 2 × 2 factorial by adding 0% or 0.017% xylanase (Econase XT, Ab Vista) to corn-soybean meal diets with 0% (lower fiber: LF) or 30% (higher fiber: HF) corn DDGS. Three collection periods consisting of a 2 d fecal collection followed by a 3 d ileal collection occurred at average BW of 46.0 ± 0.4, 54.1 ± 0.4, and 70.3 ± 0.5 kg, respectively, for a total of 24 observations per dietary treatment. Pigs remained on the same diet through the trial to test the impact of BW on enzyme response. Ileal and fecal samples were analyzed to determine the apparent ileal digestibility (AID) and apparent total tract digestibility (ATTD) of GE, DM, NDF, ADF, and nitrogen, and the AID of starch and AA. Apparent digestibility values for fat were corrected for endogenous losses and true ileal digestibility (TID) and true total tract digestibility (TTTD) of fat was reported.

Xylanase inclusion increased the AID of DM, starch, and nitrogen and tended to increase the AID of GE in LF diets, but had no effect in HF diets, resulting in XI × FL interactions ($P \leq 0.059$). Xylanase decreased the AID of NDF and tended to decrease the AID of ADF in LF diets, but had no impact in HF diets, resulting in FL × XI interactions ($P \leq 0.097$). However, the decrease in fiber digestibility may have been an artifact rather than a true result. Xylanase inclusion tended to decrease the AID of hemicellulose but increase the hindgut disappearance of NDF, ADF, and hemicellulose ($P \leq 0.100$). In LF diets, xylanase tended to decrease the ATTD of ADF but increased the ATTD of ADF in HF diets, leading to a trend for a XI × FL interaction. ($P = 0.091$). As BW increased, xylanase inclusion led to different patterns of the ATTD of DM and protein, but the xylanase treatment did not differ from the non-xylanase treatment at any of the three BW. In conclusion, there was no impact of BW on the enzyme response in 46.0 to 70.3 kg pigs. Xylanase appears to liberate nutrients for digestion in the small intestine in corn-soybean meal diets in growing pigs, but corn DDGS do not appear to be a suitable substrate for the xylanase enzyme.

CHAPTER I

LITERATURE REVIEW

Introduction

The growth of the ethanol industry has increased the demand, thereby increasing the price of corn in the United States, resulting in a need for alternative feedstuffs. Co-products of the ethanol industry vary in composition and nutrient digestibility depending on processing technique, but many are available and priced competitively for use by the animal feed industry.

Ethanol can be made using wet milling or dry milling techniques. In the dry milling process, starch is removed from corn and further fermented and processed to create ethanol. With removal of starch, which makes up approximately 70% of corn (Newman et al., 2016), other components of corn grain including fiber, protein, and fat are concentrated, creating a product known as distillers dried grains (Jaworski et al., 2015). Distillers dried grains are then often combined with condensed distillers solubles (syrup) from the distillation process and dried to create distillers dried grains with solubles (DDGS).

Technological advances have allowed the ethanol industry to further extract oil from DDGS, resulting in DDGS products that range from 4% to >10% corn oil. Distillers dried grains with solubles containing 6 to 10% corn oil have DE and ME values similar to corn; however, DDGS with 4% corn oil have slightly lower DE and ME values, and DDGS at all oil levels have lower NE values (Table 1.1; NRC, 2012). Standardized total tract digestibility of phosphorus in corn DDGS is 65%, regardless of oil level, compared to 34% in corn (NRC, 2012). Although energy and phosphorus digestibility in corn DDGS differ from corn, with the degree of

difference depending on oil level, corn DDGS can be used as a substitute for corn and soybean meal in swine diets with appropriate adjustments in formulation.

Distillers dried grains with solubles are lower in starch and approximately 3 times higher in fiber compared to corn (Stein and Shurson, 2009). Dietary fiber is primarily composed of sugars bonded and arranged in a manner that prevents them from being broken down by endogenous enzymes in the small intestine of the pig. Dietary fiber can be partially fermented by microbes in the small and large intestine of the pig, producing VFA, which can then be absorbed and utilized by the pig for energy. However, fermentation and absorption of VFA in the intestines is not as calorically efficient for the animal as enzymatic digestion and absorption in the small intestine.

It is well established that corn DDGS can be included at up to 30% in swine feed without inhibiting growth performance as long as additional energy is added to meet the caloric needs of the pig (DeDecker et al., 2005; Linneen et al., 2008). Another study has shown that corn DDGS can be included up to 60% over the grow-finish period with no effect on final BW, ADG, ADFI, or feed efficiency compared to an isocaloric diet containing 30% corn DDGS (Weber et al., 2015). However, addition of fat to the diet to increase energy levels also increases dietary costs. The challenges for the swine industry are to maintain costs, meet the pig's caloric needs, and maintain productivity while feeding higher fiber diets that are digested and absorbed less efficiently than the traditional corn-soybean meal diets.

Carbohydrates

Characterizations of carbohydrates

Traditional swine diets in the midwestern United States consist predominantly of plant feedstuffs, including, but not limited to, corn, corn co-products, and soybean meal. The carbohydrates in these plant feedstuffs are the primary source of energy in swine diets, providing approximately 54% of total energy intake in traditional nursery diets and approximately 57% of the energy intake in traditional grow-finish diets (Tables 1.2-1.3). Plant carbohydrates vary greatly in sugar monomer composition, degree of polymerization, and bond type and arrangement. These characteristics impact the nutrient and energy availability of the feedstuff when consumed by the animal.

Simple carbohydrates and most starches in plants are highly digestible by endogenous enzymes in the small intestine of the pig, and are efficiently absorbed into the blood stream for utilization. Simple carbohydrates in plants include monosaccharides (1 sugar unit) and disaccharides (2 sugar units). The two forms of starch are amylose and amylopectin. Both amylose and amylopectin consist of α-1,4 linked glucose sugars. Amylopectin also contains α-1,6 branch points at approximately every 30 α-1,4 linkage. The α-1, 4 and α-1,6 bond linkages of starches are broken down by α-amylase, which is secreted in the mouth and pancreas of the pig, liberating oligosaccharides and disaccharides for further digestion and absorption in the small intestine.

A portion of the starch in feed, termed resistant starch (RS) is highly resistant to digestion by pancreatic amylase and is not absorbed in the small intestine of healthy individuals (Englyst et al., 1982; Asp, 1992). There are four different types of RS. The first consists of starch granules

that are enclosed within the indigestible plant matrix, rendering them inaccessible to α-amylase in the small intestine. Type II RS is caused by the granular structure of starch. Some regions of starch granules are highly ordered and crystalized, rendering them inaccessible to α-amylase; gelatinization of starch must occur to make the starch in these regions available to α-amylase. The third type of RS is not present in the native starch granule, but is caused by heating and cooling during processing, which results in the reordering of amylose molecules into a crystalized structure held together with hydrogen bonds. This process is known as retrogradation. The fourth type of RS is caused by chemical modification and is not present in native starch (Lattimer and Haub, 2010).

The percentage of RS varies with feed ingredients and processing techniques. Themeier et al. (2005) reported 0.5 – 0.7% RS in low and medium amylose corn, and 49.1 – 54.4% RS in high amylose corn. Cervantes-Pahm et al. (2014a) reported 1.0% RS in yellow dent corn and 1.1% RS in Nutridense corn. The wet-milling and dry-grinding processing techniques of ethanol production increase the access to type I and II RS; however, type III RS can be created during ethanol production due to the heating and cooling of corn grains. Therefore, corn DDGS are likely to contain type III RS. Corn DDGS has been reported to contain 5.5% RS in some studies (Srichuwong and Jane, 2011), and up to 18% in others (Li et al., 2014). The resistance of starch to hydrolyzation results in some starch leaving the small intestine before complete digestion and absorption occurs. The RS then enters the large intestine where it can become a substrate for microbial fermentation or be excreted in feces (Englyst et al., 1996).

The cell walls of plants are comprised (70-90%) of non-starch polysaccharides (NSP), or complex carbohydrates, bound together by a variety of intermolecular bonds, which cannot be digested by endogenous enzymes in the pig (de Vries, 2014). Cell wall polysaccharides are made

of pentoses (arabinose and xylose), hexoses (glucose, galactose, and mannose), 6-deoxyhexoses (rhamnose and fucose), and uronic acids (glucuronic and galacturonic acids; Theander et al., 1989). The most abundant NSP categories in plant cell walls are celluloses, hemicelluloses, and pectins (Grieshop et al., 2001).

Lignin is another main component of plant cell walls and is comprised of branched networks of phenylpropane units partially linked to non-cellulosic polysaccharides in the cell wall. This portion of the plant cell wall functions in the mechanical support of plants for vertical growth and has a role in protection, as the physical and chemical changes in the plant cell wall that occur during lignification aid in pathogen resistance (Iiyama et al., 1994).

Dietary fiber

The fraction of the diet that is indigestible by endogenous mammalian enzymes in the gastrointestinal tract is referred to as dietary fiber (Theander et al., 1994). By this definition, dietary fiber includes lignin, cellulose, hemicellulose, pectins, gums, β-glucans, and RS.

Dietary fiber can also be defined chemically as "the sum of non-starch polysaccharides and lignin" (Theander et al., 1994). In 2001, the American Association of Cereal Chemists (AACC) suggested the definition of dietary fiber was "the remnants of the edible part of plants and analogous carbohydrates that are resistant to digestion and absorption in the human small intestine with complete or partial fermentation in the human large intestine." The most appropriate definition of dietary fiber has been debated for many years; however, the varying chemical composition and behavior of cell wall material in plants during digestion has prevented a consensus from being reached.

Dietary fiber is very diverse structurally and physiologically, as the type and arrangement of sugars dictate the physiological properties of fiber including solubility, viscosity, and fermentability. Dietary fiber can be classified as soluble or insoluble. Insoluble fibers include regular β-1,4-linked sugars that allow the polysaccharides to crystalize, preventing the entrance of water molecules (Oakenfull, 2001). Soluble fibers contain β-1,4 and β-1,3 linkages. The irregular structure of soluble fibers prevents the formation of crystalline structures, thus allowing the entrance of water molecules, making these polysaccharides soluble (Oakenfull, 2001). Soluble fiber has the ability to thicken or form gels when in solution, thereby increasing digestive viscosity (Dikeman and Fahey, 2006). Insoluble fiber is not commonly associated with changes in viscosity, but rather increased gut fill and passage rate (Anderson, 1985; Wu et al., 2016). The interaction of soluble fiber with water increases surface area; therefore, soluble fiber is fermented at a faster rate compared to insoluble fiber (Oakenfull, 2001).

Analytical methods for measuring dietary fiber

Many methods of fiber analysis have been developed over the years, each of which has their own advantages and limitations. Appropriate fiber analysis must be repeatable and also relate to how the fiber is processed within the body (Mertens, 2003). Dietary fiber is defined physiologically, but must be measured chemically. Therefore, the challenge with dietary fiber analysis is to find methods that can represent the digestion that occurs within the gastrointestinal tract of the body using chemical measurements.

The majority of fiber analysis methods follow the same two steps: first, digestion of non-fibrous components of the diet including protein, fat, water, minerals, and simple carbohydrates, and second, quantification of the remaining undigested residue (Urriola, 2010). The first step in

the digestion procedure can be done using chemical compounds (acid, alkali, or detergents) or enzymes (amylase, amyloglucosidases, and proteases; Urriola, 2010). Quantification of the remaining undigested residue can be accomplished gravimetrically or using chromatography, gas liquid chromatography, or high performance liquid chromatography (Urriola, 2010). Chromatography provides data in the form of peaks, which can be used to identify the chemical compounds and amount of each chemical compound present in the sample.

The oldest and most commonly used fiber analysis in the feed industry is the crude fiber method, which is part of the Weende system of proximate analysis (Henneberg and Stohmann, 1859; Bach Knudsen, 2001). The Weende method divides carbohydrates into two portions, nitrogen free extract and crude fiber (Grieshop et al., 2001). Nitrogen free extract consists of carbohydrates, sugars, starches, and hemicelluloses. Crude fiber is the portion remaining after sequential extraction with diluted acid and alkali, followed by gravimetric determination of the remaining residue after drying (Bach Knudsen, 2001). The crude fiber method consistently measures fiber in various materials and is repeatable between laboratories; however, due to the solubilisation of the structural polysaccharides and lignin, this method only measures a small, variable fraction of the fiber component (Bach Knudsen, 2001; Mertens, 2003). Therefore, there is little relationship between crude fiber measurements and the definition of dietary fiber, as the crude fiber measurement may contain anywhere from 40-100% of the cellulose, 15-20% of the pentosans from hemicellulose, and 5 to 90% of the lignin depending on the feed material (Mertens, 2003).

The detergent methods developed by Van Soest and co-workers provided an alternative to the crude fiber method that more closely related the value from the analysis to the physiological properties of dietary fiber (Van Soest et al., 1991). These methods are chemical-

gravimetric procedures that measure the fraction of fiber in the feed that is insoluble in neutral detergents (NDF) or in acid detergents (ADF). The NDF analysis measures hemicellulose, cellulose and lignin, while the ADF analysis measures cellulose and lignin, allowing the calculation of hemicellulose by difference (Bailey and Ulyatt, 1970).

There are some limitations to the detergent methods. Soluble dietary fiber including pectins, mucilages, gums, and β-glucans are not recovered; therefore, the amount of fiber can be underestimated (Grieshop et al., 2001). However, cereal grains such as corn and corn co-products contain much higher amounts of insoluble fiber compared to soluble fiber, so low soluble fiber recovery is less concerning (Bach Knudsen, 1997; Johnston et al., 2003). Hemicellulose and pectin may remain in the ADF residue (Bailey and Ulyatt, 1970), and it is possible that starch and protein may contaminate the NDF residue (Theander and Åman, 1980). Several modifications have been proposed since the original publication of the NDF method of fiber analysis, including the use of different amylase enzymes, adding the amylase at different times during the assay, and varying incubation times (Van Soest et al., 1991). Neutral detergent fiber methodologies vary among laboratories depending on which modifications are adopted, making comparisons among laboratories challenging and in some cases, inappropriate.

Total dietary fiber (TDF) can be measured using the Prosky enzymatic-gravimetric method (AOAC Official method 985.29; AOAC Int., 2005), the Uppsala enzymatic-chemical method (AOAC Official method 994.13; AOAC Int., 2005) or the McClearly method (AOAC Official method 2009.01; AOAC Int., 2012). The Prosky enzymatic-gravimetric method begins with starch gelatinization and hydrolysis to dextrins using thermostable α-amylase, followed by protein hydrolysis via protease enzymes and decreased pH. After protein hydrolysis, starch dextrins are hydrolyzed using amyloglucosidase and further decreased pH. The sample is then

precipitated using alcohol, rinsed, dried, and weighed. After weighing, one duplicate is used to calculate protein and another is incinerated to determine ash. The TDF amount is equal to the weight of the dried residue less the weight of the protein and ash calculations (Prosky et al., 1985).

The Prosky method of fiber analysis can underestimate the RS component of dietary fiber due to the gelatinization step, which eliminates the 'resistant' quality of RS. Another disadvantage of the Prosky method is that non-digestible oligosaccharides are not measured, leading to underestimation of TDF in some samples (McCleary, 2007).

The Uppsala enzymatic-chemical method for TDF measurement uses α-amylase and amyloglucosidase to hydrolyze and remove starches. After the removal of starch, soluble polysaccharides are precipitated using absolute ethanol, and the combined soluble and insoluble fiber residue is hydrolyzed to neutral sugars and uronic acids. Neutral sugars are analyzed as alditol acetates by gas-liquid chromatography, uronic acids are measured using colorimetry, and Klason lignin is measured gravimetrically as the acid-insoluble portion lost when ashing (Theander and Westerlund, 1986; Theander et al., 1995). Total dietary fiber is measured indirectly as the sum of neutral sugars, uronic acids, and Klason lignin (Theander and Westerlund, 1986). The enzymatic-chemical method provides information on monosaccharide profile as well as the functional properties of the NSP by splitting it into soluble and insoluble components (Grieshop et al., 2001). However, this method is expensive, time consuming, and requires highly skilled and trained personnel; therefore, it is not widely used in commercial practice.

The McClearly method was first described in 2007 as an integrated procedure incorporating features of other AOAC Official Methods to measure the individual components of

dietary fiber including RS, non-digestible oligosaccharides, and available carbohydrates (McCleary, 2007). This method begins with incubation of the sample in α-amylase and amyloglucosidase in similar to physiological conditions to hydrolyze starches to dextrins and glucose without gelatinization. The sample is then subjected to protease enzymes to hydrolyze proteins. Alcohol is used to precipitate soluble dietary fiber (SDF), which is then recovered by filtration. Soluble dietary fiber is measured gravimetrically as amount of filtration less protein and ash content of the sample. High molecular weight dietary fiber (HMWDF) is equal to the amount of insoluble dietary fiber (ISF) plus SDF, and includes some RS (depending on type) and high molecular weight soluble dietary fiber including β-glucans, arabinoxylans, psyllium gum, arabinogalactansome inulin, polydextrose, and resistant maltodextrins. The filtered aqueous ethanol extract can be concentrated, desalted, and analyzed to determine non-digestible oligosaccharides using HPLC (McCleary, 2007). Finally, the remaining filtrate can be used to calculate low molecular weight soluble dietary fiber (McCleary et al., 2010). Low molecular weight soluble dietary fiber includes fructo-oligosaccharides, galacto-oligosaccharides, and any remaining inulin, polydextrose, and resistant maltodextrins. This method measures all components of dietary fiber as defined by CODEX Alimentarius, but may slightly underestimate type II and IV RS.

Dietary fiber is more difficult to measure than other dietary components, such as starch, sugars, protein, fat, water, and ash. Assuming all nutrient values are additive, dietary fiber can be estimated using the values for all other diet components to calculate indigestible carbohydrates (de Lange, 2007) using the following equation:

Indigestible carbohydrates, g = DM, g – (ash + starch + sugars + protein + fat)

There are a few disadvantages to using the difference method. Calculation of dietary fiber using the difference method includes the cumulative error from each of the procedures used in the equation (i.e., DM, ash, starch, sugars, protein, fat). Also, other components of the diet that are not commonly analyzed, including polyols, alcohol, vitamins, and organic acids, are not included in the calculation. For these reasons, the value is not dependable and using the difference method for fiber determination is discouraged (Urriola, 2010).

The analytical methods used to measure dietary fiber were developed for the measurement of fiber in food products, but have been used by nutritionists for fiber measurements in ileal digesta and fecal samples in order to calculate fiber digestibility (Montoya et al., 2016). Previous reports of negative fiber digestibility values in monogastric animals, which are not physiologically possible, have called into question the accuracy of these methods when measuring dietary fiber in non-food materials (Wilfart et al., 2007; Cervantes-Pahm et al., 2014b). One proposed explanation for the negative digestibility values is that non-dietary materials from the gastrointestinal tract, particularly mucins and bacteria, are included in and contaminate dietary fiber analyses, resulting in the underestimation of fiber digestibility (Jørgensen et al., 1996; Cervantes-Pahm et al., 2014b). It has previously been shown that mucins and bacteria are present in ileal digesta samples and bacteria are present in fecal samples in quantitatively significant amounts (Cervantes-Pahm et al., 2014b; Montoya et al., 2015). Few digestibility studies have made efforts to quantify contamination by non-dietary fiber materials in fiber assays, but those that have measured non-dietary sources of fiber have reported quantifiable amounts when measured at the ileum and across the total tract (Cervantes-Pahm et al., 2014b; Montoya et al., 2015). However, dietary fiber source and amount have been shown to impact gastrointestinal secretions, thereby impacting the potential amount of contamination from non-

dietary fiber materials. Therefore, the use of correction factors for fiber may be restricted to the diet types used to determine them (Schulze et al., 1994; Jondreville et al., 2000). When analyzing dietary fiber, researchers must recognize the limitations of the laboratory assays used and, if possible, make an effort to correct for contamination by non-dietary fiber materials.

To have value, dietary fiber measurements must relate to digestion that occurs in the animal. Many methods have been developed and improved over the years, but still did not account for each component of dietary fiber and did not meet the needs of the nutritionist. The McCleary method is the first to include each component of dietary fiber currently defined and has the potential to more closely meet the needs of nutritionists. However, the method is fairly new and has not yet been widely used in animal nutrition. The McCleary method reports fiber in portions different from those reported by previous dietary fiber analyses, making comparisons across methodologies difficult. It is also expected that contamination by non-dietary fiber materials can occur when using the McCleary method for fiber analysis (Montoya et al., 2016). Animal nutritionists must choose whether to more accurately characterize dietary fiber components or to report dietary fiber in measurements currently used by the industry. Nutritionists must also be cognizant of the potential contamination of dietary fiber assays, which can lead to misrepresentation of dietary fiber digestibility.

Carbohydrate Digestion in the Pig

Simple carbohydrate digestion and absorption in the pig

In the pig, digestion of simple carbohydrates begins in the mouth with the secretion of salivary amylase, which begins hydrolyzing the α-1,4 and α-1,6 bonds present in starch. Carbohydrates entering the duodenum of the small intestine are mixed with pancreatic α-

amylase, which further hydrolyzes remaining starch bonds, liberating oligosaccharides and disaccharides including maltose, maltotriose, and dextrins. Enzymes present at the brush border of the small intestine cleave oligosaccharides and disaccharides to their monosaccharide units. These enzymes include lactase (hydrolyze lactose to glucose and galactose), maltase (hydrolyze maltose and maltotriose to glucose), sucrase (hydrolyze sucrose to glucose and fructose), and isomaltase (hydrolyze dextrins to glucose).

Monosaccharides at the brush border are transported into enterocytes through both active and passive transporters. Glucose and galactose are transported actively into enterocytes via sodium-glucose co-transporter 1 (SGLT1). Glucose can also be transported passively into the enterocyte through the insulin-dependent glucose transporter 4 (GLUT4), and fructose is transported passively into the enterocyte via glucose transporter 5 (GLUT5). Monosaccharides are then passively transported across the basolateral membrane of the enterocyte through glucose transporter 2 (GLUT2) to then enter the blood stream for utilization by the pig.

Once in the blood stream, fructose metabolism occurs primarily in the liver through the fructose 1-phosphate pathway. This pathway breaks down fructose to glyceraldehyde and dihydroxyacetone phosphate, both of which are glycolysis intermediates. Fructose can also be metabolized in other tissues through phosphorylation to fructose-6-phosphate, another intermediate in the glycolysis pathway. Absorbed galactose is also converted to a glycolysis intermediate, glucose-6-phosphate, via the galactose-glucose interconversion pathway.

The fates of absorbed glucose depend on the energy balance of the pig. In a negative energy balance, glucose will undergo glycolysis and be catabolized to pyruvate, which can enter the TCA cycle to form reducing equivalents. Reducing equivalents then enter the electron transport chain to produce ATP and provide the pig with energy. In a short-term positive energy

balance, glucose will be directed toward glycogenesis to make glycogen, the storage form of glucose. Glycogen is stored primarily in the liver and skeletal muscle, and can be broken down to increase blood glucose in times of fasting and increase available glucose in the muscle during contraction. In a long-term positive energy balance, pyruvate from the glycolysis pathway will be directed to the lipogenesis pathway and be used to synthesize triacylglycerols. Triacylglycerols are primarily stored in adipose tissue in pigs and serve as a more efficient energy source for the animal compared to glycogen.

Fermentation of fiber in pigs

Dietary fiber resists digestion by endogenous mammalian enzymes in the small intestine due to β-linkages, intricate cross-linking, or entrapment of carbohydrates in other dietary components, physically blocking them from endogenous enzymes. These carbohydrates as well as simple carbohydrates, proteins, and peptides that escape digestion in the small intestine, along with sloughed cells, mucus, and endogenous secretions, may act as substrates for fermentation by microbial populations within the small and large intestines of pigs (Bergman, 1990; Macfarlane and Macfarlane, 2012).

Fermentation is a redox (oxidation-reduction) process that occurs under anaerobic conditions (Müller, 2001). Redox reactions are chemical reactions involving a transfer of electrons between substrates, resulting in the oxidation of one substrate and the reduction of the other. During fermentation, the difference in redox potential between the initial substrate and the end product is coupled with phosphorylation of ADP to ATP. Three physiological groups of microorganisms can function in the anaerobic conditions of mammalian intestines: aerobes that

use alternate electron acceptors (nitrate or nitrite), facultative aerobes, and obligate anaerobes (Schmitz et al., 2013).

Fermentation in the pig occurs in the ileum, cecum, and colon, with the majority occurring in the cecum and proximal colon (Cummings et al., 1987). Fermentation begins with the microbes breaking down polymers, including polysaccharides, proteins, and nucleic acids, into smaller polymers or monomers, which can then be taken up by the initial microbe or by other microbes in the intestine (Schmitz et al., 2013). Once metabolized by the microbes, fermentation end products including VFA, gasses, and energy are released from the microbe into the intestinal lumen, where they are available as substrates for other microbes or utilization by the animal.

The pig is able to absorb some end products of carbohydrate fermentation for energy, primarily in the form of VFA. The predominant forms of VFA produced by carbohydrate fermentation in the intestine are acetic, propionic, and butyric acids. Volatile fatty acid production via fermentation accounts for approximately 72% of the energy content of the initial carbohydrate substrate, with the remaining 28% being utilized by microbes for growth or lost as hydrogen and methane (Miller and Wolin, 1979).

Absorption and metabolism of VFA

Previous work has shown that intracecal injection of VFA results in less than 1% of VFA excreted in feces, indicating that VFA are absorbed efficiently into the blood stream through the colon in pigs (Jørgensen et al., 1997). Absorption appears to be primarily passive, and increases linearly with increases in VFA concentration (Hollander et al., 1986). Some studies have shown that lumen pH also influences VFA absorption, with increases in pH decreasing absorption

(Hollander et al., 1986), while others have found that VFA absorption is independent of luminal pH (Von Engelhardt et al., 1989; Fleming et al., 1991).

The absorption of VFA is thought to occur by three mechanisms: diffusion of protonated VFA, anion exchange, and transporter mediated absorption. Volatile fatty acid absorption occurs by diffusion of protonated VFA, which is driven by the acidity of the colonic lumen due to protons released from Na/H exchange, $K+H^+$-ATPase, or bacterial metabolic activity; this acidity increases the concentration of protonated VFA, subsequently driving diffusion into the cell (Cook and Sellin, 1998; Wong et al., 2006). Volatile fatty acids can also be absorbed into the colonocyte as the anion in exchange for bicarbonate anions release from the cell (Fleming et al., 1991). Finally, VFA absorption can be mediated by the monocarboxylate transporter (MCT1) protein and the sodium-coupled monocarboxylate transporter (SLC5A8), both of which facilitate the transport of VFA from the colonic lumen into colonocytes in exchange for H^+ and Na^{2+} respectively (Gupta et al., 2006; Thangaraju et al., 2008).

Once absorbed, VFA are either utilized by the colonocyte or transported across the basolateral membrane of the colonocyte into the blood stream. Butyrate is primarily metabolized by the colonic epithelium cells and is the major substrate for maintenance-energy producing pathways, providing 60-70% of the energy needed (Armin Ritzhaupt et al., 1998). The use of butyrate as an energy source spares Gln for use in the small intestine and glucose for use in most other tissues (Elia and Cummings, 2007).

Volatile fatty acids not metabolized by colonocytes are transported across the basolateral side of the cell most likely via the $SCFA^{—}HCO_3^-$ antiport and the cation-SCFA anion symport (den Besten et al., 2013). Monocarboxylate transporter 4 (MCT4) has been shown to transport VFA across the basolateral membrane of colonocytes into the blood circulation in an H^+-

dependent electroneutral manner. Monocarboxylate transporter 5 (MCT5) has been shown to be present on the basolateral side of colonocytes, but its function has yet to be determined (Fig. 1.1; den Besten et al., 2013). After absorption into the blood stream, VFA can be metabolized in liver cells, muscle cells, and the brain. The liver metabolizes propionate and remaining butyrate for gluconeogenesis, and takes up 50-70% of the available acetate for lipogenesis and cholesterol synthesis (Wong et al., 2006). Skeletal muscle cells, cardiac muscle cells, and the brain can oxidize remaining acetate to generate energy; the use of acetate as an energy source spares FFA oxidation and does not stimulate the release of insulin (Elia and Cummings, 2007).

The amount of energy received from dietary carbohydrates is dependent on the location of digestion in the intestine. In the small intestine, carbohydrates are efficiently broken down by endogenous enzymes and absorbed into the blood stream for utilization. Carbohydrates entering the large intestine are fermented to VFA. Volatile fatty acid production and absorption is less efficient than digestion and absorption in small intestine because a smaller portion of the carbohydrate energy is captured; therefore, carbohydrate digestion in the small intestine is preferred. However, energy in the form of VFA is still valuable and provides essential energy to several areas of the body.

Arabinoxylans

Arabinoxylans are the primary component of the hemicellulose fraction in corn and corn co-products. They comprise approximately 48.6% of the total NSP component in both corn and corn DDGS, but make up a higher proportion of corn DDGS as the NSP component of corn DDGS is three times that of corn (Jaworski et al., 2015).

Arabinoxylans consist of a polysaccharide backbone of β-1,4-xylose residues arranged in a pyranose configuration, substituted at O2 and/or O3 with arabinofuranose residues. The xylan backbone can also be acetylated or substituted at O2 with 4-O-methyl-D-gluceronic acid (Correia et al., 2011). Although all arabinoxylans follow this same basic structure, differences in backbone size and in type and degree of backbone substitution results in high structural variation among arabinoxylans (Bastawde, 1992; Sunna and Antranikian, 1997).

The primary sugars of arabinoxylans are D-xylose and L-arabinose units (Dekker and Richards, 1976). Very few free xylose and arabinose sugars are liberated from carbohydrates in the small intestine in swine, even with enzyme supplementation. It is believed that the free xylose and arabinose sugars that are liberated can be transported through the small intestine through carrier-facilitated diffusion, most likely through a transporter that also has affinity for glucose (Salomon et al., 1961). Absorption and metabolism of xylose and arabinose sugars does not appear to be efficient, as demonstrated by the considerable amount of xylose and arabinose sugars present in urine when those sugars are included in the diet (Schutte et al., 1991; Schutte et al., 1992). However, the mechanisms of absorption and post-absorption metabolism of these sugars in monogastric animals has not been well defined. Bacteria in the small and large intestines can also ferment xylose and arabinose sugars. The apparent ileal digestibility of D-xylose and L-arabinose in pigs is 98.7 and 70.0% respectively, indicating that the majority of these sugars disappear within the small intestine either via absorption or fermentation (Schutte et al., 1991; Schutte et al., 1992).

Previous studies have reported increased total VFA when xylose and arabinose are included in swine diets, indicating that at least a portion of these sugars from complex carbohydrates are fermented in the small intestine (Schutte et al., 1991; Schutte et al., 1992).

Apparent ileal digestibility (AID) values for NDF ranging from 32.5 to 46.4% have been reported in corn-based diets and values ranging from 21.7 to 52.1% have been reported in diets containing corn DDGS, further supporting the hypothesis that fermentation of hemicellulose occurs in the small intestine (Urriola et al., 2010; Gutierrez et al., 2016).

Carbohydrase Enzymes

Carbohydrase enzymes were developed in an effort to alleviate the antinutritional effects and impaired performance when high fiber diets are fed to monogastric animals, which are caused by changes to viscosity, gut fill, and passage rate. Exogenous carbohydrase enzymes do not impact the digestion of lignin, but most often target the NSP portions of dietary fiber. The objective of carbohydrase enzymes is to break down previously undigested carbohydrates to their oligosaccharide, disaccharide, and monosaccharide components earlier in the gastrointestinal tract, shifting fiber degradation from the large intestine to the small intestine. It is hypothesized that increased fiber degradation will increase energy and nutrient utilization of feed ingredients containing dietary fiber; however, a consensus on the mechanism of increased dietary utilization by carbohydrase enzymes has not been reached.

Xylanase enzymes

Endoxylanase enzymes target the β-1,4-D-xylosidic linkages in the xylan backbone of arabinoxylans; the specific bonds targeted by endoxylanase enzymes depend on the backbone length, degree of branching of the substrate, and the presence of substituents (Reilly, 1981). Enzyme action also varies between different enzyme sources. Xylanase enzymes can be categorized as either non de-branching (non arabinose liberating) or de-branching (arabinose

liberating) based on the end products released by the enzyme reaction (Dekker and Richards, 1976; Reilly, 1981). Early hydrolysis by endoxylanase enzymes releases arabino- and xylo-oligosaccharides, with continued hydrolysis and additional enzymes required for the release of individual sugars (Dekker and Richards, 1976; Bedford and Schulze, 1998).

The mechanism for increased digestibility due to xylanase supplementation has been debated for many years, but two main hypotheses exist. The first hypothesis is that the physical structure of endosperm walls, which are indigestible to monogastric animals, trap nutrients such as starches and proteins, allowing these nutrients to essentially escape digestion (Bedford and Schulze, 1998). Xylanase enzymes may increase digestibility by breaking down the hemicellulose component of endosperm walls, releasing previously trapped nutrients (Adeola and Cowieson, 2011). A previous in-vitro study by Tervilä-Wilo et. al. (1996) demonstrated the ability of the xylanase enzyme to break down parts of plant cell walls and showed increased protein release with xylanase inclusion. However, this study also showed no change in the release of glucose with xylanase supplementation, indicating that starch was not released with the degradation of the endosperm walls (Tervilä-Wilo et al., 1996).

The second hypothesis is based on the impact of soluble fiber on intestinal digesta viscosity. Soluble NSP have been shown to increase the viscosity of intestinal digesta, which reduces intestinal contractions (Cherbut et. al., 1990), thereby decreasing mixing of digesta with endogenous enzymes (Johnston et al., 2003). A reduction in the accessibility of dietary components to endogenous enzymes reduces nutrient digestion and absorption (de Vries, 2014). Xylanases have been shown to decrease intestinal viscosity when it is induced by dietary NSP, ameliorating some of the negative effects of dietary fiber (Adeola and Bedford, 2004).

It is important to note that changes in diet digestibility do not necessarily translate to changes in growth performance. The ability of xylanase enzymes to impact growth performance depends on the type and amount of cereal grains used in the diet, the animal age, the deficiency of the limiting nutrient, and the extent of increased digestibility by the enzyme (Adeola and Cowieson, 2011). The viscosity of digesta has a larger impact on digestibility in poultry compared to swine, which may explain why carbohydrase responses in poultry have been more consistent than those in swine (Adeola and Cowieson, 2011).

Xylanase enzymes in swine diets

The majority of initial research with exogenous xylanases in swine diets was done with wheat-based diets due to wheat being the primary cereal grain in Europe, where the xylanase enzyme was originally developed (Newman, 2014). Arabinose and xylose sugars from arabinoxylans make up approximately 62% of the NSP component in wheat, with the majority of these sugars being insoluble (Jaworski et al., 2015). In past studies, the impact of xylanase on digestibility in wheat-based diets has not been consistent. Some studies have shown increased AID of energy (Yin et al., 2000; Widyaratne et al., 2009), AA (Yin et al., 2000; Widyaratne et al., 2009), starch (Lærke et al., 2015), fat (Lærke et al., 2015), fiber (Diebold et al., 2004), and NDF (Diebold et al., 2004) and increased apparent total tract digestibility (ATTD) of DM, GE, and CP (Yin et al., 2000) with xylanase inclusion in wheat-based diets, while others have reported no impact of xylanase inclusion on AID of energy and AA (Nortey et al., 2008) or the ATTD of energy and AA (Diebold et al., 2004; Nortey et al., 2008). Xylanase inclusion has been shown to increase the AID of energy and AA in diets containing wheat by-products including millrun (Nortey et al., 2007), wheat middlings (Yin et al., 2000), wheat bran (Yin et al., 2000),

and recombined wheat (Yin et al., 2000). However, other studies have shown no impact of xylanase inclusion on the AID or ATTD of energy in diets containing wheat DDGS (Widyaratne et al., 2009), wheat middlings (Nortey et al., 2008), wheat shorts (Nortey et al., 2008), wheat screenings (Nortey et al., 2008), and wheat bran (Nortey et al., 2008), and no impact on the AID of AA in diets containing wheat DDGS (Widyaratne et al., 2009), wheat middlings or wheat screening (Nortey et al., 2008).

The impact of xylanase on growth performance has also been inconsistent in wheat-based diets, with some studies showing no change in growth performance parameters (Widyaratne et al., 2009; O'Shea et al., 2014), and others showing increased ADG (Omogbenigun et al., 2004; Myers and Patience, 2014), and improved G:F (Omogbenigun et al., 2004; Nortey et al., 2007). When viscosity has been measured, the inclusion of xylanase from *Trichoderma reesi* decreased ileal viscosity in finely ground and course wheat diets, but xylanases from *Aspergillus niger* and *Bacillus subtilis* had no impact on ileal viscosity in swine (Lærke et al., 2015).

In recent years, research has been completed with exogenous xylanase supplementation in corn and corn by-product based diets, as these are cereal grains are heavily used in the United States. Corn is similar to wheat in that arabinose and xylose units from arabinoxylans make up approximately 47% of the total NSP in corn and the majority of these sugars are insoluble (Jaworski et al., 2015). This makes corn a logical substrate for xylanase supplementation.

Results from previous research with exogenous xylanase supplementation in corn and corn by-products based diets have also been inconsistent. Xylanase supplementation in corn-based diets has shown benefits in some studies, including increased ATTD of DM (Newman, 2014; Passos et al., 2015), GE (Newman, 2014; Passos et al., 2015), and NDF (Fang et al., 2007; Passos et al., 2015), as well as improvements in ADG (Fang et al., 2007; Myers and Patience,

2014) and improved feed conversion ratio (Fang et al., 2007; Jones et al., 2015). In diets containing corn-DDGS, xylanase has been shown to increase the AID of GE, DM, CP, NDF, and ADF (Kiarie et al., 2016a), and has been shown to increase ADG, although the response was not consistent through the duration of the trial (Yang et al., 2016). It has been reported that xylanase inclusion decreased jejunal digesta viscosity in corn-based diets (Passos et al., 2015). However, other trials have shown no effect of xylanase supplementation on nutrient or energy digestibility in corn-based diets (Willamil et al., 2012), or growth performance in corn-based diets (Willamil et al., 2012) or diets containing corn DDGS (Agyekum et al., 2015).

With the increased use of co-products as feedstuffs in the swine industry, the digestion and utilization of dietary fiber will continue to be increasingly important. Diets higher in fiber are less digestible, so carbohydrase enzymes may have a greater opportunity to elicit a response (Omogbenigun et al., 2004). Carbohydrase enzymes have been shown to effectively break down dietary fiber; however, the action of the enzymes and fate of enzyme reaction products within the body of the pig has yet to be determined. To better utilize the xylanase enzyme and ensure the best return on investment with corn-soybean meal based diets that are common in the United States, the action of the enzyme within the pig and the utilization of the enzyme reaction products must be better understood.

Table 1.1. Average energy values for corn DDGS at different oil levels, as-fed basis (NRC, 2012)

Energy values, Mcal/kg	Corn, Yellow Dent	Corn DDGS		
		<4% Oil	>6 and <9% Oil	> 10% Oil
Gross energy	3.933	5.098	4.710	4.849
Digestible energy	3.451	3.291	3.582	3.620
Metabolizable energy	3.395	3.102	3.396	3.434
Net energy	2.672	2.009	2.343	2.384

Table 1.2. Example phase 4 nursery diet, as-fed basis

Ingredient	Amount (%)
Corn	52.61
Corn DDGS	20.00
Soybean meal	15.00
Choice white grease	1.00
Limestone	0.44
Salt	0.50
L-Lysine HCl	0.25
DL-Methionine	0.01
L-Threonine	0.05
L-Tryptophan	0.01
Fish meal	9.67
Nursery Vit. Premix	0.15
Trace Mineral Premix	0.25
Choline Chloride, 60%	0.05

Energy from dietary components (Mcal/kg)

	Starch	Non-starch organic matter	CP	Fat
GE[1]	3.7	4.2	5.6	9.4
DE[2]	3.7	1.8	4.8	8.8
ME[3]	3.7	1.8	3.7	8.8
NE[4]	3.0	1.0	2.2	7.8

Proportion of energy from dietary components (%), DM basis[5]

	Starch	Non-starch organic matter	CP	Fat	Calculated total diet energy (Mcal/kg)	Formulated total diet energy (Mcal/kg)
% in diet, DM basis	39.2	27.5	26.1	7.2	-	-
GE	34.8	14.1	35.0	16.1	4.17	-
DE	40.3	6.9	34.9	17.9	3.55	3.60
ME	43.7	7.5	29.5	19.3	3.28	3.41
NE	48.0	5.6	23.4	23.0	2.45	2.46

[1]GE values of dietary components (NRC, 2012).
[2]Calculated by multiplying GE dietary components by digestibility coefficients (%) for ATTD of NDF and CP (Gutierrez et al., 2013), TID of EE (Gutierrez et al., 2016), and ATTD of starch (Keys and DeBarthe, 1974).
[3]Calculated correcting for % N excreted in urine in corn-soybean meal diet (Pilcher et al., 2015). Digestible energy coefficients used for starch, fiber, and fat as energy from gaseous losses is generally <1%, thus it was not included in calculation (Ewan, 2001).
[4]Calculated using coefficients for energy efficiency (Milgen, 2006).
[5]Percentages calculated as energy from dietary component/total dietary energy.

Table 1.3. Example grow/finish diet (45-68 kg), as-fed basis

Ingredient	Amount (%)
Corn	52.22
Corn DDGS	30.00
Soybean meal	13.96
Choice white grease	1.00
Monocalcium Phosphate	0.28
Limestone	1.26
Salt	0.50
L-Lysine HCl	0.37
L-Threonine	0.02
Finish Vit. Premix	0.25
Trace Mineral Premix	0.08
Choline Chloride, 60%	0.05

Energy value of dietary components (Mcal/kg)

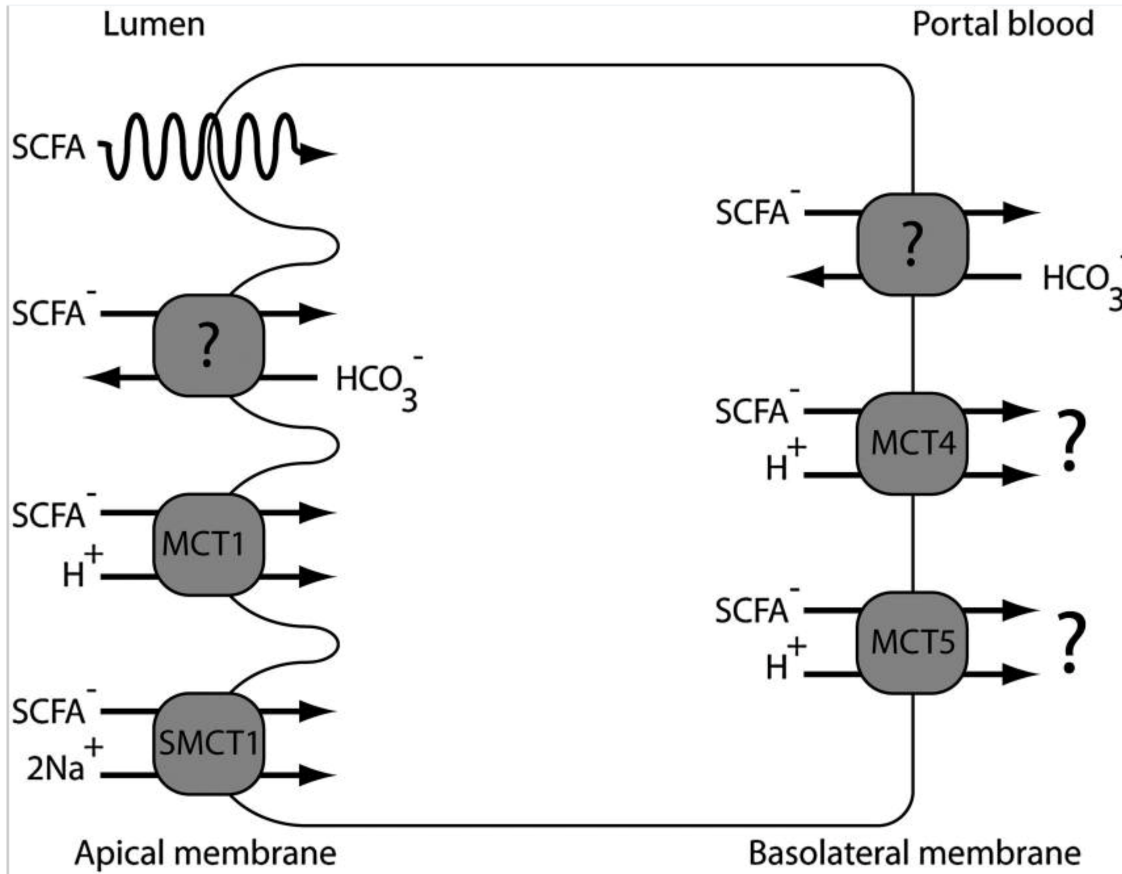
	Starch	Non-starch organic matter	CP	Fat
GE[1]	3.7	4.2	5.6	9.4
DE[2]	3.7	1.8	4.8	8.8
ME[3]	3.7	1.8	3.7	8.8
NE[4]	3.0	1.0	2.2	7.8

Proportion of energy from dietary components (%), DM basis[5]

	Starch	Non-starch organic matter	CP	Fat	Calculated total diet energy (Mcal/kg)	Formulated total diet energy (Mcal/kg)
% in diet, DM basis	40.1	30.7	22.0	7.2	-	-
GE	36.1	17.6	29.9	16.4	4.12	-
DE	42.5	8.8	30.3	18.4	3.46	3.55
ME	45.5	9.4	25.4	19.7	3.23	3.39
NE	49.7	7.0	20.0	23.3	2.41	2.46

[1]GE values of dietary components (NRC, 2012).
[2]Calculated by multiplying GE dietary components by digestibility coefficients (%) for ATTD of NDF and CP (Gutierrez et al., 2013), TTTD of EE (Gutierrez et al., 2016), and ATTD of starch (Keys and DeBarthe, 1974).
[3]Calculated correcting for % N excreted in urine in corn-soybean meal diet (Pilcher et al., 2015). Digestible energy coefficients used for starch, fiber, and fat as energy from gaseous losses is generally <1%, thus it was not included in calculation (Ewan, 2001).
[4]Calculated using coefficients for energy efficiency (Milgen, 2006).
[5]Percentages calculated as energy from dietary component/total dietary energy.

Figure 1.1. The proposed mechanism of SCFA transport in colonocytes; den Besten et al. (2013)



CHAPTER II

EFFECT OF XYLANASE SUPPLEMENTATION ON THE DIGESTIBILITY OF ENERGY, CARBOHYDRATES, AND NITROGEN IN THE SMALL AND LARGE INTESTINE AND ACROSS THE TOTAL TRACT OF GROWING PIGS AT 3 BODY WEIGHTS IN CORN-BASED AND CORN-DDGS-BASED DIETS

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Abstract

Fiber degrading enzymes have the potential to assist the pig in digestion of dietary fiber, which is increasingly important as the use of corn co-products in swine diets increases. However, previous studies with xylanase enzymes in swine have produced inconsistent results. A digestibility trial was conducted in growing pigs to better understand how xylanase impacts diet utilization by the pig by measuring xylanase impact on the digestibility of energy, nitrogen, fat, fiber, and starch in the small and large intestine and across the total tract at three BW. Thirty-two gilts (32.6 ± 0.47) were surgically fit with T-cannulae at the terminal ileum, housed individually, and assigned to 1 of 4 dietary treatments in a complete randomized design. Diets were arranged in a 2 × 2 factorial by adding 0% or 0.017% xylanase to corn-soybean meal diets with 0% (lower fiber: LF) or 30% (higher fiber: HF) corn DDGS. Three collection periods consisting of a 2 d fecal collection followed by a 3 d ileal collection occurred at average BW of 46.0 ± 0.4, 54.1 ± 0.4, and 70.3 ± 0.5 kg, respectively, for a total of 24 observations per dietary treatment.

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Ileal and fecal samples were analyzed to determine the apparent ileal digestibility (AID) and apparent total tract digestibility (ATTD) of GE, DM, NDF, ADF, and nitrogen, and the AID of starch and AA. Apparent digestibility values for fat were corrected for endogenous losses and true ileal digestibility (TID) and true total tract digestibility (TTTD) of fat was reported. Xylanase inclusion (XI) increased the AID of DM, starch, and nitrogen and tended to increase GE in LF diets, but had no affect in HF diets, resulting in fiber level (FL) × XI interactions ($P \leq 0.059$). Xylanase decreased the AID of NDF and tended to decrease the AID of ADF in LF diets, but had no affect in HF diets, resulting in FL × XI interactions ($P \leq 0.097$); however, the decrease in fiber digestibility may have been an artifact rather than a true result. Xylanase inclusion tended to decrease the AID of hemicellulose but increase the hindgut disappearance of NDF, ADF, and hemicellulose ($P \leq 0.100$). In LF diets, xylanase tended to decrease the ATTD of ADF but increased the ATTD of ADF in HF diets, leading to a trend for a XI × FL interaction ($P = 0.091$). In conclusion, xylanase appears to liberate nutrients for digestion in the small intestine in corn-soybean meal diets, but diets containing corn DDGS do not appear to be a suitable substrate for the xylanase enzyme.

Introduction

Increased use of corn co-products in swine diets prompts the need for a better understanding of the digestibility of fiber in swine. The well-documented ability of exogenous enzymes, such as phytases and β-glucanases, to increase digestibility and growth performance in swine supports the potential use of exogenous carbohydrase enzymes in swine diets to improve fiber utilization (Bedford et al., 1992; Kerr et al., 2010). Endo-xylanase enzymes catalyze the hydrolysis of β-1,4-D-xylosidic linkages in arabinoxylans, breaking apart the hemicellulose

structure to release the constituent oligosaccharides and sugars (Dekker and Richards, 1976). Until recently, the majority of xylanase research in swine has been conducted using wheat-based diets where xylanase inclusion has been shown to increase energy and AA digestibility (Nortey et al., 2008; Widyaratne et al., 2009).

In recent years, xylanase inclusion has been studied in corn-based diets as hemicellulose levels in corn are only slightly lower than in wheat (Jaworski et al., 2015). However, xylanase responses in corn-based diets in swine have been inconsistent. Some studies have reported increased energy, CP, and fiber digestibility with xylanase inclusion (Newman, 2014; Passos et al., 2015; Kiarie et al., 2016b). Increased ADG and feed conversion have also been reported (Myers and Patience, 2014; Jones et al., 2015; Yang et al., 2016). Other studies have shown no improvements in growth performance, nutrient or energy digestibility (Willamil et al., 2012; Agyekum et al., 2015).

This study was undertaken to better understand the impact of xylanase with 3 objectives: 1) to measure the impact of exogenous xylanase on the digestibility of dietary constituents, 2) to measure the impact of exogenous xylanase on the flow of energy through the small and large intestines and 3) to measure the impact of BW on the enzyme response.

Materials and Methods

All procedures for this experiment adhered to guidelines for the ethical and humane care of animals used for research and were approved by the Institutional Animal Care and Use Committee at Iowa State University (number 1-15-7918-S).

Animals, housing, and experimental design

Two groups of sixteen gilts with an average initial BW of 32.6 ± 0.47 kg were surgically fitted with T-cannulae at the terminal ileum following procedures described by Stein et al. (1998), for a total of 32 gilts on test.

Following a 7-d period to recover from surgery, pigs were housed in individual pens (1.8 by 1.9 m) with half slatted floors. Each pen was equipped with a stainless steel feeder and nipple drinker, and pigs were allowed ad libitum access to water throughout the experiment. On d 0, pigs were weighed (37.5 ± 0.3 kg) and allotted to one of 4 dietary treatments using a completely randomized design. The experiment consisted of 3 collection periods occurring on d 8 to 12, d 18 to 22 and d 38 to 42 following introduction to dietary treatment, with each collection consisting of a 2-d fecal collection followed by a 3-d ileal digesta collection. Average pig BW at collections was 46.0 ± 0.4, 54.1 ± 0.4, and 70.3 ± 0.5 kg, respectively. Pigs remained on the same dietary treatment throughout the experiment for a total of 8 observations per dietary treatment per BW.

Dietary treatments and feeding

Dietary treatments were arranged as a 2 × 2 factorial with low (LF; 0% DDGS) vs. high fiber (HF; 30% DDGS; Poet Biorefining, Jewell, IA) as the first factor, both formulated to meet or exceed the requirements of growing pigs (NRC, 2012), and the inclusion of xylanase at 0.0% vs. 0.017% (165 mg xylanase/kg of finished feed; Econase XT, AB Vista, Plantation, FL) as the second factor. Diets included chromic oxide (Cr_2O_3) at 0.4% as an indigestible marker.

Pigs were fed 3.2 times their maintenance energy requirement throughout the experiment, calculated as kg feed/day = ($BW^{0.6}$ × 197 × 3.2)/3395, where BW was average pig BW and 3395 was the estimated ME/kg of the diet (NRC, 2012). Feed allowance was recalculated within each

group based on BW measured on d 0, 12 and 22 of the experiment and was adjusted on d 13 and 23. Daily feed allotment was split into two meals of equal size fed at approximately 0800 and 1600 h.

Sample collection

Fecal grab samples were collected following each meal on d 8 to 9, 18 to 19, and 38 to 39. Ileal digesta samples were collected on d 10 to 12, 20 to 22, and 40 to 42 from 0800 h to 1600 h. The night before collections began, contents inside of cannulas were removed to ensure a representative sample was obtained. For ileal digesta collections, sterile 207-mL plastic collection bags (Whirl-Pak; Nasco, Fort Atkinson, WI) were attached to the end of the cannula via zip ties and were changed when they became ¾ full or every hour, whichever occurred first. Fecal and ileal samples were stored at -20°C immediately after collection to prevent bacterial degradation. At the end of the collection period, samples were thawed to room temperature and homogenized within animal and collection period, and subsamples were taken for laboratory analyses. Fecal subsamples were oven dried to constant weight in a convection oven for 3 days at 65°C. Ileal samples were lyophilized for approximately 7 days at -55°C. Dried samples were ground to 1 mm using a Variable Speed Digital ED-5 Wiley Mill (Thomas Scientific, Swedesboro, NJ), and then stored in a desiccator.

Subsamples of each experimental diet along with the corn, corn DDGS, and soybean meal used to manufacture the diets were collected during feed mixing. Samples were homogenized, ground to 1 mm using a Retsch grinder (model ZMI; Retsch Inc., Newtown, PA) and then stored in a desiccator.

Chemical analysis and calculations

Samples of feed, feces, and ileal digesta were analyzed in duplicate at the Iowa State University Monogastric Nutrition Laboratory (Ames, IA) unless stated otherwise. The NDF and ADF content were determined by analyzing samples in triplicate using the Ankom filter bag technique (NDF: ANKOM Technology Method 13, Van Soest et al., 1991; ADF: ANKOM Technology Method 12, Van Soest, 1973; Model A2000 and A2001 ANKOM Technology, Macedon, NY). Dry matter was determined by drying samples in a 105°C drying oven to a constant weight. Gross energy was determined by isoperibolic bomb calorimetry (Parr 6200 calorimeter; Parr Instruments Co., Moline, IL); benzoic acid (6,318 kcal GE/kg; Parr Instruments Co.) was used as the standard for calibration, and was determined to contain 6,324 ± 1 kcal GE/kg. Chromic oxide was determined using procedures described by Fenton and Fenton (1979; (PowerWave HT Microplate Spectrophotometer; BioTek, Winooski, VT). Nitrogen was determined using the combustion method (method 990.03; AOAC, 1990) with a TruMac apparatus (Leco Corporation, St. Joseph, MI). Ethylenediaminetetraacetic acid (EDTA) was used for calibration (9.56 ± 0.04% N; Leco Corporation) and was determined to contain 9.43 ± 0.01% N. Crude protein was calculated as N × 6.25. Ether extract was determined via Soxtec-Acid Hydrolysis (ISO 11085: 2009) followed by fat extraction (method 2003.06, AOAC 2006). Diet and ileal samples were analyzed for starch (method 996.11; AOAC, 2005). Dietary ingredients, mixed diets, and ileal samples were analyzed for amino acids (Ajinimoto Heartland North America, Chicago, IL). Mixed diets were analyzed for xylanase content using the ELISA method (Envirologix method AP019; AB Vista Enzyme Services, Cordova, TN) and dietary ingredients were analyzed for particle size (method 965.22, AOAC 2005; Kansas State University, Manhattan, KS).

To more accurately measure fat digestibility, values were adjusted for endogenous losses using 9.47 g/kg DMI for ileal samples and 13.64 g/kg DMI for fecal samples (Gutierrez et al., 2016). For each dietary treatment, the apparent ileal digestibility (AID) and apparent total tract digestibility (ATTD) for NDF, ADF, DM, GE, N, the AID of starch and AA, and the true ileal digestibility (TID) and true total tract digestibility (TTTD) of fat were calculated using the index method (Oresanya et al., 2008):

AID/TID/ATTD/TTTD, % = 100% - [(chromium oxide concentration in diet)(component concentration in sample)/(component concentration in diet)(chromium oxide concentration in the sample) × 100].

Hemicellulose was calculated as the difference between NDF and ADF content. The amount of dietary components remaining at the terminal ileum and the amount excreted in feces were determined using the following calculations (Pilcher et al., 2013):

Amount remaining at terminal ileum = [concentration of component in digesta × (chromium oxide in diet/chromium oxide in digesta)] and

Amount excreted in feces = [concentration of component in feces × (chromium oxide in diet/chromium oxide in feces)].

These calculations were then used to determine disappearance prior to the terminal ileum and hindgut disappearance:

Disappearance before the terminal ileum = (intake – amount remaining at terminal ileum) and

Hindgut disappearance = (amount remaining at terminal ileum – amount excreted in feces).

Statistical analysis

The PROC UNIVARIATE procedure of SAS was used to test the data for normality (SAS 9.3; SAS Inst. Inc., Cary, NC). Data points more than 3 standard deviations beyond the mean were considered outliers and were excluded from the data set. All data were analyzed using the PROC MIXED procedure of SAS (SAS 9.3; SAS Inst. Inc., Cary, NC). For digestibility analyses, fiber level, enzyme inclusion, and BW were the main effects. Ileal digesta and fecal samples were the observational units, and pig was the random effect. The model included all possible interactions among fiber level, enzyme inclusion, and BW. When analyzing the flow of energy and nutrients through the gastrointestinal tract, data collected at each BW were analyzed separately with fiber level and enzyme inclusion as main effects, and the fiber level × xylanase inclusion interaction included in the model. Differences were considered significant if $P < 0.05$, and trends if $0.05 \leq P \leq 0.10$.

Results

All pigs recovered from surgery with no complications and remained healthy throughout the experiment. All pigs fully consumed their daily feed allotment and both fecal and ileal samples were successfully collected from all pigs during each period.

The analyzed composition of each dietary treatment is included in Table 2.1. The LF diets contained less GE (3.84 vs. 4.02 Mcal/kg), NDF (6.21 vs. 11.72%), ADF (2.40 vs. 4.33%), CP (14.56 vs. 19.91%), and crude fat (3.08 vs. 4.32%), and contained more starch (56.14 vs. 37.36%) compared to the HF diets, averaged over xylanase treatment. As expected, the formulated composition in Table 2.1 shows that LF diets had higher NE (2.46 vs. 2.29 Mcal/kg) compared to the HF diets.

Impact of xylanase inclusion × fiber level on AID, hindgut fermentation, and ATTD of energy and nutrients and TTTD of fat

The inclusion of xylanase increased the AID of DM, starch, and nitrogen, and tended to increase the AID of GE in LF diets, but had no impact on digestibility in HF diets resulting in xylanase inclusion (XI) × fiber level (FL) interactions ($P \leq 0.059$; Table 2.2). Xylanase inclusion decreased the AID of NDF and tended to decrease the AID of ADF in LF diets, but had no effect on NDF or ADF digestibility in HF diets, resulting in XI × FL interactions ($P \leq 0.097$). The inclusion of xylanase tended to decrease the AID of hemicellulose ($P = 0.065$).

Xylanase inclusion tended to decrease the hindgut disappearance of DM in LF diets but increase the hindgut disappearance of DM in HF diets, leading to a trend for a XI × FL interaction ($P = 0.084$). There was a trend for XI to increase the hindgut disappearance of NDF, ADF, and hemicellulose ($P \leq 0.100$). Lower fiber diets had higher hindgut disappearance of

ADF and tended to have higher hindgut disappearance of NDF compared to HF diets ($P \leq 0.063$). Higher fiber diets had greater hindgut disappearance of fat compared to LF diets ($P = 0.016$). There was no impact of XI or FL on hindgut disappearance of GE ($P \geq 0.178$).

Xylanase inclusion had no impact on the ATTD of NDF, hemicellulose, or the TTTD fat ($P \geq 0.381$). The inclusion of xylanase decreased the ATTD of ADF in LF diets but increased the ATTD of ADF in HF diets, resulting in a trend for a XI × FL interaction ($P = 0.091$). The TTTD of fat was lower in LF diets compared to HF diets ($P < 0.001$).

Impact of BW on AID, hindgut fermentation, and ATTD of energy and nutrients and TTTD of fat

As BW increased, the AID of DM, GE and nitrogen and the hindgut disappearance of ADF increased ($P \leq 0.006$; Table 2.2). The ATTD of NDF and hemicellulose increased as BW increased ($P \leq 0.001$) and the TTTD of fat tended to increase with increased BW ($P = 0.093$).

Impact of xylanase inclusion × BW and fiber level on the hindgut disappearance of nitrogen and ATTD of DM and nitrogen

The hindgut disappearance of nitrogen increased as BW increased from 46.0 to 54.1 kg, then decreased as BW increased from 54.1 to 70.3 kg in diets without xylanase, but increased with increasing BW in diets with xylanase, resulting in a trend for a XI × BW interaction ($P = 0.088$; Table 2.3). The ATTD of DM and nitrogen increased as BW increased from 46.0 to 54.1 kg, but had no increase as BW increased from 54.1 to 70.3 kg in diets without xylanase; in diets with xylanase, the ATTD of DM did not change as BW increased 46.0 to 54.1 kg, but increased as BW increased from 54.1 to 70.3 kg and the ATTD of nitrogen increased at BW, resulting in

an XI × BW interaction ($P \leq 0.033$). The ATTD of GE increased as BW increased ($P < 0.001$). Lower fiber diets had higher ATTD of DM, GE, and nitrogen compared to HF diets ($P \leq 0.036$). Dietary fiber level did not impact the hindgut disappearance of nitrogen ($P = 0.856$).

Impact of fiber level × BW on AID of fiber and starch and ATTD of ADF

In LF diets, the AID of NDF, ADF, and hemicellulose decreased slightly as BW increased from 46.0 to 54.1 kg, then increased as BW increased from 54.1 to 70.3 kg; in HF diets, the AID of NDF, ADF, and hemicellulose increased as BW increased from 46.0 to 54.1 kg, then decreased as BW increased from 54.1 to 70.3 kg, resulting in FL × BW interactions ($P \leq 0.043$; Table 2.4). The AID of starch in LF diets did not change as BW increased from 46.0 to 54.1 kg, but increased as BW increased from 54.1 to 70.3 kg, whereas the AID of starch in HF diets did not change over the three BW, resulting in a FL × BW interaction ($P = 0.021$). The ATTD of ADF in LF diets did not change as BW increased from 46.0 to 54.1 kg, but increased as BW increased from 54.1 to 70.3 kg; the ATTD of ADF in HF diets increased over the three BW, leading to a FL × BW interaction ($P = 0.020$).

Impact of fiber level, xylanase inclusion, and BW on AID of AA

Xylanase inclusion tended to increase the AID of Asp in LF diets but decrease the AID of Asp in HF diets, resulting in a trend for a FL × XI interaction ($P = 0.063$; Table 2.5). Xylanase inclusion tended to increase the AID of Arg ($P = 0.091$). Lower fiber diets had higher AID of Arg, Cys, Glu, His, Ile, Lys, Met, Met + Cys, Phe, Ser, Thr, Trp, and Val compared to HF diets ($P \leq 0.021$). The AID of Ala and Pro were higher in HF diets compared to LF diets ($P \leq 0.027$). Other than Trp, the AID of all measured AA increased over the three BW ($P \leq 0.017$).

Impact of xylanase inclusion and fiber level on the flow of DM, GE, and NDF

Average BW: 46.0 ± 0.4 kg (d 8 to 12)

In 46 kg pigs fed LF diets, XI increased DM disappearance and tended to increase GE disappearance before the terminal ileum; in HF diets, XI decreased the disappearance of DM before the terminal ileum and had no effect on the disappearance of GE before the terminal ileum, resulting in FL × XI interactions ($P \leq 0.098$; Table 2.6). Xylanase inclusion subsequently decreased the hindgut disappearance of DM in LF diets but increased the hindgut disappearance of DM in HF diets, leading to a trend for a FL × XI interaction ($P = 0.051$).

Lower fiber diets had decreased GE remaining at the terminal ileum and decreased DM and GE excreted in feces compared to HF diets ($P < 0.001$). Xylanase inclusion had no impact on the amount of DM or GE excreted in feces ($P \geq 0.125$).

Lower fiber diets had decreased NDF disappearance before the terminal ileum, decreased hindgut disappearance of NDF, and less NDF excreted in feces compared to HF diets ($P \leq 0.030$). Xylanase inclusion decreased the amount of NDF excreted in feces, regardless of FL ($P = 0.001$).

Average BW: 54.1 ± 0.4 kg (d 18 to 22)

In 54.1 kg pigs, XI tended to increase DM and increased GE disappearance before the terminal ileum in LF diets, but had no effect in HF diets, leading to FL × XI interactions ($P \leq 0.063$; Table 2.7). Xylanase inclusion tended to decrease hindgut disappearance of DM and GE, regardless of dietary FL ($P \leq 0.087$). The inclusion of xylanase decreased the amount of GE excreted in feces in LF diets, but increased the amount of GE excreted in the feces in HF diets,

resulting in a trend for a FL × XI interaction (*P* = 0.080). Lower fiber diets had decreased DM and GE excreted in feces compared to HF diets (*P* < 0.001).

Lower fiber diets had decreased NDF disappearance before the terminal ileum and decreased hindgut disappearance of NDF compared to the HF diets (*P* ≤ 0.031). Xylanase inclusion decreased the amount of NDF excreted in feces in the LF diets, but increased the amount of NDF excreted in feces in the HF diets, leading to a trend for a FL × XI interaction (*P* = 0.078).

Average BW: 70.3 ± 0.5 kg (d 38 to 42)

When measured in 70.3 kg pigs, LF diets had increased DM disappearance before the terminal ileum, decreased hindgut disappearance of DM, and decreased DM excreted in feces compared to HF diets (*P* ≤ 0.007; Table 2.8). Xylanase inclusion tended to increase the disappearance of GE before the terminal ileum (*P* = 0.083). Lower fiber diets had less GE remaining at the terminal ileum and less excreted in feces compared to the HF diets (*P* < 0.001). Xylanase inclusion decreased the disappearance of NDF before the terminal ileum in LF diets, but had no effect in HF diets, resulting in a FL × XI interaction (*P* = 0.009). Lower fiber diets had decreased NDF remaining at the terminal ileum, hindgut disappearance of NDF, and NDF excreted in feces compared to HF diets (*P* < 0.001).

Impact of xylanase inclusion × fiber level × BW on the TID of fat

A three-way interaction between XI, FL, and BW was observed for the TID of fat (*P* = 0.024; Figure 2.1). In LF diets not including xylanase, the TID of fat did not change as BW increased from 46.0 to 54.1 kg, then increased as BW increased from 54.1 to 70.3 kg; in LF diets with xylanase, the TID did not change over the three BW. In HF diets not including xylanase,

there was a trend for the TID of fat to increase as BW increased from 46.0 to 54.1 kg, then the TID of fat decreased as BW increased from 54.1 to 70.3 kg; in HF diets with xylanase, the TID of fat did not change over the three BW.

Discussion

In this study, XI had no effect on the AID of NDF, ADF, or hemicellulose in HF diets, which is not surprising based on our current understanding of the xylanase enzyme. The hydrolysis of arabinoxylans by xylanase enzymes releases arabino- and xylo-oligosaccharides, with additional enzymes required for the release of arabinose and xylose sugars (Dekker and Richards, 1976; Bedford and Schulze, 1998). Therefore, it is likely that the dietary fiber components liberated by xylanase would still appear in the measurements of NDF. Xylanase inclusion actually decreased the AID of NDF, ADF, and hemicellulose in the LF diets, which is unexpected. The same effect was seen when measuring flow of NDF, as XI decreased NDF disappearance before the terminal ileum in the LF diets but not in the HF diets. We also observed negative digestibility values for the AID of fiber in several LF ileal digesta samples, particularly in those including xylanase. Negative fiber digestibility values are not physiologically possible in monogastric animals, but have been previously reported in the literature (Wilfart et al., 2007).

The decreased AID of fiber observed in our experiment may be due to increased mucin production, which can contaminate dietary fiber analyses. It has been determined that endogenous materials such as glycoproteins, microbes, and sloughed epithelial cells from the lumen of the gastrointestinal tract may be co-analyzed with dietary fiber when using the NDF, ADF, or TDF methods, resulting in an underestimation of dietary fiber digestion (Montoya et al., 2016). Mucins and bacteria are the primary endogenous materials that are included in and

interfere with dietary fiber analyses when measured at the small intestine (Montoya et al., 2016). Previous studies have demonstrated the ability of dietary components to influence mucin production in swine (Moré et al., 1987), and previous studies in poultry have reported increased mucin production with the inclusion of xylanase (Sharma et al., 1997; Fernandez et al., 2000). Therefore, the decreased AID of fiber in LF diets may be a by-product of contamination in the assays used to measure fiber. The decrease in the AID of dietary fiber with XI was compensated for in the hindgut, as there was no impact of XI on the ATTD of dietary fiber or the amount of NDF excreted in feces. The negative effect of XI on AID of fiber was not observed in HF diets, possibly because the diets contain higher levels of fiber, so the contribution from mucin would make up a smaller percentage of the dietary fiber collected. Therefore, contamination by mucin would have less impact.

Although the mechanism of increased digestibility via xylanase enzymes is not completely understood, one hypothesis is that xylanase breaks down the endosperm cell walls, releasing trapped nutrients that would otherwise be inaccessible to endogenous enzymes and escape digestion (Bedford, 2000). In this study, we observed that the inclusion of xylanase increased the AID of DM, starch, and nitrogen and the disappearance of GE before the terminal ileum in 46.0 and 54.1 kg pigs fed LF diets. These observations support this hypothesis of xylanase action and agree with previously published literature (Passos et al., 2015). The inclusion of xylanase had no effect on the AID of DM, starch, and nitrogen in HF diets. There was also no effect of XI on the flow of DM or GE through the digestive tract in HF diets. Xylanase has previously been shown to increase the AID of GE, DM, and CP in corn-based diets containing 30% corn co-products fed to swine (Kiarie et al., 2016); however, the co-products

used in that study were a combination of corn distillers grains with solubles and corn germ meal, whereas the diets for this study contained 30% corn distillers grains only.

During the wet-milling process of ethanol production, fermentation breaks down the endosperm walls of corn fiber, potentially releasing trapped nutrients. If trapped nutrients are released at this time, the xylanase enzyme has fewer nutrients to liberate in the gastrointestinal tract of the pig, which would explain why the xylanase enzyme elicited a response in LF diets but not in HF diets containing corn DDGS. It is also possible that protein and starch are still present in corn DDGS, but are bound in complex fiber-starch-protein matrices caused by the heating process of ethanol production, rendering them resistant to enzyme degradation (Jha et al., 2015).

It has previously been reported and is generally accepted in the industry that as pigs grow, their ability to utilize dietary energy and nutrients increases (Cunningham et al., 1962). Our data support the impact of BW on digestibility, as we observed increased AID of DM, GE, primarily driven by increases in starch and nitrogen digestibility, as BW increased. Fermentation capabilities also increased with increased BW as demonstrated by increased hindgut disappearance of nitrogen and ADF. When measured across the total tract, the digestibility DM, GE, fiber, and nitrogen increased and fat digestibility tended to increase as BW increased.

Seeing that we know BW impacts digestibility, one objective of this study was to test if BW impacted the digestibility response of the xylanase enzyme. We observed no XI × BW interaction for the digestibility of energy, fiber, nitrogen, starch, or fat in the small intestine ($P > 0.100$). Xylanase inclusion did seem to result in a smaller increase in the hindgut disappearance of nitrogen and the ATTD of DM and nitrogen from 46.0 to 54.1 kg compared to the non-xylanase treatment, followed by a larger increase from 54.1 to 70.3 kg compared to the non-

xylanase treatment; however, within BW, the xylanase treatment differed from the non-xylanase treatment in the hindgut disappearance of nitrogen only at 54.1 kg and did not differ from the non-xylanase treatment for the ATTD of DM or nitrogen at any of the three BW. Overall, xylanase inclusion did result in different patterns of DM and nitrogen digestibility. Due to our experimental design, we are not able to distinguish between the impact of BW and time on dietary treatment and cannot speculate whether the larger increase in digestibility with XI observed from 54.1 to 70.3 kg would have continued at BW over 70.3 kg or beyond 6 weeks on dietary treatment. Based on our data, there does not appear to be an impact of BW or time on dietary treatment on xylanase response in pigs from 46.0 to 70.3 kg or pigs on the enzyme for 6 weeks.

As would be expected, inclusion of 30% DDGS decreased the AID and ATTD of DM, GE, and nitrogen compared to the LF diets. The TTTD of fat was greater in the diets containing 30% DDGS compared to the LF diets. It has previously been reported that increased dietary fiber can decrease the absorption of dietary components, including fat, and increase endogenous losses of fat, possibly by promoting microbial proliferation in the intestine (Dierick et al., 1990; Le Goff and Noblet, 2001). However, these conclusions were drawn from studies using, at least in part, soluble sources of fiber. Previous research indicates that increased dietary fiber in the form of corn DDGS, which is primarily insoluble fiber, may not have the same negative impact on fat digestibility (Kil et al., 2010; Gutierrez et al., 2016). The increased TTTD of fat in the HF diets, which contained more fat than the LF diets, is most likely a consequence of endogenous losses of fat. An effort was made to account for the endogenous losses of fat by using correction factors determined by a study with pigs of similar size fed similar diets (Gutierrez et al., 2016); however, after employing the correction factor, the TID of fat was still higher than the TTTD of

fat for both HF and LF diets at each BW, indicating that the correction factor did not fully account for the endogenous fat secretions. This may have been due to the fact that the correction factors used were calculated from diets with extracted fat, and previous studies have shown that endogenous losses are higher in diets containing intact fat compared to extracted fat (Kil et al., 2010; Gutierrez et al., 2016). Within the same fat form (intact vs. extracted) and source, it is hypothesized that endogenous losses of fat remain constant regardless of fat intake (Adams and Jensen, 1984; Gutierrez et al., 2016); therefore, as fat intake increases, endogenous losses make up a lower percentage of the fat collected at the end of the gastrointestinal tract, giving the illusion of higher fat digestibility (Gutierrez et al., 2016).

In conclusion, XI increased AID of energy, starch, and nitrogen, and decreased AID of fiber in LF diets, although that may have been an artifact rather than true result, as discussed above. The inclusion of xylanase had no impact on digestibility in the HF diets. Our data show improvement in the ATTD of DM and nitrogen within the xylanase treatment occurring between 54.1 and 70.3 kg; however, it is unclear whether the larger increases in digestibility would continue beyond 70.3 kg and digestibility values for the xylanase treatment not differ from the non-xylanase treatment at any BW. Overall, xylanase supplementation slightly increased digestibility in 46.0 to 70.3 kg pigs in LF diets, and had no impact on digestibility in HF diets.

Table 2.1. Ingredient, analyzed chemical composition and formulated nutrient composition of the experimental diets, as-fed basis

	Lower fiber		Higher fiber	
Item	− Xyl[1]	+ Xyl	− Xyl	+ Xyl
Ingredient, %				
Corn[2]	77.73	77.71	50.68	50.66
Corn DDGS[3] (6.8% fat)	-	-	30.00	30.00
Soybean meal[4] (42.7% CP)	18.40	18.40	16.00	16.00
Limestone	1.18	1.18	1.45	1.45
Monocalcium Phosphate	0.94	0.94	0.35	0.35
L-Lysine HCl	0.45	0.45	0.44	0.44
DL-Methionine	0.06	0.06	-	-
L-Threonine	0.13	0.13	0.02	0.02
L-Tryptophan	0.02	0.02	0.01	0.01
L-Valine	0.04	0.04	-	-
Nursery Vitamin Premix[5]	0.25	0.25	0.25	0.25
Trace Mineral Premix[5]	0.15	0.15	0.15	0.15
Salt	0.25	0.25	0.25	0.25
Chromic oxide	0.40	0.40	0.40	0.40
Econase XT	-	0.02	-	0.02
Analyzed composition				
DM, %	90.24	90.63	90.42	90.67
GE, Mcal/kg	3.83	3.84	4.01	4.03
NDF, %	6.53	5.89	11.65	11.79
ADF, %	2.50	2.30	4.26	4.40
Starch, %	56.39	55.89	37.86	36.86
CP (N × 6.25), %	14.32	14.80	20.14	19.67
Crude fat, %	3.11	3.04	4.22	4.41
Xylanase activity, BXU/kg	<2000	33,300	3,500	32,800
Calculated nutrient composition				
NE, Mcal/kg	2.46	2.46	2.29	2.29
SID Lysine, %	1.19	1.19	1.14	1.14

[1]Xyl refers to the xylanase product ®Econase XT included at 165 mg xylanase/ kg of finished feed.

[2]Particle size of corn = 682 microns.

[3]Corn DDGS = corn dried distillers grains with solubles; particle size = 375 microns.

[4]Particle size of soybean meal = 787 microns.

[5]Provided per kg of complete diet: 6,614 IU vitamin A, 827 IU vitamin D, 26 IU vitamin E, 2.6 mg vitamin K, 29.8 mg niacin, 16.5 mg pantothenic acid, 5.0 mg riboflavin, and 0.023 mg vitamin B_{12}.

[6]Provided per kg of complete diet: 165 mg Zn as zinc sulfate, 165 mg Fe as iron sulfate, 39 mg Mn as manganese sulfate, 17 mg Cu as copper sulfate, 0.3 mg I as calcium iodate, and 0.3 mg Se as sodium selenite.

Table 2.2. Effect of xylanase inclusion × fiber level and BW on digestibility in the small intestine, hindgut fermentation, and digestibility across the total tract

	Lower fiber[1]		Higher fiber[2]			BW, kg[3]				*P*-value[4]			
Item	− Xyl[5]	+ Xyl	− Xyl	+ Xyl	SEM	46.0	54.1	70.3	SEM	Fiber	Xyl	Fiber × xyl	BW
Apparent ileal digestibility, %													
DM	72.7[a]	74.5[b]	65.6[c]	64.8[c]	0.6	68.6	68.8	70.8	0.4	<0.001	0.407	0.041	<0.001
GE	72.9[y]	74.6[y]	67.6[z]	66.8[z]	0.6	69.5	70.1	71.9	0.5	<0.001	0.453	0.059	<0.001
NDF	18.8[a]	10.4[b]	19.5[a]	18.6[a]	2.2	-	-	-	-	0.054	0.044	0.097	-
ADF	18.0[a]	7.5[b]	22.6[a]	23.1[a]	2.2	-	-	-	-	<0.001	0.030	0.017	-
Hemicellulose[6]	19.3	12.2	17.7	15.9	2.3	-	-	-	-	0.661	0.065	0.255	-
Starch	94.1[ab]	95.3[a]	94.5[ab]	93.6[b]	0.5	-	-	-	-	0.178	0.859	0.042	-
Nitrogen	72.4[a]	74.5[b]	72.2[a]	70.9[a]	0.7	71.1	72.2	74.2	0.5	0.012	0.578	0.024	<0.001
Hindgut disappearance[7], %													
DM	12.6[ab]	11.1[a]	13.2[b]	14.0[b]	0.6	12.6	13.3	12.3	0.5	0.012	0.600	0.084	0.203
GE	10.7	9.4	10.1	10.7	0.7	10.0	10.5	10.1	0.5	0.590	0.608	0.178	0.698
NDF	22.0	29.6	20.4	22.0	2.4	20.7	23.7	26.0	1.9	0.063	0.067	0.221	0.122
ADF	31.9[y]	40.0[y]	26.5[z]	28.5[z]	2.6	29.0	29.0	37.2	2.1	0.003	0.058	0.244	0.006
Hemicellulose	15.9	22.8	16.9	18.1	2.4	15.7	20.5	19.2	1.9	0.428	0.100	0.234	0.166
Fat[9]	-11.9[y]	-11.8[y]	-7.2[z]	-6.5[z]	1.9	-9.1	-10.2	-8.7	1.3	0.016	0.833	0.863	0.647
Apparent total tract digestibility[8], %													
NDF	40.9	39.9	39.9	40.6	1.1	36.9	40.0	44.1	0.9	0.879	0.909	0.462	<0.001
ADF	49.9[ab]	47.5[a]	49.1[ab]	51.6[b]	1.4	-	-	-	-	0.250	0.958	0.091	-
Hemicellulose	35.3	35.1	34.6	34.0	1.0	31.5	35.0	37.7	1.0	0.394	0.708	0.841	0.001
True total tract digestibility, %													
Fat	75.5[y]	76.2[y]	83.9[z]	81.5[z]	1.0	78.4	79.0	80.5	0.7	<0.001	0.381	0.128	0.093

[1]Lower fiber (0% corn DDGS).

[2]Higher fiber (30% corn DDGS).

[3]Average pig BW: 46.0 ± 0.4 kg (d 8 to 12), 54.1 ± 0.4 kg (d 18 to 22), 70.3 ± 0.5 kg (d 38 to 42).
d 38 to 42).

[4]*P*-values and means for BW reported when no BW × fiber level and/or xylanase inclusion interaction was observed (P > 0.100). BW × xylanase inclusion is reported in Table 2.3, and BW × fiber level interaction is reported in Table 2.4.

[5]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.

[6]Hemicellulose calculated as NDF – ADF.
[7]Data for hindgut disappearance of nitrogen included in Table 2.3 due to xylanase × BW interaction ($P \geq 0.100$).
[8]Data for ATTD of DM, GE and nitrogen included in Table 2.3 due to xylanase × BW interaction for DM and nitrogen ($P \geq 0.100$).
[9]Corrected for endogenous losses (Gutierrez et al., 2016).
[a,b,c]Within a row, means without a common superscript differ for the interaction fiber × xylanase ($P \leq 0.05$).
[y,z]Within a row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Table 2.3. Effect of xylanase inclusion × BW and fiber level on the hindgut disappearance of nitrogen and apparent total tract digestibility of GE, DM, and nitrogen

	− Xyl[1]			+ Xyl				Fiber level[2]			P-value[3]			
Item	46.0[4]	54.1	70.3	46.0	54.1	70.3	SEM	Low	High	SEM	Xyl	BW	Xyl × BW	Fiber
Hindgut disappearance, %														
Nitrogen	6.1^{ac}	8.6^{b}	7.5^{abc}	6.1^{a}	6.3^{ac}	7.9^{bc}	0.8	7.2	7.0	0.6	0.458	0.029	0.088	0.856
Apparent total tract digestibility, %														
DM	80.8^{a}	82.4^{bc}	82.8^{b}	81.5^{ac}	81.8^{ac}	83.3^{b}	0.3	85.5^{y}	78.7^{z}	0.3	0.648	<0.001	0.032	<0.001
GE	79.3	81.0	81.8	80.0	80.7	82.3	0.4	84.0^{y}	77.7^{z}	0.3	0.477	<0.001	0.128	<0.001
Nitrogen	77.1^{ab}	80.5^{cd}	81.5^{c}	77.4^{b}	78.8^{ad}	82.4^{c}	0.8	80.6^{y}	78.6^{z}	0.7	0.829	<0.001	0.033	0.036

[1]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.

[2]Fiber level: low refers to 0% corn DDGS, high refers to 30% corn DDGS in diet.

[3]Main effects of fiber reported as no fiber level × xylanase inclusion and/or BW interaction was observed ($P > 0.100$).

[4]Average pig BW: 46.0 ± 0.4 kg (d 8 to 12), 54.1 ± 0.4 kg (d 18 to 22), 70.3 ± 0.5 kg (d 38 to 42).

[a,b,c,d]Within a row, means without a common superscript differ for the interaction xylanase × BW ($P \leq 0.05$).

[y,z]Within a row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Table 2.4. Effect of fiber level × BW on the apparent ileal digestibility and apparent total tract digestibility of carbohydrates

	Lower fiber[1]			Higher fiber[2]				*P*-value[3]	
Item	46.0[4]	54.1	70.3	46.0	54.1	70.3	SEM	BW	Fib × BW
Apparent ileal digestibility, %									
NDF	13.6[ab]	11.2[b]	19.1[ac]	18.8[ac]	21.4[c]	17.0[bc]	2.2	0.572	0.011
ADF	11.7[a]	11.5[a]	15.0[ac]	22.0[bd]	26.9[b]	19.7[cd]	2.3	0.490	0.043
Hemicellulose[5]	14.7[ac]	11.0[a]	21.6[b]	16.9[ab]	18.1[bc]	15.4[ab]	2.3	0.132	0.005
Starch	94.1[a]	94.1[a]	95.9[b]	94.4[a]	93.8[a]	93.9[a]	0.5	0.081	0.021
Apparent total tract digestibility, %									
ADF	43.9[a]	46.2[ab]	56.0[c]	47.7[ab]	50.2[bd]	53.1[cd]	1.5	<0.001	0.020

[1]Lower fiber (0% corn DDGS).
[2]Higher fiber (30% corn DDGS).
[3]*P*-values for main effect of fiber reported in Table 2.2.
[4]Average pig BW: 46.0 ± 0.4 kg (d 8 to 12), 54.1 ± 0.4 kg (d 18 to 22), 70.3 ± 0.5 kg (d 38 to 42).
[5]Hemicellulose calculated as NDF – ADF.
[a,b,c,d]Within a row, means without a common superscript differ for the interaction fiber × BW ($P \leq 0.05$).

Table 2.5. Effect of xylanase inclusion × fiber level and BW on the AID of AA, %

	Lower fiber[1]		Higher fiber[2]			BW, kg[3]				*P*-value[4]			
Item	− Xyl[5]	+ Xyl	− Xyl	+ Xyl	SEM	46.0	54.1	70.3	SEM	Fiber	Xyl	Fib × Xyl	BW
Ala	74.0[a]	74.8[a]	75.8[b]	76.0[b]	0.6	74.0	75.5	76.0	0.5	0.027	0.465	0.596	0.001
Arg	83.0[a]	84.3[a]	80.8[b]	81.1[b]	0.4	81.6	82.3	83.0	0.3	<0.001	0.091	0.323	<0.001
Asp	74.3[a]	75.7[a]	69.6[b]	68.4[b]	0.7	70.6	72.1	73.3	0.4	<0.001	0.844	0.063	<0.001
Cys	60.7[a]	63.7[a]	57.5[b]	58.8[b]	1.4	57.5	59.3	63.8	0.9	0.009	0.145	0.555	<0.001
Glu	80.6[a]	81.7[a]	79.1[b]	77.3[b]	0.9	78.1	79.2	81.6	0.5	0.002	0.737	0.106	<0.001
Gly	52.8	55.7	56.3	56.0	1.6	53.2	54.1	58.3	1.0	0.252	0.420	0.331	<0.001
His	79.6[a]	80.8[a]	75.8[b]	75.7[b]	0.7	76.4	77.9	79.7	0.4	<0.001	0.430	0.376	<0.001
Ile	75.4[a]	76.5[a]	73.3[b]	73.3[b]	0.7	73.8	74.7	75.3	0.4	0.001	0.414	0.402	0.017
Leu	79.4	80.6	80.6	80.4	0.5	79.0	80.4	81.3	0.4	0.346	0.359	0.205	<0.001
Lys	83.9[a]	84.8[a]	78.4[b]	77.9[b]	0.5	80.4	81.5	81.9	0.3	<0.001	0.664	0.140	0.001
Met	86.2[a]	86.2[a]	80.3[b]	79.9[b]	0.4	82.4	83.5	83.6	0.3	<0.001	0.674	0.722	0.001
Met + Cys	75.1[a]	76.2[a]	68.8[b]	69.2[b]	0.9	70.7	72.0	74.3	0.6	<0.001	0.423	0.711	<0.001
Phe	78.3[a]	79.1[a]	77.7[b]	77.3[b]	0.5	77.0	78.3	79.0	0.4	0.021	0.687	0.245	<0.001
Pro	67.2[a]	70.6[a]	75.6[b]	75.9[b]	2.9	71.8	70.1	75.1	1.6	0.023	0.530	0.588	0.001
Ser	73.3[a]	74.0[a]	71.6[b]	71.8[b]	0.7	71.4	72.6	74.0	0.4	0.006	0.483	0.730	<0.001
Thr	72.2[a]	73.4[a]	64.7[b]	64.9[b]	0.7	67.3	68.8	70.3	0.5	<0.001	0.355	0.486	<0.001
Trp	67.0[a]	66.3[a]	62.3[b]	62.3[b]	1.0	63.8	65.4	64.5	0.7	0.001	0.709	0.716	0.106
Tyr	80.3	80.2	80.6	79.8	0.7	79.1	80.8	80.7	0.5	0.907	0.531	0.675	<0.001
Val	73.1[a]	74.5[a]	69.8[b]	70.2[b]	0.7	70.6	72.1	73.0	0.5	<0.001	0.213	0.470	<0.001

[1]Lower fiber (0% corn DDGS).
[2]Higher fiber (30% corn DDGS).
[3]Average pig BW: 46.0 ± 0.4 kg (d 8 to 12), 54.1 ± 0.4 kg (d 18 to 22), 70.3 ± 0.5 kg (d 38 to 42).
[4]Main effect of BW reported as no BW × fiber level and/or xylanase inclusion interactions were observed ($P > 0.100$).
[5]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.
[a,b]Within a row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Table 2.6. Effect of xylanase inclusion and fiber level on the flow of DM, GE, and NDF through the intestines in 46.0 ± 0.4 kg pigs (d 8 to 12)

Item	Lower fiber[1]		Higher fiber[2]		SEM	*P*-value		
	− Xyl[3]	+ Xyl	− Xyl	+ Xyl		Fiber	Xyl	Fiber×Xyl
Intake								
DM, kg/d	1.47	1.47	1.47	1.48	-	-	-	-
GE, Mcal/d	6.23	6.25	6.53	6.56	-	-	-	-
NDF, g/d	106	96	190	192	-	-	-	-
DM, g/kg DMI								
Disappearance before TI	738[a]	758[a]	671[b]	655[b]	8	<0.001	0.848	0.030
Remaining at TI	262[a]	242[a]	329[b]	345[b]	8	<0.001	0.848	0.030
Hindgut disappearance	113[a]	100[a]	116[ab]	140[b]	9	0.021	0.544	0.051
Excreted in feces	149[y]	142[y]	213[z]	206[z]	4	<0.001	0.125	0.958
GE, Mcal/kg DMI								
Intake	5.62	5.67	5.91	5.95	-	-	-	-
Disappearance before TI	4.44[a]	4.56[b]	4.45[ab]	4.42[a]	0.04	0.163	0.247	0.098
Remaining at TI	1.19[y]	1.11[y]	1.46[z]	1.52[z]	0.04	<0.001	0.864	0.103
Hindgut disappearance	0.44	0.40	0.41	0.49	0.05	0.473	0.637	0.167
Excreted in feces	0.75[y]	0.71[y]	1.05[z]	1.03[z]	0.03	<0.001	0.257	0.803
NDF, g/kg DMI								
Intake	96	87	171	174	-	-	-	-
Disappearance before TI	36[y]	28[y]	68[z]	67[z]	3	<0.001	0.195	0.231
Remaining at TI	60[y]	59[y]	104[z]	107[z]	3	<0.001	0.740	0.589
Hindgut disappearance	13[y]	18[y]	21[z]	27[z]	4	0.030	0.154	0.951
Excreted in feces	47[my]	41[ny]	82[mz]	80[nz]	1	<0.001	0.001	0.202

[1]Lower fiber (0% corn DDGS).

[2]Higher fiber (30% corn DDGS).

[3]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.

[a,b,c] Within row, means without a common superscript differ for the interaction fiber × xylanase ($P \leq 0.05$).

[m,n]Within row, means without a common superscript differ for the main effect of xylanase ($P \leq 0.05$).

[y.z]Within row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Table 2.7. Effect of xylanase inclusion and fiber level on the flow of DM, GE, and NDF through the intestines in 54.1 ± 0.4 kg pigs (d 18 to 22)

	Lower fiber[1]		Higher fiber[2]			*P*-value		
Item	− Xyl[3]	+ Xyl	− Xyl	+ Xyl	SEM	Fiber	Xyl	Fiber×Xyl
Intake								
DM, kg/d	1.66	1.67	1.67	1.67	-	-	-	-
GE, Mcal/d	7.06	7.08	7.40	7.43	-	-	-	-
NDF, g/d	120	109	215	217	-	-	-	-
DM, g/kg DMI								
Disappearance before TI	730[a]	758[b]	667[c]	659[c]	9	<0.001	0.285	0.063
Remaining at TI	270[a]	242[b]	333[c]	341[c]	9	<0.001	0.285	0.063
Hindgut disappearance	132[my]	103[ny]	140[mz]	137[nz]	9	0.021	0.076	0.137
Excreted in feces	138[y]	139[y]	193[z]	204[z]	5	<0.001	0.261	0.356
GE, Mcal/kg DMI								
Intake	6.37	6.42	6.69	6.74	-	-	-	-
Disappearance before TI	5.16[a]	5.35[b]	5.26[c]	5.26[c]	0.04	0.824	0.034	0.042
Remaining at TI	1.21[a]	1.07[b]	1.43[c]	1.47[c]	0.04	<0.001	0.274	0.045
Hindgut disappearance	0.52	0.38	0.47	0.46	0.04	0.693	0.087	0.160
Excreted in feces	0.69[a]	0.66[a]	0.96[b]	1.02[b]	0.03	<0.001	0.629	0.080
NDF, g/kg DMI								
Intake	109	98	194	197	-	-	-	-
Disappearance before TI	58	49	114	114	3	<0.001	0.162	0.147
Remaining at TI	63[y]	59[y]	101[z]	103[z]	3	<0.001	0.887	0.340
Hindgut disappearance	20	19	26	25	3	0.031	0.645	0.955
Excreted in feces	43[a]	41[a]	75[b]	78[b]	2	<0.001	0.609	0.078

[1]Lower fiber (0% corn DDGS).

[2]Higher fiber (30% corn DDGS).

[3]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.

[a,b,c] Within row, means without a common superscript differ for the interaction fiber × xylanase ($P \leq 0.05$).

[m,n] Within row, means without a common superscript differ for the main effect of xylanase ($P \leq 0.05$).

[y.z] Within row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Table 2.8. Effect of xylanase inclusion and fiber level on the flow of DM, GE, and NDF through the intestines in 70.3 ± 0.5 kg pigs (d 38 to 42)

	Lower fiber[1]		Higher fiber[2]			*P*-value		
Item	− Xyl[3]	+ Xyl	− Xyl	+ Xyl	SEM	Fiber	Xyl	Fiber×Xyl
Intake								
DM, kg/d	1.84	1.84	1.84	1.84	-	-	-	-
GE, Mcal/d	7.79	7.82	8.17	8.20	-	-	-	-
NDF, g/d	133	120	237	240	-	-	-	-
DM, g/kg DMI								
Disappearance before TI	770[y]	776[y]	683[z]	683[z]	6	<0.001	0.607	0.662
Remaining at TI	230[y]	224[y]	317[z]	317[z]	6	<0.001	0.607	0.662
Hindgut disappearance	100[y]	99[y]	121[z]	124[z]	8	0.007	0.851	0.773
Excreted in feces	131[y]	125[y]	197[z]	192[z]	4	<0.001	0.207	0.898
GE, Mcal/kg DMI								
Intake	7.03	7.08	7.38	7.43	-	-	-	-
Disappearance before TI	5.99	6.05	6.00	6.03	0.04	0.544	0.083	0.959
Remaining at TI	1.04[y]	1.03[y]	1.42[z]	1.41[z]	0.04	<0.001	0.778	0.994
Hindgut disappearance	0.40	0.42	0.47	0.48	0.04	0.149	0.747	0.927
Excreted in feces	0.64[y]	0.61[y]	0.95[z]	0.93[z]	0.02	<0.001	0.184	0.815
NDF, g/kg DMI								
Intake	133	120	237	240	-	-	-	-
Disappearance before TI	79[a]	63[b]	130[c]	132[c]	3	<0.001	0.032	0.009
Remaining at TI	54[y]	57[y]	107[z]	108[z]	3	<0.001	0.556	0.841
Hindgut disappearance	15[y]	21[y]	32[z]	34[z]	4	<0.001	0.292	0.696
Excreted in feces	39[y]	36[y]	75[z]	74[z]	2	<0.001	0.147	0.567

[1]Lower fiber (0% corn DDGS).

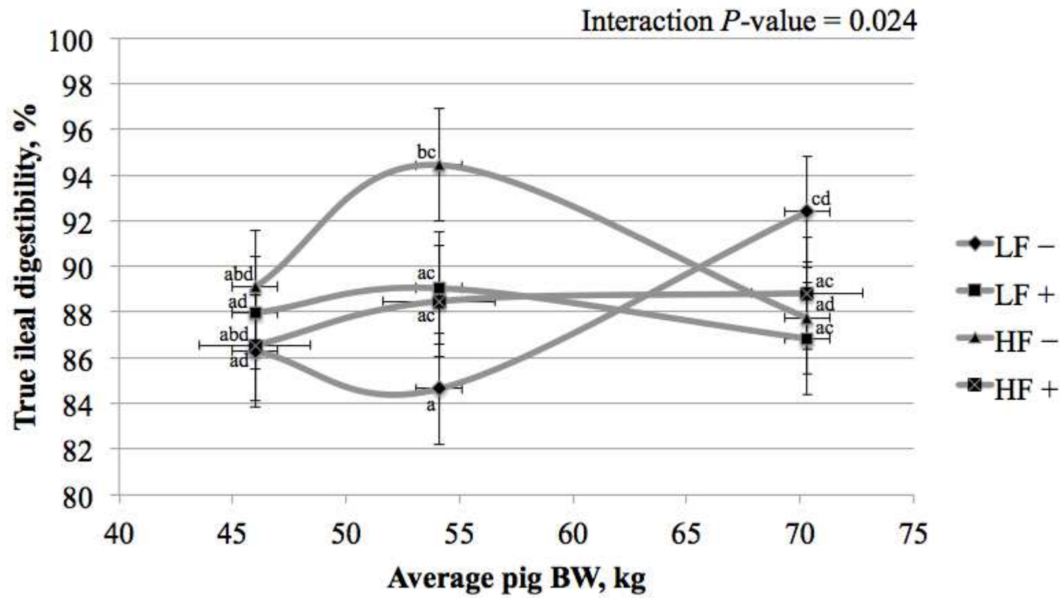
[2]Higher fiber (30% corn DDGS).

[3]Xyl refers to the xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.

[a,b,c] Within row, means without a common superscript differ for the interaction fiber × xylanase ($P \leq 0.05$).

[y,z] Within row, means without a common superscript differ for the main effect of fiber ($P \leq 0.05$).

Figure 2.1. Impact of fiber level × xylanase inclusion × BW on the TID of fat



LF: lower fiber (0% corn DDGS).
HF: higher fiber (30% corn DDGS).
Xylanase product ®Econase XT included at 0% (−) or 0.017% (+) of diet.
[a,b,c,d]Within time point, means without a common superscript differ for the interaction fiber level × xylanase inclusion × BW ($P \leq 0.05$).

CHAPTER III

SUMMARY AND CONCLUSIONS

The increased inclusion of corn co-products in swine diets has prompted the need for technologies to assist the pig in fiber degradation. The feeding of higher fiber feedstuffs not only reduces the energy concentration of the diet, but has also been shown to reduce the digestibility of other dietary components. Carbohydrase enzymes, such as xylanase, have the potential to increase digestive efficiency by breaking down dietary fiber, mitigating the negative effects on digestion. However, the inconsistencies in digestibility and growth responses to xylanase in swine have brought into question the action of the enzyme within the gastrointestinal tract of the pig. This thesis focused on measuring the impact of xylanase on digestibility of dietary components in the small and large intestines in order to gain a better understanding of the enzyme action and how the pig is able to utilize the end-products of the enzyme reaction.

We observed that xylanase inclusion increased the digestibility of energy, starch and nitrogen in the small intestine in corn-based diets, which supports the hypothesis that increased digestibility with xylanase supplementation is due to the liberation of nutrients that were previously trapped in the fiber structure of corn. Xylanase inclusion did not impact digestibility in diets containing corn DDGS; indicating that corn DDGS are not a suitable substrate for the xylanase enzyme. If the liberation of previously trapped nutrients is, in fact, the mechanism for increased digestibility by xylanase, it is possible that no response is seen in corn DDGS because trapped nutrients are already liberated during the fermentation process of ethanol production.

A second hypothesis is that xylanase supplementation increases digestive efficiency by breaking down the fibrous components in the diet, lessening the impact of dietary fiber on the

viscosity of digesta. Decreases in the viscosity of digesta with xylanase supplementation have been reported (Passos et al., 2015) and it is likely that decreases in viscosity play a part in the response to xylanase supplementation observed in poultry; however, viscosity plays a much smaller role in digestibility in swine compared to poultry (Adeola and Cowieson, 2011). Also, the fiber in corn is primarily insoluble, and thus has a lesser impact on digesta viscosity compared to soluble fiber. Therefore, changes in digestive efficiency with xylanase supplementation in corn-based diets in swine are not likely due to decreases in viscosity.

The precision of our measurements allowed us to detect differences in starch, protein, and energy digestibility with xylanase supplementation; however, in terms of growth, it is likely that these increases in digestibility mean little, as a 1.2% and 2.1% increase in starch and protein digestibility, respectively, resulted in only a 1.7% increase in energy digestibility. In the corn-soybean meal diets used in this study, a 1.7% increase in GE digestibility results in an extra 73 kcal/kg DMI:

GE release by xylanase (Mcal/kg DMI) = [(3.84 Mcal/kg /90% DM) × 1.7% change in energy release] = 0.073 Mcal/kg.

A difference in energy availability this small is not likely to be distinguishable in a growth response, as errors in growth measurements are generally too large to detect such small differences.

The ability of the xylanase enzyme to break down arabinoxylans and release trapped nutrients is limited not only by the degree of polymerization and substitution of the arabinoxylan, but also by interactions with other fibrous components of the diet. In order to entirely break down dietary fiber, multiple enzymes, including xylanases, β-glucanases, and cellulases, are necessary. Thus, future research should be aimed at testing blends of multiple carbohydrase

enzymes in corn-based diets in swine, which may produce larger, and thus, more consistent responses in digestibility and growth.

One surprising observation of this study was an apparent decrease in fiber digestibility and the negative fiber digestibility values observed with xylanase supplementation. After reviewing the literature, we concluded that the decrease in digestibility was most likely an artifact due to mucin and bacterial contamination in our NDF and ADF analyses, which resulted in an underestimation of fiber digestibility. The ability of endogenous secretions to be co-analyzed and contaminate fiber analyses has been reported for years, yet very few researchers have made an effort to quantify and correct for such contamination. Without accounting for such endogenous secretions, it is likely that reported values for fiber digestibility are incorrectly low, resulting in an underestimation of fiber digestibility in swine. In order to more accurately evaluate carbohydrase enzymes, future researchers must critically evaluate the analyses used to measure fiber and search for methods to correct for the contamination of endogenous secretions.

In conclusion, our study indicates that increased energy and nutrient digestibility with xylanase supplementation in corn-based diets in swine is likely due to the release of previously trapped nutrients. However, the digestibility response is small and is not likely to result in a measurable growth response. Rather than focusing on xylanase alone, future research should focus on carbohydrase blends, as the digestibility and growth responses may be more robust. Further research is also needed to quantify and correct for the amount of contamination by endogenous secretions in the various fiber analyses in order to more accurately measure fiber digestibility.

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