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Starch and fiber properties affect their kinetics of digestion and thereby digestive physiology in pigs

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ABSTRACT: Traditionally in swine nutrition, analyses of starch and fiber have focused on assessing quantity; however, both have a wide range of functional properties making them underappreciated nutrients. Starch ranging from low to high amylose changes from rapidly digestible in the upper gut to poorly digestible but fermentable in the lower gut thereby changing from a source of glucose to VFA source. Likewise, fibers ranging from low to high viscosity affect digesta flow and from slowly to rapidly fermentable alter production of VFA serving as energy for the gut or whole body. Our hypothesis is that total extent, kinetics, and site of digestion or fermentation of starch and fiber are important for whole body nutrient use and intestinal health. To elucidate their effects, we developed in vitro, lab-based methodologies to describe kinetics of digestion and fermentation and linked these with in vivo models including i) ileum cannulation to collect digesta, ii) portal-vein catheterization to sequentially sample blood, iii) slaughter method to collect site-specific intestinal tissue and digesta, and iv) indirect calorimetry. Using these methods, kinetics of nutrient absorption was associated with pancreatic and intestinal hormones released into the portal vein, intestinal microbiota, and gene expression in intestinal tissue and microbiota. These studies confirmed that slowly digestible starch is partially degraded in the distal small and large intestine and fermented into VFA including butyrate (10-fold increase in net portal appearance), which reduces insulin responses by 60% and whole body energy use. Starch entering the distal intestine altered mRNA abundance of nutrient transporters and was bifidogenic. Extremely viscous purified fiber dampened glycemic responses and reduced digesta passage rate by 50% thereby increasing ileal digestion of dietary nutrients whereas increased fiber in feed grains reduced nutrient digestibility. Fermentable fiber increased butyrate and insulin production. These methods will therefore support elucidation of mechanisms that link starch and fiber properties to whole body nutrient use and intestinal health.

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INTRODUCTION

Dietary starch and fiber are important nutrients for pigs but are underappreciated in their complexity. For example, starch ranging from low to high amylose changes from rapidly enzymatically digestible in the upper gut to fermentable in the lower gut including the distal small intestine, respectively, due to changes in physicochemical characteristics such as viscosity, fermentability, and water-holding capacity (Regmi et al., 2011a). Starch can therefore be a source of glucose or VFA (also known as short-chain fatty acids) and for the latter is therefore similar to fiber. In swine nutrition, the paradigm is that nondigestible carbohydrates are a negative dietary factor due to their fermentation and adverse effects on whole body nutrient use (Drew et al., 2012). In human nutrition, where health but not ADG is main objective, fermentable or resistant starch is gaining popularity due to suppression of rate of nutrient absorption and stimulation of intestinal health (Bird et al., 2008).

Similarly, dietary fiber has a contradictory status in nutritional sciences. In swine nutrition, fibers such as β-glucans and arabinoxylans are regarded as negative dietary factors due to their negative effects on nutrient digestibility and feed intake (de Lange, 2000). In

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contrast, fiber gains popularity in human nutrition due to their adverse effects on rate of nutrient digestion and, therefore, glycemic index (Jenkins et al., 2002) and stimulatory effects on intestinal health (Kudo, 2004) and is increasingly regarded as a functional food component.

Our approach has been to use in vivo and in vitro methods to study effects of physicochemical properties of starch and fiber on digestive physiology. To date, mostly purified starches and fiber sources have been used for these studies. As outlined, these methods served to initiate elucidation of mechanisms that support adaptation of pigs from carbohydrate digestion to carbohydrate fermentation.

IN VIVO METHODS

Invasive pig models to study digestion and absorption include ileal cannulation, portal-vein catheterization, and the slaughter technique (Bach Knudsen et al., 2006). Noninvasive pig models include indirect calorimetry and nutrient balance can be used to study whole body nutrient use.

Ileal Cannulation

Distal ileum cannulation allows collection of digesta (Sauer and Ozimek, 1986) as well as feces. Measures of ileal digestibility reflect enzymatic digestion, enteric fermentation in the upper gut, endogenous secretion into the gut, and (re-)absorption. With the addition of an indigestible marker, this model allows study of the total extent of digestion in the upper gut and lower gut. It has been important for the establishment of digestible AA values and can also separate digestible from fermentable starch. Nutrients, bacteria, and metabolites can be quantified in collected samples.

Portal-Vein Catheterization

Pigs are catheterized in the portal vein and carotid artery for sequential blood sampling and an ultrasonic blood flow probe is placed around the portal vein (Hooda et al., 2009). This model allows study of the rate or kinetics of digestion following a meal (Rérat et al., 1980, 1984a,b). This model thus adds a time component to the measurements of digestion. The method reflects net uptake into systemic circulation, which is the result of absorption, secretion into the gut, and absorption and use of nutrients by the portal-drained viscera. The portal vein drains the intestine and pancreas and therefore, net absorption of glucose, VFA, and other metabolites and release of incretins and pancreatic hormones into the portal vein can be measured.

Slaughter Technique

Slaughter of pigs allows the collection of intestinal tissue and digesta along the length of the gastrointestinal tract (Metzler-Zebeli et al., 2011, 2012). This model permits the study of the site of digestion. The collected tissue can be studied for overall morphology and detailed analyses of gene expression. Furthermore, digesta can be analyzed for residual nutrients and microbial populations so that the flow of nutrients such as starch and the interaction with the gut and microbial population can be tracked throughout the gastrointestinal tract. This model determines local effects on digestion and released nutrients or metabolites.

Noninvasive Models

Indirect calorimetry can assess whole body use of energy (Moehn et al., 2007). In a nutrient balance study (quantitative collection of feces and urine), whole body use of N and other nutrients but not energy can be determined.

STARCH DIGESTION AND ABSORPTION

Digestion and Absorption

Enzymatic starch digestion in the small intestine produces glucose as a final product for absorption. Starch that is not enzymatically digested can be fermented, yielding VFA that can be used as an energy source by the pig. The rate and extent of enzymatic starch digestion depends on starch chemistry, particle size, processing method, and association with other compounds (Singh et al., 2010). Among starch chemistry characteristics, amylose content is an important factor affecting starch digestibility and thus metabolic responses in vivo (Regmi et al., 2011a,b). Unlike amylopectin that is highly branched, amylose polymers have less surface area and more intramolecular hydrogen bonds (Singh et al., 2010). Therefore, amylose is digested or depolymerized at a slower rate and extent than amylopectin due to decreased accessibility for α-amylase (Batlle et al., 2000). Indeed, starch with high amylose content and slower rate and extent of in vitro digestion decreased glucose absorption and increased VFA absorption in portal-vein catheterized pigs (Regmi et al., 2011b). Therefore, starch may also function as a fiber and induce both its positive and negative effects on health. Its effects as a fiber source are described below.

In Vitro Methods to Mimic In Vivo Digestion

For nutritional purpose, starch is either described as total starch or as 3 fractions based on rate and extent of in vitro enzymatic digestion. These digested fractions include rapidly digestible starch (within 20 min), slowly digestible starch (between 20 to 120 min), and resistant starch (more than 120 min) as determined by the prominent Englyst in vitro assay (Englyst et al., 2000). This analysis mimics gastric digestion using pepsin and then enzymatic digestion

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using amyloglucosidase and invertase followed by analysis of released glucose over time. The classification into different starch fractions is linked to the glycemic index that is used in human nutrition (Jenkins et al., 1981).

For estimating net glucose flux into the portal vein, the original Englyst procedure is not a match (van Kempen et al., 2010). Possible explanations for the discrepancies between in vitro starch digestion and in vivo glucose responses include coverage of limited postprandial duration and use of discrete glucose response observations. Hence, we extended the in vitro analyses to 480 min and then converted the obtained discrete glucose release values to continuous glucose kinetics response curves using a modified Chapman Richards model (van Kempen et al., 2007). Finally, we corrected the in vitro values for gastric release of digesta and were then able to accurately predict ($R^2 = 0.95$) net portal glucose flux and the cumulative insulin response from cumulative in vitro glucose release (van Kempen et al., 2010). This method might be foundation to predict in vivo response to starch sources differing in kinetics of digestion. Then relations between starch source and, for example, insulin resistance, adiposity, and satiety can be established.

FIBER DIGESTION AND ABSORPTION

Fiber is not digested by endogenous enzymes. However, bacteria may ferment fiber (Varel and Yen, 1997), mostly in the large intestine but also in the small intestine (Jensen and Jorgensen, 1994; Jha et al., 2010; Jha and Leterme, 2012). Fiber fermentation produces VFA (mainly acetate, propionate, and butyrate) and gases such as H_2, CO_2, and CH_4 (Macfarlane and Macfarlane, 1993). The VFA are important signaling molecules (Sanderson, 2004; Xiong et al., 2004) and serve as energy source (Varel and Yen, 1997).

Digestion and Absorption

Fermentation of fiber is more variable (0 to 100%) than digestion of the macronutrients starch, fat, and CP (generally above 80%; Bach Knudsen et al., 2008). The variation in fiber fermentability is mainly due to changes in physicochemical properties of fiber such as bulk, viscosity, solubility, water-holding capacity, and fermentability. For example, viscosity may increase the proportion of the diet that is digested in the small intestine due to a reduced digesta passage rate, as demonstrated in pigs fed carboxymethyl cellulose (Hooda et al., 2011). Methods used to assess physicochemical properties should be evaluated critically. For example, viscosity of fiber will change when fiber is being fermented (Bedford and Classen, 1992). In addition, solubility is a function of the medium used in the assay, and current assays use conditions different from physiological conditions (Graham et al., 1986; Monro, 1993).

Fiber digestibility varies widely, partly due to type. In growing pigs, fiber digestibility ranges from 16% for wheat (*Triticum aestivum*) straw, 44% for wheat bran, and 70% for sugar beet (*Beta vulgaris*) pulp to 79% for soybean (*Glycine max*) hulls (Chabeauti et al., 1991). Wheat straw is poorly digested due to extensive lignification and wheat bran fiber contains poorly fermentable hemicellulose and cellulose whereas pectic substances in sugar beet pulp and soybean hulls are highly digestible (Karr-Lilienthal et al., 2005). Digestibility of cellulose is low, of soluble pectin and hemicelluloses is higher than cellulose, and of soluble barley (*Hordeum vulgare*) β-glucan is 100% by the end of the gut (Bach Knudsen et al., 1993). In contrast, insoluble branched-chain arabinoxylans from wheat, rye (*Secale cereale*), and oat (*Avena sativa*) are less digestible than soluble β-glucan (Bach Knudsen and Hansen, 1991; Glitsø et al., 1998). Soluble β-glucan, arabinoxylans, and pectins are rapidly degraded in the cecum and proximal colon whereas insoluble fiber components such as cellulose and insoluble arabinoxylans are degraded slowly in the distal colon (Bach Knudsen et al., 1993; Canibe and Bach Knudsen, 1997; Glitsø et al., 1998). Moreover, soluble and noncellulosic mannose and galactose are highly fermentable compared to the insoluble cellulosic fiber (Serena and Bach Knudsen, 2007).

Increasing dietary fiber content reduces digestibility of energy and other nutrients (Just et al., 1983; Fairbairn et al., 1999; Zijlstra et al., 1999) unless the fiber is extremely viscous such as carboxymethyl cellulose (Hooda et al., 2011). The reduction depends on the amount, source, and physicochemical properties of fiber. For example, fiber either purified or embedded within the matrix reduces CP digestibility in pigs (Bedford et al., 1992). Moreover, increased purified NDF in the diet increased endogenous protein losses and linearly decreased ileal digestibility of DM and CP (Schulze et al., 1994). The endogenous AA losses caused by dietary fiber were later defined as specific endogenous AA losses (Stein et al., 2007). Finally, digestibility of organic matter, CP, starch, and fiber was lower in diets based on hulled barley and oat than based on hulless barley in pigs (Baidoo and Liu, 1998; Jha et al., 2010). The reduced nutrient digestibility is due to physiological changes in digesta in the presence of fiber that reduce the access of endogenous enzymes to nutrients and affect passage rate of the digesta (Bach Knudsen, 2001).

Digestibility of fiber increases with physiological maturity of pigs. For example, digestible energy in fiber is 0.14 Mcal/kg DM higher in adult sows than in growing pigs (Le Goff and Noblet, 2001). This is due to a longer

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retention time consequent to the increased volume of the gastrointestinal tract combined with a lower feed intake per unit of live weight (Le Goff et al., 2002).

The large intestine is the main site of VFA absorption in pigs (Imoto and Namioka, 1978). Approximately 90% of the produced VFA are absorbed by colonocytes, which may also be used as energy source by other tissues (Wong et al., 2006). Specifically, absorbed VFA are metabolized in 3 sites: (i) colonocytes that use butyrate for energy, (ii) liver cells that metabolize residual butyrate into ketone bodies and propionate for gluconeogenesis and 50 to 70% of acetate for energy, and (iii) skeletal and cardiac muscle cells that oxidize the residual acetate (Roberfroid, 2007). The energy produced from VFA may contribute up to 15% of the ME requirements of growing pigs (Dierick et al., 1989) and up to 30% in gestating sows (Varel and Yen, 1997).

In Vitro Methods to Mimic In Vivo Digestion

Determining the rate of fiber fermentation in the porcine digestive tract and subsequent impact on the gut environment is difficult. Therefore, screening feedstuffs that differ in fiber content or functionality using in vivo techniques is impractical. Instead, in vitro gas production can measure feedstuff fermentability (Williams et al., 2005; Jha et al., 2011b), bacterial protein synthesis (Bindelle et al., 2009; Jha et al., 2011a), and bacteria profiles (Awati et al., 2005). It is hypothesized, but requires validation, that gas production combined with in vitro fermentation kinetics reflects fiber fermentation kinetics in the porcine intestine. After validation in swine models, in vitro methods can determine fiber fermentation characteristics routinely for an array of feedstuffs (Williams et al., 2005) because they are faster and less expensive than in vivo techniques. Fermentation characteristics of hulless and hulled barley, oat, wheat bran, flax seed meal, sugar beet pulp, field pea (*Pisum sativum*), and dried distillers grains with solubles have been studied in vitro and in vivo and had similar fermentation characteristics and metabolites (van Gelder et al., 2005; Jha et al., 2010, 2011a,b; Jha and Leterme, 2012). Indeed, better fermentable substrates have a higher rate of degradation and produce more gas and metabolites, such as VFA, than less fermentable substrates.

SYSTEMIC EFFECTS OF STARCH AND FIBER

Energy Metabolism

The switch from enzymatically digestible to fermentable starch will reduce net portal glucose and increase net portal VFA flux (Regmi et al., 2011b). This switch from digestible to fermentable starch will reduce energetic efficiency of starch use (Gerrits et al., 2012) and may even impact N retention (Drew et al., 2012) and fat metabolism (Yin et al., 2011) in pigs with restricted access to feed. Moreover, mildly increased amylose content in corn (*Zea mays*) was associated with reduced growth in grower but not finisher pigs with free access to feed (Moore et al., 2008), indicating that pigs may adapt to high amylose as they grow older. Similarly, switching from low to high purified fermentable fiber will increase net portal flux of VFA (Hooda, 2010), and changing from low to high viscous purified fiber may impact the site of digestion vs. fermentation of the rest of the diet (Hooda et al., 2011). The impact of changes in physicochemical properties of starch and fiber sources are not considered in databases that rely on analyses of total starch, crude fiber, ADF, NDF, total dietary fiber, and even nonstarch polysaccharides (**NSP**). The time has come to build on existing NE databases that are based on digestibility values of energy-yielding substrates (e.g., CVB, 2003) and establish feedstuff databases that consider (kinetics of) digestibility and fermentability of starch and fiber sources (Fahey et al., 2011).

Physiological Functions

Fiber in diets reduces digestibility but also affects other aspects of digestive physiology; similar effects are expected with fermentable starch. Fiber may increase endogenous N losses (Schulze et al., 1994) depending on fiber level, type (Schulze et al., 1995), and physicochemical properties such as water-holding capacity (Leterme et al., 1996). For example, soluble fiber increases digesta viscosity and endogenous N losses (Mariscal-Landin et al., 1995). High digesta viscosity stimulates epithelial cell proliferation and may contribute to loss of epithelial cells in the rat model (Gee et al., 1996). Moreover, fiber may increase mucus secretion in the small intestine (Mariscal-Landin et al., 1995) due to mechanical effects on the gut wall that may damage the mucus layer. However, soluble fiber reduces protein digestion and absorption more than insoluble fiber (Leterme et al., 1998).

Endocrinology

Starch chemistry has important effects on glucose absorption and consequently insulin and incretin release for maintaining glucose homeostasis. Resistant starch and dietary soluble fiber decrease portal glucose appearance in pigs (Ellis et al., 1995; Hooda et al., 2010; Regmi et al., 2011b); however, corresponding insulin responses were inconsistent. Portal insulin did not differ between pigs fed diets with 0 to 6% β-glucan (Hooda et al., 2010). In contrast, portal insulin was lower in pigs fed slowly vs. rapidly digestible starch (Regmi et al., 2011b). The difference in insulin response might be due to the extreme range in net portal glucose flux, reaching 3.5 mmol/min with β-glucan diets (Hooda et al., 2010) compared to 5.3

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mmol/min with rapidly digestible starch diets (Regmi et al., 2011b) at 60 min postfeeding.

Pancreatic release of insulin is not only due to net portal glucose flux but also of VFA. The VFA produced following starch and fiber fermentation influence insulin release through actions of glucagon-like peptide-1 (**GLP-1**) and glucose-dependent insulinotropic polypeptide (**GIP**), which are released from L cells in the distal small and large intestine and from K cells in the small intestine, respectively (Baggio and Drucker, 2007). In rats, VFA increased GLP-1 secretion by increasing proglucagon mRNA in L cells (Reimer and McBurney, 1996; Tappenden et al., 1996, 1998) and increasing cecal mass (Kok et al., 1998). Whereas VFA production has not been related to proglucagon mRNA and cecal hypertrophy in pigs, increased net portal VFA from fermentation of high viscous β-glucan or resistant starch was associated with increases in net portal GLP-1 (Hooda, 2010; Regmi et al., 2011b). Contrary to GLP-1 appearance, addition of NSP or resistant starch decreased net GIP appearance in pigs (Ellis et al., 1995; Hooda et al., 2010; Regmi et al., 2011b).

The association between VFA production, incretin release, and insulin secretion in pigs is not yet fully understood. Insulin secretion is initiated when GLP-1 binds to receptors on pancreatic β cells (Burcelin et al., 2007). Even though both fermentable β-glucan and resistant starch increased VFA production and net portal GLP-1 appearance, high fermentable β-glucan increased insulin release (Hooda, 2010) and resistant starch decreased insulin release (Regmi et al., 2011b). The contrast indicates that luminal glucose may more directly influence insulin responses than associations of VFA and GLP-1. The mechanisms relating luminal glucose and VFA to insulin and incretin release require a better understanding of the relation between starch chemistry and glucose homeostasis in pigs.

Microbiota

The gastrointestinal tract in pigs is colonized with a diverse population of bacteria that supports physiological development and immunologic functions (Hill et al., 2002; Chowdhury et al., 2007; Willing and Van Kessel, 2010). However, pigs can have unstable gut microbiomes at various life stages, allowing opportunity for pathogenic bacteria to colonize and cause disease (Pieper et al., 2008, 2009). A combination of digesta passage rate, digestibility, fermentability, and viscosity contributes to nutrient availability and commensal bacteria colonization in the lower gastrointestinal tract (Metzler-Zebeli et al., 2010; Regmi et al., 2011a).

Switching from dietary digestible to resistant starch provides readily available substrates for microbes in the large intestine, and dietary fiber is also used by colonic microbiota as fermentative substrates (Topping and Clifton, 2001). Diets high in amylose or resistant starch favor the production of commensal bacteria such as *Bifidobacterium* and *Lactobacillus* groups in pigs (Brown et al., 1997; Bird et al., 2007). Decreasing in vitro starch digestion rate by increasing amylose content increased available nutrients (starch and protein) in the colon, thereby increasing commensal *Bifidobacterium* spp. in feces (Regmi et al., 2011a). Moreover, dietary inclusion of highly viscous carboxymethyl cellulose increased prevalence of *Escherichia coli* virulence factors, indicating the importance of postileal nutrient flow on substrate availability in the lower gut for commensal microbial colonization (Metzler-Zebeli et al., 2010). Although certain fiber sources share physicochemical properties such as viscosity and fermentability, they do not consistently affect small intestinal digestion, large intestinal substrate availability, or microbial responses; hence, fiber sources work according to individual fractions rather than shared functional properties (Metzler-Zebeli et al., 2010).

Some oligosaccharides and polysaccharides are recognized as prebiotics for human and animal nutrition (Topping et al., 2003; Bach Knudsen et al., 2012). Nonenzymatically digestible oligosaccharides (**NDO**) are highly fermentable and decrease gastrointestinal pH producing an unfavorable environment to pH-sensitive microbes (Houdijk et al., 2002; Macfarlane et al., 2006; Bach Knudsen et al., 2012). The NDO bring about prececal prebiotic effect in weaner pigs (Houdijk et al., 2002). As pigs age, their microbiome becomes more stable and inclusion of prebiotic feedstuffs, such as resistant starch, NDO, or high amylose starch grain cultivars, have seemingly fewer effects. Supplementing fructan, a NDO, caused only minor changes in digestibility without changes in microbiota (Hedemann and Bach Knudsen, 2010b). Interestingly, when resistant starch and NDO were fed together to pigs, additive effects on colon and fecal bifidobacteria numbers were reported (Bird et al., 2009).

Combining soluble and insoluble NSP may cause similar additive effects on ileal bifidobacteria and enterobacteria populations (Owusu-Asiedu et al., 2006). Multiple studies in humans and other animals indicate that dietary resistant starch and NDO have a prebiotic effect across species (Campbell et al., 1997; Djouzi and Andrieux, 1997; Brown et al., 1998; Tuohy et al., 2001). Oat β-glucan, either concentrated or within the cereal matrix, also has a prebiotic effect in pigs (Metzler-Zebeli et al., 2010); dietary β-glucan selectively increases colonic lactobacilli and bifidobacteria (Metzler-Zebeli et al., 2011) promoting butyrate-producing bacteria (Pieper

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et al., 2008). Combined, convincing evidence exists that various starch and fiber fractions have a prebiotic effect in pigs; however, the singular or additive effects that carbohydrate fractions have on microbial diversity and colonization remain to be elucidated.

Gene Expression

Starch digestion produces glucose, which is absorbed through the apical membrane of the epithelial cell by Na^+–dependent glucose transporter 1 (**SGLT1**) (Shirazi-Beechey et al., 2011a). In contrast, fermentation of resistant starch and fiber produces VFA that are absorbed through either the Na^+–coupled monocarboxylate transporter (**SMCT**) or the monocarboxylate transporter 1 (**MCT1**) (Roy et al., 2006). Increased luminal concentration of the substrates may increase the transporters number on the apical intestinal epithelium, consequently increasing substrate uptake. For example, weaned pigs fed a diet with >50% digestible carbohydrate (starch and sugar) had increased SGLT1 expression and increased glucose uptake in the small intestine compared to pigs fed a <50% digestible carbohydrate diet (Moran et al., 2010b). Luminal glucose increases SGLT1 activity through intestinal chemosensing (Shirazi-Beechey et al., 2011a,b). Increased glucose in the intestinal lumen stimulates taste receptors T1R2 and T1R3, causing a release of α-gustducin and glucagon-like peptide-2, which stimulates transcription of mRNA encoding SGLT1, thereby increasing glucose uptake (Moran et al., 2010a; Shirazi-Beechey et al., 2011b).

Although effects of glucose on expression of SGLT1 are established (Shirazi-Beechey et al., 2011a,b), limited information exists on MCT1 and SMCT responses to luminal VFA. Slowly digestible starch may increase MCT1 expression in the colon (Woodward et al., 2012); however, the substrates that are influencing MCT1 mRNA abundance have not been established. Regardless, the presence of luminal substrates from digestion or fermentation of starch and fiber influences gene expression of transporters along the intestinal epithelium.

Value Attributes

Despite fiber reducing nutrient digestibility, fermentable fiber may improve intestine health and parts of nutrient management. Fermentable fiber modulates gut microbiota and reduces NH_3 emission (Aarnink and Verstegen, 2007) and therefore might be part of an effective package to improve gut health as an alternative to antibiotic growth promoters (Williams et al., 2001; Verstegen and Williams, 2002).

Fiber plays an important role in gut health. Fiber may assist in the control of bacterial infections, including postweaning diarrhea (Williams et al., 2001; Lalles et al., 2007), that are a major problem for the global pig industry. Pigs fed highly fermentable carbohydrates (fructan-rich chicory (*Cichorium intybus*) roots and sweet lupin) were protected against the onset of swine dysentery (Thomsen et al., 2007). Inclusion of fermentable carbohydrate in piglet feeds enhanced intestinal populations of lactobacilli and reduced diarrhea incidence and severity (Edwards, 1996). In contrast, fructan (from chicory root) did not protect weaned pigs against postweaning diarrhea in an experimental challenged *E. coli* model (Hedemann and Bach Knudsen, 2010a). Furthermore, incidence of clinical swine dysentery in growing pigs and diarrhea in weanling pigs increased for diets high in fermentable fiber and resistant starch (Pluske et al., 1998, 2003). Finally, supplementation of purified soluble fiber in nursery pig diets reduced gut health (Dritz et al., 1995). Combined, these findings indicate that a complex interaction exists between physicochemical properties of fiber and starch, intestinal microbial population, and the prevention of the onset of diarrhea resulting from pathogenic bacteria.

With a disturbed balance and less fermentable carbohydrates available for bacteria, fermentation shifts from carbohydrates to protein in the gut (Piva et al., 1996; Macfarlane and Macfarlane, 2003). However, fermentation shifts quickly back from proteolytic to saccharolytic when fermentable carbohydrates are available in the gut (Houdijk et al., 1998). Proteolytic fermentation is not preferred due to production of potentially toxic metabolites such as NH_3 and amines (Cone et al., 2005) and malodorous compounds such as skatole and indole (Jensen et al., 1995). Nutritional strategies such as reduced dietary CP (Htoo et al., 2007) or the inclusion of fermentable carbohydrates such as lactitol (Piva et al., 1996), fructooligosaccharides (Houdijk et al., 1998), resistant starch, and wheat bran (Govers et al., 1999) can reduce protein fermentation.

With increased supply of fermentable carbohydrates as an energy source, indigestible protein is more likely to be incorporated into bacterial protein (Houdijk et al., 1998). Dietary and endogenous proteins in the large intestine as well as blood urea are used by resident bacteria as N source to produce bacterial protein. Ammonia generated by bacterial urease is used by bacteria for protein synthesis, which increases the N excreted in the feces and decreases N excretion in urine (Kirchgessner et al., 1994). Thus, dietary fermentable fiber shifts N excretion from urine to feces (Zervas and Zijlstra, 2002). Fecal N excretion is a function of fermentable carbohydrates and indigestible protein (Jha and Leterme, 2012), and both should be considered while programming for N excretion and management from pigs.

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CONCLUSIONS AND FUTURE RESEARCH

Starch and fiber properties clearly affect the kinetics of their digestion and fermentation. Moreover, these properties affect digestion and absorption of other nutrients and the 3-way interaction among host, nutrients, and intestinal microbiota. These changes in nutrient flow through the lumen and across the epithelium cause an array of changes in the gut and also affect whole body nutrient use. To regulate these changes, intestinal and pancreatic hormones work in concert, likely under the direction of chemosensors in the gut. The changes in nutrient flow thus affect protein and lipid deposition, gut health, and nutrient excretion in pigs.

Gaps in knowledge remain in the underlying mechanisms that support changing the pig from a carbohydrate digester to fermenter when fed nondigestible carbohydrates. These include chemosensing, changes in nutrient transporters, gut integrity, bacteria populations, intestinal and blood profiles of nutrients and bacterial metabolites, and resultant cross-talk between the gut and pancreas. Kinetics of starch and fiber digestion and fermentation should be defined across food and feedstuffs to establish a link to food and feed formulation. For example, challenges exist that may require rapidly available energy, such as during exercise, and unique starch and fiber feedstuffs may benefit pigs challenged with intestinal pathogens.

Finally, studies using surgical models in meal-fed pigs must be translated not only to health and nutrition in meal-fed humans but also to pigs with free access to feed in pork production. This translation will add another level of complexity, because, for example, voluntary feed intake is affected by characteristics of fiber such as water-holding capacity (Kyriazakis and Emmans, 1995), GLP-1 released following starch or fiber fermentation may induce satiety (Moran and Dailey. 2011), and meal frequency impacts production and absorption of VFA (Rérat et al., 1987).

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