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FIBER DIGESTIBILITY IN GROWING PIGS FED COMMON FIBER-RICH INGREDIENTS – A SYSTEMATIC REVIEW

Pan Yang, Jinbiao Zhao♦

State Key Laboratory of Animal Nutrition, College of Animal Science and Technology, China Agricultural University, Beijing 100193, China
♦Corresponding author: jinbiaozhao@cau.edu.cn

Abstract
The application of high-fiber ingredients in the swine feed industry has some limitations considering that high amounts of fiber are resistant to endogenous enzymatic degradation in the pig's gut. However, there is growing interest in fiber fermentation in the intestine of pigs due to their functional properties and potential health benefits. Many strategies have been applied in feed formulations to improve utilization efficiency of fiber-rich ingredients and stimulate their prebiotic effects in pigs. This manuscript reviews chemical compositions, physical properties, and digestibility of fiber-rich diets formulated with fibrous ingredients for growing pigs. Evidences presented in this review indicate there is a great variation in chemical compositions and physical properties of fibrous ingredients, resulting in the discrepancy of energy and fiber digestibility in pig intestine. In practice, fermentation capacity of fiber components in the pig's intestine can be improved using strategies, such as biological enzymes supplementation and feed processing technologies. Soluble dietary fiber (SDF) and insoluble dietary fiber (IDF), rather than neutral detergent fiber (NDF) and acid detergent fiber (ADF), are recommended in application of pig production to achieve precise feeding. Limitations of current scientific research on determining fiber digestibility and short chain fatty acids (SCFA) production are discussed. Endogenous losses of fiber components from non-dietary materials that result in underestimation of fiber digestibility and SCFA production are discussed in this review. Overall, the purpose of our review is to provide a reference for feeding the pig by choosing the diets formulated with different high-fiber ingredients.

Key words: digestibility, fiber fermentation, microbiota, pig, short chain fatty acid

Dietary fiber is a series of complex compounds which cannot be digested by digestive enzymes secreted by animals, but can be partly or completely fermented by gut microbiota to produce short chain fatty acids (SCFA) in the intestine (Williams et al., 2001). Traditionally, dietary fiber intake reduces energy and nutrient digestibility, and ultimately decreases growth performance of pigs (Dégen et al., 2009). To mitigate the negative effects of dietary fiber, many studies have focused on approaches to improve utilization efficiency of dietary fiber in pigs, such as supplementation of enzymes and feed processing technologies (Zijlstra et al., 2010; Molist et al., 2010). In addition, some recent studies have reported that dietary fiber and its fermentation metabolites can maintain physiological status and benefit the immune function and health of pigs (Molist et al., 2014; Zhao et al., 2018 a). The SCFA produced by dietary fiber fermentation mainly includes acetate, propionate, and butyrate, which play an important role in regulating metabolism, immunological function, and gut cell proliferation of the host (Koh et al., 2016). Butyrate is an energy source for colonocytes to maintain gut barrier functions, whereas acetate and propionate are delivered to peripheral circulation through the portal vein to participate in metabolic activities of the liver and peripheral tissues (Liu et al., 2018). In addition, there is great variation in nutrient digestibility, fermentation capacity, and SCFA production among various fiber-rich ingredients because of their diverse physicochemical characteristics (Urriola and Stein, 2010; Bach Knudsen et al., 2013; Jaworski and Stein, 2017). To better understand the role of dietary fiber in pigs and to promote utilization of dietary fiber in pig production, this paper reviews digestibility of fibrous components in diets formulated with common fiber-rich ingredients, and summarizes factors affecting fermentation capacity of dietary fiber components.

Chemical components of dietary fiber

In general, dietary fiber is derived mainly from the cell walls of plants (Figure 1). Plant cell walls are a mixture of polysaccharides, phytate, protein, and phenol complexes, among which polysaccharides (e.g. cellulose, hemicellulose, pectin, and gums) are the major components of dietary fiber. According to solubility in water,

dietary fiber can be classified into two categories: soluble dietary fiber (SDF) and insoluble dietary fiber (IDF). The SDF is composed of pectin, β-glucan, gums, and soluble hemicellulose, and IDF is composed of cellulose, lignin, and insoluble hemicellulose (Williams et al., 2019). Alternatively, dietary fiber can be classified into neutral detergent fiber (NDF) and acid detergent fiber (ADF), which are commonly used in pig nutrition due to high cost of SDF and IDF analysis. However, NDF and ADF primarily contain cellulose, lignin, and insoluble hemicellulose, but soluble fiber components are not measured. The main physical characteristics of dietary fiber include water holding capacity, viscosity, swelling, and fermentability (Bach Knudsen et al., 2001). Water holding capacity is the ability of dietary fiber to form a colloidal suspension in water, which depends on the types of glycosidic bonds and compositions of polysaccharides present (Kelkar et al., 2012). Viscosity of dietary fiber can directly affect physiological function of the gastrointestinal tract of pigs. Viscosity of soluble fiber fractions is usually higher than that of insoluble fiber fractions (Dikeman and Fahey, 2006). In addition, dietary fibers containing long-chain polysaccharides are easier to form a net structure than those with short-chain fractions, resulting in greater viscosity. Swelling occurs when fiber solubilizes, which is dependent on water binding capacity of fiber fractions (Bach Knudsen et al., 2013). Fermentation relies on the expansion and dispersion of fiber components, which allows microbial enzymes to have more rapid and complete access to dietary fiber. Generally, varying physical characteristics of fiber among fiber-rich ingredients are associated with fiber composition and are related to the molecule structure of plant cell walls.

the cecum and proximal colon of pigs, while IDF residues are fermented primarily in the distal colon (Jaworski and Stein, 2017). Some SDF fractions can also be fermented in the small intestine of pigs (Sholly et al., 2011; Lærke et al., 2015), because fiber-degrading bacteria are found in the stomach and small intestine (Zhao et al., 2019 a). Digestibility of dietary fiber fractions in the distal ileum of pigs ranged from −7% to 40% (Bach Knudsen et al., 2013), which illustrates that large variation exists in fiber digestibility along the small intestine of pigs. Compared to xylose and arabinose, β-glucan is highly fermentable in the small intestine because of its soluble characteristics (Jha et al., 2010, 2011). Interestingly, existence of negative values for fiber digestibility suggests that there is endogenous loss of fiber components in the pig's intestine (Bach Knudsen et al., 2013), which can largely affect determination of fiber digestibility and SCFA production derived from dietary fiber. There is a large variation in fermentability of dietary fiber in the hindgut of pigs, which ranged from 48% to 95% (Jha et al., 2010; Jha and Leterme, 2012). Pectin and soluble hemicellulose are more easily fermented than cellulose, and β-glucan is almost completely fermented in the hindgut of pigs (Jha et al., 2010).

The primary microbial metabolites produced from fiber fermentation are lactate and SCFA. Lactate is produced mainly in the stomach and small intestine, while SCFAs, especially butyrate, are produced from fiber fermentation in the cecum and colon of pigs (Zhao et al., 2019 a). Nielsen et al. (2014) reported that resistant starch and arabinoxylan supplied by wheat and rye could stimulate butyrate-producing microorganisms, leading to enhanced butyrate production, whereas fermentation of
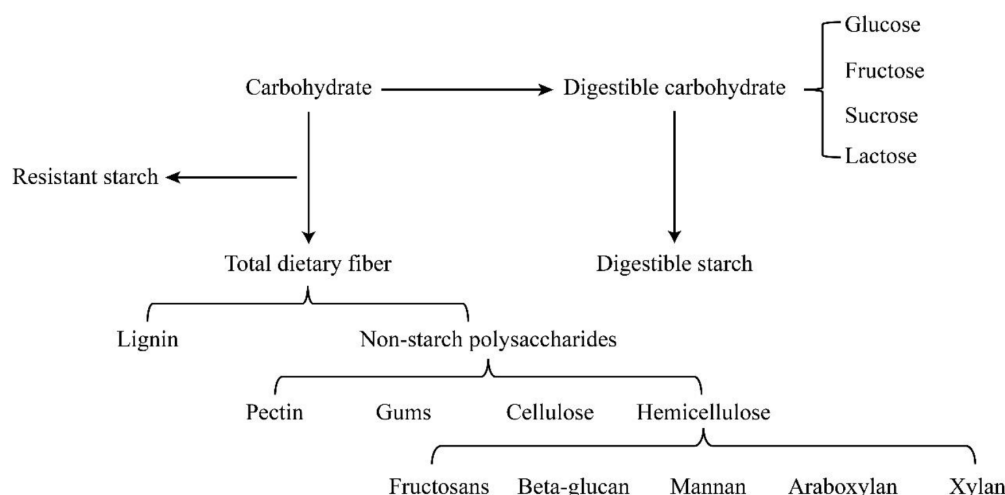

Figure 1. Classification of dietary fiber components in feed ingredients (Adapted from Bach Knudsen et al., 2013)

Dietary fiber fermentation in the intestine of pigs

Apparent total tract digestibility (ATTD) of SDF was reported to be 20% greater than that of IDF, indicating that SDF is more fermentable by gut microbiota than IDF in the intestine of pigs (Urriola et al., 2010). Most SDF fractions with high fermentability are degraded mainly in

cellulose derived from wheat increased acetate concentration. Therefore, dietary fiber source can greatly affect the fermentability of dietary fiber and the amount or type of SCFA produced in the pig intestine. In addition, our previous study showed that total SCFA concentration in ileal digesta was correlated positively with apparent il-

eal digestibility (AID) of cellulose and concentration of acetate was correlated positively with ATTD of IDF in fecal samples. A regression equation to predict fecal acetate concentration using a combination of ADF and SDF digestibility ($R^2 = 0.85$; $P = 0.06$) was better than similar equations using ATTD of ADF ($R^2 = 0.55$; $P = 0.09$) or IDF ($R^2 = 0.72$; $P = 0.03$) (Zhao et al., 2019 a). Regression equations for fecal butyrate ($R^2 = 0.65$; $P = 0.05$) and total SCFA concentrations ($R^2 = 0.61$; $P = 0.07$) were developed using ATTD of IDF (Zhao et al., 2019 a). However, more animal trials to determine fiber digestibility and SCFA concentrations must be conducted to improve accuracy and precision of prediction equations for SCFA concentrations.

Energy and fiber digestibility in diets containing common fiber-rich ingredients

Fiber-rich ingredients in feed can be categorized according to the amount and proportions of IDF or SDF fractions. Insoluble fiber sources commonly used in pig diets are hulls and brans from cereals and legumes, with representative ingredients including alfalfa meal (Zhao et al., 2018 b), oat hulls (Ndou et al., 2019), corn by-products (Li et al., 2018; Wang et al., 2019), and wheat by-products (Zhao et al., 2018 c; Casas et al., 2018). On the other hand, the most commonly-used ingredients that supply soluble fiber to pig's diets are sugar beet pulp (Zhang et al., 2013), oat bran (Lyu et al., 2018 b), and konjac flour (Li et al., 2018). Soybean hulls have both high amount of insoluble fiber and soluble fiber fractions (Jaworski and Stein, 2017). Chemical composition of fiber-rich ingredients commonly used in pig diets are summarized and presented in Table 1. Different processing technologies for a same fiber-rich ingredient would affect its fermentability of fiber. For example, the SDF proportion in sugar beet pulp ranged from 5% to 27.5% according to some previous reports (Zhao et al., 2020 a; Wang et al., 2019; Urriola and Stein, 2012; Navarro et al., 2018 a).

Table 1. Chemical composition of fibrous ingredients commonly used in diets of growing pigs (%, as-fed basis)

Item	GE	CP	DM	EE	Ash	NDF	ADF	TDF	SDF	IDF
Alfalfa meal	16.2	16.1	93.3	3.2	10.6	46.2	29.3	65.8	13.2	52.6
Canola meal	17.9	40.5	88.9	4.1	7.1	23.6	17.3	26.4	1.0	25.4
Copra expeller	19.7	21.7	96.5	11.2	5.6	48.1	23.8	43.8	1.8	42.1
Corn bran	15.9	14.8	92.0	3.9	2.5	52.0	16.2	54.1	5.9	48.2
Corn germ meal	17.8	19.9	92.3	1.9	1.7	46.4	13.3	49.3	2.8	46.5
Corn gluten feed	17.0	21.0	91.3	2.1	5.2	38.6	11.6	40.3	2.1	28.2
Corn DDGS	18.9	26.5	85.2	8.8	5.1	37.0	17.8	38.7	1.7	37.0
Flaxseed meal	19.5	33.9	93.6	7.8	6.9	41.6	14.7	30.2	–	–
Konjac flour residues	15.3	18.6	89.7	1.0	8.1	30.2	8.2	27.8	13.3	14.5
Oat bran	17.2	20.6	93.0	7.5	5.3	39.1	8.8	46.0	18.2	27.8
Oat hulls	17.2	2.5	92.3	1.7	4.8	73.5	39.8	55.8	3.9	51.9
Palm kernel expeller	17.9	15.6	90.0	5.8	5.2	50.9	24.6	46.6	0.6	46.0
Rapeseed meal	17.6	36.2	88.9	3.9	6.9	30.1	19.3	26.4	4.4	22.0
Rapeseed expeller	17.5	35.6	91.8	11.5	6.2	24.9	17.9	–	–	–
Rice bran (full-fat)	19.6	14.2	90.1	17.1	7.9	19.9	8.6	26.5	4.4	22.1
Rice bran (defatted)	15.7	15.2	91.2	1.0	10.5	30.5	18.9	35.6	1.4	34.2
Rice hulls	18.3	8.5	91.4	7.2	4.9	57.7	31.5	68.4	5.5	62.9
Soybean hulls	14.7	17.4	91.3	2.9	7.2	53.2	30.2	63.1	11.2	51.9
Sugar beet pulp	14.1	9.7	86.9	0.4	2.5	57.7	21.2	69.8	27.4	42.5
Sunflower meal	17.1	30.8	89.3	1.7	7.6	38.8	25.9	45.1	4.8	40.3
Wheat bran	16.9	17.5	88.3	2.8	5.1	37.9	11.1	42.4	4.1	38.3
Wheat middlings	16.9	17.2	87.4	3.8	4.8	33.2	9.8	37.1	2.6	34.5

The data were collected from our lab; Corn DDGS, corn distiller's dried grains with solubles; GE, gross energy; CP, crude protein; DM, dry matter; EE, ether extract; NDF, neutral detergent fiber; ADF, acid detergent fiber; TDF, total dietary fiber; SDF, soluble dietary fiber; IDF, insoluble dietary fiber.

Table 2. Apparent total tract digestibility (%) of fiber-rich diets commonly used in growing pigs in last 10 years of publications

Diet	BW (kg)	TDF (%)	NDF (%)	Inclusion level (%)	Apparent total tract digestibility (%)						Reference
					GE	TDF	SDF	IDF	NDF	ADF	
1	2	3	4	5	6	7	8	9	10	11	12
Cereal by-products											
Corn bran	42.4	17.1	17.9	25.0	82.5	30.3	68.3	28.7	36.5	28.4	Zhao et al., 2020 a
Corn germ meal	32.4	–	24.3	29.3	82.6	–	–	–	65.8	66.0	Li et al., 2018
Corn germ meal	48.4	39.8	39.6	40.2	81.8	75.5	96.1	74.6	75.7	71.6	Navarro et al., 2018 b
Corn germ meal	63.8	–	11.8	4.9	–	–	–	–	67.8	66.1	Zhang et al., 2019
Corn germ meal	63.8	–	14.1	9.7	–	–	–	–	69.2	67.6	Zhang et al., 2019
Corn germ meal	63.8	–	17.4	19.4	–	–	–	–	69.2	65.7	Zhang et al., 2019
Corn germ meal	63.8	–	20.8	29.1	–	–	–	–	74.5	70.5	Zhang et al., 2019
Corn germ meal	63.8	–	22.6	38.8	–	–	–	–	70.6	68.7	Zhang et al., 2019
Corn germ meal	63.8	–	28.2	48.5	–	–	–	–	74.0	73.1	Zhang et al., 2019
Corn germ meal	28.5	21.2	22.1	30.0	84.2	–	–	–	63.4	64.2	Lyu et al., 2018 c
Corn germ meal	48.0	–	24.3	29.5	67.0	–	–	–	67.6	66.0	Li et al., 2017
Corn germ meal	30.6	13.2	10.2	15.0	–	76.3	52.6	77.5	74.4	75.0	Navarro et al., 2018 a
Corn germ meal	30.6	19.3	15.6	30.0	–	78.0	81.0	77.8	75.7	74.4	Navarro et al., 2018 a
Corn gluten feed	28.5	24.5	21.3	30.0	78.9	–	–	–	57.1	50.2	Lyu et al., 2018 c
Corn gluten feed	48.0	–	18.6	24.4	59.9	–	–	–	29.7	30.2	Li et al., 2017
Corn gluten feed	32.4	–	18.9	24.4	82.3	–	–	–	44.0	47.2	Li et al., 2018
Corn DDGS	37.3	20.4	16.3	29.1	83.1	65.5	84.1	64.1	66.2	67.2	Jaworski and Stein, 2017
Corn DDGS	48.4	34.7	32.2	40.3	79.4	59.3	87.9	58.9	69.1	75.5	Navarro et al., 2018 b
Corn DDGS	38.0	16.2	19.0	30.0	81.0	55.5	–	–	57.2	54.8	Urriola and Stein, 2010
Corn DDGS	32.8	–	20.8	29.5	74.9	–	–	–	56.6	57.4	Li et al., 2017
Corn DDGS	32.5	22.0	–	66.7	–	28.9	64.4	20.0	45.9	36.8	Urriola et al., 2010
Corn DDGS	28.5	18.4	14.4	30.0	86.4	66.4	67.5	66.3	61.6	59.5	Abelilla and Stein, 2019
Corn DDGS	80.1	16.0	–	30.0	77.3	45.8	–	–	–	–	Urriola and Stein, 2012
Wheat bran	85.0	–	13.8	14.6	87.6	–	–	–	60.5	53.6	Zhao et al., 2018 c
Wheat bran	85.0	–	16.5	24.4	85.6	–	–	–	55.1	44.4	Zhao et al., 2018 c
Wheat bran	85.0	–	19.9	34.2	82.1	–	–	–	52.0	38.5	Zhao et al., 2018 c
Wheat bran	85.0	–	21.8	43.9	79.3	–	–	–	48.8	33.8	Zhao et al., 2018 c
Wheat bran	85.0	–	24.5	53.7	77.6	–	–	–	48.0	25.7	Zhao et al., 2018 c

Ingredient											Reference
wheat bran	35.0	18.4	14.1	9.7	81.0	–	–	–	53.6	44.0	Huang et al., 2015
wheat bran	35.0	31.9	24.2	48.3	74.1	–	–	–	61.5	43.7	Huang et al., 2015
Wheat bran	8.9	–	14.7	10.0	82.4	69.6	82.7	63.0	52.9	48.6	Yu et al., 2016
Wheat bran	30.1	–	12.9	54.8	–	–	–	–	67.0	55.1	Liu et al., 2016
Wheat bran	29.2	21.3	20.0	30.0	79.1	–	–	–	44.5	58.6	Lyu et al., 2018 b
Wheat bran	42.4	16.4	14.1	35.7	85.0	37.8	45.8	37.0	35.9	13.7	Zhao et al., 2020 a
Wheat bran	54.0	24.1	15.0	15.0	85.8	–	–	–	65.4	61.3	Jaworski et al., 2016
Wheat bran	54.0	27.6	20.6	30.0	81.1	–	–	–	64.7	52.2	Jaworski et al., 2016
Wheat middlings	25.0	–	16.4	24.1	79.0	–	–	–	39.1	30.5	Zhao et al., 2018 b
Wheat middlings	37.3	21.1	15.0	29.1	83.3	67.1	90.1	64.7	61.9	40.3	Jaworski and Stein, 2017
Wheat middlings	56.1	–	13.5	9.6	86.9	–	–	–	65.3	45.1	Huang et al., 2013
Wheat middlings	56.1	–	15.5	19.2	84.2	–	–	–	58.9	41.0	Huang et al., 2013
Wheat middlings	56.1	–	17.1	28.8	82.3	–	–	–	55.5	37.3	Huang et al., 2013
Wheat middlings	56.1	–	21.1	38.4	78.5	–	–	–	54.1	32.2	Huang et al., 2013
Wheat middlings	56.1	–	24.5	48.0	77.4	–	–	–	56.9	37.2	Huang et al., 2013
Wheat middlings	31.0	–	18.9	39.4	80.3	–	–	–	56.2	48.0	Casas et al., 2018
Wheat middlings	30.6	13.4	9.9	15.0	–	68.3	19.7	69.5	60.8	50.9	Navarro et al., 2018 a
Wheat middlings	30.6	19.8	14.6	30.0	–	66.8	61.8	67.1	58.9	44.8	Navarro et al., 2018 a
Wheat middlings	28.5	23.5	17.7	30.0	84.3	65.4	72.5	64.8	57.1	38.6	Abelilla and Stein, 2019
Full–fat rice bran	32.4	–	12.5	29.3	86.9	–	–	–	51.1	50.4	Li et al., 2018
Full–fat rice bran	28.5	18.6	20.1	30.0	81.7	–	–	–	61.8	42.2	Lyu et al., 2018 c
Full–fat rice bran	51.5	–	11.5	40.0	82.9	–	–	–	46.3	–	Casas and Stein, 2017
Defatted rice bran	28.5	21.7	22.2	30.0	74.1	–	–	–	35.3	19.8	Lyu et al., 2018 c
Defatted rice bran	42.4	16.3	15.1	50.0	82.5	39.1	43.5	38.8	32.8	12.1	Zhao et al., 2020 a
Defatted rice bran	48.0	–	12.9	29.5	80.7	–	–	–	32.6	26.9	Li et al., 2017
Defatted rice bran	51.5	–	12.2	40.0	80.9	–	–	–	49.0	–	Casas and Stein, 2017
Rice hulls	25.0	–	22.5	24.1	67.3	–	–	–	17.9	8.5	Zhao et al., 2018 b
Oat bran	29.2	18.7	17.7	30.0	83.4	–	–	–	67.2	47.3	Lyu et al., 2018 b
Oat bran	42.4	16.5	18.0	35.8	89.4	71.9	96.3	47.7	76.3	54.2	Zhao et al., 2020 a
Oat hulls	8.9	–	14.2	7.0	84.9	77.9	87.6	73.0	63.6	68.3	Yu et al., 2016
Oat hulls	35.0	25.5	18.7	10.0	–	52.6	95.5	31.6	52.6	18.7	Ndou et al., 2019
Legume by-products											
Soybean hulls	37.3	28.6	21.7	29.1	78.7	65.7	85.4	64.0	63.5	56.9	Jaworski and Stein, 2017

Table 2 – contd.

1	2	3	4	5	6	7	8	9	10	11	12
Soybean hulls	8.9	–	14.7	5.0	83.5	71.7	84.3	65.8	58.1	54.2	Yu et al., 2016
Soybean hulls	30.1	–	8.2	33.0	–	–	–	–	70.5	61.1	Liu et al., 2016
Soybean hulls	36.1	22.6	18.5	20.0	82.0	61.0	–	–	57.0	55.0	Lyu et al., 2018 a
Soybean hulls	42.4	17.1	18.1	23.5	87.1	72.3	86.4	69.5	68.6	62.3	Zhao et al., 2020 a
Soybean hulls	80.1	27.1	–	30.0	79.5	78.6	–	–	–	–	Urriola and Stein, 2012
Palm kernel meal	85.0	–	19.2	9.8	88.3	–	–	–	75.4	67.2	Huang et al., 2018
Palm kernel meal	85.0	–	22	19.5	84.4	–	–	–	70.5	58.4	Huang et al., 2018
Palm kernel meal	85.0	–	26.5	29.3	82.7	–	–	–	67.9	60.4	Huang et al., 2018
Palm kernel meal	85.0	–	26.2	39.0	79.5	–	–	–	62.3	47.5	Huang et al., 2018
Palm kernel meal	8.9	–	14.2	6.0	83.5	74.9	88.3	74.9	62.9	63.4	Yu et al., 2016
Palm kernel meal	29.2	22.3	21.2	30.0	81.0	–	–	–	66.5	58.1	Lyu et al., 2018 b
Canola meal	30.6	11.3	7.4	15.0	–	70.3	49.0	71.1	56.3	50.8	Navarro et al., 2018 a
Canola meal	30.6	12.7	9.5	30.0	–	63.8	54.1	64.4	49.7	39.9	Navarro et al., 2018 a
Canola meal	48.4	26.4	23.6	40.9	78.3	59.6	92.7	57.0	44.6	73.1	Navarro et al., 2018 b
Canola meal	27.7	–	17.9	36.0	80.8	–	–	–	59.1	41.4	Maison et al., 2015
Sugar beet pulp	36.1	26.0	17.1	22.0	85.0	81.0	–	–	74.0	79.0	Lyu et al., 2018 a
Sugar beet pulp	30.0	12.1	–	15.0	94.5	86.2	92.9	82.6	–	–	Zhang et al., 2013
Sugar beet pulp	30.0	18.8	–	25.0	91.4	86.9	94.9	83.2	–	–	Zhang et al., 2013
Sugar beet pulp	30.0	24.8	–	35.0	89.9	88.1	94.3	85.1	–	–	Zhang et al., 2013
Sugar beet pulp	30.0	32.0	–	45.0	88.4	89.7	96.3	86.7	–	–	Zhang et al., 2013
Sugar beet pulp	30.0	38.9	–	55.0	86.3	89.5	96.3	86.4	–	–	Zhang et al., 2013
Sugar beet pulp	42.4	16.6	13.6	22.5	90.3	72.5	93.6	60.8	69.6	65.2	Zhao et al., 2020 a
Sugar beet pulp	30.6	15.8	9.8	15.0	–	82.3	87.4	81.5	76.9	81.6	Navarro et al., 2018 a
Sugar beet pulp	30.6	26.7	15.2	30.0	–	85.5	89.8	84.5	78.5	82.9	Navarro et al., 2018 a
Sugar beet pulp	48.4	48.5	45.5	30.2	84.0	80.3	86.2	79.9	74.9	81.3	Navarro et al., 2018 b
Sugar beet pulp	80.1	27.9	–	30.0	83.3	78.1	–	–	–	–	Urriola and Stein, 2012
Copra expeller	48.4	43.8	48.1	30.6	84.8	77.7	97.3	76.1	76.4	78.0	Navarro et al., 2018 b
Sunflower meal	48.0	–	21.0	29.5	56.6	–	–	–	33.9	27.0	Li et al., 2017
Sunflower meal	32.4	–	21.0	29.3	79.7	–	–	–	44.4	36.3	Li et al., 2018
Rapeseed meal	27.7	–	17.7	39.0	81.3	–	–	–	59.5	45.1	Maison et al., 2015
Rapeseed meal	37.7	–	18.0	19.5	84.5	–	–	–	58.7	45.5	Li et al., 2017

Item										Reference
Rapeseed expellers	27.7	–	16.1	40.0	83.2	–	–	47.5	61.4	Maison et al., 2015
Flaxseed meal	35.0	24.9	18.2	12.0	–	80.5	65.5	42.8	80.5	Ndou et al., 2019
Peanut meal	48.0	–	12.9	19.5	88.1	–	–	52.5	64.1	Li et al., 2017
Alfalfa meal	25.0	–	19.5	24.1	68.6	–	–	18.4	30.2	Zhao et al., 2018 b
Konjac flour residues	42.2	18.7	–	15.0	87.2	–	–	61.1	62.7	Li et al., 2018
Konjac flour residues	42.2	21.0	–	30.0	83.0	–	–	72.4	63.3	Li et al., 2018

BW, body weight; Corn DDGS, corn distiller's dried grains with solubles; GE, gross energy; NDF, neutral detergent fiber; ADF, acid detergent fiber; TDF, total dietary fiber; SDF, soluble dietary fiber; IDF, insoluble dietary fiber.

Table 3. Mean ATTD of energy and fiber component in fiber-rich diets

Item	BW (kg)	Inclusion level (%)	Mean ATTD (%)					
			GE	TDF	SDF	IDF	NDF	ADF
Corn bran	42.4	25.0	82.5	30.3	68.3	28.7	36.5	28.4
Corn germ meal	50.1	27.0	78.9	76.6	76.6	76.6	70.7	69.1
Corn gluten feed	36.3	26.3	73.7	–	–	–	43.6	42.5
Corn DDGS	42.5	36.5	80.4	53.6	76.0	52.3	59.4	58.5
Wheat bran	54.9	31.1	81.7	53.7	64.3	50.0	54.6	44.1
Wheat middling	43.0	28.3	81.8	66.9	61.0	66.5	56.8	40.5
Full-fat rice bran	37.5	33.1	83.8	–	–	–	53.1	46.3
Defatted rice bran	42.6	37.4	79.6	39.1	43.5	38.8	37.4	19.6
Rice hulls	25.0	24.1	67.3	–	–	–	17.9	8.5
Oat bran	35.8	32.9	86.4	71.9	96.3	47.7	71.8	50.8
Oat hulls	22.0	8.5	84.9	65.3	91.6	52.3	58.1	43.5
Soybean hulls	39.2	23.4	82.2	69.9	85.4	66.4	63.5	57.9
Palm kernel meal	63.0	22.3	83.2	74.9	88.3	74.9	67.6	59.2
Canola meal	34.3	30.5	79.6	64.6	65.3	64.2	52.4	51.3
Sugar beet pulp	38.0	29.5	88.1	83.6	92.4	81.2	74.8	78.0
Copra expeller	48.4	30.6	84.8	77.7	97.3	76.1	76.4	78.0
Sunflower meal	40.2	29.4	68.2	–	–	–	39.2	31.7
Rapeseed meal	32.7	29.3	82.9	–	–	–	59.1	45.3
Rapeseed expellers	27.7	40.0	83.2	–	–	–	61.4	47.5
Flaxseed meal	35.0	12.0	–	80.5	97.1	65.4	80.5	42.8
Peanut meal	48.0	19.5	88.1	–	–	–	64.1	52.5
Alfalfa meal	25.0	24.1	68.6	–	–	–	30.2	18.4
Konjac flour residues	42.2	22.5	85.1	–	–	–	63.0	66.8

The mean values of each high-fiber diet presented in Table 3 were calculated based on the Table 2. BW, body weight; Corn DDGS, corn distiller's dried grains with solubles; GE, gross energy; NDF, neutral detergent fiber; ADF, acid detergent fiber; TDF, total dietary fiber; SDF, soluble dietary fiber; IDF, insoluble dietary fiber.

The ATTD of energy and fiber components in swine diets formulated with commonly-used fiber-rich ingredients are shown in Table 2. To compare energy and fiber digestibility among diets containing different high-fiber ingredients, mean ATTD of energy and fiber components were calculated and presented in Table 3. Zhao et al. (2018 b) reported that inclusion of 25% wheat middlings in diets had greater AID and ATTD of gross energy (GE) than diets containing 25% alfalfa meal or 25% rice hulls when fed to growing pigs, and the ATTD of neutral detergent fiber (NDF) and acid detergent fiber (ADF) in rice hulls diet was lower than those in wheat middlings or alfalfa meal diets. With equal TDF consumption, growing pigs fed pea hulls, pea inner fiber, or sugar beet pulp had greater ATTD of dry matter (DM) and non-starch polysaccharides (NSP) than those fed wheat bran or corn distiller's dried grains with solubles (corn DDGS) diets, but no differences in the AID of DM, NSP, and nitrogen were found among diets formulated with the other fibrous ingredients, except for sugar beet pulp (Jha and Leterme, 2012). Zhao et al. (2020 a) found that ATTD of TDF in different ingredients fed to growing pigs was 37.78% for wheat bran, 71.87% for oat bran, 72.54% for sugar beet pulp and 72.31% for soybean hulls. The poor digestibility of wheat bran can be ascribed to its high insoluble fiber content, which makes wheat bran less fermentable compared with sugar beet pulp and soybean hulls that containing highly fermentable pectin substances (Karr-Lilienthal et al., 2005). Jaworski and Stein (2017) reported that growing pigs fed a wheat middlings diet had greater apparent cecal digestibility of IDF compared with pigs fed diets containing corn DDGS or soybean hulls, and ATTD of TDF in wheat middlings diets was greater than that in corn DDGS or soybean hulls diets, indicating that fiber components in wheat middlings are more fermentable than those in corn DDGS and soybean hulls.

Effects of fiber source on nutrient digestibility and fiber fermentability in pigs depends on the physiochemical properties of various fiber-rich ingredients (Molist et al., 2014; Mpendulo et al., 2018). The different physiochemical characteristics of fiber-rich ingredients also affects SCFA production in the gut of pigs. Oat bran, rich in soluble dietary fiber in the form of β-glucan, can produce almost twice as much SCFA per gram of dietary fiber as wheat bran in pig's intestine (Zhao et al., 2019 a). Freire et al. (2000) investigated effects of adding wheat bran, sugar beet pulp, soybean hulls, or alfalfa meal at 20% of weaned pig diet on total SCFA concentration in the cecum, and reported that soybean hulls increased total SCFA concentration by 11.2%, 30.5%, and 27.2% compared with wheat bran, sugar beet pulp, and alfalfa meal, respectively. Carneiro et al. (2008) compared effects of wheat bran and maize fiber addition to weaned pig diets, and they found no difference in total SCFA concentration in the small intestine of pigs, but greater acetate and lower butyrate production in cecum when maize fiber was used in diets compared with wheat bran. Zhao et al. (2018 a) reported that feeding pigs diets containing

5% corn bran, wheat bran, or soybean hulls increased butyrate concentration in feces compared to a low-fiber control diet. Chen et al. (2014) reported that growing-finishing pigs fed 30% soybean hulls had greater acetate content in ileal digesta compared to those fed 30% wheat bran diet, and pigs fed 30% wheat bran diet had greater butyrate content in the cecum than pigs fed 30% corn fiber, soybean fiber or pea fiber. Moreover, growing pigs fed pea hulls had greater butyrate and total SCFA concentrations compared to pigs fed wheat bran and corn DDGS diets, but no difference in total SCFA content was observed among wheat bran, pea hulls, pea inner fiber, sugar beet pulp and corn DDGS diets with similar levels of TDF (Jha and Leterme, 2012). Zhao et al. (2019 a) showed that growing pigs fed an oat bran diet (at 15% TDF level) had greater lactate concentration in ileal digesta, and pigs fed soybean hulls and sugar beet pulp diets showed greater SCFA concentrations than those fed corn bran, rice bran, and wheat bran diets. Chemical and physical characteristics of intestinal digesta vary among fiber-rich ingredients at different gastrointestinal tract sites due to potential depolymerization or reduction in electrostatic repulsion among polysaccharides, resulting in varying nutrient digestibility (Capuano, 2017). Overall, these observations mentioned above support the conclusion that nutrient digestibility and fiber fermentation are influenced by dietary fiber sources due to their different physicochemical properties.

Some specific fiber components, such as cellulose, β-glucan, inulin, and resistant starch, extracted from plants have been supplied in diets to facilitate growth performance and gut health of pigs due to their benefits in promoting energy and nutrient digestibility. Gao et al. (2015) reported that growing pigs fed diets with 5% carboxymethyl cellulose sodium showed greater AID of GE, crude protein (CP), ether extract (EE), DM, and carbohydrates compared to those fed diets with 5% inulin, but the ATTD and hindgut disappearance of GE, DM, EE, and carbohydrates in a 5% inulin diet were greater than those in 5% carboxymethyl cellulose sodium diet. Wu et al. (2018) reported that weaned pigs fed a diet with 5% β-glucan showed greater ATTD of DM and GE than those fed a diet with 5% cellulose because of the greater SDF concentration in β-glucan. In addition, pigs fed a 5% carboxymethylcellulose diet showed increased viscosity, decreased digesta passage rate, greater AID of GE, CP, and DM, and greater ATTD of GE and DM in comparison with those fed a diet with 5% cellulose or β-glucan (Hooda et al., 2011).

### Key factors affecting fiber digestibility in pigs
Dietary fiber level
As dietary fiber levels increase, enzymatic digestion and nutrient digestibility in pigs is increasingly impaired. For instance, ATTD of DM, organic matter (OM), GE, and CP decreased as dietary concentration of both konjac flour residues and ramie increased (Li et al., 2018). Huang et al. (2013) reported that ATTD of NDF and

ADF in diets decreased linearly as inclusion level of wheat middlings increased from 9.6% to 48%. Zhao et al. (2018 c) and Huang et al. (2018) also showed that ATTD of NDF and ADF in diets decreased as inclusion level of wheat bran increased from 15% to 45%, or the inclusion level of palm kernel meal increased from 10% to 40%. Wilfart et al. (2007) added 0%, 20%, and 40% wheat bran to a wheat-barley-soybean meal diet and found that increased TDF level significantly decreased ATTD of DM, OM, CP, and GE, but ATTD of TDF was unaffected. In contrast, Zhang et al. (2013) reported that the ATTD of TDF, SDF, and IDF in sugar beet pulp increased linearly as the inclusion level of sugar beet pulp increased from 15% to 55%. Additionally, Bindelle et al. (2009) reported that when growing pigs were fed corn-soybean meal diets supplemented with sugar beet pulp at levels of 0%, 10%, 20%, and 30% with TDF levels increasing from 9.6% to 25.4%, ATTD of DM, OM and CP linearly decreased but ATTD of NDF linearly increased. These divergent results may be caused as fiber inclusion levels increase, dietary fiber increasingly impairs enzymatic digestion in the upper gastrointestinal tract which simultaneously supports increased microbial activity and fiber fermentation in the hindgut of pigs (Noblet and Le Goff, 2001). Positive effects of increased fiber concentration on fiber digestibility were caused by greater quantity of substrates that flowed into the large intestine to be fermented. As a result, more SCFAs were produced and energy supplied by SCFA increased in the hindgut of pigs, even though nutrient digestibility and digestible energy in diets decreased as dietary fiber levels increased (Iyayi and Adeola, 2015). For example, high NSP concentrations resulted in an increased molar proportion of lactate in stomach and ileum, and an increased molar proportion of propionate and butyrate in the ileum (Högberg and Lindberg, 2004). Overall, considering the negative response of fiber level on nutrient digestibility in the upper gut and the positive response of fiber level on fermentation and SCFA production in the hindgut of pigs, it is necessary to determine the optimal inclusion level of dietary fiber in swine diets formulation.

To further demonstrate negative effects of dietary fiber level on energy digestibility, linear equations were developed to determine which fiber analysis methods of fiber components are best for studying relationships between dietary fiber levels and energy digestibility (Figure 2). The results showed that IDF ($R^2 = 0.77$) is the best fiber component to predict energy digestibility of the diets compared with TDF ($R^2 = 0.69$), SDF ($R^2 < 0.01$), NDF ($R^2 = 0.66$) and ADF ($R^2 = 0.57$). The IDF, rather than NDF and ADF, should be used to precisely describe effects of fiber levels on dietary energy digestibility in pig production.
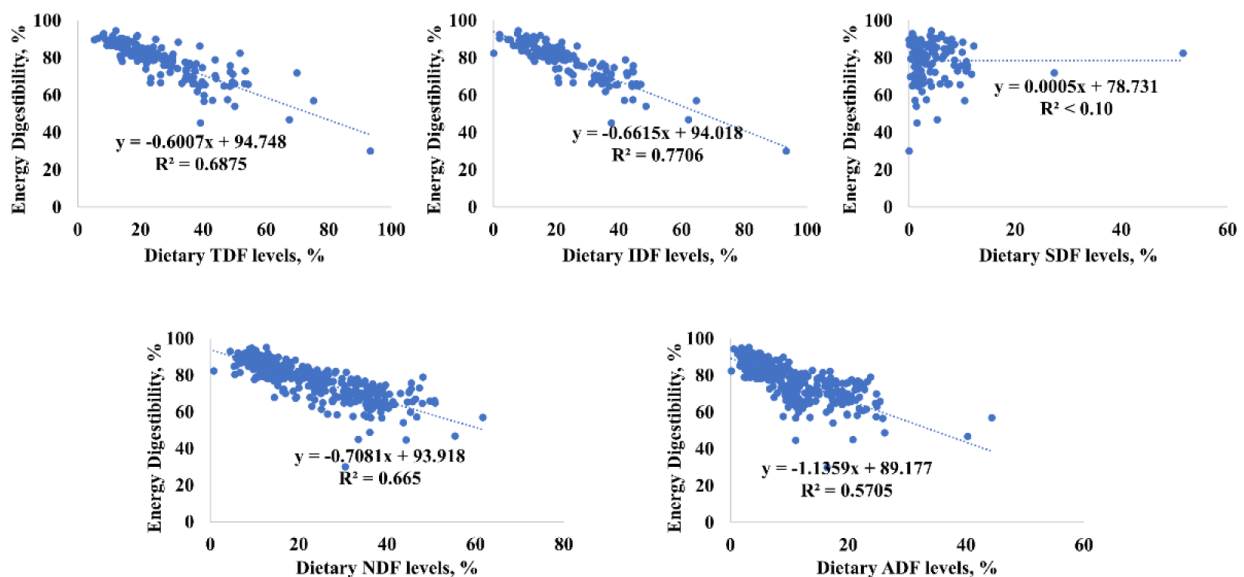
Data were separated by each dietary treatment and analyzed by analysis of variance using the PROC general linear model procedure of SAS (SAS 9.4 Institute, Cary, NC, USA) with pig as the experimental unit. The statistical models studied the effects of dietary TDF, IDF, SDF, NDF, and ADF levels on energy digestibility in growing pigs. The R^2 was used to identify which model best predicted energy digestibility. A larger R^2 represented a more accurate prediction equation. The equations developed using dietary NDF and ADF levels represented 118 dietary treatments in previously published studies (shown in Table 2), and equations developed using dietary TDF, SDF and IDF levels represented 51 dietary treatments from previously published studies.

Figure 2. Models for studying effects of dietary fiber levels on energy digestibility in growing pigs

Pig body weight and breed

Compared with young pigs, adult pigs have a more developed and larger gastrointestinal tract, slower digesta transit time, higher cellulolytic activity and enhanced fermentability by resident microflora in the gut. Gestating sows had greater ATTD of energy in diets with 40% full-fat rice bran or with 40% defatted rice bran compared with growing gilts regardless of feeding level (Casas and Stein, 2017). Pigs at 3 weeks post-weaning showed greater ATTD of all dietary components except for NDF compared to pigs just weaned (Ivarsson et al., 2011). Jørgensen et al. (2007) showed greater capacity of sows to digest fiber components and produce SCFA compared to young pigs, and demonstrated that sows could also degrade a larger proportion of dietary fiber in the small intestine than growing pigs. Sows have similar capacity to digesting soluble NSP when compared with growing pigs, even though sows can digest more insoluble NSP (Lindberg, 2014). Huang et al. (2015) reported that body weight of barrows (30 kg *vs.* 60 kg) did not affect ATTD and AID of NDF and ADF, but increased ATTD and AID of carbohydrates as inclusion levels of wheat bran increased. Zhao et al. (2020 c) reported that barrows at 60 kg had greater ATTD of TDF, SDF, and IDF, and greater hindgut disappearance of IDF and cellulose compared to barrows at 25 kg, but no differences in AID of most fiber components among barrows at different body weight stages, indicating the positive response of heavier growing pigs on dietary fiber fermentation mainly occurs in the large intestine. In addition, acetate, propionate, and total SCFA concentrations in ileal digesta and feces of barrows at 60 kg were greater than those of barrows at 25 kg (Zhao et al., 2020 c). Overall, growing pigs with higher body weight have greater capacity to digest dietary fiber components than lower body weight of pigs. Le Goff and Noblet (2001) stated that greater capacity of heavy pigs and adult sows to digest dietary fiber is due primarily to more advanced development of pig intestine, rather than enhanced intrinsic ability of gut microbiota to degrade dietary fiber.

Generally, pig breeds indigenous to China can utilize the high-fiber diets more efficiently than exotic crossbreds (Khieu et al., 2005; Len et al., 2007). Urriola and Stein (2012) reported that Meishan pigs had greater ATTD of DM, GE, CP, carbohydrates, and TDF than Yorkshire pigs when fed diets containing 29.1% corn DDGS, but no differences in ATTD of nutrients were observed between Meishan and Yorkshire pigs when fed diets containing 29.1% soybean hulls or sugar beet pulp. Greater fiber digestibility in indigenous pig breeds could be mainly attributed to their larger cecum and colon compared with the exotic breeds, leading to longer retention time of digesta and increased dietary fiber fermentation by gut microbiota (Gao et al., 2015).

Fiber-degrading enzyme

As indicated by Zijlstra et al. (2010), enzyme supplementation can be an efficient approach to enhance utilization of nutrients in fiber-rich feedstuffs. Fiber degrading enzymes, such as cellulases, β-glucanases, pectinases, and xylanases, successfully improve digestibility of fiber fractions when the type of enzyme matches available substrates and enzymes are supplied at a proper dose. Högberg and Lindberg (2004) reported supplementation of β-glucanase and xylanase in diet increased the digestibility of total NSP in the cecum, but it had no effect on ATTD of total NSP in pigs fed diets with 9.6% or 18.3% NSP derived from cereals and wheat bran. A mixture of fiber-degrading enzymes improved digestibility of most NSP fractions and their constituent sugar residues in the duodenum and ileum of pigs fed diets with 53.7% wheat bran or 33.0% soybean hulls, but did not affect the ATTD of fiber fractions (Liu et al., 2016). Therefore, an improvement of nutrient digestibility by dietary supplementation of fiber-degrading enzymes primarily occurs in the small intestine of pigs.

Jakobsen et al. (2007) reported addition of fiber-degrading enzymes, including a mixture of xylanase and β-glucanase or cellulase, improved both AID and ATTD of most fiber fractions in pigs fed a diet with 60% corn DDGS. A mixture of fiber-degrading enzymes improved digestibility of TDF and IDF in the large intestine when pigs were fed corn bran, sugar beet pulp or soybean hull diet, but did not influence fiber digestibility in the upper gut (Zhao et al., 2020 b). Lærke et al. (2015) reported there are interactive effects of fiber-degrading enzymes and chemical composition of diets on NSP digestibility in the small intestine of pigs. As a result, fiber-degraded enzymes should be chosen based on fiber ingredients in the diet to realize improvements in nutrient digestibility in the intestine.

Adaptation period

Nutrient digestibility and fiber fermentation are influenced by length of the adaptation period when pigs are fed high-fiber diets (Kil et al., 2013). Martinez-Puig et al. (2003) reported that the ATTD of OM and starch progressively increased in pigs fed 16% resistant starch when the adaptation period of diets increased from 23 days to 38 days. Similar results were also demonstrated in a long-term study with an adaptation period of 97 days (Martinez-Puig et al., 2007). Time-dependent changes in nutrient digestibility reflect the need of the gastrointestinal tract to adapt to dietary fiber supplementation. Previous studies showed that growing pigs are more easily adapted to sugar beet pulp diets compared with wheat bran diets (Roca-Canudas et al., 2007; Molist et al., 2009), which may be attributed to the greater SDF content in sugar beet pulp compared with wheat bran. Zhao et al. (2018 c) observed lower digestible energy content and ATTD of all chemical constituents when growing pigs were fed a wheat bran diet with a 7-day compared with a 14-day adaptation period. Huang et al. (2018) recommended a 21-day adaptation period for a diet containing 19.5% palm kernel meal fed to growing pigs, and suggested longer adaptation period when inclusion levels of palm

kernel meal increased. Fan et al. (2017) showed that ATTD of NDF was not different when comparing an adaptation period of 7 days and 26 days, but digestibility of other nutrients was affected in growing pigs. Considering the effects of high-fiber diets on feed intake, a 12-day adaptation period was recommended when determining net energy values of fiber-rich ingredients (Lyu et al., 2018 a). Overall, there is no consistent and specific conclusion concerning the optimal adaptation period for pigs consuming fibrous ingredients. Taking body weight and dietary fiber source into consideration, pigs with greater body weight may need shorter adaptation time especially when fed diets with high SDF and low IDF contents to achieve stable nutrient digestibility and fiber fermentability.

Feed processing technology

Reducing particle size of ingredients is beneficial in improving feed efficiency, nutrient digestibility, and fiber fermentation in swine diets (Ball et al., 2015; Rojas and Stein, 2015). Fine grinding increases surface area of diet particles, leading to greater access of digestive enzymes to nutrients (Hetland et al., 2004). Rojas et al. (2016) reported that pelleting or extrusion improved energy utilization in swine diets especially for those rich in fiber, but those processing technologies did not affect fiber digestibility in diets. Some recent studies showed that increased particle size of high-fiber ingredients is beneficial to gut health of pigs by modulating microbiota composition and SCFA production. For instance, Molist et al. (2012) reported that inclusion of coarsely ground wheat bran in diets shaped microbial community in the colon of pigs as compared with finely milled wheat bran, and addition of coarse wheat bran increased SCFA concentration. Although grinding would not change the chemical composition of feed, particle size can affect physical characteristics and digestible nutrient concentration of feed ingredients. Prebiotic effects of coarse fiber fractions on gut health of pigs might be explained by the change of physicochemical properties of digesta, such as increasing the water binding capacity, which is related to enhanced fiber fermentability and SCFA production in the hindgut of pigs (Anguita et al., 2006). Zhao et al. (2019 b) did not observe any differences in ATTD of nutrient and fiber components among pigs fed fibrous diets with different particle sizes, but coarse feed decreased the AID of GE, TDF, and IDF in diets and increased acetate concentration in feces. Overall, coarse particle size of fibrous feed decreases nutrient digestibility in small intestine, but increases fiber fermentation and SCFA production in the large intestine of pigs.

Scientific issues related to quantifying SCFA production

Interestingly, many previous studies have reported negative values for fiber digestibility, especially in the small intestine of pigs (Ji et al., 2008; Jaworski and Stein, 2017). Negative fiber digestibility is physiological abnormal, indicating the presence of endogenous components from the gastrointestinal tract that would interfere with fiber analysis and decrease digestibility of fiber components. Bacteria and mucins, which may be the main sources for 'endogenous fiber losses', contain sugar residues that could be included in TDF during analysis (Miner-Williams et al., 2012). Average ileal and total tract endogenous losses of analyzed TDF were 25.25 and 42.87 g/kg DM intake in growing pig, respectively (Cervantes-Pahm et al., 2014). Using a fiber-free diet, Montoya et al. (2016) found mucin was the main component of endogenous losses related to the SDF fraction in ileal digesta, and microbial cells were the main components of endogenous losses related to IDF fraction in ileal digesta and feces. Endogenous fiber losses in the pig intestine can be also fermented by gut microbiota to produce SCFA. Montoya et al. (2017) reported the SCFA produced from dietary fiber fermentation supplied by kiwifruit accounted for 30% of total SCFA produced *in vitro* using fecal microbiota of humans. With more dietary fiber consumed, both dietary fiber and non-dietary components entering into the hindgut increased, which in turn led to more SCFA production from both substrates. Although the non-dietary material is an important fraction of the digesta that enters into the hindgut of pigs, little information is available to quantify SCFA production from this source. Therefore, correction for endogenous loss of fiber components will improve the accuracy of SCFA produced by dietary fiber fermentation in pigs.

Most *in vivo* studies only determined SCFA produced by bacterial fermentation, while SCFA absorbed by epithelial cells of the gut is always neglected. The common method to quantify net absorption of SCFA is to employ a portal vein-catheterized pig model, in which blood samples are collected from portal vein and mesenteric artery to analyze SCFA concentrations (Bach Knudsen et al., 2000). Dietary fiber composition greatly affects net portal absorption of SCFA and concentrations of SCFA in portal vein and mesenteric artery of catheterized pigs fed cereal-based diets. An arabinoxylan-rich cereal-based diet stimulated proliferation of butyrate-producing microorganisms, butyrate production in the large intestine, and net portal absorption of butyrate to a larger extent than a resistant starch diet with equal amounts of TDF (Nielsen et al., 2014; Ingerslev et al., 2014). Therefore, absorption and net production of SCFA from gut microbiota to ferment different types of dietary fibers should be quantified to understand fermentability of dietary fibers and the possible pathways of SCFA metabolism in the gut of pigs.

Conclusion

There are large variations in fiber digestibility and SCFA concentration in small and large intestine of pigs when fed different fiber-rich ingredients. As inclusion level of dietary fiber increases or particle size of fibrous feed increases, nutrient digestibility in the small intestine of pigs decreases, but fiber fermentability and SCFA

concentration in large intestine increase. Pigs with heavier body weight or consuming feed supplemented with fiber-degrading enzymes display increased fiber fermentation capacity and SCFA concentration in the intestine compared with lighter pigs. The IDF as a best variable to predict energy digestibility are recommended in application of pig production to achieve precise feeding. Further studies should be conducted to explore impacts of physical characteristics of fiber and endogenous fiber losses on dietary fiber fermentation and SCFA production in the intestine of pigs.

Conflicts of Interest

The authors declare no conflicts of interest.

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