Animal Nutrition 7 (2021) 259–267

Contents lists available at ScienceDirect

Animal Nutrition

journal homepage: http://www.keaipublishing.com/en/journals/aninu/

Review Article

Physiological function and application of dietary fiber in pig nutrition: A review

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ARTICLE INFO

Article history:
Received 21 September 2020
Received in revised form
19 October 2020
Accepted 9 November 2020
Available online 17 April 2021

Keywords:
Dietary fiber
Pigs
Physiological function
Application

ABSTRACT

Dietary fiber (DF), divided into soluble dietary fiber (SDF) and insoluble dietary fiber (IDF), has attracted increasing attention in the field of pig nutrition. Although DF reduces nutrient digestibility and inhibits energy deposition in most cases, fiber-rich feeds have been widely used in pig diets. This is not only because of lower feed costs, but also from the continuous discovery about the nutritional value of DF, mainly including the improvement of piglet intestinal health and sow reproductive performance. The addition timing has also been further considered, which potentially enables the nutritional value of DF to be accurately used in applicable pig models. Furthermore, fiber degrading enzymes have been shown to alleviate the anti-nutritional effects of DF and have ensured the improvement effect of fiber on intestinal health in young piglet models. However, the regulatory effect of fiber on pork quality is still unclear, which requires consideration of the wide range of fiber sources and the complexity of the basic diet composition, as well as the impact of pig breeds. Taken together, future research needs to gain more insight into the combined effects of SDF and IDF, processing methods, and addition timing to improve the nutritional value of DF, and further explore the physiological functions and regulatory mechanisms of DF fermentation products short-chain fatty acids in pigs.

1. Introduction

Fiber-rich feeds such as co-products from food and biofuel industries, e.g., wheat bran (WB), corn bran (CB), soybean hulls (SBH), sugar beet pulp (SBP), and distillers dried grains with soluble (DDGS), have been applied to pig diets to save costs. These fiber-rich feeds generally were considered to have low nutritional value due to the lower digestive energy or amino acid levels compared to concentrated feeds with high starch or proteins (Woyengo et al., 2014).

Dietary fiber (DF) is the major component of fiber-rich feed, accounting for about more than 40% of the total dry matter (DM) (Woyengo et al., 2014). In traditional nutrition studies, DF was regarded as an anti-nutritional component because it cannot be broken down by the endogenous digestive enzymes and can reduce the digestibility of nutrients (Trowell, 2009; Jha and Berrocoso, 2015). Therefore, DF usually contributes to a minimal proportion in pig diets, which are typically corn and soybean meal-based, thereby making DF-rich ingredients underutilized and wasted.

However, the positive effects of DF have been increasingly investigated in recent research related to animal nutrition. DF can be fermented by intestinal microbes and provides 5%~28% energy for pigs (Kass et al., 1980). In addition, due to the prolonged satiety by DF and its relieving effect on constipation, it has become a consensus that pregnant sows can benefit from diets rich in DF (Oliviero et al., 2009; De Leeuw et al., 2008). Moreover, DF-rich diets have also shown potentially beneficial effects on gut health and meat quality of pigs (Lindberg, 2014; Han et al., 2020).

The application of DF in pig nutrition is challenging and dependent on many factors such as the wide range of sources and the complexity of the component composition. Also, the regulation of DF on meat quality of pigs has not been thoroughly and systematically studied and further research on that is warranted. Therefore, this review summarized the physiological functions and

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Peer review under responsibility of Chinese Association of Animal Science and Veterinary Medicine.

Production and Hosting by Elsevier on behalf of KeAi

https://doi.org/10.1016/j.aninu.2020.11.011

application insights of DF in pig nutrition. Additionally, we also discussed the factors that affect the efficiency of DF utilization in pigs.

2. Dietary fiber

DF is defined as the dietary components resistant to degradation by mammalian enzymes, composed of non-digestible carbohydrates (NDC) and lignin. Lignin is almost unused in the digestive tract, while NDC including resistant starch (RS), non-digestible oligosaccharides (NDO) and non-starch polysaccharides (NSP) are active components in DF (Stephen et al., 2017). RS and NDO are cell contents of plants, while NSP and lignin are mainly derived from cell walls of plants (Williams et al., 2017).

The fibrous components separated from feeds or feedstuffs have different classifications according to their analytical methods. In general, the three fiber types including crude fiber (CF), neutral detergent fiber (NDF) and total dietary fiber (TDF) are measured by the chemical-gravity method, the detergent (Van Soest) methods and the enzymatic-gravimetric method, respectively (Agyekum and Nyachoti, 2017). CF and NDF detection methods ignore most of the soluble fiber components, while the TDF is divided into soluble dietary fiber (SDF) and insoluble dietary fiber (IDF), and almost covers all fiber components. Notably, the TDF measured by the traditional enzyme gravimetric method (AOAC 985.29 and AOAC 991.43) does not cover low molecular weight SDF and RS (Lazarus and Garg, 2004). Therefore, the TDF value from this method approximately equals the content of NSP and lignin. Nowadays, the improved enzyme gravimetric method (AOAC, 2009.01 and AOAC, 2011.25) takes NDO and RS into account and provides a more comprehensive consideration in the meaning and composition of DF (McCleary, 2014; Tobaruela et al., 2018).

3. Physiological effects of dietary fiber on pig nutrition

3.1. Dietary fiber and nutrient digestibility

The results of studies investigating the effects of DF on nutrient digestibility is conflicting, wherein the great majority of studies have shown that DF reduced nutrient digestibility (Gutierrez et al., 2014; Urriola and Stein, 2010; Chen et al., 2013; Navarro et al., 2018; Zhao et al., 2019a). In contrast, high fiber diets may not reduce the digestibility of energy from results of other studies (Stein et al., 2015). Lyu et al. (2018) have shown that the addition of 30% oat bran, WB and palm kernels to the diets had no significant effect on the energy efficiency of the diets. Renteria-Flores et al. (2008) reported that increasing the level of IDF reduced the apparent total tract digestibility (ATTD) of energy and protein on sows, whereas increasing SDF intake improved energy digestibility.

Research has found that the viscosity of fiber is an important factor affecting the nutrient digestibility (Dikeman and Fahey, 2006; Wu et al., 2018). Hooda et al. (2011) reported that high-viscous DF increased the apparent ileal digestibility (AID) of nutrients by reducing digesta passage rate. Gao et al. (2015) reported that a microcrystalline cellulose diet significantly improved the ileal digestibility of crude protein in growing pigs but reduced the ATTD of gross energy (GE) and crude protein, whereas the inulin diet with lower viscous reduced the ileal digestibility of DM with no effects on the ATTD of GE and crude protein. Chen et al. (2017) reported that DF with higher viscosity increased the AID and standard ileal digestibility of amino acids, but also caused a significant increase in endogenous nitrogen loss.

3.2. Dietary fiber fermentation

3.2.1. Fermentation products

Although DF is not directly used by the endogenous digestive enzymes of pigs, intestinal microbiota can degrade DF and ferment it into gas and organic acids (OA), which is linked with the host health and metabolism (Williams et al., 2017). The gases produced from DF fermentation mainly include hydrogen, methane, and carbon dioxide, while the produced OA are mainly lactic acid and short-chain fatty acids (SCFA). Particularly, SCFA are the most important fermentation product of DF and are composed of approximately 60% acetic acid, 25% propionic acid and 15% butyric acid, respectively (Le Blanc et al., 2017).

3.2.2. Fermentation site

It is generally believed that DF is not digested and utilized in the small intestine of pigs, and its main degradation site is the large intestine. However, the fermentation of SDF could be initiated in the small intestine due to its better fermentability than IDF. For example, β-glucan was rapidly fermented and utilized in the small intestine of pigs due to its better water solubility, while arabinoxylan with less water solubility, was used in a low efficiency by the microbiota in the small intestine (Erik et al., 2012). Jaworski and Stein (2017) measured the digestibility of NSP of DDGS, wheat middling and SBH in different intestinal segments of pigs and found that the main fermentation sites of SDF are the small intestine and cecum, while the fermentation site of IDF is the colon.

3.3. Dietary fiber and intestinal microbiota

Gut microbiota is a complex and dynamic community, and it not only participates in the composition of the intestinal barrier, influencing the digestion and absorption processes, but also produces important metabolites which can play an important role in intestinal morphology, immune development and regulation of host gene expression (Blander et al., 2017; Tremaroli and Bäckhed, 2012; Yamashiro, 2017). As the main microbial energy substance, DF has been reported to regulate intestinal microflora and promote gut health (Table 1). Most of bacteria degrading DF are beneficial and can ferment DF into OA, thereby lowering the pH of the intestinal lumen, and inhibiting the proliferation of pathogenic bacteria (Williams et al., 2017). However, different DF show different effects on microbial composition and diversity. Wu et al. (2018) reported that xylan promoted the proliferation of *Bifidobacterium* whereas glucan decreased it. Mu et al. (2017) reported that compared with WB diets, weaned piglets fed alfalfa diets had increased relative abundance of *Firmicutes* and *Bacteroidetes*. Chen et al. (2014) showed that pea fiber (PF) feed significantly increased the counts of *Lactobacillus* in pig colon whereas soybean fiber increased the counts of *Escherichia coli*.

SDF with better fermentability can be efficient to change the gut microbiota of pigs, but this is not always positive. On the one hand, high viscous SDF tends to aggravate the shedding of intestinal epithelial cells and the decline of protein digestibility, which can increase the flow of undigested protein from the small intestine into the hindgut (Hooda et al., 2011; Chen et al., 2017). The increased protein in the hindgut can lead to promoted fermentation products like various amines and the proliferation of pathogenic bacteria, which have hidden dangers to the intestinal health of piglets (Fan et al., 2017). On the other hand, low viscosity SDF did not appear to increase the dangers to intestinal health. Low viscosity SDF promotes the proliferation of probiotics and has a less negative impact on nutrients and gastrointestinal physiology compared to high viscous SDF (Wu et al., 2018; Hooda et al., 2011; Gao et al., 2015; Chen et al., 2017).

Table 1
Results of studies evaluating the improvement effects of dietary fiber on gut microbes and gut health for pig.

Stage	Fiber sources	Changes in fiber type and level	Intestinal segment	Changes in gut microbes	Reference
Finishing	PF	NDF + 3%	Colon	*Lactobacillus* ↑	Che et al. (2014)
Growing	Arabinoxylan	Soluble AX + 8%	Hindgut	*Faecalibacterium prausnitzii* ↑	Williams et al. (2016)
Nursery	WB	NDF + 1.5%	Rectum	*Lactobacilli, Bifidobacteria, Faecalibacterium prausnitzii* ↑; Enterobacteriaceae ↓	Heinritz et al. (2016)
Nursery	PF	NDF + 3%	Colon	F/B ↑; *Lactobacillus* and *Prevotella* ↑	Luo et al. (2017)
Nursery	Corn bran	TDF + 2.5%	Rectum	F/B ↓; Bacteria involved in degradation of DF ↑	Zhao et al. (2019b)
Suckling	Alfalfa meal	NDF + 0.8%	Cecum and colon	*Streptococcus suis* ↓	Zhang et al. (2016)
Nursery	WB	NDF + 1.3%	Rectum	*Escherichia coli* ↓	Molist et al. (2011)
Nursery	WB and SBP	NDF + 2%	Colon	*E. coli* ↓; *Lactobacilli*-to-*Enterobacteria* ratio↑	Hermes et al. (2009)
Nursery	Extruded WB	CF + 0.5%	Colon	*E. coli*↓	Kraler et al. (2015)
Nursery	Xylan	Xylan + 5%	Cecum	*Bifidobacterium* ↑	Wu et al. (2018)
Nursery	WB	NDF + 1.5%	Colon	*Enterobacteria* ↓	(Molist Gasa et al., 2009)

PF = pea fiber; NDF = neutral detergent fiber; AX = arabinoxylan; WB = wheat bran; F/B = Firmicutes-to-Bacteroidetes ratio; TDF = total dietary fiber; DF = dietary fiber; SBP = sugar beet pulp; CF = crude fiber.

IDF has shown an inhibitory effect on pathogen colonization in many studies since it can stimulate intestinal peristalsis and reduce the colonization time of pathogenic bacteria in the intestine of pigs (Luo et al., 2017; Zhang et al., 2016; Molist et al., 2011; Hermes et al., 2009; Zhang et al., 2016). On the contrary, some studies do not support that IDF has an ability to improve pig intestinal microbiota. Owusu-Asiedu et al. (2006) reported that cellulose increased the *Enterobacteria* populations in the ileum of growing pigs, while Castillo et al. (2007) reported that growing pigs fed a diet containing 10% WB reduced the ratio of *Lactobacilli*/*Enterobacteria* during the first 3 weeks of the trial period.

3.4. Dietary fiber and energy metabolism

The absorption, transformation and deposition of energy affect the growth rate, carcass composition and meat quality of pigs. The effects of DF on energy metabolism of pigs have been extensively studied, and most studies have found that DF negatively affects energy deposition in pigs. One of the reasons is that DF dilutes the nutrient concentration of the diet and has swelling properties by absorbing water in the stomach, which increases the satiety of pigs thereby reducing energy intake (De Leeuw et al., 2008; De Jong et al., 2014; Chen et al., 2014; Li et al., 2015). DF also reduces the digestibility of nutrients in the small intestine as discussed above, which potentially results in the reduced energy absorption of pigs. Additionally, long-term high fiber intake increases the internal organ index of pigs, such as the weight of liver, spleen and intestine (Asmus et al., 2014). Since the energy requirement of organs can be around 45% of the energy intake of pigs, high fiber intake leads to more energy consumed by the organs and therefore reduced carcass weight (Tichauer et al., 2006). Furthermore, the SCFA from DF fermentation have been reported to regulate the secretion of adipokines in the intestinal epithelium of growing female pigs, especially in upregulating fasting-induced adipose factor (Fiaf), which was reported to inhibit fat deposition in humans and mice, but had not been thoroughly researched on the pigs regretfully (Weber and Kerr, 2012; Kim et al., 2010).

However, the effect of DF on energy metabolism of pigs is not always unfavorable, which is achieved through microbial metabolites SCFA, acetic acid, propionic acid, and butyric acid. Most butyric acid is directly hydrolyzed in colon cells to produce ATP (1 mol butyric acid produces 28 mol ATP) (Chambers et al., 2014). Acetic acid and propionic acid enter the liver to participate in glucolipid metabolism. Acetic acid was used for the de novo synthesis of fatty acids, while propionic acid mainly enters the gluconeogenesis pathway and inhibits cholesterol synthesis (Williams et al., 2017).

Furthermore, the inhibition of DF on energy deposition is also positive for pregnant sows. High DF diets have been shown to maintain blood glucose levels in sows because the fermentation of DF is normally a slow and continuous process, therefore is conducive to maintaining the insulin homeostasis of sows (De Leeuw et al., 2004; Quesnel et al., 2009; Serena et al., 2009). Controlling the backfat thickness is a core factor in maintaining the breeding ability and productive lifetime of the sows (Houde et al., 2010). Fiber-rich feedstuffs, such as wheat straw, SBH and alfalfa meal have been extensively used in the diets of gestating sows to prevent obesity, which helps to shorten the farrowing duration and alleviate postpartum anorexia (Veum et al., 2008; Holt et al., 2006). In recent studies, functional SDF (e.g. konjac flour and inulin) also showed improved energy metabolism of sows through regulation of insulin sensitivity and prevention of fat deposits during pregnancy (Tan et al., 2016; Zhou et al., 2017).

4. Application of dietary fiber on pig nutrition

4.1. Growth performance

Regardless of whether the feed ingredients are rich in SDF or IDF, most studies have shown that DF did not promote or even inhibited the growth performance, which was reviewed by Agyekum and Nyachoti (2017). High-fiber diets cause a significant decrease in the ADG of weaned pigs and may inhibit the deposition of lean meat in fattening pigs (De Jong et al., 2014; Magistrelli et al., 2009; Wang et al., 2016). The main reason for the reduced growth performance of pigs is the decline of nutrient digestibility and energy deposition induced by DF described above. Several studies have reported that DF helped to promote the growth performance of piglets, which is often achieved by improving intestinal health. For example, inulin promoted glucose absorption in the piglet small intestine after weaning and subsequently the dietary inulin offered a promising approach to avoid post-weaning gastrointestinal tract disorders in pigs (Awad et al., 2013). Zhao et al. (2018c) also reported that dietary CB or WB improved ADG and FCR of weaned piglets via altering gut microbiota, improving butyrate production, and enhancing gut health.

4.2. Meat quality

The effect of DF on meat quality of pig has been ignored for a long time. Results of early studies showed that high DF diets reduced carcass weight and increased intestinal weight, but few studies reported the improvement effect of DF on meat quality in pigs (Shaw et al., 2002; Stewart et al., 2013). Joven et al. (2014)

reported that replacing barley by fiber-rich olive cake in diets decreased backfat thickness, drip loss and increased pH_{45min} value on fattening pigs. Li et al. (2015) reported that the high DF diet reduced the glycolysis of fresh pork, which may be associated with the improvement of oxidative fiber composition of muscle. The muscle fibers of pigs are divided into fast-twitch and slow-twitch fibers which are associated with different glucose utilization and energy supply ways that in turn can affect the shape, lipid content, color and function of the muscle (Joo et al., 2013). Fast-twitch fibers are further divided into fast-oxidizing type (myosin corresponds to MyHC IIa), fast-degrading type (MyHC IIb) and intermediate type (MyHC IIx), while slow-twitch muscle fiber only corresponds to the slow oxidation type (MyHC I). Han et al. (2020) reported that a high-fiber diet decreased *MyHC IIb* and *MyHC IIx* mRNA and protein levels accompanied with a tendency for increased mRNA abundance of *MyHC I* of the longissimus dorsi on Erhualian pigs (a typical indigenous pig from China), but with no effects on Large White pigs. SCFA from DF fermentation were found to regulate the energy metabolism of muscle cells by affecting the synthesis and function of mitochondria, which may be a potential mechanism for DF to interfere with muscle fiber composition (Canfora et al., 2015). Taken together, the effects of DF on meat quality are poorly studied and further studies are still needed.

4.3. Reproduction of sows

Pregnant sows are often subject to strict feeding restrictions, which unfortunately causes various problems such as constipation and stereotyped behavior (Knage-Rasmussen et al., 2014). Adequate fiber intake can prevent constipation, increase satiety, and maintain normal reproductive performance (Table 2). Therefore, it has gradually become a consensus to feed pregnant sows with high fiber diets.

The addition timing influenced the effect of DF intake on sows. Ferguson et al. (2007) reported that sows fed with high DF diets 19 days before mating adjusted the follicular development and increased oocyte maturity, which was explained by the changed levels of estradiol hormone due to the addition of beet residue in the diets. High fiber diets improved weaning piglet weight in almost all studies, whilst some studies found that supplementation of high fiber diets throughout the gestation period increased the birth litter size and body weight of weaned piglets, whereas other studies have shown that feeding high-fiber diets in late gestation did not affect the birth litter size (Table 2). Additionally, high-fiber diets ingestion during the perinatal period were reported to alleviate prolonged farrowing duration by softening the feces and supplying energy from the hindgut (Feyera et al., 2017; Loisel et al., 2013). Taken together, DF has improved the reproductive performance of sows at different stages, but the selection of fiber source and level need to maintain considerable flexibility.

As shown in Table 3, research has focused on adding functional SDF to traditional high-fiber diets (rich in IDF) in recent years. Insufficient lactation ADFI is one of the core problems limiting sow reproductive performance, which is often caused by multiple factors, such as oxidative stress, inflammation, and heat stress. Konjac flour with water-swelling properties further expanded the gastrointestinal volume, which prepared sows for increased feed intake during lactation before farrowing based on a traditional high-fiber diet (Sun et al., 2015; Tan et al., 2015). Sows are believed to be facing a metabolic syndrome during the late gestation and early lactation because of vigorous metabolism and fading antioxidant capacity, wherein the imbalance of intestinal microbiota plays an important role (Cheng et al., 2018a). As promotion factors of beneficial bacteria in the intestine, functional SDF may improve the metabolic syndrome in the way of “microbiota remodeling”, thereby alleviating inflammation and oxidative stress in sows, which effectively increased the ADFI of sows during lactation (Tan et al., 2016; Zhou et al., 2017; Li et al., 2020a; Xu et al., 2020).

Additionally, the following studies have shown that maternal SDF intake helped to improve neonatal intestinal health. The maternal inulin intake during late pregnancy and lactation changed the intestinal microbiota for their suckling piglets (Paßlack et al., 2015). The addition of guar gum to maternal diets increased the population of beneficial microbiota in the intestine and reduced the diarrhea rate of piglets (Cheng et al., 2018b). Increasing the ratio of SDF to IDF in the pregnant diet of sows improved the antioxidant capacity and inhibited the inflammation of the colon for piglets (Li et al., 2020b). Briefly, maternal SDF intake is beneficial to the intestinal health of piglets, but the relevant mechanism remains to be explored, which may involve the influence of fiber nutrition on many aspects, such as the vertical transmission of intestinal microbiota, the fetal intestine development during pregnancy, and varieties of milk active ingredients.

Table 2

Results of studies evaluating the effects of traditional fiber sources on sow reproduction performance.

Feeding Period	Fiber sources	Main results	Reference
Gilts	SBP	Embryo survival ↑	Ferguson et al. (2007)
Throughout gestation for 3 consecutive parities	Wheat straw	Birth litter size, weaning litter size and litter weight ↑	Veum et al. (2008)
Throughout gestation	SBH	BW gain and lost backfat ↓; Total born number and born alive ↓; No effect on weaned litter size	Holt et al. (2006)
Throughout gestation	SBP, SBH	Stillborn ↓	Feyera et al. (2017)
Throughout gestation	SBP, SBH and Maize gluten feed compound	Stillborn ↑; Weaning litter size and litter weight ↑; Weaning to estrus interval ↓; Lactation ADFI ↑	Guillemet et al. (2007)
Throughout gestation	RS, SBH and SBP	RS and SBH reducing aggression and increasing satiety in limit-fed pregnant sows without affecting production	Sapkota et al. (2016)
Throughout gestation	SBP, SBH, WB and Maize gluten feed compound	Lactation ADFI↑; Piglet ADG, BW ↑	Quesnel et al. (2009)
Late gestation	AM and SBP	ADFI ↑; No effect on birth weight and born number	Krogh et al. (2015)
Late gestation	SBP, SBH and WB compound	Colostrum intake by individual piglets ↑; Preweaning mortality ↓	Loisel et al. (2013)
Late gestation	Lupins and oat hulls compound	Birth weight ↑; Lactation ADFI and weaning weight ↓; Body weight change on sows ↑	Langendikj and Chen (2013)
Lactation	RS	Nutrient density in maternal milk ↑; No effect on offspring performance at weaning	Yan et al. (2016)

SBP = sugar beet pulp; SBH = soybean hulls; RS = resistant starch; WB = wheat bran; AM = alfalfa meal.

Table 3
Results of studies evaluating the effects of functional fiber sources on sow reproduction performance.

Feeding Period	Fiber sources	Main results	Reference
Late gestation and lactation	Konjac flour	HOMA-IR value ↓; Antioxidants status and lactation ADFI of sows ↑	Tan et al. (2016)
Throughout gestation	Inulin	Piglet BMI ↑; Sow fat deposits ↓	Zhou et al. (2017)
Gilts	SDF compound	Intrauterine growth retardation ↓; Observed puberty 15.6 d earlier at a 12.2 kg lower body weight and a 0.84 mm lower backfat thickness.	Zhuo et al. (2017)
Throughout gestation for 2 consecutive parities	Konjac flour	Sow ADFI, weaning litter size and litter weight ↑	Tan et al. (2017)
Throughout gestation	Guar gum	Piglet growth rate ↑; Diarrhea incidence ↓	Cheng et al. (2018b)
Late gestation	Inulin	Sow ADFI, pig weaned weight and weaning survival rate ↑; Farrowing duration and stillborn ↓	Li et al., 2020a
Throughout gestation	Konjac flour	Plasma cortisol concentration and non-feeding oral behavior during gestation ↓; Lactation ADFI of sows, weaned litter size and litter weight ↑	Sun et al. (2015)
Throughout gestation for 3 consecutive parities	Konjac flour	Sow ADFI, piglet ADG and weaning litter weight ↑; Sow constipation ↓	Tan et al. (2015)

HOMA-IR = homeostatic model assessment for insulin resistance; BMI = body mass index; SDF = soluble dietary fiber.

5. Main factors affecting the utilization of dietary fiber on pigs

5.1. Growth stages and breeds of pigs

Compared with piglets, adult pigs have larger and longer intestines and more mature digestive systems, which makes them more capable of degrading fiber. Adult sows had higher ATTD of CF, NDF and TDF than that of growing pigs and finishing pigs when they were fed the same high-fiber diets (Goff et al., 2002). Gilts also had a higher energy digestibility than growing pigs, and this effect was more significant when fed a high-fiber diet, indicating that gilts have a much better capacity to degrade fiber than growing pigs (Shi and Noblet, 1993). Lindberg (2014) and Jørgensen et al. (2007) pointed out that sows had higher IDF digestibility and SCFA production, but the capacity of SDF fermentation was similar compared to growing pigs. Briefly, sows had higher DF fermenting ability than that of growing pigs, which was attributed to the difference in intestinal development and higher population of gut microbes rather than the types of intestinal microbes.

Besides the growth stages, breeds of pigs are also an important factor that affects the ability to ferment fiber. Indigenous pig breeds generally have higher fiber fermentation capacity than cultivated breeds. The study of Urriola and Stein (2012) reported that Meishan pigs fed 29.1% corn DDGS diets had significantly higher ATTD of TDF than Yorkshire pigs. When fed with high-fiber diets containing 24.1% wheat meal, alfalfa meal or rice bran, Duroc × Berkshire × Jiaxing pig showed a higher hindgut ADF digestibility than Duroc × Landrace × Yorkshire pigs, indicating the offspring of the three-way hybrid of the indigenous breeds still retained a high ability of fiber degradation (Zhao et al., 2018a). However, there has been no systematic study focusing on the reasons as to why indigenous pigs have better fiber digestibility than cultivated pigs until now. Given the importance of the intestinal environment on fiber degradation, different microbial activity in the gut and development of intestinal tissue between indigenous pig breeds and cultivated breeds could be the critical factors.

5.2. Fiber sources

The fermentation capacity of DF was highly dependent on its sources, which showed differences in fiber chemical composition and physical properties. IDF in pig diets accounted for 70% to 90% of TDF, its fermentability in the pig intestine was much lower than that of SDF, wherein the ATTD of SDF in pigs was 70% to 95% and was generally around 50% for the ATTD of IDF (Jaworski and Stein, 2017). Gao et al. (2015) reported that piglets fed 5% inulin diet showed reduced AID of NDF than those of cellulose diet, but the hindgut digestibility of NDF and ADF were much higher than those of cellulose diet, indicating that additional SDF may affect the digestion of IDF. In addition, lignin and cellulose are linked closely in plant cell wall therefore higher lignin content may inhibit the degradation of cellulose by gut microbiota (Jha and Berrocoso, 2015). For example, the NSP digestibility in wheat straw and WB with higher lignin were 62.8% and 35.6% lower than SBH, respectively (Chabeauti et al., 1991). Unfortunately, solving how to improve utilization efficiency by dissociating cellulose and lignin in plant-derived feeds remains a worldwide problem.

The concentration and distribution of SCFA produced from DF fermentation were also affected by fiber types (Table 4). The fiber source not only affected the ability of pigs to digest DF, but also changed the content of SCFA produced in different intestinal segments (Zhao et al., 2019b). Fiber from cereals such as WB and CB may be easier to ferment to produce butyric acid compared to those from legumes, such as PF, SBH and alfalfa meal, which prefer fermentation to produce acetic acid (Table 4; Table 5). Taken together, the fiber source not only affected the ability of pigs to degrade DF, but also changed the profile of SCFA in different intestinal segments.

5.3. Fiber level

Extra fiber intake often increases the concentration of volatile fatty acids (VFA) or changes the ratio of VFA in chyme or feces (Table 5). In addition, several studies showed that DF digestibility of pigs decreased with the increase of fiber level in the diets, which could partly be explained by the higher transit time of chyme along the intestine (Zhao et al., 2018b; Huang et al., 2013, 2018). Nevertheless, there were also other studies suggested that increasing fiber levels did not reduce the utilization of DF. Bindelle et al. (2009) reported that the ATTD of NDF was increased when the SBP content in the diets elevated from 0 to 30%. Wilfart et al. (2007) reported that the addition of WB (0, 20% and 40%) in the diet did not change the digestibility of DF components. In briefly, considering the complexity of different fiber sources and basic diets, there is still no consistent conclusion about the varying fiber levels on the digestibility of fiber components in pigs.

5.4. Fiber degrading enzymes

It is widely believed that the application of fiber degrading enzymes (FDE) is one of the effective strategies to improve the fermentability of fiber components. For instance, Zhang et al. (2014)

Table 4
Results of studies evaluating the effects of fiber sources with similar TDF level on fermentation production in pigs.

Growth stage	Fiber sources	Adaptation period	Intestinal segment	Difference in fermentation product concentration	Reference
Nursery	WB or SBP	15 d	Colon	BUT ↑ (WB)	Molist et al., (2009);; Jha and Leterme, (2011)
Growing	WB, pea hull, pea inner fiber, SBP or corn DDGS	10 to 12 d	Colon	VFA ↓ (WB); BUT ratio↑ (pea hull)	(Jha and Leterme, 2011)
Growing	CB, SBH or SBP	11 to 13 d	Rectum	No difference	Zhao et al. (2019a)
Finishing	CB, WB, oat bran, SBH, SBP or RB	15 d	Ileum and rectum	ACE and VFA ↑ (SBH, SBP); Lactate and VFA ↓(RB)	Zhao et al. (2019b)
Finishing	PF, WB fiber, soybean fiber or Maize fiber	160 d	Ileum and cecum	Ileal ACE ↓ (WB); Cecal BUT ↑ (WB)	Chen et al. (2014)
Growing	Flaxseed meal (SDF-rich) or oat hulls (IDF-rich)	13 to 16 d	Rectum	VFA ↑ (Flaxseed meal)	Ndou et al. (2019)
Growing	Cassava residue (SDF-rich) or Brewer's grain (IDF-rich)	27 d	Ileum, cecum and colon	ACE, PRO, BUT and VFA ↑ (Cassava residue)	Ngoc et al. (2012)
Nursery	CB, WB or SBH	28 d	Rectum	BUT ↑ in CB and WB diets	Zhao et al. (2018c)

TDF = total dietary fiber; WB = wheat bran; SBP = sugar beet pulp; BUT = butyric acid; DDGS = distillers dried grains with soluble; VFA = volatile fatty acids; CB = corn bran; SBH = soybean hulls; RB = rice bran; ACE = acetic acid; SDF = soluble dietary fiber; IDF = insoluble dietary fiber; PRO = propionic acid.

Table 5
Results of studies evaluating the effects of fiber levels on fermentation production in pigs.

Growth stage	Fiber sources	Changes in fiber level	Adaptation period	Intestinal segment	Changes in fermentation product concentration	Reference
Finishing	PF	NDF + 3%	160 d	Colon	Total SCFA ↑; ACE↑	Che et al. (2014)
Finishing	PF	NDF + 3%	160 d	Colon	ACE↑; BUT ↓ (ratio)	Luo et al. (2017)
Nursery	PF	NDF + 3%	30 d	Colon	ACE↑; BUT ↓ (ratio)	Luo et al. (2017)
Nursery	PF	NDF + 3%	30 d vs. 90 d vs. 160 d	Cecum	No effect of short-term; VFA ↑ and PRO ↓ in long-term	Luo et al. (2019)
Nursery	WB	NDF ± 1.5%	15 d	Colon	BUT ↑	Molist Gasa et al., 2009
Nursery	WB	TDF + 3.5%	18 d	Rectum	BUT ↑	Zhao et al. (2018b)
Nursery	WB	NDF + 1.3%	12 d	Rectum	Total VFA ↑	Molist et al. (2011)
Nursery	WB	NDF + 15%	49 d	Rectum	Total SCFA ↑	Heinritz et al. (2016)
Nursery	Extruded WB	CF + 0.65%	42 d	Colon	Total VFA ↑	Kraler et al. (2015)
Growing	AM	IDF + 9.0%	6 to 8 d	Ileum and rectum	ACE, PRO and total VFA ↑	Chen et al. (2013)
Nursery	Corn bran	TDF + 2.5%	28 d	Rectum	No effect	Liu et al. (2018)

PF = pea fiber; NDF = neutral detergent fiber; SCFA = short-chain fatty acids; ACE = acetic acid; BUT = butyric acid; VFA = volatile fatty acids; PRO = propionic acid; WB = wheat bran; CF = crude fiber; AM = alfalfa meal; IDF = insoluble dietary fiber; TDF = total dietary fiber.

have shown that xylanase, α-amylase, and protease improved growth rate by increasing the digestibility of DM, crude protein, and energy. Despite that, some studies have found FDE did not change the efficiency of DF utilization in pigs. Högberg and Lindberg (2004) showed that although the cecal digestibility of NSP was increased when β-glucanase and xylanase were added into a WB diet, its ATTD was not affected. The mixed enzyme preparation of cellulase, xylanase and β-glucanase in the high-fiber diets containing WB and SBH improved the ileal digestibility of NSP but did not change its ATTD (Liu et al., 2016). The above studies may indicate that the promoting effect of FDE on fiber digestibility mainly occurred in the small intestine and cecum.

Particularly, it should be realized that the FDE not only improve the utilization of DF, but also reduce the viscosity of the intestinal content to alleviate anti-nutritional effects of DF. More importantly, FDE have been used in piglets to strengthen the role of DF in protecting intestinal health in recent studies. Lærke et al. (2015) reported that xylanases decreased ileal viscosity, and improved apparent ileal fiber and nutrient digestibility of rye and wheat in growing pigs. Duarte et al. (2019) reported that xylanase reduced viscosity of digesta, mucosal malondialdehyde, crypt depth and crypt cell proliferation in the jejunum of newly weaned pigs. Chen et al. (2020) reported that the DDGS in the diets increased viscosity, whereas supplemental xylanase decreased the viscosity of jejunal digesta, improved AID of DM and GE and reduced inflammatory response in nursery pigs.

5.5. *Adaptation period*

The intestine of pigs needs an adaptation period for diets with different fiber types or levels. Studies have shown that the digestibility of fiber components stabilized and increased gradually as pigs consume high-fiber diets for extended periods of time (Van der Peet-Schwering et al., 2002; Zhao et al., 2018d). The length of the adaptation period affected the bacterial community and profile of SCFA in the pig cecum (Luo et al., 2019). The relative abundance of fiber degrading bacteria may be related to the adaptation period. For example, the colonic *Prevotella* of pigs decreased in the short-term PF diet but increased significantly during long-term feeding (Luo et al., 2017). There are currently few studies on the adaptation period. The digestibility and fermentability of the diets may affect the length of the adaptation period. The adaptation period of growing pigs to SBP rich in SDF was significantly shorter than that of WB rich in IDF, indicating gut microbes of pigs more easily adapted to fermentable SDF (Castillo et al., 2007). Additionally, the fiber level also affected the length of the adaptation period reported by Huang et al. (2018).

6. Conclusion

Appreciation of the nutritional and antinutritional function of DF on pigs has been reached dialectically with the growing understanding of its physical and chemical properties. More fiber sources, such as pea fiber, corn bran, konjac flour, and inulin, have been extensively studied in pigs, especially in piglets and sows. The regulation of intestinal microbiota has been the focus of research on the nutritional value of DF in recent years, which is not limited to the impact on intestinal health, but also covers a wide range of interventions on pig immunity and energy metabolism. However, the regulation of DF on meat quality of pigs has not been thoroughly and systematically studied. Furthermore, it remains a worldwide problem how to maximize fiber utilization efficiency on pigs. Overall, future research needs to focus more on the combined effects of SDF and IDF, processing methods, and timing of addition to improve the nutritional value of DF, and further explore the physiological functions and regulatory mechanisms of fiber fermentation products SCFA in pigs.

Author contributions

Hao Li and **Zhiqing Li**: Literature collection, Writing-Original draft preparation. **Jie Yin**, **Jiashun Chen** and **Haihan Zhang**: Writing- Reviewing and Editing. **Bie Tan** and **Xiaokang Ma**: Funding acquisition.

Conflict of interest

We declare that we have no financial and personal relationships with other people or organizations that might inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

Acknowledgments

This study was supported by Scientific Research Fund of Hunan Provincial Education Department (19B267) and National Natural Science Foundation of China (U20A2054).

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