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Dietary fiber and its role in performance, welfare, and health of pigs

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Review Article

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Abbreviations:
AA: amino acids; BW: body weight; BWG: body weight gain; CF: crude fiber; CP: crude protein; DDGS: dried distillers' grains with solubles; DF: dietary fiber; DM: dry matter; *E. coli*: *Escherichia coli*; HF: high-fiber; ISF: insoluble fiber; PWD: post-weaning diarrhea; SBP: sugar beet pulp; SCFA: short-chain fatty acids; SF: soluble fiber; WB: wheat bran

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Abstract

Dietary fiber (DF) is receiving increasing attention, and its importance in pig nutrition is now acknowledged. Although DF for pigs was frowned upon for a long time because of reductions in energy intake and digestibility of other nutrients, it has become clear that feeding DF to pigs can affect their well-being and health. This review aims to summarize the state of knowledge of studies on DF in pigs, with an emphasis on the underlying mode of action, by considering research using DF in sows as well as suckling and weaned piglets, and fattening pigs. These studies indicate that DF can benefit the digestive tracts and the health of pigs, if certain conditions or restrictions are considered, such as concentration in the feed and fermentability. Besides the chemical composition and the impact on energy and nutrient digestibility, it is also necessary to evaluate the possible physical and physiologic effects on intestinal function and intestinal microbiota, to better understand the relation of DF to animal health and welfare. Future research should be designed to provide a better mechanistic understanding of the physiologic effects of DF in pigs.

Introduction

Productivity and feed efficiency are the basic prerequisites for profitable swine production. Pigs are often fed nutrient- and energy-dense diets to meet such requirements in a cost-efficient way. The integration of fiber components in complete feeds for pigs may require additional technical effort and lead to faster satiation in the animals. This practice contradicts the natural feeding behavior of pigs, and may cause stress and behavioral problems which are considered important factors affecting welfare and health (Tokach *et al*., 2019). Therefore, welfare-oriented feeding concepts often include the administration of complete feed rich in dietary fiber (DF) or the additional administration of roughage as a satiation feed. The chemical structure of the various fiber types is crucial for the numerous direct and indirect physiological effects of DF and has been extensively reviewed (Jha and Berrocoso, 2015; Navarro *et al*., 2019; Li *et al*., 2021), whereas the physical properties have been studied sparsely (Molist *et al*., 2012). Depending on the chemical composition, but in particular on the solubility and the microbial fermentability, DF can have very different effects on the digestive tract and metabolism of pigs. Soluble fiber (SF) sources contain mix-linkage glucans, hemicelluloses, arabinoxylans, xyloglucans, galactomannans, pectins, gums, guar, and agar and non-digestible fructo- and galactooligosaccharides. Partly insoluble fibers (ISF) are composed of cellulose, lignin, and different forms of resistant starches (Gemen *et al*., 2011; Williams *et al*., 2017). DF occurs naturally in almost all plant-based feedstuffs and can also be obtained from by-products of industrial food and beverage processing, and can therefore be used as a sustainable feed component. Although DF is not considered an essential nutrient, various performance, behavior, and health-related properties are affected, depending on the quantity and quality of the fiber source. Most interestingly, DF has an impact on pigs through specific effects on the digestive tract, intestinal microbiota, and immune functions, and thereby may protect against certain intestinal disorders, contributing to better health (Lindberg, 2014). In contrast to the situation in rodent animal models, only a few studies in pigs are explicitly devoted to the mechanistic effects of fiber intake. However, the mechanistic aspect of DF is extremely important for explaining its physiologic effects on the digestive tract, microbiota, and immunity.

Here, we summarize the studies on DF in pigs as important food-producing animals, specifically considering pregnant and lactating sows, the sow–piglet couple, weaner piglets, gilts, and fattening pigs and the mode of action of DF.

DF in gestating and lactating sows

Impact of DF on performance of sows

For sows and their offspring, DF has the potential to influence physiology and health (Table 1). Several studies investigated the effect of DF inclusion in the diet on sow performance, including physiological parameters of reproduction and progeny. Particularly interesting are the effects of DF on feed intake, especially during lactation as higher feed intake in this period may promote health and performance in sows and piglets (Farmer *et al.*, 1996). An impact of DF on reproductive performance has been observed as early as the onset of puberty, which was demonstrated 15.6 days earlier in gilts fed with diets enriched with soluble DF until mating. Additionally, their litters were characterized by a reduced number of growth-retarded piglets and these litters were more uniform (Zhuo *et al.*, 2017). Regarding successful insemination, feeding sows diets rich in DF supplemented with inulin and cellulose, sugar beet pulp (SBP), wheat bran (WB) or lupins demonstrated enhancing effects on oocyte maturity, quality, and ovarian follicle reserve (Ferguson *et al.*, 2007; Weaver *et al.*, 2013; Cao *et al.*, 2019). However, no differences were observed in ovulation rate and litter size when gestating sows were fed with diets with 30% oat bran, 12% wheat straw, or 21% soybean hulls (Renteria-Flores *et al.*, 2008). The number and viability of piglets increased when sows were provided 20–30% hydrolyzed straw meal (Bergner, 1988), 38% SBP and 5.6% soybean hulls (van der Peet-Schwering *et al.*, 2003), or 3% of a mixture of guar gum and cellulose (Wu *et al.*, 2020). Mechanisms for the observed effects could be related to higher short-chain fatty acid (SCFA) production in the gut, enhanced serotonin secretion, and a T helper 2 lymphocyte (Th2)-based immune response in gestating sows with a positive impact on embryo survival. Higher birth weights were also reported when sows were fed with diets with 40% SBP during gestation, which might be related to more favorable microbial activity, as discussed by Rooney *et al.* (2019). Ground wheat straw (13%) in gestation diets for sows increased litter size and total litter weight at birth, which might be related to a higher feed intake (Veum *et al.*, 2009). However, *ad libitum* feeding of a gestation diet with 23% WB, 20% SBP, and 14% oat bran did not affect the reproductive performance of sows (Peltoniemi *et al.*, 2010). High inclusion rates of WB at 24 and 42% in gestation diets had no enhancing effect on litter size, piglet viability, and body weight gain (BWG) in primiparous sows, but resulted in increased litter performance in the next parity (Che *et al.*, 2011). The inclusion of 8% SBP and 3% cereal straw during gestation and lactation had no impact on reproductive performance (Alvarez-Rodriguez *et al.*, 2017). Similarly, no impact on performance was observed when breeding sows were fed with a mixture of SBP, alfalfa, soybean hulls, grape pomace, and lignocellulose during gestation (Priester *et al.*, 2020).

DF, nutrient digestibility, and metabolic effects on sows

Feed intake and nutrient digestibility in sows can be influenced by high-fiber (HF) diets. Specifically, serum levels of vitamin B_{12} and minerals were lower when sows received diets enriched in fibers such as 53% corn cobs, 43% WB, or 53% oat hulls. The observed effects could be related to the modulation of cecal and colonic vitamin B_{12}-producing microbiota and the mineral-binding capacity of fiber and reduced time for mineral absorption due to increased transit time (Girard *et al.*, 1995). A further study showed that diets with 15% SBP resulted in an improved overall N-retention of breeding sows, which could be explained by increased uptake of N from urea and other N-sources by the gut microbiota and therefore a lower N secretion in urine (Patráš *et al.*, 2012).

DF often showed a negative impact on total tract organic matter (OM), nutrients, and energy digestibility, but differences were observed depending on fiber sources. SBP and alfalfa meal (12 or 17%) reduced apparent total tract digestibility of energy, crude protein (CP), and in the case of alfalfa meal, non-starch polysaccharides (NSP) (Krogh *et al.*, 2015). In sows, total tract digestibility of energy, dry matter (DM), OM, CP, and ether extract were moderately reduced by the inclusion of 15% SBP and more distinct with diets containing 23% maize bran and 27% WB (Le Goff *et al.*, 2002). Diets rich in DF, specifically 9.8% sunflower meal, 9.8% WB, 19.5% SBP, and 9.8% soybean hulls reduced the circulating concentration of leptin and improved the feed intake of sows before farrowing (Quesnel *et al.*, 2009). Either 10% native or heat and pressure processed wheat or oat straw in late gestation diets lowered energy and DM digestibility in gestating sows, especially when included in the native form. Preprandial prolactin concentration was higher with oat straw, whereas postprandial insulin-like growth factor-1 (IGF-1) and prolactin were increased with processed wheat straw. Hence, oat straw was considered more beneficial compared to wheat straw, but underlying mechanisms could not be further elucidated (Agyekum *et al.*, 2019). Surprisingly, one study showed higher postprandial insulin levels in sows fed with HF diets containing each 8% soybean hulls, WB, sunflower meal, and SBP, whereas prolactin was not affected (Loisel *et al.*, 2013).

A recent study in gilts receiving an HF diet based on corn bran (30% of inclusion) also showed a decrease in DM, CP, gross energy, and fiber digestibility accompanied by increased digesta viscosity and reduced cecal fermentation. The observed effects were due to the high amount of neutral-detergent fiber (NDF) in the diets resulting in decreased nutrient and energy digestibility, reduction in relative hindgut fermentation, impairment of pig performance and dilution of dietary energy, as explained by Petry *et al.* (2021).

Effects of DF on reproductive physiology of sows

Colostrum is the first source of energy, nutrients, and bioactive compounds for newborn piglets, being replaced in this role by milk, shortly after farrowing. Therefore, modulation of colostrum, as well as milk yield and composition in lactating sows may offer an opportunity to positively influence the development and health of offspring. A diet with a mixture of soybean hulls, WB, sunflower meal, and SBP, including 8% of each fiber source at late pregnancy (from day 106 until parturition), had no effect on colostrum yield and hormones involved in lactogenesis, but it increased colostrum lipids and decreased immunoglobulin A (IgA) concentration in colostrum and milk compared to a control diet (Loisel *et al.*, 2013). A more recent study compared a diet without added fiber to gestation diets with 20% SBP or 30% WB and lactation diets with 10% SBP or 15% WB as fiber sources.

Table 1. Effects of DF sources in feed on pregnant and lactating gilts and sows

Breed, *n*	Feeding period	Fiber source and level	Digestibility	Intestine, metabolism, immune system	Productivity, reproduction	Behavior	Reference
	Gestation	HCl-treated straw meal 20–30% DM			↗ Viable and reared piglets		Bergner (1988)
Yorkshire × landrace gilts *n* = 88	Gestation	1: Corn–soybean meal 2: 43% WB + 53% corn cobs 3: Oats + 53% oat hulls		↘ Serum vitamin B_{12} and serum concentrations of minerals in diets 2 and 3			Girard *et al.* (1995)
Yorkshire × landrace gilts *n* = 48	Gestation	49% oat hulls		↗ Feed intake in lactation ↘ Water intake in gestation			Farmer *et al.* (1996)
Yorkshire × landrace *n* = 21	Gestation	Very HF: 45% oat hulls, 28% alfalfa meal, 16% WB HF: 27% oat hulls, 27% alfalfa meal, 9.4% WB CON: 15% WB *ad libitum* or in restricted amount			↘ Stereotypies and activity during 2 h post-feeding in very HF diet Feed more effective when offered *ad libitum*		Bergeron *et al.* (2000)
PIC C-15 (maternal line) × PIC 405 (sire line) gilts *n* = 42	Before conception until day 90 of gestation	CON: fortified sorghum–soybean meal HF: CON + 25% SBP		↗ White blood cell numbers in HF		↘ Standing time in HF (day 30) ↗ Sham chewing in HF	McGlone and Fullwood (2001)
Adult ovariectomized sows *n* = 4	Adult	CON MB: maize bran diet (23.5%) WB diet (27%) SBP diet (14.7%)	↘ Total tract digestibility of nutrients and energy ↗ Digestibility coefficients in SBP versus MB and WB	Energy losses from CH_4 linearly related to the digestible TDF intake (+1.4 kJ g^{-1})	BW not affected by diet		Le Goff *et al.* (2002)
Dutch landrace, Finnish landrace, and Dutch large white *n* = 444	Gestation, lactation	Gestation G-starch: 11.4% wheat + 10.2% peas + 27.4% tapioca G-NSP: 5.6% soybean hulls + 38.3% SBP Lactation L-starch: 10.5% peas + 36.7% tapioca L-NSP: 20.6% SBP			↗ Total piglets born and live-born piglets in G-NSP versus G-starch ↘ BWG and backfat gain in G-NSP versus G-starch ↗ Backfat loss during lactation in L-NSP versus L-starch		van der Peet-Schwering *et al.* (2003)
Large white × landrace crossbred gilts, *n* = 45	Puberty	50% unmolassed SBP			Beneficial effects on oocyte maturity and embryo survival in gilts		Ferguson *et al.* (2007)

(Continued)

Table 1. (*Continued.*)

Breed, *n*	Feeding period	Fiber source and level	Digestibility	Intestine, metabolism, immune system	Productivity, reproduction	Behavior	Reference
Large white × landrace crossbred	Gestation	CON HF: 9.75% sunflower meal, 9.75% WB, 19.5% SBP, 9.75% soybean hulls			HF: duration of gestation, parturition and weaning-to estrus, birth intervals, litter size, number of stillborn and weaned piglets, birth weight, sow feed intake (lactation), backfat thickness loss not affected HF: ↗ Piglet growth rate during first week HF: leaner sows at the end of gestation		Guillemet *et al.* (2007)
Duroc × imperial Swine genetics-line 422, gilts *n* = 43	From day 28 before mating and during gestation	CON: corn–soybean meal 30% oat bran diet high in SF 12% wheat straw diet high in ISF 21% soybean hull diet			↘ Live embryos in wheat-straw diet and soybean hull diet ↗ Total embryo survival rate in SF and control No differences in ovulation rate No impact on litter size DF: ↗ ADFI, ↘ BW loss		Renteria-Flores *et al.* (2008)
Large white × landrace crossbred gilts *n* = 18	Gestation (from day 26)	9.8% sunflower meal + 9.8% WB + 19.5% SBP + 9.8% soybean hulls		No fiber-related changes in glucose and insulin metabolism ↘ Secretion of leptin	↗ Appetite of lactating sows fed an HF diet during gestation ↗ Feed consumption ↗ Growth rate of piglets No sparing effect on maternal body reserves		Quesnel *et al.* (2009)
Gilts and sows of mixed parity *n* = 320	Gestation	13.4% ground wheat straw			Wheat straw: ↗ Born and weaned piglets ↗ Total litter birth and weaning weights ↗ Higher lactation feed intake in sows		Veum *et al.* (2009)
Finnish landrace × Yorkshire *n* = 926	Gestation	CON: based on barley and whey, fed once a day (2.5 kg day^{-1}, 10.3 MJ kg^{-1} NE) AD LIB: *ad libitum* fed (7.7 MJ kg^{-1}) high CF (23% WB, 20% SBP, 14% oats bran, 10% oats)			AD LIB sows: no effect on the reproductive performance (pregnancy rate, weaning to estrus interval, piglets born alive, stillborn piglets, progesterone level) CON sows: ↗ weaned piglets AD LIB sows: ↗ weight of weaning piglets		Peltoniemi *et al.* (2010)

Landrace × Yorkshire gilts *n* = 420	Gestation	LF (low fiber): 6% WB MF (middle fiber): 24% WB HF: 42% WB			LF versus HF: ↗ backfat gain in gestation and loss in lactation, ↗ litter size at farrowing/born alive (parity 1) LF and MF: ↗ litter weight (days 1 and 22 of lactation, parity 1) MF: ↗ litter size, born alive (parity 2) HF: optimal litter performance	Che *et al.* (2011)
Large white × landrace gilts *n* = 8	Prepuberty	LPAA: low CP (14%) and low CF LPAABP: low CP and high CF HP: high CP (18.8%) and low CF. HPBP: high CP and high CF. High CF diets: 15% SBP	Beet pulp fiber: ↗ Fecal N ↘ Urinary N ↗ Overall N retention (high-CP diets) DM intake not affected			Patráš *et al.* (2012)
Landrace × large white gilts *n* = 29	Gestation (from day 105)	8% soybean hulls + 8% WB + 8% sunflower meal (not dehulled) + 8% SBP		↗ Postprandial insulin levels Serum progesterone, prolactin, estradiol-17β, cortisol not affected	Colostrum yield and piglet BWG not affected ↗ Colostrum intake of LBW piglets ↘ Pre-weaning mortality ↗ Lipid and ↘ IgA content in colostrum	Loisel *et al.* (2013)
Gilts	3 weeks before puberty stimulation until day 19 of the first estrous cycle	CON 50% WB 35% lupin		LH concentrations and ovarian follicle size not affected	Improved oocyte quality and embryo survival in gilts fed HF diets	Weaver *et al.* (2013)
Danish hybrid *n* = 170	Gestation	CON Restrictive supply of CON supplemented *ad libitum* with straw (S), hay (H), clover grass silage (GS), maize silage (MS) or Jerusalem artichoke (JA)		Colostrum: total bacterial count and *E. coli* count not affected MS: ↘ LPS in colostrum ↘ C-reactive protein in colostrum in S and H diets JA: ↗ IgG-anti-LPS		Werner *et al.* (2014)
Second-parity sows Danish Landrace × Yorkshire *n* = 36	From gestation (day 105) to early lactation (day 5)	CON ALF: 16.9% alfalfa 12% SBP	↗ Digestibility in CON versus ALF and SBP ↘ Feed intake in CON versus ALF and SBP	↗ Butyrate and total SCFA in SBP versus ALF and CON in plasma ↘ Acetate in CON versus ALF and SBP in plasma ↗ Soft feces in SBP versus CON	↗ DM in colostrum in SBP versus ALF and CON ↗ Lactose in colostrum in CON; colostrum yield, suckling duration and weight gain not affected; sow weight, backfat and duration of farrowing not affected	Krogh *et al.* (2015)
Belgian landrace *n* = 30	Gestation	37% SBP		↘ NH_3 ↗ CH_4 emissions		Philippe *et al.* (2015)

(*Continued*)

Table 1. (*Continued.*)

Breed, *n*	Feeding period	Fiber source and level	Digestibility	Intestine, metabolism, immune system	Productivity, reproduction	Behavior	Reference
Topigs *n* = 21	Gestation	3% inulin		Sows: ↗ Fecal enterococci ↘ Fecal pH Suckling piglets: ↗ Stomach: Eubacteria; Cecum: enterococci, *C. leptum* ↘ Stomach: enterobacteria and *Lactobacillus amylovorus*, ammonia, *n*-butyric acid, *i*-valeric acid			Paßlack *et al.* (2015)
Gilts *n* = 22	Gestation	+35% soybean hulls		Improved skin health at weaning in piglets of sows fed with HF diet	No impact on performance		Bernardino *et al.* (2016)
York × landrace *n* = 200	Gestation	CON (corn–soybean meal based) RSTARCH (10.8% resistant starch) SBP (27.2% SBP) SOYHULLS (19.1% soybean hulls) INCSOY (14.1% soybean hulls)	SBP and SOYHULLS: ↘ Blood urea nitrogen	RSTARCH and SBP: ↗ Serum glucose RSTARCH, SBP, SOYHULLS: ↗ NEFA	Birthweight: ↘ INCSOY Litter size at farrowing and weaning weight were not affected	RSTARCH and SOYHULLS: ↗ welfare in gestating sows; ↘ aggression; ↗ satiety Sows on SBP stood more and sows on SOYHULLS rested more Chewing behavior (bar and feeder): ↗ days on diet; ↘ SOYHULLS diet When mixed: ↗ biting frequency CONTROL diet; ↘ RSTARCH diet Heart rate: ↘ SOYHULLS and INCSOY	Sapkota *et al.* (2016)
Large white × landrace *n* = 12	Lactation	Diets with a combination of two CP (14% versus 12%) and NDF (18% versus 22%) levels LF: 1.3–1.5% sunflower meal + 14.8% alfalfa meal HF: 15% sunflower meal + 10.8–11.2% alfalfa meal + 8% SBP + 3% straw meal	Low CP: no effect on apparent total tract digestibility of nutrients. HF: ↘ Apparent total tract digestibility of P, OM and NfE and ↗ apparent total tract digestibility EE		Low CP: no effect on live-weight and backfat thickness in sows; ↘ ADG in piglets. HF: no effect on sow and litter performance		Alvarez-Rodriguez *et al.* (2017)

Gilts *n* = 136	Puberty	CON + 0.8% SF (containing 17.4% rhamnose, 4.1% fucose, 11.1% arabinose, 30.6% xylose)		SF: ↘ Serum cholesterol, triglyceride, and estradiol	↘ Time until attaining observed puberty in SF-fed gilts ↘ Incidence of intrauterine growth restriction (IUGR) in SF versus CON-fed gilts ↗ Intra-litter uniformity in SF Piglets born alive, and average birthweight, were not affected		Zhuo *et al.* (2017)
Camborough plus females × C337 sires (PIC, Winnipeg, MB, Canada) *n* = 150	Late gestation (day 86 to farrowing)	CON supplemented with: 10% processed or unprocessed oat straw or 10% processed or unprocessed wheat straw	Processed straw: ↗ DM digestibility and energy content	Processed versus unprocessed wheat straw: ↗ postprandial IGF-1 and prolactin concentration Oat straw: ↗ Pre-prandial prolactin concentration Wheat straw: ↘ Pre-prandial prolactin concentration	Oat straw: ↗ sow lactation feed intake piglet weaning weight Processed versus unprocessed oat straw: ↗ piglet weaning weight No impact on piglet characteristics at birth, estimated milk production, offspring BW at market or carcass quality	No impact on feeding motivation	Agyekum *et al.* (2019)
Landrace × Yorkshire gilts *n* = 76	Puberty until slaughter	50, 75, and 100% more DF than CON with inclusion of a fiber mixture (6.4, 9.4, and 12.5%, respectively; inulin and cellulose at a ratio of 1:4)			DF: ↗ ovarian follicle reserve in gilts growth traits, and the age, bodyweight, and backfat thickness at puberty not affected		Cao *et al.* (2019)
Large white × landrace gilts *n* = 64	Gestation	ISF:SF of 3.89 (R1), 5.59 (R2), 9.12 (R3), and 12.81 (R4)		Microbial community structures in R1 and R2 differed from R3 and R4; altered SCFA composition/concentration in sow feces and neonatal colon R1 and R2 versus R3 and R4: ↗ Antioxidant enzyme activity (sows, piglets) ↗ Pro-inflammatory factor levels liver mRNA expression: ↗ Nrf2 and HO-1 ↘ NF-κB (for impact on piglets see Table 2)			Li *et al.* (2019*a*)
Large white × landrace gilts *n* = 64	Gestation	ISF:SF of 3.89 (T1), 5.59 (T2), 9.12 (T3), and 12.81 (T4) Inulin and natural cellulose	ISF: ↘ Activity of lactase, sucrase, and maltase	↘ Duodenal weight, jejunal villus height, and villus height/crypt depth in neonates ↗ Crypt depth of the jejunum in weaned piglets (for impact on piglets see Table 2)	T1 and T2 versus T3 and T4: ↗ mean piglet BW at weaning and piglet BW gain milk yield and composition not affected		Li *et al.* (2019*b*)

(*Continued*)

Table 1. (*Continued.*)

Breed, *n*	Feeding period	Fiber source and level	Digestibility	Intestine, metabolism, immune system	Productivity, reproduction	Behavior	Reference
Large white × landrace gilts *n* = 84	Gestation	CON (0% SBP; 0 g L-carnitine, CAR) CAR (0.125 g day^{-1} CAR) SBP (40% SBP) SBP + CAR (40% SBP, 0.125 g day^{-1} CAR)		SBP: ↗ Fecal consistency ↗ Weight during gestation	↗ Live weight and carcass muscle depth of progeny		Rooney *et al.* (2019)
Yorkshire × landrace *n* = 45 (sows and litters)	Gestation, lactation	Gestation: CON SBP: 20% SBP WB: 30% WB Lactation: CON SBP: 10% SBP WB: 15% WB		SBP versus CON: ↗ IgA, IL-10 in colostrum; ↗ IgA in milk WB versus CON: milk: ↗ IL-10 (for impact on piglets see Table 2)	SBP versus CON: ↗ ADFI during lactation, litter and piglet weaning weight, piglet ADG		Shang *et al.* (2019)
Danish genetic sows *n* = 96	Gestation	CON: 15% SBP, 42.6% WB HF: 21% SBP + 15% alfalfa + 10% rapeseed meal + 7% soybean hulls + 7% grape pomace + 5% lignocellulose	HF: ↗ Digestibility of CF		No effect on performance of sows and piglets		Priester *et al.* (2020)
Landrace × Yorkshire *n* = 68	Gestation	3% purified fiber mixture (50% guar gum, 50% cellulose)		↗ Butyrate ↗ *Roseburia*, *Eubacterium hallii* group, *Bacteroides* ↗ Serotonin, IL-10 ↘ IFN-γ	↗ Live-born piglets		Wu *et al.* (2020)
Gilts L337× Camborough; PIC Inc., Hendersonville, TN *n* = 60	Not specified	30% corn bran	↘ Nutrient digestibility ↗ Digesta viscosity	↘ Cecal fermentation			Petry *et al.* (2021)
Landrace × Yorkshire *n* = 30 (sows and litters)	Gestation, lactation	Gestation: 15% WB + 10% SBP Lactation: 7.5% WB + 5% SBP		Enhanced intestinal barrier function ↘ Pro-inflammatory cytokines in serum ↘ *Subdoligranulum* and *Mogibacterium* ↗ *Lactobacillus* in colonic digesta	↗ Litter weight gain in DF		Shang *et al.* (2021)
Prepubescent gilts landrace × Yorkshire *n* = 32	Puberty	CON SO: +240 soy oil g day^{-1} HF: +300 g day^{-1} inulin and cellulose at a ratio of 1:4, HFSO: HF + SO		SO: ↘ SCFA-producing microbes, reversed by fiber treatment HF: ↗ Serotonin and melatonin concentrations in serum		SO: ↗ Atretic follicles, apoptotic markers, Bax and caspase-3 Effects were reversed by fiber diet	Zhuo *et al.* (2021)

German landrace $n = 20$ (sows and gilts)	Gestation, lactation	T1: 15% SBP + 3% lignocellulose T2: 3% SBP + 15% lignocellulose	T1 versus T2: ↗ SCFA at farrowing and one week post-partum ↘ *Terrisporobacter* spp. one month ante-partum ↗ *Muribaculaceae* and microbial Shannon diversity index at farrowing (for impact on piglets see Table 2)	Grześkowiak *et al.* (2022)

Increases in litter weight at weaning and higher feed intake, IgA and interleukin-10 (IL-10) levels in colostrum and IgA in milk were observed when sows were fed with SBP, whereas IL-10 levels in milk were increased in sows fed with WB when compared to the control group. A higher feed intake was interpreted as related to increased insulin sensitivity in sows fed with SBP (Shang *et al*., 2019). The use of HF gestation diets can have an impact on sow performance that would last during lactation, even when using standard lactation diets. Thus, some parameters such as feed intake, body weight loss, or backfat loss during lactation could be ameliorated in sows that receive HF gestation diets (van der Peet-Schwering *et al*., 2003; Quesnel *et al*., 2009; Krogh *et al*., 2015). However, these effects might depend on the composition of the fiber (Renteria-Flores *et al*., 2008; Veum *et al*., 2009; Agyekum *et al*., 2019). Another study observed that diets with 9.8% WB, 19.5% SBP, and 9.8% soybean hull provided to pregnant sows (from day 26 until parturition) could not protect sows from body weight (BW) loss, despite increased average daily feed intake (ADFI) during lactation (Quesnel *et al*., 2009). When prepubescent gilts were fed a diet with a daily intake of 60 g inulin and 240 g cellulose, serotonin and melatonin concentrations in serum and follicular fluid were increased and follicular atresia reduced (Zhuo *et al*., 2021). The effects were explained by a dietary impact on the intestinal microbial serotonin synthesis.

DF affects the intestinal microbiota, gut physiology, and immune reactions in sows

The intestinal microecosystem of a sow can be shaped by DF in different ways. Here, the ratio of SF to ISF can be a decisive variable. Sows fed with either SF or ISF demonstrated different fecal profiles of SCFA, and this observation was also noted in the colon digesta of their offspring (Li *et al*., 2019*a*). Gestating sows fed diets with ISF:SF ratios of 3.89, 5.59, 9.12, and 12.81 produced piglets with the mean BW at weaning and BWG characterized by a linear decrease as the ISF:SF ratio increased. In addition, the crypt depth of the jejunum in weaned piglets linearly increased, whereas the duodenal weight, jejunal villus height, and villus height/crypt depth in newborn piglets and enzymatic activity of lactase, sucrase, and maltase linearly decreased. The observations were explained as the ISF:SF impact on development and enzymatic activity in the small intestine that enhanced piglet BW gain (Li *et al*., 2019*b*). An increase in leukocyte count was observed in sows fed diets with 25% SBP (McGlone and Fullwood, 2001). Differences in gut microbial community were associated with different ISF:SF ratios of 3.89 and 5.59 versus 9.12 and 12.81 in the sows' diets. Additionally, the intake of more SF also led to higher antioxidant enzyme activity, suppression of pro-inflammatory factors in sows and their piglets, a higher hepatic expression of Nrf2 and HO-1 and lower expression of nuclear factor-κB (NF-κB) in piglets (Li *et al*., 2019*a*). Fecal butyrate and propionate concentrations, as well as bacteria belonging to *Roseburia* and *Eubacterium-hallii* group, and *Bacteroides*, were elevated in gestating sows fed with diets with 1.5% guar gum and 1.5% cellulose (Wu *et al*., 2020). Sows fed with diets enriched with 15% WB and 10% SBP during gestation and 7.5% WB and 5% SBP in lactation showed an enhanced intestinal barrier and a reduction of *Subdoligranulum* and *Mogibacterium*, whereas *Lactobacillus* counts increased in the colon (Shang *et al*., 2021). Diets rich in oil reduced the SCFA-producing microbes, a phenomenon which was reversed when fiber (300 g inulin and cellulose per day) was added to the feed (Zhuo *et al.*, 2021). A very recent study demonstrated that sows fed diets enriched with highly fermentable DF, such as SBP (15%) compared to less fermentable lignocellulose (15%), had increased fecal SCFA, *Muribaculaceae* and microbial Shannon diversity index but decreased *Terrisporobacter* spp. during the periparturient period (Grześkowiak *et al.*, 2022).

DF and welfare of sows

Maintaining sows in groups has a positive impact on their social behavior (Verdon *et al.*, 2015). However, some individuals also tend to show aggressive attitudes with consequences on performance, welfare, and health. The inclusion of DF in diets has been reported to affect behavior in pigs. A tendency to less aggressive interactions and fewer fights was noted in sows fed diets enriched in different DF sources such as a mixture of grape pomace, lignocellulose, and soybean hulls (Priester *et al.*, 2020). Soybean hulls (19%) or resistant starch (11%) had a similar effect. Higher satiety by more constant blood glucose and non-esterified fatty acids with higher gut fill (satiety) could explain the observed effects (Sapkota *et al.*, 2016). Sham-chewing is considered a behavior related to stress in sows (Tatemoto *et al.*, 2019). Interestingly, sows kept outdoor had increased sham-chewing when fed a diet with 25% SBP, which was not observed in sows kept indoors (McGlone and Fullwood, 2001). A reduction of stereotypical behavior was observed when diets contained high amounts of DF levels from alfalfa meal (>27%) and oat hulls (27–45%) (Bergeron *et al.*, 2000). On the contrary, an HF diet (9.8% sunflower meal, 9.8% WB, 19.5% SBP) fed to pregnant gilts had limited effects on farrowing behavior and reproductive performance; however, piglets reared by sows which received the HF gestation diets showed a 13.5% higher growth rate during the first week of life (Guillemet *et al.*, 2007). When gestation diets included 35% of soybean hulls, piglets showed fewer skin lesions compared to piglets from sows fed with a low-fiber diet, indicating less aggressive interactions in the litters (Bernardino *et al.*, 2016).

In summary, both, gestation and lactation periods seem to be promising for dietary interventions in sows to also influence the fitness of their offspring. By altering the sow's physiology, colostrum composition, and intestinal microbial ecology and function through nutritional factors, it may be possible to influence the piglet's microbial development and health. However, still too little is known about the impact of diet on the microbial association between sow and offspring and the establishment of the gut microbiota in neonatal piglets. Moreover, a growing body of evidence suggests a beneficial impact of DF on sows' behavior related to stress.

DF in suckling piglets

The immune system of piglets needs to acquire passive immunity through colostrum and milk (Stokes, 2017). Thus, feeding gestating and/or lactating sows with certain DF offers an attractive way to beneficially modulate colostrum composition, and the sow's fecal microbiota and metabolites, which in turn can have a positive impact on the health of piglets.

An overview of studies on the impact of DF offered as a creep feed or supplemented formula on suckling piglets is provided in Table 2. To increase productivity in sows, a decisive breeding goal in piglet production is to enlarge litter sizes. This has an impact on the health and welfare of sows and piglets (Rutherford *et al.*, 2013). The extremely high litter size in modern sow breeds implies difficulties in raising all the piglets due to the limitation of functional teats and low individual birth weights, which may result in undernourished or deceased piglets (Kobek-Kjeldager *et al.*, 2019). Additional milk replacers in suckling piglets offer an opportunity for higher survival of piglets in large litters and an early introduction of solid feed to the piglets' diets (Van Hees *et al.*, 2019). Data on the physiological impact of DF on suckling piglets are sparse. It has been demonstrated that piglets consuming human infant formula supplemented with 1% pectin had a reduced ileal digestibility of DM and CP, lower feed intake, and BWG, as well as a decrease in energy digestibility (Fleming *et al.*, 2020). Still, suckling piglets can benefit from DF intake due to its potential to guide the developing gut microbiota in a process known as 'early microbial programming' and DF may therefore have an impact on intestinal function and health in growing animals (Li *et al.*, 2019*a*, 2019*b*). Hence, in very young piglets, DF supply may be beneficial for the early immune programming and thus, together with microbial programming, it is of particular importance for building up a better resilience against pathogens. It may contribute to the prevention of common health problems such as gut dysbiosis, leading to neonatal mortality and especially post-weaning diarrhea (PWD) (Lindberg, 2014).

It has been demonstrated that fiber-supplemented liquid feed and milk replacers for suckling piglets could improve intestinal microecology and gut epithelial health. For instance, increasing concentrations of polydextrose (0, 0.17, 0.43, 0.85, 1.7%) in infant formula, increased numbers of lactobacilli, propionic, and lactic acid linearly whereas pH and pro-inflammatory cytokine patterns decreased in the ileum digesta (Herfel *et al.*, 2011). Moreover, certain DFs have been demonstrated to reduce enteric infections in suckling piglets. Administration of 0.75% soy polysaccharides or fructo-oligosaccharides in infant formula prevented *Salmonella* Typhimurium-related diarrhea and improved gut function, probably by means of increased glutamine and total ion transport as assessed in the small intestine of suckling piglets (Correa-Matos *et al.*, 2003). DF has also been demonstrated to influence the behavior of suckling piglets. Offering a supplementary diet enriched in 5% cellulose to suckling piglets from 5 to 22 days of age, resulting in higher piglet activity, increased suckling time and interactions with pen mates, as compared to control piglets (Clouard *et al.*, 2018).

Administration of DF in a creep feed to suckling piglets may be challenging due to exposure to a high load of new antigens in the developing intestine; however, along with ingestion of sow milk, it may offer an opportunity to influence the gut microecology and health directly at an early stage of life. A recent study demonstrated an increase in SCFA in the hindgut and a reduction of the *Escherichia–Shigella* group in the colon of 3-week-old suckling piglets that were offered a creep feed supplemented with 5% cellulose from the second day onwards after birth (Van Hees *et al.*, 2019). Interestingly, piglets were reported to consume the creep diets well. Therefore, fiber-enriched creep feeds, if consumed at an early age, might be an attractive way to directly support the gut health of suckling piglets.

Nursing piglets have constant contact with sow feces after birth, which may facilitate the microbiota colonization process (Mach *et al.*, 2015). Hence, the sow diet may indirectly shape the microecosystem in their offspring's gastrointestinal tract and thereby influence piglet performance, immune status, and other attributes (Table 1). For instance, feeding the sows with diets supplemented with Jerusalem artichoke, with an estimated daily intake of 1.3 kg DM, had increased IgG serum levels in

Table 2. Effects of DF sources in feed on suckling piglets

		Main outcome			
Animals, *n*	Diet	Intestine	Productivity	Metabolism	Reference
Piglets *n* = 16 2-day-old piglets for 14 days	Human infant formula alone (CON) or supplemented with 0.75% of methylcellulose (MCEL, insol), soy polysaccharides (SPS, sol) or fructo-oligosaccharides (FOS, sol) Infection with *S.* Typhimurium	SPS and FOS groups prevented *S.* Typhimurium-diarrhea ↘ Ileal mucosal barrier function (resistance) in CON and SPS ↗ Ileal glutamine transport in SPS and FOS	↘ Post-infection physical activity in CON	↘ Ileal lactase activity in CON	Correa-Matos *et al.* (2003)
Piglets *n* = 78 1-day-old piglets for 18 days	Human infant formula supplemented with 0, 0.17, 0.43, 0.85, 1.7% polydextrose (PDX)	↗ Ileal lactobacilli with increasing PDX ↗ Propionic acid in digesta with increasing PDX ↗ Lactic acid with increasing PDX ↘ Digesta pH with increasing PDX Negative quadratic correlation of TNF-α, IL-1β, and IL-8 expression in response to PDX supplementation			Herfel *et al.* (2011)
Piglets *n* = 10 litters 5–22-day-old piglets	Milk: replacer and creep feed (LF versus HF which included 5% cellulose in substitution of 5% corn starch)		↗ Activity, suckling time, interaction with pen mates in HF diet		Clouard *et al.* (2018)
Large white × landrace gilts *n* = 64 Piglets *n* = 24 Newborn	Gestation diet: ISF:SF of 3.9 (R1), 5.6 (R2), 9.1 (R3), and 12.8 (R4) Lactation diet: corn–soybean meal based			↘ Some antioxidant markers in plasma and liver in R3 and R4	Li *et al.* (2019*a*)
Large white × landrace gilts *n* = 64 Piglets *n* = 48 Newborn and weaned	Sow feed for entire gestation: ISF:SF of 3.9 (R1), 5.6 (R2), 9.1 (R3), and 12.8 (R4) Sow feed for lactation: corn–soybean meal based	As ISF:SF increased: ↘ duodenal weight, jejunal villus height, and V:C in neonates; ↗ crypt depth of the jejunum in weaned piglets; ↘ activity of lactase, sucrase and maltase	↗ Mean piglet BW at weaning and piglet BW gain in R1 and R2 versus R3 and R4		Li *et al.* (2019*b*)
Yorkshire × landrace *n* = 45 (sows and litters)	Gestation: CON SBP: 20% SBP WB: 30% WB Lactation: CON SBP: 10% SBP WB: 15% WB	SBP: ↗ GH and IGF-1 in serum; ↘ IL-6 and ↗ IL-10, ↗ secretory immunoglobulin A (SIgA) in ileum; ↗ *Christensenellaceae* and butyrate in colon WB: ↗ GH in serum; ↗ *Lactobacillaceae* WB, SBP: ↘ serum diamine oxidase activity, endotoxin, IL-6, TNF-α; ↘ ileal TNF-α SBP versus CON: ↗ IL-10 in serum; ↗ occludin in ileum WB versus CON: ↗ GH in serum; ↗ IL-10, SIgA, ZO-1 in ileum	SBP: ↗ litter and piglet weaning weight and ADG		Shang *et al.* (2019)
Hypor libra sows *n* = 34 Piglets 2-day-old onwards	CON: high-density milk replacer, followed by a dry and highly digestible creep meal (milk replacer; creep feed) lc-AXOS: 2% fermentable long-chain arabinoxylan CELL: 5%, non-fermentable purified cellulose Lc-AXOS + CELL	↗ Large intestinal fill in Lc-AXOS ↗ Relatively large intestinal weight (lc-AXOS and CELL) ↘ Ileal pH ↗ SCFA in mid-colon in CELL ↗ Cecal propionate in lc-AXOS ↘ *Escherichia-Shigella* in CELL		Piglets consumed the fiber-containing milk supplements and creep diets well	Van Hees *et al.* (2019)

(*Continued*)

Table 2. (*Continued.*)

Animals, *n*	Diet	Main outcome			Reference
		Intestine	Productivity	Metabolism	
Yorkshire crossbred 2-day-old pigs for 21 days *n* = 36	Human infant formula supplemented with 0, 0.2, or 1% pectin		↘ BW and feed intake in 1% pectin	↘ Energy digestibility in 1% pectin ↘ Ileal digestibility of DM and CP in 1% pectin	Fleming *et al.* (2020)
German landrace *n* = 20 (sows, gilts, and their litters) Piglets 2-day-old onwards until weaning	Gestation and lactation: T1 15% SBP + 3% lignocellulose T2 3% SBP + 15% lignocellulose	T1 versus T2: ↘ *C. difficile* and *Escherichia–Shigella* in feces			Grześkowiak *et al.* (2022)

their offspring (Werner *et al.*, 2014). The addition of 3% inulin to the sows' diets during gestation and lactation resulted in increased levels of enterococci, eubacteria, and the *Clostridium leptum* group in the gut contents of suckling piglets (Paßlack *et al.*, 2015). Maternal supplementation with a combination of SBP and WB during late gestation (15% WB and 10% SBP) and lactation (7.5% WB and 5% SBP) improved growth, immune responses, intestinal morphology, barrier function, and microbiota in piglets, as compared to control diet (corn–soybean meal). Moreover, immunoglobulins and cytokines in colostrum and milk were also increased in sows fed with SBP–WB, which may have accounted for the observed beneficial effects in piglets (Shang *et al.*, 2021). In another study on maternal dietary effects on the offspring, sows fed diets enriched with SBP (15%), as compared to lignocellulose (15%), had reduced *Clostridioides difficile* concentrations and *Escherichia–Shigella* abundance in feces of their suckling piglets (Grześkowiak *et al.*, 2022).

In summary, feed supplementation with DF is a feeding strategy with the potential to control the metabolic and immune patterns and microbial colonization in sows and offspring. By feeding DF to sows, piglets could benefit from the sow–piglet association phenomenon and early microbial and immune programming. Thereby DF could offer a promising way to protect against gut pathogen dissemination in suckling piglets.

DF in weaner pigs

In several studies on specific physiological effects of DF sources in diets for weaner pigs, digestive function, intestinal microbiota, immune reactions, and occurrence of PWD were investigated (Table 3).

DF and gastrointestinal function in weaner pigs

DF influences gastrointestinal function and performance by different mechanisms. DF is often considered an anti-nutritional factor by reducing CP, amino acid (AA), and fat digestibility due to reduced enzymatic hydrolyzation, absorption, and/or increased endogenous secretion (Blank *et al.*, 2012). NDF increments are seen to result in a reduction of ileal apparent CP digestibility and reduction of the digestibility coefficient of energy in pigs (Dégen *et al.*, 2007). However, dietary inclusion of 5–15% DM of partly HCl-hydrolyzed straw meal did not lead to a reduction of BWG or feed intake (Münchow *et al.*, 1988). The reduction of digestibility can be more severe with the addition of SF as compared to ISF fiber types. In general, SF can increase the viscosity of the digesta and thus, might slow down gut transit time in the small intestine (Bach Knudsen *et al.*, 1991) due to suppressed intestinal contractions (Cherbut *et al.*, 1990), which in turn leads to reduced efficacy of digestive enzymes. In contrast, ISF may stimulate pancreatic protease enzyme activity (Langlois *et al.*, 1987). Thus, DF may reduce nutrient digestibility due to nutrient dilution, reduced nutrient absorption, reduced enzymatic breakdown, and/or increased endogenous excretion in pigs, depending on fiber type (Lenis *et al.*, 1996; Agyekum and Nyachoti, 2017). Chicory roots and ribwort at increasing concentrations of 4–16% had only a minor effect on the total apparent nutrient digestibility in piglets. Although the concentrations of coliform bacteria changed with age, there was no evidence that the DF supplements led to clear functional effects on the gastrointestinal tract (Ivarsson *et al.*, 2011). Oat husks are a typical non-fermentable and lignin-rich fiber source. At a 2% inclusion rate, the

Table 3. Effects of DF sources in feed on weaner pigs

				Main outcome				
Breed, *n*	Weaning, days	Duration of experiment, from–to, days	Fiber source	Digestibility	Intestine	Productivity	Gut physiology	Reference
Landrace *n* = 84		42–98	5, 10, 15% partly hydrolyzed straw meal in concentrate			↗ Weight gain ↗ Feed intake		Münchow *et al.* (1988)
Seghers hybrid × Piétrain *n* = 18	28	29–49	CC: 5% corn cobs CR: 2% chicory roots 12% SBP 7.5% WB		CC: ↗ total bacteria, lactobacilli, bifidobacteria in the stomach and proximal duodenum; ↘ streptococci in distal jejunum; ↗ villus length in the proximal jejunum; CR: ↗ *E. coli* in the distal jejunum and mucosa SBP: ↘ lactobacilli on the mucosa WB: ↗ *E. coli* in jejunal digesta and mucosa, ↗ lactobacilli in stomach and jejunum, ↗ bifidobacteria in the proximal part of the jejunum		CC + CR: ↘ intra-epithelial lymphocytes (IELs) of proximal and distal jejunum while SBP and WB ↗ IELs CC: ↘ apoptotic index of the mucosa of the distal jejunum WB: ↘ mitotic index in crypts	Van Nevel *et al.* (2006)
Large white × landrace *n* = 96	21	22–35	2% oat hulls	↘ Digestibility of DM and gross energy	Oat hulls: ↘ PWD (partially; rice-based diets only)	No negative impact on performance	Oat hulls: ↘ Biogenic amine concentrations	Kim *et al.* (2008)
Swedish landrace × Yorkshire *n* = 25	35	36–70	4, 8, and 16% chicory, or ribwort	Total tract apparent digestibility of DM, OM, and CP: minor effects ↗ Apparent digestibility of NSP and NDF	↘ Coliform counts with age; not affected by DF addition			Ivarsson *et al.* (2011)
Large white × landrace × Piétrain *n* = 64	21	22–33	4% WB		↗ Fecal SCFA ↘ *E. coli*			Molist *et al.* (2011)
Large white × German landrace *n* = 12		14	Exp 1: 15 or 30% WB fiber Exp 2: 15% rapeseed fiber or 15% cassava leaves fiber or 15% cassava root peels	N retentions affected by fiber level and source Fiber-associated Thr losses amounted to 3.3, 3.2, 1.2, and 1.1 g kg^{-1} fiber from WB, rapeseed, cassava leaf, and cassava root peel, respectively				Blank *et al.* (2012)

(*Continued*)

Table 3. (*Continued.*)

Breed, *n*	Weaning, days	Duration of experiment, from–to, days	Fiber source	Main outcome				Reference
				Digestibility	Intestine	Productivity	Gut physiology	
Yorkshire × landrace × Duroc *n* = 36	17	18–35	4% WB, coarse or fine		Challenge *E. coli*, day 9 WB coarse: ↗ fecal score, ↗ SCFA, ↘ Bacteroidetes, ↗ Firmicutes			Molist *et al.* (2012)
Topigs *n* = 8 weaners	42	56	3% inulin				Inulin: ↗ glucose absorption in small intestine ↗ intestinal permeability in the jejunal mucosa	Awad *et al.* (2013)
Duroc × landrace × Yorkshire *n* = 125	28	58	10% of supplemented fiber to CON (MF: maize SF: soybean fiber WB) PF: pea fiber		WB: ↗ villus height:crypt depth in the ileum WB, PF: ↗ colonic goblet cells; ↗ lactobacilli in the ileum; ↗ bifidobacteria in the colon WB: ↘ *E. coli* counts in the ileum and colon WB: ↗ ZO-1 and TLR2 mRNA in the ileum and colon MF and SF: ↗ IL-1α and TNF-α mRNA levels WB and PF: ↗ diamine oxidase activities, TGF-α, trefoil factor family and MHC-II mRNA		WB, PF: ↘ diarrhea	Chen *et al.* (2013)
Euroc × Piétrain *n* = 32	25	45–48	8% WB + 5% SBP				↘ Tissue conductance Neither an HF diet nor acute addition of SCFA enhanced urea transport across the pig cecum HP-LF diet had stimulatory effects	Stumpff *et al.* (2013)
German large white × Piétrain *n* = 48	28	28–70	CON 15% native WB 15% fermented WB 15% extruded WB		↗ Goblet cells in the ileum in native and extruded versus fermented bran *E. coli* counts in colonic chyme ↘ in the control group compared to the groups fed with WB Total SCFA in the colon ↘ by modified WB compared to native WB Lipid radicals ↘ native WB compared to the Control group	No impact on performance parameters		Kraler *et al.* (2015)

Duroc × (Landrace × Yorkshire) *n* = 180	28	29–56	10% WB SH: 5% soybean hulls OH: 7% naked oat hulls PKE: 6% palm kernel expeller BM: 5% bamboo fiber	↘ Apparent digestibility of gross energy and DM Digestibility of NSP components was different among treatments	WB: ↗ fecal bifidobacteria	CON and WB: ↗ daily gain compared to PKE and BM Fiber diets: ↗ the feed-to-gain ratio	Diarrhea incidence was not affected	Yu *et al.* (2016)
Duroc × (large white × landrace) *n* = 108	28	31–51/52–64	1% thermally treated lignocellulose (Arbocel)			↗ BW ↗ Feed intake	↗ Growth hormone axis ↘ Acute-phase proteins, IL-6 expression ↘ Diarrhea incidence	Superchi *et al.* (2017)
Large white × Piétrain *n* = 96	28	29–82	Starter and grower feed: 2.5% soybean hulls or 1.5% lignocellulose (LC)	SBH: ↗ ATTD	LC: ↘ cadaverine No overall response of SDF nor of IDF for the inclusion level	No effect on weight gain or feed conversion	No impact on immune gene expression	Slama *et al.* (2020)
Songliao black pigs *n* = 12	28	29–56	5% grape pomace (GP)		↗ *L. delbrueckii, Olsenella umbonata, S. bovis* in the cecum ↗ Villus height and villus height/crypt depth ratio (VCR) in jejunum	No difference in growth performance	↘ IL-1β, IL-8, IL-6 and TNF-α ↗ IgG in the sera of weaned piglets in the GP group	Wang *et al.* (2020)

performance of weaner pigs was not influenced, although the apparent total tract digestibility of energy and DM was reduced (Kim *et al.*, 2008).

DF and intestinal microbiota in weaner pigs

Moderate and varying effects of DF were demonstrated when either 5% corn cobs, 2% chicory roots, 12% SBP, or 7.5% WB was added to a diet for weaner pigs. Specifically, corn cobs favored lactobacilli and bifidobacteria in the stomach and proximal duodenum digesta, whereas WB increased *Escherichia coli* in the jejunum digesta and mucosa and increased levels of lactobacilli and bifidobacteria in the gastric and jejunal digesta. All in all, the changes in intestinal microbiota were moderate (van Nevel *et al.*, 2006). WB was investigated in various studies in weaner piglets. At an inclusion level of 4%, it had a stimulating effect on the formation of SCFA, at the same time reducing *E. coli* counts in the digestive tract (Molist *et al.*, 2011). The use of native, fermented, or extruded WB at 15% did not affect performance in piglets. Nevertheless, there were effects on the number of goblet cells in the ileum, which was higher when native and extruded WB were used compared to fermented WB. Intestinal counts of *E. coli* were lower in control piglets than in the groups with added WB. The modified WB variants resulted in lower concentrations of SCFA in the colon compared to unprocessed WB. Furthermore, a reduction of lipid radicals was also demonstrated when using the native WB (Kraler *et al.*, 2015). At a level of 10%, WB also increased fecal bifidobacteria (Yu *et al.*, 2016). A 4% coarsely ground WB administered to piglets increased SCFA, reduced Bacteroidetes, and increased Firmicutes (Molist *et al.*, 2012). When using 5% grape pomace, increasing concentrations of *Lactobacillus delbrueckii*, *Olsenella umbonata*, and *Selenomonas bovis* were found in the cecum of young piglets (Wang *et al.*, 2020).

DF and immune system of weaner pigs

Reduced levels of intraepithelial lymphocytes in the jejunum were detected in weaner pigs fed 2% chicory roots or 5% corn cobs, whereas an increase was observed when fed with 12% SBP or 7.5% WB; however, the functional significance was not reported (van Nevel *et al.*, 2006). The inclusion of 10% WB and pea fiber resulted in increased diamine oxidase activity and expression of transforming growth factor-alpha (TGF-α), trefoil factors and major histocompatibility complex (MHC)-II in the ileum tissues (Chen *et al.*, 2013).

The use of 1.5% lignocellulose reduced the cadaverine concentrations in the digesta, but no effects on the expression of immune-relevant genes were found in ileum, spleen, liver, or mesenteric lymph node tissues (Slama *et al.*, 2020). In another study using 5% grape pomace, the expression of some cytokines in the intestinal tissue was down-regulated (IL-1β, IL-8, IL-6, and tumor necrosis factor-alpha (TNF-α)). Additionally, the levels of IgG were increased in the serum. In that study, however, effects on the occurrence of diarrhea were not observed (Wang *et al.*, 2020).

DF and prevention of diarrhea in weaner pigs

PWD is a common problem in piglets. Oat hulls (2%) were effective when animal protein-based diets were supplemented with rice, whereas supplementation of animal protein-based diets with wheat did not protect against diarrhea. This indicates a fiber–matrix interaction and it was explained by differences in carbohydrate and proteinaceous materials entering the colon (Kim *et al.*, 2008). Importantly, the particle size of DF might be relevant for the preventive effect on PWD. When 4% coarsely ground WB was administered to piglets, significantly firmer fecal consistency was observed after a challenge with *E. coli* K88^{+}, whereas finely ground WB did not have a similar protective effect. Besides a higher binding of *E. coli* to the coarser fiber, a higher water-binding capacity of the intestinal digesta was discussed as a possible cause (Molist *et al.*, 2012).

The abovementioned studies demonstrate the importance of evaluating chemical and physical characteristics when examining the effects of DF, a fact that has been neglected in most studies. Positive effects on the incidence of diarrhea in weaner piglets were also shown when using WB in a dosage of 10%, which could be associated with multiple changes in the intestinal morphology, microbiota composition, increased zonula occludens-1, and occludin mRNA and higher diamine oxidase activities, TGF-α, trefoil factor family, and MHC-II levels in the ileum and colon tissues (Chen *et al.*, 2013). Contrarily, no protective effects on the occurrence of diarrhea after weaning could be observed when 5–10% WB, soybean hulls, or oat husks were included in the diets of weaner pigs (Yu *et al.*, 2016).

Lignocellulose is a mixture of cellulose, hemicelluloses, and lignin. When included in finely ground form at 1% in the diet, a measurable effect was noted on the occurrence of PWD. At the same time, the lignocellulose-treated group showed changes in immune parameters and acute phase proteins (Superchi *et al.*, 2017). The inclusion of 2.5% soybean hulls or 1.5% lignocellulose in a complete diet did not evoke negative effects on the performance and feed expenditure and fecal DM (Slama *et al.*, 2020).

Inulin, as a highly fermentable fiber, induced a positive effect on intestinal physiology in piglets after weaning. Specifically, the inclusion of 3% of dietary inulin in feed for gestating and lactating sows and their offspring thereafter increased glucose transport and altered intestinal barrier function in post-weaned piglets (Awad *et al.*, 2013). Similarly, a diet with 8% WB lowered epithelial resistance in the cecum of piglets (Stumpff *et al.*, 2013).

In summary, the use of fiber-rich components in the diet of weaner piglets can affect nutrient digestibility, performance, and health. The effects described depend on fiber sources, particularly with regard to their fermentability, on the matrix into which the fiber-rich feed is mixed, and on physical properties. The latter is demonstrated by the importance of particle length (Molist *et al.*, 2012). Moderately fermentable fiber sources with larger particle sizes appear to have beneficial effects on the intestinal health of piglets after weaning.

DF in fattening pigs

Adaptive potential to fiber-enriched diets in fattening pigs

The use of fiber-rich components is increasingly discussed, especially with regard to the application of more fibrous by-products in the nutrition of pigs (Table 4). Straw meal was considered early as an interesting alternative in the feeding of pigs. First investigations were performed with 5–10% hydrolyzed straw meal in fattening pigs, indicating positive dietetic effects (Bergner and Betzin, 1979) but higher intestinal nitrogen (N) losses (Simon *et al.*, 1987). When using a diet with 10% of wheat straw, no negative effects on feed intake and performance of fattening pigs could be observed. However, in the jejunum and colon, there was clear evidence of increased cell proliferation (Jin *et al.*, 1994). Pigs can obviously adapt to HF diets by an increase of the cellulolytic capacity of the intestinal microbiota. Very high inclusion rates of 50% alfalfa meal in diets for pigs induced an initial suppression of the intestinal microbial activity followed by an adaptive increase (Varel *et al.*, 1982). The numbers of cellulose-degrading bacteria in the intestine were higher and increased microbial cellulase activity was observed within 3 days (Varel *et al.*, 1984, 1987). Increased weight of the visceral organs and cellulolytic intestinal bacteria was also observed in barrows weighing 55 kg (Anugwa *et al.*, 1989). Extremely high quantities (80%) of alfalfa meal resulted in a reduced BWG and higher weights of the gastrointestinal tract, but also of the liver and kidney (Pond *et al.*, 1988). Digestibility of feed was reduced by the use of correspondingly high amounts of alfalfa despite a microbial adaptation in the sense of an increase in cellulolytic bacteria was observed (Varel *et al.*, 1988). Increasing dietary NSP content up to 19.5% led to a decrease in nutrient digestibility although it was dependent on the solubility of the NSP (Högberg and Lindberg, 2004). Digestibility of protein was reduced in growing pigs when diets contained 21% wheat aleurone fiber; 37% rye aleurone fiber reduced also the apparent digestibility of fat and starch. Rye products were more likely to be fermented in the cecum and wheat products in both the cecum and the colon (Le Gall *et al.*, 2009).

DF sources and intestinal effects on fattening pigs

The use of peas and lupins, which were either peeled or unpeeled, did not affect the true digestibility of N and AAs in pigs, indicating that the inclusion of 3–7% of crude fiber (CF) does not cause a depression in the true digestibility of N and AAs (Meier *et al.*, 1981). A reduction in the digestibility of various nutrients, which was due to a reduced intestinal transit time and an increase in fecal N excretion, was observed when 50% of ground oats was included at the expense of corn in a diet for pigs at 35 kg BW (Ravindran *et al.*, 1984). Besides digestibility, the effects of different fiber sources on the intestinal microbiota and microbial fermentation, especially the formation of SCFA, were characterized. Grass meal and SBP with levels of 13.5–17% CF for fattening pigs gave clear indications that microbial fermentation was significantly increased in the first third of the porcine colon (Schnabel *et al.*, 1990). Oat bran (15%) increased butyrate formation in the intestinal tract of pigs, especially in combination with rolled oats (Bach Knudsen *et al.*, 1991). The use of soybean hulls and wheat middling in dosages of 30% each led to a significant reduction in the net energy of the feed and performance of growing pigs, which was higher in pigs at 25.4 kg BW compared to finishers at 84.8 kg BW (Stewart *et al.*, 2013).

So far, little research has been devoted to the dependency of endogenous N losses on fiber intake and the association of true CP and AA ileal digestibility. The published studies on pigs of different production stages focused on the availability of threonine with 15% soybean hulls (Mathai *et al.*, 2016), 0, 4, 8, or 12% pectin, or 8% cellulose (Zhu *et al.*, 2005). As an outcome, pigs had a higher requirement for dietary threonine to maintain growth when the DF was increased. Among the essential AAs, the metabolism and the utilization of threonine are likely most severely influenced by DF effects on intestinal endogenous secretion and microbial activity (de Lange *et al.*, 1989; Lien *et al.*, 1997). The utilization of other AAs that are present in endogenous secretions, such as cysteine and branched-chained AAs, may be influenced as well (Zhu *et al.*, 2005). The use of alfalfa flour, SBP, or WB in doses of 44, 60, and 41%, respectively, led to a depressive effect

Table 4. Effects of DF sources in feed on fattening pigs

				Main outcome				
Breed, *n*	Age, days/ BW, kg	Duration of experiment (days), Challenge	Fiber source	Digestibility	Intestine	Productivity	Gut physiology	Reference
Landrace *n* = 4	–/64.3	42–98	39% barley + partially HCl-hydrolyzed straw meal (with ~20% utilizable carbohydrates) per animal and day		Positive effect on the digestive tract			Bergner and Betzin (1979)
n = ?			Peas and lupines, both pealed and unpeeled	No decrease in the true digestibility of nitrogen and AA when native crude fibers: 3–7%				Meier *et al.* (1981)
Duroc × Yorkshire females *n* = 12	–/60		50% alfalfa meal		Microbiota was initially suppressed, but adaptation seemed possible, apparently more so in lean than in obese pigs			Varel *et al.* (1982)
Crossbred barrows *n* = 16	–/26–32		35% alfalfa meal		↗ Cellulolytic bacteria ↘ Fecal organic acids and ammonia	HF diet: ↘ Weight gain (by 17.3%) ↗ Feed to gain ratio ↘ Carcass weight at slaughter		Varel *et al.* (1984)
Crossbred gilts *n* = 36	–/35.2		50% ground oats	↘ Digestibility DM, energy, NDF, ADF, ADL	↘ Gut transit time ↗ Fecal fiber and N excretion			Ravindran *et al.* (1984)
Chester white × landrace × large white × Yorkshire *n* = 10	8-month-old gilts	86	40% alfalfa meal		↗ fibrolytic microorganisms and their activity in the large intestine			Varel *et al.* (1987)
n = 4	–/40		Diet based on wheat and fish meal Partially hydrolyzed straw meal	Fiber: ↗ Fecal endogenous N excretion from 1.3 to 2.0 g per animal and per day				Simon *et al.* (1987)

(*Continued*)

Table 4. (*Continued.*)

				Main outcome				
Breed, *n*	Age, days/ BW, kg	Duration of experiment (days), Challenge	Fiber source	Digestibility	Intestine	Productivity	Gut physiology	Reference
Genetically lean, obese, or contemporary barrows *n* = 21	180 days/ slaughter weight	71	80% alfalfa meal at 1.5% of initial BW			Reduced to negative weight gain in pigs fed alfalfa meal	Liver, kidney, and empty segments of the gastrointestinal tract as a percentage of body weight were increased by HF	Pond *et al.* (1988)
Genetically lean, obese, or contemporary castrated male pigs *n* = 21	180 days/ slaughter weight	71	80% alfalfa meal at 1.5% of initial BW	↘ Digestibility of both diets in obese pigs *In vitro* digestibility: ↗ day 0 to 14, but not thereafter	↗ Cellulolytic bacteria when pigs were fed the HF diet			Varel *et al.* (1988)
Finishing barrows *n* = 48	–/55		HF or protein		HF: ↗ weight of the total gastrointestinal tract after 34 days and ↗ relative stomach weight up to day 48		↗ Cellulolytic bacteria in the colon	Anugwa *et al.* (1989)
Fattening pigs *n* = 12			SBP, green meal		↗ Fermentation in the first third of colon			Schnabel *et al.* (1990)
Ileal-cannulated pigs, with 16 pigs in each experiment *n* = 32			Exp. 1: 17.4% wheat aleurone, 7.2% pericarp/testa or 8.2% WB Exp. 2: 15.4% oat bran, 89.2% rolled oats or 79.4% rolled oats + 15.1% oat bran		DF addition and oats in particular increased the butyric acid molar ratio		In all the diets but the rolled oats + oat bran diets: ↘ Microbial activity as the digesta moved through the colon	Bach Knudsen *et al.* (1991)
Cross bred, *n* = 8	–/14.3	14	Diet without DF or with 10% wheat straw		No effects on visceral weights nor visceral weights per unit of eviscerated BW	No difference in feed consumption, daily gain, gain: feed, and final BW	Fiber diet: ↗ DNA synthesis in jejunum and colon, cell death, width of villi, crypt depth	Jin *et al.* (1994)

Landrace/ Yorkshire/Duroc, *n* = 50	Infection with 600 infective *A. suum* eggs and 6000 infective larvae of *O. dentatum* per pig	Diet A: whole grain ground barley + protein concentrate (3:1) Diet B: commercial full-constituent pelleted feed mixture Diet C: low DF based on barley flour + protein concentrate (3:1) Diet D: 80% barley flour + 7% inulin + 12.9% sugar beet fiber + protein concentrate (3:1) Diet E: 64% barley flour + 36% WB + protein concentrate (3:1)		↗ *O. dentatum* worm burdens diets with high levels of NSP and lignin (A and E)	Petkevicius *et al.* (1997)
Danish landrace/ Yorkshire/Duroc *n* = 20	Infection with *O. dentatum* and *Oesophagostomum quadrispinulatum*	CON: 70% barley flour, 30% protein concentrate HF: 55% barley flour, 21% oat-husk meal, 24.9% protein concentrate		HF: ↗ Efficacy of piperazine against *O. quadrispinulatum*	Praslicka *et al.* (1997)
Danish landrace/ Yorkshire *n* = 28	6000 infective *O. dentatum* larvae	Barley flour plus protein mixture Barley flour, 7–21% oat husk meal plus protein mixture, 3 levels of NDF		Diets with highest content of ISF: ↗ *O. dentatum*	Petkevicius *et al.* (1999)
German landrace × Belgian landrace × Piétrain *n* = 160 + 180 + 180		Resistant starch (maize), SBP, rye bran (RB), citrus pulp 13–20% microbially fermentable fiber 35% maize; 30% RB; 25% SBP, 20.2% citrus pulp or 14.9% RB + 6.3% SBP		Fermentable fiber: ↘ Serum cholesterol	Kreuzer *et al.* (2002)

(*Continued*)

Table 4. (*Continued.*)

				Main outcome				
Breed, *n*	Age, days/ BW, kg	Duration of experiment (days), Challenge	Fiber source	Digestibility	Intestine	Productivity	Gut physiology	Reference
Swedish Yorkshire castrates *n* = 5	14–15 weeks/ 38.0–43.6	84	Li: 14.4% WB L: 10.8% oat bran (OB), 8.3% rye bran (RB), 4.6% WB Hi: 28.7% WB H: 21.5% OB, 16.5% RB, 9.2% WB	High NSP: linear ↘ in ileal and total tract digestibility of OM, CP and energy NSP solubility: no effect on ileal digestibility of nutrients High soluble NSP: ↗ total tract digestibility of OM, fat, energy and all DF components			Total organic acid content and pH in ileal digesta were linearly related L and Li versus H and Hi: acetic acid in ileal digesta	Högberg and Lindberg (2004)
Swedish Yorkshire castrates *n* = 5	14–15 weeks/ 38.0–43.6	84	Oat bran Rye bran WB See Högberg and Lindberg (2004)				Total and coliform microbiota were influenced by the dietary NSP content	Högberg *et al.* (2004)
Yorkshire *n* = 16	–/14.3	Two subsequent periods of 14 days	0, 4, 8, or 12% pectin 8% cellulose	Increasing levels of pectin: linear ↘ of daily apparent and standardized ileal digestibility (AID and SID) of Lys and Thr; linear ↗ of daily true ileal digestibility (TID) of Thr			Linear ↘ of body protein deposition and Lys and Thr retention with increasing levels of pectin	Zhu *et al.* (2005)
Danish landrace/ Yorkshire/Duroc *n* = 32		2000 infective *T. suis* eggs	Diet 1: 30% oat hull meal Diet 2: 15% sugar beet fiber + 6% inulin		↘ Worm counts in pigs fed with diet 2 in both experiments			Thomsen *et al.* (2006)
German landrace male castrates *n* = 64	42/–	21 or 42	Wheat/ barley-based (18 g β-glucans kg^{-1} DM) or ground corn and wheat gluten (1 g β-glucans kg^{-1} DM) based diets Supplemented with 3% inulin; CON = no inulin		40% of pigs supplemented with inulin harbored bifidobacteria in the colon; only 13% receiving no inulin		20–50% inulin degraded in the jejunum, irrespective of the basal diet Inulin: ↘ colon acetate and total SCFA concentrations; ↗ relative butyrate concentration	Loh *et al.* (2006)

Landrace/Yorkshire Danish crosses (females, castrates) *n* = 28		After 3 weeks adaptation to the experimental diets all pigs were infected with a single dose of 2000 infective *T. suis* eggs	30% oat husk 16% inulin		Inulin: ↘ in *T. suis* establishment, egg excretion, and female worm fecundity		Petkevicius *et al.* (2007)
Danish landrace/ Duroc male pigs *n* = 48			1 or 2 weeks prior to slaughter: 10–13.3% dried chicory roots or 25% blue lupines			↘ Indole in chicory versus lupine fed pigs	Hansen *et al.* (2008)
German large white × Piétrain *n* = 48	–/8.3		3% WB or 1.3 or 2.6% Chinese Masson pine pollen (*Pinus massoniana*)		Fiber: ↗ villus height in jejunum and ileum	WB: ↗ NF-κB in stomach and jejunum; TNF-α, TGF-β, caspase3 in jejunum pine pollen: ↘ NF-κB, TNF-α, TGF-β, caspase3, CDK4, IGF-1 in the colon; ↗ NF-κB and TGF-β in mesenterial lymph nodes	Schedle *et al.* (2008)
Piétrain × Rattlerow Seghers crossbred *n* = 168	4–6 weeks before slaughter		Raw potato starch (RPS) RPS + WB Lupins Inulin Clinoptilolite			No impact on boar taint	Aluwe *et al.* (2009)
Duroc × landrace × Yorkshire *n* = 20	Growing females 64.9 ± 1.2 kg	10	Breads with refined fiber (WFL; 71% standard wheat flour) 81.3% whole-wheat grain (WWG) 21.4% wheat aleurone flour (WAF) 36.5% rye aleurone flour (RAF)	WAF and RAF: ↘ AD protein RAF: ↘ AD fat RAF bread: ↘ AD starch		WAF: rich in AX, fermented as much in the cecum as in the colon RAF: rich in AX, mainly fermented in cecum WFL: rich in cellulose, fermented more distally WAF: ↗ butyrate	Le Gall *et al.* (2009)
Camborough plus females × C337 sires *n* = 40	42/23		37.4% WB 18.3% pea hulls (PH) 33.3% pea inner fibers (PIF) 26.7% SBP 41.2% DDGS	Apparent total tract digestibility of N: ↘ in DDGS; intermediate in WB and SBP; ↗ in PIF and PH		PH: ↗ SCFA in the ileum and the colon ↗ NH3 in colon PIF and SBP: ↗ SCFA; ↘ NH3 and fecal N excretion	Jha and Leterme (2012)

(*Continued*)

Table 4. *(Continued.)*

Breed, *n*	Age, days/ BW, kg	Duration of experiment (days), Challenge	Fiber source	Main outcome				Reference
				Digestibility	Intestine	Productivity	Gut physiology	
Barrows, 40 Barrows, 40 Pig Improvement Company	–/25.4 –/84.8		30% soybean hulls (SBH) 30% wheat middlings (WM)			SBH, WM: ↘ NE NE of SBH not different from the NE of WM ↘ ADG, FCR, retention of lipids		Stewart *et al.* (2013)
Barrows (cannulated), Camborough × Canabrid *n* = 11	–/23	4 × 4 Latin square, 10 days each period	44.3% alfalfa 60.2% SBP 41.4% WB	SID AA: WB > alfalfa > SBP				Eklund *et al.* (2014)
Duroc × Danish landrace × Yorkshire catheterized pigs *n* = 6	–/60.2 ± 3.1 kg initial BW	5 × 6 incomplete crossover	4 breads: WF: commercial white-wheat bread RK: commercial rye bread with whole-rye kernels AX: white-wheat breads supplemented with 24.4% arabinoxylan concentrate BG: white-wheat breads supplemented with 13.3% oat β-glucan	Changes in plasma concentrations of oleic acid, AA, phosphatidyl choline, LysoPC, betaine, choline, carnitine were observed within 30–120 min postprandial				Nielsen *et al.* (2014)
n = 48	28/8.36	42	CON Native WB Fermented WB Extruded WB 15% of one WB type in each Starter			No impact on performance parameters	↗ Goblet cells in the ileum: native, extruded > fermented bran ↘ *E. coli* counts in colonic chyme in CON versus WB ↘ Total SCFA in the colon by modified WB versus native WB ↘ Lipid radicals in native WB versus CON	Kraler *et al.* (2015)
Female pigs *n* = 30		21	CON (Western-style control diet) Resistant starch diet (RS; 5.6% raw potato starch + 16.8% high-amylose maize) Arabinoxylan diet				High DF diets: ↗ Plasma butyrate concentration AX or RS: expression of some genes involved in nutrient transport, immune response and intestinal permeability affected by segment	Nielsen *et al.* (2015)

			(AX; 65.5% rye flakes + 8% enzyme-treated WB) (all diets rich in fat)				(cecum, proximal, mid or distal colon) No diet-induced effect on adipose mRNA abundance or adipocyte size	
Piétrain × Belgian landrace sows *n* = 48	21/35–117	91	0, 23, or 37% SBP	SBP: ↘ NH_3 ↗ CH_4 emissions		Growth performance was impaired		Philippe *et al.* (2015)
Landrace × Yorkshire pigs *n* = 6	–/56.5	3 × 3 Latin square 21	Bread: WFL = white wheat flour with 6.9% added purified wheat fiber WWG = 81% whole wheat grain WAF = 21% wheat aleurone flour RAF = 37% rye aleurone flour	Net SCFA absorption was similar for all diets AXA: ↗ butyrate absorption				Bach Knudsen *et al.* (2016)
German landrace × Piétrain, *n* = 8	90/27.7	49	35% WB (in a low-fat diet, compared to a high-fat/low-fiber diet)		↗ Weight of digestive organs		↘ Total bacteria in cecum; ↗ *C. leptum* in cecum; ↗ *Bifidobacterium* and ↘ *Bacteroides* and *Enterobacteriaceae*, in cecum and colon; ↘ *Prevotella* in colon ↗ total SCFA in colon	Heinritz *et al.* (2016*a*)
German landrace × Piétrain *n* = 8	90/27.7	49	35% WB (in a low-fat diet, compared to a high–fat/low-fiber diet)				Feces: ↗ lactobacilli, bifidobacteria, and *Faecalibacterium prausnitzii*; ↘ *Enterobacteriaceae* ↗ SCFA	Heinritz *et al.* (2016*b*)
G-Performer boars mated to Fertilis-25 dams (Genetiporc USA LLC, Alexandria, MN) *n* = 6 + 192 + 36 3 experiments	–/25–50 (27, 26, 29)	42, 28, 12	0, 15, or 35% soybean hulls	AA digestibility was altered				Mathai *et al.* (2016)
Yorkshire-landrace pigs (16 castrated males, 18 females) *n* = 34	56/20.6 ± 2.1	42 (14 day adaptation to diet, 28 day challenge with *T. suis*)	10% inulin		↘ Abundance of bacterial phyla linked to inflammation, such as Proteobacteria and Firmicutes ↗ Actinobacteria and Bacteroidetes		Colon: ↗ Th2-related immune genes and mucosal barrier genes (IL-13, IL-5, TFF3) ↘ Th1-related pro-inflammatory genes (IFN-γ, CXCL9, IL-1A, IL-8)	Myhill *et al.* (2018)

(*Continued*)

Table 4. (*Continued.*)

				Main outcome				
Breed, *n*	Age, days/ BW, kg	Duration of experiment (days), Challenge	Fiber source	Digestibility	Intestine	Productivity	Gut physiology	Reference
Polish large white × Polish landrace *n* = 144	–/30	98	2% long-chain inulin (LCI) 4% dried tubers of Jerusalem artichoke (JA) Multispecies probiotic (P)			↗ Daily gain by probiotics in combination with inulin sources	Inulin and probiotic: ↗ performance	Samolińska *et al.* (2018)
Duroc × landrace × Yorkshire white *n* = 36	–/22		0.5% inulin			No significant increase daily gain	↗ Serum concentrations of insulin and IGF-1 ↗ Expression level of myosin heavy chain II b (MyHC IIb) in the *Longissimus dorsi*, ↗ mammalian target of rapamycin protein (mTOR), ↘ muscle-specific ubiquitin ligase MuRF-1	Wang *et al.* (2019)
Finishing pigs *n* = 1985 (experiment 1) *n* = 1158 (experiment 2)	100 ± 2.5 kg BW (exp. 1) 105 ± 2.0 kg BW (exp. 2)	28 days (exp. 1) 35 days (exp. 2)	30% DDGS DDGS withdrawal periods: 28, 21, 14, or 0 days before marketing			No evidence for treatment differences on final BW, average daily feed intake, or feed efficiency	Optimal time to make a dietary switch from high to low fiber appears to be linear in nature and at least 28 day before marketing	Lerner *et al.* (2020)

on the standardized ileal digestibility of AA in pigs. WB had a more pronounced effect than the other two products inclusion (Eklund *et al*., 2014).

When using WB at 3% or pine pollen at 1.3 or 2.6%, positive effects on villus height in jejunum and ileum were observed in piglets with an average BW of 8.3 kg. Furthermore, there was some evidence that WB influences the expression of NF-κB in the stomach and jejunum. Also, there were effects on the expression of TNF-α, TGF-β, caspase 3, CDK4, and IGF-1 in the colon. In the mesenteric lymph nodes, the expression of NF-κB and TGF-β was upregulated (Schedle *et al*., 2008). The use of 37% WB, 28% SBP, or 41% dried distillers' grains with solubles (DDGS) from maize products in pigs resulted in a reduction in the digestibility of nutrients, while diets with 33% inner pea fiber or 18% pea hulls led to improved N utilization. Pea fiber was able to stimulate the formation of SCFA in the ileum and colon. However, the concentration of intestinal ammonia also increased (Jha and Leterme, 2012). Supplementation of wheat-barley or corn/wheat gluten-based diets with 3% inulin fed to 6-week-old pigs for 3 or 6 weeks did not affect growth but increased the prevalence of pigs with bifidobacteria in the colon (40 versus 13%) and decreased acetate and total SCFA concentrations while butyrate proportion was higher. Interestingly, 20–50% of the ingested inulin was already degraded in the jejunum (Loh *et al*., 2006). Feeding an HF diet with 37 or 23% SBP even reduced ammonia emissions from gestating sows and fattening pigs under barn conditions by 25–50%; however, it increased CH_4 emissions by 30–50% (Philippe *et al*., 2015). When using WB as a component in a diet with 4 or 24% of crude fat with sunflower margarine and sweet cream butter as a model for a 'westernized diet' for growing pigs, the weight of the digestive organs increased, and some changes in the microbiota were noted. Despite lower overall levels of bacteria in the cecum digesta, there was an increase in SCFA concentration in both the colon and cecum (Heinritz *et al*., 2016*a*, 2016*b*). Dietary carbohydrate composition may have potential in preventing intestinal disorders in certain periods of the growing phase, as could be deduced by the changes in the microbiota and coliform diversity, mainly at the ileocecal ostium when increasing NSP levels up to 19.5% (Högberg *et al*., 2004). Long-chain inulin (2%) and Jerusalem artichoke (4%) improved the performance and health-related measurements in growing pigs (Samolińska *et al*., 2018); however, 0.5% inulin failed to induce a positive impact on animal performance in another study (Wang *et al*., 2019). The inclusion of 30% DDGS in a corn–soybean meal increased dietary NDF from 8.6 to 12.8%. Feeding the diet until 28, 21, 14, or 0 days prior to slaughter did not affect feed intake and feed conversion nor the final BW (Lerner *et al*., 2020).

Metabolic effects of DF on fattening pigs

The use of HF diets in pigs not only aims to elicit effects on intestinal and microbial metabolism but also targets intermediary effects. Different aspects were considered in previous studies, such as the influence of fiber-rich components on the nutritional quality of pork products. Additionally, associated aspects, such as the impact on boar taint, which is a problem for the marketing of pork, have been investigated. The inclusion of 13–20% fermentable fiber from a mixture of SBP, rye bran, and citrus pulp led to a reduction of cholesterol levels in the blood of pigs. Altered cholesterol and bile acid re-absorption from the gut and partial bacterial degradation was considered as an explanation for the observed effects (Kreuzer *et al*., 2002). Diets with arabinoxylans from rye flakes (66%) or 6.5% raw potatoes and 17% of a maize product as resistant starch sources induced beneficial effects on genes related to colonic health and glycemic responses (Nielsen *et al*., 2015).

The use of chicory at a dosage of 10–13% reduced intestinal indole concentrations and boar taint in male pigs (Hansen *et al*., 2008). Boar taint reduction was also tested in diets using raw potato starch (10%) in a combination with WB (5 or 10%) or inulin (5%). Interestingly, no effects on boar odor were observed for an application period of 4–6 weeks before slaughter (Aluwe *et al*., 2009).

An experiment with multi-catheterized pigs provided evidence that the type of DF influences the hepatic uptake of certain SCFA. Changing the fermentable substrate from cellulose to a fiber rich in arabinoxylans resulted in increased hepatic propionate and butyrate uptake (Bach Knudsen *et al*., 2016). Using a comparative metabolomic approach with pigs and human beings, changes in the plasma concentrations of a range of plasma metabolites, including oleic acid, AAs, phosphatidylcholine, LysoPC, betaine, choline, and carnitine, were observed within 30–120 min postprandially, depending on contents and composition of DF in the diet (Nielsen *et al*., 2014).

Intestinal helminths, microbiota, and immune response in fattening pigs

Intestinal helminths are one of the most widespread infections globally in people and animals. They produce metabolites and products that can interact with the digestive process. *Ascaris suum*, *Trichuris suis*, and *Oesophagostomum dentatum* are of significant importance, as these organisms reside in the intestine, a triangular relationship exists between parasites, microbiota, and the pig immune system. These helminths may release antimicrobial products and thereby alter the host's gut microbiota, motility, growth, and gene expression. This was associated with increased production of SCFA and subsequent modulation of immune responses. In return, the microbiota can influence nematode infection at egg-hatching, larval development, and by providing pro- or anthelmintic molecules. Both nematodes and microbiota modulate the immune system and thereby indirectly the microbiome or helminths in the intestinal tract (Midha *et al*., 2021). In the interrelation between parasites, the microbiota, and the immune system, a link to the diet composition, in particular DF, seems to play a crucial role in the outcome of infection. Compared to a diet with 30% oat hull meal, the inclusion of 16% inulin or 6% inulin and 15% SBP fiber revealed a reductive impact on worm burdens of pigs infected with *T. suis* (Thomsen *et al*., 2006; Petkevicius *et al*., 2007). However, diets with high levels of NSP and lignin tended to increase *O. dentatum* worm load (Petkevicius *et al*., 1997, 1999). Additionally, piperazine treatment against intestinal parasites became more efficient when pigs received a diet with 21% oat husk meal (Praslicka *et al*., 1997). A diet with 10% dietary inulin was demonstrated to cooperatively enhance the anti-inflammatory immune response induced by the pig whipworm, *T. suis*, accompanied by changes in the microbiota composition (Myhill *et al*., 2018). Thus, a fiber supplementation in a pig infected with an intestinal nematode may synergistically influence the bacterial gut composition, the Th_2-driven immune response and lead to enhanced mucosal barrier integrity.

In summary, fattening pigs seem to easily adapt to high inclusion of DF in their diets. Supplementation of DF to fattening pigs has been shown to increase the formation of SCFA in the gut and to beneficially affect host metabolism, physiology, and immune responses. Some evidence suggests a beneficial effect of DF against intestinal parasites in fattening pigs, but more studies are still needed here. Therefore, DF offers a promising way to improve the health of fattening pigs.

Conclusion

This review demonstrates that DF has numerous positive effects on the health and well-being of pigs, including sows, piglets, and fattening pigs. DF interacts with many aspects of the pig's digestive physiology, immunology, microbiology, and even behavior. An increasing body of evidence suggests that DF can have the potential to influence piglet health through the sow diet. This makes DF an attractive feed ingredient with regard to offspring manipulation through maternal factors. The diverse origin of DF, which increasingly includes by-products of industrial food processing, leads to large variation in its composition as well as physico-chemical and biological properties. This knowledge gap calls for mechanistic studies on the intestinal and intermediary effects of DF. In addition, a better and uniform characterization and evaluation system for the fibrous feed materials is required in the future. Fibrous feed materials have a great potential to improve the sustainability of pork production under the consideration of animal welfare, but the relationships between type and structure of fiber, inclusion rates, and associated intestinal and metabolic effects are by far not clear and call for more systematic in-depth research on this topic.

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