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FIBER SUBSTRATES IN THE NUTRITION OF WEANED PIGLETS – A REVIEW

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Abstract

The present review summarizes the results of 37 experiments in which different types and levels (from 0.5 to 29.7%) of fibrous supplements were used in the formulation of diets for weaned piglets. Diets were supplemented with different sources of insoluble dietary fiber (iDF), soluble dietary fiber (sDF), or mixed DF sources. Most of the applied DF sources decreased the ileal and fecal organic matter digestibility, and they often lowered crude protein digestibility. A moderate addition (1.5–8%) of iDF sources increased average daily feed intake (ADFI) and, frequently, average daily gains (ADG). Sources of sDF as well as high inclusion levels of fiber-rich feeds tended to decrease ADFI and ADG. Improved fecal consistency, decreased diarrhea incidence and antibiotic interventions were confirmed in piglets fed diets with added lignocellulose, cooked or raw oat hulls and wheat bran. The dietary inclusion of iDF rather than sDF sources improved gastrointestinal tract (GIT) development, enzyme activity and gut morphology. An increase in the counts of beneficial gut microbiota and the concentrations of short-chain fatty acids was stimulated by diets with addition iDF or sDF sources. Such diets also slowed down proteolytic fermentation which negatively affects the colonic mucosa. Some research findings indicate that iDF sources improve intestinal barrier function. The analyzed experimental data suggest that the addition of 1.5–2% of a lignocellulose preparation, 2% of oat hulls, 4–8% of coarse wheat bran to diets for weaned piglets may be recommended to promote GIT development and health, and to improve growth performance.

Key words: fibrous feeds, digestibility, performance, diarrhea, gut health, weaned piglets

Intensive pig production combined with efforts made to reduce the costs of raising sows have led to the shortening of the lactation period to 21–28 days. Piglets weaned early in their lives are exposed to numerous stress factors, such as a loss of mother/sow, transfer to a new environment, mingling of litters, sow's milk deprivation and a change to a weaner diet, usually solid feed. The gastrointestinal tract (GIT) of a 3- to 4-week-old piglet is not quite ready for digesting plant protein, starch or fat, whereas weaning-related stress and appetite suppression (Bruininx et al., 2001) lead to undesirable changes in the small intestine, including a decrease in the villus height/crypt depth (V/C) ratio and enzyme activity, and changes in intestinal permeability (Vente-Spreeuwenburg et al., 2003; Boudry et al., 2004; Montagne et al., 2007). All of the above factors may influence nutrient digestibility and absorption, increase the incidence of post-weaning diarrhea (PWD) and compromise the growth performance of piglets. Non-antibiotic feed additives, such as enzymes, acidifiers, probiotics and phytobiotics, can be used to minimize the negative effects of weaning. Fiber supplementation is yet another strategy developed to alleviate health problems in weaned piglets (Bach Knudsen et al., 2012; Kim et al., 2012; Molist et al., 2014).

When selecting the source and level of dietary fiber, feed manufacturers and pig producers are most interested in its influence on PWD and growth performance. The objective of this review article was to collate information on the effects of fiber substrates added to post-weaning diets, with special emphasis on nutrient digestibility, the growth performance of piglets, fecal score and PWD incidence.

Table 1. Concentrations of total dietary fiber (TDF), soluble DF (sDF), insoluble DF (iDF) (g/kg DM), and the iDF/TDF ratio in selected fiber sources

Fiber sources	TDF	sDF	iDF	iDF/TDF (%)
Wheat bran[1]	449	29[a]	420[b]	93.5
Corn bran[2]	867	2	865	99.8
Barley hulls[1]	594	20[a]	574[b]	96.6
Oat hulls[1]	653	13[a]	639[b]	97.8
Rice hulls[3]	536	9	526	98.1
Buckwheat hulls[4]	918	27	891	97.1
Pea hulls[5]	730	121	609	83.4
Soybean hulls[6]	674–884	41–135	632–785	84.7–93.8
Dehydrated sugar beet pulp[1]	813	407[a]	407[b]	50.0
Potato fiber[5]	612	280	332	54.2
Citrus pulp[7]	476	344	132	27.7
Citrus pectin[8]	662	-	-	2.3
Grass meal[1]	527–595	24–38[a]	489–572[b]	92.8–96.1
Alfalfa meal[1]	457	77[a]	379[b]	82.9
Wheat straw[9]	785	-	747	95.1
Lignocellulose preparation – Vitacel[3]	714	0	714	100
Lignocellulose preparation – Arbocel[3]	632	3	629	99.5
Pure cellulose[7]	971	7	964	99.3

[a]Soluble non-cellulosic polysaccharides. [b]Sum of insoluble non-cellulosic polysaccharides, cellulose and lignin. Own elaboration based on: [1]Bach Knudsen (1997); [2]Kaholn and Chow (2000); [3]Rezaei et al. (2014); [4]Skrabanja et al. (2004); [5]Serena and Bach Knudsen (2007); [6]Cole et al. (1999); [7]Pascoal et al. (2012); [8]Sunvold et al. (1995); [9]Abad et al. (2013).

Concentrations of dietary fiber in fibrous feed

Co-products from agro-industries are the most popular fiber sources. These include cereal hulls and bran, legume hulls, grass and alfalfa meal, dehydrated sugar beet pulp, citrus pulp, pectin, potato fiber, lignocellulose preparations from wood, inulin, and cereal straw. Fibrous products differ in the content of non-starch polysaccharides (NSP) which, together with lignin, make up dietary fiber (DF). With respect to their physiological activity in the GIT of monogastric animals, fibrous feeds are classified into groups depending on whether they provide mostly insoluble (iDF) or soluble (sDF) fiber. Table 1 summarizes data on DF concentrations and iDF percentage in total DF in the most popular fibrous components added to piglet diets. The highest proportion of iDF (over 80% in TDF) was noted in hulls of oat, barley, soybean, buckwheat, alfalfa meal, wheat, rice and corn bran, lignocellulose preparations, pure cellulose and cereal straw. Sugar beet pulp and potato fiber are a rich source of sDF, but they also contain high amounts of iDF. Citrus pectin and citrus pulp provide mostly sDF. Methylcellulose, which is also sometimes used as a feed additive, is rich in sDF (McDonald et al., 2001; Hopwood et al., 2002).

Influence of dietary supplementation of fibrous feeds on ileal and fecal digestibility in weaned piglets

DF components may reduce digestibility for a variety of reasons. Soluble DF can increase digesta viscosity, impede the contact between nutrients and digestive enzymes and disturb nutrient absorption (Bach Knudsen, 2001). Insoluble DF is either poorly or not fermentable at all, and therefore more nutrients can be excreted with stools (Bach Knudsen, 2001). Moreover, iDF increases endogenous protein losses and can reduce the digestibility of CP and amino acids, in particular their ileal digestibility (Souffrant, 2001).

Most diets supplemented with fiber were less digestible than control diets (Table 2). The cecal digestibility of organic matter (OM) and crude protein (CP), but not starch, was lower in diets with low and high inclusion levels of iNSP (wheat bran) than in a diet low in NSP (Högberg and Lindberg, 2006). The dietary inclusion of 5% of sugar beet pulp did not deteriorate the digestibility of dry matter (DM) and CP (Jeaurond et al., 2008). However, 5% addition of sugar beet pulp and 8% addition of wheat bran decreased the ileal digestibility of OM, but not of CP or starch (Pieper et al., 2012). Dietary fermentable carbohydrates (introduced by 8.4% of wheat middlings, 5% of native potato starch and 4% of sugar beet pulp) significantly decreased the ileal digestibility of CP and starch (Bikker et al., 2006). Basal diets can also be a source of fiber. Piglets fed a diet based on hulled oat were characterized by significantly lower digestibility of OM, CP and starch than those receiving hulled barley, whereas piglets given hulled barley had lower digestibility of OM, CP and starch than piglets fed hulless barley (Jha et al., 2010). Diets with hulled oat, hulled barley and hulless barley contained 190, 118 and 85 g NSP/kg DM, respectively.

Total-tract (fecal) digestibility, an indicator measured more frequently, showed that the dietary supplementation with sources high in iDF, such as soybean hulls, alfalfa meal (Freire et al., 2000) or wheat bran (Högberg and Lindberg, 2006), also lowered the digestibility of OM, CP and energy. Sometimes even a small amount of added iDF, i.e. 2% of raw oat hulls (Kim et al., 2008), 4% of wheat bran (Molist et al., 2010 b), 1.27 or 2.55% of pine pollen (Schedle et al., 2008) decreased the digestibility of OM and CP. However, when 2 or 4% of cooked and expanded oat hulls (Mateos et al., 2006) or sugar beet pulp were added (Freire et al., 2000; Jeaurond et al., 2008), the fecal digestibility of OM, CP and energy did not decrease. A diet with a high amount of fermentable carbohydrates decreased the ileal digestibility of CP (by 15%; 52.9 vs. 62.1%; P<0.05) to a higher extent than its fecal digestibility (by 9%; 60.9 vs. 66.6%; P>0.05) (Bikker et al., 2006). Likewise, a diet based on hulled oat, with a high content of iNSP, enabled moving a considerable amount of protein to the large intestine where it was degraded (Jha et al., 2010), as manifested by a great difference between the fecal and ileal digestibility of CP (74 vs. 47%).

Table 2. Effect of the sources and dietary inclusion levels of supplemental fibrous feeds on the ileal and fecal apparent digestibility of organic matter (OM), crude protein (CP), starch and gross energy (GE) in weaned piglets

Sources and levels of fibrous feeds	Age of piglets	Ileal digestibility (%)			Fecal digestibility (%)			Reference
		OM	CP	Starch	OM	CP	GE	
1	2	3	4	5	6	7	8	9
Wheat bran-WB (20%)	1 and 3				[d] 86.7 b	84.7 a	87.2 a	Freire et al.
SBP (20%)[e]	wk after				88.8 a	83.3 ab	88.7 a	(2000)
Soybean hulls (20%)	wean				82.8 c	66.5c	81.5 b	
Alfalfa meal (20%)					83.1 c	79.5 b	82.4 b	
Control-FC (7.5%)[f]	26–33 d		62.1 a	97.5 a		66.6		Bikker et al.
High FC (13.4%)[g]			52.9 b	93.7 b		60.9		(2006)
Low NSP	6 wk	[h] 86 a	[h] 74 a	[h] 99	89 a	80 a	87 a	Högberg and
Low iNSP (16% WB)		75 b	64 b	98	85 a	77 ab	82 b	Lindberg (2006)
High NSP		70 b	53 c	99	81 a	72 ab	79 b	
High iNSP (30%WB)		57 c	62 b	96	76 b	70 b	73 c	
Control	27 and 37				84.6	71.3	80.6	Mateos et al.
+ Oat hulls (2%)[i]	D				84.4	73.1	80.6	(2006)
+ Oat hulls (4%)					84.6	73.2	81.3	
Control	17–45 d	[d] 65.4	67.4		83.7	78.5	85.8	Jeaurond et al.
+SBP (5%)		71.3	66.5		85.1	80.5	86.7	(2008)
Rice-based diets	1 & 2 wk				[d] 90.2 a	74.5 a	89.3 a	Kim et al.
+ oat hulls (2%)					87.2 b	71.2 b	86.7 b	(2008)
Wheat-based diet					85.6 a	77.5 a	84.3 a	
+ oat hulls (2%)					83.6 b	76.0 b	82.9 b	
Control	weaned				[d] 84.2 a	79.0 a		Schedle et al.
+Wheat bran (3%)	+5 wk				81.4 b	77.0 ab		(2008)
+Pine pollen (1.27%)[k]	of exp.				82.5 b	76.6 ab		
+Pine pollen (2.55%)					80.7 b	74.7 b		
Hulless barley (81.5%)	12.8 kg	75 a	69 a	94 a	91 a	80 a		Jha et al.
Hulled barley (81.5%)	plus 15 d	69 ab	65 ab	91 b	83 b	73 b		(2010)
Hulled oat (81.5%)	of exp.	58 b	47 b	92 b	68 c	74 b		

Table 2 – contd.

1	2	3	4	5	6	7	8	9
Control (exp.1)	10–12 d				83.3 a	83.8 a		Molist et al.
+Wheat bran (4%)	after wean				72.0 b	68.7 b		(2010b)
Control (15% CP)	20–23 d	74.0 a	63.3	95.6				Pieper et al.
+WB (8%)+SBP (5%)	after wean	63.8 b	64.0	94.0				(2012)
Control (20% CP)		67.3 a	66.2	89.2				
+WB (8%)+SBP (5%)		62.8 b	67.8	88.7				

a, b, c – $P<0.05$; [d]DM digestibility; [e]SBP – sugar beet pulp; [f]FC – fermentable carbohydrates; [g]higher FC supplied by the addition of 8.4% wheat middlings, 5% native potato starch and 4% SBP; [h]cecal digestibility; [i]cooked and expanded; [k]rich in lignin (29%).

Decreased digestibility leads to lower dietary energy concentrations. Diets supplemented with a high amount of iDF (soybean hulls or alfalfa meal) contained significantly less metabolizable energy, 12.95 and 13.24 MJ/kg, respectively, than a diet supplemented with sugar beet pulp (14.23 MJ/kg), which is characterized by high nutrient digestibility (Freire et al., 2000). Also, diets with 15.6 or 29.7% of wheat bran (Högberg and Lindberg, 2006), and diets with 2% of raw oat hulls (Kim et al., 2008) contained less (by 4 to 8%) digestible energy than the control diet. This finding should draw attention to energy concentrations in diets supplemented with fibrous feeds.

Growth performance and post-weaning diarrhea incidence in weaned piglets fed diets supplemented with different fiber substrates

Table 3 presents the effects of the inclusion of various fiber substrates in weaner diets on average daily feed intake (ADFI), average daily gain (ADG) and feed conversion ratio (FCR), measured as the gram of body weight gain per kg feed intake (g/kg) or the kg feed intake per kg body weight gain (kg/kg), as well as its impact on post-weaning diarrhea (PWD) incidence and severity. In most studies, the dietary addition of fibrous feeds with a high proportion of iDF increased ADFI, which was reported for lignocellulose preparations (Hanczakowska et al., 2008; Kroismayr et al., 2008), pure cellulose (Pascoal et al., 2012), a moderate amount of wheat bran (Högberg and Lindberg, 2006; Schedle et al., 2008; Molist et al., 2009), oat hulls with ground straw (Gerritsen et al., 2012), soybean hulls (Weber et al., 2008; Pascoal et al., 2012) and pine pollen (Schedle et al., 2008). In comparison with the control diet, ADFI increased by 4 to 54%. The supplementation of weaner diets with sNSP, i.e. 7% of pectin (Hedemann et al., 2006), 7.5% of citrus pulp (Weber et al., 2008) or 15% of inulin (Wellock et al., 2008) decreased ADFI by 7 to 28%. Diets supplemented with two fibrous feeds, one high in sDF and the other rich in iDF, exerted varied effects on feed consumption. When the amount of either of the feeds was moderate (6%), ADFI increased (Hermes et al., 2009) or was similar to that noted in the control treatment (Hermes et al., 2010). Higher supplementation with iDF, particularly in the treatment with 7% of pectin, significantly (by 40%) decreased ADFI (Hedemann et al., 2006).

Table 3. Effect of the sources and dietary inclusion levels of supplemental fibrous feeds on the growth performance of piglets and post weaning diarrhea (PWD) incidence

Sources and levels of fibrous feeds	Age of piglets	Growth performance			PWD index	Reference
		ADFI (g)	ADG (g)	FCR (g/kg)		
1	2	3	4	5	6	
22% CP, 7.5% FC[d]	26–54 d	466	313	670		Bikker et al. (2006)
22% CP, 13.4% FC[e]		478	315	660		
Control	28–37 d	302 a (100%)	186 a (100%)	616 a (100%)		Hedemann et al. (2006)
Barley hulls-BH (9%)		283 a	166 a	586 a		
Barley hulls (19%)		322 a	204 a	633 a		
Pectin (7%)		218 b (–28%)	100 b (–46%)	458 b (–26%)		
Pectin 7% +BH 9.6%		180 b (–40%)	58 b (–69%)	322 b (–48%)		
Low NSP	21–63 d	255 b (100%)	235 b (100%)	[f]1.08 ab (100%		Högberg and Lindberg, 2006
Low iNSP (16% WB)		364 a (+42%)	301 a (+28%)	1.20 ab (+11%)		
High NSP		263 b (100%)	213 b (100%)	1.24 a (100%)		
High iNSP (30% WB)		251 b (–5%)	258 ab (+21%)	0.99 b (–20%)		
Control	21–54 d	654	436	[f]1.50	[h]4.1	Mateos et al. (2006)
Oat hulls (2%)[g]		636	430	1.48	2.9	
Oat hulls (4%)		633	431	1.46	2.4	
Control	35–56 d	280 (100%)	163 (100%)	[f]1.83	50%	Hanczakowska et al. (2008)
Lignocellulose (0.5%)		317 (+13%)	180	1.87	35%	
Lignocellulose (1.5%)		348 (+24%)	185 (+13%)	1.89	33%	
Lignocellulose (2.0%)		337 (+20%)	180	1.76	16%	
Rice-based diets	21–42 d	443	223 b	[f]2.05 a	[i]5/12	Kim et al. (2008)
plus oat hulls (2%)		437	219 b	2.01 a	2/12	
Wheat-based diet		423	271 a	1.58 b	0/12	
plus oat hulls (2%)		440	277 a	1.60 b	1/12	
Control	27–62 d	538 (100%)	342[b] (100%)	[f]1.57		Kroismayr et al. (2008)
Lignocellulose (1.5%)		558 (+4%)	364[a] (+6%)	1.54		
Control	8.3 kg + 37 d of exp.	517 c (100%)	351 b (100%)	[f]1.56 (100%)		Schedle et al. (2008)
Wheat bran (3%)		735 a (+42%)	430 a (+22%)	1.73 (+11%)		
Pine pollen (1.27%)[j]		685 b (+32%)	433 a (+23%)	1.65 (+6%)		
Pine pollen (2.55%)		662 b (+18%)	411 a (+17%)	1.73 (+11%)		
Control	24–52 d	447 (100%)	319 (100%)	752 (100%)	[k]6.7	Weber et al. (2008)
Soybean hulls (7.5%)		477 (+7%)	349 (+9%)	772 (+3%)	16.7	
Citrus pulp (7.5%)		416 (-7%)	304 (–5%)	773 (+3%)	6.7	
Low sNSP (5% inulin)	27–41 d	513 (100%)	465 (100%)	[l]906 (100%)	[m]1.90	Wellock et al. (2008)
Low iNSP (5% cellul)		401 (100%)	378 (100%)	943 (100%)	1.56	
High sNSP (15% inulin)		372 (–27%)	279 (–40%)	750 (–17%)	1.08	
High iNSP (15% cellul)		344 (–14%)	294 (–22%)	855 (–9%)	1.55	

Table 3 – contd.

1	2	3	4	5	6	7
Control -20% CP	35–56 d	742 (100%)	385 b (100%)	540 b (100%)	[o] 1.8/3	Hermes
WB (4%) + SBP (2%)[n]		849 (+14%)	466 a (+21%)	570 a (+8%)	1.1/3	et al. (2009)
Control	24–34 d	199 b (100%)	–2.9	-		Molist et al.
Wheat bran (8%)		306 a (+54%)	68	-		(2009)
Sugar beet pulp (6%)		295 ab (+48%)	34	-		
Control (rice-based)	14–35 d	791	487 (100%)	[l] 616 (100%)		Hermes et al.
WB 4% + SBP 2%		779	510 (+5%)	655 (+6%)		(2010)
Control (barley-based)		671	443 (100%)	660 (100%)		
WB 4% + SBP 2%		682	461 (+4%)	676 (+2%)		
Exp. 1. Control	24–37 d	271 (100%)	157	570 (100%)	[p] 9/30	Molist et al.
Wheat bran (4%)		253 (–7%)	156	620 (+9%)	13/31	(2010b)
Control	21–33 d	177 b (100%)	103 b (100%)	[l] 582 (100%)	[r] 14/16	Molist et al.
Wheat bran – WB (4%)		185 b (+5%)	116 b (+13%)	627 (+8%)	16/16	(2011)
Zn (3 g/kg)		232 a (+31%)	153 a (+48%)	659 (+13%)	7/16	
Control (19.1% CP)	28–42 d	284 b (100%)	230 (100%)	810 a (100%)	[s] 5.3 b	Gerritsen
Oat hulls 5%+10% straw		328 a (+15%)	240 (+4%)	730 b (–10%)	5.5 a	et al. (2012)
Control	21–63 d	703 (100%)	425 (100%)	[f] 1.68 (100%)	13.9% b	Pascoal
Cellulose (1.5%)		759 (+8%)	471 (+11%)	1.62 (–4%)	11.1% c	et al. (2012)
Soybean hulls (3%)		739 (+5%)	432	1.71	25.0% a	
Citrus pulp (9%)		729 (+4%)	417	1.74	22.2% a	
Control	28–42 d	252 (100%)	130 (100%)	485 (100%)	[t] 5/22	Montagne
SBP (6%)+soybean hulls (2%)		222 (–12%)	105 (–19%)	405 (–16%)	11/23	et al. (2012)
Control	21–49 d	439	321	733 b (100%)		Herfel et al.
Stabilized rice bran (10%)		414	330	803 a (+10%)		(2013)

[l]Own calculations.

a, b, c – $P<0.05$.

[d]FC – fermentable carbohydrates; [e]higher FC supplied by the addition of 8.4% wheat middlings, 5% native potato starch and 4% SBP; [f]feed:gain (kg/kg); [g]cooked and expanded; [h]number of days with diarrhea relative to the total number of days of the trial (days 21–41); [i]pigs with diarrhea/total pigs; [j]fiber source rich in lignin (29%); [k]percentage of pigs that required antibiotic treatments; [l]own calculations; [m]mean fecal score (days 3–14) on a scale of 1 to 4 (1=firm, 4=watery); [n]SBP – sugar beet pulp; [o]piglets with diarrhea per pen over the entire experimental period; [p]pigs with diarrhea at 2 weeks after weaning; [r]diarrhea incidence on days 0–12 of exp.; [s]fecal score (from 1=liquid to 10=hard, dry) on days 1-14 after weaning; [t]diarrhea at 5 days after weaning in piglets housed under optimal and poor sanitary conditions.

Among 35 treatments with fibrous feeds, 14 were found to cause either a significant increase or a near-significant trend towards an increase in ADG, 6 resulted in a decrease in ADG whereas 15 had no effect on the ADG of piglets. In comparison with the control treatment, a higher level of growth was achieved by piglets fed diets with added iDF, i.e. 1.5% of a lignocellulose preparation (Hanczakowska et al., 2008; Kroismayr et al., 2008), 1.5% of pure cellulose (Pascoal et al., 2012), 1.27 and 2.55% of pine pollen (Schedle et al., 2008), 7.5% of soybean hulls (Weber et al., 2008), 3, 8 or 16% of wheat bran (Schedle et al., 2008; Molist et al., 2009; Högberg and Lindberg, 2006). The addition of 4% of oat bran and 2% of sugar beet pulp also significantly increased the ADG of piglets fed a diet containing 20% of CP (Hermes et al., 2009), whereas an insignificant decrease was observed in piglets fed rice- and barley-based diets (Hermes et al., 2010). The dietary inclusion of 2 or 4% of cooked oat hulls (Meteos et al., 2006), 2% of oat hulls (Kim et al., 2008), 5% of oat hulls with 10% of wheat straw (Gerritsen et al., 2012) or 10% of stabilized rice bran (Herfel et al., 2013) did not affect ADG. Diets supplemented with sDF sources such as 7% of pectin alone or in combination with 9.6% of barley hulls (Hedemann et al., 2006) or 15% of inulin (Wellock et al., 2008), decreased ADG. Diets with a high contribution of DF, such as 15% of cellulose (Wellock et al., 2008) or 6% of sugar beet pulp combined with 2% of soybean hulls (Montagne et al., 2012), decreased ADG. The results showed that elevated ADFI was often associated with higher ADG (Högberg and Lindberg, 2006; Hanczakowska et al., 2008; Schedle et al., 2008; Weber et al., 2008; Hermes et al., 2009; Molist et al., 2009; Pascoal et al., 2012).

The dietary supplementation with fiber substrates had a weaker effect on FCR than on ADFI and ADG. Diets supplemented with fiber increased ADFI, consequently raising ADG, but FCR did not change significantly (Högberg and Lindberg, 2006; Hanczakowska et al., 2008; Kroismayr et al., 2008; Weber et al., 2008). In most cases, this resulted from the dietary supplementation with ingredients with a predominant share of iDF. Significantly worse FCR values were reported in piglets fed diets with added pectin or a combination of pectin and barley hulls (Hedemann et al., 2006), or diet with a large amount of feeds rich in iDF, i.e. 10% of wheat straw plus 5% of oat hulls (Gerritsen et al., 2012).

Table 3 shows that the addition of iDF-rich sources, i.e. oat hulls (Mateos et al., 2006; Kim et al., 2008), a lignocellulose preparation (Hanczakowska et al., 2008), pure cellulose (Pascoal et al., 2012), wheat bran (2%) with a small share of sugar beet pulp (2%) to the 20% CP diet (Hermes et al., 2009) as well as oat hulls (5%) together with 10% of wheat straw (Gerritsen et al., 2012) improved the fecal score and decreased PWD incidence. It was demonstrated that coarse rather than finely ground wheat bran was more effective in preventing diarrhea (Molist et al., 2010 a, 2012). After being experimentally challenged with enterotoxigenic *E. coli*, piglets fed a diet containing 4% of coarse wheat bran had a significantly improved fecal score as compared with those fed with the same amount of finely ground wheat bran (0.6 vs. 1.5 for negative control and 1.1 for finely ground wheat bran; $P<0.01$; where 0=normal, 3=severe diarrhea). The addition of 7.5% or 3% of soybean hulls (Weber et al., 2008; Pascoal et al., 2012, respectively), 9% of citrus pulp (Pascoal et al., 2012) or a combination of 6% of sugar beet pulp with 2% of soybean hulls (Montagne et al., 2012) were not effective in reducing PWD incidence. The above study demonstrated that antibiotic treatment of piglets fed a DF-supplemented diet tends to be increasingly more common during the two weeks after weaning. However, Wellock et al. (2008) found that the addition of sNSP (inulin) and iNSP (pure cellulose), at both a low and high level, did not affect the mean fecal score on days 3 to 14 after weaning.

The influence of fiber substrates on the GIT of piglets, and the mechanisms through which they affect their growth performance and PWD incidence, have been investigated in numerous microbiological and morphological studies on the GIT status in piglets.

Response of the GIT of piglets to diets supplemented with different levels and sources of fiber

It has been demonstrated that high concentrations of iDF in a diet increase the weights of the stomach (Gerritsen et al., 2012) and large intestine (Hermes et al., 2009; Hermes et al., 2010) (Table 4). Viscous non-fermentable carboxymethylcellulose (CMC) (MacDonald et al., 2001) and sugar beet pulp (Jeaurond et al., 2008) did not affect GIT development. Soluble DF from sugar beet pulp, wheat middlings and native potato starch tended (P=0.094) to decrease the length of the small intestine 7 days after weaning (Bikker et al., 2006).

Weaned piglets are characterized by limited production of hydrochloric acid by the gastric glands, and some ingredients of post-weaning diets have acid-binding properties, which may contribute to the deficit of this acid. Hydrochloric acid plays an important role in preventing the transfer of various bacteria from the environment to the distal segments of the GIT. It has been documented that diets with added iDF (wheat bran) increase lactic acid concentrations and decrease the stomach pH (Högberg and Lindberg, 2004 and 2006).

Food digestion involves constant passage of molecules of enzymes, substrates and products of hydrolysis in the GIT. Elevated viscosity of digesta may interfere with nutrient digestion and absorption. Diets supplemented with iDF did not increase ileal digesta viscosity (Högberg and Lindberg, 2004), which in piglets fed a diet with higher CP content (20%) was even lower than in those receiving a diet with lower CP content (16%) (Hermes et al., 2009). Fiber substrates rich in sDF, such as sugar beet pulp (Van Nevel et al., 2006) and inulin (Wellock et al., 2008), did not increase ileal or cecal digesta viscosity. The only exception was CMC which significantly increased the viscosity of ileal, cecal and colon digesta (McDonald et al., 2001; Hopwood et al., 2002).

Reduced enzyme activity is observed at weaning (Vente-Spreeuwenberg et al., 2003; Boudry et al., 2004). Fibrous feeds are added to diets to stimulate the excretory functions of the GIT. Diets supplemented with substrates rich in iDF, such as barley hulls (Hedemann et al., 2006), wheat bran (Corneiro et al., 2007), wheat straw with oat hulls (Gerritsen et al., 2012), enhanced the activity of enzymes in the small intestinal (Hedemann et al., 2006; Gerritsen et al., 2012), cecal and colonic digesta (Corneiro et al., 2007). Diet supplemented with sDF sources, such as wheat middlings with sugar beet pulp and native potato starch, tended to decrease intestinal maltase activity (Bikker et al., 2006).

The intestinal architecture and mucus layer are important determinants of GIT function and health. Mucins secreted by the goblet cells of crypts prevent bacteria from adhering to the epithelium and protect deeper layers of cells from contact with undesirable substances (Barszcz and Skomiał, 2011). Diets supplemented with iDF may improve gut morphology. Barley hulls (9.6 and 19.1% in the diet) increased villus height in the small intestine and the area of neutral mucins on the villi (P=0.07) (Hedemann et al., 2006). The dietary addition of lignocellulose improved the V/C ratio from 0.842 to 1.119 in the small intestine (Hanczakowska et al., 2008). A wheat bran-fiber-diet increased the V/C ratio in the ileum, and a pea-fiber-diet increased the number of colonic goblet cells as compared with piglets on the control diet (Chen et al., 2013). Pectin (rich in sDF) added to a diet at 7.1% decreased the height of villi and crypts, and decreased the area of mucins in the small intestinal crypts (Hedemann et al., 2006). Even slightly older pigs fed diets with the addition of apple pectin (4 or 8%) had significantly higher ileal digesta viscosity and a lower number of goblet cells containing acidic mucins in the jejunal crypts (Święch et al., 2012).

Table 4. Overall effects of DF sources on the gastrointestinal tract of weaned piglets

Item	Source rich in insoluble DF	Source rich in soluble DF
	wheat bran, rice bran, hulls of oat, barley, soybean and pea, pure cellulose, alfalfa meal, lignocellulose preparations, pine pollen (rich in lignin), wheat straw	sugar beet pulp, citrus pulp, pectin, inulin, lactulose, arboxymethylcellulose (CMC)
1	2	3
GIT development	Increased weights of the stomach[1] and large intestine, as % of BW[2, 3]	No effect on GIT development[4, 5, 6]
pH and lactic acid in the stomach	Increased production and molar proportion of lactic acid in the stomach[7, 8]. Decreased stomach pH[7]	
Digesta viscosity	No increase in ileal digesta viscosity[7]. Decrease in colonic digesta viscosity in piglets fed a diet with higher (20 vs. 16%) crude protein[2]	No increase in ileal or cecal digesta viscosity[9, 10]. CMC increases ileal, cecal and colonic digesta viscosity [4, 11]
Digestive enzymes	Increased enzymatic activity in the small intestinal[1, 12], cecal and colonic digestion[13]	Decreased intestinal enzyme activity[5]
Intestinal and colon morphology	Increase in villus height in the small intestine[3, 12], villus height/crypt depth ratio[14, 15]. Increase in the area of mucins on the villi[12], and in the number of colonic goblet cells[15]	Decrease in the height of small intestinal villi and crypts[12], decrease in the number of goblet cells and the area of mucins in the small intestinal crypts[12, 16]
Microbial populations in the GIT and feces	Decreased concentrations of enterobacteria and *E. coli* bacteria in the small intestine[1, 14, 15, 17], cecum [14] and feces[18, 19]. Increased *Lactobacillus* counts in the ileum[15] and bifidobacteria counts in the colon[15, 20]	Decrease in the fecal counts of coliforms, clostridia and *Staphylococcus* spp.[21]. Decrease in the ileal and cecal F18 *E. coli* counts[22]. CMC enhances intestinal colonization by enterotoxigenic *E. coli*[4,11]
Fermentation products	Increased SCFA concentrations in the cecum[8], colon[8, 15, 23] and feces[19] and butyric acid in the cecum[8, 13], colon[8, 15, 18, 23] and feces[19]. Decreased concentrations of ammonia in the colonic digesta[24], and biogenic amines in the feces[25]	Increased SCFA concentrations in the cecum[10], colon[5, 6] and feces[21], and increased butyric acid concentrations in the cecum[10] and colon[5]. Decreased cecal[5, 6], colonic[6] and fecal concentrations of ammonia[26] and colonic amines[6]

Table 4 – contd.

1	2	3
Digesta WRC* and DM content	Reduced amount of unbound water and increased the WRC of colonic digesta[18, 23]	Decreased fecal DM content[11, 21, 26]
Digesta transit time	Shorter digesta transit time in the GIT at high lignin content of the diet[27]	
GIT markers of permeability and inflammation	Improved intestinal barrier function – up-regulation of the mRNA expression of tight junction protein (Z0-1) and TLR2 in the ileum and colon[15]	Up-regulation of the mRNA expression of pro-inflammatory cytokine IL-6 in the colon[28].

*WRC – water retention capacity. Own elaboration based on: [1]Gerritsen et al. (2012); [2]Hermes et al. (2009); [3]Hermes et al. (2010); [4]McDonald et al. (2001); [5]Bikker et al. (2006); [6]Jeaurond et al. (2008); [7]Högberg and Lindberg (2004); [8]Högberg and Lindberg (2006); [9]Van Nevel et al. (2006); [10]Wellock et al. (2008); [11]Hopwood et al. (2002); [12]Hedemann et al. (2006); [13]Corneiro et al. (2007); [14]Hanczakowska et al. (2008); [15]Chen et al. (2013); [16]Święch et al. (2012); [17]Molist et al. (2010 a); [18]Molist et al. (2010 b); [19]Molist et al. (2011); [20]Herfel et al. (2013); [21]Schiavon et al. (2004); [22]Collier et al. (2010); [23]Molist et al. (2009); [24]Schedle et al. (2008); [25]Kim et al. (2008); [26]Awati et al. (2006); [27]Freire et al. (2000); [28]Pié et al. (2007).

Commensal microflora protects the intestine from sub-optimal growth and adhesion of pathogens to gut mucosa; it stimulates the ileal immune system and provides the body with energy from SCFAs (Montagne et al., 2003; Brownlee, 2011). It has been demonstrated that the addition of iDF sources (lignocellulose, wheat bran, rice bran, pea fiber, wheat straw, oat hulls) to piglet diets improved GIT microbiota (Hanczakowska et al., 2008; Molist et al., 2010 a, b; Molist et al., 2011; Gerritsen et al., 2012; Herfel et al., 2013; Chen et al., 2013). Coarse wheat bran was more effective than finely ground wheat bran because in piglets challenged with *E. coli* K88, it distinctly lowered *E. coli* K88 counts in the ileal digesta (0.7 vs. 2.2 $\log_{10}$ CFU/g; $P<0.05$, resp.) (Molist et al., 2010 a). The development of beneficial gut microbiota was also stimulated by diets supplemented with a mixture of iDF and sDF sources, i.e. wheat bran and sugar beet pulp (Hermes et al., 2009; Molist et al., 2009), as well as sDF (Schiavon et al., 2004). The addition of citrus pulp suppressed ileal and cecal *E. coli* F18 recovery in challenged piglets (Collier et al., 2010). Except for CMC, which stimulated the intestinal colonization by *E. coli* (McDonald et al., 2001; Hopwood et al., 2002), all fibrous feeds included in diets promoted the development of beneficial gut microbiota and inhibited the growth of potential pathogens in the GIT. This was often accompanied by an improved fecal score (Hanczakowska et al., 2008; Molist et al., 2010 b and 2011; Gerritsen et al., 2012) and reduced antibiotic use (Hermes et al., 2009).

Dietary fiber is a major component of digesta that reaches the cecum and colon. Cellulose, hemicellulose and pectin fermentation increases the proportion of acetic acid. Starch fermentation increases the proportion of propionic and butyric acids (Williams et al., 2001). SCFAs have a beneficial influence on gut integrity and metabolism. Acetic acid increases colonic blood flow and enhances ileal motility (Scheppach, 1994). Propionic acid has a stimulatory effect on water absorption from colonic digesta (Williams et al., 2001). Butyric acid is a preferred source of energy for colonocytes, and it can stimulate epithelial cell growth (Scheppach, 1994). It has also been shown that butyrate reduces the interaction of *Salmonella enterica* with the intestinal epithelium (Gantois et al., 2006). Most of the fibrous feeds added to diets stimulated fermentation in the large intestine. The dietary inclusion of sDF, e.g. sugar beet pulp (Schiavon et al., 2004; Jeaurond et al., 2008), inulin (Wellock et al., 2008), and mixed sDF sources (Bikker et al., 2006), increased SCFA concentrations in the cecum and colon/feces, including lactic acid in the colon (Bikker et al., 2006; Jeauround et al., 2008). Diets containing iDF sources, such as wheat bran (Högberg and Lindberg, 2006; Molist et al., 2009; Molist et al., 2011; Chen et al., 2013) and soybean fiber (Chen et al., 2013), increased SCFA concentrations in the cecum and feces, but in many cases they also increased butyric acid concentrations (Högberg and Lindberg, 2006; Corneiro et al., 2007; Molist et al., 2009 and 2011; Chen et al., 2013), compared with the control diet. Elevated butyric acid concentrations in the large intestine suggest that the amount of starch that is not digested in the small intestine is higher in animals fed fiber-supplemented diets than in those fed control diets without fiber supplementation.

Some research findings indicate that the dietary addition of iDF (Schedle et al., 2008), sDF (Awati et al., 2006; Bikker et al., 2006; Jeaurond et al., 2008), and mixed fiber sources (Hermes et al., 2010; Pieper et al., 2012) decreases the concentrations of ammonia and amines in the large intestine (Jeaurond et al., 2008; Kim et al., 2008). This is manifested by a slower rate of proteolytic fermentation which negatively affects the GIT mucosa (Williams et al., 2001).

Insoluble DF is considered an important factor influencing the mean retention time (MRT), water absorption in the colon, fecal DM content and fecal quality. It has been shown (Molist et al., 2009 and 2010 b) that piglets fed a diet supplemented with 8% of wheat bran had a lower percentage of unbound water and a higher water retention capacity in the colonic digesta than those fed the control diet or a diet containing 6% of sugar beet pulp (Molist et al., 2009). The dietary inclusion of 1.5% of cellulose, 3% of soybean hulls or 9% of citrus pulp did not affect the MRT (Pascoal et al., 2012) but differentiated PWD incidence. In the cited study, cellulose decreased and soybean hulls and citrus pulp increased PWD incidence during the first 21 days after weaning. Soluble DF sources such as sugar beet pulp (Schiavon et al., 2004) or their mixture with inulin, lactulose (Awati et al., 2006) or soybean hulls (Montagne et al., 2012), decreased fecal DM content. On day 5 after weaning, this effect was accompanied by a higher incidence of diarrhea (Montagne et al., 2012).

Some data indicate that DF addition may affect enterotoxigenic *E. coli* (ETEC) shedding from the GIT. Wellock et al. (2008) reported that DF solubility did not affect fecal *E. coli* O149 shedding by challenged piglets, but piglets fed diets with high DF content shed fewer ETEC than those fed diets with low DF content.

The adhesive properties of DF sources have also been investigated in *in vitro* tests. *E. coli* K88 more strongly adhered to wheat bran than to other fiber substrates (Molist et al., 2011). Similarly, in a blocking test (microtitration-based model), the number of ETEC K88 cells that attached to the intestinal mucus after being co-incubated with wheat bran extract was lower as compared with those incubated with extracts of fructooligosaccharides and mannanoligosaccharides (González-Oritz et al., 2014). Both *in vivo* and *in vitro* experiments revealed that DF sources may be helpful in controlling the incidence of GIT infections in piglets.

The intestinal layer of epithelial cells and interepithelial tight junction proteins such as claudin, occludin and zonula occludens proteins (ZO-1, ZO-2, ZO-3) form an intestinal barrier and prevent the diffusion of bacteria and other antigens across the epithelium (Dulantha et al., 2011). Tumor necrosis factor-a (TNF-a), interleukins (IL-1 and IL-6), interferon-g (IFN-g) may influence epithelial permeability and ion transport, and are involved in the elimination of pathogens (Lallès et al., 2004). Between days 1 and 7 after weaning, the mRNA expression of tight junction proteins in the jejunal mucosa decreases compared with the suckling period (Hu et al., 2013). Moreover, the mRNA expression of TNF-a, IL-6 and IFN-g increases 2 to 3 days after weaning (Lallès et al., 2004; Hu et al., 2013). This suggests that weaning stress affects signaling pathways in the intestine, which may play an important role in the mechanism of enteric disorders. Some data indicate that DF may also alter intestinal permeability. Chen et al. (2013) reported that piglets fed a diet supplemented with 10% of wheat bran fiber for 30 days post-weaning had increased mRNA expression levels of tight junction protein (ZO-1) and Toll-like receptor 2 (TLR2) in the ileum and colon. However, the dietary addition of sDF sources up-regulated IL-6 mRNA expression in the colon on day 4 after weaning, suggesting stimulation of inflammatory responses (Pié et al., 2007). Therefore, it seems that piglet diets should be supplemented with iDF sources rather than sDF sources.

Conclusions

The results of studies summarized in this review article suggest that most of the applied DF sources decrease the ileal and fecal OM digestibility, and they often reduce CP digestibility. Weaned piglets fed diets supplemented with a moderate amount (1.5–8%) of fibrous feeds as sources of iDF are characterized by higher ADFI, which is often accompanied by higher ADG. Sources of sDF (pectin, inulin, citrus pulp) as well as high dietary inclusion levels of fiber-rich feeds tended to decrease ADFI and ADG. The use of iDF substrates, such as lignocellulose preparations, pure cellulose, cooked or raw oat hulls and wheat bran, improves fecal consistency and decreases PWD incidence. In comparison with sDF sources, iDF sources improve GIT function and health status. Insoluble DF supports GIT development, stimulates enzyme activity and improves gut morphology. Diets supplemented with iDF and sDF substrates contribute to an increase in the counts of beneficial gut microbiota and the concentrations of SCFAs, including butyric acid, in the GIT. Such diets also slow down proteolytic fermentation which negatively affects the colonic mucosa. Some research findings indicate that iDF sources may also improve intestinal barrier function.

Due to the various characteristics of fiber used in the applied diets (quantities and solubility), it is difficult to recommend the optimum levels of DF or NSP, including insoluble and soluble fractions, in piglet diets. However, the research results analyzed in this article imply that the addition of 1.5-2.0% of a lignocellulose preparation, 2% of oat hulls and 4-8% of coarse wheat bran to diets for weaned piglets may be recommended to promote GIT development and gut health, and to improve growth performance.

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