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Effect of different dietary fibre sources on the zootechnical performance, feeding behaviour and intestinal physiology of growing and finishing pigs

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Abstract: The aim of this study was to determine the effect of different sources of fibre in the diets of fattening pigs on performance, feeding behaviour and intestinal physiology. A total of 60 barrows and gilts (initial body weight 28.4 ± 0.4 kg) were allotted to four dietary treatments: control (CON), lignocellulose (LC), mycelium (MYC) and corn gluten feed (CGF). Diets were calculated to provide balanced available nutrient contents. Including MYC in the diet resulted in an increased average daily gain ($P < 0.05$) compared to CON and CGF, and improved gain to feed ratio ($P < 0.05$) compared to LC. Pigs in CON ($P < 0.05$) ate the fewest but largest meals, whereas treatment CGF ($P < 0.05$) showed the opposite effect, resulting in the same daily feeder occupation time. Regarding intestinal physiology, in ileum, no differences were observed between the contents of short chain fatty acids (SCFA), lactic acid and biogenic amines. In the colon, MYC showed an increased concentration of acetic acid ($P < 0.05$) as well as the total content of SCFA ($P < 0.05$), compared to LC and CGF. Distinct fermentation profiles of ammonia were recorded in ileal and colonic digesta, although contents remained below harmful concentrations. Morphometrical measurements showed differences between the fibre sources LC and MYC, as well as LC and the CON in all investigated gut sections. These results provide evidence that the inclusion of specific dietary fibre sources/contents can positively influence the gut morphology and performance of pigs. However, further studies are needed regarding the mode of action and physico-chemical characteristics of the different fibre sources as a precondition for their successful application in pig diets.

Keywords: fattening pig; dietary fibre sources; behaviour; gut physiology

In recent years the focus on high performance in pig production has shifted to include not only output but also a greater emphasis on improved animal health and welfare. Of particular interest in terms of investigations of potential animal welfare parameters from a physiological point of view are the effects on microbial metabolites, such as short chain fatty acids (SCFA), biogenic amines (bA), lactic acid or ammonia, as well as the gut morphology (Schedle et al. 2008; Schedle 2016). In terms of improving gut health, there is increasing interest in enhancing the amounts of dietary fibre (DF) supplementation in the diets of pigs. Dietary fibre is defined as the sum of soluble and insoluble

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carbohydrates with three or more monomeric units and lignin which are neither hydrolyzed by endogenous enzymes nor absorbed in the small intestine (Cummings et al. 2009). Typically, soluble dietary fibre (SDF) constitutes the minor part, and insoluble dietary fibre (IDF) is a major part of the total dietary fibre (TDF) in most feedstuffs fed to pigs (Jaworski et al. 2015). High amounts of SDF lead to increased digesta viscosity, satiety and a decreased rate of gastric emptying, whereas IDF causes an increased passage rate, bulkiness of faeces and softer faeces (Wenk 2001; Montagne et al. 2003). Alongside this traditional classification of dietary fibres, there are additional physico-chemical properties that differ between the available dietary fibre sources (Slama et al. 2019).

There have been few reported studies regarding dietary fibre and feeding behaviour. Nevertheless, several studies have confirmed a positive effect of certain quantities of DF with regard to prolonged chewing activity and increased satiety leading to a reduction of aggression and stereotypes (Kallabis and Kaufmann 2012). Despite these positive effects of DF, a reduction of energy and protein digestibility can also be observed (Noblet and Le Goff 2001). Thus, the effects of nutrient dilution and reduced digestibility have to be compensated in the diet calculations if negative effects on performance are to be avoided (Schedle 2016). Carbohydrate fermentation in the gut leads to the production of straight SCFA whereas protein fermentation leads to straight SCFA and their isomers (branched-chain fatty acids; BCFA) as well as potentially toxic substances (i.e., ammonia and bA) (Rasmussen et al. 1988; De Preter et al. 2011).

In a feed choice study, pigs chose a total dietary fibre content between of 12.3% and 14.5% (Pichler et al. 2020). Based on these results we wanted to test the effect of different dietary fibre sources, under a feeding regime that was comparable to the nutrient supply used in the feed choice study of Pichler et al. (2020). Therefore, the aim of this study was to determine the effect of different – mainly insoluble – fibre sources with different physico-chemical properties [lignocellulose (LC), mycelium (MC) and corn gluten feed (CGF)] (Slama et al. 2019) in terms of fattening performance and feeding behaviour, as well as on intestinal physiology considering a constant energy and available nutrient content between the diets. It was hypothesized that due to the nutrient-balanced diets no differences between treatments regarding the fattening performance would appear. Furthermore, we expected effects through the different fibre sources with regard to feeding behaviour and parameters regarding gut physiology.

MATERIAL AND METHODS

Animals and experiments

The research was conducted at the Austrian pig testing facility (Streitdorf, Austria) under compliance with the 1st regulation of animals keeping (BGBl. II No. 485/2004). The current study employed a total of 28 barrows and 32 gilts [28.4 ± 0.4 kg; OEHYB: ((Large White × Landrace) × Piétrain)]. The pigs were randomly allotted to 12 pens, and four dietary treatments. The pens were on a fully slatted concrete floor, with an automatic dry feeder and a nipple drinker. Each treatment group comprised seven barrows and eight gilts. Ground feed and water were provided *ad libitum*. Individual body weights (BW) were determined weekly. The automatic dry-feeding system, individually recorded every feed intake, time of feed intake and also the amount of feed as measured with a transponder chip. The individual feeding duration, feeding frequency and feed intake were calculated for each visit, day and feeding phase. For the data collected on feeding behaviour, visits that ingested 10 g or less were defined as gambolling and hence they were removed from the dataset. Animals received a grower diet (28.4 ± 0.4 kg – 74.4 ± 0.5 kg BW) and a finisher diet (74.4 ± 0.5 kg – 115.6 ± 0.2 kg BW). In addition to the common performance parameters of average daily gain (ADG), average daily feed intake (ADFI) and gain to feed ratio (G : F), calculations were also made of the daily energy intake (EI) and the energy conversion (EC). As EI was defined, the total individual energy intake was calculated as the energy content of the feed multiplied by the ADFI. The EC was defined as the weight gain in grams based on one MJ energy intake. The animals were slaughtered by skilled staff applying standardized conditions in the slaughterhouse of the pig testing facility when individual body weight reached at least 113 kg. The four dietary treatments were based on corn, barley and soybean meal (Table 1). Treatment 1 (CON) acted as a control treatment without additional dietary

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Table 1. Ingredients and chemical composition of experimental diets

	Grower				Finisher			
	CON	LC	MYC	CGF	CON	LC	MYC	CGF
Ingredients								
Corn (%)	52.18	49.50	49.50	52.88	46.11	57.54	57.54	48.44
Barley (%)	24.34	20.00	20.00	20.00	38.29	20.00	20.00	32.14
Soybean meal without hulls (%)	20.39	20.25	20.25	19.11	12.77	13.49	13.49	11.64
Sunflower oil (%)	–	2.14	2.14	–	–	1.10	1.10	–
Limestone (%)	1.39	1.32	1.32	1.43	1.30	1.25	1.25	1.36
Monocalcium phosphate (%)	0.26	0.34	0.34	0.15	0.10	0.21	0.21	–
Sodium chloride (%)	0.25	0.22	0.22	0.22	0.25	0.23	0.23	0.22
L-lysine HCl, 80% (%)	0.35	0.37	0.37	0.38	0.37	0.38	0.38	0.40
DL-methionine (%)	0.15	0.16	0.16	0.14	0.11	0.13	0.13	0.11
L-threonine (%)	0.16	0.16	0.16	0.16	0.15	0.14	0.14	0.15
L-tryptophan (%)	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.05
Lignocellulose (%)	–	5.00	–	–	–	5.00	–	–
Mycelium (%)	–	–	5.00		–	–	5.00	–
Corn gluten feed (%)	–	–	–	5.00	–	–	–	5.00
Vitamin and trace element premix (%)[1]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Phytase (IU/kg)	750	750	750	750	750	750	750	750
Chemical composition, analysed (per kg, based on 880 g/kg dry matter)								
Dry matter (g)	882	886	883	887	894	886	884	889
Predicted ME (MJ)	13.7	13.2	13.6	13.5	13.5	13.3	13.6	13.6
Predicted NE (MJ)	10.0	9.6	10.0	9.9	9.9	9.7	9.9	9.9
Crude ash (g)	46	43	43	47	42	39	40	39
Crude protein (g)	167	161	163	166	140	135	136	144
Ether extract (g)	24	44	43	25	24	37	34	23
Sugar (g)	35	37	33	33	35	28	28	29
Starch (g)	489	455	462	483	526	516	513	504
Crude fibre (g)	25	47	36	30	28	41	30	28
Acid detergent fibre (g)	31	62	51	36	33	58	52	40
Neutral detergent fibre (g)	79	106	102	93	87	107	111	113
Total dietary fibre (g)	122	160	141	125	120	150	139	136
Soluble dietary fibre (SDF, g)	4	6	11	3	7	7	10	3
Insoluble dietary fibre (IDF, g)	118	154	130	122	113	143	129	133
IDF/SDF	30	26	12	41	16	20	13	44
Ca (g)	5.7	5.9	6.5	6.6	6.5	6.2	6.2	5.7
Na (g)	1.2	1.0	1.2	1.4	1.3	1.2	1.3	1.4
P (g)	4.3	4.3	4.4	4.2	3.6	3.4	3.6	3.8

CGF = group with corn gluten feed; CON = control group; LC = group with lignocellulose; ME = metabolizable energy (GfE 2008); MYC = group with mycelium; NE = net energy (Noblet et al. 1994)

[1]Vitamin and trace element premix consisting of: vitamin A 1 200 000 IU/kg; vitamin D_3 391 200 IU/kg; vitamin E as all-racalpha-tocopherol acetate 4 000 mg/kg; vitamin K_3 840 mg/kg; vitamin B_1 480 mg/kg; vitamin B_2 1 200 mg/kg; vitamin B_6 840 mg/kg; vitamin B_{12} as cyanocobalamin 8.4 mg/kg; niacin amide 7 200 mg/kg; Ca-D-pantothenate 3 000 mg/kg; folic acid 120 mg/kg; biotin 18 mg/kg; Fe as iron-(II)-sulphate-monohydrate 12 400 mg/kg; Zn as zinc oxide 14 200 mg/kg; Mn as manganese-(II)-oxide 7 822 mg; Cu as copper-(II)-sulphate pentahydrate 2 200 mg/kg; I as calcium iodate 260 mg/kg; Se as sodium selenite 60 mg/kg; Ca-carbonate as carrier 87.7% (i.e. 33.3% Ca)

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fibre supplementation. Treatment 2 (LC) included 5% lignocellulose (SDF/IDF/TDF: 13/933/946 g/kg DM). Treatment 3 (MYC) had 5% mycelium (heat inactivated mycelium of *Aspergillus niger*, indirectly dried by steam; fermentation residue from the citric acid production; SDF/IDF/TDF: 13/756/769 g/kg DM. Treatment 4 (CGF) contained 5% corn gluten feed (a dried co-product of the corn wet milling process; SDF/IDF/TDF: 0/488/488 g/kg DM). All diets were calculated to meet or exceed the nutritional requirements of the GfE (2006) and were balanced for their content of net energy (NE), standardized ileal digestible (SID) lysine (Lys), SID methionine (Met), SID threonine (Thr), SID tryptophan (Trp), Ca, digestible P and Na.

Sampling and analyses

Feedstuff. Samples of the diets were taken immediately after mixing. The diets were analysed for dry matter (DM), crude protein (CP), crude fibre (CF), ether extract (EE), ash, starch and sugar, as well as the elements Ca, P and Na according to standard procedures (VDLUFA 2012). Total dietary fibre (TDF) analysis (Method No. AOAC 991.43, including IDF and SDF) was carried out with the ANKOM TDF Fiber Analyzer (ANKOM, Macedon, NY, USA). Due to the different DM levels, the DM was equally calculated to 88%. The metabolizable energy (ME) content was estimated using the formula for compound feed published by the society of nutrition physiology (GfE 2008). For the calculation of the net energy (NE) content the formula by Noblet et al. (1994) was applied. Amino acids were calculated as standardized ileal digestible according Sauvant et al. (2004).

Digesta. Following slaughter, and immediately after removing the gastrointestinal tract, digesta samples were taken from the end of ileum (approx. 1.5 m–10 cm prior ileo-caecal junction) and the colon ascendens (30 cm from the junction flexura centralis to the distal loop). The digesta were filled in tubes and stored at –18 °C until further analyses for DM, SCFA, bA, lactic acid and ammonia. The DM content was estimated according to VDLUFA (2012). The content of SCFA were analysed according the method of Zhao et al. (2006) with a gas chromatographic system (Agilent Technologies 7890A GC System with 7683B Injector; Santa Clara, CA, USA) and the integration was done with the appropriate software (Agilent GC ChemStation; Agilent Technologies, Santa Clara, CA, USA). The determination of the concentration of bA was done according to Saarinen (2002) with a high performance liquid chromatography system (Waters Alliance® HPLC e2695 Separations Module and software Waters Empower 2 Pro; Waters™, Milford, MA, USA) and a specific column (InertClone™ 5 µm ODS(2) 150 Å, LC Column 250 × 4.6 mm; Phenomenex®, Torrance, CA, USA). Detection was achieved with UV-Vis detector (Waters 2489 UV/Visible Detector; Waters™, Milford, MA, USA). Lactic acid and ammonia contents were analysed according to the methods of Pryce (1969) and Patton and Crouch (1977), respectively, using a spectro-photometer (Tecan Sunrise; Tecan Trading AG, Männedorf, Switzerland) for quantification.

Morphology. Immediately after slaughter, tissue samples from the proximal jejunum (~1 m distal from pylorus), the end of the ileum (approx. 10 cm prior ileo-caecal junction) and the colon ascendens (at the junction flexura centralis to the distal loop) were drawn and washed with phosphate buffered saline. After 48 h of fixation in formalin the samples were embedded in paraffin wax. Samples were cut with a microtome (Leica RM 2145; Leica Microsystems GmbH, Wetzlar, Germany) to a thickness of 5 µm and tissues were subsequently stained with Alcianblue and Periodic acid–Schiff (Leica Autostainer-XL; Leica Microsystems GmbH, Wetzlar, Germany). The tissue samples were examined with a light microscope (Leica DM 6000 B; Leica Microsystems GmbH, Wetzlar, Germany) and morphometrical measurements were carried out applying software (Leica Application Suite, v3.5.0; Leica Microsystems GmbH, Wetzlar, Germany). Histometrical measurements of villus height (from the tip of the villus to the villus-crypt junction), villus surface area (cross-sectional area of a villus measured above the crypt-villus junction), crypt depth (from the onset of crypt to the base of the crypt), crypt surface area (cross-sectional area of the luminal space of a crypt including the epithelial cells) were made on six well-orientated villi and crypts, respectively. The thickness of muscularis was also determined. Goblet cells were counted in the selected six villi and crypts. The mean of six measurements per sample was used as the aver-

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age value for further analyses. Villus crypt ratio was calculated.

Data processing. All data were processed in Microsoft Excel 2013 (Microsoft, Redmond, WA, USA) and outliers were removed. Outliers were defined as values differing by more than two times standard deviation of the mean. Additional statistical analysis was performed with the procedure GLM (general linear model, Statistical Analysis Software v9.4, SAS Institute Inc., Cary, NC, USA). The experimental factors were diet and sex, and the interaction of diet × sex. Using the Tukey-Kramer method the multiple comparison of least square means was performed and results are presented in the tables below. Differences between diets or sex were considered statistically significant at $P < 0.05$ (and $P < 0.1$ was considered as a trend). An interaction between diet and sex was considered statistically significant at $P < 0.05$, and trends at lower levels of significance were not respected.

RESULTS

As no diet × sex interactions were detected only the results for main effects are presented below. Due to health issues unrelated to diets, it was necessary to remove two animals (from CON and MYC) from the study. As shown in Table 1, the diets differed in their total nutrient content. Furthermore, the calculated balanced energy and nutrient content could not always be achieved; however, values were within the analytical tolerance and the nutrient contents reached the GfE recommendations of (GfE 2006). Table 2 presents the zootechnical performance parameters. In the grower phase there was no difference ($P > 0.1$) in average daily gain (ADG), average daily feed intake (ADFI) and the daily energy intake (EI) between treatments. However, MYC in the diet improved ($P < 0.05$) the gain : feed (G : F) and energy conversion (EC) compared to that of LC (–12.8%; –10.1%) and CGF (–10.8%; –10.1%) treatment. In the

Table 2. Effect of the fibre source and sex on zootechnical performance in the grower and finisher phases of fattening pigs

	Diet				Sex		SEM	*P*-value	
	CON	LC	MYC	CGF	♂	♀		diet	sex
Grower phase									
ADG (g)	838	856	898	836	897	816	12.5	0.100 9	0.001 0
ADFI (g)	1 768	1 917	1 811	1 958	2 024	1 703	43.0	0.270 8	0.000 1
G : F (g/kg)	469^{ab}	436^{b}	500^{a}	446^{b}	451	475	7.1	0.004 1	0.055 1
EI (MJ ME/day)	24.2	25.4	24.7	26.5	27.4	23.0	0.57	0.440 7	0.000 1
EI (MJ NE/day)	17.7	18.6	18.1	19.4	20.0	16.9	0.42	0.443 6	< 0.000 1
EC (g/MJ ME)	34.2^{ab}	33.0^{b}	36.7^{a}	33.0^{b}	33.3	35.1	0.50	0.021 4	0.055 3
EC (g/MJ NE)	46.7^{ab}	45.0^{b}	50.1^{a}	45.1^{b}	45.5	48.0	0.69	0.022 1	0.055 3
Finisher phase									
ADG (g)	868^{ab}	924^{a}	940^{a}	825^{b}	954	824	16.9	0.014 3	< 0.000 1
ADFI (g)	2 585^{b}	2 995^{a}	2 695^{ab}	2 508^{b}	2 984	2 406	66.9	0.007 9	< 0.000 1
G : F (g/kg)	332^{ab}	317^{b}	350^{a}	325^{ab}	323	339	4.5	0.048 7	0.061 1
EI (MJ ME/day)	34.9^{ab}	39.8^{a}	36.6^{ab}	34.1^{b}	40.3	32.5	0.9	0.022 9	< 0.000 1
EI (MJ NE/day)	26.6^{ab}	29.0^{a}	26.7^{ab}	24.8^{b}	29.4	23.7	0.6	0.024 1	< 0.000 1
EC (g/MJ ME)	24.2	23.8	25.4	23.9	23.9	24.8	0.3	0.219 6	0.158 7
EC (g/MJ NE)	32.9	32.7	35.0	32.9	32.8	33.9	0.4	0.191 6	0.157 4
Total									
ADG (g)	850^{b}	876^{ab}	931^{a}	828^{b}	919	819	13.0	0.005 1	< 0.000 1
ADFI (g)	2 163	2 422	2 249	2 227	2 474	2 057	47.0	0.106 1	< 0.000 1
G : F (g/kg)	388^{ab}	368^{b}	410^{a}	376^{ab}	375	396	5.1	0.016 0	0.026 8

ADFI = average daily feed intake; ADG = average daily gain; CGF = group with corn gluten feed; CON = control group; EC = energy conversion; EI = energy intake; G : F = gain to feed; LC = group with lignocellulose; MYC = group with mycelium; SEM = standard error of means

^{a,b}Mean values within a row without a common superscript differ significantly ($P < 0.05$)

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finisher phase the ADG of the treatment including LC (+12.0%) and MYC (+13.9%) were enhanced ($P < 0.05$) compared to that of the CGF. Furthermore, LC had a higher ADFI ($P < 0.05$) compared to CON (+13.7%) and CGF (+16.3%) which led to a higher daily EI ($P < 0.05$) than CGF (+5.7 MJ ME, +4.2 MJ NE). MYC improved G : F (+9.4%; $P < 0.05$) compared to that of LC. Over the total fattening phase CON (–8.7%) and CGF (–11.1%) showed reduced ADG compared to MYC ($P < 0.05$). Similar to the grower phase, a MYC supplementation improved G : F compared to the LC (–10.2%; $P < 0.05$) treatment. Regarding sex, barrows increased ($P < 0.05$) ADG (+9.0% to +13.6%), ADFI (+12.8% to +19.4%), EI (+16.1% to +19.4%), and declined ($P < 0.05$) G : F (–5.6%) in the grower, finisher and total fattening phase.

The results of the feeding behaviour are shown in Table 3. In all phases pigs in treatment group CGF consumed more but smaller meals per day than the CON ($P < 0.05$). Additionally, in the finisher phase pigs in MYC also consumed more meals (+39.6%; $P < 0.05$) per day than in CON, whereas LC showed larger meals in the finisher phase (+29.3%) and over the whole fattening phase (+23.5%) as the CGF ($P < 0.05$). Additionally, in the finisher phase, there was a trend for faster meal consumption in the LC treatment ($P < 0.1$) compared to the CGF. In both phases, pigs in CON tended to take longer meals but without any difference in the total daily feeder occupation time compared to CGF ($P < 0.1$). Barrows consumed more meals per day (+15.7% to +19.2%; $P < 0.05$) with no difference in the time per visit, leading to a longer total daily feeder occupation time ($P < 0.05$) in the finisher phase (+18.8%) and over the whole fattening phase (+14.6%; $P < 0.05$).

Table 4 shows the dry matter content and concentration of SCFA and ammonia in the ileal and colon digesta. No differences in the content of biogenic amines ($P > 0.1$) and lactic acid ($P > 0.1$) were

Table 3. Effect of the dietary fibre source and sex on the feeding behaviour in grower and finisher phase of fattening pigs

	Diet				Sex		SEM	*P*-value	
	CON	LC	MYC	CGF	♂	♀		diet	sex
Grower									
Meals/day (*n*)	21.5^{b}	26.0^{ab}	28.0^{ab}	30.8^{a}	28.7	24.4	1.1	0.010 5	0.031 6
g/meal	77.7^{a}	68.2^{ab}	64.4^{ab}	58.8^{b}	69.1	65.4	2.0	0.004 6	0.310 8
g/min	17.2	17.5	16.9	18.1	17.8	17.1	0.4	0.735 9	0.383 3
t/visit (min)	4.7$^{(a)}$	4.0$^{(ab)}$	4.0$^{(ab)}$	3.6$^{(b)}$	4.0	4.1	0.2	0.098 4	0.799 0
t/day (min)	96.9	97.3	97.2	105.6	104.7	93.8	2.4	0.431 3	0.097 0
Finisher									
Meals/day (*n*)	22.5^{b}	27.4^{ab}	31.4^{a}	33.1^{a}	31.1	26.1	1.3	0.011 4	0.034 2
g/meal	109.6^{a}	108.5^{a}	91.3^{ab}	76.7^{b}	99.9	93.2	4.4	0.013 9	0.403 6
g/min	26.9$^{(ab)}$	29.1$^{(a)}$	27.0$^{(ab)}$	24.9$^{(b)}$	27.2	26.7	0.6	0.081 7	0.620 2
t/visit (min)	4.1$^{(a)}$	3.7$^{(ab)}$	3.4$^{(ab)}$	3.1$^{(b)}$	3.7	3.5	0.1	0.075 3	0.494 1
t/day (min)	93.0	98.8	101.3	102.5	107.0	90.1	2.5	0.585 1	0.000 4
Total									
Meals/day (*n*)	22.1^{b}	26.6^{ab}	29.7^{ab}	31.4^{a}	29.5	25.5	1.1	0.013 8	0.045 7
g/meal	91.2^{a}	88.4^{a}	80.8^{ab}	67.6^{b}	84.3	79.8	2.9	0.012 2	0.394 5
g/min	21.8	23.2	21.5	21.2	22.3	21.6	0.4	0.355 9	0.417 5
t/visit (min)	4.1	3.7	3.8	3.2	3.7	3.7	0.1	0.169 0	0.827 8
t/day (min)	94.5	97.7	97.9	103.8	105.2	91.8	2.2	0.547 3	0.003 0

CGF = group with corn gluten feed; CON = control group; g/meal = amount of feed (g) per visit; g/min = amount of feed (g) per minute; LC = group with lignocellulose; Meals/day = number of daily visits at the feeder; MYC = group with mycelium; SEM = standard error of means; t/day = feeder occupation time per day in minutes; t/visit = feeder occupation time per visit in minutes

^{a,b}Mean values within a row without a common superscript differ significantly ($P < 0.05$); $^{(a,b)}$mean values within a row without a common superscript tend to differ ($P < 0.1$)

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Table 4. Effect of the dietary fibre source and of sex on the dry matter content and microbial metabolites (mmol/kg dry matter) in digesta in the ileum and colon of fattening pigs

	Diet				Sex		SEM	*P*-value	
	CON	LC	MYC	CGF	♂	♀		diet	sex
Ileum									
Dry matter (%)	9.9^{ab}	9.5^{b}	11.8^{a}	10.7^{ab}	9.9	11.0	0.3	0.023 4	0.060 5
Acetic acid (C_2)	338.7	383.1	378.2	377.8	360.1	378.8	15.74	0.755 6	0.566 8
Propionic acid (C_3)	49.2	51.8	42.3	43.5	47.2	46.2	2.26	0.414 5	0.821 9
Butyric acid (C_4)	39.9	45.1	56.0	44.4	44.5	48.2	3.74	0.506 0	0.636 0
Iso-valeric acid	5.7	6.5	5.7	5.4	6.7	5.0	0.39	0.756 9	0.029 3
Caproic acid	3.9	4.1	3.8	5.3	3.7	4.8	0.32	0.243 1	0.070 7
Total SCFA	445.0	510.0	499.2	485.0	470.2	499.4	20.5	0.715 4	0.489 2
C_2	0.78	0.79	0.79	0.80	0.79	0.79	0.007	0.815 5	0.661 0
C_3	0.12	0.12	0.09	0.10	0.10	0.11	0.008	0.508 6	0.573 9
C_4	0.10	0.09	0.12	0.10	0.10	0.10	0.006	0.371 5	0.809 1
Ammonia	5.7^{b}	9.5^{a}	7.0^{ab}	5.8^{b}	7.2	6.9	0.54	0.049 2	0.800 3
Colon									
Dry matter (%)	22.5$^{(b)}$	24.5$^{(a)}$	22.7$^{(ab)}$	23.0$^{(ab)}$	23.2	23.1	0.3	0.051 8	0.862 4
Acetic acid (C_2)	328.6^{ab}	295.5^{b}	367.7^{a}	299.5^{b}	326.9	318.8	7.14	0.000 4	0.508 2
Propionic acid (C_3)	135.2	126.0	139.6	124.1	133.4	129.1	3.19	0.255 7	0.496 7
Butyric acid (C_4)	115.8	103.2	113.1	98.8	112.3	103.2	2.93	0.116 2	0.109 7
Iso-butyric acid	11.9^{a}	11.1^{ab}	12.7^{a}	10.2^{b}	11.90	11.1	0.25	0.001 4	0.067 0
Valeric acid	15.5$^{(a)}$	12.9$^{(b)}$	14.8$^{(ab)}$	12.8$^{(b)}$	15.2	12.8	0.43	0.029 1	0.002 0
Iso-valeric acid	8.6	8.0	8.6	7.7	8.4	7.9	0.20	0.297 0	0.205 0
Caproic acid	5.4^{a}	3.1^{b}	5.6^{a}	4.6^{a}	4.9	4.5	0.22	< 0.000 1	0.253 1
Heptanoic acid	2.1	1.9	2.0	1.7	2.0	1.9	0.07	0.176 0	0.213 5
Total SCFA	626.3^{ab}	561.9^{b}	656.4^{a}	552.8^{b}	614.9	583.8	12.77	0.004 3	0.174 9
C_2	0.57	0.56	0.59	0.58	0.58	0.58	0.004	0.062 5	0.801 0
C_3	0.23	0.24	0.23	0.23	0.23	0.24	0.002	0.279 0	0.322 8
C_4	0.20	0.20	0.18	0.18	0.20	0.19	0.003	0.079 9	0.055 7
Ammonia	2.1^{a}	1.9^{ab}	1.8^{b}	1.7^{b}	2.0	1.8	0.8	0.003 0	0.017 6

C_2 = acetic acid; C_3 = propionic acid; C_4 = butyric acid ratio; CGF = group with corn gluten feed; CON = control group; LC = group with lignocellulose; MYC = group with mycelium; SEM = standard error of means; Total SCFA = sum of all detected short chain fatty acids

^{a,b}Mean values within a row without a common superscript differ significantly ($P < 0.05$); $^{(a,b)}$mean values within a row without a common superscript tend to differ ($P < 0.1$)

detected (data not shown in the table). The MYC supplementation resulted in a higher dry matter content in the ileal digesta (+24.2%) compared with that of the LC treatment ($P < 0.05$). In contrast to the ileum, the DM in the colon digesta of the LC-treated pigs increased, and there was a trend for higher DM content compared with the CON treatment ($P < 0.1$). In the ileum, no differences regarding the content of SCFA between the treatments were found, whereas in the colon treatment MYC showed a significantly higher concentration of acetic acid and total SCFA compared with that for LC (+19.6%; +14.4%) and CGF (+18.5%; +15.7%). CGF had a lower content ($P < 0.05$) of iso-butyric acid related to CON (–16.7%) and MYC (–24.5%). There was a trend for higher amounts of valeric acid in the CON compared with LC and CGF ($P < 0.1$). Treatment LC had significantly lower values of caproic acid compared with the other groups (CON: –42.6%; MYC: –44.6%; CGF: –32.6%). Including

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LC in the diet also increased ammonia content ($P < 0.05$) in ileal digesta compared with the CON (+40.0%) and CGF (+38.9%). In the colon digesta CON showed significantly higher contents of ammonia than was recorded in either MYC (+14.3%) or CGF (+19.0%). Barrows showed higher values of iso-valeric acid (+34.0%; $P < 0.05$) and, compared with gilts, there was a trend to decreased ($P < 0.1$) dry matter and caproic acid content in ileum. In the colon of barrows there were higher contents of valeric acid (+18.8%) and ammonia compared with the colon of gilts ($P < 0.05$).

Table 5 presents the results of jejunal, ileal and colonic morphometrical measurements. In treatment LC there was a trend for higher villi in the jejunum ($P < 0.1$) compared with MYC, though these differences were not observed in the ileum. There were no differences between treatments recorded for villi area in jejunum; however, in the ileum CGF showed a trend to a decreased villi area compared with LC and MYC. For treatment LC there were more goblet cells (+24.0%; $P < 0.05$) in the jejunum compared with MYC, whereas in the ileum CON showed a significant increase (+53.2%) compared with CGF. For LC there was a trend for an increased jejunal crypt depth ($P < 0.1$) compared with CON, whereas there was a trend for a decreased colonic crypt depth compared with MYC. In the jejunum LC resulted in a greater crypt area (+18.8%; $P < 0.05$) compared with MYC and CGF; however, in ileum, LC showed a trend to a larger crypt area as CON. In ileum, LC trended to an increase in crypt goblet cell number in comparison to MYC, whereas in colon a trend to a decrease in LC compared to CON was observed. MYC led to a thicker colonic muscularis (+39.9%; $P < 0.05$) compared to LC. Barrows trended to show an increase of crypt area in ileum ($P < 0.1$).

DISCUSSION

Fattening performance

The inclusion of high amounts of fibre-rich feedstuffs in the diet reduces the digestibility of many

Table 5. Effect of the dietary fibre source and sex on the gut morphology of fattening pigs

	Diet				Sex		SEM	*P*-value	
	CON	LC	MYC	CGF	♂	♀		diet	sex
Villi height (μm)									
Jejunum	393.3$^{(ab)}$	434.7$^{(a)}$	352.8$^{(b)}$	384.3$^{(ab)}$	394.3	388.2	10.5	0.050 5	0.764 7
Villi area (mm²)									
Ileum	0.060$^{(ab)}$	0.065$^{(a)}$	0.064$^{(a)}$	0.051$^{(b)}$	0.060	0.060	0.002	0.056 4	0.815 6
Villi goblet cells (*n*)									
Jejunum	23.4^{ab}	24.3^{a}	19.6^{b}	20.8^{ab}	21.9	22.1	0.60	0.021 8	0.871 7
Ileum	38.0^{a}	31.2^{ab}	31.1^{ab}	24.8^{b}	30.8	31.8	1.41	0.009 1	0.728 8
Crypt depth (μm)									
Jejunum	472.1$^{(b)}$	523.0$^{(a)}$	473.8$^{(ab)}$	488.1$^{(ab)}$	485.3	493.2	7.6	0.071 6	0.600 7
Colon	388.4$^{(ab)}$	371.0$^{(b)}$	412.3$^{(a)}$	372.6$^{(ab)}$	391.7	380.5	6.3	0.079 6	0.363 0
Crypt area (mm²)									
Jejunum	0.017^{ab}	0.019^{a}	0.016^{b}	0.016^{b}	0.016	0.018	0.000 4	0.017 4	0.180 6
Ileum	0.019$^{(b)}$	0.023$^{(a)}$	0.020$^{(ab)}$	0.020$^{(ab)}$	0.021	0.020	0.000 5	0.051 5	0.062 8
Crypt goblet cells (*n*)									
Jejunum	40.6$^{(ab)}$	44.8$^{(a)}$	38.2$^{(b)}$	39.3$^{(ab)}$	40.5	40.9	0.88	0.051 6	0.794 2
Colon	66.9$^{(a)}$	59.5$^{(b)}$	63.9$^{(ab)}$	63.3$^{(ab)}$	62.5	64.3	0.98	0.051 9	0.332 4
Muscularis (μm)									
Colon	193.4^{ab}	182.6^{b}	255.4^{a}	190.1^{ab}	206.5	204.2	9.81	0.030 0	0.901 7

CGF = group with corn gluten feed; CON = control group; LC = group with lignocellulose; MYC = group with mycelium; SEM = standard error of means

^{a,b}Mean values within a row without a common superscript differ significantly ($P < 0.05$); $^{(a,b)}$mean values within a row without a common superscript tend to differ ($P < 0.1$)

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nutrients, and as a result the available energy for the pig decreases. A higher content of dietary fibre can also be related to a decrease in performance (Schedle 2016). After an adaptation phase the dilution of nutrients, and subsequently dilution of the energy content, can increase feed intake as the animal compensates until its physical satiety is reached (Kyriazakis and Emmans 1995; Pichler et al. 2020). In the present study there was evidence of a compensatory effect of feed intake in the LC and MYC treatment, but not in the CGF treatment. The inclusion of vegetable oil in the LC and MYC diets may have had a beneficial effect on dietary preference or palatability of LC and MYC compared to CGF, thereby leading to an increased feed intake. Soluble dietary fibre was assumed to contain no additional metabolizable energy when calculating the value of the applied diets. This could be a reason for the differences regarding energy content per kg diet between LC and MYC in the finisher phase. In contrast to the results from the present study, Kraler et al. (2015) and Slama et al. (2020) reported no effect on performance in their studies with piglets where fibre-rich but nutrient-balanced diets were fed. Furthermore, Schedle et al. (2008) demonstrated that moderately increasing TDF contents can lead to increased ADG and ADFI with no difference in G : F. Gutierrez et al. (2013) showed that increasing fibre contents and a balanced energy level in the diet did not affect ADFI and ADG; however, there was an improved G : F ratio in growing pigs. An interesting result from the present study was the reduction in G : F of LC compared to MYC in all investigated feeding phases; this could be related to increased villi high, crypt depth, and goblet cell content of pigs in the LC treatment. Growth of villi and of goblet cells requires energy and protein. Hence, the differences in the performance between the treatments can be related to the different fibre sources. Slama et al. (2019) analysed 22 fibre components (inclusive the applied fibre sources in the present study) regarding their physico-chemical properties. The authors concluded that the variations in hydration and buffer capacity or swelling properties may have an effect on the physiological outcomes.

The gender dimorphism in terms of increased ADG, ADFI, and daily EI, as well as a trend to a reduction of G : F ratio in barrows compared to gilts, was seen in the present study and has also been reported in the literature (Loibl et al. 2020).

Feeding behaviour

According to the interpretation of the meal duration in our study, the following discussion considers the term 'visit' in cited studies. The observed correlation of fewer visits with increased meal size is also supported by the evidence from other studies (de Haer and de Vries 1993; Gilbert et al. 2017; Pichler et al. 2020). In general, the observed total daily feeder occupation time is similar to Pichler et al. (2020), whereas differences to the other studies cited above can be explained as follows. Despite different study designs and diet compositions it can be assumed that it is not only the diet that affects the feeding behaviour, but the animal : feeder ratio can additionally be considered as an important factor. As discussed previously, the increased number of meals per day and decreased feed amount per meal in CGF may be associated with the palatability of the diet. However, there is a further important factor, which has been neglected in the literature. This is the IDF : SDF ratio or the physico-chemical properties, which in CGF is more than the double that of the other treatments. The differences between barrows and gilts can be explained by barrows needing to eat more meals to accomplish the higher ADFI, although with similar same meal size and time at a visit.

Microbial metabolites and intestinal morphology

Acetic acid, propionic acid and butyric acid, present in a typical ratio of 60 : 20 : 20, are the most abundant SCFAs in the large intestine of mammals (Rasmussen et al. 1988; Topping and Clifton 2001) and in the present study this ratio also applied. No differences regarding the concentration of SCFA in the ileum were observed. This can be related to all diets having a physiologically low SDF content in the finisher phase, indicating very low substrate amounts for microbial fermentation. The studies of Kraler et al. (2015) and Slama et al. (2020) found similar results regarding SCFA concentration when applying nutrient-balanced diets in piglets. Furthermore, the concentration of BCFA increased in a distal direction, irrespective of the diets fed, which is in accordance with Macfarlane et al. (1992). This phenomenon can be explained by the fact that, in the small intestine, dietary protein acts as nutrient source for

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both host and microbes, leading to a competition for the available amino acids (Pierzynowski et al. 2006). In contrast to the ileum, in the colon there is a more pronounced fermentation of amino acids which leads to higher contents of BCFA (De Preter et al. 2011). Treatment MYC showed a higher acetic acid and total SCFA content in the colon compared with LC and CGF. Through the minor difference of SDF contents between the treatments, different physico-chemical properties of the different fibre sources, as reported by Slama et al. (2019), can exert a significant influence in the production of SCFA. Interestingly there were no differences in the content of bA, either in the ileum or in the colon. This effect may possibly be explained by the digestible nitrogen balanced diets and/or an adequate carbohydrate supply for the intestinal microbiota (Bikker et al. 2006; Nyachoti et al. 2006).

In comparison with the findings of Nousiainen and Suomi (1991), the higher ammonia concentration in the ileal digesta showed no negative effect on the VH, and in contrast to their study, there was no correlation between ammonia and VH in the present study (Pearson correlation: –0.108 1, $P > 0.1$; data not shown). Furthermore, LC showed the highest ammonia concentration and this treatment also had villi of increased high. The ammonia content in the study of Nousiainen and Suomi (1991) ranged between 4.3 mM and 48.8 mM. Visek (1978) reported ammonia concentration in single stomach mammals between 3.0 mM to 44 mM (both studies refer to fluid digesta). Through the generally lower ammonia content in the present study (1.7–9.5 mmol/kg dry digesta) it may be deduced that there was no influence of the ammonia content on VH. Another possibility could be the protein quality and content of the diet, as this can also influence the amount of ammonia or the pyhsico-chemical properties of the dietary fibre source (Mouille et al. 2004; Slama et al. 2019). In the present study we have assumed, that the minor differences in parameters of intestinal morphology are more affected by the differences in the physio-chemical properties of dietary fibre sources then the different amounts of dietary fibre in the diets.

CONCLUSION

The results of the present study indicate that the effect on zootechnical performance, as well as the effect on most investigated physiological parameters, was more pronounced between diets containing different dietary fibre sources than diets that differ in their dietary fibre content. This resulted in an improved G : F ratio in diets supplemented with MYC compared to LC. On the other hand, the CGF-supplemented diets showed different feeding behaviour parameters compared with the control diet. A similar picture was observed for the parameters of the intestinal physiology. Here too, the investigated parameters showed different physiological reactions between the treatments.

The results of the present study indicate the importance of knowledge of the IDF : SDF ratio in dietary fibre, as well as of physico-chemical properties in pig studies dealing with dietary fibre. Hence, further studies are necessary to provide evidence regarding the mode of action of dietary fibre sources or feed matrices of differing physico-chemical properties.

Conflict of interest

The authors declare no conflict of interest.

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