Flaxseed meal and oat hulls supplementation: impact on dietary fiber digestibility, and flows of fatty acids and bile acids in growing pigs¹

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ABSTRACT: The present study was conducted to determine the effects of adding flaxseed meal (FM) or oat hulls (OHs) in pigs' diets on digestibility of dietary fiber (DF) and fatty acids (FAs), and gastrointestinal flows of FA and bile acids (BAs). Twelve Genesus [(Duroc ♂ × Yorkshire-Landrace ♀)] castrated barrows (initial BW: 35.1 ± 0.44 kg) were individually housed and offered diets in a two-period cross-over design ($n = 8$). In each period, four pigs were assigned to one of the three corn-soybean meal-based diets without (control), or with FM or OHs. Soybean oil was added in each diet to give an FA content of 4.56%, 6.02%, and 6.05 % in the control, FM, and OH diets, respectively. Feces and ileal digesta contents were collected to determine apparent ileal (AID), total tract (ATTD) digestibility of dietary components and flows of FA and BA. Pigs fed the control diet had greater ($P < 0.05$) AID of SFA and insoluble DF and ATTD of SFA than pigs offered the OH and FM diets. The AID of total FA and MUFA in FM diet-fed pigs was lower ($P = 0.02$) compared to those fed the control and OH diets. The ATTD of CP, NDF, insoluble and total DF was lower ($P < 0.05$) in pigs fed the OH diet than in pigs that consumed the control

and FM diets. In the terminal ileum, pigs fed OH and FM diets excreted more ($P < 0.05$) primary BA and all secondary BA (except lithocholic acid) compared to control diet-fed pigs. The intestinal flows of lithocholic acid in pigs fed the FM diet were higher ($P < 0.05$) than in pigs offered the control diet. Pigs fed FM and OH diets excreted more ($P = 0.001$) fecal ursodeoxycholic and total BAs compared to pigs that consumed the control diet. The ileal flows of eicosapentaenoic and erucic acids in pigs fed the FM and OH diets were greater ($P < 0.05$) than in pigs fed the control diet. The flow of all SFA, and palmitoleic, palmitelaidic, oleic, nervonic, linoleic, eicosapentaenoic, erucic, docosatetraenoic and docosapentaenoic acids in feces were greater ($P < 0.05$) in OH diet-fed pigs compared to pigs fed other diets. In conclusion, addition of FM and OHs in pig diets reduced FA digestibility, increased gastrointestinal flows of FA and excretion of BA. Dietary supplementation with FM and OHs induces variable effects on digestibility of DF fractions and fecal flows of unsaturated FA. Future studies are needed to quantify the contribution of endogenous FA losses from the host to gastrointestinal flows of FA.

Key words: agro-industrial co-products, bile acids, dietary fiber solubility, high-fiber diets, pigs, supplementary fat

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INTRODUCTION

Low-cost agro-industrial co-products are widely used in swine diets resulting in increase in the dietary fiber (DF) composition, and consequently leading to the addition of fat to increase the dietary energy content. It is intriguing that nutrient utilization and growth performance is depressed in pigs fed nutritionally balanced diets that are supplemented with fibrous co-products and added fat (Bakker et al., 1996; Gutiérrez et al., 2013). The reduction in performance can be ascribed to overestimation of energy value of supplementary fat, inaccurate NE values of fibrous ingredients, the interaction between supplementary fat and DF or the crosstalk between gut microbiota and bile acids (BAs) responsible for emulsification of dietary fat (Capuano, 2017; Ndou et al., 2018a). The consumption of high-fiber diets altered intestinal microbiota composition, increased excretion of BA, and depressed fat digestibility more in pigs fed soluble DF-enriched diet compared to pigs fed an insoluble DF-containing diet (Ndou et al., 2017, 2018a). It is still not clear whether fecal fat originates from microbial fat production, endogenous secretions or sub-optimal absorption of added fat predisposed by fiber encapsulation of fatty acids (FAs) and BA or by deconjugation of BA. Thus, further studies are needed on intestinal FA and BA flows.

High fat and high-fiber diets induce variable effects on DF fermentability in ruminants (Onetti et al., 2001; Vergugo, 2016) and pigs fed purified fiber sources (Yan et al. 2013), but this aspect has not been extensively studied in pigs that are fed practical sources of DF and will require further investigation to better understand and develop strategies to improve utilization of dietary fat and DF-rich co-products. Therefore, the objective of this experiment was to test the null hypothesis that supplementation with flax-seed meal (FM) or oat hulls (OHs) would have similar effects on digestibility of DF and FA, fecal and ileal flows of BA and FA in growing pigs.

MATERIALS AND METHODS

The experimental protocol was reviewed and approved by the Animal Care Committee of the University of Manitoba (protocol number: F14-042/1) and the cannulated pigs were cared for in accordance with the Canadian Council on Animal Care guidelines (CCAC, 2009).

Experimental Diets, Pigs, Housing, Experimental Design, Sample Collection, and Laboratory Analyses

Details about the experimental diets (Tables 1 and 2), pigs, housing, experimental design, management

procedures, and sample collection, and other laboratory analyses were the same as those described in a companion paper reporting the effects of using a combination of in vivo (ileal cannulated pigs) and in vitro (fecal inoculum-based incubation) methodologies to predict the quantity of VFA and energy produced and absorbed in the hindgut of pigs. Thus, readers are advised to refer to that paper for more information.

Lipids were extracted from diet, ileal digesta, and fecal samples (1 g, finely ground) using a chloroform/methanol (2:1, by vol.) and 0.01% butylated hydroxytoluene (antioxidant) mixture following a method described previously (Folch et al., 1957). The extracted total lipids were weighed and reconstituted in hexane to a volume of 8 mL. Aliquots of a known volume (to contain 40 to 50 mg lipid) were obtained from each extract and dried under nitrogen gas (N₂) flux using an N-EVAP 112 evaporator (Berlin, MA) at 37 °C, and methylated using 3 mL, 3N methanolic HCl including 17:1 (Nu-Chek Prep Inc., Elysian, MN) as an internal standard (used for quantification of FA), by heating for 2 h at 80 °C. The FA methyl esters obtained were extracted into isooctane and analyzed using a Varian 450 GC with flame ionization detector (FID) and equipped with a DB225MS column (30 m×0.25 mm diameter and 0.25 µm film thickness, Agilent Technologies Canada Inc., Mississauga, ON). The program settings used for the gas chromatography–mass spectrometry (GC–MS; Varian Chromatograph System, model Star 3400; Varian Medical Systems, Palo Alto, CA) analysis were adopted from methods described by Nejlat et al. (2016). Each FA was identified by comparing its retention time to previously authenticated standard samples of known lipid composition (Lipid standards, Nu-Chek Prep, Inc., Elysian, MN).

BAs were extracted according to procedures reported by Batta et al. (1999) and modifications described by Thandapilly et al. (2018). In brief, 10 to 15 mg of the freeze-dried ileal digesta and fecal sample was weighed into culture tubes (12 × 75 mm). Norcholic acid was used as the internal standard. The samples were hydrolyzed with concentrated HCl at 60 °C for 4 h in a dry bath and subjected to salinization for 30 min at 55 °C. Prior to and after salinization, the solvents were evaporated under an N₂ flux using an N-EVAP 112 evaporator (Berlin, MA) at 60 and 55 °C, respectively. After salinization, 200 µL of hexane was added, and the samples were centrifuged at 2,800 × g for 20 min at 4 °C and analyzed by GC–MS.

Calculations for Iodine Values, Digestibility, and Flows

The iodine values (IVs) of the ingredients and diets were calculated as follows:

Table 1. Compositions of the control, flaxseed meal, and oat hulls diets (as-fed basis)

Item	Diet ¹		
	Control	FM	OH
Ingredient composition, %			
Corn	64.53	57.40	52.99
Oat hulls	—	—	10.00
Flaxseed meal	—	12.00	—
Soybean meal, 44% CP	31.00	25.49	31.50
Soybean oil	1.354	2.048	2.390
Limestone	0.683	0.667	0.640
Monocalcium phosphate	0.752	0.637	0.750
Salt	0.35	0.35	0.35
Vitamin-mineral premix ²	1.00	1.00	1.00
L-Lysine HCl	—	0.086	0.010
DL-Methionine	0.031	0.010	0.060
Threonine	—	0.012	0.010
Titanium dioxide	0.30	0.30	0.30
Calculated dietary provisions, %			
NDF	9.00	18.00	18.00
ME, kcal/kg	3,331	3,340	3,335
CP	18.10	18.70	18.01
SID Lys	0.99	0.99	0.99
SID Met	0.30	0.31	0.30
SID Met + Cys	0.58	0.61	0.55
SID Thr	0.62	0.60	0.60
SID Trp	0.21	0.17	0.18
Analyzed compositions, %			
CP	19.20	19.30	19.36
GE, kcal/kg	3,900	3,995	3,980
ADF	3.7	5.0	7.6
NDF	9.3	18.2	18.7
Soluble dietary fiber	4.7	6.9	4.5
Insoluble dietary fiber	10.5	17.6	21.1
Total dietary fiber	15.2	24.9	25.5

¹FM = flaxseed meal-containing diet; OH = oat hulls-containing diet.

²Provided the following nutrients per kilogram of air-dry diet: 8,250 IU retinol (vitamin A); 200 IU cholecalciferol (vitamin D₃); 40 UI α -tocopherol (vitamin E); 4 mg vitamin K; 1.5 mg vitamin B₁; 7 mg vitamin B₂; 2.5 mg vitamin B₆; 25 μ g vitamin B₁₂; 14 mg calcium pantothenate; 2 mg folic acid; 21 mg niacin (vitamin B₃); and 200 μ g biotin (vitamin B₇). Minerals: 15 mg Cu (as copper sulfate); 0.4 mg iodine (as potassium iodine); 120 mg iron (as ferrous sulfate); 20 mg Mn (as manganese oxide); 0.3 mg Se (as sodium selenite); 110 mg Zn (as zinc oxide).

IV = $([C16:1] \times 0.95) + ([C18:1] \times 0.86) + ([C18:2] \times 1.732) + ([C18:3] \times 2.616) + ([C20:1] \times 0.785) + ([C22:1] \times 0.723)$, in which the brackets indicate concentration (percentage) of FA [adopted from American Oil Chemists' Society by [Metcalf and Schmitz \(1961\)](#)].

The determined apparent ileal (AID) and total tract digestibility (ATTD) were calculated as follows:

$$\text{AID or ATTD}(\%) = \left(1 - \frac{(\text{Nutrient}_{F/I} \div \text{Nutrient}_D) \times T_D}{(T_D \div T_{F/I})} \right) \times 100,$$

where Nutrient_{F/I} is the contents of dietary components (g/kg DM) in the feces (F) or ileal (I) digesta, respectively; Nutrient_D is the content of each nutrient (g/kg DM) in the diet; T_D is the titanium dioxide (g/kg DM) in the diet; and $T_{F/I}$ is the concentrations of titanium dioxide (g/kg DM) in feces (F) or ileal (I) digesta, respectively.

The concentrations of BA in the terminal ileal digesta, and the feces were normalized for the feed DMI using the following equation:

$$\text{Normalized BA concentration (mg/g DMI)} =$$

$$\text{BA concentration (mg/g DM)} \times (T_D / T_{F/I}).$$

The flow of FA in the terminal ileum or feces was calculated using the following equation:

$$\text{Flow}_{\text{nutrient}} (\text{g/kg DMI}) =$$

$$\text{Nutrient}_{F/I} \times (T_D \div T_{F/I}),$$

where Flow_{nutrient} is the flow of dietary components; Nutrient_{F/I} is the concentration of each dietary component in feces (F) or ileal (I) digesta, respectively.

Statistical Analysis

Data were analyzed using a generalized linear mixed model procedure of SAS (SAS, Institute, Inc., Cary, NC). Comparisons of means were performed using the Tukey–Kramer honestly significance difference test. Significant differences among means were declared at an α of $P \leq 0.05$, and trends declared for P -values between 0.05 and 0.10 were discussed.

RESULTS

Apparent Ileal and Total Tract Digestibility

The AID of DM, SFA, and insoluble dietary fiber (IDF) and ATTD of MUFA were greater ($P < 0.05$) for pigs fed the FM and OH diets than for pigs fed the control diet (Table 3). There were no significant dietary effects observed on AID of CP, NDF and soluble dietary fiber (SDF), and ATTD of SDF. The AID of MUFA and total fatty acids (TFA) and ATTD of TFA in FM diet-fed pigs was lower than in pigs fed OH or control diets ($P < 0.01$). The AID of ADF and ATTD of PUFA were greater ($P < 0.01$) in pigs that consumed the control and OH diets than in pigs fed the FM diet. A tendency was observed in which the AID of total dietary fiber (TDF) ($P = 0.082$) in pigs fed the control diet was greater than in that were offered the OH diet. The ATTD of SFA was greater ($P = 0.005$) in pigs fed the OH diet than in pigs that

Table 2. Fatty acids profile of the ingredients, control, flaxseed meal, and oat hulls diets (% as-fed)

Item (%)	Ingredients				Diet ¹		
	Corn	Soybean	Flaxseed meal	Oat hulls	Control	FM	OH
Saturated fatty acids (SFA)							
Lauric (C12:0)	0.01	0.00	0.01	0.00	0.01	0.01	0.01
Myristic (C14:0)	0.04	0.07	0.07	1.20	0.07	0.06	0.08
Pentadecylic (C15:0)	0.07	0.18	0.06	0.39	0.07	0.06	0.07
Palmitic acid (C16:0)	12.23	15.72	7.15	31.84	12.68	10.71	12.01
Margaric (C17:0)	0.09	0.20	0.06	0.26	0.11	0.10	0.11
Stearic (C18:0)	1.75	4.10	2.09	3.45	2.85	2.94	3.15
Arachidic (C20:0)	0.00	0.24	0.19	0.97	0.36	0.31	0.35
Behenic (C22:0)	0.18	0.36	0.15	0.81	0.24	0.23	0.27
Lignoceric (C24:0)	0.24	0.26	0.00	0.00	0.17	0.00	0.00
ΣSFA	15.06	21.14	9.95	39.48	16.57	14.59	16.22
Monounsaturated fatty acids (MUFA)							
Palmitoleic (C16:1n-7)	0.12	0.09	0.09	0.41	0.11	0.10	0.11
Palmitelaidic (C16:1t)	0.05	0.01	0.03	0.02	0.03	0.03	0.02
Oleic (C18:1n-9)	25.50	9.04	11.86	0.99	22.54	21.89	22.42
Vaccenic (C18:1n-7)	0.48	1.39	0.68	33.59	0.74	0.78	0.89
Gadoleic (C20:1)	0.35	0.15	0.14	1.58	0.27	0.23	0.25
ΣMUFA	26.51	10.61	12.81	37.17	23.69	23.04	23.70
Polyunsaturated fatty acids (PUFA)							
Linoleic (C18:2)	56.77	57.32	14.10	21.21	54.99	45.84	54.07
Linolenic (C18:3n-6)	0.00	0.00	0.00	0.00	0.00	0.01	0.01
α-Linolenic (C18:3n-3)	1.61	10.90	62.97	2.14	4.73	16.46	5.95
Eicosadienoic (C20:2)	0.02	0.03	0.08	0.00	0.03	0.04	0.03
Eicosatrienoic (C20:3n-3)	0.00	0.00	0.08	0.00	0.00	0.01	0.00
Eicosapentaenoic (C20:5n-3)	0.03	0.00	0.00	0.00	0.00	0.01	0.02
Erucic (C22:1n-9)	0.00	0.00	0.01	0.57	0.00	0.01	0.01
Nervonic (C24:1n-9)	0.00	0.00	0.17	0.32	0.00	0.17	0.16
ΣPUFA	58.43	68.25	77.24	23.35	59.74	62.37	60.07
ΣFA ²	—	—	—	—	4.56	6.02	6.05
Calculated IV, g/100 g ³	125	136	200	45	127	142	129

¹FM = flaxseed meal-containing diet; OH = oat hulls-containing diet.

²FA = fatty acids.

³IV = iodine value.

consumed the control and FM diets. The ATTD of DM ($P < 0.01$) and IDF ($P < 0.01$) in pigs fed OH diet was lower compared to those fed the control or FM diets. The ATTD of ADF ($P = 0.068$) in pigs fed the control and FM diets tended to be greater than in those offered the OH diet. The ATTD of CP was lower ($P < 0.001$) in pigs fed the FM and OH diets, respectively, than in pigs fed the control diet. The AID of NDF and TDF was greater ($P = 0.001$) in pigs fed the FM diet than in those fed the control or OH diets.

Ileal FAs Acids Flows

The ileal flows of capric, linoleic, linolenic, eicosadienoic, eicosatrienoic, arachidonic, and docosapentaenoic acids were not different ($P > 0.10$) in pigs fed all the diets (Table 4). The flows of lauric, myristic, margaric, stearic, behenic, lignoceric,

palmitoleic, eicosapentaenoic, and erucic acids in the terminal ileum of pigs fed FM and OH diets were greater ($P < 0.05$) compared to that in pigs fed the control diet. The ileal flows of pentadecylic ($P = 0.076$), arachidic ($P = 0.089$), and gadoleic ($P = 0.078$) acids in OH diet-fed pigs tended to be greater than in pigs that consumed the control diet. The ileal flow of palmitic acid was greatest ($P = 0.032$) in pigs offered OH diet, followed by those fed the FM diet and then those fed the control diet. The flows of palmitelaidic and oleic acids were greater ($P < 0.05$) in the terminal ileum of pigs that consumed the FM diet than those fed the control diet. The flows of vaccenic and α-linolenic acids in the terminal ileum of pigs fed the OH and control diets were lower ($P < 0.05$) than in those fed the FM diet. Pigs fed the FM diet tended to have higher ($P = 0.089$) ileal flows of nervonic acid compared to pigs that consumed the control or OH diets.

Table 3. Apparent ileal and total tract digestibility (%) of dietary components in growing pigs fed the control, flaxseed meal, and oat hulls diets ($n = 8$)

	Diet ¹				
Item	Control	FM	OH	SEM	<i>P</i>
Apparent ileal digestibility					
DM	72.4 ^a	59.9 ^b	58.0 ^b	3.10	0.008
CP	78.9	71.0	75.9	2.64	0.140
SFA	77.4 ^a	62.1 ^b	66.3 ^b	3.24	0.001
MUFA	70.4 ^a	34.1 ^c	55.2 ^b	6.99	0.007
PUFA	76.4 ^a	64.0 ^b	67.8 ^b	2.91	0.047
TFA	89.7 ^a	80.1 ^c	84.1 ^b	1.13	0.017
ADF	4.4 ^a	−23.4 ^b	11.9 ^a	8.61	0.004
NDF	32.8	42.6	34.9	4.42	0.323
Soluble dietary fiber	68.9	65.9	61.0	5.11	0.219
Insoluble dietary fiber	45.5 ^a	29.2 ^b	27.3 ^b	3.10	0.001
Total dietary fiber	48.3 ^A	35.5 ^{AB}	28.2 ^B	6.37	0.082
Apparent total tract digestibility					
DM	90.6 ^a	86.3 ^b	75.3 ^c	1.55	0.001
CP	90.1 ^a	86.1 ^b	83.2 ^c	0.97	<0.001
TFA	89.6 ^a	72.4 ^c	77.2 ^b	0.58	<0.001
SFA	67.5 ^c	72.6 ^b	78.4 ^a	1.04	0.005
MUFA	83.0 ^a	70.0 ^b	75.9 ^b	0.22	0.002
PUFA	78.4 ^a	57.1 ^c	67.2 ^b	0.29	0.017
ADF	48.2 ^A	42.8 ^A	18.7 ^B	9.46	0.068
NDF	67.3 ^b	80.5 ^a	52.6 ^c	3.74	<0.001
Soluble dietary fiber	95.8	97.1	95.5	1.17	0.636
Insoluble dietary fiber	74.9 ^a	65.4 ^a	31.6 ^b	4.47	<0.001
Total dietary fiber	67.3 ^b	80.5 ^a	52.6 ^c	3.52	<0.001

^{a-c}Mean values within a row with unlike superscripts differ ($P < 0.05$). ^{A-C}Mean values within a row with unlike superscripts differ ($0.05 > P \leq 0.05$).

¹FM = flaxseed meal-containing diet; OH = oat hulls-containing diet; TFA = the sum of all fatty acids.

Fecal FAs Acids Flows

The fecal flow of capric, vaccenic, and arachidonic acids was greater ($P < 0.05$) in pigs fed the OH diet than in those fed the control diet (Table 5). The flows of lauric, pentadecylic, palmitic, margaric, stearic, lignoceric, palmitoleic, palmitelaidic, oleic, nervonic, linoleic, eicosatrienoic, eicosapentaenoic, docosatetraenoic, and docosapentaenoic acids in feces of OH diet-fed pigs were greater ($P < 0.05$) than in pigs fed the control or FM diets. The fecal flows of myristic, arachidic, behenic, and erucic acids were greater ($P = 0.01$) in pigs fed the OH diet, followed by the FM diet-fed pigs and lowest in those fed the control diet. Dietary inclusion of FM or OHs did not affect ($P > 0.10$) the fecal flows of gadoleic, linolenic, and eicosadienoic acids in all pigs.

Gastrointestinal Concentrations of BAs

The concentration of chenodeoxycholic + cholic acids, deoxycholic, isodeoxycholic, and ursodeoxycholic acids in the terminal ileum of pigs fed

the FM and OH diets was higher ($P < 0.05$) than in control diet-fed pigs (Table 6). The concentration of ileal lithocholic acid in pigs fed the FM diet was higher ($P < 0.05$) than in pigs offered the control diet. The ileal concentrations of secondary and total BA in pigs fed the control diet were lower ($P < 0.01$) compared to those that consumed FM and OH diets.

In fecal contents, there were no differences ($P > 0.10$) in the concentration of chenodeoxycholic acid + cholic, deoxycholic, and isodeoxycholic acids (Table 4). The concentration of lithocholic acid excreted in feces of pigs fed the control and OH diets was lower ($P < 0.001$) than in pigs fed the FM diet. Pigs fed the FM and OH diets excreted more ($P = 0.001$) fecal ursodeoxycholic, secondary, and total BAs compared to those that consumed the control diets.

DISCUSSION

Our recent experiment investigated the effects of dietary supplementation with FM and OHs on growth performance, blood lipids, and on

Table 4. Ileal fatty acid flows (mg/kg DMI) in growing pigs fed control, flaxseed meal, and oat hulls diets ($n = 8$)

Item	Diet ¹			SEM	<i>P</i>
	Control	FM	OH		
Saturated fatty acids					
Capric (C10:0)	0.3	0.7	0.1	0.31	0.300
Lauric (C12:0)	3.7 ^b	10.3 ^a	8.2 ^a	1.43	0.014
Myristic (C14:0)	22.5 ^b	41.6 ^a	47.0 ^a	6.7	0.043
Pentadecyclic (C15:0)	19.2 ^B	31.9 ^{AB}	39.9 ^A	6.11	0.076
Palmitic acid (C16:0)	2,838 ^c	5,208 ^b	4,787 ^a	62.0	0.032
Margaric (C17:0)	36.5 ^b	52.4 ^a	59.3 ^a	4.41	0.005
Stearic (C18:0)	769 ^b	1,220 ^a	1,091 ^{ab}	111	0.041
Arachidic (C20:0)	96.2 ^B	159 ^{AB}	166 ^A	23.22	0.089
Behenic (C22:0)	63.4 ^b	126 ^a	115 ^a	15.67	0.029
Lignoceric (C24:0)	71.4 ^b	153.3 ^a	138.2 ^a	19.22	0.011
Monounsaturated fatty acids					
Palmitoleic (C16:1n-7)	36.9 ^b	52.8 ^a	61.1 ^a	4.91	0.004
Palmitelaidic (C16:1t)	14.2 ^b	29.1 ^a	21.3 ^{ab}	4.48	0.013
Oleic (C18:1n-9)	6,171 ^b	9,080 ^a	8,275 ^{ab}	1,165	0.007
Vaccenic (C18:1n-7)	−3.7 ^b	106 ^a	4.2 ^b	25.71	0.013
Gadoleic (C20:1)	68.1 ^B	110 ^{AB}	135 ^A	20.99	0.078
Nervonic (C24:1n-9)	−0.1	3.0	0.1	1.03	0.098
Polyunsaturated fatty acids					
Linoleic (C18:2)	87.6	5,831	2,531	1,869	0.105
Linolenic (C18:3n-6)	10,756	14,084	16,356	2,779	0.377
α-Linolenic (C18:3n-3)	521 ^b	1,975 ^a	814 ^b	271.0	0.003
Eicosadienoic (C20:2)	11.1	16.9	13.1	2.37	0.224
Eicosatrienoic (C20:3n-3)	−0.2	0.1	1.7	1.03	0.359
Arachidonic (C20:4n-6)	9.00	14.0	14.4	2.67	0.259
Eicosapentaenoic (C20:5n-3)	18.9 ^b	40.7 ^a	57.1 ^a	8.27	0.012
Erucic (C22:1n-9)	5.3 ^b	10.3 ^a	11.7 ^a	1.51	0.016
Docosatetraenoic (C22:4n-6)	18.0	4.6	2.7	10.86	0.534

^{a-c}Mean values within a row with unlike superscripts differ ($P < 0.05$). ^{A-C}Mean values within a row with unlike superscripts differ ($0.05 > P \leq 0.05$).

¹FM = flaxseed meal-containing diet; OH = Oat hulls-containing diet.

concentrations of intestinal VFA, BA, and neutral sterols in pigs (Ndou et al., 2017). Previous studies have also reported the nutritive value of FM in terms of the energy value, and digestibility of CP, phosphorus, crude fat, and AA and gastrointestinal microbial activity in pigs (Kiarie et al., 2007; Eastwood et al., 2009; Kim et al., 2017; Ndou et al., 2018ab) and utilization of FM and OHs in poultry (Jiménez-Moreno et al., 2009; Leung et al., 2018). However, the effects of supplementing with soluble or insoluble sources of DF on fermentability of DF fractions, digestibility and flow of FA had been ignored in pigs fed nutritionally balanced corn and soybean meal-based diets. FM and OHs were selected based on previous studies and preliminary analysis that showed that FM and OHs are rich in soluble and insoluble fiber, respectively (Ndou et al., 2017, 2018a,b). Therefore, the objective of the present study was to determine the effects of supplementing with FM or OHs on DF and FA utilization

in growing pigs fed nutritionally balanced corn-soybean meal-based diets. The consumption of FM and OHs induces hypocholesteremia in growing pigs (Ndou et al., 2017) and depends on the physical properties fiber source (Ndou et al., 2013a,b). Cholesterol is a precursor for the synthesis of BA (Agnihotri and Khan, 2015) and is produced at the expense of metabolizable energy needed for growth performance (Cerqueira et al., 2016). BAs emulsify FA and facilitate the crosstalk between lipid metabolism and gastrointestinal microbiota that are capable of fermenting DF (Capuano, 2017; Ndou et al., 2018a). Thus, the role of DF solubility on BA flows in ileal digesta and fecal contents was also investigated in the present study.

The observation that addition of FM and OHs reduced AID of MUFA, SFA, PUFA, and TFA may be ascribed to the fact that the presence of DF could have induced sub-optimal absorption of added lipids predisposed by encapsulation of FA

Table 5. Fatty acid flows (mg/kg DMI) in feces of growing pigs fed control, flaxseed meal, and oat hulls diets ($n = 8$)

	Diet ¹				
Item	Control	FM	OH	SEM	<i>P</i>
Saturated fatty acids					
Capric (C10:0)	0.4 ^b	0.1 ^b	1.2 ^a	0.19	0.022
Lauric (C12:0)	5.3 ^b	9.8 ^b	15.8 ^a	1.48	<0.001
Myristic (C14:0)	73 ^c	138 ^b	219 ^a	14.95	<0.001
Pentadecyclic (C15:0)	167 ^b	271 ^b	481 ^a	36.12	<0.001
Palmitic acid (C16:0)	1,351 ^b	1,850 ^b	3,704 ^a	242.1	<0.001
Margaric (C17:0)	98 ^b	144 ^b	270 ^a	21.42	<0.001
Stearic (C18:0)	5,059 ^b	7,252 ^b	13,081 ^a	754	<0.001
Arachidic (C20:0)	97 ^c	146 ^b	228 ^a	13.53	<0.001
Behenic (C22:0)	36.9 ^c	58.8 ^b	95.2 ^a	5.46	<0.001
Lignoceric (C24:0)	43.6 ^b	62.0 ^b	113.8 ^a	6.82	<0.001
Monounsaturated fatty acids					
Palmitoleic (C16:1n-7)	1.4 ^b	2.2 ^b	3.8 ^a	0.35	<0.001
Palmitelaidic (C16:1t)	2.4 ^b	3.7 ^b	5.6 ^a	0.60	0.004
Oleic (C18:1n-9)	1,101 ^b	1,615 ^b	3,119 ^a	235.3	<0.001
Vaccenic (C18:1n-7)	101 ^b	229 ^{ab}	375 ^a	54.56	0.010
Gadoleic (C20:1)	11.1	9.4	18.1	3.87	0.278
Nervonic (C24:1n-9)	2.0 ^b	3.2 ^b	6.5 ^a	0.63	<0.001
Polyunsaturated fatty acids					
Linoleic (C18:2)	193 ^b	338 ^b	544 ^a	50.81	<0.001
Linolenic (C18:3n-6)	-0.2	7.3	0.4	3.75	0.298
α-Linolenic (C18:3n-3)	24.6 ^b	89.2 ^a	42.2 ^b	6.82	<0.001
Eicosadienoic (C20:2)	1.5	0.8	1.8	0.59	0.463
Eicosatrienoic (20:3n-3)	0.2 ^b	0.4 ^b	1.9 ^a	0.46	0.039
Arachidonic (C20:4n-6)	1.3 ^b	1.9 ^{ab}	2.8 ^a	0.30	0.014
Eicosapentaenoic (C20:5n-3)	1.3 ^b	2.1 ^b	4.1 ^a	0.47	0.001
Erucic (C22:1n-9)	2.4 ^c	5.7 ^b	9.3 ^a	0.99	<0.001
Docosatetraenoic (C22:4n-6)	60 ^b	86 ^b	131 ^a	13.56	0.007
Osbond (C22:5n-6)	16.7 ^b	13.3 ^b	39.1 ^a	6.15	0.015

^{a,b,c}Mean values within a row with unlike superscripts differ ($P < 0.05$).

¹FM = flaxseed meal-containing diet; OH = Oat hulls-containing diet.

within the DF matrices or by deconjugation of BA. The high DF content and WHC of nonstarch polysaccharides in FM and OHs may also bind some of the BA present in the digesta contents, thereby reducing emulsification and absorption of dietary lipids (Ferreebe and Dawson, 2015; Capuano, 2017). Supporting these postulations is the increase in the ileal flows of BA, FA, and the low digestibility values or fermentability of DF fractions in the upper gastrointestinal tract. Moreover, the observation that FM supplementation reduced the digestibility of TFA and fermentability of insoluble DF more than OHs further supports the notion proposed by Ndou et al. (2017) that these DF sources behave differently during transit in the gastrointestinal tract (GIT). This implies that, as a well-known rich source of soluble and mucilaginous NSP with high swelling and water holding capacity, FM might have increased digesta viscosity, thereby preventing nutrient absorption (Bhatti, 1993; Kiarie et al.,

2007; Takahashi et al., 2009). These findings also concur with our observation that feed efficiency was reduced more in pigs fed the FM diet compared to those fed the control and OH diets (Ndou et al. 2017). Conversely, OHs increased the insoluble DF content, which in turn reduces transit time of intraluminal contents of small intestines (Jiménez-Moreno et al., 2009), thereby reducing FAs absorption observed in OH diets-fed pigs. However, we did not measure passage rate in the current study.

Another plausible explanation for the reduction in digestibility of TFA in pigs fed FM and OHs is that DF from these co-products increases the substrate for microbial activities which facilitates deconjugation of BA and reduces their ability to solubilize and emulsify dietary lipids (Ahn et al., 2003). The deconjugated BAs are then bound to bacterial cells and DF, thereby increasing their excretion as well as that of lipids. Reinforcing this are the greater ileal and fecal flows of BA and FA

Table 6. Normalized concentrations (mg/kg DMI) of bile acids (Bas) in ileal and fecal contents of growing pigs fed control, flaxseed meal, and oat hulls diets ($n = 8$)

	Diet ¹				
Item	Control	FM	OH	SEM	<i>P</i>
Terminal ileum					
Chenodeoxycholic + cholic acid	11.8 ^b	23.0 ^a	22.6 ^a	1.59	<0.001
Deoxycholic acid	2.3 ^b	4.4 ^a	4.0 ^a	0.42	0.032
Isodeoxycholic acid	0.3 ^b	0.5 ^a	0.5 ^a	0.05	0.002
Lithocholic acid	0.2 ^b	0.4 ^a	0.4 ^{ab}	0.06	0.039
Ursodeoxycholic acid	1.7 ^b	3.6 ^a	4.1 ^a	0.34	<0.001
Secondary BAs ²	4.9 ^b	8.9 ^a	8.9 ^a	0.78	0.002
Total BAs ³	16.8 ^b	31.9 ^a	31.5 ^a	2.26	<0.001
Feces					
Chenodeoxycholic + cholic acid	0.03	0.05	0.08	0.02	0.150
Deoxycholic acid	0.1	0.1	0.3	0.06	0.120
Isodeoxycholic acid	0.03	0.1	0.04	0.01	0.605
Lithocholic acid	0.3 ^b	0.8 ^a	0.3 ^b	0.05	<0.001
Ursodeoxycholic acid	0.6 ^b	1.7 ^a	1.4 ^a	0.19	0.001
Secondary BAs ²	1.1 ^b	2.1 ^a	2.0 ^a	0.27	0.001
Total BAs ³	1.1 ^b	2.7 ^a	2.1 ^a	0.26	0.001

^{a,b,c}Mean values within a row with unlike superscripts differ ($P < 0.05$).

¹FM = flaxseed meal-containing diet; OH = oat hulls-containing diet; normalized BA concentration (mmol/kg DMI) = BA concentration (mmol/kg DM) $\times$ (titanium in diets $\div$ titanium content in feces or ileal digesta).

²Calculated as: deoxycholic + isodeoxycholic + lithocholic + ursodeoxycholic acid.

³Calculated as: chenodeoxycholic + cholic + deoxycholic + isodeoxycholic + lithocholic + ursodeoxycholic acid.

in pigs fed FM and OH diets compared to those fed the control diet in the current study. Therefore, high viscosity of digesta which is likely to have been induced by soluble fiber in pigs fed the FM diet hampered diffusion of lipid micelles in the small intestine thereby further reducing FA absorption (Bhatti, 1993; Kiarie et al., 2007). Additionally, insoluble DF from OHs could have indirectly reduced transit time of intraluminal contents of GIT (Jiménez-Moreno et al., 2009), thereby reducing digestibility of nutrients in the stomach and small intestines.

A similar trend was observed between AID and ATTD of TFA in which case pigs fed the FM diet had the lowest digestibility values than those fed the OH diets was in line with observations by Ndou et al. (2017) who reported that fecal digestibility of crude fat was lower in pigs fed OHs compared to pigs fed FM. It is intriguing that when compared with the control diet, the ATTD of TFA was lower than the AID of TFA among the FM and OH diets. By extrapolation, with reference to the control diet, the AID of TFA in FM and OH diets was reduced by 9.58% and 5.66%, respectively. In the feces, digestibility of TFA was reduced by 17.26% and 10.48% in FM and OH diets, respectively. At the same time, the quantity of BA excreted in the terminal ileum and feces was more than 50% among FM and OH diets. These values are in agreement with

peculiar findings from previous research that total tract digestibility of fat was more negative (–54%) than ileal fat digestibility (–19%) in pigs (Graham et al., 1986). Moreover, more fascinating observations which also coincided with our findings also revealed that consumption of fermentable DF from oatmeal increased fecal fat excretion by 47% and fecal BA by 35% compared with the control group in humans (Judd and Truswell, 1981). Therefore, it is highly likely that the decrease in digestibility of FA in the present study is attributable to not only deconjugation of BA but also to the microbial production of FA in the hindgut of pigs fed FM and OH diets. Supporting this assertion is the increased values of fecal flows than that of ileal flows of FA in pigs fed the FM and OH diets which confirm that microbial activities are a major contributory factor in elevating fecal fat in pigs fed high-fiber diets. Moreover, the negative values for the flow of vaccenic, nervonic and eicosatrienoic acids in the terminal ileum can be ascribed to the contribution of endogenous secretions of FA from the host to the gastrointestinal flows of FA.

Apart from their role as detergents to facilitate digestion and absorption of fats in the GIT, BAs are not only detergents that emulsify fats but are signaling molecules that also regulate the farnesoid X receptor (FXR) and in turn alter lipid, glucose and energy metabolism (Marcil et al., 2002; Ferrebee

and Dawson, 2015; Nie et al., 2015). The increase in the flows of chenodeoxycholic and cholic acids in the terminal ileum of FM and OH diets-fed pigs could be ascribed to the dilution of these primary BA by the nondigestible fibers (Ndou et al., 2017). Although no diet-induced effects were observed on the fecal flow of primary BA, deoxycholic acid, and isodeoxycholic acids, differences in NSP composition between the FM and OHs could explain why lithocholic acid was excreted more in pigs fed OHs compared to those that consumed FM. This observation is in agreement with findings in our recent study that hypocholesterolemia was distinctively pronounced more in OH diet-fed pigs than in FM diet-fed pigs (Ndou et al., 2017). Furthermore, OHs are rich sources of insoluble DF that are highly lignified (Bach Knudsen, 1997), and lignin acts as a resin or a bile salt-sequestering agent by reducing reabsorption of gastrointestinal BA (Fardet, 2010). The lack of dietary effects in the flow of deoxycholic and isodeoxycholic acids in feces cannot be explained by measurements in the present experiment. However, similarities in chenodeoxycholic and cholic acids among all diets could be ascribed to that almost 95% of are rechanneled back to the liver through the enterohepatic circulatory system (Graffner et al., 2016). Another plausible explanation which is supported by findings from our previous study (Ndou et al., 2017) is the observation that fecal flows of ursodeoxycholic acids increased and this can be ascribed to microbial activity that promoted production of secondary BA (Stevens and Hume, 1998; Ahn et al., 2003). Mechanisms by which primary BA are transformed into their secondary forms are through gut microbial 7α -dihydroxylation and $7\alpha/\beta$ -epimerization (Stevens and Hume, 1998; Ahn et al., 2003; Wahlström et al., 2016).

A plethora of treatment-induced differences were observed on the ileal flows of pentadecyclic, palmitelaidic, vaccenic, gadoleic, nervonic, and α -linolenic acids and almost all the fecal flows of FA except gadoleic, linoleic, and eicosadienoic acids between FM and OH diets-fed pigs. The differences in the flows of these gastrointestinal FA observations suggest that soluble and insoluble DF induce variable effects on the ability of gut microbiota to alter changes in FA profiles in the GIT. The increase in the ileal flow of n-3 FA such as α -linolenic and eicosapentaenoic acids observed in the current study is in agreement with findings reported by Martínez-Ramírez et al. (2013) and indicates a likelihood of activity of the $\Delta 6$ - and $\Delta 5$ -desaturases and chain-elongases in the upper sections of the

GIT of the pig. The increase in the ileal and fecal flows of PUFA such as eicosadienoic, eicosatrienoic, arachidonic, erucic, docosatetraenoic, and docosapentaenoic acids that were virtually absent in the diets can also suggest that microbial fermentation in different regions of the GIT contributes to the proportion of unsaturated FA in the digesta of nonruminant animals (Martínez-Ramírez et al., 2013). Supporting this speculation is the increase in the presence of *trans* FA which are likely to be of microbial origin (Martínez Marín et al., 2013). Therefore, the presence of long-chain unsaturated FA in gastrointestinal contents can be used as reliable indicators to assess the effects of feeding DF and its fermentability on lipid metabolism (Santas et al., 2012). These findings also indicate that endogenous secretions of FA from the host into gastrointestinal contents might have contributed to the ileal and fecal flows of these FA. To the best of our knowledge no studies have reported to quantify the endogenous FA profiles in the GIT of growing pigs.

It is also of interest to note that the ATTD of the sum of FA in pigs fed the FM diet in the current study was lower than ATTD of crude fat observed by Ndou et al. (2017) for a similar diet. A similar trend was also reported for other diets by Jørgensen et al. (1992, 2000), Duran-Montgé et al. (2007), and Martínez-Ramírez et al. (2013) and these findings including ours indicated that other fat-soluble components might have lower digestibility than FA. Another reason might be related to the difference in the methodology used to quantify the lipid content of fecal samples. As such the present method would preferentially extract the conjugated FA implying that the lack of use of an acidified solvent prior to FA extraction could have imposed a limitation to our results. This suggests that FA extraction might have been more efficient than the crude fat extraction and the use of acidified solvent would eliminate the bias to the results. Therefore, more work is needed to compare the effects of different methods of lipid extraction (including ether extract or crude fat with hexane, acid-hydrolyzed fat extract or FAs extraction using menthol and chloroform mixtures). Another limitation in the present study is that although there were diet-induced effects on the flow of FA and BA in the terminal ileum as well as in the feces, it is difficult to identify the actual source of lipids excreted either in the terminal ileum or feces. This implies that the application of isotope-labeled FA in future studies would facilitate characterization of gastrointestinal FA originating from the diet, endogenous secretions, or microbial

activities following deconjugation of BA and/or microbial bioconversion of supplementary FA or endogenous lipids into microbial FA. Thus, more research is also needed to identify the actual sources and flows of FA and BA derivatives and how these are influenced by changes in physicochemical properties of digesta or microbiota composition from one gastrointestinal segment to the other.

In conclusion, addition of FM and OHs in pig diets reduced FA digestibility, increased Gastrointestinal (GI) flows of FA and excretion of BA. Dietary supplementation with FM and OHs induced variable effects on digestibility of DF fractions and fecal flows of unsaturated FA. Future studies are needed to quantify the contribution of endogenous FA losses from the host to gastrointestinal flows of FA.

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