Digestion of carbohydrates and utilization of energy in sows fed diets with contrasting levels and physicochemical properties of dietary fiber[1]

A. Serena,[2] H. Jørgensen, and K. E. Bach Knudsen[3]

Department of Animal Health, Welfare and Nutrition, University of Aarhus,
Faculty of Agricultural Sciences, PO Box 50, DK-8830 Tjele, Denmark

ABSTRACT: Three experimental diets were used to investigate the digestion of carbohydrates and utilization of energy in sows fed diets with different levels and physicochemical properties of dietary fiber (DF). The low-fiber diet (LF; DF, 16%; soluble DF, 4.8%) was based on wheat and barley. The high-fiber 1 diet (HF1; DF, 41%; soluble DF, 11%) was based on wheat and barley supplemented with the coproducts: sugar beet pulp, potato pulp, and pectin residue, and the high-fiber 2 diet (HF2; DF, 44%; soluble DF, 7.3%) was based on wheat and barley supplemented with approximately 1/3 of the coproducts used in diet HF1 and 2/3 of brewers spent grain, seed residue, and pea hull (1:1:1, respectively). The diets were studied in 2 series of experiments. In Exp. 1, the digestibility and ileal and fecal flow of nutrients were studied in 6 ileal-cannulated sows placed in metabolic cages designed as a repeated 3 × 3 Latin square design. In Exp. 2, energy metabolism was measured in respiration chambers using 6 sows in a repeated 3 × 3 Latin square design. The DF level influenced the ileal flow of most nutrients, in particular carbohydrates, which increased from 190 g/d when feeding the LF diet to 538 to 539 g/d when feeding the HF diets; this was also reflected in the digestibility of OM and carbohydrates (P < 0.05). The ranking of total excretion of fecal materials was HF2 > > HF1 > LF, which also was reflected in the digestibility of OM, protein, and carbohydrates. Feeding HF diets resulted in greater CH_4 production, which was related to the amount of carbohydrates (r = 0.79) and OM (r = 0.72) fermented in the large intestine, but with no difference in heat production (12.2 to 13.1 MJ/kg of DM). Retained energy (MJ/kg of DM) was decreased when feeding HF1 compared with LF and negative when feeding HF2. Feeding sows HF1 reduced the activity of animals (5.1 h/24 h) compared with LF (6.1 h/24 h; P = 0.045).

Key words: coproduct, carbohydrate, digestibility, energy metabolism, sow

INTRODUCTION

The major fraction of diet for pigs is dietary carbohydrates, which can be divided according glycosidic linkages into sugars, oligosaccharides, and 2 broad classes of polysaccharides, starch and nonstarch polysaccharides (**NSP**). Nonstarch polysaccharides together with lignin make up the fiber fraction and will be assumed to constitute dietary fiber (**DF**; Theander et al., 1994; Bach Knudsen, 1997). The bulk of disaccharides and starch can be broken down by the action of pancreatic and mucosal enzymes in the small intestine (Bach Knudsen and Jørgensen, 2001). There are no enzymes capable of cleaving some types of oligosaccharides and NSP, but a fraction may be lost due to microbial fermentation in the stomach and small intestine (Bach Knudsen and Jørgensen, 2001). A fraction of starch, however, may also pass the small intestine undegraded (Englyst et al., 1992). The carbohydrates not digested by endogenous enzymes in the small intestine will pass to the large intestine, where they stimulate microbial growth and production of short-chain fatty acids (**SCFA**).

We have recently performed an extensive characterization of the coproducts sugar beet pulp, potato pulp, pea hull, seed residues, brewers spent grain, and pectin residue (Serena, 2005). Sugar beet pulp and potato pulp were characterized by being high in soluble DF

(**S-DF**); pectin residue and pea hull medium in S-DF are brewers spent grain and seed residue high in insoluble DF (**I-DF**). These differences are expected to affect the digestibility in the gastrointestinal tract. Coproducts characterized as having a high concentration of S-DF may delay gastric emptying because of high water-binding capacity and viscosity, whereas coproducts characterized as having a high concentration of I-DF can be expected to increase fecal excretion because of a relatively decreased microbial degradation in the large intestine.

The aim of the present study was to investigate carbohydrate digestion and energy utilization of 3 diets formulated from concentrated carbohydrate-rich feedstuffs or coproducts from the vegetable food and agricultural industries combined into 2 diets with contrasting chemical and physicochemical properties.

MATERIALS AND METHODS

Animals and Surgery

Experiments complied with the guidelines of The Danish Animal Experiments Inspectorate, Ministry of Justice, Copenhagen, Denmark, with respect to animal experimentation and care of the animals under study.

The study was composed of 2 experiments. In Exp. 1, digestibility and flow of macronutrients were evaluated, and in Exp. 2 dietary energy metabolism was measured.

After 10 d of adaptation to the environment, each sow was surgically fitted with a T-cannula in the terminal ileum, as described by Jørgensen et al. (1992). After a 7-d day postsurgery recovery period, the experiment was initiated. During the experiment, particular attention was paid to keep the sows washed, and skin irritation was minimized by the liberal application of a lanolin-based, zinc oxide cream.

Exp. 1. The digestion experiment was carried out using 6 sows (first- or second-parity sows, Danish Landrace × Yorkshire; Aarhus University, Faculty of Agricultural Sciences Swineherd, Foulum, Denmark) with an initial BW of 208 ± 23 kg. The experiment was designed as a repeated, 3 × 3 Latin square, with 6 sows fed 3 different diets during 3 periods per block.

Exp. 2. Six sows (4 sows from Exp. 1; first- or second-parity sows, Danish Landrace × Yorkshire; Aarhus University, Faculty of Agricultural Sciences Swineherd) with an initial BW of 206 ± 23 kg were placed in respiration chambers. The experiment was designed as a repeated, 3 × 3 Latin square, with 6 sows fed the same 3 experimental diets as in Exp. 1 during 3 periods per block.

Diets and Feeding (Exp. 1 and 2)

Sows were fed 3 experimental diets: a low-fiber (LF) control diet and 2 generic high-DF diets, high fiber 1 (HF1) or high fiber 2 (HF2), with different proportions

between S-DF and I-DF (Table 1). The LF diet was based on wheat and barley, and the 2 HF diets were based on wheat and barley and supplemented with different coproducts (potato pulp, KMC, Kartoffelmelcentralen Amba, Brande, Denmark; sugar beet pulp, Danisco Sugar A/S, Assens, Denmark; pectin residue, CP Kelco ApS, Lille Skensved, Denmark; brewers spent grain, Carlsberg A/S, Fredericia delivered by Agro-Korn A/S, Videbæk, Denmark; pea hull, Prodana Seeds A/S, Odense, Denmark; and seed residues, DLF Trifolium A/S, Roskilde, Denmark). Wet coproducts (sugar beet pulp, potato pulp, pectin residue, and brewers spent grain) were all heat-dried to contain >87.5% DM.

The diets were formulated to contain different types and concentrations of DF. The LF diet contained 15% DF, and the 2 HF diets contained approximately 40% DF. The HF1 diet had a high concentration of S-DF provided from sugar beet pulp, potato pulp, and pectin residue, and HF2 had a high concentration of I-DF obtained by substitution of approximately two-thirds of the former coproducts with pea hull, seed residue, and brewers spent grain. The diets were formulated to meet the Danish minimum recommendations for essential macro- and micronutrients (Jørgensen and Tybirk, 2005) and milled to pass a 2-mm screen. Chromic oxide (2.0 g/kg of feed) was added as a digestibility marker. The sows were fed once daily (at 0700 h) with 2,000 g (as fed) to standardize the intake of DF and had free access to water.

Collection of Digesta and Fecal Materials for the Digestibility Measurement (Exp. 1)

During most of the adaptation period (7 d) to the diets and the period of ileum collection, the sows were housed individually in 8-m^2 smooth-walled pens with a concrete floor. The last 2 d of the adaptation period, the sows were placed in metabolic cages (adaptation for the metabolic cages). During the collection of feces, the sows were placed in metabolic cages. Feces were collected for the first 3 d followed by 3 d of collecting the ileal digesta quantitatively from 0700 to 1700 h, with 1 d between collections. Ileal digesta were collected in plastic tubes attached to the cannula. The tubes were emptied when full or if they had been attached for 60 min. The daily collected ileal digesta were pooled and stored at –20°C. Water-binding capacity and viscosity of ileal material were measured at 0900 and 1300 h.

Respiration Chambers for the Determination of Energy Metabolism (Exp. 2)

During most of the adaptation period (7 d) to the diets, the sows were housed individually in 8-m^2 smooth-walled pens with a concrete floor. The last 2 d of the adaptation period, the sows were placed in metabolic cages (adaptation for the metabolic cages). During the collection of feces and urine for 3 d, the sows were placed in the metabolic cages in the respiration cham-

Table 1. Ingredients and composition of the low-fiber (LF), high-fiber 1 (HF1), and high-fiber 2 (HF2) diets[1]

	Diet		
Item	LF	HF1	HF2
Ingredient, % as-fed basis			
Barley	42.0	14.5	14.5
Wheat	42.0	14.5	14.5
Sugar beet pulp	—	14.0	5.0
Pectin residue	—	14.0	5.0
Potato pulp	—	14.0	5.0
Seed residue	—	—	13.5
Pea hulls	—	—	13.5
Brewers spent grain	—	—	13.5
Soy oil	5.0	5.0	5.0
Soybean meal, toasted	7.5	21.2	8.6
Vitamin and mineral premix[2]	0.2	0.2	0.2
Monocalcium phosphate	2.2	1.0	0.8
Calcium carbonate	0.6	1.1	0.4
NaCl	0.3	0.3	0.3
Chromic oxide	0.2	0.2	0.2
Chemical composition, % of DM unless otherwise indicated			
Ash	5.8	6.4	6.4
CP	14.2	19.1	16.8
Fat	8.7	8.5	9.9
Total carbohydrates	66.2	59.9	60.4
Sugars	2.1	2.9	1.7
Fructan	0.9	0.4	0.7
Starch	50.1	21.0	21.0
Total nonstarch polysaccharides[3]	14.0 (4.8)	35.6 (11.0)	37.0 (7.3)
Cellulose	2.5	13.7	15.2
Noncellulosic polysaccharides	11.4 (4.8)	21.9 (11.0)	21.8 (7.3)
Klason lignin	1.9	5.6	7.1
Dietary fiber	15.9 (4.8)	41.2 (11.0)	44.1 (7.3)
Cr_2O_3	0.24	0.22	0.22
Enzyme-digestible OM	89.5	87.3	74.7
GE, MJ/kg	17.5	18.5	18.0
Essential amino acids, g/kg of DM			
Lysine	6.46	10.2	7.96
Methionine + cystine	5.31	5.80	5.31
Threonine	5.10	7.01	6.06
Viscosity,[4] mPa·s	0.89	1.64	1.16
Swelling, L/kg of DM	3.45	6.48	5.70
Water-binding capacity, kg/kg of DM	1.32	3.55	3.18

[1]Mean of the 2 batches used in Exp. 1 and Exp. 2.

[2]Provided the following per kilogram of final diet: 8,800 IU of vitamin A, 1,000 IU of vitamin D_3, 60 mg of all *rac* DL-α-tocopherol acetate, 2.2 mg of menadione, 2.2 mg of thiamine, 5.5 mg of riboflavin, 3.3 mg of pyridoxine, 16.5 mg of D-pantothenic acid, 22 mg of niacin, 1.65 mg of folic acid, 220 μg of biotin, 22 μg of cyanocobalamin, 60 mg of butylated hydroxytoluene, 100 mg of Fe as $FeSO_4 \cdot 7H_2O$, 150 mg of Zn as ZnO, 28 mg of Mn as MnO, 20 mg of Cu as $CuSo_4 \cdot 5H_2O$, 304 μg of I as KI, and 300 μg of Se as Na_2SeO_3.

[3]Values in parentheses are soluble NSP.

[4]mPa·s = millipascal seconds.

bers, where gas exchanges (concentration of O_2, CO_2, and CH_4) and movements (lay or stay, measured by a photocell) were measured for 48 h (on d 2 and 3 of feces and urine collection) using the open-air system, as described by Jørgensen et al. (1996). The volume of the outgoing air from the chambers was measured continuously from the differential pressure over both sides of an orifice (Hartmann & Braun, Frankfurt, Germany). Heat production (**HP**) was estimated from calculations of gas exchange. The climate in the respiration chambers was kept constant, and a 12-h (0600 to 1800 h) light-dark cycle was maintained. Temperature and relative humidity in the respiration chambers were kept constant at approximately 20°C and 55%, respectively, which were similar to the climate in the pens.

Analytical Methods and Calculations

All chemical analyses were performed in duplicate, and physicochemical properties were performed in triplicate. Chromic oxide, lactic acid, SCFA, nitrogen in urine, viscosity, and water-binding capacity were measured in wet material, and all other analyses were done on freeze-dried materials. Dry matter was measured by drying (mostly 20 h) to a constant weight at 103°C, and ash was determined according to the AOAC

(1990). Protein (N × 6.25) was determined by the Kjeldahl method (reference no. 978.02; AOAC, 1990) using a Kjeltec 1035 autoanalyser (Foss Tecator A/B, Höganäs, Sweden), and fat was acid hydrolyzed, extracted with diethyl ether, and analyzed by the method of Stoldt (1952). Enzyme-digestible OM was measured as described by Boisen and Fernández (1997), energy by using a LECO AC 300 automated calorimeter system 789–500 (LECO, St Joseph, MO), and carbon as described by Neergaard et al. (1969). Chromic oxide was determined using the method of Schürch et al. (1950), and total lactic acid and SCFA were analyzed by gas chromatography (Jensen et al., 1995). Enzymatic-colorimetric methods were used to analyze for starch (Bach Knudsen, 1997), sugars (glucose, fructose, and sucrose), and fructan (Larsson and Bengtsson, 1983). Total NSP and their constituent sugars were determined by gas-liquid chromatography for neutral sugars and by a colorimetric method for uronic acids, using a modification of the methods described by Theander and Åman (1979) and Englyst et al. (1982) and as described by Bach Knudsen (1997).

Cellulose content was calculated as:

$$\text{cellulose} = \text{NSP}_{\text{glucose (12 mol/L of } H_2SO_4)} - \text{NSP}_{\text{glucose (2 mol/L of } H_2SO_4)},$$

total noncellulosic polysaccharides was calculated as:

$$\text{total noncellulosic polysaccharides} = \text{rhamnose} + \text{fucose} + \text{arabinose} + \text{xylose} + \text{mannose} + \text{galactose} + \text{glucose} + \text{uronic acids},$$

soluble noncellulosic polysaccharides was calculated as:

$$\text{soluble noncellulosic polysaccharides} = \text{total noncellulosic polysaccharides} - \text{insoluble noncellulosic polysaccharides},$$

and DF was calculated as:

$$\text{DF} = \text{total noncellulosic polysaccharides} + \text{cellulose} + \text{lignin}.$$

Klason lignin was measured gravimetrically as the residue resistant to hydrolysis by 12 mol/L of H_2SO_4 (Theander and Åman, 1979).

Viscosity was measured in extracts of diets and digesta following the procedure of Johansen et al. (1997), which briefly was as follows: 30 g of ileum digesta were centrifuged (10,000 × g for 20 min at 4°C) to separate solid (sediment) from liquid (supernatant) digesta. The diets (2 g) were dissolved and extracted for 1 h at 40°C

in 8 mL of 0.9% sodium chloride with 0.02% sodium azide (NaCl + NaN$_3$) and centrifuged at 10,000 × g for 20 min at 4°C. Just after centrifugation, the supernatant fraction of the digesta was removed by suction, and the viscosity of the supernatant was measured in a Brookfield DV-11 cone/plate viscometer (Brookfield Engineering Laboratories Inc., Stoughton, MA) at 38°C and shear rates in the range of 2.25 to 450 s^{-1}. Values of apparent viscosity at a shear rate of 30 s^{-1} are reported. The remaining supernatant was frozen and stored for subsequent analysis.

The procedure for swelling was briefly as follows: 300 mg of sample was dissolved in 10 mL of NaCl + NaN$_3$ and placed in a shaking water bath (150 movements/min) at 39°C in 20 h. The swelling capacity (L/kg of DM) was measured 1 h after turning off the water bath.

To calculate the fraction of solid digesta, the 50-mL centrifuge tubes containing the sediment were turned upside down to drain residual supernatant for at least 30 min before reweighing. The fraction of digesta (g/kg) present in the sediment was calculated. The sediment was then freeze-dried and the tubes weighed again to determine the DM content. The water-binding capacity was calculated as the amount of water retained in the sediment after centrifugation and removed after the drying procedure.

The water-binding capacity (kg of water/kg of DM) of the sediment fraction of digesta was calculated as:

$$\text{water-binding capacity} = \frac{(\text{WW} - \text{DW})}{\text{DW}},$$

where WW = the wet weight and DW = the dry weight of the material.

Calculations and Statistical Analysis

The content of polysaccharide residues was calculated as anhydro sugars, and all apparent digestibilities, flow, and net disappearance were calculated relative to the Cr_2O_3 concentration:

$$\text{digestibility of X } (\% \text{ of intake}) = \left(1 - \frac{Cr2O3_{(\text{diet})} \times X_{(\text{ileum/feces})}}{Cr2O3_{(\text{ileum/feces})} \times X_{(\text{diet})}}\right) \times 100,$$

where X = the concentration of specific nutrients or energy in the diet and the ileal or feces materials. When calculating starch digestibility, it is assumed that free glucose in ileum digesta derives from starch.

The recovery (flow) of nutrient X at the ileum or in the feces was calculated as:

$$\text{recovery of X (g/d)} = \text{intake of X (g/d)} \times (100 - \text{digestibility of X})/100,$$

and the flow of lactic acid and SCFA was calculated on the basis of the flow of wet digesta at the ileum or in feces multiplied by the concentration of lactic acid and SCFA.

The average daily HP was calculated according to Brouwer (1965) as described in Christensen et al. (1988) using the RQ, as follows:

$$HP_{RQ}, KJ = 16.181V_{O2} + 5.023V_{CO2}$$
$$- 5.989N - 2.168V_{CH4},$$

where V_{02}, V_{CO2}, and V_{CH4} = the volume (L) of oxygen, carbon dioxide, and methane consumed and produced daily and N = the amount (g) of nitrogen excreted in the urine daily.

The results were analyzed by a GLM procedure (SAS Inst. Inc., Cary, NC) according to the following model:

$$X_{ijk} = \mu + \alpha_i + \beta_j + C_k + \varepsilon_{ijk,}$$

where ε_{ijk} $(0,o^2)$, α_i = the diet 1, 2, and 3; β_j = period 1, 2, and 3; and C_k = the sow 1,...6. The level of significance was $P < 0.05$.

The relationship between disappearances of carbohydrates or OM in the large intestine and CH_4 production were calculated using PROC REG of SAS, as

$$Y = \beta_0 + \beta_1X_1 + \varepsilon,$$

where Y = the dependent variable (i.e., CH_4); X = the independent variable; β_0 = the intercept; and β_1 = a coefficient representing the contribution of the independent (i.e., carbohydrates or OM) variables.

RESULTS

The 3 experimental diets (Table 1) were formulated to provide different levels and types of DF. This was reflected in the composition of the DF fraction where NCP was approximately 2 times greater in the 2 HF diets than the control, cellulose 5.5 to 6 times greater than in the control, and lignin 2.8 to 3.6 times greater than the control. The HF1 diet had a greater absolute concentration of S-DF compared with LF and HF2. The differences in DF levels and types also translated to the physicochemical properties in which the greatest viscosity, swelling, and water-binding capacity were detected for diet HF1 followed by diets HF2 and LF. In our diet formulation, proper adjustment was done to ensure a sufficient supply of amino acids, but unexpectedly, diet HF1 had a greater protein concentration than planned.

There were in general only minor variations in viscosity and water-binding capacity of digesta materials among the 3 diets and between morning and afternoon samples (data of mean values are shown in Table 2). However, the water-binding capacity of ileal material when feeding diet LF was decreased (3.25 kg/kg of DM)

in the afternoon compared with the morning (4.29 kg/kg of DM). Also, there was a more decreased viscosity (1.50 mPa·s) during the morning than during the afternoon (2.00 mPa·s) sampling when feeding HF2.

Feeding HF diets resulted in a 1.7 to 1.8 times greater ileal flow of digesta compared with diet LF (Table 2). The increase in digesta flow was seen for OM and ash. The greatest contributor to the increased flow of OM was carbohydrates, which increased from 190 to 538 to 539 g/d, whereas the increase detected for protein, fat, organic acids, and residue was smaller although generally greater than for diet LF. There was a substantial absorption of liquid from the large intestine of 4.4, 9.0, and 7.6 L when feeding LF, HF1, and HF2, respectively, making the fecal excretion almost similar for diets LF and HF1 but still greater for diet HF2. For OM, the greatest amount of excreted fecal material was HF2 > > HF1 > LF. This trend was also observed for protein, whereas it was only for diet HF2 that ash, carbohydrates, and fat were greater.

The amount and type of DF also affected diet digestibility (Table 3). The HF diets had ($P < 0.05$) decreased digestibility of OM, carbohydrates, and starch in ileum and of OM and carbohydrates in total tract compared with LF. Furthermore, the diet with the high concentration of S-DF (HF1) had greater apparent digestibility of protein in ileum compared with the other diets. The total tract digestibility of OM, protein, fat, carbohydrates, starch, and total NSP and noncellulosic polysaccharides was also greater with diet HF1 than HF2. The digestibility of cellulose was low in ileum for all diets and only slightly positive in total tract when feeding diet LF. The digestibility of noncellulosic polysaccharides and total NSP was different ($P < 0.05$) among all diets in the total tract, in which the greatest digestibility was for diet HF1 (noncellulosic polysaccharides, 82%; total NSP, 78%) and the least for LF (noncellulosic polysaccharides, 60%; total NSP, 48%).

The sows in the current study were fed a constant amount of feed, which resulted in an intake of DE that was decreased when feeding HF2 compared with the other diets (Table 4). Substitution of cereals with coproducts moved a substantial proportion of the digestion to the large intestine; with diet HF2, 21% of DE disappeared in the large intestine; with diet HF1, it was 28%, whereas it was only 10% with diet LF. A greater ($P > 0.05$) amount of energy was excreted by the urine when feeding diet HF1 than when feeding diet LF, which could be caused by the greater intake of protein from this diet. When feeding both HF diets, 3 to 3.6 times greater amounts of CH_4 were produced, and HF2 resulted in decreased amount of DE compared with the other diets. There was no difference in the HP (expressed as MJ/kg of DM) between the diets. Retained energy was negative when feeding diet HF2, whereas it was greater than zero for the other 2 diets.

The relationship between carbohydrates digested in the large intestine (g/d) and the CH_4 production expressed as (kJ/d) was

Table 2. Flow and composition of ileal and fecal materials of sows fed low-fiber (LF), high-fiber 1 (HF1), or high-fiber 2 (HF2) diets[1]

Item	Ileum				Feces			
	Diet				Diet			
	LF	HF1	HF2	SEM	LF	HF1	HF2	SEM
Total wet material, g/d	5,560[b]	10,113[a]	9,519[a]	522	1,184[b]	1,121[b]	1,948[a]	98
Total DM, g/d	544[b]	972[a]	1,004[a]	54	346[b]	389[b]	589[a]	26
Total DM, g/kg of wet material	97	96	106	2.3	294[b]	349[a]	306[ab]	9.1
Ash, g/d	121[b]	152[a]	163[a]	5.1	78[b]	75[b]	109[a]	4.0
OM, g/d	423[b]	821[a]	841[a]	50	268[c]	318[b]	486[a]	23
Total carbohydrates,[2] g/d	190[b]	538[a]	539[a]	42	132[b]	145[b]	236[a]	12
Total carbohydrates,[2] g/kg of DM	340[b]	552[a]	535[a]	25	383	373	401	9.0
CP, g/d	83[b]	108[a]	122[a]	4.7	47[c]	69[b]	98[a]	5.2
CP, g/kg of DM	153[a]	111[b]	122[b]	5.1	136[c]	178[a]	167[b]	4.6
Fat, g/d	42[b]	38[b]	52[a]	1.8	45[b]	44[b]	60[a]	1.9
Fat, g/kg of DM	78[a]	39[b]	52[b]	4.2	130[a]	113[b]	101[b]	3.3
Organic acids, g/d	2[b]	3[a]	3[a]	0.2	2	2	3	0.2
Organic acids, g/kg of DM	3	3	3	0.1	6	5	5	0.3
Residue,[3] g/d	107[b]	134[a]	126[ab]	4.2	41[b]	59[b]	90[a]	5.7
Water-binding capacity, kg/kg of DM	3.77	4.43	4.55	0.2				
Viscosity, mPa·s[4]	1.50	2.00	1.75	0.1				

[a–c]Within ileum or feces, means without a common superscript are different among diets ($P < 0.05$).

[1]Values are the means of 6 sows from Exp. 1.

[2]Assumed that starch is approximately 0 in fecal material.

[3]Residue = OM − carbohydrates − fat − protein − organic acid.

[4]mPa·s = millipascal seconds.

$$Y = 160 + 1.369 \times carbohydrates, r = 0.79; P = 0.002$$

and between OM digested in the large intestine (g/d) and CH_4 production (kJ/d) was

$$Y = 132 + 1.132 \times OM, r = 0.72; P = 0.008.$$

Activity expressed as standing hours per 24 h was measured during the period in the respiration chambers. Activity was decreased ($P = 0.045$) when feeding diet HF1 (5.11 h/24 h) compared with LF (6.10 h/24 h), and there was a tendency ($P = 0.08$) for decreased activity when feeding HF1 compared with HF2 (5.96 h/24 h). There was no difference in activity between HF2 and LF ($P = 0.78$). In the period in which the sows were placed in metabolic cages, the average BW gain was 281 g/d.

DISCUSSION

In the present study, a simple T-cannula was used to study the digestibility in terminal ileum and without causing any problems with blockage even though the 2 HF diets were very high in DF. In this context, it should be noted that in the present study, the sows were allowed to move freely around in relatively large

Table 3. Digestibility (% of intake) of nutrients in ileum and total tract of sows fed low-fiber (LF), high-fiber 1 (HF1), or high-fiber 2 (HF2) diets[1]

Item	Ileum				Total tract			
	Diet				Diet			
	LF	HF1	HF2	SEM	LF	HF1	HF2	SEM
Ash	−23[a]	−44[b]	−35[ab]	3.1	21[a]	29[a]	12[b]	2.1
OM	75[a]	53[b]	51[b]	2.9	84[a]	82[b]	72[c]	1.4
CP	68[a]	69[a]	61[b]	1.3	82[a]	80[a]	68[b]	1.5
Fat	74	76	71	0.7	71[a]	72[a]	67[b]	0.7
Carbohydrates	84[a]	51[b]	52[b]	3.9	89[a]	87[b]	79[c]	1.1
Starch	96[a]	92[b]	91[b]	0.8	99.9[a]	99.7[a]	97[b]	0.3
Total nonstarch polysaccharides	41[a]	23[b]	26[ab]	3.2	48[c]	78[a]	67[b]	3.2
Cellulose	11	6	4	3.8	9[b]	72[a]	64[a]	6.8
Noncellulosic polysaccharides	50	34	40	2.9	60[c]	82[a]	69[b]	2.3
Soluble nonstarch polysaccharides	67[a]	32[b]	52[ab]	4.2	—	—	—	—

[a–c]Within ileum or total tract, means without a common superscript are different among diets ($P < 0.05$).

[1]Values are the means of 6 sows from Exp. 1.

Serena et al.

Table 4. Energy utilization of sows fed low-fiber (LF), high-fiber 1 (HF1), or high-fiber 2 (HF2) diets[1]

Item[2]	Diet			SEM
	LF	HF1	HF2	
DM intake, g/d	1,820[b]	1,840[a]	1,840[a]	2.30
GE intake, MJ/d	31.89[c]	33.21[a]	33.09[b]	1.44
DE intake, MJ/d	26.26[a]	26.03[a]	22.32[b]	4.60
ME intake, MJ/d	24.92[a]	23.97[a]	20.67[b]	4.64
ME, MJ/kg of DM	13.69[a]	13.03[a]	11.23[b]	0.30
Energy disappearance, % of DE				
Ileum[3]	90[a]	72[b]	79[b]	3.00
Large intestine	10[a]	28[b]	21[b]	2.40
Energy, % of DE as				
Urine	4.1[b]	5.2[a]	4.9[ab]	0.22
CH_4	0.8[b]	2.7[a]	2.4[a]	0.25
H_2	0.03[a]	0.04[a]	0.03[a]	0.01
ME	95[a]	92[b]	93[b]	0.42
Utilization of ME				
HP_{RQ}, MJ/kg of DM	13.1[a]	12.9[a]	12.2[a]	0.23
RE, MJ/kg of DM	0.55[a]	0.17[a]	−0.99[b]	0.28
HP_{RQ}/ME, %	96[b]	99[b]	109[a]	28
RE/ME, %	4.0[a]	1.3[a]	−8.8[b]	0.20

[a–c]Within a row, diets without a common superscript are different ($P < 0.05$).

[1]Values are the means of 6 sows from Exp. 2.

[2]HP = heat production and RE = retained energy, where RE = ME − HP_{RQ}.

[3]Data based on 4 animals from Exp. 1.

pens including during ileal collections. This collection procedure is probably more representative of normal conditions compared with collection of ileum in metabolic cages and may have helped to pass the digesta through the gastrointestinal tract (Bakker and Jongbloed, 1994).

In the present study, the dietary composition had a major effect on the flow of digesta and nutrients up to the end of the small intestine as well as the degradation of nutrients in the large intestine. The flow of digesta at the terminal ileum was almost 2 times greater in sows fed on the HF diets compared with sows fed on the LF diet. This demonstrates the importance of the dietary levels of DF and the physiochemical properties expressed in terms of viscosity, water-binding capacity, and swelling. Although diet HF1 contained more S-DF and, consequently, had a greater viscosity, water-binding capacity, and swelling than diet HF2, this difference was not reflected in the flow of either wet digesta or dry solid. The lack of significant differences in the physiochemical properties of ileal digesta between the 2 HF diets could be due to the fact that in vitro solubility of DF polysaccharides can differ significantly from the in vivo data as pointed out by data of Monro (1993) and Miquel et al. (2001). We also know that the amount of S-DF to a large extent is determined by the extraction procedure and that the amount of S-DF in pectin-containing materials, such as sugar beet pulp and potato pulp, is overestimated (Marlett et al., 1989; Monro, 1993).

The present study clearly demonstrated that type and level of DF had a pronounced effect on the site of energy, OM, and carbohydrate digestion. Thus, when feeding the LF diet, up to 84% of the carbohydrates were digested in the small intestine compared with only 51 to 52% when feeding the 2 HF diets. This caused a substantially much greater flow of carbohydrates to the large intestine. In the large intestine, the most noticeable difference in the disappearance pattern of nutrients among the 3 diets is related to the disappearance of carbohydrates when consuming the HF diets (303 to 393 g/d) as compared with the low-DF (58 g/d) diet. The data show that the disappearance of carbohydrates in the large intestine was greater with diet HF1 than with HF2. The insoluble and more lignified DF in diet HF2 compared with diet HF1 restricts the microbial degradation of nutrients in the large intestine (Bach Knudsen and Hansen, 1991; Flourié, 1992).

The digestibility of the other dietary constituents than DF can potentially be influenced by the DF level, because cell walls may hinder the access of hydrolytic enzymes to the cell contents (Bach Knudsen et al., 1993). A negative correlation between DF and digestibility is well established in growing pigs as well as in adult pigs (Fernandez et al., 1986; Jørgensen et al., 1996; Olesen et al., 2001). The digestibility of protein and fat, however, did not in general follow the same pattern as has been shown in other studies. In the present study, only the ileal digestibility of protein was decreased when feeding diet HF2 compared with diet LF. The HF1 diet had a greater concentration of protein than the other diets and thereby increased apparent protein digestibility (Yan et al., 1995; Jørgensen et al., 1996; Theil et al., 2002). The differences in terms of digestibility among the diets at the ileum were also observed for the total gastrointestinal tract. However, more surprising

was the decreased digestibility of starch in the small intestine with the 2 HF diets compared with LF, which is much lower than found in studies with growing pigs (Bach Knudsen and Jørgensen, 2001).

The digestibility of NSP at the terminal ileum was greater for diet LF, whereas it was the same as shown in growing pigs (~24%) for the 2 HF diets (Bach Knudsen and Jørgensen, 2001). Consistent with the chemical nature of cell wall NSP, the digestibility of noncellulosic polysaccharides, especially soluble noncellulosic polysaccharides, was greater than of cellulose for all diets. The digestibility of cellulose was not significantly decreased for HF2 than for HF1, but the more lignified DF fraction in diet HF2 probably resulted in the slightly decreased digestibility of cellulose in this diet compared with HF1. However, the very low digestibility of cellulose with diet LF is more difficult to understand, because many studies with growing-finishing pigs (Low, 1985; Fadel et al., 1989) have shown greater digestibilities in spite of an increased gastrointestinal retention time in sows than in pigs (Van Soest, 1985; Shi and Noblet, 1993). The digestibility of noncellulosic polysaccharides was in line with our expectations and fully explained by the type of polysaccharides in the DF fraction and the degree of lignification as discussed in Serena (2005). A study by Olesen et al. (2001) further confirmed that the degradation of DF was greater with a sugar beet pulp-supplemented diet compared with a low-DF control diet. An increased adaptation period to the feed could eventually have given a greater digestibility of NSP particularly when feeding the HF2 diet (Longland et al., 1993). However, overall, our results show that the sows are very efficient in using DF as an energy source.

The 3 levels of carbohydrate fermentation in the large intestine are correlated with the CH_4 production. These findings are consistent with other studies by Jørgensen et al. (1996, 2000) and Olesen et al. (2001). The inverse relationship between energy disappearances in the small versus the large intestine in response to the dietary DF level is also in agreement with Jørgensen et al. (2000). However, contrary to the findings of Jørgensen et al. (1996) is the significantly greater amount of DE excreted in the urine when feeding the diet with the high level of S-DF compared with the LF diet. A confounding factor, however, could be the greater intake of protein (Theil et al., 2002) when feeding HF1.

In our study, HP was not increased with feeding HF diets as observed by Jørgensen et al. (1996), who showed an increased HP due to increased microbial degradation of DF components. It cannot be excluded that these contrasting results are due to a reduction in activity-related HP (Schrama et al., 1996, 1998; Schrama and Bakker, 1999) when the sows are placed in metabolic cages (sows had a minimum space when placed in metabolic cages and minimum activity).

The decreased activity in this experiment when feeding HF1 is in agreement with the findings of Rijnen et al. (2003) and is presumably caused by the high level of S-DF that delayed gastric emptying (Rainbird and Low, 1996) and caused a decreased rate of nutrient absorption (Serena, 2005). We also noticed that the average BW gain increased (281 g/d) during the time spent in the respiration chambers, which could be due to increased amount of material in the gut caused by a decreased activity.

The sows of the present study were fed a constant amount of 2,000 g/d. This resulted in a decreased intake of DE when feeding diet HF2 compared with the other 2 diets. The sows fed LF and HF1 were fed in agreement with energy for maintenance (387 to 400 kJ/kg of $BW^{0.75}$ per day; Le Goff et al., 2002), whereas the amount of energy provided by diet HF2 did not meet the maintenance requirement of the sows. Because of the decreased digestibility caused by the DF level, the ME intake from the HF diets was also decreased, and the sows consuming diet HF1 and HF2 should have consumed 5 and 22% more DM, respectively, to provide equal amounts of ME. This would not have been a factor when consuming diet HF1, whereas with diet HF2, the amount of feed could not be increased any further. This is presumably a reflection of the relatively low digestibility of all nutrients with diet HF2, which caused the physical capacity of the digestive tract to set the limit for feed intake.

In conclusion, the study shows that feeding the HF diets resulted in a significant increase in flow of nutrients through the intestinal tract, thereby moving the digestion distal in the gastrointestinal tract; a significantly greater amount of nutrients was provided as fermentation products rather than by nutrients absorbed from the small intestine. It was also shown that the degradation of DF components was linked to the composition of the DF fraction in particular the degree of lignification. A correlation was shown between the fermentation of carbohydrates in the large intestine and the CH_4 production, whereas there was no apparent effect of site of carbohydrate degradation and the HP possibly, because the energy balances were near zero. Feeding the diet with the high level of S-DF further resulted in decreased activity compared with the other 2 diets.

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