Absorption of carbohydrate-derived nutrients in sows as influenced by types and contents of dietary fiber

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ABSTRACT: The current investigation was undertaken to study the absorption and plasma concentration of carbohydrate-derived nutrients [glucose, short-chain fatty acids (SCFA), and lactate] and the apparent insulin production in sows fed diets containing contrasting types and contents of dietary fiber. Six sows were fed 3 experimental diets, low fiber (LF; 177 g of dietary fiber and 44 g of soluble fiber/kg of DM), high soluble fiber (HF-S; 429 g of dietary fiber and 111 g of soluble fiber/kg of DM), and high insoluble fiber (HF-I; 455 g of dietary fiber and 74 g of soluble fiber/kg of DM), in a repeated crossover design. Variations in dietary concentration and solubility of dietary fiber were obtained by substituting starch-rich wheat and barley in the LF diet with dietary fiber-rich co-products (sugar beet pulp, potato pulp, pectin residue, brewers spent grain, pea hulls, and seed residue, which have distinct physicochemical properties). The main carbohydrate component of the LF diet was starch and nonstarch polysaccharides (cellulose and noncellulosic polysaccharides) for the 2 high dietary fiber diets. Consumption of the LF diet resulted in increased and rapid glucose absorption at 0 to 4 h postfeeding. With the HF-I diet, the glucose absorption pattern was similar but at a decreased rate, whereas it was decreased and delayed with the HF-S diet (diet, \(P < 0.001\); time, \(P < 0.001\)). These differences were also reflected in the insulin response. The quantitative absorption of SCFA at 0 to 10 h postfeeding was greater when feeding the HF-S diet compared with the LF diet (\(P < 0.001\)) and intermediate when feeding the HF-I diet (\(P < 0.001\)). The study showed that feeding the high dietary fiber diets resulted in an increased and more uniform uptake of SCFA than when feeding the LF control. Moreover, the HF-S diet reduced diurnal variation in glucose and insulin concentrations.

Key words: absorption, catheterized sow, glucose, insulin, short-chain fatty acid

INTRODUCTION

Sugars, oligosaccharides, starch, and nonstarch polysaccharides (NSP) are the main organic constituents of feeds for pigs. Because various carbohydrate components are digested and absorbed at different sites and rates in the gastrointestinal tract (Bach Knudsen, 2005; Bach Knudsen et al., 2006), differences in the dietary carbohydrate composition can be used proactively to modulate the uptake of carbohydrate-derived nutrients, glucose, short-chain fatty acids (SCFA), and lactate (LA), and thereby affect the feeling of satiety and behavior of the animals (Brouns et al., 1997; Danielsen and Vestergaard, 2001; de Leeuw and Ekkel, 2004; de Leeuw et al., 2005b).

The chemical composition, glycosidic linkages, and cross-linkages of polysaccharides in the dietary fiber (DF; NSP + lignin) matrix have a profound effect on the physicochemical properties of the feed (Bach Knudsen, 2001; Serena and Bach Knudsen, 2007a). For instance, soluble DF may raise luminal viscosity and increase the water-binding capacity (WBC) of digesta in the small intestine (Canibe and Bach Knudsen, 2002), thereby slowing the movement of digesta and the rate of glucose absorption (Holt et al., 1979; Ellis et al., 1995). Insoluble DF, on the other hand, has relatively little influence on events in the stomach and small intestine (Low et al., 1986; Rainbird and Low, 1986), but the chemical and structural composition and degree of lignification of the DF will have a profound influence on the fermentation in the large intestine (Bach Knudsen,
It is hypothesized that substitution of starch for DF-rich feedstuffs will result in a shift in the nature and diurnal variation of energy that is provided to the animal. The main purpose of the present investigation was to study the qualitative and quantitative aspects of carbohydrate assimilation in catheterized sows fed 3 experimental diets varying in types and contents of DF. Variations in DF contents and physicochemical properties were obtained by substituting starch-rich wheat and barley in the control diet with DF-rich sugar beet pulp, potato pulp, pectin residue, brewers spent grain, pea hulls, and seed residue, which have distinct physicochemical properties (Serena and Bach Knudsen, 2007a).

MATERIALS AND METHODS

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

Diets

The diets (Table 1) were prepared from wheat and barley supplemented with different co-products from the Danish vegetable food and agricultural industries [potato pulp, KMC (Brande, Denmark); sugar beet pulp, Danisco Sugar A/S (Assens, Denmark); pectin residue, CPKelco ApS (Lille Skensved, Denmark); brewers spent grain, Agro-korn A/S (Videbæk, Denmark); pea hulls and seed residue, DLF Trifolium A/S (Roskilde, Denmark)]. The variation in the chemical and physicochemical composition of these co-products collected over a 2-yr period has been published recently (Serena and Bach Knudsen, 2007a). The diets were formulated to contain different contents and types of DF. A low-DF diet (LF; 177 g of DF/kg of DM) was prepared from wheat and barley as the main carbohydrate source, and 2 high-DF diets (approximately 440 g of DF/kg of DM) were prepared by substituting the wheat and barley with sugar beet pulp, potato pulp, and pectin residue (HF-S) and with approximately one-third sugar beet pulp, potato pulp, and pectin residue and two-thirds brewers spent grain, pea hulls, and seed residue (HF-I). The diets were formulated to meet the Danish recommendations for essential macro- and micronutrients (Jørgensen and Tybirk, 2005) and were milled to pass through a 2-mm screen. In our diet formulation, proper adjustment was made to ensure a sufficient supply of digestible AA, which was the reason for the greater protein concentration of the 2 high-DF diets compared with the LF diet (Table 2). The amount of carbohydrates was greatest in the LF diet (698 g/kg of DM) and similar in the HF-S and HF-I diets (628 to 622 g/kg of DM). Diet LF had the greatest starch content, whereas it was much less in the 2 high-DF diets. The 2 high-DF diets were similar in total NSP (367 to 369 g/kg of DM) and similar in cellulose and noncellulosic polysaccharides (NCP), but with variable proportions of soluble-to-insoluble NCP (30:70 in the HF-S diet and 20:80 in the HF-I diet). The different chemical compositions translated into differences in the physicochemical properties of the diets. Swelling and WBC were greatest in the HF-S diet and least in the LF diet.

Animal Experiment

Measurement of the quantitative absorption of nutrients was carried out as a 3 × 3 repeated crossover design, with 6 sows fed the 3 different diets (i.e., LF, HF-S, and HF-I, for 7 d per diet period). Nonpregnant sows with an initial average BW of 202 ± 28 kg were selected after weaning their first litter (Peter Bøjlesen, Vammen, Denmark). After 10 d of adaptation, each sow was surgically fitted with 2 catheters. The first was placed in the portal vein (1.2 mm i.d. and 2.3 mm o.d.; Cole-Parmer, Vernon Hills, IL), and the second was placed in the mesenteric artery (1.0 mm i.d. and 1.8 mm o.d.; Cole-Parmer), and also with an ultrasonic blood flow probe (28A probe, 28 mm; Transonic System Inc., Ithaca, NY) around the portal vein. A flowmeter (Transonic T206 flowmeter with P-option; Transonic System Inc.) was used to measure the blood flow rate. After a 7-d recovery period from the surgery, the sows were introduced to 1 of the 3 experimental diets. During the experimental period, the sows were fed once daily at 1000 h (leftover feed was removed af-

Table 1. Composition of experimental diets, low fiber (LF), high soluble fiber (HF-S), and high insoluble fiber (HF-I)

<table>
<thead>
<tr>
<th>Ingredient, g/kg (as-fed basis)</th>
<th>LF</th>
<th>HF-S</th>
<th>HF-I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>420</td>
<td>145</td>
<td>145</td>
</tr>
<tr>
<td>Wheat</td>
<td>420</td>
<td>145</td>
<td>145</td>
</tr>
<tr>
<td>Sugar beet pulp</td>
<td>—</td>
<td>140</td>
<td>50</td>
</tr>
<tr>
<td>Pectin residue</td>
<td>—</td>
<td>140</td>
<td>50</td>
</tr>
<tr>
<td>Potato pulp</td>
<td>—</td>
<td>140</td>
<td>50</td>
</tr>
<tr>
<td>Seed residue</td>
<td>—</td>
<td>—</td>
<td>135</td>
</tr>
<tr>
<td>Pea hulls</td>
<td>—</td>
<td>—</td>
<td>135</td>
</tr>
<tr>
<td>Brewers spent grain</td>
<td>—</td>
<td>—</td>
<td>135</td>
</tr>
<tr>
<td>Soybean oil</td>
<td>50</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Soybean meal (toasted)</td>
<td>75</td>
<td>216</td>
<td>84</td>
</tr>
<tr>
<td>Marker (chronic oxide)</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Ca(H2PO4)2</td>
<td>22</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>CaCO3</td>
<td>6</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>NaCl</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Vitamin-mineral mix1</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

1Provided per kilogram of final diet: 8,800 IU of vitamin A as retinyl acetate; 1,000 IU if vitamin D3 as cholecalciferol; 60 mg of all rac 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 BHT; 100 mg of Fe as FeSO4·7H2O; 150 mg of Zn as ZnO; 28 mg of Mn as MnO; 20 mg of Cu as CuSO4·5H2O; 304 μg of I as KI; and 300 μg of Se as Na2SeO3.
The daily feeding level was 2,000 g of feed (as-fed basis), and the sows had free access to water (Table 3). Sows were placed in farrowing pens during the collection of blood from the portal vein and mesenteric artery. Blood samples were collected on the last day of each period at −120, −60, 0, 15, 30, 45, 60, 90, and 120 min after feeding, and at 60-min intervals up to 600 min. Blood flow in the portal vein was measured at the same time as blood collection as a mean of 4 readings in 1 min, and hematocrit was measured at −60 and 360 min after feeding. The blood was collected into 2 Na-heparinized plastic tubes (9 and 4 mL) and 1 EDTA-heparinized plastic tube (2 mL; Greiner Bio-One GmbH, Kremsmünster, Austria) and centrifuged (1,800 × g for 10 min at 8°C). Plasma was frozen until further analysis. The plasma from the Na-heparinized tubes was analyzed for glucose, SCFA, and insulin. The plasma from the EDTA-heparinized tubes was used for analysis of LA. On the days of blood sampling, any feed that remained was collected.

### Analytical Methods

All chemical analyses were performed in duplicate on freeze-dried materials. The DM was measured by drying to a constant weight (mostly 20 h) at 103°C, and ash was analyzed according to the AOAC (1990) method. Nitrogen was determined by the Kjeldahl method (AOAC, 1990), and protein was calculated as N × 6.25. Fat was extracted with diethyl ether after acid hydrolysis and analyzed as described by Stoldt (1952). The diets were analyzed for sugars (glucose, fructose, and sucrose) and fructans as described by Larsson and Bengtsson (1983), and starch and NSP as described by Bach Knudsen (1997). Total NSP was divided into cellulose, soluble NCP, and insoluble NCP by their constituent sugars by GLC for neutral sugars and by colorimetry for uronic acid (Bach Knudsen, 1997). Klason lignin was measured as the sulfuric acid-insoluble residue as described by Theander and Åman (1979). The diets were analyzed for WBC and viscosity as described by Canibe and Bach Knudsen (2002) and Johansen et al. (1997), respectively. Briefly, the procedure for swelling was as follows: 300 mg of sample was weighed into a 15-mL conical centrifuge tube with 0.1-mL divisions, dissolved in 10 mL of 0.9% NaCl:0.02% Na2SO4 and placed in a shaking water bath (150 movements/min) for 20 h at 39°C. The swelling capacity (L/
kg of DM) was measured by reading the volume that fiber occupied 1 h after removing the water bath.

Plasma was analyzed for SCFA (acetate, propionate, butyrate, valerate, caproinate, isovalerate, and isobutyrate) essentially as described by Brighenti (1998) by using 2-ethyl butyrate (Fluka No. 03190; Sigma Aldrich, St. Louis, MO), rather than isovaleric acid, as an internal standard. The LA was measured according to the method described by Noll (1984), and insulin was analyzed as described by Lövendahl and Purup (2002). Glucose concentrations in plasma were analyzed by a glucose-oxidase kit (Trinder, 1969).

**Calculations and Statistical Analysis**

Absorption of glucose, LA, and SCFA into the portal vein and apparent production of insulin in the portal vein were calculated from the porto-arterial differences and the portal flow measurement as described by Rérat et al. (1984):

\[
q = (C_p - C_a) \times F(dt), \text{ and}
\]

\[
Q = \sum_{t_0}^{t_n} q_t,
\]

where \( q \) is the amount of glucose, LA, or SCFA absorbed and the amount of insulin produced within the time period \( dt \), \( C_p \) is the concentration in the portal vein, \( C_a \) is the concentration in the mesenteric artery, \( F \) is blood flow in the portal vein, and \( Q \) is the amount absorbed from \( t_0 \) to \( t_n \) or the amount of insulin produced from \( t_0 \) to \( t_n \). The calculated insulin production can only be described as apparent because insulin has a pulsatile secretion that is broken down by the liver and kidneys and that has a variable half-life value (10 to 30 min). The energy coefficients reported by Weast et al. (1984) were used when converting millimoles to energy for glucose, LA, and the SCFA mix.

Differences between diets and time in concentrations (mesenteric artery and portal vein) of glucose, LA, SCFA (acetate, propionate, butyrate, valerate, caproinate), and branched-chain fatty acids (isobutyrate and isovalerate), and absorption of glucose, LA, and SCFA were analyzed as repeated measurements by using PROC MIXED (SAS Inst. Inc., Cary, NC), with a level of significance at \( P \leq 0.05 \):

\[
X_{ijk} = \mu + \alpha_i + \beta_j + \nu_k + (\alpha\beta)_{ij} + \epsilon_{ijkl},
\]

where \( X_{ijk} \) is the dependent variable, \( \mu \) is the overall mean, \( \alpha_i \) is the diet (\( i = 1, 2, \) or 3), \( \beta_j \) is the week (\( j = 1, 2, \) or 3), \( \nu_k \) is the sow (\( k = 1 \) to 6), \( (\alpha\beta)_{ij} \) is the 2-factorial interaction between diet and period. The correlation between total apparent glucose absorption and apparent insulin production was calculated as the Pearson product-moment correlation coefficient by using PROC CORR of SAS.

**RESULTS**

To obtain a fixed reference point for the measurements of postprandial changes in nutrients in the blood, the eating period was initially restricted to 45 min. Only 1 sow fed the HF-I diet did not consume all the allowance on 1 of the sampling days.

There were no differences in blood flow among sows fed the 3 diets (\( P = 0.26 \); Table 4). Mean blood flow for all diets was 19.8 mL/(kg of BW·min). Blood flow was 3.4 L/min before feeding, increasing to 4.0 L/min in the absorptive phase and to 4.2 L/min in the postabsorptive phase (data not shown).

The concentrations of glucose and insulin in the portal vein and in the mesenteric artery are shown in Table 4. There was a rapid postprandial increase in glucose concentration in the portal vein when feeding the LF diet (Figure 1A). Glucose concentration increased from 3.4 mmol/L at feeding (time 0 h) to 7.0 mmol/L after 1 h, and slowly decreased to 4.5 mmol/L in the portal vein 10 h after feeding. When feeding the HF-I diet, there was also a rapid response in the portal vein 1 h after feeding and the same descending pattern in glucose concentration up to 10 h after feeding as observed with the LF diet. However, when feeding the HF-S diet, a decreased and delayed glucose response in the portal vein was observed. The concentration of glucose in the portal vein throughout the day was also more stable when feeding the HF-S diet compared with the other diets. However, in the mesenteric artery, the concentration was similar when sows were fed the 3 different diets.

The absorption (mmol/h) of glucose was greater when feeding the LF diet than when feeding the high-DF diets (Table 4). Before feeding, no differences were
Table 4. Plasma concentrations (0 to 10 h postfeeding) in the mesenteric artery and portal vein, blood flow in the portal vein, and absorption in sows fed low fiber (LF), high soluble fiber (HF-S), or high insoluble fiber (HF-I)^1

<table>
<thead>
<tr>
<th>Item</th>
<th>Mesenteric artery</th>
<th>Portal vein</th>
<th>P-value</th>
<th>Portal vein</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LF</td>
<td>HF-S</td>
<td>HF-I</td>
<td>SEM</td>
<td>Diet</td>
</tr>
<tr>
<td>Flow, L/min</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Glucose, mmol/L</td>
<td>3.70</td>
<td>3.46</td>
<td>3.55</td>
<td>0.27</td>
<td>0.001</td>
</tr>
<tr>
<td>Absorption, mmol/h</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Insulin, µmol/L</td>
<td>73</td>
<td>42</td>
<td>50</td>
<td>5.01</td>
<td>0.05</td>
</tr>
<tr>
<td>Lactate, mmol/L</td>
<td>0.56</td>
<td>0.57</td>
<td>0.55</td>
<td>0.05</td>
<td>0.43</td>
</tr>
<tr>
<td>SCFA, µmol/L</td>
<td>223</td>
<td>512</td>
<td>432</td>
<td>33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Acetate, µmol/L</td>
<td>205</td>
<td>483</td>
<td>409</td>
<td>31</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Propionate, µmol/L</td>
<td>6.2^a</td>
<td>8.4^a</td>
<td>7.1^b</td>
<td>0.59</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Butyrate, µmol/L</td>
<td>5.3^a</td>
<td>12^a</td>
<td>9.7^a</td>
<td>0.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Valerate, µmol/L</td>
<td>0.7^a</td>
<td>0.9^a</td>
<td>0.9^a</td>
<td>0.06</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Caproionate, µmol/L</td>
<td>3.3</td>
<td>3.7</td>
<td>3.1</td>
<td>0.28</td>
<td>0.37</td>
</tr>
<tr>
<td>BCFA, µmol/L</td>
<td>2.4^a</td>
<td>4.0^a</td>
<td>3.1^a</td>
<td>0.27</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Isobutyrate, µmol/L</td>
<td>1.6^a</td>
<td>1.9^a</td>
<td>1.5^b</td>
<td>0.12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Isovalerate, µmol/L</td>
<td>1.2^a</td>
<td>2.2^a</td>
<td>1.6^b</td>
<td>0.14</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Absorption of SCFA, mmol/h</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

^aWithin a row, means without a common superscript letter differ (P < 0.05).

^1Values are means; n = 6.

^2D × T = diet × time.

^3SCFA = short-chain fatty acids.

^4BCFA = branched-chain fatty acids.
observed among the diets, whereas feeding the LF diet led to a greater absorption of glucose in the absorptive and postabsorptive phases compared with feeding the 2 high-DF diets ($P < 0.001$; Figure 1B). In the absorptive phase, glucose absorption was delayed when feeding the HF-S diet compared with feeding the LF and HF-I diets ($P < 0.001$). The portal glucose absorption relative to the intake of starch and sugars (% of intake) was less in the absorptive and postabsorptive phases when feeding the HF-S diet (26 and 17%, respectively) compared with the HF-I (33 and 27%, respectively) and LF (34 and 34%, respectively) diets.

The concentration of insulin in the portal vein mimicked glucose to a large extent (Figure 2A): a rapid response when feeding the LF diet, a decreased and less attenuated response when feeding the HF-I diet, and a more decreased and less attenuated response when feeding the HF-S diet. Four hours after feeding, insulin concentration in the portal vein was similar for all 3 diets (70 to 80 pmol/L), and this persisted up to 10 h postfeeding. The apparent insulin production (Figure 2B) at 0 to 10 h postfeeding was not different among the 3 diets (Table 4). The total apparent insulin production (0 to 10 h after feeding) was correlated ($r = 0.75$, $P = 0.009$) with the total apparent glucose absorption (0 to 10 h after feeding). In the absorptive phase, the correlation was greater when feeding the HF-S diet ($r = 0.96$, $P < 0.001$) than when feeding the other diets (LF: $r = 0.78$, $P = 0.01$; HF-I: $r = 0.69$, $P = 0.04$).

Feeding the HF-S diet decreased portal vein concentration of LA, whereas there was no difference in either mesenteric artery concentrations of LA or the
The absorption of LA decreased from approximately 57 mmol/h in the absorptive period (diet, \( P = 0.96 \)) to approximately 37 mmol/h in the postabsorptive period (diet, \( P = 0.54 \)). The statistical analyses revealed that there was an effect of time (\( P = 0.002 \)) only in the absorptive phase.

The 3 diets established 3 different concentrations of SCFA in the portal vein: least for the LF diet, intermediate for the HF-I diet, and greatest for the HF-S diet (Figure 3A). These concentration differences were also observed in the mesenteric artery for all acids except capronic acid (Table 4). The absorption of SCFA (Figure 3B) was consistently greater before and after feeding when sows were consuming the 2 high-DF diets (diet, \( P < 0.001 \), 0.001, and 0.002 for before feeding, in the absorptive phase, and in the postabsorptive phase, respectively). However, there was an effect of time only in the absorptive phase (time, \( P = 0.04 \)). The total absorption of SCFA at 0 to 10 h was greater when feeding the HF-S diet compared with feeding the LF diet, with the HF-I diet being between the 2 diets (Table 4).

The apparent uptake of energy (MJ/h) from glucose and SCFA varied considerably among diets in the 3

![Figure 2](image_url). Portal and arterial concentrations (A) or production (B) of insulin in sows fed diets containing low fiber (LF), high soluble fiber (HF-S), or high insoluble fiber (HF-I). Values are means ± SEM; n = 6. P-values (apparent production): (−2 to 0 h) diet, \( P = 0.49 \), and time, \( P = 0.55 \); (0 to 4 h) diet, \( P = 0.09 \), and time, \( P < 0.001 \); (4 to 10 h) diet, \( P = 0.66 \), and time, \( P = 0.66 \). Mesenteric artery (-- -- --); portal vein (——); LF (○ ○ ○); HF-S (■ ■ ■); HF-I (□ □ □).
periods (before feeding, absorptive phase, and postabsorptive phase), whereas for LA, there was no diet effect (Table 5). A period effect was further observed for glucose and LA, but not for SCFA, which was relatively constant at all sampling periods. Whereas the uptake of total energy varied by a factor of 2.3 from before feeding to the absorption phase for the HF-S diet, the ratio was 7.3 for the LF diet, with the HF-I diet being between the 2 diets ($P < 0.001$). Collectively, the apparent uptake of energy (0 to 10 h postfeeding) from carbohydrate-derived nutrients was 14.5, 8.2, and 8.3 MJ in the LF, HF-S, and HF-I diets, respectively (Table 6). Although the intake of ME was similar for sows fed the LF and HF-S diets, the accumulated uptake of

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**Figure 3.** Portal and arterial concentrations (A) or absorption (B) of total short-chain fatty acids in sows fed diets containing low fiber (LF), high soluble fiber (HF-S), or high insoluble fiber (HF-I). Values are means ± SEM; n = 6. *P*-values (absorption): (−2 to 0 h) diet, $P < 0.001$, and time, $P = 0.88$; (0 to 4 h) diet, $P < 0.001$, and time, $P = 0.04$; (4 to 10 h) diet, $P = 0.002$, and time, $P = 0.24$. Mesenteric artery (——); portal vein (——); LF (○); HF-S (■); HF-I (□).
glucose was only one-third when feeding the HF-S diet compared with the LF diet, whereas the energy from SCFA was more than twice as high with the HF-S compared with the LF diet.

**DISCUSSION**

The current investigation was designed to study the qualitative and quantitative absorption of products deriving from carbohydrate assimilation in sows fed diets that varied in types and contents of DF. To our knowledge, this kind of study has never been carried out with sows before; therefore, we do not have comparable literature data regarding the flow rate in the portal vein. In the present study, the portal flow rate in sows [19.8 mL/(kg of BW·min)] was greater in absolute terms, but less than that shown for growing pigs [33.0 to 38.8 mL/(kg of BW·min)] when using ultrasonic flow probe techniques as in the current study (Ellis et al., 1995; Bach Knudsen et al., 2000, 2005), the electromagnetic flow probe technique [40 to 42.5 mL/(kg of BW·min); Rérat et al., 1984], or dye [31.7 to 36.5 mL/(kg of BW·min); van der Meulen et al., 1997a,b] when expressed per kilogram of BW. The most likely cause for the reduced blood flow is the decreased proportion of visceral organs in mature and almost fully grown animals compared with young growing animals (Doornenbal and Tong, 1981).

The most noticeable differences among diets were the contents of starch and the types, contents, and degrees of lignification of the polysaccharides that made up the DF fraction. Although the concentrations of NSP, cellulose, and NCP were practically the same in the 2 high-DF diets, the proportions of soluble and insoluble NCP varied substantially, which was related to the differences in the DF composition of the raw materials in the high-DF diets (Serena and Bach Knudsen, 2007a). The greater solubility of DF in the HF-S diet was responsible for the greater WBC and swelling compared with the DF in the HF-I diet, whereas the high degree of lignification of the HF-I diet was responsible for the decreased total tract digestibility of energy for this diet compared with the other 2 diets (Serena et al., 2008b).

The contrasting starch contents and chemical and physicochemical properties of DF in the experimental diets were key factors regulating the rate at which glucose was absorbed into the portal vein. The glucose absorption pattern in the absorptive phase when feeding the LF diet was increased and was similar to that shown for growing pigs fed a concentrated diet (Ellis et al., 1995; van der Meulen et al., 1997b; Bach Knudsen et al., 2000, 2005). This was caused by the open structure of cereal starch, which enabled easy access for the salivary and pancreatic α-amylases in the small intestine (Englyst et al., 1992; Gallant et al., 1992; Lang et al., 1999). For the HF-I diet, the absorption profile resembled that of the LF diet, but in quantita-
tive terms, the uptake was decreased because of the decreased starch load. We believe that this was because the starch in the 2 diets came from the same source (the cereals) and that insoluble DF present in the HF-I diet had little, if any, influence on either gastric emptying or the movement of digestion products in the lumen of the small intestine (Low et al., 1986; Rainbird and Low, 1986). However, when feeding the HF-S diet, the portal glucose concentration was decreased and peak glucose was reached at a later stage than with the 2 other diets. We presume that this was due to delayed gastric emptying (Rainbird and Low, 1986; Flourié, 1992) and a bulky luminal environment (Serena et al., 2008a), which may have slowed down amylolysis and the movement of digestion products (Rainbird et al., 1984; Low et al., 1986; Rainbird and Low, 1986). However, a contributing factor could be the potato starch in the HF-S diet (16% of total starch), with a reduced prececal digestibility (Sun et al., 2006) and reduced absorption rate (van der Meulen et al., 1997a).

Our quantitative and qualitative direct measurements of glucose absorption with the HF-S diet confirmed the measurements in peripheral blood (jugular vein) observed by Vestergaard (1997), who compared a control diet similar to the LF diet with a high-DF diet with added sugar beet pulp. Whereas other studies fed growing pigs a concentrated diet supplemented with highly viscous guar gum (Nunes and Malmlof, 1992; Ellis et al., 1995) and documented the importance of the viscosity of digesta (Flourié, 1992) in regulating glucose absorption, our study with the HF-S diet pointed more toward WBC and swelling as regulatory factors in the movement of digestion products (Rainbird et al., 1984). However, our results concerning the insulin response in the portal vein and mesenteric artery confirm the jugular vein insulin responses in sows fed a low-DF diet, and diets high in soluble and insoluble DF, respectively (Vestergaard, 1997). It is also clear from the studies of de Leeuw et al. (2004, 2005a) that fermentable DF has a stabilizing effect on insulin concentration in sows.

The diets resulted in 3 levels of carbohydrate fermentation in the large intestine (Serena et al., 2008b), which were directly reflected in the portal concentrations of all SCFA as well as in total SCFA absorption. For the LF diet, the SCFA concentrations in the portal vein were comparable with values found in growing-finishing pigs fed diets with approximately the same DF level (Giusi-Perier et al., 1989; Bach Knudsen et al., 2000), whereas the concentration was much greater when feeding the 2 high-DF diets. For these diets, portal concentrations were far greater than those reported for growing pigs and were similar to those observed for sheep (approximately 1.6 mmol/L; Bergman, 1990), but were less than those observed for cows (approximately 2.9 mmol/L; Huntington and Reynolds, 1983). Therefore, these data point to the importance of NSP as a measure of the fraction of dietary carbohydrates fermented in the large intestine and the portal and systemic concentrations of SCFA (Bach Knudsen, 2005).

It is also clear from this comparison that the SCFA concentrations in the portal vein of sows more closely resembled those of herbivores, which rely primarily on SCFA as an energy source, than those of pigs fed concentrated diets (Bergman, 1990). In spite of the oxidation of SCFA in the various body tissues, the SCFA concentration ranking in the portal vein would be reflected in the peripheral tissues.

Although the polysaccharides in the high-DF diets had different physicochemical properties and fermentabilities (Serena et al., 2008a,b), they did not lead to differences in the SCFA profile. In this aspect, the results of this study were different from other studies in which one type of DF polysaccharide was the predominant source for fermentation. For instance, the fermentation of cellulose stimulates acetate formation (Giusi-Perier et al., 1989), whereas arabinoxylans and resistant starches are substrates that stimulate butyrate formation (van der Meulen et al., 1997a; Bach Knudsen et al., 2005).

### Table 6. Apparent energy absorption 0 to 10 h postfeeding in sows fed low fiber (LF), high soluble fiber (HF-S), or high insoluble fiber (HF-I)^1

<table>
<thead>
<tr>
<th>Item</th>
<th>LF</th>
<th>HF-S</th>
<th>HF-I</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glucose, MJ</td>
<td>12.11^a (84)^2</td>
<td>3.59^b (44)</td>
<td>5.14^d (62)</td>
<td>1.69 (3.5)</td>
</tr>
<tr>
<td>Lactate, MJ</td>
<td>0.68 (5)</td>
<td>0.61 (7)</td>
<td>0.53 (6)</td>
<td>0.07 (0.4)</td>
</tr>
<tr>
<td>SCFA, MJ</td>
<td>1.68^c (11)</td>
<td>3.95^d (49)</td>
<td>2.64^d (32)</td>
<td>0.32 (3.3)</td>
</tr>
<tr>
<td>Total absorbed energy, MJ</td>
<td>14.5^a</td>
<td>8.2^b</td>
<td>8.3^b</td>
<td>3.07</td>
</tr>
<tr>
<td>Absorbed energy, % of ME</td>
<td>58</td>
<td>34</td>
<td>40</td>
<td></td>
</tr>
</tbody>
</table>

^1Within a row, means without a common superscript letter differ (P < 0.05).
^2Values are means; n = 6.
^3SCFA = short-chain fatty acids.
Absorbed LA contributed only 5 to 7% of absorbed carbohydrate-derived nutrients, with virtually no influence from the dietary composition. As was discussed by Serena and Bach Knudsen (2007b), this is a reflection of the absorption profile of LA being better synchronized to that of glucose than that of SCFA.

Because of the substantial oxidation of energy in splanchnic tissues (Brundin and Wahren, 1991), the portal appearance of energy could only be considered as apparent. However, it is evident from this study that a decreased proportion of the absorbed energy was delivered to the body during the first 10 h post-feeding when feeding the high-DF diets compared with the low-DF diet. It should also be noted that, whereas the portal flux of starch declined gradually during the late absorptive phase to reach nonsignificant levels in the last 2 h before feeding, the portal flux of SCFA in the last 2 h before feeding was at approximately the same level as 10 h after feeding when feeding the 2 high-DF diets.

The 2 high-DF diets altered several factors that are thought to influence the feeling of satiety. First, substitution of NSP for starch results in a shift in the nature of absorbed energy from readily absorbed glycogenic energy to more slowly released SCFA. Second, a direct consequence of the reduced diurnal variation in absorbed energy is less fluctuation in insulin. Third, DF-rich diets resulted in more materials in the stomach and the remaining gut system (Serena et al., 2008a). Thus, sows consuming high-DF diets can be expected to be satiated for a longer period of time, which is regulated in the short-term by the physical presence of digesta in the gut, which influences the stretch and chemoreceptors in the stomach and duodenum, and in the long run by metabolic means obtained through the decreased diurnal variation in energy uptake (Read et al., 1994). These conditions can be expected to reduce the incidence of aggressiveness, stress, and stereotype behavior in sows induced by hunger (Brouns et al., 1997; Ramonet et al., 1999; Bergeon et al., 2000; Danielsen and Vestergaard, 2001; Grieshop et al., 2001).

In conclusion, we showed a clear influence of dietary composition on the rate and types of carbohydrate-derived nutrients to the body. The study showed that DF-rich diets provided a greater and more uniform SCFA uptake than did the low-DF diet, and that the diet high in soluble DF provided a more regulated glucose and insulin response. It is expected that decreased diurnal variation in portal energy appearance may counteract the aggressiveness, stress, and stereotypic behavior caused by hunger in sows.

LITERATURE CITED


Absorption of nutrients in sows


