Sites of nutrient digestion in growing pigs: Effect of dietary fiber

A. Wilfart,* L. Montagne,† P. H. Simmins,‡ J. van Milgen,* and J. Noblet*2

*INRA, UMR1079 Systèmes d’Elevage Nutrition Animale et Humaine, F-35590 Saint Gilles, France; †Agrocampus Rennes, UMR1079 Systèmes d’Elevage Nutrition Animale et Humaine, F-35590 Saint Gilles, France; and ‡Danisco Animal Nutrition, Marlborough Wiltshire, SN8 IXN, United Kingdom

ABSTRACT: The impact of dietary fiber on fecal digestion is well-known and provides a comprehensive approach toward nutrient digestibility and availability. Little quantitative information is available on digestion of fiber in the different segments of the gastrointestinal tract (GIT). The objectives of this study were to obtain a method allowing the quantification of the digestive process in different segments of the GIT and to study the impact of dietary fiber on nutrient digestibility. Six barrows (average initial BW of 30 kg and fitted with a simple T-cannula at the proximal duodenum and caudal ileum) were used in a replicated 3 × 3 Latin square design. In each period, pigs were offered 1 of 3 diets differing in fiber content (low, medium, and high). Differences in fiber content were created by replacing wheat and barley with wheat bran. Titanium dioxide was included in the diet as an indigestible marker to determine the apparent digestibility coefficients in different segments of the GIT. The apparent digestibility of ash, CP, DM, and OM increased in the different segments of the GIT. Duodenal digestibility coefficients were negative for ash (e.g., −39.9% for the medium- and high-fiber diets), indicating important endogenous mineral secretions by the stomach and digestive glands. The duodenal digestibility of other nutrients and OM were positive but close to zero and numerically lower in the diets with the greater fiber contents. The fiber content in the diet did not affect the apparent ileal digestibility of nutrients. Increasing the fiber content in the diet affected the fecal digestibility of CP, ether extract, and energy (P < 0.01). The method used for studying sites of digestion in the digestive tract provides promising results, but it is limited due to the high variability that is likely caused by sampling limitations and variation between animals.

Key words: dietary fiber, digestion, endogenous secretion, pig

INTRODUCTION

Feed formulation is based on the principle that nutritional values of feed ingredients are additive. However, it is known that digestibility is affected by physical and chemical characteristics of the feed (Le Goff and Noblet, 2001), dietary supplements, feed processing (Lahaye et al., 2004), animal factors, and feeding level (Noblet and Shi, 1994). In addition, the type and site of digestion (i.e., enzymatic digestion in the small intestine and fermentation in the large intestine) will determine the type of nutrients that are absorbed. Although considering digestibility as a single (ileal or fecal) characteristic is of practical importance, it cannot account for interactions among nutrients or for interactions between the animal and nutrients.

Mathematical modeling is a method for integrating theories and observations to obtain a comprehensive view of complex biological systems (Sauvant, 1992). To our knowledge, only 3 models describing ileal or total tract digestion have been developed for pigs (Usry et al., 1991; Bastianelli et al., 1996; Rivest et al., 2000). Digestion is an integrated process of hydrolysis, absorption, fermentation, secretion, and transit. The importance of each of these processes depends on the type and quantity of nutrients supplied, and on the site of digestion. Dietary fiber is known to influence several aspects of the digestive processes (Noblet and Perez, 1993). However, there is relatively little quantitative information on digestibility and transit in different segments of the gastrointestinal tract (GIT).

The objectives of the current study were to quantify the contributions of stomach, small intestine, and large
intestine to total tract nutrient digestibility, and also to
determine the impact of dietary fiber content on passage
rates of nutrients in these segments according to dietary
fiber content. The present paper presents the digestibil-
ity results.

MATERIALS AND METHODS

Diets and Feeding

Three experimental diets based on wheat, barley, soy-
bean meal, and wheat bran were formulated (Table 1). Diets with different dietary fiber contents were created by
partly replacing wheat and barley by wheat bran. The low- (LF), medium- (MF), and high-fiber (HF) diets contained 17, 21, and 27% of total dietary fiber, respectively. Rapseed oil was used to equalize the lipid content in the diets (2.5%). Titanium dioxide (0.3%) was included as an inert marker for digestibility calculations. The diets were offered to the pigs as pellets.

All pigs were offered the same quantity of feed for a
given week, which corresponded to approximately 80 g
of DM·(kg of BW)−0.6·d−1. This quantity was adjusted
weekly. The ration was distributed in 6 equal portions
every 4 h using an automatic feeder. Water was available
ad libitum throughout the experiment. Feed refusals and
spillage, if any, were collected daily and analyzed for
DM content.

Animals, Experimental Design,
and Digesta Collection

All pigs came from the herd of the Institut National
de la Recherche Agronomique (Saint-Gilles, France). The
care and use of animals were performed according to
the Certificate of Authorization to Experiment on Living
Animals provided by the French Ministry of Agriculture.
Two blocks of 3 littermate barrows (Pietrain × (Large
White × Landrace)) were used. At approximately 33 kg
of BW, pigs were fitted with simple T-cannula at the
proximal duodenum (20 cm caudal to the pylorus; i.e.,
just caudal to the pancreatic and biliary ducts), and in
the caudal ileum according to procedures adapted from
Sauer et al. (1983). The silicone cannulas had internal
diameters of 1.3 and 1.7 cm for duodenum and ileum,
respectively. Prior to the use of halothane anesthesia,
pigs were sedated with an i.m. injection of ketamine.
After surgery, pigs were individually housed in metabo-


tism crates in a temperature-controlled room (23 ± 1°C),
and were allowed a 2-wk recovery period. During this
period, feed allowance was increased gradually to attain
1.7 kg/d at the end of the recovery period.

Each block of pigs was used in a 3×3 Latin square
design, using a different diet in each period. Experimen-
tal periods lasted 14 d each, and pigs were weighed
weekly. The first week of each period was used to adapt
the animals to the diet and to take duodenal and ileal
samples to be used for the determination of nutrient
digestibility (i.e., the objective of the current paper). The
second week was used to determine transit kinetics by
feeding the animals a single marked meal (data not
shown).

On d 6 and 7 of each experimental period, samples of
duodenal and ileal digesta were collected 3 times (at
0900, 1200, and 1730) in sterilized plastic bags (Whirl-
pak, Nasco, Fort Atkinson, WI). The total quantity of
digesta collected (approximately 120 g as fresh material)
represented about 1% of the DM intake. Fecal samples
were collected during a 13-h period (from 0730 to 2030)
on d 10. Duodenal, ileal, and fecal samples were weighed
and frozen (−20°C) immediately after collection. Before
analysis, samples were freeze-dried and finely ground.
Samples from each collection day (3 samples/d) were
pooled by animal (within period and diet) and stored at
4°C. After the experiment, pigs were euthanized, and
an autopsy was performed to evaluate the tissue around
the cannula.

Table 1. Formulation and chemical composition of the experimental diets

<table>
<thead>
<tr>
<th>Component, % (as-fed basis)</th>
<th>Diet 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Item</td>
<td>LF</td>
</tr>
<tr>
<td>Total dietary fiber</td>
<td>16.5</td>
</tr>
<tr>
<td>Insoluble dietary fiber</td>
<td>13.2</td>
</tr>
<tr>
<td>Soluble dietary fiber</td>
<td>3.3</td>
</tr>
<tr>
<td>GE, MJ/kg of DM</td>
<td>18.2</td>
</tr>
<tr>
<td>Calculated composition 3</td>
<td></td>
</tr>
<tr>
<td>Lysine, %</td>
<td>0.67</td>
</tr>
<tr>
<td>Digestible energy, MJ/kg</td>
<td>13.2</td>
</tr>
<tr>
<td>ME, MJ/kg</td>
<td>12.7</td>
</tr>
<tr>
<td>NE, MJ/kg</td>
<td>9.6</td>
</tr>
</tbody>
</table>

1LF, MF, and HF = diets containing a low, medium, or high content of dietary fiber, respectively.
2The vitamins and minerals mixture provided the following (per kilogram of diet): 5,000 IU of vitamin A, 1,000 IU of vitamin D3, and 20 IU of vitamin E; 2.0 mg of thiamin; 4.0 mg of riboflavin; 1.0 mg of pyridoxine; 20 μg of cobalamin; 15 mg of niacin; 9.9 mg of D-pantothenate; 200 μg of biotin; 1 mg of folic acid; 2.0 mg of menadione; 1.7 kg/d at the end of the recovery period.
3Calculated from Sauvant et al. (2004).
Analytical Methods

Laboratory analyses were carried out on feed, duodenal and ileal digesta, and fecal samples for each animal. Diets were analyzed for DM, OM, and ether extract (AOAC, 1990). Crude protein (N × 6.25) was analyzed according to the Dumas method (AOAC, 1990), and GE was measured using an adiabatic bomb calorimeter (IKA, Staufen, Germany). Fiber fractions (NDF, ADF, and acid-detergent lignin) of diets were determined according to the method described by Njaa (1961). Fecal samples were analyzed for DM, OM, CP, ether extract (after acid hydrolysis), GE, and the fiber fractions, as described before for feed samples. Because of the limited availability of samples, starch, TDF, and insoluble dietary fiber contents were measured only in ileal samples, whereas DM, ash, and CP were analyzed in duodenal and ileal samples as described previously.

Calculations and Statistical Analyses

The apparent duodenal, ileal, and fecal digestibility of nutrients and energy was calculated using the nutrient-to-marker ratio in the diet and digesta or feces according to the following equation:

\[
\text{Apparent digestibility} = 1 - \left( \frac{Z}{\text{TiO}_2} \right) \times 100,
\]

where \(Z\) and \(Z_{\text{diet}}\) are the nutrient (or energy) concentrations in digesta (or feces) and in the diet, respectively; and \(\text{TiO}_2\) and \(\text{TiO}_2_{\text{diet}}\) represent the concentration of titanium dioxide in digesta (or feces) and in the diet, respectively. In this calculation, digestibility refers to the cumulative digestibility at the end of each digestive segment (i.e., duodenal, ileal, and fecal digestibility). Apparent digestibility was also calculated for each digestive segment relative to the nutrient and energy supply to that segment. In addition, nutrient concentrations in digesta were calculated relative to 100 g of DM intake. Expressing the results as concentrations (nutrient per 100 g of DM intake) makes it possible to partly overcome the differences in the nutrient contents between the diets. It also allows quantifying of the contribution of each nutrient to the overall flow of DM.

Data were analyzed according to the GLM procedure (SAS Inst. Inc., Cary, NC). Experimental period (n = 3), diet (n = 3), and pig (n = 6) were included in the statistical model. Results are presented as least squares means with residual standard deviation (RSD). The RSD is the root mean square of the residual error and applies to the whole model, not an individual estimate within the model. Contrasts were used to determine differences between treatments.

RESULTS

One of the pigs was removed from the statistical analysis for the third period because of lack of appetite during this period. All other pigs appeared healthy during the experiment, and diets were readily consumed. The BW of the pigs was not affected by the diet and averaged 38, 48, and 59 kg during the 3 successive periods, which corresponds to an average daily gain of 757, 686, and 606 g/d, respectively. The average consumption of water by pigs was 2.7, 3.1, and 3.4 L/d for the LF, MF, and HF diets, respectively; these values were not statistically different. Autopsy of the pigs did not reveal complications of the surgical procedure. Duodenal and ileal cannulae were positioned 18 cm from the pylorus and 17 cm prior to the ileo-cecal valve, respectively. Visual observation of the digestive tract did not reveal disorders, and cicatrization around the cannula was not excessive.

Apparent digestibility of most nutrients increased along the GIT from the duodenum onwards (Table 2). For all diets, duodenal ash digestibility was negative (−45.0, −39.9, and −39.9% for the LF, MF, and HF diets, respectively). According to the ash content of the diets, this corresponds to apparent endogenous ash secretions of 2.5 and 2.8 g/100 g of DM intake for the LF and HF diets, respectively. The ash flow entering the duodenum was 40% larger than the ash intake (Table 3) and indicates the importance of endogenous mineral secretions prior to the duodenum (e.g., due to saliva and gastric secretions). Apparent digestibility of dietary ash increased along the gut and was positive at the end of the ileum. Fecal ash digestibility ranged from 40 to 50%. Dietary fiber did not affect duodenal or ileal ash digestibility, but affected (P = 0.01) fecal ash digestibility with decreased values for HF diet compared with the LF diet (43.4 vs. 51.3%).

The apparent CP digestibility was low at the proximal duodenum for all diets (15, 12, and 7% for LF, MF, and HF diets, respectively) and was not affected by the diet composition. As anticipated, apparent ileal and fecal CP digestibilities were largely positive, averaging 73 and 84% for the 3 diets, respectively. Apparent ileal digestibility of CP was not affected by fiber content, but fecal CP digestibility was lower (P < 0.01) in fiber-rich diets (81.3% for HF vs. 87.3% for LF). The results for the ileal TDF digestibility were negative for LF and MF diets (−31 and −5%, respectively), but positive for HF diet. Fecal apparent TDF digestibility was positive for all diets. Virtually all starch was digested at the end of the small intestine, and digestibility was not affected by the diet. No starch could be detected in a few fecal samples.
Table 2. Effect of the fiber content in the diet on apparent duodenal, ileal, and fecal digestibility of dietary components

<table>
<thead>
<tr>
<th>Dietary component and site of digestion</th>
<th>Diet 2</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>LF  45.0</td>
<td>MF -39.9</td>
</tr>
<tr>
<td>Ileum</td>
<td>11.1</td>
<td>19.7</td>
</tr>
<tr>
<td>Feces</td>
<td>51.3</td>
<td>46.1</td>
</tr>
<tr>
<td>CP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>14.5</td>
<td>11.9</td>
</tr>
<tr>
<td>Ileum</td>
<td>70.4</td>
<td>73.3</td>
</tr>
<tr>
<td>Feces</td>
<td>87.3</td>
<td>84.4</td>
</tr>
<tr>
<td>Ether extract</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feces</td>
<td>77.0</td>
<td>70.6</td>
</tr>
<tr>
<td>Starch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ileum</td>
<td>99.1</td>
<td>99.1</td>
</tr>
<tr>
<td>Total dietary fiber</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ileum</td>
<td>-30.6</td>
<td>-5.1</td>
</tr>
<tr>
<td>Feces</td>
<td>46.1</td>
<td>44.5</td>
</tr>
<tr>
<td>OM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>19.8</td>
<td>11.9</td>
</tr>
<tr>
<td>Ileum</td>
<td>64.7</td>
<td>65.0</td>
</tr>
<tr>
<td>Feces</td>
<td>86.7</td>
<td>82.7</td>
</tr>
<tr>
<td>DM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>16.1</td>
<td>8.6</td>
</tr>
<tr>
<td>Ileum</td>
<td>61.6</td>
<td>62.1</td>
</tr>
<tr>
<td>Feces</td>
<td>84.7</td>
<td>80.4</td>
</tr>
<tr>
<td>Energy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feces</td>
<td>85.0</td>
<td>80.5</td>
</tr>
</tbody>
</table>

1Adjusted means, %.
2LF, MF, and HF = diets containing a low, medium, or high content of dietary fiber, respectively; n = 6.
3The residual standard deviation (RSD) is the root mean square of the residual error and applies to the whole model, not an individual estimate within the model.

that were analyzed for verification. Fecal digestibility of ether extract decreased \((P < 0.01)\) with increasing dietary fiber content (77.0 vs. 65.2% for LF and HF diets, respectively).

For OM, the duodenal, ileal, and fecal digestibilities followed the trends seen for the individual nutrients. Apparent digestibility was modest up to proximal duodenum and increased in the subsequent segments of the digestive tract. In association with a negative duodenal apparent digestibility of ash, duodenal digestibility of DM was reduced compared with OM digestibility and was decreased to the extent that negative values were observed for some pigs offered the HF diet. Moreover, increasing the fiber content of the diet decreased the fecal OM digestibility \((P < 0.01)\), had no effect on ileal digestibility, and tended to decrease \((P = 0.10)\) the duodenal OM digestibility. Energy digestibility followed a pattern similar to that of DM or OM \((P < 0.01)\). There was a pig effect \((P = 0.03)\) for fecal digestibility of DM, OM, TDF, ash, and a tendency \((P = 0.09)\) for CP but not for duodenal and ileal digestibility, indicating an individual specificity of the digestion process at the fecal stage. There was no period effect for any of the measured criteria.

The nutrient flows of digesta in the different segments of the GIT relative to DM intake are presented in Table 3. Except for ether extract, nutrient concentrations were different in the experimental diets. As indicated by the digestibility results, the duodenal flow of ash was greater than the intake, implying apparent endogenous secretions equivalent to approximately 2.7 g of ash per 100 g of DM intake; this value was not affected by the dietary fiber content. The (numerical) differences among diets for ash flow at the proximal duodenum were absent at the ileum and the rectum. Flows of CP, starch, ether extract, and TDF at the duodenum and the ileum were not affected by the diet. However, flows of CP, ether extract TDF, and of OM and DM were greater \((P < 0.01)\) for HF compared with LF diets at the rectum. For instance, the calculated rate of absorption in the large intestine was almost 2 times as high for the LF diet as for the HF diet (20.8 vs. 11.2 g per 100 g of DM intake; Table 3). Finally, data in Table 3 indicated that the DM excreted at the rectum was mainly composed of TDF (50 to 60%) and that the increased fecal DM excretion observed for the HF diet was mainly due to increased TDF excretion.

**DISCUSSION**

The in vivo method used in the current study allows the quantification of digestion at the proximal duodenum, the terminal ileum, and the rectum in the same animal. Although the multicannulation technique has
Table 3. Effect of the fiber content in the diet on the concentration of components in the feed, at the beginning of the duodenum, at the end of the ileum, and in the feces

| Component      | Site        | LF (g per 100 g of DM intake) | MF (g per 100 g of DM intake) | HF (g per 100 g of DM intake) | RSD<sup>3</sup> | Probability
|----------------|-------------|------------------|------------------|------------------|-----------------|----------------
| Ash            | Feed        | 5.8              | 6.4              | 7.1              |                 |                 |
|                | Duodenum    | 8.3              | 9.0              | 9.9              | 1.9             | 0.76            | 0.11<sup>0.45</sup> |
|                | Ileum       | 7.5              | 7.2              | 7.6              | 2.3             | 0.92            | 0.21<sup>0.95</sup> |
|                | Feces       | 3.7              | 3.9              | 4.4              | 1.5             | 0.95            | 0.17<sup>0.74</sup> |
| CP             | Feed        | 17.5             | 18.5             | 19.6             |                 |                 |
|                | Duodenum    | 14.9             | 16.3             | 18.2             | 2.9             | 0.90            | 0.21<sup>0.26</sup> |
|                | Ileum       | 5.2              | 5.0              | 4.9              | 1.2             | 0.26            | 0.65<sup>0.91</sup> |
|                | Feces       | 2.2              | 2.9              | 3.7              | 0.3             | 0.81            | 0.10<sup>&lt;0.01</sup> |
| Ether extract  | Feed        | 2.5              | 2.4              | 2.4              |                 | 0.70            | 0.10<sup>&lt;0.01</sup> |
|                | Feces       | 0.7              | 0.9              | 1.1              | 0.1             |                 | 0.25            | 0.13<sup>0.68</sup> |
| Starch         | Feed        | 52.1             | 45.4             | 38.2             |                 | 0.24            | 0.53<sup>0.91</sup> |
|                | Ileum       | 0.5              | 0.4              | 0.4              | 0.1             |                 | 0.25            | 0.13<sup>0.68</sup> |
| Total dietary fiber | Feed        | 16.5             | 20.9             | 27.0             |                 | 0.10            | 0.53<sup>0.91</sup> |
|                | Ileum       | 21.6             | 22.1             | 21.2             | 3.2             |                 |                 | 0.78<sup>&lt;0.01</sup> |
|                | Feces       | 8.9              | 11.6             | 14.0             | 0.8             |                 | 0.74            | 0.10<sup>&lt;0.01</sup> |
| OM             | Feed        | 94.2             | 93.6             | 92.9             |                 |                 |
|                | Duodenum    | 75.6             | 82.8             | 85.3             | 7.3             | 0.24            | 0.21<sup>0.15</sup> |
|                | Ileum       | 33.3             | 32.7             | 30.9             | 5.4             | 0.21            | 0.52<sup>0.78</sup> |
|                | Feces       | 12.5             | 16.2             | 19.7             | 1.0             | 0.44            | 0.04<sup>&lt;0.01</sup> |
| DM             | Duodenum    | 90.1             | 97.5             | 101.4            | 8.6             | 0.28            | 0.18<sup>0.16</sup> |
|                | Ileum       | 40.9             | 40.1             | 38.3             | 6.3             | 0.25            | 0.51<sup>0.81</sup> |
|                | Feces       | 16.0             | 20.6             | 24.3             | 1.3             | 0.40            | 0.40<sup>&lt;0.01</sup> |

<sup>1</sup>Adjusted means, g per 100 g of DM intake.  
<sup>2</sup>LF, MF, and HF = diets containing a low, medium, or high content of dietary fiber, respectively; n = 6.  
<sup>3</sup>The residual standard deviation (RSD) is the root mean square of the residual error and applies to the whole model, not an individual estimate within the model.

been used in ruminants (Faichney, 1975; Siddons et al., 1985; Faichney, 1993) and preruminant calves (Montagne et al., 2001), it has only been used in few studies with pigs. For pigs, digestion has been studied frequently at the rectum (Darcy-Vrillon et al., 1991; Kavanagh et al., 2001; Le Goff et al., 2002) and to a lesser extent at the terminal ileum (Shi and Noblet, 1993; Buraczewska, 2001; Souffrant, 2001). In the case of amino acids for which ileal digestibility has to be measured, ileal T-cannula or ileo-rectal anastomosis have been mainly used. The ileo-rectal anastomosis has the disadvantage that the cecum and colon will cease to function and that special diets are required to maintain animals in good health. The present technique expands on that of using the ileal T-cannula in a way that the contribution of the stomach (and pancreas and liver) can be separated. It is evident that this technique requires a more significant surgical intervention. For ease of sampling, it is also important that the pigs get accustomed to human intervention.

Nevertheless, the method has some limitations, one of these being the high variability of the results. In Table 2, the RSD was much greater for the duodenal and ileal digestibility results compared with the fecal digestibility data. The variability among animals is known to contribute to the overall high variability of ileal digestibility estimates (Van Leeuwen et al., 1996). The main reason for this is that considerably smaller quantities of samples are obtained from the duodenum and ileum (approximately 13 g of DM each) compared with fecal samples (270 g of DM). The use of T-cannulas involves a partial collection of digesta (Fuller et al., 1994), and the method has been criticized because of the small quantities of digesta taken and the possibility that collected samples are not representative of the total digesta (Titgemeyer, 1997). Furthermore, the presence of the cannula may alter the normal passage of digesta as suggested by Radcliffe et al. (2005), which may result in perturbations of digestive processes after the cannula. Furthermore, Yin et al. (2000) suggested that the small diameter of T-cannula may induce a change in pressure at the base of the cannula when it is opened. This could result in separation of the larger and finer particles, an effect that may be greater for diets rich in fiber. Furthermore, as gastric emptying follows a pulsatory pattern, it is not known if the sample is taken at the beginning, the middle, or the end of the pulse. Moore (1959) suggested that variability in duodenal digestibility depended on the interval between feeding, the individual pig, and the duration of eating. In our study, the interval between feedings (every 4 h) and the duration of eating were regular and similar for the pigs, and it can be hypothesized that ileal digesta passage was relatively constant (Van Leeuwen et al., 1997). This highlights the suggestion that the observed variability is inherent to the individual animal. Although not significant, the probabilities for an individual pig effect were lower for the duodenal than for ileal digestibility (Table 2) and may suggest
that endogenous secretions were affected by the animal. These observations also indicate that duodenal and ileal sample sizes should be increased to attenuate this methodological variability.

A rather surprising result was the negative apparent ileal digestibility of TDF with the LF diet, and to a smaller extent, with the MF diet. This indicates that more TDF was measured at the ileum than in the feed. Similar results have been obtained by other authors also using wheat bran as a source of fiber (Graham et al., 1986; Jorgensen et al., 1996). It has been suggested that contamination with endogenous and microbial matter may contribute to the polysaccharide content of the sample (Graham et al., 1986; Jorgensen et al., 1996). The method of Prosky et al. (1985), which is a gravimetric method, may be sensitive to this contamination, resulting in an artificial increase in fiber content and underestimation of fiber digestion. Thus, the rather surprising result for the ileal digestibility of TDF may have originated from the combination of sampling or analytical errors and the relatively high variability of results. The results for ileal digestibility of OM were also surprising. Indeed, the enrichment of fiber in the diet was achieved by a replacement of starch with fiber. Taking into account the high digestibility of starch at the ileum, it can be anticipated that diets with a low fiber content (and thus with a high starch content) are more digestible than those having a high fiber content. However, our results showed that there is no effect of fiber on ileal digestibility of OM. This finding is inconsistent with literature data (Shi and Noblet, 1994; Leming and Lindberg, 2001; Högberg and Lindberg, 2004). Also, the fiber content in the diet did not affect CP digestibility, which is not consistent with results reported by Owusu-Asiedu et al. (2006). This absence of an effect of fiber on OM and CP apparent digestibility might be partly explained by the negative digestibility of fiber at the ileum.

Digestion of nutrients begins soon after ingestion of the diet, and digestibility becomes greater along the gut. However, the apparent duodenal digestibility of ash was negative (Table 2), indicating a secretion of endogenous material prior to the cannula. Apparent ash digestibility became positive at the end of ileum. Because the duodenal cannula was positioned just after the entrance of the pancreatic and biliary ducts, the samples of duodenal digesta collected presumably contained endogenous secretions from the pancreas and liver in addition to saliva and gastric secretions. The apparent duodenal digestibility of CP was low but positive. These low values are the result of a combination of 2 processes. First, there is an endogenous input in the form of lumen of proteins (e.g., mucins, enzymes, and proteins from desquamated cells) originating from the mouth, esophagus, stomach, proximal duodenum, pancreas, and liver. Also, hydrolysis of protein and absorption of amino acids may start at the stomach (Buraczewska, 1981) or immediately after the stomach with a subsequent disappearance of CP from proximal duodenum. The apparent duodenal CP digestibility ranged from 7% (HF) to 14% (LF), illustrating that the digestion and absorption of dietary CP is greater than the endogenous secretions before the proximal duodenum. For growing pigs, Souffrant (1991) estimated the endogenous N secretion from saliva to be 0.22 g/d, whereas Corring (1980) estimated it to be 0.40 g/d. Estimates of gastric N secretion range between 2.0 (Souffrant, 1991) to 3.3 g/d (Simon et al., 1986). Other sources include pancreatic (2.5 to 6.7 g of N/d; Souffrant, 1991) and biliary secretions (1.9 to 3.0 g of N/d; Sambrook, 1978; Juste, 1982). According to Zebrowska and Kowalczyk (2000), the total N secretion in the stomach and proximal duodenum is approximately 9 g/d in 30-kg pigs or 20 to 25% of the dietary protein intake. Furthermore, the endogenous N secretion depends on the presence and nature of dietary fiber, and to a lesser extent, on the quantity of feed (Souffrant, 1991; Zebrowska and Kowalczyk, 2000). Our study did not confirm these values but indicated a nonnegligible absorption of N compounds before the proximal duodenum. Other methods (e.g., isotopes techniques) or cannulation at other sites would have been necessary to quantify these aspects (Lahaye et al., 2004).

In agreement with the results of Noblet and Perez (1993) and Le Goff and Noblet (2001), increasing the fiber content in the diet decreased the apparent fecal digestibility of nutrients and OM. Moreover, the measured fecal digestibility of OM and energy was similar to the digestibility values calculated from the feed ingredients (Sauvant et al., 2004). The decrease in fecal ash and CP observed for the HF diet compared with the LF diet (Table 2) could be the result of a specific digestive processes due to the increased fiber content. In fact, a lower apparent digestibility can be explained by increased endogenous secretions, or a decreased hydrolysis and absorption of nutrients, or both. Wheat bran, which was the major fiber source in our trial, is relatively resistant to microbial degradation (Stephen and Cummings, 1980; Donangelo and Eggum, 1985), resulting in an increase in fecal dry matter and fecal bulk (Bach Knudsen and Hansen, 1991). Consequently, because of its physical presence (40% for the HF diet), wheat bran is one of the most effective dietary fiber sources for increasing the rate of passage in the digestive tract (Jorgensen et al., 1996). Digestion in the hindgut is affected by the time that the digesta is subjected to fermentation, and a rapid passage of digesta may diminish the effectiveness of this process (Morel et al., 2006). This can be a factor that partially explains the decrease of fecal digestibility in association with the increase of dietary fiber. Similar observations have been reported by Högberg and Lindberg (2004) who compared fecal digestibility of diets containing cereals or high- and insoluble-fiber (30% wheat bran).

The stomach, small intestine, and large intestine do not have the same implication in the digestive process, and their contribution differs depending on the nutrient considered. If endogenous secretions are ignored, the large intestine seems to be the major site of mineral absorption (54 vs. 25% before the end of the ileum).
However, because of the important secretion of endogenous minerals before the duodenal cannula, and in agreement with the results of Partridge (1978), the small intestine is in fact a major site of absorption of mineral arriving in the duodenum (40 vs. 33% in the large intestine). According to published data, different minerals are absorbed at different sites. Calcium and P are absorbed in the first half of the small intestine, Na in the ileum and the colon, Mg only in the colon, and K is absorbed in all regions of the digestive tract (Partridge, 1978). The effect of dietary fiber on the contribution of small and large intestine on ash absorption was not significant.

In addition to its role in the secretion of minerals, the segment prior to the proximal duodenum has a role in the hydrolysis and absorption of proteins. In the current study, 11% of CP was absorbed prior to the duodenum. In agreement with studies reported in the literature (Dierick et al., 1983; Just et al., 1985; Shi and Noblet, 1993), the present experiment also indicates that a large proportion of ingested CP (62%) is digested in the small intestine, whereas only 12% of CP is digested in the large intestine. Compared with the quantities of CP entering the small and large intestine, the apparent digestibilities of CP were on average 69 and 49% in each segment, respectively. These values are greater than results of Kass et al. (1980) who showed, for alfalfa diets, an apparent CP digestibility of 48 to 69% for the small intestine, and 20 to 35% for the large intestine. In agreement with results of Shi and Noblet (1993), the CP digestibility in the large intestine was reduced when the dietary fiber content is increased in the current study. In fact, this may be indicative of ammonia flux toward the large intestine due to the presence of fermentable OM. This would result in a shift of N loss from the urine to the feces. Starch was totally digested at the end of the ileum in our study and it can be assumed that most starch is digested in the ileum (Bach Knudsen and Hansen, 2004). It is generally assumed that dietary fat is digested before the end of the ileum (Shi and Noblet, 1994) with some hindgut production of microbial fat (Shi and Noblet, 1993). Therefore, total tract digestibility of fat might then be lower than ileal digestibility (Högberg and Lindberg, 2004).

On average for the 3 diets, 13% of the dietary OM was digested before the proximal duodenum, 52% in the small intestine (and thus 65% before the end of the ileum), and 17% in the large intestine. In other words, 16, 63, and 21% of the digested OM was degraded before the proximal duodenum, in the small intestine, and in the large intestine, respectively. The OM digestibility was lower than that of Shi and Noblet (1993), who estimated that the contribution of the large intestine to OM digestibility was 25%. The values obtained in the current study were greater than those observed by Högberg and Lindberg (2004) and Laplace et al. (1989). In fact, diet composition seems to have a major effect on the contribution of the hindgut to the OM digestibility. For example, Shi and Noblet (1993) obtained minimal and maximal contributions of 13 and 32%, respectively, and these values were obtained with low- (9.7% NDF) and high-fiber diets (26% NDF).

In conclusion, the methodology used in this study allows the quantification of digestion in different segments of the gastrointestinal tract using the same animal. There was a high residual variability in the present experiment, especially for the duodenal and ileal digestibility values. This variability might probably be reduced if greater quantities of duodenal and ileal digesta are collected.

LITERATURE CITED

Effect of fiber on digestibility in pigs


