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Digesta transit in different segments of the gastrointestinal tract of pigs as affected by insoluble fibre supplied by wheat bran

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Digestibility is the result of two competing processes: digestion and digesta transit. To develop or parameterise mechanistic models of digestion, both processes have to be quantified. The aim of this study was to determine the effect of insoluble dietary fibre on the transit in the gastrointestinal tract of pigs. Six barrows (33 kg initial body weight and fitted with two simple T-cannulas at the proximal duodenum and distal ileum) were used in a double 3 × 3 Latin square design. Pigs were offered diets differing in total dietary fibre content (170, 220 and 270 g/kg DM) at 4 h intervals. A single meal marked with YbO_2 and Cr-EDTA was used to determine the kinetics of markers concentrations of the solid and liquid phases, respectively. The mean retention time (MRT), calculated by the method of the moments, averaged 1, 4 and 38 h in the stomach, small intestine and large intestine, respectively. Increasing the insoluble fibre content in the diet had no effect on MRT in the stomach and decreased the MRT of both phases in the small intestine ($P<0{\cdot}05$). In the large intestine, increasing the insoluble fibre content decreased the MRT of the liquid phase ($P=0{\cdot}02$) and tended to decrease the MRT of the solid phase ($P=0{\cdot}06$). Transit of the solid phase in the large intestine was 4–8 h slower than transit of the liquid phase. Analysis of marker excretion curves indicated that the small and large intestine should be represented mathematically to have both a tubular (propulsion) and compartmental (mixing) structure.

Insoluble fibre: Model: Pig: Transit

Digestibility is the result of several processes occurring in the gastrointestinal tract (GIT) including transit, hydrolysis or fermentation, absorption and endogenous secretions. It is known that digestion is affected by the physical and chemical characteristics of the feed (Le Goff & Noblet, 2001), feed processing (Lahaye *et al.* 2004), animal factors and feeding level (Noblet & Shi, 1994). The importance of each of these phenomena depends on the type and quantity of nutrients supplied and on the site of digestion. Despite the fact that there is quite a body of literature on factors affecting digestion, relatively few efforts have been made to integrate the results of these studies to obtain a global approach towards digestion.

Mathematical modelling is a method to integrate theories and observations in order to obtain a comprehensive view of complex biological systems (Sauvant, 1992). To our knowledge, three models describing ileal or total tract digestion have been developed for pigs (Usry *et al.* 1991; Bastianelli *et al.* 1996; Rivest *et al.* 2000). In these models, digestibility is predicted by separately quantifying transit, endogenous secretions, degradation, absorption and microbial fermentation. One of the major drawbacks of using these models to predict digestibility of feedstuffs is the fact that little quantitative information exists concerning the kinetics of digestion and transit in the different segments of the GIT. Moreover, the representation of the different anatomical compartments differs between these models. Although gastric empting is represented as a mass–action law, driven by the total DM mass (Usry *et al.* 1991; Bastianelli *et al.* 1996) or protein mass (Rivest *et al.* 2000) in the stomach, different approaches are used for the representation of the small intestine. Both Usry *et al.* (1991) and Rivest *et al.* (2000) divided the small intestine into small segments where transit is represented as the passage from one segment to another one by either a stochastic (Usry *et al.* 1991) or a compartmental process (Rivest *et al.* 2000). On the other hand, Bastianelli *et al.* (1996) represented the small intestine by two compartments separated by a delay function. The large intestine was only represented in the model of Bastianelli *et al.* (1996) as a single compartment with outflow depending on the DM present in the compartment.

In order to use mathematical models to predict the (ileal and faecal) digestibility of feeds, response curves for the different digestives processes have to be developed. In addition, a suitable representation of the anatomical structures is required. The objectives of the present study were to quantify the passage kinetics in different segments of the GIT and to propose

Abbreviations: BW, body weight; GIT, gastrointestinal tract; HF, high fibre; LF, low fibre; MF, medium fibre; MRT, mean retention time; MRT_C, mean retention time in a compartmental structure; NDF, neutral detergent fibre; RSD, residual standard deviation; SDRT, standard deviation of retention time; TDF, total dietary fibre.

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an appropriate mathematical representation of transit in each segment of the GIT. As dietary fibre is expected to influence several aspects of the digestive processes (Noblet & Perez, 1993; Bach Knudsen & Jorgensen, 2001; Le Goff & Noblet, 2001), diets differing in insoluble fibre content were used to evaluate its effect on transit time.

Materials and methods

Animals and animal housing

Details of the experimental procedure have been reported by Wilfart *et al.* (2007). Briefly, two blocks of three littermate barrows (Pietrain × (Large White × Landrace)) with an average initial weight of 33 kg were obtained from the herd of the Institut National de la Recherche Agronomique (Saint-Gilles, France). Pigs were housed in metabolism crates 1 week prior to surgery. The barrows were fitted with two simple T-cannulas, one in the proximal duodenum 20 cm after the pylorus (i.e. after the pancreatic and biliary ducts) and one in the distal ileum. Following the surgery, pigs returned to the metabolism cages in a temperature-controlled room (23 ± 1°C) and were allowed a 2-week recovery period. During this period, feed allowance was increased gradually to attain 1·7 kg/d at the end of the recovery period.

The animal experiment was performed according to the Certificate of Authorization to Experiment on Living Animals (certificate numbers 07 704 and 04 739 provided by the French Ministry of Agriculture to J. van Milgen and J. Noblet, respectively). After the experiment, pigs were euthanased and an autopsy was performed to evaluate the consequences of canulation.

Experimental design and diets

Each block of pigs was used in a 3 × 3 Latin square design, using a different diet in each period. Experimental periods lasted 14 d each and pigs were weighed weekly. All pigs were offered the same quantity of feed for a given week, which corresponded to approximately 80 g DM/(kg body weight (BW))$^{0·60}$/d. The ration was distributed in six equal portions every 4 h using an automatic feeder. Water was freely available from a low-pressure drinking nipple. Feed refusals and spillage, if any, were collected daily and analysed for DM content.

The first 9 d of each period were used to adapt the animals to the diet and to take duodenal and ileal samples to be used as blank samples (days 6 and 7). Transit kinetics were determined between day 10 and day 14 by feeding the animals a single meal marked with chromium-EDTA (Cr-EDTA) to follow the liquid phase (Gomez *et al.* 1992) and ytterbium oxide (Yb_2O_3) to follow the solid phase (Le Goff *et al.* 2002). The pulse meal was followed by partial collection of duodenal and ileal digesta and total collection of faeces.

Three experimental diets were formulated based on wheat, barley, soybean meal and wheat bran (Table 1). Diets differed in insoluble fibre content and were created by replacing wheat and barley by wheat bran. The low- (LF), medium- (MF) and high-fibre (HF) diets contained respectively 170, 220 and 270 g/kg DM of total dietary fibre (TDF). The difference in fibre content was essentially due to a difference in non-soluble fibre (Table 1). Rapeseed oil was used to maintain a constant lipid content in the diets (2·5 %), and diets were iso-energetic on a gross energy basis. The diets were offered to the pigs as pellets.

Table 1. Formulation and analysed chemical composition of experimental diets

	Diets		
Item	LF	MF	HF
Components (as fed, g/kg)			
Wheat	410·50	312·25	214·00
Barley	410·50	312·25	214·00
Soya-bean meal	140·00	140·00	140·00
Wheat bran	0·00	200·00	400·00
Rapeseed oil	7·00	3·50	0·00
Dicalcium phosphate	11·00	11·00	11·00
Calcium carbonate	10·00	10·00	10·00
Vitamins and minerals mixture*	8·00	8·00	8·00
Titanium dioxide	3·00	3·00	3·00
Chemical composition†			
Ash	50·0	55·9	61·3
Crude protein (N × 6·25)	152·3	161·0	170·2
Ether extract	21·5	21·0	21·0
Starch	453·1	395·3	332·7
Neutral-detergent fibre	127	163·3	207·4
Acid-detergent fibre	29·4	39·4	50·7
Acid-detergent lignin	2·3	4·3	7·7
Total dietary fibre	143·8	182·1	234·8
Insoluble fibre	115·1	161·7	199·4
Soluble fibre‡	28·7	20·5	35·4
Gross energy (MJ/kg DM)	15·8	15·8	16·0
Lysine, g/kg§	5·8	6·3	6·7
Digestible energy, MJ/kg§	11·5	10·7	10·0
Metabolisable energy, MJ/kg§	11·1	10·3	9·5
Net energy, MJ/kg§	8·3	7·6	6·9

LF, low fibre content; MF, medium fibre content; HF, high fibre content

* The vitamins and minerals mixture provided the following (per kg of diet): 2·7 mg of retinyl palmitate; 25 μg of cholecalciferol; 20·0 mg of DL-α-tocopherol acetate; 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-panthotenate; 200 μg of biotin; 1 mg of folic acid; 2·0 mg of menadione; 500 mg of choline chloride; 100·2 mg of Zn; 10·0 mg of Cu; 37·0 mg of Mn; 80·0 mg of Fe; 202 μg of I; 100 μg of Co; 150 μg of Se.

† Standardised for 0·87 DM

‡ Calculated by the difference between total dietary fibre and insoluble fibre.

§ Calculated from the data obtained in composition and nutritional value of feed materials (Sauvant *et al.* 2004).

Measurement of the rate of passage and digesta collection

Prior to administration of the marked meal, duodenal, ileal and faecal samples were collected for each animal on day 6 and day 7, and were used as blank samples, and for a digestibility study (Wilfart *et al.* 2006). The measurement period began on day 10 with the distribution of a single meal marked with 1 g of Yb_2O_3 and 40 ml of cr-EDTA. Both markers were incorporated directly in the feed, which was distributed manually. On average, the pigs ate the marked meal in 10 min. The time at which the pigs finished eating their marked meal was considered as time 0 (t_0).

Duodenal samples were collected 10, 20, 30, 45, 60, 90, 120, 180, 360 and 720 min after the ingestion of the marked meal. Ileal samples were collected 45, 90, 135, 180, 225, 270, 315, 360, 450, 540, 720 and 1440 min after the consumption of the marked meal. As the digesta flow is irregular, actual times of digesta collection were recorded. If no sample could be collected within 5 min of the intended collection time, the cannula was closed in order to avoid disturbing the intestinal migrating myoelectric complex (C. H. Malbert, personal communication). Faecal samples were not taken by grab-sampling, but by surveying faecal excretions at regular intervals up to 105 h after ingestion of the marked meal. On the day of the

distribution of the marked meal, faecal excretion was checked hourly from 08.30 to 21.30 h. One survey at night occurred at 02.30 h. For the following 5 d, faecal excretion was verified hourly between 07.30 and 19.00 h with an additional midnight survey on the second and third days after marker administration.

For each duodenal and ileal sample, approximately 20 g of fresh matter was collected in sterilised plastic bags (Whirl-pak, Nasco, USA). Faecal samples were collected quantitatively. All duodenal, ileal and faecal samples were weighed and frozen (−20°C) immediately after collection. Before analyses, samples were freeze-dried, finely ground and stored at 4°C.

Chemical analyses

Diets were analysed for DM, ash and ether extract as described by the Association of Official Analytical Chemists (1990). Organic matter was calculated by the difference between DM and ash. Crude protein (N × 6·25) was analysed according to the method of Dumas (Association of Official Analytical Chemists, 1990) and gross energy was measured using an adiabatic bomb calorimeter (IKA, Staufen, Germany). Fibre fractions (neutral-detergent fibre (NDF), acid-detergent fibre and acid-detergent lignin) were determined in the diets according to the method of Van Soest & Wine (1967) using a sequential procedure with prior amylolytic treatment. The TDF and insoluble fibre were determined according to the method of Prosky *et al.* (1985, 1992). Soluble fibre was estimated as the difference between TDF and insoluble fibre. Starch content was measured using an enzymatic method (Thivend *et al.* 1965).

Freeze-dried digesta and faecal samples were used for determination of DM. The samples were ashed subsequently at 520°C according to the method of the Association of Official Analytical Chemists (1990). Cr and Yb were extracted from the ashed residue according to the method of Siddons *et al.* (1985) as modified by Lallès & Poncet (1990), and analysed using an atomic absorption spectrometer (Varian 220FS, Springvale, Australia).

Calculations and statistical analyses

The mean retention time (MRT) in duodenum, ileum and total tract was calculated by a non-compartmental method. The term 'non-compartmental' was used as no attempt was made to relate the MRT to anatomical or physiological compartments (Lallès *et al.* 1991). The calculation of the MRT with this method does not require a specific hypothesis concerning the marker excretion pattern and is often referred to as the method of the moments. The MRT between ingestion of the marker and excretion in faeces was obtained using the following equation for total cumulative marker collection (Faichney, 1975):

$$\mathrm{MRT}_{\mathrm{faeces}} = \sum_{i=1}^{n} M_i t_i$$

where t_i is the time (in hours) between the ingestion of the marked meal and the ith defecation, and M_i is the quantity of marker excreted in the ith defecation. As this equation cannot be used for partial collection of digesta (Faichney, 1975; Lallès *et al.* 1991), the equation of Thielemans *et al.* (1978) was used for duodenal and ileal samples:

$$\mathrm{MRT}_{\mathrm{digesta}} = \left(\sum_{i=1}^{n} C_i t_i\right) / \left(\sum_{i=1}^{n} C_i\right)$$

MRT excretion in the duodenum and ileum were analysed using a one-compartment model where C_i is the marker concentration at time t_i after ingestion of the marked meal. The MRT in the small intestine was calculated by the difference between the MRT at the end of the ileum and the MRT at the duodenum. Similarly, the MRT in the large intestine was calculated as the difference between total tract MRT and the MRT at the end of the ileum.The calculation of the MRT according to the method of the moments does not require defining a mathematical model of marker excretion. However, this is required when constructing a mechanistic model of digestion in monogastric animals. The kinetics of marker excretion in the duodenum and ileum were analysed using a one-compartment model with Erlang retention times and a discrete lag time (Matis *et al.* 1989):

$$\text{marker concentration} = C_0 \frac{\lambda^n \times (\text{time} - \tau)^{n-1} \times \exp(-\lambda \times (\text{time} - \tau))}{(n-1)!}, \text{ for } t > \tau$$

$$\text{marker concentration} = 0, \text{ for } t < \tau$$

where C_0 is a scale parameter related to the quantity of marker given, λ and n are shape parameters of the Erlang distribution of residence times, and τ is the discrete lag time (hours). This model is based on the assumption of steady-state conditions where the pulse dose of the marker is accompanied by a continuous feed supply. Results of the analysis are reported by replacing the shape parameters of the Erlang distribution by the mean retention time in the compartment ($\mathrm{MRT_C} = n/\lambda$) and the standard deviation of retention times in the compartment ($\mathrm{SDRT} = \sqrt{(n/\lambda^2)}$). Because n is an integer value, each curve of marker concentration was fitted with values of n ranging successively from 1 to 9. The parameter estimates of the curve with the lowest residual standard deviation (RSD) were retained to calculate the $\mathrm{MRT_C}$ and SDRT. This method separates the MRT at the end of each segment (duodenum, ileum and faecal excretion) into a part due to a tubular structure (τ) and a part due to a compartmental structure ($\mathrm{MRT_C}$). The MRT at the end of each segment can be calculated as $\mathrm{MRT_C} + \tau$.

Faecal marker excretion data were analysed using the same conceptual model, but based on cumulative faecal marker excretion (Matis *et al.* 1989):

$$\text{cumulative marker excretion} = C_0(1 - \exp(-\lambda \times t)) \times \sum_{i=0}^{n-1} \frac{(\lambda \times t)^i}{i!}, \text{ for } t > \tau$$

$$\text{cumulative marker excretion} = 0, \text{ for } t < \tau$$

Data were analysed using an analysis of variance with the mixed linear models (Proc Mixed) procedure of Statistical Analysis Systems statistical software version 8·1 (SAS Institute, Cary, NC, USA) including period and diet as fixed effects

and animal as a random effect. The relationship between MRT and fibre content in the diet was also analysed using a regression analysis. Results for each marker are presented as least-squares means with RSD.

Results

General observations

The pigs appeared to be in good health throughout the experiment and readily ate the distributed meals. Results concerning faecal collection are presented in Table 2. An increase in dietary fibre content numerically increased ($P=0{\cdot}12$) the number of faecal collections and increased the total quantity of fresh and dry faeces excreted ($P<0{\cdot}01$). The DM content of digesta and faeces was not affected by the dietary fibre content.

The marker recovery rate (i.e. quantity of marker recovered in all samples relative to marker administration) averaged 0·90 for Yb (ranging from 0·82 to 0·97) and 0·93 for Cr (ranging from 0·88 to 0·98).

Mean retention time by the non-compartmental methods

The MRTs for both the solid and liquid phases are given in Table 3. The MRT averaged 1 h up to the proximal duodenum (further referred to as the stomach), 4 h from the proximal duodenum to the distal ileum (small intestine) and 37 h from the distal ileum to the faecal excretion (large intestine, average for the solid and liquid phase). Total tract transit time averaged 45 h for the solid phase and 39 h for the liquid phase.

Increasing the dietary fibre content reduced or tended to reduce the MRT in the small intestine, large intestine and total tract for the solid and liquid phase. The relationship between total tract MRT (h) and NDF content in the diet (g/kg DM) was linear for the solid ($MRT_{solid} = 70{\cdot}2 - 99$ NDF, $R^2 = 0{\cdot}78$) and liquid phases ($MRT_{liquid} = 77{\cdot}2 - 173$ NDF, $R^2 = 0{\cdot}77$). The reduction in total tract MRT due to an increase in fibre content was mainly caused by a reduction in MRT in the large intestine.

The MRT in the stomach was not affected by the fibre content in the diet. The difference in MRT between the solid and the liquid phases averaged 10 min and was not affected by fibre level ($P=0{\cdot}17$). In the small intestine, an increase in fibre content reduced the MRT, but there was no difference between the solid and the liquid phases of digesta ($P=0{\cdot}95$). In the large intestine, the increase in dietary fibre reduced the MRT more for the liquid phase than for the solid phase. The solid phase MRT was 9 h shorter for the HF diet compared with the LF diet, whereas it was 16 h shorter for the liquid phase. A similar difference was observed for the total tract MRT.

Table 2. Effect of dietary fibre on the number and weight of faecal collections*

Item	Diet				*P* value
	LF	MF	HF	RSD	Diet
No. of faecal collections	18·33	20·00	24·00	4·30	0·12
Fresh faeces weight (kg)	3·38[a]	4·74[b]	6·52[c]	0·88	<0·01
Dry faeces weight (kg)	1·06[a]	1·32[a]	1·93[b]	0·26	<0·01
Average DM content (% as is)					
Duodenal digesta	11·1	11·9	8·0	3·1	0·12
Ileal digesta	10·5	12·2	11·4	2·7	0·59
Faeces	31·5	30·2	29·4	2·8	0·44

LF, low fibre content; MF, medium fibre content; HF, high fibre content; RSD, residual standard deviation.

[a,b,c] Within a row, least squares means values without a common superscript letter differ ($P>0{\cdot}05$)

* Faeces collection occurred during a 105 h period following the distribution of the marked meal (see Material and methods). The actual number of defecations may be greater than the number of faecal collections.

Table 3. Mean retention time (h) of solid and liquid phase markers in the different segments of the gastrointestinal tract estimated by the method of the moments

Item	Diets*			RSD†	*P* value
	LF	MF	HF		Diet
Solid phase marker (YbO_2)					
Stomach*	1·0	1·1	1·3	0·3	0·25
Small intestine*	4·3[a]	3·9[b]	3·7[b]	0·3	0·02
Large intestine*	44·4[a]	39·4[ab]	35·6[b]	5·3	0·06
Total tract*	49·7[a]	44·3[ab]	40·5[b]	5·3	0·05
Liquid phase marker (Cr-EDTA)					
Stomach*	0·8	0·8	0·9	0·2	0·67
Small intestine*	4·4[a]	4·0[ab]	3·9[b]	0·3	0·13
Large intestine*	41·3[a]	36·1[ab]	24·9[ab]	8·1	0·02
Total tract*	46·6[a]	41·0[a]	29·7[b]	8·1	0·02

LF, low fibre content; MF, medium fibre content; HF, high fibre content; RSD, residual standard deviation.

[a,b] Within a row, least squares means without a common superscript letter differ ($P>0{\cdot}05$)

* Stomach, up to the the duodenal cannula; small intestine, between the duodenal and ileal cannulas; large intestine, from the ileal cannula onwards; total tract, stomach + small intestine + large intestine.

Qualitative description of marker excretion curves

The calculation of the MRT by the non-compartmental method has the advantage that no specific mathematical model of marker excretion is required. The drawback of the approach is that the results can only be expressed in terms of MRT. By using a model, additional relevant traits can be obtained that describe the pattern of marker excretion (e.g. time of first marker appearance). Several models exist for this purpose but, in order to evaluate the feasibility of using these, a visual appraisal of the data has to be carried out.

Figure 1 illustrates a typical marker excretion curve observed for duodenal digesta. Maximum marker concentration was typically observed within the first 30 min following ingestion of the marked meal, and marker excretion was complete 6 h after ingestion. In this experiment, a single marked meal was followed by the intake of normal (non-marked) meals every 4 h. If one assumes that the marker behaves as the feed and in the absence of endogenous secretions, one would expect to observe a constant marker concentration up to 4 h. Due to the ingestion of meals, the marker concentration would be expected to attain a new level instantaneously every 4 h. As can be seen in Fig. 1, this is not the case as the marker excretion curves appear to decline exponentially. Moreover, the decline is not continuous as, following the initial maximum marker

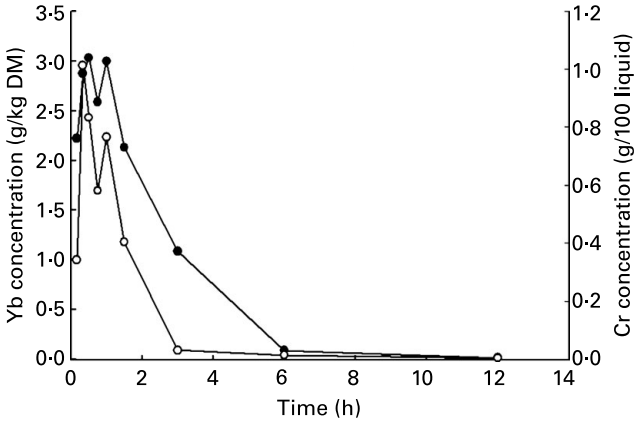

Fig. 1. Example of excretion curves for ytterbium (Yb) and chromium (Cr) in digesta collected at the proximal duodenum. ●, solid phase marker; ○, liquid phase marker.

concentration and an initial decline, marker concentration increased during 1–2 observations followed by a decline. This type of curve was observed for more than half of all cases, and for both solid and liquid phase markers.

Figure 2 shows an example of the change in solid marker concentration at the duodenal and ileal cannula (the duodenal excretion marker curve is the same as that in Fig. 1). Ileal marker excretion occurred approximately 4 h later than duodenal marker excretion (see also Table 2). First ileal marker appearance occurred 2 h after the ingestion of the marked meal, and marker ileal excretion was complete after approximately 12 h.

Due to the fact that a total collection method was used for excretion of faecal markers, the kinetics of faecal marker excretion are shown as a cumulative marker excretion curve (Fig. 3). The first appearance of the marker occurred after approximately 20 h, and marker excretion was complete 50–60 h after ingestion of the marked meal. There was some variability in the kinetics of marker excretion between animals and diets. The ascending part of the curve (i.e. from first marker appearance to full marker recovery) was represented by 1–8 points.

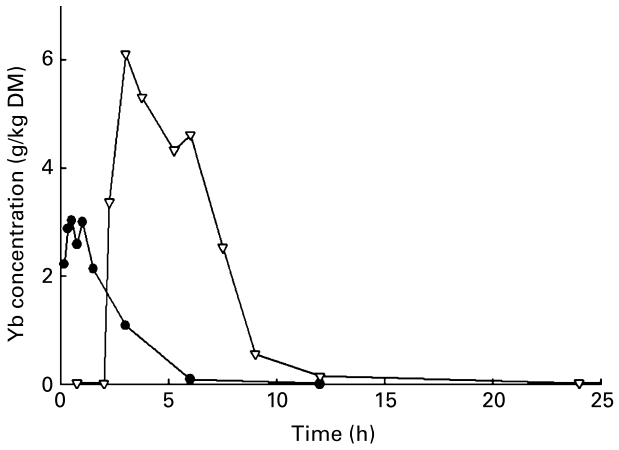

Fig. 2. Example of excretion curves for ytterbium in digesta collected at the proximal duodenum and the terminal ileum. ●, duodenum; ∇, ileum.

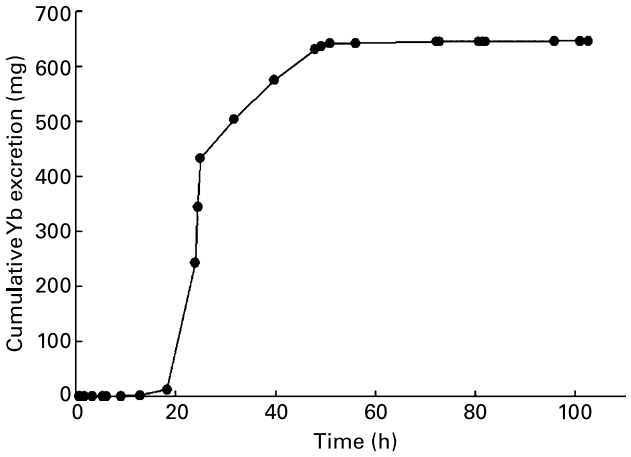

Fig. 3. Example of a cumulative faecal excretion curve for ytterbium.

Compartmental modelling of marker excretion

This method allows the kinetics of marker excretion to be distinguished as occurring in two (mathematical) parts: a tubular structure without mixing of digesta and a compartmental structure with mixing. The time delay (or lag time, τ) between ingestion of the marked meal and the first appearance of the marker is indicative for the tubular structure and represents a fixed retention time for the digesta. A compartmental structure implies that the retention time of digesta is variable and the (Erlang) distribution of retention times is represented by MRT_C and SDRT.

As indicated before, the pattern of duodenal marker excretion showed some unanticipated behaviour. As the proposed statistical model does not account for this behaviour, only ileal and faecal data were used in this analysis, and the

Table 4. First marker appearance (τ, h), mean compartmental retention time (MRT_C, h) and standard deviation of compartmental retention times (SDRT, h) for solid and liquid phase markers in ileal digesta and faeces*

	Diets				*P* value
Item	LF	MF	HF	RSD	Diet
Solid phase marker					
Ileal digesta					
τ	2·5	2·2	2·3	0·6	0·72
MRT_C	3·2	3·0	3·5	1·2	0·77
SDRT	1·9	2·0	2·3	0·9	0·75
Faeces					
τ	31·0	33·7	29·7	11·5	0·83
MRT_C	15·3	6·3	6·7	6·8	0·09
SDRT	12·1	5·2	5·6	5·6	0·11
Liquid phase marker					
Ileal digesta					
τ	2·9	2·3	2·8	1·2	0·65
MRT_C	2·3	2·7	2·1	1·3	0·69
SDRT	1·1	1·5	1·0	0·4	0·18
Faeces					
τ	27·0	21·0	20·5	10·0	0·49
MRT_C	13·9	11·6	8·7	5·8	0·34
SDRT	11·1	8·6	7·5	6·3	0·62

LF, low fibre content; MF, medium fibre content; HF, high fibre content; RSD, residual standard deviation.

* Obtained using a one-compartment model with Erlang retention times and a discrete lag-time (Matis *et al.* 1989). See text for details.

results are shown in Table 4. In general, the MRT calculated by the method of Faichney (1975) and Thielemans *et al.* (1978) (at the end of each segment of the GIT) and the MRT obtained by compartmental modelling ($MRT = \tau + MRT_C$) were well correlated and correlation coefficients ranged from 0·66 to 0·92.

For ileal digesta, τ was of a similar magnitude to the MRT_C (on average 2.7 h). In contrast, for faecal data, τ was considerably greater than MRT_C. The distribution of compartmental retention times was much more homogenous for ileal digesta than for the faeces. The SDRT was roughly half of the MRT_C for ileal digesta, whereas the SDRT and MRT_C were of similar magnitude for the faeces. Due to the high residual variation, few of the traits were significantly affected by the diet, period or pig. The ileal τ was not affected by the diet and averaged 2.5 h (Table 4). The ileal MRT_C was different ($P=0·03$) for solid and liquid phases (averaging 3.3 and 2.4 h, respectively). Period tended to affect ($P=0·06$) the liquid phase MRT_C.

The first faecal appearance of the marker occurred earlier for the liquid marker than for the solid marker (22.8 versus 31.4 h, $P=0·01$) but the difference did not depend on the fibre content of the diet. The faecal MRT_C of the solid phase tended to be affected by the diet ($P=0·09$) with a longer MRT_C for the LF diet. There was no effect of the marker on MRT_C. The difference in SDRT between markers was different only for ileal digesta ($P<0·01$). The difference between solid and liquid marker excretion was not affected by the diet, period or pig.

Discussion

Methodological considerations

Digesta consist of a fluid and a solid phase. However, the solid phase is known to be heterogeneous in nature, for example due to different particles sizes (Gomez *et al.* 1992). Cr-EDTA is a frequently used marker for the liquid phase (Siddons *et al.* 1985). Although it is present mainly in the liquid fraction of the digesta, small quantities of Cr-EDTA may be associated with the solid phase (Warner, 1969). Yb is associated preferentially with particles smaller than 1·5 mm (Siddons *et al.* 1985). As particles leaving the stomach of the pig are typically smaller than 2 mm (Low, 1990), it can be assumed that Yb is a suitable marker for the solid phase (Pond *et al.* 1986). Moreover, the affinity of Yb for the solid phase is greater than that of Cr-EDTA, so that both markers can be used together (Siddons *et al.* 1985).

Effect of dietary fibre on total mean retention time

Across treatments, the average total tract MRT was 45 h for the solid phase and 39 h for the liquid phase in the present study. The increase in the (insoluble) fibre content in the diet resulted in a decrease in total tract MRT (Table 3), which is in agreement with results reported previously (Stanogias & Pearce, 1985; Le Goff *et al.* 2002; Van Leeuwen *et al.* 2006). The origin of the effect of fibre on transit is still unclear. The increase in fibre content in the diet decreases the digestibility of DM (Shi & Noblet, 1993; Le Goff *et al.* 2002) and thus increases the quantity of indigestible DM present in the digestive tract (Owusu-Asiedu *et al.* 2006). It has been suggested that the presence of bulk exerts a direct physical action in the small and large intestine, which increases peristaltic action stimulating propulsive colonic motility (Laplace, 1981; Le Goff *et al.* 2002).

It is difficult to compare transit data reported in the literature as (absolute) values for total tract MRT vary greatly. Van Leeuwen *et al.* (2006) reported an average total MRT of 75 h for pigs weighing between 50 and 120 kg. Le Goff *et al.* (2002) observed that the MRT increased slightly with the BW of growing pigs, with average MRT increasing from 33 h at 33 kg BW to 37 h at 78 kg BW. Potkins *et al.* (1991) reported that the MRT ranged from 25 to 38 h for pigs having an average BW of 38 kg. Latymer *et al.* (1990) found a peak marker concentration at 43 h in 25 kg pigs. There are different aspects that can contribute to the wide range of MRT data reported in the literature. The main difference between studies is the nature of fibre in the diet, the BW of the animals, markers employed and the calculation and/or definition of MRT. Fibre sources used in the studies differ widely, and the nature of the fibre (e.g. soluble and insoluble fibre) has been shown to affect transit time (Le Goff *et al.* 2002). Also the BW of the animal may affect the MRT, as shown by Le Goff *et al.* (2002). Although the BW varied widely between studies (from 20 to 120 kg), the reported effect of BW on the MRT (Le Goff *et al.* 2002) does not seem to be sufficient to explain the difference between studies. Although the fibre content in the diet undeniably affects the MRT (within studies), the magnitude of reported MRT values remains very large. Although methodological aspects (e.g. calculation method of MRT, feed intake level) may play a role in the absolute values of MRT, it is difficult to quantify these effects.

Mean retention time in different segments of the digestive tract

In the present experiment, the MRT in the stomach was 1 h. Reported literature values for the MRT in the stomach vary greatly. Guerin *et al.* (2001) reported a value of 1 h for the half emptying time for a diet containing wheat bran, whereas Van Leeuwen *et al.* (2006) reported a value of 7 h for the half emptying time. The results of our study did not indicate an effect of the fibre content in the diet on the MRT in the stomach, suggesting that the addition of an insoluble fibre source such as wheat bran has little or no effect on gastric emptying. Nevertheless, the effect of dietary fibre on gastric emptying is not very clear and is controversial. Dietary fibre (both soluble and/or insoluble fibre) has been reported to delay (Miquel *et al.* 2001; Van Leeuwen *et al.* 2006), to have no effect (Rainbird & Low, 1986) or to accelerate (Potkins & Lawrence, 1984; Guerin *et al.* 2001) gastric emptying. The MRT of the liquid marker in the stomach was on average 0.25 h less than the MRT of the solid marker (Table 3). In general, the solid phase of digesta has been shown to leave the stomach more slowly than the liquid phase (Laplace, 1980; Low, 1990; Gregory *et al.* 1990).

The results of this study indicate that an increase in the fibre content in the diet results in a reduction in the MRT in the small intestine. Wenk (2001) suggested that fibre stimulates peristaltic action, thereby reducing the transit time in the small intestine. Jorgensen *et al.* (1996) reported a 5- to 6-fold increase in the flow of digesta through the terminal

ileum of pigs fed an HF diet (4 g of DM per g of non-starch polysaccharide added in the diet). On the other hand, Van Leeuwen *et al.* (2006) did not observe an effect of fibre on transit time in the small intestine. In the literature, the effect of fibre on MRT in the small intestine remains unclear as most studies determined transit time at the terminal ileum, which is the aggregate of the effects of fibre in the stomach and the ileum. In fact, some authors did not find an effect of fibre (Latymer *et al.* 1990; Potkins *et al.* 1991) or found that it even increased MRT at the terminal ileum (Hanson *et al.* 1986; Van Leeuwen *et al.* 1997). Apart from the confounding of the stomach and small intestine, these differences may also be related to dietary factors such as particle size (Potkins *et al.* 1991), water holding capacity of fibre and bulk of the digesta (Stanogias & Pearce, 1985).

The first solid phase marker appeared at the terminal ileum at approximately the same time as the liquid phase marker (Table 4). Latymer *et al.* (1990) also did not find a different first appearance of solid and liquid phase markers at the end of the small intestine. Nevertheless, the MRT at the terminal ileum was on average 0.5 h longer for the solid phase marker than for the liquid phase marker, which was essentially due to a difference in MRT_C (Table 4). This suggests that the longer MRT of the solid phase is caused in a compartmental structure (where mixing takes place) and not in the tubular structure (with propulsion). This is partly caused by a longer MRT of the solid phase in the stomach (Table 3). However, it also suggests that in the small intestine the solid phase is retained longer by segmentation contractions than the liquid phase.

The MRTs in the stomach and small intestine are very rapid compared with the MRT in the large intestine. It was on average 35 h (range 26–44 h) in the large intestine, which represents 87 % of the total MRT. The hindgut has been shown to be the main contributor to the total tract MRT (Keys & Debarthe, 1974; Latymer *et al.* 1990). Recently, Van Leeuwen *et al.* (2006) reported a value of 49 h for the MRT in large intestine of growing pigs. In the hindgut, an increase in the fibre content of the diet resulted in a decrease in MRT of both the solid and liquid phases of digesta. It is generally admitted that fibre stimulates the transit through the total GIT in pigs (Potkins *et al.* 1991). It has been suggested that the effect of fibre is related to the increase of microbial activity in the large intestine (Ravindran *et al.* 1984; Van Leeuwen *et al.* 2006), and possible effects of the volume of undigested contents in the intestines as factors influencing digesta transit in the hindgut. Insoluble lignified dietary fibre mainly reduced the faecal transit time (Wenk, 2001). Wheat bran has a high proportion of insoluble lignified cell walls (Selvendran, 1984), and has been reported to be one of the most effective fibre sources to increase faecal bulk and to decrease total tract MRT (Spiller *et al.* 1986).

The kinetics of marker excretion

After having received a single marked meal, pigs were fed every 4 h. The time between meals was long relative to the rate of gastric emptying. A decline in marker concentration (within a time frame of the first 4 h) can therefore be caused not by the arrival of newly ingested feed but more probably by the arrival of endogenous secretions. The fact that there is an important decline in marker concentration during the first 4 h (Fig. 1) suggests that endogenous secretions (from stomach, pancreas and gall bladder) are considerable.

The kinetics of gastric emptying for both phases typically followed a similar pattern. If the stomach is considered as a single, mixing compartment with a constant supply of feed and/or endogenous secretion, gastric emptying may be represented by an exponential function (Elashoff *et al.* 1982). Figure 1 illustrates that the observations differed from a smooth, exponentially declining function and that, following an initial decline, the marker concentration temporarily increased. Two hypotheses can be put forward to explain this phenomenon. The first hypothesis concerns a possible pulsatile excretion of DM, resulting in a dilution of the observed marker concentration. This would result in a 'dip' in the marker excretion curve. A single, pulsatile secretion of endogenous DM in a compartment (e.g. the stomach) would result in a reduction in marker concentration without a subsequent increase in marker concentration after the endogenous secretion. On the other hand, a pulsatile secretion after the compartment (e.g. by the pancreas or gall bladder) would result in a temporary reduction in marker concentration. The positioning of the duodenal cannula (after the pancreatic duct) makes the latter a more plausible hypothesis. In conscious pigs, pancreatic secretion exhibits a biphasic circadian pattern with a phase of basal secretion and a phase of meal-related enzyme-rich secretion. Basal pancreatic secretion is periodic and changes in parallel with duodenal motor activity (Abello *et al.* 1988). Pancreatic secretion increases in both volume and enzyme concentration following food ingestion (Pierzynowski *et al.* 1999). When digesta flow from the stomach to the duodenum, pancreatic secretion is stimulated (Xu, 2003). The protein output from the pancreas increases immediately after a meal, resulting in a postprandial peak (Pierzynowski *et al.* 1999). There appears to be no effect of meal patterns on the volume of bile secretion, although the bile salt concentration increases 2–3 h after a meal. Consequently, a postprandial pulsatile increase of endogenous secretions by the pancreas and/or gall bladder can contribute to diluting the concentration of both the liquid and solid phase markers.

A second hypothesis is that the solid phase marker may be partially retained by the stomach and released later. This would then result in the occurrence of a second peak of marker excretion. The anatomy of the stomach could explain the retention of particles by the sequestration in the gastric antrum (Prove & Ehrlein, 1983) and/or a sedimentation of solids in the gastric sinus through gravity (Brown *et al.* 1993). Although differences in gravity may potentially explain an irregular solid marker excretion, this is less likely to be the case for the liquid marker. Nevertheless, the liquid marker excretion curve was also irregular. Consequently, the first hypothesis is the most plausible explanation for the excretion curves of the duodenal markers.

It is clear that the observed phenomena make it difficult to propose a simple model structure for the stomach to analyse the experimental data. The positioning of the duodenal cannula may have complicated the data analysis. In the absence of a suitable alternative, modelling the stomach (before the pancreatic duct) as a single compartment may still be the best approach. Elashoff *et al.* (1982) suggested that the solid

marker excretion curve may differ from the liquid marker excretion curve through the occurrence of an initial lag phase for the solid emptying. In our study, we could not determine such a lag phase as the first duodenal sample was taken 10 min after completion of the meal (which corresponds to approximately 20 min after the onset of the meal). For forthcoming experiments, it may be important to sample soon after the onset of the meal and to increase the frequency of sampling during the first 20 min to follow the first appearance of markers in duodenal digesta.

The lag time (τ) that occurred prior to the first appearance of markers at the ileal digesta is due to the presence of a non-mixing tubular structure prior to the ileal cannula (Table 4). The MRT_C for ileal digesta indicates the presence of a compartmental structure prior to the cannula, part of which is caused by the stomach. However, the fact the MRT_C for ileal digesta (Table 4) is much greater than the MRT for the stomach (Table 3) suggests that the small intestine is also a mixing compartmental structure in addition to the tubular structure. In the literature, the small intestine has been represented as a multi-compartmental system, using a succession of small sections of constant (Usry *et al.* 1991) or decreasing (Rivest *et al.* 2000) lengths. Such a representation accounts for both the tubular and the compartmental aspects of transit. Alternatively, Bastianelli *et al.* (1996) represented the small intestine as two compartments combined with a discrete delay function. The fact that intestinal motility comprises both peristaltic (propulsion) and mixing movements suggests that the small intestine should be represented mathematically by both a compartmental and a tubular structure.

Faecal marker excretion curves were obtained by periodically surveying the animals and (passive) faecal collection. Others continuously observed the animals and collected the faeces immediately after excretion (Stanogias & Pearce, 1985). It is clear that in both cases, data and results should be interpreted with caution as they represent collection or defecation patterns and not a continuous transit of digesta. In the present study, faecal collection could theoretically occur 6 h after excretion (if defecated at night), thereby overestimating the MRT.

The cumulative faecal marker excretion curve showed a lag phase of >20 h. This is approximately 16 h after the peak marker excretion at the ileum and 8 h after the last marker detection at the ileum. This implies that transit in the large intestine should also be represented by a tubular structure (propulsion) in addition to a compartmental structure. The only digestion model for pigs specifically including the large intestine is that of Bastianelli *et al.* (1996). They represented the large intestine as a single compartment with a fractional outflow rate depending on the DM present in the compartment. This representation means that digesta entering the compartment may be excreted immediately. Data from the present study as well as the anatomy of the large intestine seem to justify the representation of the large intestine as a tubular and compartmental structure (or as a multi-compartmental structure).

Implications

Development of mathematical models of digestion is an important way to account for interactions that exist between different nutrients and between nutrients and the animal. The quantification of digesta transit is an essential step in developing these models. As little information is available in the literature, the results of the present study can help to develop an appropriate mathematical representation for each segment of the GIT, and to quantify the effect of wheat bran as a source of insoluble fibre on passage kinetics.

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References

Abello J, Laplace JP & Corring T (1988) Biliary and pancreatic secretion component of the migrating myoelectric complex in the pig. Effect of intraduodenal pH. *Reprod Nutr Dev* **29**, 953–967.

Association of Official Analytical Chemists (1990) *Official Methods of Analysis*, 15th ed., Arlington, VA: Association of Official Analytical Chemists.

Bach Knudsen K & Jorgensen H (2001) Intestinal degradation of dietary carbohydrates from birth to maturity. In *Digestive Physiology of Pigs*, pp. 109–120 [J Lindberg and B Ogle, editors]. Wallingford: CABI Publishing.

Bastianelli D, Sauvant D & Rerat A (1996) Mathematical modeling of digestion and nutrient absorption in pigs. *J Anim Sci* **74**, 1873–1887.

Brown BP, Schulze-Delrieu K, Schrier JE & Abu-Yousef MM (1993) The configuration of the human gastrointestinal junction in the separate emptying of liquids and solids. *Gastroenterology* **105**, 433–440.

Elashoff JD, Reedy TJ & Meyer JH (1982) Analysis of gastric emptying data. *Gastroenterology* **83**, 1306–1312.

Faichney G (1975) The use of markers to partition digestion within the gastrointestinal tract of ruminant. In *Digestion and Metabolism of the Ruminant*, pp. 277–291 [IW Mac Donald and ACI Warner, editors]. Sidney: The University of New England.

Gomez L, Lallès JP, Bogaërt C & Poncet C (1992) Kinetics of particulate and solute marker passage in sheep supplemented with catiomycin and lasalocid antibiotics. Comparisons among methods for calculating mean retention time. *Reprod Nutr Dev* **32**, 173–190.

Gregory PC, McFadyen M & Rayner DV (1990) Pattern of gastric emptying in the pig: relation to feeding. *Br J Nutr* **64**, 45–58.

Guerin S, Ramonet Y, Le Cloarec J, Meunier-Salaün MC & Malbert CH (2001) Changes in intragastric meal distribution are better predictors of gastric emptying rate in conscious pigs than are meal viscosity or dietary fibre concentration. *Br J Nutr* **85**, 343–350.

Hanson CF, Maxwell CV & Winterfeldt EA (1986) Passage time, digestibility and breath concentration from pigs fed fiber. In *Swine in Biomedical Research*, Vol. 2, pp. 967–979 [ME Tumbleson, editor]. New York: Plenum Press.

Jorgensen H, Zhao XQ & Eggum B (1996) The influence of dietary fibre and environmental temperature on the development of the gastrointestinal tract, digestibility, degree of fermentation in the hind-gut and energy metabolism in pigs. *Br J Nutr* **75**, 365–378.

Keys JE & Debarthe JV (1974) Site and extent of carbohydrate, dry matter, energy and protein digestion and the rate of passage of grain in swine. *J Anim Sci* **39**, 57–62.

Lahaye L, Ganier P, Thibault J & Sève B (2004) Technological processes of feed manufacturing affect protein endogenous losses and amino acid availability for body protein deposition in pigs. *Anim Feed Sci Technol* **113**, 141–156.

Lallès JP, Delval E & Poncet C (1991) Mean retention time of dietary residues within the gastrointestinal tract of the young ruminant: a comparison of non-compartmental (algebraic) and compartmental (modelling) estimation methods. *Anim Feed Sci Technol* **35**, 139–159.

Lallès JP & Poncet C (1990) Rate of passage of digesta during and after weaning in calves fed concentrate diets containing pea or soya-bean meal. *Livest Prod Sci* **24**, 333–345.

Laplace JP (1980) Stomach and small intestine motility in the pig: electromyography in nutritional studies. In *Currents Concepts of Digestion and Absorption in Pigs. Technical Bulletin No. 3*, pp. 24–31 [AG Low and IG Partridge, editors]. Shinfield: National Institute for Research in Dairying.

Laplace JP (1981) The transit of digesta in the different parts of the digestive tract of the pig. In *Nutrition in Health and Disease and International Development*, pp. 847–872 [AE Harper and K Davis, editors]. New York: Alan. R. Liss, Inc.

Latymer EA, Low AG, Fadden K, Sambrook IE, Woodley SC & Keal HD (1990) Measurement of transit time of digesta through sections of gastrointestinal tract of pigs fed with diets containing various sources of dietary fibre (non-starch polysaccharides). *Arch Anim Nutr* **40**, 667–680.

Le Goff G & Noblet J (2001) Comparative digestibility of dietary energy and nutrients in growing pigs and adult sows. *J Anim Sci* **79**, 2418–2427.

Le Goff G, van Milgen J & Noblet J (2002) Influence of dietary fibre on digestive utilization and rate of passage in growing pigs, finishing pigs and adult sows. *Anim Sci* **74**, 503–515.

Low AG (1990) Nutritional regulation of gastric secretion, digestion and emptying. *Nutr Res Rev* **3**, 229–252.

Matis JH, Wehrly TE & Ellis WC (1989) Some generalized stochastic compartment models for digesta flow. *Biometrics* **45**, 703–720.

Miquel N, Bach Knudsen K & Jorgensen H (2001) Impact of diets varying in dietary fibre characteristics on gastric emtying in pregnant sows. *Arch Anim Nutr* **55**, 121–145.

Noblet J & Perez JM (1993) Prediction of digestibility of nutrients and energy values of pig diets from chemical analysis. *J Anim Sci* **71**, 3389–3398.

Noblet J & Shi XS (1994) Effect of body weight on digestive utilization of energy and nutrients of ingredients and diets in pigs. *Livest Prod Sci* **37**, 323–338.

Owusu-Asiedu A, Patience JF, Laarveld B, Van Kessel AG, Simmins PH & Zijlstras RT (2006) Effects of guar gum and cellulose on digesta passage rate, ileal microbial populations, energy and protein digestibility, and performance of grower pigs. *J Anim Sci* **84**, 843–852.

Pierzynowski SG, Jakob S, Erlwanger KH, Tsuzuki S, Fushiki T, Gregory PC, Botermans JAM & Weström BW (1999) Possible feedback mechanisms involved in exocrine pancreatic secretion in pigs and rats. In *Biology of the Pancreas in Growing Animals*, pp. 261–271 [SG Pierzynowski and R Zabielski, editors]. Amsterdam: Elsevier.

Pond WG, Pond KR, Ellis WC & Matis JH (1986) Markers for estimating digesta flow in pigs and the effects of dietary fiber. *J. Anim. Sci.* **63**, 1140–1149.

Potkins ZV & Lawrence TLJ (1984) Studies on the effects of composition and physical form of the diet on gastric abnormalities and nutrient utilization in the growing pig. *Anim Prod* **38**, 534.

Potkins ZV, Lawrence TLJ & Thomlinson JR (1991) Effects of structural and non-structural polysaccharides in the diet of the growing pig on gastric emptying rate and rate of passage of digesta to the terminal ileum and through the total gastrointestinal tract. *Br J Nutr* **65**, 391–413.

Prosky L, Asp N, Furda I, DeVries J, Schweizer T & Harland B (1985) Determination of total dietary fiber in foods and food products: collaborative study. *J Assoc Off Anal Chem* **68**, 677–679.

Prosky L, Asp N, Schweizer T, DeVries J & Furda I (1992) Determination of insoluble and soluble dietary fiber in foods and food products: collaborative study. *J Assoc Off Anal Chem* **75**, 360–367.

Prove J & Ehrlein HJ (1983) Motor function of gastric antrum and pylorus for evacuation of low and high viscosity meals in dogs. *Gut* **23**, 150–156.

Rainbird AL & Low AG (1986) Effect of various types of dietary fibre on gastric emptying in growing pigs. *Br J Nutr* **55**, 111–121.

Ravindran V, Kornegay ET & Webb KE (1984) Effects of fiber and virginiamycin on nutrient absorption, nutrient retention and rate of passage in growing swine. *J Anim Sci* **59**, 400–408.

Rivest J, Bernier JF & Pomar C (2000) A dynamic model of protein digestion in the small intestine of pigs. *J Anim Sci* **78**, 328–340.

Sauvant D (1992) La modélisation systémique en nutrition. *Reprod Nutr Dev* **32**, 217–230.

Sauvant D, Perez JM & Tran G (editors) (2004) *Tables of Composition and Nutritional Value of Feed Materials: Pig, Poultry, Sheep, Goats, Rabbits, Horses, Fish*. Wageningen: Wageningen Academic Publishers, Paris: INRA Editions.

Selvendran RR (1984) The plant cell wall as a source of dietary fibre: chemistry and structure. *Am J Clin Nutr* **39**, 320–337.

Shi XS & Noblet J (1993) Contribution of the hindgut to digestion of diets in growing pigs and adult sows: effect of diet composition. *Livest Prod Sci* **34**, 237–252.

Siddons RC, Paradine J, Beever DE & Cornell PR (1985) Ytterbium acetate as a particulate-phase digesta-flow marker. *Br J Nutr* **54**, 509–519.

Spiller GA, Story JA, Wong LG, Nunes JD, Alton M, Petro MS, Furumoto EJ, Whittam JH & Scala J (1986) Effect of increasing levels of hard wheat fiber on fecal weight, minerals and steroids and gastrointestinal transit time in healthy young women. *J Nutr* **116**, 778–785.

Stanogias G & Pearce GR (1985) The digestion of fibre by pigs. 1. The effects of amount and type of fibre on apparent digestibility, nitrogen balance and rate of passage. *Br J Nutr* **53**, 513–530.

Thielemans MF, François E, Bodart C & Thewis A (1978) Mesure du transit gastrointestinal chez le porc à l'aide de radiolanthanides. Comparaison avec le mouton. *Ann Biol Anim Biochim Biophys* **18**, 237–247.

Thivend P, Mercier C & Guilbot A (1965) Dosage de l'amidon dans les milieux complexes. *Ann Biol Anim Biochim Biophys* **5**, 513–526.

Usry JL, Turner LW, Stahly TS, Bridges TC & Gates RS (1991) GI-tract simulation model of the growing pig. *Trans Am Soc Agric Eng* **34**, 1879–1890.

Van Leeuwen P, Doorenbos J, McCracken K, Ebbinge J & Verstegen M (1997) Digesta passage at the terminal ileum in pigs. In *Digestive Physiology in Pigs*, pp. 531–534 [JP Laplace, C Fevrier and A Barbeau, editors]. Paris: EAAP Publication No. 88. Paris: INRA.

Van Leeuwen P, van Gelder AH, de Leeuw JA & van der Klis JD (2006) An animal model to study digesta passage in different compartments of the gastro-intestinal tract (GIT) as affected by dietary composition. *Curr Nutr Food Sci* **2**, 97–105.

Van Soest PJ & Wine RH (1967) Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. *J Assoc Off Anal Chem* **50**, 50–55.

Warner ACI (1969) Binding of the 51Cr complex of ethylenediamine tetraacetic acid to particulate matter in the rumen. *Vet. Rec* **81**, 441–442.

Wenk C (2001) The role of dietary fibre in the digestive physiology of the pig. *Anim Feed Sci Technol* **90**, 21–33.

Wilfart A, Montagne L, Simmins H, van Milgen J & Noblet J (2007) Sites of nutrient digestion in growing pigs: effect of dietary fiber. *J Anim Sci* **85**, 976–983.

Xu RJ (2003) Gastrointestinal secretory function. In *The Neonatal Pig: Gastrointesinal Physiology and Nutrition*, pp. 117–155 [RJ Xu and PD Cranwell, editors]. Nottingham: Nottingham University Press.