British Journal of Nutrition (2000), **84**, 85–94

The effect of dietary fibre on energy utilisation and partitioning of heat production over pregnancy in sows

Y. Ramonet, J. van Milgen*, J. Y. Dourmad, S. Dubois, M. C. Meunier-Salaün and J. Noblet

Institut National de la Recherche Agronomique, Station de Recherches Porcines, 35590 St-Gilles, France

(Received 5 May 1999 – Revised 6 October 1999 – Accepted 9 December 1999)

A low (L) and high-fibre (H) diet were fed to six multiparous sows during gestation in a 2×2 repeated Latin square design. A single meal per day was given that provided 37·2 MJ digestible energy/d. The kinetics of heat production (HP) and its partitioning (fasting HP, activity HP, and thermic effect of feeding (TEF)) were determined. The TEF was partitioned between a dynamic component (TEF_{st}) and a constant component (TEF_{lt}). Digestibility of energy and nutrients was lower for the diet H. In spite of the lower metabolisable energy (ME) intake (33·9 *v*. 35·4 MJ/d for diets H and L respectively), HP was higher for diet H (30·5 *v*. 28·9 MJ/d) resulting in a lower energy retention. The estimated fasting HP was 270 kJ/kg body weight$^{0.75}$ per d at day 0 of gestation and increased with advancement of pregnancy. The TEF_{lt} was not significantly different from zero for diet L, but represented 4·1 % of ME intake for diet H. The TEF_{st} was not affected by the diet but diet H delayed the postprandial peak of HP. Total TEF was higher for diet H than for diet L (11·7 *v*. 8·2 % of ME intake). The longer duration of eating with diet H was compensated for by less physical activity between meals, so that activity HP was equivalent for both diets. The activity HP represented 20 % of ME intake but was variable between sows. The ME requirements for maintenance averaged 440 kJ/kg body weight$^{0.75}$per d. Feeding high-fibre diets increases HP, delays the postprandial peak of HP and maintains the basal HP at a higher level.

High-fibre diet: Heat production: Sow: Pregnancy: Physical activity

The use of fibre in sow diets has been investigated with regard to their nutritional effects (Stanogias & Pearce, 1985*a*; Shi & Noblet, 1993*a*) and the consequences on the reproductive performances (Matte *et al*. 1994; Vestergaard & Danielsen, 1998). More recently, in order to improve the welfare of restrictively fed sows, high-fibre diets were recommended to reduce the feeding motivation of animals that may result in stereotyped behaviour (Robert *et al*. 1993; Brouns *et al*. 1997; Ramonet *et al*. 1999). Different hypotheses have been proposed to explain this effect of fibre level on behaviour of sows. One hypothesis is a prolonged supply of energy in connection with increased fermentation in the hindgut. Therefore, it is important to quantify the nyctohemeral utilisation of energy according to the dietary fibre level and the probable extra energy expenditure that may be due to ingestion, digestion and metabolism of fibrous diets (Noblet *et al*. 1993*a*; Schrama *et al*. 1998).

The objective of the present study was to determine the effect of dietary fibre level on energy utilisation and components of heat production (HP) during four successive periods in pregnant sows. The procedure involved continuous measurement of HP and its partitioning between the fasting HP, the thermic effect of feeding (TEF) and the energy expenditure related to physical activity (van Milgen *et al*. 1997).

Materials and methods

Animals and housing

Six multiparous Large-White sows were assigned during gestation to two dietary treatments in a repeated 2×2 Latin-square design, each sow being fed alternatively one of the two experimental diets during four successive 21 d periods. Three sows were planned to receive one diet at the first period and the three other sows, the other diet. The experiment started after confirmation of pregnancy, 3 weeks after mating. During each period, sows were adapted to the diet for 10 d and subsequently moved to metabolism cages. The animals, each in their metabolic cage, were transferred individually to an open-circuit respiration chamber for collection of faeces and urine and energy balance and HP measurements for 7 d. Sows were kept in the respiration chamber for 2 additional d in order to estimate their fasting HP. One sow refused to eat the high-fibre diet during the

Abbreviations: BW, body weight; DE, digestible energy; H, high-fibre diet; HP, heat production; L, low-fibre diet; ME, metabolisable energy; RE, retained energy; TEF, thermic effect of feeding.

* **Corresponding author:** Dr J. van Milgen, fax +33 2 23 48 50 80, email jaap@st-gilles.rennes.inra.fr

first collection period, whereas leg problems occurred for another animal. Both sows were removed from the experiment but only one replacement sow was available. This animal started the experiment in the second period, 56 d after mating. Parity number of sows effectively used in the experiment was 4·2 (SE 2·5) and their mean live weight was 233 kg (SE 31) at insemination. Sows were slaughtered at the end of pregnancy.

Two respiration chambers with a volume of 12 m^3 were available for measurement of gas exchanges in individual pigs. Metabolic cages were equipped with two i.r. beams located at the front and the rear of the cages to detect standing or sitting activity of the animals. Interruption of an i.r. beam for at least 20 s was considered to represent a standing activity (i.e. sitting or standing). In addition, the metabolic cage was mounted on force sensors to detect physical activity. Sensors produced an electric signal considered to be proportional to physical activity of the animal. To ensure that the animals remained within their thermoneutral zone, the temperature in the respiration chamber was maintained at 22°C. In order to measure the duration of feed intake, feeders were placed on load cells.

Diets and feeding

The two experimental diets were formulated to contain either a low level of dietary fibre (diet L) or a high level of dietary fibre (diet H). Diet L was based on wheat, barley and soyabean-meal whereas in diet H, the wheat and soyabean-meal fraction was replaced by a mixture of fibre-rich feeds of different origin. Ingredient composition and chemical characteristics of diets are reported in Table 1. The increased fibre content in diet H is accompanied by a reduction in the starch content. Effects attributed to fibre should therefore be seen relative to a reduction in starch content.

Diets were offered as pellets. On the basis of the results of a previous digestibility study (Ramonet *et al*. 1999), daily feed allowance was calculated to provide the same daily digestible energy (DE) supply (37·2 MJ/d, which corresponded to 2·7 and 3·3 kg feed/d for diets L and H respectively). Similar to practical conditions, energy allowance was kept constant during pregnancy. Daily supplies of neutral-detergent fibre and starch were 324·8 g and 1355 g for diet L, and 1124 g and 658 g for diet H respectively. Similar to a previous experiment (Ramonet *et al*. 1999), the diet was fed as a single meal given at 08.45 hours during the adaptation and collection period. Following the 7 d collection period, the fasting HP was measured during a 2 d period. A single meal was given at 08.45 hours of the first day of this period, after which no more food was distributed. Water was available *ad libitum* from a water-tank throughout the experimental period.

Measurements

Sows were weighed at the beginning (day 1), at the end of the collection period (day 7), as well as after fasting (day 9). During each balance trial, a urinary catheter was inserted into the bladder of sows for the 7 d of total urine collection. Urine was collected daily in an HCl solution, pooled over successive days and weighed at the end of the period, and sampled for analysis. Faeces were collected daily, pooled, and, at the end of the period, weighed, mixed, subsampled, and freeze-dried for analysis. Feed and faeces were analysed for DM, ash, crude protein, and Weende crude fibre according to the Association of Official Analytical Chemists (1990) and their gross energy contents were measured with an adiabatic bomb calorimeter. Cell wall fractions (neutral-detergent fibre, acid-detergent fibre and acid-detergent lignan) were determined according to Van Soest *et al*. (1991) with preceding amylolytic treatment. N in urine was determined on fresh material. The energy content of urine was obtained after freeze-drying approximately 50 ml in polyethylene bags.

Concentrations of O_2, CO_2 and CH_4 in the respiration chamber were measured continuously. The [O_2] was measured with paramagnetic differential analyser (Oxygor 6N, Maihak AG, Hamburg, Germany) whereas [CO_2] and [CH_4] were measured with two absorption i.r. analysers (Unor 6N, Maihak AG). However, only one CH_4-analyser was available for both chambers, so that the CH_4 concentration was measured for each sow during 3 or 4 d (out of 7) during each experimental period.

The signal of the force sensors, and the weight of the trough and water-tank were measured 50–60 times/s. When the weight of the trough or the water-tank was detected as unstable, the corresponding beginning and ending time and the change in weight of the trough or water-tank were recorded. Measurements of gas concentrations, signals of the force sensors and weights of trough and water-tank were averaged over 10 s and stored on a microcomputer for

Table 1. Composition of the experimental diets

	Diets	
	L	H
Ingredients (g/kg)		
Barley	162·0	162·0
Wheat	657·0	–
Soyabean meal	112·5	–
Sunflower meal	–	130·0
Wheat bran	–	130·0
Sugar-beet pulp	–	260·0
Soyabean hulls	–	130·0
Corn-gluten feed	–	130·0
Molasses	30·0	30·0
Calcium carbonate	13·0	6·5
Dicalcium phosphate	11·0	7·0
NaCl	4·5	4·5
Vitamin and mineral premix	10·0	10·0
Chemical analysis		
Dry matter (g/kg)	876	875
Crude protein (N × 6·25; g/kg DM)	159	158
Crude fibre (g/kg DM)	41	183
NDF (g/kg DM)	140	396
ADF (g/kg DM)	43	207
ADL (g/kg DM)	11	35
Starch (g/kg DM)	577	234
Fat (g/kg DM)	19	24
Gross energy (MJ/kg DM)	17·74	17·78

L, low-fibre diet; H, high-fibre diet; DM,dry matter; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin.

further analysis. The aim of these simultaneous measurements was to relate the instantaneous variation in [O_2] and [CO_2] to physical activity of the sow and eating events in the chamber.

Calculations and statistical analysis

Apparent digestibility coefficients of energy and the different chemical fractions were calculated according to standard procedures (Noblet & Shi, 1993). Daily HP was calculated from gas exchanges, including CH_4 production, according to the formula of Brouwer (1965). The retained energy (RE) corresponded to the difference between metabolisable energy (ME) intake and HP. Energy retained as protein was calculated from the N balance whereas energy retained as lipids corresponded to the difference between RE and energy retained as protein.

The kinetics of O_2 and CO_2 production by the animal were estimated as described by van Milgen *et al.* (1997). In this approach, the [O_2] and [CO_2] in the respiration chamber are modelled by accounting for the physical aspects of gas exchanges and for the O_2 consumption and CO_2 production by the animal. The objective is to adjust model variables relating to the O_2 consumption and CO_2 production by the animal, so that variation between observed and predicted [O_2] and [CO_2] is minimal. The model is described as a series of differential equations, which are integrated numerically using SimuSolv (Steiner *et al.* 1990). Dependent variables in the model were [O_2] and [CO_2] in the respiration chamber whereas independent variables included time, level of physical activity (signal of force sensor) and quantity of feed intake. In practice, the model provides estimates of gas exchanges due to resting (litre/min), physical activity (litre/unit of force) and feed intake (litre/g). Subsequently, corresponding unitary HP were calculated from the respective O_2 consumption and CO_2 production as described by Brouwer (1965), excluding the correction for urine N and CH_4 production.

The four major components of the model are the fasting HP, the long-term TEF (TEF_{lt}), the short-term TEF (TEF_{st}), and the physical activity (van Milgen *et al.* 1997) and an example is given in Fig. 1. The fasting HP (kJ/d) corresponds to the asymptotic heat production 48 h after distribution of the last meal and was assumed constant. Also animals in the fed state were assumed to have a constant, basal HP (kJ/d). The difference between fasting HP and basal HP corresponds to TEF_{lt} and is indicative for long-term metabolic processes such as fermentation and metabolism of nutrients. Ingestion of a meal and associated short-term physiological events such as digestion and absorption cause a temporary increase of HP (TEF_{st}). This phenomenon was modelled as a compartmental system, which was parameterised to include the unitary TEF_{st} (kJ/g of feed) and the time required after ingestion of a meal to attain 50 % of the corresponding HP (total TEF (T_{TEF}); h). The daily TEF_{st} (kJ/d) corresponds then to the product of unitary TEF_{st} and the mean daily feed intake. The total TEF then corresponds to the sum of TEF_{st} and TEF_{lt}. Finally, activity (i.e. the signal of the force sensor) also results in increased HP to which a component of HP can be attributed. The daily HP due to physical activity was calculated as the product of unitary HP (kJ/unit of force) and total force detected over a day.

The distribution of daily activity HP between eating (i.e. instability of the trough), standing (i.e. the difference between total duration of standing and duration of eating) and lying periods was calculated as the product of activity HP (kJ/unit of force) and the total force measured during these periods. The RQ was calculated as the ratio CO_2 production : O_2 consumption.

Model variables of HP were estimated for each day of measurement. In the subsequent statistical analysis, the mean

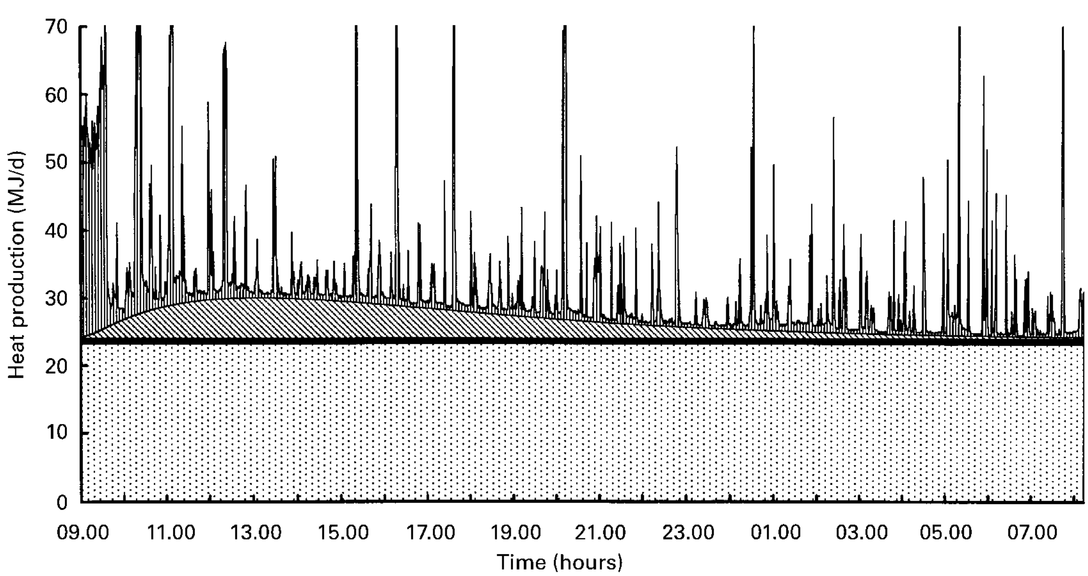

Fig. 1. Dynamics of heat production in a pregnant sow fed a high-fibre diet (diet H).The animal consumed its daily food allowance as a single meal. Daily heat production was 31·6 MJ/d and its components included the fasting heat production (▨; 73·3 %), long-term effect of feeding (⊠; 2·6 %), short-term effect of feeding (▧; 8·6 %) and heat production due to physical activity (▥; 15·5 %). For details of diet and procedures see Table 1 and p. 86.

of daily variables was used for each sow and for each stage of pregnancy (excluding the first day in the respiration chamber). However, when a technical problem happened (e.g. loss or blockage of bladder catheter), that day of measurement was not included in the estimation of components of HP or calculation of energy balance over the measurement period. All results were subjected to ANOVA that included the effects of animal, diet, stage of pregnancy and the diet × stage interaction using the GLM procedure of SAS (version 6.04, 1990; Statistical Analysis Systems Inst. Inc., Carey, NC, USA). The diet × stage interaction was not significant for any of the measurements and was therefore excluded from the model.

Results

The weight of faeces produced by animals was three times higher with diet H (2418 g/d) than with diet L (729 g/d) due, in part, to a significant difference in the DM content of faeces (30·5 *v.* 38·4 % for diets H and L respectively; $P < 0{\cdot}001$). In connection with this difference in faeces weight, it can be anticipated that sows fed diet H had a higher gut fill than when fed diet L. Covariance analysis of body-weight (BW) measurements with sow and diet as main effects and stage of pregnancy (d) as covariate indicated that sows, when fed diet H, were on average 8·8 kg heavier than when they received diet L ($P < 0{\cdot}05$). Consequently, the live weight of each sow was adjusted to a situation as if they were fed diet L. After completion of the experiment, sows were slaughtered; mean litter size was 12·2 (SE 3·8) piglets.

Digestibility of dietary nutrients and nitrogen balance

The digestibility coefficients of energy and nutrients are given in Table 2. Digestibility coefficients of organic matter, crude protein and energy were higher for diet L than for diet H and were not affected by stage of pregnancy. Sows digested about two-thirds of the dietary neutral-detergent fibre, which resulted in intakes of 221 and 757 g digestible neutral-detergent fibre/d for diets L and H respectively. The corresponding amounts of starch were 1355 and 658 g/d. Diet composition had an important effect on daily CH_4 production, which was 3·8-times higher for diet H (31·6 litre/d, 3·36 % of DE intake) than for diet L (8·2 litre/d, 0·85 % of DE intake). The higher energy loss in urine with diet H was related to a higher dietary N intake for this treatment (+ 12·3 g/d) and a subsequently higher N excretion (Table 3). Therefore, the ME : DE ratio was lower for the H diet. The N retention increased over pregnancy and maximum retention was observed during the last collection period, about 97 d after mating. The N retention was not affected by diet composition. Consequently, advancement of pregnancy was associated with a significant reduction of

Table 2. Digestibility and energy values of the diets*
(Mean values and relative standard deviations)

	Diet			Statistical significance of difference between means (ANOVA): *P*		
	L	H	RSD	Diet	Sow	Stage
No. of observations	9	10				
DM of faeces (g/kg)	384	305	18	< 0·001	0·026	NS
Daily faeces excreted (g)	729	2418	111	< 0·001	0·010	0·024
Mean body weight (kg)	259·6	261·1	3·6			
DM intake (g/d)	2355	2831	68			
Apparent digestibility						
DM	0·881	0·742	0·084	< 0·001	0·040	NS
Organic matter	0·911	0·767	0·077	< 0·001	0·024	NS
Crude protein	0·885	0·702	0·172	< 0·001	NS	NS
Crude fibre	0·535	0·647	0·300	< 0·001	NS	NS
NDF	0·678	0·675	0·287	NS	0·025	NS
ADF	0·538	0·670	0·331	< 0·001	0·014	NS
ADL	0·512	0·318	0·454	< 0·001	NS	NS
Fat	0·539	0·348	0·371	< 0·001	0·027	NS
Energy	0·897	0·740	0·077	< 0·001	0·028	NS
CH_4 (litre/d)	8·2	31·6	4·2	< 0·001	0·068	NS
Energy value of CH_4 (% DE)	0·85	3·36	0·50	< 0·001	NS	NS
Energy value of urine (% DE)	4·48	5·62	0·52	0·001	NS	0·017
ME : DE (%)	94·7	91·0	0·7	< 0·001	NS	0·011
Energy values (MJ/kg DM)						
DE	15·9	13·2	0·1	< 0·001	0·025	0·090
ME	15·1	11·9	0·2	< 0·001	NS	0·008

L, low-fibre diet; H, high-fibre diet; DM, dry matter; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin; ME, metabolisable energy; DE, digestible energy.
* For details of diets and procedures see Table 1 and p. 86.

Table 3. Effect of diet composition and stage of gestation on nitrogen and energy balance of sows*
(Mean values and relative standard deviations)

	Diet		Stage					Statistical significance of difference between means (ANOVA): *P*		
	L	H	1	2	3	4	RSD	Diet	Sow	Stage
No. of observations	9	10	4	5	5	5				
No. of day of gestation			36	57	78	97				
Body weight (kg)	259·6	261·1	244·8[a]	258·0[b]	266·2[c]	272·7[d]	3·6	NS	< 0·001	< 0·001
Nitrogen balance (g/d)										
Intake	59·5	71·8	65·8	64·4	65·9	66·6	2·1	< 0·001	NS	NS
Total losses	44·6	54·3	55·5[c]	52·6[bc]	48·5[b]	41·2[a]	4·2	< 0·001	NS	0·002
Faecal losses	6·9	21·3	14·7	14·3	14·0	13·6	1·2	< 0·001	0·179	NS
Urinary losses	37·3	32·7	40·3[c]	37·9[bc]	34·3[b]	27·3[a]	3·9	0·038	NS	0·003
Gaseous losses	0·4	0·3	0·5	0·3	0·2	0·3	0·2	NS	0·011	NS
Retention	14·9	17·5	10·3[a]	11·9[ab]	17·4[b]	25·4[c]	4·4	NS	NS	0·002
Energy balance (MJ/d)										
DE intake	37·4	37·3	37·2[ab]	36·3[a]	37·9[b]	37·9[b]	0·9	NS	0·022	0·082
ME intake	35·4	33·9	34·2[ab]	33·6[a]	35·3[b]	35·6[b]	1·0	0·013	0·094	0·039
Heat production	28·9	30·5	28·4[a]	27·6[a]	30·6[b]	32·1[b]	1·3	0·045	0·068	0·002
Retained energy (MJ/d)										
Total	6·48	3·46	5·77	5·98	4·66	3·49	1·81	0·006	NS	NS
Retained as protein	0·53	0·62	0·36[a]	0·42[ab]	0·62[b]	0·90[c]	0·15	NS	NS	0·002
Retained as lipid	5·95	2·83	5·40[c]	5·56[c]	4·04[bc]	2·58[ab]	1·72	0·004	NS	0·079
Retained energy (% of ME intake)										
Total	18·4	10·1	16·8	17·4	13·2	9·7	4·9	0·006	NS	NS
Retained as protein	1·5	1·8	1·1[a]	1·2[ab]	1·7[b]	2·5[c]	0·4	NS	NS	0·002
Retained as fat	16·9	8·3	15·7[b]	16·1[b]	11·4[ab]	7·2[a]	4·7	0·004	NS	0·049
Respiratory quotient	0·99	0·98	0·99[ab]	1·01[b]	0·98[ab]	0·95[a]	0·03	NS	NS	0·057

L, low-fibre diet; H, high-fibre diet; ME, metabolisable energy; DE, digestible energy.
[a,b,c,d] Mean values within a row with unlike superscript letters were significantly different, $P < 0.05$.
* For details of diets and procedures see Table 1 and p. 86.

urinary N excretion and an increase of the ME : DE ratio from 0·92 at stage 1 to 0·94 at stage 4.

Energy balance

Daily DE intake was similar for both diets, but due to higher energy losses as CH_4 and in urine, the daily ME intake was higher for diet L (Table 3). Despite the higher ME intake, HP was lower for diet L which resulted in a significantly higher energy retention. Consequently, the RE represented 18·4 and 10·1 % of ME intake for diets L and H respectively. As N retention was similar for both diets, the additional energy retention with diet L was then deposited exclusively as fat. Total HP increased with advancement of pregnancy, so that total energy retained was lower, especially at stages 3 and 4.

The combination of higher HP and higher protein retention with advancement of pregnancy resulted in a marked reduction of fat deposition during the later stages of pregnancy. This situation was more pronounced for diet H. The lower RQ at stages 3 and 4 confirms this result. These variations of HP and N balance with advancement of gestation and diet composition resulted in marked changes in the partitioning of ME. Indeed, the partitioning of RE between protein and fat showed that energy retained as protein was two-fold higher in the last stage of gestation than in the first stage. Conversely, energy retained as fat decreased markedly with advancement of pregnancy.

Behaviour

Duration of standing activity averaged 212 min/d and ranged from 135 to 387 min. Standing activity was neither affected by the diet nor by the sow (Table 4). The time spent eating was 50 % higher for diet H than for diet L (54 *v*. 35 min for diets H and L respectively).

Irrespective of the behaviour of the animal, the energy cost of standing averaged 20 kJ/min standing activity. In fact, this average value corresponds to the combined cost of standing during the meal and standing while not eating, that averaged 31·5 and 17·8 kJ/min respectively. These latter values were not affected by diet composition. The difference between both estimates can be considered as the energy cost of ingestion which thus averaged 13·7 kJ/min. Due to the longer duration of ingestion, activity HP during eating was higher for diet H than for diet L (1·54 *v*. 1·11 MJ/d respectively). Expressed per g of feed, when the energy cost of standing was removed from activity HP during eating, these costs of eating are then 0·183 and 0·234 kJ/g, which correspond to 497 and 748 kJ/meal for diets L and H respectively ($P < 0.05$).

Components of heat production

In fed animals, the basal HP tended to be higher for diet H than for diet L and increased during pregnancy (Table 5); it

Table 4. Standing and physical activity of sows*
(Mean values and relative standard deviations)

	Diet			Statistical significance of difference between means (ANOVA): *P*		
	L	H	RSD	Diet	Sow	Stage
Behaviour (min/d)						
Eating	35	54	8	<0·001	0·006	NS
Standing	195	220	59	NS	NS	NS
Activity HP (MJ/d)						
Total	6·61	6·88	0·97	NS	0·004	NS
Standing and/or eating	1·11	1·54	0·23	0·003	0·027	NS
Standing and/or not eating	3·06	2·74	0·78	NS	0·006	NS
While lying	2·50	2·60	0·54	NS	0·020	0·047
Standing HP (kJ/min)	21·8	19·5	4·6	NS	NS	NS
Standing HP (kJ/kg $BW^{0·75}$ per min)	0·33	0·30	0·07	NS	NS	NS

L, low-fibre diet; H, high-fibre diet; HP, heat production.
* For details of diets and procedures see Table 1 and p. 86.

was 9·5 % higher at stage 4 than at stage 1. The daily TEF_{st} was 859 and 802 kJ/kg of ingested feed for diets L and H respectively. When expressed per kg metabolic body size ($BW^{0·75}$) and per d, TEF_{st} was not affected by the diet (36 and 40 kJ/kg $BW^{0·75}$ per d for diets L and H respectively). The HP profile for diet L attained a higher level and attained it earlier after the ingestion of the meal (Fig. 2). On the other hand, diet H delayed HP after ingestion of the meal. Indeed, the time to produce 50 % of the T_{TEF} was 1·12 h longer for diet H than for diet L (6·35 and 7·47 h for diets L and H respectively; $P = 0·017$).

Activity HP averaged 105 kJ/kg $BW^{0·75}$ per d, with considerable variation between animals. The most important component of activity HP occurred when sows were standing. Ingestion of the meal represented 26 and 35 % of standing activity HP for diets L and H respectively. However, irrespective of the diet, 36 % of activity HP occurred when sows were lying.

The fasting HP, estimated for zero activity, averaged 313 kJ/kg $BW^{0·75}$ per d and was not affected by the diet. But it increased significantly over pregnancy. This variation of fasting HP with advancement of pregnancy could be expressed by the following curvilinear relationship between fasting HP (kJ/kg $BW^{0·75}$) and stage of gestation (d): fasting HP (kJ/kg $BW^{0·75}$ per d) $= 270 + 0·00648\, d^2$. The TEF_{lt}, which was calculated as the difference between basal HP and fasting HP, differed from zero for diet H ($P = 0·026$) but not for diet L ($P = 0·910$). The total TEF ($TEF_{lt} + TEF_{st}$) was 35 % higher for diet H than for diet L and it decreased during pregnancy.

Table 5. Effect of experimental diets and stage of gestation on partitioning of heat production in pregnant sows*
(Mean values and relative standard deviations)

	Diet		Stage					Statistical significance of difference between means (ANOVA): *P*		
	L	H	1	2	3	4	RSD	Diet	Sow	Stage
Estimated variables (kJ/kg $BW^{0·75}$ per d)										
Fed animals										
ME intake	550	523	554	523	537	532	17	0·013	0·001	NS
Total HP	456	478	473	444	472	496	21	0·078	0·002	NS
Components of HP										
Basal HP	322	334	324[b]	304[a]	331[b]	355[c]	21	0·067	0·007	< 0·001
TEF_{st}	36	40	46	38	35	33	8	NS	NS	NS
Activity HP	103	106	102	102	106	108	15	NS	0·002	NS
Fasted animals										
Fasting HP	313	313	297[a]	290[a]	314[a]	353[b]	21	NS	0·021	0·004
Calculated variables (kJ/kg $BW^{0·75}$ per d)										
Components of HP										
TEF_{lt}	9	21	27	14	17	3	16	NS	NS	NS
Total TEF	45	61	73[b]	52[ab]	52[ab]	36[a]	15	0·050	NS	0·037
Standing and/or eating HP	17	24	20	20	19	21	3	0·004	0·032	NS
Standing and/or not eating HP	48	43	50	46	49	36	12	NS	0·004	NS
Activity while lying HP	38	39	32	36	38	51	8	NS	0·026	0·069

L, low-fibre diet; H, high-fibre diet; ME, metabolisable energy; HP, heat production; TEF_{st}, short-term effect of feed; TEF_{lt}, long-term effect of feed; TEF, thermic effect of feeding.
[a,b,c] Mean values within a row with unlike superscript letters were significantly different, $P < 0·05$.
* For details of diets and procedures see Table 1 and p. 86.

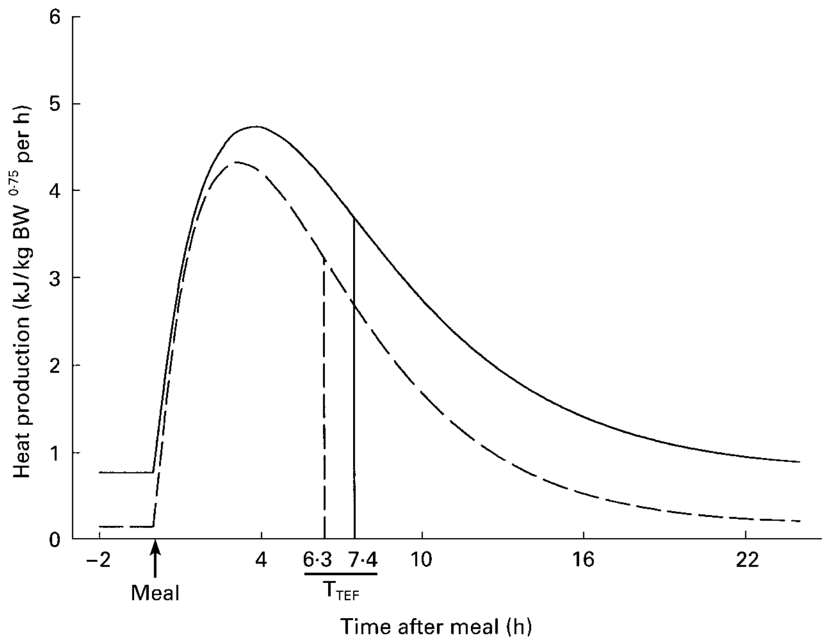

Fig. 2. Effect of experimental diets on thermic effect of feeding (TEF) after ingestion of a high-fibre diet (——) and a low-fibre diet (– – –). The zero-level of heat production corresponds to fasting heat production. The TEF was partitioned between a constant component (TEF_{lt}), which corresponds to the initial value and asymptotic value, and a dynamic component (TEF_{st}). The time required after ingestion of the meal to attain 50 % of the corresponding TEF_{st} (T_{TEF}) is indicated. BW, body weight. For details of diets and procedures see Table 1 and p. 86.

The basal HP represented 58·6 and 64·1 % of ME intake for diets L and H respectively (Table 6). In connection with similar ME intakes and increase of basal HP over pregnancy, the fraction of ME intake for basal HP was 7 percentage points higher in the last stage of gestation than in the first stage. The TEF represented a higher proportion of ME intake for diet H than for diet L (11·7 and 8·2 %). Activity HP was the most variable component of energy expenditure between sows and averaged 20 % of ME intake. The partitioning of HP indicated that fasting HP was the main component of total HP and represented about two-thirds of HP, irrespective of the diet. The remainder was due to TEF (11 % of total HP) and activity HP (22 % of total HP).

Table 6. Partitioning of metabolisable energy* intake
(Mean values and relative standard deviations)

	Diet		Stage					Statistical significance of difference between means (ANOVA): *P*		
	L	H	1	2	3	4	RSD	Diet	Sow	Stage
Heat production (% of ME intake)										
Basal HP	58·6	64·1	58·2[a]	57·5[a]	61·7[a]	65·0[b]	3·6	0·014	0·062	0·016
TEF										
Total	8·2	11·7	13·4[b]	10·1[ab]	9·8[ab]	6·7[a]	2·7	0·024	NS	0·038
TEF_{st}	6·6	7·7	8·5	7·4	6·4	6·3	1·6	NS	NS	NS
TEF_{lt}	1·7	4·1	4·9	2·7	3·3	0·5	2·8	NS	NS	NS
Activity HP	18·7	20·2	18·5	19·4	19·8	20·1	2·5	NS	0·003	NS
Heat production (% of total HP)										
Fasting HP	67·9	65·3	62·9[a]	65·4[a]	66·8[ab]	71·4[b]	3·8	NS	0·031	0·052
Basal HP	70·0	69·8	68·7	68·5	70·4	71·9	2·7	NS	0·006	NS
TEF										
Total	9·9	12·8	15·6[b]	11·7[b]	10·9[ab]	7·2[a]	3·1	NS	NS	0·023
TEF_{st}	7·8	8·3	9·8	8·6	7·3	6·7	1·7	NS	NS	NS
TEF_{lt}	2·1	4·5	5·8	3·1	3·6	0·5	3·3	NS	NS	NS
Activity HP	22·2	21·9	21·5	22·9	22·3	21·4	2·6	NS	0·003	NS

L, low-fibre diet; H, high-fibre diet; ME, metabolisable energy; HP, heat production; TEF_{st}, short-term effect of feed; TEF_{lt}, long-term effect of feed; TEF, thermic effect of feeding.
[a,b,c] Mean values within a row with unlike superscript letters were significantly different, $P < 0·05$.
* For details of diets and procedures see Table 1 and p. 86.

Discussion

Energy metabolism in pregnant sows

In the present experiment, fasting HP increased with the stage of pregnancy. This change is probably associated with changes in body composition and differences in metabolic activity of tissues. Indeed, in pregnant sows, uterine energy deposition and weight of uterus increases, mainly in the last third of gestation (Noblet *et al*. 1985). In addition, the gravid uterus is a metabolically active tissue, as suggested by Freetly & Ferrell (1997) who measured that the increase in HP of the gravid uterus of ewes accounted for approximately 49 % of the increase in total HP during pregnancy. When pregnant sows are fasted, catabolism of maternal tissues occurs to maintain nutrient deposition in reproductive tissues as a priority. The combination of increased importance of uterine tissues and the increased rate of energy deposition in the uterus with advancement of pregnancy is the most probable explanation for the higher fasting HP at stages 3 and 4. On the other hand, fasting HP as measured at stages 1 and 2 should be less influenced by gestation status. The extrapolation of the relationship between fasting HP and stage of gestation provides an estimate of fasting HP at day 0 of gestation (270 kJ/kg $BW^{0{\cdot}75}$) which is comparable to the values measured by Noblet *et al*. (1993*a*) in non-pregnant adult sows (261 kJ/kg $BW^{0{\cdot}75}$).

The ME requirement for maintenance (ME_m) can be calculated as the difference between ME intake and ME requirements for fat and protein deposition. Assuming energetic efficiencies in pregnant sows of 0·80 and 0·60 for ME deposited as fat and protein, respectively (Noblet *et al*. 1990), it can be calculated that ME_m averaged 437 kJ/kg $BW^{0{\cdot}75}$ per d in the present study. This value is similar to the average value of 440 kJ ME/kg $BW^{0{\cdot}75}$ per d used in energy recommendations for primiparous and multiparous sows (Agriculture and Food Research Council, 1990; Noblet *et al*. 1990; National Research Council, 1998). Despite the fact that fasting HP increased with stage of pregnancy, ME_m did not change with gestation, in agreement with Noblet & Etienne (1987) and Noblet *et al*. (1997). The calculation of ME_m is based on a zero energy balance (i.e. the intercept of the multivariate regression of ME intake on protein and lipid deposition) and does not account for the redistribution of energy between tissues. The fasting HP on the other hand is measured in individual animals and accounts, at least partially, for the priority energy metabolism of the uterus. As a result, the ME_m and fasting HP in gestating sows do necessarily reflect the same phenomena.

Energy retained as protein increased after mid-pregnancy, as observed in multiparous (Everts & Dekker, 1994) or nulliparous sows (Noblet & Etienne, 1987). This increase may be related to the enhanced N retention in products of conception during the later stages of pregnancy (Noblet *et al*. 1985, 1997; Dourmad *et al*. 1996). Since BW increases during pregnancy, a greater fraction of ME is designated to meeting maintenance requirements in late pregnancy. The combination of increased HP related to the daily ME_m and greater amounts of ME for protein and uterine energy deposition results in a reduced supply of ME for fat deposition when ME intake is kept constant. Under such conditions, fat deposition will be reduced with advancement of pregnancy; it was even negative for sows fed the diet H at stage 4.

Physical activity in pregnant sows

The mean energy cost of standing activity averaged 0·30 kJ/kg $BW^{0{\cdot}75}$per min standing and is similar to that found in sows by Cronin *et al*. (1986) and Noblet *et al*. (1993*b*). Approximately 20 % of ME intake in pregnant sows is then used for physical activity. The force sensors give more detailed information about the energy cost of activity than the measurement of standing activity alone. Using the combination of both methodologies, results of this study indicate that 36 % of activity related HP was produced when sows were lying.

In pregnant tethered sows housed in practical conditions, an average of 250 min was spent standing per d (Cariolet & Dantzer, 1984) but considerable between-animal variation can exist (Ramonet *et al*. 1999). Moreover, standing time and stereotyped behaviours increase in multiparous sows or in animals with poor body condition (Cariolet & Dantzer, 1984). Consequently, physical activity can be quite variable and represents a major factor causing differences in energy balance between sows (Noblet *et al*. 1997). For instance, energy expenditure due to an increase of 100 min standing activity per d represents the energetic equivalent of about 150 g of the L diet per d.

It has been reported that fibrous diets can reduce standing and stereotyped activity in sows (Robert *et al*. 1993; Brouns *et al*. 1994) and in growing pigs (Schrama *et al*. 1998). In sows housed in a piggery and fed the same diets as in the present experiment, Ramonet *et al*. (1999) showed that the duration of standing was 363 min/d when sows were fed diet L and 291 min/d when fed diet H. This effect could not be confirmed in the present study. This may be due to the fact that, in the present study, the sows were kept alone in the respiration chamber and were completely isolated from the environment. Their body condition at mating was also much better than in the study of Ramonet *et al*. (1999). In addition, the effect of a high-fibre diet on the time spent standing by animals can be dependent on the nature of ingredients (Brouns *et al*. 1995; Ramonet *et al*. 2000).

Effect of dietary fibre on energy utilisation in pregnant sows

In agreement with results of previous studies (Calvert *et al*. 1985; Stanogias & Pearce, 1985*a*; Noblet & Shi, 1993; Ramonet *et al*. 1999), the digestibility coefficients of energy and nutrients decreased when the level of dietary fibre in the diet was increased. In addition, a larger fraction of energy would be degraded in the hindgut when dietary fibre content is increased. According to an equation of Shi & Noblet (1993*a*), the fraction of dietary energy digested in the hindgut would be 18 and 43 % of total digested energy for diets L and H respectively. The difference in the contribution of hindgut in providing energy is confirmed by CH_4 production which represented 3·4 % of DE content for diet H and 0·8 % for diet L. The CH_4 production observed with diet H is higher than the highest values reported by Shi & Noblet (1993*b*). Similar to energy, the presence of fibre in the diet of pigs reduces the apparent faecal digestibility of N (Stanogias & Pearce, 1985*a*; Noblet & Perez, 1993).

Despite a lower daily ME intake, total HP of sows was higher for diet H than for diet L. This increase of HP is in agreement with the net energy prediction equations of Noblet *et al*. (1993*a*) showing a higher heat increment with high-fibre or high-protein diets. This difference between diets was mainly due to the differences in TEF. Indeed, TEF was higher for diet H than for diet L (8·2 and 11·7 % of ME intake for diets L and H respectively). This resulted in a lower RE for diet H, even though DE intakes were equivalent for both diets. To obtain a similar RE for both diets, it would be necessary to increase the ME intake of the diet H by about 3·4 MJ/d (i.e. 330 g).

A decrease in activity with fibrous diets has been observed in some studies (Robert *et al*. 1993; Schrama *et al*. 1998; Ramonet *et al*. 1999), with a subsequent lower activity HP. This decrease of activity HP with fibrous diets could compensate for the higher TEF as observed by Schrama *et al*. (1998) in growing pigs fed with diets containing different levels of NSP. For sows of the present experiment, a total compensation would require a reduction of 170 min/d of standing activity for diet H. Although Ramonet *et al*. (1999) observed a reduction in activity due to a high-fibre diet in sows housed in practical conditions, the reduction was of much smaller magnitude (74 min/d). Therefore, for a similar amount of DE, the decreased activity with high-fibre diets is insufficient to compensate for the increased TEF and the lower efficiency of volatile fatty acids produced during fermentation.

In connection with a delayed and more continuous supply of nutrients from the hindgut, basal HP was higher with diet H than in diet L. Because there was no difference in fasting HP between both diets, TEF_{lt} was higher for diet H than for diet L. For sows fed diet L, TEF_{lt} was not different from zero, whereas it represented 4·1 % of ME intake for the fibrous diet. The TEF_{lt} represents long-term metabolic phenomena such as metabolism and fermentation without a distinguishable pattern of HP that can be related to the ingestion of feed. The larger fraction of DE digested in the hindgut for diet H can explain the difference between basal and fasting HP. In contrast, the TEF_{st} was similar irrespective of the feed. The mean duration of T_{TEF} was 1·2 h higher for diet H diet than for diet L. In man, the peak value of HP occurs 3 h after ingestion of a low-fibre meal and 30 to 90 min later with high-fibre meals (Scalfi *et al*. 1987). Absorption of nutrients with fibrous diets may follow similar kinetics to TEF. Fibrous diets also delay the gastric emptying in pigs (Rainbird & Low, 1986) and the absorption of nutrients such as glucose and amino acids (van den Brand *et al*. 1998; Ramonet *et al*. 2000). In contrast, microbial fermentation of dietary fibre in the large intestine results in the production of volatile fatty acids (Stanogias & Pearce, 1985*b*) which becomes important between 5 and 12 h after the meal (Rérat, 1996; Michel & Rérat, 1998). Because of the higher and more prolonged HP, the use of fibrous diet can be interesting in cold environments. Indeed, using diets high in straw or alfalfa, Noblet *et al*. (1989) showed that increased HP associated with metabolic utilisation of ME of such diets fed to sows exposed to cold climatic conditions was efficiently used for thermoregulation.

In conclusion, when pregnant sows are fed the same quantity of DE, the use of a high-fibre diet increases the HP and less energy will be available for protein and lipid deposition. This increase in HP is mainly due to long-term processes related to fermentation and associated end-products. When feeding gestating sows a high-fibre diet, it is important to account for this extra energy loss. However, reduced physical activity often associated with the use of high-fibre diets may only attenuate or partially compensate this difference in HP. Feeding a high-fibre diet also delays the postprandial peak of HP and provides a more continuous supply of nutrients which may explain the reduction of stereotyped behaviours of pregnant sows fed such diets.

Acknowledgements

The authors gratefully acknowledge G. Reuzeau, Y. Lebreton and A. Roger for their technical assistance.

References

Agriculture and Food Research Council, Technical Committee on Responses to Nutrients (1990) Report Number 4, Nutrient requirements of sows and boars. *Nutrition Abstract Reviews (Series B)* **60**, 383–406.

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

Brouns F, Edwards SA & English PR (1994) Effect of dietary fibre and feeding system on activity and oral behaviour of group housed gilts. *Applied Animal Behaviour Science* **39**, 215–223.

Brouns F, Edwards SA & English PR (1995) Influence of fibrous feed ingredients on voluntary intake of dry sows. *Animal Feed Science and Technology* **54**, 301–313.

Brouns F, Edwards SA & English PR (1997) The effect of dietary inclusion of sugar-beet pulp on the feeding behaviour of dry sows. *Animal Science* **65**, 129–133.

Brouwer E (1965) Report of sub-committee on constants and factors. In *Energy Metabolism. Proceedings of the 3rd Symposium held at Troon, Scotland, May, 1964. European Association for Animal Production Publication* no. 11, pp. 441–443 [KL Blaxter, editor]. London: Academic Press.

Calvert CC, Steele NC & Rosebrough RW (1985) Digestibility of fiber components and reproductive performance of sows fed high levels of alfalfa meal. *Journal of Animal Science* **61**, 595–602.

Cariolet R & Dantzer R (1984) Motor activity of pregnant tethered sows. *Annales de Recherches Vétérinaires* **15**, 257–261.

Cronin GM, Van Tartwijk MFM, Van Der Hel W & Verstegen MWA (1986) The influence of degree of adaptation to tether-housing by sows in relation to behaviour and energy metabolism. *Animal Production* **42**, 257–268.

Dourmad JY, Etienne M & Noblet J (1996) Reconstitution of body reserves in multiparous sows during pregnancy: effect of energy intake during pregnancy and mobilization during the previous lactation. *Journal of Animal Science* **74**, 2211–2219.

Everts H & Dekker RA (1994) Effect of nitrogen supply on the retention and excretion of nitrogen and on energy metabolism of pregnant sows. *Animal Production* **59**, 293–301.

Freetly HC & Ferrell CL (1997) Oxygen consumption by and blood flow across the portal-drained viscera and liver of pregnant ewes. *Journal of Animal Science* **75**, 1950–1955.

Matte JJ, Robert S, Girard CL, Farmer C & Martineau GP (1994) Effect of bulky diets based on wheat bran or oat hulls on

reproductive performance of sows during their first two parities. *Journal of Animal Science* **72**, 1754–1760.
Michel P & Rérat A (1998) Effect of adding sugar beet fibre and wheat bran to a starch diet on the absorption kinetics of glucose, amino-nitrogen and volatile fatty acids in the pig. *Reproduction Nutrition Development* **38**, 49–68.
National Research Council (1998) *Nutrient Requirement of Swine*, 10th revised ed. Washington, DC: National Academy Press.
Noblet J, Close WH, Heavens RP & Brown D (1985) Studies on the energy metabolism of the pregnant sow. 1. Uterus and mammary tissue development. *British Journal of Nutrition* **53**, 251–265.
Noblet J, Dourmad JY, Dividich Jl & Dubois S (1989) Effect of ambient temperature and addition of straw or alfalfa in the diet on energy metabolism in pregnant sows. *Livestock Production Science* **21**, 309–324.
Noblet J, Dourmad JY & Etienne M (1990) Energy utilization in pregnant and lactating sows: modeling of energy requirements. *Journal of Animal Science* **68**, 562–572.
Noblet J & Etienne M (1987) Metabolic utilization of energy and maintenance requirements in pregnant sows. *Livestock Production Science* **16**, 243–257.
Noblet J, Dourmad JY, Etienne M & Le Dividich J (1997) Energy metabolism in pregnant sows and newborn pigs. *Journal of Animal Science* **75**, 2708–2714.
Noblet J & Perez JM (1993) Prediction of digestibility of nutrients and energy values of pig diets from chemical analysis. *Journal of Animal Science* **71**, 3389–3398.
Noblet J & Shi XS (1993) Comparative digestibility of energy and nutrients in growing pigs fed ad libitum and adult sows fed at maintenance. *Livestock Production Science* **34**, 137–152.
Noblet J, Shi XS & Dubois S (1993*a*) Metabolic utilization of dietary energy and nutrients for maintenance energy requirements in sows: basis for a net energy system. *British Journal of Nutrition* **70**, 407–419.
Noblet J, Shi XS & Dubois S (1993*b*) Energy cost of standing activity in sows. *Livestock Production Science* **34**, 127–136.
Rainbird AL & Low AG (1986) Effect of various types of dietary fibre on gastric emptying in growing pigs. *British Journal of Nutrition* **55**, 111–121.
Ramonet Y, Meunier-Salaün MC & Dourmad JY (1999) High fiber diets in pregnant sows: digestive utilization and effects on the behavior of the animals. *Journal of Animal Science* **77**, 591–599.
Ramonet Y, Robert S, Aumaître A, Dourmad JY & Meunier-Salaün MC (2000) Influence of the nature of dietary fibre on the digestive utilisation, some metabolite and hormonal profiles and the behaviour of pregnant sows. *Animal Science* **70**, 275–286.
Rérat A (1996) Influence of the nature of carbohydrate intake on the absorption chronology of reducing sugars and volatile fatty acids in the pig. *Reproduction Nutrition Development* **36**, 3–19.
Robert S, Matte JJ, Farmer C, Girard CL & Martineau G-P (1993) High-fiber diets for sows: Effects on stereotypes and adjunctive drinking. *Applied Animal Behaviour Science* **37**, 297–309.
Scalfi L, Coltorti A, D'Arrigo E, Carandente V, Mazzacano C, Palo Md & Contaldo F (1987) Effect of dietary fibre on postprandial thermogenesis. *International Journal of Obesity* **11**, 95–99.
Schrama JW, Bosch MW, Verstegen MWA, Vorselaars AHPM, Haaksma J & Heetkamp MJW (1998) The energetic value of nonstarch polysaccharides in relation to physical activity in group-housed, growing pigs. *Journal of Animal Science* **76**, 3016–3023.
Shi XS & Noblet J (1993*a*) Contribution of the hindgut to digestion of diets in growing pigs and adult sows: effect of diet composition. *Livestock Production Science* **34**, 237–252.
Shi XS & Noblet J (1993*b*) Digestible and metabolizable energy values of ten feed ingredients in growing pigs fed ad libitum and sows fed at maintenance level; comparative contribution of the hindgut. *Animal Feed Science and Technology* **42**, 223–236.
Stanogias G & Pearce GR (1985*a*) The digestion of fibre by pigs. 1. The effects of amount and type of fibre on apparent digestibility, nitrogen balance and rate of passage. *British Journal of Nutrition* **53**, 513–530.
Stanogias G & Pearce GR (1985*b*) The digestion of fibre by pigs. 2. Volatile fatty acid concentrations in large intestine digesta. *British Journal of Nutrition* **53**, 531–536.
Steiner EC, Rey TD & McCroskey PS (1990) *Simusolv – Modelling and Simulation Software*. Midland, MI: The Dow Chemical Company.
van den Brand H, Soede NM, Schrama JW & Kemp B (1998) Effects of dietary energy source on plasma glucose and insulin concentrations in gilts. *Journal of Animal Physiology and Animal Nutrition* **79**, 27–32.
van Milgen J, Noblet J, Dubois S & Bernier JF (1997) Dynamic aspects of oxygen consumption and carbon dioxide production in swine. *Bristish Journal of Nutrition* **78**, 397–410.
Van Soest PJ, Robertson JB & Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and non starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597.
Vestergaard EM & Danielsen V (1998) Dietary fibre for sows: effects of large amounts of soluble and insoluble fibres in the pregnancy period on the performance of sows during three reproductive cycles. *Animal Science* **68**, 355–362.