The Influence of Different Fiber and Starch Types on Nutrient Balance and Energy Metabolism in Growing Pigs

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ABSTRACT : A repeated 4×4 Latin square design was conducted with eight ileal cannulated castrates to examine the effect of source of starch and fiber on nutrient balance and energy metabolism. Pigs were fed on one of the four experimental diets: Control diet (C) mainly based on cooked rice; and diets P, S and W with the inclusion of either raw potato starch, sugar beet pulp or wheat bran supplementation, respectively. With the exception of an increased ($p<0.05$) energy loss from methane production with diet S observed, no significant differences ($p>0.05$) in the ratio of metabolizable energy (ME)/digestible energy, the utilization of ME for fat deposition and for protein deposition, energy loss as hydrogen and urinary energy were found between diets. The efficiency of utilization of ME for maintenance was lower ($p<0.05$) with diets P and S than with diet C. The inclusion of fiber sources (sugar beet pulp or wheat bran) or potato starch reduced the maintenance energy requirement. The fecal energy excretion was increased ($p<0.05$) with either sugar beet pulp or wheat bran supplementation, while it was unaffected ($p>0.05$) by addition of potato starch. In comparison with diets C and P, a lowered ileal or fecal digestibility of energy with diets S and W was observed ($p<0.05$). Feeding sugar beet pulp caused increased ($p<0.05$) daily production of methane and carbon dioxide and consequently increased energy losses from methane and carbon dioxide production, while it did not influence the daily hydrogen production ($p>0.05$). An increased ($p<0.05$) proportion of NSP excreted in feces was seen by the supplementation of wheat bran. Higher NSP intake caused an increased daily amount of NSP in the ileum, but the ileal NSP proportion as a percentage of NSP intake was unaffected by diets. Feeding potato starch resulted in increased daily amount of starch measured in the ileum and the proportion of ileal starch as a percentage of starch intake, while no significant influence on fecal starch was found. Higher ($p<0.05$) daily amount of fecal starch and the proportion of fecal starch as a percentage of starch intake were found with fiber sources supplementation compared with diets C and P. By increasing the dietary NSP content the fecal amount of starch increased ($p<0.01$). *(Asian-Aust. J. Anim. Sci. 2004. Vol 17, No. 2 : 263-270)*

Key Words : Energy Metabolism, Dietary Fiber, Potato Starch, Rice, Growing Pigs

INTRODUCTION

The future of the pig industry will depend on the ability of this species to compete with humans for the available food supply. As human demand for conventional high-energy cereals progressively increases, alternative feed resources will be used increasingly for livestock production. Alternative feed resources include milling and distillery by-products as well as forages. Wheat by-products and maize by-products are acceptable energy sources for pig. The potential of forages as energy sources for pig depends considerably on such factors as cell wall content, degree of microbial fermentation in the large intestine and extent of absorption and utilization of the volatile fatty acids produced (Pond, 1987).

Plant materials are rich sources of carbohydrates. Dietary carbohydrates consist of a diverse group of substances with various fates in the entire gastrointestinal

tract and physiological properties of differing importance to animal health. Dietary fiber (DF) has been defined as the complex macromolecular substances in food plants that are not degraded by mammalian digestive enzymes (Bach Knudsen, 2001). With the exception of lignin, all of the materials called DF are carbohydrates in nature (Kritchevsky, 1988). DF is thought to mediate protective effects on the colonic epithelium through their fermentation products and fecal bulking capacity (Bach Knudsen and Hansen, 1991; Wang et al., 2002; Wang et al., 2003a, b). In addition, Zhu et al. (2003) reported that feeding high fiber resulted in a lowered rate of lipogenesis and a tendency of an increased capacity to utilize acetyl-CoA in pigs. Non-starch polysaccharides (NSP) are the carbohydrate components of DF and are the predominant substrates for anaerobic fermentation. NSP can, to a certain degree, be broken down by the microflora permanently colonizing the gastrointestinal tract and their breakdown in all non-ruminants including human and pig mainly occurs in the hindgut by microbial fermentation (Jensen, 1990; Jørgensen et al., 1996; Wang et al., 2003a). High concentrations of bacteria can be found in the hindgut of pigs and the density of culturable bacteria in the colon is $10^{10\text{-}11}$ CFU/g digesta (Jensen, 1988; Jensen and Jørgensen, 1994; Wang et al., 2003b), consisting of more than 500 different species, of which only few have been described in detail (Moore et al.,

Table 1. Ingredients and chemical composition of experimental diets (air dry basis)

Diet[a]	C	P	S	W
Ingredients (g/kg)				
Wheat bran	-	-	-	194.1
Sugar beet pulp	-	-	118.4	-
Potato starch	-	94.0	-	-
Cooking rice	769.6	693.3	661.0	612.0
Fishmeal	87.8	84.6	88.8	80.9
Soya bean meal	39.0	37.6	39.5	38.8
Casein	48.8	47.0	49.3	29.1
Cellulose	9.8	9.4	9.9	9.7
Vegetable oil	29.3	18.8	19.7	19.4
Wheat	7.8	7.8	6.1	8.5
Dicalcium phosphate	2.6	2.4	2.4	2.5
Vitamin/mineral mixture [c]	2.0	1.9	2.0	1.9
NaCl	2.0	2.0	2.0	2.0
Chromic oxide (marker)	1.3	1.2	1.2	1.1
Chemical composition (g/kg DM)				
S-NSP[b]	8.7	9.2	47.2	13.5
I-NSP[b]	34.0	31.0	68.3	93.0
NSP[b]	42.7	40.2	115.5	106.5
Klason lignin	11.7	8.3	15.5	17.7
Dietary fiber	54.4	48.5	131.0	124.2
Starch	606.3	626.1	522.2	521.5
Ash	37.5	34.4	40.6	44.8
Gross energy (MJ/kg DM)	19.0	19.0	19.0	19.1
Protein (Nx6.25)	198.8	191.9	191.3	190.0
HCl-fat	47.2	45.8	47.8	53.8

[a] C, control; P, potato starch; S, sugar beet pulp; W, wheat bran.
[b] S-NSP, soluble non-starch polysaccharides; I-NSP, insoluble non-starch polysaccharides; NSP, non-starch polysaccharides.
[c] Supplied (/kg diet): retinol acetate 1,720 μg; cholecalciferol 25 μg; dl-α-tocopherol acetate 60 mg; menadione 2.2 mg; thiamine 2.2 mg; riboflavin 4 mg; D-pantothenic acid 11 mg; pyridoxine 3.3 mg; niacin 22 mg; biotin 60 μg; cyanocobalamin 0.02 mg; 50 mg Fe as $FeSO_4 \cdot 7H_2O$; 80 mg Zn as ZnO; 27.72 mg Mn as Mn_3O_4; 20 mg Cu as $CuSO_4.5H_2O$; 198 μg I as KI; 300 μg Se as Na_2SeO_3.

1987). The hindgut is the major site for microbial fermentation in non-ruminant species (Breves and Stück, 1995), although, to a lesser extent, microbial metabolism may also occur in the upper gastrointestinal tract (Bergman, 1990). The hydrolytic digestive function in the large intestine of pig, human and other non-ruminants is carried out by the anaerobic bacteria flora in the hindgut (Moore et al., 1987).

From a nutritional point of view, starch can be divided into three fractions: Rapidly digestible starch (RDS), slowly digestible starch (SDS) and resistant starch (RS). RDS and SDS can be digested completely in the small intestine, while RS is resistant to digestive enzymes (Englyst et al., 1996). Potato starch belongs to the RS type. Freshly cooked rice, which is thought to be rapidly and completely digested in the small intestine, belongs to the RDS type in this case (Wang et al., 2002). Starch that is resistant to degradation in the small intestine will pass into the large intestine, where it may act in a similar manner to the NSP fraction. Some NSP

cause a reduced gastrointestinal tract transit time and also an increased stool output (Bach Knudsen et al., 1993), and there are various mechanisms proposed to explain these effects. One suggestion is that the carbohydrates escaping digestion in the small intestine act as the main substrates of carbon and energy to the colonic microbial fermentation action (Macfarlane and Macfarlane, 1993), stimulating microbial growth and increasing bacterial cell mass (Stephan and Cummings, 1980) and generating fermentation end-products such as short-chain fatty acids (SCFA) and gases (H_2, CO_2, CH_4) (Fleming et al., 1983). These end-products are of particular interest to animal and human nutrition because of the interactions with the host in a variety of ways and contribute to many metabolic processes. The SCFA produced are rapidly absorbed from the gut lumen and subsequently utilized by the host animal as substrates of energy metabolism and can provide a substantial amount of the metabolizable energy (Cummings and Macfarlane, 1991; Macfarlane and Macfarlane, 1993; Jørgensen et al., 1996). Earlier studies performed in pigs by Steven et al. (1980) and Bugaut (1987) indicated that the energy contribution of SCFA to the basal metabolic rate is 30-76%. Also Latymer and Low (1984) reported that over 90% of ^{14}C labeled-acetic acid as injected into the caecum of pigs was absorbed and metabolized by the host animal.

The aim of the present research was to investigate the influence of two starch sources (cooked rice (C) and raw potato starch (P)) and of two fiber sources (sugar beet pulp (S) and wheat bran (W)) on balance of NSP and starch, as well as on energy metabolism in growing pigs.

MATERIALS AND METHODS

The experiment with castrates was performed at the Danish Institute of Agricultural Sciences, Foulum, Denmark. The experimental protocol with the guide for the care and use of animals was in accordance with the guidelines established by the Danish Ethical Commission.

A total of eight healthy crossbred (Danish Landrace×Yorkshire) male castrated pigs, with an average initial body weight (BW) of 30 kg, were used in the current study. Surgery was performed at 33-35 kg BW and all pigs were fitted with a permanent 'T' cannula placed in the ileum approximately 150 mm anterior to the ileo-caecal valve. Following surgery, the pigs were placed individually in 4 m^2 smooth-walled pens with a concrete floor and allowed a 2 week recuperation period.

Rice was cooked (1 atm, 121°C, 20 min) with water in a 1:2 ratio in the early morning every day. The four experimental diets (Table 1) based on freshly cooked rice were as follows: a control diet (C); a diet with addition of raw potato starch (P); a diet with a high content of soluble fibre based on dried sugar beet pulp (S) and a diet with a

Table 2. Live weight (LW) and feed intake (FI) during the balance periods

	Diet*			
	C	P	S	W
Period I				
LW, kg	33	30	32	32
FI, kg DM/d	1.22	1.28	1.46	1.45
Period II				
LW, kg	40	47	45	45
FI, kg DM/d	1.42	1.82	1.81	1.83
Period III				
LW, kg	63	57	55	60
FI, kg DM/d	1.87	1.93	1.81	2.19
Period IV				
LW, kg	69	72	72	68
FI, kg DM/d	1.95	2.29	2.40	2.19

* For details, see Table 1.

high content of insoluble fibre based on the wheat bran (W). Fishmeal, casein and soybean meal were used as protein sources. In the present study, the various types of starch for freshly cooked rice and raw potato starch were measured by controlled enzymic hydrolysis and determination of the released glucose using glucose oxidase as described by Englyst et al. (1992). The values of RDS, SDS, RS and total starch expressed as a percentage of the dry matter for freshly cooked rice were 71, 13.5, 0.5 and 85%, respectively. For raw potato starch, the corresponding values were 9, 12, 75 and 96%, respectively. As an internal marker to measure the digestibility, diets C, P, S and W contained 1.3, 1.2, 1.2 and 1.1 g Cr_2O_3/kg feed, respectively. According to bodyweight of pigs, the daily feed allowance was provided in three equal meals at 0700, 1500 and 2300, respectively (Table 2), and water was freely available at all times.

The experiment was carried out in a repeated 4×4 Latin square design with eight castrates fed on one of the four diets, with experimental periods of 15 d, comprising 7 d of adaptation to each diet, followed by 3 d of quantitative collection of feces and urine, 3 d of collection of ileal digesta, 2 d of recording gas exchange in four consecutive periods. In the adaptation and the collection periods the pigs were housed individually in 4 m^2 smooth-walled pens with a concrete floor and individual stainless steel metabolic cages, respectively. Ileal digesta samples were totally collected for 12 h, comprising 0900-1100 and 1300-1500 on day 13, 0800-1000 and 1200-1400 on day 14, and 0700-0900 and 1100-1300 on day 15. Feces were collected every 6 h daily on day 10-12, frozen and stored at -20°C and mixed thoroughly before sampling for analysis. The ileal digesta were collected on ice, frozen immediately after collection, stored at -20°C and mixed thoroughly for further analysis. Urine was quantitatively collected for three days and aliquot samples frozen until analysis. The gas exchange was measured over periods of 24 h on pigs placed in separate chambers as described by Jørgensen et al. (1996).

The concentrations of O_2, CO_2 and CH_4, temperature, relative humidity, and rate of flow from each chamber were recorded automatically on-line every second minute, from which the composition of the gas was measured fifteen times per h.

All analyses were performed in duplicates. Dry matter (DM) contents of feed samples, digesta and feces were determined by drying at 105°C for 20 h to constant weight. Crude protein (CP; N×6.25) was determined in a Kjell-Foss 1620 autoanalyser (Foss Electric A/S, Denmark) by the Kjeldahl method. The gross energy content was measured with an adiabatic bomb calorimeter (IKA Calorimeter C 400; Janke and Kunkel, Germany). Ash was analysed according to the Association of Official Analytical Chemists (AOAC method 942.05, 1990). Fat (HCl-fat) was extracted with diethyl ether after acid hydrolysis (Stoldt, 1952). Cr_2O_3 was determined according to Fenton and Fenton (1979). Starch was measured as described by Bach Knudsen (1997). Total NSP and constituent sugars were determined as alditol acetates by GLC, uronic acids by colorimetry and Klason lignin by gravimetry as described by Bach Knudsen (1997). Cellulose was determined as the difference in NSP-glucose content obtained for total NSP and that obtained after hydrolyzing starch-free residues directly with 2 M H_2SO_4. Dietary fiber is calculated as the sum of total NSP and Klason lignin.

All calculations of gas exchange were performed on the mean of 24 h respiration measurements and carried out on a group basis with eight pigs per group. The average daily heat production was calculated from gas exchange measurements according to Brouwer (1965). Both the respiratory quotient (RQ) and carbon-nitrogen (CN) balance methods were used to calculate heat production (Christensen et al., 1988). Metabolizable energy (ME) includes energy losses from urine and CH_4. Energy lost in urine was calculated from urinary nitrogen using the value of 40.8 KJ/g of urinary nitrogen (Hoffmann and Klein, 1980). Results are presented as mean values and root mean square error (RMSE). The results were tested statistically in an analysis of variance test using a General Linear Model (GLM) procedure. If no significant differences were found between periods, the results from different periods were pooled. When significant overall differences were found, pairwise comparisons between treatment groups were made in a Least Square Means (LSMeans) test and the results indicated in the tables. All statistical tests were performed on a computerized statistical software package (SAS, 1990).

RESULTS

The pigs were in good health and none of them was removed throughout the experiment.

There were no significant differences (p>0.05) in the

Table 3. Energy utilization fed on the experimental diets (n=8)

Diet [a]	C	P	S	W	RMSE	P [b]
Energy % of DE as						
ME	96.82	96.92	96.47	96.49	0.73	ns
Urine	2.73	2.56	2.68	3.06	0.67	ns
CH_4	0.29^a	0.38^a	0.63^b	0.38^a	0.15	*
H_2	0.11	0.09	0.06	0.09	0.08	ns
Utilization of ME as						
HP(RQ)/ME	0.52^a	0.49^b	0.48^b	0.51^{ab}	0.03	*
HP(CN)/ME	0.61	0.57	0.57	0.59	0.05	ns
Maintenance/ME	0.23^a	0.20^b	0.20^b	0.21^b	0.01	**
RE/ME	0.41	0.45	0.45	0.43	0.05	ns
Net energy/ME	0.63	0.64	0.65	0.64	0.04	ns
% of RE as						
RE-fat	61.76	68.44	68.72	69.52	8.20	ns
RE-protein	38.24	31.56	31.28	30.48	8.20	ns

DE, digestible energy; ME, metabolizable energy; HP, heat production; Maintenance, 336 KJ/kg metabolic body weight ($kg^{0.75}$, Just et al., 1983); RE, retained energy; RE-fat, retained energy in fat (39.8 KJ/g); RE-protein, retained energy in protein (23.9 KJ/g).
Values in the same row with different superscript letters were significantly different (p<0.05).
[a] For details, see Table 1. [b] ns, p>0.05, * p<0.05, ** p<0.01.

Table 4. Energy balance in pigs fed on the experimental diets (n=8)

Diet [a]	C	P	S	W	RMSE	P [c]
DM intake, kg/d	1.62^a	1.82^b	1.88^b	1.92^b	0.12	**
GE [b] intake, MJ/d	30.82^a	34.65^b	35.72^b	36.69^b	2.33	**
DE intake, MJ/d	29.27^a	32.81^b	32.83^b	31.79^b	2.11	*
ME intake, MJ/d	28.33^a	31.78^b	31.68^b	30.62^b	2.06	*
Fecal energy, MJ/d	1.55^a	1.84^a	2.89^b	4.90^c	0.53	*
Urine energy, MJ/d	0.82	0.88	0.91	1.02	0.24	ns
CH_4 energy, MJ/d	0.09^a	0.13^a	0.23^b	0.13^a	0.06	**
H_2 energy, MJ/d	0.03	0.02	0.02	0.02	0.02	ns
HP(RQ), MJ/d	14.47	15.26	14.80	15.42	0.70	ns
HP(CN), MJ/d	16.92	18.10	17.65	17.66	0.93	ns
RE, MJ/d	11.41	13.68	14.03	12.96	2.11	ns
RE-fat, MJ/d	7.34	9.73	9.84	9.28	2.27	ns
RE-protein, MJ/d	4.07	3.96	4.19	3.68	0.92	ns
Net Energy, MJ/d	17.80	20.08	20.41	19.34	2.21	ns
Ileal energy digestibility coefficient	0.88^a	0.86^a	0.79^b	0.78^b	0.02	***
Fecal energy digestibility coefficient	0.95^a	0.94^a	0.92^b	0.86^c	0.01	***

Values in the same row with different superscript letters were significantly different (p<0.05).
[a] For details, see Tables 1 and 3. [b] GE, gross energy. [c] ns, p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

ratio of metabolizable energy (ME)/digestible energy, energy loss as H_2 and energy voided in urine (Table 3), whereas an increased (p<0.05) energy loss as CH_4 in pigs fed on diet S was found.

As compared with diet C, heat production as a proportion of ME and the ratio of maintenance/ME were lower (p<0.05) with diets P and S according to the RQ method. No significant differences (p>0.05) in the utilization of ME for fat deposition and for protein deposition between the experimental diets were observed.

Higher daily gross energy (GE), DE and ME intake in pigs fed on diets P, S and W than in those fed on diet C were measured (p<0.05) (Table 4). Feeding fiber sources (sugar beet pulp or wheat bran) resulted in an increased (p<0.05) fecal energy excretion, while it was unaffected (p>0.05) by addition of potato starch.

Feeding fiber sources (sugar beet pulp and wheat bran) and potato starch tended to increase the daily heat production either according to the RQ (p=0.070) or the CN (p=0.141) methods. The daily energy retention of fat was higher (p<0.05) with diet S than with diet C, while no significant difference (p>0.05) in the daily energy retained in protein was found between these two diets.

As compared with diets C and P, a lowered ileal or fecal digestibility of energy with diets S and W was observed (p<0.05). Feeding sugar beet pulp caused increased (p<0.05) daily production of methane and carbon dioxide, while it have unaffected the daily hydrogen production (p>0.05) (Table 5).

A higher (p<0.05) daily amount of fecal NSP with diets S and W compared with diet C was observed (Table 6). While feeding wheat bran resulted in an increased (p<0.05)

Table 5. Amount of methane, carbon dioxide and hydrogen expired and oxygen consumed in pigs fed on the experimental diets (n=8)

Diet [a]	C	P	S	W	RMSE	P [b]
CH_4 expired, L/d	2.3[a]	3.3[a]	5.7[b]	3.2[a]	1.45	**
H_2 expired, L/d	2.7	2.1	1.5	1.9	1.55	ns
CO_2 expired, L/d	790[a]	852[b]	837[b]	819[ab]	32.9	**
O_2 consumed, L/d	656	687	664	708	40.1	ns

Values in the same row with different superscript letters were significantly different (p<0.05). [a] For details, see Table 1. [b] ns, p>0.05, ** p<0.01.

Table 6. Flow/balance of non-starch polysaccharides (NSP) and starch in pigs fed on the experimental diets (n=8)

Diet [a]	C	P	S	W	RMSE	P [b]
NSP						
NSP intake, g/d	69.2[a]	72.6[a]	216.4[b]	205.5[b]	24.51	***
NSP in ileal digesta, g/d	58.2[a]	59.0[a]	187.7[b]	190.3[b]	23.06	***
NSP in ileum, % intake	84.8	82.2	87.0	93.4	8.95	ns
NSP in feces, g/d	9.8[a]	14.0[ab]	23.3[b]	93.5[c]	9.36	***
NSP in feces, % intake	14.6[ab]	20.9[b]	11.0[a]	45.8[c]	5.81	***
Starch						
Starch intake, g/d	1,078.5	1,090.3	1,072.5	1,041.3	82.10	ns
Starch in ileal digesta, g/d	15.3[a]	51.9[b]	17.2[a]	13.4[a]	15.11	*
Starch in ileum, % intake	1.4[a]	4.5[b]	1.7[a]	1.2[a]	0.98	**
Starch in feces, g/d	0.4[a]	0.4[a]	0.7[b]	1.1[c]	0.14	**
Starch in feces, % intake	0.03[a]	0.04[a]	0.06[b]	0.10[c]	0.01	**

Values in the same row with different superscript letters were significantly different (p<0.05).
[a] For details, see Table 1. [b] ns, p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

proportion of NSP excreted in feces, the decreased (p<0.05) ratio of fecal NSP/NSP intake was seen with sugar beet pulp supplementation. Higher NSP intake caused an increased daily amount of NSP in the ileum, but the ileal NSP proportion as expressed in percentage of NSP intake was unaffected (p>0.05) by diets.

Feeding potato starch resulted in increased (p<0.05) daily amount of starch measured in the ileum and the proportion of ileal starch in percentage of starch intake, while no significant influence on fecal starch was observed (p>0.05). Higher daily amount of fecal starch and the proportion of fecal starch in percentage of starch intake were found with fiber sources supplementation compared with diets C and P (p<0.05).

DISCUSSION

The proportion of starch in the terminal ileum in percentage of starch intake is very low (1.2-4.5), in good agreement with previous findings indicating that starch digestion was almost complete in the small intestine irrespective of diet (Just, 1982; Lindberg and Cortova, 1995; Phuc and Lindberg, 2000; Wang et al., 2002). The present study indicated that no significant differences in the daily starch intake between diets were observed, however a higher daily amount of starch in the terminal ileum with inclusion of raw potato starch was found as compared with the others (52 vs. on average 15 g). This suggests that the type of starch is responsible for its utilization, and the lower starch digestion in the small intestine should be explained by the structural differences between the RDS- (freshly

cooked rice) and RS-type starch (raw potato starch). However, starch digestion in the small intestine was uninfluenced by the inclusion of either soluble (sugar beet pulp) or insoluble dietary fiber (wheat bran). Furthermore, the great difference in the size of starch granules between cooked rice and raw potato starch could have affected starch digestion in the small intestine. Starch digestion in the large intestine was unaffected by the inclusion of raw potato starch, while feeding fiber sources (sugar beet pulp or wheat bran) caused the reduced degradation of starch in the large intestine. This suggested that the digestion of starch was completed as a result of the microbial activity in the large bowel and was independent of the type of starch. In agreement with the current study, Tomlin and Read (1990) reported that RS might act in a similar manner to the unabsorbed NSP, which could be degraded by the microflora in the hindgut (Moore et al., 1987).

In the current study, the NSP degradation in the hindgut was unaffected by addition of raw potato starch or soluble dietary fiber (sugar beet pulp), while the inclusion of insoluble fibrous constituents like wheat bran resulted in a lowered degradation of NSP in the large intestine. This suggested that a depression of microbial metabolism took place with the inclusion of wheat bran, which could be related to a faster transit time, a reduction in microbial activity or a physical hindrance of degradation (Graham et al., 1986).

In the current study, feeding soluble dietary fiber (sugar beet pulp) resulted in increased fermentation end-products such as methane and carbon dioxide, suggesting that soluble fiber source caused an increase in microbial activity in the

intestinal tract, and consequently more fermentation end-products including gases could be achieved through microbial fermentation. In general, of energy supply two physiologically and energetically different pathways called pre-caecal and post-ileal digestion exist in pigs, and the energetic influence of dietary energy arising from microbial fermentation is expected to be lower than that of carbohydrates absorbed as monosaccharides in the small intestine (Dierick et al., 1989). The difference results from additional losses as methane, hydrogen and fermentation heat and from a lower efficiency of the utilization of volatile fatty acids in the intermediary metabolism. Dierick et al. (1989) reported that approximately 41-66% of the energy value of carbohydrate digested in the large intestine of pigs is lost as heat in the fermentation processes and as methane and heat during the conversion to volatile fatty acids and then to body tissues. In contrast, only 25-30% of its energy value digested in the small intestine is lost as heat during the conversion to body tissues.

The present study clearly demonstrated that the daily amount of fecal energy was increased by the inclusion of fiber sources (sugar beet pulp or wheat bran). This implies that dietary fiber effects on energy utilization could be observed by an increased energy output in feces, mainly due to a high content of lignin in the fiber supplemented diets (16 and 18 g/kg DM with diets S and W, respectively).

Influence of diet composition on energy expenditure partly stems from energy losses from hydrogen, carbon dioxide and methane production, and heat production during the microbial fermentation. In the present study daily amount (1.5-2.7 L/d) of and energy loss (0.06-0.11%) from hydrogen production in percentage of DE intake were rather low and unaffected by addition of either fiber sources or potato starch. This suggests that energy loss from hydrogen production, which is normally considered to be of minor importance in total energy metabolism, is small and hardly affects energy expenditure (Jørgensen et al., 1996). In contrast, several studies have shown that the measurement of hydrogen production could be used to quantify the extent of microbial fermentation within the gastrointestinal tract (Wolever et al., 1986; Jensen and Jørgensen, 1994; Jørgensen et al., 1996). The results from the current study indicated that the ratio of maintenance/ME, that is the efficiency of utilization of ME for maintenance, decreased due to the inclusion of either fiber sources or potato starch. This suggested that feeding fiber sources or potato starch caused a lower maintenance energy requirement, which should be closely related to the concentrations of SCFA generated from the microbial fermentation in the hindgut. Friend et al. (1964) reported that volatile fatty acids could meet 15-28% of the maintenance energy requirement. Similarly, one earlier study performed by Kennelly et al. (1981) using the caecal isotope-dilution rate to evaluate

volatile fatty acid production rates has shown that 19.7% of maintenance energy could result from volatile fatty acid in pigs fed on barley-based diets, and only 10-15% in pigs fed on diets with the inclusion of different levels of alfalfa. This suggests that a lowered value (expressed as % of maintenance energy requirement) was obtained from volatile fatty acids due to the inclusion of fiber source (alfalfa). In contrast, Kass et al. (1980) suggested that volatile fatty acid could contribute 6.9, 11.3, 12.5 and 12.0% of maintenance energy requirement in pigs fed on diets containing 0, 200, 400 and 600 g alfalfa/kg, respectively.

Addition of dietary fiber or potato starch showed a lowered ratio of HP to ME and consequently a slightly increased ratio of RE to ME in the present study, indicating that in comparison to the control diet, the transformation of metabolizable energy into retained energy was more efficient in diets with dietary fiber or resistant starch supplementation. In contrast to our findings, earlier studies have shown that increasing fiber levels cause higher heat production and lower retained energy in proportion of ME (Just et al., 1983; Noblet et al., 1985), which is associated with additional energy costs of ingestion and digestion and fermentation of the large amount of organic matter. This should be explained by the fact that diets based on high level of cooked rice result in a higher digestibility of organic matter in the small intestine and thus a relatively small amount of organic matter flowing into the large intestine as compared with conventional diets.

The present study indicated that higher energy loss from methane production was found with diet S as compared with the others (0.63 vs. on average 0.35% of DE). This suggests that feeding soluble dietary fiber caused an intensively microbial fermentation and consequently a higher amount of methane from 2.9 to 5.7 L/d and carbon dioxide from 804 to 837 L/d expired with the except of hydrogen production.

In the current study the daily heat production according to either the RQ or the CN methods, daily retained energy and the utilization of ME for fat deposition tended (p<0.10) to increase with the inclusion of dietary fiber or potato starch. This can be explained by the fact that higher DM and GE intake were found in these diets.

CONCLUSION

Feeding soluble dietary fiber caused an increased daily amount of methane production and thus an additional energy loss from methane production. The pig fed on diets with the inclusion of either dietary fiber or resistant starch had a higher maintenance requirement. A higher daily DM intake resulted in a higher energy loss from feces. The decreased ileal and fecal digestibility of energy were found

in pigs fed on diets with the inclusion of dietary fiber. Feeding potato starch obviously affected the starch balance, while no significant effect on the NSP flow was observed with addition of potato starch. The inclusion of soluble dietary fiber (wheat bran) increased daily NSP excreted from feces and thus reduced the utilization of NSP by the microflora in the hindgut.

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