

# Energetic Utilization of Dietary Fiber in Pigs

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# Energetic Utilization of Dietary Fiber in Pigs

Martin Rijnen

## **Proefschrift**

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## Voorwoord

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# **Chapter 1**

## **General Introduction**

## General Introduction

### Introduction

The interest of pig nutritionists in the role of dietary fiber (DF) in animal functioning is increasing. Priority and increased demand of available high-energy cereals for direct human use world-wide and increased availability of fiber-rich co-products from human food industries have promoted an increased use of fiber-rich feed ingredients in pig nutrition (Noblet & Le Goff, 2001).

Stimulation of the development of the autochthonous microflora of pigs by specific dietary fermentable carbohydrates is one interesting possibility for the replacement of antibiotics in animal diets. This 'prebiotic' effect of dietary fermentable carbohydrates will stimulate the production of short chain fatty acids, and it may enhance 'colonization resistance' and reduce protein fermentation in the hindgut (Williams et al., 2001). Other possible benefits, such as well-being of animals, improvement of gut transit and reduction of stomach ulcers also increased the use of fiber-rich feed ingredients (Low, 1985). During the last decade, pig nutritionists and also the general public changed their attitude towards animal nutrition and production, which has increased the interest in the use of dietary fiber. Nutritionists are becoming more aware that nutrition is more than providing nutrients to animals: nutrition serves several other functions, such as the biological properties of some of its components and the resulting change in, for example, well-being of animals.

In most net energy (NE) based feed evaluation systems, energy of digestible nutrients (i.e., crude protein (CP), crude fat, starch, sugars, and dietary fiber) is used to calculate the NE content of a diet or feed ingredient (e.g., Noblet et al., 1994; CVB, 2000). Unlike starch, which is hydrolyzed by pancreatic amylase to glucose, DF is not hydrolyzed by mammalian enzymes. Dietary fiber is fermented by the gastrointestinal microflora.

In energy utilization studies, the NE content of DF fractions is derived by using digestibility data and multiplying it with the efficiency with which the absorbed products from fermentable DF (fDF) can be used for energy retention (ER). This latter is termed energy for production. Generally, utilization of energy from fDF is considered to be lower than the utilization of energy from digestible starch (Boisen & Verstegen, 2000). Therefore, in feed evaluation systems, feed ingredients with high contents of fDF have lower NE values than feed ingredients with similar levels of digestible starch (e.g., CVB, 2000).

The composition of DF fractions from different origin (e.g., in contents of pectin, cellulose, and hemicellulose) can differ widely (Wenk, 2001). Therefore, it is questionable whether a fixed value for the efficiency with which energy from fDF is utilized, is sufficient. Schrama et al. (1998), demonstrated that group-housed growing

pigs were able to use energy from fDF from sugar beet pulp silage with a similar efficiency as energy from digestible starch from tapioca. This relative high NE value of fDF from sugar beet pulp silage compared to NE values used in current feed evaluation systems, was related to a decreased energy expenditure for physical activity (i.e., activity-related heat production [AHP]). This led to an adapted NE value for sugar beet products in the Dutch feed evaluation system for pigs (CVB, 1997).

The currently used feed evaluation systems are mainly based on data from individually housed growing pigs (e.g., Noblet et al., 1994; Boisen & Verstegen, 2000; CVB, 2000). These systems assume that energy requirements for maintenance are not affected by dietary composition. In growing pigs (e.g., Schrama et al., 1996; 1998) and sows (e.g., Robert et al., 1993; Brouns et al., 1994; Ramonet et al., 2000a), however, differences in dietary composition (i.e., increased DF content) affected physical activity; with physical activity usually being considered as a part of maintenance requirements. The impact of DF content on physical activity indicates that the energy requirements for maintenance are not a constant. Housing conditions (i.e., individual vs group-housing) might play a role. Quantitative data on the effects of dietary composition and housing conditions on the energetic utilization of fDF in relation to physical activity, however, are lacking.

The investigations carried out in the present thesis mainly focused on energetic utilization of fDF. The relationship between the energetic utilization of fDF and AHP was also an important subject of the experiments. Bach Knudsen (2001), Longland & Low (2001), Mosenthin et al. (2001), Noblet & Le Goff (2001), Pluske et al. (2001), and Williams et al. (2001) have recently reviewed other actions of DF.

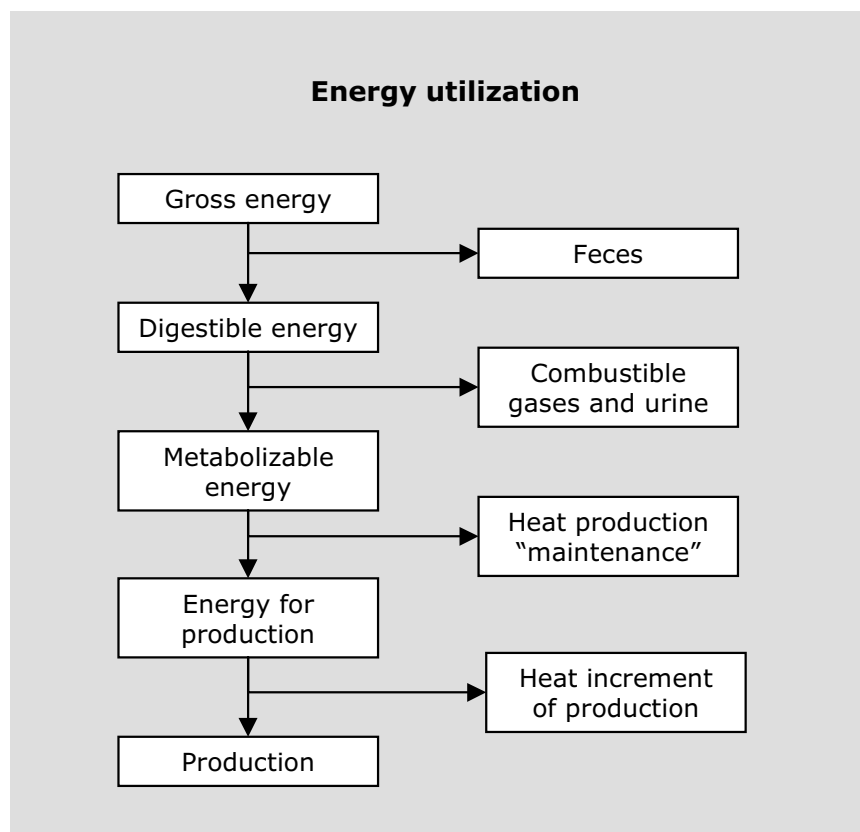
Before the hypotheses of the present thesis are described some background information is given on the Dutch feed evaluation system for pigs.

## **The Dutch Feed Evaluation System for Pigs (NE)**

Like most NE based feed evaluation systems, the Dutch feed evaluation system uses digestibility and production data to calculate the NE content of a feed ingredient. The basis of the current Dutch NE feed evaluation system is the classical description of energy utilization (Figure 1).

A diet or feed ingredient contains an amount of gross energy (GE), which is equal to the combustion heat of that diet or feed ingredient. Part of this GE will be excreted with the feces, from which the apparent fecal digestibility of energy for that diet or feed ingredient can be calculated. The remaining part is digestible energy (DE). Part of the DE will be lost with urine and combustible gases (mainly CH<sub>4</sub> and H<sub>2</sub>). The remaining part is metabolizable energy (ME). Part of the ME will be used for maintenance processes, like respiration, blood flow, muscle tone, ion balance, tissue turnover, regulation of body temperature, ingestion of feed, and physical activity

(Black, 2000). All energy used for maintenance processes will be lost as heat. The remaining part of ME can be used for production processes, like growth and milk production. This energy will be used with an efficiency of less than unity. The inefficiency part will be lost as heat (i.e., heat increment of feed intake and processing). Total heat production can be measured using direct or indirect calorimetry. The total amount of ME minus heat production for production is the NE content of a diet or feed ingredient (i.e., above maintenance).



**Figure 1.** Classical description of energy utilization.

The NE value of a feed ingredient in feed evaluation systems, like the Dutch NE system, indicates how much the energy retention of a pig will increase with an increased intake of one extra unit of that feed ingredient. Such systems are made under some assumptions:

- 1) Energy that is used for maintenance is assumed to be constant; NE being the extra ER with an extra unit of a feed ingredient or diet above maintenance.
- 2) Additional energy from a certain nutrient is used with a constant efficiency that has been established for that nutrient. This can also be phrased as the linear increase in ER with an increase in the intake of a certain digestible component (e.g., protein, lipids, sugars, starch, or dietary fiber).

The amounts of digested nutrients (i.e., digestible CP, crude fat, starch, sugars, and fermentable DF) or in other words the apparent fecal digestibilities of the nutrients

that are present in a diet or feed ingredient are the starting point of a NE based feed evaluation system. The second step of NE based feed evaluation systems is the conversion of digestible nutrients into NE (i.e., energy retention). For this conversion, fixed partial efficiencies for each nutrient are assumed. The energetic efficiencies with which the different energy yielding nutrients are utilized for production, as used in the Dutch feed evaluation system, are shown in Table 1. The partial efficiency of digestible nutrients is the ratio between the NE value and the enthalpy value of a digestible nutrient (Table 1).

The described second step of NE based feed evaluation systems covers in fact two energetic processes: conversion from DE to ME and conversion from ME to NE. The difference between DE and ME is the energy lost with combustible gases and urine. As described above, energy that is available for production (i.e., ME minus energy used for maintenance) is used with certain efficiency. The partial efficiencies resemble the conversion of ME to NE. For most nutrients this is similar to the conversion of DE to NE, except for two nutrients. First, for digestible crude protein the energy losses via the urine (i.e., nitrogen losses as urea) are included. Second, for fDF the energy losses via combustible gasses (i.e., CH<sub>4</sub> and H<sub>2</sub>) are included. In NE systems, NE values are based on regressions of extra energy retention on extra intake of digestible or metabolizable energy. Therefore, the contribution of the different nutrients to the NE value is mostly not measured individually.

**Table 1.** Values for enthalpy, net energy (NE), heat increment, and partial efficiencies for digestible nutrients as used in the Dutch feed evaluation system for pigs (CVB, 2000)

Nutrient	Enthalpy MJ/kg	NE value MJ/kg	Heat increment MJ/kg	Partial efficiency %
Crude protein	23.6	10.8	12.8	46
Crude fat	39.3	36.1	3.2	92
Sugars <sup>a</sup>	15.8	12.2	3.6	77
Starch	17.5	13.5	4.0	77
Dietary fiber	17.5	9.5	8.0	54

<sup>a</sup> Mono- and disaccharides expressed in glucose units.

In the current Dutch feed evaluation system for pigs, the assumed partial efficiency with which energy from fDF is used for energy retention is less than the partial efficiency for digestible starch. The partial efficiency for fDF is defined as 70% of the partial efficiency of digestible starch (i.e., partial efficiency of 77% for digestible starch and 54% for fDF; Table 1). This efficiency of about 70% of that of digestible starch is generally adopted (CVB, 2000; Bach Knudsen, 2001; Longland & Low, 2001; Noblet & Le Goff, 2001). This lower NE value of fDF compared with digestible starch is

based on biochemical calculations, energy evaluation studies using direct or indirect calorimetry, and infusion studies (Just et al., 1983; Noblet et al., 1994; Jørgensen et al., 1996a; 1997). There are some differences in the efficiencies of digestible nutrients among different NE evaluation systems, which are described by Boisen & Verstegen (2000). Some of these differences are related to the definition of dietary fractions. The definition of DF, as used in this thesis, is described below.

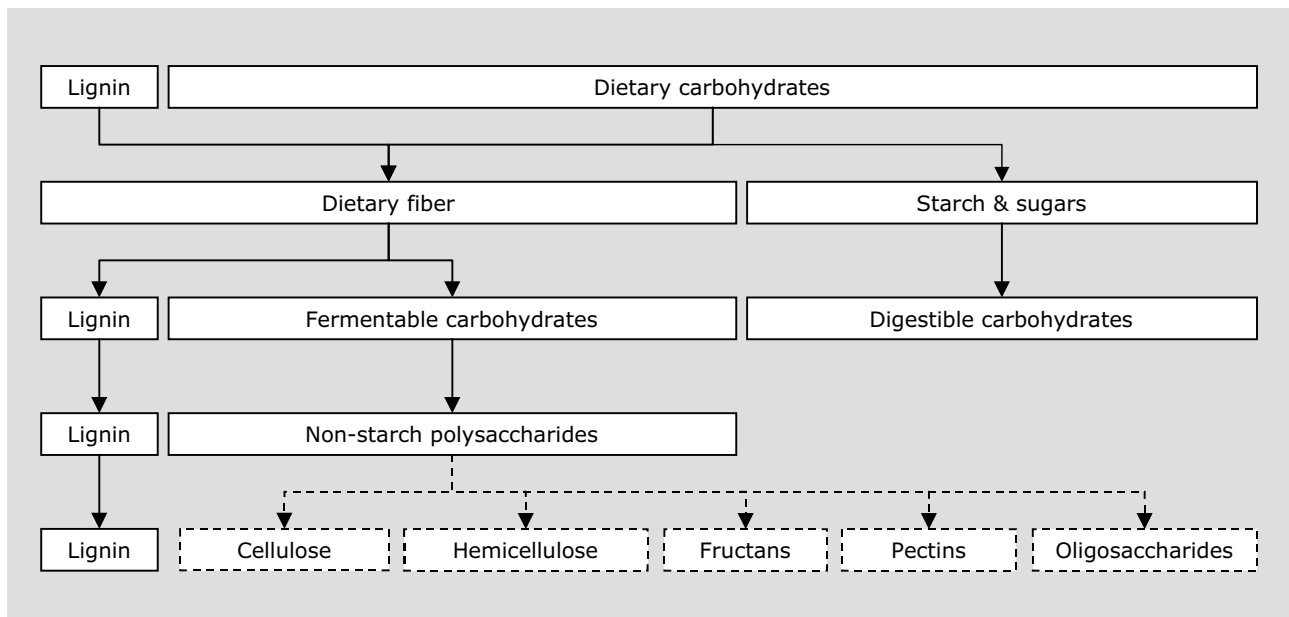
### **Definition of Dietary Fiber**

In the studies presented in this thesis, the focus was on the energetic utilization of fDF and its relation to physical activity in pigs. As described before, NE based feed evaluation systems use a fixed value for the energetic efficiency of fDF. In the Dutch feed evaluation system, for example, the energetic efficiency of fDF is 9.5 kJ/g (CVB, 2000). Because the DF fraction of a diet or feed ingredient consists of many different kinds of fermentable constituents, it is questionable whether a fixed value for the energetic efficiency applies to all fermentable constituents.

Generally, the organic matter of a diet or feed ingredient consists of CP, crude fat, carbohydrates, and occasionally volatile components, like short chain fatty acids. Pigs' enzymes will digest part of the carbohydrates (i.e., digestible carbohydrates). The remaining of the carbohydrates is resistant to hydrolysis by the digestive enzymes of pigs, but can be (partly) fermented by the micro-organisms in the pig's gut. Bach Knudsen (2001) has recently reviewed different aspects of DF and their analyses. Different definitions of the fermentable fraction of a diet or feed ingredient can be given, and are dependent on the used method for analyses or calculations (as shown in Figure 2). Usually, lignin is not considered as fermentable, but included in the DF fraction. In the studies presented in this thesis, we defined the DF fraction as fermentable carbohydrates plus lignin, calculated as follows:

$$\text{DF} = \text{DM} - (\text{crude ash} + \text{crude protein} + \text{crude fat} + \text{starch} + \text{sugars})$$

Fiber-rich feed ingredients differ widely in their fiber content, composition, and fecal digestibility. Digestibility of DF from different botanical origin has been studied extensively during the last decade. Generally, the soluble part of DF is more readily digested, whereas the insoluble part is less digestible (Noblet & Bach Knudsen, 1997; Noblet & Le Goff, 2001). Digestibility of DF also increases with the age of pigs (Fernandez & Jørgensen, 1986; Noblet & Shi, 1994; Le Goff, 2001), which may be related to an increased mean retention time of digesta in the gastrointestinal tract (Le Goff et al., 2002b).



**Figure 2.** Schematic presentation of the carbohydrate fraction of a diet.

## Physical Activity and Energy Evaluation

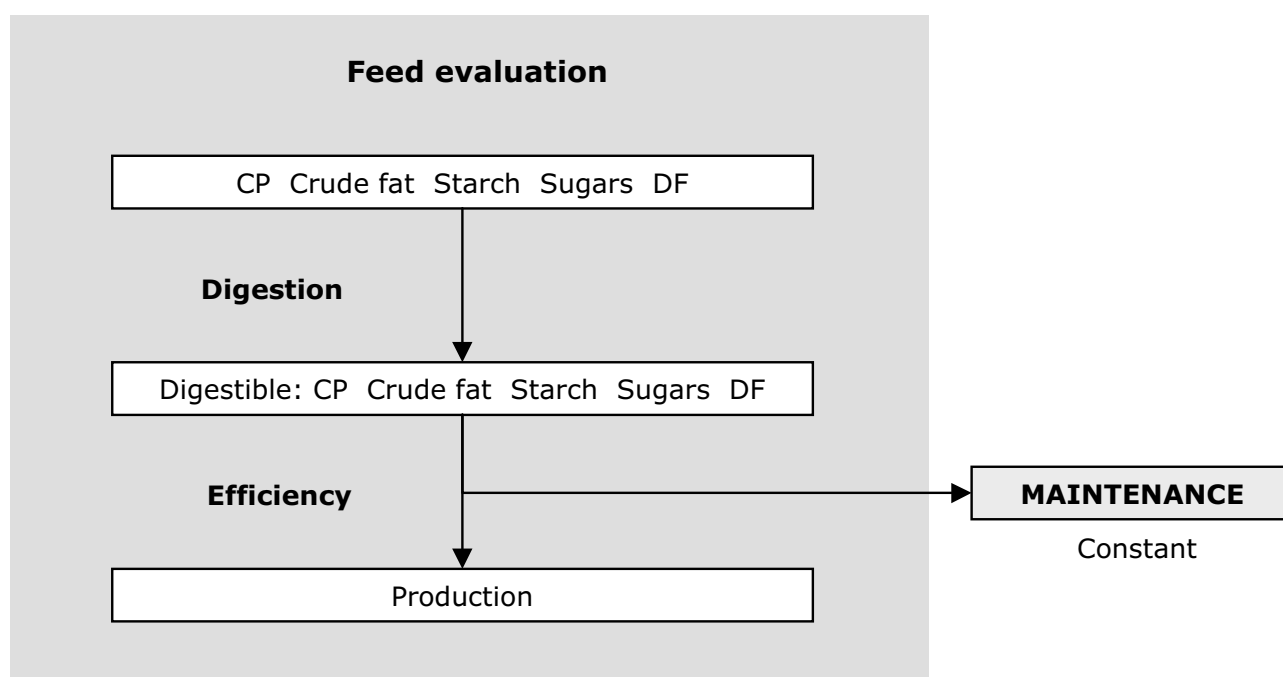
Most NE feed evaluation systems assume that the energy requirements for maintenance are a constant (Figure 3). Major energy-demanding processes for maintenance of an animal include those associated with blood flow, respiration, muscle tone, ion balance, tissue turnover, control of body temperature, resistance to disease, and those associated with the ingestion of feed and physical activity. All energy used for maintenance processes can be measured as heat production. Total heat production also includes heat production due to the inefficiency of production.

Energy spend on physical activity can vary between 5 and 28% of total energy expenditure for maintenance processes (several authors, as cited by Grieshop et al., 2000). Aspects related to the animal, its environment as well as feeding level can affect the amount of energy that is spent on physical activity (Jakobsen et al., 1994).

Some animal related factors that might affect AHP are genotype, age, sex, and coping-style. Susenbeth & Menke (1991), for example, reported indications that the percentage of body fat was negatively correlated with AHP. There was, however, some confounding with feeding level, because with an increased feeding level, differences between genetic lines decreased. Verstegen et al. (1982) and Nienaber et al. (1985) reported that AHP decreased when weight ( $\approx$  age) of pigs increased. In addition, Noblet et al. (1993) reported that the energy cost of physical activity is much higher in pigs ( $416 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) than in sheep, cattle, poultry, and rats (94, 55, 120, and 35  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , respectively). The reason for these species differences is not clear.

Some environmental factors, which can affect AHP, are housing conditions, ambient temperature, disease, and stress. From comparing data from Noblet et al. (1998) and

Verstegen et al. (1982), it seems that individual housed pigs spend less time (i.e., energy) on physical activity than group-housed pigs. This might be due to the fact that pigs that are housed individually in metabolic crates or respiration chambers have less room for physical activity than group-housed pigs. Individually housed animals have no room for walking or interaction with other pigs. Quantitative data on the effects of housing conditions on AHP, however, are lacking. There are also differences in calculation procedures for measuring physical activity between studies. In addition, some studies reported a decrease in AHP when animals were exposed to disease or stress (e.g., Van Diemen et al., 1995; Gentry et al., 1997; Heetkamp et al., 1998).



**Figure 3.** Schematic presentation of a net energy feed evaluation system.

Apart from animal and environmental related factors, nutrition can also affect AHP. Halter et al. (1980) and Susenbeth & Menke (1991) reported that AHP decreased with increasing feeding levels. Quantitative data considering relationships between feeding level and AHP, however, are lacking. Diet composition can also affect AHP (e.g., Schrama et al., 1996; 1998). They reported that AHP decreased when group-housed growing pigs consumed increasing amounts of DF from sugar beet pulp silage. Schrama et al. (1998) estimated that this decrease in AHP was about 3.9 kJ/g of fDF intake. In their experiment, this was equal to about 8% of the ME requirements for maintenance. A similar decrease in AHP was found when gelatinized maize starch was replaced by raw potato starch (Schrama & Bakker, 1999). Schrama & Bakker (1999) also tested the effect of dietary bulkiness on AHP by adding milled wheat straw to the diets. They concluded that fermentation in the gastrointestinal tract was responsible for the decrease in AHP and not dietary bulkiness.



Since there is an increasing interest in fiber-rich feed ingredients for pigs, it is important to know the impact of DF, and more specifically of the different DF sources, on physical activity to improve the current NE systems for pigs.

Apart from the effects of DF intake on physical activity, other dietary components, like fat, alcohol, tryptophan, and melatonin might also affect physical activity or behavior of animals. In humans, it was reported that diet composition (fat vs carbohydrates) affected alertness, mood (Wells & Read, 1994) as well as cognitive performance (Lloyd et al., 1993). Kwakernaak (1998) reported that broilers became more quiet when dietary fat content increased. Addition of tryptophan increased the ability of pigs to handle stressful situations (Meunier-Salaun et al., 1991; Adeola & Ball, 1992). Tryptophan plays an important role in the release of serotonin in the brain of animals. An increased ratio between tryptophan and large neutral amino acids increases the amount of tryptophan that can be transported through the blood-brain barrier. An increased concentration of tryptophan in the brain increases the secretion of serotonin, which had a decreasing effect on physical activity and stress (Leathwood, 1987; Kogan et al., 1994). Adding melatonin to a broiler diet decreased AHP (Apeldoorn et al., 1999). Broilers spent 102 and 89  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  on physical activity when they were fed 0 and 40 ppm of melatonin with their diet, respectively. Other diet related factors might be feeding frequency and physical characteristics of a diet. Quantitative data on these topics, however, are lacking.

### **Some Mechanisms of Dietary Fiber**

Dietary bulkiness can affect the degree of satiety in animals and therefore affect the time (and energy) that is spent on physical activity (including eating). Schrama & Bakker (1999) concluded that dietary bulkiness had no effect on the energy expenditure on activity in growing pigs, fed at a feeding level of 2.5 times the energy requirements for maintenance. In sows, which are fed close to maintenance, however, Fraser (1975) found that the addition of straw to a diet made the sows more quiet (i.e., more time was spent lying). Feeding level is possibly an important factor in the effects of dietary bulkiness on AHP. An increased amount of feed in the stomach will stimulate receptors present in the stomach wall (Pasquali et al., 1990). For animals fed at maintenance level this is possibly more important than for animals fed at higher feeding levels. Pasquali et al. (1990) concluded that in humans the stretch receptors in the stomach wall adapt to a certain pressure caused by ingested food. Therefore, dietary bulkiness seems only to have a short-term effect on the feeling of satiety. The size of the stomach increases when more feed is ingested and therefore the stimulation of receptors in the stomach wall will diminish.

During fermentation of DF in the gastrointestinal tract, short chain fatty acids are produced by the guts' microflora. The gut wall absorbs these short chain fatty acids,

which provide the animal with energy. These short chain fatty acids can supply between 5 and 28% of the amount of energy that is requirement for maintenance (several authors, as cited by Grieshop et al., 2000). These short chain fatty acids possibly affect the behavior of an animal and thus may have biological activity. In ruminants, volatile fatty acids reduce feed intake (Forbes, 1995), and therefore possibly reduce energy spent on physical activity, because animals are less stimulated to search for feed. In non-ruminants, however, direct relationships between fermentation in the gastrointestinal tract and feed intake or feeding behavior have not been studied. If there is such a direct effect of short chain fatty acids on physical activity, this would mean that for example moisture rich co-products and fermented diets, which contain high levels of short chain fatty acids and ethanol (Scholten et al., 1999), might also affect AHP.

Furthermore, feeding of DF will result in a shift of the type of energy that is provided to the animal. Digestion of starch provides animals with glucogenic energy. Propionic acid that is formed during fermentation is also a source of glucogenic energy, whereas, butyric and acetic acid are sources of lipogenic energy. Digestible carbohydrates, like starch and sugars, will be degraded quickly after ingestion, and will provide the animal with energy soon after intake. Fermentable carbohydrates, however, will be degraded more slowly, and will therefore provide the animal with energy for a longer period after feed intake. Schrama et al. (1997) reported that heat production corrected for physical activity showed less variation, when fermentable carbohydrates were fed, compared with feeding digestible carbohydrates. Thus, it was shown that the intake of DF resulted in a more gradual uptake of dietary energy compared to the intake of digestible carbohydrates. It is, however, not clear if the pattern of energy uptake during the day has a relationship with energy spent on physical activity. The rate of digestion and the digestive products need to be known to understand the described effects.

If DF intake has direct or indirect effects on energy metabolism it might be worthwhile to change energy evaluation systems to include this information in order to have a better prediction of the NE content of a diet or feed ingredient.

## **Research Questions and Thesis Outline**

The energetic utilization of fermentable DF and its relation to physical activity was the main topic of this thesis. Schrama et al. (1998) reported a relatively high NE value of fermentable DF from sugar beet pulp silage in group-housed growing pigs. This high NE value was related to a decrease in energy expenditure for physical activity with fermentable DF in the diet. Several authors report differences in digestibility of DF between growing pigs and sows and in addition to that, it was hypothesized that similar differences in the energetic utilization of fermentable DF between adult sows

and growing pigs is present. It was also hypothesized that the effect of fermentable DF from sugar beet pulp silage on energy expenditure for physical activity was present for group-housed sows. To study these hypotheses, a dose response experiment with different dietary contents of sugar beet pulp silage was carried out using non-pregnant, non-lactating, group-housed sows. Effects on energy metabolism and the energetic utilization of fermentable dietary fiber from sugar beet pulp silage are reported in Chapter 2. In Chapter 3, effects of feeding sugar beet pulp silage on physical activity are discussed.

The effects of sugar beet pulp silage as reported by Schrama et al. (1998) might be related to DF or fermentable DF intake, or to the composition of the DF fraction. It was hypothesized that the energetic utilization of fermentable DF is dependent on the composition or botanical origin of fermentable DF. It was also hypothesized that energy expenditure for physical activity of group-housed growing pigs is related to fermentable DF intake. Therefore, a dose response experiment has been carried out with five levels of solvent-extracted coconut meal and five levels of soybean hulls to test these hypotheses. In Chapter 4, the energetic utilization of fermentable DF from solvent-extracted coconut meal and soybean hulls is reported. In Chapter 5, the effects of solvent-extracted coconut meal and soybean hulls on physical activity are discussed.

Schrama & Bakker (1999) studied the separated and combined effects of dietary bulkiness and fermentation on energy metabolism and physical activity in group-housed growing pigs. They concluded that dietary bulkiness had no effect on physical activity, whereas increased fermentation in the hindgut decreased physical activity. Increased fermentation in the hindgut increases metabolic activity of cell wall tissues. It was therefore hypothesized that dietary bulkiness and fermentation in the gastrointestinal tract have different effects on the empty weight of different parts of the gastrointestinal tract. In Chapter 6, effects of dietary bulkiness and fermentation on empty weights of the gastrointestinal tract and its different parts are reported.

Most data that are used for net energy based feed evaluation systems are derived from experiments with individually housed growing pigs. Several authors report differences in feed intake, fecal digestibilities, and growth between individually and group-housed pigs. It was hypothesized that housing conditions have an effect on the energetic utilization of fermentable DF in growing pigs. It was also hypothesized that housing conditions will affect the energy expenditure for physical activity with possible effects on the energetic utilization of fermentable DF. In the experiment described in Chapter 7, the effects of housing conditions on energy metabolism, physical activity and the energetic utilization of fermentable DF are discussed. In Chapter 8, the results of the three experiments described in this thesis are discussed. The discussion focuses on the energetic utilization of fermentable DF and possible mechanisms for the found differences, such as energy expenditure for physical activity, energy retention, and the rate of fermentation.



## **Chapter 2**

### **Effects of Dietary Fermentable Carbohydrates on Energy Metabolism in Group-Housed Sows**

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## Effects of Dietary Fermentable Carbohydrates on Energy Metabolism in Group-Housed Sows

### Abstract

The effect of dietary fiber (DF) content on the metabolic rate in group-housed sows was studied. Twelve groups of six non-pregnant sows were each fed one of the four experimental diets similar in composition except for the starch and DF content. Exchanging sugar beet pulp silage (SBPS) for tapioca created the difference in starch and DF ratio in the diet. On DM basis, diets contained 0, 10, 20, or 30% SBPS. Sows were group-housed and fed at 1.30 times the assumed maintenance energy requirements. Nitrogen and energy balances were measured per group during a 7-d experimental period, which was preceded by a 33-d adaptation period. Both digestibility and metabolizability of energy decreased with increasing dietary SBPS content ( $P < 0.05$ ). Heat production and energy retention were unaffected by the exchange of starch for DF ( $P > 0.1$ ). Based on energy retention data and apparent fecal digestibilities of crude protein, crude fat, starch, and DF, the estimated net energy value of fermented DF was 13.4 kJ/g. The present study shows that group-housed sows are capable of using energy from fermented DF (i.e., DF from SBPS) as efficiently as energy from digested starch (i.e., starch from tapioca).

### Introduction

Nonlactating sows are fed at a low feeding level, and thus dietary energy is mainly used for reproduction and for maintenance processes. In practical feed evaluation, digestion and utilization data are used to calculate the net energy content of a feed ingredient or diet. The currently used feed evaluation systems are based on individually housed, growing pigs (e.g., Noblet et al., 1994; CVB, 1998).

The utilization of energy from dietary fiber (DF) is considered to be 30% lower than that from starch (Noblet et al., 1994). Therefore, in feed evaluation systems, feed ingredients with a high content of fermentable carbohydrates have lower net energy values than feed ingredients with similar levels of digestible starch (e.g., CVB, 1998). Shi & Noblet (1993b) and Noblet & Bourdon (1997) concluded from their experiments that digestibilities differ between sows and growing pigs. However, information on possible differences in utilization of energy from DF between sows and growing pigs is lacking. It can be hypothesized that adult sows use energy from DF more efficiently than currently adopted in feed evaluation systems.

Additionally, it is important to know the energetic efficiency of fermented DF in sows, because in Dutch pig husbandry it is mandatory that sows without piglets receive 34% of DF in their diet. In the present study, the efficiency of energetic utilization of fermented DF was quantified in group-housed, nonpregnant sows.

## **Materials and Methods**

### ***Animals and Housing***

The experiment consisted of a 33-d preliminary period followed by a 7-d experimental period. The preliminary period allowed the sows to adjust to the experimental diets and housing conditions. A total of 72 crossbred sows (Great Yorkshire × [Dutch Landrace × Great Yorkshire]) were used. These sows were divided into 12 groups of six animals each. Group was the experimental unit in this study. The 12 groups were randomly assigned to one of the four experimental diets. These diets differed mainly in starch and DF content. Sows originated from one farm, which was located 30 km from the laboratory. Three weeks before the preliminary period, sows were synchronized with REGUMATE (Hoechst Roussel Vet, Amsterdam, The Netherlands) and PG600 (Intervet BV, Boxmeer, The Netherlands). At the start of the preliminary period, sows weighed on average 221 kg (SEM = 5.6) and had an average parity of 4.1 (SEM = 0.56). Groups were formed at the start of the preliminary period.

Thirteen days before the experimental period, each group (i.e., six sows) was placed in one of two identical, large, environmentally controlled respiration chambers with a floor-space of 16.6 m<sup>2</sup> (Verstegen et al., 1987b). In the chambers, environmental temperature was kept constant at 20°C, which is thermoneutral for group-housed sows at the experimental feeding level (ARC, 1981; Verstegen et al., 1987c). Relative humidity was maintained at approximately 65%. Air velocity was < 0.2 m/s. Sows were exposed to 12 h of light (from 0700 to 1900) and 12 h of darkness (from 1900 to 0700).

### ***Feeding***

During the experiment, sows within the groups received one of four experimental diets. The diets (Table 1) were formulated to be similar in composition, except for their contents of starch and dietary fiber. In order to create the difference in the ratio between starch and DF, sugar beet pulp silage (SBPS) was exchanged for tapioca (on DM basis). However, the CP content of SBPS is higher than that of tapioca. So, in order to equalize the digestible lysine content, the amount of potato protein was lowered with increasing levels of SBPS. The four experimental diets contained, on a DM basis, respectively 0, 10, 20, and 30% SBPS (Table 1). Once a week, fresh SBPS was collected from a silo with SBPS at the experimental dairy farm. At the experimental pig unit, SBPS was stored at 4°C.

Sows were fed according to their metabolic BW. During this study the feeding level of all groups was 1.30 times the maintenance energy requirements. A value of 440 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup> was assumed as the ME requirement for maintenance (Verstegen, 1987). The sows were group-fed, using one long trough. Sows were fed once a day at 0800, and the daily amount of feed was based on the average metabolic BW of the animals per group. If present, feed refusals were collected 30 min after feeding in order to

record daily feed intake. The feed was given as liquid feed. The amount of water added to the feed was 2.3 L/kg DM. It was assumed that the DM content of the concentrates was 880 g/kg. The DM content of SBPS was measured weekly (data not shown). In addition, animals were given ad libitum access to drinking water during the experiment. Except for the SBPS content, feed and water for the next day were put into the trough immediately after the previous feeding. Soaking time was approximately 23 h. Sugar beet pulp silage was added to and mixed with the feed at the time of feeding.

### **Measurements**

Individual BW was measured weekly from the start of the preliminary period onward. During the experimental period, apparent fecal digestibilities of CP, crude fat, starch, NDF, ADF, ADL, and GE were measured by using the acid-insoluble ash (AIA) marker method. The dietary AIA contents were increased by adding 1.5% diatomaceous shell powder to the experimental diets (Table 1). During the 7-d experimental period, diets were sampled daily. The daily samples of the supplementary feed and SBPS were collected separately. During 5 d of the experimental period, grab samples of feces were collected daily during feeding. Feces were collected per group of sows (i.e., per chamber), and a sample was pooled per group per experimental period. After the collection of the grab samples, the rest of the feces were removed from the floor. Therefore, the grab samples were representative of the feces excreted each day.

Feed (i.e., supplementary feed and SBPS, separately) and feces were analyzed for DM, ash, AIA, CP, crude fat, starch, NDF, ADF, ADL, and GE. Feeds were also analyzed for free sugars. All analyses were carried out in duplicate. The DM content was measured by drying to constant weight at 103°C. Ash content was measured by incineration in an oven at 550°C. Nitrogen content was measured with the Kjeldahl method with K<sub>2</sub>SO<sub>4</sub> and HgO as catalysts. The CP content was calculated as N × 6.25. After extraction with 3 N HCl, the residue was extracted with ether and the crude fat content was measured. The AIA concentration was measured by treating the residue of the ash determination with 3 N HCl to solubilize minerals. The AIA was filtered and weighed after incineration. The starch content was analyzed enzymatically. Free sugars (mono- and disaccharides) were removed by alcohol extraction (ethanol 40%). After gelatinization of the starch by heating in an autoclave for 3 h at 130°C, starch was hydrolyzed to glucose with a mixture of enzymes (10 mg of amyloglucosidase, 1 mg of  $\alpha$ -amylase and 12.5 mg of  $\mu$ L-pullulanase in 5 mL of H<sub>2</sub>O per sample) at pH 4.8 (Brunt, 1993). Subsequently, glucose was measured using hexokinase and G6P-dehydrogenase. Total sugar content was determined in the same way, without removing free sugars. Sugar content (mono- and disaccharides) was calculated as total sugars minus starch content. Cell wall constituents (NDF, ADF, and ADL) were determined according to the methods of Van Soest & Wine (1967) to characterize the DF fraction. Gross energy values were determined by adiabatic bomb calorimetry.



Dietary fiber content was calculated by subtracting CP, crude fat, starch, sugar, and ash content from the DM content. All starch and sugars present in the diets were easily degradable. The mean digestibility of the starch content was 99.9% (data not shown). We assumed that fecal digestibility of sugars was 100%. Therefore, fecal DF was calculated as DM minus fecal CP, crude fat, starch, and ash.

Energy and nitrogen balances per group were measured during the experimental period. Feces with urine were collected quantitatively per group and sampled for energy and nitrogen analysis. Gross energy values were determined by adiabatic bomb calorimetry and nitrogen contents by Kjeldahl. Intake of ME per group was calculated from the energy content of feed, feces with urine, and methane production. Total heat production (HP) was measured at 9-min intervals by determining exchange of oxygen, carbon dioxide, and methane as described by Verstegen et al. (1987b). These gaseous exchanges were used to calculate HP according to the formula of Brouwer (1965). During the last 6 d of the experimental period, HP was measured. Total energy retention (ER) was calculated by subtracting HP from ME intake. The retention of N was estimated from N in feed, in feces plus urine, in aerial  $\text{NH}_3$ , and in  $\text{NH}_4^+$  of water that condensed on the heat exchanger. Energy retention as protein (ERp) was derived from the N retention, and the energy retention as fat (ERf) was calculated from ER and ERp as described by Henken et al. (1991).

### **Statistical Analysis**

Group was the experimental unit. Apparent fecal digestibilities, DM intake, digestible nutrient intake, energy and N balance as well as mean values of HP were analyzed for the effect of diet by ANOVA. The present study focused on the efficiency with which fermented dietary fiber (fDF) was used energetically by the sows. Therefore, methane production, HP, and ER were also analyzed for the effect of diet by linear regression of these traits on daily intakes of fDF (expressed in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The SAS software (SAS Inst. Inc., Cary, NC) was used in all statistical evaluations. Data on GE, ME, ER, ERp, ERf, and HP are expressed in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ .

**Table 1.** Composition of experimental diets

Item	Diet			
	0% SBPS	10% SBPS	20% SBPS	30% SBPS
Ingredient, g/kg DM				
Sugar beet pulp silage <sup>a</sup>	-	100	200	300
Tapioca <sup>b</sup>	288	192	96	-
Potato protein	12	8	4	-
Wheat	100	100	100	100
Wheat middlings	195	195	195	195
Gelatinized maize starch	146	146	146	146
Extracted soybeans	150	150	150	150
Soybean oil	10	10	10	10
Extracted sunflower seed	50	50	50	50
CaCO <sub>3</sub>	11	11	11	11
Monocalcium phosphate	10	10	10	10
NaCl	3	3	3	3
Vitamin and mineral mix <sup>c</sup>	10	10	10	10
Diamol <sup>d</sup>	15	15	15	15
Analyzed content, g/kg DM				
CP	169	169	173	174
Crude fat	25	25	25	24
Starch	454	393	326	265
Dietary fiber <sup>e</sup>	264	323	384	444
Sugars <sup>f</sup>	3	6	8	8
Ash	85	84	85	84
NDF	136	170	211	250
ADF	73	89	108	124
ADL	21	20	19	17

<sup>a</sup> In the calculation of the diet, the DM content of sugar beet pulp silage was fixed at 900 g/kg. According to CVB (1996), sugar beet pulp silage (SBPS) contained on DM basis 101 g/kg CP, 7 g/kg crude fat, 0 g/kg starch, 13 g/kg sugars, and 800 g/kg dietary fiber.

<sup>b</sup> According to CVB (1996), tapioca contained on DM basis 28 g/kg CP, 45 g/kg crude fat, 788 g/kg starch, 16 g/kg sugars, and 117 g/kg dietary fiber.

<sup>c</sup> Provided the following amounts of vitamins and minerals per kilogram of complete diet: vitamin A, 9,000 IU; vitamin D<sub>3</sub>, 1,800 IU; vitamin E 40 mg; riboflavin, 5 mg; niacinamide, 30 mg; d-pantothenic acid, 12 mg; choline chloride, 350 mg; vitamin B<sub>12</sub>, 40 µg; vitamin K, 3 mg; vitamin C, 50 mg; folic acid, 1 mg; biotin, 0.1 mg; Co as CoSO<sub>4</sub>·7H<sub>2</sub>O, 2.5 mg; I as KI, 0.5 mg; Fe as FeSO<sub>4</sub>·7H<sub>2</sub>O, 400 mg; Mn as MnO<sub>2</sub>, 70 mg; Zn as Zn SO<sub>4</sub>·H<sub>2</sub>O, 200 mg; Cu as CuSO<sub>4</sub>·5H<sub>2</sub>O, 80 mg; Se, 0.06 mg (Selplex 50, organic Se 0.1%).

<sup>d</sup> Diamol is diatomaceous shell powder (HCl insoluble ash, apparent digestibility marker).

<sup>e</sup> Dietary fiber (DF) contents were derived by subtracting the CP, crude fat, starch, sugars, and ash content from the DM content.

<sup>f</sup> Mono- and disaccharides as glucose units.

## Results and Discussion

### **General**

The number of groups and animals used in the analyses is given in Table 2. Six sows were removed at the start of the experimental period. Five sows came into estrus during the preliminary week prior to the experimental period and were removed. One sow was removed because of leg problems.

At the start of the 7-d experimental period, average BW was 229 kg (SEM = 12.3) and average parity was 4.1 (SEM = 1.11); both were not different among treatment groups. During the experimental period no feed refusals occurred. Consequently, the daily DM intake of the groups was similar for the different dietary treatments (Table 2;  $P > 0.1$ ) and averaged  $38.3 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ . The daily growth of the sows during the experimental period averaged  $342 \text{ g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$  (SEM = 120.6).

In Tables 2, 3, and 4, effects of diet are given. According to the experimental design, SBPS was exchanged for tapioca. Therefore, the shown effects of diet reflect effects of the change in the ratio between tapioca and SBPS (i.e., starch vs DF).

### **Apparent Fecal Digestibilities**

The mean apparent fecal digestibilities per diet are given in Table 3. The apparent fecal digestibilities of OM, CP, and crude fat decreased ( $P < 0.10$ ,  $P < 0.05$ , and  $P < 0.001$ , respectively), whereas that of DF increased ( $P < 0.001$ ) with increasing dietary SBPS content. In the present study, experimental diets differed mainly in the content of tapioca and SBPS and slightly in potato protein content (Table 1). Therefore, differences in fecal digestibilities of the experimental diets are the consequence of differences in digestibilities between tapioca and SBPS. The increase in apparent fecal DF digestibility with an increase in dietary SBPS content (on DM basis) is in line with literature data on digestibility values of tapioca and SBPS (CVB, 1998). In accordance with the increase in apparent fecal digestibility of DF, the apparent fecal digestibilities of NDF and ADF increased with increasing dietary SBPS content ( $P < 0.001$ ). Between diets, there were no differences in apparent fecal digestibility of ADL. In pigs, the DF fraction of sugar beet pulp has a relatively high apparent fecal digestibility ( $> 80\%$ ) compared with other feed ingredients (Dierick et al., 1989; Zhu et al., 1990; CVB, 1998), because the DF fraction of SBPS is readily fermented (Vervaeke et al., 1989). In general, the apparent fecal digestibilities in the present study were higher than that observed in a similar study with group-housed, growing pigs (Schrama et al., 1998). This is in agreement with several other studies in which digestibilities in sows and growing pigs were compared (Shi & Noblet, 1993a,b; Noblet & Bourdon, 1997).

**Table 2.** Mean daily DM intake and daily intake of digestible nutrients (in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) for the diets differing in sugar beet pulp silage (SBPS) content fed to group-housed sows during the experimental period

Item	Diet				SEM	<i>P</i> - value
	0% SBPS	10% SBPS	20% SBPS	30% SBPS		
No. of groups	3	3	3	3	-	-
No. of sows	16	16	17	17	-	-
DM intake	38.05	38.38	38.53	38.34	0.14	0.180
Digestible nutrient intake						
CP	5.44	5.26	5.33	5.29	0.08	0.469
Crude fat	0.65	0.53	0.48	0.39	0.02	<0.001
Starch	17.19	15.14	12.64	10.19	0.22	<0.001
Sugars	0.11	0.23	0.23	0.25	0.07	0.574
DF <sup>a</sup>	7.06	9.18	11.61	13.73	0.19	<0.001
NDF	2.80	4.04	5.68	7.14	0.14	<0.001
ADF	1.29	1.89	2.72	3.27	0.05	<0.001
ADL	0.15	0.10	0.12	0.06	0.03	0.281

<sup>a</sup> Dietary fiber (DF) contents were derived by subtracting the CP, crude fat, starch, sugars, and ash content from the DM content and assuming an apparent digestibility of 100% for sugars.

The aim of the present study was to evaluate the energetic utilization of fermented DF (fDF) compared to that of digested starch. In order to do this evaluation, the amounts of digestible nutrients consumed by the sows fed the experimental diets have to be known. As shown in Table 2, the main difference between the experimental treatments consisted of an alteration of the intake of both digestible starch and fermentable DF ( $P < 0.001$ ). The intake of digestible starch ranged from 10.2 to 17.2  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  and decreased with an increase in dietary SBPS content (on DM basis). The intake of fermentable DF ranged from 7.1 to 13.7  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  and increased with an increase in dietary SBPS content (on DM basis). In accordance with the increase in the intake of fermentable DF, the intake of both fermentable NDF and ADF increased with increasing dietary SBPS content ( $P < 0.001$ ).

**Table 3.** Mean apparent fecal digestibility (in %) for the diets differing in sugar beet pulp silage (SBPS) content fed to group-housed sows

Item	Diet				SEM	P - value
	0% SBPS	10% SBPS	20% SBPS	30% SBPS		
OM	87.5	86.3	85.8	85.0	0.5	0.064
CP	83.7	81.1	80.1	79.0	0.9	0.034
Crude fat	66.2	60.0	50.1	42.5	2.0	<0.001
DF <sup>a</sup>	70.6	74.3	78.4	80.6	1.0	<0.001
NDF	54.1	61.8	69.9	74.5	1.7	<0.001
ADF	46.4	55.4	65.2	69.1	1.6	<0.001
ADL	18.1	12.2	16.8	9.7	3.7	0.405

<sup>a</sup> Dietary fiber (DF) contents were derived by subtracting the CP, crude fat, starch, sugars, and ash content from the DM content and assuming an apparent digestibility of 100% for sugars.

### **Partitioning of Energy**

The changes in energy partitioning, as a result of changes in dietary SBPS content, are given in Table 4. Total energy lost in feces, urine, and methane was affected by diet. This is indicated by the declining metabolizability (ME:GE) with increasing dietary SBPS content ( $P < 0.05$ ). The apparent fecal digestibility of energy also decreased with increasing dietary SBPS content (DE:GE, Table 4). Despite the differences in the composition of the basal diets between studies, Schrama et al. (1998) also found, in a similar experiment with growing pigs, that the metabolizability and digestibility of energy declined with increasing SBPS content. In growing pigs the decline in metabolizability and digestibility per percentage of dietary SBPS (Schrama et al., 1998) was higher than in sows.

The results from the present study and from a similar study with growing pigs (Schrama et al., 1998) show higher apparent fecal digestibilities of energy in sows than in growing pigs (e.g., with 10% dietary SBPS [on DM basis], 83.6% vs 80.5%, respectively). This is in line with other studies that compared digestibilities between sows and growing pigs (Shi & Noblet, 1993b; Noblet & Bourdon, 1997). Both Shi & Noblet (1993b) and Noblet & Bourdon (1997) found higher apparent fecal digestibilities of energy in sows than in growing pigs, especially with diets with high levels of DF. The superiority of sows can be attributed to a higher fermentation capacity of the hindgut in heavier animals, the fermentation rate being increased by the low feeding level and the subsequent slow rate of passage (Shi & Noblet, 1993b; 1994).

**Table 4.** Energy partitioning (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) in group-housed sows fed diets differing in sugar beet pulp silage (SBPS) content

Trait	Diet				SEM	P - value
	0% SBPS	10% SBPS	20% SBPS	30% SBPS		
GE intake	674	680	686	683	2	0.035
DE:GE, %	85.1	83.6	83.0	81.8	0.7	0.043
ME:GE, %	77.6	76.1	74.9	72.2	0.9	0.015
Methane	3.7	6.2	6.3	7.9	0.5	<0.001
ME intake	523	518	514	493	7	0.057
Heat production	435	439	434	419	6	0.213
Energy retention						
Total (ER)	88	79	80	74	10	0.792
Protein (ERp)	17	14	16	21	4	0.664
Fat (ERf)	71	65	64	53	10	0.655

Methane production increased with increasing dietary SBPS content ( $P < 0.001$ , Table 4). This increase in methane production is lower than that seen in a similar experiment with growing pigs (Schrama et al., 1998). This is probably due to the lower feeding level in the present study compared to the study of Schrama et al. (1998), 1.30 and 2.5 times maintenance, respectively. In the present study, methane production ( $\text{CH}_4$ ;  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) was related to the daily fDF intake (fDF;  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) as follows:

$$\text{CH}_4 = 0.50 \text{ (SE 1.19)} + 0.53 \text{ (SE 0.11)} \times \text{fDF} \quad R^2 = 0.70 \quad [1]$$

In non-ruminants, fermentation of DF occurs mainly in the cecum and colon. Therefore, methane is mainly produced in this part of the gastrointestinal tract. As shown in other studies with pigs (Kirchgessner et al., 1991; Zhu et al., 1993; Shi & Noblet, 1994), increasing fDF intake resulted in an increase in methane production. In the present study the increase in methane production was 0.53 kJ per gram fDF intake ( $P < 0.001$ ; Eq. [1]). This increase is lower than that in a similar study with growing pigs (Schrama et al., 1998). When using an enthalpy value of 17.5 kJ/g for DF, it can be calculated that for each unit of DF that is digested (fermented), 3.0% of its GE content is lost as methane. This observed value is lower than that in studies with growing pigs (Kirchgessner et al., 1991; Zhu et al., 1993; Shi & Noblet, 1994; Bakker, 1996; Schrama et al., 1998), which ranged from 4.1 to 9.5%. These differences among various studies might be related to dietary factors, levels of fermentable carbohydrate sources in the diets (Bakker, 1996), and differences in microflora present in the gastrointestinal tract of pigs (Schrama et al., 1998). In

addition, differences in methane production might also reflect differences between animal classes (sows vs growing pigs).

In the present study, the exchange of starch with DF in the experimental diets tended to decrease ME intake ( $P < 0.10$ ). This small reduction in ME intake with increasing dietary SBPS content did not lead to significant differences between dietary treatments in total heat production (HP) or total energy retention (ER).

### **Net Energy Evaluation**

The present study assessed the energetic efficiency of fDF. Theoretically, the energetic efficiency of fDF can be obtained from the linear regression between HP and fDF or from the linear regression between ER and fDF. This is only possible if the intakes of other digestible nutrients (i.e., CP, crude fat, starch, and sugars) are equal in all experimental diets. In the present study, apart from changes in daily intake of fDF and starch, some minor differences in daily intake of other digestible nutrients occurred (i.e., crude fat; Table 2). In order to get the unbiased relationship between HP and fDF and between ER and fDF, HP and ER were corrected first toward the same daily intake of digestible CP, crude fat, starch, and sugars (CorHP and CorER, respectively). The intake of digestible nutrients was measured per group of sows, with the actual feed intake and the measured apparent fecal digestibilities. The values of heat increment of digestible CP, crude fat, starch, and sugars used for this correction were 12.8, 3.2, 4.0, and 3.9 kJ/g, respectively, and were derived from energetic efficiency of, respectively, 46, 92, 77, and 77% for these digested nutrients as used in the current Dutch NE evaluation system for pigs (CVB, 1998).

The CorHP in relation to the daily fDF intake is presented in Figure 1. In the present study, CorHP ( $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was related to fDF ( $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) as follows:

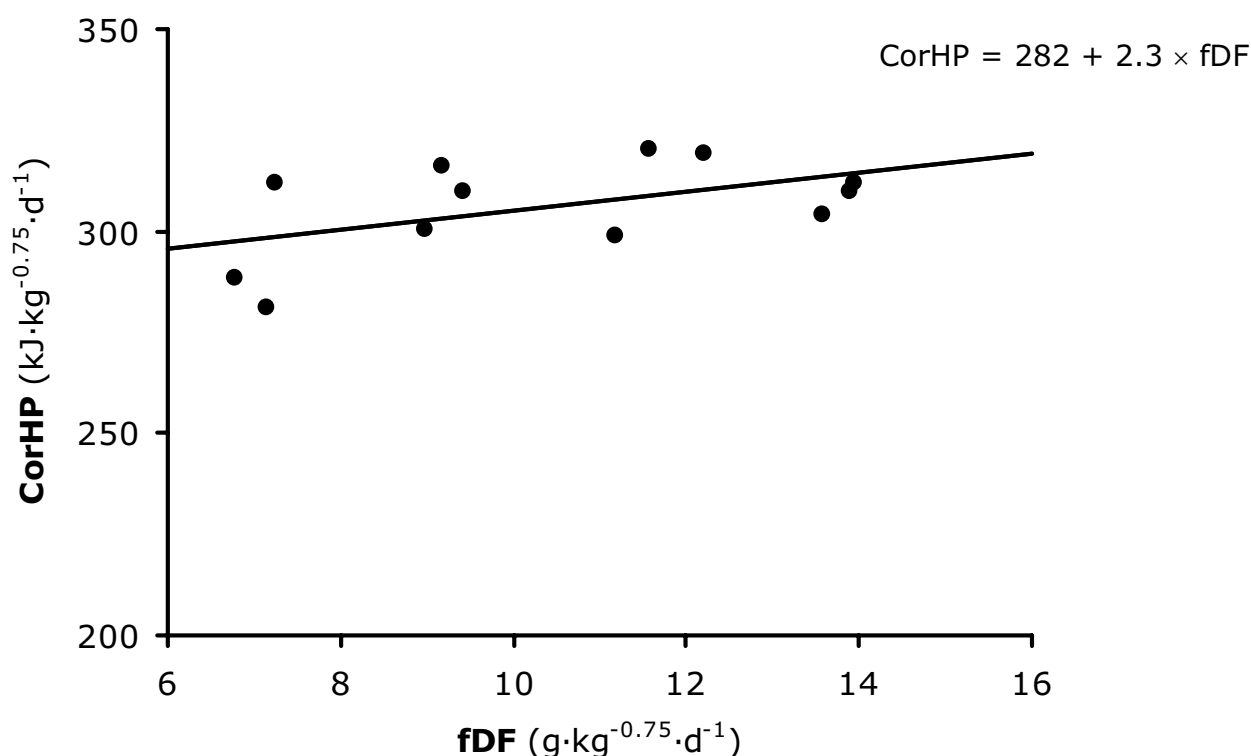
$$\text{CorHP} = 282 (\text{SE } 13) + 2.3 (\text{SE } 1.3) \times \text{fDF} \quad R^2 = 0.25 \quad [2]$$

And CorER ( $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was related to fDF ( $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) as follows:

$$\text{CorER} = -324 (\text{SE } 17) + 13.4 (\text{SE } 1.6) \times \text{fDF} \quad R^2 = 0.88 \quad [3]$$

The heat increment for fDF (CorHP) was 2.3 kJ/g (Eq. [2]). The estimated value for heat increment of fDF was different ( $P < 0.001$ ) from the heat increment value of fDF of 8 kJ/g used in the current Dutch NE evaluation system for pigs (CVB, 1996).

The energetic efficiency estimated in Eq. [3] was 13.4 kJ/g (77%) for fDF. The difference between the estimated energetic efficiency from Eq. [2] and [3] (i.e., 15.2 and 13.4 kJ/g, respectively) is due to increased methane and urinary energy losses with increasing levels of DF. These losses are not corrected for when estimating the energetic efficiency using CorHP. Therefore, discussion is focused on the estimated energetic efficiency using CorER.



**Figure 1.** Relationship between total heat production (HP) and daily intake of fermented dietary fiber (fDF) (●) in group-housed sows. The HP data were corrected (CorHP) for similar daily intakes of digestible CP, crude fat, starch, and sugars. For this correction, the measured daily digestible nutrient intakes (Table 2) were used and the values for the heat increment by digested CP, crude fat, starch, and sugars of 12.8, 3.2, 4.0, and 3.9 kJ/g, respectively, were used.

The energetic efficiency for fDF was higher than that given in literature on growing pigs: 26% by Just et al. (1983); 57% by Hoffmann et al. (1990); 58% by Noblet et al. (1994); and 45% by Bakker (1996). The energetic efficiency of fDF estimated in the present study (77%) is similar to the value for fDF in group-housed growing pigs (85%) found by Schrama et al. (1998), who estimated the energetic efficiency using CorHP. Moreover, in the present study, the energetic efficiency of fDF was not different ( $P > 0.10$ ) from the energetic efficiency of digestible starch (13.5 kJ/g) used in the current Dutch NE evaluation system for pigs (CVB, 1996). However, it differed ( $P < 0.05$ ) from the energetic efficiency of fDF (9.5 kJ/g) as currently used (CVB, 1996).

As stated before, the estimated energetic efficiency in the present study differs from other research with individually housed, growing pigs. This difference may be caused by the experimental design, such as the housing conditions (i.e., individually housed vs group-housed), duration of adaptation period, age and breed of animals, calculation method, and differences in physical activity. The effect of housing



conditions on the energetic efficiency needs to be further investigated. Furthermore, different types of fermentable DF were used in different studies. In the present study, only SBPS, with high levels of pectin in the DF, was studied. Therefore, differences between studies might also be due to variation in the composition of the DF fraction of the diet. Further research is needed to investigate the difference in utilization of DF from various feed ingredients.

## **Implications**

The present study showed that in group-housed sows the energetic efficiency of fermented dietary fiber from sugar beet pulp silage was not different from that of digested starch from tapioca. This is in contrast with the theory that fermentable dietary fiber is utilized with a lower efficiency than digested starch, as currently used in feed evaluation systems. Future research is required to unravel the mechanisms involved. The magnitude of the effects on energy metabolism is especially important for diets (feed ingredients) with a considerable amount of fermentable dietary fiber.



## **Chapter 3**

### **Effects of Dietary Fermentable Carbohydrates on Behavior and Heat Production in Group-Housed Sows**

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## Effects of Dietary Fermentable Carbohydrates on Behavior and Heat Production in Group-Housed Sows

### Abstract

The effects of dietary fiber (DF) on behavior and heat production in group-housed sows were studied. Twelve groups of six nonpregnant sows were fed one of four experimental diets that were similar in composition except for starch and DF contents. Exchanging sugar beet pulp silage (SBPS) for tapioca created the difference in dietary starch and DF ratio. On a dry matter (DM) basis, diets contained 0, 10, 20, or 30% SBPS. Sows were group-housed. Intake of fermentable DF (fDF) for diets containing 0, 10, 20, or 30% SBPS averaged 7.06, 9.18, 11.61, and 13.73 g·kg<sup>-0.75</sup>·d<sup>-1</sup>, respectively. Sows were fed once a day at 0800. Dry matter intake for diets containing 0, 10, 20, or 30% SBPS, averaged 38.05, 38.38, 38.53, and 38.35 g·kg<sup>-0.75</sup>·d<sup>-1</sup>, respectively, and ME intake averaged 523, 518, 514, and 493 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup>, respectively. On average, sows spent 177 min/d on physical activity, of which 8.8% was spent on eating. Time spent in physical activity was affected by diet ( $P = 0.005$ ). Sows fed 0 or 10% SBPS spent more time on physical activity than sows fed 20 or 30% SBPS ( $P = 0.002$ ). Energy cost of physical activity averaged 464 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup> (SEM 31) and was similar for diets ( $P = 0.679$ ). Total heat production (HP) and activity-related heat production (AHP) were affected by diet ( $P < 0.05$ ). Sows tended to be quieter when fDF intake increased ( $P = 0.063$ ). The effect of fDF intake on HP and AHP was not constant during the day. During the night period, fDF intake did not effect HP and AHP ( $P > 0.10$ ). During the day period, increased fDF intake decreased HP ( $P = 0.006$ ) and tended to decrease AHP ( $P = 0.062$ ). During eating, increased fDF intake increased HP ( $P = 0.012$ ) and tended to increase AHP ( $P = 0.074$ ). Despite similar DM intake, sows fed 0 or 10% SBPS spent less time eating than sows fed 20 or 30% SBPS ( $P = 0.009$ ). Feed consumption rate was higher ( $P = 0.003$ ) in groups fed 0 or 10% SBPS than in groups fed 20 or 30% SBPS. Feed consumption rate decreased by 0.19 g DM·kg<sup>-0.75</sup>·min<sup>-1</sup> ( $P = 0.003$ ) for each gram of fDF intake. The energy saving effect of physical activity on the NE value of fDF from SBPS ranged between 2.3 and 3.7 kJ/g of fDF intake. In conclusion, intake of fDF from SBPS affected energy expenditure for physical activity ( $P = 0.063$ ); however, this effect was not constant during the day.

### Introduction

Most (net) energy feed evaluation systems are based on digestion and utilization data and are used to calculate the potency of a feed ingredient or diet for energy deposition and maintenance. In growing pigs (e.g., Schrama et al., 1996; 1998) and sows (e.g., Robert et al., 1993; Brouns et al., 1994; Ramonet et al., 1999), differences in dietary ingredients affected physical activity. Consequently, this effect

on physical activity will influence the energetic efficiency with which pigs utilize their diet. However, reported results on effects of dietary fiber (DF) on time spent on physical activity are not very consistent. Some authors report a decrease in physical activity by feeding fiber-rich diets to individually (e.g., Ramonet et al., 1999; 2000b) or group-housed sows (e.g., Brouns et al., 1994; Danielsen & Vestergaard, 2001), whereas others report no effects (e.g., Whittaker et al., 1998; Ramonet et al., 2000a). Moreover, it can be hypothesized that effects of DF on physical activity are dependent on their botanical origin (Noblet & Le Goff, 2001). Schrama et al. (1998) reported dose response effects of sugar beet pulp silage (SBPS) on physical activity in growing pigs. Dose response studies on the effects of dietary composition on physical activity of sows, however, are lacking.

It can be hypothesized that the level of dietary SBPS affects physical activity of group-housed sows. Furthermore, it can be hypothesized that an effect of dietary SBPS on physical activity of sows is not constant during the day. In the present study, effects of dietary SBPS content and intake of fermentable DF (fDF) from SBPS on physical activity and heat production in group-housed sows were studied.

## **Materials and Methods**

### ***General***

Twelve groups of six sows were used. The experiment consisted of a 33-d preliminary period followed by a 7-d experimental period. Groups were randomly assigned to one of four experimental diets. These diets differed mainly in starch and DF content by an exchange of SBPS for tapioca (on DM basis). The four experimental diets contained, on DM basis, 0, 10, 20, or 30% SBPS, respectively. Sows were group-fed, using a long trough. Sows receiving the 0% SBPS diet were fed at 1.3 times the assumed maintenance energy requirements. Sows fed the other diets received similar amounts of DM. Groups were housed in environmentally controlled respiration chambers (Verstegen et al., 1987b). Sows were exposed to 12 h of light (about 300 lx, from 0700 to 1900) and 12 h of partial darkness (about 10 lx, from 1900 to 0700) to allow video recordings. Details on animals, housing conditions, and diets are reported by Rijnen et al. (2001).

### ***Measurements***

For each group, time spent on eating was measured using time-lapse video recorders. The recording of eating time started as soon as the sows had access to the feed and stopped when the trough was empty (i.e., observed from video recordings). With these data and measured DM intake, feed consumption rate per group was calculated. Total heat production (HP) was measured at 9-min intervals by determining exchange of oxygen, carbon dioxide, and methane (indirect calorimetry) as described by

Verstegen et al. (1987b). These gaseous exchanges were used to calculate HP according to the formula of Brouwer (1965). During the last 6 d of the experimental period, HP was measured continuously.

Behavior of the sows was recorded using time-lapse video recorders during two different days (i.e., two whole 24-h periods) within the 7-d experimental period. An instantaneous scan sampling technique (as described by Altmann, 1974) was used to analyze the video recordings for behavioral characteristics (Table 1). The analyses of video recordings for behavioral characteristics were done at 3-min intervals. At these 3-min intervals, the number of sows that exhibited a specific behavior was recorded. With these data, the percentage of time of all sows that was spent on a specific behavior was calculated. The average of each performed behavioral characteristic was calculated for the same 9-min intervals as HP (i.e., average of three sampling moments). The behavioral characteristic "standing" includes standing up, standing, eating, walking, and lying down (Table 1). Therefore, physical activity is defined as standing up, standing, eating, walking, lying down, plus sitting. Per group and per day (i.e., per 24-h period), the 9-min data on HP were related to physical activity according to the following equation:

$$HP_{ij} = \mu + D_i + \beta \times X_j + e_{ij} \quad [1]$$

where  $HP_{ij}$  = heat production during day period  $i$  and 9-min period  $j$ , in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $\mu$  = overall mean;  $D_i$  = fixed effect of day period  $i$  ( $i = 1$  (from 0700 to 2200), 2 (from 2200 to 0700));  $X_j$  = physical activity of sows during 9-min period  $j$ , in percentage of time of all sows spent on "standing plus sitting";  $\beta$  = regression coefficient of heat production on physical activity; and  $e_{ij}$  = error term.

Heat production and physical activity exhibit circadian rhythms (e.g., Aschoff et al., 1974; Schrama et al., 1996). The circadian rhythm in HP is only partially accounted for by physical activity, which has been demonstrated in pigs (van der Hel et al., 1984; Henken et al., 1991). Therefore, a fixed effect of day period with two levels was included in Eq. [1]. The day was divided into a day period from 0700 to 2200, during which the sows were most active, and a night period from 2200 to 0700, during which sows were inactive. The increase in HP around feeding time is not fully related to the elevated physical activity (Verstegen et al., 1987a; Noblet et al., 1993). In the calculation according to Eq. [1], data around feeding time, from 0800 to 0900, were excluded. These data were omitted in order to avoid possible bias by inclusion of heat increment associated with feed ingestion in the relationship between HP and physical activity.

The activity-related heat production (AHP) was calculated as follows:

$$\text{AHP}_j = b \times X_j \quad [2]$$

where  $\text{AHP}_j$  = activity related heat production during 9-min period  $j$ , in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $X_j$  = physical activity during 9-min period  $j$  of the video recordings, in percentage of time of all sows spent on “standing plus sitting”;  $b$  = the estimated regression coefficient from HP on physical activity from Eq. [1]. Heat production not related to physical activity or resting heat production (RHP) was derived by subtracting AHP from HP. Activity-related HP and RHP were calculated for each 9-min period, including the 1-h period around feeding (i.e., from 0800 to 0900).

The energy cost for physical activity ( $\text{EC}_{\text{act}}$  in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was derived from the regression coefficient from HP on physical activity, as follows:

$$\text{EC}_{\text{act}} = 100 \times b \quad [3]$$

where  $b$  = the estimated regression coefficient from the regression of HP on physical activity from Eq. [1].

### Statistical Analysis

Group was the experimental unit. Mean values of HP, AHP, RHP, and the behavioral characteristics were analyzed for the effect of diet by ANOVA. In addition, least square means were used for treatment comparisons. A contrast method was used to analyze differences between low- and high-fiber diets (i.e., 0%+10% vs 20%+30% SBPS). Moreover, HP, AHP, and RHP were analyzed for the effect of diet by linear regression of these traits on the daily intake of fDF (expressed in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The SAS software (SAS Inst. Inc., Cary, NC) was used in all statistical evaluations. The data on HP, AHP, and RHP are expressed in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ .

**Table 1.** Ethogram of the behavioral characteristics of group-housed sows fed diets differing in sugar beet pulp silage content during 2 d of the experimental period<sup>a</sup>

Item	Definition
Standing	The sow stands upright on four legs, including walking. Standing up, lying down, and eating are also included.
Sitting	The sow sits with backside and forelegs on the floor (“dog-like”).
Lying breast	The sows lays on her legs with her head and spinal column upright.
Lying flank	All varieties of lying except for “lying breast”, the sow is passive and not alert.

<sup>a</sup> Physical activity is defined as the total of the behavioral characteristics “standing” plus “sitting” (i.e., standing up, standing, walking, lying down, eating, plus sitting).

## Results and Discussion

### General

The number of groups and animals used in the analyses is given in Table 2. Six sows were removed at the start of the experimental period because they came into estrus or had leg problems. At the start of the experimental period, average BW was 229 kg (SEM = 12.3). Average parity of sows was 4.1 (SEM = 1.11). During the experimental period, no feed refusals occurred. Consequently, the daily DM intake of the groups was similar for the different dietary treatments ( $P = 0.180$ ; Table 2) and averaged  $38.3 \text{ g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ .

According to the experimental design, SBPS was exchanged for tapioca (on DM basis). Therefore, the observed effects of diet (Tables 2, 3, 4, 5, and 6) reflect effects of the change in the ratio between tapioca and SBPS (i.e., digestible starch vs fDF). The main difference between the experimental treatments consisted of an alteration in the intake of digestible starch and fDF ( $P < 0.001$ ; Table 2). The intake of digestible starch decreased with increasing dietary SBPS content. The intake of fDF increased with increasing dietary SBPS content. Consequently, ME intake tended to decrease with increasing SBPS content ( $P = 0.057$ ; Table 2). Apparent fecal digestibilities and digestible nutrient intakes have been reported elsewhere (Rijnen et al., 2001).

**Table 2.** Mean daily dry matter, metabolizable energy, digestible starch, and fermentable dietary fiber intake of group-housed sows receiving diets differing in sugar beet pulp silage (SBPS) content

Item	Number of groups	Number of sows	DM intake, $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	ME intake, $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	Digestible nutrient intake, $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$	
					Starch	DF <sup>a</sup>
0% SBPS	3	16	38.05	523	17.19	7.06
10% SBPS	3	16	38.38	518	15.14	9.18
20% SBPS	3	17	38.53	514	12.64	11.61
30% SBPS	3	17	38.34	493	10.19	13.73
SEM	-	-	0.14	7	0.22	0.19
<i>P</i> -value	-	-	0.180	0.057	<0.001	<0.001

<sup>a</sup> Dietary fiber (DF) contents were derived by subtracting the crude protein, crude fat, starch, sugars, and ash content from the dry matter content and assuming an apparent digestibility of 100% for sugars.



### **Behavioral Characteristics**

Studies on the effects of DF on the behavior of sows have been focused mainly on feeding motivation, feeding rate, aggressive behavior, and the occurrence of oral stereotyped activities (as reviewed by Meunier-Salaün et al., 2001). To study these effects, most studies analyze behavior during short periods during the day, mostly related to feeding time (e.g., Braud et al., 1998; Whittaker et al., 1999; Danielsen & Vestergaard, 2001). In the present study, however, general activity (or postures) was analyzed for during 24-h periods.

In the present study, sows spent on average 163 min/d standing, 14 min/d sitting, 272 min/d lying on breast, and 991 min/d lying on their flanks (Table 3). Furthermore, in the present study, dietary composition affected activity level of group-housed sows ( $P < 0.01$ ; Table 3). Contrast analysis showed that sows fed 0 or 10% SBPS spent more time "standing" and "standing+sitting" than sows fed 20 or 30% SBPS ( $P < 0.01$ ).

In the present study, time spent on physical activity (i.e., "standing plus sitting") averaged 177 min/d, which is low compared with data in literature. In the literature, average time spent on physical activity ranges between 190 min/d (Noblet, 1990) and 363 min/d (Ramonet et al., 1999) for individually housed sows, and between 202 and 435 min/d for group-housed sows (Brouns et al., 1994). In addition, the variation between individual sows in time spent on physical activity is large (e.g., Cariolet & Dantzer, 1984; Noblet et al., 1993). Differences between studies in time spent on activity might be due to housing conditions, feeding level (Terlouw & Lawrence, 1993), physical condition (Cariolet & Dantzer, 1984), and characteristics of the diet (Meunier-Salaün et al., 2001), like DF content and origin (e.g., Ramonet 1999; 2000a,b).

Reported effects of DF on physical activity of sows are not very consistent. Due to difference among experiments in breeds, diets, feeding level, recording periods, and housing conditions, it is difficult to look at effects of DF between studies (Meunier-Salaün et al., 2001). Ramonet et al. (2000a), for example, reported no effect of DF level (i.e., mixed fiber sources) on standing behavior, whereas Ramonet et al. (1999) reported decreased standing activity with similar diets. Ramonet et al. (2000a), however, used individually housed sows insulated in respiration chambers, whereas Ramonet et al. (1999) used individual pens. Terlouw & Lawrence (1993) did not find a difference between individually tethered and loose-housed sows in total activity during the day. Furthermore, several authors report a difference in total activity time caused by feeding level; a high feeding level decreased time spent on physical activity (e.g., Halter et al., 1980; Susenbeth & Menke, 1991; Terlouw & Lawrence, 1993). This is important, because in most studies feeding level (in kg) is increased because of the decreased dietary energy density when DF content increases.

Moreover, differences between studies might be related to the level and botanical origin of DF (Noblet & Le Goff, 2001). Most reported effects of DF on physical activity

during the day have been found using sugar beet pulp as fiber source (e.g., Brouns et al., 1994; Brouns et al., 1998; Ramonet et al., 2000b). The decrease in physical activity with higher dietary SBPS content in the present study is similar to the decrease in physical activity with high dietary sugar beet pulp content as reported by Brouns et al. (1994) and Ramonet et al. (2000b). In addition, Ramonet et al. (1999) reported a decrease in standing activity of sows, which were fed a diet high in mixed fiber sources. Ramonet et al. (2000b) reported a decrease in standing activity with high dietary content of wheat bran. Specific components or physicochemical properties of specific DF sources might be of importance for the effect on behavior and activity (Brouns et al., 1995; Noblet & Le Goff, 2001). Moreover, fermentation characteristics (e.g., fermentation rate) of specific fiber sources in the gastrointestinal tract might be of importance.

**Table 3.** Behavioral characteristics, in percentage of time spent per day (24 h), of group-housed sows fed diets differing in sugar beet pulp silage (SBPS) content

Item	Behavioral characteristics <sup>a</sup>				
	Standing	Sitting	Standing+sitting	Lying breast	Lying flank
0% SBPS	11.6 <sup>cd</sup>	1.0	12.7 <sup>cd</sup>	16.9	70.5
10% SBPS	14.3 <sup>d</sup>	1.4	15.7 <sup>d</sup>	17.3	67.0
20% SBPS	9.4 <sup>c</sup>	0.9	10.3 <sup>c</sup>	18.8	70.9
30% SBPS	9.8 <sup>c</sup>	0.7	10.4 <sup>c</sup>	22.7	66.8
SEM	0.7	0.4	0.8	3.6	3.8
<i>P</i> -value	0.004	0.629	0.005	0.662	0.810
<i>P</i> -value contrast <sup>b</sup>	0.001	0.303	0.002	0.333	0.972

<sup>a</sup> The definitions of the behavioral characteristics are described in the ethogram (Table 1).

<sup>b</sup> A contrast method was used to analyze differences between low- and high-fiber diets (i.e., 0%+10% vs 20%+30% SBPS).

<sup>c, d</sup> Within a column, means with different superscripts differ ( $P < 0.05$ ).

### Energy Cost of Activity

In sows, the energy cost of activity can be divided into energy cost of sitting, standing, sitting up and standing up (16.4, 34.1, 35.5, and 49.0 kJ·kg<sup>-0.75</sup> per 100 min, respectively; Kelley et al., 1978), and walking. It is possible that housing conditions or feeding frequency interact with energy cost of activity, because sitting up and standing up cost more energy than sitting and standing, respectively (Kelley et al., 1978).

In the present study, EC<sub>act</sub> averaged 464 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup> (SEM 31.0; Table 4), or 32.2 kJ·kg<sup>-0.75</sup> per 100 min, and did not differ between diets ( $P = 0.679$ ). The EC<sub>act</sub> of

group-housed sows in the present study is similar to values for individually housed sows, reported by Kelley et al. (1978), Noblet et al. (1993), and Ramonet et al. (2000a) (i.e., 34.1, 27.3, and 30  $\text{kJ}\cdot\text{kg}^{-0.75}$  per 100 min, respectively). It can be hypothesized that cost of activity in sows does not depend on housing conditions (i.e., individually vs group-housed). Due to our experimental setup it was not possible to make a distinction between energy cost for different physical activities or movements.

### **Total Heat Production and Activity-related Heat Production**

Total HP and AHP of the sows are shown in Table 4. Total HP was calculated for the same 2 d when the videotapes were recorded. Total HP and AHP were affected by diet ( $P < 0.05$ ), whereas RHP was not ( $P = 0.331$ ). Among others, Terlouw & Lawrence (1993), reported that a higher feeding level resulted in lower physical activity. In the present study, however, ME intake tended to decrease with increasing dietary SBPS content ( $P = 0.057$ ; Table 2), whereas sows fed 0% or 10% SBPS spent more energy on activity than sows fed 20 or 30% SBPS ( $P = 0.006$ ). The mean AHP of group-housed sows in the present study ( $56 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) is similar to the AHP value of  $62 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  reported by Noblet et al. (1993). The small difference between the two values might be due to the higher feeding level in the present study compared with the study of Noblet et al. (1993) since there is an effect of feeding level on time spent on activity (e.g., Halter et al., 1980; Susenbeth & Menke, 1991). Compared to the present study, Ramonet et al. (2000a) reported a higher average value of AHP in individually housed pregnant sows of  $105 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ . This might be due to differences in the method of measuring activity between studies (i.e., force sensors and video recordings, respectively).

The mean AHP in the present study represented 12.7% of HP, and ranged from 10.7 to 15.6% among groups. This percentage is in agreement with literature values (e.g., Halter et al., 1980; Verstegen et al., 1987a; Noblet et al., 1993). Ramonet et al. (2000a) reported a higher average percentage of AHP of total HP (i.e., 22%) in individually housed pregnant sows, which might be related to differences in the method of measuring activity between studies. In conclusion, dietary composition altered energy expenditure on physical activity of group-housed sows.

Increased fDF intake, at similar DM intake, decreased the 24-h mean HP ( $P = 0.039$ ; Table 5) and tended to decrease the 24-h mean AHP ( $P = 0.063$ ; Table 5). Sows tended to spend 2.3 kJ less on physical activity per gram increase of fDF intake. Schrama et al. (1998) found that growing pigs spent 3.9 kJ less on physical activity per gram of fDF intake. This difference between animals maybe related to body mass (Porzig & Liebenberg, 1977). It can also be due to the high feeding level in growing pigs (Halter et al., 1980; Susenbeth & Menke, 1991; Terlouw & Lawrence, 1993). Moreover, in the present study, video recordings were used for 2 d to measure physical activity, whereas Schrama et al. (1998) used a radar device for 6 d to measure physical activity. Furthermore, in the present study there were small

differences in ME intake between diets ( $P = 0.057$ ; Table 2). Feeding level can affect physical activity (e.g., Terlouw & Lawrence, 1993). In the present study, however, the effect of ME intake on AHP could have partially masked the pure effect of fDF.

**Table 4.** Mean total heat production (HP), activity-related heat production (AHP), resting heat production (RHP), and energy cost for physical activity ( $EC_{act}$ ) (in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) of group-housed sows fed diets differing in sugar beet pulp silage (SBPS) content

Item	HP	HPcor <sup>a</sup>	AHP	RHP	$EC_{act}$
0% SBPS	437	437	58 <sup>cd</sup>	379	462
10% SBPS	443	444	70 <sup>c</sup>	373	443
20% SBPS	434	435	51 <sup>cd</sup>	383	495
30% SBPS	420	425	47 <sup>d</sup>	373	455
SEM	5	5	4	4	31
<i>P</i> -value	0.043	0.128	0.019	0.331	0.679
<i>P</i> -value contrast <sup>b</sup>	0.023	0.067	0.006	0.702	0.495

<sup>a</sup> HPcor = HP data were correct for differences in ME intake (i.e., 0.2 kJ for each kJ ME).

<sup>b</sup> A contrast method was used to analyze differences between low- and high-fiber diets (i.e., 0%+10% vs 20%+30% SBPS).

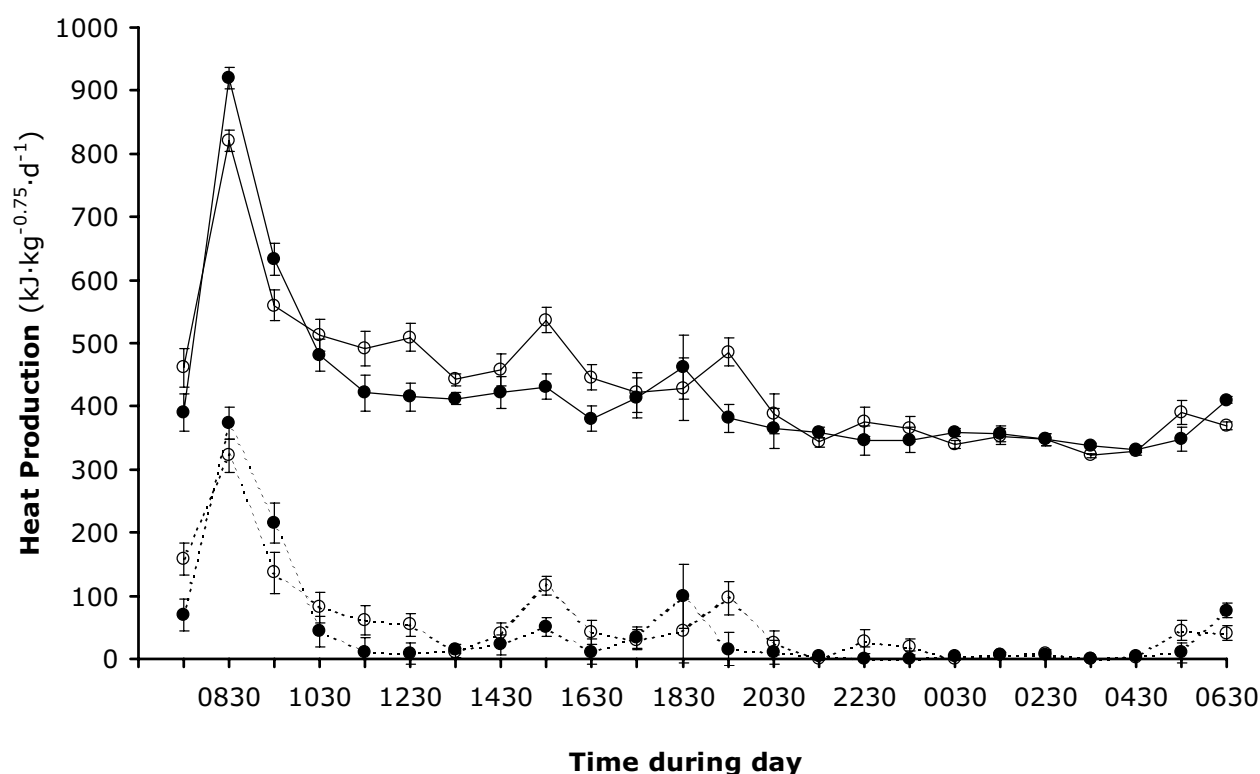
<sup>c, d</sup> Within a column, means with different superscripts differ ( $P < 0.05$ ).

## Circadian Rhythms

### General

The circadian rhythms of average HP and average AHP of the 0 and 30% SBPS groups are illustrated by Figure 1. Sows were exposed to 12 h of light (from 0700 to 1900) and 12 h of partial darkness (from 1900 to 0700), and fed once a day (at 0800). Similar to the results reported by Noblet et al. (1993), HP and AHP were highest during eating and decreased until about 12 h after the meal. The first increase in HP and AHP during the afternoon (at 1530) was due to an animal keeper entering the respiration chamber to check health of the sows. The second increase in HP and AHP was due to automatically turning down the lights at 1900. Both peaks were therefore caused by the experimental setup.

On average, sows fed the diet with 30% SBPS had a lower ( $P < 0.01$ ) HP during the greater part of the day (from 0700 to 2200), except for the eating period (from 0800 to 0900), during which the sows fed 30% SBPS were more active ( $P < 0.05$ ). No differences ( $P > 0.05$ ) in HP or AHP occurred during the night period (from 2200 to 0700).



**Figure 1.** Circadian rhythm in total heat production (—) and activity related heat production (- - -) of group-housed sows fed 0% (○) or 30% (●) sugar beet pulp silage with the diet.

#### *Total Heat Production and Activity-related Heat Production*

To evaluate the variation in HP and AHP within the day, the day was divided into three parts. The part from 2200 to 0700 was designated as the night period. The night period was part of the partial darkness period. Video recording showed that physical activity was minimal during the night period. This is in agreement with the findings of Cariolet & Dantzer (1984) and Ramonet et al. (2000b), who found that sows had reduced activity during the night period. From 0700 to 2200 (i.e., the remainder of the day) was designated as the day period. The third part was the eating period, from 0800 to 0900, during which time the sows were most active. The linear relationships between fDF intake and HP, and AHP, are calculated for 24 h, the night period, day period, eating period, and 24 h without the eating period (Table 5).

Averaging over the whole day (24 h), HP decreased with increasing fDF intake ( $P = 0.039$ ). During the night period, fDF intake did not affect HP ( $P = 0.509$ ). During the day period, however, HP decreased with increasing fDF intake ( $P = 0.006$ ). During eating, HP increased with increasing fDF intake ( $P = 0.012$ ). After removing the data of the eating period from the whole day, HP decreased with increasing fDF intake ( $P = 0.027$ ).

**Table 5.** Linear relationships between fermentable dietary fiber intake (fDF in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) and total heat production (HP), and activity-related heat production (AHP) (in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) in group-housed sows fed diets differing in sugar beet pulp silage content

Item	Relationship	P-value	RSD	R <sup>2</sup>
<b>HP</b>				
Mean, per 24 h <sup>a</sup>	$y = 461 (\pm 12) - 2.62 (\pm 1.10) \times \text{fDF}$	0.039	9.6	0.36
During night period <sup>b</sup>	$y = 344 (\pm 16) + 1.06 (\pm 1.54) \times \text{fDF}$	0.509	13.5	0.05
During day period <sup>c</sup>	$y = 530 (\pm 17) - 4.82 (\pm 1.37) \times \text{fDF}$	0.006	12.0	0.55
During eating <sup>d</sup>	$y = 727 (\pm 44) + 12.52 (\pm 4.10) \times \text{fDF}$	0.012	35.8	0.48
Mean without eating <sup>e</sup>	$y = 449 (\pm 14) - 3.27 (\pm 1.26) \times \text{fDF}$	0.027	11.0	0.40
<b>AHP</b>				
Mean, per 24 h	$y = 80 (\pm 12) - 2.31 (\pm 1.11) \times \text{fDF}$	0.063	9.7	0.30
During night period <sup>b</sup>	$y = 20 (\pm 7) - 0.45 (\pm 0.67) \times \text{fDF}$	0.516	5.8	0.04
During day period <sup>c</sup>	$y = 116 (\pm 17) - 3.43 (\pm 1.63) \times \text{fDF}$	0.062	14.3	0.31
During eating <sup>d</sup>	$y = 280 (\pm 39) + 7.36 (\pm 3.69) \times \text{fDF}$	0.074	32.3	0.28
Mean without eating <sup>e</sup>	$y = 71 (\pm 12) - 2.73 (\pm 1.09) \times \text{fDF}$	0.031	9.5	0.39

<sup>a</sup> Correcting HP for differences in ME intake (i.e., 0.2 kJ for each kJ ME) changes the relationship:  $\text{HP} = 454 (\pm 11) - 1.77 (\pm 1.04) \times \text{fDF}$  ( $P = 0.118$ ).

<sup>b</sup> The night period is defined as the period from 2200 to 0700.

<sup>c</sup> The day period is defined as the period from 0700 to 2200.

<sup>d</sup> The eating period is defined as the period from 0800 to 0900.

<sup>e</sup> Mean without eating is defined as the mean per 24 h without the eating period.

ME intake tended to be lower when SBPS content increased ( $P = 0.057$ ; Table 2). Assuming that HP varies by about 0.2 kJ for each kJ ME, HP may be corrected for differences in ME intake (Table 4). Correcting HP for differences in ME intake changes the relationship between HP and fDF intake:

$$\text{HP} = 454 (\pm 11) - 1.77 (\pm 1.04) \times \text{fDF} \quad (P = 0.118) \quad [4]$$

It can be concluded that differences in ME intake might accentuate or mask effects of treatments on HP. In the present study, it is unlikely that the differences in ME intake accentuate the effect of fDF intake on physical activity, because the lower feeding level (i.e., ME intake) with increasing SBPS content would increase physical activity and not diminish it, as found in the present study.

Averaging over the whole day (24 h), AHP tended ( $P = 0.063$ ) to decrease with increasing fDF intake. During the night period, fDF intake did not affect AHP ( $P = 0.516$ ). During the day period, however, AHP tended ( $P = 0.062$ ) to decrease with increasing fDF intake. During eating, AHP tended ( $P = 0.074$ ) to increase with increasing fDF intake. After removing the data of the eating period from the whole

day, AHP decreased with increasing fDF intake ( $P = 0.031$ ). There were no effects of fDF intake on RHP (data not shown).

About 90% of the decrease in mean HP per gram of fDF intake (2.62 kJ/g;  $P = 0.039$ ) was caused by the decrease in mean AHP per gram of fDF intake (2.31 kJ/g;  $P = 0.063$ ). During eating, about 60% of the increase in HP per gram of fDF intake (12.52 kJ/g;  $P = 0.012$ ) was caused by the increase in AHP per gram of fDF intake (7.36 kJ/g;  $P = 0.074$ ).

The observed tendencies for alteration of physical activity by dietary composition is in agreement with other studies with growing pigs (Schrama et al., 1998), gilts (Brouns et al., 1994), and sows (e.g., Robert et al., 1993; Brouns & Edwards, 1994; Ramonet et al., 1999; 2000b). As reviewed by Meunier-Salaün et al. (2001), most effects of fibrous diets on sow behavior were found using sugar beet pulp as fiber source. A decrease in activity level of sows with increasing sugar beet pulp intake might be related to the high water-holding capacity of the diets and delayed gastric emptying and/or specific effects of short chain fatty acids that are produced during fermentation in the hindgut (Meunier-Salaün et al., 2001). Furthermore, the total fermentability and/or fermentation rate related to the botanical origin of DF might be of importance for an effect of DF on behavior of pigs (e.g., feeding motivation).

In conclusion, the effect of fDF intake on energy expenditure for physical activity was not constant during the day. Sows tended ( $P = 0.074$ ) to spend more energy on physical activity during eating with increasing fDF intake, but less during the remainder of the day (i.e., 24 h without eating,  $P = 0.031$ ).

### **Physical Activity and Net Energy**

The regression coefficients in the relationships between mean AHP and fDF intake (Table 5) can be interpreted as the saving effect of physical activity on the NE value of the fDF fraction. During 24 h, the saving effect of AHP on the NE value of fDF was 2.3 kJ per g of fDF intake ( $P = 0.063$ ; Table 5). The NE value of the fDF fraction of a diet or feed ingredient (in kJ/g) can be calculated by correcting HP of pigs for similar digestible nutrient intakes, followed by a regression of fDF intake on the corrected HP (Rijnen et al., 2001). A second method to calculate the saving effect of physical activity on the NE value of fDF is the difference in regression coefficients between regression of fDF intake on HP during the 24-h period and HP during the night period. This method assumes that sows are not active during the night period. According to this method and the regression coefficients in Table 5, the saving effect of physical activity on the NE value of fDF from SBPS was 3.7 kJ/g of fDF intake. According to the relationship between AHP and fDF intake (Table 5) and the calculation as described above, the saving effect of physical activity of sows on the NE value of fDF from SBPS ranges between 2.3 and 3.7 kJ per g of fDF intake (i.e., fDF from SBPS). Assuming a NE value of fDF from SBPS of 13.4 kJ/g (Rijnen et al., 2001), the energy saving effect

of physical activity of sows on the NE value of fDF from SBPS ranges between 18 and 28% of its NE content.

**Table 6.** Mean total eating time (min) and feed consumption rate of group-housed sows fed diets differing in sugar beet pulp silage (SBPS) content

Item	Total eating time min	Feed consumption rate <sup>a</sup>	
		g DM/min	g DM·kg <sup>-0.75</sup> ·min <sup>-1</sup>
0% SBPS	11.8	192	3.3
10% SBPS	12.5	177	3.1
20% SBPS	19.8	124	2.0
30% SBPS	18.1	132	2.2
SEM	2.0	19	0.2
<i>P</i> -value	0.048	0.081	0.016
<i>P</i> -value contrast <sup>b</sup>	0.009	0.016	0.003

<sup>a</sup> Dry matter (DM) intake for 0%, 10%, 20%, and 30% SBPS were 38.05, 38.38, 38.53, and 38.34 g·kg<sup>-0.75</sup>·d<sup>-1</sup>, respectively.

<sup>b</sup> A contrast method was used to analyze differences between low- and high-fiber diets (i.e., 0%+10% vs 20%+30% SBPS).

### Feed Consumption Rate

The present study shows that fDF intake (i.e., fDF from SBPS) of sows had opposite effects on HP during eating and during the remainder of the day. Therefore, the eating period (from 0800 to 0900) is discussed more closely.

Mean eating time was 16 min (Table 6), which is in agreement with the mean eating time in individually housed sows (13 min) reported by Noblet et al. (1993). Mean eating time is also similar to reported eating times of sows fed low-fiber diets (Braud et al., 1998; Ramonet et al., 1999; 2000b). Despite similar DM intake among different treatments in the present study, mean eating time was affected by diet ( $P = 0.048$ ; Table 6). Contrast analysis showed that sows fed 0 or 10% SBPS spent less time on eating than sows fed 20 or 30% SBPS ( $P = 0.009$ ). Several authors reported an increased time spent on eating when DF content increased (e.g., Brouns et al., 1994; Braud et al., 1998; Ramonet et al., 1999; 2000b).

In the present study, 8.8% of total activity (177 min/day) of the sows was spent on eating. Noblet et al. (1993) reported that sows spent 5.8% of their total activity time on eating. This is in agreement with the sows fed 0 or 10% SBPS in the present study (i.e., 6.0% of total activity time was spent on eating). Sows fed 20 or 30% SBPS spent a larger percentage of their total activity time on eating (i.e., 12.7%), which is in agreement with sows fed high-fiber diets (i.e., 14.2%) in the study from Ramonet et al. (1999).



The feed consumption rate in the present study averaged 156 g DM/min or  $2.7 \text{ g DM} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$ . The average feed consumption rate was higher than that reported by Dourmad (1993; 95 g/min), Noblet et al. (1993; 120 g/min), and Brouns et al. (1997; 108 g/min), and similar to that of sows fed low-fiber diets as reported by Ramonet et al. (1999 and 2000b; 152 g/min and 149 g/min, respectively). In the present study, rate of feed consumption (expressed in  $\text{g DM} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$ ) was affected by diet ( $P = 0.016$ ; Table 6). On average, feed consumption rate was higher for groups fed 0 or 10% SBPS than for groups fed 20 or 30% SBPS ( $P = 0.003$ ). This is in agreement with findings of several authors, who reported that feed consumption rate of sows fed a control diet was higher than that of sows fed a diet containing high percentages of sugar beet pulp (Brouns et al., 1997; Braud et al., 1998; Ramonet et al., 2000b). As reviewed by Meunier-Salaün et al. (2001), the low feed consumption rate of diets containing high levels of sugar beet pulp might be due to reduced feeding motivation level, increased mastication time, or lowered palatability due to physical and/or metabolic processes during digestion of sugar beet pulp. Guérin et al. (2001) showed a higher water-holding capacity and delayed gastric emptying for diets with sugar beet pulp. Furthermore, differences in feed consumption rates between studies might be due to differences in housing conditions, as suggested by Nielsen (1999). Besides, differences between the present study and other studies might also be due to differences in feed preparation (i.e., mash feed vs pellets or meal).

Finally, it was found in the present study that for each gram increase of fDF intake (i.e., fDF from SBPS) the feed consumption rate decreased by 11 g DM/min ( $P = 0.012$ ) or  $0.19 \text{ g DM} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$  ( $P = 0.003$ ). Diet composition affected time spent on eating and feed consumption rate of sows.

## **Implications**

In feed evaluation systems for pigs, behavior or physical activity is often excluded. Dietary factors, however, can affect energy expenditure on physical activity. The present study shows that energy spent on physical activity decreases when sows eat more fermentable carbohydrates from sugar beet pulp silage. Effects on heat production and activity-related heat production are not constant during the day. In this way, the eating period is very important. Feed consumption rate decreases and total eating time increases with increasing dietary fiber contents. Moreover, the impact of dietary fiber on physical activity, metabolic rate, and feed consumption rate might be related to the source or botanical origin of dietary fiber. Therefore, there might be differences in energetic utilization between different sources of dietary fiber. Mechanisms involved, however, are not clear yet.



## **Chapter 4**

### **Effects of Two Different Sources of Dietary Fiber on Energy Metabolism in Group-Housed Growing Pigs**

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## Effects of Two Different Sources of Dietary Fiber on Energy Metabolism in Group-Housed Growing Pigs

### Abstract

The energetic efficiency of two types of dietary fiber (DF) in group-housed growing pigs was studied. Twenty clusters of 14 barrows (50 kg) were fed one of ten diets. Diets differed in type and content of fermentable DF (fDF) and digestible starch. Five diets contained solvent-extracted coconut meal (SECM) and five diets contained soybean hulls (SBH) as main fDF source. The main contrast in the experimental diets was achieved by adding different levels of either SECM or SBH to the diets. On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of SECM or SBH. Pigs were group-housed (seven pigs per subgroup) and fed at 2.5 times the assumed maintenance energy requirements. All clusters were fed similar amounts of calculated NE, ileal digestible protein and amino acids, vitamins, and minerals. After a 32-d preliminary period, nitrogen and energy balances were measured per cluster during a 7-d experimental period in environmentally controlled respiration chambers. Digestibility of dietary energy decreased with increasing DF intake ( $P < 0.001$ ). Metabolizability of dietary energy decreased with increasing fDF intake ( $P < 0.001$ ). Methane production increased with increasing fDF intake ( $P < 0.001$ ). Based on heat production data and apparent fecal digestibility of nutrients, the estimated energetic efficiency of fDF from SECM was 63%, and from SBH 58%. The calculated energetic efficiency of fDF was not affected by type of dietary fermentable carbohydrates ( $P > 0.10$ ). The average energetic efficiency of fDF for energy retention above maintenance (61%) was about 80% of that of digestible starch as used in the currently used NE based feed evaluation systems for pigs. It can be concluded that the energetic efficiency of fDF did not differ between the two types of fDF (i.e., fDF from SECM or SBH) used in the present study.

### Introduction

In most NE based feed evaluation systems, energy of digestible nutrients (i.e., CP, crude fat, starch, sugars, and dietary fiber [DF]) is used to calculate the NE content of a diet or feed ingredient (Noblet et al., 1994; CVB, 1998). The DF fraction of a diet contains all plant polysaccharides that are not hydrolyzed by endogenous enzymes of the mammalian digestive system (nonstarch polysaccharides plus lignin) (Wenk, 2001). Microbes in the gut, however, may degrade DF. The NE content of DF fractions is calculated by using digestibility data and a certain efficiency with which NE from fermentable DF (fDF) is used for production. In most cases, utilization of energy from fDF is considered to be 70% of the energetic efficiency of digestible starch (Noblet et al., 1994; CVB, 1998).

The use of fiber-rich feed ingredients in pig diets is increasing (Noblet & Le Goff, 2001). This increased use of fiber-rich ingredients may benefit well being of pigs (Low, 1985; Williams et al., 2001). The composition of DF fractions of different origin (e.g., in content of pectin, NDF, ADF, and ADL) can differ widely (Wenk, 2001). These differences in composition lead to differences in digestibility of DF from different botanical origin (Noblet & Le Goff, 2001). Moreover, it is questionable that a single value is applicable for the efficiency with which energy from fDF is utilized. It was found, for example, that group-housed growing pigs (Schrama et al., 1998) and group-housed sows (Rijnen et al., 2001) were able to use energy from fDF from sugar beet pulp silage as efficiently as energy from digestible starch from tapioca.

It can be hypothesized that the botanical origin of DF affects the efficiency with which energy from fDF is utilized in pigs. In the present study, the efficiency with which group-housed growing pigs utilize energy from fDF from two different sources was studied.

## **Materials and Methods**

### ***Animals and Housing***

A total of 280 crossbred barrows ([Dutch Landrace × Great Yorkshire] × Pietrain) were used. Pigs originated from one farm, which was located 30 km from the laboratory. The experiment consisted of a 32-d preliminary period followed by a 7-d experimental period. The preliminary period allowed the pigs to adjust to the experimental diets and housing conditions. Pigs were divided into 20 clusters of 14 pigs each. Cluster was the experimental unit in this experiment. The clusters were assigned to one of the ten experimental diets. The study was conducted in 10 trials. At the start of the preliminary period, pigs weighed on average 37.3 kg (SEM = 1.2 kg). Clusters were formed at the start of the preliminary period. During the first 20 d of the preliminary period, pigs were group-housed per cluster. Thirteen days before the experimental period, each cluster was placed in one of two identical, large, environmentally controlled respiration chambers (Verstegen et al., 1987b). Within each chamber, pigs were group-housed in one of two pens with a floor-space of 8.3 m<sup>2</sup> each (i.e., seven pigs per subgroup). Thus, each cluster consisted of two subgroups. In the chambers, environmental temperature was kept constant at 20°C, which is thermoneutral for group-housed growing pigs at the experimental feeding level (ARC, 1981; Verstegen, 1987). Relative humidity was maintained at about 65%. Air velocity was < 0.2 m/s. Pigs were exposed to 12 h of light (about 300 lx, from 0700 to 1900) and to 12 h of darkness (about 10 lx, from 1900 to 0700).

### **Feeding**

The aim of the present study was to assess the energetic utilization of fDF from two different sources. Therefore, ten diets were formulated. Five diets contained different levels of solvent-extracted coconut meal (SECM) (Diets 1 to 5) and five diets contained different levels of soybean hulls (SBH) (Diets 6 to 10). Dietary compositions and analyzed nutrient compositions of the diets are shown in Table 1 and 2, respectively. For all diets, pigs were fed the same amount of calculated NE, with similar intakes of ileal digestible protein and amino acids, vitamins, and minerals. Due to this set up, pigs receiving the different diets were fed different amounts of DM, because the NE content decreases with increasing DF content (Table 1). On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of either SECM or SBH with their diet (Table 3).

During the experiment, pigs within clusters received one of the ten experimental diets. Pigs were fed according to the average metabolic BW (kg<sup>0.75</sup>) per subgroup. Each subgroup was fed at 2.5 times the assumed maintenance energy requirements. The NE requirements for maintenance were assumed to be 293 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup> (Verstegen et al., 1973). Pigs were group-fed twice a day at 0800 and 1530, using one long trough per subgroup. The daily amount of feed per subgroup was based on the mean metabolic BW per subgroup, adjusted for an expected ADG of 600 g. If present, feed refusals were collected 45 min after feeding in order to record ADFI. Feed was given as mash feed and the amount of water added to the feed was 2.3 L/kg DM. Feed and water were mixed immediately before feeding (i.e., no soaking time). In addition, pigs were given ad libitum access to drinking water during the whole experiment.

### **Measurements**

Individual BW was measured weekly from the start of the preliminary period onward. The ADFI was calculated from supplied feed and feed refusals. During the experimental period, apparent fecal digestibility of DM, OM, CP, crude fat, GE, NDF, ADF, and ADL were measured by using the AIA marker method. The dietary AIA content was increased by adding diatomaceous shell powder to the experimental diets (Table 1). During the 7-d experimental period, diets were sampled daily. During 5 d of the experimental period, grab samples of feces were collected daily after feeding at 0800 and 1530. Feces were collected per cluster of pigs (i.e., per chamber), and a sample was pooled per experimental period. After collection of grab samples, the remainder of the feces was removed from the floor. Therefore, grab samples were representative of feces excreted between feeding times.

Feed and feces were analyzed for DM, ash, AIA, CP, crude fat, GE, NDF, ADF, and ADL. Feeds were also analyzed for starch and free sugars. All analyses were carried out in duplicate. The DM content was measured by drying to constant weight at 103°C. Ash content was measured by incineration in an oven at 550°C. Nitrogen

content was measured with the Kjeldahl method using  $K_2SO_4$  and  $HgO$  as catalysts. The crude fat content was measured after hydrolysis with 3 *N* HCl and extraction of the residue with petroleum ether (boiling range 40 to 60°C). The AIA content was measured by treating the residue of the ash determination with 3 *N* HCl to solubilize minerals. The AIA was filtered and weighed after incineration. The starch content was analyzed enzymatically. Free sugars (mono- and disaccharides) were removed by alcohol extraction (ethanol 40%). After gelatinization by heating in an autoclave for 3 h at 130°C, starch was hydrolyzed to glucose with a mixture of enzymes (10 mg of amyloglucosidase, 1 mg of  $\alpha$ -amylase and 12.5 mg of  $\mu$ L-pullulanase in 5 mL of  $H_2O$  per sample) at pH 4.8 (Brunt, 1993). Subsequently, glucose was measured using hexokinase and G6P-dehydrogenase. The sugar content was measured after extracting feed samples with ethanol. Carbohydrates in the filtrate, were hydrolyzed with 0.1 *N* HCl and after using free sugars as a reducing agent to oxidize copper, the content was measured using a spectrophotometer. Cell wall constituents (NDF, ADF, and ADL) were determined according to the methods of Van Soest & Wine (1967). Gross energy values were measured using bomb calorimetry.

Dietary fiber was calculated by subtracting the contents of CP, crude fat, starch, sugar, and ash from the DM content. All starch and sugars present in the diets were easily degradable. Results of the analyses of one feces sample for each diet showed that the content of starch and free sugars was less than 2 g/kg (data not shown). Therefore, we assumed fecal digestibility of starch and sugars to be 100%. Fecal DF was calculated as DM minus fecal CP, crude fat, and ash.

During the experimental period, energy and nitrogen balances were measured per cluster. Feces with urine were collected quantitatively per cluster and sampled for energy and nitrogen analysis. Intake of ME per cluster was calculated from the energy content of feed, feces with urine, and methane production. Total heat production (HP) was measured at 9-min intervals by determining exchange of oxygen, carbon dioxide and methane as described by Verstegen et al. (1987b). This gaseous exchange was used to calculate HP according the formula of Brouwer (1965). During the last 6 d of the experimental period, HP was measured continuously. Total energy retention (ER) was calculated by subtracting HP from ME intake. The retention of N was estimated from N in feed, in feces plus urine, in aerial  $NH_3$ , and in  $NH_4^+$  of water that condensed on the heat exchanger. Energy retention as protein (ERp) was derived from the N retention and subtracting ERp from ER derived the energy retention as fat (ERf).

**Table 1.** Composition of experimental diets (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Ingredient <sup>a</sup> , g/kg											
Extracted coconut meal <sup>b</sup>	50.0	178.6	295.5	402.2	500.0	-	-	-	-	-	-
Soybean hulls <sup>c</sup>	-	-	-	-	-	47.6	170.5	282.6	385.4	480.0	-
Gelatinized maize starch	350.0	250.0	159.1	76.1	-	333.3	238.6	152.2	72.9	-	-
Potato protein	35.0	25.0	15.9	7.6	-	34.5	26.1	18.5	11.5	5.0	-
Wheat	286.0	294.0	301.3	307.9	314.0	351.1	344.8	339.0	333.6	328.8	-
Extracted soybeans	211.3	188.1	167.0	147.8	130.2	184.5	159.1	135.9	114.6	95.0	-
Soybean oil	25.3	24.6	24.1	23.6	23.1	5.2	10.2	14.7	18.9	22.6	-
Sucrose	-	-	-	-	-	3.7	14.3	24.1	33.0	41.2	-
CaCO <sub>3</sub>	13.8	13.1	12.5	11.8	11.4	12.4	10.1	7.9	5.9	4.2	-
NaCl	3.1	3.0	2.8	2.7	2.6	3.0	2.8	2.7	2.6	2.5	-
Monocalcium phosphate	8.8	7.3	5.9	4.7	3.5	8.6	8.3	8.0	7.9	7.7	-
Amino acids	1.5	1.7	1.9	2.2	2.4	1.4	1.1	1.0	0.8	0.7	-
Choline chloride 50%	0.4	0.4	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.3	-
Vitamin and mineral mix <sup>d</sup>	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	-
Cr-maize starch mix	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	-
Diatomaceous shell powder	12.5	11.9	11.4	10.9	10.4	11.9	11.4	10.9	10.4	10.0	-
NE content, MJ/kg	10.38	9.88	9.43	9.02	8.65	9.88	9.43	9.02	8.65	8.30	-

<sup>a</sup> In the calculation of the diets, nutrient compositions of the feed ingredients from CVB (1998) were used in addition to the analyzed content of DM, CP, crude fat, and ash for solvent-extracted coconut meal, soybean hulls, potato protein, wheat, extracted soybeans, and maize starch.

<sup>b</sup> According to CVB (1998) solvent-extracted coconut meal contained (on as fed basis): DM, 896 g/kg; CP, 211 g/kg; ash, 65 g/kg; crude fat, 29 g/kg; starch, 10 g/kg; sugars, 100 g/kg; NSP, 478 g/kg; NDF, 449 g/kg; ADF, 230 g/kg; ADL, 38 g/kg.

<sup>c</sup> According to CVB (1998) soybean hulls (on as fed basis): DM, 885 g/kg; CP, 145 g/kg; ash, 52 g/kg; crude fat, 32 g/kg; starch, 21 g/kg; sugars, 13 g/kg; NSP, 622 g/kg; NDF, 511 g/kg; ADF, 361 g/kg; ADL, - g/kg.

<sup>d</sup> Provided the following amounts of vitamins and minerals per kg of the complete diet: vitamin A, 7,000 IU; vitamin D<sub>3</sub>, 1,700 IU; vitamin E 20 IU; vitamin K<sub>3</sub>, 1.5 mg; vitamin B<sub>1</sub>, 1.5 mg; vitamin B<sub>2</sub>, 4.0 mg; d-pantothenic acid, 11 mg; niacin, 18 mg; vitamin B<sub>12</sub>, 0.018 mg; folic acid, 0.1 mg; vitamin B<sub>6</sub>, 1.0 mg; Co, 0.15 mg; I, 0.75 mg; Fe, 75 mg; Mn, 30 mg; Zn, 50 mg; Cu, 25 mg; Se, 0.30 mg.



**Table 2.** Analyzed nutrient composition of experimental diets, in g/kg (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Dry matter	888	891	894	893	891		884	891	897	902	909
Crude ash	57	61	65	67	71		53	53	53	53	54
Crude protein	182	188	196	203	210		168	175	177	180	182
Crude fat	30	38	40	42	44		19	30	46	64	76
Starch	457	393	320	253	190		489	410	333	273	201
Sugars <sup>a</sup>	35	42	49	55	61		36	50	65	78	88
Dietary fiber <sup>b</sup>	127	169	224	273	315		119	173	223	254	308
NDF	69	113	166	210	247		70	115	154	191	229
ADF	38	69	103	135	163		38	73	104	135	160
ADL	10	21	33	45	55		7	8	9	10	11
Gross energy, MJ/kg	16.3	16.5	16.6	16.6	16.6		15.9	16.4	16.8	17.2	17.6

<sup>a</sup> Reducing sugars expressed in glucose units.<sup>b</sup> Content of dietary fiber was calculated as DM - (CP + crude fat + ash + sugars + starch).**Table 3.** Supplied amounts of experimental diets during the experimental period

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
NE <sup>a</sup> , kJ·kg <sup>-0.75</sup> ·d <sup>-1</sup>	733	733	733	733	733	733	733	733	733	733	733
Feed <sup>b</sup> , g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	70.6	74.1	77.7	81.3	84.7		74.1	77.7	81.3	84.7	88.3
SECM <sup>c</sup> , g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	3.5	13.2	23.0	32.7	42.4		-	-	-	-	-
SBH <sup>c</sup> , g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	-	-	-	-	-	-	3.5	13.2	23.0	32.7	42.4

<sup>a</sup> Amount of NE supplied to clusters of pigs.<sup>b</sup> Amount of feed supplied to clusters of pigs.<sup>c</sup> Amount of solvent-extracted coconut meal (SECM) or soybean hulls (SBH) supplied to clusters of pigs.

### **Statistical Analysis**

In the present study, cluster was the experimental unit. Apparent fecal digestibilities, DM intake, energy and N balance, and mean values of HP were analyzed for effects of diet by ANOVA. Moreover, the aim of the present study was to estimate the energetic efficiency with which fDF was utilized. Therefore, metabolizability of dietary energy, methane production, and HP were analyzed for the effect of diet by linear regression of these traits on the daily intake of fDF (expressed in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The SAS software (SAS Inst. Inc., Cary, NC) was used in all statistical evaluations.

## **Results and Discussion**

### **General**

The number of clusters and animals used are given in Table 4. One cluster (diet 5) was removed from the experiment, because the lights in the chamber were on during the whole experimental period due to a technical failure. Five pigs (on diet 4, 5, 8, and 10) were removed at the start of the experimental period due to health problems. One pig (diet 5) was removed during the experimental period due to health problems.

At the start of the 7-d experimental period, live BW averaged 57.0 kg (SEM = 1.1) and was affected by diet ( $P < 0.05$ ), due to differences in feed refusals and ADG during the preliminary period (data not shown).

During the experimental period no feed refusals occurred, except for one cluster (diet 5) in which 0.2% of the total feed supply was refused. For each diet, feeding level was adjusted to the calculated dietary NE content to supply all clusters with similar amounts of NE (Table 3). Consequently, daily DM intake was affected by diet ( $P < 0.001$ ; Table 4). During the experimental period, ADG was affected by diet ( $P < 0.01$ ; Table 4).

### **Apparent Fecal Digestibility**

The mean apparent fecal nutrient digestibilities per diet are given in Table 5. The apparent fecal digestibility of DM, OM, CP, crude fat, DF, and NDF were affected by diet ( $P < 0.05$ ). When the content of SECM or SBH increased, the apparent fecal digestibility of DM, OM, and CP decreased. The apparent fecal digestibility of crude fat was similar for all diets containing SECM, but increased for diets with increasing content of SBH.

The main sources of DF (i.e., SECM and SBH) were exchanged for gelatinized maize starch. However, to supply clusters with similar amounts of calculated NE, digestible protein and amino acids, sugars and digestible crude fat, diets differed more in composition than only in source and dose of DF, and content of gelatinized maize starch (Table 1). These differences in composition between diets caused differences in

apparent fecal digestibility of nutrients by differences in apparent fecal digestibility of the used feed ingredients (CVB, 1998).

For the digestibility of crude fat, however, differences between diets with SECM and SBH were large. This was due to the high crude fat content of the used SBH compared to the tabulated value (CVB, 1998) (97.0 and 32.3 g/kg DM, respectively). Furthermore, an increased dietary crude fat content leads to an increased apparent fecal digestibility of crude fat (Bakker, 1996). This was, however, not accounted for in diet formulation for the present study. Therefore, clusters that received diets with increasing levels of SBH received more dietary energy than was accounted for in diet formulation.

Digestibility of DF varies with the botanical origin of DF, which is directly related to the physicochemical properties of DF (Noblet & Le Goff, 2001). In the present study, average digestibility of DF for diets with SECM (72.8%; SEM 1.2) was higher ( $P = 0.002$ ) than that for diets with SBH (66.0%; SEM 1.1). The average digestibility of the different components of DF (i.e., NDF, ADF, and ADL) was also higher for diets with SECM than for diets with SBH ( $P < 0.01$ ).

### ***Partitioning of Energy***

#### *General*

The effects of diet on energy partitioning are shown in Table 6. Diet affected the intake of GE, DE, and ME ( $P < 0.001$ ), due to the experimental set up (i.e., feeding the same amount of calculated NE).

#### *Digestibility of Energy*

Digestibility of dietary energy (DCe, in %) was affected by diet ( $P < 0.001$ ), and decreased with increasing daily intake of SECM or SBH. This decrease is in agreement with the results of Noblet & Le Goff (2001), who reported that DCe decreased with increasing dietary content of DF or NDF (g/kg DM). In the present study, DCe was related to DF and NDF content (g/kg DM;  $P < 0.001$ ) as follows:

$$\text{DCe} = 99.0 \text{ (SE 0.9)} - 0.066 \text{ (SE 0.004)} \times \text{DF} \quad \text{RSD} = 1.16 \quad \text{R}^2 = 0.96 \quad [1]$$

$$\text{DCe} = 95.9 \text{ (SE 0.8)} - 0.075 \text{ (SE 0.004)} \times \text{NDF} \quad \text{RSD} = 1.23 \quad \text{R}^2 = 0.95 \quad [2]$$

In the present study, the effects of DF and NDF (g/kg DM) on DCe were not different between the two sources of DF ( $P > 0.10$ ). The effect of dietary NDF content on DCe (i.e., a decrease in DCe of 0.075% per g of NDF content; Eq. [2]) is similar to the reported effect of NDF content from soybean products on DCe by Noblet & Le Goff (0.073% per g of NDF content; 2001). The average DCe in the present study (83.2%) was similar to that reported by Noblet & Le Goff (2001) for soybean products (84.9%).

**Table 4.** Number of clusters, pigs used, and mean initial BW, daily DM intake, and growth during the experimental period in group-housed growing pigs fed the experimental diets

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls					Effect of diet
		1	2	3	4	5	6	7	8	9	10	SEM
No. of clusters	2	2	2	2	2	1	2	2	2	2	2	-
No. of pigs	28	28	28	28	27	11	28	28	26	28	27	-
BW, kg	55.7	56.2	54.9	58.0	53.4		54.1	59.7	58.4	59.0	58.8	1.1
DM intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	62.2 <sup>a</sup>	65.4 <sup>b</sup>	68.6 <sup>c</sup>	72.1 <sup>d</sup>	75.3 <sup>e</sup>		64.9 <sup>b</sup>	68.3 <sup>c</sup>	71.9 <sup>d</sup>	75.2 <sup>e</sup>	78.9 <sup>f</sup>	0.016
DF intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	8.9 <sup>a</sup>	12.6 <sup>b</sup>	17.4 <sup>c</sup>	22.2 <sup>d</sup>	26.6 <sup>e</sup>		8.7 <sup>a</sup>	13.3 <sup>b</sup>	18.4 <sup>c</sup>	21.3 <sup>d</sup>	27.1 <sup>e</sup>	0.3
ADG	622 <sup>abc</sup>	645 <sup>abcd</sup>	591 <sup>ab</sup>	639 <sup>abc</sup>	532 <sup>a</sup>		672 <sup>abcd</sup>	714 <sup>bcd</sup>	714 <sup>bcd</sup>	802 <sup>cd</sup>	788 <sup>d</sup>	29
												0.003

a, b, c, d, e, f Within a row, means with different superscripts differ ( $P < 0.05$ ).

**Table 5.** Mean apparent fecal nutrient digestibility (in %) during the experimental period in group-housed growing pigs fed the experimental diets

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls					Effect of diet
		1	2	3	4	5	6	7	8	9	10	SEM
DM	89.0 <sup>a</sup>	86.6 <sup>ab</sup>	82.8 <sup>bcd</sup>	80.8 <sup>cde</sup>	76.3 <sup>e</sup>		89.5 <sup>a</sup>	86.1 <sup>abc</sup>	82.7 <sup>bcd</sup>	79.8 <sup>de</sup>	76.0 <sup>e</sup>	1.0
OM	91.7 <sup>a</sup>	89.1 <sup>ab</sup>	85.2 <sup>bcd</sup>	82.9 <sup>cde</sup>	78.1 <sup>e</sup>		91.9 <sup>a</sup>	88.4 <sup>abc</sup>	84.8 <sup>bcd</sup>	81.7 <sup>de</sup>	78.0 <sup>e</sup>	1.0
CP	84.2 <sup>a</sup>	80.1 <sup>abc</sup>	73.8 <sup>bcd</sup>	70.9 <sup>de</sup>	63.5 <sup>e</sup>		85.1 <sup>a</sup>	81.7 <sup>ab</sup>	77.5 <sup>abcd</sup>	74.5 <sup>bcd</sup>	71.8 <sup>cde</sup>	1.5
Crude fat	72.2 <sup>ab</sup>	78.5 <sup>a</sup>	77.6 <sup>a</sup>	80.0 <sup>a</sup>	78.7 <sup>a</sup>		59.8 <sup>c</sup>	66.7 <sup>bc</sup>	73.0 <sup>ab</sup>	78.4 <sup>a</sup>	78.1 <sup>a</sup>	1.4
DF	74.6	73.9	72.4	73.2	70.2		70.9	68.2	66.9	62.8	61.4	2.5
NDF	71.2	73.4	74.5	74.7	73.1		66.2	64.6	62.2	60.7	57.3	3.2
ADF	64.9	65.5	65.5	67.3	64.7		60.7	58.1	56.0	53.7	48.6	4.0
ADL	42.3	33.3	35.1	34.2	34.9		35.9	30.3	23.7	13.7	14.5	6.3

a, b, c, d, e Within a row, means with different superscripts differ ( $P < 0.05$ ).

As reviewed by Noblet & Le Goff (2001), effects of DF (or NDF) on DCE is dependent on the botanical origin of DF, and consequently its content of pectins, hemicellulose, cellulose, and lignin. This could, however, not been proven in the present study, which is probably due to the smaller difference in composition between DF from SECM and SBH than expected. For example, the expected (i.e., calculated) content of hemicellulose and cellulose were 185 and 86 g/kg, respectively, for Diet 5 (SECM), and 105 and 134 g/kg, respectively, for Diet 10 (SBH) (CVB, 1998). Whereas, the analyzed content of hemicellulose and cellulose were 85 and 108 g/kg, respectively, for Diet 5, and 68 and 149 g/kg, respectively, for Diet 10.

#### *Metabolizability of Energy*

Metabolizability of dietary energy (ME:GE; Table 6) was affected by diet ( $P < 0.001$ ). This effect is in line with the effect on DCE. Moreover, diets were formulated to provide clusters with similar amounts of calculated NE, therefore, there are differences in metabolizability and ME intake among diets. In the present study, ME:GE was related to fDF intake ( $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $P < 0.001$ ), as follows:

$$\text{ME:GE} = 94.0 \text{ (SE 1.0)} - 1.31 \text{ (SE 0.08)} \times \text{fDF-intake} \quad \text{RSD} = 1.35 \quad R^2 = 0.95 \quad [3]$$

The relationship between ME:GE and fDF intake was not affected by the source of fDF ( $P = 0.110$ ). The decrease in metabolizability of dietary energy by an increase in fDF intake is similar to the decrease in ME:GE by an increase in crude fiber from cellulose as reported by Just et al. (1983). Intake of ME was similar for all groups fed diets with SECM, but increased with increasing SBH content. This increase is due to the high crude fat content of the used SBH, as described above.

#### *Methane Production*

Methane production was affected by diet ( $P = 0.010$ ). Methane production ( $\text{CH}_4$  in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was related to fDF intake ( $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $P < 0.001$ ) as follows:

$$\text{CH}_4 = -0.51 \text{ (SE 1.40)} + 0.95 \text{ (SE 0.11)} \times \text{fDF-intake} \quad \text{RSD} = 1.92 \quad R^2 = 0.83 \quad [4]$$

The relationship between methane production and fDF intake was not affected by the source of fDF ( $P = 0.254$ ). On average, methane production increased with 0.95 kJ per gram of fDF intake. Using an enthalpy value of 17.5 kJ per gram of fDF, 5.4% of the energy content of fDF was lost as methane. This result is similar to the mean result (4 to 5%) reported by Noblet & Le Goff (2001).

**Table 6.** Energy partitioning (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) during the experimental period in group-housed growing pigs fed the experimental diets

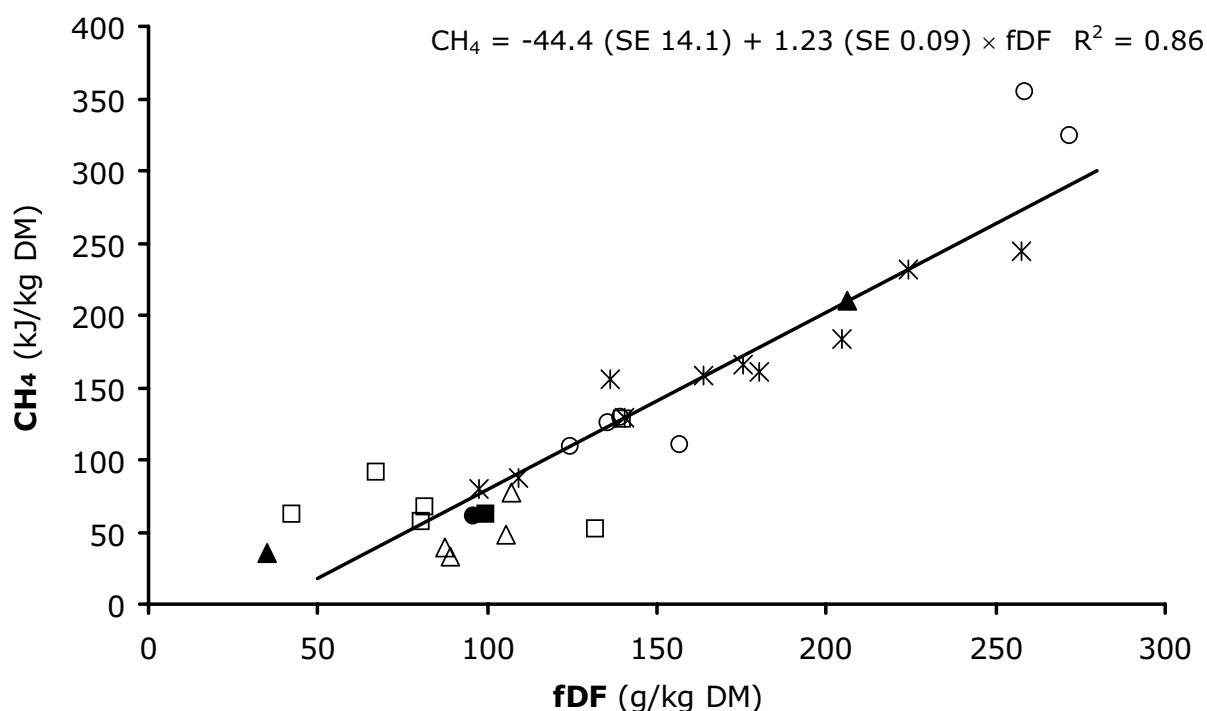
Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls					Effects of diet	
		1	2	3	4	5	6	7	8	9	10		SEM
GE intake		1143 <sup>a</sup>	1207 <sup>b</sup>	1272 <sup>c</sup>	1339 <sup>d</sup>	1402 <sup>e</sup>	1167 <sup>a</sup>	1256 <sup>c</sup>	1345 <sup>d</sup>	1432 <sup>f</sup>	1526 <sup>g</sup>	5	<0.001
DE intake		1023 <sup>a</sup>	1048 <sup>ab</sup>	1048 <sup>ab</sup>	1072 <sup>abc</sup>	1047 <sup>ab</sup>	1048 <sup>ab</sup>	1083 <sup>abc</sup>	1111 <sup>bcd</sup>	1142 <sup>cd</sup>	1162 <sup>d</sup>	13	<0.001
ME intake		983 <sup>ab</sup>	991 <sup>ab</sup>	960 <sup>a</sup>	970 <sup>a</sup>	959 <sup>a</sup>	998 <sup>ab</sup>	1035 <sup>bc</sup>	1062 <sup>cd</sup>	1094 <sup>cd</sup>	1111 <sup>d</sup>	11	<0.001
DCE, %		89.6 <sup>a</sup>	86.8 <sup>ab</sup>	82.4 <sup>bc</sup>	80.1 <sup>cd</sup>	74.7 <sup>d</sup>	89.9 <sup>a</sup>	86.2 <sup>ab</sup>	82.5 <sup>bc</sup>	79.9 <sup>cd</sup>	76.2 <sup>d</sup>	13.2	<0.001
ME:GE, %		86.1 <sup>a</sup>	82.0 <sup>ab</sup>	75.4 <sup>cd</sup>	72.4 <sup>de</sup>	68.5 <sup>e</sup>	85.5 <sup>a</sup>	82.4 <sup>ab</sup>	78.9 <sup>bc</sup>	76.4 <sup>cd</sup>	72.8 <sup>de</sup>	0.8	<0.001
Methane		5.3 <sup>a</sup>	8.2 <sup>ab</sup>	10.7 <sup>ab</sup>	16.2 <sup>b</sup>	17.9 <sup>b</sup>	5.0 <sup>a</sup>	10.3 <sup>ab</sup>	11.0 <sup>ab</sup>	12.0 <sup>ab</sup>	14.0 <sup>ab</sup>	1.8	0.010
Heat production		639 <sup>ab</sup>	635 <sup>a</sup>	652 <sup>abc</sup>	648 <sup>abc</sup>	672 <sup>bcd</sup>	656 <sup>abc</sup>	656 <sup>abc</sup>	673 <sup>cd</sup>	677 <sup>cd</sup>	692 <sup>d</sup>	6	<0.001
Energy retention													
Total (ER)		344 <sup>abcde</sup>	356 <sup>abcde</sup>	308 <sup>de</sup>	322 <sup>cde</sup>	289 <sup>e</sup>	342 <sup>bcde</sup>	380 <sup>abcd</sup>	388 <sup>abc</sup>	417 <sup>ab</sup>	419 <sup>a</sup>	14	<0.001
Protein (ERp)		144 <sup>a</sup>	132 <sup>abc</sup>	120 <sup>abc</sup>	117 <sup>bc</sup>	114 <sup>c</sup>	140 <sup>abc</sup>	140 <sup>abc</sup>	142 <sup>ab</sup>	145 <sup>a</sup>	142 <sup>ab</sup>	4	0.005
Fat (ERf)		200 <sup>ab</sup>	224 <sup>abcd</sup>	188 <sup>ab</sup>	205 <sup>abc</sup>	174 <sup>a</sup>	203 <sup>abc</sup>	240 <sup>abcd</sup>	246 <sup>bcd</sup>	272 <sup>cd</sup>	278 <sup>d</sup>	12	0.002

a, b, c, d, e, f, g Within a row, means with different superscripts differ ( $P < 0.05$ ).

As suggested by Schrama et al. (1998), differences among studies in energy losses as methane seem to be related to dietary factors (e.g., type and level of DF) or differences in microbiota present in the hindgut of pigs. Shi & Noblet (1994) reported differences in methane production for growing pigs of different BW and for different dietary compositions. Noblet & Le Goff (2001) indicate that the variation between studies in the extent of methane production per unit of fermented DE is high.

As suggested by Shi & Noblet (1994), methane production in pigs cannot be considered as a reliable predictor of rate of fermentation in the digestive tract of pigs. In dose response studies with group-housed pigs, as in the present study, there are clear relations between methane production and fDF intake from the same source of fermentable carbohydrates (Schrama et al., 1998; Rijnen et al., 2001). In studies that use more sources of fermentable carbohydrates, no clear relationships were reported (e.g., Shi & Noblet, 1994).

The total amount of methane production by monogastric animals is low compared to that of ruminants (Jensen, 1996). In ruminants, the molar percentage of the different volatile fatty acids (VFA) produced during fermentation influences the production of methane in the rumen. Acetate and butyrate promote methane production while propionate formation can be considered as a competitive pathway for hydrogen use in the rumen. Moreover, the microbial ecosystem of the rumen involved in propionate formation can alter with dietary conditions. In the hindgut of monogastrics, as in the rumen, methanogens use  $H_2$  to reduce  $CO_2$  to methane, and non-methanogens use  $H_2$  to reduce  $CO_2$  to acetate, which can be absorbed into the blood (Moss et al., 2000). It can be hypothesized that the composition of the DF fraction of diets affects the composition of microbiota in the hindgut and the pattern of VFA production in growing pigs, which might affect methane production. In the present study, however, there was no significant difference between methane production of pigs fed diets with SECM compared to pigs fed diets with SBH ( $P = 0.28$ ). In addition, there was a high variation in methane production from the different clusters of pigs. In order to compare the results in methane production from the present study with previous data, literature data on methane production in growing pigs are shown in Figure 1. The relationship obtained from these studies shows that methane production increases with 1.2 kJ for each gram of additional fDF in the diet. Using an enthalpy value of 17.5 kJ/g fDF, energy loss as methane represents about 7% of the energy of fDF. This result is slightly higher than the mean value (4 to 5%) reported by Noblet & Le Goff (2001). Within most practical diets for growing pigs, the loss of energy as methane will be limited.

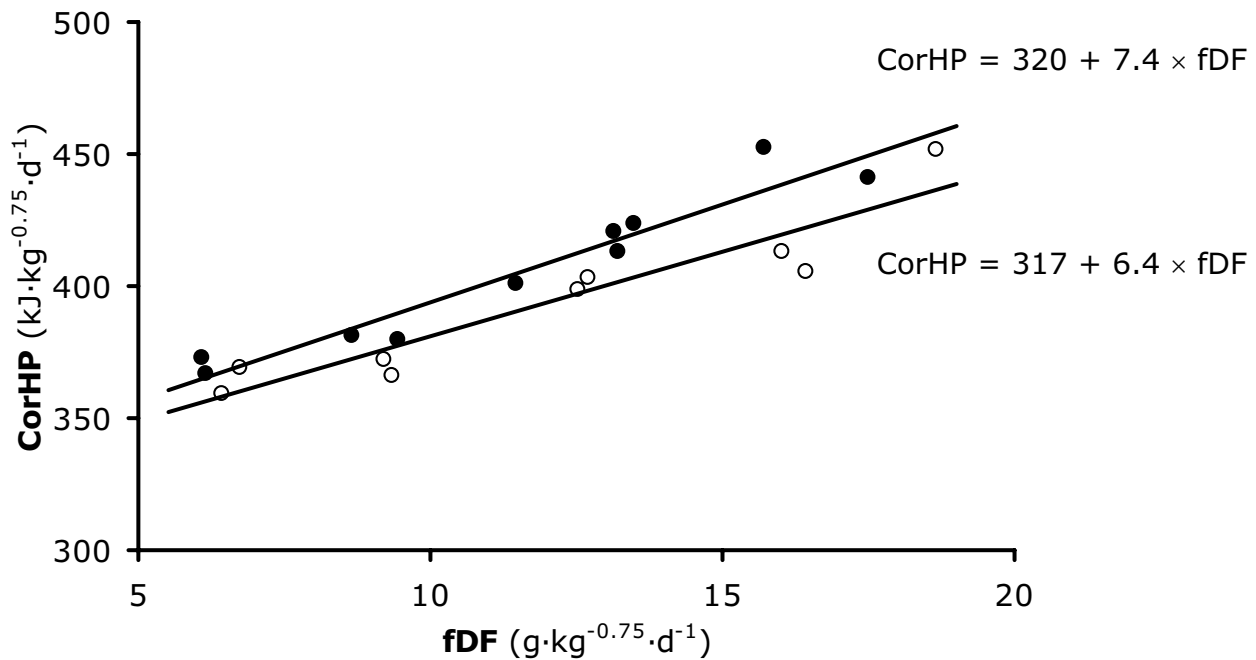


**Figure 1.** Relationship between methane energy losses (CH<sub>4</sub>, kJ/kg DM) and fermentable dietary fiber (fDF, g/kg DM); fDF is calculated as the difference between digestible organic matter and the sum of digestible crude protein, crude fat, starch, and sugars (■ Shi & Noblet, 1993b; □ Noblet & Shi, 1994; ● Noblet et al., 1994; ○ Bakker, 1996; ▲ Jørgensen et al., 1996a; △ Le Goff et al., 2001; \* present study).

### Net Energy Evaluation

The aim of the present study was to assess the energetic efficiency of fDF. As described by Rijnen et al. (2001), the heat increment of fDF can be obtained from the linear regression between HP and fDF intake, after correcting HP for differences in digestible nutrient intakes and methane production (CorHP). The intake of digestible nutrients was measured per cluster of pigs, using the actual feed intake and the measured apparent fecal digestibility of nutrients. The values of heat increment of digestible CP, crude fat, starch, and sugars used for the correction of HP were 12.8, 3.2, 4.0, and 3.6 kJ/g, respectively. These heat increments were derived from the energetic efficiency of 46, 92, 77, and 77%, respectively, for the digested nutrients used in the current Dutch NE evaluation system for pigs (CVB, 1998). As described by Boisen & Verstegen (2000), there are minor differences in the energetic efficiencies as used in different NE based feed evaluation systems. The relationships between CorHP and daily fDF intake from SECM and SBH are presented in Figure 2.





**Figure 2.** Relationships between total heat production (HP) and daily intake of fermentable dietary fiber (fDF) for solvent-extracted coconut meal (○) or soybean hulls (●) in group-housed growing pigs. Heat production data were corrected (CorHP) for similarity in daily intakes of digestible CP, crude fat, starch, and sugars. For this correction, the measured daily digestible nutrient intakes were used and the values for the heat increment by digested CP, crude fat, starch, and sugars of 12.8, 3.2, 4.0, and 3.6 kJ/g, respectively, were used.

In the present study, CorHP (kJ·kg<sup>-0.75</sup>·d<sup>-1</sup>) was related to fDF (g·kg<sup>-0.75</sup>·d<sup>-1</sup>) as follows:

Diets with solvent-extracted coconut meal:

$$\text{CorHP} = 317 (\text{SE } 10) + 6.4 (\text{SE } 0.8) \times \text{fDF} \quad R^2 = 0.89 \quad [5]$$

Diets with soybean hulls:

$$\text{CorHP} = 320 (\text{SE } 10) + 7.4 (\text{SE } 0.8) \times \text{fDF} \quad R^2 = 0.93 \quad [6]$$

The heat increment of fDF for diets with SECM or SBH was 6.4 and 7.4 kJ/g of fDF intake, respectively. The estimated value for heat increment of fDF from SECM tended to be lower ( $P = 0.098$ ) than the heat increment value of 8.0 kJ/g fDF used in the current Dutch NE evaluation system for pigs (CVB, 1998). The estimated value for heat increment of fDF from SBH did not differ ( $P = 0.445$ ) from the heat increment value of 8.0 kJ/g fDF used in the current Dutch NE evaluation system for pigs (CVB,

1998). The energetic efficiency of fDF from solvent-extracted coconut meal and from soybean hulls was 63% and 58%, respectively, using an enthalpy value of 17.5 kJ/g for fDF. Moreover, the estimated values for the energetic efficiency of fDF did not differ between SECM and SBH ( $P = 0.81$ ). Therefore, the hypothesis that the energetic efficiency of fDF would differ between different sources of fDF could not be proven in the present study. This might be due to the smaller difference in composition of the DF fractions (i.e., content of NDF, ADF, and ADL) of the used SECM and SBH than expected from CVB (1998), as described earlier. It can be hypothesized that a larger difference in composition of DF fractions might cause larger differences in the heat increment of fDF for different sources of DF.

The energetic efficiency of fDF from SECM and from SBH were lower ( $P < 0.05$ ) than the energetic efficiency of 77% of digestible starch used in most NE based evaluation system for pigs. The energetic efficiencies for fDF, estimated in the present study, were lower than the energetic efficiencies for fDF from sugar beet pulp silage reported by Schrama et al. (1998) and Rijnen et al. (2001). In those experiments the energetic efficiency of fDF from sugar beet pulp silage was estimated in either growing pigs (Schrama et al., 1998) or sows (Rijnen et al., 2001). The DF fraction of sugar beet pulp silage contains high levels of pectin, compared to the DF fractions used in the present study.

Between studies, there seem to be differences in energetic efficiency of fDF from different types of fermentable carbohydrates. This still might be related to differences in composition of DF, but also to the pattern of VFA production, the velocity of fermentation in the gastrointestinal tract, or to specific components in feed ingredients. More research is needed to unravel the mechanisms involved.

## **Chapter 5**

### **Effects of Two Different Dietary Fermentable Carbohydrates on Activity and Heat Production in Group-Housed Growing Pigs**

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## Effects of Two Different Dietary Fermentable Carbohydrates on Activity and Heat Production in Group-Housed Growing Pigs

### Abstract

The effects of two sources of dietary fiber (DF) on behavior and heat production (HP) in group-housed growing pigs were studied. Twenty clusters of 14 barrows (50 kg) were fed one of 10 diets. Diets differed mainly in type and content of fermentable DF (fDF), and in content of digestible starch. Five diets contained solvent-extracted coconut meal (SECM), and five diets contained soybean hulls (SBH) as main fDF source. On an as-fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of SECM or SBH. A total of 280 crossbred growing pigs were used, divided into clusters of 14 pigs each. Pigs were group-housed and fed at 2.5 times the assumed maintenance energy requirements. All clusters were fed similar amounts of NE, ileal digestible protein and amino acids, vitamins, and minerals. Consequently, DM intake differed among diets because NE content decreases with increasing DF content. After a 32-d preliminary period, HP was measured per cluster during a 7-d experimental period in environmentally controlled respiration chambers. Behavior of the pigs was recorded using time-lapse video recorders during two different days within the experimental period. Intake of digestible starch and fDF was different ( $P < 0.001$ ) among diets, whereas intake of digestible CP was similar for all diets. On average per day, pigs spent 153 min standing, 42 min sitting, 202 min lying on chest, and 1043 min lying on their flanks. Pigs fed SECM diets spent on average less time ( $P < 0.05$ ) lying on chest than pigs fed SBH diets. Total time spent on physical activity (i.e., "standing plus sitting": 195 min/d) was not affected by diet. Total HP and resting HP were affected by diet and were on average lower ( $P < 0.01$ ) for pigs fed SECM diets than for pigs fed SBH diets. Activity-related heat production (AHP) averaged 65 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup>, and was not affected by diet. There was a linear relationship between fDF intake and HP ( $P < 0.001$ ) and there was no relationship between fDF intake and AHP. During separated parts of the day, fDF intake also affected HP. The saving effect of physical activity on the NE values of fDF from SECM and SBH were 0.56 and 0.84 kJ for each gram of fDF intake, respectively. Both these saving effects were not significantly different from zero. We conclude that fDF from SECM and SBH did not affect energy expended on physical activity by growing pigs, and that the NE value of fDF from SECM and SBH was not affected by changes in physical activity.

### Introduction

Most (net) energy feed evaluation systems are based on digestion and utilization data to calculate the potency of a feed ingredient or diet for energy deposition and maintenance. These systems assume that energy requirements for maintenance are unaffected by dietary composition. In growing pigs (e.g., Schrama et al., 1996; 1998)

and sows (e.g., Robert et al., 1993; Brouns et al., 1994; Rijnen et al., 2003a), however, differences in dietary ingredients affected physical activity. The impact of dietary composition on physical activity indicates that energy requirements for maintenance are not constant. In addition, currently used feed evaluation systems are mostly based on experiments with individually housed growing pigs (e.g., Noblet et al., 1994; CVB, 1998).

Schrama et al. (1998) reported that physical activity of growing pigs was decreased with increasing dietary fiber (DF) content (i.e., DF from sugar beet pulp silage [SBPS]). Rijnen et al. (2003a) reported that physical activity of group-housed sows also tended to decreased with increasing DF content (i.e., DF from SBPS), and that this effect was not constant during the day.

Comparison between studies suggests that there might be differences in energetic utilization of fermentable DF (fDF) from different sources of dietary fermentable carbohydrates (Schrama et al., 1998). These differences in energetic utilization of fDF might be related to differences in energy expenditure for physical activity. It can be hypothesized that different sources of DF have different effects on behavior and energy expenditure for physical activity of pigs. In the present study, effects of two sources of DF on behavior and heat production in group-housed growing pigs were studied.

## **Materials and Methods**

### ***General***

A total of 280 crossbred barrows ([Dutch Landrace × Great Yorkshire] × Pietrain) were used. The experiment consisted of a 32-d preliminary period followed by a 7-d experimental period. Pigs were divided into 20 clusters of 14 pigs each (i.e., two groups of seven pigs each). Cluster was the experimental unit in this experiment. The clusters were randomly assigned to one of the ten experimental diets. The aim of the present study was to study the effects of fDF intake from two different sources at different levels on behavior and activity-related heat production (AHP) in group-housed growing pigs. Therefore, ten diets were formulated. Five diets contained different levels of solvent-extracted coconut meal (SECM) (Diets 1 to 5) and five diets contained different levels of soybean hulls (SBH) (Diets 6 to 10). Dietary compositions and analyzed nutrient compositions of the diets are shown in Table 1 and 2, respectively. For all diets, pigs were fed the same amount of calculated NE, with similar intakes of ileal digestible protein and amino acids, vitamins, and minerals. The main contrast in the experimental diets was achieved by adding different levels of either solvent-extracted coconut meal (SECM) or soybean hulls (SBH) to the diets (Table 1 and 2). On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of either SECM or SBH with their diet. Diets with the lowest DF content (diets 1

and 6) contain DF contents that are normally used in practical diets and can therefore be considered as control diets within diets with the same DF source. Pigs were fed according to the average metabolic BW ( $\text{kg}^{0.75}$ ) per subgroup. Each subgroup was fed at 2.5 times the assumed maintenance energy requirements. The NE requirements for maintenance were assumed to be  $293 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  (Verstegen et al., 1973). Pigs were group-fed twice a day at 0800 and 1530 from two long troughs per cluster. Feed was given as mash feed and the amount of water added to the feed was 2.3 L/kg of DM.

At the start of the preliminary period, clusters were formed and pigs weighed on average 37.3 kg (SEM = 1.2). Thirteen days before the experimental period, each cluster was placed in one of two identical, large, environmentally controlled respiration chambers (Verstegen et al., 1987b) and divided into two groups (i.e., seven pigs each). Thus, each cluster consisted of two subgroups. In the chambers, environmental temperature was kept constant at 20°C, which is thermoneutral for group-housed growing pigs at the experimental feeding level (ARC, 1981; Verstegen, 1987). Relative humidity was maintained at about 65%. Air velocity was < 0.2 m/s. Pigs were exposed to 12 h of light (about 300 lx, from 0700 to 1900) and 12 h of partial darkness (about 10 lx, from 1900 to 0700) to allow video recordings.

### **Measurements**

Total heat production (HP) was measured at 9-min intervals by determining exchange of oxygen, carbon dioxide, and methane (indirect calorimetry) as described by Verstegen et al. (1987b). These gaseous exchanges were used to calculate HP according the formula of Brouwer (1965). During the last 6 d of the experimental period, HP was measured continuously.

Behavior of the pigs was recorded using time-lapse video recorders during two different days (i.e., two 24-h periods) within the experimental period. An instantaneous scan sampling technique (as described by Altmann, 1974) was used to analyze the video recordings for behavioral characteristics (Table 3). The analyses of video recordings for behavioral characteristics were done at 3-min intervals. At these 3-min intervals, the number of pigs that exhibited a specific behavior was recorded. With these data, the percentage of time of all pigs that was spent on a specific behavior was calculated.

**Table 1.** Composition of experimental diets (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Ingredient <sup>a</sup> , g/kg											
Extracted coconut meal <sup>b</sup>	50.0	178.6	295.5	402.2	500.0	-	-	-	-	-	-
Soybean hulls <sup>c</sup>	-	-	-	-	-	47.6	170.5	282.6	385.4	480.0	-
Gelatinized maize starch	350.0	250.0	159.1	76.1	-	333.3	238.6	152.2	72.9	-	-
Potato protein	35.0	25.0	15.9	7.6	-	34.5	26.1	18.5	11.5	5.0	-
Wheat	286.0	294.0	301.3	307.9	314.0	351.1	344.8	339.0	333.6	328.8	-
Extracted soybeans	211.3	188.1	167.0	147.8	130.2	184.5	159.1	135.9	114.6	95.0	-
Soybean oil	25.3	24.6	24.1	23.6	23.1	5.2	10.2	14.7	18.9	22.6	-
Sucrose	-	-	-	-	-	3.7	14.3	24.1	33.0	41.2	-
CaCO <sub>3</sub>	13.8	13.1	12.5	11.8	11.4	12.4	10.1	7.9	5.9	4.2	-
NaCl	3.1	3.0	2.8	2.7	2.6	3.0	2.8	2.7	2.6	2.5	-
Monocalcium phosphate	8.8	7.3	5.9	4.7	3.5	8.6	8.3	8.0	7.9	7.7	-
Amino acids	1.5	1.7	1.9	2.2	2.4	1.4	1.1	1.0	0.8	0.7	-
Choline chloride 50%	0.4	0.4	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.3	-
Vitamin and mineral mix <sup>d</sup>	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	-
Cr-maize starch mix	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	-
Diatomaceous shell powder	12.5	11.9	11.4	10.9	10.4	11.9	11.4	10.9	10.4	10.0	-
NE content, MJ/kg	10.38	9.88	9.43	9.02	8.65	9.88	9.43	9.02	8.65	8.30	-

<sup>a</sup> In the calculation of the diets, nutrient compositions of the feed ingredients from CVB (1998) were used in addition to the analyzed content of DM, CP, crude fat, and ash for solvent-extracted coconut meal, soybean hulls, potato protein, wheat, extracted soybeans, and maize starch.

<sup>b</sup> According to CVB (1998) solvent-extracted coconut meal contained (on as fed basis): DM, 896 g/kg; CP, 211 g/kg; ash, 65 g/kg; crude fat, 29 g/kg; starch, 10 g/kg; sugars, 100 g/kg; NSP, 478 g/kg; NDF, 449 g/kg, ADF; 230 g/kg; ADL, 38 g/kg.

<sup>c</sup> According to CVB (1998) soybean hulls (on as fed basis): DM, 885 g/kg; CP, 145 g/kg; ash, 52 g/kg; crude fat, 32 g/kg; starch, 21 g/kg; sugars, 13 g/kg; NSP, 622 g/kg; NDF, 511 g/kg, ADF; 361 g/kg; ADL, - g/kg.

<sup>d</sup> Provided the following amounts of vitamins and minerals per kg of the complete diet: vitamin A, 7,000 IU; vitamin D<sub>3</sub>, 1,700 IU; vitamin E 20 IU; vitamin K<sub>3</sub>, 1.5 mg; vitamin B<sub>1</sub>, 1.5 mg; vitamin B<sub>2</sub>, 4.0 mg; d-pantothenic acid, 11 mg; niacin, 18 mg; vitamin B<sub>12</sub>, 0.018 mg; folic acid, 0.1 mg; vitamin B<sub>6</sub>, 1.0 mg; Co, 0.15 mg; I, 0.75 mg; Fe, 75 mg; Mn, 30 mg; Zn, 50 mg; Cu, 25 mg; Se, 0.30 mg.

**Table 2.** Analyzed nutrient composition of experimental diets, in g/kg (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Dry matter	888	891	894	894	893	891	884	891	897	902	909
Crude ash	57	61	65	65	67	71	53	53	53	53	54
Crude protein	182	188	196	196	203	210	168	175	177	180	182
Crude fat	30	38	40	40	42	44	19	30	46	64	76
Starch	457	393	320	320	253	190	489	410	333	273	201
Sugars <sup>a</sup>	35	42	49	49	55	61	36	50	65	78	88
Dietary fiber <sup>b</sup>	127	169	224	224	273	315	119	173	223	254	308
NDF	69	113	166	166	210	247	70	115	154	191	229
ADF	38	69	103	103	135	163	38	73	104	135	160
ADL	10	21	33	33	45	55	7	8	9	10	11
Gross energy, MJ/kg	16.3	16.5	16.6	16.6	16.6	16.6	15.9	16.4	16.8	17.2	17.6

<sup>a</sup> Reducing sugars expressed in glucose units.<sup>b</sup> Content of dietary fiber was calculated as DM - (CP + crude fat + ash + sugars + starch).



The average of each performed behavioral characteristic was calculated for the same 9-min intervals as HP (i.e., average of 3 sampling moments). The behavioral characteristic "standing" includes standing up, standing, eating, walking, and lying down (Table 3). Therefore, physical activity is defined as standing up, standing, eating, walking, lying down, plus sitting. Per group and per day (i.e., per 24-h period), the 9-min data on HP were related to physical activity according to the following equation:

$$HP_{ij} = \mu + D_i + \beta \times X_j + e_{ij} \quad [1]$$

where  $HP_{ij}$  = heat production during day period  $i$  and 9-min period  $j$ ;  $\mu$  = overall mean;  $D_i$  = fixed effect of day period  $i$  ( $i = 1$  (from 0700 to 2200) or  $2$  (from 2200 to 0700));  $X_j$  = physical activity of pigs during 9-min period  $j$ ;  $\beta$  = regression coefficient of heat production on physical activity from video recordings, in percentage of time of all pigs spent on "standing plus sitting"; and  $e_{ij}$  = error term.

Heat production and physical activity exhibit circadian rhythms (e.g., Aschoff et al., 1974; Schrama et al., 1996). The circadian rhythm in HP is only partially accounted for by physical activity, which has been demonstrated in pigs (van der Hel et al., 1984; Henken et al., 1991). Therefore, a fixed effect of day period with two levels was included in Eq. [1]. The day was divided into a day period from 0700 to 2200, during which the pigs were most active, and a night period from 2200 to 0700, during which the pigs were inactive. The increase in HP around feeding time is not fully related to the elevated physical activity (Verstegen et al., 1987a; Noblet et al., 1993). In the regression according to Eq. [1], data around feeding times, from 0800 to 0900 and from 1530 to 1630 were excluded. These data were omitted in order to avoid possible bias by inclusion of heat increment associated with feed ingestion in the relationship between HP and physical activity.

The activity-related heat production (AHP in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was calculated as follows:

$$AHP_{ij} = b \times X_j \quad [2]$$

where  $AHP_{ij}$  = physical activity-related heat production during 9-min period  $j$ ;  $X_j$  = physical activity during 9-min period  $j$  of the video recordings;  $b$  = the estimated regression coefficient from HP on physical activity from Eq. [1]. Heat production not related to physical activity or resting heat production (RHP) was derived by subtracting AHP from HP. Activity-related HP and RHP were calculated for each 9-min period, including the 1-h periods around feeding, from 0800 to 0900 and from 1530 to 1630.

The energy cost for physical activity ( $EC_{act}$  in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) was derived from the regression of HP on physical activity, as follows:

$$EC_{act} = 100 \times b \quad [3]$$

where  $b$  = the estimated regression coefficient from the regression of HP on physical activity from Eq. [1].

### **Statistical Analysis**

Cluster was the experimental unit. Mean values of HP, AHP, RHP, and the behavioral characteristics were analyzed for effects of diet by ANOVA. The present study focused on the effects of fDF intake from two different sources on HP and AHP during the day. Therefore, HP, AHP, and RHP were analyzed for the effect of diet by linear regression of these traits on the daily intake of fDF (expressed in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ). The LSMEANS procedure was used for treatment comparisons. A contrast method was used to analyze differences between diets with SECM and diets with SBH. The SAS software (SAS Inst. Inc., Cary, NC) was used in all statistical evaluations. The data on HP, AHP, and RHP are expressed in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ .

**Table 3.** Ethogram of the behavioral characteristics of group-housed growing pigs during two days of the experimental period<sup>a</sup>

Item	Definition
Standing	Pigs stand upright on four legs, including walking. Standing up, lying down, and eating are also included.
Sitting	Pigs sit with backside and forelegs on the floor ("dog-like").
Lying breast	Pigs lie on their legs with their head and spinal column upright.
Lying flank	All varieties of lying except for "lying breast", pigs are passive and not alert.

<sup>a</sup> Physical activity is defined as the total of the behavioral characteristics "standing" plus "sitting" (i.e., standing up, standing, walking, lying down, eating, plus sitting).

## **Results**

### **General**

The numbers of clusters and animals used are given in Table 4. One cluster of pigs (diet 5) was removed from the analyses, because the lights in the chamber were on during the whole experimental period due to a technical failure. Six pigs were removed during the experiment due to health problems.

At the start of the 7-d experimental period, live BW averaged 57.0 kg (SEM = 1.1) and was affected by diet ( $P < 0.05$ ) due to differences in feed refusals and ADG during the preliminary period (data not shown).

For each diet, feeding level was adjusted to the calculated dietary NE content to supply all clusters with similar amounts of NE, because NE content decreases with increasing DF content. Consequently, daily DM intake was affected by diet ( $P < 0.001$ ; Table 4). In agreement with the experimental set-up, the main difference between the experimental diets consisted of an alteration of the intake of digestible starch and fDF ( $P < 0.001$ ; Table 4), whereas the intake of digestible CP was similar for all diets ( $P > 0.05$ ).

**Table 4.** Number of clusters and pigs used, mean BW and daily intakes of dry matter, digestible crude protein (CP), starch, and fermentable dietary fiber (in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) of group-housed growing pigs fed the experimental diets

Item	Number of clusters	Number of pigs	BW, kg	DM intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	Digestible nutrient intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		
					CP	Starch	DF <sup>a</sup>
Diets with SECM <sup>b</sup>							
1	2	28	55.7	62.2 <sup>c</sup>	10.9	32.0 <sup>c</sup>	6.6 <sup>c</sup>
2	2	28	56.2	65.4 <sup>d</sup>	11.0	28.8 <sup>d</sup>	9.3 <sup>cd</sup>
3	2	28	54.9	68.6 <sup>e</sup>	11.1	24.5 <sup>e</sup>	12.6 <sup>de</sup>
4	2	27	58.0	72.1 <sup>f</sup>	11.3	20.3 <sup>f</sup>	16.2 <sup>ef</sup>
5	1	11	53.4	75.3 <sup>g</sup>	10.5	16.5 <sup>g</sup>	18.7 <sup>f</sup>
Diets with SBH <sup>b</sup>							
6	2	28	54.1	64.9 <sup>d</sup>	10.5	36.0 <sup>h</sup>	6.1 <sup>c</sup>
7	2	28	59.7	68.3 <sup>e</sup>	11.0	31.5 <sup>c</sup>	9.1 <sup>cd</sup>
8	2	26	58.4	71.9 <sup>f</sup>	11.0	26.5 <sup>i</sup>	12.3 <sup>de</sup>
9	2	28	59.0	75.2 <sup>g</sup>	11.1	22.9 <sup>e</sup>	13.4 <sup>ef</sup>
10	2	27	58.8	78.9 <sup>h</sup>	11.4	17.3 <sup>g</sup>	16.6 <sup>f</sup>
SEM	-	-	1.1	0.3	0.2	0.2	0.5
P-value	-	-	0.016	<0.001	0.077	<0.001	<0.001

<sup>a</sup> Content of dietary fiber (DF) was calculated as DM - (CP + crude fat + ash + sugars + starch), and intake of fermentable DF was calculated under the assumption of apparent fecal digestibilities of 100% for sugars and gelatinized starch.

<sup>b</sup> On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  of either solvent-extracted coconut meal (SECM) or soybean hulls (SBH) with their diet (diet 1 to 5 and diet 6 to 10, respectively).

<sup>c, d, e, f, g, h, i</sup> Within a column, means with different superscripts differ ( $P < 0.05$ ).

### Behavioral Characteristics

On average per day, pigs spent 153 min standing, 42 min sitting, 202 min lying on chest, and 1043 min lying on their flanks (Table 5). The average time spent on physical activity (i.e., behavioral characteristics “standing plus sitting”) was 195 min/d. None of the behavioral characteristics was affected by diet ( $P > 0.10$ ). Contrast analyses showed that pigs which received a diet with SECM spent less time lying on their chest than pigs that received diets with SBH (192 and 210 min/d, respectively,  $P = 0.037$ ). Total time spent on physical activity was not affected by diet ( $P = 0.966$ ).

**Table 5.** Behavioral characteristics, in percentage of time spent per 24 h, of group-housed growing pigs fed the experimental diets

Item	Behavioral characteristics <sup>a</sup>				
	Standing	Sitting	Standing+sitting	Lying chest	Lying flank
Diets with SECM <sup>b</sup>					
1	9.0	4.0	13.0	13.8	73.2
2	10.8	2.9	13.7	13.1	73.2
3	10.9	2.7	13.6	14.7	71.8
4	10.9	2.4	13.3	12.5	74.1
5	13.2	1.4	14.5	12.3	73.2
Diets with SBH <sup>b</sup>					
6	10.8	3.9	14.7	15.2	70.2
7	11.4	2.9	14.3	14.3	71.4
8	11.2	2.6	13.8	15.3	70.9
9	9.5	2.7	12.2	14.6	73.2
10	10.1	3.1	13.2	13.6	73.2
SEM	1.8	0.5	1.4	0.9	1.5
<i>P</i> -value	0.946	0.161	0.966	0.310	0.622
<i>P</i> -value contrast <sup>c</sup>	0.752	0.259	0.997	0.037	0.190

<sup>a</sup> The definitions of the behavioral characteristics are described in the ethogram (Table 3).

<sup>b</sup> On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of either solvent-extracted coconut meal (SECM) or soybean hulls (SBH) with their diet (diet 1 to 5 and diet 6 to 10, respectively).

<sup>c</sup> A contrast method was used to analyze differences between SECM and SBH diets.

### Energy Cost of Activity

The energy cost of physical activity averaged 479 kJ·kg<sup>-0.75</sup>·d<sup>-1</sup> (SEM 27; Table 6), and tended to be affected by diet ( $P = 0.080$ ). This was caused by a significant difference in energy cost of physical activity between pigs on diet 1 and pigs on diet 9 ( $P < 0.05$ ).

Within diets with the same source of fermentable carbohydrates no effect on energy cost of physical activity occurred ( $P > 0.05$ ).

### **Total Heat Production and Activity-related Heat Production**

#### *General*

Total HP, AHP, and RHP of the growing pigs is given in Table 6. Total HP was calculated for the same 2 d when videotapes were recorded. Both HP and RHP were affected by diet ( $P < 0.05$ ). Treatment comparison showed that within diets with SECM, HP of pigs on diet 5 differed from HP of pigs on diets 1 and 2 ( $P < 0.05$ ). Within diets with SBH, HP of pigs on diet 9 and 10 differed from HP of pigs on diet 6 and HP of pigs on diet 10 also differed from HP of pigs on diet 7 ( $P < 0.05$ ). Effects of diet on RHP were only significant between pigs on diet 2 and diet 10. Contrast analyses showed that pigs which received diets with SECM had a lower RHP than pigs which received diets with SBH ( $P < 0.01$ ). On average, AHP was  $65 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  and was not affected by diet ( $P = 0.820$ ; Table 6).

**Table 6.** Mean total heat production (HP), activity-related heat production (AHP), resting heat production (RHP), and energy cost for physical activity ( $\text{EC}_{\text{act}}$ ) (in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) of group-housed growing pigs fed the experimental diets

Item	HP	AHP	RHP	$\text{EC}_{\text{act}}$
Diets with SECM <sup>a</sup>				
1	641 <sup>c</sup>	53	588 <sup>cd</sup>	409 <sup>c</sup>
2	640 <sup>c</sup>	69	571 <sup>c</sup>	505 <sup>cd</sup>
3	653 <sup>cde</sup>	67	586 <sup>cd</sup>	494 <sup>cd</sup>
4	648 <sup>cd</sup>	61	587 <sup>cd</sup>	453 <sup>cd</sup>
5	671 <sup>def</sup>	64	606 <sup>cd</sup>	444 <sup>cd</sup>
Diets with SBH <sup>a</sup>				
6	656 <sup>cde</sup>	66	589 <sup>cd</sup>	455 <sup>cd</sup>
7	661 <sup>cdef</sup>	71	590 <sup>cd</sup>	498 <sup>cd</sup>
8	675 <sup>efg</sup>	63	612 <sup>cd</sup>	460 <sup>cd</sup>
9	685 <sup>fg</sup>	69	616 <sup>cd</sup>	564 <sup>d</sup>
10	697 <sup>g</sup>	64	631 <sup>d</sup>	493 <sup>cd</sup>
SEM	4	7	8	27
<i>P</i> -value	<0.001	0.820	0.013	0.080
<i>P</i> -value contrast <sup>b</sup>	<0.001	0.389	0.005	0.085

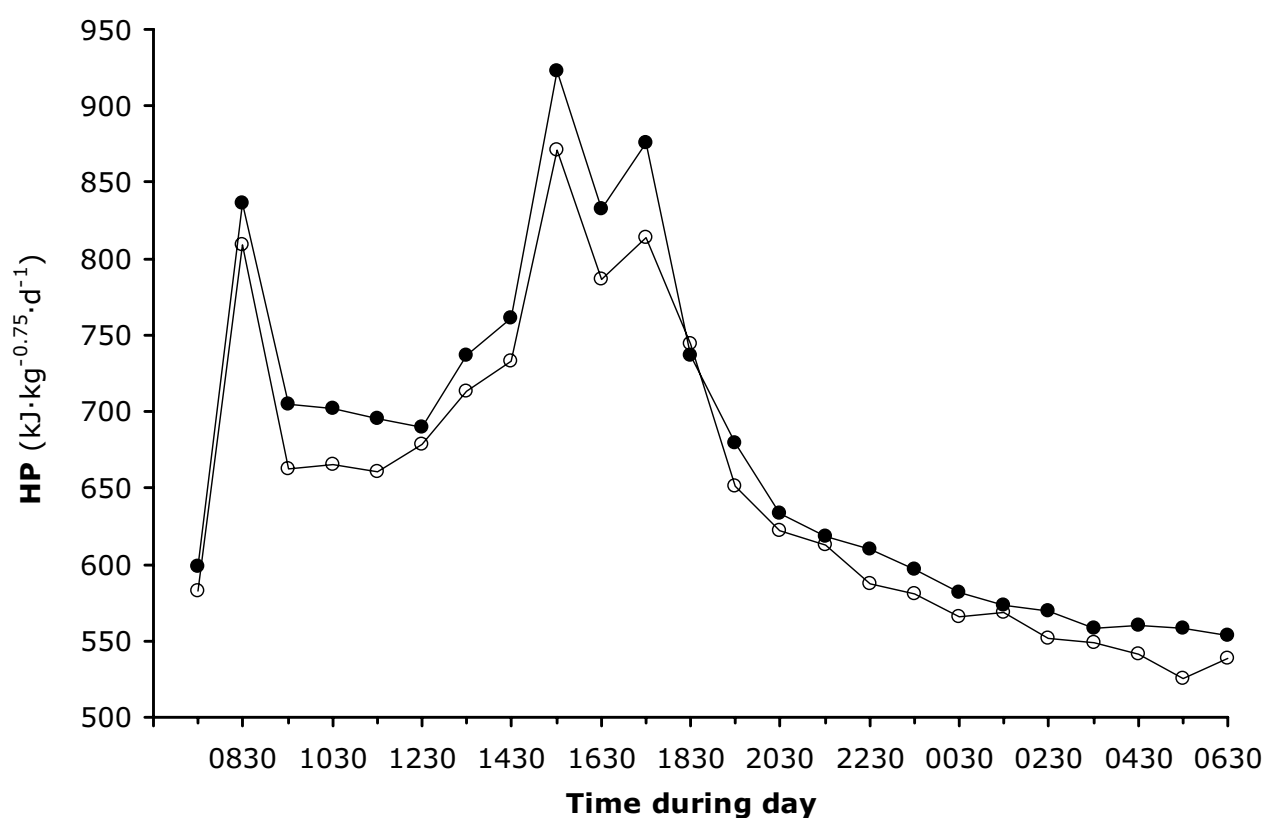
<sup>a</sup> On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  of either solvent-extracted coconut meal (SECM) or soybean hulls (SBH) with their diet (diet 1 to 5 and diet 6 to 10, respectively).

<sup>b</sup> A contrast method was used to analyze differences between SECM and SBH diets.

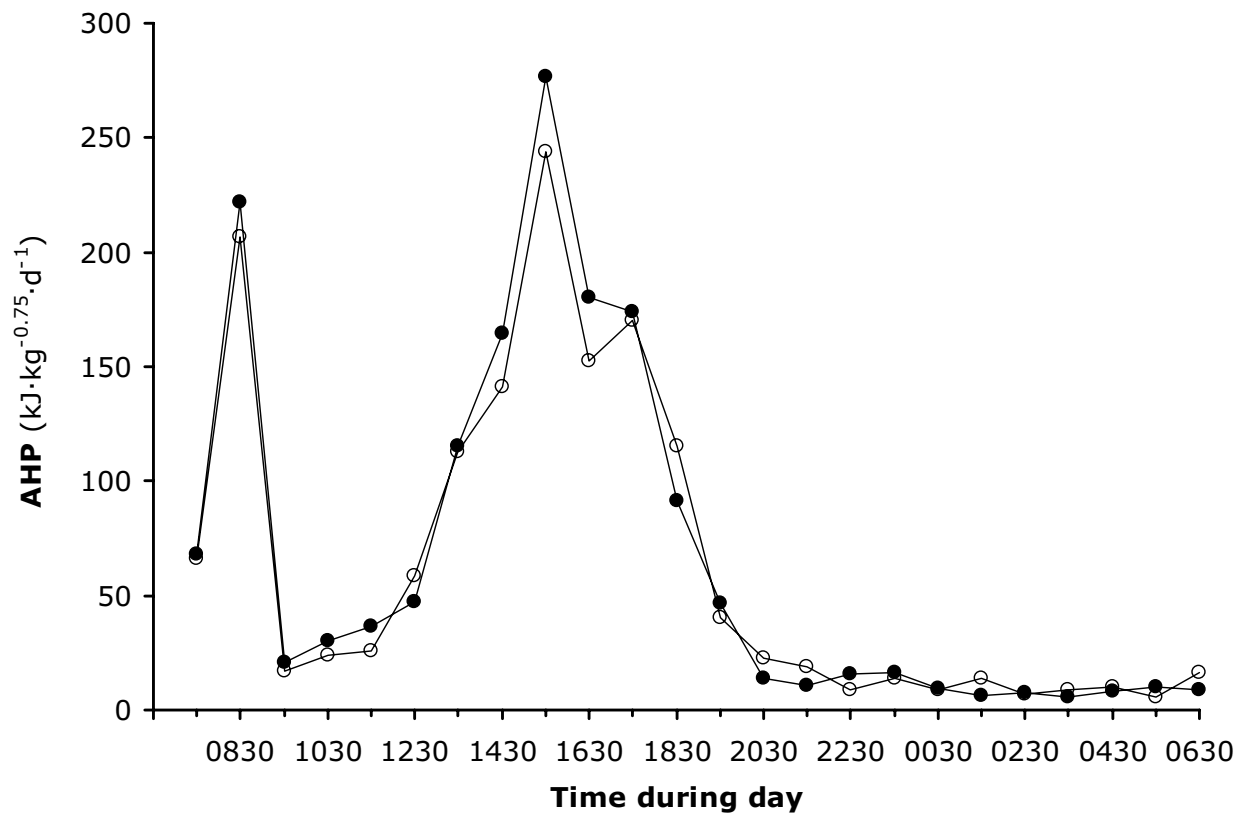
<sup>c, d, e, f, g</sup> Within a column, means with different superscripts differ ( $P < 0.05$ ).

### Circadian Rhythms

The average circadian rhythms of HP and AHP of groups of pigs fed different levels of dietary SECM or SBH are illustrated by Figures 1 (HP) and 2 (AHP). Pigs were exposed to 12 h of light (about 300 lx from 0700 to 1900) and 12 h of partial darkness (about 10 lx from 1900 to 0700), and fed twice a day (at 0800 and 1530). Total HP and AHP were highest during eating and decreased after the meal (i.e., one peak between 0800 and 0900 and one peak between 1530 and 1630). Figure 2 shows that the activity level of pigs is close to zero during the night period (between 2200 and 0700). Figure 2 also shows that AHP decreases very rapidly after the morning meal (0800) to values close to zero, while AHP remains high during the whole afternoon (from about 1200 to 2000).



**Figure 1.** Circadian rhythms in heat production (HP) of group-housed growing pigs, averaged for diets with different contents of solvent-extracted coconut meal (○) or soybean hulls (●).



**Figure 2.** Circadian rhythms in activity-related heat production (AHP) of group-housed growing pigs, averaged for diets with different contents of solvent-extracted coconut meal (○) or soybean hulls (●).

The linear relationships between fDF intake and HP are calculated for the whole day (24 h), night period, day period, eating period, and for 24 h without the eating period (Table 7). The linear relationships between fDF intake and AHP are reported for 24 h (Table 7). Average over the whole day (24 h), HP increased with increasing fDF intake ( $P < 0.001$ ). There was no effect of the source of fermentable carbohydrates ( $P > 0.10$ ; Table 7). There was, however, an interaction between the source of fermentable carbohydrates and fDF intake ( $P = 0.017$ ). The increase in HP was less with an increased intake of fDF from SECM than with an increased intake of fDF from SBH. The effects of fDF on HP were similar during the night period and the day period. During eating, HP was not affected by fDF intake ( $P = 0.145$ ). Average over the whole day (24 h), fDF intake did not affect AHP ( $P = 0.999$ ). During the separated parts of the day, fDF also did not affect AHP ( $P > 0.10$ ; data not shown).

**Table 7.** Linear relationships between intake of fermentable dietary fiber (fDF in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) and total heat production (HP), and activity-related heat production (AHP) (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) in group-housed growing pigs fed the experimental diets

Item	Fiber source	Relationship	<i>P</i> -value <sup>a</sup>				
			S	fDF	S × fDF		
HP							
Mean, per 24 h	SECM <sup>b</sup>	$y = 626 (\pm 7) + 1.82 (\pm 0.55) \times \text{fDF}$	0.826	<0.001	0.017		
	SBH <sup>b</sup>	$y = 629 (\pm 7) + 4.01 (\pm 0.59) \times \text{fDF}$					
During night period	SECM	$y = 524 (\pm 11) + 2.38 (\pm 0.83) \times \text{fDF}$	0.670	<0.001	0.060		
	SBH	$y = 518 (\pm 11) + 4.85 (\pm 0.89) \times \text{fDF}$					
During day period	SECM	$y = 688 (\pm 7) + 1.49 (\pm 0.56) \times \text{fDF}$	0.472	<0.001	0.027		
	SBH	$y = 695 (\pm 7) + 3.51 (\pm 0.60) \times \text{fDF}$					
During eating	SECM	$y = 834 (\pm 21) + 0.73 (\pm 1.63) \times \text{fDF}$	0.541	0.145	0.371		
	SBH	$y = 852 (\pm 21) + 2.94 (\pm 1.75) \times \text{fDF}$					
Mean, without eating	SECM	$y = 604 (\pm 7) + 2.07 (\pm 0.54) \times \text{fDF}$	0.928	<0.001	0.014		
	SBH	$y = 605 (\pm 7) + 4.28 (\pm 0.58) \times \text{fDF}$					
AHP							
Mean, per 24 h	SECM	$y = 56 (\pm 9) + 0.50 (\pm 0.74) \times \text{fDF}$	0.243	0.999	0.371		
	SBH	$y = 73 (\pm 10) - 0.50 (\pm 0.79) \times \text{fDF}$					

<sup>a</sup> S = effect of source of dietary fermentable carbohydrates (i.e., solvent-extracted coconut meal or soybean hulls); fDF = effect of fermentable dietary fiber intake; S × fDF = effect of source of fDF on regression coefficient.

<sup>b</sup> On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  of either solvent-extracted coconut meal (SECM) or soybean hulls (SBH) with their diet (diet 1 to 5 and diet 6 to 10, respectively).

## Discussion

### Behavioral Characteristics

Schrama et al. (1998) reported that group-housed growing pigs spent less energy on physical activity when the intake of dietary sugar beet pulp silage (SBPS) increased. This implies that pigs spent less time on physical activity when the intake of dietary sugar beet pulp silage increased. Rijnen et al. (2003a) reported that group-housed sows decreased time spent on physical activity when more sugar beet pulp silage was added to the diet. In the present study, however, there were no differences in time spent on physical activity between group-housed growing pigs fed different levels of SECM or SBH.



**Energy Cost of Activity**

In pigs, energy cost of physical activity can be divided into energy cost of sitting, standing, sitting up, standing up, and walking (Kelly et al, 1978). In the present study, the energy cost of physical activity averaged  $479 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  and ranged between 409 and  $564 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  for dietary treatments. Some reported values for the energy cost of physical activity of growing pigs are 369, 428, 435  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  (cited by Noblet et al., 1993 from different studies), 269, 401, and 528  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  (Van Milgen et al., 1998). Considering the data from the present study and data from literature, it seems that the energy cost of physical activity varies widely between growing pigs. Van Milgen et al. (1998) reported effects of BW and breed/castration on the energy cost of physical activity. Van Milgen et al. (1998) suggested that housing conditions and feeding level (i.e., fasted vs fed animals) might affect the energy cost of physical activity. Furthermore, the technique for measuring or assessing energy cost for physical activity might interact with the energy cost of activity. The energy cost of physical activity depends on the activity pattern of the pigs during the day (i.e., duration of activity, number of changes in position, type of activity and movements). Because sitting up and standing up cost more energy than sitting and standing, respectively (Kelley et al., 1978), the number of times that a pig stands up or lies down will interact with the energy cost for physical activity. Van Milgen et al. (1998) reported that positional movements as well as metabolic efficiency of movement contribute more to the energetic cost of activity than the act of rising itself.

In the present study, pigs were group-housed and able to walk freely in the pen. In most studies which report data on energy cost of physical activity, however, pigs were housed individually (e.g., Hörnicke, 1970; Susenbeth & Menke, 1991; Van Milgen et al., 1998). This difference in housing conditions might be a cause for the high energy cost of physical activity found in the present study (on average  $479 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) compared with literature data (on average  $407 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ; Noblet et al., 1993; Van Milgen et al., 1998). This might be related to differences in the number of positional changes and movements. This, however, was not analyzed for in the present study.

In literature, the energy cost of physical activity in individually housed sows is on average  $448 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  or  $31.1 \text{ kJ}\cdot\text{kg}^{-0.75}$  per 100 min (averaged for Kelley et al., 1978; Noblet et al., 1993; Ramonet et al., 2000a; Le Goff et al., 2002). In literature, the energy cost of physical activity in individually housed growing pigs is on average  $407 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  or  $28.3 \text{ kJ}\cdot\text{kg}^{-0.75}$  per 100 min (averaged for Noblet et al., 1993; Van Milgen et al., 1998). These literature data suggest that the energy cost of physical activity is about 10% higher for individually housed sows than for individually housed growing pigs. Rijnen et al. (2003) assessed the energy cost of physical activity in group-housed sows (i.e.,  $446 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  or  $31.0 \text{ kJ}\cdot\text{kg}^{-0.75}$  per 100 min) and suggested that the energy cost of physical activity in sows did not depend on housing conditions. In the present study the energy cost of physical activity was  $479 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$  for group-housed growing pigs. These data suggest that the energy cost of

physical activity is about 7% lower for group-housed sows than for group-housed growing pigs. This might be due to differences in circadian rhythms in physical activity between group-housed sows and group-housed growing pigs (i.e., duration of activity, number of changes in position, type of activity and movements). In the study from Rijnen et al. (2003), sows were quiet during the whole day except for feeding time and two small peaks in activity during the afternoon, while in the present study, pigs were active during the whole afternoon. The difference in energy cost of physical activity between group-housed sows and group-housed growing pigs is in agreement with findings from Van Milgen et al. (1998) that positional movements contribute more to the energetic cost of activity than the act of rising itself.

Literature data described above and data from the present study suggest that there may be an interaction between energy cost of physical activity for sows and growing pigs and housing conditions (individually vs group-housing).

### ***Heat Production and Activity-related Heat Production***

#### ***General***

The average AHP ( $65 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) is lower than the reported average value for AHP of growing pigs by Schrama et al. ( $89 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; 1998). This difference might be related to differences in activity levels between pigs with different genetics. This difference might also be related to the difference in the used techniques for measuring physical activity. In the present study, video recordings were used for analyzing physical activity, whereas Schrama et al. (1998) used a radar device (Wenk & van Es, 1976). One important difference between these two methods is that in the present study the video recordings were analyzed for physical activity using 3-min intervals, whereas the radar device measures physical activity continuously (Schrama et al., 1998). Video recordings were only from 2 d during the experimental period, whereas the radar device measured activity during the whole experimental period (i.e., 6 d; Schrama et al., 1998).

#### ***Circadian Rhythms***

Similar to the results reported by Noblet et al. (1993), Schrama et al. (1996), and Rijnen et al. (2003a), in the present study, HP and AHP were highest during eating and decreased after the meal (i.e., one peak between 0800 and 0900 and one peak between 1530 and 1630; Figure 2). The circadian rhythm in AHP from the present study (Figure 2) is very similar to the circadian rhythm in AHP of group-housed growing pigs fed either a high-starch diet or a high-DF diet as reported by Schrama et al. (1996).

In the present study, fDF intake did not affect AHP. There were no differences in AHP between pigs fed diets with SECM and pigs fed diets with SBH. These sources of dietary fermentable carbohydrates mainly contained hemicellulose (SECM) and

cellulose (SBH) (CVB, 1998). The differences in composition of the DF fractions (i.e., contents of NDF, ADF, and ADL) of the used SECM and SBH, however, were smaller than expected (Table 2).

The absence of an effect of fDF intake on energy expenditure for physical activity in the present study is in contrast with the observed alteration of physical activity by dietary composition in other studies (e.g., Brouns et al., 1994; Schrama et al., 1998; Rijnen et al., 2003a). Both Schrama et al. (1998) and Rijnen et al. (2003a) reported that additional intake of fDF from SBPS decreased energy expenditure for physical activity. There is, however, a large difference in composition of the DF fraction used in the present study compared to the experiments of Schrama et al. (1998) and Rijnen et al. (2003a). In the last studies, pigs were fed different levels of SBPS, which contains high levels of pectin, whereas in the present study, fDF consisted mainly of hemicellulose and cellulose. From comparison between studies, it can be hypothesized that the botanical origin and the composition of the fDF fraction is still of importance for an effect on physical activity. This, however, could not be proven in the present study with growing pigs or in the study of Le Goff et al. (2002) with individually housed sows. Beside possible effects on AHP of growing pigs related to differences in composition of the dietary DF, also the pattern of volatile fatty acid (VFA) production, the velocity of fermentation in the gastrointestinal tract, or specific components in feed ingredients might be of importance. More research is needed to unravel the mechanisms involved.

### ***Physical Activity and Net Energy***

In experiments with growing pigs (Schrama et al., 1998) and sows (Rijnen et al., 2003a) an increased intake of fDF from dietary SBPS decreased AHP. This means that the NE value of fDF from SBPS was affected by physical activity. Translated into practical values for the NE value of fDF, this means that reduced activity causes higher NE values. The saving effect of physical activity on the NE value of fDF can be derived from the difference in calculated NE value of fDF during the whole day and during the sleeping period. This saving effect of physical activity on the NE value of fDF can also be derived from the difference in regression coefficient from the regression of fDF on HP during the whole day and during the night period, assuming that the pigs were not active during the night period (Rijnen et al., 2003a).

In the present study, regression coefficients for linear regression of fDF on average HP (24h) from SECM and SBH were 1.82 and 4.01 kJ per g of fDF intake, respectively (Table 7). Regression coefficients for linear regression of fDF on HP during the night period from SECM and SBH were 2.38 and 4.85 kJ per g of fDF intake, respectively (Table 7). This means that the saving effect of physical activity on the NE values of fDF from SECM and SBH were 0.56 and 0.84 kJ per gram of fDF intake, respectively (Table 8). Neither of these saving effects of physical activity on the NE values of fDF from SECM and SBH was significantly different from zero. The results from this

calculation are similar to the found effects of fDF on AHP during 24 h (neither value was significantly different from zero; Table 7). The effect of physical activity on the NE value of fDF from SECM was not different from that of SBH ( $P > 0.10$ ). This might be due to the smaller difference in composition of the DF fraction (i.e., contents of NDF, ADF, and ADL) than expected (Table 2).

**Table 8.** Net energy saving effect of fermentable dietary fiber (fDF) intake by a decrease in energy expended on physical activity by pigs (in kJ/g fDF intake)

DF source <sup>a</sup>	BW, kg	NE saving effect of physical activity		
		Video <sup>b</sup>	24 h – sleeping <sup>c</sup>	Reference
SBPS	50	2.9 <sup>c</sup>	3.7 <sup>c</sup>	Schrama, not published <sup>d</sup>
SECM	50	0.5	0.6	Present study
SBH	50	-0.5	0.8	Present study
SBPS	220	2.3	3.7	Rijnen et al., 2003a

<sup>a</sup> SBPS = sugar beet pulp silage; SECM = solvent-extracted coconut meal; SBH = soybean hulls.

<sup>b</sup> Data from video recordings on 2 d were used for linear regression of fDF on activity-related heat production to calculate the NE saving effect of physical activity on the NE value of fDF (in kJ/g fDF intake).

<sup>c</sup> Differences in regression coefficients from linear regression of fDF intake on HP during 24 h and during the sleeping period (from 2200 to 0700) were used to calculate the NE saving effect of physical activity on the NE value of fDF (in kJ/g fDF intake). Data for 6 d (i.e., experimental period) were used.

<sup>d</sup> Data were calculated from unpublished data of Schrama et al. In the corresponding study (Schrama et al., 1998), the NE saving effect of physical activity on the NE value of fDF was calculated from linear regression on activity-related heat production, using a radar device to measure physical activity (i.e., 3.9 kJ/g fDF intake).

Table 8 shows results from different studies for the NE saving effect of fDF from different feed ingredients by a decrease in energy expenditure on physical activity of pigs. These results show differences between different fibrous feed ingredients for the NE saving effect of fDF intake by a decrease in AHP. The NE value of fDF from sugar beet pulp silage was significantly increased by a decrease in AHP when more SBPS was fed, while the NE values of fDF from SECM and SBH were not affected by physical activity. The reasons for differences between fibrous feed ingredients for their effect on AHP and NE values of fDF are not clear. A major difference between SBPS and SECM and SBH is the high content of soluble fibers in SBPS compared to SECM and SBH. This difference will result in different physicochemical properties of the intestinal contents, such as viscosity and water holding capacity. Therefore, differences might be related to differences in composition of dietary DF, the pattern of VFA production,

the velocity of fermentation in the gastrointestinal tract, or to specific components in feed ingredients.

### **Implications**

Many feed evaluation systems for pigs are compiled under the assumption that energy costs for maintenance are constant, including physical activity. In literature, intake of fermentable carbohydrates is suggested to decrease physical activity in pigs. The present study showed no effects on activity-related heat production for solvent-extracted coconut meal and soybean hulls. Between studies, however, there are differences in effects of fermentable carbohydrates on energy expended on physical activity. Composition of fermentable carbohydrates, along with velocity of fermentation in the hindgut might be of importance for effects of fermentable carbohydrates on energy expenditure for physical activity. This implies that different fiber-rich feed ingredients might have different net energy values for the fiber fraction of that specific feed ingredient. Further research is needed to investigate the mechanisms involved in differences in net energy values of fiber-rich feed ingredients.



## **Chapter 6**

### **Effects of Dietary Fiber on Empty Weights of the Gastrointestinal Tract of Group-Housed Growing Pigs**

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## Effects of Dietary Fiber on Empty Weights of the Gastrointestinal Tract of Group-Housed Growing Pigs

### Abstract

Two experiments on the effects of dietary fiber (DF) on the empty weights of the gastrointestinal tract (GIT) and its separated parts are reported. In experiment 1, the effects of ten different diets were studied. Five diets contained different levels of solvent-extracted coconut meal (SECM) and five diets contained different levels of soybean hulls (SBH) as DF source. Pigs were group-housed and on as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of either SECM or SBH with their diet. After 39 d, euthanasia was performed on six pigs per dietary treatment. In experiment 2, the effects of fermentation and dietary bulkiness were studied. Pigs were group-housed and fed diets containing either gelatinized maize starch, gelatinized maize starch plus 15% milled wheat straw, raw potato starch, or raw potato starch plus 15% milled wheat straw. After 26 d, euthanasia was performed on 12 pigs per dietary treatment. For both experiments, the GIT was removed after euthanasia and divided into four parts: stomach, small intestine, cecum, and large intestine. The different parts were emptied and weighed. Results of experiment 1 showed that the empty weights of the total GIT, stomach, and large intestine were affected by diet composition ( $P < 0.01$ ). The empty weight of the large intestine was higher for pigs fed SECM than for pigs fed SBH ( $P < 0.05$ ). An increased intake of DF and fermentable DF increased the empty weight of the total GIT by increased empty weights of the stomach, and large intestine ( $P < 0.001$ ). In experiment 2, stimulation of fermentation in the GIT (i.e., gelatinized maize starch vs potato starch) increased the empty weight of the total GIT ( $P < 0.01$ ) by an increased empty weight of the large intestine ( $P < 0.05$ ). Increased dietary bulkiness (i.e., no wheat straw vs wheat straw) increased the empty weight of the total GIT ( $P < 0.05$ ) by an increased empty weight of the stomach ( $P < 0.01$ ). In both experiments, no effects were found on the empty weights of the small intestine and cecum ( $P > 0.10$ ). It can be concluded from the present studies that increased dietary volume mainly increased the empty weight of the stomach, whereas stimulation of fermentation in the GIT mainly increased the empty weight of the large intestine.

### Introduction

The interest of pig nutritionists in the role of dietary fiber (DF) is increasing. Priority and increased demand of high-energy cereals for direct human use and increased availability of fiber rich co-products from human food industries have promoted an increased use of fiber-rich feed ingredients in pig nutrition (Noblet and Le Goff, 2001). In addition, other benefits, such as increased well-being of animals, improvement of



gut transit and reduction of stomach ulcers (Low, 1985) increased the use of fiber-rich feed ingredients. Effects of DF on behavior was studied in growing pigs (e.g., Schrama et al., 1996; 1998) and sows (e.g., Danielsen et al., 2001; Meunier-Salaün et al., 2001). It seems that increased intake of DF reduces aggressive behavior in sows (Danielsen et al., 2001), and decreases time and energy spent on activity in sows (Rijnen et al., 2003a) and growing pigs (Schrama et al., 1998). This might be due to differences in satiety by dietary bulkiness (Wenk, 2001), but also to fermentation in the gastrointestinal tract (GIT) (Schrama & Bakker, 1999).

Moreover, many authors studied the effects of DF on the weight of the GIT and its separated parts (e.g., Pond et al., 1989; Jørgensen et al., 1996b). The reported effects, however, are not very consistent and might depend on the type and level of DF. In addition, data on dose response effects of different DF sources on the empty weights of the GIT are scarce (Kass et al., 1980). It can be hypothesized that the type and dose of DF is related to the empty weight of the GIT. Siba et al. (1996) reported a relationship between volatile fatty acid (VFA) production and large intestinal weight. It can be hypothesized that dietary bulkiness and stimulation of fermentation in the GIT have different effects on different parts of the GIT.

In the present study, two experiments on effects of DF on the empty weights of the GIT and its different parts are reported. The aim of the first experiment was to study the effects of the dose and source of DF on the empty weights of the GIT. The aim of the second experiment was to study the effects of dietary bulkiness and fermentable DF on the empty weights of the GIT.

## **Materials and Methods**

### ***Animals and Housing***

#### ***Experiment 1***

A total of 280 crossbred barrows ([Dutch Landrace × Great Yorkshire] × Pietrain) were used, divided into 20 clusters of 14 pigs each. Clusters were randomly assigned to one of ten experimental diets. At the start of the experiment, pigs weighed on average 37.3 kg. Pigs were fed the experimental diets for 39 d. During the first 20 d of the experiment, pigs were group-housed per cluster. After 20 d, clusters of pigs were placed in one of two identical, large, climatically controlled respiration chambers (Verstegen et al., 1987b). Within each chamber, pigs were group-housed in one of two pens of 8.3 m<sup>2</sup> each. Therefore, each cluster consisted of two subgroups of seven pigs each. In the chambers, environmental temperature was kept constant at 20°C, relative humidity was kept constant at 65%, air velocity was < 0.2 m/s, and pigs were exposed to 12 h of light (from 0700 to 1900) and 12 h of partial darkness (1900 to 0700). More details on animals and housing conditions are reported by Rijnen et al. (2003b).

### *Experiment 2*

A total of 112 crossbred barrows ([Dutch Landrace × Great Yorkshire] × Great Yorkshire) were used, divided into eight clusters of 14 pigs each. Clusters were assigned to one of four experimental diets. At the start of the experiment, pigs weighed on average 40.6 kg. Pigs were fed the experimental diets for 26 d. Each cluster of pigs was housed in one of two identical, large, climatically controlled respiration chambers (Verstegen et al., 1987b). Within each chamber, pigs were group-housed in one of two pens of 8.3 m<sup>2</sup> each. Therefore, each cluster consisted of two subgroups of seven pigs each. Housing and environmental conditions were the same as in experiment 1. More details on animals and housing conditions are reported by Schrama & Bakker (1999).

## **Feeding**

### *Experiment 1*

The goal of first experiment was to assess the effects of two different sources of DF on the empty weights of different parts of the GIT of group-housed growing pigs. Therefore, ten diets were composed. Five diets contained different levels of solvent-extracted coconut meal (SECM) (Diets 1 to 5) and five diets contained different levels of soybean hulls (SBH) (Diets 6 to 10). The DF fraction of SECM contains a high level of hemicellulose and the DF fraction of SBH a high level of cellulose (CVB, 1998). On as fed basis, pigs received 3.5, 13.2, 23.0, 32.7, or 42.4 g·kg<sup>-0.75</sup>·d<sup>-1</sup> of either SECM or SBH with their diet. Dietary compositions and analyzed nutrient compositions of the diets are shown in Table 1 and 2, respectively. For all diets, pigs were fed the same amount of calculated NE (i.e., 2.5 times the assumed energy requirements for maintenance), with similar intakes of ileal digestible protein and amino acids, vitamins, and minerals. Due to this set up, pigs receiving the different diets were fed different amounts of DM, because the dietary NE content decreases with increasing DF content (Table 4).

### *Experiment 2*

The goal of the second experiment was to assess the effects of fermentation of DF and dietary bulkiness separately and in combination on the empty weights of different parts of the GIT of group-housed growing pigs. Therefore, four diets were composed according to a 2 × 2 factorial design (maize starch, maize starch + straw, potato starch, and potato starch + straw). For studying the effect of fermentation without affecting dietary bulkiness, gelatinized maize starch, being a source of ileal digestible starch, in the control diet was (on DM basis) replaced for raw potato starch, being a source of resistant starch, in the high-fermentation diets. With this replacement, a similar dietary volume was maintained while increasing the amount of starch being fermented vs digested. Adding 15% milled wheat straw to the diets included the bulkiness of the diets. The wheat straw was obtained by milling of pelleted wheat

straw through a 3-mm sieve, and had a particle size of < 5 mm. In growing pigs, straw has a low nutritional value because of its nearly absent (Münchow et al., 1989), or even negative content of digestible energy (Shi & Noblet, 1993). We, therefore, assumed that wheat straw had no nutritional value for pigs and provided only volume to the diet. Compositions of the experimental diets of experiment 2 are given in Table 3. Pigs assigned to the "Maize diet" (i.e., without straw) were fed at 2.5 times the assumed energy requirements for maintenance. The feeding levels for the other diets were based on that of the "Maize diet". Pigs receiving the "Maize + straw diet" received 15% more DM per kg<sup>0.75</sup> than pigs receiving the "Maize diet" to obtain the same amount of NE as pigs receiving the Maize diet. Pigs receiving the "Potato" and "Potato + straw diet" were fed the same amount of DM per kg<sup>0.75</sup> as pigs receiving the "Maize diet" and "Maize + straw diet", respectively. Hence, no correction was made for the lower NE value of raw potato starch compared to gelatinized maize starch.

#### *Experiment 1 and 2*

All pigs were fed according to their metabolic BW (kg<sup>0.75</sup>). Pigs were weighed every week, and feeding level was based on the average metabolic weight per subgroup, adjusted for an expected ADG of 600 g. Pigs were fed twice a day (at 0800 and 1530). Feed was given as mash feed. The amount of water added to the feed was 2.3 L/kg of DM. In addition, pigs had ad libitum access to drinking water during the whole experiment.

### **Measurements**

#### *Experiment 1*

Feed intake, fecal digestibilities of DM, CP, crude fat, ash, and DF, and N and energy balances of the clusters of pigs were measured during the experimental period. These data are reported and discussed elsewhere (Chapter 4). At the end of the experiment (i.e., after 39 d), three pigs per cluster (i.e., 6 pigs per treatment) were slaughtered. At slaughter, pigs had an average live BW of 63.0 kg. First, pigs were anesthetized and thereafter euthanasia was performed. Pigs received their final meal 1, 3, or 5 hours before euthanasia. After euthanasia, first the total GIT was removed from the animal and weighed. Second, the GIT was divided into 4 parts: stomach, small intestine, cecum, and large intestine. The full and empty weights of the different parts were measured. The weight of the mesentery, including the pancreas was also measured. The empty weight of the total GIT was calculated as the sum of the empty weights of the different parts of the GIT. All weights are expressed in g/kg BW.

**Table 1.** Composition of experimental diets (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Ingredient <sup>a</sup> , g/kg											
Extracted coconut meal <sup>b</sup>	50.0	178.6	295.5	402.2	500.0	-	-	-	-	-	-
Soybean hulls <sup>c</sup>	-	-	-	-	-	47.6	170.5	282.6	385.4	480.0	-
Gelatinized maize starch	350.0	250.0	159.1	76.1	-	333.3	238.6	152.2	72.9	-	-
Potato protein	35.0	25.0	15.9	7.6	-	34.5	26.1	18.5	11.5	5.0	5.0
Wheat	286.0	294.0	301.3	307.9	314.0	351.1	344.8	339.0	333.6	328.8	328.8
Extracted soybeans	211.3	188.1	167.0	147.8	130.2	184.5	159.1	135.9	114.6	95.0	95.0
Soybean oil	25.3	24.6	24.1	23.6	23.1	5.2	10.2	14.7	18.9	22.6	22.6
Sucrose	-	-	-	-	-	3.7	14.3	24.1	33.0	41.2	41.2
CaCO <sub>3</sub>	13.8	13.1	12.5	11.8	11.4	12.4	10.1	7.9	5.9	4.2	4.2
NaCl	3.1	3.0	2.8	2.7	2.6	3.0	2.8	2.7	2.6	2.5	2.5
Monocalcium phosphate	8.8	7.3	5.9	4.7	3.5	8.6	8.3	8.0	7.9	7.7	7.7
Amino acids	1.5	1.7	1.9	2.2	2.4	1.4	1.1	1.0	0.8	0.7	0.7
Choline chloride 50%	0.4	0.4	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.3	0.3
Vitamin and mineral mix <sup>d</sup>	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	1.0
Cr-maize starch mix	1.3	1.2	1.1	1.1	1.0	1.2	1.1	1.1	1.0	1.0	1.0
Diatomaceous shell powder	12.5	11.9	11.4	10.9	10.4	11.9	11.4	10.9	10.4	10.0	10.0
NE content, MJ/kg	10.38	9.88	9.43	9.02	8.65	9.88	9.43	9.02	8.65	8.30	8.30

<sup>a</sup> In the calculation of the diets, nutrient compositions of the feed ingredients from CVB (1998) were used in addition to the analyzed content of DM, CP, crude fat, and ash for solvent-extracted coconut meal, soybean hulls, potato protein, wheat, extracted soybeans, and maize starch.

<sup>b</sup> According to CVB (1998) solvent-extracted coconut meal contained (on as fed basis): DM, 896 g/kg; CP, 211 g/kg; ash, 65 g/kg; crude fat, 29 g/kg; starch, 10 g/kg; sugars, 100 g/kg; NSP, 478 g/kg; NDF, 449 g/kg; ADF, 230 g/kg; ADL, 38 g/kg.

<sup>c</sup> According to CVB (1998) soybean hulls (on as fed basis): DM, 885 g/kg; CP, 145 g/kg; ash, 52 g/kg; crude fat, 32 g/kg; starch, 21 g/kg; sugars, 13 g/kg; NSP, 622 g/kg; NDF, 511 g/kg; ADF, 361 g/kg; ADL, - g/kg.

<sup>d</sup> Provided the following amounts of vitamins and minerals per kg of the complete diet: vitamin A, 7,000 IU; vitamin D<sub>3</sub>, 1,700 IU; vitamin E 20 IU; vitamin K<sub>3</sub>, 1.5 mg; vitamin B<sub>1</sub>, 1.5 mg; vitamin B<sub>2</sub>, 4.0 mg; d-pantothenic acid, 11 mg; niacin, 18 mg; vitamin B<sub>12</sub>, 0.018 mg; folic acid, 0.1 mg; vitamin B<sub>6</sub>, 1.0 mg; Co, 0.15 mg; I, 0.75 mg; Fe, 75 mg; Mn, 30 mg; Zn, 50 mg; Cu, 25 mg; Se, 0.30 mg.

**Table 2.** Analyzed nutrient composition of experimental diets, in g/kg (as fed basis)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
Dry matter	888	891	894	894	893	891	884	891	897	902	909
Crude ash	57	61	65	65	67	71	53	53	53	53	54
Crude protein	182	188	196	196	203	210	168	175	177	180	182
Crude fat	30	38	40	40	42	44	19	30	46	64	76
Starch	457	393	320	320	253	190	489	410	333	273	201
Sugars <sup>a</sup>	35	42	49	49	55	61	36	50	65	78	88
Dietary fiber <sup>b</sup>	127	169	224	224	273	315	119	173	223	254	308
NDF	69	113	166	166	210	247	70	115	154	191	229
ADF	38	69	103	103	135	163	38	73	104	135	160
ADL	10	21	33	33	45	55	7	8	9	10	11
Gross energy, MJ/kg	16.3	16.5	16.6	16.6	16.6	16.6	15.9	16.4	16.8	17.2	17.6

<sup>a</sup> Reducing sugars expressed in glucose units.<sup>b</sup> Content of dietary fiber was calculated as DM - (CP + crude fat + ash + sugars + starch).

*Experiment 2*

Feed intake, N and energy balances of the clusters of pigs were measured during the experimental period. These data are reported and discussed elsewhere (Schrama & Bakker, 1999). Pigs were anesthetized and thereafter euthanasia was performed. About 17 h before euthanasia pigs received their final meal. After euthanasia, first the total GIT was removed from the animal and weighed. Second, the GIT was divided into 4 parts: stomach, small intestine, cecum, and large intestine. The different parts were emptied and weighed. The empty weight of the total GIT was calculated as the sum of the empty weights of the different parts of the GIT. All weights are expressed in g/kg BW.

**Table 3.** Composition of experimental diets for experiment 2, in g/kg (as fed)

Item	Gelatinized maize starch		Raw potato starch	
	No straw	Straw	No straw	Straw
Ingredient				
Gelatinized maize starch <sup>a</sup>	350.0	304.3	-	-
Raw potato starch <sup>a</sup>	-	-	365.1	318.4
Milled wheat straw	-	130.4	-	127.8
Basal diet <sup>b</sup>	650.0	565.2	634.9	553.8
Analyzed nutrient composition				
Dry matter	880	882	884	885
Crude ash	45	51	46	52
Crude protein	155	137	153	133
Crude fat	23	22	21	20
Starch and sugars	459	393	465	400
Dietary fiber <sup>c</sup>	198	279	199	280
NDF	85	160	82	163
ADF	43	85	39	90
ADL	5	9	5	10
NE content, MJ/kg <sup>d</sup>	9.74	8.47	8.16	7.11

<sup>a</sup> Maize and potato starch were exchanged on a DM basis. The analyzed DM content of maize and potato starch were 929 and 870 g/kg, respectively.

<sup>b</sup> The basal diet contained on as fed basis: 461.5 g/kg barley; 363.1 g/kg soybean meal; 90.0 g/kg alfalfa meal; 46.2 g/kg cane molasses; 12.2 g/kg CaCO<sub>3</sub>; 11.1 g/kg monocalcium phosphate; 8.5 g/kg soybean oil; 3.8 g/kg NaCl; 1.5 g/kg vitamin and mineral mix; 1.1 g/kg L-lysine-HCl; 0.6 g/kg DL-methionine; 0.5 g/kg Choline chloride.

<sup>c</sup> Content of dietary fiber was calculated as dry matter - (crude protein + crude fat + crude ash + sugars + starch).

<sup>d</sup> In the calculation of the NE content, nutrient compositions of the feed ingredients from CVB (1994) were used, and the NE value of wheat straw was assumed to be zero for pigs.

### **Statistical Analysis**

Pig was the experimental unit. The data on the empty weights of the total GIT and its different parts (in g/kg BW) were analyzed separately for the two experiments.

For experiment 1, the empty weights of the total GIT and its different parts were analyzed for effects of diet (1 to 10) by a one-way ANOVA. Analyses showed that the moment of slaughtering (i.e., 1, 3, or 5 h after feeding) did not affect the empty weights of the GIT or its different parts (data not shown). Therefore, moment of slaughtering was excluded from the final model. LSMEANS were used for treatment comparisons. A contrast method was used to analyze differences between diets with SECM and diets with SBH. Moreover, experiment 1 focused on the dose response effects of DF and fermentable DF (fDF) intake on the empty weights of the GIT and its different parts. Therefore, the empty weights of the total GIT and its different parts were also analyzed for the effect of diet by linear regression of these traits on the daily intake of DF and fDF (expressed in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ), using the main source of DF as a class variable. For Experiment 2, the empty weights of the total GIT and its different parts were analyzed for effects of the experimental treatments (including interactions) by a 2-way ANOVA. Regression effects could not be analyzed for the second experiment, because it was not possible to make the distinction between digested and fermented starch from the used raw potato starch. The SAS software (SAS Inst. Inc., Cary, NC) was used in all statistical evaluations.

## **Results**

### **General**

#### *Experiment 1*

Average calculated NE intake (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) and intakes of DM, starch, DF, and fDF (in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) for the dietary treatments are shown in Table 4. According to the experimental set-up, the amount of calculated NE intake was the same for all pigs, whereas DM, DF, fDF, and starch intakes were different between dietary treatments. These data are discussed elsewhere (Chapter 4).

#### *Experiment 2*

Average calculated NE intake (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) and intakes of DM, starch, and DF (in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) for the dietary treatments are shown in Table 5. According to the experimental set-up, the amount of calculated NE intake was the same for all pigs receiving diets with the same carbohydrate source and higher for pigs receiving diets with gelatinized maize starch than for pigs receiving diets with raw potato starch. Also according to the experimental set-up, DM intake was higher for pigs receiving diets with straw than for pigs receiving diets without straw. The DF intake increased and starch intake remained the same when straw was added to the diets. These data are discussed elsewhere (Schrama & Bakker, 1999).

**Table 4.** Supplied amounts of NE, fermentable feed ingredients, and intakes of DM, dietary fiber (DF), digestible starch and fermentable dietary fiber (fDF) of group-housed growing pigs fed the experimental diets (*Experiment 1*)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls				
		1	2	3	4	5	6	7	8	9	10
NE <sup>a</sup> , kJ·kg <sup>-0.75</sup> ·d <sup>-1</sup>		733	733	733	733	733	733	733	733	733	733
SECM <sup>b</sup> , g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		3.5	13.2		32.7	42.4	--	--	--	--	--
SBH <sup>b</sup> , g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		--	--	--	--	--	3.5	13.2	23.0	32.7	42.4
DM intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		62.2	65.4	68.6	72.1	75.3	64.9	68.3	71.9	75.2	78.9
DF <sup>c</sup> intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		8.9	12.6	17.4	22.2	26.6	8.7	13.3	18.4	21.3	27.1
Starch intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		32.0	28.8	24.5	20.3	16.5	36.0	31.5	26.5	22.9	17.3
fDF <sup>c</sup> intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>		6.6	9.3	12.6	16.2	18.7	6.1	9.1	12.3	13.4	16.6

<sup>a</sup> Amount of calculated NE supplied to the pigs.

<sup>b</sup> Amount of solvent-extracted coconut meal (SECM) or soybean hulls (SBH) supplied to the pigs.

<sup>c</sup> Content of dietary fiber (DF) was calculated as DM - (CP + crude fat + ash + sugars + starch).



**Table 5.** Supplied amounts of NE, DM, dietary fiber (DF), and starch of group-housed growing pigs fed diets differing in carbohydrates source and straw addition (*Experiment 2*)

Item	Gelatinized maize starch		Raw potato starch	
	No straw	Straw	No straw	Straw
NE <sup>a</sup> , kJ·kg <sup>-0.75</sup> ·d <sup>-1</sup>	733	733	628	628
DM intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	67.0	77.1	67.1	77.2
DF <sup>b</sup> intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	15.1	24.4	15.1	24.4
Starch <sup>c</sup> intake, g·kg <sup>-0.75</sup> ·d <sup>-1</sup>	34.9	34.4	35.3	34.9

<sup>a</sup> Amount of NE supplied to the pigs.

<sup>b</sup> Content of dietary fiber (DF) was calculated as DM - (CP + crude fat + ash + sugars + starch). Non-digestible starch from potato starch is not included in this fraction.

<sup>c</sup> Starch plus sugars, fermentable starch from potato starch is also included in this fraction.

### **Empty Weights of the Gastrointestinal Tract**

#### *Experiment 1*

Effects of the experimental diets on empty weights of the GIT and its different parts are given in Table 6. Diet affected the empty weights of the total GIT, stomach, and large intestine ( $P < 0.01$ ; Table 6). The source of DF (i.e., SECM or SBH) had no effect on the empty weights of the total GIT, stomach, small intestine, and cecum ( $P > 0.10$ ). The empty large intestine and the mesentery (i.e., including pancreas) were heavier ( $P < 0.05$ ) for pigs fed diets with SECM (15.8 and 7.8 g/kg BW, respectively) than for pigs fed diets with SBH (14.5 and 6.1 g/kg BW, respectively).

#### *Experiment 2*

Effects of carbohydrate source and addition of straw on the empty weights of the GIT and its different parts are given in Table 7. No interaction between carbohydrate source and the addition of wheat straw was found. Carbohydrate source affected the empty weight of the total GIT ( $P = 0.010$ ) and the large intestine ( $P < 0.001$ ). The empty weight of the total GIT of pigs fed raw potato starch (43.2 g/kg BW) was higher than that of pigs fed gelatinized maize starch (39.7 g/kg BW). This was due to the higher empty weight of the large intestine of pigs fed raw potato starch (18.5 g/kg BW) than that of pigs fed gelatinized maize starch (14.3 g/kg BW). Addition of straw to the diet affected the empty weight of the total GIT ( $P = 0.033$ ) and the stomach ( $P = 0.004$ ). The empty weight of the total GIT of pigs fed straw (42.9 g/kg BW) was higher than that of pigs fed no straw (40.0 g/kg BW). This was mainly due to the higher empty weight of the stomach of pigs fed straw (6.7 g/kg BW) compared to pigs fed no straw (6.0 g/kg BW).

**Table 6.** Mean live body weight (in kg) and effects of the experimental diets on empty weights of the gastrointestinal tract (GIT) and its different parts (in g/kg BW) in growing pigs (*Experiment 1*)

Item	Diet No.	Diets with solvent-extracted coconut meal					Diets with soybean hulls					P – value <sup>a</sup>	
		1	2	3	4	5	6	7	8	9	10	SEM	D
Body weight	61.1	60.5	61.1	65.9	55.9	59.0	67.6	64.8	65.1	69.4	2.0	-	-
Total GIT <sup>b</sup>	42.5 <sup>ef</sup>	45.9 <sup>def</sup>	46.1 <sup>def</sup>	46.8 <sup>defg</sup>	52.7 <sup>d</sup>	44.7 <sup>ef</sup>	41.1 <sup>f</sup>	45.9 <sup>def</sup>	49.0 <sup>de</sup>	47.5 <sup>def</sup>	1.7	0.001	0.272
Stomach	6.4 <sup>g</sup>	6.7 <sup>fg</sup>	6.9 <sup>efg</sup>	7.1 <sup>defg</sup>	8.2 <sup>d</sup>	6.6 <sup>fg</sup>	6.7 <sup>fg</sup>	7.4 <sup>defg</sup>	7.9 <sup>de</sup>	7.6 <sup>def</sup>	0.2	<0.001	0.238
Small intestine	21.9	21.8	22.2	21.4	22.1	23.5	19.3	21.4	23.5	21.5	1.1	0.277	0.935
Cecum	1.8	1.9	2.1	2.1	2.4	2.0	1.8	2.7	1.8	2.0	0.3	0.452	0.901
Large intestine	12.4 <sup>g</sup>	15.5 <sup>efg</sup>	14.9 <sup>efg</sup>	16.2 <sup>ef</sup>	20.0 <sup>d</sup>	12.6 <sup>fg</sup>	13.4 <sup>efg</sup>	14.4 <sup>efg</sup>	15.7 <sup>efg</sup>	16.3 <sup>de</sup>	0.8	<0.001	0.011
Mesentery <sup>c</sup>	7.7	6.8	8.3	8.6	7.4	6.8	7.9	6.5	4.3	4.8	1.0	0.090	0.013

<sup>a</sup> D = effect of diet (diet 1 to 10); Contrast = A contrast method was used to analyze differences between diets with solvent-extracted coconut meal and diets with soybean hulls.

<sup>b</sup> Total empty weight of the gastrointestinal tract (GIT) was calculated as the sum of the empty weights of the different parts of the GIT.

<sup>c</sup> The weight of the mesentery including the pancreas.

<sup>d, e, f, g</sup> Within a row, means with different superscripts differ ( $P < 0.05$ ).

**Table 7.** Mean live body weight (in kg) and effects of carbohydrate source and straw addition on empty weights of gastrointestinal tract (GIT) and its different parts in growing pigs (in g/kg BW), using carbohydrate source and straw addition as class variables in ANOVA (*Experiment 2*)

Item	Gelatinized maize starch		Raw potato starch		SEM	P - value <sup>a</sup>		
	No straw	Straw	No straw	Straw		C	S	C × S
Body weight	53.9	55.6	54.7	57.0	1.5	-	-	-
Total GIT	37.7	41.6	42.3	44.2	1.3	0.010	0.033	0.443
Stomach	6.2	6.7	6.0	6.8	0.2	0.859	0.004	0.428
Small intestine	16.1	18.2	16.5	16.6	0.7	0.382	0.117	0.143
Cecum	1.7	1.7	1.7	1.8	0.1	0.308	0.988	0.467
Large intestine	13.7	14.9	18.0	19.0	0.7	<0.001	0.151	0.886

<sup>a</sup> C = Effect of carbohydrate source; S = Effect of straw addition; C × S = Interaction between carbohydrate source and straw addition.

#### **Effects of Dietary Fiber Intake on Empty Weights of the GIT**

The linear relationships between the intake of DF and the empty weights of the total GIT, stomach, and large intestine are given in Table 8. There was no relation between the intake of DF and the empty weights of the small intestine, cecum, or mesentery (data not shown). The empty weight of the total GIT increased when DF intake increased ( $P < 0.001$ ). Per gram of extra DF intake, the empty weight of the GIT increased with 0.37 g per kg BW. The empty weight of the stomach and the empty weight of the large intestine also increased with an increasing DF intake ( $P < 0.001$ ). On average, about 20% and 75% of the increase in empty weight of the GIT with increasing DF intake is due to an increased empty weight of the stomach and large intestine, respectively. There was no effect of DF source on the increase in empty weights of the total GIT or its different parts.

#### **Effects of Fermentable Dietary Fiber Intake on Empty Weights of the GIT**

The linear relationships between the intake of fDF and the empty weights of the total GIT, stomach, and large intestine are given in Table 9. There was no relation between the intake of fDF and the empty weights of the small intestine, cecum, or mesentery (data not shown). Similar to the effects of DF intake, the empty weight of the total GIT increased when fDF intake increased ( $P < 0.001$ ). Per gram of extra fDF intake, the empty weight of the GIT increased with 0.58 g per kg BW. The empty weight of the stomach and the empty weight of the large intestine also increased with an increasing intake of fDF ( $P < 0.001$ ). On average, about 20% and 75% of the increase in empty weight of the GIT with increasing fDF intake is due to an increased empty weight of the stomach and large intestine, respectively.

**Table 8.** Relationships between the intake of dietary fiber (DF, in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) and empty weights of the gastrointestinal tract (GIT), stomach, and large intestine (in g/kg BW) in growing pigs (*Experiment 1*)

Item	Relationship with DF intake	<i>P</i> - value <sup>b</sup>	
		DF	Source
Total GIT,		<0.001	0.279
SECM	$Y = 46.9 (\text{SE } 0.8) + 0.47 (\text{SE } 0.12) \times \text{DF}$		
SBH	$Y = 45.6 (\text{SE } 0.8) + 0.28 (\text{SE } 0.12) \times \text{DF}$		
Stomach,		<0.001	0.518
SECM	$Y = 7.1 (\text{SE } 0.1) + 0.09 (\text{SE } 0.02) \times \text{DF}$		
SBH	$Y = 7.2 (\text{SE } 0.1) + 0.07 (\text{SE } 0.02) \times \text{DF}$		
Large intestine,		<0.001	0.112
SECM	$Y = 15.8 (\text{SE } 0.4) + 0.35 (\text{SE } 0.06) \times \text{DF}$		
SBH	$Y = 14.5 (\text{SE } 0.4) + 0.22 (\text{SE } 0.06) \times \text{DF}$		

<sup>a</sup> SECM = solvent-extracted coconut meal; SBH = soybean hulls.

<sup>b</sup> DF = effect of DF intake; Source = effect of source of DF on regression coefficient.

**Table 9.** Relationships between the intake of fermentable dietary fiber (fDF, in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) and empty weights of the gastrointestinal tract (GIT), stomach, and large intestine (in g/kg BW) in growing pigs (*Experiment 1*)

Item	Relationship with fDF intake	<i>P</i> - value <sup>b</sup>	
		fDF	Source
Total GIT,		<0.001	0.577
SECM	$Y = 46.4 (\text{SE } 0.8) + 0.66 (\text{SE } 0.17) \times \text{fDF}$		
SBH	$Y = 46.0 (\text{SE } 0.8) + 0.50 (\text{SE } 0.22) \times \text{fDF}$		
Stomach,		<0.001	0.883
SECM	$Y = 7.0 (\text{SE } 0.1) + 0.12 (\text{SE } 0.03) \times \text{fDF}$		
SBH	$Y = 7.3 (\text{SE } 0.1) + 0.13 (\text{SE } 0.03) \times \text{fDF}$		
Large intestine,		<0.001	0.457
SECM	$Y = 15.5 (\text{SE } 0.4) + 0.49 (\text{SE } 0.08) \times \text{fDF}$		
SBH	$Y = 14.8 (\text{SE } 0.4) + 0.39 (\text{SE } 0.10) \times \text{fDF}$		

<sup>a</sup> SECM = solvent-extracted coconut meal; SBH = soybean hulls.

<sup>b</sup> fDF = effect of fDF intake; Source = effect of source of fDF on regression coefficient.

## **Discussion**

### **General**

Various experiments on the effects of DF on the empty weights of the GIT and its different parts have been reported in rats (e.g., Ikegami et al., 1990; Zhao et al., 1995a,b), poultry (e.g., Jørgensen et al., 1996a; Iji et al., 2001) and pigs (e.g., Pond et al., 1988; Jørgensen et al., 1996b; Pluske et al., 1998). These studies, however, do not report very consistent results, as indicated for pigs in Table 10. In general, an increased DF intake results in an increased weight of the large intestine. This is similar to the results from the present study. It might be concluded from data in Table 10 that effects of DF on empty weights of different parts of the GIT depend on the level of DF intake and the form in which DF has been included (isolates or integrated part of cell wall structure). Moreover, Freire et al. (2000) reported an effect of DF source on the empty weights of the stomach, small intestine, and large intestine in weaned piglets. They, however, did not use a control diet with limited content of DF and therefore the effect of DF addition could not be estimated. Bakker (1996) reported that increased dietary bulkiness (i.e., addition of pure cellulose) did not affect the empty weight of the total GIT, cecum, and large intestine, whereas increased fermentation (i.e., addition of SBH) increased the empty weights of the total GIT, cecum, and large intestine.

Dose response studies with DF are scarce (Kass et al., 1980; Zhao et al., 1995a). Zhao et al. (1995a) reported that the empty weight of the stomach, small intestine, cecum, and large intestine of rats increased with increasing DF intake. Kass et al. (1980) reported that the weight of the total GIT, small intestine, cecum, and colon of pigs increased with increasing dietary inclusion levels of alfalfa meal. Pluske et al. (1998) fed growing pigs diets with either a source of soluble DF (i.e., guar gum), or a source of resistant maize starch, or both soluble DF and resistant maize starch, or Australian sweet lupines. They reported a positive correlation between intakes of soluble DF or soluble DF plus resistant starch and the empty weight of the large intestine (cecum plus colon), which resulted in a negative correlation between the daily intake of soluble DF plus resistant starch and dressing proportion. Pluske et al. (1998), however, did not find a relationship between daily intake of total DF or resistant starch on the empty weight of the large intestine (cecum plus colon). This is in contrast with the results from present study in which DF intake had significant effects on the empty weight of the total GIT, stomach, and large intestine (i.e., except for the addition of straw).

### **Stomach**

In literature, effects of DF on the empty weight of the stomach seem to depend on the level of DF, but reported effects are not consistent (Table 10). In experiment 1 of the present study, the empty weight of the stomach increased with increasing DF or fDF

intake (Table 8 and 9). The source of DF did not affect the empty weight of the stomach (Table 6). In experiment 2 of the present study, addition of straw to the diet increased the empty weight of the stomach, whereas stimulation of fermentation did not (Table 7). The cause for increased stomach weights with increasing dietary bulkiness might be due to the fact that the stomach temporarily stores ingested feed which normally has a greater bulkiness when the DF content increases. Contradictory effects of DF on gastric emptying are reported in literature presumably due to differences among studies in the form in which DF has been included (i.e., isolates or integrated part of cell wall structure) (Bach Knudsen, 2001). The inhibitory effect of DF on liquids emptying is clearly demonstrated, whereas the effect of DF on the emptying of the solid phase is more controversial (Guerin et al., 2001). Guerin et al. (2001) reported that intragastric meal distribution and viscosity of the gastric contents are better predictors for gastric emptying than DF content. They also showed that the botanical origin of DF affected gastric emptying (Guerin et al., 2001). In experiment 1 of the present study, DM intake increased with increasing DF content. In experiment 2 of the present study, DM intake was higher for diets with wheat straw. This increased meal volume may cause differences in gastric emptying (Moran et al., 1999). It can be concluded from the present study that increasing dietary volume increased the empty weight of the stomach.

### ***Small Intestine***

In the present study, no effect of diet composition on the empty weight of the small intestine was found. Bach Knudsen (2001) reported an average digestibility of DF in the small intestine of 0.20 with large variations between experiments. An effect of DF on the empty weight of the small intestine may be due to the degree of fermentation in the small intestine, which increases absorption of volatile fatty acids. It can be hypothesized that fermentation in the small intestine in the present study was stimulated to a limited amount with the used sources of DF. With increasing DF, however, the amount of digesta that needs to be transported by the small intestine will increase. Low (1989) also reported that various sources of DF appear to stimulate salivary, gastric, biliary, pancreatic, and intestinal secretions. This probably will increase energy utilization by the gastroduodenal region of the GIT.

### ***Cecum***

From Table 10, it seems that an effect of DF on the empty weight of the cecum is dependent on the inclusion level of DF and the origin of DF. Isolates, like guar gum and resistant starch, did not affect the empty weight of the cecum (Pluske et al., 1998), whereas DF as integrated part of cell wall structure did affect the empty weight of the cecum (e.g., Pond et al., 1988; Pluske et al., 1998). In the present study, however, no effects of SECM, SBH, raw potato starch, or straw addition on the empty weight of the cecum were found. This is probably due to the relative high variation in

weight of the cecum compared to that of the large intestine and to the short retention time in the cecum compared to the large intestine (Glitsø et al., 1999).

### ***Large Intestine***

In experiment 1 of the present study, the empty weight of the large intestine increased with increasing DF of fDF intake (Table 8 and 9). And the source of DF affected the empty weight of the large intestine (Table 6). In experiment 2 of the present study, stimulation of fermentation in the GIT increased the empty weight of the large intestine (Table 7). The increase of the empty weight of the large intestine is consistent in literature (Table 10). Because the retention time of digesta is normally much longer in the large intestine than in the stomach or small intestine (Bach Knudsen, 2001), the large intestine houses large numbers of bacteria (Moore et al., 1987). Therefore, the most active sites for fermentation are the cecum and the proximal colon (Bach Knudsen, 2001). Nyachoti et al. (2000) reported that a barley-canola meal diet and a barley-canola meal-alfalfa diet increased the empty weight of the large intestine, which was mainly due to an increased weight of the mucosa of the large intestine and not the muscular layer. This implies that stimulation of fermentation in the hindgut stimulates the growth of metabolic active tissue for the absorption of volatile fatty acids and less the growth of muscle tissue in the hindgut. Fleming et al. (1992) reported that the source or quantity of DF could influence cellular proliferation of the distal colon. Moreover, Siba et al. (1996) reported a relationship between VFA production and large intestinal weight. Increased DF content will also increase the amount of digesta that needs to be transported through the gut. Fleming et al. (1992), however, did not report a significant correlation between digesta volume and cellular proliferation in the distal colon. They suggested that DF influence intestinal cell proliferation through many mechanisms, some of which are interactive. Increased DF content can also decrease retention time in the GIT, dependent on the botanical origin of DF (Le Goff et al., 2002b), which will probably increase energy used for motility of the GIT. An increased weight of metabolic active tissue of the GIT has implications for energy metabolism of pigs as reported by Koong et al. (1985).

It can be concluded from the present study that inclusion of DF has two distinctive effects on the empty weights of the different parts of the GIT. The relative importance of these effects seems to depend on the characteristics of DF. First, dietary volume increased mainly the empty weight of the stomach, to make the stomach able to carry more dietary weight. This suggests growth of muscle tissue of the stomach. Second, stimulation of fermentation in the GIT increased mainly the empty weight of the large intestine. This suggests growth of metabolic active tissue of the large intestine. Dietary fiber will increase dietary volume and fermentation in the hindgut, which may influence energy utilization of pigs.

**Table 10.** Effects of dietary fiber on empty weights of the gastrointestinal tract (GIT), and its different parts from various studies in pigs

Fiber source	Inclusion level <sup>a</sup>	Total GIT	Stomach	Small intestine	Cecum	Large intestine	Reference
Alfalfa	200	NS <sup>b</sup>	NS	NS	NS	NS	Kass et al., 1980
Alfalfa	400	↑ <sup>c</sup>	NS	NS	NS	↑	Kass et al., 1980
Alfalfa	600	↑	NS	↑	↑	↑	Kass et al., 1980
Alfalfa	800	- <sup>d</sup>	↑	↑	↑	↑	Pond et al., 1988
Alfalfa	400	↑	↑	NS	-	NS <sup>e</sup>	Anugwa et al., 1989
Alfalfa	400	-	NS	↑	-	↑ <sup>e</sup>	Pond et al., 1989
Pea fiber + pectin	350 + 25	↑	↑	NS	↑	↑	Jørgensen et al., 1996b
Guar Gum (GG)	50	-	-	-	NS	↑	Pluske et al., 1998
Resistant maize starch	80	-	-	-	NS	NS	Pluske et al., 1998
GG + RS	50 +70	-	-	-	NS	↑	Pluske et al., 1998
Sweet lupins	250	-	-	-	↑	↑	Pluske et al., 1998
Alfalfa	300	↑	-	NS	↑	↑	Nyachoti et al., 2000
Barley + canola meal	610 + 225	NS	-	NS	NS	↑	Nyachoti et al., 2000

<sup>a</sup> Dietary inclusion level in g/kg.

<sup>b</sup> NS = not significant.

<sup>c</sup> ↑ = increased empty weight ( $P < 0.05$ )

<sup>d</sup> - = not reported in reference.

<sup>e</sup> Cecum plus colon.



## **Chapter 7**

### **Effects of Housing Conditions and Dietary Fiber on Energy Metabolism and Physical Activity in Growing Pigs**

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## Effects of Housing Conditions and Dietary Fiber on Energy Metabolism and Physical Activity in Growing Pigs

### Abstract

The effects of housing conditions, dietary fiber (DF) from sugar beet pulp (SBP), and their interaction on energy metabolism and physical activity were studied in growing pigs. It was hypothesized that group-housed pigs were able to utilize energy from fermentable DF more efficiently than individually housed pigs by the ability of lowering their energy expenditure for physical activity. A 13-d experimental period was preceded by a 13-d preliminary period. The experiment was designed in a  $2 \times 2$  factorial arrangement with housing conditions (individual vs group-housing) and dietary composition (starch vs DF) as factors. In the sugar beet pulp (SBP) diet (high in DF), 15% of the gelatinized maize starch from the control diet (high in starch) was replaced with 17.5% SBP. In total, 10 individually housed pigs, and 140 group-housed pigs (i.e., 10 groups of 14 pigs each) were studied in five trials. Each trial consisted of two balance periods, and per balance period N and energy balances were measured simultaneously in four respiration chambers. Apparent fecal digestibilities of all nutrients were also measured per balance period. No interaction between housing conditions and diet composition was found. Apparent fecal digestibilities of all nutrients and dietary energy, except for DF, were higher for individually housed pigs than for group-housed pigs ( $P < 0.05$ ). Metabolizability of dietary energy was 3.7 percentage units higher ( $P < 0.001$ ) for individually housed pigs than for group-housed pigs. Housing conditions did not affect total heat production (HP), activity-related HP (AHP), and total energy retention (ER). The ratio between AHP and HP was lower ( $P = 0.066$ ) for individually housed pigs than for group-housed pigs. Individually housed pigs had a higher ( $P < 0.001$ ) ER as protein than group-housed pigs ( $151$  vs  $137 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Digestibilities were different between the experimental diets. Metabolizability of dietary energy was 3.5 percentage units higher ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet. Diet composition did not affect HP, and pigs fed the control diet had a higher ( $P = 0.055$ ) AHP than pigs fed the SBP diet ( $80$  vs  $68 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Diet composition did not affect total ER, but pigs fed the control diet had a higher ( $P < 0.01$ ) ER as protein than pigs fed the SBP diet ( $150$  vs  $138 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The heat increment values of fermentable DF (fDF) from SBP, uncorrected and corrected for AHP, were 3.8 and 5.2 kJ/g, respectively. This corresponds to NE values of 13.7 and 12.3 kJ/g, respectively. Fermentable DF intake decreased AHP ( $P = 0.058$ ), and there was no effect of housing conditions on estimated NE values. It can be concluded that the effect of fDF from SBP on AHP was not affected by housing conditions and that the energetic utilization of fDF from SBP was not affected by housing conditions.

## **Introduction**

In nutritional, feed evaluation, and other experimental studies, pigs are mostly housed individually, whereas in commercial conditions pigs are group-housed. Various studies reported effects of housing conditions for pigs on behavior (e.g., Terlouw & Lawrence, 1993; Cerneau et al., 1997), feeding patterns (e.g., De Haer & De Vries, 1993; Nielsen et al., 1996; Bornett et al., 2000a,b), performance (e.g., Bustamante et al., 1996; Gomez et al., 2000) and apparent fecal digestibilities (e.g., Bakker & Jongbloed, 1994; Kemme et al., 1997; Gomez et al., 2000). Growth performance is usually improved when pigs are housed individually compared with group-housed pigs (Gomez et al., 2000). This might at least partly be explained by the higher fecal digestibility of nutrients in these pigs (e.g., Bakker & Jongbloed, 1994; Gomez et al., 2000). However, little is known about effects of housing conditions on energy utilization in pigs.

Energy evaluation systems for pigs in most countries (e.g., ARC, 1981; Noblet et al., 1994; NRC, 1998; CVB, 2000) predict the potential of feed ingredients for growth and maintenance. These systems are largely based on experiments with individually housed growing pigs and assume constant energy requirements for maintenance. In growing pigs (e.g., Schrama et al., 1996; 1998) and sows (e.g., Brouns et al., 1994; Ramonet et al., 1999; Rijnen et al., 2003a), differences in dietary fiber (DF) content affected physical activity. Consequently, this effect on physical activity will influence the energetic efficiency with which pigs utilize their diet. In literature, results on effects of DF on energy expenditure for physical activity are not very consistent. In growing pigs, decreasing effects of DF intake on energy expenditure for physical activity are only reported for experiments with group-housed pigs (e.g., Schrama et al., 1998; Schrama & Bakker, 1999). It is hypothesized that housing conditions (i.e., restriction of physical activity and behavior) may interfere with the energetic utilization of DF by influencing a pig's physical activity. This hypothesis is based on (i) decreasing the opportunity for altering physical activity of individually housed pigs and (ii) the absence of social interactions when pigs were housed individually. The aim of the experiment was to assess the effects of housing conditions and carbohydrate source separately and in combination on energy metabolism and physical activity of growing pigs.

## **Materials and Methods**

### ***Animals, Diets, and Housing***

The 13-d experimental period was preceded by a 13-d preliminary period. The preliminary period allowed the pigs to adjust to the experimental diets, housing conditions and handling (i.e., weighing and collecting feces). The experiment was

designed in a  $2 \times 2$  factorial arrangement with housing conditions, and dietary carbohydrate composition as factors. For studying the first factor, pigs were housed either individually or in groups. For studying the second factor, two diets were composed (Table 1). The control diet consisted of a basal diet supplemented with gelatinized maize starch and potato protein. For composition of the sugar beet pulp (SBP) diet, gelatinized maize starch from the control diet was partly replaced by SBP. For this exchange, 15% of the gelatinized maize starch from the control diet was replaced with 17.5% SBP, based on an assumed apparent fecal digestibility of the DF fraction of SBP of about 85% (Schrama et al., 1998). Composition of the basal diet is shown in Table 2.

In total, 10 pigs were housed individually and 140 pigs were housed in groups (i.e., 10 groups of 14 pigs each). Individually housed and group-housed pigs were assigned to one of two experimental diets. The experiment was conducted in five trials ( $n = 5$  observations per treatment; Table 3). Pigs were ([Great Yorkshire  $\times$  Finish Landrace]  $\times$  Tyborg-G) barrows. At the start of the preliminary period, pigs were about 14 weeks old and weighed on average 38.0 kg (SEM 0.3). During the preliminary period, individually housed pigs were fed the experimental diets and housed in metabolic crates with a size of about 0.9 m<sup>2</sup>, which allowed the pigs to move and turn around in the crates. Metabolic crates were placed in one room, which allowed the pigs to hear and see each other. To collect feces quantitatively, a plastic bag was attached to the rear end of the pigs as described by Van Kleef et al. (1994). During the preliminary period, group-housed pigs were fed the experimental diets and group-housed in conventional pens (i.e., 14 pigs per group).

Individually housed pigs were fed according to their metabolic LW (kg<sup>0.75</sup>) and group-housed pigs were group-fed according to their mean metabolic LW. Feed intake was adjusted daily for an expected ADG of 600 g/d. During the first three days of the preliminary period (i.e., after transportation to the experimental facilities), the feeding level of all pigs on the control diet was gradually increased from 1.25 to 2.5 times the maintenance requirements. From the fourth day of the preliminary period until the end of the experiment, pigs on the control diet were fed at a feeding level of 2.5 times maintenance. The NE requirements for maintenance were assumed to be 293 kJ·kg<sup>0.75</sup>·d<sup>-1</sup> (Verstegen et al., 1973). To ensure similar intakes of the basal diet, pigs fed the SBP diet were fed a similar amount of the basal diet as pigs fed the control diet. Therefore, pigs received the SBP diet at a feeding level (in g/d) that was 1.5% higher than pigs fed the control diet. The calculated nutrient intakes per dietary treatment are shown in Table 1.

**Table 1.** Composition and calculated daily intake of the experimental diets

	Composition		Daily intake	
	Control	SBP	Control	SBP
Ingredients	g/kg	g/kg	g/kg <sup>0.75</sup>	g/kg <sup>0.75</sup>
Basal diet <sup>a</sup>	750.0	738.9	53.6	53.6
Gelatinized maize starch <sup>b</sup>	200.0	49.3	14.3	3.6
Potato protein <sup>c</sup>	50.0	39.4	3.6	2.9
Sugar beet pulp <sup>b</sup>	-	172.4	-	12.5
Total	1000.0	1000.0	71.5	72.6
Analyzed nutrients	g/kg DM	g/kg DM	g/kg <sup>0.75</sup>	g/kg <sup>0.75</sup>
Dry matter, g/kg	899	896	64.2	65.0
Crude ash	73	83	5.2	6.0
Crude protein	209	215	14.9	15.6
Crude fat	38	30	2.7	2.2
Starch	498	359	35.6	26.0
Sugars	74	72	5.3	5.2
Dietary fiber <sup>d</sup>	109	241	7.8	17.5
NDF	50	110	3.6	8.0
ADF	29	65	2.1	4.7
ADL	6	9	0.4	0.7

<sup>a</sup> Composition of the basal diet is given in Table 2.

<sup>b</sup> On as fed basis, 15% maize starch from the control diet was exchanged for 17.5% sugar beet pulp (SBP), based on fecal digestibility of dietary fiber from SBP of about 85%.

<sup>c</sup> On as fed basis, 1% potato protein from the control diet was excluded from the sugar beet pulp diet, because of the digestible protein content in sugar beet pulp (91 g/kg; CVB, 2000).

<sup>d</sup> Dietary fiber content was calculated as DM - (crude ash + crude protein + crude fat + starch + sugars).

The experimental period of each trial consisted of two successive balance periods, which lasted 6 d and 7 d, respectively. At the start of the experimental period, individually housed pigs were placed in one of two identical, size-adjustable climatic respiration chambers, set to about 0.9 m<sup>2</sup>, in which the pigs were isolated from their environment. Group-housed pigs were placed in one of two identical, large climatic respiration chambers (Verstegen et al., 1987b). Within each chamber, pigs were group-housed in two pens of 8.3 m<sup>2</sup> each (i.e., seven pigs per pen; 14 pigs per respiration chamber). In all chambers ambient temperature was kept at 20°C, which is above the lower critical temperature of pigs at the experimental feeding levels (Verstegen, 1987); relative humidity was maintained at about 65%, and air velocity was < 0.2 m/s; and pigs were exposed to 12 h of light (about 300 lx from 0700 to 1900) and 12 h of partial darkness (about 10 lx from 1900 to 0700).

Individually housed pigs were fed using a trough with a drinking nipple for ad libitum access to drinking water. Group-housed pigs were group-fed per pen using a long trough, and separated drinking nipples for ad libitum access to drinking water. Pigs received their daily feed in two equal portions at 0800 and 1530. Pigs had access to the feed for 45 min. The feed was given as dry feed (pellets).

**Table 2.** Ingredient composition of basal diet<sup>a</sup>

Ingredient	g/kg
Wheat	333.3
Extracted soybeans	312.0
Gelatinized maize starch	200.0
Soybean oil	40.0
Cane molasses	40.0
CaCO <sub>3</sub>	16.0
Monocalcium phosphate	12.0
NaCl	5.3
DL-Methionin	1.3
Diatomaceous shell powder	26.7
Vitamin and mineral premix <sup>b</sup>	13.4

<sup>a</sup> Included in the experimental diet on as fed basis (Table 1).

<sup>b</sup> Supplied the following per kilogram of the control diet (Table 1): vitamin A, 5,000 IU; vitamin D3, 1,000 IU; vitamin E, 7.5 mg; vitamin B12, 15 µg; vitamin K, 0.4 mg; riboflavin, 3.5 mg; niacinamid, 20 mg; d-pantothenic acid, 5 mg; choline chloride, 200 mg; CoSO<sub>4</sub>.7H<sub>2</sub>O, 1 mg; KI, 0.5 mg; organic Se, 0.06 mg; FeSO<sub>4</sub>.7H<sub>2</sub>O, 400 mg; CuSO<sub>4</sub>.5H<sub>2</sub>O, 80 mg; MnO<sub>2</sub>, 70 mg; ZnSO<sub>4</sub>.H<sub>2</sub>O, 200 mg.

**Table 3.** The number of animals and experimental units per experimental treatment<sup>a</sup>

Item	Group housing		Individual housing	
	Control	SBP	Control	SBP
Trial i (i = 1, 2, 3, 4, 5)	14/1	14/1	1/1	1/1

<sup>a</sup> Control = control diet; SBP = sugar beet pulp diet; 14/1 = 14 pigs / 1 experimental unit; 1/1 = 1 pig / 1 experimental unit.

### **Measurements**

Individual LW was recorded at the start of the preliminary period, at day 7, day 13 (start of experimental period), day 19, and day 26. If present, feed refusals were collected 45 min after feeding. The ADFI was determined from supplied feed and refusals.

Per balance period, apparent fecal digestibility of DM, ash, OM, N, crude fat, NDF, ADF, ADL, and GE were measured by using the acid-insoluble ash (AIA) marker method. Adding diatomaceous shell powder to the basal diet (Table 2) increased the dietary AIA content. During the experimental period, diets were sampled daily and pooled per experimental period. For individually housed pigs, feces were collected daily and quantitatively for each individual pig using plastic stoma bags attached to the rear end of the pigs as described by Van Kleef et al. (1994). Daily collected feces were pooled per balance period per respiration chamber. For group-housed pigs, fecal grab samples were collected twice per day after feeding at 0800 and 1530, during five days of both balance periods. Feces were collected per group of pigs (i.e., per chamber), and samples were pooled per balance period per respiration chamber. After collection of grab samples, the remainder of the feces was removed from the floor. Therefore, grab samples were representative for feces excreted between feeding times.

Feed and feces samples were analyzed for DM, ash, AIA, N, crude fat, NDF, ADF, ADL, and GE. Feed was also analyzed for sugars. All analyses were carried out in duplicate. The DM and N content of the feces was measured in fresh samples, and the remaining analyses were carried out in freeze-dried samples. The DM content was measured by drying to constant weight at 103°C. Ash content was measured by incineration in an oven at 550°C. The AIA content was determined by treating the residue of the ash determination with 3 N HCl to dissolve minerals and subtracting the solved part from total ash. The AIA was filtered and weighed after incineration. Nitrogen content was measured with the Kjeldahl method, and CP content was calculated as N x 6.25. The crude fat content was measured after hydrolysis with 3 N HCl and extraction of the residue with petroleum ether (boiling range 40 to 60°C). Cell wall constituents (NDF, ADF, and ADL) were measured according to the methods of Van Soest & Wine (1967). Gross energy values were measured using bomb calorimetry. The starch content of the used gelatinized maize starch was analyzed enzymatically. With the starch content of the gelatinized maize starch, starch contents of the experimental diets were calculated. Free sugars (mono- and disaccharides) were removed by alcohol extraction (ethanol, 40%). After gelatinization by heating in an autoclave for 3 h at 130°C, starch was hydrolyzed to glucose with a mixture of enzymes (10 mg of amyloglucosidase, 1 mg of  $\alpha$ -amylase and 12.5 mg of  $\mu$ L-pullulanase in 5 ml of H<sub>2</sub>O per sample) at pH 4.8 (Brunt, 1993). Subsequently, glucose was measured using hexokinase and G6P-dehydrogenase. The sugar content was determined after extracting feed samples with ethanol. Carbohydrates in the

filtrate, were hydrolyzed with 0.1 *N* HCl and after using free sugars as a reducing agent to oxidize copper, the content was measured using a spectrophotometer.

Dietary fiber (DF) content was calculated by subtracting the content of CP, crude fat, starch, sugars, and ash from the DM content. Fecal digestibility of starch and sugars was assumed to be 100%. Therefore, fecal DF was calculated as DM minus fecal CP, crude fat, and ash.

Per balance period, energy and N balances were measured per respiration chamber. For individually housed pigs, feces and urine were collected quantitatively and separately per balance period and sampled for GE and N analysis. For group-housed pigs, excreta (i.e., feces plus urine) were collected quantitatively per balance period per group and sampled for GE and N analysis. Gross energy was analyzed in freeze-dried samples and N in fresh samples.

Intake of ME per respiration chamber was calculated from energy content of feed, excreta, and methane production. Urinary energy losses were calculated by the difference from digestible energy intake and the sum of ME intake and methane production.

Heat production (HP) was measured in 9-min intervals by measuring the exchange of oxygen, carbon dioxide, and methane as described by Verstegen et al. (1987b). From these gaseous exchanges, HP was calculated according to the formula of Brouwer (1965). During each balance period, HP was measured, omitting the first, incomplete day of each balance period. Furthermore, the first half-hour after offering feed was omitted from the data (i.e., from 0800 to 0830 and from 1530 to 1600), because HP measurements were disturbed when using the air lock to feed the individually housed pigs. To make a good comparison between housing treatments, HP data of the first half-hour of feeding were omitted for all experimental treatments. Total energy retention (ER) was calculated by subtracting HP from ME intake. The retention of N was calculated from N in feed, in excreta, in aerial NH<sub>3</sub>, and in NH<sub>4</sub><sup>+</sup> of water that condensed on the heat exchanger. Energy retained as protein (ERp) was derived from retained N. Energy retention as fat (ERf) was calculated by subtracting ERp from ER.

Physical activity was recorded in the same time intervals as HP. For individually housed pigs, physical activity was measured per pig (i.e., per respiration chamber) with one radar-Doppler device according to the method described by Wenk & Van Es (1976). For group-housed pigs, physical activity was measured per pen with a radar-Doppler device (i.e., two devices per respiration chamber). The principle of this method is that due to the Doppler effect all movements (i.e., of animals) result in a change in frequency of the reflected radar waves emitted by the devices. Activity is then being calculated, within mentioned intervals, as the number of electrical pulses generated by the devices when changes in radar frequency crosses certain threshold values.



For individually and group-housed pigs, the 9-min data on HP were related to activity counts using the following equations:

$$HP_{ij} = \mu + D_i + \beta_1 \times X_{1j} + e_{ij} \quad (\text{individually housed pigs}) \quad [1]$$

$$HP_{ij} = \mu + D_i + \beta_1 \times X_{1j} + \beta_2 \times X_{2j} + e_{ij} \quad (\text{group-housed pigs}) \quad [2]$$

where  $HP_{ij}$  = heat production during day period  $i$  and 9-min period  $j$ ;  $\mu$  = overall mean;  $D_i$  = fixed effect of day period ( $i = 1$  (from 0700 to 2200) or  $2$  (from 2200 to 0700));  $X_{1j}$  and  $X_{2j}$  = activity counts during 9-min period  $j$  of radar-Doppler device 1 and 2, respectively;  $\beta_1$  and  $\beta_2$  = regression coefficients of heat production on activity counts of radar-Doppler device 1 and 2, respectively; and  $e_{ij}$  = error term.

Heat production and physical activity exhibit circadian rhythms (Aschoff et al., 1974; Schrama et al., 1996; Rijnen et al., 2003a). The circadian rhythm in HP is only partly accounted for by physical activity, which has been demonstrated in pigs (Van der Hel et al., 1984; Henken et al., 1991) and calves (Schrama et al., 1994). Therefore, a fixed effect of day period with two levels was included in Eq. [1] and [2]. Days were divided into an active period from 0700 to 2200 and an inactive period from 2200 to 0700 (Rijnen et al., 2003a). The increase in HP after feeding is not fully accounted for the elevated physical activity (Verstegen et al., 1987a). In the regressions according to Eq. [1] and [2], data around feeding time, from 0800 to 0900 and from 1530 to 1630, were excluded. These data were omitted to avoid possible bias by inclusion of the heat increment associated with feed ingestion in relationship between HP and physical activity.

For individually and group-housed pigs, activity-related heat production (AHP) was calculated by:

$$AHP_j = \beta_1 \times X_{1j} \quad (\text{individually housed pigs}) \quad [3]$$

$$AHP_j = \beta_1 \times X_{1j} + \beta_2 \times X_{2j} \quad (\text{group-housed pigs}) \quad [4]$$

where  $AHP_j$  = activity-related heat production during 9-min period  $j$ ;  $X_{1j}$  and  $X_{2j}$  = activity counts during 9-min period  $j$  of radar-Doppler device 1 and 2, respectively; and  $\beta_1$  and  $\beta_2$  = the estimated regression coefficient from HP on physical activity from Eq. [1].

Heat production corrected for physical activity, or resting heat production (RHP), was calculated by subtracting AHP from HP. Both AHP and RHP were calculated for each 9-min period of HP.

**Statistical Analysis**

For all traits for individually housed pigs, the pig was the experimental unit. For all traits for group-housed pigs, the group was the experimental unit. Averaged over the two balance periods, all traits were analyzed for the effect of housing conditions, diet composition and their interaction using a two-way ANOVA, with trial as extra independent variable, according to the following model:

$$y_{ijk} = \mu + T_i + H_j + D_k + (H \times D)_{jk} + e_{ijk} \quad [5]$$

where  $y_{ijk}$  = dependent variable;  $\mu$  = overall mean;  $T_i$  = effect of trial ( $i = 1, 2, 3, 4, 5$ );  $H_j$  = effect of housing conditions ( $j = 1, 2$ );  $D_k$  = effect of diet composition ( $k = 1, 2$ );  $(H \times D)_{jk}$  = interaction between housing conditions and diet composition;  $e_{ijk}$  = error term.

Moreover, the present study focused on effects of fermentable DF (fDF) intake from SBP on HP and AHP. Therefore, HP and AHP were analyzed for the effect of housing conditions by linear regression of these traits on the daily intake of fDF (expressed in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Statistical Analysis Systems, statistical software package version 6.12 (SAS Inst. Inc., Cary, NC, USA) was used for all statistical evaluations.

**Results****General**

In Table 4, the number of pigs used per experimental treatment is given. In total, nine group-housed pigs (three on the control diet and six on the SBP diet) were removed from the experiment due to leg problems and/or low feed intakes. For group-housed pigs on the control diet during trial 1, no AHP was recorded due to failure of one radar device. During the experimental period, no feed refusals occurred.

At the start of the experimental period, LW averaged 43.9 kg (SEM 0.5) and was slightly lower ( $P < 0.05$ ) for individually housed pigs than for group-housed pigs. Individually housed pigs had a higher ( $P < 0.01$ ) ADG (637 g/d) than group-housed pigs (524 g/d). Diet composition did not affect ADG ( $P > 0.10$ ).

**Apparent Fecal Digestibilities**

In Table 4, data for apparent fecal digestibilities on the experimental treatments are given. No interaction between housing conditions and carbohydrate source was present. The digestibility of DM, ash, OM, CP, crude fat, and NDF were higher ( $P < 0.05$ ) for individually housed pigs than for group-housed pigs (i.e., 1.7, 1.7, 1.7, 5.1, 6.2, and 1.3 percentage units higher, respectively). Digestibility of DF, ADF, and ADL were unaffected by housing conditions and averaged 73.7, 70.3 and 38.9%, respectively. Digestibility of dietary energy was 2 percentage units higher ( $P < 0.001$ ) for individually housed pigs than for group-housed pigs.

Digestibility of DM, ash, OM, CP, crude fat, and ADL was higher ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet (i.e., 3.5, 5.9, 2.8, 4.1, 17.4, and 11.8 percentage units higher, respectively). Digestibility of DF, NDF, and ADF were lower ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet (i.e., 13.5, 13.0, and 11.0 percentage units lower, respectively). Digestibility of dietary energy was 3.5 percentage units higher ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet, which resulted in differences in DE intake between diets.

**Table 4.** Influence of housing conditions (individual vs group-housing) and diet composition (control diet vs sugar beet pulp [SBP] diet) on mean initial LW, ADG, and apparent fecal digestibilities in growing pigs

	Group		Individual		SEM	P-value <sup>a</sup>		
	Control	SBP	Control	SBP		D	H	D × H
No. of exp. units	5	5	5	5	-	-	-	-
No. of pigs	69	68	5	5	-	-	-	-
Initial LW, kg	44.2	44.7	43.0	43.5	0.5	0.279	0.018	0.962
ADG, g/d	536	511	668	607	25	0.106	0.001	0.486
Apparent fecal digestibilities, in %								
Dry matter	88.7	85.2	90.3	86.9	0.1	<0.001	<0.001	0.794
Crude ash	52.6	47.2	54.8	48.3	0.6	<0.001	0.018	0.446
Organic matter	91.5	88.6	93.1	90.4	0.1	<0.001	<0.001	0.587
Crude protein	84.7	80.4	89.6	85.7	0.5	<0.001	<0.001	0.635
Crude fat	72.2	54.3	77.9	61.0	1.9	<0.001	0.007	0.785
Dietary fiber	65.8	79.8	68.1	81.0	1.0	<0.001	0.102	0.558
NDF	64.6	78.0	66.3	78.8	0.5	<0.001	0.032	0.389
ADF	64.0	75.4	65.5	76.2	0.9	<0.001	0.234	0.661
ADL	44.5	34.5	45.0	31.5	2.1	<0.001	0.574	0.407
Energy	89.6	86.1	91.5	88.2	0.2	<0.001	<0.001	0.575

<sup>a</sup> D = effect of diet, H = effect of housing conditions, D × H = interaction between diet and housing conditions.

### Energy Partitioning

In Table 5, data on energy partitioning for the experimental treatments are given. Except for DM, and GE intake, no interaction between housing conditions and carbohydrate source was present.

**Table 5.** Influence of housing conditions (individual vs group-housing) and diet composition (control diet vs sugar beet pulp [SBP] diet) on DM intake (in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ), and energy partitioning (in  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) in growing pigs

	Group		Individual		SEM	<i>P</i> -value <sup>a</sup>		
	Control	SBP	Control	SBP		D	H	D × H
DM intake	64.1	64.7	62.2	64.0	0.2	<0.001	<0.001	0.022
GE intake	1191	1192	1156	1179	5	0.020	<0.001	0.035
Methane	9.5	12.7	10.6	12.6	0.5	<0.001	0.322	0.232
Urinary energy	71	63	42	48	5	0.859	<0.001	0.178
ME intake	987	951	1005	979	6	<0.001	0.003	0.443
ME:GE, in %	82.8	79.7	87.0	83.0	0.4	<0.001	<0.001	0.339
ME:DE, in %	92.4	92.6	95.0	94.1	0.5	0.481	0.001	0.292
Heat Production								
Total	641	641	663	641	11	0.338	0.312	0.343
Activity-related	82	74	78	62	6	0.055	0.182	0.459
Resting	556	567	585	580	9	0.767	0.036	0.405
pAHP <sup>b</sup> , in %	12.8	11.6	11.7	9.6	0.8	0.043	0.066	0.557
Energy Retention								
Total (ER)	346	310	342	338	13	0.160	0.375	0.262
Protein (ERp)	142	133	158	144	3	0.003	<0.001	0.446
Fat (ERf)	204	177	184	194	15	0.585	0.920	0.240

<sup>a</sup> D = effect of diet, H = effect of housing conditions, D × H = interaction between diet and housing conditions.

<sup>b</sup> pAHP = AHP/HP × 100.

### Effects of Housing Conditions

Metabolizability of dietary energy (ME:GE) was 3.7 percentage units higher ( $P < 0.001$ ) for individually housed pigs than for group-housed pigs, which resulted in a higher ( $P < 0.05$ ) ME intake for individually housed pigs than for group-housed pigs (993 vs 969  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Urinary energy excretion was lower ( $P < 0.001$ ) for individually housed pigs than for group-housed pigs, and housing conditions did not affect methane production. Housing conditions did not affect HP and AHP, which averaged 646 and 74  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , respectively. As a percentage of HP, AHP was 1.5 percentage units lower (pAHP;  $P = 0.066$ ) for individually housed pigs than for group-housed pigs. Individually housed pigs had a higher ( $P < 0.05$ ) RHP than group-housed pigs (582 v. 561  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Housing conditions did not affect ER and ERf, which averaged 334 and 190  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , respectively. Individually housed pigs had a higher ( $P < 0.001$ ) ERp than group-housed pigs (151 vs 137  $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ).

### *Effects of Diet Composition*

Metabolizability of dietary energy (ME:GE) was 3.5 percentage units higher ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet, which resulted in a higher ( $P < 0.01$ ) ME intake for pigs fed the control diet than for pigs fed the SBP diet (996 vs 967  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ). Urinary energy excretion was unaffected by diet composition, and methane production was lower ( $P < 0.001$ ) for pigs fed the control diet than for pigs fed the SBP diet. Diet composition did not affect HP, which averaged 646  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ . Pigs fed the control diet had a higher ( $P = 0.055$ ) AHP than pigs fed the SBP diet (80 vs 68  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ). As a percentage of HP, AHP was 1.7 percentage units higher (pAHP;  $P = 0.043$ ) for pigs fed the control diet than for pigs fed the SBP diet. Diet composition did not affect RHP, which averaged 573  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ . Diet composition did not affect ER and ERf. Pigs fed the control diet had a higher ( $P < 0.01$ ) ERp than pigs fed the SBP diet (150 vs 138  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ).

## **Discussion**

### **General**

This study was carried out to assess the effects of housing conditions (i.e., individual or group-housing) and dietary carbohydrate source (i.e., digestible or fermentable carbohydrates) separately and in combination on energy metabolism and physical activity in growing pigs.

Interactions between housing conditions and diet composition were not present, except for DM intake (in  $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ) and consequently for GE intake (in  $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ). The experimental set-up caused this interaction, because pigs were fed according to their metabolic LW at the start of each balance period with an expected ADG of 600 g/d. Therefore, differences in ADG for pigs on the experimental treatments in relation to the assumed ADG caused the interaction between housing conditions and diet composition. There was no interaction between housing conditions and diet composition for DM intake when it was expressed in g/d.

A higher ADG for individually housed pigs than for group-housed pigs on the control diet could be expected from literature (e.g., De Haer & De Vries, 1993; Bustamante et al., 1996; Gomez et al., 2000). These studies, however, were conducted with pigs with ad libitum access to feed that led to a higher ADFI for individually housed pigs than for group-housed pigs with no or small effects on feed efficiency. In the present study, pigs were fed restrictively and we expected an interaction between housing conditions and diet composition on AHP. This was expected to increase feed efficiency in group-housed pigs on the SBP diet. Therefore, differences in ADG between housing conditions were not taken into account in the experimental design.

It should be noted that no interaction between housing conditions and dietary composition was present for apparent fecal digestibilities, energy metabolism and physical activity in growing pigs on the experimental treatments.

### ***Housing Conditions***

#### ***Apparent Fecal Digestibilities***

In line with the present study, higher digestibilities of DM, OM, and CP for individually housed pigs compared with group-housed pigs are reported in literature (De Haer & De Vries, 1993; Bakker & Jongbloed, 1994; Kemme et al., 1997; Gomez et al., 2000). In the present study, digestibility of crude fat was also higher for individually housed pigs than for group housed pigs, with large variation among animals and groups. In line with the present study, Gomez et al. (2000) found a trend ( $P < 0.10$ ) for higher digestibility of dietary energy for individually housed growing gilts compared with group-housed growing gilts (80.7 vs 81.8 %), fed a corn based diet. This trend was found for young pigs from 18 to 50 kg LW (Gomez et al., 2000).

De Haer & De Vries (1993) reported a lower feed intake per meal, a lower rate of feed intake (in g/min), a higher number of meals per day, and a longer time spent on eating per day for individually housed pigs compared with group-housed pigs. They also reported that an increased time spent per day on eating was negatively correlated with the apparent fecal digestibilities of DM and CP for individually housed pigs and not for group-housed pigs. Gomez et al. (2000) suggested that higher apparent fecal digestibilities in individually housed pigs might be related to the number of meals per day, because for group-housed pigs feeding is correlated to frequency of aggressive acts. Therefore, group-housed pigs might have a lower number of meals per day than individually housed pigs, with only small differences in total feed intake per day. This causes a higher rate of feed intake in group-housed pigs, which might reduce the exposure of feed to digestive secretions and an increased rate of passage through the small intestine (Gomez et al., 2000). In the present study, however, all pigs were fed restrictively and twice a day with a limited time to access the feed. Competition for feed was, however, still present for group-housed pigs, which might have affected rate of feed intake. A higher retention time of digesta in the gut for individually housed pigs compared with group-housed pigs was reported by Metz & Dekker (1985), which resulted in on average 1.8 percentage units higher DM digestibility. In the present study, the differences in digestibilities between housing conditions might be caused by an increased mean retention time of digesta by individual housing. Increased retention time of digesta for individually housed pigs might be related to a lower physical activity of those pigs. In the present study, pAHP was lower ( $P = 0.066$ ) for individually housed pigs than for group-housed pigs, but AHP was only numerically lower ( $P > 0.10$ ) for individually housed pigs than for group-housed pigs (Table 5). When correlating AHP and pAHP with the apparent fecal

digestibilities, we did not find any relationships between AHP or pAHP and apparent fecal digestibilities. In the present study, housing conditions did not affect the apparent fecal digestibility of DF, but did affect the digestibility of NDF. This is at least partly due to the larger variation in DF digestibility.

It can be concluded that apparent fecal digestibilities of all nutrients, except for DF, are higher for individually housed pigs than for group-housed pigs on the experimental diets.

### *Energy Partitioning*

Individually housed pigs had a higher ME intake ( $P < 0.05$ ) than group-housed pigs due to a 3.7 percentage units higher metabolizability of dietary energy ( $P < 0.001$ ). In addition to differences in digestion (i.e., 2 percentage units) the difference in metabolizability was due to a lower energy excretion with urine for individually housed pigs compared with group-housed pigs. Methane production was not affected by housing conditions. This is also shown by a higher ( $P < 0.01$ ; Table 5) ME to DE ratio for individually housed pigs compared with group-housed pigs. The higher ( $P < 0.01$ ) ERp for individually housed pigs compared with group-housed pigs is in line with the lower energy excretion with urine. There was no difference in the ratio between digestible CP intake (in  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) and ME intake ( $P > 0.10$ ). It is unlikely that group-housed pigs had a limiting digestible CP intake for protein deposition.

De Haer & De Vries (1993) and Gomez et al. (2000) found a numerically higher ( $P > 0.10$ ) lean growth rate for individually housed pigs than for group-housed pigs. Petersen et al. (1998) reported no differences in lean growth between individually and group-housed pigs. De Haer & De Vries (1993) reported a higher backfat thickness for individually housed pigs than for group-housed pigs with similar feed intake. Petersen et al. (1998) reported a higher total body fat for individually housed pigs than for group-housed pigs, which was due to significantly more fat retention in the shoulder and legs of individually housed pigs. It was suggested that the higher energy expenditure for spontaneous physical activity and lower feed intake of group-housed pigs might have caused the lower fat retention (Petersen et al., 1998). In the present study, feed intake and AHP were similar for both housing conditions, but pAHP was lower ( $P = 0.066$ ) for individually housed pigs than for group-housed pigs. No effects were found on ERf.

It can be concluded that the ME to GE ratio was higher for individually housed pigs than for group-housed pigs due to higher fecal digestibility of dietary energy and lower energy excretion with urine. Total ER was not affected by housing conditions, but more energy was retained as protein for individually housed pigs.

## **Diet Composition**

### *Apparent Fecal Digestibilities*

In the present study, experimental diets differed mainly in the contents of maize starch and SBP. There was also a small difference in potato protein content. Therefore, differences in fecal digestibilities reflect differences in digestibilities of the components in maize starch, SBP and to a lesser extent potato protein. The higher digestibility of OM, CP, and dietary energy for pigs fed the control diet compared with pigs fed the SBP diet is in line with the differences in tabulated digestibility values of maize starch, potato protein, and SBP (CVB, 2000). The lower digestibility of DF for pigs fed the control diet compared with pigs fed the SBP diet is in line with literature data (e.g., Schrama et al., 1998). Le Goff et al. (2002b) reported no effect of adding SBP to diets for growing pigs on mean retention time of digesta in the gut.

To assess the energetic utilization of fDF from SBP, the intake of digestible nutrients were calculated from DM intake, diet composition, and fecal digestibilities. Digestible starch and DF intake differed between dietary treatments ( $P < 0.001$ ). The intake of starch was 31.4 and 23.1  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  (SEM 0.1) and the intake of DF was 4.6 and 12.5  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  (SEM 0.1) for pigs fed the control diet and pigs fed the SBP diet, respectively. Intake of digestible CP did not differ between the experimental diets and averaged 11.5  $\text{g} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  (SEM 0.1).

### *Energy Partitioning*

In the present study, metabolizability of dietary energy was 3.5 percentage units higher for pigs fed the control diet than for pigs fed the SBP diet. In addition to differences in digestion, the higher metabolizability for pigs fed the control diet was due the lower methane production for pigs fed the control diet compared with pigs fed the SBP diet, whereas diet composition did not affect urinary energy losses. The ME to DE ratio was unaffected by diet composition ( $P > 0.10$ ; Table 5). The higher metabolizability for pigs fed the control diet is in line with the difference in metabolizability (i.e., 3.5 percentage units) between the control diet and the 15% SBP-silage diet as reported by Schrama et al. (1998). Total heat production was similar for both diets, which corresponds to results from Schrama et al. (1998). Furthermore, Schrama et al. (1998) reported a lower ( $P < 0.10$ ) AHP when dietary SBP-silage content increased. Despite smaller differences, the present results also showed that AHP was higher ( $P = 0.055$ ) for pigs fed the control diet than for pigs fed the SBP diet.

### *Net Energy Value of Fermentable Dietary Fiber from Sugar Beet Pulp*

The aim of the present study was to assess the energetic efficiency of fermentable DF (fDF) from SBP for growth in relation to energy expenditure for physical activity. As described by Schrama et al. (1998) and Rijnen et al. (2001), the energetic efficiency



of fDF, uncorrected and corrected for AHP, can be derived from the linear relationships between HP and fDF intake and between RHP and fDF intake, respectively. In order to get unbiased relationships, HP and RHP were corrected for daily intakes of digestible CP, crude fat, starch, and sugars and for the production of methane (CorHP and CorRHP, respectively). The values for the heat increment of digestible CP, crude fat, starch, and sugars used for this correction were 12.8, 3.2, 4.0, and 3.6 kJ/g, respectively. These heat increments were derived from the assumed energetic efficiencies for these digested nutrients (i.e., 46, 92, 77, and 77 %, respectively) used in the current Dutch NE evaluation system for pigs (CVB, 2000). The NE saving effect of physical activity can be derived from the relationship between AHP and fDF intake. Results are shown in Table 6.

**Table 6.** Estimated heat increment of fermentable dietary fiber (fDF) from sugar beet pulp, uncorrected and corrected for activity-related heat production (AHP), and the effect of AHP on the NE value of fDF (in kJ/g fDF intake)<sup>a</sup>

Item	Housing conditions <sup>b</sup>			P-value <sup>c</sup>			
	Individual	Group	SEM	Mean	SEM	H × fDF	fDF
Heat increment	2.05	5.47	1.86	3.76	1.33	0.213	0.011
Heat increment, corr.	3.92	6.42	1.59	5.18	1.20	0.280	<0.001
AHP	-1.87	-0.89	0.95	-1.39	0.68	0.478	0.058

<sup>a</sup> Heat increment was estimated from linear relationships between heat production (HP) and resting heat production (RHP), and fermentable dietary fiber (fDF) intake, after correcting HP and RHP for daily intakes of digestible nutrients using fixed heat increments (see text). The shown data are the regression coefficients.

<sup>b</sup> For group-housed pigs on the control during trial 1, no AHP was recorded due to failure of one radar device. Therefore, the sum of the heat increment corrected for AHP and the effect of AHP on the NE value of fDF is not equal to the heat increment uncorrected for AHP.

<sup>c</sup> H × fDF = effect of housing conditions on estimated value; fDF = effect of fermentable dietary fiber intake.

The mean heat increment of fDF from SBP, uncorrected for AHP, was 3.8 kJ/g, which corresponds to a NE value of 13.7 kJ/g. Schrama et al. (1998) reported a NE value of fDF from SBP-silage of 14.7 kJ/g in group-housed growing pigs. When correcting data from Schrama et al. (1998) for methane production, the NE value of fDF from SBP-silage was 14.1 kJ/g, which is in line with the NE value found in the present study. Rijnen et al. (2003a) also reported a high NE value of fDF from SBP-silage in group-housed sows (i.e., 13.4 kJ/g). Most feed evaluation system use a NE value of fDF that is 70% of the NE value of digestible starch as reviewed by Boisen & Verstegen (2000) (e.g., 9.5 kJ/g; CVB, 2000).

Both Schrama et al. (1998) and Rijnen et al. (2003a) reported that a decrease in AHP with increasing SBP-silage content was a main cause for the relatively high NE value

of fDF from SBP-silage. Bakker and Schrama (1999) reported that increased fermentation of starch (i.e., raw potato starch) decreased AHP of group-housed growing pigs. In the present study, AHP also decreased with increasing fDF intake ( $P = 0.058$ ). Differences in the effect of fDF intake on AHP between studies might also be related to the used starch source and the amount of starch that is fermented in the gastrointestinal tract. After correcting the heat increment value for AHP of fDF from SBP, the average heat increment value was 5.2 kJ/g, which corresponds to a NE value of 12.3 kJ/g. This is still over 90% of the NE value of digestible starch. It can be concluded that the high NE value of fDF from SBP is not only caused by differences in AHP. Noblet & Le Goff (2001) suggested differences in NE values for DF from different botanical origin.

Schrama et al. (1998) suggested that housing conditions might affect the energetic efficiency of fDF. In the present study it was hypothesized that group-housed pigs are able to adjust their energy expenditure on physical activity, whereas individually housed pigs have a decreased opportunity for altering physical activity and absence of social interactions. In the present study, however, individually housed pig had a numerically lower ( $P > 0.10$ ) heat increment of fDF than group-housed pigs, which is in contrast with the hypothesis of the present study. The effect of AHP on the NE value of fDF from SBP was numerically higher ( $P > 0.10$ ) for individually housed pigs than for group-housed pigs. These results show that individually housed pigs are able to lower their energy expenditure on physical activity at least with the same magnitude as group-housed pigs.

It is known that individually housed pigs suffer from more stress than group-housed pigs, because of the lack of social interactions. Individually housed pigs, however, had higher apparent fecal digestibilities than group-housed pigs, except for DF, ADF, and ADL, which might be caused by differences in mean retention time of digesta. Digestibility of NDF was also higher for individually housed pigs than for group-housed pigs. It is suggested that mean retention time of digesta in the hindgut was higher for individually housed pigs than for group-housed pigs, which increased the energetic efficiency of fDF. It is also suggested that in stressful situations DF has a greater effect than under practical conditions.

The hypothesis of the present study that the energetic efficiency of fDF from SBP is higher for group-housed pigs than for individually housed pigs, due to differences in energy expenditure for physical activity has to be rejected. The addition of SBP to the diet lowered energy expenditure for physical activity both in group-housed and individually housed pigs. Both digestibility and metabolizability of dietary energy were higher for individually housed pigs than for group-housed pigs, which means that there will be differences in the NE values of feed ingredients and diets between individually and group-housed pigs.

# **Chapter 8**

## **General Discussion**

## **General Discussion**

### **Introduction**

The experiments in this thesis focused on the energetic utilization of fermentable dietary fiber (fDF) in pigs. As described in Chapter 1, many studies or reviews concerning different effects of dietary fiber (DF) in pigs have been published recently (e.g., Bach Knudsen (2001), Noblet & Le Goff (2001), Pluske et al. (2001), Wenk (2001), and Le Goff (2001)). These and more recent publications on the use of DF show the increased interest of pig researchers and pig industry in the use of fiber-rich feed ingredients for pigs. De Lange (2000) and Grieshop et al. (2001) give good overviews on the use of DF in practical pig diets and their compositions.

The starting point of the studies presented in this thesis was the relative high NE value of fDF of sugar beet pulp silage (SBPS), and the decreasing effect of SBPS on activity-related heat production (AHP) of group-housed growing pigs (Schrama et al., 1998). Several hypotheses were raised to investigate possible mechanisms for the found effects. The first experiment was conducted to study the energetic utilization of fDF from SBPS in group-housed sows, and the effects of SBPS on behavior of group-housed sows (Chapter 2 and 3). The second experiment was conducted to study the energetic utilization of fDF from two other sources of fDF in group-housed growing pigs, and to study if the found effect of SBPS on AHP was also present for other DF sources (Chapter 4 and 5). In the third experiment, the effect of housing conditions (individual vs group-housing) on the energetic utilization of fDF was studied, because the high NE value of SBPS was only found in group-housed pigs (Chapter 7). In this chapter, the results from the studies described in this thesis are discussed.

### **Some Aspects of Net Energy**

Living organisms are characterized by a highly ordered state and thus by a low entropy of the biomass and need a constant supply of oxygen and energy for turnover. Living animals breakdown organic molecules from their own body and from their environment (nutritional sources) and combust them with oxygen to carbon dioxide and water. The free energy produced in the breakdown of these molecules can be stored as chemical energy or used as ATP. The breakdown from body components requires replacement by ingested nutrients and nutrients are also needed for growth and production.

In energy based feed evaluation systems attempts are made to quantify the energy that can be derived from ingested nutrients by animals. In the future this will probably be as ATP that can be derived from ingested feed. It should be realized that in the past it was difficult to measure ATP. It was already realized a long time ago that in

addition to energy some nutrients are required to enable animals to synthesize products for growth or for its products (e.g., milk and eggs). For the potential use of feed by animals we need its feeding value. The feeding value can be expressed as energy or as building matter. In this respect it is important to note that these functions cannot be combined in one figure. This was noted a long time ago because Armsby (1922) wrote: "Feed has two distinct functions and these are incommensurable. It is impossible to combine the value of a feed as source of protein or other structural material with its value as a source of energy and to express that result in a single number." That also means that the energy value should be used as energy and other components should be valued otherwise.

In some cases of animal husbandry, feed may be regarded as fuel (energy) and its nutritive content expressed as Joules, and in other cases as building blocks, such as amino acids or fatty acids. For energy evaluation, net energy is considered an excellent concept for expressing efficiency of feed utilization since the time of Kellner around 1900. The advantage is that net energy can be used as replacement equivalent of feed ingredients or diets for energy.

Since 1958, symposia on energy metabolism in farm animals are held every 3 years and it was discussed how the energy value of diets and feed ingredients should be expressed. It is generally agreed that first the amount of nutrients which are being absorbed from the feed should be known. Energy values should quantify how these absorbed nutrients can be each used for maintenance and production processes.

### **Concerns of NE-Systems**

In most net energy (NE) based feed evaluation systems, energy of digestible nutrients (i.e., crude protein, crude fat, starch, sugars, and dietary fiber) is used to calculate the NE content of a diet or feed ingredient (e.g., Noblet et al., 1994; CVB, 2000). To determine NE, energy retention (ER) or heat production (HP) needs to be measured. Energy retention can be measured with the comparative slaughter technique or by measuring the carbon-nitrogen balance (or energy-nitrogen balance). Heat production is the sum of the heat increment by the digestion, fermentation, metabolism of nutrients, and energy used for maintenance processes to sustain life and maintain body temperature (Ewan, 2001). In Chapter 1, more details are given of NE based feed evaluation systems. The NE value of a feed ingredient in feed evaluation systems indicates how much the energy retention of a pig will increase with an increased intake of one extra kg of that feed ingredient.

NE systems are made under some assumptions:

- 1) Energy that is used for maintenance is assumed to be constant; NE being the extra ER with an extra unit of a feed ingredient or diet above maintenance.

- 2) Additional energy from a certain nutrient is used with a constant efficiency that has been established for that nutrient. This can be also phrased as the linear increase in ER with an increase in the intake of a certain digestible component (e.g., protein, lipids, sugars, starch, or dietary fiber).
- 3) For estimating the NE of a diet, the ratio between ER as protein and as fat has to be constant or ER as protein has to be constant.
- 4) No difference in fecal digestibility and utilization is made between the physiological stages of pigs (i.e., piglets, growing pigs, finishing pigs, and sows).

Maintenance requirements are often excluded from feed evaluation systems by the assumption of being constant (i.e., marginal systems). Maintenance requirements as such are not estimated in the experiments described in this thesis. For clarification, some details are given about the various definitions of maintenance requirements. Maintenance requirements can be estimated from measurements of HP following periods of fasting (i.e., HP at zero ER). Measurements of fasting HP vary with the length of fasting, with previous nutritional history, and with the difference in physical activity between fasted and fed animals; it may not relate to the maintenance requirements of the normal animal. Maintenance requirements can also be estimated from the relationship between ER and ME intake (i.e., ME intake at zero ER). At zero ER, however, growing animals will continue to deposit protein and mobilize fat. Multiple regression between ME intake and retention of fat and protein provides an estimate of the ME requirements when no fat or protein is retained and is the third method of estimating maintenance requirements (Ewan, 2001).

When AHP can be altered with diet composition, the assumption that energy used for maintenance is a constant is not valid, which is the first concern of NE feed evaluation systems (see above). This is, however, dependent on the definition of maintenance as shown above. It raises the question whether maintenance requirements should include the total of physical activity, or that the maintenance requirements should include only part of physical activity and that the other part of physical activity is a characteristic of the feed ingredients that are used. Because feeding level (i.e., ME intake) can affect physical activity, it seems obvious that part of the physical activity is related to the used diet. This means that part of physical activity is included in the NE content of a diet or feed ingredient, because NE is defined as the extra ER above maintenance with the extra inclusion of additional feed.

The second assumption of NE feed evaluation systems (see above) is both used and studied in the experiments described in this thesis. As discussed in Chapter 2, the energetic efficiency of fDF can be estimated from the regression between HP and fDF intake, after correcting HP for digestible nutrient intakes. For estimating the energetic efficiency of fDF we use constant efficiencies for digestible CP, fat, starch, and sugars to estimate differences in the energetic efficiency of fDF. If the used efficiencies for digestible CP, fat, starch, and sugars are not constant or incorrect, the estimate of the

energetic efficiency of fDF is also not correct, because all variation in the constants of the efficiencies will be summarized for fDF. The other assumptions of NE feed evaluation systems will be discussed below.

Increased DF levels might negatively affect digestibility and rate of absorption of nutrients from protein, lipids, and starch. These effects can be attributed to the effects of DF on gut microflora, viscosity and water-holding capacity of the digesta, and to the 'mechanical' properties of DF (De Lange, 2000). It is also important to recognize possible contribution of DF to interactive effects between other nutrients on digestibilities, as reported by Bakker (1996). During the experiments presented in the present thesis, apparent fecal digestibilities of all nutrients were measured and used for estimating the energetic efficiency of fDF. Therefore, if DF had interacted with digestibilities of other nutrients, this would have been account for. If, however, DF affected the absorption or energetic utilization of other nutrients, then the estimated energetic efficiencies of fDF (as described in Chapter 2, 4, and 7) are biased.

### **Apparent Fecal Digestibilities**

The first step in NE based feed evaluation systems is the apparent fecal digestibility of all nutrients (Figure 3; Chapter 1). The focus of the present thesis was not on fecal digestibilities of nutrients, but on the energetic utilization of fDF. However, to estimate the energetic utilization of fDF, the fecal digestibilities need to be known.

The main cause for differences in fecal digestibilities between the used diets in the experiments described in this thesis, is the difference in the used feed ingredients. Differences in digestibilities for nutrients from various feed ingredients are reported in feeding tables (e.g., CVB, 2000).

Housing conditions can also cause differences in fecal digestibilities as shown in Chapter 7. The fecal digestibilities that are used for diet formulation are largely based on data derived from studies with individually housed growing pigs (e.g., CVB, 2000). With the higher digestibilities for individually housed pigs than for group-housed pigs (Chapter 7), this means that digestibilities are overestimated when used for group-housed pigs. It is suggested that the NE values for pigs, as reported in feeding tables, are overestimated for their use in practical diets, because of the lower digestibilities in group-housed pigs compared to values in feeding tables.

Le Goff & Noblet (2001) have reported differences in and relationships between fecal digestibilities of individually housed growing pigs and sows (averaged over 77 diets). It was clearly shown that the fecal digestibilities of dietary nutrients and energy, except for ether extract, were higher for sows than for growing pigs (Le Goff & Noblet, 2001). Similar differences were found between group-housed sows (Chapter 2) and group-housed growing pigs (Schrama et al., 1998), which were fed similar diets under similar experimental conditions. For example, the total tract digestibility of dietary energy was about 3 percentage units higher for sows than for growing pigs (Le Goff &

Noblet, 2001). This is equal to the difference in total tract digestibility of dietary energy for group-housed sows (Chapter 2) and group-housed growing pigs (Schrama et al., 1998). Possible explanations are the lower feeding level and longer mean retention time of the digesta in the gastrointestinal tract of sows compared to growing pigs (Le Goff et al., 2002b). Le Goff & Noblet (2001) showed an interaction between dietary protein content and physiological stage of pigs on the fecal digestibility of crude protein. Comparing data in this thesis (Chapter 2) with Schrama et al. (1998) a similar result was found: the fecal digestibility of crude protein decreased more in sows than in growing pigs with increasing dietary SBPS content. It was suggested that this may be due to the higher excretion of protein in cell bound protein, in relation to the lower fermentability of DF in growing pigs (Le Goff & Noblet, 2001). In addition, Cahn et al. (1998) showed that more nitrogen is excreted via the feces (i.e., as microbial protein) and less via the urine when the intake of DF increased. It is suggested that this effect is greater in sows than in growing pigs, because of the normally higher nitrogen excretion via the urine and the higher fermentability of DF in sows compared to growing pigs. It is suggested that different NE values of feed ingredients should be used for sows and growing pigs, because of the differences in fecal digestibilities. This is already adopted in some parts of the swine industry.

### Energetic Utilization of Dietary Fiber

The main focus of the experiments in this thesis was to study the energetic utilization of fDF. Some mean results of these experiments are summarized in Table 1.

**Table 1.** Mean ME intake, ratio between energy retention as protein (ERp) and fat (ERf), activity-related heat production (AHP), and the estimated net energy value of fermentable dietary fiber (fDF), uncorrected (NE) and corrected (NEcor) for the effect of fDF on physical activity, as reported in this thesis.

fDF <sup>a</sup> Source	Physiological Stage	Housing Conditions	ME intake, kJ·kg <sup>-0.75</sup> ·d <sup>-1</sup>	Ratio ERp/ERf	AHP, kJ·kg <sup>-0.75</sup> ·d <sup>-1</sup>	NE, kJ/g	NEcor, kJ/g
SBPS	Growing pigs	Group	972	0.79	89	14.1	10.2
SBPS	Sows	Group	512	0.28	57	14.7	12.4
SECM	Growing pigs	Group	973	0.63	63	11.1	10.5
SBH	Growing pigs	Group	1060	0.58	67	10.1	9.3
SBP	Growing pigs	Group	969	0.72	78	12.0	11.1
SBP	Growing pigs	Individual	992	0.80	70	15.4	13.5

<sup>a</sup> SBPS = sugar beet pulp silage; SECM = solvent-extracted coconut meal; SBH = soybean hulls; SBP = dried sugar beet pulp.



***Effects of Physiological Stage: Growing Pigs vs Sows***

The first aim of this thesis was to study whether the high energetic utilization of fDF from SBPS in growing pigs (Table 1; Schrama et al., 1998) was also found in sows. Both experiments used similar diets, with increasing SBPS (exchanged for tapioca), and were conducted under similar experimental conditions (e.g., group-housing, ambient temperature, etc.). The NE value of fDF from SBPS for growing pigs was 14.1 kJ/g (adapted from Schrama et al., 1998), and that for sows was 14.7 kJ/g (Chapter 2, corrected for methane production). In literature, no results are reported on possible differences in energetic utilization of fDF between growing pigs and adult sows. The found difference in the energetic utilization of fDF is small, and might be related to differences in feeding level and ER between growing pigs and sows. The lower feeding level in sows in relation to the higher mean retention time of digesta in the gastrointestinal tract might cause the slightly higher energetic efficiency in sows compared to growing pigs.

***Effects of Activity-related Heat Production***

The effect of fDF on AHP was higher in growing pigs than in sows (difference between the uncorrected and corrected NE value; Table 1). This was also due to the fact that with a similar contrast in AHP the contrast in fDF intake was greater in the experiment with sows (Chapter 3) than in the experiment with growing pigs (Schrama et al., 1998). After correcting the NE values for AHP, the difference in the energetic utilization between growing pigs and sows becomes larger (Table 1).

***Differences in Energy Retention***

In NE based feed evaluation systems, a constant ER<sub>p</sub> to ER<sub>f</sub> ratio or a constant ER<sub>p</sub> is assumed. The ratio between ER<sub>p</sub> and ER<sub>f</sub> (Table 1) is much lower in sows than in growing pigs, indicating the relatively higher ER<sub>f</sub> in sows than in growing pigs. When more energy is retained as fat, dietary energy is used more efficiently. Differences in the energetic utilization between sows and growing pigs will be shown in the NE value of fDF, because the energetic efficiencies for the other digestible nutrients are assumed to be constant. In line with the relatively lower ER<sub>p</sub> in sows compared to growing pigs, differences in ME to DE ratio was 3.9 percentage units lower for sows (Chapter 2) than for growing pigs (Schrama et al., 1998), due to differences in energy losses with urine. Le Goff & Noblet (2001) reported that the ME/DE ratio was 1.7 percentage units lower for individually housed sows than for individually housed growing pigs, due to the higher energy losses in urine in adult sows compared to growing pigs. In NE based feed evaluation systems, the higher energy losses with urine is integrated in the energetic efficiency with which digestible protein is used for ER. The differences between urinary energy losses between sows and growing pigs suggest that the energetic utilization is different between sows and growing pigs. With the calculations used in the present thesis, all differences in energetic utilization are

attributed to the energetic utilization of fDF. In the present thesis, differences in methane production were accounted for when estimating the energetic efficiency of fDF. Differences in methane production between sows and growing pigs will attenuate the difference in energetic utilization between sows and growing pigs, because of an increased methane production with increasing digestibility of DF. It is suggested that housing conditions (i.e., individual vs group-housing) might affect the differences that are found between growing pigs and adult sows.

#### *Botanical Origin of Dietary Fiber*

As shown by Le Goff et al. (2002b), the difference in digestion of DF from different plant sources between growing pigs and adult sows was less important for DF from SBP than for maize bran. It is suggested that differences in energetic utilization of fDF between adult sows and growing pigs is also dependent on the botanical origin of fDF.

#### *Conclusions*

It can be concluded that the energetic utilization of fDF is dependent on physiological stage of pigs (i.e., adult sows vs growing pigs). Differences might be due to differences in ER (i.e., ERp or ERf), differences in energy losses with urine and methane, and differences in physical activity. The found difference in energetic utilization of fDF might partly be due to differences in energetic utilization of digestible crude protein. Differences in energetic utilization of fDF might also depend on the botanical origin of fDF.

#### ***Energetic Utilization of Dietary Fiber in Growing Pigs***

The main objective of the research presented in this thesis was to study the energetic utilization of fDF in growing pigs. The following questions were asked:

- 1) Are there differences in energetic utilization of fDF from different DF sources?
- 2) Do differences in AHP explain differences in energetic utilization of fDF?
- 3) Do differences in housing conditions affect the energetic utilization of fDF?

#### *Differences in Energetic Utilization of fDF from Different Sources*

De Lange (2000) reported the composition of DF fractions of different botanical origin in contents of soluble and insoluble nonstarch polysaccharides, and polysaccharide structure. These differences in composition lead to differences in digestibility of DF from different botanical origin (Noblet & Le Goff, 2001). In Table 1, the energetic utilization of fDF from sugar beet pulp silage (SBPS), dried sugar beet pulp (SBP), solvent-extracted coconut meal (SECM), and soybean hulls (SBH) is given for group-housed growing pigs. The NE value of fDF was the highest for SBPS, and higher for SBP than for SECM and SHB. It can be concluded that there are differences in the energetic utilization of fDF from different origin. Some possible mechanisms for those differences are discussed below.

*Effects of Activity-related Heat Production on the NE Value of Fermentable DF*

When correcting the NE values for fDF from the used feed ingredients for the effects of fDF on AHP, the NE values of the fDF fractions are very similar (Table 1). This is in contrast with the NE values uncorrected for AHP. The difference is due to the fact that SBPS had a large effect on AHP and SBP had a small effect on AHP, whereas SECM and SBH had no significant effect on AHP. This means that an effect of fDF on AHP is not a general effect for all sources of fDF and it is probably related to their botanical origin. Effects of fDF on AHP will affect the NE value as used in feed evaluation systems, but has up till now only been found in sugar beet pulp (silage). This explains the relative high NE value of fDF from SBP compared to other feed ingredients. It should be noted that Schrama & Bakker (1999) also reported a decrease in AHP when raw potato starch was fed to growing pigs instead of gelatinized maize starch.

Energy expenditure for physical activity has been reported to depend on feeding level (Susenbet & Menk, 1991), type of feed (Schrama et al., 1998; Chapter 3 and 7), body weight, and breed/castration of pigs (Van Milgen et al., 1998). The AHP of group-housed pigs on the control diet in the experiments reported by Schrama et al. (1996:  $118 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; 1998:  $106 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) was higher than for the pigs on the control diets in the experiment described in Chapter 5 (53 and  $66 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The group-housed pigs on the control diet in the experiment described in Chapter 7 had an intermediate AHP ( $82 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ), with a lower effect of fDF on AHP than reported by Schrama et al. (1998). All pigs (i.e., barrows) were housed under the same experimental housing conditions with the same feeding level, and about the same body weight. However, different crossbred pigs were used. It is suggested that differences in AHP found between studies are due to the used breeds. It is hypothesized that a certain threshold level of physical activity is needed to find effects of diet composition on AHP. In other words, when pigs have very low AHP values, no effect of diet composition can be expected.

It can be concluded that there are differences in the energetic utilization of fDF and that those differences can be largely explained by differences in AHP. Effects on AHP might be dependent on source of fDF and breed of pigs.

*Differences in Energy Retention*

As explained in the discussion on differences in the energetic utilization between adult sows and growing pigs, the ratio between ERp and ERf might play a role. There are some differences in the ratio between ERp and ERf in the studies with group-housed growing pigs (Table 1). The ERp/ERf ratio was, however, highest for pigs fed SBPS that had the highest NE value. This is in contrast to the differences found between adult sows and growing pigs. The differences in the ERp/ERf ratio probably depends on the used breeds of pigs, because there was only limited difference in digestible crude protein intake between SBPS, SBP, SECM, and SBH (10.1, 11.3, 11.0, and 11.0

$\text{g}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ). However, it is possible that there were some differences in intakes of ileal digestible crude protein and amino acids.

#### *Effects of Housing Conditions on the NE Value of Fermentable DF*

It was hypothesized that the energetic efficiency with which pigs utilize fDF was higher for group-housed pigs than for individually housed pigs, because of their ability to lower their energy expenditure for physical activity. In Chapter 7, however, it was shown that there was no significant effect of housing conditions on the energetic utilization of fDF. Numerically, the energetic efficiency of fDF was even higher for individually housed pigs than for group-housed pigs. The ERp/ERf ratio was higher for individually housed pigs than for group-housed pigs. This means that the ERp/ERf ratio did not mask the higher energetic utilization of fDF in individually housed pigs compared to group-housed pigs.

Differences in housing conditions are considered to have some effect on AHP in pigs (e.g., Schrama et al., 1998; Van Milgen et al., 1998; Noblet et al., 2001). Group-housed pigs have the possibility for all types of spontaneous physical activity and social interactions, whereas pigs individually housed in cages only have the possibility to stand, lay, and sit. In contrast to what was expected the effect of fDF intake on AHP was numerically higher for individually housed pigs than for group-housed pigs ( $P = 0.478$ ). After correcting for AHP, the difference in energetic utilization of fDF between individually housed pigs and group-housed pigs becomes smaller.

It can be concluded that individually housed pigs can alter their energy expenditure on physical activity. It can also be concluded that there seem to be differences in the energetic utilization of fDF between individually housed pigs and group-housed pigs. In most feed evaluation studies pigs are housed individually, which might have an effect on the use of the obtained NE values for practical housing conditions.

#### *Increased Fermentation or Dietary Bulkiness*

Schrama et al. (1998) suggested that the high NE value of SBPS was caused by the more gradual uptake of dietary energy when increasing levels of DF were fed (Schrama et al., 1998). A more gradual uptake of dietary energy is inevitable when more DF is fed, because more dietary energy will derive from fermented matter. Despite the substantial fermentation before the hindgut (De Lange, 2000), DF will for the greater part be fermented in the hindgut, whereas starch is digested in the upper part of the gastrointestinal tract. Schrama & Bakker (1999) reported that an increased fermentation in the gastrointestinal tract by adding resistant starch to the diet lowered AHP. A high level of dietary bulkiness had no effect on AHP. This suggests that increased fermentation had an effect on the energetic utilization of fDF, because of the effect on AHP. However, there was no effect of increased fermentation with SECM or SBH on the energetic utilization of fDF by an effect on AHP. It can be

concluded that stimulation of fermentation is not a general cause for differences in energetic utilization of fDF in pigs.

#### *Ratio between Protein and Dietary Fiber in the Hindgut*

In ruminant nutrition it is well known that an optimal ratio between rumen degradable protein and fermentable DF is necessary for optimal growth of the microflora in the rumen. About 150 g of rumen degradable protein is necessary for each kg of fermentable matter. For pigs, it is well known that the addition of DF will cause a lower excretion of nitrogen with the urine (as urea) and a higher protein excretion with the feces (as microbial protein) (Cahn et al., 1998). However, limited information is available on the optimal ratio between the amount of protein that is needed in the hindgut for optimal fermentation. An excessive amount of protein in the hindgut will lead to fermentation of protein that will lead to formation of ammonia that will be excreted as urea. A limited amount of protein in the hindgut will lead to unsatisfactory growth of the microflora, with sub-optimal production of fermentation products. With an optimal ratio between energy (fDF) and protein in the hindgut, the energy costs of fermentation in the hindgut are probably less than with an excessive or limited amount of protein or fDF. More microbial protein in addition to more endogenous protein will be lost with the feces, at the same time less nitrogen has to be excreted with the urine. This means that less nitrogen will be associated with less energy cost for the animal. For the experiments described in this thesis, it is suggested that difference in the ratio between protein and fDF in the hindgut might have caused differences in the energetic utilization of fDF. More research is needed to study the optimal ratio between protein and energy for optimal fermentation in the hindgut.

#### *Errors with the Measurement of (Fermentable) Dietary Fiber*

With the estimation of the energetic efficiency of fDF, the quantification or definition of DF is important. During the years more techniques have been developed with increasing accuracy. With all analytical procedures to measure DF contents there will be some organic matter left that is not quantified. Combining the measurements of total dietary fiber (TDF; Prosky et al., 1988), and ADL (Van Soest & Wine, 1967) will have the closest relationship with DF as defined in Chapter 1 (i.e.,  $DF = DM - [Ash + CP + CFAT + starch + sugars]$ ), without the need to analyze all individual sugars that are present in DF.

For estimating the energetic efficiency of fDF, we used the definition of DF as used in the Dutch feed evaluation system (see above and Chapter 1). With this definition of DF, all errors within the measurement of all nutrients will have consequences on accuracy of the calculated DF content of diets and feed ingredients. The estimate of the total tract digestibility of DF will be affected in a similar way. The risk for errors is in fact even higher, because chemical analyses are done in both the feed and feces. It should therefore be noted that differences in estimated energetic efficiency of fDF

might be emphasized or masked by differences in analyses. A thorough knowledge and possibly improvement of chemical analyses of major components of diets and feed ingredient (e.g., starch and DF) is suggested.

### *Specific Effects of Sugar Beet Pulp*

The results of the experiments described in this thesis showed a relative high NE value for fDF from SBP-products. Effects on AHP seem to explain a major part of this high NE value. There are, however, some other specific aspects of SBP that possibly are involved in the high NE value. Some of these aspects are discussed below.

Guerin et al. (2001) reported that intragastric meal distribution and viscosity of the gastric contents are better predictors for gastric emptying than DF content. They also showed that the botanical origin of DF affected gastric emptying. In fact, their experiment showed that compared to wheat bran and a control diet, SBP had a greater retention time in the proximal stomach, a more steady rate of distal stomach filling, and retrograde movements from the distal into the proximal stomach. It was suggested that the effected emptying rate of the stomach might cause the drastic reduction of feed intake in adult sows fed SBP. Differences in gastric emptying were not explained by differences in viscosity or volume of the feed (Guerin et al., 2001). The complexity and composition of the polysaccharide structure in the pectic substance from SBP (Oosterveld, 1997) might play an important role. If such effects are specific to certain feed ingredients, this might also explain differences in NE values of fDF from different sources.

Dried sugar beet pulp can contain small amounts of betaine (about 2.5 g/kg). Betaine can donate methyl-groups, which may result in reduced requirements for methionine, choline, and betaine. Some studies in pigs demonstrated that dietary supplementation of betaine can improve daily weight gain and feed efficiency. The improved performance in pigs with betaine supplementation seemed enhanced when pigs are exposed to nutritional (e.g., low concentration of dietary energy, restricted feeding) and/or environmental stress (health status, housing conditions). The effects of betaine suggest that dietary betaine supplementation affects the energy partitioning of growing pigs (Schrama et al., 2003). It is suggested that the betaine content of SBP has an effect on the estimated NE value.

In the studies with the highest NE values for fDF (Table 1), SBPS was used. Sugar beet pulp silage is a fermented feed ingredient, which contains fermentation products like short chain fatty acids and alcohol (Scholten et al., 1999). The effects of fermented diets on energy partitioning in pigs are not investigated yet. It can be suggested that fermented diets will affect the energetic utilization in pigs.

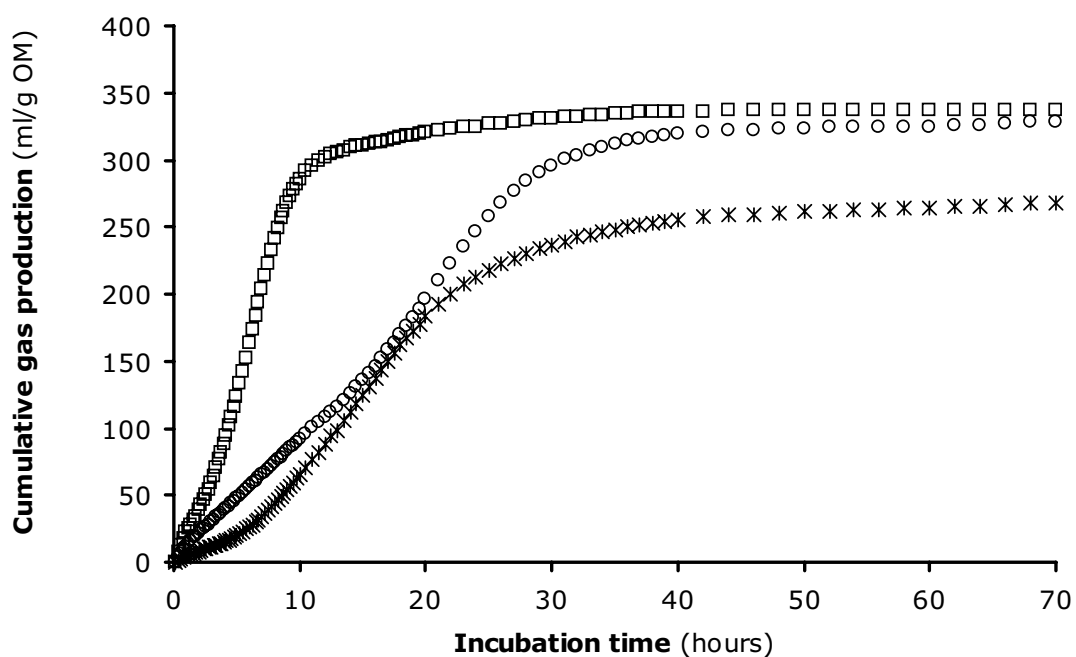
### **Rate of Fermentation and Energetic Utilization**

In this study, it appears that the rate of fermentation might explain the found differences in energetic utilization of fDF from different sources. To study this mechanism, the fermentation kinetics of DF fractions of SBP, SECM, and SBH were measured using the gas production technique as described by Cone et al. (1996) and Groot et al. (1996) (Figure 1). Gas production was measured during 72 hours (four replicates per feed ingredient with the same inoculum). As inoculum for gas production, a pooled sample of feces from four growing pigs on a standard diet was used. The feed ingredients were pre-digested with pancreatic enzymes before the gas production measurements. Cumulative gas production curves were analyzed with a non-linear model as described by Groot et al. (1996), using standard procedures to calculate the fermentation characteristics. The first two hours of gas production were excluded from the analyses to correct for fermentation of residual digestible components. The fermentation characteristics were analyzed for the effect of feed ingredient. The correlations between the mean fermentation characteristics per feed ingredient and the *in vivo* measured NE values of fDF were also analyzed.

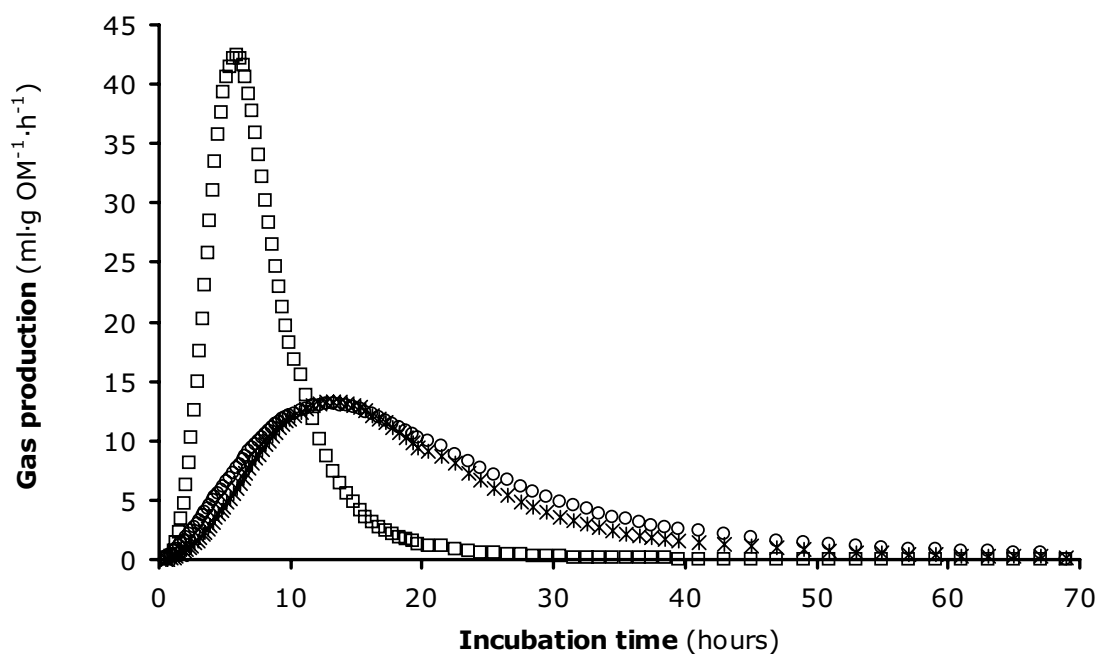
The cumulative gas production curves (Figure 1), show that the onset of fermentation of DF from SBP is faster than that of SECM and SBH, and that the total cumulative gas production of DF from SBP and SBH is higher after 72 hours than that of SECM. This means that within 72 hours the microbes in the used inoculum were able to ferment DF from SBP and SBH to a greater extent than that of SECM. The first derivative of the cumulative gas production (Figure 2) shows differences in rate of fermentation of the used feed ingredients. The rate of fermentation is faster for DF from SBP than for SECM and SBH. The fermentation characteristics were calculated from both figures and are shown in Table 2.

Total cumulative gas production after 72 hours ( $GP_{72}$ ), was highest for SBP and higher for SBH than for SECM. The half time of fermentation (b) was highest for SBP and higher for SECM than for SBH. The time of maximal gas production ( $T_i$ ), maximal gas production per hour (i), and the time of maximal fractional degradation rate ( $TR_m$ ) were highest for SBH and equal for SECM and SBH. The maximal fractional degradation rate ( $R_m$ ) was highest for SBP and higher for SECM than for SBH. Total *in vitro* volatile fatty acid (VFA) production was similar for the used feed ingredients.

The correlations between the *in vitro* fermentation characteristics and the *in vivo* NE values of fDF from the used feed ingredients are shown in Table 2. The half time of *in vitro* fermentation correlated well with the *in vivo* measured NE value of fDF ( $P = 0.050$ ). The maximal fractional degradation rate tended to correlate with the *in vivo* measured NE value of fDF ( $P = 0.096$ ).



**Figure 1.** Cumulative gas production curves of sugar beet pulp ( $\square$ ), soybean hulls ( $\circ$ ) and solvent-extracted coconut meal ( $\ast$ ).



**Figure 2.** First derivative of the cumulative gas production curves of sugar beet pulp ( $\square$ ), soybean hulls ( $\circ$ ) and solvent-extracted coconut meal ( $\ast$ ).



**Table 2.** Correlation between *in vitro* fermentation characteristics<sup>a</sup> and *in vivo* net energy values<sup>b</sup> of fermentable dietary fiber from sugar beet pulp (SBP), solvent-extracted coconut meal (SECM), and soybean hulls (SBH).

Feed	GP <sub>2</sub> ml/g OM	GP <sub>72</sub> ml/g OM	a ml/g OM	b h	c	Ti h	i ml/h	TRm h	Rm %/h	VFA mmol/g OM	NE kJ/g
SBP	38 <sup>c</sup>	337 <sup>c</sup>	295 <sup>c</sup>	6.4 <sup>c</sup>	3.39 <sup>c</sup>	5.38 <sup>c</sup>	42.5 <sup>c</sup>	8.3 <sup>c</sup>	0.288 <sup>c</sup>	7.72 <sup>c</sup>	13.7
SECM	8 <sup>d</sup>	269 <sup>d</sup>	265 <sup>d</sup>	16.0 <sup>d</sup>	2.81 <sup>d</sup>	12.26 <sup>d</sup>	13.3 <sup>d</sup>	19.7 <sup>d</sup>	0.090 <sup>d</sup>	6.55 <sup>c</sup>	11.1
SBH	22 <sup>e</sup>	329 <sup>e</sup>	332 <sup>e</sup>	18.2 <sup>e</sup>	2.39 <sup>e</sup>	12.50 <sup>d</sup>	13.1 <sup>d</sup>	20.8 <sup>d</sup>	0.068 <sup>e</sup>	7.30 <sup>c</sup>	10.1
SEM	2	2	3	0.3	0.02	0.20	0.4	0.3	0.003	0.35	-
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.110	-
Correlation between <i>in vitro</i> fermentation characteristics and <i>in vivo</i> measured NE values											
r	0.743	0.370	-0.319	-0.996	0.981	-0.974	0.969	-0.984	0.989	0.591	-
P-value	0.467	0.759	0.793	0.050	0.114	0.145	0.160	0.113	0.096	0.597	-

<sup>a</sup> GP<sub>2</sub>, cumulative gas production after 2 h (ml/g OM); GP<sub>72</sub>, cumulative gas production after 72 h (ml/g OM); a<sub>2</sub>, asymptote (ml/g OM); b, half time of fermentation (h); c, switching characteristic; Ti, time point of maximal gas production (h); i, maximal gas production (ml/h); TRm, time point of maximal fractional degradation rate (h); Rm, maximal fractional degradation rate (%/h); VFA, total volatile fatty acid production after 72 hours (mmol/g OM); NE, net energy value (kJ/g).

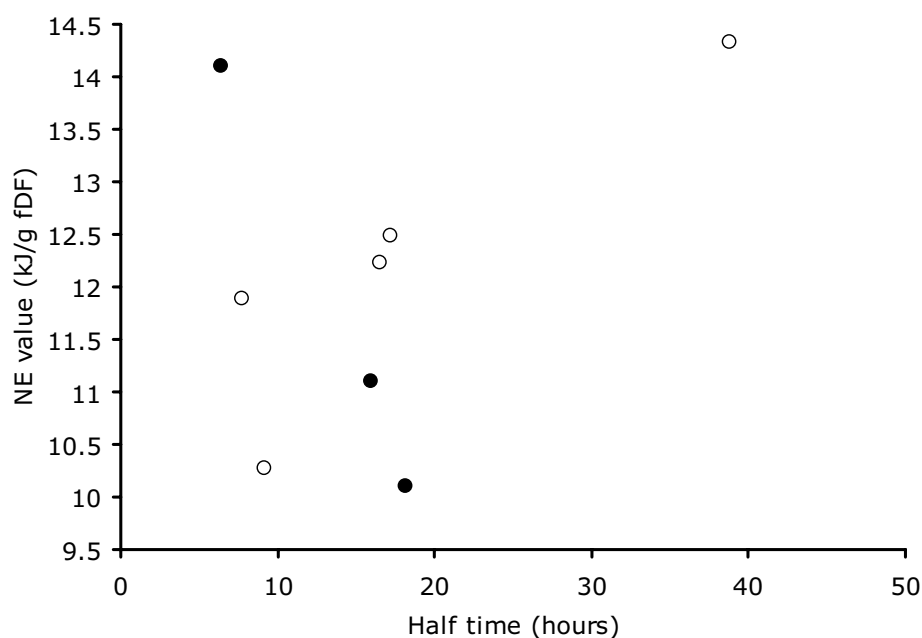
<sup>b</sup> The NE values of fDF from solvent-extracted coconut meal (SECM) and soybean hulls (SBH) are estimated in Chapter 4, and the NE value of sugar beet pulp (SBP) is the average NE value from Chapter 7 and Schrama et al. (1998).

<sup>c, d, e</sup> Mean values within a column with different superscripts differ ( $P < 0.05$ ).

Beside the correlations between the half time of the total gas production, maximal fractional degradation and the NE value of fDF, other parameters that indicate rate of fermentation seem to be better correlated with NE values of fDF than parameters that indicate total fermentability (Table 2). This is logical, because *in vitro* fermentation lasted 72 h, whereas the mean total retention time of digesta in the gastrointestinal tract of growing pigs is about 33 h (Le Goff et al., 2002b). In addition, the conditions for fermentation are better *in vitro* than *in vivo*, because of the more moist substance and higher initial number of bacteria (JW Cone, personal communication).

The rate of fermentation will determine the location in the gastrointestinal tract where fermentation of fDF will take place, and the amount of short chain fatty acids (SCFA) that are produced and absorbed. It seems logical that a higher rate of fermentation will increase SCFA production in upper parts of the gastrointestinal tract, which leaves more time for absorption compared with fermentation in lower parts of the gastrointestinal tract. Effects of different DF sources on passage rate of digesta also play a role in the location of SCFA absorption. From these findings, it was hypothesized that the rate of *in vitro* fermentation of DF can predict the *in vivo* NE value of fDF for growing pigs, which would be a handful tool for the swine industry.

This hypothesis was the start of a next experiment, in which the *in vitro* fermentation characteristics and the *in vivo* NE values of 5 different fDF sources are being studied. Preliminary results of that ongoing experiment, however, do not confirm the hypothesis (Figure 3; Rijnen et al., unpublished data).



**Figure 3.** *In vivo* measured NE values of fermentable dietary fiber (fDF) of 8 different feed ingredients with their corresponding half time of *in vitro* gas production (b, Table 2) from the present thesis (●) and unpublished data (○).

## Implications

### *General*

The use of nontraditional and by-product feed ingredients is increasing in swine nutrition. These feed ingredients commonly cost less when expressed per unit of feeding value than traditional feed ingredients and contain high levels of DF. With this change a thorough understanding of these compounds is necessary (Grieshop et al., 2001). This also includes knowledge of digestive and energetic utilization of DF.

It is generally accepted that pigs will consume diets to meet their energy needs (NRC, 1987). Feed intake will therefore be maximal in ad libitum fed pigs. Excessive contents of DF can, however, result in reduced feed intake due to dietary bulkiness or reduced palatability (NRC, 1998). Growth rate and feed efficiency are usually depressed with increasing DF contents.

It was shown in Chapter 6 that the increased intake of DF increased weights of the gastrointestinal tract, which might increase energy requirements for maintenance and will decrease the dressing proportion of pigs. The effects of feeding fiber-rich diets to pigs on the quality of their end products (e.g., meat) is not explored extensively yet. The amount of manure might increase when using fiber-rich diets, which will have higher costs at farmer level. An understanding of the issues stated here are important to predict effects of fiber-rich diets in practice. Lower feeding costs, lower management costs, improved health status, and/or improved well being of pigs should have a surplus at the farmer level, when fiber-rich diets are introduced.

### *Feed Evaluation Systems*

In NE based feed evaluation systems, energy requirements for maintenance are assumed to be constant. The question rises whether energy expenditure on physical activity should be fully imbedded in energy requirements for maintenance or that energy expenditure for physical activity is a characteristic of feed ingredients. It has been shown in the present thesis that the effect of different DF sources on the energy expenditure for physical activity is not equal for all sources of DF (sugar beet pulp (silage), solvent-extracted coconut meal, soybean hulls). Therefore, energy expenditure for physical activity is at least partly a characteristic of the used feed ingredients. This leads to the conclusion that the NE value of fDF is not equal for all sources of fDF, but seems to depend on the feed ingredient from which it originates. Therefore, one fixed value for the efficiency with which fDF is used for production is incorrect. Exact mechanisms, however, are not clear yet.

The NE values used in feed evaluation systems are mainly based on experiments with individually housed pigs and biochemical calculations. The present thesis showed that the NE value of fDF was not significantly affected by housing conditions. Numerically, however, the NE value of fDF is lower for group-housed pigs than for individually housed pigs. However, there were differences in digestibility and

metabolizability of dietary energy, which will lead to differences in the NE value of feed ingredients between individually and group-housed growing pigs. The NE value of a feed ingredient will be lower for group-housed pigs than for individually housed pigs. This means that the NE values obtained from studies with individual pigs will probably overestimate the NE values for group-housed pigs.

## Conclusions

In this thesis the energetic utilization of fermentable dietary fiber in relation to energy expenditure for physical activity has been studied. From the results some conclusions can be drawn:

- The NE value of fermentable dietary fiber of sugar beet pulp silage in group-housed sows was high compared to NE values used in feed evaluation systems. This was partly due to the decreased energy expenditure for physical activity with increasing dietary contents of sugar beet pulp silage.
- The effect of dietary fiber from sugar beet pulp silage on heat production and behavior of group-housed sows was not constant during the day.
- Fermentable dietary fiber from sugar beet pulp products will result in less heat than fermentable dietary fiber from solvent-extracted coconut meal and soybean hulls in group-housed growing pigs. This suggests that the energetic efficiency of fermentable dietary fiber is affected by the botanical origin of dietary fiber.
- The relative high energetic utilization of fermentable dietary fiber from sugar beet pulp products is related to the lowered energy expenditure on physical activity when sugar beet pulp products are fed to growing pigs.
- The net energy saving effect of sugar beet pulp products by a decrease in energy expenditure for physical activity, was not found for other dietary fiber sources (i.e., solvent-extracted coconut meal and soybean hulls). Therefore, energy expenditure for physical activity is at least partly a characteristic of the used feed ingredients. This suggests that the NE value of fermentable dietary fiber is related to the source of dietary fiber, and that using the same value for the efficiency, with which all fermentable dietary fibers are utilized, is incorrect.
- Increasing intake of (fermentable) dietary fiber will decrease the dressing proportion of pigs.
- Housing conditions did not have a significant effect on the energetic utilization of fermentable dietary fiber from sugar beet pulp. However, housing conditions had a great effect on the digestive and energetic utilization of dietary energy: individually housed pigs being more efficient than group-housed pigs. This suggests that the NE value of a diet or feed ingredient obtained from studies with individually housed growing pigs will overestimate the NE value for group-housed growing pigs.
- The rate of fermentation might play an important role in the energetic utilization of fermentable dietary fiber in pigs.

**Summary**  
**&**  
**Samenvatting**

## Summary

### ***Introduction***

The interest of pig nutritionists in the role of dietary fiber (DF) in animal functioning is increasing. Priority and increased demand of available high-energy cereals for direct human use increased the availability of fiber-rich co-products from human food industries. This has promoted an increased use of fiber-rich feed ingredients in pig nutrition. Unlike starch, which is hydrolyzed by pancreatic amylase to glucose, DF is not hydrolyzed by mammalian enzymes. Dietary fiber is fermented by the gastrointestinal microflora. The net energy (NE) content of DF fractions is derived by using digestibility data and multiplying it with the efficiency with which the absorbed products can be used for energy retention (ER). Generally, utilization of energy from fermentable DF (fDF) is considered to be lower than that from digestible starch. Therefore, in feed evaluation systems, feed ingredients with high contents of DF have lower NE values than feed ingredients with similar levels of digestible starch. These systems assume that energy requirements for maintenance are constant and that energy from a certain nutrient above maintenance is used with constant efficiency. In group-housed growing pigs fed different levels of sugar beet pulp silage (SBPS) a relatively high energetic utilization of fDF was found. In fact it was similar to that of digestible starch. This relatively high NE value of fDF from SBPS was related to the lowered activity-related heat production (AHP) with increasing dietary SBPS contents. In the present systems, physical activity is usually being considered part of maintenance, but part of physical activity may also be a specific effect of specific feed ingredients or nutrients. Further quantitative data on the energetic utilization of fDF in relation to physical activity are lacking. The composition of DF fractions of different botanical origin can differ widely. Therefore, it is questionable whether a fixed value for efficiency with which energy from fDF is utilized, is sufficient. The studies in this thesis describe the effects of DF on energy metabolism and behavior in sows (Chapter 2 and 3), the effects of different sources of DF on energy metabolism, physical activity and the gastrointestinal tract in growing pigs (Chapter 4, 5, and 6), and the effects of housing conditions on the energetic utilization of fDF (Chapter 7).

### ***Effects of Dietary Fiber in Group-Housed Sows***

The first experiment was conducted to study whether the high energetic efficiency of fDF from SBPS and its effect on AHP that was found in group-housed growing pigs, was also valid in group-housed sows (Chapter 2 and 3). Therefore, dose-response effects of SBPS on energy metabolism and behavior were studied in group-housed sows. Twelve groups of six non-pregnant, non-lactating sows were each fed one of the four experimental diets that were similar in composition except for the starch and DF content. Exchanging SBPS for tapioca created the difference in starch and DF ratio. On DM basis, diets contained 0, 10, 20, or 30% SBPS. Sows were group-housed and fed

once a day at 1.30 times the assumed energy requirements for maintenance. Nitrogen and energy balances were measured per group in environmentally controlled respiration chambers during a 7-d experimental period, which was preceded by a 33-d adaptation period. Behavioral characteristics of the sows were recorded during 2 d of the experimental period with time-lapse video recorders.

Digestibility and metabolizability of dietary energy decreased with increasing dietary SBPS content. Total heat production (HP) and ER were unaffected by the exchange of starch for DF. Based on ER data and intakes of digestible crude protein, crude fat, starch, and sugars, the estimated NE value of fDF was 13.4 kJ/g. On average, sows spent 177 min/d on physical activity, of which 8.8% was spent on eating. Sows fed 0 or 10% SBPS spent more time on physical activity than sows fed 20 or 30% SBPS. Sows tended to have lower AHP when fDF intake increased. The effect of fDF intake on HP and AHP was not constant during the day. During the night period, fDF intake did not effect HP and AHP. During the day period, increased fNSP intake decreased HP and tended to decrease AHP. During eating, increased fNSP intake increased HP and tended to increase AHP. Sows fed 0 or 10% SBPS spent less time eating than sows fed 20 or 30% SBPS. Consequently, feed consumption rate was higher in groups fed 0 or 10% SBPS than in groups fed 20 or 30% SBPS. The energy saving effect of AHP on the NE value of fDF from SBPS ranged between 2.3 and 3.7 kJ/g of fDF intake.

The experiment showed that group-housed sows were capable of using energy from fDF (i.e., fDF from SBPS) as efficiently as energy from digested starch (i.e., starch from tapioca). The intake of fDF from SBPS lowered energy expenditure for physical activity; however, this effect was not constant during the day.

### ***Effects of Dietary Fiber on Energy Metabolism and Activity in Pigs***

The experiment described in Chapter 4 and 5 was conducted to study whether the energetic efficiency of fDF was dependent on DF source and whether a general effect on AHP could be expected from different sources of DF. Therefore, the effects of two types of DF on energy metabolism and behavior were studied in group-housed growing pigs. Twenty clusters of 14 barrows (50 kg) were fed one of the ten experimental diets. Diets differed mainly in type and content of fDF and digestible starch. Five diets contained different levels of solvent extracted coconut meal (SECM) and five diets contained different levels of soybean hulls (SBH) as main DF source. Pigs were group-housed and fed at 2.5 times the assumed energy requirements for maintenance. All clusters were fed similar amounts of calculated NE, ileal digestible protein and amino acids, vitamins, and minerals. Consequently, DM intake differed among diets because NE content decreases with increasing DF content. Nitrogen and energy balances were measured per cluster in environmentally controlled respiration chambers during a 7-d experimental period, which was preceded by a 32-d preliminary period. Behavioral characteristics of the pigs were recorded during 2 d of the experimental period with time-lapse video recorders.

The intake of digestible starch and fDF was different among diets, whereas intake of digestible CP was similar for all diets. Digestibility of dietary energy decreased with increasing DF intake. Metabolizability of dietary energy decreased with increasing fDF intake. Methane production increased with increasing fDF intake. Based on HP data and apparent fecal digestibilities of nutrients, the estimated energetic efficiency of fDF from SECM was 63%, and from SBH 58%. These energetic efficiencies were not significantly different. The average energetic efficiency of fDF for ER above maintenance (i.e., 61% or 10.7 kJ/g fDF) was about 80% of that of digestible starch as used in the Dutch NE based feed evaluation systems for pigs. Total time spent on physical activity (195 min/d) was not affected by diet. Total HP and resting HP were affected by diet and were on average lower for pigs fed SECM diets than for pigs fed SBH diets. Activity-related HP averaged  $65 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , and was not affected by diet. There was a linear relationship between fDF intake and HP, but there was no relationship between fDF intake and AHP. During different parts of the day, fDF intake also affected HP. The saving effect of physical activity on the NE values of fDF from SECM and SBH were 0.56 and 0.84 kJ/g of fDF intake, respectively. These energy saving effects were not significantly different from zero.

The experiment showed that the energetic efficiency of fDF did not differ between the two types of fDF (i.e., fDF from SECM or SBH) used in the experiment. The intake of fDF from SECM or SBH did not affect AHP in growing pigs and the NE value of fDF from SECM and SBH was not affected by changes in physical activity.

### ***Effects of Fermentation and Bulkiness on the Gastrointestinal Tract***

Data from two experiments were used to study the effects of DF on the empty weights of the gastrointestinal tract (GIT) and its different parts (Chapter 6). In experiment 1, the effects of ten different diets were studied (Chapter 4 and 5). After 39 d, euthanasia was performed on six pigs per dietary treatment. In experiment 2, the effects of fermentation and dietary bulkiness were studied. Pigs were group-housed and fed diets containing either gelatinized maize starch, gelatinized maize starch plus 15% milled wheat straw, raw potato starch, or raw potato starch plus 15% milled wheat straw. After 26 d, euthanasia was performed on 12 pigs per dietary treatment. For both experiments, the GIT was removed after euthanasia and divided into four parts: stomach, small intestine, cecum, and large intestine. The different parts were emptied and weighed. Results of experiment 1 showed that the empty weights of the total GIT, stomach, and large intestine were affected by diet composition. The empty weight of the large intestine was higher for pigs fed SECM than for pigs fed SBH. An increased intake of DF and fDF increased the empty weight of the total GIT by increased empty weights of the stomach, and large intestine. In experiment 2, stimulation of fermentation in the GIT (i.e., gelatinized maize starch vs potato starch) increased the empty weight of the total GIT by an increased empty weight of the large intestine. Increased dietary bulkiness (i.e., no wheat straw vs wheat straw) increased



the empty weight of the total GIT by an increased empty weight of the stomach. In both experiments, no effects of diets were found on the empty weights of the small intestine and cecum.

The experiments showed that increased dietary volume mainly increased the empty weight of the stomach, whereas stimulation of fermentation in the GIT mainly increased the empty weight of the large intestine.

### ***Housing Conditions and Energetic Utilization of Dietary Fiber***

Data used in NE based feed evaluation systems are mainly based on experiments with individually housed growing pigs. Therefore, the effects of housing conditions, DF, and their interaction on energy metabolism and physical activity were studied in growing pigs. It was hypothesized that group-housed pigs were able to utilize energy from fermentable DF more efficiently than individually housed pigs by the ability of lowering their energy expenditure for physical activity. A 13-d experimental period was preceded by a 13-d preliminary period. The experiment was designed in a  $2 \times 2$  factorial arrangement with housing conditions (individual vs group-housing) and dietary composition (starch vs DF) as factors. In the sugar beet pulp (SBP) diet (high in DF), 15% of the gelatinized maize starch from the control diet (high in starch) was replaced with 17.5% SBP. In total, 10 individually housed pigs, and 140 group-housed pigs (i.e., 10 groups of 14 pigs each) were used. The experiment was conducted in five trials. Each trial consisted of two balance periods, and per balance period nitrogen and energy balances were measured simultaneously in four respiration chambers. Apparent fecal digestibilities of all nutrients were measured per balance period.

No interaction between housing conditions and diet composition was found. Apparent fecal digestibilities of dietary energy and all nutrients, except for DF, were higher for individually housed pigs than for group-housed pigs. Metabolizability of energy was 3.7 percentage units higher for individually housed pigs than for group-housed pigs. Housing conditions did not affect HP, AHP, and ER. Individually housed pigs had a higher ER as protein than group-housed pigs ( $151$  vs  $137 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The ratio between AHP and HP was lower for individually housed pigs than for group-housed pigs. Metabolizability of energy was 3.5 percentage units higher for pigs fed the control diet than for pigs fed the SBP diet. Diet composition did not affect HP. Pigs fed the control diet had a higher AHP than pigs fed the SBP diet ( $80$  vs  $68 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Diet composition did not affect total ER, but pigs fed the control diet had a higher ER as protein than pigs fed the SBP diet ( $150$  vs  $138 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). The heat increment values of fDF from SBP, uncorrected and corrected for AHP, were 3.8 and 5.2 kJ/g, respectively. This corresponds to NE values of 13.7 and 12.3 kJ/g, respectively. Fermentable DF intake decreased AHP, and there was no significant effect of housing conditions on the estimated NE values. However, numerically the energetic efficiency of fDF was higher in individually housed pigs than in group-housed pigs. Both digestibility and metabolizability of dietary energy were higher for individually housed

pigs than for group-housed pigs, which means that there will be differences in the NE value of feed ingredients and diets between individually and group-housed pigs.

### Conclusions

In this thesis the energetic utilization of fermentable dietary fiber in relation to energy expenditure for physical activity has been studied. From the results some conclusions can be drawn:

- The NE value of fermentable dietary fiber of sugar beet pulp silage in group-housed sows was high compared to NE values used in feed evaluation systems. This was partly due to the decreased energy expenditure for physical activity with increasing dietary contents of sugar beet pulp silage.
- The effect of dietary fiber from sugar beet pulp silage on heat production and behavior of group-housed sows was not constant during the day.
- Fermentable dietary fiber from sugar beet pulp products is utilized more efficiently than fermentable dietary fiber from solvent extracted coconut meal and soybean hulls in group-housed growing pigs. This suggests that the energetic efficiency of fermentable dietary fiber is affected by the botanical origin of dietary fiber.
- The relative high energetic utilization of fermentable dietary fiber for sugar beet pulp products is related to the lowered energy expenditure on physical activity when sugar beet pulp products are fed to growing pigs.
- The net energy saving effect of sugar beet pulp products by a decrease in energy expenditure for physical activity, was not found for other dietary fiber sources (i.e., solvent extracted coconut meal and soybean hulls). Therefore, energy expenditure for physical activity is at least partly a characteristic of the used feed ingredients. This suggests that the NE value of fermentable dietary fiber is related to the source of dietary fiber, and that one fixed value for the efficiency with which fermentable dietary fiber is used, is incorrect.
- Increasing intake of (fermentable) dietary fiber will decrease the dressing proportion of pigs.
- Housing conditions did not have a significant effect on the energetic utilization of fermentable dietary fiber from sugar beet pulp. However, housing conditions had a great effect on the digestive and energetic utilization of dietary energy: individually housed pigs being more efficient than group-housed pigs. This suggests that the NE value of a diet or feed ingredient obtained from studies with individually housed growing pigs will overestimate the NE value for group-housed growing pigs.
- The rate of fermentation might play an important role in the energetic utilization of fermentable dietary fiber in pigs.

## Samenvatting

### ***Inleiding***

Diervoedingsdeskundigen hebben een toenemende belangstelling voor de rol die voedingsvezels kunnen spelen in het functioneren van dieren. De groeiende vraag naar beschikbare, hoogwaardige granen voor humane consumptie hebben geleid tot een verhoogde beschikbaarheid van vezelrijke bijproducten vanuit de levensmiddelen-industrie. Dit heeft bijgedragen aan het toenemende gebruik van vezelrijke grondstoffen in de varkensvoeding. In tegenstelling tot zetmeel, dat door enzymen uit de maag en pancreas wordt afgebroken, worden voedingsvezels oftewel overige organische stof (OOS) niet afgebroken door lichaamseigen enzymen van varkens. Voedingsvezels kunnen echter afgebroken worden door de microben in het maagdarmkanaal. De netto energie (NE) waarde van de verteerbare OOS-fractie (vOOS-fractie) van het voer kan berekend worden met verteringscijfers die vermenigvuldigd worden met de efficiëntie waarmee de afgebroken nutriënten worden geabsorbeerd en aangezet in het lichaam (= energieretentie [ER]). In voederwaarderingsystemen wordt de energetische efficiëntie van de vOOS-fractie normaal gesproken lager ingeschat dan de energetische efficiëntie van de zetmeelfractie. Daarom hebben grondstoffen met een hoog gehalte aan vOOS een lager gehalte aan NE dan grondstoffen met een vergelijkbaar gehalte aan verteerbaar zetmeel. Voederwaarderingsystemen maken veelal gebruik van twee aannames; ten eerste wordt verondersteld dat de energie die gebruik wordt voor onderhoudsprocessen constant is; ten tweede wordt aangenomen dat de energie van nutriënten die gebruik wordt voor ER (dus boven onderhoud) met een constante energetische efficiëntie per nutriënt wordt vastgelegd in het lichaam. In onderzoek met in groepen gehuisveste varkens is gevonden dat de energetische efficiëntie van de vOOS-fractie van bietenperspulsilage (BPPS) relatief hoog is. De energetische efficiëntie was gelijk aan die van verteerbaar zetmeel. Deze hoge efficiëntie was gerelateerd aan een verlaagd energieverbruik voor fysieke activiteit, oftewel activiteitsgerelateerde warmteproductie (AHP). In de huidige voederwaarderingsystemen wordt AHP meestal bestempeld als onderdeel van de onderhoudsbehoefte. Een deel van de AHP kan echter ook gerelateerd zijn aan specifieke grondstoffen of nutriënten. De samenstelling van de OOS-fractie is sterk verschillend tussen grondstoffen van verschillende botanische herkomst. Het is daarom de vraag of een vaste waarde voor de energetische efficiëntie van vOOS correct is. In dit proefschrift wordt aandacht besteed aan de effecten van vOOS op het energiemetabolisme en gedrag van zeugen (Hoofdstuk 2 en 3). Vervolgens worden effecten van verschillende vOOS-bronnen op het energiemetabolisme, de fysieke activiteit en gewichten van het maagdarmkanaal van vleesvarkens toegelicht (Hoofdstuk 4, 5 en 6). Tenslotte wordt het effect van huisvestingssysteem op de energetische efficiëntie van vOOS behandeld.

### **Effecten van OOS op in Groepen Gehuisveste Zeugen**

Het eerste onderzoek dat beschreven is in dit proefschrift (Hoofdstuk 2 en 3) is uitgevoerd om te bestuderen of de hoge energetische efficiëntie waarmee, in groepen gehuisveste, vleesvarkens vOOS van BPPS benutten ook geldig is voor in groepen gehuisveste zeugen. Ten tweede is bestudeerd of het effect van BPPS op de AHP van in groepen gehuisveste vleesvarkens ook geldig is voor in groepen gehuisveste zeugen. Om dit te onderzoeken, zijn de effecten van een oplopend gehalte aan BPPS op het energiemetabolisme en het gedrag van in groepen gehuisveste zeugen bestudeerd. In totaal zijn 12 groepen van zes guster zeugen gebruikt. Aan iedere groep werd één van de vier experimentele voeders verstrekt. De voeders hadden een gelijk samenstelling met uitzondering van de gehalten aan zetmeel en OOS door de uitwisseling van BPPS tegen tapioca. Op drogestof (DS) basis bevatte de voeders 0, 10, 20 of 30% BPPS. De zeugen werden in groepen gehuisvest en één keer per dag gevoerd op een voerniveau van 1,3 maal de onderhoudsbehoefte. Gedurende de 7 dagen durende experimentele periode, die vooraf werd gegaan door een 33 dagen durende voorperiode, werden per groep de stikstof- en energiebalansen gemeten in klimaatrespiratiecellen. Gedurende 2 dagen van de experimentele periode werd het gedrag van de zeugen opgenomen met videorecorders.

De verteerbaarheid en metaboliseerbaarheid van de energie in het voer nam af met een oplopend gehalte aan BPPS. De totale warmteproductie (HP) en de ER werden niet beïnvloed door de uitwisseling tussen zetmeel en OOS. Op basis van de ER data en de opname aan verteerbaar ruw eiwit, ruw vet, zetmeel en suikers, werd een NE gehalte voor vOOS berekend van 13,4 kJ/g. Per dag besteedde de zeugen gemiddeld 177 min aan fysieke activiteit, waarvan 8,8% besteed werd aan vreten. Zeugen die gevoerd werden met voeders met 0 of 10% BPPS besteedde meer tijd aan fysieke activiteit dan zeugen die gevoerd werden met voeders met 20 of 30% BPPS. Er was een tendens dat zeugen een lagere AHP hadden wanneer de opname van vOOS toenam. Het effect van de vOOS-opname op HP en AHP was echter niet constant gedurende de dag. Gedurende de nachtperiode had vOOS-opname geen effect op HP en AHP. Gedurende de dagperiode, nam de HP af en tendeerde AHP tot een afname bij een toenemende vOOS-opname. Tijdens het vreten leidde een toenemende vOOS opname tot een verhoogde HP en was er een tendens tot een verhoogde AHP. Zeugen die 0 of 10% BPPS gevoerd werden besteedde minder tijd aan vreten dan zeugen die 20 of 30% BPPS gevoerd werden. De zeugen die 0 of 10% BPPS gevoerd werden hadden dan ook een hogere voeropnamesnelheid. De verlaging van de AHP met toenemende opname van vOOS had een energiebesparend effect op de NE-waarde van de vOOS-fractie van BPPS, dat lag tussen de 2,3 en 3,7 kJ/g vOOS opname.

Er is geconcludeerd dat in groepen gehuisveste zeugen de energie uit vOOS van BPPS net zo efficiënt benutten als energie uit verteerbaar zetmeel van tapioca. De opname van vOOS van BPPS leidde tot een lager energieverbruik voor fysieke activiteit, maar dit effect was niet constant gedurende de dag.

### **Effecten van OOS op in Groepen Gehuisveste Vleesvarkens**

Het onderzoek beschreven in Hoofdstuk 4 en 5 is uitgevoerd om te bestuderen of de energetische efficiëntie van vOOS afhankelijk is van de vOOS-bron. Tevens is bestudeerd of er een algemeen geldend effect is van vOOS op de fysieke activiteit van vleesvarkens. Om dit te onderzoeken zijn de effecten van twee verschillende vOOS-bronnen op het energiemetabolisme en het gedrag van in groepen gehuisveste vleesvarkens bestudeerd. In totaal zijn 20 groepen van 14 vleesvarkens (van ca. 50 kg) gebruikt. Aan iedere groep vleesvarkens werd één van de 10 experimentele voeders verstrekt. De voeders verschillende met name in het type en gehalte aan vOOS en verteerbaar zetmeel. Aan vijf voeders werden verschillende gehalten aan kokosschroot toegevoegd en aan de andere vijf voeders werden verschillende gehalten aan sojahullen toegevoegd. De varkens werden in groepen gehuisvest en gevoerd op een voerniveau van 2,5 maal de onderhoudsbehoefte. Alle groepen kregen een gelijke hoeveelheid aan berekende NE, ileaal verteerbaar eiwit en aminozuren, vitaminen en mineralen. Als gevolg daarvan verschilde de DS opname tussen de experimentele rantsoenen, aangezien het NE gehalte van het voer afneemt met een oplopend gehalte aan OOS. Gedurende een 7 dagen durende experimentele periode, die vooraf gegaan werd door een 32 dagen durende voorperiode, werden per groep de stikstof- en energiebalansen gemeten in klimaatrespiratiecellen. Het gedrag van de varkens werden gedurende 2 dagen van de experimentele periode opgenomen met videorecorders.

De opname van verteerbaar zetmeel en vOOS was verschillend tussen de rantsoenen, terwijl de opname van verteerbaar ruw eiwit voor alle voeders gelijk was. De verteerbaarheid van de energie in het voer nam af met een toenemende OOS-opname. De metaboliseerbaarheid van de energie in het voer nam af met een toenemende vOOS-opname. De methaanproductie nam toe met een oplopende vOOS-opname. Op basis van de HP gegevens en de fecale verteerbaarheden van de nutriënten, was de berekende energetische efficiëntie van vOOS uit kokosschroot 63% en die van vOOS uit sojahullen 58%. Deze energetische efficiënties verschilden niet significant van elkaar. De gemiddelde energetische efficiëntie van vOOS voor ER (61% of 10,7 kJ/g vOOS) was ongeveer 80% van de energetische efficiëntie van verteerbaar zetmeel, zoals in het Nederlandse voederwaarderingssysteem gebruikt wordt. De totale tijd die besteed werd aan fysieke activiteit (195 min/dag) werd niet beïnvloed door de voersamenstelling. Warmteproductie (HP) en HP gecorrigeerd voor AHP werden wel beïnvloed door de voersamenstelling. Gemiddeld was HP en HP gecorrigeerd voor AHP lager voor varkens die kokosschroot verstrekt kregen dan voor varkens die sojahullen verstrekt kregen. De AHP was gemiddeld  $65 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  en werd niet beïnvloed door de voersamenstelling. Er bestond een lineaire relatie tussen de vOOS-opname en HP, maar niet tussen de vOOS-opname en AHP. De verlaging van AHP met toenemende vOOS-opname had een energiebesparend effect op de NE-waarde van de vOOS-fracties van kokosschroot en sojahullen. Dit energiebesparende

effect was respectievelijk 0,56 en 0,84 kJ/g vOOS-opname voor kokosschroot en sojahullen. Beide waarden waren niet significant afwijkend van nul.

Er is geconcludeerd dat de energetische efficiëntie van vOOS niet verschilde tussen de 2 typen vOOS die gebruikt werden. De opname van vOOS had geen effect op de energiebesteding aan fysieke activiteit van vleesvarkens.

### ***Effecten van Fermentatie en Bulk op Gewichten van het Maagdarmkanaal***

De gegevens van twee experimenten werden gebruikt om de effecten van OOS op de gewichten van het maagdarmkanaal (MDK) en de gewichten van de afzonderlijke delen van het MDK te bestuderen (Hoofdstuk 6). In het eerste experiment werden de effecten van 10 voeders bestudeerd (zie Hoofdstuk 4 en 5). Na 39 dagen werden er zes dieren per voersoort geëuthanaseerd. In het tweede experiment werden de effecten van fermentatie in het MDK en het volume van het voer bestudeerd. De varkens werden in groepen gehuisvest en kregen voeders met ontsloten maïszetmeel, ontsloten maïszetmeel plus 15% gemalen tarwestro, natief aardappelzetmeel of natief aardappelzetmeel plus 15% gemalen tarwestro. Na 26 dagen werden er 12 dieren per voersoort geëuthanaseerd. Voor beide experimenten geldt dat na euthanasie het MDK werd verwijderd en verdeeld in 4 delen: de maag, dunne darm, blinde darm en dikke darm. De afzonderlijke delen werden leeggemaakt en gewogen. Het eerste experiment liet zien dat een toename in de opname aan OOS en vOOS resulteerde in een gewichtstoename van het lege MDK door een gewichtstoename van de maag en dikke darm. Het gewicht van de lege dikke darm was hoger voor varkens gevoerd met kokosschroot dan voor varkens gevoerd met sojahullen. In het tweede experiment leidde de stimulatie van fermentatie in het MDK (ontsloten maïszetmeel vs natief aardappelzetmeel) tot gewichtstoename van het lege MDK door een gewichtstoename van de dikke darm. Een vergroot volume van het voer (geen stro toevoeging vs stro toevoeging) leidde tot een gewichtstoename van het lege MDK door een gewichtstoename van de maag. In beide experimenten werden er geen effecten gevonden van voersamenstelling op de gewichten van de dunne darm en de blinde darm.

Er is geconcludeerd dat een toename van het volume van het voer hoofdzakelijk leidde tot een toename van het gewicht van de maag, terwijl stimulatie van fermentatie in het MDK met name leidde tot een gewichtstoename van de dikke darm.

### ***Effect van Huisvesting op de Energetische Benutting van vOOS***

De huidige voederwaarderingssystemen voor varkens zijn vooral gebaseerd op experimenten met individueel gehuisveste dieren. De effecten van huisvesting, OOS en hun interactie op het energiemetabolisme en de fysieke activiteit van vleesvarkens zijn bestudeerd. De hypothese werd gesteld dat in groepen gehuisveste varkens de energie in vOOS efficiënter konden benutten dan individueel gehuisveste varkens, omdat ze meer mogelijkheden hebben om hun AHP te verlagen. De 13 dagen durende experimentele periode werd vooraf gegaan door een 13 dagen durende voorperiode.

Het experiment was opgezet in een  $2 \times 2$  factoriële opzet met huisvestingssysteem (individueel vs groep) en voersamenstelling (zetmeel vs OOS) als factoren. In het bietenpulpvoer (BP), met een hoog gehalte aan OOS, werd 15% van het ontsloten maïszetmeel uit het controlevoer vervangen door 17,5% BP. In totaal werden 10 individueel gehuisveste vleesvarkens en 140 in groepen gehuisveste vleesvarkens (10 groepen van elk 14 dieren) gebruikt. Het experiment bestond uit 5 deelexperimenten. Elk deelexperiment bestond uit 2 balansperioden. In iedere balansperiode werden de stikstof- en energiebalansen gemeten in 4 klimaatrespiratiecellen. Ook werden de fecale verteerbaarheden van de nutriënten per balansperiode gemeten.

Er zijn geen interacties gevonden tussen huisvestingssysteem en voersamenstelling. De fecale verteerbaarheden van energie en nutriënten waren hoger in individueel gehuisveste varkens dan in groepen gehuisveste varkens, behalve voor de OOS-fractie. De metaboliseerbaarheid van energie was 3,7%-eenheden hoger in individueel gehuisveste varkens dan in groepen gehuisveste varkens. Het huisvestingssysteem had geen effect op HP, AHP en ER. Individueel gehuisveste varkens hadden een hogere ER in de vorm van eiwit dan varkens die in groepen gehuisvest waren ( $151$  vs  $137 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Metaboliseerbaarheid van energie was 3,5%-eenheden hoger voor varkens gevoerd met het controlevoer dan voor varkens gevoerd met het BP-voer. De voersamenstelling had geen effect op de HP en de varkens die gevoerd werden met het controlevoer hadden een hogere AHP dan varkens die gevoerd werden met het BP-voer ( $80$  vs  $68 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). De voersamenstelling had geen effect op ER, maar varkens gevoerd met controlevoer hadden een hogere ER in de vorm van eiwit dan varkens gevoerd met het BP-voer ( $150$  vs  $138 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ). Het NE-gehalte van vOOS uit BP, respectievelijk ongecorrigeerd en gecorrigeerd voor AHP, was 13,7 en 12,3 kJ/g vOOS. De AHP nam af met een toenemende opname aan vOOS en er was geen effect van huisvestingssysteem op de geschatte NE-waarde van vOOS uit BP. Numeriek was de energetische efficiëntie van vOOS echter hoger voor individueel gehuisveste varkens in vergelijking met in groepen gehuisveste varkens.

Er is geconcludeerd dat effecten van BP op AHP en de energetische efficiëntie van vOOS van BP niet beïnvloed werden door het huisvestingssysteem. Door de overige gevonden verschillen kunnen er echter wel verschillen bestaan in NE waarden van grondstoffen tussen individueel en in groepen gehuisveste varkens.

### **Conclusies**

In dit proefschrift is onderzoek verricht naar de energetische benutting van vOOS in relatie tot de energiebesteding aan fysieke activiteit. Uit de resultaten komen de volgende conclusies naar voren:

- De energetische efficiëntie waarmee in groepen gehuisveste zeugen vOOS uit bietenperspulsilage benutten is hoog in vergelijking met de waarden die gebruik worden in voederwaarderingssystemen. Deze hoge energetische efficiëntie wordt deels veroorzaakt door een verlaagd energieverbruik voor fysieke activiteit bij een toenemende opname van bietenperspulsilage.
- Het effect van vOOS uit bietenperspulsilage op de warmteproductie en het gedrag van in groepen gehuisveste zeugen is niet constant gedurende de dag.
- De vOOS-fractie van bietenpulp wordt door in groepen gehuisveste vleesvarkens efficiënter benut dan de vOOS-fractie van kokosschroot en sojahullen. Dit suggereert dat de energetische efficiëntie waarmee vOOS wordt benut afhankelijk is van de botanische herkomst van de desbetreffende vOOS-fractie.
- De relatief hoge energetische efficiëntie waarmee vOOS uit bietenpulp wordt benut is gerelateerd aan een verlaagd energieverbruik voor fysieke activiteit, wanneer bietenpulp gevoerd wordt aan vleesvarkens.
- Het energiebesparende effect van bietenpulp door een verlaagd energieverbruik voor fysieke activiteit is niet gevonden voor andere vOOS-bronnen (kokosschroot en sojahullen). Dit betekent dat een deel van de energiebesteding aan fysieke activiteit een karakteristiek is van de gebruikte grondstoffen. Dit suggereert dat de energetische efficiëntie waarmee vOOS wordt benut gerelateerd is aan de botanische herkomst van vOOS. Het suggereert ook dat een vaste waarde voor de energetische efficiëntie waarmee vOOS wordt benut niet correct is.
- Een verhoogde opname van (v)OOS leidt tot een verhoging van de slachtverliezen van vleesvarkens.
- Huisvestingssysteem (individueel vs groep) had geen significant effect op de energetische benutting van vOOS uit bietenpulp. Huisvestingssysteem had echter een groot effect op de vertering en benutting van de energie in het voer: individueel gehuisveste varkens waren efficiënter dan in groepen gehuisveste varkens. Dit suggereert dat de netto energie waarden van een voer of grondstof die afkomstig zijn uit proeven met individueel gehuisveste varkens, de nette energie waarde voor in groepen gehuisveste varkens overschatten.
- De snelheid van fermentatie speelt mogelijk een belangrijke rol bij de energetische efficiëntie waarmee varkens vOOS benutten.



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## **Curriculum Vitae**

Martin Rijnen (baptismal names: Martinus Maria Johannes Ardina) was born on the 2nd of April 1974 in Oisterwijk, The Netherlands. After his fourth birthday he grew up in Deurne, The Netherlands. In 1993 he graduated from secondary grammar school. In the same year he started a study Animal Science at Wageningen University. In March 1998 he finished his masters after MSc research in animal nutrition at the Research Institute for Pig Husbandry, and a traineeship in dairy nutrition at Massey University, New Zealand. In January 1998 he was appointed as researcher at the Research Institute for Pig Husbandry. His main research topics were the use of cereals and liquid diets for pigs. In November 1998 he started his Ph.D. research at Wageningen University, chairs Adaptation Physiology and Animal Nutrition. In January 2002 he started working at Beuker Vochtrijke Diervoeders B.V., where he was working as nutritionist and quality manager for liquid co-products for pigs and cattle. Since December 2002 he is working as a nutritionist at Hendrix UTD B.V. (a Nutreco company), and one of his main tasks is innovation in pig nutrition.

Martin Rijnen (doopnamen: Martinus Maria Johannes Ardina) werd geboren op 2 april 1974 te Oisterwijk. Vanaf zijn vierde jaar is hij opgegroeid in Deurne. In 1993 haalde hij zijn VWO diploma aan het St. Willibrord Gymnasium te Deurne. In datzelfde jaar begon hij met de studie Zoötechniek aan de Wageningen Universiteit. Na zijn stage in de rundveevoeding aan Massey University in Nieuw Zeeland, heeft hij twee afstudeervakken uitgevoerd bij het Praktijkonderzoek Varkenshouderij te Rosmalen. Beide afstudeervakken hadden betrekking op het gebruik en de fermentatie van vochtrijke diervoeders voor varkens. In maart 1998 haalde hij zijn doctoraal diploma Zoötechniek met diervoeding als hoofdvak. In januari 1998 begon hij als onderzoeker bij het Praktijkonderzoek Varkenshouderij te Rosmalen, met als belangrijkste onderzoeksthema's het gebruik van granen en brijvoer voor varkens. In november 1998 begon hij met een promotieonderzoek aan Wageningen Universiteit, leerstoelgroepen Adaptatiefysiologie en Diervoeding. Vanaf januari 2002 was hij werkzaam bij Beuker Vochtrijke Diervoeders, waarbij voedings- en kwaliteitstechnische aspecten van vochtrijke diervoeders voor varkens en rundvee centraal stonden. Sinds december 2002 werkt hij als fundamenteel nutritionist bij Hendrix UTD (onderdeel Nutreco), waarbij innovatie van varkensvoeding een belangrijk deel van de functie omvat.

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