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Dietary energy sources affect the partition of body lipids and the hierarchy of energy metabolic pathways in growing pigs differing in feed efficiency^{1,2}

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ABSTRACT: The use and partition of feed energy are key elements in productive efficiency of pigs. This study aimed to determine whether dietary energy sources affect the partition of body lipids and tissue biochemical pathways of energy use between pigs differing in feed efficiency. Forty-eight barrows (pure Large White) from two divergent lines selected for residual feed intake (RFI), a measure of feed efficiency, were compared. From 74 d to 132 ± 0.5 d of age, pigs ($n = 12$ by line and by diet) were offered diets with equal protein and ME contents. A low fat, low fiber diet (LF) based on cereals and a high fat, high fiber diet (HF) where vegetal oils and wheat straw were used to partially substitute cereals, were compared. Irrespective of diet, gain to feed was 10% better ($P < 0.001$), and carcass yield was greater (+2.3%; $P < 0.001$) in the low RFI compared with the high RFI line; the most-efficient line was also leaner (+3.2% for loin proportion in the carcass, $P < 0.001$). In both lines, ADFI and ADG were lower when pigs were fed the HF diet (−12.3% and −15%, respectively, relatively to LF diet; $P < 0.001$). Feeding the HF diet reduced the perirenal

fat weight and backfat proportion in the carcass to the same extent in both lines (−27% on average; $P < 0.05$). Lipid contents in backfat and LM also declined (−5% and −19%, respectively; $P < 0.05$) in pigs offered the HF diet. The proportion of saturated fatty acids (FA) was lower, but the percentage of PUFA, especially the EFA C18:2 and C18:3, was greater ($P < 0.001$) in backfat of HF-fed pigs. In both lines, these changes were associated with a marked decrease ($P < 0.001$) in the activities of two lipogenic enzymes, the fatty acid synthase (FASN) and the malic enzyme, in backfat. For the high RFI line, the hepatic lipid content was greater ($P < 0.05$) in pigs fed the HF diet than in pigs fed the LF diet, despite a reduced FASN activity (−32%; $P < 0.001$). In both lines, the HF diet also led to lower glycogen content (−70%) and lower glucokinase activity (−15%; $P < 0.05$) in the liver. These results show that dietary energy sources modified the partition of energy between liver, adipose tissue, and muscle in a way that was partly dependent of the genetics for feed efficiency, and changed the activity levels of biochemical pathways involved in lipid and glucose storage in tissues.

Key words: feed efficiency, fiber, glucokinase, lipid partition, lipogenesis

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INTRODUCTION

The increasing pressures on food production and feed supplies challenge the need of genotypes with an improved feed efficiency and ability to cope with alternative feed resources such as fibrous feedstuff. The greater feed efficiency of pigs selected for a low residual feed intake (RFI), a measure of feed efficiency, has been mainly established on standard diets (Gilbert et al., 2007). Adverse effects on weight gain and feed efficiency have been observed when pigs selected for a high RFI but not for a low RFI were shifted to a high

fiber, low energy diet for 3 wk (Montagne et al. 2014). This suggests that low RFI pigs may have a better ability to cope with a diet rich in fiber. Because fiber is poorly degraded along the digestive tract (De Lange et al., 2006), it is usually considered as a diluent of pig diets. Therefore, adding fat to a fiber diet has been shown as a relevant strategy to improve dietary energy value and feed efficiency (Myer and Combs, 1991). However, this strategy changes the nutrients and energy source as compared with a low fat diet, with possible consequences on the energy use by pigs. Indeed, fatty acids (FA) are oxidized for ATP synthesis with the same efficiency as glucose, but are deposited in tissues with a much greater energetic efficiency (Birkett and de Lange, 2001). The effects on performance and body composition remain, however, difficult to predict, as illustrated by the interplay between dietary fat content and fiber type in determining backfat depth (Yan et al., 2013). The responses could also be dependent of the genetics for feed efficiency. Indeed, lipid metabolic pathways are down-regulated in low RFI pigs (Lkhagvadorj et al., 2010) and metabolic specificities in the way low vs. high RFI pigs use energy in tissues have been suggested (Le Naou et al., 2012).

This study aimed to determine body composition and tissue energy metabolism in pigs differing in feed efficiency, and offered contrasting diets for nutrients and energy source.

MATERIALS AND METHODS

Animals and Diets

The care and use of pigs were performed in compliance with the guidelines of the French Ministry of Agriculture and Fisheries for animal research, and was approved by a local ethical committee (Rennes, France).

From Large White pure animals, two lines were divergently selected for low RFI vs. high RFI since 2000, as described by Gilbert et al. (2007). Briefly, daily feed intake (ADFI) was measured on group-housed boars fed ad libitum from 35 to 95 kg BW. Candidates for selection were tested over a fixed BW range. Two traits were recorded and used to calculate the predicted feed intake: ADG from 35 to 95 kg, and ultrasonic backfat thickness (UBT) at 95 kg averaged from 6 different measures (right and left shoulder, right and left midback, right and left loin). The R^2 of the model used to compute the predicted feed intake was 0.66. A phenotypic RFI selection index was computed as a linear combination of those traits as follows:

$$\text{RFI} = \text{ADFI} - (1.24 \times \text{ADG}) - (31.9 \times \text{UBT}),$$

in which ADFI and ADG (measured in grams) and UBT (measured in millimeters) were corrected for the effects of contemporary group and pen size before computation.

The present study refers to Generation 8 of selection. Forty-eight barrows ($n = 24$ per RFI line from 12 pairs of full or half sibs) were chosen at weaning (27 ± 1.9 d of age and 8.2 ± 0.2 kg BW on average) from the selection herd (INRA GenESI, Le Magneraud, France). Within each line, 6 different sires and 12 different sows were used. Two successive transfers of piglets to the postweaning facilities of INRA Pegase (Saint-Gilles, France) were done at a 3-wk interval. There, they were housed in collective pens (one pen per line and per replicate) and offered free access to a standard prestarter diet (10.2 MJ NE/kg, 19.2% CP, and 12.8 g/kg digestible lysine) during the first 2 wk postweaning, and a standard starter diet (9.9 MJ NE/kg, 18.4% CP, and 11.4 g/kg digestible lysine) during the next 5 wk postweaning. At 74.0 ± 0.3 d of age, pigs were moved to growing facilities, where they were housed individually (full-slatted floor) allowing individual feed intake recording. After 2 d, the starter diet was progressively replaced by an experimental diet (75/25, 50/50, 50/50, and 25/75) during a 4-d period. Thereafter, pigs received the experimental diet in a phase-feeding program: the growing diet was distributed during the first 6 wk after the feeding trial has started, and the finishing diet which differed mainly for the protein and amino-acid contents, was distributed thereafter until slaughter at the same age (132 ± 0.5 d of age). Within each line, pigs ($n = 12$ per line and per diet) were offered either a low fat, low fiber (LF) diet or a high fat, high fiber (HF) diet. The LF diet was mainly based on cereals (wheat and barley) and soybean meal. The HF diet was formulated by the partial replacement of cereals by ground straw (11.5% of the diet; 5 mm grinding) and a mixture of rapeseed and soybean oils (7.5% of the diet) to provide the same protein and ME contents as the LF diet (Table 1). Fiber was considered as a diluting factor of diet, because energy digestibility of wheat straw for growing pigs is only 13% (De Lange et al., 2006). All diets were prepared and pelleted (4.5 mm) at the experimental mill of INRA Pegase (Saint Gilles). Samples of diets were stored at 4°C and freeze-dried later for chemical analyses. Feed swelling capacity was estimated (Quemeneur et al., 2013) to be 3.4 and 3.9 mL/g of DM for the grower formulas of LF and HF diets, respectively, as well as to be 3.3 and 3.7 mL/g of DM for the finisher formulas of LF and HF diets, respectively.

Pigs were weighed when entering in the growing facilities, every 2 wk thereafter, and on the morning of the slaughter day. Individual feed consumption was recorded weekly (feed offered minus refusals) during the 8 wk of the feeding trial. Throughout the experiment, animals had free access to water. The ADG, ADFI, and G:F were calculated for the test period.

Table 1. Ingredients, chemical and nutritional compositions of the experimental diets¹

Diet	Growing		Finishing	
	HF	LF	HF	LF
Ingredients, g/kg (as-fed basis)				
Wheat	269.5	362.2	330.9	417.2
Barley	269.5	362.2	330.9	417.2
Soybean meal	233.5	199.9	116.1	84.9
Corn starch	0	27.5	0	35.7
Crushed wheat straw	114.5	0	112.6	0
Rapeseed oil	25.1	3.4	25.1	3.5
Soybean oil	50.1	6.8	50.3	6.7
L-Lysine HCl	2.8	3.2	2.9	3.3
L-Threonine	1.17	1.20	10.3	10.5
L-Tryptophane	0.28	0.26	0.22	0.19
DL-Methionine	1.04	0.76	0.46	0.38
Salt	4.5	4.50	4.50	4.50
Calcium carbonate	10.5	10.5	10.0	10.0
Dicalcium phosphate	12.5	12.5	10.0	10.0
Vitamins and minerals premix	5.0	5.0	5.0	5.0
DM, g/100 g	88.0	87.4	87.2	86.9
Chemical composition, % (as-fed basis)				
Ash	5.4	5.0	4.7	4.3
OM	82.6	82.4	82.5	82.6
CP	17.3	17.4	13.1	13.4
Fat	7.0	2.1	7.4	2.2
Starch	30.8	42.6	36.2	48.5
NDF	17.7	12.8	18.3	11.5
ADF	8.5	3.8	7.9	3.5
GE, MJ/kg	17.5	15.9	17.3	15.8
Nutritional values				
ME, MJ/kg	12.9	12.9	12.9	12.9
NE, MJ/kg	9.8	9.6	10.0	9.9
Digestible lysine, g/kg	9.5	9.5	7.0	7.0
Digestible threonine, g/kg	0.62	0.62	0.46	0.46
Digestible methionine, g/kg	0.32	0.30	0.21	0.21
FA composition, % extracted FA				
C18:2 n-6	41.0	45.3	41.6	44.6
C18:3 n-3	5.6	5.0	5.7	4.7
Saturated FA	13.9	18.5	13.8	19.0
Mono-unsaturated FA	36.2	27.0	36.4	25.9
Poly-unsaturated FA	54.6	49.8	50.0	55.1
Ratio n-6:n-3	5.0	5.3	5.4	4.8

¹A low fat, low fiber diet (LF) and a high fat, high fiber diet (HF) were formulated at the same protein and ME contents. For each dietary group, a growing diet was distributed to pigs from 76 d of age onwards for 6 wk, and a finishing diet which differed for the protein and amino-acid contents, was distributed thereafter and until slaughter. FA = fatty acid.

In vivo Backfat Depth

Backfat thickness (BFT) was measured by ultrasound (VETKOPLUS, Noveko Inc., Boucherville, QC, Canada) on the left and right sides of the body, at the last rib level, when pigs entered the grower facilities and at 4 and 7 wk after the feeding trial had started.

Animal Slaughtering and Sample Collection

Two hours after the first morning meal, pigs were killed by electronarcosis followed by jugular exsanguination. At bleeding, a blood sample (10 mL) was collected on EDTA and centrifuged for 15 min at $2,500 \times g$ and 4°C . Plasma was stored at -20°C for later analyses. Backfat (comprising all fat layers) was immediately sampled by an incision along the dorsal right side of the body at the last rib level. The carcass was then prepared by removing digestive, urogenital, and respiratory tracts. The digestive tract was weighed (full and empty), and the weight of the digestive content was calculated. Backfat thickness was obtained by optical measurements (one spot between the 3rd and 4th last rib) on the hot carcass (CGM, Sydel, Lorient, France). Liver and kidneys were weighed, and the liver was immediately sampled. Perirenal fat was removed, weighed, and sampled. Within 20 min after slaughter, a sample of the LM was also collected at the last rib on the right side of the carcass, just below the sampling location of backfat. Tissue samples were cut into small pieces, snap frozen in liquid nitrogen and stored at -75°C until biochemical analyses. A portion of liver was also freeze-dried.

The carcass was then chilled at 4°C . After 36 h of chilling, the left and right half side of the carcass were weighed. The left side of the carcass was dissected into its main cuts (backfat, belly, loin, ham, and shoulder). The entire LM was then dissected from the loin, weighed, and a sample was freeze-dried. All cuts weights were then expressed as percentage of the left chilled carcass weight.

Chemical and Biochemical Analyses

All analyses were performed in duplicate. Frozen (backfat and perirenal fat) or freeze-dried (LM, liver, and diets) subsamples were ground. Freeze-dried samples were first analyzed using methods of the International Standardization Organization (<http://www.iso.org>, verified September 26, 2014) for DM (ISO 6496-1983). Ash content (ISO-5984) was determined in diets. Gross energy content (ISO 9831-1998) was measured in diets with an adiabatic bomb calorimeter (IKA C5000, IKA, Staufen, Germany). Feeds were also analyzed for cell wall constituents (NDF and ADF) according to van Soest and Wine (1967), and for starch content (ISO 6493-2000) using a digital polarimeter (ADP220, Bellingham, UK). The N content in diets, LM, and liver samples was analyzed according to the Dumas procedure (NF V18-120, 1997; <http://www.afnor.org/en>, verified September 26, 2014) with a Rapid N cube (Elementar France, Villeurbanne, France), and protein content ($\text{N} \times 6.25$) was deduced. Lipid contents of diets and tissues were determined by the application of supercritical CO_2 and solvent extraction (Sahena et al., 2009) with an automatic system (Leco TFE 2000 Instrument, Leco Corporation, St. Joseph, MI). The glycogen content was determined in liver

and LM according to the method described by Good et al. (1933) with minor adaptations (Montagne et al., 2014). In LM, the glycolytic potential (**GP**) was also calculated as $GP = 2[(\text{glycogen}) + (\text{glucose}) + (\text{glucose-6-phosphate})] + (\text{lactate})$, as described previously (Monin and Sellier, 1985). Glucose and glucose-6-phosphate were determined together using the enzymatic method (Glucose HK Kit; ABX Diagnostics, Montpellier, France). Glycogen content was determined from glucose determination after hydrolysis by amyloglucosidase. Lactate content was determined using a dedicated commercial kit (Lactate PAP; BioMérieux, Marcy-l'Etoile, France). Glucose (Glucose RTU, BioMérieux) and triglyceride (TG PAP 1000 kit, BioMérieux) concentrations were also determined in plasma. All measurements were performed on a clinical chemistry analyzer Konelab 20i (Thermo Fisher Scientific, Courtaboeuf, France).

Fatty Acid Composition

Fatty acid compositions of diets and backfat were determined after methylation of lipids extracted as described above. The boron trifluoride methanol was used according to procedures developed by Morrison and Smith (1964). Analyses were performed on a gas chromatograph (Nelson Analytical, Manchester, NH) equipped with a fused-silica capillary column (30 m \times 0.25 mm i.d.), with a base-deactivated silica stationary phase (a 0.25- μm film thickness) filled with a stationary phase (80% bisecyanopropyl and 20% cyanopropylphenyl) and using margaric acid (C17:0) as the internal standard. The furnace temperature was 180°C, and injector and detector temperatures were 240°C. For all samples, retention times and peak areas were determined. Peaks were identified by comparison with the retention times of standard FA methyl esters. Individual FA, as well as the sum of SFA, MUFA, or PUFA, were reported as percentages of the total FA identified in each sample.

Enzyme Activities of Nutrient

Oxidative Catabolism and Glycogenesis

Specific activities of enzymes were monitored in selected tissues. To evaluate the oxidative ability, the β -hydroxylacyl-CoA dehydrogenase (**HAD**) involved in β -oxidation of FA, and citrate synthase (**CS**) participating to oxidation of nutrients in the Krebs cycle, were measured. Briefly, frozen samples of the liver, LM, and backfat (approximately 300 mg each) were homogenized in a 0.1 M phosphate buffer (pH = 7.5) containing EDTA (2 mM). Mixtures were sonicated (60 s, 50 Hz) and centrifuged (13 min, 1,500 \times g, 4°C). Supernatants were stored in ice. Specific activities were assayed at 340 nm absorbance for HAD (Bass et al., 1969) and at 405 nm absorbance for CS (Srere, 1969), using the clinical chemistry analyzer Konelab 20i.

In addition, the activities of the glucokinase (**GCK**) participating to glycogenesis and considered as a glucose sensor, and of the hexokinase (**HK**), using glucose as substrate to produce glucose-6-phosphate, were measured in the liver and LM, respectively, using a spectrophotometric method (Panserat et al., 2000). Briefly, liver or LM samples (500 mg) were homogenized (dilution 1:9) in ice-cold buffer [50 mM Tris, 5 mM EDTA, 2 mM 1,4-dithiothreitol (**DTT**) and protease inhibitors cocktail (Complete, Roche Diagnostic, Meylan, France); pH 7.4]. Homogenates were centrifuged at 4°C for 10 min at 900 \times g. Enzyme activity was measured at 37°C by coupling ribulose-5-phosphate formation from glucose-6-phosphate to the reduction of NADP, using purified glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase (Sigma) as coupling enzymes. One unit of enzyme activity was defined as the amount that phosphorylates 1 μmol glucose per min. The GCK activity in liver was estimated by subtracting the rate of Nicotinamide adenine dinucleotide phosphate (**NADPH**) formation (at 340 nm) in the presence of 0.5 mM glucose (scoring low-Km HK activity) from that obtained in the presence of 100 mM glucose (scoring total HK activity) and taking into account the possible interference of glucose 1-dehydrogenase activity, as follows:

$$\text{GCK} = \text{HKT} - \text{HK} - \text{GDH}/3,$$

where HKT referred to total HK activity, and GDH to glucose 1-dehydrogenase activity.

To calculate enzyme specific activities, protein content in the assayed supernatants was measured using Bradford reagent with BSA as standard (Bradford, 1976).

Lipogenic Enzyme Activities

Activities of lipogenic enzymes were assessed in backfat, perirenal fat, LM, and liver. Tissue samples were first homogenized in 0.25 M ice-cold sucrose solution containing EDTA (1 mM) and DTT (1 mM). Mixtures were ultracentrifuged at 100,000 \times g during 1 h at 4°C. The resulting supernatants containing cytosolic proteins were collected and frozen at -75°C until use. Specific activities of malic enzyme (**ME1**), glucose-6-phosphate dehydrogenase (**G6PDH**), and fatty acid synthase (**FASN**) were assayed spectrophotometrically at 340 nm absorbance (Bazin and Ferré, 2001). The measurements have been first adapted in volumes of supernatants and reagents for using the KoneLab 20i apparatus. Activities were expressed per units of cytosolic proteins.

Statistical Analysis

Data were analyzed using the SAS Software (v. 9.2; SAS Inst. Inc., Cary, NC) by ANOVA using the GLM

Table 2. Performance as influenced by line and diet during the growing-finishing period

Pigs	RFI ¹ line		Diet		RSD	P-value ²	
	High	Low	HF	LF		Line	Diet
<i>n</i>	24	24	24	24	–	–	–
Start BW, kg	26.9	26.1	26.2	26.8	4.3	0.539	0.624
End BW, kg	73.3	77.8	70.9	80.2	5.5	0.008	<0.001
Age at slaughter, d	132	133	132	133	4	0.121	0.492
ADG, g/d	796	882	770	907	73	<0.001	<0.001
ADFI, ³ g/d	2,307	2,250	2,216	2,340	106	0.099	0.004
G:F	0.351	0.386	0.361	0.374	0.020	<0.001	0.131
HCW, kg	54.0	58.6	52.0	60.6	4.3	<0.001	<0.001
Carcass yield, %	73.5	75.2	73.2	75.5	1.7	0.001	<0.001
Digestive content, ⁴ kg	6.55	5.87	6.99	5.42	0.89	0.010	<0.001
Empty digestive tract, ³ kg	5.30	4.86	5.20	4.97	0.39	0.001	0.140

¹RFI = residual food intake.

²There was no interaction ($P > 0.10$) between genetic line (high or low RFI) and diet (LF: low fiber low fat; HF: high fiber high fat) for any analyzed traits. Least squares means for the effects of Line and of Diet are shown.

³Corrected for differences in end-of-test BW.

⁴Corrected for ADFI to account for difference in the size of the last meal.

procedure. Line, diet, and the interaction between line and diet were considered as fixed effects, and replicate was considered as a random effect. End-of-test BW and ADFI during the test period were also considered as covariates to decipher changes induced by nutrients and energy source from changes related to growth allometry. Data are shown as pooled least squares means when the statistical analysis did not reveal any line \times diet interaction. Differences were considered significant for $P \leq 0.05$, and $0.05 < P \leq 0.10$ was discussed as a trend.

RESULTS

Growth Performance

No interactions ($P > 0.10$) between line and diet were observed for growth traits, so only the separate effects of line and diet are presented (Table 2). Irrespective of diet, ADG was 11% greater ($P < 0.001$) in the low RFI line than the high RFI line, and this line-associated difference was observed whatever the periods considered in the feeding trial (0 to 3 wk, 3 to 6 wk, and 6 wk to end; data not shown). During the test, there was a trend for a reduction in ADFI (-57 g/d; $P < 0.10$) in the low RFI line compared with the high RFI line (Table 2). Altogether, G:F was 10% greater ($P < 0.001$) in the low RFI pigs than in the high RFI pigs. At slaughter, carcass yield was greater ($+2.3\%$; $P = 0.001$) in the low RFI pigs than in the high RFI pigs. Digestive content was reduced by 10.4% ($P = 0.010$) in the formers. The empty digestive tract was also lighter (-8% ; $P = 0.010$) in the low RFI pigs than in the high RFI pigs when data were adjusted for differences in end-of test BW (Table 2), whereas there was no line-associated difference ($P = 0.30$) when no correction was applied (data not shown).

Irrespective of line, pigs offered the HF diet had a 15% lower ADG ($P < 0.001$) and a 12% lower ADFI (2.13 vs. 2.43 kg/d on average; $P < 0.01$) during the test period. The difference in ADFI between diets was less marked at the beginning of the test (0 to 3 wk: -10%) than thereafter (3 to 6 wk or 6 wk to end: -13% on average; data not shown). When data were corrected for end-of-test BW, ADFI was also lower in the HF-fed pigs than in the LF-fed pigs (Table 2). As a result, G:F during the test did not differ between diets ($P = 0.131$). At slaughter, BW and carcass yield were reduced ($P < 0.001$) in pigs fed the HF diet compared with those fed the LF diet. The digestive content was 29% heavier ($P < 0.001$) in pigs fed the HF diet. No dietary-associated difference was observed for the weight of the empty digestive tract when difference in BW at slaughter was taken into account (5.08 kg on average; $P = 0.140$), although it was lighter in HF-fed pigs than in LF-fed pigs when no correction was applied (4.91 kg vs. 5.25 kg, respectively; $P = 0.03$).

Carcass Composition

There were no interactions ($P > 0.10$) between line and diet for carcass composition (Table 3), so line and diet effects are shown separately. Liver and kidney weights were lower ($P < 0.005$) in the low RFI line than in the high RFI line. The loin proportion in the carcass and the LM relative weight were greater ($P < 0.05$) in the low RFI pigs than in high RFI pigs, and ham percentage did not differ between the two lines, resulting in a greater proportion of lean pieces ($+2\%$, $P < 0.01$) in the low RFI pigs. The sum of the main fatty pieces in the carcass (backfat and belly) was conversely lower (-9% ; $P < 0.01$) in the low RFI pigs than in the high RFI pigs; however, BFT, weight

Table 3. Body composition as influenced by line and diet during the growing-finishing period

Composition	RFI ¹ line		Diet		RSD	P-value ²	
	High	Low	HF	LF		Line	Diet
<i>n</i>	24	24	24	24	–	–	–
Start BFT, ² mm	4.9	5.1	4.9	5.1	0.9	0.300	0.550
BFT 4 wk, mm	6.7	6.8	6.3	7.2	1.0	0.960	0.004
BFT 7 wk, mm	8.7	8.7	8.0	9.4	1.3	0.910	0.001
End BFT, mm	14.1	13.6	11.9	15.8	2.5	0.496	<0.001
Organ weight, ³ g							
Perirenal fat	535	534	455	613	92	0.967	<0.001
Kidneys	320	279	301	299	29	<0.001	0.874
Liver	1,740	1,600	1,608	1,731	146	0.004	0.030
Carcass composition, %							
Backfat	7.3	6.8	5.9	8.2	1.0	0.113	<0.001
Belly	13.4	12.3	12.4	13.4	2.1	0.072	0.103
Ham	22.8	23.0	23.4	22.3	0.72	0.382	<0.001
Shoulder	25.1	25.7	25.7	25.1	2.0	0.390	0.247
Loin	27.8	28.7	28.8	27.8	0.73	<0.001	<0.001
LM	4.96	5.38	5.28	5.06	0.004	0.050	0.048
Fatty pieces ⁴	20.8	19.1	18.3	21.6	2.02	0.009	<0.001
Lean pieces ⁵	75.7	77.3	77.9	75.1	2.03	0.008	<0.001

¹RFI, residual food intake.

²There was no interaction ($P > 0.10$) between genetic line (high or low RFI) and diet (LF: low fiber low fat; HF: high fiber high fat) for any traits including backfat thickness (BFT) assessed at the beginning of the growing-finishing period, and 4 or 7 wk later. Least squares means for the effects of Line and of Diet are shown.

³Data corrected for differences in BW at slaughter.

⁴The sum of backfat and belly.

⁵The sum of shoulder, ham, and loin.

of perirenal fat, and backfat proportion in the chilled carcass did not differ between the two lines (Table 3). Corrected by ADFI of pigs during the test, backfat proportion in the carcass was however slightly reduced ($P = 0.05$) for the low RFI line (6.8% of the carcass) compared with the high RFI line (7.4% of the carcass). Similarly, backfat proportion was reduced in the low RFI pigs compared with the high RFI pigs when data were adjusted for differences in end BW (6.79 vs. 7.37%; $P = 0.08$) or in carcass weight (6.71 vs. 7.45%; $P = 0.03$).

In both lines, pigs fed the HF diet had greater ($P < 0.001$) proportions of loin (+3.5%) and ham (+4.9%) as compared with pigs fed the LF diet (Table 3). Conversely, feeding the HF diet reduced body adiposity compared with feeding the LF diet, as illustrated by lower perirenal fat weight (–26%), thinner backfat (–25%), and lower proportion of backfat in the carcass (–28%; $P < 0.001$). The difference between diets for BFT was already significant 4 wk after the start of the feeding trial (–12.5%; $P = 0.004$; Table 3). Relatively to ADFI during the feeding test, perirenal fat proportion in the body and backfat proportion in the chilled carcass were still lower in HF-fed pigs (0.61 and 6.4%, respectively) compared with LF-fed pigs (0.78 and 7.8%, respectively; $P < 0.001$). Similarly, the dietary-associated differences observed in the relative proportions of fatty and lean pieces were significant even after correction for differences in end-

of-test BW (e.g., 6.2% vs. 8.1% for backfat proportion in HF-fed and LF-fed pigs, respectively; $P < 0.001$) as well as for carcass weight (data not shown).

Glycemia and Triglyceridemia

Plasma concentrations of glucose (1.45 ± 0.08 g/L on average) and triglycerides (508 ± 47 mg/L on average) did not differ between RFI lines. Plasma triglyceride concentrations were 1.8-fold greater ($P < 0.001$) in HF-fed pigs (650 ± 47 mg/L) than in LF-fed pigs (357 ± 47 mg/L). Conversely, plasma glucose concentrations tended ($P = 0.10$) to be lower in pigs fed the HF diet (1.35 ± 0.08 g/L) than in pigs fed the LF diet (1.55 ± 0.08 g/L); this dietary-associated variation in glucose concentrations reached significance (1.26 vs. 1.63 g/L, respectively; $P = 0.02$) when data were corrected for difference in BW at slaughter.

Tissue Composition

There were no differences in protein and moisture contents in the LM between lines and diets (Table 4). In liver, moisture content was greater in the low RFI pigs fed HF diet compared with those fed LF diet, whereas there was no feeding-associated variation in moisture content within the high RFI line. Hepatic glycogen content was

Table 4. Tissue composition¹ as influenced by line (high or low residual food intake, RFI) and diet (LF, low fiber low fat; HF, high fiber high fat)

Tissue	High RFI		Low RFI		RSD	P-value ²		
	HF	LF	HF	LF		Line	Diet	L × D
<i>n</i>	12	12	12	12	–	–	–	–
LM								
Protein, g/100 g tissue wet wt.	22.4	23.1	22.9	23.1	1.9	0.599	0.431	0.708
Moisture, g/100 g tissue wet wt.	74.5	73.5	74.3	73.4	2.1	0.800	0.152	0.925
Glycogen, g/100 g tissue wet wt.	0.97	1.00	0.97	1.02	0.18	0.859	0.457	0.813
Glycolytic potential, μEq lactate/g of tissue	214	210	204	214	22	0.651	0.657	0.297
Liver								
Protein, g/100 g tissue wet wt.	20.1	19.2	19.5	19.4	1.1	0.512	0.129	0.200
Moisture, g/100 g tissue wet wt.	72.8a	73.3ab	73.5b	72.7a	0.9	0.733	0.705	0.028
Glycogen, g/100 g tissue wet wt.	1.66	2.32	1.82	3.09	0.65	0.337	0.049	0.527

^{a,b}Difference ($P < 0.05$) between least squares means in the same row.

¹Contents in protein ($N \times 6.25$), moisture, and glycogen were expressed in g/100 g tissue wet weight. Glycolytic potential was expressed in μEq lactate/g of tissue.

²Effects of genetic line (low or high RFI), diet, and the interaction between line and diet (L × D). Least squares means in the four experimental groups are shown.

similar in the low RFI line and the high RFI lines, whereas it was 41% lower ($P = 0.05$) for pigs fed the HF diet than in pigs fed the LF diet. There were no dietary-associated differences in glycogen content or in the GP in LM.

An interaction between line and diet was denoted for lipid content in some tissues, so that data are presented for the 4 experimental groups (Fig. 1). There was no significant difference in the amount of lipids in backfat and LM between the high and low RFI lines. Irrespective of line, feeding the HF diet led to lower lipid contents ($P < 0.05$) in backfat and LM when compared with the LF diet. In perirenal fat, there was a trend ($P = 0.102$) for an interaction between diet and line, so that the reduction in lipid content in HF-fed pigs with LF-fed pigs was observed for the high RFI line only (77.2 vs. 80.3%, respectively; $P = 0.030$). For hepatic lipid content, diet and line also interacted ($P = 0.017$): lipid content was 18% greater ($P < 0.05$) for the high RFI pigs fed the HF diet than fed the LF diet, whereas it was similar with both diets for the low RFI pigs.

There was no interaction ($P > 0.10$) between line and diet for FA composition in backfat, so line and diet effects for the most important FA are shown separately (Table 5). The low RFI pigs tended ($P < 0.08$) to have a lower proportion of SFA, which was related to the lower proportions ($P < 0.02$) of C10:0 to C15:0 FA in that line (data not shown) without any variations in the relative percentages of the predominant SFA C16:0 and C18:0, when compared with the high RFI line. The low RFI pigs had a greater percentage ($P = 0.010$) of MUFA, which was mainly due to the greater proportion of C18:1 n-9 in this line compared with the high RFI line (38.7 vs. 37.4%, respectively; $P = 0.006$). The PUFA content (21.7% of total FA) and the ratio of n-6 to n-3 FA (5.4 on average) in backfat were similar ($P > 0.40$) in both lines. Irrespective of line, feeding the HF diet resulted in

a marked decrease ($P < 0.001$) in the proportion of SFA, including lower ($P < 0.001$) proportions of C16:0 and C18:0 when compared with the LF diet. There was also a slight decrease in the proportion of MUFA in backfat of HF-fed pigs (Table 5), which was related to the lower percentages of C16:1, C20:1, and C18:1 n-9 to a lesser extent, in HF-fed pigs compared with LF-fed pigs. Conversely, pigs offered the HF diet had lipids with a 2.3-fold greater proportion of PUFA ($P < 0.001$), which was due to greater ($P < 0.001$) proportions of C18:2, C18:3, and C20:2 compared with LF-fed pigs. The ratio of n-6 to n-3 families was also modified by the diet, toward a predominance of n-6 FA in pigs offered diet HF when compared with those offered diet LF.

Energy Metabolism in Tissues

There was no interaction ($P > 0.10$) between line and diet for lipogenic activities, so line and diet effects are shown separately (Table 6). The specific activities of FASN, ME1, and G6PDH did not differ between RFI lines in adipose tissues and liver. In LM, activities of ME1 and G6PDH were lower ($P < 0.005$) in the low RFI pigs than in the high RFI pigs. Irrespective of line, activities of lipogenic enzymes in backfat, perirenal fat and LM were much lower ($P < 0.001$) for pigs fed diet HF than for pigs fed diet LF. In liver, FASN activity was reduced by 32% ($P < 0.001$) in HF-fed pigs compared with LF-fed pigs, but hepatic activities of ME1 and G6PDH producing NADPH did not differ between diets.

Concerning enzymes involved in the nutrient catabolism, tissue-specific responses to line or diet were observed (Table 7). In backfat, the oxidative enzyme activities were increased by 17% for HAD and 7% for CS ($P < 0.10$) in the low RFI line compared with the high RFI line, and they were lower (–19% on average,

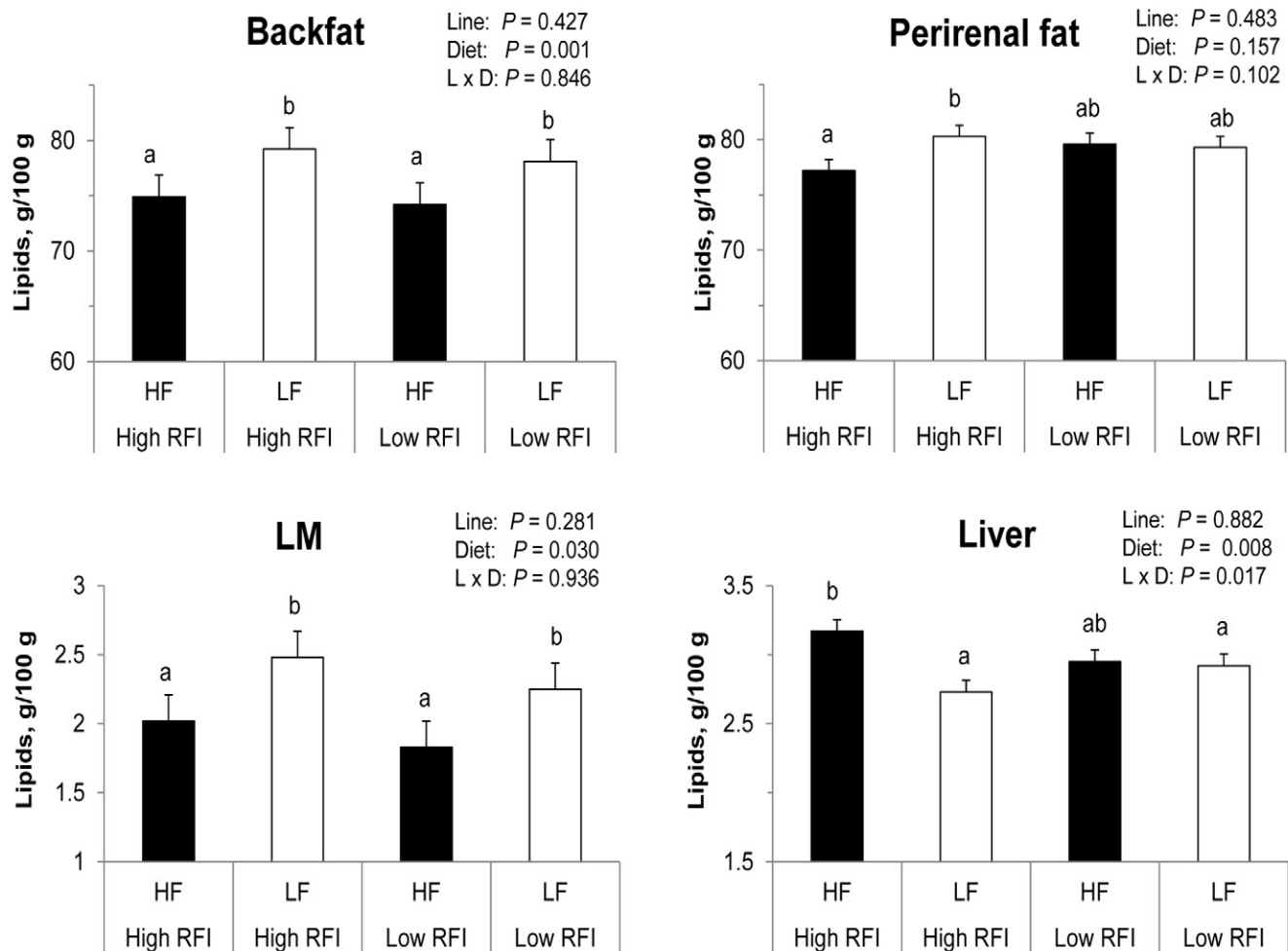


Figure 1. Lipid content in tissues. Pigs from two lines divergently selected for residual feed intake (RFI) were offered either a low fat, low fiber (LF, white bars) diet or a high fat, high fiber (HF, black bars) during the growing period. Data were analyzed with line, diet, and the interaction between line and diet (L × D) as the main effects. Least squares means in the four experimental groups are shown.

$P < 0.005$) when pigs were fed the HF diet. In liver, HAD activity was lower ($P < 0.02$) in the low RFI pigs than in the high RFI pigs, and CS activity did not vary between the two lines. Feeding the HF diet had no effect on hepatic activities of these mitochondrial oxidative enzymes. In the LM, the activities of these enzymes were similar whatever the line and the diet. However, the ratio of HK to CS in muscle was 31% lower ($P = 0.03$) when pigs were fed the HF diet than with the LF diet.

Finally, GCK activity in liver was greater ($P < 0.001$) in the low RFI line than in the high RFI line (Table 7). Irrespective of line, feeding a HF diet led to a reduction of hepatic GCK activity (-15% , $P < 0.05$) as compared with the LF diet. Altogether, the ratio of GCK to CS activities in liver was 36% greater ($P < 0.001$) in the low RFI line than in the high RFI line, and feeding HF diet tended to reduce this ratio by 13% ($P < 0.10$) when compared with diet LF.

DISCUSSION

This study clearly shows that, irrespective of diet, pigs selected for a low RFI exhibited improved growth performance and carcass merit than pigs selected for a high RFI. The improved G:F of pigs selected for low RFI was expected, because RFI is a unique measure of feed efficiency (Koch et al., 1963); however, the greater ADG measured in the low RFI pigs during the growing period ($+87$ g/d) was not in line with the selection objective to keep BW constant (Gilbert et al., 2007) and with previous data showing no difference in growth rate between lines of pigs divergently selected for RFI (Harris et al., 2012; Faure et al., 2013). Because the difference in ADG between low and high RFI groups was observed for any given interval, the hypothesis of line-associated differences in growth precocity during the grower period can be discarded. Testing pigs over a fixed age range rather than over a fixed BW range as in the selection procedure may be rather partly responsible for this discrepancy on ADG between studies. At slaughter, the bet-

Table 5. Fatty acid composition¹ in subcutaneous adipose tissue as influenced by line and diet

FA	RFI Line		Diet		RSD	P-value ²	
	High	Low	HF	LF		Line	Diet
<i>n</i>	12	12	12	12	–	–	–
SFA	37.7	36.6	29.3	45.0	2.1	0.071	<0.001
C14:0	1.06	0.98	0.86	1.18	0.09	0.007	<0.001
C16:0	21.6	21.2	17.6	25.2	1.1	0.172	<0.001
C18:0	13.8	13.3	9.7	17.4	1.3	0.195	<0.001
MUFA	40.5	41.8	40.4	41.8	1.7	0.010	0.010
C16:1	1.58	1.70	1.47	1.81	0.2	0.094	<0.001
C18:1	37.4	38.7	37.6	36.4	1.6	0.007	0.078
C20:1	1.32	1.29	1.22	1.39	0.24	0.683	0.017
PUFA	21.8	21.6	30.2	13.2	1.9	0.700	<0.001
C18:2	16.4	16.3	23.5	9.2	1.7	0.950	<0.001
C18:3	1.56	1.53	2.51	0.61	0.24	0.518	<0.001
C20:2	1.19	1.17	1.48	0.87	0.60	0.907	0.001
C20:3	1.22	0.98	1.12	1.08	0.84	0.321	0.872
n-6/n-3	5.25	5.60	6.02	4.84	1.6	0.450	0.014

¹The most quantitatively important fatty acids (FA) of SFA, MUFA, or PUFA families are indicated as the proportion of all individual identified FA.

²Effects of genetic line, diet, and the interaction between line and diet (L × D).

ter carcass yield in the low RFI pigs than in the high RFI pigs confirms previous data obtained in a former generation of selection (Faure et al., 2013). The present study further indicates that this benefit was due to the lesser development of the digestive tract and lower digestive content in that line. Carcass composition was also affected by selection with heavier muscled carcasses for the low RFI pigs in this study, as reported in other experiments (Lefaucheur et al., 2011; Smith et al., 2011; Faure et al., 2013). This difference could be related to reduced protein degradation in pigs selected for a low RFI (Cruzen et al., 2013), although we have reported no difference in the activities of some enzymes related to protein catabolism in the former generation of pigs selected for RFI (Le Naou et al., 2012). A limited line-associated difference in the proportion of fat tissues in the carcass, with no change in BFT, was shown herein; whereas marked differences in carcass adiposity between RFI lines have been reported in the former generations of selection for pigs at the market BW (Le Naou et al., 2012; Faure et al., 2013). Early line difference in BFT is not expected because BFT at 95 kg BW is included in the computation of the RFI selection index (Gilbert et al., 2007). The finding that line difference for BFT becomes significant for 19 wk onwards (Faure et al., 2013), which was the end point of the present experiment, also support our data. Pigs were investigated at this young age to reveal causal rather than associated mechanisms that may underline adiposity variation. At this age, as well as at a later age in the finishing period (Le Naou et al., 2012), the activities of enzymes involved in lipogenesis in backfat were not affected by RFI selection. However, it is conceivable that a shift in the balance be-

tween lipogenesis and lipolysis explained difference in body fat development between RFI lines. Importantly, the current study reported greater activities of HAD and CS in backfat of low RFI pigs compared with the high RFI pigs. A proper functioning of mitochondria is essential for ATP synthesis needed for various metabolic pathways in adipocytes, with the induction of lipolysis being notably associated with stimulation of various mitochondrial proteins participating to tricarboxylic acid cycle and FA oxidation (Cho et al., 2009). However, the role of mitochondrial oxidation rate in white adipose tissue has been largely neglected in the literature relative to energy homeostasis. In pigs, Vincent et al. (2012) have reported greater expression of several genes related to mitochondrial energy metabolism in subcutaneous adipose tissue of a lean breed compared with a fat breed. In mice, the levels of approximately half of the gene transcripts encoding mitochondrial proteins in epididymal fat are decreased during the development of obesity (Wilson-Fritch et al., 2004). Finally, induction of mitochondrial oxidative phosphorylation and of (UCP1-independent) beta-oxidation in white adipocytes has been suggested as a key to lean phenotype in both humans and rodents (Flachs et al., 2013 for a review). Altogether, we suggest that oxidative capacity of mitochondria in adipose tissue needs to be reconsidered in future studies on feed efficiency in swine, regarding its potential role in energy homeostasis and body composition. An opposite response of HAD activity to RFI selection was observed in the liver, with the lowest hepatic HAD activity in the low RFI pigs fitting with previous data obtained in a former generation of selection (Le Naou et al., 2012). Similarly, Grubbs and colleagues (2013)

Table 6. Activities of enzymes related to lipogenesis¹ in tissues as influenced by line and diet

Tissue	RFI line ²		Diet		RSD	P-value ³	
	High	Low	HF	LF		Line	Diet
<i>n</i>	24	24	24	24	–	–	–
Backfat							
FASN	77	70	60	88	21	0.243	<0.001
Malic enzyme	1,313	1,200	840	1,671	271	0.153	<0.001
G6PDH	498	518	439	577	87	0.444	<0.001
Perirenal fat							
FASN	104	100	83	121	32	0.629	<0.001
Malic enzyme	1,550	1,534	876	2,209	472	0.906	<0.001
G6PDH	667	740	558	849	161	0.129	<0.001
Muscle							
Malic enzyme	9.9	8.6	8.6	9.9	1.5	0.004	0.003
G6PDH	1.01	0.76	0.79	0.98	0.21	<0.001	0.004
Liver							
FASN	11.3	12.8	9.7	14.3	2.9	0.100	<0.001
Malic enzyme	11.0	9.5	9.7	10.8	3.8	0.188	0.302
G6PDH	50.8	53.2	52.8	51.2	7.8	0.287	0.477

¹Specific activities of the fatty acid synthase (FASN), malic enzyme, and the glucose-6-phosphate dehydrogenase (G6PDH) were expressed as nmol per min and per mg of cytosolic proteins.

²RFI, residual feed intake.

³There was no interaction ($P > 0.10$) between genetic line (low or high RFI) and diet (LF, low fiber, low fat; HF, high fiber, high fat), so that least squares means for the effects of Line and of Diet are shown.

have found lower abundance of HAD and of acyl-CoA dehydrogenase, another enzyme involved in FA oxidation, in isolated liver mitochondria of low vs. high RFI pigs. The RFI selection had also lowered GCK activity, the low affinity hepatic HK; therefore, GCK-to-CS ratio was greater in liver of the low RFI pigs, which means likely that the gluconeogenic pathway has been favored by selection for feed efficiency.

Despite line-associated differences in performance and tissue energy metabolism, feeding a HF diet adversely affected feed intake, growth rate and carcass yield in a similar manner in the two RFI lines when compared with feeding a LF diet. Recently, Montagne et al. (2014) have suggested that the low RFI pigs may have a better ability than the high RFI pigs to cope with a high fiber but low energy diet during a 3-wk interventional period. Nevertheless, the results of the present study comparing the responses to contrasted diets with equal ME content during the whole growing period did not support this idea. The duration of the feeding trial, the type of fibers included in diets, and the level of dietary energy might be involved in these discrepancies. In both lines, the reduction in ADFI observed when feeding the HF diet is likely due to increased physical constraints as illustrated by the greater swelling capacity of this diet compared with the LF diet, which may have resulted in longer time spent eating (Whittemore et al., 2002; De Lange et al., 2006) and early satiety (Kerr and Shurson, 2013). The reduction in carcass yield resulted likely from a greater gut fill and increased development of the digestive tract

in HF-fed pigs, which might be associated with the high fiber content of this diet (Millet et al., 2012). Although extractable fat was included in the HF diet, thus leading to a slightly greater NE content than in the LF diet, this did not prevent the decrease in ADG nor had it benefits on G:F. These data disagree with Myer and Combs (1991), showing that adding fat improves feed efficiency of growing pigs whether diets contain fiber or not. This means that, even if dietary energy concentration is important to consider, the main determinant of growth performance in pigs housed individually is daily ingested energy (Quiniou and Noblet, 2012).

The dietary-associated changes in body adiposity were difficult to predict, due to antagonistic effects of dietary fat level and fiber content on BFT (Yan et al., 2013). Because differences in backfat proportion between HF-fed and LF-fed pigs were significant even when data were corrected for individual differences in ADFI, BW or carcass weight, we suggest that the lower adiposity of pigs fed the HF diet was not simply the consequence of their lower energy intake or their slower growth rate. Rather, the differences in tissue lipid contents were likely associated with reduced lipogenic rates when feeding the HF diet, an assumption that is supported by lower proportions of palmitate (C16:0) and oleate (C18:0) in backfat, the first synthesized FA from carbohydrate sources, and lower specific activities of key lipogenic enzymes. These data are in accordance with the observation that dietary fat inhibits lipogenesis in isolated porcine adipocytes (Benmansour et al.,

Table 7. Activities of oxidative enzymes and glucokinase in tissues as influenced by line and diet¹

Tissue	RFI line ²		Diet		RSD	P-value ³	
	High	Low	HF	LF		Line	Diet
<i>n</i>	24	24	24	24	–	–	–
Backfat							
HAD	0.221	0.259	0.214	0.266	0.06	0.025	0.003
CS	0.252	0.269	0.235	0.286	0.03	0.088	<0.001
LM							
HAD	0.031	0.030	0.030	0.031	0.01	0.846	0.811
CS	0.056	0.060	0.059	0.057	0.02	0.412	0.684
HK	0.876	0.877	0.801	0.952	0.43	0.996	0.233
HK/CS	16.54	15.58	13.08	19.04	9.23	0.721	0.031
Liver							
HAD	0.011	0.010	0.011	0.011	0.001	0.017	0.961
CS	0.092	0.096	0.094	0.095	0.015	0.441	0.750
GCK	19.46	28.75	22.45	25.74	2.37	<0.001	0.041
GCK/CS	213	301	243	270	63	<0.001	0.100

¹Specific activities of the hydroxyl-acyl-CoA dehydrogenase (HAD), citrate synthase (CS), hexokinase (HK), and glucokinase (GCK) expressed as $\mu\text{moles per min and per mg of cytosolic proteins}$.

²RFI, residual feed intake.

³There was no interaction ($P > 0.10$) between genetic line (low or high RFI) and diet (LF, low fiber, low fat; HF, high fiber, high fat), so that least squares means for the effects of Line and of Diet are shown.

1991). In liver, the lower activity of the FASN in HF-fed pigs compared with LF-fed pigs also matches with the recent finding that reduced BFT and reduced hepatic expression of FASN might be associated in pigs (Munoz et al., 2013), so that liver may have an input into lipid metabolism and body composition even in peri-pubertal pigs (Ponsuksili et al., 2007). Conversely, the finding that proportions of C18:2 and C18:3, which are essential PUFA, were dramatically higher in backfat of HF-fed pigs, argues for the direct deposition of a portion of dietary lipids in backfat; however, despite lower oxidation rates of FA in backfat with the HF diet, this was not enough to sustain backfat development to the rate of lipid deposition obtained with the distribution of the LF diet. Because it has been recently shown that dietary fibers attenuate the fat accumulation expected with the distribution of a high fat diet in grower pigs (Yan et al., 2013), one explanation might be that part of ingested lipids in HF-fed pigs, which resulted in greater plasma triglyceride concentrations in HF-fed pigs than in LF-fed pigs, was sequestered elsewhere than in peripheral tissues in those pigs. We have no direct evidence for that, but the greater hepatic lipid content measured for the high RFI line when feeding the HF diet as compared with the LF diet argues for lipid trapping by digestive organs, at least in this line. This fits with the assumption of increased energy needs in HF-fed pigs to sustain a greater development of the digestive tract and a heavier digestive content, and to cope with an increase in populations of cellulolytic and hemicellulolytic bacterial species in the intestine in response to the ingestion of diet high in plant cell wall materials (Varel and Yen, 1997).

The RFI-specificity of this response is likely to be associated with the greater maintenance requirements in the high RFI line (Barea et al., 2010), considering also the fact that both digestive content, gastrointestinal tract and liver weights were heavier in the high RFI pigs than in the low RFI pigs in the present study.

Finally, changing energy source and nutrients in pig diet had also resulted in variations in hepatic glycogen content in both lines. The decreased GCK activity in the liver of pigs fed the HF diet is consistent with the lower hepatic glycogen content reported herein as compared with the LF-fed pigs. Indeed, this enzyme is expressed in tissues such as liver to allow trapping excess of glucose for glycogen synthesis (Printz et al., 1993). Because this enzyme is considered as a glucose sensor in mammals (Matschinsky, 1990), the reduced GCK activity in HF-fed pigs likely results from the lower plasma glucose level observed after the distribution of this low starch diet. Similar changes in GCK activity during the post-prandial period have been observed when other species are fed diets with decreasing carbohydrate contents (Mithieux, 1996; Tranulis et al., 1996). In muscle, the ratio of HK, playing a pivotal role in glucose transport and metabolism by trapping glucose through phosphorylation, to CS, involved in tricarboxylic acid cycle within mitochondria, was lower in pigs fed the HF diet compared with pigs fed the LF diet. This theoretically favors oxidation over glycolysis in the HF-fed pigs, and may indicate a better coordination of cytosolic and oxidative metabolisms (Simoneau and Kelley, 1997) in those pigs. This observed difference in the HK/CS ratio in muscle of HF-fed vs. LF-fed pigs agrees with the observation

that ratio of glycolytic to oxidative enzymes is generally lower in lean than in obese Human subjects (Simoneau and Kelley, 1997).

Conclusions

Irrespective of feed energy sources, feed conversion efficiency, carcass yield, and composition of pigs selected for a low RFI were favorable. Irrespective of the line, feeding a high-fat diet with a high level of coarsely ground fibers reduced feed intake with adverse consequences on growth rate, compared with feeding a LF diet. There was an interaction with genetics for feed efficiency in the partition and use of feed energy and nutrients, so that lipid contents responded in a tissue-specific manner to this diet. Not only the hierarchy in lipid metabolic pathways was affected, but also the glycolytic metabolism was involved in the variations of tissue composition according to dietary energy sources.

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