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Energy utilization in pigs selected for high and low residual feed intake[1]

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ABSTRACT: Genetic selection on residual feed intake (RFI) can be used as an alternative method to G:F to improve feed efficiency in pigs. The objective of this study was to determine the effects of selection for RFI on digestive and metabolic utilization of energy in 2 lines of purebred French Large White castrated male pigs obtained from a divergent selection experiment over 6 generations. The RFI$^+$ (high RFI) line consumed more feed than predicted from performance compared with the RFI$^-$ (low RFI) line. Digestibility of energy and nutrients, total heat production (HP), HP related to physical activity, and energy and N balance were measured in respiration chambers for a 6-d period in pigs offered feed ad libitum. Pigs remained in the chamber for an additional day and did not receive any feed to estimate the fasting HP and calculate the thermic effect of feeding. Five pairs of 2 littermates from the same farrowing batch were used in each line. Because 2 respiration chambers were available for the trial, pigs were measured regularly during the 25- to 95-kg growing period. Two pigs per chamber were used until pigs reached 45 kg of BW, and 1 pig per chamber was used thereafter. Individual feed intake and BW gain were measured continuously from weaning to the end of the trial. Pigs were fed 3 diets with decreasing CP contents during the 25 to 45 (period 1), 45 to 65 (period 2), and 65 to 95 (period 3) kg of BW periods. Average daily feed intake was greater in RFI$^+$ pigs than in RFI$^-$ pigs between 25 and 65 kg of BW (2,128 vs. 1,891 g/d; $P < 0.01$) and G:F was 8% greater in RFI$^-$ pigs compared with RFI$^+$ pigs ($P < 0.01$). There was no line effect on digestibility coefficients or N retention, irrespective of the experimental period studied. Nitrogen retention was 31.2, 28.7, and 20.8 g/d at periods 1, 2, and 3, respectively ($P < 0.001$). The HP was greater in RFI$^+$ pigs than in RFI$^-$ pigs (1,497 vs. 1,383 kJ·kg of BW$^{-0.60}$·d^{-1}; $P < 0.01$), with no subsequent line effect on energy retention. The activity-related HP tended to be greater in RFI$^+$ pigs than in RFI$^-$ pigs (250 vs. 218 kJ·kg of BW$^{-0.60}$·d^{-1}; $P = 0.09$), and the fasting HP was 10% greater ($P = 0.04$) in RFI$^+$ pigs than in RFI$^-$ pigs (846 vs. 771 kJ·kg of BW$^{-0.60}$·d^{-1}). The thermic effect of feeding, expressed as a percentage of ME intake, was the same for both lines of pigs (average, 14.7%). In conclusion, the RFI$^+$ pigs are energetically less efficient because of their greater HP related to physical activity and basal metabolic rate.

Key words: energy utilization, fasting heat production, growing pig, heat production, residual feed intake

INTRODUCTION

Improving feed efficiency is one of the major objectives of current animal breeding to reduce feed costs and enhance the availability of plant resources for other purposes. Estimated during the growing period, the residual feed intake (**RFI**) is defined as the difference between the actual feed intake of an animal and that theoretically required for maintenance and growth (Gilbert et al., 2007). The RFI has been proposed as an alternative to G:F to measure feed efficiency in cattle (Arthur et al., 2001; Nkrumah et al., 2007), laying hens

(Bordas and Mérat, 1981; Luiting and Urff, 1991), pigs (Gilbert et al., 2007; Cai et al., 2008), and fish (Silverstein et al., 2005; Grima et al., 2008).

The variation in RFI reflects differences in digestion processes, metabolic utilization of feed intake, or both in animals of similar BW and production levels (Nguyen et al., 2005). In cattle, RFI has been positively correlated with CH_4 emissions and heat production (**HP**) or retained energy (**RE**), but not with maintenance energy requirements (**ME_m**) or efficiency of utilization of ME for growth (Nkrumah et al., 2006; Castro Bulle et al., 2007). Luiting et al. (1991) suggested that up to 85% of the difference in HP between lines of hens differing in RFI can be related to differences in physical activity. In contrast, data concerning genetic variation in feed digestibility and partitioning of ME related to differences in RFI do not exist for growing pigs.

The purpose of the current study was to estimate the relationship between RFI and digestibility coefficients and energy partitioning (i.e., HP, physical activity, and basal metabolic rate) in growing pigs, using digestibility and balance trials combined with HP measurements in respiration chambers in 2 divergent Large White lines selected for high (**RFI^+**) or low (**RFI^-**) RFI and differing significantly in that trait (Gilbert et al., 2007).

MATERIALS AND METHODS

The study was conducted in accordance with the French legislation on animal experimentation and ethics, and the senior researchers are authorized by the French Ministry of Agriculture to conduct experiments on living animals at the INRA facilities in Saint-Gilles, France.

Animals and Experimental Design

The aim of this study was to investigate to what extent differences in nutrient digestion and energy partitioning contribute to differences in RFI. In this study, 2 lines of purebred French Large White castrated male pigs with differences in RFI but showing similar growth rate and body composition were used. The RFI^+ or RFI^- lines had, respectively, a greater or reduced feed consumption relative to the feed intake predicted from their performance. However, over successive generations, there has been a tendency for greater growth rate and body fatness in the RFI^+ line (Gilbert et al., 2007; Sellier et al., 2010). The experimental animals were obtained from a divergent selection experiment for RFI, which was begun at INRA in 2000. The design of the selection program and the estimates of genetic parameters over the first 4 generations of selection have been described by Gilbert et al. (2007). Animals used in the current study belonged to the sixth generation of selection. In generation 6, the line difference amounted to 2.8 genetic SD units of the selection criteria recorded on selected males (Sellier et al., 2010).

At weaning (i.e., at approximately 4 wk of age), castrated male piglets were transported from the selection herd (INRA-Génétique et Expérimentation en Productions Animales, Le Magneraud, France) to the laboratory in Saint-Gilles (INRA, France) for balance tests, which consisted of 6-d trials, during which the N, energy (through indirect calorimetry), and P balances were determined in pigs offered feed ad libitum. These balance tests were followed by 1 fasting day to estimate the fasting HP (**FHP**). In each line, experimental animals consisted of 5 pairs of 2 littermates from 5 sows sired by 4 or 5 different boars. A total of 20 animals were therefore used in the trial, and trials began at an initial BW of approximately 25 kg. Because only 2 large respiration chambers were available, 2 balance tests were performed each week, using 2 littermate pigs per chamber, until the pigs weighed 40 to 45 kg, after which 1 pig per chamber was used for heavier pigs. The total experimental period was divided in 3 periods (**P1**: 25 to 45 kg of BW; **P2**: 45 to 65 kg of BW; and **P3**: 65 to 95 kg of BW). Because of a decrease in AA requirements relative to BW, the CP content was decreased over successive periods. In practice, 4 pairs of pigs were tested at each period, whereas pigs in the last pair were considered as possible substitutes. Similarly, after 40 to 45 kg of BW, the remaining pig within each pair was considered a possible substitute. In addition, 1 pair of pigs measured at P2 was not systematically measured at P3. Therefore, the overall design could not be considered a repeated measures design.

Genetic values of the 20 pigs used in the balance trials were estimated based on individual feed intake of 1,065 controlled pigs of generations 0 to 6, using the REML methodology (Patterson and Thompson, 1971) applied to a multitrait individual animal model (Gilbert et al., 2007). Average differences in genetic values for pigs sampled for the present study from the RFI^+ line and the RFI^- line were very close to those estimated for the contemporary group of generation 6 for growth and feed intake traits (Sellier et al., 2010). The differences were 21.1 points for the selection index (compared with 21.0 points for the contemporary group), 229 g for ADFI (compared with 225 g), 14 g for ADG (compared with 19 g), and 0.27 for G:F (compared with 0.23).

Housing and Feeding

Pigs were offered commercial weaner and starter diets ad libitum until reaching 25 kg of BW. The starter diet was then progressively replaced (over 3 d) by the diet used in P1. All diets were formulated on an as-fed basis and were based on a corn, wheat, and barley mixture and soybean meal (Table 1). The supply of AA met or exceeded the current French recommendations, expressed on a standardized ileal digestible AA basis (Henry, 1993; Sève and Le Floc'h, 1998). Other nutrients and energy content were formulated to meet or exceed the requirements of pigs for the experimental

periods studied. During the energy balance measurements, feed and water were offered ad libitum. To control the variation in feed intake between littermates, pigs within a litter were offered the same quantity of feed, which was slightly below their ad libitum intake capacity, between the balance trial periods. During the experiment, pigs were housed in pens (with 2 pigs per pen) until reaching 30 to 35 kg of BW and were housed in individual metabolism cages thereafter. During the balance trials, pigs were housed in one of the two 12-m^3 open-circuit respiration chambers based on a design similar to that used by Vermorel et al. (1973). In the respiration chamber, animals remained in their pens or metabolism cages, which were mounted on force sensors (Type 910A, Kistler, Winterthur, Switzerland). These sensors produce an electrical signal to measure the physical activity of the pigs. In each respiration chamber, feeders were placed on a load cell to continuously measure feed intake and traits of feeding behavior (i.e., time, size, and duration of each meal) through changes in trough weights (van Milgen et al., 1997). Only results for total daily feed intake are presented. The respiration chambers were climate controlled to maintain a constant temperature and relative humidity (24°C and 70%, respectively) during the balance trials. A 12-h lighting time span (from 0800 to 2000 h) was used.

Measurements

Pigs were weighed after an overnight fast at the beginning and at the end of P1, P2, and P3 to determine their ADG. Feed intake was measured each week, taking into account possible feed refusals or spillage. During the balance trials, pigs were weighed when they were moved into the respiration chamber before the morning meal and on the mornings before and after the fasting day. Feed refusals (if any) were collected daily, weighed, and then subjected to DM determination. Feed samples were taken at the time of diet preparation and were pooled for each balance trial for immediate DM determination and further analyses.

Feces and urine (the latter in a container with H_2SO_4) were collected separately each day per pig (or per 2 pigs in P1) during the 6-d period and stored at 2°C. Subsequently, pooled fecal and urine samples (d 1 to 6 per pig or groups of 2 pigs in P1) were weighed, mixed, subsampled, and freeze-dried for chemical analyses. A second sample of homogenized feces was obtained to estimate the DM content by desiccation at 103°C for 48 h.

In the respiration chamber, gas concentrations (i.e., CO_2, O_2, and CH_4) of outgoing air and the ventilation rate were measured continuously according to the methods described by van Milgen et al. (1997). The O_2 concentration was measured with a paramagnetic differential analyzer (Oxymat 6, Siemens AG, Munich, Germany), whereas infrared analyzers were used to measure the concentrations of CO_2 (Ultramat 6, Siemens

AG or Unor 600, Maihak AG, Hamburg, Germany) and CH_4 (Unor 6N, Maihak AG). Because only 1 CH_4 analyzer was available for the 2 respiration chambers, the CH_4 concentration was measured using an alternating scheme of 3 d of measurement per chamber. Gas extraction rate was measured by a mass gas flow meter (Hasting Teledyne Brown Engineering, Hampton, VA). Gas concentrations, the signals of the force sensors, the weight of pig feeders, gas flow rate, and physical conditions in the chamber (i.e., temperature, humidity, and barometric pressure) were measured 60 times/s, averaged over 10-s intervals, and averages were recorded for further calculations. Ammonia losses recovered in condensed water and outgoing air were collected according to the methods described by Noblet et al. (1987).

Chemical Analyses

The DM content of representative feed samples, feces, and feed refusals was determined according to AOAC (1990) methods. Samples of feed, feces, urine (as fresh material), condensed water, and extracted air were analyzed for N according to the Dumas procedure (Leco 3000, Leco Corporation, St. Joseph, MI). In addition, ash, P (spectrophotometric method: ashing at 550°C and dissolving in 16 N HNO_3), and GE (IKA C5000, IKA, Staufen, Germany) contents in feces and feed samples were determined. For urine, the GE content was determined after freeze-drying approximately 30 mL of urine in polyethylene bags. The P content of urine was also determined. Finally, feed samples were analyzed for ether extract (Soxtec Avanti 2050; Foss, Höganäs, Sweden), starch (the Ewers polarimetric method; European Economic Community, 1972), Weende crude fiber, NDF, ADF (Ankom 2000 Fiber Analyzer, Ankom Technology, Macedon, NY), and ADL (Van Soest and Wine, 1967).

Calculations

For calculations, all data were expressed per pig and per day, even in the early periods with 2 pigs per respiration chamber (i.e., average of the 2 pigs). For the periods during which pigs were housed in pairs (i.e., until reaching 40 to 45 kg of BW), the individual feed intake for calculating the growth performance over P1 and the total trial was estimated by dividing ADG of each pig by the G:F measured in the 2 pigs. Nitrogen retention (**NR**) was calculated as the difference between N intake and N losses in feces, urine, condensed water, and extracted air. The P retention was calculated as the difference between P intake and P losses in feces and urine. The DE and ME values of the diet were calculated according to the methods described by Noblet et al. (1987). The CH_4 production, expressed as a percentage of DE intake over a part of the balance period, was small and rather variable between successive days for a given animal and between animals. Therefore, in the calculation of ME, the overall mean

Table 1. Ingredients and chemical composition of the diets (as-fed basis)

Item	Experimental period[1]		
	P1	P2	P3
Ingredient, %			
Corn	23.48	25.39	30.15
Wheat	23.00	23.00	22.40
Barley	23.00	23.00	21.60
Soybean meal	21.70	18.70	16.30
Sunflower oil	0.50	0.00	0.00
Molasses	2.00	2.00	2.00
Wheat bran	3.00	5.00	5.00
Dicalcium phosphate	1.30	1.10	0.90
Calcium carbonate	0.80	0.70	0.60
Salt	0.40	0.40	0.40
L-Lysine·HCl	0.220	0.180	0.140
DL-Methionine	0.040	0.000	0.000
L-Threonine	0.060	0.030	0.010
l-Tryptophan	0.005	0.000	0.000
Vitamin-mineral premix[2]	0.500	0.500	0.500
Analyzed chemical composition,[3] %			
CP	17.7	16.1	15.7
Ash	5.22	4.83	4.54
Ether extract	2.4	1.8	2.2
GE, kJ/g	16.03	15.97	16.06
Crude fiber	3.2	3.3	3.3
NDF	12.3	11.8	11.9
ADF	4.1	3.9	4.4
ADL	0.23	0.19	0.63
Starch	42.1	44.3	45.2
Ca	0.92	0.82	0.72
P	0.66	0.63	0.57
Nutritional value,[3]			
ME,[4] kJ/g	12.79	12.64	12.71
NE,[4] kJ/g	9.48	9.41	9.54
Digestible AA[5]			
Lys, %	0.90	0.81	0.72
Met + Cys, %	0.56	0.50	0.48
Thr, %	0.59	0.52	0.47
Trp, %	0.18	0.17	0.15
(Met + Cys):Lys	62	62	67
Thr:Lys	65	65	66
Trp:Lys	20	21	21

[1]P1 = 25 to 45 kg of BW; P2 = 45 to 65 kg of BW; P3 = 65 to 95 kg of BW.

[2]Supplied per kilogram (as-fed basis) of diet: vitamin A, 5,000 IU; vitamin D_3, 1,000 IU; vitamin E, 20 IU; menadione, 2 mg; thiamine, 2 mg; riboflavin, 4 mg; niacin, 15 mg; pantothenic acid, 10 mg; pyridoxine, 1 mg; biotin, 0.2 mg; folic acid, 1 mg; cyanocobalamin, 0.02 mg; choline chloride, 500 mg; Fe, 80 mg as ferrous carbonate; Cu, 10 mg as copper sulfate; Zn, 100 mg as zinc oxide; Mn, 37 mg as manganous oxide; I, 0.2 mg as calcium iodate; Se, 0.2 mg as sodium selenite; and Co, 0.1 mg as cobalt sulfate.

[3]Adjusted for 87.3% of DM.

[4]Values for ME and NE were calculated according to the method of Sauvant et al. (2004).

[5]Standardized ileal digestible AA, calculated from the digestibility of feed ingredients (Sauvant et al., 2004).

of methane energy loss during the trial was used for all animals. The first day in the respiration chamber was considered an adaptation day and was not included in the final calculations. Total HP was calculated from O_2 consumption and CO_2 production according to the equation of Brouwer (1965), which included average CH_4 production and urinary N excretion. Energy retention was calculated as the difference between ME intake and HP over the measurement period. Assuming an energy value of protein gain of 23.6 kJ/g, energy retained as protein (**RE_p**) was calculated from the N balance. Energy retained as fat (**RE_f**) was calculated

as the difference between total RE and RE_p. The RQ corresponds to the ratio between CO_2 production and O_2 consumption.

Simultaneous measurements of O_2 and CO_2 concentrations, physical activity (i.e., the signal of force sensors), and feeding behavior (i.e., the signal of load cells) in the respiration chamber, and physical characteristics of gas exchanges in the chamber were used as inputs to calculate the components of HP according to the modeling approach described by van Milgen et al. (1997). Briefly, the variations in O_2 and CO_2 concentrations in the chamber were related to O_2 consumption and CO_2

production by the pig. Actually, during periods when the pigs were fed, the model provided estimates of gas exchanges attributable to resting state, physical activity, and short-term thermic effect of feeding (**TEF**). During the fasting day, it provides estimates of gas exchanges attributable to fasting and physical activity during fasting. The ACSL/Optimize program (AEgis Simulation, AEgis Technologies, Huntsville, AL) was used to obtain estimates of model parameters describing gas exchanges. Components of total HP related to physical activity (**AHP**), feed intake (short-term TEF), and resting metabolism (resting HP) were calculated from these model parameters using only the estimated O_2 consumption and CO_2 production (Brouwer, 1965). The FHP was obtained from gas exchanges measured during the fasting day. The difference between resting HP and FHP was considered to correspond to the long-term TEF, whereas the sum of the long-term TEF and short-term TEF corresponded to the total TEF. All energy traits were calculated on a daily basis and further expressed relative to $BW^{0.60}$ (Noblet et al., 1999).

Statistical Analyses

Data were subjected to ANOVA using the GLM procedure (SAS Inst. Inc., Cary, NC), and the individual pig (or the pair of pigs in P1) was used as the experimental unit for all data. The effects included in the ANOVA model were line, growing period, and their interaction. Least squares means for the effects were computed (LSMEANS statement in the GLM procedure) and the differences between the effects of levels were tested with a Student t-test (PDIFF option in the LSMEANS statement). The performance and energy balance results were also analyzed by covariance to refine the analysis of the overall treatment difference. The initial BW (i.e., BW at the beginning of the period) and ADG over the period were then included as covariates for data on, for instance, feed intake. Adjustment for a similar energy intake or RE as a covariate was also included in the energy balance data. The ME_m was estimated according to the model proposed by Kielanowski (1965): $ME = ME_m + RE_p/k_p + RE_f/k_f$. In this model, we assumed that the ME_m requirement varied with BW (i.e., $ME_m = a_iBW^{0.60}$), assuming a potentially different a_i for each line of pigs; the values of k_p and k_f are supposed to be identical for both lines. This model allows the estimation of the partial efficiencies of using ME for protein and fat deposition (i.e., k_p and k_f, respectively) and the effect of line on ME_m (i.e., a_i). Differences were considered significant at $P < 0.05$.

RESULTS

Throughout the experiment, pigs appeared to be healthy. However, we observed that feed intake ceased to increase as pigs reached 70 to 80 kg of BW and that feed intake was even reduced in some pigs. These reductions were often associated with appearance of leg problems, probably related to the prolonged stay in metabolism cages, which limited their physical activity. For this reason, 4 pigs (2 in each line) were removed from the study after 70 kg of BW and the others were progressively removed after being measured for the P3 stage. Growth performance data were thus available for all the animals up to approximately 70 kg of BW. Table 2 shows growth performance data for the immediate postweaning period (from 8.5 to 24.3 kg of BW) and the growing period (from 24.3 to 67.7 kg of BW). During the immediate postweaning period, growth performance was affected by the line of pigs, with a greater ADFI (692 vs. 529 g/d; $P < 0.01$) and a greater ADG (452 vs. 366 g/d; $P = 0.01$) in RFI^+ pigs. As expected, the G:F was less in the RFI^+ line. During the growing period, ADFI was also greater and G:F was less in RFI^+ pigs than in RFI^- pigs ($P < 0.01$). In contrast, ADG was not affected by the pig line. Because of the reduced ADG during the immediate postweaning period, RFI^- pigs were lighter at the beginning of the growing period. Adjustment of ADFI and G:F for initial BW emphasizes the reduced feed efficiency of the RFI^+ pigs ($P = 0.04$).

Table 3 shows the results of the balance trials and the effect of the pig line and growth period on nutrient and energy digestibility and on N and P balances. There was no interaction between line and growth period for any trait. Both ADFI and ADG tended to be greater in RFI^+ pigs than in RFI^- pigs during the balance periods (184 g/d for ADFI and 159 g/d for ADG; $P \leq 0.10$). As expected, ADFI increased with increasing BW (1,752 to 2,456 g/d from P1 to P3, respectively; $P < 0.001$), but the increase between P2 and P3 was negligible. Digestibility coefficients of nutrients or energy were not affected by the pig line. Smaller digestibility coefficients for DM ($P < 0.05$), ash ($P < 0.001$), and P ($P < 0.01$) were observed in P3 (86.2, 52.4, and 50.1%, respectively) compared with the other 2 periods (averaging 87.2, 61.0, and 60.8%, respectively). The digestibility coefficient of N was greater in P2 than in P1 ($P < 0.05$) and was intermediary in P3. The digestibility coefficient of energy was not affected by line or growth period. The differences in digestibility coefficients between the periods must be interpreted with caution because diets were slightly different, with less CP and more starch in diets fed to the heavier pigs. Similarly to the digestibility coefficients, the energy utilization of DE (expressed as ME:DE) and energy values of the diets (ME and NE in MJ/kg of DM) were affected by the period, but not by the pig line. In agreement with the ADG, the N balance results confirmed the reduction ($P < 0.001$) in NR in P3 (20.8 g/d) compared with those in P1 (31.2 g/d) and P2 (28.7 g/d). The NR did not differ between the pig lines. Unlike the NR, the P retention was less in P1 and P3 (5.5 and 5.2 g/d, respectively) compared with P2 (7.1 g/d). In addition, P retention was greater in RFI^+ pigs than in RFI^- pigs (6.2 vs. 5.6 g/d; $P < 0.05$), but, when expressed per kilogram of BW gain, it was not different between lines ($P = 0.44$).

Table 2. Effects of line on growth performance of pigs during the immediate postweaning (1- to 6-wk) and growing (6- to 12-wk) periods (least squares means; 4 observations per line and per period)

	Line[1]			
Item	RFI[+]	RFI[−]	RSD[2]	P-value[3]
Immediate postweaning period				
Initial BW, kg	8.81	8.17	1.17	0.24
Final BW, kg	26.3	22.4	2.6	<0.01
Duration, d	38.8	39.0	0.3	0.15
ADFI,[4] g/d	692	529	101	<0.01
ADG, g/d	452	366	69	0.01
G:F[4]	0.654	0.689	0.026	<0.01
Growing period[5]				
Initial BW, kg	26.3	22.4	2.6	<0.01
Final BW, kg	70.5	64.9	4.0	<0.01
Duration, d	47.9	47.9	—	—
ADFI,[4] g/d	2,128	1,891	134	<0.01
Adjusted ADFI,[4,6] g/d	2,060	1,960	75	0.03
ADG, g/d	923	888	56	0.18
G:F[4]	0.435	0.469	0.020	<0.001
Adjusted G:F[4,6]	0.441	0.463	0.017	0.04

[1]RFI[+] = high residual feed intake; RFI[−] = low residual feed intake.

[2]RSD = residual SD (18 df), which is the root mean square of the error that applies to the whole model.

[3]Effect of line.

[4]Adjusted for 87.3% of DM.

[5]Approximately from 25 to 70 kg of BW because of reduced feed intake and the appearance of leg problems in some pigs at BW greater than 70 kg.

[6]Adjusted least squares means, with ADG during the growing period and BW at the beginning of the growing period as covariates.

Energy balance data according to pig line and growing period are presented in Table 4. No line × period interaction was observed for any of the traits. The ME intake (kJ·kg of $BW^{-0.60}·d^{-1}$) tended to be greater in RFI[+] pigs than in RFI[−] pigs. When adjusted for a similar RE, ME intake was greater in RFI[+] pigs (84 kJ·kg of $BW^{-0.60}·d^{-1}$). Consequently, RFI[−] pigs produced 8% less HP than RFI[+] pigs. This reduction was mainly related to a 10% reduction in FHP (771 vs. 846 kJ·kg of $BW^{-0.60}·d^{-1}$; $P = 0.04$) and a tendency for a reduced AHP (−15% in the RFI[−] line; $P = 0.09$). Adjustment of HP or FHP to a constant RE confirmed these observations. The RE and its partitioning between protein and fat were not affected by the pig line. The RQ values were similar for both lines. In agreement with differences in HP between the lines, the CO_2 production was greater in RFI[+] pigs than in RFI[−] pigs. Finally, the overall efficiency of ME utilization [100 − (TEF + AHP)/ME intake] was the same in the 2 lines.

Expressed per unit of metabolic BW, ME intake in P3 was less than in P1 and P2 (−30%; Table 4). Consequently, RE and HP were 45 and 20% less in P3 than in the other 2 periods. Neither AHP nor TEF was affected by the experimental period. The decreased ME intake in P3 was associated with decreased RE, both as fat and as protein, because the RE_p decreased progressively over successive periods ($P < 0.001$), whereas the RE_f increased, but only between P1 and P2. The RQ increased between P1 and P2 in connection with the increased fat retention, and it decreased between

P2 and P3 in connection with the reduced ME intake. Adjustment of the CO_2 production for a constant RE confirmed the decreased ME intake, and thus RE, during P3. Because ME intake was less during P3, both AHP and TEF, expressed as a percentage of ME intake, were greater during P3. As a consequence of these changes in the components of HP and the utilization of ME between periods, the efficiency of ME for NE was the least ($P < 0.001$) in P3.

Estimates of the ME_m according to the approach of Kielanowski (1965) were 841 and 920 kJ·kg of $BW^{-0.60}·d^{-1}$ for RFI[−] and RFI[+] pigs, respectively ($P = 0.02$), and the average values for k_p and k_f were 0.60 (1/1.68) and 0.75 (1/1.33), respectively (equations not shown). These ME_m values are less than those calculated as FHP/k (where **k** is the NE:ME ratio; 1,104 and 1008 kJ·kg of $BW^{-0.60}·d^{-1}$, for RFI[+] and RFI[−], respectively; Table 4).

DISCUSSION

The present study is part of a larger project to establish new selection criteria and strategies for the sustainable development of pig production. The concept of RFI was first proposed by Koch et al. (1963) in beef cattle. It represents the feed intake in excess of that required for average growth and maintenance requirements (Foster et al., 1983). There are some reports that selection for decreased RFI improves G:F but with a

Table 3. Effects of line and experimental period on the nutrient and energy digestion, and N and P balance in pigs (least squares means; 4 observations per line and per period)

Item	Line[1]		Experimental period[2]			RSD[3]	P-value[4]	
	RFI[+]	RFI[-]	P1	P2	P3		Line	Period
BW,[5] kg	59.9	59.7	32.3[a]	59.1[b]	88.0[c]	6.7	0.93	<0.001
ADFI,[6] g/d	2,309	2,125	1,752[a]	2,443[b]	2,456[b]	270	0.10	<0.001
ADG, g/d	1,029	870	1,013[b]	1,058[b]	777[a]	225	0.09	0.03
Digestibility coefficient, %								
DM	86.9	86.8	87.3[b]	87.1[b]	86.2[a]	0.9	0.76	0.04
OM	88.5	88.5	88.7	88.9	88.0	0.9	0.96	0.12
Ash	59.3	57.0	65.1[c]	56.9[b]	52.4[a]	2.8	0.05	<0.001
N	84.6	85.2	83.6[a]	86.5[b]	84.6[ab]	2.0	0.44	0.03
Energy	86.7	86.8	86.9	87.3	86.1	1.0	0.91	0.06
P	58.1	56.3	64.3[b]	57.3[b]	50.1[a]	7.2	0.54	<0.01
Methane energy,[7] % of DE	0.40	0.40	0.40	0.40	0.40	—	—	—
Energy utilization								
ME, % of DE	96.1	96.3	96.7[c]	96.0[b]	95.7[a]	0.2	0.09	<0.001
Energy values, MJ/kg of DM								
DE	15.94	15.94	16.02	15.96	15.84	0.18	0.93	0.11
ME	15.31	15.34	15.49[b]	15.33[b]	15.16[a]	0.17	0.59	<0.01
NE[8]	11.69	11.69	12.13[b]	11.91[b]	11.03[a]	0.47	0.97	<0.001
N balance, g/d								
Intake	61.2	56.4	51.8[a]	63.0[b]	61.6[b]	6.7	0.09	<0.01
Absorbed	51.8	48.1	43.3[a]	54.5[b]	52.1[b]	5.7	0.11	<0.01
Retained	28.0	25.9	31.2[b]	28.7[b]	20.8[a]	3.3	0.11	<0.001
P balance, g/d								
Intake	11.85	10.89	8.97[a]	13.12[b]	12.03[b]	1.35	0.08	<0.001
Excreted								
Feces	5.09	4.85	3.29[a]	5.61[b]	6.02[b]	1.12	0.58	<0.001
Urine	0.53	0.41	0.15[a]	0.43[b]	0.85[c]	0.22	0.16	<0.001
Retained	6.23	5.62	5.53[a]	7.08[b]	5.16[a]	0.71	0.04	<0.001
Retained P:BW gained, g/kg	6.36	7.07	5.49	6.93	7.73	2.30	0.44	0.14

[a–c]Within a row, period means without a common superscript differ ($P < 0.05$).

[1]RFI[+] = high residual feed intake; RFI[-] = low residual feed intake.

[2]P1 = 25 to 45 kg of BW; P2 = 45 to 65 kg of BW; P3 = 65 to 95 kg of BW.

[3]RSD = residual SD (25 df), which is the root mean square of the error that applies to the whole model.

[4]Effects of line or period. The line × period interaction was not significant for any trait.

[5]BW in the middle of the balance period.

[6]Adjusted for 87.3% DM.

[7]The average methane energy loss (% of DE intake) was used in calculations of ME for all pigs; statistical analysis was not possible.

[8]Calculated as the sum of fasting heat production and retained energy (Noblet et al., 1994); the latter is obtained as the difference between ME and total heat production.

negative correlated effect on growth rate, as described in beef cattle by Hoque et al. (2009). Growth performance data over the growing-finishing period in the current experiment, even though obtained for a small number of animals, confirm those obtained in the selection herd over the successive generations (Gilbert et al., 2007; Sellier et al., 2010) and indicate that selection for decreased RFI can reduce ADFI and improve G:F without adversely affecting the ADG. However, the specific response over the postweaning period with a greater ADG in RFI[+] pigs should be confirmed with a large number of animals. This will be studied with the data collected in the larger selection experiment that is currently underway. Preliminary calculations on the data collected in the selection farm on the siblings of the pigs used in the present trial and on all the available measurements up to the sixth generation confirm the statistically significant difference between the 2 lines in growth over the postweaning period and BW at the end

of the postweaning period. However, these differences between the 2 lines are approximately one-third of the differences observed in the present trial. This indicates that pigs sampled for the present study would represent extreme differences between the lines in terms of early growth. In any case, these divergent responses among trials for response to selection on RFI are not surprising because the consequences of selection for a feed efficiency trait (e.g., better G:F) on the growth traits (e.g., BW at a given age or ADG) are variable among species, experiments, or response criteria used in the selection program, or all three (Arthur et al., 2001).

Variations in RFI indicate differences in nutrients and energy digestibility, metabolic efficiency of nutrient use, basal metabolic rate and energy expenditure, or all these (Labroue et al., 1999). Digestion of nutrients and energy can be an important source of variation in RFI in ruminants (Richardson and Herd, 2004; Herd and Arthur, 2009), but this seems to be less in laying hens

Table 4. Effects of line and experimental period on heat production (HP) and energy balance in pigs (least squares means; 4 observations per line and per period)

Item	Line[1]		Experimental period[2]			RSD[3]	P-value[4]	
	RFI$^+$	RFI$^-$	P1	P2	P3		Line	Period
BW,[5] kg	60.4	60.0	32.6^a	59.7^b	88.4^c	6.6	0.88	<0.001
Energy balance, kJ·kg of BW$^{-0.60}$·d^{-1}								
ME intake	2,793	2,604	2,984^b	2,877^b	2,235^a	267	0.09	<0.001
HP	1,497	1,383	1,559^b	1,488^b	1,273^a	100	<0.01	<0.001
Adjusted ME intake[6]	2,709	2,625	2,723	2,666	2,611	74	0.01	0.11
Adjusted HP[6]	1,473	1,390	1,488	1,431	1,376	74	0.01	0.11
Retained energy								
As protein	404	382	588^c	379^b	213^a	50	0.29	<0.001
As fat	893	838	837^{ba}	1,010^b	749^a	170	0.43	0.01
Total	1,296	1,221	1,425^b	1,389^b	962^a	187	0.32	<0.001
RQ[7] components of HP, kJ·kg of BW$^{-0.60}$·d^{-1}	1.14	1.14	1.12^a	1.16^b	1.14^{ab}	0.03	0.73	0.02
FHP[7]	846	771	911^b	846^b	669^a	88	0.04	<0.001
Adjusted FHP[6,7]	840	773	892^a	830^a	697^b	84	0.06	0.02
AHP[7]	250	218	227	245	230	46	0.09	0.70
TEF[7]	392	390	409	392	373	74	0.94	0.60
CO$_2$ production,[8] L·kg of BW$^{-0.60}$·d^{-1}								
Measured V$_{CO2}$[7]	78.5	72.7	80.6^b	79.3^b	66.9^a	5.6	0.01	<0.001
Adjusted V$_{CO2}$[6,7]	77.0	73.1	76.0	75.6	73.6	3.6	0.01	0.63
Estimated ME$_m$[9]	1,104	1,008	1,163^b	1,087^b	917^a	91	0.02	<0.001
ME utilization, % of ME								
NE	76.3	76.2	78.3^b	77.7^b	72.7^a	2.6	0.90	<0.001
TEF[7]	14.3	15.2	13.7^a	13.6^a	16.8^b	2.5	0.38	0.02
Short-term TEF[7]	7.6	8.2	6.6^a	8.7^b	8.4^b	1.3	0.33	<0.01
Activity	9.2	8.5	7.6^a	8.5^a	10.4^b	1.9	0.38	0.01

$^{a-c}$Within a row, period means without a common superscript differ ($P < 0.05$).

[1]RFI$^+$ = high residual feed intake; RFI$^-$ = low residual feed intake.

[2]P1 = 25 to 45 kg of BW; P2 = 45 to 65 kg of BW; P3 = 65 to 95 kg of BW.

[3]RSD = residual SD (25 df), which is the root mean square of the error that applies to the whole model.

[4]Effects of line or period. The line × period interaction was not significant for any trait.

[5]Mean BW in the middle of the period inside the respiration chamber.

[6]Corrected least squares means with retained energy (kJ·kg of BW$^{-0.60}$·d^{-1}) as a covariate; the effect of pig line on the slope of adjustment was not significant.

[7]RQ = (CO$_2$/O$_2$); FHP = fasting HP; AHP = activity HP; TEF = thermic effect of feeding; V$_{CO2}$ = volume of CO$_2$.

[8]V$_{CO2}$ produced in the fed state.

[9]ME$_m$ = maintenance energy requirements (kJ·kg of BW$^{-0.60}$·d^{-1}). Calculated as FHP/k (k was estimated as NE:ME).

and broilers (Luiting et al., 1994; Carré et al., 2008) and in pigs (de Haer et al., 1993; present study). Differences in metabolism are assumed to be the major factor contributing to differences in feed efficiency. Gabarrou et al. (2000) found that selected cockerels with a reduced RFI showed a reduced plasma triiodothyronine concentration as plasma insulin concentrations increased in an insulin tolerance test. These animals behaved as hypothyroidic when compared with nonselected animals, which can be related to the decreased lean BW gain and diet-induced thermogenesis observed in these cockerels. In energy balance trials (involving indirect calorimetry and activity measurements), Luiting et al. (1991) observed a greater HP in laying hens selected to represent an increased RFI, which is in agreement with results of the present study. These authors suggested that changes in the basal metabolic rate, physical activity, and diet-induced thermogenesis may have contributed to the differences in HP. The modeling method that was used in the present experiment to partition total HP indicates that FHP and AHP were, or tended to be, greater in RFI$^+$ pigs than in RFI$^-$ pigs. The

estimation of FHP can be influenced by the length of the fasting period (van Milgen and Noblet, 2003), the pig genotype (van Milgen et al., 1998), or the preceding feeding amount (de Lange et al., 2006). Thus, correcting FHP for a similar ME intake or a constant energy gain increased the statistical precision in determining differences in this trait. The differences observed in FHP and AHP are in agreement with some of the suggestions made by Luiting et al. (1991), who concluded that variation in both activity-related HP and basal metabolic rate explained the variations in total HP. According to de Haer et al. (1993), eating activity may influence, to a larger extent, the variations in HP. These authors found that pigs with decreased RFI had reduced feed intake activity (i.e., fewer daily meals and less time eating) than RFI$^+$ pigs. In a recent study of feeding behavior under conventional housing conditions in pigs from the same selection program as in the present study (Gilbert et al., 2009), the RFI$^-$ pigs had fewer meals and spent less time eating per day, confirming the present results obtained in respiration chambers. Similar to our study, reduced physical activity related

to reduced RFI was described by McPhee et al. (2001) in sows and by Lepron et al. (2007) in growing pigs. In both cases, the RFI$^-$ pigs were less active and had fewer changes in posture than the RFI$^+$ pigs. Finally, it is important to point out that our activity measurements were obtained under specific housing conditions (i.e., metabolism crates). Measurements of activity under conventional housing conditions would be necessary to confirm the results of the current study.

Variation in HP related to an increased TEF between animals differing in RFI has been reported in poultry (Gabarrou et al., 1997). These authors suggested that chickens selected for decreased RFI had less TEF than control line chickens. In ruminants, O_2 consumption by the portal-drained viscera (i.e., gastrointestinal tract, pancreas, and spleen) has been positively related to feed intake (Ortigues and Doreau, 1995). In growing pigs, the portal-drained visceral organs account for only 5% of BW but up to 20% of total O_2 consumption (Yen et al., 1989). Moreover, van Milgen et al. (1998) found that the contribution of viscera (i.e., gastrointestinal tract, liver, pancreas, spleen, kidneys, heart, lungs, bladder, and reproductive organs) to FHP was more than 4 times greater than in lean tissue of growing pigs. It is then possible that selection for decreased RFI and reduced feed intake may decrease the O_2 consumption of these organs.

The genetic selection for decreased RFI has been associated with a decreased ME_m in beef cattle (Herd and Bishop, 2000) and laying hens (Luiting et al., 1991). In contrast, Castro Bulle et al. (2007) did not find differences in ME_m between lines of beef cattle selected for different RFI. Although little information is available in the literature for growing pigs, our results indicate greater ME_m values in RFI$^+$ pigs, estimated either from the model of Kielanowski (1965) or as FHP/k. The approach of Kielanowski (1965) results in a reduced estimate of ME_m (841 and 920 kJ·kg of $BW^{-0.60}·d^{-1}$ for RFI$^-$ and RFI$^+$, respectively) compared with the estimation through FHP/k (1,008 and 1,104 kJ·kg of $BW^{-0.60}·d^{-1}$ for RFI$^-$ and RFI$^+$, respectively). That difference may be due to the decreased FHP observed in the last experimental period studied [e.g., the model of Kielanowski (1965) assumes a constant ME_m, and thus FHP, for the whole experimental period]. The ME_m values from the second model used (i.e., FHP/k) are in close agreement with those found in the literature for pigs of different genetic types and sexes (936 to 1,122 kJ·kg of $BW^{-0.60}·d^{-1}$; Noblet et al., 1999). Preferred estimates for k_p and k_f values proposed by Noblet et al. (1999) were 0.60 and 0.80 for k_p and k_f, respectively. The efficiencies in the present experiment (0.60 and 0.75) are in agreement with those reported by the NRC (1998). Even if our estimates of k_p and k_f in the present trial are associated with an apparently smaller ME_m estimation, they are in good agreement with the ranges cited before and they illustrate the multicolinearity of coefficients for protein and lipid retention and ME_m (Noblet et al., 1999).

The classical estimation of HP proposed by Brouwer (1965) was further developed by the modeling approach of van Milgen et al. (1997), which allows calculation of the different components of HP. Little information is available in the literature concerning the components of energy expenditure or HP in growing pigs, and most of these studies have been carried out in our laboratory (van Milgen et al., 2001; Noblet et al., 2003; Lovatto et al., 2006). Measured values for FHP typically range from 700 to 800 kJ·kg of $BW^{-0.60}·d^{-1}$, which is consistent with our results (from 669 to 911 kJ·kg of $BW^{-0.60}·d^{-1}$ for average values per line or per period). The average value of the cost of the physical activity observed in the current study (8.7% of ME) is in close agreement with values reported in the literature (i.e., 7.1 to 9.4% of ME; van Milgen et al., 2001; Noblet et al., 2003; Lovatto et al., 2006). Finally, our estimate of approximately 76% for the efficiency of ME utilization (NE:ME) is consistent with the value of 75% reported in the literature (Noblet et al., 1994, 2001; Le Bellego et al., 2001). In contrast, the differences observed in the present experiment for this variable in both growth periods and lines may be related to different distributions of TEF and activity during the day, and thus to variation in the dynamics of HP.

In the present study, important physiological processes (e.g., feed intake, HP and its partitioning, and ME_m) have been studied and discussed in relation to RFI. However, little information is available in the literature on the relationship between these traits and specific biological pathways (Herd and Arthur, 2009). In recent years, some biochemical, molecular, and genomic studies have been developed to understand the mechanisms contributing to the basis for variation in RFI in beef cattle or poultry (Hill and Azain, 2009). The energy production (i.e., ATP) in mitochondria has an essential role in whole-body metabolic processes. Thus, it is expected that an altered mitochondrial function may modify the feed efficiency. Differences in mitochondrial membrane potential in poultry (Ojano-Dirain et al., 2007) or in mitochondrial respiration in steers (Kolath et al., 2006) have been reported. However, to our knowledge, no comparable information is available concerning growing pigs, and unfortunately, these biochemical and molecular variables were not measured in the current study.

In conclusion, this study indicates that a substantial genetic change in the dynamics of energy partitioning in the growing animal has occurred in 2 divergent lines of Large White pigs selected to differ in RFI. Pigs from the RFI$^+$ line exhibited a greater HP than those from the RFI$^-$ line. This difference was mainly due to a greater basal metabolic rate and, to a lesser extent, to increased physical activity. Energy retention and its partitioning between protein and fat did not differ between the 2 lines. Further research is required to better understand the behavioral, physiological, biochemical, molecular, and genomic mechanisms responsible for variation in RFI in pigs.

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