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Selection for residual feed intake in growing pigs: Effects on sow performance in a tropical climate^{1,2}

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ABSTRACT: The aim of the study was to evaluate the consequences of a divergent selection for residual feed intake (RFI) during growth in a temperate environment (TEMP) on sow performance in a tropical environment (TROP). Sows came from a selection experiment conducted at INRA in which 2 lines were selected for larger (RFI⁺) or smaller (RFI⁻) feed intake than predicted from performance. In the first analysis, a subsample of data obtained in TROP conditions (49 lactations) was compared to those obtained in TEMP on their sibs mated with the same boars (54 lactations). In the second analysis, data obtained in the TROP environment (82 lactations) were analyzed for testing the effect of season (warm vs. hot) and line on sow performance. Except for the lactation length, the interaction between line and climatic environment was not significant for the others traits ($P > 0.05$). The ADFI expressed per kilogram of litter BW gain tended to be higher in the RFI⁺ line bred in the TROP environment ($P = 0.080$), together with piglet BW at weaning, which tended to be lower ($P = 0.080$). The ADFI was lower in TROP than in TEMP (4.56 vs. 5.86 kg/d; $P = 0.003$), with negative consequence on litter BW gain and maternal BW loss. The RFI⁻ sows tended to eat less feed than RFI⁺ sows

during lactation (4.55 vs. 5.86 kg/d; $P = 0.099$). Litter BW at weaning was higher in the RFI⁻ line. The RFI⁻ sows ate significantly less feed to produce 1 kg of litter than the RFI⁺ sows and tended to lose a larger amount of BW during lactation than the RFI⁺ sows (2.40 vs. 3.02 kg/kg and -0.66 vs. -0.39 kg/d, respectively, $P < 0.10$). Whatever the line, ADFI was reduced by about 21% in the hot season ($P < 0.05$). Litter BW gain was depressed ($P < 0.05$) in the hot season (1.72 vs. 2.08 kg/d in the warm season; $P = 0.023$). Lactation maternal BW loss tended to increase in the hot season (1.10 vs. 0.71 kg/d in the warm season; $P = 0.016$), but back fat loss remained constant ($P = 0.295$). In the TROP environment, the amount of feed required to produce 1 kg of litter was not influenced by the line in the warm season (2.53 kg/kg on average; $P = 0.99$), but it tended to be lower in the RFI⁻ line when compared to the RFI⁺ line in the hot season (2.06 vs. 3.45 kg/kg; $P = 0.050$). This higher apparent efficiency in RFI⁻ sows was mainly related to greater maternal body reserve mobilization (i.e., BW and back fat losses). In conclusion, selection for low RFI during growth in a TEMP environment did not impair sow and litter performance in tropical conditions.

Key words: lactating sow, pig, residual feed intake, thermal stress, tropical environment

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INTRODUCTION

Thermal heat stress is one of the major problems that affect the efficiency of pig production in tropical regions and also in temperate (TEMP) regions during the summer months and/or during hot spells. In lactating sows, reduction in ADFI is the main adjustment response to

reduce metabolic heat production and maintain body temperature within a physiologically safe range (Renaudeau et al., 2012a). Above 22°C, ADFI is reduced with negative consequences on litter growth rate and maternal BW loss (Black et al., 1993; Quiniou and Noblet, 1999).

Residual feed intake (**RFI**) is the difference between the expected intake of the pigs and what they actually consume. Genetic selection for decreased RFI in pigs is a promising strategy to improve feed efficiency without affecting growth rate and body composition (Dekkers and Gilbert, 2010). Selection experiments to reduce RFI during growth have resulted in a reduction of ADFI in sow during lactation in TEMP environments, together with an increase in maternal BW loss (Young et al., 2010; Gilbert et al., 2012). We hypothesized that these correlative effects would be accentuated in sows reared in hot conditions. Low RFI pigs are energetically more efficient mainly because of their reduced maintenance requirements (Barea et al., 2010). The correlated reduced heat production could be an advantage in hot conditions. However, recent results showed that thermoregulatory responses during growth were rather similar in 2 growing pig lines selected for high and low RFI (Renaudeau et al., 2013).

The aim of the study was to evaluate the effect of hot conditions on the performance of lactating sows produced from 2 lines divergently selected for RFI during growth in a TEMP environment. The first objective was to compare sow performance of the 2 lines under tropical conditions to those from their counterparts reared in a TEMP environment. The second objective was to determine if selection for RFI would influence the effects of season on sow and litter performance reared in a tropical climate.

MATERIALS AND METHODS

This study was conducted in accordance with the French legislation on animal experimentation and ethics, and the senior researchers were authorized by the French Ministry of Agriculture to conduct experiments on living animals at the INRA facilities in Plateforme Tropicale Expérimentale Animale (**PTEA**; Petit Bourg, France) and Génétique, Expérimentation et Systèmes Innovants (**GenESI**; Toulouse, France).

Experimental Design and Animal Management

Sows were issued from lines divergently selected in an experiment conducted at INRA GenESI in a TEMP environment (latitude 46°N, longitude 0°W) for 7 generations. More details on the selection experiment and herd management are given by Gilbert et al. (2007, 2012). In generation 7, the line difference amounted to 3.1 genetic SD units for the selection criteria (i.e., RFI) recorded on male candidates for selection (H. Gilbert, unpublished

data). At about 30 kg BW, 20 gilts from the eighth generation of selection from both lines ($n = 10/\text{line}$), sibs of those breeding at the European farm, were transported to experimental facilities at INRA PTEA, which is located in a tropical climate area (**TROP**, latitude 16°N, longitude 61°W; Fig. 1). Females in the 2 environments were inseminated with fresh semen coming from boars selected from the 2 lines to produce the ninth generation. The boars were housed in the INRA artificial insemination facilities of GenESI (TEMP conditions). In the TROP environment, the 20 gilts were distributed in 2 initial 10-gilt batches. In TROP conditions, the first-, second-, and third-parity litters were pure RFI line pigs issued from RFI-selected boars (5 boars in the high RFI line [**RFI**⁺] and 4 boars in the low RFI line [**RFI**⁻] from the 6 boars selected to produce the ninth generation); the fifth-parity litters were produced from a mating with unselected Large White (**LW**) boars. In the TEMP environment, 26 sows were inseminated with the same RFI boars as the sows in the TROP environment. They were distributed in 4 batches separated by 3 wk, and they were mated with the RFI boars in parities 2 to 5. Parity 1 was produced with unselected Large White and Piétrain boars and was not retained for this analysis.

In the TROP environment, sows were housed in a semiopen building in which variations in ambient temperature, relative humidity, and photoperiod closely followed outdoor conditions. In the TEMP environment, sows were housed in a conventional building in which ambient temperature was controlled but not recorded. Ambient temperature was set at about 20°C during the lactation period. Relative humidity was not controlled. Photoperiod closely followed outdoor conditions.

Whatever the line and the environment, females were inseminated using fresh semen. During the gestation period, sows were group housed and were restrictively fed a standard commercial diet containing 12.5 to 13.0 MJ of DE/kg, a minimum of 140 g CP/kg, and 7.0 g lysine/kg. During lactation, sows reared in TROP conditions were fed a corn-soybean meal diet. In TEMP conditions, lactation diet formulation was based on a mixture of cereals (corn, wheat, and triticale) and soybean meal. Even though the ingredients differed between environments, the proximate chemical composition of the diets was similar in TEMP and TROP climates (13.5 MJ DE/kg, 160 g CP/kg, and 10.5 g lysine/kg). Feed allowance during gestation was individually calculated to standardize body condition at farrowing to 21 to 22 mm back fat thickness (Dourmad et al., 2008). At 7 to 10 d before parturition, sows were moved to individual farrowing pens on a slatted metal floor. At the beginning of the lactation period, sows were restrictively fed until d 5 to avoid overconsumption at the beginning of lactation and agalaxia problems. Thereafter, sows were fed ad libitum

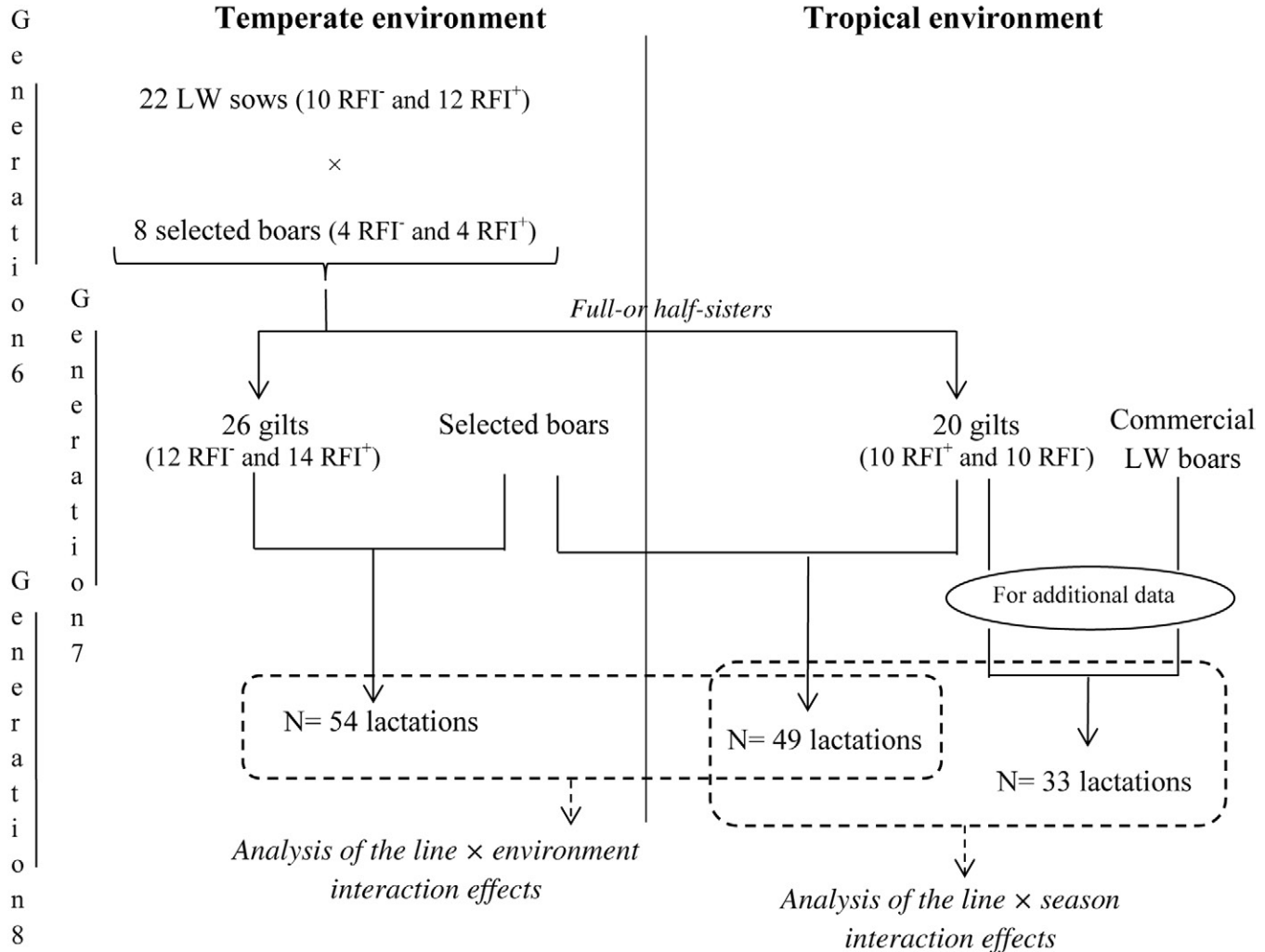


Figure 1. Design of the data production for analyzing the effects of a divergent selection for RFI during growth in a temperate environment on lactating sow performances according to the seasonal variations in the tropical environment and the environment (temperate vs. tropical). RFI = residual feed intake; LW = Large White.

with a maximal feed allowance of 9.9 kg/d. After birth, piglets were handled for tooth cutting, umbilical cord treatment, and labeling, together with tail docking. On d 3, they received an intramuscular injection of 200 mg of iron dextran. When sow or piglet survival was endangered and when it was possible, cross-fostering was performed within line during the first 24 h after birth. The percentage of cross-fostered piglets in the 2 environments was less than 5%. Between d 3 and 7, male piglets were castrated, except in parity 5 in the TEMP environment. During the last week of lactation (d 21 to weaning), piglets were offered a commercial creep feed containing 15.3 MJ DE/kg, 200 g CP/kg, and 14.7 g lysine/kg. Infrared lights provided supplemental heat for the piglets during the first 21 d of the lactation period. At weaning, the sows were moved to a breeding facility and were presented to a mature boar twice daily to detect onset of standing estrus. From 28 d after mating, all sows were checked for pregnancy diagnosis using ultrasonography (Agroscan, E.C.M., Angoulême, France).

Measurements

In both environments, sows were weighed 2 to 3 d before farrowing and at weaning. In the TROP environment, an additional weighing was performed on the farrowing day, and back fat thickness measurements were taken ultrasonically (Agroscan, E.C.M.) 2 to 3 d before farrowing and at weaning, at 65 mm from the midline at the point beside the shoulder and at the last rib on each flank. Back fat measurements were averaged at each stage for further analyses. In both environments, the total numbers of piglets born, born alive, and stillborn, together with the pre-weaning mortality, were recorded for each litter to compute litter size at birth, d 1 (i.e., after cross-fostering), and weaning. Piglets were individually weighed at birth, on the same day during the third week of lactation (mean age = 21.1 ± 2.5 d; this stage is hereafter called d 21), and at weaning (mean age = 28.5 ± 2.4 d). Two ADFI during lactation were computed: for the entire lactation period and for the period when the sows were fed ad libitum only (i.e., from d 6 to weaning). The ADFI from birth to d 21 and during the

entire lactation were expressed as a proportion of the litter BW gain during the corresponding period. In the TROP environment, the rectal temperature and respiratory rate of each sow were measured on Monday and Thursday at 0700 and 1200 h from farrowing to weaning. The average daily rectal temperature and respiratory rate measurements were pooled by sows over the lactation period for analysis. For litter performance, growth rate was calculated over the first 3 wk of lactation (i.e., from d 1 to d 21), the last week of lactation (i.e., from d 21 to weaning), and the whole lactation period. For these calculations, we assumed that piglet BW did not change between birth and d 1. Ambient temperature and relative humidity were continuously recorded only in TROP conditions (1 measurement every 30 s) in the farrowing room, using a probe (Campbell Scientific Ltd., Shepshed, UK) placed 1 m above the floor.

Calculations and Statistical Analyses

An outline of the data collection and analyses is presented in Fig. 1. Two sets of analyses were applied to the data set. First, the analysis focused on the effects of the line \times environment interactions on sow's performance. A subsample of the data recorded in the TROP environment (i.e., only data obtained in sows mated with RFI boars, $n = 49$ lactations) was compared to data obtained in the TEMP location from their sibs mated with the same boars. Because sow BW after farrowing was not available in the TEMP environment, a predicting equation was first established from data in the TROP environment; sow BW after farrowing (BW_{af} , kg) was predicted from BW before farrowing (BW_{bf} , kg) and total litter BW at farrowing (LBW , kg): $BW_{af} = 1.3 + 1.003 \times BW_{bf} - 0.989 \times LBW$ ($R^2 = 0.95$, residual SD [RSD] = 10.4 kg). This equation was used to approximate sow BW after farrowing in the TEMP environment. Data from the 2 environments were compared using a linear mixed model (MIXED procedure of SAS, SAS Inst. Inc., Cary, NC) including the fixed effects of climatic environment (TEMP vs. TROP), line (RFI⁺ vs. RFI⁻), and sire of sows within line (8 levels), together with appropriate 2-factor interactions among the fixed effects. The effect of batch of sows within each environment (14 levels) was included as a random effect. As repeated measurements were performed in each sow, the repeated option of the MIXED procedure was used to account for within-subject correlation. The age of the sow at farrowing was used as a covariate for all traits. When compared to the theoretical farrowing date, the actual farrowing date was somewhat variable according to the climate/season and the line with subsequent variations in piglets' age at d 21 and at weaning. For this reason, average piglet BW at d 21 and at weaning were adjusted for the same piglet age at d 21 and at weaning, respectively. Changes in maternal BW during lactation were adjusted for the same BW at farrowing.

Data obtained in the TROP environment (82 lactations, Fig. 1) were analyzed alone to test the effect of season and line on a sow's performance. Daily maximum, minimum, and mean of the ambient temperature and relative humidity were averaged for each farrowing batch ($n = 12$). These explanatory variables were then submitted for principal component analysis (PRINCOMP procedure of SAS) to reduce data dimensionality and enable us to split the total experiment period into 2 seasons. The effects of season (warm vs. hot), line (RFI⁺ vs. RFI⁻), parity (5 levels: 1, 2, 3, 4, and ≥ 5), and groups of sows within season (12 levels) and their interactions were tested on sow and litter performance according to a linear mixed model (MIXED procedure of SAS). As repeated measurements were performed for each sow, the repeated option was used to account for within-subject correlation. Average piglet BW at d 21 and at weaning were adjusted for the same piglet age at d 21 and at weaning, respectively. Changes in maternal BW and back fat thickness were adjusted for the same BW and back fat thickness at farrowing, respectively. The farrowing rate and the numbers of sows returning into estrus were compared between lines and seasons using a χ^2 test (FREQ procedure of SAS) with 3 degrees of freedom.

For all previous analyses, an approximated Tukey correction was applied to the nominal P -values of the tests to account for multiple comparisons of least squares means.

RESULTS

Environment \times Line Interaction on Sow and Litter Performances

In the TROP environment, mean daily ambient temperature and relative humidity were 24.9°C ($\pm 1.5^\circ\text{C}$) and 95.3% ($\pm 6.0\%$), respectively, for the subsample of records retained for this analysis. In the TEMP environment, ambient temperature was set at 20.0°C, and relative humidity never exceeded 60.0%.

The average parity number, and thus age of the sow at farrowing, was lower in TROP than in the TEMP environment (Table 1). All the other traits presented in Table 1 were then adjusted for the age of the sow at farrowing. The lactation length was greater (+2 d; $P = 0.014$) in TROP than in the TEMP environment. These effects were related to a shorter duration of gestation period in the RFI⁻ line in the tropical climate compared to the other line \times environment combinations. The feed intake (ADFI) during the whole lactation period was reduced by about 20% in TROP compared to TEMP (4.56 vs. 5.86 kg/d; $P = 0.003$). Whatever the line, the total number of piglets born was not significantly affected by the environment, but the stillbirth rate was greater in the TROP climate (15.4% vs. 4.8%; $P = 0.013$). A similar trend was observed for piglet

Table 1. Effects of line and climatic environment on sow and litter performances (least squares means)¹

	Temperate		Tropical		RSD ²	P-value ³		
	RFI ⁺	RFI ⁻	RFI ⁺	RFI ⁻		Line	E	L × E
No. of lactations	27	27	24	25				
Parity	2.7	2.5	2.0	1.9	0.1	0.023	<0.001	0.305
Lactation length, d	28.0 ^a	28.0 ^a	28.6 ^a	31.3 ^b	1.4	0.014	0.033	0.016
ADFI, kg/d								
Whole lactation	5.89	5.83	4.94	4.17	0.58	0.099	0.003	0.166
Ad libitum period	6.41	6.29	5.60	4.62	0.69	0.071	0.017	0.156
ADFI, kg/kg litter BW gain								
Lactation ⁵	2.53	2.39	3.51	2.42	0.96	0.024	0.259	0.080
Birth to d 21 ⁶	2.52	2.37	4.02	2.59	1.38	0.032	0.155	0.080
Sow BW, kg								
Before farrowing	263	245	254	251	13	0.206	0.938	0.383
At farrowing	244	227	234	226	13	0.134	0.688	0.560
At weaning	234	210	219	202	8	0.006	0.292	0.552
Lactation loss, ⁷ kg/d	0.25	0.56	0.52	0.75	0.41	0.061	0.017	0.765
Litter size (LS)								
Total born	12.2	14.0	14.3	15.1	2.2	0.125	0.266	0.529
Total born alive	11.7	13.1	12.1	13.1	2.3	0.104	0.878	0.733
At d 1	12.4	13.1	11.5	13.2	1.6	0.089	0.727	0.461
At weaning	9.8	10.9	8.0	9.4	1.8	0.038	0.087	0.822
Stillbirths, % of total born	3.3	6.3	16.3	14.5	8.2	0.807	0.013	0.337
Death rate, % of LS on d 1	18.6	15.0	30.0	28.8	17.0	0.554	0.068	0.765
Piglet BW, kg								
At d 1	1.45	1.36	1.26	1.33	0.14	0.845	0.229	0.173
At d 21	6.35 ^a	6.04 ^a	5.52 ^b	6.32 ^a	0.45	0.287	0.463	0.021
At d 21 ⁸	6.29	6.11	5.64	5.90	0.37	0.847	0.183	0.260
At weaning	8.61	8.05	7.55	8.02	0.67	0.870	0.268	0.088
Litter BW, kg								
At d 1	17.9	18.0	14.6	17.6	2.5	0.033	0.111	0.027
At d 21	63.5	66.3	44.7	58.8	10.7	0.022	0.032	0.118
At d 21 ⁹	62.1	65.0	50.0	53.0	10.0	0.259	0.008	0.985
At weaning	84.2	87.6	60.8	74.7	14.7	0.067	0.254	0.266
At weaning ⁹	82.6	86.2	67.4	66.7	13.9	0.684	0.005	0.543
Litter BW gain, kg/d								
d 1 to 21	2.29	2.41	1.36	1.68	0.46	0.130	0.001	0.482
d 21 to weaning	2.64	2.72	2.29	2.26	0.68	0.876	0.197	0.771
d 1 to weaning	2.39	2.50	1.60	1.82	0.50	0.232	0.004	0.695

¹RFI⁺: high residual feed intake; RFI⁻: low residual feed intake.²Residual SD.³From an analysis of variance including the effects on line (L), environment (E), age of the sow at farrowing, group of sows, sire origin within line (S), and L × E and S × E interactions as fixed effects and the age of the sow at farrowing as a covariate. The repeated option of the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC) was used to take into account the multiple measurements on each sow.⁵ADFI from farrowing to the day before weaning/litter BW gain from birth to weaning.⁶ADFI from farrowing to d 21/litter BW gain from birth to d 21.⁷Adjusted for the same maternal BW at farrowing, 232 kg (mean value for the data set).⁸Adjusted for the same age of piglet at d 21, 21.5 d (mean value for the data set).⁹Adjusted for the same lactation length, 28.5 d (mean value for the data set).

death rate during the lactation period (29.4% vs. 16.8%; $P = 0.068$). As a consequence, the litter size at weaning was lower in the TROP climate than in the TEMP climate (8.7 vs. 10.4 piglets; $P = 0.087$). The average piglet BW at birth, at d 21, and at weaning was not influenced by the environment ($P > 0.05$). Litter BW gain during the first 21 d and during the whole lactation period were significantly reduced in TROP compared with TEMP (1.52 vs. 2.35 kg/d and 1.71 vs. 2.45 kg/d, respectively; $P < 0.01$). Litter BW at d 21 and at weaning were 12.0 and 17.4 kg

higher in TEMP than in TROP. As a result, the amount of feed necessary for the sows to produce 1 kg of litter BW was not significantly different between environments despite the numerically higher value in TROP (2.96 vs. 2.46 kg/kg in TEMP environment). Whatever the line, sows lost more BW in the TROP environment than in the TEMP environment (0.63 vs. 0.35 kg/d; $P = 0.017$).

On average, the RFI⁻ sows tended to eat less feed than the RFI⁺ sows during lactation (4.55 vs. 5.86 kg/d; $P = 0.099$; Table 1). Even though the line × environment

was not significant ($P = 0.166$), the ADFI depression in the TROP climate seemed to be emphasized in the RFI⁻ line (-28%) when compared to the RFI⁺ line (-16%). The average litter sizes at d 1 and at weaning were greater in the RFI⁻ line than in the RFI⁺ line (+1.1 and +1.2 piglets, respectively; $P < 0.089$). The average piglet BW at birth, after 3 wk of lactation, and at weaning were not significantly affected by the line. The litter BW at d 21 and at weaning were higher in the RFI⁻ line because of numerically larger litter size at birth and a longer lactation length, especially in the TROP climate. The environment \times line interaction was significant for piglet BW at d 21 ($P = 0.021$) and tended to be significant for piglet BW at weaning ($P = 0.088$). This effect was mainly related to a longer lactation length for RFI⁻ than for RFI⁺ pigs in the TROP environment, whereas the line difference was not significant in the TEMP environment (Table 1). As a result, the RFI⁻ sows ate significantly less feed to produce 1 kg of litter than the RFI⁺ sows (2.40 vs. 3.02 kg/kg; $P = 0.024$). This difference tended to be accentuated in the TROP environment ($P = 0.080$). Irrespective of the environment, the RFI⁻ sows tended to lose a larger amount of BW during lactation (-0.66 vs. -0.39 kg/d; $P = 0.061$) than the RFI⁺ sows (Table 1).

Seasonal Variation of Tropical Climate and Line on Sow and Litter Performances

On average, the daily ambient temperature and relative humidity were 23.5°C ($\pm 0.4^\circ\text{C}$) and 93.6% ($\pm 3.4\%$) during the warm season. The corresponding values for the hot season were 25.7°C ($\pm 0.8^\circ\text{C}$) and 96.7% ($\pm 1.4\%$), respectively. As presented in Table 2, most of the traits related to sow reproduction and thermoregulatory responses were not significantly affected by the line \times season interaction. As a result, least squares means related to the season and line effects are presented separately in Table 2, and details on the interaction are given in Fig. 2 when necessary.

The ADFI was significantly affected by season, with the feed consumption in the hot season reduced by about 21% during the entire lactation period (Table 2). The litter sizes at birth and at weaning were not affected by the season (Table 2). Litter BW gain was depressed in the hot season compared to the warm season during the first 3 wk of lactation (1.60 vs. 1.96 kg/d; $P = 0.015$) and the whole lactation period (1.72 vs. 2.08 kg/d; $P = 0.023$). In contrast, litter BW gain during the fourth week of lactation was not influenced by season ($P = 0.197$). As a consequence, ADFI relative to litter BW gain was not affected ($P > 0.05$) by the season (2.64 kg/kg on average; $P = 0.651$). Lactation maternal BW loss increased in the hot season compared to the warm season (1.10 vs. 0.71 g; $P = 0.016$), but back fat loss did not change according to the season (0.13 mm/d on average; $P = 0.$

295). The respiratory rate significantly increased in the hot season (+9.2 breaths per minute [bpm]; $P = 0.006$), whereas the rectal temperature was not affected by season (38.8°C on average; $P = 0.290$).

Whatever the season, ADFI was reduced in the RFI⁻ line compared to the RFI⁺ line during the entire lactation period and the ad libitum period (4.12 vs. 4.71 kg/d and 4.58 vs. 5.33 kg/d, respectively; $P < 0.05$). The litter sizes at birth, on d 1, and at weaning were not significantly influenced ($P > 0.05$) by the divergent selection for RFI (Table 2). However, the stillbirth rate appeared to be lower in the RFI⁻ than in the RFI⁺ line (9.6% vs. 17.9%; $P < 0.001$). The average piglet BW on d 1 was higher in the RFI⁻ line compared to the RFI⁺ line (1.49 vs. 1.27 kg; $P = 0.008$). Similarly, average piglet BW at d 21 was higher in the RFI⁻ line than in the RFI⁺ line (+650 g on average; $P < 0.05$). At weaning, the line effect on the average piglet BW was not significant (7.43 kg on average; $P = 0.279$). Even though the line effect was not significant ($P = 0.154$), the litter BW at weaning was about 10 kg higher in the RFI⁻ line. As a result, sow feed intake relative to litter BW gain was reduced in the RFI⁻ line compared to the RFI⁺ line, similar to line differences for ADFI (Table 2). The sow BW before and after farrowing were not influenced by the line ($P > 0.05$). Adjusted for the same BW at farrowing, the daily BW loss during lactation was much higher in the RFI⁻ sows than in the RFI⁺ sows (1.18 vs. 0.60 kg/d; $P < 0.01$). Back fat thickness at farrowing and at weaning were significantly lower in the RFI⁻ sows (-3.0 mm on average), but the back fat change adjusted for the same back fat at farrowing was not affected by the line (0.14 mm/d on average). The rectal temperature was similar in both lines (38.8°C on average; $P = 0.243$), and respiratory rate tended to be lower in the RFI⁻ than in the RFI⁺ line (52.9 vs. 61.1 bpm; $P = 0.069$).

The line \times season interaction effect was significant for the duration of lactation, with a longer lactation length for RFI⁻ sows reared during the hot season (30.5 vs. 28.7 d on average for the others treatments; $P = 0.049$). For the total lactation period, the amount of feed required to produce 1 kg of litter was not influenced by the line in the warm season (2.53 kg/kg on average, $P = 0.99$), but it tended to be lower in the RFI⁻ line when compared to the RFI⁺ line in the hot season (2.06 vs. 3.45 kg/kg; $P = 0.050$; Fig. 2). The maternal body reserve mobilization (i.e., daily BW and back fat losses adjusted for the same BW and back fat at farrowing, respectively) was significantly higher in RFI⁻ sows only in the hot season (Fig. 2). The average litter BW at weaning was numerically greater during the hot season for the RFI⁻ line compared to the RFI⁺ line (71.0 vs. 55.3 kg; $P = 0.177$) but remained constant according to the line in the warm season (73.1 kg on average). A significant season \times line interaction effect

Table 2. Effects of line and season on sow and litter performances (least squares means)

Item	Line ¹		Season ²		RSD ³	P value ⁴		
	RFI ⁺	RFI ⁻	Warm	Hot		Line	Season	L × S
No. of lactations	38	44	37	45				
Parity	3.5	3.0	3.2	3.2	0.5	<0.001	0.714	0.161
Lactation length, d	28.7	29.6	28.7	29.6	1.6	0.292	0.122	0.049
ADFI, kg/d								
Whole lactation	4.71	4.12	4.92	3.91	0.57	0.048	<0.001	0.804
Ad libitum period	5.33	4.58	5.54	4.38	0.70	0.037	<0.001	0.945
ADFI, kg/kg litter BW gain								
Lactation ⁵	3.02	2.26	2.53	2.75	1.17	0.032	0.651	0.050
Birth to d 21 ⁶	3.17	2.27	2.63	2.81	1.22	0.010	0.625	0.093
Sow BW, kg								
Before farrowing	282	271	278	275	12	0.249	0.411	0.991
At farrowing	261	251	261	250	12	0.262	0.017	0.979
At weaning	240	217	238	219	13	0.012	<0.001	0.156
Lactation loss, kg/d ⁷	0.60	1.18	0.71	1.10	0.39	0.007	0.016	0.068
Sow BT, mm								
At farrowing	23.9	20.6	22.5	21.9	2.5	0.014	0.428	0.217
At weaning	19.7	16.7	18.7	17.7	2.0	0.022	0.169	0.484
Lactation loss, mm/d ⁸	0.12	0.15	0.12	0.14	0.06	0.162	0.295	0.044
Rectal temperature, °C	38.7	38.8	38.7	38.8	0.2	0.243	0.290	0.039
Respiratory rate, ⁹ bpm	61.1	52.9	52.4	61.6	5.8	0.069	0.006	0.845
Litter size (LS)								
Total born	15.1	14.1	14.8	14.4	2.6	0.139	0.647	0.536
Total born alive	12.2	12.7	12.8	12.1	2.1	0.479	0.284	0.303
At d 1	11.2	12.1	11.8	11.5	1.8	0.146	0.544	0.189
At weaning	8.8	9.6	9.7	8.7	2.4	0.290	0.165	0.129
Stillbirths, % of total born	17.9	9.6	12.1	15.4	10.1	<0.001	0.298	0.029
Death rate, % of LS on d 1	31.0	35.7	27.3	29.5	22.0	0.383	0.736	0.486
Piglet BW, kg								
At d 1	1.27	1.49	1.34	1.42	0.22	0.008	0.238	0.219
At d 21	5.33	6.13	5.92	5.54	0.63	0.022	0.086	0.169
At d 21 ¹⁰	5.34	5.99	5.92	5.41	0.61	0.023	0.019	0.019
At weaning	7.24	7.79	7.73	7.29	0.86	0.181	0.129	0.319
At weaning ¹⁰	7.24	7.63	7.73	7.14	0.82	0.280	0.038	0.778
Piglet BW gain, g/d								
d 1 to 21	173	196	199	170	29	0.067	0.006	0.881
d 21 to weaning	247	228	245	230	54	0.449	0.391	0.775
d 1 to weaning	188	203	209	182	29	0.254	0.011	0.758
Litter BW, kg								
At d 1	14.3	18.0	15.9	16.4	2.9	0.002	0.511	0.024
At d 21 ¹⁰	47.8	57.7	56.0	49.4	12.4	0.065	0.106	0.091
At weaning ¹⁰	63.7	73.3	73.0	64.0	16.8	0.154	0.101	0.095
Litter BW gain, kg/d								
d 1 to 21	1.66	1.91	1.96	1.60	0.44	0.180	0.015	0.367
d 21 to weaning	2.36	2.24	2.45	2.15	0.75	0.643	0.197	0.201
d 1 to weaning	1.82	1.98	2.08	1.72	0.47	0.387	0.023	0.242

¹RFI⁺: high residual feed intake; RFI⁻: low residual feed intake.²Warm season: between May and October (temperature = 23.5°C and relative humidity = 93.6%); hot season: between November and April (temperature = 25.7°C and relative humidity = 96.7%).³Residual SD.⁴From an analysis with a general linear mixed model including the effects on line (L), season (S), L × S interaction, and group of sows within S as fixed effects. The repeated option of the Mixed procedure of SAS (SAS Inst. Inc., Cary, NC) was used to take into account the multiple measurements on each sow.⁵ADFI from farrowing to the day before weaning/litter BW gain from birth to weaning.⁶ADFI from farrowing to d 21/litter BW gain from birth to d 21.⁷Adjusted for the same maternal BW at farrowing, 247 kg (mean value for the data set).⁸Adjusted for the same maternal BT at farrowing, 21.5 mm (mean values for the data set).⁹bpm: breaths per minute.¹⁰Adjusted for the same lactation length, 28.7 d (mean values for the data set).

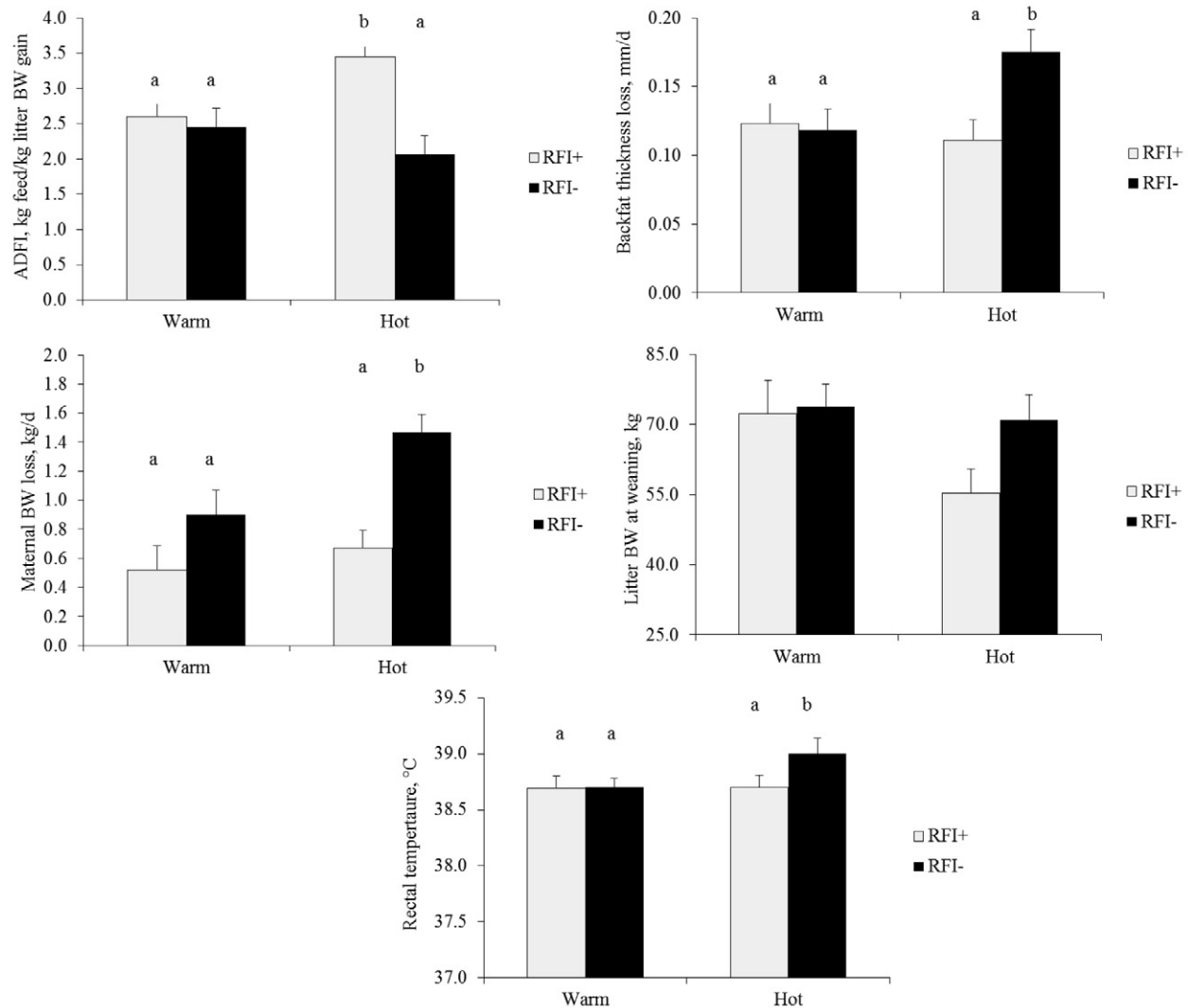


Figure 2. Line to season interaction effect on ADFI over total lactation (kg feed/kg litter BW gain), maternal BW, and back fat losses during lactation (adjusted for the same BW and back fat at farrowing, respectively), litter BW at weaning, and rectal temperature (°C). Warm season: between May and October ($T = 23.5^{\circ}\text{C}$ and $\text{RH} = 93.6\%$); hot season: between November and April ($T = 25.7^{\circ}\text{C}$ and $\text{RH} = 96.7\%$). Whatever the traits, each bar is the least squares means corresponding to a combination of line \times season factors, together with its SE (number of data points = 16, 21, 22, and 23 lactations for the warm RFI⁺, warm RFI⁻, hot RFI⁺, and hot RFI⁻ groups, respectively). ^{a,b}Within each plot, least squares means with different letters differ ($P < 0.10$). RFI = Residual feed intake.

was noticed, with a greater rectal temperature in the hot season for the RFI⁻ line (Fig. 2).

The percentage of lactations with a delayed estrus (i.e., with weaning-to-estrus interval higher than 5 d) and the farrowing rate (i.e., percentage of mated sows that farrow) were not affected by season or line (on average, 15.0% and 89.0%, respectively; results not shown).

DISCUSSION

Effect of Line on Lactating Sows and Litter Performance

The consequences of selection for RFI during growth on sow and litter performances in temperate conditions have already been reported by Gilbert et al. (2012) for the INRA selection experiment and by Young et al. (2010) for a selection experiment performed at

Iowa State University. On the basis of more than 1,000 records each, both studies have reported a reduction of voluntary feed intake and an improvement of the litter BW at weaning in RFI⁻ sows when compared to RFI⁺ sows (Gilbert et al., 2012) or unselected sows (Young et al., 2010). According to these studies, RFI⁻ sows mobilize a larger amount of body reserves than their RFI⁺ counterparts to compensate their lower feed intake level. The line differences in litter growth reflect both the growth potential of the piglets to use feed more efficiently, as a correlated response to selection during the growing period, and the milk production of sows (Gilbert et al. 2012). In the present experiment, results from the comparison of sows from the 2 selected lines are rather similar to those previously reported. However, because of the reduced number of records in temperate conditions ($n = 54$) and the high within-line variability

for sow and litter performances, the power of statistical tests was reduced, and the line effect in the TEMP environment was rarely statistically significant.

Effect of Climate on Sows and Litter Performance

In the present study, the effects of climate were assessed by comparing sow performances between the TEMP and the TROP climates and between the warm and hot seasons in the TROP environment. Apart from differences in the mean ambient temperature (**Ta**), the TEMP and TROP environments differed widely in terms of relative humidity levels (40%–60% vs. >90%, respectively) and diurnal changes in **Ta**. The **Ta** remained rather constant over the day in the TEMP environment, whereas it showed a nycthemeral variation of $\pm 4^{\circ}\text{C}$ to 5°C with minimum and maximum values of **Ta** at about 0700 and 1400 h in the TROP climate. The negative effect of high **Ta** on daily feed intake during lactation has been extensively described (Lynch, 1977; Black et al., 1993; Quiniou and Noblet, 1999). This depressed feed intake is usually reported as an adaptive trait for reducing metabolic heat production in heat-stressed lactating sows. From the comparison of ADFI in TEMP (about 20.0°C) and TROP (24.9°C on average) environments, each degree increase for **Ta** resulted in a reduction of daily feed intake equivalent to about $270 \text{ g} \cdot \text{d}^{-1} \cdot ^{\circ}\text{C}^{-1}$. This value is higher than the previously reported reduction of $160 \text{ g} \cdot \text{d}^{-1} \cdot ^{\circ}\text{C}^{-1}$ in ADFI measured in LW lactating sows between 22°C and 25°C with a relative humidity below 60% (Quiniou and Noblet, 1999). Even though many factors could be involved, this discrepancy could be partly related to the high relative humidity (>90%) in TROP conditions, which is recognized as a factor that exacerbates the effect of high ambient temperature on feed intake by limiting the capacity of evaporative heat losses (Huynh et al., 2005; Renaudeau, 2005). From the comparison between warm and hot seasons (i.e., between 23.5°C and 25.7°C) in the TROP environment, the drop in ADFI (i.e., $459 \text{ g} \cdot \text{d}^{-1} \cdot ^{\circ}\text{C}^{-1}$) agreed with values obtained in previous studies with the same experimental conditions (Renaudeau et al., 2003a; Gourdine et al., 2004; Silva et al., 2009; 492, 350, and $584 \text{ g} \cdot \text{d}^{-1} \cdot ^{\circ}\text{C}^{-1}$, respectively).

A lower piglet survival during the farrowing and lactation periods was observed in the TROP environment than in the TEMP environment, even in the warm season. According to the positive correlation between litter size and the number of stillborn piglets, the effect of TROP climate on stillbirth rate could be partly attributed to a slightly higher litter size at birth. From a literature survey, the risk of stillbirth significantly increases when **Ta** in the farrowing area exceeds 22°C (Vanderhaeghe et al., 2010). A high **Ta** increases the duration of parturition with subsequent deleterious effects on piglet survival

(Borges et al., 2005; Babicz et al., 2012). Even though many factors other than **Ta** can be involved in preweaning mortality, the numerically higher loss of piglets during lactation can be associated with either an indirect consequence of problems related to parturition or a direct effect of reduced sow ADFI and subsequent lower milk production in the TROP climate.

Litter growth rate during the first 3 wk of lactation was lower in TROP than in TEMP conditions (-0.830 kg/d on average). As piglets did not eat creep feed during this period, the litter BW gain was directly related to sow's milk production (Noblet and Etienne, 1989). The depressed milk production in hot conditions is linked to the reduced sow feed intake. However, as milk production is highly correlated with litter size (Auldist et al., 1998), the drop in milk production in TROP conditions could also be related to a smaller number of nursed piglets in that environment. The reduction of litter growth rate during the first 3 wk of lactation from the warm to the hot season was less than the difference found between TEMP and TROP climates (-0.360 vs. -0.830 kg/d). In the TROP environment, the average daily **Ta** is usually higher than the upper limit of the thermal comfort zone of the lactating sow (i.e., 22°C ; Black et al., 1993; Quiniou and Noblet, 1999), and therefore, sows are heat stressed even during the warm season, with a negative effect on milk production. As a consequence, the smaller reduction of litter growth rate over the first 3 wk of lactation from the warm to the hot season could be related to the reduced milk yield in the warm season. Independent of the climatic conditions, the litter BW gain during the fourth week of lactation was found to be higher than from d 1 to 21 of lactation (results not shown), likely because of creep feed consumption during this period (Renaudeau and Noblet, 2001). Expressed as a percentage of litter BW gain during the first 3 wk of lactation, the improvement of litter growth rate during the fourth week was higher when sows were kept in the hot condition ($+33\%$ vs. $+12\%$ between the TROP and TEMP environments and $+25\%$ vs. $+15\%$ in hot and warm seasons). These results suggest that in heat-stressed conditions, piglets would be able to compensate to some extent for insufficient milk production by increasing their consumption of creep feed during the last week of lactation.

In modern sows, nutrient requirements for milk production are rarely fully covered by voluntary feed intake, even in thermoneutral conditions. The related nutritional deficit can be partly compensated by maternal body reserve mobilization. Under thermal heat stress, reduced ADFI emphasizes this deficit and increases the intensity of sow body tissue depletion (Renaudeau et al., 2012b). The TROP sows numerically lost more BW than TEMP sows, but this trait showed a great variability between sows ($\text{CV} = 66\%$). This high variability could be partly

explained by the heterogeneity of the population of sows considered in the present study (i.e., first parity and multiparous sows from RFI⁺ and RFI⁻ lines) and/or different strategies used by the sows of the 2 lines to respond to the piglet demands. In fact, these sows tend to either eat more and mobilize their body reserves to a lesser extent (RFI⁺ sows) or eat less and extensively mobilize their reserves (RFI⁻ sows; Gilbert et al., 2012). In the TROP climate, sow BW loss was larger in the hot than in the warm season. Similar to previous studies (Black et al., 1993; Quiniou and Noblet, 1999), the present work confirms that the high body reserve mobilization under thermal heat stress is not sufficient to cover energy requirements of the lactating sow and to maintain milk production. This inability to compensate for the lactation energy deficit could be explained by a limited amount of “available” maternal body reserves of the modern sow (Noblet et al., 1998). However, comparing heat-stressed sows to pair-fed thermoneutral counterparts, Messias de Bragança et al. (1998) and Renaudeau et al. (2003b) showed the former lose less BW and produce less milk than the latter do. Consequently, the reduced milk production in hot conditions could also result from a lower ability of the sow to mobilize a large amount of body reserves when heat stressed. One could hypothesize that the limitation of body reserve mobilization could be another adaptive strategy, with reduced feed intake, to reduce heat production.

Impact of Divergent Selection for RFI on Performance of Sows Reared in Hot Conditions

In the TROP environment, sow and litter responses were affected by the divergent selection for RFI during the growing period conducted in the TEMP environment. One unexpected result of the present study was the magnitude of the drop of ADFI in the TROP compared to the TEMP environment, which was numerically greater for RFI⁻ sows than for RFI⁺ sows. However, a similar effect was not found between the hot and warm seasons in the TROP climate. First, our results would indicate that for a moderate thermal heat stress, RFI⁻ sows have to rely more on a reduced ADFI than RFI⁺ sows to decrease their metabolic heat production and maintain their body temperature within a physiologically safe range. In contrast, results on growing pigs from these selected lines submitted to a severe heat stress (30°C) with moderate humidity showed a similar impact on ADFI in both lines (Renaudeau et al., 2013; Campos et al., 2014). The discrepancy between both sets of results could be related to the higher susceptibility to heat stress of lactating sows than growing pigs and also to the high relative humidity in the present study. This apparent higher susceptibility of RFI⁻ sows to the TROP climate, as expressed by the

reduction of appetite, is in agreement with the hypothesis that an animal with a low RFI could have fewer possibilities to cope with stress (Luiting et al., 1994). From that, it can be hypothesized that the energetic requirements for sustaining body temperature in hot conditions would exceed the residual part of energy intake in RFI⁻ sows, leading to enhanced decline in heat production and ADFI.

Regarding the interaction between line and climatic environment on litter performance, the litter BW at 21 d and at weaning in the RFI⁻ line were higher in the TROP environment, whereas a limited line effect was observed in the TEMP climate. Similarly, the effect of season on litter BW at weaning was attenuated in the RFI⁻ sows. The line × environment interaction on litter BW became nonsignificant when adjusted for the same litter size and duration of lactation. In other words, the higher litter BW in the RFI⁻ line bred in TROP conditions was mainly explained by both its larger litter size and the longer duration of lactation. This longer duration of lactation meant that for RFI⁻ sows in TROP the duration of gestation was shorter. Unfortunately, we do not have a clear explanation for this surprising result.

Irrespective of the environment, the ratio ADFI/litter BW gain, which can be interpreted as a gross feed conversion ratio, was lower in the RFI⁻ line than in the RFI⁺ line, and this difference was emphasized in the TROP conditions. On average, during the whole lactation period, RFI⁻ sows needed about 1.09 kg less feed to produce 1 kg of litter BW gain in the TROP environment. The corresponding result in the TEMP conditions was 0.15 kg. However, this gross efficiency criterion does not account for energy used for milk production available from mobilization of body reserves. Sows that mobilize a larger proportion of tissue reserves will appear more efficient than sows losing less BW. In our study, this apparent higher lactation efficiency in RFI⁻ sows was mainly explained by a larger body reserve mobilization, especially in hot conditions, as a direct consequence of their reduced feeding level. The RFI for lactating sows could be defined as the difference between observed ADFI and the predicted ADFI required for maintenance and milk production (estimated from litter size and litter BW gain during the first 3 wk of lactation; Gilbert et al., 2012). Nutrient requirements for litter growth met by changes in body reserves (estimated from maternal BW and back fat losses) were considered for the prediction of ADFI. Following the procedure described Gilbert et al. (2012), RFI, i.e., ADFI corrected for the milk production and body resource utilization, was computed by including the fixed effects of the batch and the parity to test the line difference in the tropical environment. Despite the small amount of data available, the *R*² of the multiple regression analysis was 75%. The regression equation explained 75% of ADFI variability despite the

small amount of data available, but the residual variance of the test model was large (i.e., 480 g/d for RSD of the model with line and season effects and their interaction). In the previous model, the season effect was partly confounded with the batch effect and could not be properly estimated. The sow RFI was 174 g/d lower in the RFI⁻ line than in the RFI⁺ line, but the line difference was not significant ($P = 0.263$). Altogether, this tends to indicate that a slight advantage for RFI during lactation is maintained in the TROP environment for the low RFI line, as was found previously in a temperate environment (Gilbert et al., 2012).

A high body reserve mobilization during lactation and/or a poor body condition at weaning may compromise postweaning reproductive performance, especially in first-litter sows (Peltoniemi et al., 2000; Auvigne et al., 2010). As data were not available on weaning to estrus interval (WEI) in TEMP climate, the line \times environment interaction on postweaning reproductive performance could not be investigated. Data available in the TROP environment did not provide evidence that RFI⁻ sows have a prolonged weaning to estrus interval or a reduced proportion of mated sows that farrow. This result was in agreement with previous results published by Gilbert et al. (2012). In addition, it was not possible to evaluate the potential effect of maternal BW loss on the litter size in the following farrowings. However, focusing on primiparous sows, 3 out of the 10 RFI⁻ sows bred in the TROP environment had a delayed WEI (i.e., >5 d; average WEI = 7.3 d), whereas all RFI⁺ sows had a WEI less than or equal to 5 d ($\chi^2 = 2.88$; $P = 0.089$). Even though it was obtained from a very limited number of animals, this result confirms that first litter sows are particularly vulnerable to a nutritional deficit during lactation.

Conclusions

From the results obtained in the present study, selection for reduced RFI during growth in a TEMP environment did not have detrimental effects on the performance of sows raised in hot conditions. In contrast, RFI⁻ sows in TROP climate are apparently more efficient at producing milk, mainly because they mobilize a large amount of their body stores. The RFI⁻ sows saved about 12 kg of feed over the total duration of lactation and weaned heavier litters (+14 kg). More generally, the question of the choice of the lactating sow most adapted to hot conditions arises. In thermoneutral conditions, it is generally accepted that everything must be done to maximize lactation feed intake to ensure a high milk production with a limited mobilization of maternal body reserves (Eissen et al., 2003). In hot conditions, change in ADFI is one of the main adaptive responses for coping with heat stress. As a consequence, selection for

increasing sow ADFI would lead to an increase in the animal's susceptibility to heat stress. The genetic antagonism between rectal temperature and ADFI in lactating sows (Gourdine et al., 2013) tends to confirm this hypothesis. Sows have a high ability to store maternal body reserves during gestation and to mobilize them during lactation. The efficiency of utilization of energy for milk production is higher when energy comes from body reserves than from feed intake (0.88 vs. 0.72; Noblet et al., 1990). Thus, from an energetic point of view, a high mobilization of body stores for maintaining milk production could be a valuable strategy for reducing metabolic heat production and feed efficiency in hot conditions (Bergsma et al., 2009). These maternal body reserves can be replenished by deposition of body tissues during the following gestation period. From that, lactation performance under heat stress could be improved by identifying and selecting animals within a population that have a greater reliance on body tissue mobilization to support milk production, associated with a greater ability to rebuild resources afterward. However, further research must be done to evaluate the consequences of such selection on reproductive and longevity traits.

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