Animal (2010), **4:8**, pp 1308–1318 © The Animal Consortium 2010
doi:10.1017/S1751731110000339

Detecting QTL for feed intake traits and other performance traits in growing pigs in a Piétrain–Large White backcross

H. Gilbert[1,2†], J. Riquet[3], J. Gruand[4], Y. Billon[4], K. Fève[3], P. Sellier[1,2], J. Noblet[5] and J. P. Bidanel[1,2]

[1]*INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78350 Jouy-en-Josas, France;* [2]*AgroParisTech, UMR1313 Génétique Animale et Biologie Intégrative, F-75231, Paris 05, France;* [3]*INRA, UMR444 Génétique Cellulaire, Auzeville, BP52627, F-31326 Castanet-Tolosan, France;* [4]*INRA, UE967 Génétique Expérimentale en Productions Animales, F-17700 Surgères, France;* [5]*INRA, UMR1079 Systèmes d'Elevage, Nutrition Animale et Humaine, F-35590 Saint Gilles, France*

(Received 19 August 2009; Accepted 15 January 2010; First published online 4 March 2010)

Knowing the large difference in daily feed intake (DFI) between Large White (LW) and Piétrain (PI) growing pigs, a backcross (BC) population has been set up to map QTL that could be used in marker assisted selection strategies. LW × PI boars were mated with sows from two LW lines to produce 16 sire families. A total of 717 BC progeny were fed ad libitum *from 30 to 108 kg BW using single-place electronic feeders. A genome scan was conducted using genotypes for the halothane gene and 118 microsatellite markers spread on the 18 porcine autosomes. Interval mapping analyses were carried out, assuming different QTL alleles between sire families to account for within breed variability using the QTLMap software. The effects of the halothane genotype and of the dam line on the QTL effect estimates were tested. One QTL for DFI (*$P < 0.05$ *at the chromosome-wide (CW) level) and one QTL for feed conversion ratio (*$P < 0.01$ *at the CW level) were mapped to chromosomes SSC6 – probably due to the halothane alleles – and SSC7, respectively. Three putative QTL for feed intake traits were detected (*$P < 0.06$ *at the CW level) on SSC2, SSC7 and SSC9. QTL on feeding traits had effects in the range of 0.20 phenotypic s.d. The relatively low number of QTL detected for these traits suggests a large QTL allele variability within breeds and/or low effects of individual loci. Significant QTL were detected for traits related to carcass composition on chromosomes SSC6, SSC15 and SSC17, and to meat quality on chromosome SSC6 (*$P < 0.01$ *at the genome-wide level). QTL effects for body composition on SSC13 and SSC17 differed according to the LW dam line, which confirmed that QTL alleles were segregating in the LW breed. An epistatic effect involving the halothane locus and a QTL for loin weight on SSC7 was identified, the estimated substitution effects for the QTL differing by 200 g between Nn and NN individuals. The interactions between QTL alleles and genetic background or particular genes suggest further work to validate QTL segregations in the populations where marker assisted selection for the QTL would be applied.*

Keywords: QTL, pig, feed intake, feed efficiency, Piétrain × Large White

Implications

Feed efficiency of the growing pig has long been selected, and improved, through indirect selection for faster growth and leaner carcass. Further reduction of body fatness could, however, affect meat quality and reproductive performance. Today, single-place electronic feeders provide accurate measures of individual feed intakes of pigs reared in collective pens. Information is still rather scarce on quantitative trait loci affecting daily feed intake, feed conversion ratio or residual feed intake of growing pigs. This study reports the results of a QTL detection experiment pertaining to feed intake traits and other production traits.

† E-mail: helene.gilbert@jouy.inra.fr

Introduction

Residual feed intake (RFI) represents the fraction of total feed intake (TFI) that is 'unexplained' by maintenance requirements and production costs. Thus, low RFI is interpreted as improved feed efficiency with no difference in production traits while high RFI corresponds to a high feed intake for a given production level (Kennedy *et al.*, 1993; Archer *et al.*, 1999). Residual feed intake, compared with feed conversion ratio (FCR), which is traditionally used to measure feed efficiency, is a linear combination of traits, statistically more robust than the ratio of feed consumed to body weight gain, which defines FCR. Among the numerous QTL mapping designs implemented so far in the pig, only very few have included feed intake measurements (Geldermann *et al.*, 2003; Houston *et al.*, 2005;

Mohrmann *et al*., 2006; Duthie *et al*., 2008). Some QTL have been detected for TFI over a given period of time or average daily feed intake (DFI) between fixed body weight (BW). Less than 20 QTL have been identified so far for feed efficiency, mostly through FCR measurements. Additionally, some single genes, that is, *halothane* (Leach *et al*., 1996), *MC4R* (Kim *et al*., 2000) and *IGF2* (van Laere *et al*., 2003) have been found to affect feed intake and feed efficiency.

This study aimed at detecting QTL for DFI and feed efficiency measured by RFI or FCR in an experimental backcross (BC) between Piétrain (PI) and Large White (LW) breeds. These two breeds show large differences for DFI and, to a lower extent, feed efficiency and feeding behaviour (Labroue *et al*., 1999). Growth, carcass composition and meat quality traits were also recorded on BC progeny so QTL detection could also be applied to these traits.

Material and methods

Animals

Sixteen sire families were produced using PI × LW sires available in French artificial insemination (AI) centres. Sires were chosen so as to be as lowly related as possible. Sires were mated to LW sows reared in two INRA farms (Rouillé, Vienne and Le Magneraud, Charente-Maritime). The dams belonged to generations 0 (founders), 1, 2 or 3 from two divergent lines selected for either high or low residual feed intake (RFI^+ and RFI^-, respectively) during the growth period (Gilbert *et al*., 2007). Line divergence for RFI was 0.3 phenotypic s.d. of the trait at generation 3. In order to avoid potential interactions between sire haplotype segregation in dam families and the effect of selection on the dams, each boar was mated only with sows from a single RFI line.

The present analysis was carried out on 717 female and castrated male BC progeny issued from 4 to 12 litters per sire. BC animals were distributed into four yearly series of four sire families each. In each series, animals were produced in four successive farrowing batches, with a 3-week interval between contiguous batches. These batches then became postweaning and fattening batches and defined four contemporary groups per series. The study was conducted in accordance with the national regulations for human care and use of animals in research.

All animals were raised in the same postweaning unit in Rouillé experimental farm. At least one female pig and one castrated male pig were then allotted to pens of 8 to 12 animals equipped with ACEMA 64 single-place electronic feeders (Pontivy, Cedex, France) (Labroue *et al*., 1994) to record individual feed intake. Facilities available in Rouillé comprised four rooms of four pens each. A contemporary group was defined as the group of about 45 pigs contemporarily tested in the same room, with animals penned by sex. Animals were offered a pelleted diet based on cereals and soybean meal and containing 10 MJ of net energy per kilogram and 160 g of crude protein per kilogram, with a minimum of 0.80 g of digestible lysine per MJ of net energy.

Traits recorded

The test period considered for growth and feed intake traits started 3 days after the pigs entered fattening pens at an average BW (BW_0) of 30 kg and ended the day before slaughter at an average BW (BW_1) of 108 kg. During growth, in addition to feed intake, live backfat thickness (BFT, average value of six ultrasonic measurements taken on each side of the spine, 4 cm from the mid-dorsal line at the levels of the shoulder, the last rib and the hip joint) and BW were recorded at 11, 15, 19 and 23 weeks of age. Feed intake and BW measurements were used to compute average daily gain (ADG), DFI, TFI and FCR over the whole test period. At the end of the test, after a fasting period of approximately 20 h, pigs were weighed to obtain slaughter weight (SW). The transport of pigs from the farm to the abattoir (Celles-sur-Belle (Deux-Sèvres) for the first three series with 33 slaughter dates; Saint-Maixent (Deux-Sèvres) for the last series with 12 slaughter dates) lasted around 1 h. Groups of animals slaughtered the same day always contained progeny (at least 7 and at most 25 pigs) from the two dam lines. Waiting time at the abattoir before slaughter was at least 1 h. Stunning method in both abattoirs was electro-narcose. Shortly after slaughter, the hot carcass (with head and feet) was weighed and dressing percentage was defined as the ratio of hot carcass weight to SW. Carcasses were pre-cooled during 1 h to decrease their temperature from 40°C to 35°C, and then chilled in a cooling room to reach 7°C after 17 h. The day after slaughter, cold carcass weight, carcass length (from the atlas to the anterior edge of the pubian symphysis), carcass BFT (on the mid-dorsal line at the level of shoulder, last rib and hip joint) and head weight were measured. The right half-carcass was then submitted to a standardized cutting procedure and the weights of ham, loin, belly, shoulder, backfat and feet were recorded. Lean meat content (LMC) was estimated as a linear combination of the weights of three carcass cuts (ham, loin and backfat), expressed as a percentage of the half-carcass weight (Tribout and Bidanel, 2000).

RFI was estimated by multiple regression of DFI on ADG, LMC and AMBW. The latter trait is average metabolic BW during the test period ($AMBW = (BW_1^{1.6} - BW_0^{1.6})/[1.6\,(BW_1 - BW_0)]$; Noblet *et al*., 1999). The equation was:

$$\mathrm{RFI\,(g)} = \mathrm{DFI\,(g)} - 1.30 \times \mathrm{ADG\,(g)} + 2.79 \times \mathrm{LMC\,(\%)} - 104.9 \times \mathrm{AMBW\,(kg)}.$$

The model used to compute the multiple regression equation also included the fixed effects of contemporary group, sex and pen size. The R^2 of the multiple regression model used to compute the predicted feed intake was 0.78.

Meat quality measurements were performed 24 h *post mortem*. Ultimate pH (pH_u) measurements were taken on *adductor femoris* (AF), *semimembranosus* (SM), *gluteus superficialis* (GS), *longissimus dorsi* (LD) and *semispinalis capitis* (SC) muscles using a Knick Portamess 911 pH meter with a glass electrode. Meat colour was assessed on GS and *gluteus medius* (GM) muscles through the three coordinates L*, a* and b* of the CIELAB colour space using a Minolta

CR-300 photocolorimeter (Minolta, Carrieres S/Seine, France). Water-holding capacity (WHC) was assessed using a piece of filter paper put on the freshly cut surface of the GS muscle and measuring the time (in 10 s) required for the paper to become wet (a higher value is associated with better WHC). This trait was recorded in the Celles-sur-Belle abattoir only. A linear combination of three of the above measurements (pH_u SM, L * GS and WHC GS) was used as a meat quality index (MQI), defined as a predictor of the 'technological yield' (ratio of the weight of saleable cooked ham to the weight of defatted and boneless fresh ham) in cured–cooked ham processing (Tribout and Bidanel, 2000).

Genotyping

Genotypes for 118 microsatellite markers spread on the 18 porcine autosomes were determined on the BC progeny, the dams and 12 of the 16 sires. Blood samples of the four remaining AI sires could not be collected before they were culled, so that DNA samples were not available. The panel of microsatellites was designed to maximise the average heterozygosity of the sires. A total of 1684 cM was covered, with an average density of 18.1 cM (Table 1). Genotyping was performed in both Labogena (Jouy-en-Josas) and the Genomic Platform (Toulouse) facilities. Phases for all chromosomes were built with certainty from the progeny for the 16 sires, including the four sires for which DNA was missing. Average informativity per chromosome (Table 1), computed as the average transmission probability of sire haplotypes at each position along the panel, was 0.84, ranging from 0.79 for chromosome 16 to 0.88 for chromosome 15. Sires were all heterozygous Nn for the *HAL* gene, whereas dams were homozygous NN. Mutations previously described for *HAL* (C1843T) (Fujii *et al*., 1991), *IGF2* (G3072A) (van Laere *et al*., 2003) and *MC4R* (N298D) (Kim *et al*., 2000) were genotyped by PCR restriction fragment length polymorphism for the all the progeny, available sires and dams for *HAL*, and only sires for *IGF2* and *MC4R*.

Statistical analyses

The analyses were carried out by using a two-step procedure. Trait data were corrected for usual fixed effects using the GLM procedure of the SAS software. The fixed effects included in the model were contemporary batch (16 levels), farm of birth (2 levels), pen size (5 levels) and sex (2 levels) for growth and carcass composition traits. For meat quality traits, the combination of slaughter day and abattoir (45 levels) was added in the model and the pen size was removed. Slaughtering for a given contemporary batch was distributed into three to seven slaughter dates, with some overlapping between successive batches. SW was included as a covariate in the model used for carcass traits, except for joint weights, which were analysed using hot carcass weight as a covariate.

QTL detection was performed on the residuals of the above-mentioned mixed models using the QTLMap software developed at INRA (Elsen *et al*., 1999). QTLMap allows interval mapping to be performed without any hypothesis on

Table 1 *Marker distribution on the chromosomes, bounds of the positions covered and average informativity*

Chromosome (SSC)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Number of markers	9	8	7	8	4	10	9	5	8	6	6	6	5	6	5	6	6	4
First/last marker positions (cM)	3 (138)	1 (128)	17 (129)	5 (126)	72 (133)	9 (165)	0 (177)	46 (123)	1 (137)	20 (121)	9 (85)	1 (105)	35 (102)	21 (108)	17 (89)	15 (93)	17 (98)	5 (56)
Marker density[1]	17	18	19	17	20	17	22	19	19	20	15	21	17	17	18	16	16	17
Informativity (%)	84	85	87	83	82	83	82	87	83	81	87	81	86	80	88	79	82	87

[1]Average distance (cM) between adjacent markers.

the number of QTL alleles and the allele frequencies within breeds. Sire contrasts between PI and LW haplotypes were tested assuming that the population was structured as a set of independent half-sib families. Test statistics were approximate likelihood ratio tests (LRT), computed for the most probable sire haplotype. QTL effects reported in the following were computed as the mean of absolute values of individual sire QTL substitution effects.

In the first QTL detection analysis, a polygenic effect for the sire, a QTL effect and a residual were included in the model. A second QTL detection analysis was carried out with a model including the additional effects of the halothane genotype and of the interaction between the halothane genotype and the QTL. The halothane genotype effects were thus computed and a test on the dependency of the QTL effects upon the halothane genotype of the progeny was performed.

In the above-mentioned analyses, all dams were considered as belonging to the same LW population. In order to estimate potential effects of dam lines on the QTL effect estimates, a final test was applied to QTL detected in the first analysis: separate QTL effect estimates were obtained for the group of sires mated with RFI^{+} dams and for the group of sires mated with RFI^{-} dams. The difference of QTL effects estimated within the each group of sire families was tested with a Student's *t*-test.

The differences of the QTL effects depending on the halothane genotype or on the dam line were estimated only for QTL detected in the first QTL analysis. For both tests, a Bonferroni correction was applied to the *P*-value to account for the number of independent results tested, considering that tests were applied on 86 QTL grouped on 17 chromosomes for three major groups of traits: only tests with nominal $P < 0.001$ were retained, which corresponds to a proportion of 0.05 false positive at the experiment level.

Results

Means, s.d. and numbers of progeny recorded for each trait are reported in Table 2.

Halothane locus effects

Sires were all heterozygous Nn for the *HAL* gene, whereas all dams were homozygous NN. The mean differences between NN and Nn progeny are presented for all traits in Table 2. NN progeny compared with Nn progeny had significantly higher trait values for DFI, ADG, carcass length, backfat weight, ultimate pH of LD muscle, water-holding capacity and MQI, whereas their ham weight, loin weight, dressing percentage and LMC were significantly lower. When expressed in phenotypic s.d. units, the highest difference between NN and Nn progeny (0.58 s.d.) was found for LMC.

A significant increase in FCR was observed in NN compared with Nn progeny ($P < 0.05$). The difference between NN and Nn pigs for residual feed intake was not significant, whereas all its components (DFI, ADG and LMC) were strongly affected by the *HAL* locus.

QTL for DFI and feed efficiency

Only two QTL were detected for DFI and feed efficiency in $P < 0.05$ at the chromosome-wide (CW) level (Table 3), but marginally significant QTL ($P < 0.10$ at the CW level) were also found. Among the 13 resulting QTL, 8 were significant at least at the ($P < 0.06$) CW level for four chromosomes: SSC2 for daily and TFI (at 2 and 77 cM, respectively), on SSC6 for FCR at 125 cM and DFI at 83 cM (significant at $P < 0.05$ at the CW level), on SSC7 for FCR (significant at $P = 0.001$ at the CW level) in a region about 74 cM and on SSC9 for DFI and residual feed intake at about 104 cM. Average substitution effects for these QTL were rather similar, representing about 20% of the phenotypic s.d. of the traits.

QTL for growth traits

QTL detected for growth traits are shown in Table 4. The main QTL affected average daily BW gain on SSC7 ($P < 0.01$ at the genome-wide level) at 104 cM. Two chromosomal regions were detected at the ($P < 0.01$) CW level for birth weight, on SSC6 at 17 cM and on SSC14 at 31 cM. Both chromosomes showed QTL at the ($P < 0.05$) CW level for early weight, at 28 days of age or 70 days of age. Additional QTL regions were found at the ($P < 0.05$) CW level for growth traits on SSC1, 9, 12 and 13.

QTL for body and carcass composition traits

QTL detected for body and carcass composition traits are listed in Table 5. Four chromosomal regions were significant at the ($P < 0.01$) CW level. On SSC2, a QTL for BFT measured at the last rib was detected at position 126 cM ($P < 0.01$ at the CW level). On SSC6 (at about 70 cM), the significance was 0.01 at the genome-wide level for the QTL affecting dressing percentage, ham weight and LMC. On SSC15, QTL with most likely positions ranging from 43 to 76 cM for live backfat from 15 weeks of age to the end of control period and shoulder weight were detected ($P < 0.05$ at the genome-wide level). In this region, a QTL for LMC with a lower significance level ($P < 0.05$ at the CW level) was detected. On SSC17, QTL for feet weight (at 90 cM), loin weight (at 17 cM) and carcass length (at 45 cM) were mapped at the $P < 0.01$ CW level, the position 90 cM showed associations with live BFT measurements at all stages, at lower significance levels ($P < 0.05$ at the CW level). QTL effects on SSC15 and SSC17 ranged from 0.19 to 0.40 s.d. units of the traits. Additional QTL regions were detected ($P < 0.05$) at the CW level for body and carcass composition traits on SSC1, 2, 3, 5, 7, 8, 12, 13, 16 and 18.

QTL for meat quality traits

QTL affecting meat quality traits are listed in Table 6. On SSC6, the significance of $P < 0.01$ at the genome-wide level was reached at about 70 cM for QTL affecting water-holding capacity. QTL substitution effect was 0.27 s.d. units of the traits. Three chromosomal regions were significant at the ($P < 0.01$) CW level, namely on SSC1 for a* measured on GM muscle, SSC5 for a* measured on GS muscle, and SSC4 for L* measured

Table 2 *Means, s.d. and number of recorded progeny (number) and halothane genotype effect for each trait*

Trait	Number	Mean	s.d.	NN – Nn (s.d. unit)[1]
Feed intake and feed efficiency				
Daily feed intake (kg)	673	2.13	0.18	0.40****
Total feed intake (kg)	673	206	19	0.10
Residual feed intake (kg/day)	637	0	0.10	0.09
Feed conversion ratio (kg/kg)	668	2.66	0.19	0.17*
Growth traits				
Birth weight (kg)	673	1.6	0.3	−0.06
Weight 28 days (kg)	671	9.5	1.5	0.00
Weight 70 days (kg)	673	29.7	3.9	0.16†
Slaughter weight (kg)	673	108.4	4.3	0.14†
Average daily gain from 70 days of age to slaughter (kg)	673	0.79	0.07	0.25***
Body composition traits[2]				
BFT 11 weeks (mm)	350	7.7	0.9	0.04
BFT 15 weeks (mm)	350	9.4	1.4	0.14
BFT 19 weeks (mm)	350	11.3	1.8	0.25†
BFT 23 weeks (mm)	289	12.9	1.9	0.17
Cold carcass weight (kg)	654	84.7	2.9	−0.25**
Dressing percentage (%)	654	78.5	1.5	−0.54****
Carcass length (mm)	654	978	23	0.40****
Backfat thickness at last rib (mm)	654	17.6	3.1	0.09
Backfat thickness at hip joint (mm)	653	12.3	2.4	0.28***
Backfat thickness at shoulder (mm)	655	30.5	4.1	0.21*
Backfat weight (kg)	645	1.84	0.29	0.48****
Belly weight (kg)	646	5.68	0.31	0.22*
Feet weight (kg)	640	0.93	0.06	0.27**
Ham weight (kg)	652	10.66	0.35	−0.56****
Head weight (kg)	645	4.54	0.23	0.31***
Loin weight (kg)	647	10.57	0.45	−0.34****
Shoulder weight (kg)	644	9.23	0.32	0.18*
Lean meat content (%)	637	64.1	2.2	−0.58****
Meat quality traits				
Ultimate pH AF	653	5.80	0.20	0.02
Ultimate pH GS	657	5.54	0.15	0.08
Ultimate pH LD	658	5.71	0.17	0.35****
Ultimate pH SC	595	6.12	0.27	−0.14
Ultimate pH SM	654	5.63	0.17	−0.05
L * GM	656	41.6	3.7	−0.02
L * GS	656	50.2	3.5	−0.17†
a * GM	653	12.6	2.1	−0.07
a * GS	653	6.2	1.7	−0.13
b * GM	654	8.6	1.6	−0.04
b * GS	654	8.6	1.3	−0.08
Water-holding capacity GS (10 s)	478	9.8	5.8	0.53****
Meat quality index	478	10.4	2.7	0.42****

GS = *gluteus superficialis*; GM = *gluteus medius*; AF = *adductor femoris*; LD = *longissimus dorsi*; SC = *semispinalis capitis*; SM = *semimembranosus*.
[1]Difference between the NN performance trait and the Nn performance trait expressed in proportion of phenotypic s.d.
[2]BFT = average live backfat thickness.
†$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

on the GM muscle. Additional QTL were detected at the ($P < 0.05$) CW level on chromosomes 1, 4, 7, 8, 11, 12, 13, 17 and 18 for L*, a* or b* measures of both GM and GS muscles or for ultimate pH of LD, SC and AF muscles.

QTL detection with the halothane genotype as a fixed effect
QTL detection including the fixed effect of the halothane genotype in the model of analysis was carried out. On SSC6, all the tests being significant in the previous analyses at about 70 cM were no longer significant with the model accounting for the halothane genotype, indicating that the QTL detected in the region might be due to the *HAL* gene. Nevertheless, two QTL previously detected, for birth weight at 17 cM and FCR at 125 cM, remained significant in the new analysis, indicating that QTL other than *HAL* are segregating on SSC6.

Table 3 *QTL detected for feed intake and feed efficiency, maximum LRT value, corresponding* P*-values (at CW level) and position (cM) and mean of QTL substitution effects estimated within sire families*

SSC	Trait	Maximum LRT	*P*-value	Position	Effect physical units	Effect s.d. units
2	Daily feed intake (kg)	34.9	0.052	2	0.032	0.18
	Total feed intake (kg)	35.6	0.057	77	3.8	0.20
5	Residual feed intake (kg/day)	31.5	0.098	99	0.018	0.18
6	Feed conversion ratio (kg/kg)	34.3	0.055	125	0.04	0.20
	Daily feed intake (kg)	41.8	0.012	83	0.039	0.22
7	Feed conversion ratio (kg/kg)	45.3	0.001	74	0.04	0.19
	Daily feed intake (kg)	32.4	0.072	58	0.034	0.19
8	Feed conversion ratio (kg/kg)	31.0	0.088	46	0.03	0.18
	Total feed intake (kg)	31.1	0.091	46	3.7	0.20
9	Daily feed intake (kg)	33.7	0.059	104	0.036	0.20
	Residual feed intake (kg/day)	34.8	0.052	103	0.024	0.23
15	Feed conversion ratio (kg/kg)	32.9	0.061	51	0.04	0.19
	Daily feed intake (kg)	33.1	0.065	47	0.029	0.16

LRT = likelihood ratio test; CW = chromosome wide.

Table 4 *QTL detected for growth traits, maximum LRT value, corresponding significance level and position (cM), and mean of QTL substitution effects estimated within sire families*

SSC	Trait	Maximum LRT	Significance level[1]	Position	Effect physical units	Effect s.d. units
1	Weight 70 days (kg)	40.0	$^{+}$	129	0.8	0.22
6	Birth weight (kg)	43.4	$^{++}$	17	0.10	0.30
	Weight 70 days (kg)	36.6	$^{+}$	73	0.6	0.17
7	Average daily gain (kg)	51.1	**	104	0.018	0.26
	Weight 70 days (kg)	36.1	$^{+}$	177	1.1	0.29
9	Average daily gain (kg)	35.2	$^{+}$	125	0.012	0.17
12	Weight 28 days (kg)	38.7	$^{+}$	84	0.4	0.25
13	Birth weight (kg)	37.1	$^{+}$	55	0.07	0.20
14	Birth weight (kg)	45.4	$^{++}$	31	0.08	0.23
	Weight 28 days (kg)	38.2	$^{+}$	67	0.4	0.24
	Weight 70 days (kg)	35.6	$^{+}$	29	0.8	0.20

LRT = likelihood ratio test.
[1]Chromosome-wide significance levels: $^{+}P < 0.05$; $^{++}P < 0.01$ and genome-wide significance levels: $*P < 0.05$; $**P < 0.01$.

Applying a QTL detection model including the halothane genotype and the interaction between the halothane genotype and the QTL showed significant results for one QTL region previously detected. The interaction for the SSC7 QTL affecting loin weight was highly significant ($P < 0.0001$). Comparing the sire QTL substitution effect estimates depending on their progeny genotypes, an average difference of 0.20 kg of loin was found between Nn and NN pigs. The estimated QTL substitution effects were thus on average larger in an Nn than in an NN genetic background.

QTL effect estimates depending on the dam line

QTL effect estimates were significantly different depending on the LW dam line for five of the QTL previously detected (Table 7). On SSC6 and SSC7, significant differences of similar magnitude were found for birth weight and loin weight (estimated QTL effects of +70 g in the RFI^{+} dam line compared with the RFI^{-} dam lines). On SSC12, effects for ultimate pH measured on the SC muscle were significantly higher when estimated in the RFI^{-} line. The largest differences ($P < 0.0001$) were found for estimated QTL effects relating to live BFT on SSC13 and SSC17, with higher QTL effects found in the RFI^{-} line compared with the RFI^{+} line.

Discussion

Design and QTL model

The population used here for the detection of QTL affecting feed intake and feed efficiency was a cross between LW × PI boars from AI centres and LW female pigs from two lines divergently selected for residual feed intake. The progeny were recorded for individual feed intake to allow the computation of individual consumption and feed efficiency, as usually performed in breeding company to predict lean growth and FCR. The effect of feeding pigs with single-place electronic feeders instead of multiple place feeders used in commercial pig farms is not accurately established. One may assume that feeding behaviour is changed due to a reduced competition for food access. The actual extent of this change

Table 5 *QTL detected for body composition traits, maximum LRT value, corresponding significance level and position (cM), and mean of QTL substitution effects estimated within sire families*

SSC	Trait	Maximum LRT	Significance level[1]	Position	Effect physical units	Effect s.d. units
1	Backfat thickness at shoulder (mm)	38.1	+	114	0.8	0.19
	Shoulder weight (kg)	40.7	+	58	0.07	0.21
2	Backfat thickness at last rib (mm)	42.9	++	126	0.7	0.21
	LMC (%)	38.1	+	94	0.4	0.19
	Shoulder weight (kg)	41.1	+	109	0.07	0.21
3	Backfat thickness at last rib (mm)	34.4	+	66	0.5	0.17
	BFT 19 weeks (mm)	21.8	+	70	0.4	0.27
5	Shoulder weight (kg)	33.7	+	111	0.07	0.23
	BFT 23 weeks (mm)	19.4	+	72	0.4	0.27
6	Backfat weight (kg)	42.9	++	71	0.06	0.22
	Carcass length (mm)	45.7	++	83	5.3	0.23
	Dressing percentage (%)	63.0	**	71	0.4	0.25
	Feet weight (kg)	45.6	++	69	0.01	0.22
	Ham weight (kg)	71.7	**	88	0.10	0.28
	LMC (%)	66.0	**	87	0.6	0.28
	Loin weight (kg)	45.0	++	54	0.10	0.23
7	Cold carcass weight (kg)	37.2	+	36	0.6	0.03
	Loin weight (kg)	35.3	+	41	0.10	0.23
8	Backfat weight (kg)	33.9	+	96	0.06	0.19
12	Head weight (kg)	39.7	+	64	0.11	0.32
13	Feet weight (kg)	35.6	+	47	0.01	0.22
	BFT 23 weeks (mm)	23.1	+	102	0.5	0.31
15	BFT 15 weeks (mm)	27.9	++	43	0.3	0.33
	BFT 19 weeks (mm)	34.8	**	48	0.5	0.32
	BFT 23 weeks (mm)	32.3	*	46	0.6	0.40
	Ham weight (kg)	35.1	+	61	0.07	0.19
	LMC (%)	39.3	++	54	0.4	0.20
	Shoulder weight (kg)	45.0	*	76	0.08	0.26
16	BFT 23 weeks (mm)	23.4	+	93	0.7	0.53
	Carcass length (mm)	38.6	+	60	4.6	0.20
	LMC (%)	35.6	+	58	0.5	0.21
17	BFT 11 weeks (mm)	24.5	+	98	0.3	0.35
	BFT 15 weeks (mm)	24.7	+	90	0.4	0.40
	BFT 19 weeks (mm)	26.0	+	98	0.6	0.35
	BFT 23 weeks (mm)	21.2	+	61	0.5	0.33
	Carcass length (mm)	63.1	**	45	5.6	0.24
	Feet weight (kg)	44.7	++	90	0.02	0.29
	Loin weight (kg)	39.0	++	17	0.11	0.24
18	Dressing percentage (%)	33.6	+	31	0.3	0.18

LRT = likelihood ratio test; BFT = average live backfat thickness; LMC = lean meat content.
[1]Chromosome-wide levels: $^{+}P < 0.05$; $^{++}P < 0.01$ and genome-wide levels: $^{*}P < 0.05$; $^{**}P < 0.01$.

is unknown, while being probably limited as shown by the agreement between breed differences found in the two environments (e.g. Labroue *et al*., 1994, 1999).

The halothane mutation was segregating in all the sire families. It had a significant and moderate effect on DFI, ADG and LMC, that is, the components of feed efficiency, but its direct effect was of marginal magnitude on FCR and RFI, in agreement with previous studies: differences between NN and Nn individuals in DFI or FCR were found to be significant or marginally significant in some studies (Leach *et al*., 1996; Thaller *et al*., 2000) but not significant in other studies (Larzul *et al*., 1997; Tor *et al*., 2001). Thus, the halothane mutation appears to account for a marginal part of the genetic variability between the breeds for feed efficiency traits. Similarly, the halothane locus was shown to significantly affect growth, body and carcass composition, as well as meat quality. Estimated effects were in the usual range of literature estimates (Larzul *et al*., 1997).

Labroue *et al*. (1999) found a lower DFI, by 19%, in the PI breed compared with the LW breed, which would correspond to 2 to 3 s.d. of the trait, and reported a small difference in feed efficiency between the two breeds. On the other hand, selection experiments (Gilbert *et al*., 2007; Cai *et al*., 2008) showed that these traits can be efficiently selected, which suggests QTL allele segregation within breeds. To account for this phenomenon, we applied a QTL model that made no

Table 6 *QTL detected for meat quality traits, maximum LRT value, corresponding significance level and position (cM), and mean of QTL substitution effects estimated within sire families*

SSC	Trait	Maximum LRT	Significance level[1]	Position	Effect physical units	Effect s.d. units
1	a * GM	48.1	$^{++}$	72	0.4	0.21
	Ultimate pH SC	39.1	$^{+}$	138	0.06	0.23
4	L * GM	42.6	$^{++}$	9	1.1	0.28
	Ultimate pH LD	38.2	$^{+}$	5	0.04	0.22
5	a * GS	40.5	$^{++}$	115	0.5	0.28
6	Water-holding capacity (s)	43.6	**	70	14	0.27
8	a * GS	36.1	$^{+}$	46	0.3	0.21
11	L * GS	38.9	$^{+}$	9	0.7	0.18
12	Ultimate pH SC	36.8	$^{+}$	1	0.09	0.31
13	Ultimate pH AF	36.3	$^{+}$	54	0.05	0.22
17	b * GM	35.6	$^{+}$	94	0.3	0.20
	L * GM	38.3	$^{+}$	75	0.7	0.19
18	a * GM	36.3	$^{+}$	43	0.3	0.19
	Ultimate pH SC	35.6	$^{+}$	38	0.07	0.25

LRT = likelihood ratio test; AF = *adductor femoris*; GM = *gluteus medius*; GS = *gluteus superficialis*; LD = *longissimus dorsi*; SC = *semispinalis capitis*.
[1]Chromosome-wide levels: $^{+}P < 0.05$; $^{++}P < 0.01$ and genome-wide levels: $*P < 0.05$; $**P < 0.01$.

Table 7 *Significant differences (P < 0.001) between mean values of QTL substitution effects estimated within sire families for sires mated with dams from the line selected for high residual feed intake (RFI^{+}) and for sires mated with dams from the line selected for low residual feed intake (RFI^{-})*

SSC	Trait	Effect (physical units)		*t*-test
		RFI^{+}	RFI^{-}	
6	Birth weight (kg)	0.14	0.07	***
7	Loin weight (kg)	0.14	0.07	***
12	Ultimate pH SC	0.05	0.12	***
13	BFT 23 weeks (mm)	0.2	0.7	****
	Feet weight (kg)	0.01	0.02	***
17	BFT 11 weeks (mm)	0.2	0.5	****
	BFT 23 weeks (mm)	0.3	0.6	***

BFT = average live backfat thickness; SC = *semispinalis capitis*.
$***P < 0.001$; $****P < 0.0001$.

assumption on the number of QTL alleles segregating in the parental breeds of the cross. The alternative, that is, a line cross model where QTL alleles are assumed to be different and fixed in the parental breeds (Haley and Knott, 1992), has been shown to be more powerful to detect QTL when the hypothesis of QTL fixation is correct, or at least when the effects of the alleles in one breed are consistently higher than the effects of the alleles in the other breed. Practically, Student's *t*-tests on sire QTL effects were performed to identify heterozygous sires (not shown). For most of the detected QTL, some sires were found to be homozygous, confirming that most of the QTL alleles are not reciprocally fixed in the LW and the PI breeds. Finally, line cross tests require that the breed origin of the sire phases can be inferred, which was not the case in our study; the boars were in service in commercial AI centres and their parents could not be genotyped. As a consequence, it was not possible to orientate the effect of the PI alleles compared with LW alleles in the design and, for example, QTL presenting cryptic effect could not be detected with this design.

We performed a simulation study to evaluate the expected detection power of our design (data not shown). With a 5% type I error, for a QTL effect of 0.5 s.d. of the trait, the power was 72% if two QTL alleles were alternatively fixed in the breeds, and 30% if they were segregating with equal proportions in the two breeds. For an effect of 1 s.d., the power reached 100% in the former case and 90% in the latter one. Additionally, in a BC design, the QTL effects are estimated as contrasts between the LW/LW and the PI/LW genotypes in the sire progeny. Consequently, higher power was provided to detect QTL with either additive effects, or (partial) dominance of the PI alleles over the LW alleles. However, in this context, only few QTL were detected for feed intake and feed efficiency. This might be a consequence of low individual effects of the QTL alleles segregating in PI *v.* LW, combined with a high allelic polymorphism in the breeds. In addition, if some QTL had dominant LW alleles over PI alleles, they would not be detected. Moreover, even if the average informativity of our markers was high, some chromosomal regions were not covered, like the sex chromosomes or the beginning of chromosomes 5 and 8. Some QTL may have been missed, as other studies have reported QTL effects in these chromosomal regions (e.g. QTL for ham weight and carcass leanness were reported on SSC8 by Duthie *et al*., 2008).

Feed intake traits

SSC2. A QTL for DFI and FCR has recently been mapped on SSC2 (Duthie *et al*., 2008), in a cross between PI sires and commercial crossbred dams issued from LW, Landrace and Leicoma breeds. This QTL was similar to that we detected for DFI ($P < 0.06$ at the CW level). The most likely position (2 cM) in our study corresponds to the IGF2 region, but the IGF2 mutation found in the Meishan breed by van Laere *et al*. (2003) was not segregating in our PI × LW boars.

Houston *et al*. (2005) have detected QTL for DFI in this region and also rejected the published IGF2 mutation as a causal factor. The QTL effect observed in our study could similarly come from a different mutation or a different locus in the IGF2 region.

A QTL for TFI was found to be marginally significant ($P < 0.06$) in a different SSC2 region (at 77 cM), fairly close to QTL affecting carcass BFT and LMC located in the region about 100 cM. QTL for DFI (Duthie *et al*., 2008) and for tissue composition of the ham (Heuven *et al*., 2009) in a commercial cross including the PI breed were detected in this same region. Correlations between the effects of the SSC2 QTL on different traits indicated that haplotypes increasing TFI might be physically linked to haplotypes increasing BFT, in the direction of known genetic correlations (Johnson *et al*., 1999). On the contrary, their correlations with the QTL effects on LMC showed no clear pattern, suggesting that two different loci could segregate in the region. This would offer the opportunity to decrease feed intake, and backfat, while improving LMC by selection of favourable haplotypes in the region.

SSC7. To our knowledge, no QTL affecting FCR had previously been mapped to the swine leucocyte antigen complex (SLA) region on SSC7. We detected in this region a low significant QTL for DFI, cold carcass weight and loin weight. Thus, our results do not point out major QTL affecting body composition in the SLA region as those detected in crosses involving the Meishan breed (Bidanel and Rothschild, 2002). On the other hand, a highly significant QTL for ADG was mapped to SSC7 (position $\sim$100 cM), close to the region where Houston *et al*. (2005) mapped QTL for average feeding rate, and close to previously reported QTL affecting growth rate (Bidanel and Rothschild, 2002). Some QTL were identified in crosses involving the PI breed in chromosomal regions close to the maximum LRT position in our analysis (Nezer *et al*., 2002; Edwards *et al*., 2008).

A highly significant influence of the halothane genotype on the QTL effects estimated for loin weight on SSC7 was detected. If some interactions between the halothane mutation and the *RN* major gene have been previously reported (Le Roy *et al*., 2000), this is to the best of our knowledge the first time that an interaction between a QTL and the halothane mutation is demonstrated. An epistatic interaction can be suspected between the loci, where the effect of the SSC7 QTL would be enhanced or diminished when the *n* allele is present at the halothane locus. The *n* mutation is responsible for sudden increases in calcium levels in the cytoplasm during challenges: the uncontrolled sarcoplasmic Ca^{2+} release via the ryanodine receptor activates actomyosin filaments, leading to muscle contractions and triggers glycogenolysis resulting in anoxia, muscle acidosis and heat production (Laville *et al*., 2009), which could here activate/inactivate some metabolic pathways related to the SSC7 QTL.

SSC5 and SSC8. We detected a number of suggestive QTL on SSC5 and SSC8, where QTL have previously been detected for feed intake traits, but at rather different locations. For example, Lee *et al*. (2003) detected a SSC5 QTL for FCR in F_2 Meishan $\times$ PI pigs at position 200 cM, whereas the QTL that we detected for residual feed intake ($P < 0.10$) was located at 99 cM. Similarly, a QTL affecting FCR was mapped at 99 cM to SSC8 by Beeckmann *et al*. (2003) in the same population as Lee *et al*. (2003). The putative ($P < 0.10$) QTL detected on SSC8 for both FCR and TFI in our study had most likely position about 45 cM, with CI that would not overlap that of the QTL detected by Beeckmann *et al*. (2003).

SSC6 and SSC9. Few QTL were previously reported for feed intake traits on SSC6 and SSC9. In crosses between the PI breed and a European white breed, a QTL affecting DFI was mapped by Mohrmann *et al*. (2006) to the region of SSC6 (position $\sim$130 cM) in which we found a putative QTL for FCR. We found a marginally significant QTL ($P < 0.06$) for DFI at 104 cM on SSC9, whereas Cepica *et al*. (2003) mapped a QTL for food consumption at 193 cM. The latter location is the end of the linkage group delimited by marker SW1349 in our study and their study. The same chromosomal region affected ADG in our study and in the study of Duthie *et al*. (2008). However, these latter authors did not show any effect on feed intake. In our study, QTL effects on ADG were positively correlated with QTL effects on DFI, which agrees with the genetic correlation between these traits (Johnson *et al*., 1999). This would imply that the alleles increasing ADG would be linked to alleles increasing DFI.

SSC15. On chromosome 15 (position $\sim$50 cM), we found a putative QTL affecting both FCR and DFI, co-located with highly significant QTL for BFT at 15, 19 and 23 weeks of age and carcass lean content. One QTL had previously been published on the proximal part of this chromosome as affecting a feed intake pattern (average feed per visit) in a Meishan $\times$ LW cross (Houston *et al*., 2005). Other QTL had been located in the same region for BFT, by Kuryl *et al*. (2003) in a Meishan or PI $\times$ Wild Boar cross, and by Kim *et al*. (2006) in a Yorkshire $\times$ Duroc cross. As fat deposition requires more energy and nutrients than protein deposition, QTL alleles leading to a reduced feed intake could be directly related to QTL alleles associated with a reduced fat deposition. Unfavourable genetic correlations between meat quality traits and feed efficiency measured by RFI or FCR have been reported in the literature (Tribout and Bidanel 2000; Gilbert *et al*., 2007) within the LW breed. In this study, excluding the halothane gene for which the *N* allele is fixed in the LW population, no chromosomal region showed joint effects on both categories of traits. This suggests that genetic associations between meat quality traits and feed efficiency might have different origins depending on the breed, resulting in different genetic correlations in this particular cross. An alternative explanation would be a lack of power in our design to detect all QTL effects. The QTL are located in the region of the *RN* gene (Milan *et al*., 2000), but further analyses remain necessary to evaluate the effect of this gene for this particular QTL.

SSC1. No QTL affecting feed intake and feed efficiency was detected on SSC1 in our study. Kim *et al.* (2000) reported a G/A substitution in position 1426 in the *MC4R* gene, which increased BFT, ADG and DFI. Among these traits, we mapped a QTL for BFT and weight at 70 kg BW at the end of the long arm of SSC1, at about 50 cM from the putative position of the *MC4R* gene on the linkage map. In addition, the genotypes of the 16 PI × LW sires were determined for the *MC4R* polymorphism. Five sires were found heterozygous, 8 homozygous AA, 3 homozygous GG, but concentrating the QTL detection analyses on heterozygous sire families did not reveal additional QTL for those traits.

Other traits

QTL regions were detected with no effect on feed intake traits. A highly significant region was mapped to chromosome 17, affecting traits related to skeletal development in pigs. The QTL mapped to positions 45, 90 and 17 cM, respectively. Further examination showed that the QTL affecting carcass length at position 45 cM would be a ghost QTL: when two segregating QTL are linked on a chromosome, a QTL detection can point out a unique QTL with large effects between the two positions. In our case, complementary tests suggested the existence of two pleiotropic QTL, one about 20 cM affecting carcass length and feet weight, and the second about 90 cM affecting carcass length and loin weight. Some QTL were formerly reported for traits related to skeletal development on SSC17, for carcass length at about 30 cM in a Landrace × Hampshire cross (Karlskov-Mortensen *et al.*, 2006) and at 70 cM in a PI × Meishan cross (Pierzchala *et al.*, 2003), and for femur dimension at 87 cM (Andersson-Eklund *et al.*, 2000). Suggestive QTL for L* and b* measured in the *gluteus medium* were also mapped in this region in our population, as did Fan *et al.* (2008) in a Berkshire × Yorkshire population for L* in the same chromosomal region.

QTL effect estimates depending on the dam line

Significant differences of the QTL effects estimated in the RFI^+ line genetic background compared with the RFI^- line genetic background were identified. They affected body composition and early growth. Body composition was affected by early selection in the divergent lines (Gilbert *et al.*, 2007), which might indicate that different chromosomal regions were selected for these traits on SSC13 and SSC17 in the dam lines. Experiments in plants revealed variation of QTL effect estimations depending on line crosses (Lecomte *et al.*, 2004), QTL × genetic background interactions (Lecomte *et al.*, 2004) and QTL × environment interactions (Moreau *et al.*, 2004). Demonstration in livestock populations is harder to obtain, but the greatest genetic heterogeneity in animal breeds compared with plant lines suggests even greater possibilities of interactions. This questions the across-breed generality of QTL effects found in experimental populations and their utilisation for selection in commercial populations, and suggests the necessity of a systematic validation of QTL effects in the populations and environments of production to achieve an optimal marker assisted selection of QTL.

Conclusion

In this study, few significant QTL for feed intake and feed efficiency were identified and they were generally associated with other major production traits, such as higher growth rate or leaner carcass. QTL alleles seemed to be segregating almost systematically within the breeds, and have relatively small effects on feeding traits. The LW dam line and the halothane genotype showed significant effects on QTL effect estimates. Both these results confirm once again the necessity to validate QTL effects in target populations before applying marker-assisted selection. As a consequence, the biology of those economically important traits appears to be driven by multiple and various loci, with potentially multiple regulatory pathways that guaranty relative stability in the expression of feeding traits. If this situation makes it more difficult to map QTL or use marker assisted selection, it might ensure high genetic potential for improvement of feeding traits through multiple biological routes, thus maintaining genetic diversity in the pig breeds for these traits.

Acknowledgements

The authors thank the reviewers for their constructive comments. This research was supported by grants from the Integrated Project SABRE from the European Sixth Research and Technological Development Framework Programme.

References

Andersson-Eklund L, Uhlhorn H, Lundeheim N, Dalin G and Andersson L 2000. Mapping quantitative trait loci for principal components of bone measurements and osteochondrosis scores in a wild boar × Large White intercross. Genetical Research 75, 223–230.

Archer JA, Richardson EC, Herd RM and Arthur PF 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. Australian Journal of Agricultural Research 50, 147–151.

Beeckmann P, Moser G, Bartenschlager H, Reiner G and Geldermann H 2003. Linkage and QTL mapping for *Sus scrofa* chromosome 8. Journal of Animal Breeding and Genetics 120(suppl. 1), 66–73.

Bidanel JP and Rothschild M 2002. Current status of quantitative trait locus mapping in pigs. Pig News and Information 23, 39N–53N.

Cai W, Casey DS and Dekkers JCM 2008. Selection response and genetic parameters for residual feed intake in Yorkshire swine. Journal of Animal Science 86, 287–298.

Cepica S, Schröffel J Jr, Stratil A, Hojny J, Pierzchala M, Kuryl J, Brunsch C, Sternstein I, Davoli R, Fontanesi L, Reiner G, Bartenschlager H, Moser G and Geldermann H 2003. Linkage and QTL mapping for *Sus scrofa* chromosome 9. Journal of Animal Breeding and Genetics 120(suppl. 1), 74–81.

Duthie C, Simm G, Doeschl-Wilson A, Kalm E, Knap PW and Roehe R 2008. Quantitave trait loci for chemical body composition traits in pigs and their positional associations with body tissues, growth and feed intake. Animal Genetics 39, 130–140.

Edwards DB, Ernst CW, Tempelman RJ, Rosa GJM, Raney NE, Hoge MD and Bates RO 2008. Quantitative trait loci mapping in an F2 Duroc × Pietrain resource population: I. Growth traits. Journal of Animal Science 86, 241–253.

Elsen JM, Mangin B, Goffinet B, Boichard D and Le Roy P 1999. Alternative models for QTL detection in livestock. I. General introduction. Genetics Selection Evolution 31, 213–224.

Fan B, Glenn KL, Geiger B, Mileham A and Rothschild MF 2008. Investigation of QTL regions on chromosome 17 for genes associated with meat colour in the pig. Journal of Animal Breeding and Genetics 125, 240–247.

Fujii J, Otsu K, Zorzato F, de Leon S, Khanna VK, Weiler JE, O'Brien PJ and MacLennan DH 1991. Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. Science 253, 448–451.

Geldermann H, Müller E, Moser G, Reiner G, Bartenschlager H, Cepica S, Stratil A, Kuryl J, Moran C, Davoli R and Brunsch C 2003. Genome-wide linkage and QTL mapping in porcine F_2 families generated from Pietrain, Meishan and Wild Boar crosses. Journal of Animal Breeding and Genetics 120, 363–393.

Gilbert H, Bidanel JP, Gruand J, Caritez JC, Billon Y, Guillouet P, Noblet J and Sellier P 2007. Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. Journal of Animal Science 85, 3182–3188.

Haley CS and Knott SA 1992. A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. Heredity 69, 315–324.

Heuven HCM, van Wijk RHJ, Dibbits B, van Kampen TA, Knol EF and Bovenhuis H 2009. Mapping carcass and meat quality QTL on *Sus Scrofa* chromosome 2 in commercial finishing pigs. Genetics Selection Evolution 41, 4.

Houston RD, Haley CS, Archibald AL and Rance KA 2005. A QTL affecting daily feed intake maps to Chromosome 2 in pigs. Mammalian Genome 16, 464–470.

Johnson ZB, Chewning JJ and Nugent RA 1999. Genetic parameters for production traits and measures of residual feed intake in Large White swine. Journal of Animal Science 77, 1679–1685.

Karlskov-Mortensen P, Bruun CS, Braunschweig MH, Sawera M, Markljung E, Enfält AC, Hedebro-Velander I, Josell A, Lindahl G, Lundström K, von Seth G, Jørgensen CB, Andersson L and Fredholm M 2006. Genome-wide identification of quantitative trait loci in a cross between Hampshire and Landrace I: carcass traits. Animal Genetics 37, 156–162.

Kennedy BW, van de Werf JHJ and Meuwissen THE 1993. Genetic and statistical properties of residual feed intake. Journal of Animal Science 71, 3239–3250.

Kim CW, Hong YH, Yun SI, Lee SR, Kim YH, Kim MS, Chung KH, Jung WY, Kwon EJ, Hwang SS, Park DH, Cho KK, Lee JG, Kim BW, Kim JW, Kang YS, Yeo JS and Chang KT 2006. Use of microsatellite markers to detect quantitative trait loci in Yorkshire pigs. Journal of Reproduction and Development 52, 229–237.

Kim KS, Larsen N, Short T, Plastow G and Rothschild MF 2000. A missense variant of the porcine melanocortin-4 receptor (*MC4R*) gene is associated with fatness, growth, and feed intake traits. Mammalian Genome 11, 131–135.

Kuryl J, Pierzchala M, Hojny J, Reiner G, Bartenschlager H, Moser G and Geldermann H 2003. Linkage and QTL mapping for *Sus scrofa* chromosome 15. Journal of Animal Breeding and Genetics 120(suppl. 1), 119–125.

Labroue F, Guéblez R, Meunier-Salaün MC and Sellier P 1999. Feed intake behaviour of group-housed Piétrain and Large White growing pigs. Annales de Zootechnie 48, 247–261.

Labroue F, Guéblez R, Sellier P and Meunier-Salaün MC 1994. Feeding behaviour of group-housed Large White and Landrace pigs in French central test stations. Livestock Production Science 40, 303–312.

Larzul C, Le Roy P, Guéblez R, Talmant A, Gogué J, Sellier P and Monin G 1997. Effect of halothane genotype (*NN, Nn, nn*) on growth, carcass and meat quality traits of pigs slaughtered at 95 or 125 kg live weight. Journal of Animal Breeding and Genetics 114, 309–320.

Laville E, Sayd T, Terlouw C, Blinet S, Pinguet J, Fillaut M, Glénisson J and Chérel P 2009. Differences in pig muscle proteome according to HAL genotype: implications for meat quality defects. Journal of Agricultural and Food Chemistry 57, 4913–4923.

Leach LM, Ellis M, Sutton DS, McKeith FK and Wilson ER 1996. The growth performance, carcass characteristics, and meat quality of halothane carrier and negative pigs. Journal of Animal Science 74, 934–943.

Lecomte L, Duffé P, Buret M, Servin B, Hospital F and Causse M 2004. Marker-assisted introgression of five QTLs controlling fruit quality traits into three tomato lines revealed interactions between QTLs and genetic backgrounds. Theoretical and Applied Genetics 109, 658–668.

Lee SS, Chen Y, Moran C, Stratil A, Reiner G, Bartenschlager H, Moser G and Geldermann H 2003. Linkage and QTL mapping for *Sus scrofa* chromosome 5. Journal of Animal Breeding and Genetics 120(suppl. 1), 38–44.

Le Roy P, Moreno C, Elsen JM, Caritez JC, Billon Y, Lagant H, Talmant A, Vernin P, Amigues Y, Sellier P and Monin G 2000. Interactive effects of the HAL and RN genes on carcass quality traits in pigs: preliminary results. In EAAP Publication No 100: quality of meat and fat in pigs as affected by genetics and nutrition (ed C Wenk, JA Fernandez and M Dupuis), pp. 139–142. Wageningen Pers, Wageningen, The Netherlands.

Milan D, Jeon JT, Looft C, Amarger V, Robic A, Thelander M, Rogel-Gaillard C, Paul S, Iannuccelli N, Rask L, Ronne H, Lundström K, Reinsch N, Gellin J, Kalm E, Le Roy P, Chardon P and Andersson L 2000. A mutation in PRKAG3 associated with excess glycogen content in pig skeletal muscle. Science 288, 1248–1251.

Mohrmann M, Roehe R, Knap PW, Plastow GS and Kalm E 2006. Quantitative trait loci associated with AutoFOM grading characteristics, carcass cuts and chemical body composition during growth of *Sus scrofa*. Animal Genetics 37, 435–443.

Moreau L, Charcosset A and Gallais A 2004. Use of trial clustering to study QTL*environment effects for grain yield and related traits in maize. Theoretical Applied Genetics 110, 92–105.

Nezer C, Moreau L, Wagenaar D and Georges M 2002. Results of a whole genome scan targeting QTL for growth and carcass traits in a Pietran × Large White intercross. Genetics Selection Evolution 34, 371–387.

Noblet J, Karege C, Dubois S and van Milgen J 1999. Metabolic utilisation of energy and maintenance requirements in growing pigs: effect of sex and genotype. Journal of Animal Science 77, 1208–1216.

Pierzchala M, Cieslak D, Reiner G, Bartenschlager H, Moser G and Geldermann H 2003. Linkage and QTL mapping for *Sus scrofa* chromosome 17. Journal of Animal Breeding and Genetics 120(suppl. 1), 132–137.

Thaller G, Dempfle L, Schlecht A, Wiedemann S, Eichinger H and Fries R 2000. Effect of the MHS locus on growth, carcass and meat quality traits in F_2 crosses between Mangalitza and Piétrain breeds. Archiv für Tierzucht 43, 263–275.

Tor M, Estany J, Villalba D, Cubilo D, Tibau J, Soler J, Sanchez A and Noguera JL 2001. A within-breed comparison of RYR1 pig genotypes for performance, feeding behaviour, and carcass, meat and fat quality traits. Journal of Animal Breeding and Genetics 118, 417–427.

Tribout T and Bidanel JP 2000. Genetic parameters of meat quality traits recorded on Large White and French Landrace station-tested pigs in France. In EAAP Publication No 100: quality of meat and fat in pigs as affected by genetics and nutrition (ed C Wenk, JA Fernandez and M Dupuis), pp. 37–41. Wageningen Pers, Wageningen, The Netherlands.

Van Laere AS, Nguyen M, Braunschweig M, Nezer C, Collette C, Moreau L, Archibald AL, Haley CS, Buys N, Tally M, Andersson G, Georges M and Andersson L 2003. A regulatory mutation in IGF2 causes a major QTL effect on muscle growth in the pig. Nature 425, 832–836.