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To cite this version:

Thierry Tribout, Nathalie N. Iannuccelli, Tom T. Druet, Hélène Gilbert, Juliette Riquet, et al.. Detection of quantitative trait loci for reproduction and production traits in Large White and French Landrace pig populations.. 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, 2006, Brazil, France. pp.Inconnu. ⟨hal-02816661⟩

HAL Id: hal-02816661

https://hal.inrae.fr/hal-02816661v1

Submitted on 9 Dec 2025

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DETECTION OF QUANTITATIVE TRAIT LOCI FOR REPRODUCTION AND PRODUCTION TRAITS IN LARGE WHITE AND FRENCH LANDRACE PIG POPULATIONS

T. Tribout[1], N. Iannuccelli[2], T. Druet[1], H. Gilbert[1], J. Riquet[2], R. Gueblez[3], M.J. Mercat[3], J. P. Bidanel[1], D. Milan[2], P. Le Roy[1]

[1] INRA Station de Génétique Quantitative et Appliquée, 78352 Jouy-en-Josas Cedex, France, [2] INRA Laboratoire de Génétique Cellulaire, 31326 Castanet-Tolosan Cedex, France, [3] Institut Technique du Porc - Pôle Génétique et Qualité, BP 3, 35650 Le Rheu, France

INTRODUCTION

During the last decade, many QTL detection experiments have been conducted in the pig, most of the time using experimental designs based on crosses between two distant breeds, as for example Meishan and Large White (Bidanel *et al.* 2001). Very few experiments have been conducted in pure breeds (e.g. Evans *et al.* 2003), even though the QTL detected in such populations should be more directly usable in breeding programs. In France, the use of artificial insemination hyperprolific boars in collective maternal breeds has resulted in the constitution of large families, potentially suitable for QTL detection. The present paper reports the results of a genome-wide scan for production and reproduction traits in Large White (LW) and French Landrace (FL) populations, taking advantage of the existence of such families.

MATERIAL AND METHODS

Material. This experiment was based on a granddaughter design (Weller *et al.* 1990) including 3 generations in each family: a male founder (generation 1), his sons and daughters (generation 2 = "parents"), and sons and daughters of these latter (generation 3 = "grandsons" and "granddaughters"). Animals of generations 1 and 2 were genotyped for genetic markers. Phenotypic traits were recorded on generation 3 as usually in such a design, but the performances of the genotyped parents were also considered to maximize information.

The French porcine national database, used for the genetic evaluation of collective breeds (Tribout *et al.* 1998), was used from 1996 to 2001 to identify the "largest" existing purebred families. Desired requirements were a minimum of 30 parents per male founder, and 40 offspring or more with records per parent. DNA samples were taken from the national porcine DNA bank for boars born after 1998, or collected on farm for still living dams and older sows. Phenotypic traits considered for the QTL detection were those routinely collected for selection purposes and stored in the French porcine national database:

- total number of piglets born, number of piglets born alive and number of stillborn piglets per litter (TOTp, LIVp, DEADp) recorded on purebred sows in selection and multiplication herds;
- live weight (LWOT) and the mean (OS_M) of 6 ultrasonic measurements of backfat thickness (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, last rib and hip joint) recorded at the end of the on farm testing period (148 days of age and 95 kg on average) on male and female candidates in selection herds. The age of animals at the end of the on farm test

was preadjusted to 100 kg (AGE100) using regression coefficients depending on batch mean performance for growth.
The design finally included 239 parents (166 males and 73 females) distributed in 8 half-sib families (5 in LW female line and 3 in FL breeds). Family size averaged 30 genotyped animals per male founder (ranging from 15 to 62) for production traits, but was smaller for reproduction traits (24 genotyped parents on average, ranging from 7 to 56). On average, parents had 215 offspring with records for production traits and 70 daughters with records on 3.9 litters for reproduction traits, but data volume greatly differed among parents.

Methods. A total of 558 microsatellites mapped on the USDA map (Rohrer *et al.* 1994) or on the PIGMaP map (Archibald *et al.* 1995) were analyzed on 7 of the 8 founder males. An average heterozygosity of 52% was observed. A set of 144 markers covering the 18 pairs of autosomes was selected. The average distance between two microsatellites was 13.3 cM (SD=9.7 cM), and average marker informativity was 0.77.
QTL detection was carried out by within-male founder linear regression with the model described by Boichard *et al.* (2003), using the QTLMAP software (Elsen *et al.* 1999). Only the most likely phase was retained for each founder to calculate phase transmissions in the design.
The dependant variable Y_{ij} for the jth parent from the ith male founder was computed by generalizing the "daughter yield deviation" approach described by VanRaden and Wiggans (1991) to include the parents own performances. Y_{ij} for production traits (one performance per animal) was calculated as:

$$Y_{ij} = \frac{y_j + \frac{\lambda}{1+2\lambda}\sum_{k=1}^{N_d}(y_{d_k} - \frac{\hat{u}_{m(k)}}{2})}{W}, \text{ where } W = 1 + \frac{\lambda N_d}{2(1+2\lambda)}, \lambda = \frac{\sigma_e^2}{\sigma_a^2} = \frac{\text{residual variance}}{\text{additive genetic variance}},$$

N_d is the number of sons or daughters of parent j with a record, y_j and y_{dk} are, respectively, the performance of parent j and of its kth son/daughter adjusted for the environmental effects, and $\hat{u}_{m(k)}$ is the estimated additive genetic value of the second parent of the kth son/daughter of j.
The Y_{ij} for reproduction traits were similarly computed, except that females of generations 2 and 3 could have several records and that the permanent environmental effect had been previously absorbed in equations of additive genetic effects in the MME coefficient matrix.
The estimates of environmental effects and of additive genetic values $\hat{u}_{m(k)}$ were computed with the PEST software (Groeneveld *et al.* 1990). Single trait mixed animal models were used, including all performances recorded in the populations from 1992 to 2003 for production traits and from 1992 to 2005 for reproduction traits, and using five generations of ancestors. LW and FL populations were considered separately. Genetic parameters used in PEST had been estimated using version 4.5 of the VCE software (Neumaier and Groeneveld 1998) with the same mixed models on subsamples of the files described above. The models used in PEST and VCE, and the effects for which the performances were adjusted are detailed in table 1.
For each trait and each chromosome, 30 000 within-family permutations were performed to estimate empirical chromosome-wide significance levels of the test statistics (Churchill and Doerge 1994). The average substitution effect of significant QTL was calculated as the mean of the substitution effects estimated for male founders considered heterozygous for the QTL

(*i.e.* whose family contribution to the overall likelihood ratio test exceeded the value of a χ^2 distribution with one degree of freedom and a probability of 5%).

Table 1. Models used and effects for which performances were adjusted to calculate Y_{ij}

Trait	Effects included in the model
TOTp, LIVp, STILLp	Parity$^{F\ adj}$, age at farrowing within parity$^{C\ adj}$, month of farrowing$^{F\ adj}$, combination(herd year mating type)$^{F\ adj}$, boar mate$^{R\ adj}$, permanent environmental effect^{R}, breeding value^{R}
LWGT, AGE100	Age at the end of on farm test$^{C\ adj}$, birth litter$^{R\ adj}$, combination(herd year batch)$^{F\ adj}$, breeding value^{R}
US_M	Live weight at the end of on farm test$^{C\ adj}$, birth litter$^{R\ adj}$, combination(herd year batch)$^{F\ adj}$, breeding value^{R}

^{F} fixed effect; ^{C} covariate; ^{R} random effect; records were adjusted for effects noted ^{adj}

RESULTS AND DISCUSSION

The QTL detected with a chromosome-wide significance level of 5% are shown in table 2. Significant and large effects (from 0.3 to 1.3 phenotypic standard deviations) were found for all traits except AGE100 and TOTp. The results suggest a QTL on SSC4 for LWGT (p=0.05), and three QTL were found for fatness, on SSC2 (p=0.037), SSC3 (p=0.009) and SSC17 (p=0.014). Several loci affecting fatness and growth were reported by other authors in the same areas (consult for example PigQTLdb, Hu *et al.* 2005). From these results, some of the polymorphisms existing between divergent populations also seem to be observable in commercial breeds.

On the contrary, very few QTL were detected in other studies for litter size, and the 6 QTL found for LIVp and STILLp do not match any of them.

Table 2. QTL with a chromosome-wide significance level (p-value) of 5% or better

Trait	σ_{ph} - h^2 ^{A}	SSC	Location of maximum (cM) *[C.I.5%]* ^{B}	p-value	Heterozygous founders ^{C}	Average substitution effect
US_M (mm)	1.5 – *0.47*	2	15 *[3 – 29]*	0.037	FL_3 LW_1	1.0 mm
US_M (mm)	1.5 – *0.47*	3	105 *[97 – 129]*	0.009	FL_2 LW_2	1.2 mm
US_M (mm)	1.5 – *0.47*	17	28 *[15 – 55]*	0.014	FL_1 LW_2 LW_3	2.0 mm
LWGT (kg)	8.7 – *0.29*	4	62 *[38 - 73]*	0.050	FL_2 LW_5	7.4 kg
STILLp (piglets)	1.4 – *0.09*	6	88 *[79 - 94]*	0.018	FL_2 FL_3 LW_1	0.6 pig.
STILLp (piglets)	1.4 – *0.09*	11	66 *[49 - 84]*	0.035	FL_2 LW_1	1.0 pig.
STILLp (piglets)	1.4 – *0.09*	14	28 *[21 - 37]*	0.045	FL_1 FL_3 LW_3	0.4 pig.
LIVp (piglets)	3,1 – *0.10*	7	27 *[24 - 38]*	0.036	FL_2 LW_3	1.3 pig.
LIVp (piglets)	3,1 – *0.10*	16	9 *[2 - 32]*	0.050	LW_4	2.5 pig.
LIVp (piglets)	3,1 – *0.10*	18	1 *[1 - 8]*	0.013	FL_1 LW_5	1.2 pig.

^{A} phenotypic standard deviation and heritability of the trait (average parameters of the 2 breeds)
^{B} lod drop-off 5% confidence interval of the QTL location ^{C} i^{th} male founder within breed

None of the 10 QTL detected here reached a genome-wide significance level, probably because of the limited number of families (reducing the chances of having heterozygote founders for QTL) and their relatively low size. Very large families in commercial populations are indeed scarce, the intense use of a limited number of artificial insemination boars being undesirable for genetic diversity reasons. Moreover, once a large family was identified in the national database, some of its members (parents or even founder) were already culled and their DNA was no longer available. Nevertheless, considering 18 chromosomes and a total of 6 traits (corresponding to 4 independent traits), about only 4 false positive results were expected at a 5% elementary significance level, which is lower than the 10 QTL detected. This implies that several of the QTL reported here represent true QTL effects.

CONCLUSION

Several QTL were detected for fatness, growth and litter size. These results tend to show that a part of the phenotypic variance observed in commercial populations can still be explained by segregation at large effect QTL, despite a long and intensive selection work being made on these traits. Further work remains to be done, such as considering litter size performances of crossbred daughters to increase the power of the design. Some other traits will be investigated, such as litter size at weaning, reproduction intervals … Finally, from these preliminary detections, further studies will be required to confirm the QTL reported and to map them more accurately. Segregation of the alleles of effective loci in various commercial populations also has to be investigated.

AKNOWLEDGEMENTS

Genotyping was performed on the CRGS platform of Génopole Toulouse Midi Pyrénées. This project was funded in part by grants from the French Ministry of Agriculture (programme Actions Innovantes) and from Génopole Toulouse Midi Pyrénées. The French collective breeding organisations are acknowledged for participating in the project, particularly for making data available and for blood sampling of animals.

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A genome-wide scan was performed in Large White (LW) and French Landrace (FL) pig populations in order to identify QTL affecting reproduction and production traits. This experiment was based on a granddaughter design, including 5 LW and 3 FL families identified in the French porcine national database. Animals were genotyped for 144 microsatellite markers. Three production and three reproduction traits were considered. Ten QTL were detected with a chromosome-wide significance level of 5%, for average backfat thickness (SSC2, 3, 17) and live weight (SSC4) at the end of the on farm test, and for the number of stillborn piglets (SSC6, 11, 14) and of living piglets born (SSC7, 16, 18) per litter.