Short Communication

QTL analysis of production traits on SSC3 in a Large White×Meishan pig resource family

B. Zuo[1], Y.Z. Xiong[1#], Y.H. Su[2], C.Y. Deng[1], M.G. Lei[1], F.E. Li[1], R. Zheng[1] and S.W. Jiang[1]

[1] Key Laboratory of Swine Genetics and Breeding, Ministry of Agriculture & Key Lab of Agricultural Animal Genetics, Breeding and Reproduction, Ministry of Education, College of Animal Science and Veterinary Medicine, Huazhong Agricultural University, Wuhan, 430070, P. R. China
[2] Key Laboratory of Molecular Cell Biology and New Drug of LiaoNing Province, JinZhou Medical College, JinZhou, 121000, P. R. China

Abstract

In order to locate the genetic regions that are responsible for economically important traits, a resource population was established by crossing Large White boars and Meishan sows. Phenotypic data of a total of 287 F_2 offspring were collected from 1998 to 2000 and QTL analysis conducted using nine microsatellites on *Sus scrofa* chromosome 3 (SSC3). Least square regression interval mapping revealed two significant QTL effects on dressing percentage and moisture in *m. longissimus dorsi*, respectively. They were located at 136 cM and 22 cM in the genetic linkage map, near the marker Sw349 and Swr1637, respectively. QTL for dressing percentage had an additive effect of -1.035 ± 0.296% and a dominance effect of 1.056 ± 0.481%, and the explained phenotypic variance was 15.9%. The additive and dominance effects of QTL for moisture in *m. longissimus* dorsi were -0.025 ± 0.076% and 0.365 ± 0.101%, respectively, indicating that this QTL seemed to be significantly dominant in action. The present study confirms previously identified QTL and provides an important step in the search for the actual major genes involved in the traits of economic interest.

Most production traits in pigs such as growth, fatness and meat quality are quantitative traits controlled by many genes, termed quantitative trait loci (QTL). Genes influencing quantitative traits can be identified through two different strategies: the candidate gene approach and the whole genome scan approach. In practice, a combination of both strategies is often used, i.e. positional candidate gene approach: QTL mapping will reveal chromosomal regions that have an impact on the trait and subsequently functional candidate genes can be selected from this region (O'Brien *et al.*, 1999). In order to identify the genes or genetic regions responsible for quantitative traits, a pig reference population has been established using three Large White boars and seven Meishan dams as parents. The F2 offspring of the resource population were slaughtered in three contemporary groups between 1998 and 2000. It was shown that there existed significant QTL affecting growth and meat quality traits on *Sus scrofa* chromosome 3 (SSC3) in 140 F_2 individuals slaughtered in the last half year of 2000 (Zuo *et al.*, 2003a; b). Many other studies also reported that SSC3 harboured QTL for growth (Casas-Carrillo *et al.*, 1997; De Koning *et al.*, 2001; Malek *et al.*, 2001), carcass traits (Anderson-Eklund *et al.*, 1998) and meat quality (Milan *et al.*, 1998). The aim of the present study was to confirm previously identified QTL for growth and carcass traits using the combined data of 287 F2 offspring from 1998 to 2000.

The pigs were slaughtered following a standard protocol (Xiong & Deng, 1999). The average weight at slaughter was 87.9 ± 6.14 kg. Growth and carcass traits analyzed, were birth weight and carcass weight, growth rate from birth to the end of test, carcass length, dressing percentage, longissimus muscle area and average backfat depth over three positions. Meat quality traits included meat pH of *m. semipinalis capitis*, moisture in *m. longissimus dorsi*, water holding capacity and intramuscular fat in *m. longissimus dorsi*.

The animals were genotyped for nine microsatellite loci: Sw2021, Swr1637, Sw1443, Sw2618, Sw2047, Sw2408, Sw349, Sw717, S0165. The procedure of genotyping as described by Zuo *et al.* (2003b) was followed. All animals in the experiment were halothane tested. Of all animals, 16 animals including one Large White boar, two F1 boars and thirteen F_2 offspring were carriers of the halothane negative gene.

Linkage analysis was performed using the CRIMAP version 2.4 (Green *et al.*, 1990). Web software (http://qtl.cap.ed.ac.uk) was used to carry out QTL analysis. For all traits, interval mapping using least square regression methods was applied, following the line-cross model (Haley *et al.*, 1994). Using multi-marker information, three probabilities were calculated at 1-cM intervals along the chromosome. $P_{(QQ)}$ is the probability that an F_2 offspring inherited two Large White alleles, $P_{(qq)}$ that it inherited two Meishan alleles, and $P_{(Qq)}$ that it inherited one from each breed. At every centimorgan (cM) across the genome, the following model was fitted:

$$y_{ijklm} = u + s_i + f_j + g_k + Hal_l + \beta cov_{ijklm} + c_{am}\,a + c_{dm}\,d + e_{ijklm}$$

where y_{ijklm} is the phenotype of the mth F_2 offsping; u is the overall mean; s_i is the ith sex effect (i = 1, 2); f_j is the full-sib family (j = 1 ~ 41); g_k is the contemporary group (k = 1~3); Hal_l is the fixed effect of halothane gene (l = 1 ~ 2). The βcov_{ijklm} differed depending on the trait. It is carcass weight for the traits carcass length, dressing percentage, longissimus muscle area and average backfat depth and the covariate is the age at slaughter for meat quality traits. a and d are the estimated additive and the dominance effects of a putative QTL, respectively. c_{am} is the additive coefficient of the mth individual at a putative QTL in the genome and the probability $P_{(QQ)}$ - $P_{(qq)}$. c_{dm} is the dominant coefficient of the mth individual at a putative QTL in the genome and $P_{(Qq)}$, e_{ijklm} is the residuals error. In this study, the additive effects were estimated for Large White QTL allele. Thus, positive values of the additive effects denote an increase of the trait due to the Large White QTL allele. Additive genetic fraction of adjusted F_2 phenotypic variance (σ_y^2) explained by a QTL was computed assuming that alternative alleles were fixed in each breed; i.e., $h^2_Q = a^2/2\sigma_y^2$ (Ovilo *et al.*, 2000). Chromosome-wise significance thresholds were calculated empirically by permutation tests.

The most probable order produced by build option is as follows (Kosambi cM; sex-average values): Sw202121.4-Swr1637-16.5-Sw1443-10.9-Sw2618-29.9-Sw2047-31.0-Sw2408-25.9-Sw349-19.4-Sw717-17.1-S0165. The marker order was identical to that reported by the USDA-MARS (http://www.genome.iastate.edu/pig), but the distances were longer than those in the USDA map. This difference between the maps may be the result of typing errors that are known to increase map lengths (Marklund *et al.*, 1996), as well as different reference populations used.

The result of QTL mapping is presented in Table 1 and Figure 1. There was significant evidence for the presence of two QTL affecting dressing percentage and moisture in *m. longissimus dorsi*, respectively. For dressing percentage, the most probable location of QTL was found at 136 cM, close to the marker SW349. The additive effect of Large White allele was -1.035%, suggesting that the allele with higher dressing percentage originated from the Meishan breed. There was also an indication of a dominance effect with 1.056% at this QTL, and the effect was positive in contrast to additive effect. This QTL explains 15.9% of the phenotype variation. To our knowledge, this is the first study reporting a significant QTL for dressing percentage on SSC3. As this convincing QTL for dressing percentage is not in accordance with the expected effect due to selection, the beneficial effect of the Meishan allele on dressing percentage makes this QTL an interesting candidate for marker-assisted selection.

Another significant QTL for moisture in *m. longissimus dorsi* was detected at about 22 cM position, around the marker Swr1637, confirming that SSC3 contains QTL for meat quality reported earlier (Milan *et al.*, 1998; Zuo *et al.*, 2003b). This QTL seemed to be significantly dominant in action, and the positive dominance effect indicated that heterozygotes had 0.75% more moisture than the average mean of the two homozygotes. In general, only QTL with fairly large effects were expected to reach statistical significance, but the additive fraction of phenotype variation was only 0.05%. The formula ($h^2_Q = a^2/2\sigma_y^2$) only applies if the lines are fully inbred and in the F2 p = q = 0.5. If the QTL alleles are segregating in the parental lines (Large White or Meishan) this formula is no longer correct. In this instance, the estimation of the fraction of the phenotype that is explained by QTL tended to be lower, because the dominant effects have been neglected in this original formula. No significant evidence for QTL was found for any other traits.

Table 1 QTL analysis for production traits on SSC3

Traits	Marker interval	Location cM	Additive effect	Dominance effect	Variance%	F-value
Birth weight, kg	Swr1637-Sw1443	32	0.032 ± 0.030	0.101 ± 0.045	0.44	2.94
Growth rate from birth to end of test, kg/d	Sw1443	40	0.001 ± 0.0006	0.001 ± 0.001	0.01	2.8
Carcass length, cm	Swr1637-Sw1443	24	0.250 ± 0.483	1.128 ± 0.653	0.70	1.49
Dressing percentage, %	Sw349	136	1.035 ± 0.296	1.056 ± 0.481	15.9	6.96*
Average backfat depth, cm	Sw2408-Sw349	117	0.008 ± 0.054	0.298 ± 0.113	0.01	3.47
Longissimus muscle area, cm^2	Sw1443	38	1.012 ± 0.531	0.076 ± 0.781	10.7	1.86
Meat pH	Sw349	135	0.048 ± 0.021	-0.009 ± 0.033	0.57	2.60
Moisture, %	Swr1637	22	-0.025 ± 0.076	0.365 ± 0.101	0.05	6.5*
Water holding capacity, %	Sw2408-Sw349	124	1.107 ± 0.668	0.938 ± 1.395	10.7	1.77
Intramuscular fat, %	Swr1637	21	0.026 ± 0.065	-0.192 ± 0.086	0.06	2.77

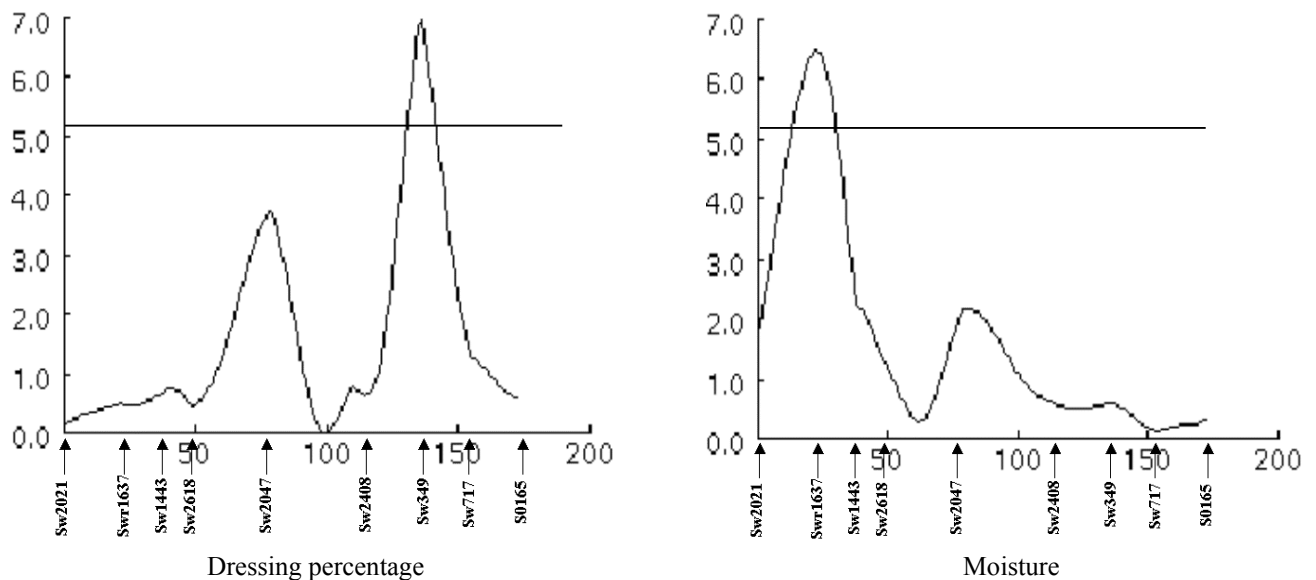* represents significance above the 5% chromosome-wise level

Figure 1 F ratio curves for evidence of QTL. The X-axis indicates the relative position on the linkage map, the Y-axis represents the F-ratio. Horizontal line indicates 5% chromosome-wise significance. Left figure represents QTL graphs for dressing percentage. Right figure represents QTL graphs for moisture in the *m. longissimus dorsi*

A long-term goal in QTL mapping is to identify the causative genes at the molecular level (Knott *et al.*, 1998). However, owing to the low precision of the QTL mapping, it is difficult to identify actual major genes with existing technology. With the development of comparative genomics, identification of the genes in a well-defined human chromosomal region homologous to a pig QTL region will identify numerous positional candidate genes for the trait. The increasing development of detailed comparative maps assists in the identification of candidate genes responsible for the mapped QTL. Zoo-FISH analysis and chromosome painting have shown an extended conservation of synteny between SSC3 and human chromosome (HSA) 2, 7 and 16 (Goureau *et al.*, 1996). Some functional genes that have been mapped around this region, such as *ATP2A1*, *POMC* and *TAF1B*, could be considered as possible candidates. Further studies will be aimed at fine mapping of the chromosome regions of interest and comparative candidate gene analysis so that the

possible QTL (actual) gene could be isolated and characterized. Eventual identification of candidate genes associated with the traits of interest will contribute to the improvement of targeted traits in pigs.

Acknowledgements

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