

QTL analysis for carcass composition and meat quality traits on SSC7q1.1-q1.4 region in Large White × Meishan F₂ pigs

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ABSTRACT: Significant QTL for carcass and meat quality traits on *Sus scrofa* chromosome 7 (SSC7) were detected in various Meishan derived resource populations, especially on q1.1-q1.4 region. In order to confirm and narrow the QTL in this region, seven single-nucleotide polymorphisms (SNPs) and one insertion or deletion located in eight genes (*BTNL1*, *SLC39A7*, *COL21A1*, *PPARD*, *GLP1R*, *MDFI*, *GNMT*, and *PLA2G7*) were included for linkage mapping in a Large White × Meishan resource population, as well as two flanking microsatellite markers (*SW2155* and *SW352*). Ten chromosome-wise significant QTL and two suggestive QTL were found. QTL affecting carcass weight and dressing percentage were mapped within the interval *BTNL1* and *SLC39A7*. QTL for skin weight and percentage, bone weight and percentage in carcass were located between the interval *PPARD* and *GLP1R*. QTL for fat weight and percentage in carcass were detected between *GNMT* and *PLA2G7* genes, while QTL for loin muscle width was found between *GLP1R* and *MDFI*. The results of this study will help to facilitate identifying the causative molecular genetic variation in this region.

Keywords: single nucleotide polymorphism; linkage map; quantitative trait locus; *Sus scrofa* chromosome 7

The carcass composition and meat quality traits such as fat weight, skin weight, loin muscle area, lean meat weight, water holding capacity, and intramuscular fat are economically important traits in pig production. Most of these traits are quantitative traits which are controlled by polygene with pleiotropic effects. So far, quantitative trait loci (QTL) mapping for important economically traits in swine has been conducted to identify the molecular genetic basis of these quantitative traits, leading to significant progress (Bidanel and Rothschild, 2002; Hu et al., 2005). According to the PigQTLdb (<http://www.animalgenome.org/QTLD/db/pig.html>), there was abundant evidence of significant QTL affecting carcass composition and muscle traits on *Sus scrofa* chromosome 7 (SSC7). Chinese fat-type Meishan pig

breed and the lean-type Large White pig breed show significant differences in muscle growth and meat quality traits (Yang et al., 2011). Using the F₂ resource population derived from the intercross of Large White boars and Meishan dams, we detected significant QTL for carcass and meat quality traits on SSC7 (Zuo et al., 2004). Most of these QTL were located on SSC7p1.1-q1.4 region, which was in good agreement with many results reported in various Meishan-derived populations (Milan et al., 1998; Rohrer et al., 1998; De Koning et al., 1999; 2001; Rattink et al., 2000; Bidanel et al., 2001; Sato et al., 2003; Demeure et al., 2005). Due to the development of sequencing technologies, still more single nucleotide polymorphisms (SNPs) are being used in linkage mapping and even in QTL mapping. SNP maps

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are becoming the gold standard for genetic markers, even for linkage analyses (Bellenguez et al., 2009). In this study, a genetic linkage map based on eight SNPs and two microsatellite markers were constructed to confirm and narrow the QTL localization of carcass composition and meat quality traits in this region.

MATERIAL AND METHODS

Animals and traits

The study was approved by the Animal Care Committee at the Huazhong Agricultural University. The Large White × Meishan resource population used in the linkage and QTL analysis was derived from the intercross of Large White and Meishan pigs and was formed by 54 F₁, 315 F₂ and 21 grandparent animals in 37 full-sib families. The animals were born and raised on the Huazhong Agricultural University Jingpin pig farm. All pigs were fed twice daily with diets formulated according to age under the standardized feeding and management regimen, and had free access to water. The F₂ pigs were slaughtered at 200 days on average, with the slaughter weight of 87.0 ± 7.07 kg. After the pigs' slaughter, the traits were measured according to procedures given in the literature (Xiong and Deng, 1999).

The carcass traits were measured and calculated as follows: dressing percentage (DP, %) was determined using carcass weight (CW, kg) as a proportion of body weight; left side of each carcass was dissected by separating bone, muscle, fat, and skin, each component was individually weighed; body fat percentage (FP, %), skin percentage (SP, %), bone percentage (BP, %), and lean meat percentage (LMP, %) were calculated relative to the carcass weight; loin eye height (LEH, cm) and loin eye width (LEW, cm) were the maximum height and width of the loin; loin eye area (LEA, cm²) was computed according to the formula LEA = LEH × LEW × 0.7.

Drip loss rate (DLR, %) and water holding capacity (WHC, %) were measured by the press technique, in which columnar samples of meat (height 1 cm, diameter 2.523 cm) were pressed for 5 min between 36 medium-speed filter papers under 35 kg using a swelling press. One day postmortem, the intramuscular fat percentage of the last thoracic vertebral *longissimus dorsi* (IMF, %) was determined by chloroform-methanol extraction. Water moisture (WM, %) was measured after meat samples had been placed in a drying oven at 102°C for 18 h.

SNP identification and genotyping

Seven novel markers including six SNPs and one insertion or deletion within seven genes (*BTNL1*, *COL21A1*, *PPARD*, *GLP1R*, *MDFI*, *GNMT*, and *PLA2G7*) on SSC7 q1.1-q1.4 region were developed by comparative sequencing, and then detected using PCR or PCR-restriction fragment length polymorphisms (RFLP) in more pigs (Huang et al., 2011). The SNP in *SLC39A7* gene and two flanking microsatellite markers (*SW2155* and *SW352*) available on SSC7 were also included in the linkage map (Zuo et al., 2004; Zhang et al., 2007; Chen et al., 2009). Animal genotyping was performed by PCR or PCR-RFLP with the application of the restriction endonucleases and separated in agarose gel or polyacrylamide gel.

Statistical analysis

Linkage analysis was performed using CRIMAP version 2.4 by integrating two flanking microsatellites and eight markers (Green et al., 1990). The most probable order and position of DNA markers were produced by Build option of CRIMAP. Least square regression interval mapping was used for QTL detection (Haley et al., 1994). QTL analysis was carried out with QTL Express (<http://qtl.cap.ed.ac.uk>). Using multi-marker information, three probabilities were calculated at 1-cM intervals along the chromosome. $P_{(QQ)}$, $P_{(qq)}$, and $P_{(Qq)}$ are the probability that F₂ offspring inherited two Large White alleles, two Meishan alleles, and one from each breed, respectively. At each centimorgan (cM) across the genome, the following model was fitted:

$$y_{ijk} = u + s_i + f_j + \beta \text{cov}_{ijk} + c_{ak} a + c_{dk} d + e_{ijk}$$

where:

- y_{ijk} = trait record of the k^{th} offspring
- u = overall mean
- s_i = the i^{th} sex effect ($i = 1, 2$)
- f_j = full-sib family ($j = 1-37$)
- βcov_{ijk} = carcass weight for the carcass traits and the age at slaughter for meat quality traits, respectively
- a, d = estimated additive and dominance effects of a putative QTL, respectively
- c_{ak} = additive coefficient of the k^{th} individual at a putative QTL and the probability $P_{(QQ)} - P_{(qq)}$
- c_{dk} = dominant coefficient of the k^{th} individual at a putative QTL and $P_{(Qq)}$
- e_{ijk} = residual error

Weight and age at slaughter were used as the covariate for carcass traits and meat quality traits, respectively.

In this study, the additive effects are 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. Chromosome-wise significant thresholds are obtained with 1000 repetitions of the permutation test (Churchill and Doerge, 1994). The percentage of phenotype variances explained by QTL (h_Q^2) is calculated by the formula:

$$h_Q^2 = (\text{MS}_{\text{reduce}1} - \text{MS}_{\text{full}}) / \text{MS}_{\text{reduce}} \times 100\%$$

where:

MS_{full} , $\text{MS}_{\text{reduce}1}$, $\text{MS}_{\text{reduce}}$ = residual mean square (MS) of the model with all detected QTL, with the rest detected QTL except for a given one and without all detected QTL, respectively (Liu et al., 2009)

SW2155 – 25.3 – *BTNL1* – 1.6 – *SLC39A7* – 5.3 – *COL21A1* – 3.6 – *PPARD* – 2.4 – *GLP1R* – 3.2 – *MDFI* – 2.2 – *GNMT* – 6.6 – *PLA2G7* – 8.9 – *SW352*. The sex-averaged linkage map spanned 59.1 cM, with an average marker interval of 6.57 cM. Results of the QTL analysis were presented in Table 1. A total of ten significant QTL and two suggestive QTL were detected. *F*-ratio curve for six significant QTL on *SSC7q1.1-q1.4* was shown in Figure 1.

We located QTL with impacts on CW and DP at 26 cM position in the interval *BTNL1* and *SLC39A7*. The QTL for CW and DP could explain approximately 3.35% and 3.76% fraction of the phenotypic variation, respectively. Individuals homozygous for the Large White allele had 2.31 kg more for CW and 2.75% for DP than those homozygous for Meishan alleles. Meishan allele caused decrease in CW and DP, which was consistent with breed phenotype. As carcass weight can reflect an indirect measure of dressing percentage, several studies identified significant QTL for carcass weight on *SSC7* (Andersson-Eklund et al., 1998; Sato et al., 2003; Yue et al., 2003). A significant QTL affecting carcass weight between *TNFB* and *S0102* was found in

RESULTS AND DISCUSSION

The most probable order produced by Build option is as follows (Kosambi cM; sex-average values):

Table 1. Results of QTL analysis for carcass composition and meat quality traits

Traits	Position (cM) ¹	Marker interval	$a \pm \text{SE}$	$d \pm \text{SE}$	h_Q^2	F_{Max}	P_c
CW (kg)	26	<i>BTNL1-SLC39A7</i>	-1.16 ± 0.34	0.05 ± 0.52	3.35	5.75	< 0.05
DP (%)	26	<i>BTNL1-SLC39A7</i>	-1.38 ± 0.39	0.10 ± 0.58	3.76	6.35	< 0.05
SW (kg)	36	<i>PPARD-GLP1R</i>	0.48 ± 0.11	0.12 ± 0.14	7.40	11.94	< 0.01
SP (%)	36	<i>PPARD-GLP1R</i>	0.77 ± 0.17	0.12 ± 0.22	7.31	11.81	< 0.01
BW (kg)	36	<i>PPARD-GLP1R</i>	0.45 ± 0.13	0.15 ± 0.18	4.03	6.75	< 0.05
BP (%)	36	<i>PPARD-GLP1R</i>	0.83 ± 0.20	0.15 ± 0.26	5.72	9.31	< 0.01
LMW (kg)	39	<i>GLP1R-MDFI</i>	-0.53 ± 0.31	-0.32 ± 0.43	0.73	2.000	non
LMP (%)	58	<i>PLA2G7-SW352</i>	0.16 ± 0.44	-1.18 ± 0.65	0.69	1.95	non
LEH (cm)	59	<i>PLA2G7-SW352</i>	-0.19 ± 0.10	-0.29 ± 0.13	1.81	3.53	non
LEW (cm)	40	<i>GLP1R-MDFI</i>	-0.21 ± 0.06	-0.07 ± 0.09	4.25	7.09	< 0.05
LEA (cm ²)	48	<i>GNMT-PLA2G7</i>	-1.24 ± 0.42	0.13 ± 0.70	2.43	4.41	non
FW (kg)	51	<i>PLA2G7-SW352</i>	-0.83 ± 0.25	0.08 ± 0.40	3.25	5.6	< 0.05
FP (%)	51	<i>PLA2G7-SW352</i>	-1.22 ± 0.40	0.38 ± 0.64	2.33	5.04	suggestive
DLR (%)	0	<i>SW2155</i>	-1.77 ± 0.50	-0.11 ± 1.00	3.77	6.35	< 0.05
WHC (%)	0	<i>SW2155</i>	2.45 ± 0.69	-0.00 ± 1.38	3.82	6.42	< 0.05
IMF (%)	25	<i>SW2155-BTNL1</i>	-0.12 ± 0.05	-0.03 ± 0.07	1.50	3.05	non
WM (%)	56	<i>PLA2G7-SW352</i>	0.21 ± 0.08	0.28 ± 0.12	2.92	5.10	suggestive

a = additive effect, d = dominance effect, h_Q^2 = fraction of phenotypic variance explained by the QTL, P_c = *P*-value for the chromosome-wise test, CW = carcass weight, DP = dressing percentage, SW = skin weight, SP = skin percentage, BW = bone weight, BP = bone percentage, LMW = lean meat weight, LMP = lean meat percentage, LEH = loin eye height, LEW = loin eye width, LEA = loin eye area, FW = fat weight, FP = body fat percentage, DLR = drip loss rate, WHC = water holding capacity, IMF = intramuscular fat percentage of the last thoracic vertebral *longissimus dorsi* muscle, WM = water moisture Negative values of the additive effects denote a decrease of the trait due to Meishan alleles

¹corresponding to F_{Max}

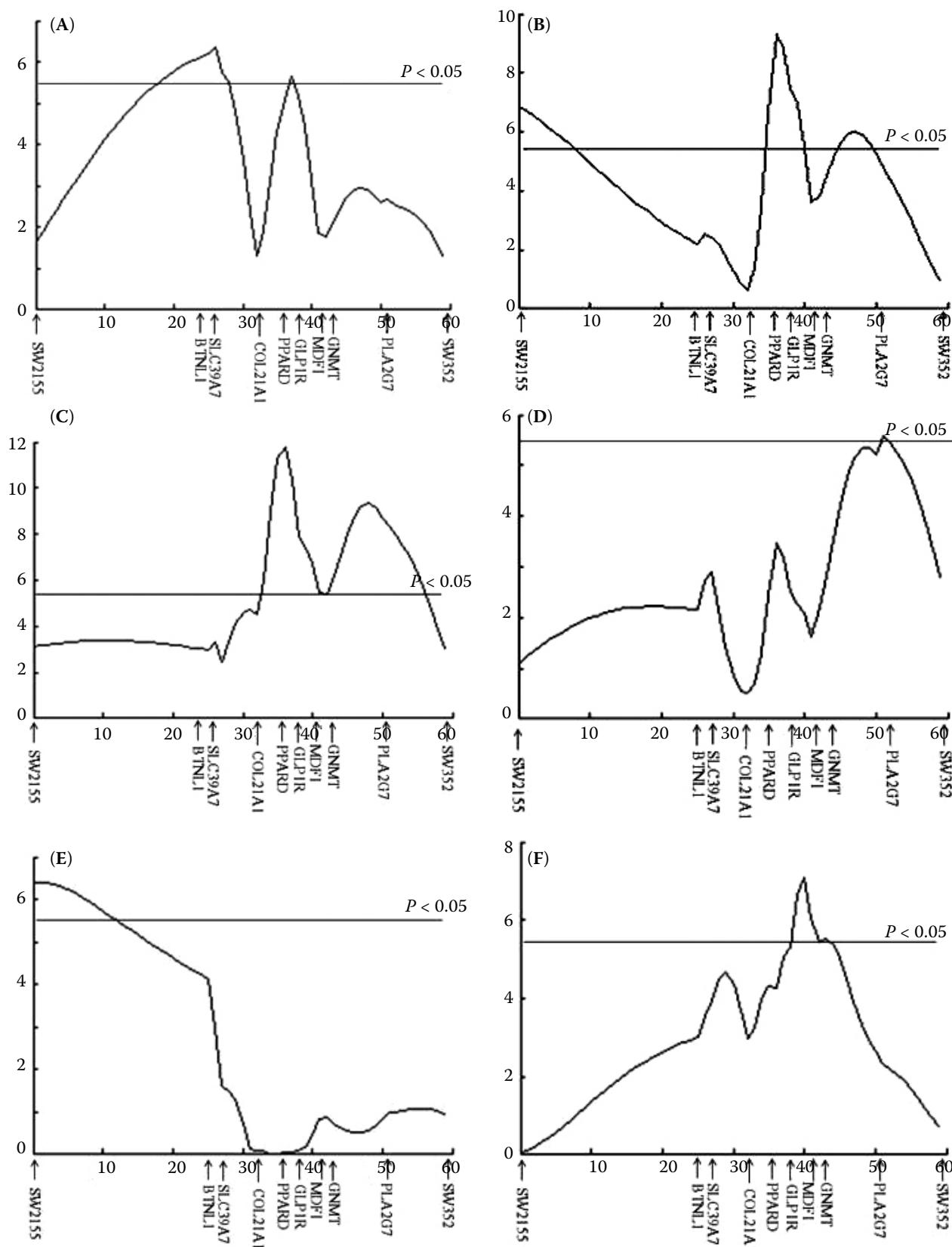


Figure 1. *F*-ratio curve for significant QTL on pig chromosome 7q1.1-q1.4. (A) DP, (B) BP, (C) SP, (D) FP, (E) WHC, (F) LEW

X-axis indicates the relative positions on the linkage map, Y-axis represents the *F*-ratio

F_2 generations of Wild Boar, Pietrain, and Meishan pigs (Andersson-Eklund et al., 1998), which was confirmed and narrowed by the mapping results of dressing percentage in this study, as both *BTNL1* and *SLC39A7* genes were all located within *TNFB* and *S0102* interval.

The most significant QTL were those affecting SW and SP, for which the respective *F*-statistics of 11.94 and 11.81 was obtained. The highest probability for QTL position was at 36 cM flanked with *PPARD* and *GLP1R*. The QTL for SW and SP could explain approximately 7.40% and 7.31% fraction of the phenotypic variation, respectively. Compared with individuals homozygous for Large White allele, those homozygous for the Meishan allele had more SW and SP, and the alleles increasing SW and SP were inherited from Meishan breed. One missense mutation (G32E) in *PPARD* gene is of functional significance as it mediates down-regulation of β -catenin and its target gene expression that is crucial for fat deposition in skin (Ren et al., 2011). We thus speculate that this mutation might have pleiotropic effects on skin weight and percentage in pigs. The QTL affecting BW and BP were mapped to the same marker interval as SW and SP QTL, with the most probable position of 36 cM. The QTL for BW and BP could explain about 4.03% and 5.72% of the phenotypic variation. Meishan allele had an increasing effect of 0.45 kg and 0.82% on BW and BP, respectively. The positive effects of Meishan allele on SP were in agreement with its breed phenotype, whereas the opposite occurred for BP.

The QTL for FW and FP were located at 51 cM between *PLA2G7* and *SW352*. The two QTL could explain 3.25% and 2.33% of phenotypic variance, respectively. Meishan allele was additive and presented positive and desirable effects, which was opposite to breed characteristics. A QTL affecting fatness in a way opposite to expectations based on breed phenotype was mapped to *SSC7* in Meishan-derived pig resource population, such as Meishan \times Large White population and Meishan \times Duroc population (Rohrer et al., 1998; De Koning et al., 1999, 2001; Rattink et al., 2000; Rohrer, 2000; Bidanel et al., 2001; Sato et al., 2003; Demeure et al., 2005). The effect of FW and FP QTL was concordant with the above-reported QTL. However, the position was different with the reported QTL, as most of the fatness QTL resided around *PPARD* gene. Thus there might be another significant QTL in this region.

Another significant QTL for LEW explaining 4.25% fraction of phenotypic variance was detected

at the 40 cM position between *GLP1R* and *MDFI*. The additive effect of the QTL was 0.21 cm, with the Large White allele increasing the LEW. Although several studies reported that there were significant QTL affecting LP and LEA around this region using different experimental animals (Sato et al., 2003; Yue et al., 2003; Sanchez et al., 2006; Uemoto et al., 2008), no QTL for LP and LEA with significant level were detected in the present study. This phenomenon might be due to the differences of experimental designs as well as statistical models. However, it is worthwhile to notice an important functional candidate gene, *MDFI*, which was tightly linked to the QTL for LEW. Functional analysis showed that *MDFI* inhibits the transactivation activity of MyoD family members and represses myogenesis, and immunofluorescence microscopy also revealed that *MDFI* associates with MyoD family members in the cytoplasm and retains them by masking their nuclear localization signals (Pan et al., 2005; 2006). Recent evidence supported a conclusion that *MDFI* can suppress myogenesis by inhibiting TCF/LEF-1 and that canonical Wnt signalling may relieve the suppression through elevating beta-catenin levels, which in turn relieve *MDFI*-mediated suppression (Pan et al., 2005; 2006). So it is interesting to continue the genetic analysis for this gene in pigs.

The significant QTL for both DLR and WHC have the same location around *SW2155*, and these effects reached statistical significance at 5% chromosome-wise level. At 56 cM, there was a suggestive indication of QTL affecting WM between *PLA2G7* and *SW352*, similar to the previous results (Zuo et al., 2004). Increased proportion of Meishan allele yielded meat with more moisture and water holding capacity. Additionally, no significant QTL was observed for IMF.

The order of eight genes was also shown on the BAC fingerprint contig from the Wellcome Trust Sanger Institute. From this map, the new refined region from *BTNL1* to *PLA2G7* spans for approximately 20 Mb, and the corresponding human region contains about 160 annotated genes. For example, the BW and BP QTL are located within the interval between *PPARD* and *GLP1R* which contains about 28 putative porcine genes. Therefore, the refined QTL and the positional candidate genes within them will facilitate identifying the gene responsible and ultimately the causative molecular genetic variation.

In summary, this study detected ten significant QTL and two suggestive QTL for carcass composition and meat quality traits. The results confirmed

and narrowed the previous QTL on SSC7q1.1-q1.4. Further studies are required to fine-map these QTL with additional markers and populations.

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