Asian-Aust. J. Anim. Sci.
Vol. 24, No. 12 : 1651 - 1659
December 2011

www.ajas.info
http://dx.doi.org/10.5713/ajas.2011.11221

Characterization of QTL for Growth and Meat Quality in Combined Pig QTL Populations

Y. Li[a], B. H. Choi[1,a], Y.-M. Lee, M. Alam, J.-H. Lee[2], K.-S. Kim[3], K.-H. Baek* and J.-J. Kim[a]
School of Biotechnology, Yeungnam University, Gyeongsan, Korea

ABSTRACT : This study was conducted to detect quantitative trait loci (QTL) for thirteen growth and meat quality traits in pigs by combing QTL experimental populations. Two F_2 reference populations that were sired by Korea native pig (KNP) and dammed by Landrace (LN) or Yorkshire (YK) were generated to construct linkage maps using 123 genetic markers (mostly microsatellites) and to perform QTL analysis on porcine chromosomes (SSCs) 1, 2, 3, 6, 7, 8, 9, 11, 13, 14, and 15. A set of line-cross models was applied to detect QTL, and a series of lack-of-fit tests between the models was used to characterize inheritance mode of QTL. A total of 23, 11 and 19 QTL were detected at 5% chromosome-wise level for the data sets of KNP×LN, KNP×YK cross and joint sets of the two cross populations, respectively. With the joint data, two Mendelian expressed QTL for live weight and cooking loss were detected on SSC3 and SSC15 at 1% chromosome-wise level, respectively. Another Mendelian expressed QTL was detected for CIE a on SSC7 at 5% genome-wise level. Our results suggest that QTL analysis by combining data from two QTL populations increase power for QTL detection, which could provide more accurate genetic information in subsequent marker-assisted selection. (**Key Words :** QTL, Joint Data, Meat Quality, Korean Native Pig, Landrace, Yorkshire)

INTRODUCTION

In the last several decades, pig QTL studies have been aimed at detecting QTL to improve efficiency of pig production as well as to ensuring nutritional meat products for pork consumers (Rothschild et al., 2007). So far, a large number of QTL for pig production and meat quality has been identified (5,466 QTL in PigQTLdb, www.animalgenome.org).

Since the 20th century, Korean native pigs (KNP) have drastically decreased due to their low productivity in Korea (Kim et al., 2002). The KNP possesses unique genetic characteristics that are distinct from European pig breeds (Kim et al., 2002; Jeon et al., 2003; Kim et al., 2005b). However, the KNP has good meat qualities such as high glucose content, low fat and low cholesterol (Jeon et al., 2003; Kim et al., 2005a).

QTL analysis by combining multiple QTL populations has been studied. By joining genotypic and phenotypic data from different populations, the power to detect QTL and the accuracy of estimating QTL effect has increased (Dekkers et al., 2003; Kim et al., 2005c).

QTL models with parent-of-origin effect have been implemented to identify genes that have gene expression patterns in non-Mendelian patterns. The parent-of-origin effects can be estimated whether QTL alleles that descend from either parent contribute to offspring phenotypes (de Koning et al., 2002). In several QTL studies, successful discoveries of QTL with parent-of-origin effects for growth, body composition and meat quality were reported in pigs (Thomsen et al., 2004; Guo et al., 2008; Liu et al., 2008).

There are several reports, in which QTL for growth and meat quality were detected in KNP populations (Lee et al., 2003; Kim et al., 2005a; Kim et al., 2007). However, these QTL studies were based on single QTL experimental populations.

The objective of this study was to identify and characterize QTL for growth and meat quality traits by joining two KNP populations.

* Corresponding Author : Kwang-Hyun Baek. Tel: +82-53-810-3029, Fax: +82-53-801-3027, E-mail: khbaek@ynu.ac.kr
[1] Animal Genomics and Bioinformatics Division, National Institute of Animal Science, Suwon, Korea.
[2] Gyeongbuk Livestock Research Institute, Yeongju, Gyeongbuk 750-781, Korea.
[3] Department of Animal Science, Chungbuk National University, Cheongju, Korea.
[a] The three authors contributed equally to this work.
Received July 12, 2011; Accepted August 19, 2011

MATERIALS AND METHODS

Population structure, phenotypic and molecular data

Two F_2 resource populations were constructed with KNP sires and Landrace (LN) or Yorkshire (YK) dams. The F_0, F_1 and F_2 individuals from the KNP×LN and KNP×YK crosses were raised at National Livestock Research Institute in Songhwan and Cheju, Korea, respectively. In the KNP×LN (KNP×YK) cross population, five (5) KNP sires and nine (19) LN dams were mated to produce F_1s, of which 11 (23) sires and 30 (33) dams were selected and mated to produce 193 (251) F_2 offspring. The F_2 individuals were slaughtered at approximately seven months of age. Some details about raising and management of the experimental population and data recording were described in Choy et al. (2002a), Choy et al. (2002b), and Moon et al. (2009).

Thirteen traits for growth and meat quality that were measured in both populations were selected; live weight at slaughter (kg), crude ash (%), crude protein (%), crude fat (%), drip loss (%), cooking loss (%), water holding capacity (%), shear force (kg), ham pH 2 4-h, CIE L, CIE a, CIE b, and moisture (%) of meat. Table 1 contains the mean and standard deviation for the respective growth and meat quality traits.

At slaughter, animals were stunned by flowing 300 volts electric current of 1.25-1.50 amperes for one to five seconds. Bleeding was performed at vertical position to minimize post-mortem changes, and the scalding tank was maintained at around 60°C for subsequent carcass processing. Samples from muscle *longissimus dorsi* were taken to measure moisture (%), crude protein (%), crude lipid (%), and crude ash (%) following the protocol of AOAC (1990). Warner-Bratzler shear force was measured according to Wheeler et al. (2000), and pH was taken with a portable needle-tipped electrode (NWKbinar pH-K21, Germany) at 24-h after slaughter. Drip loss was also measured at 24-h postmortem period by weighing the sample before and after vacuum storage. Cooking loss was calculated from the weight loss after cooking for 40 min in an 80°C water bath. Water holding capacity (WHC) was measured after some adaptations from Kristensen and Purslow (2001). One gram (g) of homogenized tissue was placed in a 2 ml centricon tube (VIDAS, France), followed by its placement in a 50 ml centrifugation tube, heated in a 70°C water bath for 30 min, and centrifuged at 100 g (Hitatchi, SCR20BA, Japan) for 10 min at 18°C room temperature. WHC was measured as the percentage of weight loss of the sample tissues after centrifugation. Objective meat colors CIE (*L*, *a*, *b*) were determined by a Minolta Chroma meter (CR-301, Minolta, Japan) on fresh cut surface after a 30-min blooming at 1°C. Meat color was expressed by commission and the color meter was calibrated against a white tile provided by the manufacturer.

To facilitate the joint analysis of the data from both populations, phenotypes were standardized by dividing the residual standard deviation (population specific) prior to QTL analysis. Individuals having missing marker genotypes or phenotypes were eliminated from the data set.

To generate linkage maps, a total of 121 genetic markers, mostly microsatellites, were used for the eleven *Sus scrofa* chromosomes (*i.e.* SSCs 1, 2, 3, 6, 7, 8, 9, 11, 13, 14, and 15). Nine, 15, 12, 13, 15, 9, 7, 7, 12, 12, and 10 markers were selected and genotyped for the respective SSCs. Among the genetic markers, 3, 3, 2, 6, 5, 4, 3, 4, 2, 3, and 4 markers on the respective SSCs were genotyped in both the KNP×LN and the KNP×YK cross populations.

Statistical analysis

Linkage map : The linkage maps were constructed for the KNP×LN, KNP×YK or joining data of the two

Table 1. The Means and standard deviations for traits in the KNP×LN and KNP×YK population

Trait	KNP×LN			KNP×YK		
	N	Mean	SD	N	Mean	SD
Moisture (%)	193	73.53	1.91	248	73.90	1.62
Live weight (kg)	193	88.88	14.85	240	93.55	10.38
Crude ash (%)	193	1.03	0.15	250	1.05	0.13
Crude protein (%)	193	22.44	1.22	248	22.19	1.54
Crude lipid (%)	193	2.36	2.79	247	2.49	1.25
Drip loss (%)	193	3.66	2.38	249	5.00	1.57
Water-Holding capacity (%)	193	60.88	5.08	248	57.31	5.56
Cooking loss (%)	193	33.21	4.02	250	32.16	3.45
Shear force (kg)	193	3.82	1.28	246	1.71	0.39
Ham pH2 4-h	193	5.62	0.24	243	5.61	0.20
CIE L	193	51.27	4.94	249	52.59	5.13
CIE a	193	10.58	2.66	251	5.76	2.02
CIE b	193	6.69	2.09	251	7.38	1.73

populations. Crimap software (vs 2.4) was applied (Green et al., 1994).The option, TWOPOINT, was initially performed to cluster the markers into different linkage groups. Subsequently, the framework map for each linkage group was established by choosing the BUILD option (Keats et al., 1991). The FLIPSN option was then applied to determine final linkage maps.

QTL analyses : Two types of least squares interval mapping models were used for detection of QTL, *i.e.* with Mendelian or parent-of-origin QTL effects. For each trait, appropriate fixed factors or covariates were fitted in the models ($p<0.05$) using a GLM procedure in SAS (SAS 9.1, SAS Institute Inc., Cary, NC, USA.).

Firstly, the Mendelian line-cross (Mend) model was chosen as a base model, in which one QTL single-trait model was fitted at each 1 cM position (Haley et al., 1994).

Line-cross model (LC-i):

$$y_{ijk} = X_{ijk}b_{ijk} + \alpha_k P_{a(ijk)} + dP_{d(ijk)} + e_{ijk}$$

Where, y_{ijk} is the standardized phenotype for F_2 progeny j of F_1 sire i in population k (KNP×YK or KNP×LN), X_{ijk} and b_{ijk} are the design matrix and solution vector for fixed effects and covariates and e_{ijk} is a residual. Following the line-cross model of Haley et al. (1994), coefficients α_k and d_k are the additive and dominance effects of breed-origin alleles at a putative QTL at the fitted position for population k, $P_{\alpha(ijk)}$ for an individual is the difference between the probabilities of being homozygous for the QTL allele that originated from KNP or LN (YK), and $P_{d(ijk)}$ is the probability of an individual being heterozygous for line origin QTL alleles. The LC-i model was derived by dropping population interaction effects.

A full expression model as a second QTL model was formulated following Thomsen et al. (2004) and Kim et al. (2005c):

Full model (Full-i):

$$y_{ijk} = X_{ijk}b_{ijk} + \alpha_{(pat)k}P_{(pat)ijk} + \alpha_{(mat)k}P_{(mat)ijk} + d_k P_{(d)ijk} + e_{ijk}$$

Where, y_{ijk}, X_{ijk}, b_{ijk} and e_{ijk} are as defined previously, and $\alpha_{(pat)k}$, $\alpha_{(mat)k}$, and d_k are the paternally and maternally inherited effects for population k, and dominance QTL coefficients, respectively. Coefficient $P_{pat(ijk)}$ is the probability of animal j inheriting a LN (YK) allele vs. a KNP allele from its sire i for population k, $P_{mat(ijk)}$ is the probability of animal j inheriting a LN (YK) allele vs. a KNP allele from its dam i for population k, and $P_{d(ijk)}$ is the probability of animal j being heterozygous. The full model was derived by dropping population interaction effects.

The next models were the paternal (Pat-i) and maternal (Mat-i) expression models, and the null model:

Paternal expression model (Pat-i):

$$y_{ijk} = X_{ijk}b_{ijk} + \alpha_{(pat)k}P_{(pat)ijk} + e_{ijk}$$

Maternal expression model (Mat-i):

$$y_{ijk} = X_{ijk}b_{ijk} + \alpha_{(mat)k}P_{(mat)ijk} + e_{ijk}$$

Null model: $y_{ijk} = X_{ijk}b_{ijk} + e_{ijk}$

Where, all terms were defined previously. Pat-i and Mat-i models were derived by dropping population interaction effects.

Characterization of the detected QTL were carried out using a panel of lack-of-fit tests between alternate models and, classification of QTL types, i.e. parent-of-origin or Mendelian QTL was performed according to the decision trees in Thomsen et al. (2004). One QTL is defined to be paternally (maternally) expressed when its allelic effect is significant if inherited from the sire (dam) and non-significant if inherited from the dam (sire) of progeny at the same time. However, a partially expressed QTL shows allelic effects from both parents when inherited, although the magnitude of effects are differential depending on the sex of the parents, from which it was inherited.

For the joint analyses, breed origin alleles were assumed to be unique *a priori*. Thus, the population interaction models were used for QTL detection and for tests of parent-of-origin effects. Significance of population specific QTL effects were then tested for the inferred mode of expression based on a lack of fit test between the interaction and single effect models. These tests were conducted at the 5% comparison-wise level at the best position for the inferred population-interaction model (Kim et al., 2005c).

Significance tests

For QTL detection, empirically derived 5% chromosome-wise (CW) significance thresholds were used for each model and trait by using 10,000 permutations following Churchill and Doerge (1994). Further, the empirically derived thresholds for Paternal (Pat) *vs.* Null models were also used for Full vs. Mend model as it was suggested that, for the parent of origin models, significance tests with the equal degrees of freedom had similar significance thresholds (Thomsen et al., 2004). Similarly, Mend *vs.* Null model thresholds were utilized in Full *vs.* Pat and Full vs. Maternal (Mat) model. The lack-of-fit tests were performed at a 5% comparison-wise level using standard *F* statistic thresholds. Genome-wise (GW)

significance levels were obtained following de Koning et al. (2001) as

$$P_{genome-wise} = 1-(1-P_{chromosome-wise})^{1/r}$$

Where, r = ratio of distance between first and last markers on a chromosome and total genomic coverage on all 11 chromosomes. Multiple QTL were declared on a chromosome if significant effects were separated by at least 40 (30) cM for QTL significant at the 5% CW (GW) level (Kim et al., 2005d).

RESULTS AND DISCUSSION

Linkage map

The total length of the linkage maps including eleven chromosomes were estimated as 1.59, 1.74, and 1.02 Morgan having an average marker distance of 16.1, 17.0, and 24.2 cM from joint, KNP×LN, and KNP×YK data, respectively. Marker orders were consistent across data sets, except for markers when tightly linked (results not shown). The estimated linkage map positions of the markers showed a good agreement with the previous map studies available in the public database of the USDA-MARC swine genome map (http://www.marc.usda.gov/genome/genome.html). For most chromosomes, the map lengths based on the joint and KNP×LN data were greater compared to the distances between corresponding markers in the USDA and KNP ×YS data (results not shown).

Overall QTL results

Table 2 depicted a list of significant QTLs for growth and meat quality traits. A total of 23, 11, and 19 QTLs were detected in the KNP×LN, KNP×YK, and joint data at 5% CW level, respectively. Among the joint QTLs, eight QTL had population specific effects, while 11 QTL had population common effects (Tables 2 and 6).

In the KNP×LN cross population, the number (23) of significant QTL was much greater than that (11) in the KNP×YK cross population. When using the joint data, the number (19) of detected QTL was also greater than the number of significant QTL in the KNP×YK population. This may be partly due to the small number of available genetic markers (44) in the KNP×YK cross, and thus due to low marker informativeness in the test chromosomes.

The joint QTL analyses revealed 10 Mendelian and 9 parent-of-origin QTLs. Among the parent-of-origin QTLs, four QTL were paternally or maternally expressed, and one QTL was partially expressed (Table 3). In the KNP×LN (YK) cross population, 12 (7) QTLs were Mendelian expressed, and two (two), six (two), and three (zero) QTL were paternally, maternally, and partially expressed, respectively (Table 3).

Single population analyses

In the KNP×LN cross population, four QTLs were detected in SSC8 for moisture, crude protein, crude lipid, and shear force respectively. Also, three QTL were detected on each of SSCs 11, 14, and 15, respectively (Table 4). Compared with Kim et al. (2007) in which the same population was used, a new QTL for live weight was detected on SSC6. However, the QTL for live weight that were detected on SSCs 7 and 14 at 5% CW and 10% GW levels respectively in Kim et al. (2007), were not confirmed in this study. This may be partly due to different linkage maps, *i.e.* as two populations were combined, much longer intervals between markers were generated in the joint data on which the maps were used for QTL analyses in the KNP ×LN cross population, causing much lower marker informativeness in some QTL regions (results not shown). The QTL for ham pH 24-h that was detected at 1% CW level on SSC1 explained the greatest proportion of phenotypic variance (9.1%) in the KNP×LN cross. The QTLs for shear force, live weight, and cooking loss were also detected at 1% CW level on SSCs 3, 6, and 13, respectively (Table 4). Except for the two QTLs for moisture and shear force on SSC7, all QTLs with Mendelian expression had complete or over dominant alleles effects. Most maternally expressed QTLs had increasing effects for Landrace alleles in the KNP×LN cross population (Table 4).

Table 2. Number of QTL detected in the breed cross data from Landrace (LN),Yorkshire (YK),and in the joint data (Joint) on SSC 1, 2, 3, 6, 7, 8, 9, 11, 13, 14, and 15 at different level of significance

Significance level	KNP×LN	KNP×YK	Joint[a]
5% Chromosome-wise	19	8	16 (8,8)
1% Chromosome-wise	4	0	2 (0,2)
5% Genome-wise	0	3	1 (0,1)
Total	23	11	19 (8,11)

[a] QTL number of the population interaction term in the first digit of parenthesis.

Table 3. Number of QTL detected for different QTL expression type in the breed cross data from Landrace (LN), Yorkshire(YK), and in the joint data (Joint) on SSC1, 2, 3, 6, 7, 8, 9, 11, 13, 14 and 15

QTL type	KNP×LN	KNP×YK	Joint[a]
Mend	12	7	10 (4,6)
Pat	2	2	4 (1,2)
Mat	6	2	4 (2,2)
Partial	3	0	1 (1,0)
Total	23	11	19 (8,11)

[a] QTL number of the population interaction term in the first digit of parenthesis.

Table 4. QTL for growth and meat quality that were detected at the 5% chromosome-wise level in the Korean native pig and Landrace cross population

SSC	Trait	cM[a]	-log$_{10}$P[b]	%σ_p^{2}[c]	QTL type[d]	QTL effect[e]			Bracketing markers
1	CIE L	66	2.30	6.0	Mend	-1.28 (0.46)	-1.36 (0.73)		sw1332~s0008
1	Ham pH2 4-h	55	3.54	9.1	Mend*	0.07 (0.02)	0.11 (0.04)		sw1332~s0008
2	Shear force	102	2.55	6.3	Mend	0.29 (0.14)	-0.50 (0.21)		sw1883~sw1695
2	Ham pH2 4-h	57	2.35	7.4	Partial	0.05 (0.02)	-0.04 (0.02)	-0.09 (0.05)	sw1650~sw1686
3	Cooking loss	108	2.59	5.2	Mat	0.84 (0.29)			sw902~sw142
3	Shear force	120	2.99	5.8	Mat*	0.32 (0.10)			sw142~s0167
6	Live weight	47	3.14	6.3	Pat*	4.23 (1.25)			sw1353~sw1057
7	Moisture	53	2.36	5.9	Mend	0.67 (0.20)	0.12 (0.32)		sw2155~sw1369
7	Shear force	58	3.20	7.9	Mend	0.50 (0.13)	0.14 (0.19)		sw2155~sw1369
8	Moisture	21	2.39	5.9	Mend	0.76 (0.28)	0.92 (0.54)		s0098~sw205
8	Crude protein	43	2.46	6.4	Mend	-0.03 (0.15)	0.88 (0.26)		s0098~sw205
8	Crude lipid	28	3.01	7.8	Mend	-0.78 (0.41)	-2.61 (0.84)		s0098~sw205
8	Shear force	6	2.27	5.6	Mend	0.35 (0.15)	-0.60 (0.24)		s0098~sw205
11	Crude protein	27	2.08	4.0	Mat	-0.26 (0.10)			sw1632~s0182
11	Drip loss	75	2.09	5.5	Mend	0.21 (0.23)	1.19 (0.38)		sw1377~sw1465
11	Shear force	56	2.11	6.4	Partial	0.02 (0.10)	-0.33 (0.10)	0.05 (0.18)	sw1684~sw1377
13	Cooking loss	0	2.98	6.1	Mat*	1.00 (0.39)			s0219~sw1378
14	Live weight	96	2.74	7.0	Mend	-0.06 (1.43)	7.52 (2.10)		s0007~sw63
14	Crude protein	101	2.54	5.1	Mat	0.26 (0.09)			s0007~sw63
14	CIE b	0	2.80	7.3	Mend	0.45 (0.17)	0.69 (0.28)		sw1125~sw857
15	Moisture	0	2.19	6.6	Partial	-0.25 (0.14)	0.47 (0.14)	0.22 (0.26)	sw2072~s0004
15	Water holding capacity	113	3.55	7.1	Mat	1.50 (0.43)			sw1683~sw1983
15	Cooking loss	128	3.41	4.9	Pat	-0.65 (0.30)			sw1983~sw1119

[a] Position at which the test-statistic value was maximized for the inferred QTL model.

[b] Negative logarithm of the comparison-wise p-value of the test static against the null hypothesis of no QTL at the most likely position for the inferred QTL model.

[c] Proportion (%) of phenotypic variance explained by QTL ((RSS_{noQTL}-RSS_{QTL})/RSS_{noQTL}), where RSS is residual sum of squares for the model with or without QTL.

[d] Declared QTL type. Mend = Mendelian expression, Pat = Paternal expression, Mat = Maternal expression, Partial = Partial expression. * Significant at the 0.01 chromosome-wise level.

[e] Additive and dominance estimates for Mend QTL, paternal (maternal) estimate for Pat (Mat) QTL, paternal, maternal and dominance estimates for partial QTL. All estimates are expressed in residual phenotype standard deviations.

Table 5. QTL for growth and meat quality that were detected at the 5% chromosome-wise level in the Korean native pig and Yorkshire cross population

SSC	Trait	cM[a]	-log$_{10}$P[b]	%σ_p^{2}[c]	QTL type[d]	QTL effect[e]		Bracketing markers
1	Crude lipid	59	3.97	8.6	Mend**	0.37 (0.21)	-1.47 (0.38)	sw1430~sw65
1	Crude protein	0	2.67	6.2	Mend**	0.70 (0.22)	-0.83 (0.55)	s1851~sw1430
1	Moisture	0	3.11	7.2	Mend**	-1.05 (0.28)	0.49 (0.69)	s1851~sw1430
1	Shear force	0	2.22	3.9	Pat	-0.01 (0.01)		s1851~sw1430
2	Drip loss	39	1.81	2.9	Mat	-0.06 (0.12)		swr783~s0141
2	Shear force	124	1.61	2.6	Pat	-0.01 (0.00)		sw1844~s0036
7	Crude lipid	6	4.04	7.3	Mat	0.53 (0.13)		sw1856~sw1701
8	Crude ash	44	2.03	1.2	Mend	-0.21 (0.17)	0.22 (0.23)	sw1312~sw61
8	Water-holding capacity	0	2.06	4.8	Mend	0.82 (0.48)	-1.76 (0.64)	s0069~s0225
14	Crude protein	65	2.22	5.2	Mend	0.28 (0.19)	-0.95 (0.34)	sw761~sw2515
14	Moisture	73	2.45	5.7	Mend	-0.61 (0.22)	0.65 (0.32)	sw761~sw2515

[a] Position at which the test-statistic value was maximized for the inferred QTL model.

[b] Negative logarithm of the comparison-wise p-value of the test static against the null hypothesis of no QTL at the most likely position for the inferred QTL model.

[c] Proportion (%) of phenotypic variance explained by QTL ((RSS_{noQTL}-RSS_{QTL})/RSS_{noQT}), where RSS is residual sum of squares for the model with or without QTL.

[d] Declared QTL type. Mend = Mendelian expression, Pat = Paternal expression, Mat = Maternal expression, Partial = Partial expression. ** Significant at the 0.05 genome-wise level.

[e] Additive and dominance estimates for Mend QTL, paternal (maternal) estimate for Pat (Mat) QTL. All estimates are expressed in residual phenotype standard deviations.

In the KNP×YK population, 11 QTLs were detected on five chromosomes, *i.e.* SSCs 1, 2, 7, 8 and 14 (Table 5). The three Mendelian QTL for crude lipid, crude protein, and moisture were detected on SSC1 at 5% GW level. The two QTL for crude lipid and crude protein had KNP increasing additive effects and YK increasing dominance effects, and *vice versa* for the moisture QTL (Table 5). Most Mendelian QTL (except for the moisture on SSC1) had complete or over dominant effects. However, no QTL for cooking loss, ham pH 24-h, or any meat color trait that was detected in the KNP×LN population, was not confirmed in the KNP×YK population (Table 5). This might be partly due to the use of small number of markers that were sparsely located on the test chromosomes (results not shown).

Joint population analysis

Among the 19 detected QTL in the joint data, 11 QTLs had population-common effects, while the eight QTLs were

Table 6. QTL for growth and meat quality that were detected at the 5% chromosome-wise level in the joint population analysis

SSC	Trait	cM[a]	-log$_{10}$P[b]	%σ_p^{2}[c]	QTL type[d]	QTL effect[e]		Bracketing markers
1	Live weight	121	3.12	2.8	Mat	-0.11 (0.06)		sw65~sw1970
2	Crude ash	77	3.62	5.3	Mend-i	-0.36 (0.81)	-0.72 (0.82)	sw1686~sw1026
						2.68 (0.60)	1.99 (0.62)	
2	Shear force	49	3.51	5.2	Mend-i	-0.10 (0.89)	-0.11 (0.85)	sw2516~sw1650
						-0.53 (0.19)	0.39 (0.18)	
2	CIE b	42	3.06	3.5	Mat-i	0.28 (0.48)		sw2516~sw1650
						-0.82 (0.22)		
3	Live weight	125	2.35	2.7	Mend*	0.14 (0.05)	-0.02 (0.05)	s0167~sw314
3	Crude lipid	48	2.08	1.8	Pat	-0.25 (0.10)		sw1443~sw487
6	Water holding capacity	163	2.53	2.9	Pat-i	0.22 (0.33)		sw322~sw1328
						-1.01 (0.30)		
7	Drip loss	161	2.38	3.8	Mend-i	0.40 (0.53)	0.71 (0.45)	sw632~sw0101
						0.22 (0.28)	-0.69 (0.26)	
7	CIE L	95	2.54	2.9	Mat-i	2.65 (1.18)		swr2036~sw175
						1.81 (0.68)		
7	CIE a	52	4.25	4.8	Mend**	-0.07 (0.06)	0.22 (0.07)	sw2155~sw1369
7	CIE b	49	2.49	2.8	Mend	-0.06 (0.17)	0.49 (0.18)	sw2155~sw1369
8	Moisture	6	2.65	3.0	Mend	0.06 (0.18)	-0.49 (0.17)	s0098~sw205
8	Crude protein	173	3.18	2.9	Pat	-0.86(0.25)		opn~s0178
9	Cooking loss	68	2.23	1.9	Pat	-0.17(0.06)		sw940~sw2074
9	Shear force	0	2.65	4.2	Mend-i	0.30(0.66)	0.29(0.54)	sw983~sw21
						0.70(0.17)	0.31(0.19)	
11	Live weight	67	2.15	2.5	Mend	0.15(0.06)	-0.00(0.06)	sw1684~sw1377
11	Crude protein	21	2.6	5.0	Partial-i	0.39(0.77)[f]	1.40(1.11)	s0385~sw1632
						1.24(0.81)		
						2.88(2.47)	-0.2(0.92)	
						1.88(0.75)		
15	Water holding capacity	85	2.47	2.2	Mat	0.44(0.43)		sw1119~swr2121
						0.79(0.27)		
15	Cooking loss	49	3.12	3.6	Mend*	-0.12(0.06)	0.13(0.06)	sw1683~sw1983

[a] Position at which the test-statistic value was maximized for the inferred QTL model.

[b] Negative logarithm of the comparison-wise p-value of the test static against the null hypothesis of no QTL at the most likely position for the inferred QTL model.

[c] Proportion (%) of phenotypic variance explained by QTL ((RSS_{noQTL}-RSS_{QTL})/RSS_{noQT}), where RSS is residual sum of squares for the model with or without QTL.

[d] Declared QTL type. Mend = Mendelian expression, Pat = Paternal expression, Mat = Maternal expression, Partial = Partial expression. For the joint analyses,-*i* indicates significance of the population interaction term with the assumption of different effects for the two maternal breed alleles (or population). * Significant at the 0.01 chromosome-wise level. ** Significant at the 0.05 genome-wise level.

[e] Additive and dominance estimates for Mend QTL, paternal (maternal) estimate for Pat (Mat) QTL, paternal, maternal and dominance estimates for partial QTL. Estimates in the first and second lines for type-*i* (population-specific QTL) are for the KNP×Landrace and KNP×Yorkshire population, respectively. All estimates are expressed in residual phenotype standard deviations.

[f] Estimate of the paternal effect in the first line and of the maternal effect in the second line.

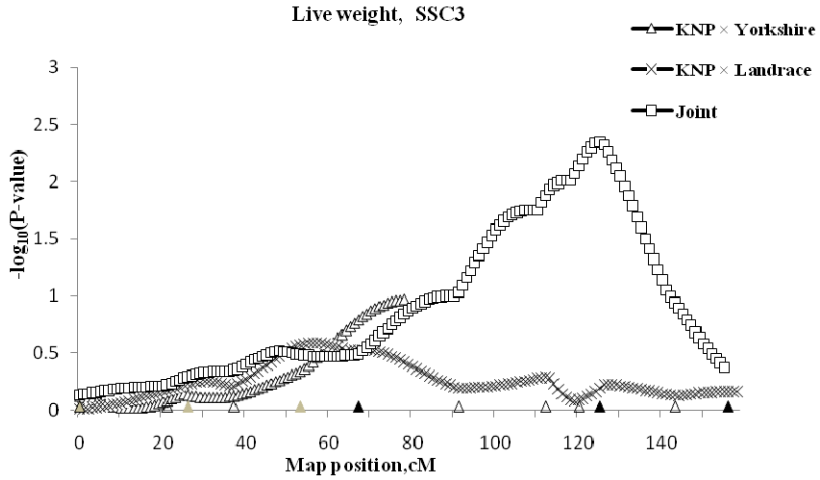

Figure 1. Mendelian QTL profiles for live weight on SSC3 in the joint or individual populations. Markers genotyped in the Landrace and Yorkshire cross populations are indicated by open and gray triangles on the x-axis, with black triangles indicating markers genotyped in both populations.

population-specific, *i.e.* the QTL effects were different between the two KNP-crossed populations, which was influenced by maternal (LN or YK) genetic background effects (Table 6).

One Mend QTL for CIE a was detected on SSC7 at 5% GW level, and two Mend QTL for live weight and cooking loss were detected on SSC3 and SSC15, respectively, at 1% CW level. Some QTLs that were not detected in the individual populations were detected in the joint analysis, *e.g*, the QTLs for live weight on SSC3, for CIE a on SSC7, and for cooking loss on SSC15, respectively (Figures 1, 2, and 3). These results indicate the evidence of increasing power to detect QTL when combining two populations (Kim et al., 2005c).

Rohrer et al. (2006) reported a Mend QTL for live weight in the distal region of SSC3 in a Duroc-Landrace F_2 population. We also detected a Mend QTL at 125 cM of the same chromosome in the joint data (Figure 1 and Table 6). Ovilo et al. (2002) found a Mendelian QTL for CIE a that were flanked by SW2155 and SW1369 on SSC7, where the QTL for the same trait was also detected at 5% GW level in the joint data of this study (Figure 2 and Table 6).

Rohrer et al. (2006) reported a Mend QTL for cooking loss on SSC15, and Edwards et al. (2008) also discovered a Mend QTL for the same trait in an F_2 population of Duroc-Pietrain cross. In the similar QTL regions, we detected one QTL for cooking loss between SW1683 and SW1983 (Figure 3 and Table 6).

The detection of two additive QTLs for live weight on SSC3 and SSC11 in the joint analyses indicates potentially commercial use of the KNP sires, because the KNP alleles had weight-increasing effects. This results support

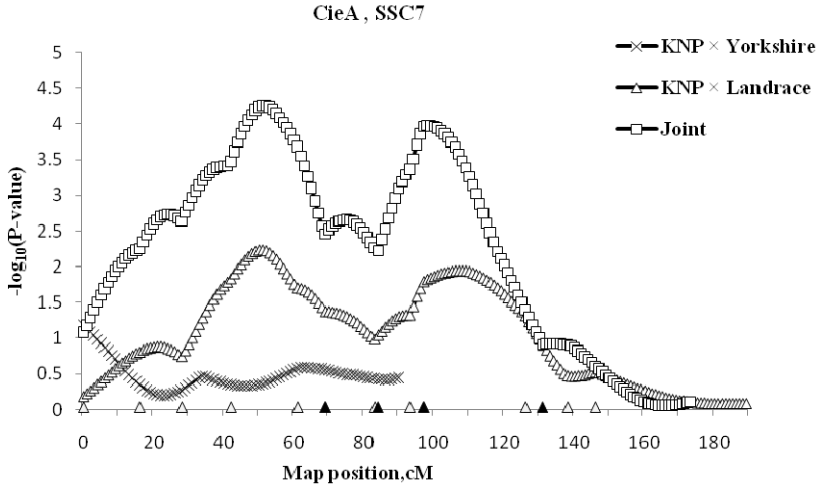

Figure 2. Mendelian QTL profiles for Cie A on SSC7 in the joint or individual populations. Markers genotyped in the Landrace and Yorkshire cross populations are indicated by open and gray triangles on the x-axis, with black triangles indicating markers genotyped in both populations.

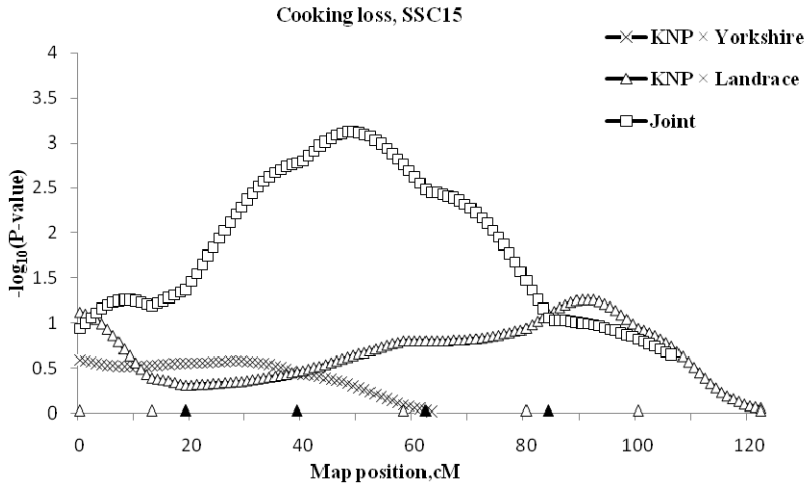

Figure 3. Mendelian QTL profiles for cooking loss on SSC15 in the joint or individual populations. Markers genotyped in the Landrace and Yorkshire cross populations are indicated by open and gray triangles on the x-axis, with black triangles indicating markers genotyped in both populations.

usefulness of an unselected breed, because of the cryptic and favorable alleles that exist in the KNP breed (Kim et al., 2005d).

Kim et al. (2007) reported Mendelian and parent-of-origin QTLs in the same population of this study. However, we genotyped additional 43 markers in the chromosomal regions of interest. Some new QTLs were detected in the joint data, while other QTLs that were detected in the KNP×LN population were not confirmed in the joint data (Tables 4 and 6). The limited QTL discovery in the joint data may be partially due to missing genotypes and longer marker intervals and thus lower marker informativeness in the KNP×YK cross, compared to the KNP×LN. This might cause QTL detection errors and/or biased estimates of QTL position and effect. Thus, care needs to be taken in interpreting detection and characterization of QTL.

In polygamous species, imprinting (or parent-of-origin) effect is considered to primarily affect the genes that regulate the transfer of maternal resources to offspring (Georges et al., 2007). In this study, we found nine parent-of-origin QTL in the joint data, among which six QTL had increasing effects for Landrace or Yorkshire breeds (Table 6). This results reflect consistent breeding schemes that have been practiced in western breeds for selecting genes with favorable effects on growth and meat quality (Cameron, 1994).

In conclusion, by combining the two KNP sired populations, several new QTLs were detected that were not identified when the QTL analyses was performed in the single populations. These QTLs need to be confirmed in further genomic studies, which then can be incorporated into marker assisted selection programs for genetic improvement of Korean native pigs.

ACKNOWLEDGEMENTS

This research was supported by the Yeungnam University research grants in 2008.

REFERENCES

AOAC. 1990. Official methods of analysis. 15th Ed. Association of official analytical chemists. Washington, DC, USA.

Cameron, N. D. 1994. The value of pig selection experiments. Proceedings of the 5th World Congress on Genetics Applied to Livestock Production 19:41-48.

Choy, Y. H., G. J. Jeon, T. K. Kim, B. H. Choi and H. W. Chung. 2002a. Ear type and coat color on growth performances of crossbred pigs. Asian-Aust. J. Anim. Sci. 15:1178-1181.

Choy, Y. H., G. J. Jeon, T. K. Kim, B. H. Choi, I. C. Cheong, H. K. Lee, K. S. Seo, S. D. Kim, Y. I. Park and H. W. Chung. 2002b. Genetic analyses of carcass characteristics in crossbred pigs between Landrace sows and Korean wild boars. Asian-Aust. J. Anim. Sci. 15:1080-1084.

Churchill, G. A. and R. W Doerge. 1994. Empirical threshold values for quantitative trait mapping. Genetics 138:963-971.

De Koning, D. J., H. Bovenhuis and J. A. van Arendonk .2002. On the detection of imprinted quantitative trait loci in experimental crosses of outbred species. Genetics 161: 931-938.

De Koning, D. J., B. Harlizius, A. P. Rattink, M. A. Groenen, E. W. Brascamp and J. A. van Arendonk. 2001. Detection and characterization of quantitative trait loci for meat quality traits in pigs. J. Anim. Sci. 79:2812-2819.

De Koning, D. J., A. P. Rattink, B. Harlizius, J. A. van Arendonk, E. W. Brascamp and M. A. Groenen. 2000. Genome-wise scan for body composition in pigs reveals important role of imprinting. Proc. Natl. Acad. Sci. USA 97:7947-7950.

Dekkers, J. C., J. J. Kim, M. Malek, H. Thomsen, H. Lee, H. H. Zhao and M. F. Rothschild. 2003. A genome scan to detect QTL affecting growth, composition, and meat quality trait in a

Berkshire×Yorkshire cross. Pages 1-21 in Proc. 28th National Swine Improvement Federation, Des Moines, IA.

Edwards, D. B., C. W. Ernst, N. E. Raney, M. E. Doumit, M. D. Hoge and R. O. Bates. 2008. Quantitative trait locus mapping in an F2 Duroc×Pietrain resource population: II. Carcass and meat quality traits. J. Anim. Sci. 86:254-266.

Georges, M. 2007. Mapping, fine mapping, and molecular dissection of quantitative trait Loci in domestic animals. Annu. Rev. Genomics Hum. Genet. 8:131-162.

Green, P., K. Fallis and S. Crooks. 1994. Documentation for CRIMAP version 2.4, Washington University School of Medicine, St. Louis, MO.

Guo, Y. M., G. J. Lee, A. L. Archibald and C. S. Haley. 2008. Quantitative trait loci for production traits in pigs: a combined analysis of two Meishan×Large White populations. Anim. Genet. 39:486-495.

Haley, C. S., S. A. Knott and J. M. Elsen. 1994. Mapping quantitative trait loci in crosses between outbred lines using least squares. Genetics 136: 1195-207.

Jeon, J. T., E. W. Park, H. J. Jeon, T. H. Kim, K. T. Lee and I. C. Cheong. 2003. A large-insert porcine library with seven fold genome coverage: a tool for positional cloning of candidate genes for major quantitative traits. Mol. Cells 16:113-116.

Keats, B. J., S. L. Sherman, N. E. Morton, E. B. Robson, K. H. Buetow, P. E. Cartwright, A. Chakravarti, U. Francke, P. P. Green and J. Ott. 1991. Guidelines for human linkage maps: an international system for human linkage maps (ISLM, 1990). Genomics 9:557-560.

Kim, E. H., B. H. Choi, K. S. Kim, C. K. Lee, B. W. Cho, T. H. Kim and J. J. Kim. 2007. Detection of Mendelian and parent-of-origin quantitative trait loci in a cross between Korean native pig and Landrace. I. growth and body composition traits. Asian-Aust. J. Anim. Sci. 20:669-676.

Kim, K. S., J. S. Yeo and J. W. Kim. 2002. Assessment of genetic diversity of Korean native pig (*Sus scrofa*) using AFLP markers. Genes Genet. Syst. 77:361-368.

Kim, T. H., B. H. Choi, H. K. Lee, H. S. Park, H. Y. Lee, D. H. Yoon, J. W. Lee, G. J. Jeon, I. C. Cheong, S. J. Oh and J. Y. Han. 2005a. Identification of quantitative traits loci (QTL) affecting growth traits in pigs. Asian-Aust. J. Anim. Sci. 18: 1524-1528.

Kim, T. H., K. S. Kim, B. H. Choi, D. H. Yoon, G. W. Jang, K. T. Lee, H. Y. Chung, H. Y. Lee, H. S. Park and J. W. Lee. 2005b. Genetic structure of pig breeds from Korea and China using microsatellite loci analysis. J. Anim. Sci. 83:2255-2263.

Kim, J. J., M. F. Rothschild, J. Beever, S. -Zas Rodriguez and J. C. Dekkers. 2005c. Joint analysis of two breed cross populations in pigs to improve detection and characterization of quantitative trait loci. J. Anim. Sci. 83:1229-1240.

Kim, J. J., H. Zhao, H. Thomsen, M. F. Rothschild and J. C. Dekkers. 2005d. Combined line-cross and half-sib QTL analysis of crosses between outbred lines. Genet. Res. 85:235-48.

Kristensen, L. and P. P. Purslow. 2001. The effect of ageing on the water-holding capacity of pork: Role of cytoskeletal proteins. Meat Sci. 58:17-23.

Lee, H. K., S. S. Lee, T. H. Kim, G. J. Jeon, H. W. Jung, Y. S. Shin, J. Y. Han, B. H. Choi and I. C. Cheong. 2003. Detection of imprinted quantitative trait loci (QTL) for growth traits in pigs. Asian-Aust. J. Anim. Sci. 16:1087-1092.

Liu, G., J. J. Kim, E. Jonas, K. Wimmers, S. Ponsuksili, E. Murani, C. Phatsara, E. Tholen, H. Juengst, D. Tesfaye, J. L. Chen and K. Schellander. 2008. Combined line-cross and half-sib QTL analysis in Duroc-Pietrain population. Mamm. Genome. 19: 429-438.

Moon, J. K., K. S. Kim, J. J. Kim, B. H. Choi, B. W. Cho, T. H. Kim and C. K. Lee. 2009. Differentially expressed transcripts in adipose tissue between Korean native pig and Yorkshire breeds. Anim. Genet. 40:115-118.

Ovilo, C., A. Clop, J. L. Noguera, M. A. Oliver, C. Barragan, C. Rodriguez, L. Silio, M. A. Toro, A. Coll, J. M. Folch, A. Sanchez, D. Babot, L. Varona and M. Perez-Enciso. 2002. Quantitative trait locus mapping for meat quality traits in an Iberian×Landrace F2 pig population. J. Anim. Sci. 80:2801-2808.

Rohrer, G. A., R. M. Thallman, S. Shackelford, T. Wheeler and M. Koohmaraie. 2006. A genome scan for loci affecting pork quality in a Duroc-Landrace F population. Anim. Genet. 37: 17-27.

Rothschild, M. F., Z. L. Hu and Z. Jiang. 2007. Advances in QTL mapping in pigs. Int. J. Biol. Sci. 3:192-197.

Thomsen, H., H. K. Lee, M. F. Rothschild, M. Malek and J. C. Dekkers. 2004. Characterization of quantitative trait loci for growth and meat quality in a cross between commercial breeds of swine. J. Anim. Sci. 82:2213-2228.

Wheeler, T. L., S. D. Shackelford and M. Koohmaraie. 2000. Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles. J. Anim. Sci. 78: 958-965.