Quantitative trait loci analysis for growth and carcass traits in a half-sib family of purebred Japanese Black (Wagyu) cattle[1]

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ABSTRACT: We used a half-sib family of purebred Japanese Black (Wagyu) cattle to locate economically important quantitative trait loci. The family was composed of 348 fattened steers, 236 of which were genotyped for 342 microsatellite markers spanning 2,664 cM of 29 bovine autosomes. The genome scan revealed evidence of 15 significant QTL (<5% chromosome-wise level) affecting growth and carcass traits. Of the 15 QTL, six QTL were significant at the 5% experiment-wise level and were located in bovine chromosomes (BTA) 4, 5, and 14. We analyzed these three chromosomes in more detail in the 348 steers, with an average marker interval of 1.2 cM. The second scan revealed that the same haplotype of the BTA 4 region (52 to 67 cM) positively affected LM area and marbling. We confirmed the QTL for carcass yield estimate on BTA 5 in the region of 45 to 54 cM. Five growth-related QTL located on BTA 14, including slaughter and carcass weights, were positively affected by the same region of the haplotype of BTA 14 (29-51 cM). These data should provide a useful reference for further marker-assisted selection in the family and positional cloning research. The research indicates that progeny design with moderate genotyping efforts is a powerful method for detecting QTL in a purebred half-sib family.

Key Words: Carcass Traits, Cattle, Half-Sib Family, Progeny Design, Quantitative Trait Loci

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Introduction

A major goal of livestock genome research is to understand the basis of the genetic contribution to variations in production traits. Andersson et al. (1994) first reported a cluster of loci affecting growth and fatness on pig chromosome 4 in wild boar and Large White pigs based on the interval mapping method described by Haley et al. (1994). Using similar designs, several studies reported the location of QTL in experimental resource families constructed by crossbreeding animals from relatively different breeds. In beef cattle, most QTL mapping studies have used crosses between *Bos indicus* and *Bos taurus* breeds (e.g., Keele et al., 1999; Stone et al., 1999; Casas et al., 2000).

When progeny are grouped according to the marker allele received from a heterozygous parent, the presence of alternative alleles at the linked QTL tends to generate a difference in the mean quantitative value between the two progeny groups. Weller et al. (1990) simulated the power of daughter and granddaughter designs to determine linkages between marker loci and QTL in dairy cattle, and concluded that the granddaughter design generally requires fewer marker assays to have equivalent power to the daughter design. Moody et al. (1996) simulated the grand progeny design (**GPD**) to detect QTL in a purebred beef cattle population, and hypothesized that large amounts of genotyping are required to achieve reasonable power and only QTL with moderate to large effects could be identified. Neither the GPD nor the progeny design have been used for QTL mapping in beef cattle, probably due to the high cost, although these strategies might provide information on haplotypes of immediate application to marker-assisted selection. The objective of this research was to identify QTL for growth and carcass traits using the progeny design in a paternal half-sib family composed of 348 fattened purebred Japanese Black (Wagyu) steers.

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Table 1. Phenotypic data for growth and carcass traits of a half-sib family

Trait[a]	Average	SD	Range	Skewness	Kurtosis	Heritability estimate[b]
Primary screen (236 animals)						
BW-1, kg	291.6	26.5	199 to 380	−0.085	0.902	0.30
BW-2, kg	718.6	52.7	585 to 864	−0.008	−0.209	0.36
CW, kg	447.0	37.3	351.2 to 553.5	0.095	−0.348	0.39
LMA, cm^2	54.6	7.6	38 to 81	0.597	0.373	0.47
RT, cm	8.2	0.8	6.2 to 10.4	0.112	0.001	0.41
SFT, cm	2.9	0.8	0.8 to 5.8	0.328	0.291	0.55
YE, %	75.0	1.2	72.2 to 78.5	0.322	0.099	0.53
BMS	6.6	2.1	2 to 12	0.261	−0.733	0.52
ADG-1, kg	1.06	0.11	0.78 to 1.34	0.132	0.184	0.13
ADG-2, kg	0.71	0.09	0.49 to 0.96	0.069	0.085	0.15
Secondary screen (348 animals)						
BW-1, kg	289.7	26.0	199 to 380	−0.052	0.715	0.30
BW-2, kg	713.8	55.6	576 to 864	−0.024	−0.267	0.36
CW, kg	443.3	39.0	347.2 to 553.5	0.083	−0.341	0.39
LMA, cm^2	53.5	7.5	33 to 81	0.571	0.661	0.47
YE, %	74.8	1.2	71.5 to 78.5	0.285	0.163	0.53
BMS	6.5	2.1	2 to 12	0.257	−0.661	0.52
ADG-1, kg	1.06	0.11	0.78 to 1.34	0.031	−0.012	0.13
ADG-2, kg	0.70	0.09	0.49 to 0.98	0.158	0.058	0.15

[a]Body measurements recorded were BW-1, BW-2, ADG-1, and ADG-2. Weight at 276 ± 12 d was used for ADG-1 and BW-1. Weight at 30 mo was used for ADG-2 and BW-2. See the text for further description of BW and ADG terms. Trait records for carcass weight (CW), LM area (LMA), rib thickness (RT), s.c. fat thickness (SFT), and beef marbling score (BMS) were obtained from Japan Meat Grading Association. Carcass yield estimate (YE) was calculated from LMA, RT, left-side CW, and SFT.
[b]Mukai et al. (1995).

Materials and Methods

Phenotype Measurement

A paternal half-sib family of 348 steers was constructed from carcass data and pedigree records collected by the Japan Waygu Registry Association (Kyoto, Japan). Samples of DNA for these steer were available as part of a systematic program for collecting DNA at slaughterhouses. Steers were slaughtered at approximately 30 mo of age. Body measurements recorded were ADG before fattening (**ADG-1**), BW at 9 mo before fattening (**BW-1**), ADG from 9 to 30 mo during fattening (**ADG-2**), and BW at slaughter (**BW-2**). Carcasses were dissected at the sixth and seventh rib section according to the Japanese meat grading system by certified graders from the Japan Meat Grading Association (Tokyo) to measure carcass traits. Traits measured were cold carcass weight (**CW**), LM area (**LMA**), rib thickness (**RT**), s.c. fat thickness (**SFT**), carcass yield estimate (**YE**), and beef marbling score (**BMS**). The YE is the estimated ratio of wholesale cuts from which the surface fat was trimmed, to carcass weight as a percentage and is calculated by the following equation:

$$\text{YE, \%} = 69.419 + 0.130 \times \text{LMA} + 0.667 \times \text{RT} - 0.025 \times \text{CWL} - 0.896 \times \text{SFT}$$

where CWL is a cold left-side carcass weight. This equation has been used officially for grading in all Japanese carcass markets since 1988. The BMS was scored from one to 12 with a standard model panel, in which higher scores correspond to more marbling. Table 1 summarizes the data of the 10 traits, including growth and carcass traits. Heritability estimates in Table 1 were taken from a study of Wagyu cattle (n = 8,329) by Mukai et al. (1995).

Genome Screen

Samples of DNA were prepared from semen, blood, or adipose tissue according to standard protocols, and the DNA concentration was adjusted to 20 ng/μL. A genome screen was conducted using microsatellite markers (Kappes et al., 1997; http://sol.marc.usda.gov/cattle). Polymerase chain reaction was performed in a volume of 15 μL containing 20 ng of genomic DNA, 1.67 m*M* $MgCl_2$, 6.25 pmol each primer, 0.2 m*M* deoxynucleotides (dNTPs), and 0.375 U of *Taq* DNA polymerase (ABgene, Epsom, U.K.). The thermal cycling conditions were optimized for each primer set as recommended (Kappes et al., 1997), and the other reaction conditions were set as recommended by the manufacturer. Following polymerase chain reaction, alleles were resolved by electrophoresis in polyacrylamide gels using an ABI 377 sequencer (Applied Biosystems, Foster City, CA) and genotype data were captured using GENESCAN and Genotyper software (Applied Biosystems).

Table 2. Summary of QTL location and chromosome-wise and experiment-wise probabilities

Trait[a]	BTA[b]	cM	*F*-statistic	FDR[c]
BW-1, kg	14	33	11.8**	0.039
BW-2, kg	3	108	11.2*	0.043
BW-2, kg	14	45	28.8††	0.034
CW, kg	14	45	28.1††	0.011
LMA, cm^2	2	98	9.4*	0.097
LMA, cm^2	4	64	15.4†	0.010
SFT, cm	14	49	10.3*	0.094
YE, %	5	50	23.7††	0.026
BMS	4	75	17.0†	0.011
BMS	5	30	9.4*	0.094
BMS	13	75	9.4*	0.096
BMS	14	53	9.8*	0.096
ADG-1, kg	14	32	23.5††	0.020
ADG-2, kg	5	136	11.0**	0.057
ADG-2, kg	14	49	12.8**	0.022

*5% chromosome-wise significance level.
**1% chromosome-wise significance level.
†5% experiment-wise significance level.
††1% experiment-wise significance levels, respectively.
[a]Weight at 276 ± 12 d was used for ADG-1 and BW-1. Weight at 30 mo was used for ADG-2 and BW-2. See the text for further description of BW and ADG terms. Trait records for carcass weight (CW), LM area (LMA), s.c. fat thickness (SFT), beef marbling score (BMS), and carcass yield estimate (YE).
[b]Bovine chromosome.
[c]False discovery rate.

Statistical Analyses

Correction of genotype errors, reconstruction of haplotypes, and *F*-statistic profiling were performed with the interval mapping method for half-sib family analysis (Haley et al., 1994; Seaton et al., 2002). Briefly, the phase of a sire's chromosomes was determined at each pair of two consecutive heterozygous markers using allele transmission information to offspring so that recombination between two markers was minimized. The statistical model for QTL analysis was that of linear regression of the phenotypic value of the probabilities of QTL genotypes at a given location. The sire's two alleles at a putative QTL at a given location were denoted by Q and q. Probabilities of offspring QTL genotypes denoted by $Prob(Q)$ were calculated from the observed genotypes of markers linked to the QTL. A linear regression analysis was performed using the following model:

$$y_i = \mu + Prob(Q)_i\, a + e_i$$

where μ is the fixed effect, a is the allele substitution effect of q to Q, and y_i, $Prob(Q)_i$, and e_i are unadjusted phenotypic value, probability of Q genotype at a given location, and the residual error for individual i, respectively. An F-statistic value was calculated from the minimum sum of squares of residual errors under the model with the least squares estimators of μ and a, and the minimum sum of squares under the null model corresponding to no QTL, where $a = 0$ is assumed. To evaluate whether the QTL effect was well estimated, the information content was calculated as a variance of $Prob(Q)_i$ divided by 0.25, the possible maximal variance of $Prob(Q)_i$ (Knott et al., 1998). Analyses of QTL were performed at 1-cM intervals along the chromosome. For all analyses, marker locations were obtained from the Shirakawa-USDA linkage map (Ihara et al., 2004). The LOD drop-off method was used to calculate the support interval for each putative QTL (Ott, 1992). Thresholds for significance of the F-statistic value were obtained by 10,000 random permutations of the phenotypic data. The largest F-value over all analysis points for each analysis was recorded, and the 1 and 5% thresholds were defined as the 100th and 500th ranked F-values. For chromosome-wise and experiment-wise thresholds, the largest statistic value on each chromosome and on all chromosomes was recorded. The largest statistic values among all the traits for each permutation were recorded to obtain overall significance levels with multiple tests of multiple traits.

Table 3. Summary of eight QTL fine-mapped on bovine chromosomes 4, 5, and 14

Trait[a]	BTA[b]	cM[c]	*F*-statistic value	*Q* to *q* allele substitution effect	QTL contribution, %[d]
LMA, cm^2	4	60 (52 to 67)	19.3	3.56	4.8
BMS	4	55 (52 to 62)	30.5	1.18	8.2
YE, %	5	52 (45 to 54)	23.5	0.61	5.6
BW-1, kg	14	34 (30 to 42)	12.1	9.67	3.4
BW-2, kg	14	50 (48 to 50)	48.7	38.11	12.3
CW, kg	14	50 (48 to 51)	44.5	25.75	11.4
ADG-1, kg	14	33 (29 to 39)	15.8	0.045	4.4
ADG-2, kg	14	50 (45 to 51)	15.8	0.044	6.7

[a]Weight at 276 ± 12 d was used for ADG-1 and BW-1. Weight at 30 mo was used for ADG-2 and BW-2. See the text for further description of BW and ADG terms. Carcass trait are weight (CW), LM area (LMA), beef marbling score (BMS) and carcass yield estimate (YE).
[b]Bovine chromosome.
[c]Support interval in parentheses.
[d]A QTL contribution (%) in the family was calculated as follows: (variance explained by the linear regression model/total variance) × 100.

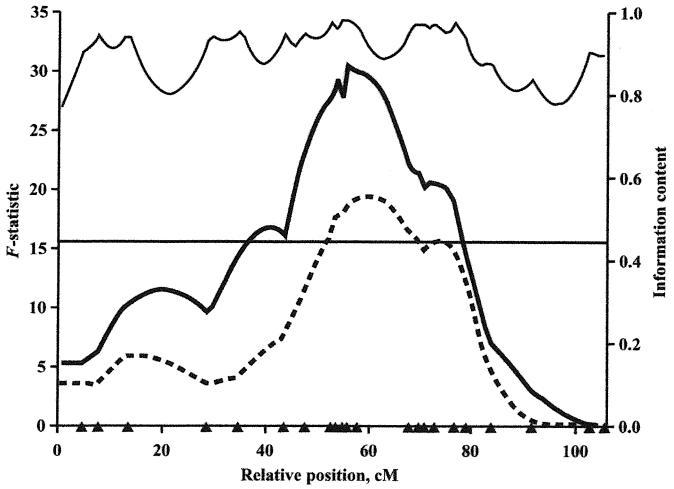

Figure 1. *F*-statistic profiles for carcass LM area (-----) and beef marbling score (—) on BTA 4 (cM position; x-axis). The horizontal line indicates the threshold for the 0.1% chromosome-wise level. The upper line indicates information content (right y-axis). Marker positions are identified as triangles above the x-axis and were BMC1410, BL1030, BMS1788, RM188, BMS1237, BMS2646, BMS1840, RM067, TGLA116, BMS885, BM1224, BM6437, BMS779, RM232, BMS2571, BM6458, Oar-CP26, MNB-42, DIK123, BMS648, TGLA159, and BR303, respectively.

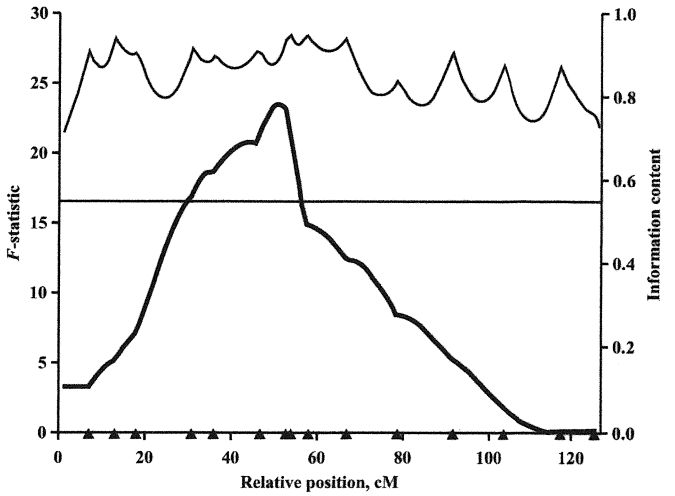

Figure 2. *F*-statistic profile for carcass yield estimate (—) on BTA 5 (cM position; x-axis). The horizontal line indicates the threshold for the 0.1% chromosome-wise level. The upper line indicates information content (right y-axis). Marker positions are identified as triangles above the x-axis and were BM6026, BMS610, BP1, BL23, Oar-FCB5, CSSM034, BL4, UWCA52, RM084, BMS490, BMS1216, BMS1248, BM315, BM733, and BMS597, respectively.

To control the thresholds for error rate of multiple-trait analysis, we applied the false discovery rate (**FDR**) suggested by Weller et al. (1998). False discovery rate is the expected proportion of true null hypotheses within the class of rejected null hypotheses. The *P*-values corresponding to multiple comparisons are ordered such that $P_{(1)} \leq P_{(2)} \leq \ldots \leq P_{(k)} \ldots \leq P_{(n)}$, where n is the total number of tests and $P_{(k)}$ is the P value corresponding to the null hypothesis of the kth test. Defining $q = nP_{(i)}/i$, the FDR can be controlled at some level q^* by determining the largest i for which $q^* \leq nP_{(i)}/i$. That is, under this condition, among i rejected null hypotheses, the expected proportion of falsely rejected hypotheses is no greater than q^*.

Results and Discussion

Population for QTL Analysis

The pedigree and carcass trait data for each steer were obtained from the Japan Wagyu Registry Association and the Japan Meat Grading Association, respectively. Each parentage relationship was confirmed with microsatellite marker genotypes. The paternal half-sib family of a specific bull used was composed of 348 steers, 236 of which were used for the first genome scan, and all 348 steers were used for the second scan. Deviation from normality was tested for each of 10 traits, including BW-1, BW-2, CW, LMA, RT, SFT, YE, BMS, ADG-1, and ADG-2. Their skewness and kurtosis values are shown in Table 1. The Wagyu steers were slaughtered at an older age (882 ± 36 d) and at heavier weights (714 ± 56 kg) than in previous studies (467 d and 493 kg, Casas et al., 2003; Kim et al., 2003). Thus, QTL results

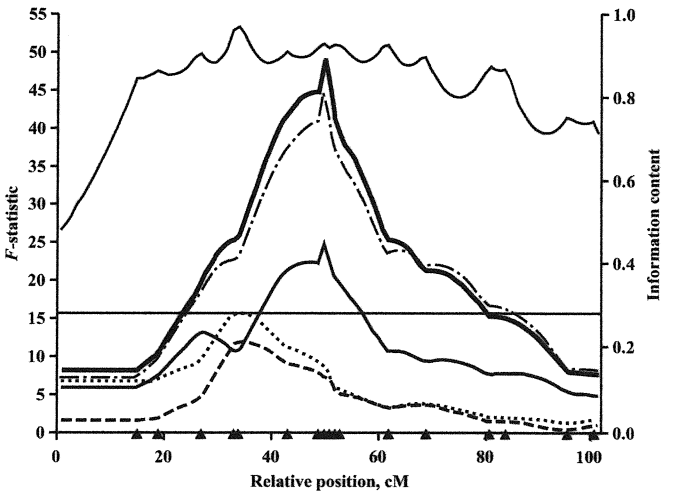

Figure 3. *F*-statistic profiles for weights at 9 mo (— — —) and 30 mo (—), carcass weight (— · —), ADG-1 (----) and ADG-2 (—) on BTA 14 (cM position; x-axis). The horizontal line indicates the threshold for the 0.1% chromosome-wise level. The upper line indicates information content (right y-axis). Marker positions are identified as triangles above the x-axis and were BM1508, BMS1678, ILSTS001, MNB-14, RM180, BMS1941, BM8215, BL1009, DIK062, ILSTS008, BM302, BMS740, BMS108, BM4513, BM4305, BL1036, and BM6425, respectively.

from these two studies and ours must be compared with caution.

QTL Mapping Results by the First Genome Scan

We genotyped 342 microsatellite markers on 29 autosomes across 236 steers in a paternal half-sib family for the first genome scan. The present linkage map for the 29 autosomes spanned 2,664 cM with an average marker interval of 7.8 cM. The information content ranged from 0.62 to 0.89, with an average of 0.84. The QTL mapping results are summarized in Table 2. We initially identified 26 QTL for nine traits at the 5% chromosome-wise level. The QTL detected were examined in terms of FDR due to multiple trait analysis of whether FDR were less than 0.10, where the QTL would be reliable (Weller et al., 1998). Eleven QTL had calculated FDR of greater than 0.10 and were thus excluded. Of the resulting 15 QTL, we located three QTL for two traits in the same regions as previously reported: CW on BTA 14 (Kim et al. 2003); BMS on BTA 5 (Stone et al., 1999) and BTA 14 (Casas et al., 2003; Thaller et al., 2003). We mapped QTL for SFT on BTA 14, whereas the back fat thickness trait was located in the same region by Stone et al. (1999), Casas et al. (2000, 2001), and Moore et al. (2003). The QTL for BMS and SFT were detected in the same region of BTA 14 where Barendse (1999) observed an association of marbling with the microsatellite *CSSM66* near *thyroglobulin*, and Grisart et al. (2002) and Winter et al. (2002) identified a gene responsible for milk fat content as *diacylglycerol O-acyltransferase*. Twelve QTL, however, were first observed in this work.

Confirmation of Significant QTL by the Second Genome Scan

Of the 15 QTL, six QTL for six traits were significant at the 5% experiment-wise level and were located on three chromosomes: LMA and BMS on BTA 4, YE on BTA 5, and three growth-related traits (ADG-1, BW-2, and CW) on BTA 14. Two other QTL affecting growth-related traits (BW-1 and ADG-2) were also located on BTA 14 as shown in Table 2. Thus, we investigated the three chromosomes comprising the eight QTL using 348 steers with increased markers as the second scan and estimated their allele effects. Table 3 summarizes the second scan results with QTL positions, F-statistic values, Q to q allele substitution effects, and QTL contributions (ratio of variance explained by the regression model to total variance) at the positions where the highest F-statistic values were recorded. For the second scan of BTA 4, 22 microsatellite markers were genotyped as shown in Figure 1. The QTL for LMA and BMS were located at 52 to 67 cM of the support interval with the high F-statistic values. The same haplotype derived from a bull was related to positive effects on LMA and BMS. The contribution ratios of QTL for LMA and BMS were calculated to be 4.8 and 8.2%, respectively. The results support the notion by Moody et al. (1996) that GPD could detect QTL with large effects, although we used the progeny design. We confirmed the YE QTL on BTA 5 (45 to 54 cM) with an F-statistic value of 23.5 by genotyping 15 microsatellite markers as shown in Figure 2. The contribution ratio for YE corresponded to 5.6%. We used 17 microsatellite markers to confirm the QTL for five growth-related traits (BW-1, BW-2, CW, ADG-1, and ADG-2) on BTA 14. Three QTL for ADG-2, BW-2, and CW were located on 45-51 cM of BTA 14, whereas BW-1 and ADG-1 were on 29 to 42 cM (Figure 3). Notably, the five growth-related traits were positively affected by the same haplotype. The contribution ratios for these five growth-related traits ranged from 3.4 to 12.3% of the total variances, respectively, supporting the notion by Moody et al. (1996). Mukai et al. (1995) estimated a significant correlation between BW-2 and CW with a coefficient of 0.87 in a purebred Wagyu population. Kim et al. (2003), however, observed a significant QTL for CW, but not for BW-2, on BTA 14 in an Angus × Brahman family. Finally, FDR for the eight QTL were less than 0.01 in the second scan, confirming the presence of these QTL.

Our progeny design to detect QTL was composed of one paternal half-sib family comprising more than 200 progeny and informative microsatellite markers with a 7 to 8 cM marker interval with an information content of approximately 0.85. Results indicated that this design is useful for detecting QTL in a Wagyu purebred population. Mapping of QTL based on a single sire, however, will uncover only a fraction of the segregating QTL present in the population. Additional analyses of half-sib families will provide valuable information for marker-assisted breeding of the population.

Implications

The progeny design in a purebred Wagyu population successfully detected quantitative trait loci. Eight quantitative trait loci exhibited large effects immediately applicable to marker-assisted selection in the family. The refined quantitative trait loci regions on bovine chromosomes 4, 5, and 14 are promising targets for positional cloning research.

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