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Bovine quantitative trait loci analysis for growth, carcass, and meat quality traits in an F_2 population from a cross between Japanese Black and Limousin

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ABSTRACT: A genome-wide scan for QTL affecting economically important traits in beef production was performed using an F_2 resource family from a Japanese Black × Limousin cross, where 186 F_2 animals were measured for growth, carcass, and meat-quality traits. All family members were genotyped for 313 informative microsatellite markers that spanned 2,382 cM of bovine autosomes. The centromeric region of BTA2 contained significant QTL (i.e., exceeding the genome-wide 5% threshold) for 5 carcass grading traits [LM area, beef marbling standards (BMS) number, luster, quality grade, and firmness), 8 computer image analysis (CIA) traits [LM lean area, ratio of fat area (RFA) to LM area, LM area, RFA to musculus (M.) trapezius area, M. trapezius lean area, M. semispinalis lean area, RFA to M. semispinalis area, and RFA to M. semispinalis capitis area], and 5 meat quality traits (contents of CP, crude fat, moisture, C16:1, and C18:2 of LM). A significant QTL for withers height was detected at 80.3 cM on BTA5. We detected significant QTL for the C14:0 content in backfat and C14:0 and C14:1 content in intermuscular fat around the 62.3 to 71.0 cM region on BTA19 and for C14:0, C14:1, C18:1, and C16:0 content and ratio of total unsaturated fatty acid content to total SFA content in intramuscular fat at 2 different regions on BTA19 (41.1 cM for C14:1 and 62.3 cM for the other 4 traits). Overall, we identified 9 significant QTL regions controlling 27 traits with genome-wide significance of 5%; of these, 22 traits exceeded the 1% genome-wide threshold. Some of the QTL affecting meat quality traits detected in this study might be the same QTL as previously reported. The QTL we identified need to be validated in commercial Japanese Black cattle populations.

Key words: bovine, F_2 family, meat quality, quantitative trait loci

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INTRODUCTION

Many studies have successfully detected QTL for economically important traits of beef cattle such as growth, carcass, and meat quality traits by using crossbred experimental populations (Keele et al., 1999; Stone et al., 1999; Casas et al., 2000, 2003; MacNeil and Grosz, 2002; Kim et al., 2003). Alexander et al. (2007a,b) recently reported the results of QTL analysis of a population for which Japanese Black and Limousin cattle were the parents.

Since 1994, we have generated an F_2 resource population derived from crosses between Japanese Black sires and Limousin dams to map loci affecting economically important traits. A unique characteristic of

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Table 1. Composition of the recipient dams of the F_2 population

	Age (yr)										
Breed	2	3	4	5	6	7	8	9	12	13	Total
Angus		2	1	6	3	1	2	4	1	1	21
F_1[1]							1				1
Hereford					2	2					4
Japanese Black		2	3								5
Japanese Shorthorn	52	42	43	8							145
Limousin	10										10
Total	62	46	47	14	5	3	3	4	1	1	186

[1]Derived from the cross of Japanese Black × Murray Gray.

the Japanese Black breed is the high fat content in the meat (so-called highly marbled beef), which is an important criterion for beef quality in the present Japanese market. May et al. (1993) described the difference in fatty acid compositions of the intramuscular fat of Wagyu crossbred and Angus steers, and Kuber et al. (2004) reported that Wagyu steaks had lower Warner-Bratzler shear force values than did Limousin steaks (note that most cattle known as Wagyu are Japanese Black breeds). Given those findings, Japanese Black cattle may have other economically favorable traits, in addition to marbling, compared with other breeds. In contrast to Japanese Black cattle, Limousin cattle produce leaner meat and have a larger body size. We chose these 2 breeds, the phenotypes of which differ dramatically, to construct an experimental F_2 resource family for bovine QTL analysis.

In this report, we describe QTL underlying the difference in growth, carcass, and meat quality traits between Japanese Black and Limousin cattle. We incorporated physicochemical property traits of the F_2 beef, including the fatty acid composition of backfat, intermuscular fat, and LM i.m. fat. We also identified QTL for computer image analysis (**CIA**) traits.

MATERIALS AND METHODS

Animal care and use was according to the protocol approved by the National Livestock Breeding Center Animal Care and Use Committee.

Generation and Feeding of F_2 Population

F_2 Population. An F_2 resource population was generated at the Tokachi and Ohu branches of the National Livestock Breeding Center in Japan. The animals used as parents were 2 Japanese Black (**JB**) sires (JB-A and JB-B) and 2 Limousin (**L**) dams (L-A and L-B). The F_1 animals were obtained by crossing JB-A with L-A (family A) and JB-B with L-B (family B). Family A consisted of 2 F_1 males and 17 F_1 females, and family B consisted of 2 F_1 males and 15 F_1 females. To avoid obtaining progeny homozygous for latent recessive hereditary disease loci that may be present in the 2 JB sires, F_2 animals were obtained by crossing F_1 males and their nonsibling F_1 females (between family A and B) using embryo transfer techniques. Both F_1 families were produced and raised at the Tokachi branch, and fertilized eggs were collected in a frozen state. The majority of the frozen eggs were then sent to the Ohu branch and used to produce F_2 animals. We produced 37 F_2 animals at the Tokachi branch from July 1999 to January 2000. The remaining 149 F_2 animals were produced at the Ohu branch during 4 periods: October to December 1999 (18 cattle); April to June 2000 (44 cattle); January to March 2001 (52 cattle); and July to October 2001 (35 cattle). The recipient dams of the F_2 population consisted of 6 breeds, and ages were distributed from 2 to 13 yr (Table 1).

Feeding Conditions. A total of 186 F_2 animals were weaned at 56 d of age. Calves were raised by artificial suckling. In the period from weaning to immediately before the fattening stage (rearing period), animals were fed with mixed feed (Snow Brand Seed Co. Ltd., Sapporo, Japan), with free intake of hay, water, and mineral salts. At 8 mo of age, F_2 animals were moved to fattening stalls and began to receive the mixed feed for the fattening stage. The mixed feed comprised 30.2% barley corn, 39.4% dent corn, 15.1% wheat bran, 3.4% rice bran, 4.0% wheat flour, 5.7% soybean waste, 1.0% NaCl, and 1.0% monocalcium phosphate. The digestible CP of this diet was 11.4% and the total digestible nutrients were 83.1%. All of these percentages were calculated on a DM basis. The amount of mixed feed provided during the fattening stage was calculated considering the energy requirement given in the Japanese Feeding Standard for beef cattle (JLIA, 1995). To accurately control feed intake, every F_2 animal was tagged with individual recognition equipment for an automatic feeding system. The allowed proportions of hay and mixed feed for the fattening stage were 25:75 for animals <14 mo old, 15:85 for animals 15 to 20 mo old, and 10:90 for animals 21 to 24 mo old. Hay, water, and mineral salts were fed without restriction.

Phenotype Measurements

Growth and Carcass Traits. The F_2 animals were weighed at birth, 4 wk of age, and on the first and last day of the fattening period. Withers height (from

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the ground to the peak between shoulder blades), hip cross height (from the ground to the intersecting point of hip points line and the median line), body length (from lower edge of the scapula to the end of the ischial tuberosity), chest girth and width (close behind the fore foot), hip length (from the hip cross to back end of the ischial bone), hip point width (between the points of the hip), rump width, and pin bone (back end of the ischial bone) width were measured 1 d before slaughter. The F_2 animals were slaughtered at the age of 24 mo (731.62 ± 5.01 d of age). At the meat plant, HCW of the F_2 animals were obtained, and carcass quality was evaluated about 48 h after slaughter by certified graders belonging to the Japan Meat Grading Association (Tokyo, Japan). Graded traits were LM area, rib thickness (the length from the abdominal lining to the external side of latissimus dorsi at around the midpoint of entire rib bone of the cross section), backfat thickness (the length from the external side of latissimus dorsi to carcass surface on the vertical line from the lower end of iliocostalis to carcass surface), beef marbling standards (**BMS**; No. 1 to 12), beef color standards (No. 1 to 7), beef fat standards (No. 1 to 7), luster, firmness, and texture. All graded traits were measured at the sixth rib bone side of the cross section between the sixth and seventh rib bones.

Meat Quality Traits. Physicochemical property traits of the F_2 beef were measured. The rib roast blocks of the seventh to eighth rib bone were sampled in all F_2 animals. The LM was excised from the block and minced for analysis of moisture, crude fat, and CP content as described by Okumura et al. (2007), where approximately 50 g of LM was excised and put in a plastic bag, and then incubated for 1 h in a constant-temperature bath at 70°C, and reweighed to calculate the cooking loss value. This incubated muscle was then cut thinly to yield pieces that were 1 cm × 1 cm × 5 cm cuboids) and used to measure the Warner-Bratzler shear force (Salter, Kent, UK). Meat color was measured as described by Sato et al. (2003). In addition, we determined the fatty acid content of 3 parts of the rib loin block: backfat (on M. trapezius), intermuscular fat (between M. rhomboideus and LM), and intramuscular fat (of LM). Fat extractions were done as described by Folch et al. (1957), and extracted fat was saponified with potassium hydrate-ethanol solution and methylesterified with boron trifluoride-methanol complex. Processed fat was analyzed by gas chromatography (6890A, Agilent Technologies Japan Ltd., Tokyo, Japan) under the following conditions: the temperature of the inlet was 150°C, the oven was warmed from 150 to 220°C, and the temperature of the detector sensor was 220°C. We used helium gas as a carrier, a capillary column (TC-70, 0.25 mm i.d. × 60 m, df (the phase thickness of the inside of the capillary column) = 0.25 μm; GL Science, Tokyo, Japan), and flame-ionization detector for detection.

Computer Image Analysis Traits. Digital images of the carcass cross section were taken between the sixth and seventh ribs using photographic equipment developed by Kuchida et al. (2001a). This equipment comprised 2 parts: a dome with 570 white light-emitting diodes and a digital camera (2 megapixels, FinePix2900Z, Fuji Film, Tokyo, Japan) with a wide conversion lens (WL-FX29, Fuji Film). The distance between the camera and the surface of the carcass was fixed, and the lens was always parallel to the carcass cross section. As a result, area and length could be measured with high accuracy using the equipment. Obtained digital images were then analyzed using software developed by Kuchida et al. (2000). The total muscle area, lean area, and fat area of LM, M. trapezius, M. semispinalis, and M. semispinalis capitus were calculated by this software. Here, the total muscle area represents the internal area of the muscle outline form. Therefore, the lean and fat areas are summed to give total muscle area. The ratio of the length of minor and major axes of LM was also calculated.

Genotyping

We extracted DNA from blood using automatic extraction equipment (NA1000, Kurabo, Osaka, Japan), and the final DNA concentration was adjusted to 20 ng/μL. A genome screen was conducted with microsatellite markers (Kappes et al., 1997; Ihara et al., 2004). Polymerase chain reaction amplification was performed in a volume of 15 μL containing 20 ng of genomic DNA, 1.67 m*M* $MgCl_2$, 6.25 pmol of each primer, 0.2 m*M* deoxynucleotides, and 0.375 U of *Taq* DNA polymerase (ABgene, Epsom, UK). The annealing temperatures of each marker in thermocycling steps were optimized by referencing those recommended by Ihara et al. (2004). Amplifications were performed under the following conditions: 5 min at 94°C, 30 cycles of 30 s at 94°C, 30 s at annealing temperature, 30 s at 72°C, and a final extension of 7 min at 72°C. After PCR amplification, reaction products were fractionated on an ABI377 DNA sequencer (Applied Biosystems, Foster City, CA), and fragment analysis was performed with GeneScan and Genotyper software (Applied Biosystems).

Linkage Analysis

Linkage maps for the 29 bovine autosomes were constructed by using CRI-MAP (Green et al., 1990), and the constructed map was used for the whole-genome QTL scan. The information content of markers was calculated by the method described by Knott et al. (1998).

A QTL analysis for each trait was performed by the method developed by Haley et al. (1994). The statistical model is based on linear regression of phenotypes on the probabilities of QTL genotypes at a given location. We assumed that the grandparental breeds, Limousin and Japanese Black, were fixed for alternative alleles at a QTL. Two alleles at a putative QTL at a given location were denoted by Q and q. There are 3

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possible genotypes, QQ, Qq, and qq, for a QTL at the given location on an autosome. The probabilities of the QTL genotypes [denoted as Prob(QQ), Prob(Qq), and Prob(qq)] were calculated from the observed genotypes of markers linked to the QTL. The calculation was done as described by Haley et al. (1994). In analyses of actual data, some fixed effects other than QTL effects including sex-associated differences, breeds, and ages of the recipient cows, seasons, and locations were taken into account.

Let the effects of genotypes QQ, Qq, and qq be denoted by a, d, and $-a$, respectively. We assumed that the phenotypic value of a trait is written for the ith individual in F_2 as follows:

$$y_i = \sum_j x_{ij} b_j + c_{ai} a + c_{di} d + e_i,$$

where b_j is the jth element of the vector of fixed effects, which includes overall mean, sex effect, breeds of the recipients (6 breeds), ages of the recipients (10 levels), and combinations of seasons and locations (5 levels); x_{ij} is the (i,j)th element of the design matrix associating b_j to y_i; c_{ai} is the coefficient for the additive component for individual i at the given location that is calculated from the probabilities of QTL genotypes and equal to Prob(QQ) – Prob(qq); c_{di} is the coefficient for the dominance component for individual i at the given location, which is equal to Prob(Qq); and e_i is the residual error. Model parameters μ, h, a, and d are estimated by a least squares method. That is, estimators of the parameters are obtained such that the sum of squares,

$$S = \sum_{i=1}^{n} \left(y_i - \sum_j x_{ij} b_j - c_{ai} a - c_{di} d \right)^2,$$

is minimized, where n is the number of individuals of F_2. Denoting least squares estimators of b_j, a, and d by the terms $\hat{b}_j$, $\hat{a}$, and $\hat{d}$, the minimal sum of squares is obtained as

$$S_1 = \sum_{i=1}^{n} \left(y_i - \sum_j x_{ij} \hat{b}_j - c_{ai} \hat{a} - c_{di} \hat{d} \right)^2.$$

Under the null model corresponding to no QTL, where $a = d = 0$ is assumed, the minimal sum of squares is denoted by S_0. Detection of a significant QTL is declared based on the ratio involving S_1 and S_0. In this report, we used the F-ratio, $[(S_0 - S_1)/2]/[S_1/(n - 20)]$, as a statistic for detecting QTL, where it should be noted that degrees of freedom of 20 is assigned to the fixed effects. Significance thresholds were obtained by a permutation test with 1,000 repetitions for each trait.

Correlation coefficients among the 27 F_2 phenotypes for which significant QTL were detected were calculated by PROC CORR (SAS Inst. Inc., Cary, NC).

RESULTS AND DISCUSSION

Phenotype Measurement and Marker Selection

The 76 traits measured are summarized in Table 2. One trait of particular interest was the BMS number, because in the Japanese market, the value of a beef carcass is heavily dependent on this grading score. Although BMS numbers are categorized as 1 to 12 in Japanese grading systems, the highest number in our F_2 population was 7. Furthermore, the distribution of the BMS numbers was extremely biased and was skewed toward lower scores (Figure 1).

The 4 parents of our F_2 family were genotyped with bovine autosomal microsatellite markers (Kappes et al., 1997; Ihara et al., 2004) to select informative markers. Contrary to our expectations, the allele types were quite similar between the 2 parental breeds for many markers, so we could not help eliminating a large part of them (data not shown). Overall, we genotyped these 4 parents for a total of 1,755 markers. We selected the markers in consideration of the marker distances based on the published bovine linkage map (Kappes et al., 1997; Ihara et al., 2004) and the number of characteristic alleles that could distinguish the origin among 4 parental animals or 2 parental breeds.

Linkage Analysis and QTL Mapping

From the marker linkage analysis, 313 markers were mapped to 29 bovine autosomal chromosomes over 2,382 cM, and the average distance between markers was 8.4 cM. With this linkage map, we detected QTL on BTA2, 5, and 19 (Table 3). We identified 9 QTL for 27 traits at the 5% genome-wide threshold level; QTL for 22 traits were significant at the 1% genome-wide level. Details of the significant QTL are presented in Figures 2, 3, and 4. In the QTL analysis, we took into account the fact that our F_2 population was produced at 2 different stations over different time periods. We also took into account the effects of recipient dams of the F_2 population, including their breed and age, as they might have an effect on the performance of the offspring (Table 1).

We mapped significant QTL for 5 carcass grading traits (Figure 2, panel A), 8 CIA traits (Figure 2, panels C to E), and 5 meat quality traits (Figure 2, panel B) to the same centromeric region of BTA2. Among the CIA traits, LM lean area showed the greatest F-ratio of all QTL identified in this study (Figure 2, panel C; Table 3). In addition, QTL for M. semispinalis and M. trapezius lean area were detected at 4.7 and 2.0 cM, respectively, on BTA2 (Figure 2, panel C). Animals that

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Table 2. Performance, growth, traits of carcass grade, meat quality, computer image analysis (CIA), and fatty acid composition of F_2 animals from an intercross of F_1 animals derived from 2 Japanese Black sires and 2 Limousin dams

Trait	n	Mean	SD	Minimum	Maximum
Growth[1]					
Birth BW, kg	186	34.4	5.1	20.0	47.0
BW at 4 wk of age	186	48.1	5.8	28.5	63.0
BW daily gain in fattening period	186	0.9	0.1	0.7	1.2
BW on first day of fattening	186	227.4	26.7	157.0	291.7
BW on last day of fattening	186	678.0	62.6	536.0	842.0
Withers height, cm	186	138.7	5.8	125.0	154.0
Hip cross height, cm	186	141.4	5.9	127.0	157.2
Body length, cm	186	136.2	5.9	122.5	154.0
Chest girth,[2] cm	186	219.5	7.8	198.0	243.0
Chest width,[2] cm	186	74.0	2.9	67.4	81.4
Hip length, cm	186	54.6	3.4	46.0	63.0
Hip point width, cm	186	53.0	2.5	47.0	59.0
Rump width, cm	186	51.3	3.1	41.0	60.0
Pinbone width, cm	186	30.2	3.1	23.0	41.0
Carcass grade					
Carcass weight, kg	186	424.8	40.1	332.5	534.0
Carcass grade (1 to 5)	186	2.4	0.6	2.0	4.0
LM area, cm^2	186	52.3	6.5	39.0	80.0
Rib thickness, cm	186	6.7	0.7	5.4	9.7
Back fat thickness, cm	186	3.1	1.0	0.3	5.7
Beef marbling standards (1 to 12)	186	3.0	1.0	2	7
Beef color score (1 to 7)	186	4.2	0.5	2	5
Luster (1 to 5)	186	2.9	0.5	2	4
Firmness (1 to 5)	186	2.5	0.6	2	4
Texture (1 to 5)	186	3.0	0.3	2	4
Beef fat score (1 to 7)	186	3.0	0.1	2	4
Meat quality					
Moisture, %	186	62.7	4.4	49.2	71.1
Crude fat content, %	186	17.7	5.9	6.2	35.4
CP content, %	186	19.0	1.4	15.2	21.9
Cooking loss, %	186	27.3	2.2	19.6	32.8
Warner-Bratzler shear force, kg/cm^2	186	5.6	1.5	1.9	10.7
Redness (a* value)	186	16.2	1.8	10.6	20.7
Yellowness (b* value)	186	9.3	1.9	4.3	13.6
Lightness (L* value)	186	47.1	3.8	36.8	58.0
Computer image analysis					
LM area, cm^2	186	47.3	6.5	33.7	76.4
LM lean area, cm^2	186	37.0	6.3	23.2	64.0
LM fat area, cm^2	186	10.3	3.2	4.4	22.4
RFA[3] to LM area, %	186	21.9	6.3	7.9	40.1
LM major axis, pixels	186	580.5	57.6	53.0	762.8
LM minor axis, pixels	186	415.8	46.2	21.4	507.1
Ratio of minor and major axes of LM	186	0.7	0.1	0.4	0.9
M. semispinalis capitus area, cm^2	186	8.7	2.9	1.2	16.1
M. semispinalis capitus lean area, cm^2	186	6.6	2.3	0.9	12.8
M. semispinalis capitus fat area, cm^2	186	2.0	0.8	0.3	4.2
RFA to M. semispinalis capitus area, %	186	23.2	5.0	9.3	36.1
M. semispinalis area, cm^2	186	31.8	3.9	21.5	42.0
M. semispinalis lean area, cm^2	186	22.7	3.1	15.5	31.1
M. semispinalis fat area, cm^2	186	9.1	2.3	3.4	15.2
RFA to M. semispinalis area, %	186	28.5	5.7	12.1	45.6
M. trapezius area, cm^2	186	35.0	5.1	20.7	55.2
M. trapezius lean area, cm^2	186	26.8	4.0	17.1	39.2
M. trapezius fat area, cm^2	186	8.2	3.1	2.9	24.1
RFA to M. trapezius area, %	186	23.1	6.9	9.4	43.6
Fatty acid composition					
Backfat					
C14:0 content, %	178	3.1	0.5	2.1	5.1
C14:1 content, %	178	1.4	0.5	0.5	5.7
C16:0 content, %	178	23.7	1.6	19.2	30.5
C16:1 content, %	178	6.0	1.0	3.8	12.6

Continued

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Table 2 (Continued). Performance, growth, traits of carcass grade, meat quality, computer image analysis (CIA), and fatty acid composition of F_2 animals from an intercross of F_1 animals derived from 2 Japanese Black sires and 2 Limousin dams

Trait	n	Mean	SD	Minimum	Maximum
C18:0 content, %	178	8.2	1.6	0.1	13.2
C18:1 content, %	178	51.9	2.7	42.6	58.8
C18:2 content, %	178	2.7	0.8	1.5	5.2
US/S[4]	178	1.8	0.2	1.1	2.3
Intermuscular fat					
C14:0 content, %	177	3.7	0.7	2.3	8.2
C14:1 content, %	177	1.0	0.3	0.4	2.2
C16:0 content, %	177	25.1	2.4	9.4	31.2
C16:1 content, %	177	4.8	0.8	3.1	7.7
C18:0 content, %	177	12.7	2.3	3.2	20.5
C18:1 content, %	177	47.2	3.0	40.5	55.7
C18:2 content, %	177	2.5	0.8	1.4	4.9
US/S	177	1.4	0.2	0.9	2.0
Intramuscular fat					
C14:0 content, %	184	3.7	0.6	2.3	6.6
C14:1 content, %	184	0.8	0.3	0.3	2.0
C16:0 content, %	184	28.4	2.0	22.5	34.6
C16:1 content, %	184	4.2	0.7	2.1	7.0
C18:0 content, %	184	12.7	1.9	4.9	18.4
C18:1 content, %	184	44.7	2.6	37.4	51.8
C18:2 content, %	184	2.8	0.8	0.1	6.4
US/S	184	1.2	0.1	0.8	1.7

[1]Withers height = the length from the ground to the peak between shoulder blades; hip cross height = the length from the ground to the intersecting point of hip points line and the median line; body length = the length from the lower edge of the scapula to the end of the ischial tuberosity; hip length = the length from the hip cross to the back end of the ischial bone; hip point width = the length between the points of the hip; pinbone width = the length between the ischial tuberosities.

[2]Measured at close behind the fore foot.

[3]RFA = ratio of fat area.

[4]The ratio between total unsaturated fatty acid and total SFA.

inherited the Limousin alleles had larger lean area in those 3 muscles than did those that inherited the Japanese Black alleles. A QTL for LM area was detected at the same position of 1.0 cM on BTA2 (Figure 2, panel D); animals that inherited the Limousin allele had a greater muscle area. Because a positive correlation between muscle area and lean area in our F_2 family occurred in every muscle measured by CIA (data not shown), animals that inherited the Limousin alleles at this QTL had greater muscle area with leaner meat.

In contrast, the QTL for RFA to LM, M. semispinalis, M. semispinalis capitus, and M. trapezius area were detected at 4.7 cM on BTA2 (Figure 2, panel E), as was the QTL for BMS number (Figure 2, panel A). Furthermore, QTL for crude fat content of LM and the C16:1 content of intramuscular fat were detected at 5.7 and 0 cM, respectively, on BTA2 (Figure 2, panel B). In all these cases, animals that inherited the Japanese Black alleles had greater values. Kuchida et al. (2000; 2001b) described significant relationships between crude fat content and RFA ($r = 0.98$), and between RFA and BMS number ($r = 0.93$), respectively. They suggested that crude fat content and RFA are useful data for evaluating marbling objectively. This suggestion is consistent with the results of our study.

All of our F_2 animals showed BMS numbers of 2 to 5, except for one animal that had a 6 and one that had a 7 (Figure 1). This indicates the lower intramuscular fat content of the F_2 population than of purebred Japanese Black cattle. In fact, Okumura et al. (2007) noted that the crude fat content (%) of Japanese Black cattle slaughtered at 24 mo of age (identical to the age at slaughter for our F_2 population) was 37.0 ± 4.4, whereas that in our F_2 population was 17.7 ± 5.9 (Table 2). Summarizing these results, we suggest that the Limousin alleles, which produced larger lean and muscle area, had a more extreme effect than those of the Japanese Black alleles, which produced beef with greater BMS, RFA, crude fat, and C16:1 content. Using a population that inherited the muscle hypertrophy locus, Casas et al. (1998) detected a QTL for ribeye area, marbling, and fat thickness. Their results were similar to ours not only in the type of phenotypes affected, but also in the QTL regions reported; the multiple QTL were in the same chromosomal region. Furthermore, using a Wagyu × Limousin crossbred F_2 population, Alexander et al. (2007a) detected a QTL for LM area in the centromeric region of BTA2.

Recently, Sellick et al. (2007) reported the effect of the F94L mutation of the myostatin gene. They treated this gene as a positional candidate of the QTL for meat percentage, eye muscle area, and silverside (meat block composed of M. gluteobiceps and M. semitendinosus) percentage detected in the 0 to 15 cM region of BTA2. They analyzed a population derived from a Jersey × Limousin cross and explained that the F94L mutation

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Table 3. Summary of QTL location, genome-wide probability, and additive and dominance effects

Trait	Genome-wide probability[1]		Location		F-ratio[2]	Additive[3] effect	Dominance[3] effect	Variance explained
	5%	1%	BTA	cM				
Growth								
Withers height, cm	9.06	11.82	5	80.3	10.59*	−1.87	−1.44	0.06
Carcass grade								
Carcass grade (1 to 5)	9.41	12.08	2	4.7	16.27†	0.32	0.09	0.16
LM area, cm^2	9.29	11.71	2	1.0	26.63†	−4.35	−1.95	0.23
Beef marbling score (1 to 12)	9.31	11.22	2	4.7	23.65†	0.61	0.19	0.21
Luster (1 to 5)	9.47	11.00	2	4.7	18.47†	0.25	0.11	0.16
Firmness (1 to 5)	9.47	11.87	2	4.7	14.51†	0.32	0.05	0.15
Meat quality								
Moisture	9.16	10.79	2	5.7	24.58†	−2.83	−1.39	0.21
Crude fat content	9.12	11.29	2	5.7	26.37†	3.85	1.94	0.23
CP content	9.18	10.98	2	4.7	32.57†	−0.96	−0.50	0.27
Computer image analysis								
LM area, cm^2	9.46	11.78	2	1.0	20.29†	−3.95	−0.90	0.18
LM lean area, cm^2	9.13	11.25	2	3.0	43.21†	−5.02	−2.04	0.33
RFA[4] to LM area, %	9.47	12.00	2	4.7	28.55†	4.18	2.28	0.25
RFA to M. semispinalis capitus area, %	9.22	11.59	2	4.7	11.91†	2.36	0.93	0.12
M. semispinalis lean area, cm^2	8.97	11.07	2	4.7	15.55†	−1.73	−0.13	0.15
RFA to M. semispinalis area, %	9.49	11.06	2	4.7	14.45†	2.56	2.26	0.14
M. trapezius lean area, cm^2	9.21	10.9	2	2.0	28.37†	−2.73	−0.58	0.22
RFA to M. trapezius area, %	9.17	11.27	2	4.7	11.69†	3.27	1.35	0.12
Fatty acid composition								
Backfat								
C14:0 content, %	9.38	11.71	19	62.3	9.65*	−0.22	−0.06	0.11
Intermuscular fat								
C14:0 content, %	9.49	12.06	19	62.3	27.47†	−0.39	−0.08	0.18
C14:1 content, %	9.44	11.40	19	71.0	13.59†	−0.18	0.04	0.15
Intramuscular fat								
C14:0 content, %	9.19	11.01	19	62.3	30.44†	−0.43	−0.13	0.28
C14:1 content, %	9.19	11.18	19	41.1	12.50†	−0.14	−0.13	0.14
C16:0 content, %	9.14	11.73	19	62.3	10.68*	−0.86	−0.39	0.11
C16:1 content, %	9.17	11.14	2	0.0	9.18*	0.23	0.23	0.09
C18:1 content, %	9.28	10.78	19	62.3	21.12†	1.56	0.42	0.20
C18:2 content, %	9.36	12.20	2	2.0	19.22†	−0.27	−0.23	0.07
US/S[5]	8.96	10.66	19	62.3	9.65*	0.06	0.03	0.09

[1]Genome-wide F-statistic thresholds at the 1% and 5% levels as determined by permutation tests.
[2]Asterisk (*) and dagger (†) represent the 5% and 1% genome-wide significance levels, respectively.
[3]Additive (a) and dominance (d) QTL effects correspond to the genotype values of +a, d, and –a for animals having inherited 2 Japanese Black alleles, 1 of each allele, or 2 Limousin alleles, respectively. If the additive effect is positive, the Japanese Black allele increases the phenotypic value; if it is negative, the Japanese Black allele decreases it (conversely, the Limousin allele increases the phenotypic value). Dominance effects are relative to the mean of the 2 homozygous genotypes.
[4]RFA = ratio of fat area.
[5]The ratio between total unsaturated fatty acid and total SFA.

of the myostatin gene originated from the Limousin breed and significantly increased these traits. Their results seem applicable to our findings. Myostatin is one of the strong candidate genes for QTL of BTA2 detected in our F_2 population.

Interestingly, a QTL for C18:2 content of LM was detected at 2 cM on BTA2 (Figure 2, panel B). Animals that inherited the Limousin alleles had greater content of C18:2. This fatty acid is a constituent of CLA, which has recently been studied for its favorable effect on human health, especially for reducing human cancer cell growth (De La Torre et al., 2006). The C18:2 fatty acid in beef cannot be synthesized in the bovine body, but originates from feedstuffs. Therefore, it seems strange that the genetic effect was observed on this trait. On the other hand, several studies have reported the difference in C18:2 content between muscle and adipose of cattle (Hristov et al., 2005; Noci et al., 2005). According to these studies, C18:2 is more abundant in muscle than in adipose. In our F_2 population, animals that inherited the Limousin allele had leaner meat, as described above. Furthermore, there was a weak but positive correlation between C18:2 content and both CP content and LM lean area (r = 0.11 and 0.12, respectively). Conversely, there was a negative correlation between C18:2 and both crude fat content and RFA to LM area (r = −0.12 and −0.13, respectively). These results may relate to the fact that the QTL for C18:2 content was detected at the centromeric end of BTA2.

There are several reports on candidate gene analysis of BMS and subcutaneous fat depth (**SFD**) traits using similar Wagyu × Limousin F_2 populations. Jiang et al.

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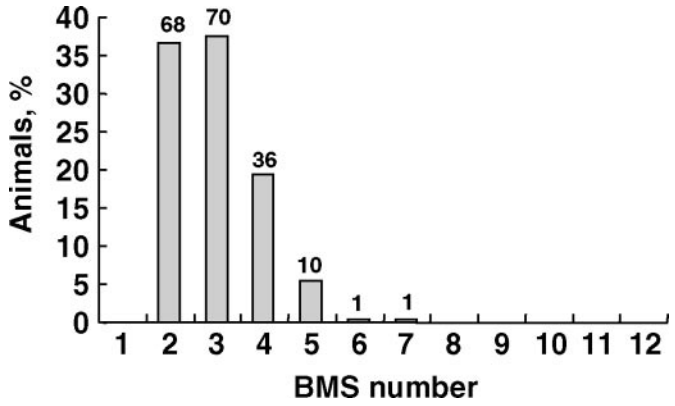

Figure 1. Bar chart of the beef marbling standards (BMS) numbers of 186 F_2 animals. The x-axis indicates the BMS numbers (1 to 12), the y-axis indicates the percentage, and the numeral on each bar represents the number of F_2 animals with that particular BMS.

(2005) detected genetic variation in the mitochondrial transcription factor A (*TFAM*) gene and determined its significant effect on both BMS and SFD. Michal et al. (2006) analyzed the bovine fatty acid binding protein 4 (*FABP4*) gene as a candidate, and found a significant relationship between detected SNP and these 2 traits. Wibowo et al. (2007) reported a significant effect of mutations detected in the corticotrophin-releasing hormone (**CRH**) gene on BMS and SFD. The first TFAM gene is located on BTA28, and the latter 2 genes (FABP4 and CRH) are both located on BTA14. We detected no significant (or suggestive) QTL for BMS or backfat thickness on those chromosomes. One possible explanation for this observation was the difference in parental individuals between those 2 F_2 populations. In our F_2 population, the mutations detected in these 3 genes might be fixed in the 2 breeds. In addition, the difference in the measuring procedure of BMS and SFD between the United States and Japan might have caused the different results.

We detected a QTL for withers height at 80.3 cM on BTA5 (Figure 3). Animals that inherited the Limousin alleles were taller than those that inherited the Japanese Black alleles. Quantitative trait loci for birth weight were detected in this region (Casas et al., 2003; Kim et al., 2003) by use of a *Bos indicus* × *Bos taurus* crossbred family. Mizoshita et al. (2004) detected a QTL for carcass yield on BTA5 in a half-sib population of purebred Japanese Black cattle, but the position was different from our QTL. Li et al. (2004) detected a QTL for preweaning ADG and ADG on feed in the 73.5- to 77.6-cM region on BTA5 using a crossbred population developed from several bovine breeds. Those investigators considered IGF-I to be a positional candidate and included information regarding IGF-I polymorphisms in their analysis. Although we measured 14 growth-associated traits in total, including birth weight and ADG during the fattening period, the genome-wise significant QTL was detected only for withers height.

On BTA19, we detected QTL for fatty acid composition (Figure 4, panels A to C). In addition, QTL for C14:0 content were detected at 62.3 cM for backfat (Figure 4, panel A); QTL for C14:0 and C14:1 content were detected at 62.3 and 71.0 cM for intermuscular fat (Figure 4, panel B) and at 62.3 and 41.1 cM for intramuscular fat (Figure 4, panel C). For each of these 3 loci, animals that inherited the Limousin alleles showed increased C14:0 and C14:1 content. We also detected QTL for C16:0 and C18:1 content and the ratio of total unsaturated fatty acid content to total SFA content of intramuscular fat at 62.3 cM on BTA 19 (Figure 4, panel C). Individuals that inherited the Japanese Black allele at this QTL demonstrated reduced C16:0 content, but increased C18:1 content and the ratio of total unsaturated fatty acid content to total SFA content. The degree of fatty acid composition in the intramuscular fat is an important factor for the eating quality of beef. Generally, the melting points of unsaturated fatty acids are less than those of SFAs, so beef with more unsaturated fatty acid in the intramuscular fat has superior eating quality and good texture. In addition, Mandell et al. (1998) suggested that C18:1 content has a favorable effect on beef flavor. In contrast, Fernandez and West (2005) stated that C12:0, C14:0, and C16:0 are considered to be associated with hypercholesterolemia, because they increase the concentration of low-density lipoprotein in human plasma, and Bláha et al. (2000) suggested that SFA concentrations and coronary atherosclerosis are related. Considering these points, we suggest that our findings here may facilitate the production of beef that is both pleasant to eat and healthier for human consumption. Furthermore, Viitala et al. (2003) detected a QTL for milk fat percentage at 67 cM on BTA19. Subsequently, Roy et al. (2006) studied the bovine fatty acid synthase (*FASN*) gene as a candidate gene for the QTL and found various SNP that had significant effects on milk fat percentage. Morris et al. (2007) detected QTL for fatty acid composition in both adipose tissue and milk fat in the 60 to 80 cM region on BTA19; the locations of those QTL overlap those that we detected. Morris et al. (2007) also analyzed *FASN* as a candidate gene for this QTL and found that the SNP haplotype had a significant effect on fatty acid composition; *FASN* may also be a strong candidate gene for controlling fatty acid composition in our F2 family. On the other hand, Alexander et al. (2007b) analyzed the fatty acid composition of the LM of their Wagyu × Limousin F_2 population, and carried out QTL mapping on this trait, but did not detect significant QTL on BTA19. A possible reason for this result is the difference in parental individuals of the 2 Wagyu × Limousin reference populations. Whereas their F_2 population originated from 8 Wagyu bulls and 108 Limousin females, our family was constructed from only 2 Japanese Black sires and 2 Limousin females. Our 2 Japanese Black

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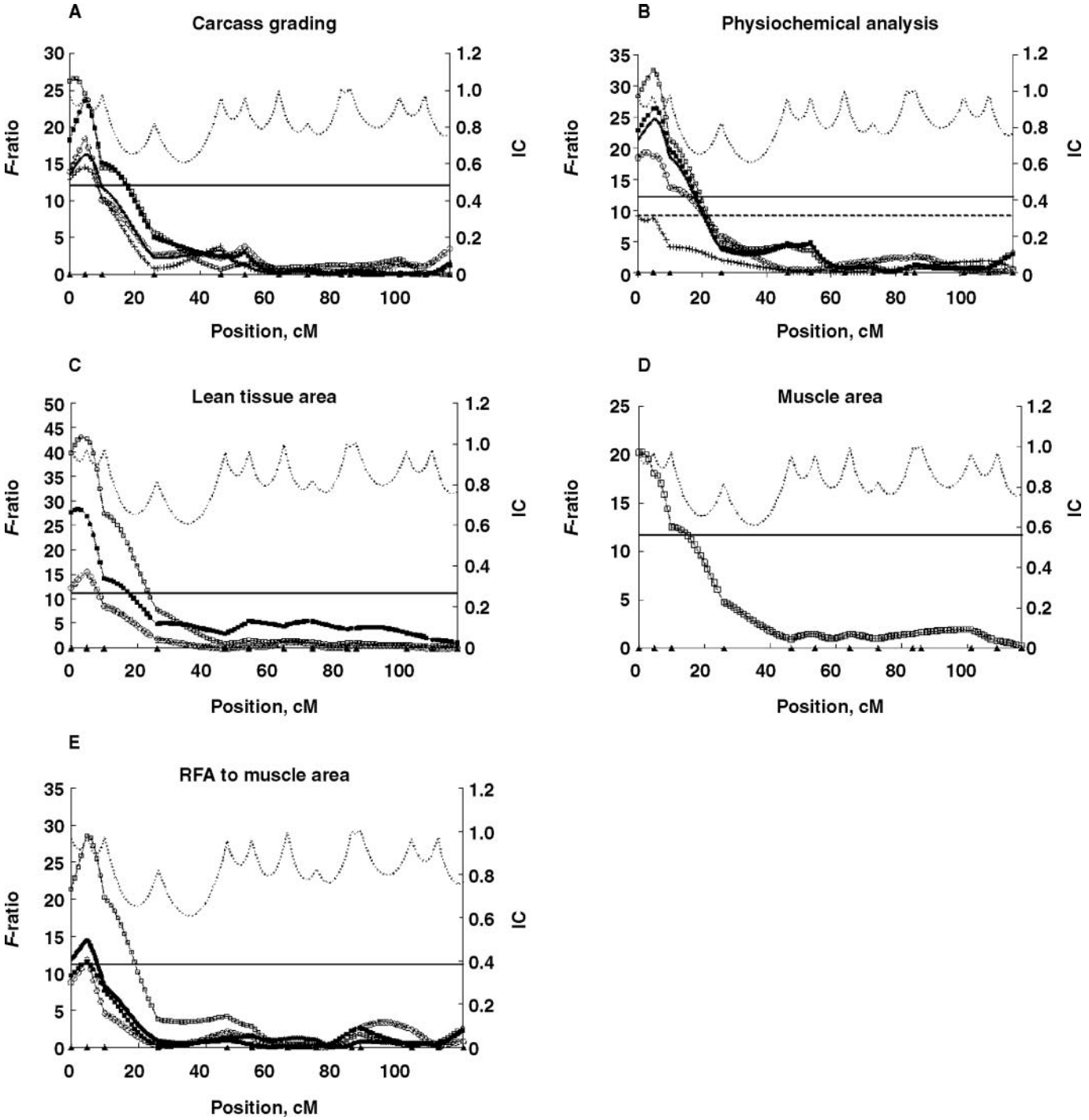

Figure 2. Plot of the *F*-ratios from multilocus least squares analysis (Haley et al., 1994) of carcass grade and physicochemical property traits on BTA2. The x-axis indicates the relative position on the linkage map; the left-hand y-axis represents the *F*-ratio; and the right-hand y-axis (dotted curve) indicates information content (IC). Triangles on the x-axis indicate marker positions. Markers were *MNS-2*, *DIK621*, *ILSTS026*, *DIK1081*, *DIK1140*, *BM4440*, *RM041*, *TGLA226*, *DIK1109*, *MM8D3*, *INRA135*, *IDVGA-37*, and *IDVGA-2*. The horizontal lines indicate genome-wide threshold values for 5% level (dotted line) and 1% level (solid line). (A) QTL profile of carcass grade traits: □ = LM area; ■ = beef marbling standards; ○ = luster; — = carcass grade; and + = firmness. (B) QTL profile of physicochemical property traits: □ = CP content; ■ = crude fat content; — = moisture content; ○ = C18:2 content; + = C16:1 content of intramuscular fat. (C) QTL profile of lean area: □ = LM; ■ = M. trapezius; ○ = M. semispinalis. (D) QTL profile of muscle area: □ = LM. (E) QTL profile of ratio of fat area (RFA) to muscle area: □ = LM; ■ = M. trapezius; ○ = M. semispinalis capitus; — = M. semispinalis. There is no public information for marker *DIK621*. The primer sequences of marker *DIK621* were forward primer = TCATGGCCATCATACATCAAG, reverse primer = CCCCTTTCCAAACCCATAAT.

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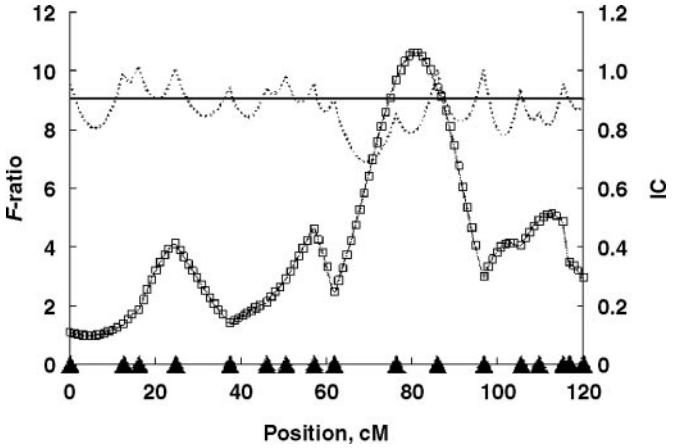

Figure 3. Plot of the *F*-ratios from multilocus least squares analysis (Haley et al., 1994) of withers height (□) on BTA5. The x-axis indicates the relative position on the linkage map; the left-hand y-axis represents the *F*-ratio; and the right-hand y-axis (dotted curve) indicates information content (IC). Triangles on the x-axis indicate marker positions. Markers were *BMS1095*, *BMS610*, *BP1*, *RM103*, *BMS1898*, *MS2106*, *CA084*, *ETH10*, *MNS-44*, *BMS1248*, *BM315*, *DIK2206*, *DIK2287*, *DIK2122*, *BM733*, *DIK2035*, and *BMS597*. The horizontal line indicates threshold values for genome-wide 1% level.

sires were considered excellent individuals in 1995, so several favorable genes (for meat qualities) might be fixed in the 2 sires. It could be said that the structure of our F_2 population was more suitable for detecting effective QTL. Interestingly, Alexander et al. (2007b) detected significant QTL for fatty acid composition on the centromeric region of BTA2, where we also detected the QTL on C16:1 and C18:2. The latent factor with effects on beef fatty acid composition may also be located in this region.

We observed several pairs of traits that showed highly positive or negative correlations among the 27 QTL-detected traits in this study. For example, BMS number had a strong positive relationship with RFA and LM muscle area (r = 0.85), but also showed a negative correlation with CP content (r = −0.78). Notably, QTL of those 3 traits were located at the same position, 4.7 cM on BTA2. This suggests that markers targeted for one trait may improve performance of the other trait. The opposite result might occur for other trait combinations. We may have to pay attention to this matter when consideration is given to marker-assisted selection.

Overall, the findings we report here provide fundamental information on the transmission of bovine quantitative traits. Because the QTL we detected may represent only breed-associated differences between Japanese Black and Limousin cattle, we need to confirm these QTL effects in a purebred Japanese Black population to obtain information useful in breeding Wagyu cattle.

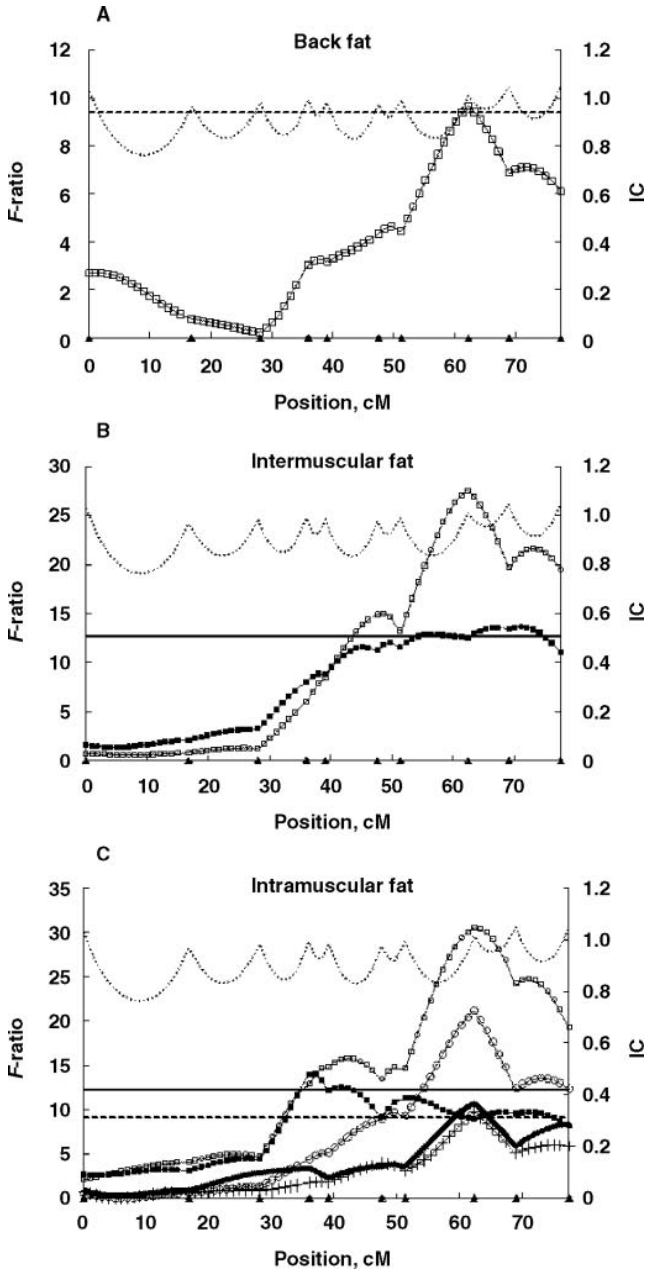

Figure 4. Plot of the *F*-ratios from multilocus least squares analysis (Haley et al., 1994) for fatty acid composition traits on BTA19. The x-axis indicates the relative position on the linkage map; the left-hand y-axis represents the *F*-ratio; and the right-hand y-axis (dotted curve) indicates information content (IC). Triangles on the x-axis indicate marker positions. Markers were *DIK2452*, *X82261*, *INRABERN148*, *URB044*, *CSSME070*, *BMS2389*, *BM17132*, *IOBT34*, *NLB-CMK39*, and *DIK688*. The horizontal lines indicate threshold values for genome-wide 5% level (dotted line) and genome-wide 1% level (solid line). (A) QTL profile of fatty acid composition in backfat: □ = C14:0 content. (B) QTL profile of fatty acid composition in intermuscular fat: □ = C14:0 content; ■ = C14:1 content. (C) QTL profile on fatty acid composition of LM intramuscular fat: □ = C14:0 content; ■ = C14:1 content; ○ = C18:1 content; — = C16:0 content; and + = the ratio between total unsaturated fatty acid and total SFA.

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