Whole genome fine mapping of quantitative trait loci for ultrasound and carcass merit traits in beef cattle

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[1]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5 (zhiquan.wang@ales.ualberta.ca); and [2]Agriculture and Agri-Food Canada, Lacombe Research Centre, 6000 C&E Trail, Lacombe, Alberta, Canada T4L 1W1 (email: changxi.li@agr.gc.ca).
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Nalaila, S. M., Stothard, P., Moore, S. S., Wang, Z. and Li, C. 2011. **Whole genome fine mapping of quantitative trait loci for ultrasound and carcass merit traits in beef cattle**. Can. J. Anim. Sci. **91**: 61–73. Quantitative trait loci (QTL) mapped to large chromosomal regions have limited utility as DNA markers for marker-assisted selection (MAS) and are less informative as a reference for the identification of the underlying causative quantitative trait nucleotides (QTN). The objective of this study was to conduct a whole genome fine mapping of QTL for ultrasound and carcass merit traits in beef cattle using a greater density of single nucleotide polymorphism (SNP) markers, and to identify SNP markers within the QTL regions that are associated with the traits. A total of 418 steers from 28 sires were used in this study with nine ultrasound and seven carcass merit traits that were collected as part of a feedlot trial conducted from 2003 to 2005 at the University of Alberta Kinsella ranch. Sires and their progeny were genotyped for a total of 4592 SNP markers distributed across all 29 bovine autosomes (BTA). Across-family analyses detected 12 QTL for five ultrasound traits on nine chromosomes and 18 QTL for six carcass merit traits on 10 chromosomes ($P < 0.05$). Within-family analyses identified 78 significant QTL for nine ultrasound and seven carcass merit traits ($P < 0.01$). The use of a denser panel of SNP markers allowed fine mapping of QTL to smaller chromosomal regions ranging from 0.6 to 11 cM compared with relatively larger QTL regions of 4 to 24 cM reported in previous studies. Furthermore, single SNP marker association analyses identified 22 SNPs that were significantly associated with three ultrasound and four carcass merit traits under 12 QTL regions ($P < 0.05$). These identified SNP markers significantly associated with the traits under the fine mapped QTL regions provide genomic tools for potential application of MAS and a reference to assist with the identification of QTN causing variations in ultrasound and carcass merit traits in beef cattle.

Key words: Beef cattle, carcass merit, quantitative trait loci, single nucleotide polymorphisms

Nalaila, S. M., Stothard, P., Moore, S. S., Wang, Z. et Li, C. 2011. **Cartographie fine des QTL du génome à l'origine des paramètres de l'examen aux ultrasons et de la qualité de la carcasse chez les bovins de boucherie**. Can. J. Anim. Sci. **91**: 61–73. Les locus quantitatifs (QTL) associés aux grandes régions chromosomiques n'ont guère d'utilité en tant que marqueur génétique dans les programmes de sélection assistée par marqueurs (SAM) et s'avèrent moins instructifs pour l'identification des nucléotides quantitatifs (QTN) sous-jacents dont ils dérivent. La présente étude devait préciser l'emplacement des QTL qui codent les paramètres de l'examen aux ultrasons et de la qualité de la carcasse signalés antérieurement pour les bovins de boucherie sur l'ensemble du génome, grâce à une plus grande densité de marqueurs à polymorphisme mononucléotidique (SNP), et ainsi identifier les marqueurs SNP dans la partie du QTL associée aux caractères en question. En tout, 418 bouvillons issus de 28 géniteurs ont été utilisés dans le cadre de cette étude sur 9 caractères de l'examen aux ultrasons et 7 de la qualité de la carcasse. L'étude s'inscrivait dans un essai d'élevage en parc d'engraissement réalisé de 2003 à 2005 au ranch Kinsella de l'Université de l'Alberta. Le génotypage des géniteurs et de leur progéniture a révélé 4 592 marqueurs SNP répartis sur les 29 autosomes bovins (ATB). Les analyses entre familles ont dévoilé 12 QTL pour 5 paramètres de l'examen aux ultrasons, sur 9 chromosomes, et 18 QTL pour 6 paramètres de la qualité de la carcasse, sur 10 chromosomes ($P < 0{,}05$). Les analyses à l'intérieur de chaque famille ont pour leur part révélé 78 QTL significatifs pour les 9 paramètres de l'examen aux ultrasons et 7 paramètres de la qualité de la carcasse ($P < 0{,}01$). L'utilisation d'un jeu de marqueurs SNP plus dense a permis d'affiner l'emplacement des QTL dans de plus petites régions chromosomiques allant de 0,6 à 11 cM, comparativement aux régions de 4 à 24 cM, beaucoup plus vastes, signalées dans d'autres études. Par ailleurs, les analyses d'association avec les marqueurs SNP uniques ont permis d'identifier 22 SNP

Abbreviations: **ADG**, average daily gain; **AVE_BF**, carcass average back fat; **BTA**, bovine autosome; **CMAR**, carcass marbling; **CREA**, carcass ribeye area; **CWT**, carcass weight; **GRDFAT**, carcass grade fat; **LMY**, ean meat yield; **MAS**, marker assisted selection; **QTL**, quantitative trait loci; **QTN**, quantitative trait nucleotides; **SNP**, single nucleotide polymorphism; **UBF**, ultrasound measurements of backfat thickness; **UMAR**, ultrasound measurements of marbling score; **UREA**, ultrasound measurements of rib eye area; **YGRADE**, yield grade

présentant des liens significatifs avec 3 paramètres de l'examen aux ultrasons et 4 paramètres de la qualité de la carcasse dans 12 régions à QTL ($P < 0,05$). Les marqueurs significativement associés aux QTL qui ont été plus finement cartographiés fournissent des outils génomiques qui pourront être employés pour la SAM et serviront de point de référence lors de l'identification des QTN à l'origine des paramètres de l'examen aux ultrasons et de la qualité de la carcasse chez les bovins de boucherie.

Mots clés: Bovins de boucherie, qualité de la carcasse, locus quantitatifs, polymorphisme mononucléotidique

Carcass merit traits in beef cattle are of particular interest to the beef industry as they are related to both the efficiency of beef production and consumer preferences for meat consumption and, as a result, they affect the profitability of the industry. A sustainable beef industry depends on efficient production and constant improvement in meat quality. Carcass merit traits are among the quantitative traits that are measured relatively late in an animal's production cycle. Incorporating the genes or DNA markers influencing carcass traits into the traditional genetic evaluation and selection programs using marker assisted selection (MAS) holds a great promise to accelerate the rate of genetic improvement by increasing the accuracy of genetic evaluation and shortening the generation interval (Dekkers and Hospital 2002). However, in order to implement MAS effectively, closely linked DNA markers or gene alleles or preferably functional quantitative trait nucleotides (QTN) influencing the quantitative traits of interest need be identified, characterized and validated.

In beef cattle, most of the early gene-discovery studies conducted to identify quantitative trait loci (QTL) of economical importance including carcass merit traits used microsatellite markers alone or in combination with single nucleotide polymorphism (SNP) markers (Beever et al. 1990; Keele et al. 1999; Stone et al. 1999; Casas et al. 2000; Li et al. 2006). Candidate gene and positional candidate gene approaches have also been used to identify polymorphisms that affect carcass merit traits in beef cattle (Grobet et al. 1997; Moore et al. 2003; Nkrumah et al. 2004). In a previous study, a genome-wide scan for QTL affecting ultrasound and carcass backfat thickness was conducted in a hybrid beef steer population using a combination of 100 microsatellite and 355 SNP markers with 8 to 30 markers per chromosome (Li et al. 2006). However, the QTL were localized to large chromosomal regions (4 to 24 cM), which is likely due to the low density of markers used, thus limiting their usefulness in the development of marker assisted selection strategies and as a reference for identifying causative QTN.

In cattle and other species, SNPs have become a widely used DNA marker type for QTL mapping and association analyses due to its high abundance in the genome, possible direct cause of the phenotype variation, relative high stability and suitability for high throughput genotyping in comparison with other DNA markers. The objective of this study was to conduct a whole-genome scan to identify and fine map QTL regions for ultrasound and carcass merit traits in beef cattle by using a denser SNP marker set and to identify SNP markers within the QTL regions that are associated with the ultrasound and carcass merit traits through association analyses.

MATERIALS AND METHODS

Animal Resources and Phenotypic Data

A total of 418 steers from 28 sire families at the University of Alberta's Kinsella Research Station were used in this study. The animals were managed and cared for according to the guidelines of the Canadian Council on Animal Care (CCAC 1993). The composition of this population has been previously described by Nkrumah et al. (2007a, b). Briefly, it was produced by crossing Angus, Charolais, or University of Alberta hybrid bulls and a hybrid dam line. The hybrid dam line was obtained by crossing among three composite cattle lines, namely beef synthetic 1, beef synthetic 2, and dairy × beef synthetic for more than 10 yr. The beef synthetic 1 was composed of 33% Angus, 33% Charolais, and 20% Galloway with the reminder from other beef breeds. The beef synthetic 2 was composed of about 60% Hereford and 40% other beef breeds. The dairy × beef synthetic line was made up of approximately 60% dairy breeds (Holstein, Brown Swiss, or Simmental) and 40% beef breeds mainly Angus and Charolais (Goonewardene et al. 2003). Steers were produced over 3 yr from a multiple-sire breeding program on pasture and the sire of each calf was later determined using a panel of microsatellite markers (Nkrumah et al. 2007a, b).

Traits Studied and Measurements

The measurements of ultrasound traits were obtained as part of the phenotypic data collection during the feedlot tests that were conducted at the University of Alberta's Kinsella Research Station in 2003, 2004 and 2005 with two batches of steers tested per year, and the carcass merit traits were collected in the abattoir, which was described by Nkrumah et al. (2004, 2007a, b). Briefly, ultrasound measurements of rib eye area (UREA), backfat thickness (UBF) at the 12th to 13th ribs, and marbling score (UMAR) were recorded at 28-d intervals during the feeding tests for a period of approximate 100 d using an Aloka 500V real-time ultrasound with a 17-cm, 3.5-MHz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC). Average daily gains for ultrasound ribeye area (ADG_UREA), ultrasound backfat (ADG_UBF), and ultrasound marbling score (ADG_UMAR) were estimated using a

linear regression analysis. Carcass weight (CWT) was measured as a summation of the left and right halves of each carcass. Carcass grade fat (GRDFAT) was measured at the 12th–13th rib. Carcass marbling (CMAR) is a measure of the intramuscular fat with a score of 1 to <2 for trace marbling, 2 to <3 for slight marbling, 3 to <4 for small to moderate marbling, and ≥ 4 for slightly abundant or more marbling. Carcass average back fat (AVE_BF) is the fat thickness measured over the ribeye muscle at 12th rib. Lean meat yield (LMY), an estimate of the saleable meat, was estimated using the following equation:

$$\begin{aligned}\text{lean meat yield (\%)} &= 57.96 + [0.202 \times \text{longissimus thoracis area (cm}^2)] \\ &\quad - [0.027 \times \text{warm carcass weight (kg)}] \\ &\quad - [0.703 \times \text{average backfat thickness (mm)}]\end{aligned}$$

as described by Basarab et al. (2003). Carcass ribeye area (CREA) was measured on the cross section of the longissimus dorsi muscle between the 12th and 13th ribs. Yield grade (YGRADE) refers to the proportion of lean meat and was classified as follows: $1 = \geq 59\%$; $2 = 54$ to 58%; and $3 = < 54\%$. A total of 418 steers with phenotypic and genotype data were available for this study. However, only 370 steers from 16 sire families were used for the interval QTL mapping analyses, with an average 23 progeny per sire and a half-sib family size that ranged between 9 and 56. Families where the number of offspring was fewer than 9 were excluded from the interval QTL mapping analyses. The average age at start of test and at slaughter was 251 and 389 d, respectively. However, carcass merit data were available on 342 steers. The descriptive statistics of the ultrasound and carcass merit traits considered in the study are presented in Table 1.

Table 1. Descriptive statistics of ultrasound and carcass merit traits

Variable	Steers, *n*	Mean	SD
Mean ultrasound marbling score	418	4.01	0.56
Average daily gain ultrasound marbling score	418	0.01	0.005
Mean ultrasound backfat (mm)	418	3.89	1.67
Average daily gain ultrasound backfat (mm)	418	0.03	0.019
Mean ultrasound ribeye area (cm^2)	418	55.74	7.14
Average daily ultrasound ribeye area (cm^2)	418	0.17	0.07
Ultrasound marbling	418	5.19	0.78
Ultrasound backfat (mm)	418	9.32	3.56
Ultrasound ribeye area (cm^2)	418	83.55	10.57
Carcass weight (kg)	342	312.4	31.9
Grade fat (mm)	342	10.73	4.31
Average backfat (mm)	342	12.21	4.25
Carcass ribeye area (cm^2)	342	84.06	9.29
Lean meat yield (%)	342	57.92	3.81
Carcass marbling score	342	2.49	0.54
Yield grade	342	1.72	0.72

DNA Isolation and SNP Genotyping

A 10-mL blood sample was collected by jugular venipuncture from each steer during the feedlot tests. Calf genomic DNA was extracted from blood samples using a standard saturated salt, phenol-chloroform method (Miller et al. 1988). Steers were genotyped for a total of 4592 SNP markers. The 4592 SNP markers were chosen based on their location on a radiation hybrid map that was constructed based on marker loci across eight breeds of cattle (McKay et al. 2007). The 4592 SNP markers were distributed on all 29 bovine autosomes (BTA) spanning 2914.4 cM of the linkage maps with a range of number of SNPs per chromosome from 58 (BTA 27) to 334 (BTA5) and an average distance of 0.63 cM between SNP markers. The approximate locations of the 4592 SNP markers in cM were inferred based on a composite physical map of the bovine genome of Snelling et al. (2007).

Whole Genome QTL Fine Mapping

Phenotypes for ultrasound and carcass merit traits were pre-adjusted for the fixed effects of feedlot batch-year contemporary groups (six levels for two feedlot batches over 3 yr) and sire breeds using PROC GLM (SAS 9.1.3 Institute, Inc., Cary, NC), and the resulting residuals were used as phenotypes for the interval QTL mapping analyses. A whole genome QTL scan was first conducted using an across-family analysis through the multiple marker regression approach (Knott et al. 1996). Animal age at the start of the test was included as a covariate for ultrasound trait QTL scan and animal age at slaughter was included as a covariate for carcass merit trait QTL scan, as implemented in the *QTL Express* software (Seaton et al. 2002). The across-family QTL scan tests the QTL effects nested within sire families and provides evidence of the segregation of QTL in the overall experimental population. Subsequently, a within-family QTL analysis was carried out to further examine which sire family was potentially segregating for the putative QTL.

Both the across-family and within-family QTL scans were performed at a 1-cM marker interval and the *F*-statistic tests were plotted along the chromosome. The chromosome-wise significance thresholds of the *F*-statistic tests for both the across-family analyses and the within-family QTL analyses were obtained by 10 000 permutations (Churchill and Doerge 1994) also as implemented in the *QTL Express* software (Seaton et al. 2002). The genome-wide significance thresholds, P_{genome}, were determined for across-family analyses by applying a Bonferroni correction to the chromosome-wise thresholds, $P_{\text{chromosome}}$, as described by de Koning et al. (1998):

$$P_{\text{genome}} = 1 - (1 - P_{\text{chromosome}})^n,$$

where n is the number of chromosomes tested in the analysis.

The QTL search was first conducted using the one-QTL model. Background QTL effects were analyzed for chromosomes that showed multiple QTL peaks on *F*-statistic profiles. The most significant QTL were fitted as co-factors to determine the presence of another QTL on the same linkage group. Results showed no evidence of multiple QTL on chromosomes that showed multiple peaks on the *F*-statistics profiles for the traits under investigation.

Single SNP Association Analyses under Identified QTL Regions

Single nucleotide polymorphisms under the significant QTL regions identified in across-family analyses were further assessed for their associations with the phenotypic traits using a single SNP marker association analysis. The association analysis was conducted using the Mixed Model Procedure of SAS (SAS 9.1.3 Institute Inc., Cary, NC) and the unadjusted phenotypic values of the data set including 418 steers with 28 sires and 298 dams. The model included the fixed effects of breed of sire (Charolais, Angus, or hybrid), batch-year effect (six levels), SNP genotype effect and random effects of sire and dam of animal. Sires were considered to be unrelated and therefore the random effect of sire was included in the model to account for expected covariances among paternal half-sibs as described in Nkrumah et al. (2007a). Animal age at the start of the test was included as a covariate for the analysis of ultrasound traits. Animal age at slaughter was included as a covariate for the association analyses of carcass merit traits. The additive effect of a SNP marker was estimated as half the difference between genotypic values of the two homozygous genotypes. The dominance deviation was estimated as the deviation of heterozygote genotypic value from the mean of the two homozygous genotypic values (Falconer and Mackay 1996).

RESULTS AND DISCUSSION

QTL for Ultrasound and Carcass Merit Traits

The whole genome across-family QTL scan identified 12 QTL that were significantly associated with five ultrasound measures on nine BTA at a chromosome-wise significance level of 5% with four QTL exceeding the 1% chromosome-wide significance threshold (Table 2). For the carcass merit traits, a total of 18 significant QTL for six carcass merit traits were identified on 10 chromosomes at a chromosome-wise significance level of 5%, whereas five QTL exceeded the 1% chromosome-wise significance threshold (Table 3). However, none of the above QTL reached the genome-wide significance level of 5% (Tables 2 and 3). Examples of QTL profiles for the across-family analyses are shown on Figs. 1 to 5.

The within-family QTL analyses identified 53 QTL with significant effects for 9 ultrasound traits on 23 chromosomes in 14 sire families (Table 4) and 25 QTL regions for 7 carcass merit traits on 16 chromosomes in 11 families at the chromosome-wise threshold of 1% (Table 5). The within-family QTL analysis confirmed 4 QTL for ultrasound traits and 11 QTL for carcass merit traits that were identified by the across-family QTL analyses. For the remaining 15 across-families QTL identified, the within-family QTL analyses detected significant QTL nearby for 4 of them (Tables 2 and 3).

The average QTL 95% confidence interval of the 30 QTL identified in the across-family QTL analyses was 2.9 cM with a range of 0.6 to 11 cM. Three of the 30 across-family QTL regions identified in this study were localized to similar chromosomal regions that were reported previously by other studies using different beef cattle populations (Casas et al. 2001, 2003; Takasuga et al. 2007), providing additional support for the findings. These include QTL for ADG_UREA, MEAN_UBF and UMAR on BTA 5, 8 and 21 respectively. The ADG_UREA QTL on BTA 5 within the interval of 43.9 to 45.3 cM is consistent with longissimus muscle area QTL at 53 (38–66 cM) reported by Casas et al. (2003). The QTL for MEAN_UBF identified on BTA 8 (7.0 to 8.1 cM) is consistent with a previous identified QTL for fat thickness located in an interval between 6 and 30 cM (Casas et al. 2001). On BTA 21, the chromosomal region of 37.9 to 40 cM for UMAR QTL is consistent with marbling score QTL detected at 40 cM by Takasuga et al. (2007) in Japanese Black Cattle.

Six of the remaining 27 across-family QTL regions were close to regions reported on the same chromosomes by other studies (Kim et al. 2003; Li et al. 2006; Takasuga et al. 2007). These comprised the QTL for CWT, UBF, GRDFAT, and AVE_BF on BTA 6, 13, 15 and 18 (Table 2 and 3). The CWT QTL on BTA 6 (18 to 20 cM) and 18 (53.9 to 55.6 cM) were closely located to carcass weight QTL reported at 38 cM (Takasuga et al. 2007) and between 33.4 and 40.2 cM (Kim et al. 2003), respectively. UBF QTL on BTA 13 at 34.1 to 36.7 cM in this study is also close to the QTL location for subcutaneous fat at 28 cM reported by Takasuga et al. (2007) in Japanese Black cattle. The QTL for UBF, GRDFAT and AVE_BF detected on BTA 15 in this study were also reported in a previous study using the same beef cattle population (Li et al. 2006). However, the QTL locations were shifted by 11 to 25 cM, which is likely due to an updated version of the bovine composite map used in this study. It may also represent different QTL as a denser maker set was used in this study for QTL detection in comparison to the previous study (Li et al. 2006). However, further investigation is required to confirm these QTL regions. The remaining 21 QTL identified by the across-family analyses in this study were not reported previously. Although using a higher density of markers could increase the resolution of QTL detection (Meuwissen and Goddard 2000), further studies using a larger sample size are needed to verify these QTL regions.

Table 2. Locations and QTL effects for ultrasound traits based on across-family analyses

Trait[z]	BTA	QTL peak (cM)	QTL 95% interval (cM)	*F*-ratio	$P_{chromosome}$	P_{genome}	QTL%[y]
MEAN_UBF	8	8	7.0–8.1	2.63	0.0093**	0.2374	7.1[xw]
	15	15	14.0–16.5	2.28	0.0477*	0.7577	5.7[xwv]
	27	58	57.7–59.0	2.39	0.0098**	0.2484	6.1
UBF	12	1	0.0–1.6	2.69	0.0496*	0.7713	7.8
	13	35	34.1–36.7	2.60	0.0497*	0.7720	7.4[v]
	15	43	41.0–47.0	3.46	0.0090**	0.2306	11.0
	23	0	0.0–8.0	2.45	0.0425*	0.7162	6.1
MEAN_UMAR	15	14	11.5–17.2	2.74	0.0394*	0.6883	7.7[v]
UMAR	13	39	37.9–39.6	2.73	0.0365*	0.6598	7.2[w]
	21	39	37.9–40.0	2.53	0.0448*	0.7353	6.4[w]
ADG_UREA	5	45	43.9–45.3	2.96	0.0074**	0.1938	8.3[v]
	11	88	87.7–88.6	2.61	0.0384*	0.6786	8.3

[z]MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; MEAN_UMAR = mean ultrasound marbling; UMAR = ultrasound marbling; ADG_UREA = average daily gain ltrasound ribeye area.
[y]QTL contribution (%) = (residual mean square of reduced model–residual mean square of full model)/total phenotypic variance.
[x]QTL confirmed at $P < 0.01$ in within-family analysis.
[w]QTL confirmed at $P < 0.05$ in within-family analysis.
[v]QTL detected at nearby region in within-family analysis.
*, ** $P < 0.05$ and $P < 0.01$, respectively.

In addition to the across-family analyses, we also performed a within-family QTL analyses to further investigate the sire families segregating the QTL. For the 30 QTLs identified in the across-family analyses, 15 were confirmed by the within-family QTL analyses at the significance level of 5% (Table 2 and 3). However, another 15 QTLs identified by the across-family analysis were not confirmed by the within-family QTL analyses at the significance level of 5%. Significant QTL effects that were obtained by pooling together several sire families with weak to moderate QTL effects may not be identified as a significant QTL within individual families, which was discussed in a previous QTL mapping study by Nkrumah et al. (2007a) for different traits. In addition, marker heterozygosity differences between sires could be the cause of the shift of QTL locations between across-family and within-family analyses (de Koning et al. 1999). It was noted that additional QTL

Table 3. Locations and QTL effects for carcass merit traits based on across-family analyses

Trait[z]	BTA	QTL peak (cM)	QTL 95% interval (cM)	*F* ratio	$P_{chromosome}$	P_{genome}	QTL%[y]
CWT	6	19	18.0–20.0	3.01	0.0375*	0.6699	8.7
	15	84	82.0–86.0	3.13	0.0491*	0.7678	9.2
	18	54	53.9–55.6	3.21	0.0097**	0.2462	9.5[w]
	21	34	33.9–34.5	2.63	0.0418*	0.7101	7.2[w]
LMY	5	16	15.5–18.0	2.70	0.0466*	0.7494	8.5[w]
	15	16	14.5–17.0	2.80	0.0065**	0.1723	8.9[w]
GRDFAT	1	9	8.5–12.0	2.46	0.0389*	0.6836	7.3[w]
	15	15	12.5–17.5	3.33	0.0085**	0.2193	11.1[wv]
	18	3	2.8–3.5	2.43	0.0428*	0.7186	7.2
	27	59	58.0–59.0	2.33	0.0495*	0.7706	6.7[w]
AVE_BF	5	8	0.0–11.0	2.74	0.0440*	0.7288	8.6
	15	16	13.0–17.5	3.45	0.0093**	0.2373	11.7[w]
CREA	1	6	4.0–6.1	2.69	0.0494*	0.7699	8.0[w]
	6	111	109.0–111.4	2.66	0.0434*	0.7238	7.9[x]
	10	16	15.9–16.5	2.34	0.0403*	0.6967	6.5
CMAR	1	4	0.0–5.2	2.66	0.0443*	0.7313	7.9[v]
	25	1	0.9–1.6	2.75	0.0092**	0.2351	8.3[w]
	29	20	19.0–20.7	2.56	0.0489*	0.7663	7.4

[z]CWT = carcass weight; LMY = lean meat yield; GRDFAT = carcass grade fat; AVE_BF = average backfat; CREA = carcass ribeye area; CMAR = carcass marbling.
[y]QTL contribution (%) = (residual mean square of reduced model–residual mean square of full model)/total phenotypic variance.
[x]QTL confirmed at $P < 0.01$ in within-family analysis.
[w]QTL confirmed at $P < 0.05$ in within-family analysis.
[v]QTL detected at nearby region in within-family analysis.
*, ** $P < 0.05$ and $P < 0.01$, respectively.

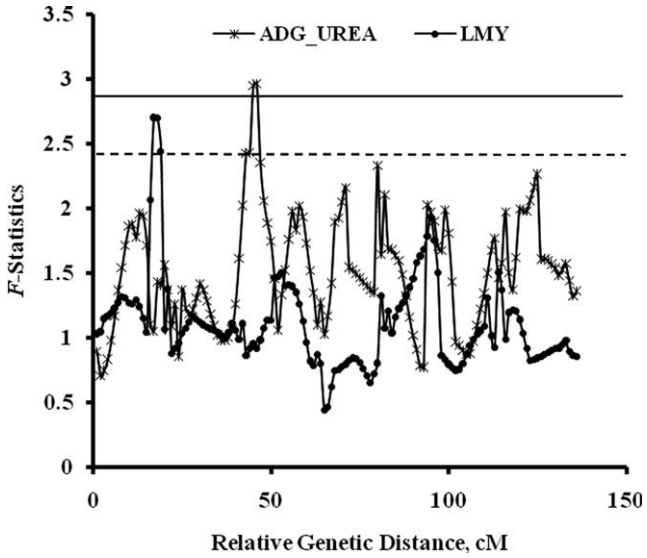

Fig. 1. QTL profiles for across-family analyses on bovine chromosome 5. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10 000 permutations. ADG_UREA = average daily gain ultrasound ribeye area; LMY = lean meat yield.

were identified in the within-family analysis in comparison to the across-family QTL analyses. It is likely that the effects of some of these QTL were overestimated due to a small number of informative offspring per sire half-sib family (Beavis 1998; Xu 2003) although half-sib families with fewer than nine offspring were not included in the analyses.

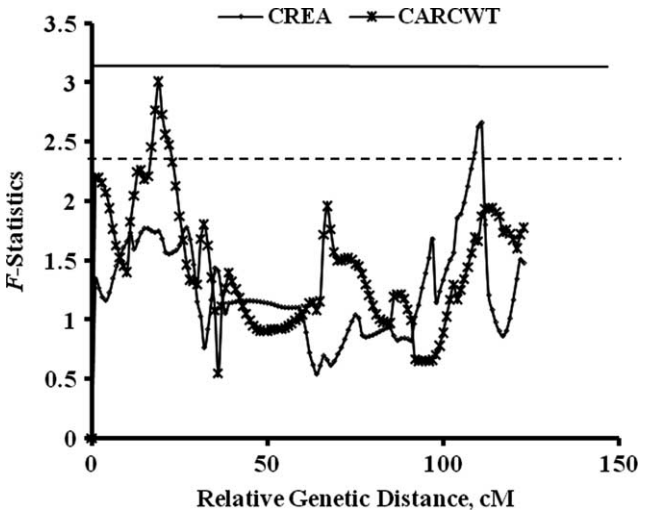

Fig. 2. QTL profiles for across-family analyses on bovine chromosome 6. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10 000 permutations. CREA = carcass ribeye area; CARCTW = carcass weight.

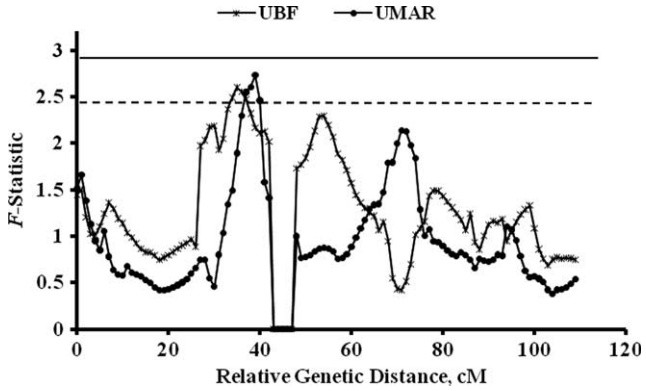

Fig. 3. QTL profiles for across-family analyses on bovine chromosome 13. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10 000 permutations. UBF = ultrasound backfat; UMAR = ultrasound marbling.

It was observed that the ultrasound and carcass merit measurements made on similar traits did not share the same QTL. Possible explanation of the inconsistency between ultrasound and carcass merit traits QTL may be due to moderate correlations between ultrasound and carcass merit traits, which implies that matching evidence for both traits would not necessarily be expected (Johnson et al. 2005). It may also be due to the fact that different genes are involved at the various developmental stages.

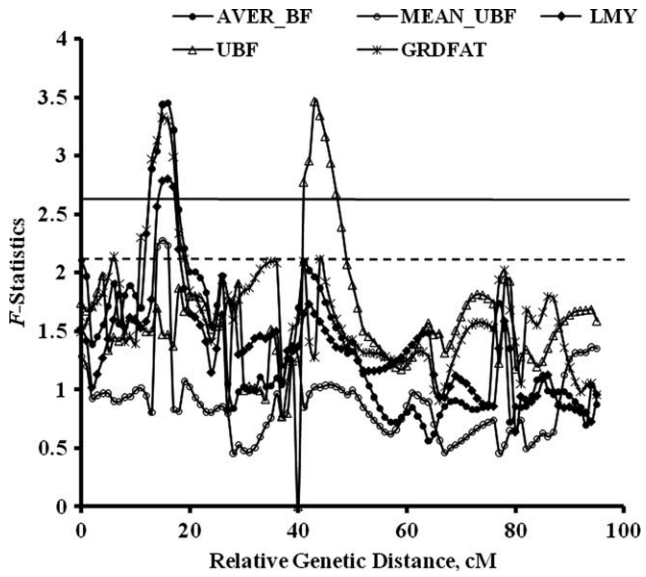

Fig. 4. QTL profiles for across-family analyses on bovine chromosome 15. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10 000 permutations. MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; LMY = lean meat yield; GRDFAT = carcass grade fat; AVER_BF = average backfat.

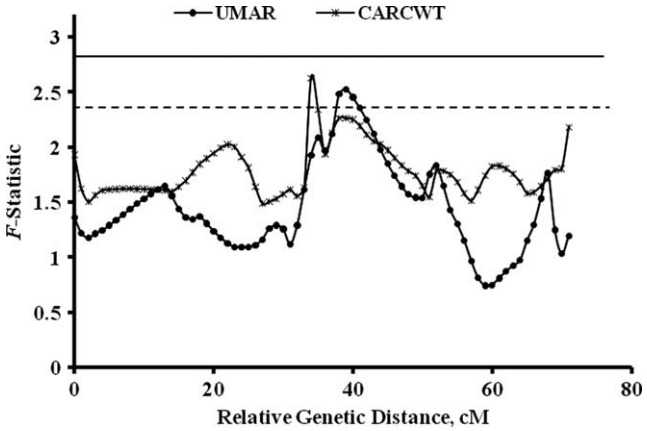

Fig. 5. QTL profiles for across-family analyses on bovine chromosome 21. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold level based on 10 000 permutations. UMAR = ultrasound marbling; CARCWT = carcass weight.

SNPs Associated with Ultrasound and Carcass Merit Traits

Single SNP association analyses were performed for SNPs under or near the 30 significant QTL regions that were identified in the across-family study. The analysis detected 22 SNPs under 12 QTL regions that were significantly associated with seven ultrasound and carcass merit traits. These included eight SNPs that showed significant associations ($P<0.05$) with ultrasound traits of MEAN_UBF, UBF, and MEAN_UMAR on BTA 15 and 23, whereas for the carcass merit traits, a total of 14 SNPs had significant associations ($P<0.05$) with LMY, GRDFAT, AVE_BF and CMAR on BTA 1, 5, 15, 18, and 29 (Table 6). Information regarding positions of the SNPs on the chromosomes and their potential function of the above 22 SNPs was obtained from the databases of the National Center for Biotechnology Information (NCBI) (Table 7).

SNP ss38334774, which is located at 14.1 cM on BTA 15, was found to have a significant additive effect on MEAN_UBF, in which genotype AA had a higher MEAN_UBF value. The SNP is located in an intron of the *Zinc finger and BTB domain-containing protein 16* (*ZBTB16*) gene (Table 7). In Human, the *ZBTB16* gene encodes a transcription factor that may play a role in myeloid maturation and in the development and maintenance of other differentiated tissues (Fischer et al. 2008). However, the role of the *ZBTB16* gene in regulating fat deposition in beef cattle needs further investigation.

Six SNPs were found to be significantly associated with UBF, of which three were located on BTA 15 in the region of 41.7–49.6 cM and three on BTA 23 in the region of 3.6–8.9 cM. The three SNPs on BTA 15 had significant additive effects on UBF with the genotype GG of ss38325273 and TT of ss38323563 and ss38323565 SNPs having significant lower UBF. On BTA 23, ss38323823 SNP had a significant additive effect on UBF with the genotype GG having significantly lower UBF than genotype TT. The ss38323823 SNP also had a significant dominance effect on UBF. Both the ss38335355 and ss38335358 SNPs on BTA 23 have only two genotypes, i.e., AA and AG, detected in the population. The genotype AA of both SNPs has significantly higher UBF than AG. Of the six SNPs associated with UBF, SNP ss38325273 on BTA15 is located in an intron of the *phosphodiesterase 3B, cGMP-inhibited* (*PDE3B*) gene, while SNPs ss38323563 and ss38323565 are located in the intronic region of the *RAB6A* gene. Among the three SNPs for UBF on BTA 23, the SNP ss38323823 is near the *BAK1* gene, while SNPs ss38335355 and ss38335358 are close to the *C23H6ORF142* gene. The product of the *PDE3B* gene is cGMP-inhibited 3′,5′-cyclic phosphodiesterase B protein. Lobbert et al. (1996) reported that the human homologue *PDE3A* gene in rat is involved in fat metabolism. Furthermore, the *PDE3B* protein is the membrane component of adipose tissue microsomes, adipocytes and erythrocytes in human, rat and rabbit (Kitamura et al. 1999; Hanson et al. 2008), which suggests that the *PDE3B* gene may also play an important role in the deposition of body fat in beef cattle.

The ss38331825 SNP on BTA 15 had a significant association with MEAN_UMAR and exhibited a significant additive effect on MEAN_UMAR with genotype GG having a significantly low trait value. This SNP is a synonymous SNP located in the *USP2* (*ubiquitin specific peptidase 2*) gene. In human, the isopeptidase ubiquitin-specific protease-2a (USP2a) enzyme is the product of *USP2* gene that regulates the stability of fatty acid synthase in cancer cells. Inactivation of the *USP2a* function causes decreased fatty acid synthase protein and increased apoptosis (Graner et al. 2004), which warrants further investigation of the function of the gene in beef cattle.

For the carcass merit traits, four SNPs on BTA 5 and two SNPs on BTA 15 showed significant associations with LMY. On BTA 5, ss38324422 and ss38339138 SNPs have significant additive effects on LMY. Animals with genotype CC of ss38324422 and GG of ss38339138 had significantly lower LMY than animals with the other two SNP genotypes. Likewise ss38334596 SNP had a significant dominance effect on LMY with genotype TC having lower LMY than the two homozygous SNP genotypes. However, further study is needed to confirm the dominance effect of ss38334596 SNP on the LMY. The ss61473002 SNP had two genotypes detected in the population and animals with AG genotype had higher LMY than those with GG genotype. On BTA 15, both the ss38332149 and ss38332148 SNP had significant additive effects on LMY whereby animals with CC genotypes for ss38332149 SNP and AA genotypes for ss38332148 SNP showed a higher amount of LMY than

Table 4. QTL locations and effects for ultrasound traits based on within-family analyses

Trait[z]	BTA	QTL location (cM)	Family	Estimate	SE	*P* value[y]
ADG_UBF	4	12	4	−0.022	0.005	0.0076
ADG_UBF	4	69	8	0.020	0.004	0.0090
ADG_UBF	4	79	9	−0.003	0.002	0.0070
ADG_UBF	8	51	6	−0.011	0.003	0.0096
ADG_UBF	12	30	6	0.014	0.004	0.0097
ADG_UBF	13	60	13	−0.026	0.007	0.0080
ADG_UBF	29	44	1	0.890	0.209	0.0074
MEAN_UBF	2	110	12	3.873	0.098	0.0087
MEAN_UBF	8	126	10	−3.633	0.681	0.0083
MEAN_UBF	8	7	17	3.238	0.592	0.0097
MEAN_UBF	9	23	12	4.275	0.293	0.0063
MEAN_UBF	14	0	2	1.414	0.329	0.0097
MEAN_UBF	15	16	14	−2.129	0.452	0.0068
MEAN_UBF	15	31	17	−2.166	0.448	0.0086
MEAN_UBF	24	47	10	2.683	0.586	0.0092
MEAN_UBF	27	2	4	−1.552	0.372	0.0098
MEAN_UBF	29	18	17	−2.219	0.430	0.0086
UBF	17	83	2	4.711	1.188	0.0089
UBF	18	4	9	3.895	0.451	0.0068
UBF	21	29	4	−3.169	0.826	0.0079
UBF	21	48	8	−4.373	0.844	0.0087
UBF	25	64	6	−2.501	0.696	0.0092
ADG_UMAR	2	9	18	0.008	0.001	0.0065
ADG_UMAR	4	60	3	0.004	0.001	0.0141
ADG_UMAR	20	61	18	−0.009	0.001	0.0083
MEAN_UMAR	1	32	4	0.754	0.158	0.0091
MEAN_UMAR	8	20	8	−0.781	0.176	0.0091
MEAN_UMAR	10	66	4	−0.398	0.095	0.0090
MEAN_UMAR	12	89	6	−0.288	0.083	0.0086
MEAN_UMAR	13	1	14	−0.692	0.157	0.0095
MEAN_UMAR	14	18	17	−0.609	0.109	0.0096
UMAR	5	30	12	−15.904	1.053	0.0074
UMAR	9	1	7	1.044	0.253	0.0095
UMAR	10	110	3	−0.760	0.197	0.0078
UMAR	18	8	4	−0.799	3.763	0.0092
UMAR	19	71	4	−1.144	0.280	0.0084
ADG_UREA	3	91	8	−0.066	0.012	0.0096
ADG_UREA	9	59	18	0.106	0.013	0.0085
ADG_UREA	21	31	4	0.049	0.012	0.0083
ADG_UREA	21	19	10	−0.087	0.018	0.0088
ADG_UREA	27	40	4	0.043	0.012	0.0067
MEAN_UREA	2	33	2	−10.176	1.943	0.0089
MEAN_UREA	2	39	8	8.665	2.113	0.0083
MEAN_UREA	10	71	9	11.692	0.298	0.0020
MEAN_UREA	12	61	10	−7.597	1.680	0.0088
MEAN_UREA	13	44	2	9.401	2.002	0.0095
MEAN_UREA	13	25	8	8.542	1.905	0.0081
MEAN_UREA	19	37	13	8.483	1.828	0.0090
MEAN_UREA	23	19	3	4.545	1.181	0.0084
MEAN_UREA	27	53	17	−14.375	2.276	0.0094
UREA	9	63	18	19.073	1.947	0.0070
UREA	12	77	9	−15.518	0.708	0.0092
UREA	20	12	1	−10.106	1.814	0.0096

[z]ADG_UBF = average daily gain ultrasound backfat; MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; ADG_UREA = average daily gain ultrasound ribeye area; MEAN_UREA = mean ultrasound ribeye area; UREA = ultrasound ribeye area; ADG_UMAR = average daily gain ultrasound marbling; MEAN_UMAR = mean ultrasound marbling; UMAR = ultrasound marbling.
[y]Only 1% chromosome-wise significance level are reported for within-family QTL effects.

the other two SNP genotypes. Three of the four SNPs on BTA5 are located in the intronic regions of *LIN7A* gene, while SNP ss38334596 is located in the intron of *SYT1* gene. Gene *LIN7A* encodes Lin-7 homolog A protein in bovine, and its molecular function based on thorough investigation has not been reported in cattle. The *SYT1* gene encodes synaptotagmin-1 protein. Molecular function of synaptotagmin-1 protein is not fully understood. However, a study on the phosphorylation of synaptotagmin-1by casein kinase II in bovine has shown that

Table 5. QTL locations and effects for carcass merit traits based on within-family analyses

Trait[z]	BTA	QTL location (cM)	Family	Estimate	SE	*P* value[y]
CWT	9	39	8	60.984	11.268	0.0093
CWT	15	20	8	47.946	9.278	0.0096
CWT	15	37	10	−60.282	12.564	0.0019
CWT	28	36	13	−52.616	10.712	0.0083
CWT	29	41	13	56.330	10.715	0.0098
LMY	1	121	9	−13.238	1.071	0.0063
LMY	2	11	9	11.902	1.855	0.0033
LMY	9	0	14	−6.172	1.433	0.0091
LMY	13	98	18	11.873	2.412	0.0069
LMY	16	19	5	3.520	0.825	0.0085
LMY	16	84	14	6.626	1.601	0.0082
GRDFAT	9	51	9	10.264	0.549	0.0092
GRDFAT	15	77	5	−3.684	0.826	0.0083
GRDFAT	17	93	4	−4.213	1.062	0.0096
GRDFAT	25	52	7	7.737	2.059	0.0092
GRDFAT	29	0	4	−4.294	1.177	0.0085
AVE_BF	16	84	14	−6.578	1.699	0.0099
CREA	6	107	2	20.606	3.915	0.0099
CREA	25	28	5	9.060	2.267	0.0093
CREA	26	42	8	−19.21	4.454	0.0089
CMAR	4	43	10	0.992	0.226	0.0096
CMAR	20	52	9	−1.847	0.070	0.0099
CMAR	23	30	14	0.721	0.181	0.0078
YGRADE	10	90	6	0.589	0.155	0.0084
YGRADE	16	84	14	−1.182	0.272	0.0094

[z]CWT = carcass weight; LMY = lean meat yield; GRDFAT = carcass grade fat; AVE_BF = average backfat; CREA = carcass ribeye area; CMAR = carcass marbling; YGRDAE = carcass yield grade.
[y]Only 1% chromosome-wise significance level are reported for within-family QTL effects.

it is a Ca^{2+} binding and phospholipid binding protein whose functions may involve synaptic vesicle exocytosis (Davletov et al. 1993). SNP ss38332148 and ss38332149 on BTA15, which also have significant associations with AVE_BF, however, are located near the gene and its function remains unclear.

Three SNPs on BTA 1, 18 and 27 were found to have significant associations with GRDFAT. The ss66538078 SNP on BTA 1 had a significant additive effect on GRDFAT with genotype CC having low grade fat. The ss38322834 and ss38324558 SNPs on BTA 18 and 27, respectively, showed both additive and dominance effects on GRDFAT. Animals with TC genotypes for the ss38322834 SNP and CC for the ss38324558 SNP had high grade fat values compared with those with alternative genotypes. SNP ss38322834 SNP on BTA 18 is located in the intron of *LOC506171* gene encoding a similar protein to phospholipase C, gamma 2 protein. The phospholipase C, gamma 2 enzyme plays important role on leptin signaling and leptin-mediated activation of human platelets (Dellas et al. 2007). Leptin is a hormone that is involved in regulation of appetite, energy expenditure and body composition (Houseknecht et al. 1998). The SNPs on *leptin* gene have shown significant associations with several carcass traits in beef cattle including grade fat (backfat), ultrasound backfat thickness and lean meat yield (Nkrumah et al. 2004), which implies that the *LOC506171* gene may play an important role in the regulation of GRDFAT through interaction with the *leptin* gene.

The ss38339295 SNP on BTA 5 showed a significant dominance effect and a slightly significant additive effect on AVE_BF with the GG genotype having higher trait values. The SNP is located close to *MYF6* gene, which encodes myogenic factor 6 protein. In mice, the *MYF6* gene is homologous to bovine *MYF6* gene and plays a role in cell differentiation processes (Pin and Konieczny 2002). In cattle, the *MYF6* gene is considered to be involved in regulation of skeletal muscle development (Maak et al. 2006; Hudson et al. 2009), which may also affect fat deposition through energy partitioning, which needs further investigation.

Of the 30 significant QTL regions detected in the across-family analyses, 12 QTL regions for ultrasound and carcass merit traits were supported by SNPs in the proximate QTL locations with significant SNP associations, whereas 18 QTL regions had no SNP that showed significant associations with traits (Tables 6 and 7). The absence of significant association for SNPs under or near the significant QTL regions identified by the across-family QTL analyses could be a result of the single SNP marker association analysis having a relatively low power of detecting QTL compared with the multiple marker interval QTL mapping method. Therefore, further increasing the sample size and the density of SNP markers under the QTL regions may lead to the identification of SNPs associated with the traits. Nevertheless, this

Table 6. Location, genotype frequency and effects of SNPs significantly associated with ultrasound and carcass merit traits

Trait	BTA	SNP name	SNP genotypes (no. of animals)[z] and estimate (± SE)			SNP location (cM)	a[y] ± SE	Prob[x]	d[w] ± SE	Prob[v]
MEAN_UBF	15	ss38334774	AA (97) 3.93 ± 0.17	AG (209) 3.73 ± 0.13	GG (106) 3.47 ± 0.16	14.1	0.228 ± 0.10	0.0202	0.027 ± 0.12	0.8235
UBF	15	ss38325273	CC (13) 10.63 ± 0.79	GC (142) 9.17 ± 0.27	GG (254) 8.64 ± 0.22	41.7	0.994 ± 0.41	0.0151	−0.462 ± 0.47	0.3235
		ss38323563	GG (169) 9.08 ± 0.26	TG (186) 8.96 ± 0.23	TT (59) 7.93 ± 0.40	41.7	0.572 ± 0.23	0.0164	0.458 ± 0.29	0.1253
		ss38323565	GG (172) 9.03 ± 0.27	TG (180) 9.01 ± 0.25	TT (60) 7.99 ± 0.41	49.6	0.516 ± 0.24	0.0301	0.502 ± 0.30	0.0963
UBF	23	ss38323823	GG (275) 8.86 ± 0.26	TG (132) 8.71 ± 0.31	TT (8) 11.21 ± 1.05	8.9	−1.177 ± 0.53	0.0268	−1.329 ± 0.57	0.0194
		ss38335355	AA (358) 8.99 ± 0.20	AG (55) 8.13 ± 0.40	–	3.6	0.859 ± 0.42	0.0398	–	–
		ss38335358	AA (359) 8.99 ± 0.20	AG (56) 8.12 ± 0.40	–	3.8	0.865 ± 0.41	0.0366	–	–
MEAN_UMAR	15	ss38331825	AA (19) 4.13 ± 0.10	AG (153) 4.03 ± 0.05	GG (237) 3.91 ± 0.04	20.2	0.107 ± 0.05	0.0444	0.007 ± 0.06	0.9058
LMY	5	ss38324422	CC (29) 56.83 ± 0.76	TC (161) 57.75 ± 0.39	TT (227) 58.73 ± 0.37	16.0	−0.950 ± 0.39	0.0163	−0.027 ± 0.47	0.9541
		ss38334596	CC (294) 58.52 ± 0.35	TC (102) 56.95 ± 0.54	TT (6) 59.00 ± 1.62	17.3	−0.218 ± 0.81	0.7664	−1.809 ± 0.86	0.0353
		ss38339138	GG (39) 56.59 ± 0.72	TG (186) 58.09 ± 0.38	TT (186) 58.58 ± 0.39	14.8	−1.019 ± 0.38	0.0070	0.526 ± 0.45	0.2458
		ss61473002	AG (139) 58.91 ± 0.42	GG (270) 57.73 ± 0.35	–	16.6	1.177 ± 0.46	0.0111	–	–
LMY	15	ss38332149	CC (182) 58.64 ± 0.33	TC (176) 57.99 ± 0.37	TT (51) 57.08 ± 0.60	8.7	0.778 ± 0.32	0.0153	0.130 ± 0.42	0.7539
		ss38332148	AA (179) 58.57 ± 0.34	AG (173) 57.97 ± 0.39	GG (51) 57.11 ± 0.61	8.7	0.729 ± 0.33	0.0266	0.125 ± 0.43	0.7687
GRDFAT	1	ss66538078	CC (165) 10.08 ± 0.36	TC (195) 10.34 ± 0.36	TT (51) 11.74 ± 0.64	8.7	−0.830 ± 0.35	0.0197	−0.564 ± 0.46	0.2214
GRDFAT	18	ss38322834	CC (3) 16.69 ± 2.20	TC (76) 9.71 ± 0.57	TT (339) 10.42 ± 0.30	4.7	3.135 ± 1.10	0.0047	−3.843 ± 1.18	0.0013
GRDFAT	27	ss38324558	CC (334) 10.14 ± 0.33	TC (79) 10.50 ± 0.53	TT (3) 16.77 ± 2.21	58.8	−3.313 ± 1.12	0.0032	−2.952 ± 1.20	0.0141
AVE_BF	5	ss38339295	CC (354) 11.91 ± 0.31	CG (60) 11.17 ± 0.61	GG (3) 15.67 ± 2.19	10.4	−1.881 ± 1.10	0.0889	−2.627 ± 1.22	0.0331
AVE_BF	15	ss38332149	CC (182) 11.36 ± 0.32	TC (176) 11.97 ± 0.36	TT (51) 12.98 ± 0.63	8.7	−0.808 ± 0.35	0.0224	−0.195 ± 0.45	0.6678
		ss38332148	AA (179) 11.40 ± 0.34	AG (173) 12.03 ± 0.39	GG (51) 12.96 ± 0.65	8.7	−0.779 ± 0.36	0.0311	−0.149 ± 0.46	0.7489
CMAR	29	ss38322162	CC (6) 1.97 ± 0.20	TC (83) 2.44 ± 0.07	TT (327) 2.46 ± 0.05	21.6	−0.241 ± 0.10	0.0147	0.221 ± 0.11	0.0460
		ss38324688	AG (33) 2.22 ± 0.10	GG (380) 2.48 ± 0.04	–	18.8	−0.253 ± 0.10	0.0093	–	–

[z]Number of animals shown in parentheses.
[y]a, additive effect.
[x]Prob, probability that the additive effect equals zero.
[w]d, dominance deviation.
[v]Prob, probability that the dominance deviation equals zero.

Table 7. Summary of position and gene annotation for SNPs significantly associated with ultrasound and carcass traits

Trait	BTA	SNP name	SNP position (bp)	Function class	In Gene ID	In Gene name	In Gene description
MEAN_UBF	15	ss38334774	22919210	intron	534401	ZBTB16; MGC127918	zinc finger and BTB domain containing 16
UBF	15	ss38325273	36854388	intron	533323	PDE3B	phosphodiesterase 3B, cGMP-inhibited
		ss38323563	52710350	intron	616537	RAB6A	RAB6A, member RAS oncogene family
		ss38323565	52710098	intron	616537	RAB6A	RAB6A, member RAS oncogene family
UBF	23	ss38323823	8498505	nearest_gene	514090	BAK1	BCL2-antagonist/killer 1
		ss38335355	101039	nearest_gene	790110	C23H6ORF142	chromosome 6 open reading
		ss38335358	101057	nearest_gene	790110	C23H6ORF142	chromosome 6 open reading
MEAN_UMAR	15	ss38331825	28495153	synonymous contig reference	522980	USP2; MGC137635	ubiquitin specific peptidase 2
LMY	5	ss38324422	12423627	intron	528379	LIN7A	lin-7 homolog A (C. elegans)
		ss38334596	9087028	intron	281511	SYT1	synaptotagmin I
		ss38339138	12403425	intron	528379	LIN7A	lin-7 homolog A (C. elegans)
		ss61473002	12451776	intron	528379	LIN7A	lin-7 homolog A (C. elegans)
LMY	15	ss38332149	20509763	nearest_gene	538766	MGC134087; MGC134087	hypothetical LOC538766
		ss38332148	20509821	nearest_gene	538766	MGC134087; MGC134087	hypothetical LOC538766
GRDFAT	1	ss66538078	6350258	intron	540879	C1H21ORF7	chromosome 21 open reading frame 7 ortholog
GRDFAT	18	ss38322834	7459380	intron	506171	LOC506171	similar to phospholipase C, gamma 2
GRDFAT	27	ss38324558	42710278	nearest_gene	616397	ZMAT4	zinc finger, matrin type 4
AVE_BF	5	ss38339295	12323876	nearest_gene	281336	MYF6	myogenic factor 6 (herculin)
AVE_BF	15	ss38332149	20509763	nearest_gene	538766	MGC134087; MGC134087	hypothetical LOC538766
		ss38332148	20509821	nearest_gene	538766	MGC134087; MGC134087	hypothetical LOC538766
CMAR	29	ss38322162	16888647	nearest_gene	506046	CCDC90B; MGC155307	coiled-coil domain containing 90B
		ss38324688	15572469	nearest_gene	506046	CCDC90B; MGC155307	coiled-coil domain containing 90B

study used both an interval mapping QTL genome scan and single SNP marker association to fine map QTL regions and to detect SNPs affecting ultrasound and carcass merit traits in beef cattle. Both methods analyze one position of the genome or one marker at a time, which could possibly result in high incidences of false positives due to multiple testing. However, 10 000 permutations were carried out to set the significance threshold in order to combat false positives due to multiple testing in the whole genome QTL scan. Also, the QTL effects may be overestimated due to the fact that each QTL or SNP marker was analyzed independently, or due to a small number of animals in the genotype subclasses (Beavis 1998). Therefore, another study is underway to use a Bayesian approach to evaluate associations of all SNP markers simultaneously in a single model, which will overcome some of the limitations associated with the interval mapping genome scan and the single SNP association analyses. Also, the use of 4592 SNPs in the current study may not capture all existing linkage disequilibrium between SNP markers and QTL on the bovine genome. Therefore, the use of the BovineSNP50 assay with a total of 58336 SNPs (Matukumalli et al. 2009) would be more powerful in narrowing down reported QTL and identifying SNPs influencing complex traits. Nevertheless, the fine mapped QTL regions and SNPs that were identified in this study will provide a reference for the identification of DNA markers for ultrasound and carcass merit traits for the implantation of MAS in beef cattle genetic improvement programs.

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