Genome-wide scans for QTL affecting carcass traits in Hereford × composite double backcross populations[1]

M. D. MacNeil[2] and M. D. Grosz[3,4]

USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301

ABSTRACT: A genome-wide scan for chromosomal regions influencing carcass traits was conducted spanning 2.413 morgans on 29 bovine autosomes using 229 microsatellite markers. Two paternal half-sib families of backcross progenies were produced by mating Hereford × composite gene combination (**CGC**) bulls to both Hereford and CGC dams. Progeny of the first sire (n = 146) were born in 1996 and progeny of the second sire (n = 112) were born in 1997. Each year cattle were fed out and slaughtered serially when they were between 614 and 741 d of age. Phenotypes measured at harvest were: live weight; carcass weight; fat depth; marbling; percentage kidney, pelvic, and heart fat (KPH); and rib eye area. Dressing percentage and USDA Yield Grade were calculated from these data. The phenotypes were adjusted to age-, live weight-, and fat depth-constant endpoints using analysis of covariance. The resulting residuals were analyzed by interval mapping to detect QTL. Within family, nominal significance was established by permutation analysis. Approximate genome-wide significance levels were established by applying the Bonferroni correction to the nominal probability levels. Regression and error sums of squares and degrees of freedom were pooled across families when suggestive linkage identified in one family was confirmed in the other. The results indicate promising locations for QTL affecting live weight on BTA 17 and marbling on BTA 2 that segregate in *Bos taurus*. Also, previously identified linkage between central markers on BTA 5 and USDA Yield Grade was confirmed in one family. Greater marker saturation in these regions coupled with refined methods for data analysis will lead to more precise determination of QTL positions.

Key Words: Beef Cattle, Carcasses, Quantitative Trait Loci

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Introduction

Development of saturated genetic marker maps (Barendse et al., 1997; Kappes et al., 1997) has allowed the identification of QTL affecting traits of economic importance. Identifying QTL has potential to significantly increase the rate of genetic improvement through implementation of marker assisted selection. For traits that are difficult and(or) expensive to measure, are lowly heritable, occur late in life, or are determined postmortem, marker assisted selection may substantially increase the rate of response relative to selection based on estimated breeding value alone (Davis and DeNise, 1998). In addition, marker-assisted selection provides the opportunity to dissect genetically correlated traits supplementing quantitative approaches to select for one trait while simultaneously selecting against or restricting response in a correlated trait. The application of marker-assisted selection by elite breeders of beef cattle seedstock has the potential to significantly increase both the efficiency of production and the quality and desirability of the end product.

Fort Keogh Livestock and Range Research Laboratory created three generation resource populations comprised of backcross calves for identifying QTL. Earlier investigations identified a QTL affecting birth weight on bovine chromosome (**BTA**) 2 (Grosz and MacNeil, 2001) and localized the spotting locus on BTA 6 (Grosz and MacNeil, 1999). The objective of this research was to identify genomic intervals, which may contain genes affecting carcass traits.

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[2]Correspondence: 243 Fort Keogh (phone: 406-232-8213; fax: 406-232-8209; E-mail: mike@larrl.ars.usda.gov).

[3]Present address: Monsanto, 700 Chesterfield Parkway North, Chesterfield, MO 63198.

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Materials and Methods

Three generation double backcross populations were initiated with the production of F_1 bulls by mating Line 1 Hereford (MacNeil et al., 1992) bulls to a composite gene combination (**CGC**; Newman et al., 1993a,b) cows. The resulting F_1 bulls, #94574 and #94730, were then bred by AI and natural service to Line 1 and CGC dams to produce backcross progenies in 1996 (n = 146) and 1997 (n = 112), respectively. Composite Gene Combination is a stabilized composite population consisting of ½ Red Angus, ¼ Tarentaise, and ¼ Charolais germplasm. Composite cows were at least four generations removed from the foundation matings of Charolais and Tarentaise bulls to Red Angus females.

The calves were born between March 19 and May 7 in 1996 and between March 19 and May 9 in 1997. The average birth date was April 9. Each calf was weighed within 24 h after birth and again at weaning when the calves averaged approximately 180 d of age. After weaning, the calves were returned to native range pastures and were supplemented with 0.7 kg per calf per day of both barley cake and alfalfa pellets. In mid-January, the calves were moved from the range and were fed silage and chopped hay to achieve anticipated gains of 0.5 to 0.8 kg per day. In late April, the calves were again returned to native range where they grazed until August. Subsequently, the calves were moved to an individual feeding facility equipped with electronic feeding gates (American Calan, Inc., Nothwood, NH). Beginning in October, after an adjustment period, the calves were individually fed a mixed ration containing 56% corn silage, 42% barley grain, and 2% protein supplement on a dry matter basis. This ration contained an estimated 2.7 Mcal metabolizable energy and 11% CP.

Before initiating harvest, all steers and heifers were randomly assigned to a slaughter date. Beginning January 7 and weekly thereafter, six steers and six heifers were transported to a local abattoir and slaughtered using standard industry procedures. Hot carcass weight was measured the day of slaughter and other carcass measures were taken after 48 h of storage at 2°C. Dressing percentage was calculated as 100 times the ratio of hot carcass weight to live weight taken 1 d before slaughter. Longissimus muscle area between the 12th and 13th sternal ribs was measured using a planar grid. Fat thickness over the longissimus muscle was taken at the 12th rib. The kidney, pelvic, and heart fat (**KPH**) was estimated and recorded as a percentage of carcass weight. Marbling was evaluated by subjective comparison of the amount of fat within the longissimus muscle between the 12th and 13th ribs with photographic standards (National Livestock and Meat Board, 1981).

To derive age-, live weight-, and fat-depth-constant phenotypes, the observed phenotypes were analyzed by least squares, using a model that included fixed effects for year of birth (1996 or 1997), breed of dam (Line 1 or CGC), sex (heifer or steer), linear effects of either age (days), live weight (kilograms), or fat depth (centimeters), as appropriate, and all possible interactions. Quadratic effects of the continuous variate and its interactions with breed of dam and sex were also evaluated and were retained in the model when they approached significance ($P < 0.10$). Animals with residual values for any trait greater than 3.5 SD were removed from all subsequent analyses. The residual deviations between observed and expected values were the phenotypes for interval mapping of QTL. This approach provides the partial regression for the QTL effect given all effects in the model used to calculate the residuals and assumes no interaction between QTL effects and the other fixed effects. Homogeneity of variance of the residual deviations in backcrosses to Line 1 and CGC was evaluated.

An initial panel of microsatellite markers was identified on the basis of relative position, fragment size (to facilitate multiplexing), and scoring ease from the genomics database at the USDA-ARS, U.S. Meat Animal Research Center (Kappes et al., 1997; USDA, 2000). Informative markers spanning the genome were identified by genotyping each F_1 bull and his sire and dam. In the second family, markers found to be informative in the first family were evaluated first and then additional markers were identified from the USDA-ARS bovine linkage map (Bishop et al., 1994; Kappes et al., 1997) to fill gaps created by noninformative markers. The suite of informative markers used for the genome scan of progeny of #94574 included 170 microsatellite markers and in the spanning 2.328 M (morgans) representing all 29 bovine autosomal chromosomes. Thus, in the first family, the average number of markers per chromosome was 5.9, the average gap between adjacent markers was 16.5 cM, and the largest gap between adjacent markers was 40.5 cM on BTA 25. The suite of informative markers used for the genome scan of progeny of #94730 included 161 microsatellite markers and in the spanning 2.189 M of the 29 bovine autosomal chromosomes. Thus, in the second family, the average number of markers per chromosome was 5.6, the average gap between adjacent markers was 16.6 cM, and the largest gap between adjacent markers was 47.4 cM on BTA 10. In both families, each chromosome contained at least four informative markers, with the exceptions of BTA 28 in the first family and BTA 26 in the second family, for which only three informative markers were identified. All PCR reactions were done as described by Bishop et al. (1994).

Chromosomal linkage maps (Table 1) were produced using BUILD and ALL functions of CRIMAP (Green et al., 1990) based on the genotypic data. Paternal contribution at marker loci was determined using the CHROMPIC function of CRIMAP. Alleles from the composite and Line 1 were assigned values of 0 and 1, respectively. When definitive assignment of the paternal allele was not possible, the paternal allele was coded as missing. The information content at each marker location was computed following Spelman et al. (1996).

Table 1. Markers, their relative positions (cM), and information content (%) used in mapping quantitative trait loci

BTA	Centromeric markers											Telomeric markers	
1	AGLA17	BMS574	ILSTS104	BMS4002	RM326	BM9019	BM8246	BMS4028	BM1824	BMS4043	URB104		
	0.0	13.4	25.0	48.2	52.9	66.0	74.2	93.6	112.7	131.9	142.7		
	71.3	99.7	97.9	88.4	98.7	84.7	98.7	98.7	98.1	99.4	72.9		
2	TGLA44	TEXAN-2	TGLA377	URB042	CSSM042	BMS1300	BMS1126	BMS1866	BMS1987	BM2113	IDVGA37	IDVGA2	FCB11
	0.0	29.0	30.0	35.5	37.4	49.8	56.0	75.5	98.7	105.5	106.3	124.1	127.3
	97.8	96.8	98.4	97.2	97.7	88.4	98.8	99.6	83.2	95.1	94.7	91.6	89.8
3	MB101	UWCA7	BMS2904	BMS819	BL41	BMS2790	BMS937	BM3020	BM4301	BMS835	BMC5227		
	0.0	0.0	4.9	6.6	24.8	36.5	44.5	67.5	71.5	81.5	102.9		
	97.2	97.2	98.7	94.8	79.9	98.7	84.0	86.2	88.5	96.5	98.3		
4	BMS1788	BMS1237	BM1224	BMS2809	ILSTS062	BM1500	IDVGA51	AGLA227					
	0.0	24.4	44.2	53.6	53.7	62.0	74.4	93.9					
	98.8	95.5	99.3	98.8	98.8	85.5	77.2	95.4					
5	BMS1095	BP1	BMS1315	BMS1617	ETH10	BM1819	BM315	BM49	BM8126				
	0.0	13.5	30.5	45.0	52.3	62.2	80.2	96.0	104.1				
	99.7	99.7	98.3	98.3	89.6	97.1	99.6	96.3	73.5				
6	ILSTS093	BM1329	BM143	BMS1242	BM4528	BM4621	ILSTS035	MB062	BP7	BMC4203	BL1038		
	0.0	27.6	37.1	37.5	53.2	57.9	63.5	69.0	74.5	93.8	112.1		
	97.0	76.9	99.2	99.6	91.0	98.6	95.1	98.5	87.2	93.6	96.2		
7	BM9289	BMS713	BMS1116	BM741	UWCA20	BM6117	BMS2258	BMS1331	BM7208	MB057	BMS1247		
	0.0	0.0	7.0	34.9	46.4	50.7	62.6	73.7	81.4	91.6	115.7		
	96.7	96.7	98.1	74.8	88.2	88.3	99.4	98.4	97.2	80.2	93.3		
8	Z27077	RM321	BMS1591	BM310	INRA129	BMS2072	BM3412	BM711	BMS836	SRC221			
	0.0	12.1	20.2	20.2	46.0	52.7	64.9	70.6	96.9	101.8			
	67.8	82.1	94.8	94.8	86.1	85.6	89.5	98.5	84.9	86.3			
9	BMS2177	BMS425	ILSTS037	RM216	BMS555	CSSM025	ILSTS084	TGLA73	BMS2377	BMS2251	BMS2063	BMS1967	
	0.0	2.9	20.1	21.4	31.3	40.0	45.6	55.6	61.7	65.3	76.7	105.1	
	98.4	93.1	95.2	95.2	85.8	89.0	89.6	83.8	90.5	90.1	96.8	52.9	
10	BMS6418	CSSM038	BMS528	BMS861	ILSTS053	BMS419	INRA037	BMS2641	BMS2614				
	0.0	0.2	10.4	28.7	28.7	41.5	53.4	64.1	88.9				
	96.8	96.4	98.2	95.2	95.4	84.5	97.2	79.7	99.0				
11	BM827	BMS2621	INRA177	BM7169	INRA111	MB110	BMS989	ILSTS028	BMS2208				
	0.0	0.0	23.0	35.8	42.5	49.8	72.9	85.5	92.7				
	89.8	89.8	98.9	90.3	90.1	97.3	100.0	100.0	74.1				
12	BMS410	BM6116	RM178	RM094	BM6404	BMS585	MB100	BMS1316					
	0.0	23.8	23.9	42.4	54.1	69.1	77.8	91.9					
	98.6	97.3	97.3	97.7	99.1	83.2	88.9	98.6					
13	BMS1742	ILSTS059	BMS1580	RM327	BMS995								
	0.0	22.8	32.0	43.7	72.4								
	95.9	97.7	86.4	97.8	96.5								
14	BMS1678	BL1009	RM011	BL1029	BMS108	BM2934	BM6425						
	0.0	12.9	16.0	26.6	31.2	46.3	61.3						
	96.7	94.4	93.0	99.2	93.0	99.6	98.9						

Continued

Table 1 continued. Markers, their relative positions (cM), and information content (%) used in mapping quantitative trait loci

15	BMS2533	INRA50	MB076	Z27076	BMS540	BMS2076	BMS927	BMS429
	0.0	25.1	29.4	38.9	53.0	60.3	76.8	79.9
	98.8	81.9	91.8	99.8	85.0	86.9	85.3	82.9
16	BM6430	BMS1348	BM9034	CSSM028	BM719	MB103	HUJ625	
	0.0	4.2	27.0	53.2	67.8	78.4	81.6	
	86.1	95.8	94.2	97.0	81.6	90.1	87.3	
17	RM156	BMS2220	BMS1101	ILSTS023	IDGVA-40	ILTSTS058	BM1233	
	0.0	14.2	28.9	37.5	50.3	65.4	79.4	
	98.3	98.7	97.6	99.9	79.6	69.3	69.3	
18	BMS3004	BMS2559	UWCA28	INRA121	INRA063	BM7109	IDGVA-55	TGLA227
	0.0	0.0	11.9	23.7	41.0	41.3	61.2	81.1
	94.0	94.0	96.8	97.5	92.9	93.1	96.6	98.9
19	BMS745	BMS2142	BM17132	IDVGA-44	ETH3	BMC1013		
	0.0	25.2	35.5	55.4	55.7	81.8		
	99.0	99.0	99.9	97.6	97.4	96.5		
20	BM3517	BMS1282	TGLA304	ILSTS068	BMS1128	BMS703	BMS521	
	0.0	16.9	17.0	21.4	37.0	50.2	85.6	
	96.7	95.4	95.8	87.4	78.9	95.8	50.7	
21	BM8115	MB071	AGLA223	IDVGA-45	TGLA337	BMS743	IDVGA-30	
	0.0	4.4	19.3	34.5	56.1	78.4	86.0	
	96.0	88.5	79.1	96.3	97.7	82.1	79.1	
22	MB116	BMS742	INRA194	BMS2573	BM2613	BMS980	BMS1932	
	0.0	12.4	18.4	30.6	42.2	47.2	59.5	
	98.5	87.7	87.0	99.4	92.1	92.1	98.2	
23	INRA064	BM47	BM1258	BMS468	RM185	BM1443		
	0.0	10.2	23.4	27.1	32.4	57.3		
	75.7	83.7	99.0	94.6	86.5	98.6		
24	BMS917	BMS2270	BMS466	BMS3024				
	0.0	12.9	28.2	48.5				
	95.5	98.0	99.4	99.6				
25	BMC4216	CA074	BMS1232	BP28	BMS1353	BM7207	AF5	
	0.0	9.4	9.5	28.8	44.7	50.0	59.9	
	91.7	94.9	94.7	70.2	83.6	87.9	98.3	
26	BMS651	MB067	BM1314	BM188	BMS882	BM7237	ILSTS091	
	0.0	18.8	31.5	39.9	49.4	61.5	71.7	
	57.4	74.1	86.2	97.7	86.2	80.7	69.1	
27	BM3507	BMS2137	INRA183	CSSM036	INRA027			
	0.0	11.7	15.4	27.0	35.0			
	98.9	90.7	92.9	99.3	99.0			
28	BMC6020	BMS510	BMS2658	BM2515				
	0.0	16.8	28.9	41.7				
	98.2	98.2	98.7	65.5				
29	ILSTS057	RM044	RM040	BMC1206	ILSTS081			
	0.0	14.0	27.9	46.7	51.3			
	96.3	97.0	95.3	83.9	79.1			

Table 2. Means, standard deviations, and regression coefficients on age at harvest, weight at harvest, and carcass fat depth for carcass traits of backcross progenies of Line 1 Hereford × CGC composite bulls

			Regression on		
Trait	Mean	SD	age, d	Live weight, kg	Fat depth, cm
Live weight, kg	557	46.7	0.66 ± 0.11		49.5 ± 7.6
Carcass weight, kg	325	28.5	0.47 ± 0.07	0.6011 ± 0.0104	34.0 ± 4.6
Dressing percentage	58.2	1.5	0.015 ± 0.004	0.0051 ± 0.0019	1.06 ± 0.25
Rib eye area, cm^2	79.6	8.0	0.026 ± 0.018	0.0881 ± 0.0083	1.37 ± 1.31
Fat depth, mm	1.2	0.37	0.0039 ± 0.0009	0.0029 ± 0.0004	
Percentage KPH fat	2.1	0.56	0.0003 ± 0.0010	0.0017 ± 0.0005	0.24 ± 0.07
USDA Yield Grade	2.9	0.56	0.0065 ± 0.0013	0.0038 ± 0.0007	1.25 ± 0.06
Marbling score[a]	5.5	0.85	0.0109 ± 0.0020	0.0057 ± 0.0011	0.49 ± 0.14

[a]Marbling score: 4.00 = $Slight^0$, 5.50 = $Small^{50}$, 7.00 = $Moderate^0$, etc.

Within paternal half-sib family, interval mapping was by least squares according to the method of Knott et al. (1996). For each individual, the probability of having inherited the Line 1 allele from its sire was calculated every 2 cM conditional on its marker phase at the nearest adjacent flanking markers. At each chromosomal position, the regression of phenotype on the conditional probability of having inherited the Line 1 allele from the F_1 sire was indicative of the additive genetic or QTL effect at that locus. Nominal significance was established by permutation analysis (Churchill and Doerge, 1994; Lui, 1997). After establishing the QTL effect, within the separate families, the phenotypes were randomly assigned to marker genotypes. These shuffled data reflecting the null hypothesis of no relationship between phenotype and genotype within family were analyzed as described for estimating the QTL effect. For each chromosomal position, the resulting regression coefficient was saved. This process was repeated 2,000 times for each family. Upon completing the analyses of all random permutations of the data, the resulting vector of regression coefficients at each chromosomal position was sorted from largest to smallest. The within family QTL effect at that locus was then positioned relative to elements of the vector of regression coefficients from analyses of the permutated data, and the probability of a more extreme regression coefficient occurring by chance at that locus was found. This procedure takes into account the particular characteristics of the experiment in arriving at nominal probability levels specific to each locus (Churchill and Doerge, 1994). The procedure also has the advantage that no assumptions are required with respect to distributional properties of either phenotypes or genetic markers (Weller, 2001). Approximate genome-wide significance levels were established by applying the Bonferroni correction to the nominal probability levels as described in Knott et al. (1998). Subsequent to the de-

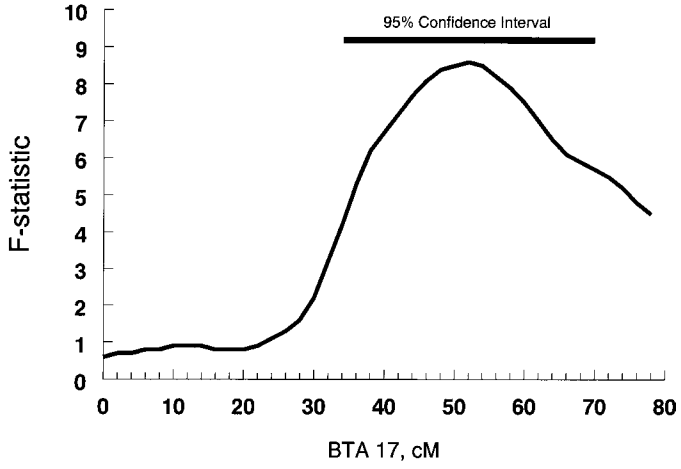

Figure 1. Map of F-statistics from pooled within family regressions of age-constant live weight on conditional probability of inheriting an allele from Line 1 Hereford at 2-cM intervals on bovine chromosome 17 (BTA 17).

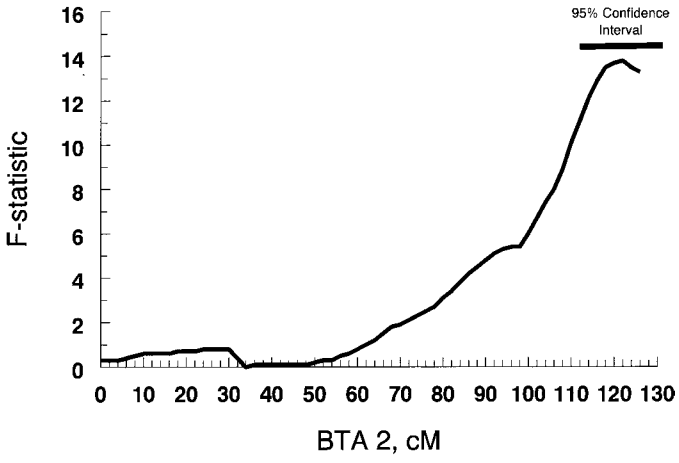

Figure 2. Map of F-statistics from pooled within family regressions of age-constant marbling score on conditional probability of inheriting an allele from Line 1 Hereford at 2-cM intervals on bovine chromosome 2 (BTA 2).

Table 3. Suggestive linkage affecting carcass traits at age-, live weight-, and fat depth-constant endpoints in backcross progeny of Line 1 Hereford × CGC composite bull #94574

Trait	BTA	Relative position, cM	Substitution effect[a]
Age-constant endpoint			
Live weight, kg	9	44	–18.7
	17	50	–24.1
Carcass weight, kg	2	114	–15.1
Dressing percent	16	22	0.95
Rib eye area, cm^2	12	34	–5.01
Fat depth, cm	16	66–72	–0.28
KPH fat, %	17	76	–0.23
	18	64	0.24
USDA Yield Grade	5	30	0.28
	16	68	–0.37
Marbling score[b]	2	120	–0.59
	29	2	0.46
Live weight-constant endpoint			
Carcass weight, kg	16	26	4.2
	24	34	4.8
Rib eye area, cm^2	12	34	–4.67
Fat depth, cm	16	72	–0.26
USDA Yield Grade	12	34	0.32
	16	70	–0.34
Marbling score	2	122	–0.47
Fat depth-constant endpoint			
Live weight, kg	12	74	–23.7
	18	78	22.6
Carcass weight, kg	12	70	–13.7
	24	40	14.2
Dressing percent	16	26	0.93
	24	24	0.82
	29	0	–0.74
Rib eye area, cm^2	12	36	–5.12
KPH fat, %	17	78	–0.23
USDA Yield Grade	12	34	0.19
Marbling score	2	120	–0.55
	18	74	0.47
	26	4	0.44

[a]Effect resulting from a Line 1 Hereford allele replacing an allele from CGC.
[b]Marbling score: 4.00 = $Slight^0$, 5.50 = $Small^{50}$, 7.00 = $Moderate^0$, etc.

tection of a QTL, homogeneity of the effect in both backcrosses was tested in a model fitting the probability of inheriting the Line 1 allele at the most likely position for the QTL, all effects used to derive the residuals, and the interaction of the QTL effect with breed of dam. When a QTL effect reached the genome-wide significance threshold $P < 0.05$ in both families, the sums of squares and degrees of freedom for regressions and for error were pooled across families, and the resulting F-statistic was calculated to map the confirmed QTL effect. Ninety-five percent confidence intervals for QTL effects were approximated by the method of Darvasi and Soller (1997) for a saturated genetic map.

Results and Discussion

In general, marker information content was greater than 90% (Table 1). Reduced information content resulted primarily from the lack of an informative marker at either end of a chromosome in one family or the other and the resulting need to infer the marker genotype at that locus as the conditional probability of inheriting the Line 1 allele based on a single and somewhat distant marker. Other factors, such as missing genotypes for individual animals and unequal segregation of alternative alleles, had little effect on the information content of these markers. Information content is also less between markers than at the marker loci (Weller, 2001).

Phenotypic means, residual standard deviations, and regressions on age, live weight, and fat depth at harvest are shown in Table 2. While there was a trend toward reduced residual variance in progeny of Line 1 dams, this trend was not significant for any phenotype, and the data were not transformed to further equalize the residual variances in the two backcrosses. Assignment of the cattle to harvest date was at random. Thus, statistical control, through analyses of covariance with respect to age, live weight, and fat depth was used to

Table 4. Suggestive linkage affecting carcass traits in backcross progeny of Line 1 Hereford × CGC composite bull #94730

Trait	BTA	Relative position, cM	Substitution effect[a]
Age-constant endpoint			
Live weight, kg	17	50	–24.1
	29	38	–26.5
Carcass weight, kg	29	36	–14.8
Rib eye area, cm^2	14	40	4.95
	21	8	4.68
KPH fat, %	2	22	–0.27
USDA Yield Grade	21	0	–0.24
Marbling score[b]	2	122	–0.59
Live weight-constant endpoint			
Carcass weight, kg	5	40	–6.6
Dressing percent	5	40	–0.99
	10	44	1.02
Rib eye area, cm^2	14	46	4.45
KPH fat, %	2	20	–0.28
USDA Yield Grade	21	2	–0.29
Marbling score	2	118	–0.63
	29	42	0.63
Fat depth-constant endpoint			
Live weight, kg	16	22	–28.1
Carcass weight, kg	16	20	–15.1
Dressing percent	1	110	–0.71
	5	40	–0.84
	10	46	0.96
Rib eye area, cm^2	21	4	4.51
KPH fat, %	2	26	–0.24
USDA Yield Grade	14	38	–0.25
Marbling score	29	48	0.55

[a]Effect resulting from a Line 1 Hereford allele replacing an allele from CGC.
[b]Marbling score: $4.00 = Slight^0$, $5.50 = Small^{50}$, $7.00 = Moderate^0$, etc.

derive the measures of the carcass traits adjusted to these endpoints. Adjusted phenotypes at these alternative endpoints are highly correlated. Thus, presentation of results and discussion of them focuses on the results for the age-constant endpoint.

Shown in Figures 1 and 2 are maps of QTL effects on age-constant live weight and marbling, respectively. The genome-wide probability levels of these effects being detected due to chance were $P < 0.05$ in both of the paternal half-sib families. The joint probability that a similarly located QTL would be observed by chance in both families is remote.

The maximum QTL effect on age constant live weight was located at 52 cM on BTA 17. In both families, the effect of the QTL was similar with progeny receiving the allele from Line 1 being approximately 24 kg lighter at harvest than contemporaries receiving the allele from CGC. The 95% confidence interval for the location of this effect spanned the interval from 35 to 69 cM. Microsatellite markers used in this research and in this interval were ILSTS023, IDGVA-40, and ILSTS058. The significance of this QTL was markedly reduced when the live weight phenotype was adjusted to the constant fat depth endpoint.

The maximum QTL effect on age constant marbling score was located at 122 cM on BTA 2. In both families, the effect of the QTL was similar with progeny receiving the allele from Line 1 having approximately 0.6 score units less marbling at harvest than contemporaries receiving the allele from CGC. The 95% confidence interval for the location of this effect spanned the interval from 112 to 132 cM. This confidence interval includes the microsatellite markers IDVGA-2 and FCB11 and extends beyond them toward the telomere of BTA 2. This QTL for marbling is coincident with a QTL for birth weight that was previously identified in backcross progeny of #94574 (Grosz and MacNeil, 2001). This QTL was also observed when the phenotypic data were adjusted to a constant live weight or fat depth (Tables 3 and 4), except that it only approached genome-wide significance ($P = 0.06$) in progeny of #94730 at the fat-constant endpoint.

Chromosomal regions where significant QTL effects on phenotype were detected in one of the two paternal half-sib families are listed in Tables 3 and 4. With one exception, the QTL effects did not differ in progenies of Line 1 Hereford and CGC composite females. Because Line 1 and CGC are both not fully inbred lines, there is no reason to believe alternative alleles are fixed in either population and, thus, that the F_1 sires would necessarily be informative for all QTL. As a consequence, even existing QTL effects are not necessarily

expected to have either the same sign or be of the same magnitude in both families. The observed QTL effects were extreme relative to a very high proportion of the random permutations of genotypes and phenotypes within the respective paternal half-sib families. The associated nominal significance level of each is approximately equal to the threshold suggested by Lander and Kruglyak (1995) to establish "suggestive" linkage. Because the criterion for suggestive linkage is based on the expectation of one false positive result per genome scan, many of these effects are probably due to chance. However, they are reported here to provide an opportunity to use them in confirming the presence of QTL detected in future experiments. Most, but not all, of these putative QTL are similar across the endpoints examined. In addition, because the phenotypes considered here are correlated, thus the same QTL was detected for several phenotypes.

Genome-wide scans may identify QTL for use in marker-assisted selection programs. In this context, the potential for type II error is a serious concern. Except for the QTL affecting live weight on BTA 17 and the QTL affecting marbling on BTA 2, the linkage between markers and quantitative trait loci identified in Tables 3 and 4 is tenuous without subsequent conformation in independent families. Also, 95% confidence intervals for the location of these QTL effects range from 28 to 83 cM, substantially broader than those required for effective marker assisted selection. However, genome-wide scans for QTL are also preliminary investigations in the scientific process that ultimately leads to identification of major genes. In this context, conformation of suggestive linkage is a logical progression of research and application of a stringent type I error rate necessary to control type II error will result in many true effects being missed (Weller, 2001).

Previous studies have identified QTL in *Bos Taurus* × *Bos Indicus* populations and in crosses segregating inactive forms of myostatin (Stone et al., 1999; Casas et al., 2000). In these two independent studies, QTL were identified on BTA 5 (50 to 80 cM) affecting rib bone, dressing percentage, fat depth, retail product yield, and yield grade. Stone et al. (1999) also discussed suggestive evidence for QTL on BTA 5 affecting rib fat. In this study, a QTL on BTA 5 was identified affecting USDA Yield Grade in progeny of #94574 (Table 2). Contributing to this effect was a QTL affecting carcass weight at 36 cM on BTA 5 that approached genome-wide significance ($P < 0.1$). Collectively, these studies seemingly confirm the linkage of a QTL affecting yield grade to central markers on BTA 5.

The results presented here pertain to alleles that segregate in crosses between Line 1 Hereford and the CGC composite. To be useful in marker assisted selection, alleles with important effects that segregate within a population must be identified. The present results provide an indication of loci that may be useful in marker assisted selection programs, but within Line 1 and CGC segregation of alleles with important effects at these loci remains to be established.

Implications

Discovering regions of the *Bos taurus* genome in which QTL that affect economically relevant carcass traits are segregating provides a foundation for localizing these QTL and identifying closely linked markers. When they are identified, these closely linked markers can be used in marker assisted selection to supplement traditional progeny testing for genetic improvement of carcass attributes.

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