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Quantitative trait loci with effects on feed efficiency traits in Hereford × composite double backcross populations

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Summary

Two half-sib families of backcross progeny were produced by mating F_1 Line 1 Hereford (L1) × composite gene combination (CGC) bulls with L1 and CGC cows. Feed intake and periodic weights were measured for 218 backcross progeny. These progenies were genotyped using 232 microsatellite markers that spanned the 29 BTA. Progeny from L1 and CGC females was analysed separately using composite interval mapping to find quantitative trait loci (QTL) affecting daily dry matter intake (DMI), average daily gain (ADG), feed conversion (FCR) and residual feed intake (RFI). Results from both backcrosses were pooled to find additional QTL. In the backcross to L1, QTL were detected for RFI and DMI on BTA11, FCR on BTA16, and ADG on BTA9. In the backcross to CGC, QTL were detected for RFI on BTA10, FCR on BTA12 and 16 and ADG on BTA15 and 17. After pooling, QTL were detected for RFI on BTA 2, 6, 7, 10, 11, 13 and 16; for FCR on BTA 9, 12, 16, 17 and 21; for ADG on BTA 9, 14, 15, 17; and for DMI on BTA 2, 5, 6, 9, 10, 11, 20 and 23.

Keywords feed conversion, quantitative trait loci, residual feed intake.

Improved efficiency of feed utilization should reduce cost of beef production (Crews 2005). Selection based on ratio measures of feed efficiency may cause undesired increases in mature size and feed requirements (Archer *et al.* 1999). Alternatively, residual feed intake (RFI; Koch *et al.* 1963) has sufficient genetic variation for use as a selection tool with little risk of increased cow size (Hoque *et al.* 2006; Nkrumah *et al.* 2007a). Therefore, our objective was to find QTL affecting measures of feed intake and associated measures of efficiency.

Data were obtained from 218 backcross progeny of two F_1 Line 1 Hereford (L1) by composite gene combination (CGC) composite bulls bred to L1 (N = 120) and CGC (N = 98) cows previously described by MacNeil & Grosz (2002). Animals were weighed twice at the beginning and end of the test period in which feed intake was measured. As a result of serial harvest for collection of carcass data, time on feed varied from 82 to 167 days. Calves were individually fed a ration with 45% DM, 2.7 Mcal metabolizable energy/kg DM and 11% crude protein using electronic feeding gates (American Calan, Inc.).

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Feed conversion (FCR) was DMI/ADG, where DMI is the average daily dry matter intake (kg/day) and ADG is the average daily gain (kg/day) during the test period. Phenotypic RFI was calculated using multiple regression:

$$\mathrm{DMI} = b_0 + b_1 \times \mathrm{ADG} + b_2 \times \mathrm{WT} + b_3 \times \mathrm{year}_{1997} + b_4 \times \mathrm{sex}_2 + \mathrm{RFI}$$

where WT is the average weight (kg) during test, year is the year of birth (1996 or 1997), sex denotes steer or heifer, b_0 is the intercept, b_1–b_4 are the partial regression coefficients and RFI is the residual assumed$N(0, \sigma^2_{\mathrm{RFI}})$.

Beyond the 229 microsatellites used previously (MacNeil & Grosz 2002), three microsatellites were identified from the USDA-MARC map (Kappes *et al.* 1997) to enhance coverage of a QTL on BTA16. A new linkage map of BTA16 (Table 1) was constructed using CRI-MAP version 2.4 (Green *et al.* 1990). Markers (relative position) on BTA16 were: BM6430 (0.0), BMS1348 (4.1), BM121 (12.0), BM1311 (20.2), BM9034 (31.6), BMS1907 (48.5), CSSM028 (60.9), BM719 (76.3), MB103 (86.2) and HUJ623 (90.3).

Within each backcross, QTL effects were identified by composite interval mapping (CIM) using QTL cartographer (Wang *et al.* 2007). Experiment-wise and chromosome-wise significance thresholds were established by permutation analysis (Churchill & Doerge 1994). Threshold levels were chosen for type I error rates of 0.10, 0.05 and 0.01. Empirical 95% confidence intervals were determined by

Table 1 Quantitative trait loci detected in backcross progeny of Line 1 Hereford (L1) and CGC composite females by composite interval mapping.

Trait	Cross	BTA	Location (cM)	LOD	Effect	95% CI
RFI (kg/day)	L1	11	23.0	4.0**	−0.50	13–34
	CGC	10	28.6	2.5#	0.34	17–39
FCR (kg/kg)	L1	16	10.0	3.1**	−2.1	0–12.4
	CGC	12	77.8	2.7*	1.32	58–90
	CGC	16	30.3	3.8**	2.8	25–40.1
	CGC	16	50.2	3.1**	−3.2	49–56
ADG (kg)	L1	9	21.0	3.0*	−0.14	10–28
	CGC	15	29.2	1.9#	−0.21	28–41
	CGC	17	50.2	1.9#	0.58	46–64
DMI (kg/day)	L1	11	23.1	2.7#	−0.48	6–33
	CGC	16	40.2	2.5#	−1.04	35–46

Effect measures substitution of an allele from L1 for one from CGC.
Chromosome-wise significance thresholds, #$P < 0.10$, *$P < 0.05$, **$P < 0.01$
RFI, residual feed intake; QTL, feed conversion ratio; ADG, average daily gain; DMI, daily dry matter intake.

identifying positions flanking the QTL peak with LOD score two less than the maximum LOD. Results from CIM in both backcrosses were pooled to identify QTL that were significant across backcrosses by converting likelihood ratios to *P*-values (Ott 1991). For LR <0.1, the *P*-values were set to 0.72 to remove bias from the distribution of the *P*-values

$$\sum_{i=1}^{2}(-2\ln P_i)$$

which is distributed as χ^2 with $2n$ degrees of freedom was used as a test statistic (Province 2001). Correction for multiple comparisons followed Cheverud (2001) and 95% confidence intervals were estimated following Darvasi & Soller (1997). Confidence intervals were wide, because of marker spacing and number of observations.

Daily gain and feed intake averaged 1.11 kg/day (SD 0.36) and 8.37 kg/day (SD 0.68) respectively. Shown in Table 1 are QTL detected from each backcross. The effect indicates substitution of an allele from L1 for one from CGC. The QTL affecting RFI differ from those of Nkrumah *et al.* (2007b). However, the QTL affecting: FCR at 30.3 cM on BTA 16, ADG on BTA17, and DMI on BTA11 were co-located with QTL found by Nkrumah *et al.* (2007b).

Pooled results from both backcrosses considered jointly are shown in Table 2. All QTL found previously within the backcrosses remained significant. Additional QTL affecting RFI were found on BTA 2, 6, 7 and 13. The additional QTL affecting: RFI on BTA 2 and 7, FCR on BTA16 and 17, ADG on BTA14 and 17, and DMI on BTA5 and 11 validate those reported by Nkrumah *et al.* (2007b). Results from this study also support the QTL affecting ADG found by Alexander *et al.* (2007) on BTA9 and 17 and by Kneeland *et al.* (2004) on BTA14. The QTL on BTA11 found here affecting RFI is also supported by Sherman *et al.* (2009). The lack of further agreement between studies may point to either population specific differences in segregation or experimental differences in protocol that lead to differences among conceptually similar phenotypes.

Table 2 Quantitative trait loci detected pooling results from backcross progenies of Line 1 Hereford (L1) and CGC composite females.

Trait	BTA	Location (cM)	Bonferroni adjusted *P*-value	Effect	95% CI width (cM)
RFI (kg/day)	2	126	<0.01	−0.31	52
	6	55	<0.01	−0.24	79
	7	93	<0.05	−0.27	55
	10	31	<0.001	0.47	50
	11	29	<0.001	−0.17	30
	13	18	<0.05	0.10	81
	16	43	<0.05	0.16	19
FCR (kg intake /kg gain)	9	25	<0.05	0.75	73
	12	73	<0.01	0.87	53
	16	10	<0.01	−1.2	32
	16	28	<0.001	1.9	24
	16	50	<0.01	−1.7	23
	17	32	<0.05	−0.17	71
	21	62	<0.05	0.30	64
ADG (kg)	9	17	<0.01	−0.10	45
	14	20	<0.05	0.01	94
	15	29	<0.05	−0.11	88
	17	20	<0.01	0.01	58
DMI (kg/day)	2	126	<0.001	−0.33	45
	5	14	<0.01	−0.01	68
	6	81	<0.05	−0.13	63
	9	42	<0.001	−0.38	34
	10	35	<0.05	0.25	73
	11	18	<0.05	−0.24	46
	16	37	<0.01	0.34	17
	20	25	<0.05	0.24	70
	23	44	<0.05	0.08	77

RFI, residual feed intake; FCR, feed conversion ratio; ADG, average daily gain; DMI, daily dry matter intake.
Effect measures substitution of an allele from L1 for one from CGC.

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