



Identification of quantitative trait loci for wool traits in Iranian Baluchi sheep

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Received: 29 November 2011; Accepted: 7 June 2012

ABSTRACT

Regions on 3 ovine chromosomes (OAR1, 5 and 25) were selected to study quantitative trait loci (QTL) segregating for wool traits in Baluchi sheep, an indigenous sheep breed in Iran. Progenies (503) from 13 half-sib families were genotyped for 15 microsatellite markers. The average number of progeny per sire was 38 and ranged between 16 and 59. Wool traits (14) were analyzed and phenotypes were corrected for fixed effects of birth year, sex, flock, litter size and shearing date (year and season). The QTL analyses were performed using regression-based interval mapping. The results revealed 4 QTL on OAR1 for fibre type traits (hetero-type and Kemp fibres type per cent in fleece), coefficient of variation of fibre diameter and greasy fleece weight, one QTL on OAR5 for clean fleece weight and 7 QTL on OAR25 for fibre type traits (Hetro-type, Kemp and True wool fibres per cent), greasy and clean fleece weight, coefficient of variation of average fibre diameter and the per cent of fibre diameter between 40 and 50 μm .

Key words: DNA markers, QTL mapping, Baluchi sheep, fleece traits, Microsatellite marker

The construction of comprehensive marker maps in different species is feasible through techniques of molecular biology (Schibler *et al.* 1998, Maddox *et al.* 2001) that allow mapping of QTL influencing economically important traits, including fleece and wool traits. The development of efficient and robust linear regression methods to detect QTL (Haley and Knott 1992, de Koning *et al.* 2001) made it possible to locate the chromosomal regions influencing traits of interest. There is a great interest in study of genes of major effect and identifying QTL to improve wool quality and hence, production efficiency. Wool traits such as greasy fleece weight, clean fleece weight, fibre diameter and staple length are very important selection criteria in wool sheep breeding programmes. Most of the wool traits are moderate to high heritable (Hanford *et al.* 2006).

QTLs were detected for fibre diameter, staple length, coefficient of variation of fibre diameter, greasy and clean fleece weight and Kemp per cent (Parsons *et al.* 1994, Ponz *et al.* 2001, Beh *et al.* 2001, Allain *et al.* 2006, Cano *et al.* 2007, Bidinost *et al.* 2008). However, it is necessary to

confirm the previously detected QTL before QTL information can be included for selection or substantial resources are invested into identification of causal polymorphisms. Therefore, confirming this QTL in Baluchi sheep will increase confidence of these QTL being real. The total sheep population of Iran is 54 million heads which consisted of 27 breeds and ecotypes (ASRI 2004). The Baluchi sheep is one of the most frequent breeds, which constitutes about 30% of the total sheep population of Iran. It plays an important role in meat and wool production in the area. The wool yield is being used for carpet production. The coat colour in this breed is white and was adapted to the harsh local climate condition. The objective of the present study was to identify QTL affecting wool quality and quantity traits in half-sib design in Baluchi sheep, through the analysis of specific regions of chromosomes 1, 5 and 25.

MATERIALS AND METHODS

Animal and phenotype: The experimental population for the QTL study consisted of 503 Baluchi sheep belonging to 13 paternal half-sib families from 2 flocks at Research Centre of Baluchi sheep. The average family size was 38 offspring per sire, ranging from 16 to 59. Wool data from rams and ewes with lambing records were included in these analyses (929 records/trait in 2009 and 2010). To achieve normality, some traits were transformed prior to QTL analyses.

Wool-quantity traits were recorded on all progenies. Mid-side fleece samples were taken from individuals at 15–17

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months of age and staple length (SL, mm) and greasy fleece weight (GFW, g) were measured. Then, wool samples were washed and analyzed in a laboratory for determining clean fleece weight (CFW, g), yield (YLD,%), average fibre diameter (FD; μm), coefficient of variation of FD (CVFD;%), percentage of fibre with FD 20 μm or less (FD20;%), percentage of fibre between 21 and 30 μm (FD21-30;%), percentage of fibre between 31 and 40 μm (FD31-40;%), percentage of fibre between 41 and 50 μm (FD41-50;%), percentage of fibre with FD more than 50 μm (FDUP50;%), percentage of Kemp fibre and continuous medullated fibres (KEMP;%), percentage of discontinuous medullated fibres (HET;%), and the percentage of true wool (TRUE,%).

Microsatellite genotyping: Based on results from previous QTL studies on the sheep 15 microsatellite markers were selected from the available web-based sheep genetic map (<http://www.thearkdb.org/arkdb/>) on chromosome 1, 5 and 25. Our linkage analysis covered specific regions on OAR1 (8 microsatellites from 80.8 to 234.6 cM), OAR5 (4 markers from 12.8 to 95.7 cM) and OAR25 (3 markers from 0 to

52.6 cM), with an average distance between markers of 19.22, 20.72 and 17.5 cM respectively.

Blood samples of the 13 sires and their progenies were collected from jugular vein in tube with EDTA as anticoagulant. The blood samples were frozen at -20°C . The DNAs were extracted from frozen blood using DNA extraction kit. Purity of extracted DNA was assessed using a spectrophotometer. PCR amplifications were carried out in 25 μl reactions with 20–50 ng genomic DNA as template. Reaction mixtures contained 0.05 μl Taq DNA polymerase, 1 μM dNTP, 2.5 μl Tris-HCl, KCl and MgCl_2 . The cycling protocol was as follows: An initial denaturation step at 95°C for 10 min was applied, followed by 35 cycles with the following steps: 94°C for 30s, 48 – 62°C for 55s and 72°C for 30s (Table 1). The reactions were terminated by a final extension step at 72°C for 10 min. The primer, amplification conditions and other information were obtained from the Roslin Institute (University of Edinburgh) website (<http://www.roslin.ed.ac.uk/>). Firstly all sires were genotyped at all microsatellite markers before offspring were genotyped for

Table 1. Information on markers studied, sequence of the PCR primers and PCR amplification conditions

Marker name	Chr.	Po. (cM)	Primer F (forward) R (reverse)	PCR product (bp)	Annealing temperature ($^{\circ}\text{C}$)
BM6465	1	80.8	F: AGGAGCAAGCATCTTTAATGTG R: TGCCAGGCTATAGAAGGACTT	119–133	62
BMS1636	1	91.9	F: CATTATTCAGTGCCTTTGGATG R: GTGTTGGAGTTCTTCAGCAGG	180–200	60
BM4129	1	101.9	F: AACCTTTATTAGGGGAGTTCGG R: TAAGCTGTGGAGTGCAGCAA	120–150	55.5
BMS2321	1	152.1	F: TCACCTCACAAAATACACAATGC R: CCAAACCTCCATAATCACCATT	150–170	49
BMS4000	1	195.3	F: TCCCTCCTTGATGGATTGAG R: TTGAAGTAGCCTGAGAAAAGGG	230–250	58
BMS2572	1	207.4	F: ATGTTGCAGGCTTGTGGAG R: TCGACCCGACCGTAAAAAG	190–220	62
BM7145	1	227	F: ATTATGTTCCAGATTCCATTCCA R: CAGCACTGTTTCATAAACTATGGG	130–170	52.5
BM8246	1	234.6	F: AATGACAAATTGAGGGGAGACG R: AGAGCCCAGTATCAATTCTTCC	220–250	58.7
RM0006	5	12.8	F: CTACAATATCTGGTCACTGGA R: GATCACCATATTTATGAGATGG	119–130	56
BM0741	5	36.2	F: GCCCCTGAAGGAATGGTG R: CCAAAAAGTCTCTATCTCCAAA	156–186	55.5
BM7247	5	64.3	F: AAAGTAAGGCCTGCAGTAT R: CTTTCCCTAGAACTTACAAAG	105–121	58
BM1853	5	95.7	F: GCCTTTTGTAGGTGTTTCATTG R: GGTTGCAAAGAGTCAGACATG	105–121	59
MCM200	25	0.0	F: ACCAAACAGTGTCTCAACC R: GAACAGTCCTTAGATGCCA	130–150	57.3
BM6466	25	43.9	F: GGGAACAAATCACTGGGC R: AGCTGATATTTGAGCATCCAA	200–220	56.5
BMS1714	25	52.6	F: ATTTATCCCAAGAGGTTCCA R: TGAATCTGGTGAACAGGAAT	120–140	49

Chr., Chromosome; Po., position of locus on chromosome.

the markers which were heterozygous in the respective sire.

PCR products were run on 8% polyacrylamide gel using electrophoresis and the gels dried and scanned. Image of gels were scored independently by 2 researchers and the results incorporated in a database containing marker genotype and phenotypic data.

QTL analysis: Initially, the wool trait records were analyzed by least squares analysis of variance (SAS Institute, version 9.2) to identify known fixed effects including birth-year, sex, litter size, flock, shearing date and birth weight (as covariate) with significance ($P < 0.05$) and such effects were included in the mixed model for variance component estimation. Further, (co)variance components were estimated with mixed model by DMU 5.0 (Madsen *et al.* 2011) from single-trait analyses using animal model:

$$y = X\beta + Za + e$$

In this model, y was a vector of observations for different wool traits, β was vector of fixed effects influencing traits, a was the direct additive effect with the normal distribution $N(0, A\sigma_a^2)$, where A is the additive relationship matrix and σ_a^2 is the additive genetic variance and e was a randomly distributed vector of residuals. X and Z were the corresponding incidence matrices relating observation to the respective fixed effects and random animal effects respectively.

Single-QTL model: QTL analyses were conducted using a univariate multi-marker regression approach for interval mapping in half-sib families (Knott *et al.* 1996) with GridQTL software (Seaton *et al.* 2006). The probability of inheriting a particular sire allele was calculated at 1-cM intervals for each offspring, conditional on the marker genotypes of individual and its sire. Subsequently, the phenotype of each wool trait was regressed on the inheritance probabilities, at each location along with each chromosome for each family. Across family analysis was applied to

calculate the estimation of putative QTL effect for each sire included in the analysis for the genomic region under investigation. This was done by nesting regression within sires, because not all sires will be heterozygous for all QTL and the linkage between the QTL and the sire haplotype may vary from sire to sire. For each regression an F-ratio of the model including the phase probability versus the same model without the phase probability was calculated. The best estimated position for a QTL in each family, for each trait, was taken to be the location with the largest F-ratio. Chromosome-wide significance thresholds were assessed using permutation tests, and bootstrap procedures were used to obtain confidence intervals, both implemented in GridQTL using 10 000 re-samplings (Churchill and Doerge 1994, Visscher *et al.* 1996).

Two-QTL model: A two-dimensional QTL search was carried out for only those traits where significant evidence for a single QTL was detected, and this was conducted over 3 chromosomes.

RESULTS AND DISCUSSION

From all of fixed effects, birth-year had a significant effect on most of wool traits except wool quality traits such as HET, MED, TRUE and FD41-50 μm . Sex of progeny only affected the greasy and clean fleece weight and staple length. The mean of fibre diameter was different in 2 flocks, and shearing-date (based on year and season) affected greasy and clean fleece weight, staple length and the per cent of fibre diameter between 30 to 40 μm . Body weight considered as covariate for all of wool traits, but had not significant effect on these traits. Litter size did not differ substantially quality and quantity of wool traits.

Estimates of genetic and phenotypic parameters from single trait analyses for wool traits are shown in Table 2. Estimates of direct heritability for greasy fleece weight

Table 2. Phenotypic and genetic parameters of fleece traits in Baluchi sheep (records related 2009 to 2010)

Traits	N	Average	SD	σ_a^2	r	h^2	SE (h^2)
GFW (gr)	925	1519	540	10634	43836	0.19	0.08
YLD (%)	925	72.35	7.80	6.03	19.64700	0.23	0.01
CFW (%)	925	1103	430	6973.60	28146	0.20	0.01
SL (cm)	925	6.70	1.55	0.9999	1.07420	0.48	0.18
FD20 μm (%)	925	0.58	0.15	0.0040	0.02800	0.18	0.12
FD21-30 μm (%)	925	0.25	0.10	0.0004	0.02700	0.01	0.07
FD31-40 μm (%)	925	0.09	0.04	0.0100	0.04600	0.18	0.14
FD41-50 μm (%)	925	0.46	0.03	0.0070	0.16100	0.04	0.08
FDUP50 μm (%)	925	0.03	0.05	0.0060	0.00500	0.55	0.23
FD (μm)	925	25.11	3.56	1.8313	3.84340	0.32	0.07
CVFD (%)	925	42.87	8.28	9.1300	59.3000	0.13	0.11
HET (%)	925	0.03	0.03	0.0001	0.0009	0.16	0.09
KEMP (%)	925	0.02	0.03	0.0001	0.0008	0.20	0.08
TRUE (%)	925	0.95	0.04	0.8682	1.330	0.65	0.44

σ_a^2 , Additive genetic variation; r, residual error; h^2 , heritability; SE (h^2), standard error of heritability.

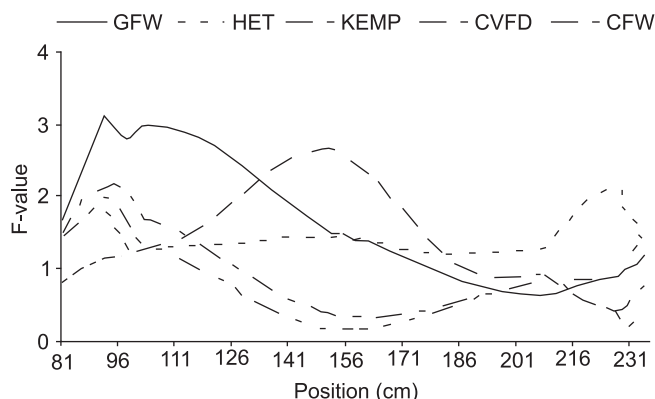


Fig. 1. The F-value profile obtained from across family analysis for wool traits on sheep chromosome.

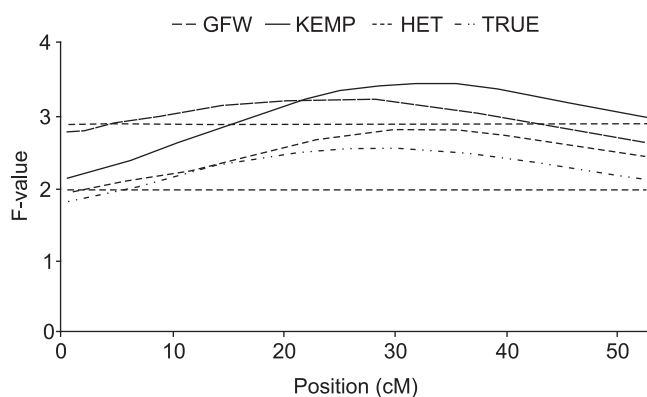


Fig. 3. The F-value profile obtained from across family analysis for wool traits on sheep chromosome 25.

(GFW), clean fleece weight (CFW) and wool yield (YLD) were 0.19, 0.20 and 0.23 respectively. The heritability estimates for fleece weight traits were within the range of estimates (0.15 to 0.55) for dual-purpose breeds (Safari *et al.* 2005), but Hanford *et al.* (2006) reported heritability for GFW 0.68. Estimate of heritability for staple length was 0.48, also heritability of wool quality, e.g. FD20 μ m, FD31-40 μ m, FDUP50 μ m, Hetero-type, Kemp and True wool per cent were 0.18, 0.18, 0.55, 0.16, 0.20 and 0.65 respectively.

The results of detected QTL for wool traits are shown in Table 3 and Figs 1-3. Chromosome 1 showed segregation of 4 putative QTL at position of 92, 95, 152 and 228 cM affecting GFW, CVFD, KEMP and HET traits respectively ($P < 0.01$ chromosome-wide significance level for GFW and $P < 0.05$ chromosome-wide significance level for CVFD, HET and KEMP).

The only QTL segregation on chromosome 5 was related to CFW at 88 cM with effects 0.97 phenotypic standard deviation (SD_p) in family 2382 ($P < 0.05$). There was a highly significant QTL on OAR25 affecting KEMP and GFW. Seven putative QTL related to wool traits were detected on this chromosome, i.e. GFW at 23 cM, TRUE at 28 cM, KEMP at 32 cM, FD41-50 μ m at 35 cM, HET at 42 cM, CFW at 46

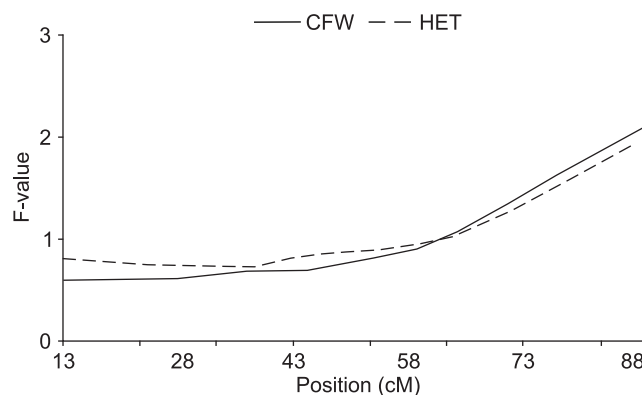


Fig. 2. The F-value profile obtained from across family analysis for wool traits on sheep chromosome 5.

cM and CVFD at 52cM. The effect of QTL for GFW were 0.57 to 0.75 SD_p in families 1314 and 1414 and KEMP with effects from 1.06 to 1.96 SD_p in families 1062 and 1414 ($P < 0.01$).

Confidence interval for all QTL situations included the complete region studying on chromosome (results not showed). The effect/standard deviation ranged from 0.33 to 2 phenotypic standard deviation (Table 3).

Significant results for the two-QTL models are presented in Table 4. For FD20, two QTL were detected on OAR1, one at position of 94 cM and the other at 176 cM. Two putative QTL were detected for FD21-30, one at position 93 cM and the other at 179 cM. For GFW two QTL were detected but they were located very close to each other and could be one QTL. Also two-QTL model for CVFD and HET were significant. Two-QTL model for OAR5 and 25 was not significant.

In the present study, we reported 12 putative QTL for wool traits on chromosome 1 (4 QTL), chromosome 5 (1 QTL) and chromosome 25 (7 QTL) in Baluchi sheep. The putative QTLs affecting hetero-type (HET), Kemp and true wool percentage were observed on chromosome 1. The position of the putative QTLs related to these traits was far from each others. The results indicated that these traits could be controlled by different set of genes.

A QTL influencing coefficient of variation of fibre diameter on chromosome 1 was also detected. Cano *et al.* (2007) detected a putative QTL for CVFD at position of 96 cM on chromosome 1 in Angora goat. Owing to homology of sheep and goat (Maddox 2005) it is confirmed that a QTL related to fibre diameter is located at this position of the chromosome.

In sheep, there are a few reports available for the linkage between genes and QTL with wool production traits (Ponz *et al.* 2001, Bray *et al.* 2002, Purvis and Franklin 2005). The putative QTL for wool traits which was found in Baluchi sheep on chromosome 1 could be related to keratin (KRT) and keratin-associated protein (KRTAP) similar gene families as pointed out by McLaren *et al.* (1997). The Kemp fibres

Table 3. QTL segregation for wool traits in Baluchi sheep

OAR	Position (cM)	Traits	F-value (chromosome-wide thresholds)	Family	Effects	Nearest marker	Effect/SD _p	95% C.I
1	92	GFW	3.12 (2.4, 2.9) **	1314	841.97	BMS1636	0.56	81–230
				1414	540.86		0.41	
	92	CFW	1.97 (2.2–2.9) NS	1314	567.60	BMS1636	0.49	81–232
	95	CVFD	2.2 (2.2–2.9) *	1062	23.52	BMS1636	0.50	81–230
	96	TRUE	1.95 (2.2–2.7) NS	2348	0.56	BMS1636	0.59	81–232
	152	KEMP	2.64 (2.3, 2.9) *	1001	0.87	BMS2321	1.47	85–233
5	228	HET	2.11 (2.06–2.9) *	1433	0.78	BM7145	1.56	81–232
	88	CFW	2.09 (2.06, 2.5) *	2382	1215.78	BM1853	0.97	19–88
	88	HET	1.97 (2.2–2.8) NS	2382	1.21	BM1853	0.67	13–88
25	23	GFW	3.26 (2.2, 2.9) **	1414	989.13	BM6466	0.75	4–52
				1314	849.42		0.57	
	28	TRUE	2.57 (2.2, 2.8) *	1001	1.29	BM6466	1.35	16.5–52
				1414	0.86		0.91	
	32	KEMP	3.46 (2.2, 2.9) **	1414	0.051	BM6466	1.96	0–52
				1062	0.034		1.06	
	35	FD41-50	2.4 (2.2, 2.8) *	1414	0.05	BM6466	1.06	0–52
				1001	0.065		1.44	
	42	HET	2.83 (2.3, 2.9) *	1001	0.056	BM6466	2.0	20–52
				1414	0.024		0.33	
	46	CFW	2.01 (2.0–2.9) *	2310	857.43	BM6466	0.79	0–52
	52	CVFD	2.18 (2.1, 2.8)*	2310	39.91	BMS1714	0.92	0–52
				1001	50.73		1.21	

* chromosome-wide significant level in $p < 0.05$ and ** chromosome-wide significant level in $P < 0.01$.

SD_p, QTL effect in phenotypic standard deviation units.

Table 4. Significant result of two-QTL model analyses on wool traits on chromosome 1.

Trait	F value (2QTL vs. 0QTL)	F value (2QTL vs. 1QTL)	QTL ₁ (cM)	QTL ₂ (cM)
FD20 µm or less	1.91 ^{NS}	2.11*	94	176
FD21-30 µm	1.93 ^{NS}	2.16*	93	179
GFW	2.33*	1.50 ^{NS}	91	103
CFW	1.66 ^{NS}	1.33 ^{NS}	93	191
CVFD	1.97 ^{NS}	2.08*	95	183
HET	2.04*	1.93 ^{NS}	88	228
FD	1.57 ^{NS}	1.48 ^{NS}	96	207
MED	1.64 ^{NS}	0.65 ^{NS}	91	126
TRUE	1.55 ^{NS}	1.14 ^{NS}	98	132

*Chromosome-wide level significant ($p < 0.05$); ^{NS} nonsignificant; QTL₁, The first QTL position in two-QTL model; QTL₂, the second QTL position in two-QTL model.

are large modulated fibres with a latticed deficient in sulphur. OAR1 harbors one of the keratin-associated-protein clusters (KAP, KAP7 and KAP8) involved in the formation of matrix surrounding cortex wool microfibrils (McLaren *et al.* 1997, Ede *et al.* 1995, Parsons *et al.* 1993). Another important wool follicle protein, i.e. trichohyalin (THH), encoded by a single

gene, was also mapped in chromosome 1 (McLaren *et al.* 1997). A linkage between this keratin cluster gene and fibre diameter in a merino half-sib was observed (Parsons *et al.* 1994) confirming that KAP cluster genes are strong candidate for the wool quality traits in Baluchi sheep.

In this study only one QTL on chromosome 5 was detected which was related to CFW trait. Two keratin genes families (KRT8 and KRT1B) were assigned to chromosome 5 in sheep, goat and cattle (Fries *et al.* 1991, Schibler *et al.* 1998, Pinton *et al.* 2000), all of them could be related to the QTL found on chromosome 5 in Baluchi sheep.

Significant QTLs affecting several wool traits were observed on chromosome 25, suggesting the evidence of a gene with major effect on wool traits. Ponze *et al.* (2001) in INRA401 breed have described three QTLs related to FD, CVFD and staple length traits. Allain *et al.* (2006) in a Lacaune × Sarda backcross detected four QTLs for fleece characteristics on OAR25, including greasy fleece weight, mean diameter, coefficient of variation of diameter fibre and medullated fibre per cent.

The present study contributes to the understanding of chromosomal regions that explain part of the variability of wool quality in Baluchi sheep and was also able to confirm previously reported QTL. This information may help in fine-mapping these QTL and utilization through marker-assisted selection for improvement of wool traits in future.

ACKNOWLEDGMENTS

This study was funded and supported by the Department of Animal Science, Ferdowsi University of Mashhad, Iran. The authors also acknowledge the staff of the Research Centre of Baluchi sheep in north-east of Iran.

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