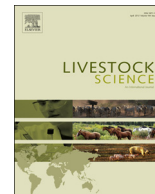




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Short communication

Polymorphisms of α -lactalbumin, β -lactoglobulin and prolactin genes are highly associated with milk composition traits in Spanish Merino sheep



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ABSTRACT

Traditionally, Merino Sheep has been used for wool and meat production. However, in Spain, it is used for manufacturing valuable artisanal cheeses. Therefore, milk production is becoming a very important trait to be considered. In this research, the effects of the different genetic variants of milk whey proteins α -lactalbumin (*LALBA*) and β -lactoglobulin (*LGB*), and prolactin hormone (*PRL*) on milk quality traits have been estimated in 1114 lactations from 396 genotyped Merino ewes of an experimental flock. Nucleotide substitutions g.133C > T (A and B alleles) of *LALBA* gene and g.1617T > C (A and B alleles) of *LGB* gene and a deletion, g.460_483del, of *PRL* gene (A and B alleles) were analysed. Hardy-Weinberg Equilibrium (HWE) and fixation index (F_{IS}) analyses detected that the genotyped Merino population have not been selected for the analyzed loci. Haplotype analyses of milk whey protein loci (*LALBA* and *LGB*) located at *Ovis aries* chromosome 3 (OAR3), indicate that alleles are independently inherited. So, we only studied the genetic effects of single genes on milk traits. Allele substitution and genotypes effects on milk yield and composition traits were estimated using a linear mixed model. Significant effects of *LALBA* *A (p. Ala²⁷), *LGB* *A (p. Tyr³⁸) and *PRL* *B (del24 bp) alleles on milk quality traits standardized to 120 days have been observed. *LALBA* *A allele is significantly associated with higher percentages of fat (FP; $\alpha = +0.26\%$, $P = 0.001$), protein (PP; $\alpha = +0.22\%$, $P = 0.001$), solids non fat (SNF; $\alpha = +0.17\%$, $P = 0.001$) and total solids (TS; $\alpha = 0.42\%$, $P = 0.0002$). *LGB* *A allele shows significant positive effect on PP ($\alpha = +0.136\%$, $P = 0.032$) and FP ($\alpha = +0.140\%$, $P = 0.070$). *PRL* *B allele shows only a significant positive effect on PP ($\alpha = +0.131\%$, $P = 0.026$). These positive effects could be of great interest for the cheese industry. Variants could be used as suitable markers to perform association analyses in commercial farms in order to implement a cheese yield selection program based on genotype information.

1. Introduction

The biological function of α -lactalbumin is crucial for milk secretion while β -lactoglobulin seems related with the transport of retinol and fatty acids (García-Gómez et al., 2012; Selvaggi et al., 2014). On the other hand, prolactin is an essential hormone for mammary gland development, for lactogenesis and for expression of milk protein genes (Horseman, 1999). The encoding genes of α -lactalbumin (*LALBA*), β -lactoglobulin (*LGB*) and prolactin (*PRL*) have been detected in chromosome regions associated to milk performance traits in dairy sheep. In this sense, *LALBA* gene was identified as candidate gene that influenced on milk protein percentage in Spanish Churra sheep (Gutiérrez-Gil et al., 2009). A non-synonymous SNP described in this gene, which

causes the amino acid exchange p.Val27Ala, has been associated with a higher milk protein and fat contents (García-Gómez et al., 2012). In *LGB* ovine gene, the missense variant g.1617T > C, responsible of the substitution p.Tyr38His, was associated with milk fat and protein contents (Corral et al., 2010) and cheesemaking properties in several breeds (Selvaggi et al., 2015). Recently, this mutation has been confirmed as a remarkable variant in a candidate gene related to milk protein content (Suárez-Vega et al., 2017). The *PRL* gene is located into a QTL confidence interval related with milk yield traits (Gutiérrez-Gil et al., 2009). Vincent and Rothschild (1997) described *Hae*III PCR-RFLP variants (A and B) in this gene. Subsequently, the B allele was characterized by a 24 bp deletion within the intron 2 of this gene (Orford et al., 2010). The variants A and B have been associated with milk-

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related traits in Serra da Estrela and East Friesian sheep breeds (Ramos et al., 2009; Staiger et al., 2010).

Currently, Merino is a dual purpose (fine wool and meat) sheep breed. Although milk yield is scarce and lactations are short, in Spain milk of ewes from some flocks is used to make cheeses of high quality (DOP "Queso de la Serena" and DOP "Torta del Casar"). For this reason, breeders and cheese industries are interested in the improvement of milk performance traits. In this sense, knowledge of the effects of protein loci variants on milk production and composition traits could be used in selection schemes to improve these traits. The aim of this study was to evaluate the effects of the genetic polymorphisms of *LALBA* and *LGB* milk whey proteins genes and prolactin (*PRL*) gene on milk yield and composition traits in an experimental flock of Merino sheep.

2. Materials and methods

2.1. Phenotypic data and DNA extraction

Milk recording data with a total of 1114 lactations of 396 Merino ewes from an experimental flock were used. Daily milk yield of each ewe was recorded fortnightly. The first record was measured at weaning (between 30 and 60 days after lambing). Lactation records included milk yield and fat, protein, non-fat solids, total solids and lactose percentages standardized to 120 days. In addition, birth-weaning interval, year-season of lambing, type of birth and age of dam were recorded.

DNA was isolated from individual whole blood samples of each 396 ewes using the UltraClean™ DNA BloodSpin Kit (MO BIO, Carlsbad, CA, USA) following the manufacturer's protocol.

2.2. *LALBA*, *LGB* and *PRL* polymorphisms

In the *LALBA* gene, we analyzed the missense variant g.139C > T located at exon 1. This SNP (rs403176291) is responsible for the p.Ala27Val substitution, which differentiates *LALBA* *A and *LALBA* *B alleles (GenBank accession # KY485138.1 and KY485139.1, respectively). Regarding *LGB* gene, a non-synonymous variant g.1617T > C located at exon 2 was analyzed. This SNP (rs430610497) causes the p.Tyr38His substitution, which discriminates among *LGB* *A and *LGB* *B alleles. The deletion g.460_483del, located at intron 2 for *PRL* *B allele" was also analyzed (see Supplementary Table S1 for details).

2.3. Statistical analyses

Genotype frequencies were tested for Hardy-Weinberg equilibrium and Wright's F_{IS} statistic (Weir and Cockerham, 1984) using GENEPOP v. 4.2 computer package (Raymond and Rousset, 1995). Haplotype frequencies for the nucleotide substitutions of *LALBA* and *LGB* genes located at *Ovis aries* chromosome 3 (OAR3) were estimated using EH software (Xie and Ott, 1993). Furthermore, the occurrence of linkage disequilibrium between the two genes was estimated.

The genotypes effects on milk yield (first milk recording yield and milk yield standardized to 120 days) and composition (percentages of fat, protein, non-fat solids, total solids and lactose standardized to 120 days) were estimated using the following linear mixed model (procedure REML) from SAS® 9.3 (SAS Institute Inc., Cary, NC, USA):

$$Y = X\beta + Zu + e$$

where, Y was the vector of observations for milk yield and composition traits; β was the vector of fixed factors: *LALBA*, *LGB* and *PRL* genotypes, year-season of lambing, age of ewe, type of lambing and lambing – weaning interval; X was the incidence matrix for these effects; u was the vector of random ewe effects; Z was the incidence matrix for random ewe effects and e was a vector of the residual effects, $N(0, I\sigma_e^2)$. Linear combinations of parameters values $L'\beta$ (L being a vector of

Table 1

Allele and genotype frequencies, expected (unbiased) heterozygosity (Hnb) frequencies, F_{IS} index and the Hardy-Weinberg equilibrium (HWE) found in the genetic variants analyzed in Merino sheep.

Gene	Alleles	Freq.	Genotypes	Freq.	HWE P-value	Hnb	Fis
<i>LALBA</i>	A	0.765	AA	0.578	NS	0.360	–0.038
	B	0.235	AB	0.374			
			BB	0.048			
<i>LGB</i>	A	0.751	AA	0.560	NS	0.374	–0.021
	B	0.249	AB	0.382			
			BB	0.058			
<i>PRL</i>	A	0.642	AA	0.396	NS	0.460	–0.065
	B	0.358	AB	0.490			
			BB	0.114			

Freq. = frequency; NS = Not Significant.

coefficients) and their corresponding variances $V(L'\beta)$, estimated with this model, allowed to test differences genotype means using a t distribution.

To estimate the allele substitution effect (α) of each gene on the traits under analysis we used the same linear mixed model, replacing the effect of genotype by the number of copies of alleles (0, 1 or 2) as covariate in the model.

3. Results

3.1. Genetic variability

Table 1 shows allele and genotypes frequencies, expected heterozygosity (Hnb), F_{IS} index and Hardy-Weinberg equilibrium (HWE) estimated for each locus. Haplotype frequencies and linkage disequilibrium results (Supplementary Table S2), indicate no association between g.133C > T and g.1617T > C variants of *LALBA* and *LGB* genes, respectively. Estimated frequencies of the haplotypes were similar than expected frequencies. Therefore, although both milk whey protein genes are located at OAR3, alleles are independently inherited. So, we only studied the genetic effects of single genes on milk traits.

3.2. Genotype effects on milk traits

Genotype effects on milk performance traits of variants of milk whey protein genes *LALBA* and *LGB*, and *PRL* hormone are shown in Table 2. In general, no significant differences were found on milk yield among genotypes derived from the analyzed polymorphisms, however, on milk quality traits significant favorable effects have been detected. *LALBA* gene polymorphism had highly significant effects on percentages of fat (FP), protein (PP), solids nonfat (SNF) and total solids (TS) in milk standardized to 120 days. The ewes of genotype *LALBA* AA displayed higher levels than their *LALBA* AB and *LALBA* BB counterparts. Least square means of genotypes derived from *LGB* gene variants had also effects on milk traits FP, PP, SNF and TS standardized to 120 days. For all these milk quality traits, except for SNF, ewes with *LGB* AA genotype displayed higher percentages than the *LGB* BB ewes. Prolactin (*PRL*) polymorphism significantly affected protein content (PP) in Merino breed. Homozygote ewes carrying of the deletion – *PRL* BB genotype – presented higher protein content when compared with the ones carrying genotype *PRL* AA.

3.3. Allele substitution effects on milk traits

Table 3 shows the allele substitution effects of *LALBA* *A, *LGB* *A and *PRL* *B alleles. In general, significant favorable effects on milk quality traits have been detected. *LALBA* *A allele was significantly associated with a higher FP ($\alpha = +0.26\%$, $P = 0.001$), PP ($\alpha = +0.22\%$, $P = 0.001$), SNF ($\alpha = +0.17\%$, $P = 0.001$) and TS ($\alpha = 0.42\%$, $P = 0.0002$) percentages. *LGB* *A allele only showed

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