Association Between a Polymorphism at the Stearoyl CoA Desaturase Locus and Milk Production Traits in Italian Holsteins

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ABSTRACT

Associations between stearoyl-CoA desaturase (*SCD*) gene polymorphisms and milk production traits (milk, fat, and protein yields, fat and protein contents, somatic cell score) were investigated on a sample of 701 lactations of 313 Italian Holsteins. Test-day records (5,097) were analyzed with a mixed linear model that included the fixed effects of herd, date of test, parity, genotype at the *SCD* locus, and lactation interval nested within *SCD* genotype, and the random effect of cow. An effect of the *SCD* genotype on milk and protein yields was detected, with VV cows producing more milk (about 2 kg/d) and protein (about 0.07 kg/d) compared with AA cows. The contribution of the *SCD* locus to the phenotypic variance of the 2 traits was about 0.015. These results suggest a possible use of the *SCD* locus in gene-assisted selection programs for the improvement of milk production traits in dairy cattle, although large-scale studies in different breeds are required.

Key words: dairy cattle, stearoyl-CoA locus, polymorphism, milk production trait

INTRODUCTION

Advancements in the identification of loci and chromosomal regions affecting traits of economic interest open appealing perspectives for the improvement of milk production traits in dairy cattle. Gene-assisted selection, that is, the use of functional mutations directly responsible of differences in phenotypes, is at present the most efficient option of marker-assisted selection (Dekkers, 2004). Loci with known effects on physiology of milk production have been proposed as candidate genes and relationships between their poly-

morphisms and several dairy traits have been tested (Hayes and Goddard, 2001; Grisart et al., 2002; Khatib et al., 2007, 2008).

The stearoyl-CoA desaturase (*SCD*) locus has been suggested as a candidate gene affecting milk fatty acid (FA) profile (Gautier et al., 2006), a fundamental aspect of milk nutritional quality (Bauman et al., 2006; Soyeurt et al., 2006). The *SCD* gene encodes a key enzyme of lipid metabolism able to introduce a double bond at the Δ^9 position in a large spectrum of FA (Ntambi, 1999; Ntambi and Miyazaki, 2004). The *SCD* locus has been mapped on *Bos taurus* autosome (BTA)26 (Campbell et al., 2001). Three single nucleotide polymorphisms (SNP) in complete linkage disequilibrium resulting in 2 haplotypes have been detected in exon 5 (Taniguchi et al., 2004). The third SNP causes the substitution of valine (allele V) with alanine (allele A) on the 293rd residue. Because valine is highly conserved across mammals, it is considered the ancestral amino acid in that position (Taniguchi et al., 2004). The *SCD* polymorphism has been found in Holstein-Friesian, Jersey, Brown Swiss, and Japanese Black cattle breeds (Taniguchi et al., 2004). Recently, an SNP polymorphism at the 3' untranslated region (UTR) of the *SCD* gene has been detected (Kgwatala et al., 2007).

Significant relationships between the polymorphisms in exon 5 of the *SCD* locus and the FA profile of carcass fat (Taniguchi et al., 2004) and, more recently, of milk fat (Mele et al., 2007; Moiola et al., 2007) have been reported for cattle. In particular, an effect of the *SCD* genotype on monounsaturated FA content and in the desaturase activity of the *SCD* enzyme has been detected in Italian Holsteins (Mele et al., 2007).

The aforementioned results suggest a possible use of the *SCD* locus in gene-assisted selection programs for the genetic improvement of milk fat quality in dairy cattle. Moreover, it is reasonable to hypothesize that a gene involved in energetic pathways may affect other productive traits as milk, fat, and protein yields that

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Table 1. Number of records (n), raw test-day means and standard deviations for milk, fat, and protein yields (kg/d), fat and protein contents, and SCS for cows of different parities

Trait	Parity								
	First			Second			Third		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
Milk yield (kg/d)	2,564	29.94	6.21	1,760	33.29	9.91	1,512	36.59	10.44
Fat content (%)	2,462	3.634	0.786	1,695	3.705	0.877	1,468	3.614	0.789
Fat yield (kg/d)	2,462	1.066	0.258	1,695	1.206	0.400	1,468	1.301	0.411
Protein content (%)	2,462	3.395	0.380	1,695	3.402	0.405	1,468	3.268	0.358
Protein yield (kg/d)	2,462	1.002	0.178	1,695	1.110	0.277	1,468	1.176	0.291
SCS	2,460	2.605	1.765	1,695	2.937	1.949	1,468	3.177	2.016

represent the main breeding goals in current selection schemes. To verify this hypothesis, the relationships between the SNP polymorphism located in exon 5 of the *SCD* locus and milk production traits in Italian Holstein cattle were investigated in this work.

MATERIALS AND METHODS

The data set contained 5,097 test-day (**TD**) records for milk, fat, and protein yields, fat and protein contents, and SCS measured on 701 lactations of 313 Italian Holstein cows. The original data set consisted of cows sampled from 21 half-sib families (14 ± 2 daughters per bull) and distributed in 34 herds (9 ± 3 cows per herd) located in the northeast of Italy. Data were recorded by the Italian Association of Animal Breeders within the official dairy recording plan in the period 1998–2004 (Table 1). Edits were based on the number of tests per lactation (>2) and on parity (<4).

The exon 5 region of the *SCD* gene was amplified by PCR and the genotype at the *SCD* locus for each cow was determined by an adapted single strand conformation polymorphism (SSCP) method (Ceriotti et al., 2004). Results were further checked by sequencing the DNA fragment that contained the polymorphism (Mele et al., 2007). Distributions of TD records, lactations, and cows across different *SCD* genotypes and parities are reported in Table 2. Genotypes were not in Hardy-Weinberg equilibrium (chi-square $P = 0.0002$), probably because of the limited size of the sample.

Data were analyzed with the following single-trait mixed linear model:

$$y_{ijklmn} = TD_i + H_j + PAR_k + SCD_l + DIM_m(SCD_l) + c_n(SCD_l) + e_{ijklmn} \quad [1]$$

where y = test for milk, fat, or protein yields, fat or protein percentage, somatic cell score; TD = fixed effect of the date of the test (797 levels); H = fixed effect of the herd (32 levels); PAR = fixed effect of the parity (3 levels, 1st, 2nd, 3rd); SCD = fixed effect of the *SCD* genotype (AA, AV, VV); DIM = fixed effect of the stage of lactation (10 levels of 30 d each); c = random effects of each individual cow (313 levels), nested within *SCD* genotype; and e = random residual.

Pairwise comparisons among different levels of fixed effects included in model [1] were performed using a Bonferroni adjusted test. The fixed effect of the *SCD* locus allows for the estimation of the gene effect on the considered trait averaged for the whole lactation. Statistical significance of the *SCD* effect was tested against variance of cow nested within *SCD* genotype according to repeated measures design theory (Littell et al., 1998). The average effect of gene substitution at the *SCD* locus was calculated as regression of the estimated least squares means of the 3 genotypes on the number of V alleles, weighted for the observed genotypic frequencies. The DIM factor nested within *SCD* was included in the model to estimate lactation curves of the different *SCD* genotypes (Stanton et al., 1992).

Random effects of cow and residual were assumed to be distributed with mean zero and (co)variance matrices $I\sigma_c^2$ and $I\sigma_e^2$, respectively. They allow for the

Table 2. Absolute frequencies of lactations and cows across the stearoyl CoA desaturase locus (*SCD*) genotypes and tests across parities and *SCD* genotypes

<i>SCD</i> genotype	Lactations, n	Cows, n	Tests by parity, n		
			First	Second	Third
AA	18	81	635	503	399
AV	431	190	1,535	1,072	996
VV	89	42	368	214	107

Table 3. Least squares means of test day for milk (MY), fat (FY), and protein (PY) yields (kg/d), fat (FC) and protein (PC) contents, and SCS for cows of different parities and stearoyl CoA desaturase locus (*SCD*) genotype

Item	MY		FC		FY		PC		PY		SCS	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Parity												
1	31.56 ^A	0.36	3.516 ^{AB}	0.039	1.095 ^A	0.015	3.312 ^A	0.018	1.038 ^A	0.012	2.481 ^A	0.100
2	34.96 ^B	0.41	3.538 ^A	0.045	1.216 ^B	0.017	3.336 ^A	0.020	1.152 ^B	0.013	2.699 ^B	0.115
3	38.00 ^C	0.54	3.426 ^B	0.060	1.289 ^C	0.023	3.240 ^B	0.026	1.225 ^C	0.016	2.994 ^C	0.152
<i>SCD</i> genotype												
AA	33.86 ^A	0.55	3.554	0.060	1.186	0.022	3.300	0.028	1.110 ^{A,a}	0.017	2.805	0.150
AV	34.52 ^A	0.39	3.524	0.043	1.193	0.016	3.301	0.020	1.126 ^{AB,a}	0.012	2.735	0.110
VV	36.13 ^B	0.71	3.402	0.078	1.221	0.029	3.287	0.036	1.180 ^{B,b}	0.022	2.634	0.195

^{a,b}Means within columns with different superscripts differ ($P < 0.05$).

^{A-C}Means within columns with different superscripts differ ($P < 0.01$).

REML estimation of variance components associated to individual cow (σ_c^2) and residual (σ_e^2). The variance associated with the *SCD* locus (σ_{SCD}^2) was calculated according to Falconer and Mackay (1996):

$$\sigma_{SCD}^2 = 2pq[a + d(q - p)]^2$$

where p and q are the frequencies of alleles A and V , respectively; a is half the difference between the 2 homozygotes; and d is the dominance deviation. The contribution of the stearoyl-CoA locus to the total phenotypic variance of the trait considered (r_{SCD}^2) was then calculated as

$$r_{SCD}^2 = \frac{\sigma_{SCD}^2}{\sigma_{SCD}^2 + \sigma_c^2 + \sigma_e^2}.$$

Finally, to test for possible spurious associations between *SCD* polymorphism and milk production traits

due to polygenic effects, contrasts among different *SCD* genotypes were estimated also by analyzing data with a model with the same structure of [1], but with the cow effect split into an additive genetic and a permanent environmental effect. The genetic (co)variance was structured by an additive relationship matrix that included cows with observations and their known ancestors up to 8 generations back in the pedigree, with a total number of 7,387 animals. To avoid model overparameterization, considering also the size of the data set, the permanent environmental (co)variance was modeled as $\mathbf{I}\sigma_{ep}^2$, where σ_{ep}^2 actually absorbs TD variation within and between lactations. (Co)variance components were estimated by a 6-trait REML animal model, by using the VCE software (Groeneveld, 1996).

RESULTS AND DISCUSSION

Herd, date of the test, and parity affected all the traits considered in the analysis (F -test significance

Figure 1. Estimated average lactation curves for milk yield of cows with different stearoyl-CoA desaturase genotypes.

Table 4. Substitution effect of an alanine into a valine at the stearoyl CoA desaturase locus (*SCD*; mean $\pm$ SE) and contribution of the *SCD* locus at the phenotypic variance for milk and protein yields

Trait	α	σ_{SCD}^2	σ_c^2	σ_e^2	r_c^2	r_{SCD}^2
Milk yield (kg)	1.040 $\pm$ 0.27	0.702	13.11	27.33	0.317	0.015
Protein yield (kg)	0.032 $\pm$ 0.008	0.0007	0.012	0.028	0.295	0.016

level $P < 0.001$), whereas a significant effect of the polymorphism at the stearoyl Co-A locus was found only for milk ($P = 0.015$) and protein ($P = 0.011$) yields.

Effects of parity and *SCD* genotype are summarized in Table 3. As expected, least squares means of daily yields of milk, fat, and protein, and SCS tended to increase with parity, whereas fat and protein percentages showed an opposite trend.

Cows with genotype VV at the *SCD* locus showed the greatest daily milk yield (Table 3), with more than 2 kg/d compared with AA cows; heterozygous cows were in an intermediate position. Moreover, the difference between homozygous genotypes appeared to be constant across different lactation stages (Figure 1), whereas the behavior of the heterozygote was less regular. The allele substitution effect of alanine into valine was 1.04 kg/d, and the contribution of the *SCD* polymorphism to the phenotypic variance was about 1.5% (Table 4).

There was no effect of the *SCD* genotype on protein content, whereas the protein yield of VV cows was significantly greater than that of AA cows, with a difference of about 0.070 kg/d. In the case of protein yield, the difference between homozygous genotypes was constant throughout the lactation (Figure 2). The allele substitution effect was 0.032 kg/d, with a contribution to the phenotypic variance of protein yield of about

1.6%. No effect of *SCD* genotype on fat content and SCS was observed (Table 3), even though VV cows showed lower values for both traits.

Differences among *SCD* genotypes for milk and protein yields were confirmed by the analysis carried out with the relationship matrix (Table 5): VV cows were always the most productive for both traits, and differences among the 2 homozygous means were 2.15 and 0.055 kg/d for milk and protein yield, respectively.

Estimates of heritability for all milk production traits considered (Table 6) are in agreement with previous reports on the Italian Holstein population (Muir et al., 2007) and, in general, with values reported in literature for dairy cattle (Ikonen et al., 2004; Ojala et al., 2005; Interbull, 2007).

Genetic correlations among yield and composition traits (above the diagonal of Table 6) are in agreement with the large literature available for these traits (Samoré et al., 2002; Miglior et al., 2007): in particular, high and positive genetic correlations between yield traits (ranging from about 0.56 to 0.87) and negative values for correlations between milk yield and fat and protein contents (about -0.42) can be observed. Finally, all correlations involving SCS were low (<0.12).

Results of the present work showed an association between a polymorphism at exon 5 of the *SCD* locus and milk and protein yields. Such an association ap-

Figure 2. Estimated average lactation curves for protein yield of cows with different stearoyl-CoA desaturase genotypes.

Table 5. Effects (Est) and standard errors (SE) of stearoyl CoA desaturase locus (*SCD*) genotypes for milk (MY), fat (FY), and protein (PY) yields (kg/d), fat (FC) and protein (PC) contents, and SCS estimated with the model that included the additive genetic and permanent environmental effects¹

<i>SCD</i> genotype	MY		FC		FY		PC		PY		SCS	
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
AV	0.784	0.59	-0.002	0.06	0.022	0.02	0.004	0.03	0.023	0.02	-0.105	0.15
VV	2.151	0.84	-0.118	0.09	0.040	0.03	-0.053	0.04	0.055	0.03	-0.289	0.21

¹Values are expressed as a deviation from the reference genotype AA.

pears to be constant across different lactation stages and it is still confirmed when the polygenic background is accounted for. The magnitude of the gene effect, both in terms of substitution effect and contribution to the phenotypic variance of the traits, is comparable to results reported for the most well-known example of a gene found to affect milk production traits in cattle, the acyl-CoA diacylglycerol acyltransferase (*DGAT1*) gene (Grisart et al., 2002). Moreover, also for *DGAT1*, the occurrence of an effect of the same sign on both milk and protein yield has been reported (Grisart et al., 2002; Kühn et al., 2004).

Several studies have reported QTL located on BTA26 affecting milk, fat, and protein yields in Holsteins (Plante et al., 2001; Boichard et al., 2003; Viitala et al., 2003; Jiang et al., 2005; Druet et al., 2006). Moreover, some genes involved in lipid metabolism that are located on this chromosome including *SCD*, LPF (gastric lipase), or GPAM (glycerol-3-phosphate acyltransferase mitochondrial) have been suggested as possible candidate genes harboring the functional mutation detected by the QTL analysis. However, results of the work of Gautier and coworkers (2006) that used microsatellites close to these genes seem to exclude the possibility that the position of the *SCD* locus matches the location of any of the QTL affecting milk production traits found on BTA26.

Finally, in previous research carried out on the same animals, VV cows showed lower contents of oleic, myristoleic, and monounsaturated fatty acids and a lower desaturase activity compared with AA cows (Mele et

al., 2007). Actually, milk fat represents the major cost of milk synthesis (more than one half; Bauman et al., 1985), mainly due to energy requirements for FA neosynthesis and desaturation. It is therefore reasonable to hypothesize that in cows with greater desaturase activity, fewer nutrients are directed toward milk and protein yields. This relationship is partially confirmed by results obtained by Kay et al. (2005) that found that Holstein cows selected for milk fat yield produced more milk than cows from control line but with reduced Δ^9 -desaturase activity and lower monounsaturated FA content.

CONCLUSIONS

A polymorphism at the *SCD* locus was found to be associated with daily milk and protein yields in a sample of Italian Holsteins. Moreover, the effect of the genotype was quite constant across lactation stages. The association between *SCD* locus and milk production traits could be exploited in programs of gene-assisted selection for the genetic improvement of milk production traits, with particular regard to milk and protein yield. In any case, large-scale studies in the same and other dairy cattle populations are required to confirm the effect found in the present work and relationships with milk nutritional qualities.

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Table 6. Estimates of heritability (on the diagonal) and genetic correlations (above the diagonal) among milk (MY), fat (FY), and protein (PY) yields (kg/d), fat (FC) and protein (PC) contents, and SCS¹

Trait	MY	FC	FY	PC	PY	SCS
MY, kg/d	0.263	-0.417	0.564	-0.425	0.866	0.059
FC, %		0.283	0.511	0.614	-0.151	-0.124
FY, kg/d			0.194	0.117	0.693	-0.093
PC, %				0.378	0.082	-0.106
PY, kg/d					0.250	-0.005
SCS, points						0.126

¹Standard errors of heritability estimates ranged from 0.017 to 0.027; standard errors of correlations estimates ranged from 0.026 to 0.109.

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