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Associations of milk protein polymorphism and milk production traits and udder health traits in Finnish Ayrshire cows

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INTRODUCTION

Milk with good coagulation properties is expected to give more cheese with desirable composition than milk with poor properties. In addition, high casein concentration, especially κ-casein concentration, and casein number are beneficial in cheese production. Some milk protein genotypes, especially κ-casein genotypes with the B allele, have been reported to have favorable associations with the above characteristics (e.g., Davoli et al. 1990; van den Berg et al. 1992; Macheboeuf et al. 1993; Ikonen et al. 1997; Ikonen et al. 1999a; Ikonen et al. 1999c).

It has been proposed that milk protein genotypes could be used as a criterion in selection to improve cheese production properties of milk. Before the milk protein genotypes can be considered in selection of breeding animals, the effects of the genotypes on milk production traits and other related traits have to be established. So far, the effects of the β-κ-casein (β-κ-CN) genotypes and haplotypes, and β-lactoglobulin (β-LG) genotypes from data of Finnish Ayrshire cows have been studied on the first lactation milk production traits (Ikonen et al. 1999b; Ikonen et al. 2001), on fertility traits (Ruottinen et al. 2004) and on body weight (Ojala et al. 2004).

The objectives of the study were to estimate the effects of the β-κ-casein and β-lactoglobulin genotypes, and β-κ-casein haplotypes on milk production traits and udder health traits from the first three lactations of Finnish Ayrshire cows.

MATERIALS AND METHODS

Data

Cows in the data set were born in 1984 through 1993, and were from 1548 herds in eastern Finland. The original data set with 20 928 cows was checked for validity and completeness of the information with regard to the traits studied and pedigree. In addition, 54 cows were excluded due to rare β-κ-casein genotypes, and 582 due to a too small half-sib group to deduce their haplotypes. After editing, 18 104 cows had records on the first lactation, and 15 722 and 12 124 records on the second and third lactations, which totaled 45 950 records. Cows were offspring of 695 sires.

Records for 305-d milk production traits, somatic cell scores (SCS) and veterinarian treatments for mastitis were received from the databases of Agricultural Data Processing Centre and Finnish Animal Breeding Association. Somatic cell count (SCC) is recorded bimonthly in the national milk recording. The bimonthly SCC (1000 cells/ml) have been preadjusted for the effects of stage of lactation and parity. Adjustment factors were computed from the complete milk recording data in the context of the national evaluation of breeding values. In this study, SCS for a cow was the within lactation mean of the natural logarithm of the preadjusted SCCs. In the health recording scheme, cows are recorded with mastitis (score 1) if diagnosed and treated by a veterinarian within a period of 7 d before through 150 d after calving. The rest of the cows are considered to be healthy (score 0). In addition to treating clinical, subclinical and chronic mastitis as a binary trait, the frequencies for them (Table 1) were transformed to units of phenotypic standard deviations on the continuous underlying scale of liability as described by Lynch and Walsh (1998).

The β- and κ-casein and β-lactoglobulin genotypes were determined using isoelectric focusing in polyacrylamide gels (Erhardt 1989). Due to the close linkage between the β- and κ-casein loci (e.g., Ferretti et al. 1990; Threadgill and Womack 1990), they were merged into 14 β-κ-CN composite genotypes. In order to infer the β-κ-CN haplotypes for the cows heterozygous for both β- and κ-CN loci, the size of paternal half-sib group was required to be at least 9. The most likely genotypes of the sires were inferred based on the β-κ-CN genotypes of their daughters. The casein haplotypes for the sires were inferred by minimizing the number of recombination events that occurred in the daughters. Subsequently, the haplotype a daughter had inherited from the sire was inferred assuming the recombination fraction between the β- and κ-CN loci was zero. The procedure seemed justified given the tight linkage between the casein loci. The β-κ-CN haplotypes for cows homozygous for both β- and κ-CN loci or heterozygous for only one of them were possible to deduce based on their β-κ-CN genotypes without a condition on the size of paternal half-sib group.

Statistical Analyses

To obtain the necessary variance components, the traits studied were analyzed assuming the following univariate linear model, (Model 1):

$$y_{ijklm} = \mu + yrs_i + age_j + do_k + herd_l + pe_m + a_m + e_{ijklm}$$

where
y_{ijklm} = an observation on a cow for 305-day milk, fat or protein yield, fat or protein content, somatic cell score, or clinical, subclinical or chronic mastitis on the first three lactations
μ = overall mean
yrs_i = fixed effect of year-season of calving class $_{i,\ i = 1,\ldots,36}$
age_j = fixed effect of age at calving class within a lactation $_{j,\ j = 1,\ldots,20}$
do_k = fixed effect of days open class $_{k,\ k = 1,\ldots,8}$
$herd_l$ = fixed effect of herd $_{l,\ l = 1,\ldots,1548}$
pe_m = random permanent environmental effect of animal $_{m,}$ N ($\mathbf{0}$, $\mathbf{I}\sigma^2_{pe}$)
a_m = random additive genetic effect of animal $_{m,}$ N ($\mathbf{0}$, $\mathbf{A}\sigma^2_a$)
e_{ijklm} = random residual effect, N ($\mathbf{0}$, $\mathbf{I}\sigma^2_e$).

Covariances among permanent environmental, animal and residual effects were assumed to be zero. The **A-**matrix included relationships among a total of 40 653 individuals of which 18 104 were cows with records and 22 549 their parents or grandparents.

Year of calving was grouped in 9 classes (1986 to 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, and 1996 to 1998), and each year in 4 seasons (by the months 3 to 5, 6 to 8, 9 to 11, and 12 to 2), which totaled 36 year-season subclasses. Age at calving was grouped within the 3 lactations into a total of 20 classes: ≤ 23, 24, 25, 26, 27 to 28, and ≥ 29 months within the first lactation, ≤ 35, 36, 37, 38, 39 to 40, 41 to 42, 43 to 45, and ≥ 46 months within the second lactation, and ≤ 48, 49, 50, 51, 52, 53 to 54, 55 to 57, and ≥ 58 months within the third lactation. Days open was grouped in 8 classes: ≤ 60, 61 to 80, 81 to 100, 101 to 120, 121 to 160, 161 to 240, ≥ 240 days, and a class for missing information.

To test the effects of the β-κ-CN and β-LG genotypes on the traits studied, the data were analyzed assuming the following model, (Model 2):

$$y_{ijklmno} = \mu + \beta\text{-}\kappa\text{-CNgen}_i + \beta\text{-LGgen}_j + yrs_k + age_l + do_m + herd_n + pe_o + a_o + e_{ijklmno}$$

where
$y_{ijklmno}$ = an observation on a cow for 305-day milk, fat or protein yield, fat or protein content, or somatic cell score on the first three lactations
$\beta\text{-}\kappa\text{-CNgen}_i$ = fixed effect of β-κ-CN genotype $_{i,\ i = 1,\ldots,14}$
$\beta\text{-LGgen}_j$ = fixed effect of β-LG genotype $_{j,\ j = 1,\ 2,\ 3}$
The other effects were the same as in Model 1.

The variance components estimated based on Model 1 (Table 2) were used in performing the analyses based on Model 2. To estimate the effects of the six β-κ-CN haplotypes they were fitted in Model 2 one at a time in place of the β-κ-CN genotype. Three classes, cows carrying either 2, 1 or no copy of a haplotype, were possible for the four most common β-κ-CN haplotypes, whereas only the last two classes were possible for the two rarest haplotypes.

The data were edited using the WSYS-L program package (Vilva 2004). Variance components for the random effects and the estimates of the genetic parameters with their standard errors (SE) were computed using the REML VCE4 program package (Groeneveld 1997). Statistical significance of the fixed factors was tested by F-test using the PEST program package (Groeneveld 1990). The differences between the classes of a factor with their SE were computed using the PEST.

RESULTS AND DISCUSSION

Basic Statistics

The means of the milk production traits and SCS (Table 1) are in agreement with the population average in the Finnish Ayrshire during the time period. The relative magnitude of the variation was largest for 305-d milk, fat and protein yields, but was clearly smaller for fat and protein contents and SCS, which agrees with the general order of magnitude of variation in the traits. The frequency of clinical mastitis in the data set (Table 1) was about the same magnitude as in the Finnish Ayrshire (Pösö and Mäntysaari 1996), but they were smaller than in the French Holstein (Rupp and Boichard 1999) and Swedish Holstein (Carlén et al. 2004).

Estimates of Genetic Parameters

Estimates of heritability for the 305-d milk production traits (Table 2) were slightly smaller or about the same magnitude as the corresponding estimates from another data of the Finnish Ayrshire (Pösö and Mäntysaari 1996), from Holstein data in France (Rupp and Boichard 1999) and from Holstein data in Sweden (Carlén et al. 2004). The magnitude of the estimate of heritability for SCS in this study was in a good agreement with the estimates in the previous studies.

Estimates of repeatability and heritability for clinical, subclinical and chronic mastitis were zero both for the binary and transformed. The traits for mastitis were analyzed also using bivariate models, in which either milk yield or SCS was in the model as a correlated trait, but the estimates of heritability were zero in this case as well. The estimates of heritability for clinical mastitis have been reported to be 0.02 to 0.05 in the Finnish Ayrshire (Pösö and Mäntysaari 1996), 0.02 in the French Holstein (Rupp and Boichard 1999) and 0.01 to 0.03 in the Swedish Holstein (Carlén et al. 2004).

Effects of β-κ-CN and β-LG genotypes

The most common β-κ-CN genotypes in the data set (Table 3) were A_1A_2AE (29%), A_2A_2AA (23%), A_1A_2AA (13%), A_1A_1EE (9%), A_1A_1AE (9%), A_1A_2AB (6%), A_1A_1BE (4%), A_1A_1AB (2%) and A_1A_1AA (2%). The rarest β-κ-CN genotypes were A_2A_2AB (1.4%), A_1A_2BE (0.4%), A_1A_1BB (0.4%), A_1A_2BB (0.2%) and A_1A_2EE (0.1%). Frequencies of the β-LG genotypes were: BB (51%), AB (41%) and AA (8%). Frequencies of the β-κ-CN composite genotypes and the β-LG genotypes were quite similar in the first three lactations.

Because the estimates of repeatability and heritability for the mastitis traits were zero, the effects of the β-κ-CN and β-LG genotypes were estimated only for 305-d milk production traits and SCS. The effect of the β-κ-CN genotypes was statistically significant on all traits, except fat yield, whereas the effect of the β-LG genotypes was significant (at least with $p < 0.05$) on traits other than SCS (Table 3). The effects of the rarest β-κ-CN genotypes were associated with large SE in most of the traits.

The two most common genotypes, A_1A_2AE and A_2A_2AA, were the best and their effect on 305-d milk yield was about equal to each other (Table 3). The rest of the genotypes were about 80 to 160 kg inferior in milk yield relative to A_2A_2AA genotype. The effects of the β-κ-CN genotypes on fat content were opposite to those on milk yield. All most common β-κ-CN genotypes were about 0.03 to 0.11 %-units superior in fat content relative to the A_2A_2AA genotype. The genotypes A_1A_1AB and A_1A_2AB were superior in protein content (0.01 to 0.02 %-units) and in SCS (0.02 to 0.03 units) relative to the A_2A_2AA genotype. The genotypes A_1A_1AE and A_1A_1EE were inferior in protein content (0.03 to 0.04 %-units) and in SCS (0.02 units). The most common genotype A_1A_2AE had a tendency for increased fat but decreased protein content and increased SCS relative to the A_2A_2AA genotype. The difference between the comparable extreme genotypes was equal to about 20% of phenotypic standard deviation (σ_P) in the traits studied, except the fat yield.

The β-LG AA genotype was about 60 kg superior in 305-d milk yield and 0.08%-units inferior in fat content relative to the BB genotype (Table 3). The effects of the heterozygote AB genotype were about in the middle of the two homozygotes.

The effects of the β-κ-CN and β-LG genotypes on the milk production traits from the first three lactations agreed in general with those estimated from the first lactation records (Ikonen et al. 1999b). The results were also parallel with the results of comparable studies, e.g., in Dutch black and white cows (Bovenhuis et al. 1992) and in Holstein cows (Ojala et al. 1997).

Effects of β-κ-CN haplotypes

The four most common β-κ-CN haplotypes in the data set (Table 4) were A_2A (46%), A_1E (29%), A_1A (16%) and A_1B (6%), whereas the two rarest haplotypes were A_2E (2%) and A_2B (1%). The effects of the two rarest β-κ-CN haplotypes were not statistically significant (at least with $p < 0.05$) on the traits studied, except for one case.

Excluding fat yield, the effects of the four most common β-κ-CN haplotypes were statistically significant (at least with $p < 0.05$) on most of the traits (Table 4). The most common β-κ-CN haplotype A_2A was associated with the highest milk yield, lowest fat content, increased protein content and slightly decreased SCS. The second most common A_1E haplotype was associated with low milk yield, high fat content, low protein content and high SCS. The A_1A haplotype was associated with low milk yield, high fat content, slightly decreased protein content and increased SCS. The relatively rare A_1B haplotype was associated with the lowest milk yield, highest fat and protein content, and lowest SCS. The comparable extreme haplotypes differed about 15% of σ_P in milk yield, about 20% in SCS, close to 30% in fat content, and over 30% in protein yield and content.

The effect of the β-κ-CN haplotypes tended to be additive on most of the milk production traits. Non-additive effects of the β-κ-CN haplotypes on the traits may be explained, in part, by the limited number of observations in some classes and large SE associated with the effects. Another explanation may be that a particular β-κ-CN haplotype appears in a single form with various haplotypes. Thus, the estimate of a single haplotype may be influenced by the effect of other haplotypes carried by the cows. It is also possible that some closely linked genes, QTL, may be associated with the effects of some casein haplotypes in chromoseme 6, e.g., in Finnish Ayrshire bulls (Velmala et al. 1995; Velmala et al. 1999) and in Norwegian Cattle bulls (Lien et al. 1995).

The effects of the β-κ-CN haplotypes on the milk production traits from the first three lactations agreed in general with those estimated from the first lactation records (Ikonen et al. 2001). The results were also parallel with the results in the comparable studies in the literature, e.g., in Finnish Ayrshire bulls (Velmala et al. 1995).

Conclusions

Milk yield was superior for the β-κ-CN genotypes with the β-CN A_2-allele as opposed to the A_1-allele. Both the B- and E-alleles in the κ-CN locus increased fat content. The κ-CN B-allele increased the protein content and decreased SCS, whereas the E-allele decreased the protein content and increased SCS. The relatively rare β-κ-CN haplotype A_1B was associated with the lowest milk yield, highest fat and protein content, and lowest SCS. The haplotype A_1E was associated with low milk yield, high fat content, the lowest protein content and highest SCS. The most common β-κ-CN haplotype A_2A was associated with the highest milk yield, lowest fat content, moderate protein content and slightly decreased SCS. The

comparable extreme haplotypes differed about 15% of σ_P in milk yield, about 20% in SCS, close to 30% in fat content, and over 30% in protein yield and content.

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Table 1. Number of observations, and mean and variation of the 305-d milk production traits and somatic cell score, and frequency of mastitis in the first three lactations of Finnish Ayrshire cows.

Trait	No. of cows	No. of records	Mean	Standard deviation	Coeff. of variation, %
Milk yield, kg	18 104	45 950	6 605	1 401	21
Fat yield, kg	18 104	45 950	295	62	21
Protein yield, kg	18 104	45 950	217	46	21
Fat content, %	18 104	45 950	4.50	0.56	12
Protein content, %	18 104	45 950	3.30	0.22	7
Somatic cell score	17 902	45 177	6.02	0.22	4

Lactation	No. of cows	Clinical mastitis, %	Subclinical mastitis, %	Chronic mastitis, %
First	18 104	8.0	0.1	1.8
Second	15 722	8.1	0.6	2.1
Third	12 124	7.9	1.1	2.5

Table 2. Estimate for additive genetic, permanent environmental and residual variances, and repeatability and heritability of the 305-d milk production traits and somatic cell score in Finnish Ayrshire cows.

Trait	Additive genetic var.	Permanent environm. v.	Residual variance	Estimate of repeatability	Estimate of heritability ± SE
Milk yield, kg	220 992	199 173	425 413	0.50	0.26 ± 0.01
Fat yield, kg	360	427	1 118	0.41	0.19 ± 0.01
Protein yield, kg	143	209	443	0.44	0.18 ± 0.01
Fat content, %	0.108	0.032	0.100	0.59	0.45 ± 0.01
Protein content, %	0.028	0.004	0.014	0.69	0.60 ± 0.01
Somatic cell score	0.005	0.008	0.028	0.32	0.13 ± 0.01

Table 3. Effect (Est.) of the β-κ-casein (β-κ-CN) and β-lactoglobulin (β-LG) genotypes on the 305-d milk production traits and somatic cell score in the first three lactations of Finnish Ayrshire cows.

Genotype	No. of cows[1]	Milk yield $\bar{y}$=6605kg σ_P=920kg	Fat yield $\bar{y}$=295kg σ_P=44kg	Protein yield $\bar{y}$=217kg σ_P=28kg	Fat content $\bar{y}$=4.50% σ_P=0.49%	Protein content $\bar{y}$=3.30% σ_P=0.21%	Somatic cell score $\bar{y}$=6.02 σ_P=0.20
	18 104	Est. ± se	Est. ± se	Est. ± se	Est. ± se	Est. ± se	Est. ± se
<u>β-κ-CN</u>							
A_1A_1AA	400	-93 ± 42	0.4 ± 2.0	-4.1 ± 1.3	0.07 ± 0.02	-0.03 ± 0.01	0.01 ± 0.01
A_1A_1AB	418	-163 ± 42	0.1 ± 1.9	-4.3 ± 1.3	0.11 ± 0.02	0.01 ± 0.01	-0.03 ± 0.01
A_1A_1AE	1533	-116 ± 25	0.7 ± 1.2	-5.5 ± 0.8	0.09 ± 0.01	-0.03 ± 0.01	0.02 ± 0.01
A_1A_1BB	71	-206 ± 93	-3.6 ± 4.3	-3.7 ± 2.8	0.10 ± 0.05	0.05 ± 0.02	-0.02 ± 0.02
A_1A_1BE	738	-107 ± 33	1.4 ± 1.5	-4.1 ± 1.0	0.10 ± 0.02	-0.01 ± 0.01	-0.01 ± 0.01
A_1A_1EE	1664	-96 ± 25	0.0 ± 1.2	-5.9 ± 0.8	0.07 ± 0.01	-0.04 ± 0.01	0.02 ± 0.01
A_1A_2AA	2335	-83 ± 21	-0.1 ± 1.0	-3.1 ± 0.6	0.06 ± 0.01	-0.01 ± 0.00	0.00 ± 0.00
A_1A_2AB	1153	-117 ± 28	-2.0 ± 1.3	-2.2 ± 0.8	0.04 ± 0.01	0.02 ± 0.01	-0.02 ± 0.01
A_1A_2AE	5249	-9 ± 17	1.2 ± 0.8	-2.0 ± 0.5	0.03 ± 0.01	-0.02 ± 0.00	0.01 ± 0.00
A_1A_2BB	36	-21 ± 131	3.3 ± 6.1	-1.8 ± 4.0	0.05 ± 0.07	-0.02 ± 0.03	-0.01 ± 0.03
A_1A_2BE	72	38 ± 93	1.8 ± 4.3	-1.3 ± 2.8	0.02 ± 0.05	-0.04 ± 0.02	0.02 ± 0.02
A_1A_2EE	24	-66 ± 161	4.3 ± 7.5	-6.1 ± 4.9	0.14 ± 0.08	-0.06 ± 0.04	-0.01 ± 0.03
A_2A_2AA[2]	4159	0	0	0	0	0	0
A_2A_2AB	252	10 ± 54	-2.4 ± 2.5	-0.1 ± 1.7	-0.05 ± 0.03	-0.01 ± 0.01	0.01 ± 0.01
	p[3]	0.0000	0.58	0.0000	0.0000	0.0000	0.0000
<u>β-LG</u>							
AA	1429	62 ± 24	-1.7 ± 1.1	3.0 ± 0.7	-0.08 ± 0.01	0.01 ± 0.01	-0.00 ± 0.01
AB	7482	30 ± 13	-1.5 ± 0.6	1.7 ± 0.4	-0.05 ± 0.01	0.01 ± 0.00	-0.00 ± 0.00
BB[2]	9193	0	0	0	0	0	0
	p[3]	0.01	0.047	0.0000	0.0000	0.003	0.97

[1]No. of records 45 950 in the first three lactations.
[2]The genotype of comparison.
[3]p: level of statistical significance of the factor in F-test.

Table 4. Effect (Est.) of the β-κ-casein (β-κ-CN) haplotypes on the 305-d milk production traits and somatic cell score in the first three lactations of Finnish Ayrshire cows.

β-κ-CN haplotype, no. of copies	No. of cows[1]	Milk yield $\bar{y}$=6605kg σ_P=920kg	Fat yield $\bar{y}$=295kg σ_P=44kg	Protein yield $\bar{y}$=217kg σ_P=28kg	Fat content $\bar{y}$=4.50% σ_P=0.49%	Protein content $\bar{y}$=3.30% σ_P=0.21%	Somatic cell score $\bar{y}$=6.02 σ_P=0.20
	18 104	Est. ± se	Est. ± se	Est. ± se	Est. ± se	Est. ± se	Est. ± se
$\underline{A_1A}$							
2	400	-61 ± 41	0.1 ± 1.9	-2.1 ± 1.3	0.04 ± 0.02	-0.01 ± 0.01	0.01 ± 0.01
1	5 027	-60 ± 15	-0.1 ± 0.7	-1.8 ± 0.5	0.04 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
0[2]	12 677	0	0	0	0	0	0
	p[3]	0.0004	0.99	0.0005	0.0000	0.45	0.60
$\underline{A_1B}$							
2	71	-164 ± 93	-3.9 ± 4.3	-1.2 ± 2.8	0.07 ± 0.05	0.06 ± 0.02	-0.03 ± 0.02
1	2 183	-88 ± 20	-0.8 ± 0.9	-0.9 ± 0.6	0.05 ± 0.01	0.03 ± 0.00	-0.03 ± 0.00
0[2]	15 850	0	0	0	0	0	0
	p[3]	0.0001	0.51	0.36	0.0001	0.0000	0.0000
$\underline{A_1E}$							
2	1 664	-48 ± 23	0.2 ± 1.1	-4.3 ± 0.7	0.04 ± 0.01	-0.04 ± 0.01	0.03 ± 0.00
1	7 037	5 ± 13	1.4 ± 0.6	-1.5 ± 0.4	0.02 ± 0.01	-0.02 ± 0.00	0.01 ± 0.00
0[2]	9 403	0	0	0	0	0	0
	p[3]	0.045	0.07	0.0000	0.0003	0.0000	0.0000
$\underline{A_2A}$							
2	4 159	95 ± 19	-0.5 ± 0.9	4.6 ± 0.6	-0.08 ± 0.01	0.03 ± 0.00	-0.01 ± 0.00
1	8 248	53 ± 14	-0.2 ± 0.7	2.4 ± 0.4	-0.04 ± 0.01	0.01 ± 0.00	-0.01 ± 0.00
0[2]	5 697	0	0	0	0	0	0
	p[3]	0.0000	0.84	0.0000	0.0000	0.0000	0.008
$\underline{A_2B}$							
1	522	46 ± 38	-1.4 ± 1.8	1.5 ± 1.2	-0.06 ± 0.02	-0.01 ± 0.01	0.01 ± 0.01
0[2]	17 582	0	0	0	0	0	0
	p[3]	0.23	0.41	0.21	0.0045	0.55	0.42
$\underline{A_2E}$							
1	603	50 ± 34	1.1 ± 1.6	1.1 ± 1.0	-0.02 ± 0.02	-0.01 ± 0.01	0.01 ± 0.01
0[2]	17 501	0	0	0	0	0	0
	p[3]	0.14	0.50	0.30	0.19	0.48	0.23

[1]No. of records 45 950 in the first three lactations.
[2]The class of comparison, i.e., the cows not carrying the haplotype.
[3]p: level of statistical significance of the factor in F-test.