

Milk protein genes *CSN1S1*, *CSN2*, *CSN3*, *LGB* and their relation to genetic values of milk production parameters in Czech Fleckvieh

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ABSTRACT: Genotypes of milk protein genes, alpha_{s1}-casein (*CSN1S1*), beta-casein (*CSN2*), kappa-casein (*CSN3*) and beta-lactoglobulin (*LGB*), were detected in 440 individuals of Czech Fleckvieh breed using a PCR-RFLP method. Breeding values of genotyped animals were obtained from the Official Database of Progeny Testing. A granddaughter design including 5 grandsires, 33 sons and 402 granddaughters was used for evaluation. Statistical analysis was carried out in SAS program using a restricted maximum likelihood method (REML). The aim of this study was to determine allele and genotype frequencies of observed genes and to find the relation between genotypes of genes and milk production parameters expressed by the breeding values of animals. The positive findings of frequencies of *CSN3* allele *B* (0.38) and genotype *BB* (13%) were detected in the observed population. Significant differences were found between genotypes of loci *CSN1S1*, *CSN2* and *CSN3* and breeding values for milk production parameters. Genotypes of *LGB* locus were not significantly related to any of the milk production parameters. Significant effects were found between *CSN1S1* locus and average breeding value for milk yield, *CSN2* locus and breeding values for all parameters except for protein content and *CSN3* locus and breeding values for protein content and protein yield. These findings contribute to a better understanding of the genetic constitution of Czech Fleckvieh breed and help with the application of the information to breeding.

Keywords: milk protein genes; cattle; caseins; beta-lactoglobulin; milk production

The milk protein genes alpha_{s1}-casein (*CSN1S1*), beta-casein (*CSN2*), kappa-casein (*CSN3*) and beta-lactoglobulin (*LGB*) are relevant in relation to milk production parameters and milk protein quality. Such genes that are correlated with performance parameters explain a part of the genetic variance and can improve the estimation of breeding value. Therefore they can be used as a suitable supplement to conventional breeding procedures (Příbyl, 1995). Their polymorphism related to the differences in animal performance can be taken into account in the selection process.

Casein genes are situated on bovine chromosome 6. The most frequent alleles in *CSN1S1* gene are *B* and *C*, allele *A* occurs occasionally. Allele *B* is prevalent compared to allele *C* (Boettcher et al., 2004). Eenennaam and Medrano (1991) found high milk yield as well as protein content associated with genotype *CC* as compared to genotypes *BC* and *BB*. Beta-casein is important for the casein micelle structure and common alleles in the *CSN2* gene are *A*¹, *A*², *A*³, *B* and *C* (Jann et al., 2002; Zwierzchowski, 2005). According to Ng-Kwai-Hang (1998) allele *A*³ is associated with

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higher milk production. The *CSN3* gene encodes milk protein that is important for the structure and stability of casein micelles (Alexander et al., 1988). Allele *B* is associated with higher milk protein content and milk quality (Boettcher et al., 2004; Caroli et al., 2004) and allele *A* tends to increase milk yield (Neubauerová, 2001). Kučerová et al. (2005) found a high breeding value for milk yield associated with genotype *AA* and a high breeding value for protein content associated with genotypes *BB* and *BE* in Czech Fleckvieh. The gene for beta-lactoglobulin (*LGB*) encodes mainly whey protein and is situated on bovine chromosome 11 (Eggen and Fries, 1995). The most frequent alleles are *A* and *B* (Panicke et al., 1996). Kaminski et al. (2002) found the highest breeding values for yield parameters related to genotype *AA* in comparison with genotypes *AB* and *BB*.

Alleles of the observed loci differ by point mutations in the sequences encoding certain amino acids. These mutations result in amino acid changes. Allele *B* of *CSN1S1* locus encodes Glu at position 192 while allele *C* encodes Gly at the same position (Eigel et al., 1984). Alleles *A*¹ and *A*² of *CSN2* locus differ in amino acid position 67, where *A*¹ encodes His and *A*² encodes Pro (Eigel et al., 1984). Allele *A*³ changes His to Gln at position 106, allele *B* changes Pro to His at position 67 and Ser to Arg at position 122 (Lien et al., 1992). *CSN3* allele *A* encodes Thr and Asp at positions 136 and 148, respectively, while allele *B* encodes Ile and Ala at the same positions (Eigel et al., 1984). Allele *E* changes Ser to Gly at position 155 (Erhardt, 1989). Allele *A* of *LGB* locus encodes amino acids Asp and Val at positions 64 and 118, respectively, while allele *B* encodes Gly and Ala at the same positions (Eigel et al., 1984).

Two approaches have been used for analysing the relation between genotypes and production parameters. Some studies reported the association between genotypes and phenotypes of cows (e.g. Bovenhuis et al., 1992; Ojala et al., 1997; Ikonen et al., 1999) while other studies reported an association between genotypes of sires and their breeding values (e.g. Ron et al., 1994; Sabour et al., 1996; Kaminski et al., 2002).

In our study we used a granddaughter design (Weller et al., 1990) to estimate the effects of milk protein genes. The aim of this study was to determine allele and genotype frequencies of the observed milk protein genes and find their relation to milk production parameters expressed by the breeding values of animals.

MATERIAL AND METHODS

Genotypes of milk protein genes, alpha_{s1}-casein (*CSN1S1*), beta-casein (*CSN2*), kappa-casein (*CSN3*) and beta-lactoglobulin (*LGB*), were detected in 440 individuals of Czech Fleckvieh using a Polymerase Chain Reaction and Restriction Fragment Length Polymorphism method (PCR-RFLP) (Schellander et al., 1992; Lien and Rogne, 1993; Chung et al., 1998). Electrophoresis on agarose gel was used for visualisation of fragments. DNA was obtained from blood samples of cows (Kawasaki, 1990) or semen of sires (Ashwell et al., 1996).

Identification of casein variants (*CSN1S1* – *B*, *C* and *CSN3* – *A*, *B*, *E*) was carried out according to Lien and Rogne (1993). *CSN2* variants *A*¹, *A*², *A*³ and *B* were identified according to Lien et al. (1992). *LGB* variants *A* and *B* were detected according to Agrawala et al. (1992). The PCR conditions slightly differed in comparison with the above-mentioned studies: *CSN1S1* – 3 min at 94°C, followed by 40 cycles of 30 s at 94°C, 45 s at 63°C and 60 s at 72°C; *CSN2* and *CSN3* – 1 min at 95°C, followed by 35 cycles of 30 s at 95°C, 25 s at 66°C (*CSN2*) or 62°C (*CSN3*) and 30 s at 72°C; *LGB* – 3 min at 95°C, followed by 40 cycles of 60 s at 95°C, 30 s at 60°C and 30 s at 72°C.

Breeding values of the observed animals were obtained from Official Database of Progeny Testing. A granddaughter design including 5 grandsires with 33 progeny-tested sons (sires) and 402 granddaughters (cows at first standardized lactation) was used in the analysis.

As the first step of analyses, allele and genotype frequencies were calculated. Statistical analysis was carried out in programme SAS 9.1 using the MIXED procedure, REML method and the following mixed model:

$$\mathbf{y} = \mu + \sum_{i=1}^4 \mathbf{W}\mathbf{g}_i + \mathbf{Z}\mathbf{s} + \mathbf{e}$$

where: \mathbf{y} = the vector of breeding value recorded for each individual on the observed parameter (milk, protein and fat yield, protein and fat content)

μ = the fixed effect including the overall trait mean

\mathbf{W} = the matrix associating the observations with the additive effects of milk protein genes (*CSN1S1*, *CSN2*, *CSN3* and *LGB*) represented by the vector \mathbf{g}

Z = the matrix associating the observations with random effects of sires represented by the vector s
 e = the vector of random residual effects

RESULTS AND DISCUSSION

Average breeding values of grandsires were positive in yield parameters but negative in content parameters (Table 1). In the sires the average breeding values for protein yield and protein content were positive while other breeding values were negative. This could be due to the fact that only several sires were later evaluated as bulls improving the parameters. The third generation consisted of all granddaughters at first lactation and only their average breeding values for protein and fat content were positive while other values were negative. This was expected due to the breeding values of sires.

Two alleles, B and C , were detected in $CSN1S1$ locus and their frequencies are presented in Table 2. Similar results in Czech Fleckvieh breed (B 0.92 and C 0.08) were found by Hanuš and Beber (1995).

The most frequent genotype of $CSN1S1$ locus was BB (80.2%). The frequency of genotype BC ranged from 18.2% to 20.0% between generations. Genotype CC was the least frequent (1.6%).

A significant effect of $CSN1S1$ locus was found only on breeding value for milk yield (Table 3). A significant difference was detected between genotypes BB and BC but the average breeding values of all observed parameters were the highest in animals with genotype CC . However, genotype CC was detected only in seven animals, which is not sufficient for a definite conclusion. Eenennaam and Medrano (1991) also found the highest protein content and milk yield associated with genotype CC and reported that genotype CC tended to increase milk yield as well as protein content. On the other hand, Havlíček (1996) detected only genotypes BB and BC in Czech Fleckvieh breed and reported higher milk, protein and fat yields as well as higher protein content associated with genotype BC compared to genotype BB . The above-cited studies were focused on the relation between genotypes of $CSN1S1$ locus and milk production parameters (not breeding values for milk production parameters). However, a com-

Table 1. Basic statistics of grandsires, sires and granddaughters

Breeding value for	Basic statistics of grandsires				
	n	\bar{x}	$s_{\bar{x}}$	min.	max.
Milk yield (kg)	5	+346	251	+97	+815
Protein yield (kg)	5	+10.2	11.8	-8	+25
Protein content (%)	5	-0.07	0.14	-0.27	+0.12
Fat yield (kg)	5	+6.2	13.0	-14	+19
Fat content (%)	5	-0.18	0.18	-0.39	+0.12
Breeding value for	Basic statistics of sires				
	n	\bar{x}	$s_{\bar{x}}$	min.	max.
Milk yield (kg)	33	-133	430	-1 181	+629
Protein yield (kg)	33	+2.3	15.0	-48	+25
Protein content (%)	33	+0.02	0.11	-0.22	+0.25
Fat yield (kg)	33	-7.39	19.1	-60	+38
Fat content (%)	33	-0.03	0.19	-0.50	+0.47
Breeding value for	Basic statistics of granddaughters				
	n	\bar{x}	$s_{\bar{x}}$	min.	max.
Milk yield (kg)	402	-69	242	-731	+1052
Protein yield (kg)	402	-1.5	7.6	-24	+24
Protein content (%)	402	+0.02	0.05	-0.16	+0.15
Fat yield (kg)	402	-1.74	10.5	-28	+34
Fat content (%)	402	+0.02	0.10	-0.28	+0.39

Table 2. Genotype and allele frequencies in the animals studied

Gene	Geno- type	Genotype frequencies (%)				Allele	Allele frequencies (%)			
		total	GS	S	GD		total	GS	S	GD
<i>CSN1S1</i>	<i>BB</i>	80.2	80.0	81.8	80.1	<i>B</i>	0.893	0.900	0.899	0.892
	<i>BC</i>	18.2	20.0	18.2	18.2	<i>C</i>	0.107	0.100	0.101	0.108
	<i>CC</i>	1.6			1.7					
<i>CSN2</i>	<i>A1A1</i>	2.8			3.0	<i>A1</i>	0.177	0.200	0.227	0.178
	<i>A1A2</i>	29.7	40.0	45.5	29.6	<i>A2</i>	0.809	0.800	0.773	0.808
	<i>A2A2</i>	64.7	60.0	54.5	64.5	<i>A3</i>	0.006	0	0	0.006
	<i>A2A3</i>	1.2			1.2	<i>B</i>	0.008	0	0	0.009
	<i>A2B</i>	1.6			1.7					
<i>CSN3</i>	<i>AA</i>	35.4	20.0	21.2	35.8	<i>A</i>	0.598	0.500	0.465	0.603
	<i>AB</i>	46.8	60.0	51.6	46.5	<i>B</i>	0.378	0.500	0.435	0.371
	<i>AE</i>	2.3			2.5	<i>E</i>	0.024	0	0	0.026
	<i>BB</i>	13.0	20.0	18.2	12.4					
	<i>BE</i>	2.5			2.7					
<i>LGB</i>	<i>AA</i>	26.2	20.0	18.2	26.4	<i>A</i>	0.511	0.500	0.515	0.512
	<i>AB</i>	49.8	60.0	66.6	49.5	<i>B</i>	0.489	0.500	0.485	0.488
	<i>BB</i>	24.0	20.0	15.2	24.1					

total $n = 440$, GS = grandsires ($n = 5$), S = sires ($n = 33$), GD = granddaughters ($n = 402$)

parison of these results with our results shows similar findings.

Four alleles (A^1 , A^2 , A^3 and B) of *CSN2* locus were detected in the genotyped animals (Table 2). Significant differences between the genotypes of *CSN2* locus were found in breeding values for milk yield, protein yield, fat yield and fat content (Table 3). Genotype A^1A^1 was associated with the highest breeding value for milk yield while the highest breeding values for protein and fat yields were associated with genotype A^2A^3 . The lowest breeding values were associated with genotype A^2B . As there were only five animals with genotype A^2A^3 and seven animals with genotype A^2B in the examined group of animals, the results of these genotype groups cannot be used to draw reliable conclusions. Contrary to our results, Ng-Kwai-Hang (1998) found the highest milk yield but lower protein content to be associated with genotype A^1A^3 . They also reported a significant effect of allele A^3 on milk production. According to Beaglehole and Jackson (2003) and Laugesen and Elliott (2003), allele A^1 increases the risk of diseases such as diabetes, coronary heart disease and ischaemic heart disease in people consuming such milk. On the other hand, they did not find any negative effect of allele A^2 . However, this posi-

tive effect of allele A^2 is not fully consistent with its effect on milk production parameters. In our study, the breeding values of animals with genotype A^2A^2 were negative for yield parameters but positive for content parameters compared to the animals with genotype A^1A^1 . It points to the tendency of allele A^2 to influence content parameters while allele A^1 increases milk yield.

The frequencies of alleles A , B and E for *CSN3* locus are shown in Table 2. The effect of allele B mainly on higher protein content and protein quality was reported (Boettcher et al., 2004; Caroli et al., 2004) while the effect of allele A tends to increase milk yield (Neubauerová, 2001). Negative effects of allele E on milk production parameters and protein quality were found by Ikonen et al. (1997). The frequencies of *CSN3* genotypes AA and BB 35.4% and 13.0% were detected for all genotyped animals. Only low frequencies of genotypes including allele E were found whereas genotype EE was not found at all.

Differences between the genotypes of *CSN3* locus in breeding values for protein content and protein yield were significant (Table 3). Genotype BB was associated with the highest breeding value for protein content but a lower

Table 3. The relation between genotypes of milk protein genes and breeding values of milk production parameters

Genotype	<i>n</i>	Average breeding values for				
		milk yield (kg)	protein yield (kg)	protein content (%)	fat yield (kg)	fat content (%)
<i>CSN1S1</i>						
<i>BB</i>	353	−66.8 ^a	−1.65	+0.012	−3.69	−0.019
<i>BC</i>	80	−140.3 ^a	−3.14	+0.025	−5.02	+0.005
<i>CC</i>	7	−14.3	+0.89	+0.027	+1.33	+0.021
<i>CSN2</i>						
<i>A1A1</i>	12	+27.4 ^a	+1.45 ^a	+0.010	+0.04 ^a	−0.025 ^a
<i>A1A2</i>	131	−80.7 ^b	−0.64 ^b	+0.028	−1.46 ^b	+0.028 ^a
<i>A2A2</i>	285	−52.7 ^c	−0.81 ^c	+0.018	−0.73 ^c	+0.021
<i>A2A3</i>	5	+8.2	+1.66 ^d	+0.039	+1.24	−0.002
<i>A2B</i>	7	−271.3 ^{abc}	−8.15 ^{abcd}	+0.013	−11.40 ^{abc}	−0.011
<i>CSN3</i>						
<i>AA</i>	156	−113.3	−2.31 ^a	+0.022	−3.15	+0.020
<i>AB</i>	206	−62.6	−0.45 ^a	+0.019 ^a	−1.84	+0.003
<i>AE</i>	10	−92.0	−1.62	+0.010	−3.56	−0.008
<i>BB</i>	57	−102.1	−2.22	+0.038 ^a	−3.67	+0.007
<i>BE</i>	11	+0.9	+0.11	+0.018	−0.07	−0.011
<i>LGB</i>						
<i>AA</i>	115	−54.4	−0.69	+0.019	−2.37	−0.010
<i>AB</i>	219	−76.6	−1.06	+0.025	−2.36	+0.006
<i>BB</i>	106	−90.4	−2.13	+0.021	−2.64	+0.011

^{a,b,c,d} means the significant difference $P < 0.05$ between two genotypes marked with the same letter in one column of the same milk protein gene

breeding value for protein yield while genotype *BE* was related to the highest breeding value for protein yield but a lower value for protein content. It means that allele *E* together with allele *B* gives an effect similar to genotype *AA*. However in this study, genotype *AA* was associated with the low average breeding value for milk yield. Kučerová et al. (2005) reported higher breeding values for protein content but lower ones for protein yield associated with genotype *BB* while higher breeding values for milk yield but lower ones for protein content associated with genotype *AA* in Czech Fleckvieh breed. Kaminski et al. (2002) also found the highest breeding value for milk yield but the lowest breeding value for protein content related to genotype *AA*. On the other hand, Neubauerová (2001) did not find any association between *CSN3* genotypes and the observed breeding values for milk production parameters. According to Boettcher et al. (2004)

and Caroli et al. (2004), genotype *BB* increases protein content and protein quality but decreases milk yield. Genotype *AA* tends to increase milk yield but it decreases content parameters (Neubauerová, 2001).

Only two alleles, *A* and *B*, for locus *LGB* were detected in the genotyped animals (Table 2). Similar frequencies were reported by Hanuš and Beber (1995) in Czech Fleckvieh breed. The observed frequency of genotype *AB* ranged from 49.5% to 66.6% between generations while the frequencies of genotypes *AA* and *BB* ranged from 18.2% to 26.4% and from 15.2% to 24.1%, respectively.

Although there were evident differences in the average breeding values of animals with different *LGB* genotypes (Table 3), they were not significant. The highest breeding values for milk and protein yields were associated with genotype *AA* while the highest breeding value for protein content was related to genotype *AB*. Neither did

Neubauerová (2001) find any association between *LGB* genotypes and the observed breeding values for milk production parameters. On the other hand, Kaminski et al. (2002) reported the relation between *LGB* genotypes and breeding values for protein yield.

The novel aspect of a valuable share of alleles and genotypes with positive effects on milk production parameters and milk quality as well as the association between milk protein genes and breeding values for milk production parameters contribute to a better understanding of the genetic constitution of Czech Fleckvieh breed and help with the application of the information to breeding process.

CONCLUSION

The positive finding of a valuable share of *CSN3* allele *B* and genotype *BB* was detected in the observed population of Czech Fleckvieh breed. Genotype *BB* increased protein and fat content in milk. The association between milk protein genes *CSN1S1*, *CSN2*, *CSN3* and breeding values for milk production parameters was found while *LGB* locus was not significantly related to any milk production parameter. The findings contribute to a better understanding of the role of the observed genes in Czech Fleckvieh breed and help with the application of the information to breeding process.

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