

Milk protein polymorphism in Swiss dairy cattle

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Individual cow milk samples from (a) 208 original Swiss Simmental (OSS), (b) 220 of their crosses (Simmental cattle = FV) with American Red Holstein (RH), (c) 215 original Swiss Brown (OSB) and (d) 390 of their crosses (Brown cattle = BV) with American Brown Swiss (BS) were genotyped for the variants of milk caseins (Cn) and β -Lactoglobulin (β -Lg). In addition, the association between κ -Cn genotypes and milk yield was studied.

Reasonable differences in the allele frequencies were found between the breeds. Compared to pure-bred OSS, crossing with RH resulted in a decrease in the frequencies of α_{s1} -Cn C, β -Cn B and κ -Cn B and in an increased frequency of β -Lg B. Within OSB, increased crossing with BS resulted in a decrease in the frequencies of α_{s1} -Cn C and β -Cn B and in increased frequencies of κ -Cn B and β -Lg B.

A significant association between the κ -Cn locus and milk yield could only be shown for the OSS breed.

Key words: Swiss dairy cattle, milk protein polymorphism, kappa-casein and milk yield

Introduction

In the past, dairy cattle breeders paid more attention to quantitative criteria (yield and fat content of milk) than to other criteria. Lately, however, milk protein polymorphism (qualitative criteria) has received considerable attention from the dairy industry because of its effect on the manufacturing properties of milk and the yield and quality of the products. Consequently, in the last 30 years the distribution of the genetic variants of milk proteins - caseins (Cn) and β -lactoglobulin (β -Lg) - in different breeds has been studied and the possible benefits of considering protein genotypes in selection programmes have been discussed. The vast number of studies on the association between protein polymorphism and the physiochemical properties of milk in different breeds has recently been reviewed

by JAKOB and PUHAN (1992). The main results were that there are favourable milk protein variants which are associated with the technological properties of milk: α_{s1} -Cn C is associated with firmer curd, β -Cn B with shorter coagulation times, β -Lg B with high casein number and κ -Cn B with shorter renneting time (DAVIES and LAW 1977, KROEKER et al. 1985, SCHAAR 1984, JAKOB and PUHAN 1986, MARIANI et al. 1976, TERVALA et al. 1985, MARZIALI and NG-KWAI-HANG 1986, MCLEAN 1986, AALTONEN and ANTILA 1987).

Reports on the association between κ -Cn genetic variants and milk yield are somewhat conflicting. Whereas ALEANDRI et al. (1990) and NG-KWAI-HANG et al. (1990) found no significant associations, results from other groups (LIN et al. 1989) indicate that there is indeed a relationship. However, because of economic interests, it has been

suggested that favourable milk protein genotypes, α_{s1} -Cn CC, β -Cn BB, κ -Cn BB and β -lactoglobulin BB, should be included into the criteria for selecting dairy cattle.

The objectives of this investigation were to study the frequencies of the genetic variants of α -, β -, κ -Cn and β -Lg in two original Swiss breeds and in their crosses with two related American breeds and to analyze the association between κ -Cn genetic variants and milk yield. The reason for including only κ -Cn variants in the statistical analysis was that the Braunvieh Cattle Breeders Federation in Switzerland has decided to consider these variants in breeding programmes; animals with κ -Cn BB- and/or AB type are recommended for planned matings (ZOGG 1990).

Material and methods

Animal material

The two main dairy breeds in Switzerland are Simmental cattle, known in Switzerland as "Simmentaler Fleckvieh" (FV), and Brown cattle, known in Switzerland as "Braunvieh" (BV). FV are crosses between original Swiss Simmental (OSS) and American Red Holstein (RH), and BV are crosses between original Swiss Brown (OSB) and American Brown Swiss (BS). Together they represent 87.90% (Simmental cattle = 45.51% and Brown cattle = 42.39%) of the total recorded cows (593,361). Only a few farmers still breed OSS and OSB.

Within one week a total of 1,033 individual milk samples from 68 farms were analyzed, representing the following dairy breeds in Switzerland:

- Original Swiss Simmental = OSS
- Simmental cattle (crosses OSS x RH) = FV
- Original Swiss Brown = OSB
- Brown cattle (crosses OSB x BS) = BV

The milk was genotyped for variants of α_{s1} -Cn, β -Cn, κ -Cn and β -Lg using isoelectric focusing (SEIBERT et al. 1985).

Statistical analysis

To study the association between κ -Cn variants and milk yield (305-day lactation yield), an analysis of variance was carried out using the General Linear Model (GLM) Procedure Type SSIII (SAS 1988). The model included the fixed effects of κ -Cn locus and lactation number as classification variables. Only the phenotypes κ -Cn AA, AB and BB were included, but not phenotypes including κ -Cn C and E alleles because of their low frequencies in this material (Table 2). The herd effect was ignored because from some farms less than 5, from others more than 30 records were available. Sires were not included in the model because of lack of data for sires used in the studied original Swiss breed herds (OSS and OSB).

The officially recorded milk yield, i.e., a 305-day lactation yield, was used in the statistical analysis. First-lactation records as well as records of cows with a lactation number higher than 10 were excluded because they were not available for all breeds. Moreover, 67 samples were excluded because of identification difficulties of their casein variants, leaving 954 samples for statistical analysis.

The model used to analyze the data was

$$Y_{ijk} = \mu + V_i + L_j + e_{ijk}$$

where:

Y_{ijk} = milk yield of the ijk^{th} individual

μ = overall mean

V_i = fixed effect of the i^{th} κ -Cn allele ($i = \text{AA, AB and BB}$)

L_j = fixed effect of the j^{th} lactation number ($j = 2, 3, \dots, 10$)

e_{ijk} = residual random term

Results and discussion

Allele frequencies of α_{s1} -, β -Cn and β -Lg

The allele frequencies are shown in Table 1. Regarding homozygote genotypes of the favourable genetic variants, α_{s1} -Cn CC, β -Cn BB and β -Lg

Table 1. Allele frequencies of α_{s1} -, β - and κ -casein and β -lactoglobulin for original Swiss Brown and Simmental cattle and their crosses with American Brown Swiss and Red Holstein.

Protein variants	n =	Breed ¹⁾			
		OSS	FV	OSB	BV
α_{s1} -casein					
A		0	0	0.002	0
B		0.932	0.956	0.812	0.933
C		0.068	0.044	0.186	0.067
β -casein					
A1		0.215	0.443	0.159	0.138
A2		0.630	0.458	0.571	0.655
B		0.059	0.021	0.267	0.196
C		0.096	0.078	0.003	0.011
κ -casein					
A		0.514	0.593	0.539	0.409
B		0.486	0.396	0.424	0.575
C		0	0	0.037	0.016
E		0	0.010	0	0
β -lactoglobulin					
A		0.424	0.326	0.623	0.396
B		0.570	0.674	0.370	0.598
D		0.006	0	0.007	0.006

- ¹⁾ OSS = original Swiss Simmental
 FV = original Swiss Simmental \times Red Holstein
 OSB = original Swiss Brown
 BV = original Swiss Brown \times American Brown Swiss

BB, differences were found between the breeds (Table 2). Contrary to the OSB and BV population, the rare C allele of α_{s1} -Cn appeared only in heterozygous (BC) of the OSS and FV population. The rare A allele of α_{s1} -Cn was found in the OSB population and appeared only in a heterozygous form (AB).

In OSS, the frequencies of α_{s1} -Cn C and β -Cn B (0.068 and 0.059) were higher than in FV (0.044 and 0.021), whereas the opposite was true for β -Lg B (0.570 compared to 0.674). In comparison, the average frequencies for α_{s1} -Cn C, β -Cn B and β -Lg B for the Holstein breed are 0.03, 0.02 and 0.61, respectively (NG-KWAI-HANG et al. 1984, McLEAN et al. 1984, ALEANDRI et al. 1990). A comparison of the allele frequencies of the Holstein

breed and OSS showed that the allele frequencies of FV are between these breeds. For the German Simmental cattle population, the allele frequencies were 0.09 for α_{s1} -Cn C, 0.07 for β -Cn B and 0.53 for β -Lg B (SEIBERT et al. 1987), which are close to those shown for OSS. This indicates that German Simmental cattle is crossbred with RH to a lesser degree than FV in Switzerland.

Differences were also found between OSB and BV. In OSB, the frequencies of α_{s1} -Cn C (0.267) and β -Cn B (0.186) were higher than in BV (0.067 and 0.196 respectively), whereas the frequency of β -Lg B was lower for OSB (0.370) than for BV (0.598). LI and GAUNT (1972) reported the frequency 0.02 for α_{s1} -Cn C and 0.10 for β -Cn B for Brown Swiss in the USA. For the Brown cattle in Italy the frequency for α_{s1} -Cn C was 0.119, for β -Cn B 0.280 and for β -Lg B 0.499 (RUSSO and MARIANI 1971). The frequencies 0.064, 0.258 and 0.559, respectively, were reported for the same breed more recently by MARIANI (1987). A comparison of these allele frequencies in Italy shows that the frequencies of α_{s1} -Cn C and β -Cn B had decreased over this period, whereas the frequency of β -Lg B had increased, meaning that the gene flow from BS in the populations of Brown cattle in Italy and Switzerland is similar.

It is difficult to find an appropriate explanation for the differences between the allele frequencies in the original Swiss breeds, OSS and OSB, on one hand, and in their crosses, FV and BV, with the American breeds, BS and RH, on the other. One of the reasons might be the crossing itself due to differences found between the original Swiss breeds and their crosses (Table 2). It is known that crossbreeding of original Swiss Simmental with American Red Holstein, and also of original Swiss Brown with American Brown Swiss, began around 1970 and is constantly increasing. Genetic improvement in dairy cattle has principally been dependent on quantitative genetics. This would suggest that dairy breeders have indirectly selected in favour of some genetic variants which are in positive correlation with the quantitative characteristics. This is affecting and altering the genetic make-up of milk proteins. It can be concluded that the variation in the frequencies of milk protein

Table 2. Genotype frequencies of α_{s1} -, β - and κ -casein and β -lactoglobulin for each breed and the differences between original and crossed breeds.

Genotype	Breed ¹⁾						
	OSS	FV	Difference	OSB	BV	Difference	
	n =	177	193		204	380	
α_{s1} -Cn							
AB	0	0	0	0.005	0	+0.005	
BB	0.864	0.912	-0.048	0.642	0.876	-0.234	
BC	0.136	0.088	+0.048	0.333	0.113	+0.220	
CC	0	0	0	0.020	0.011	+0.009	
β -Cn							
A1A1	0.051	0.223	-0.172	0.020	0.026	-0.006	
A1A2	0.282	0.378	-0.096	0.181	0.166	+0.015	
A1B	0.017	0.016	+0.001	0.093	0.058	+0.035	
A1C	0.028	0.047	-0.019	0.005	0	+0.005	
A2A2	0.373	0.202	+0.171	0.314	0.434	-0.120	
A2B	0.079	0.026	+0.053	0.333	0.258	+0.075	
A2C	0.153	0.109	+0.044	0	0.018	-0.018	
BB	0.006	0	+0.006	0.054	0.037	+0.017	
BC	0.011	0	+0.011	0	0.003	-0.003	
κ -Cn							
AA	0.294	0.358	-0.064	0.279	0.168	+0.111	
AB	0.531	0.451	+0.080	0.480	0.466	+0.014	
AE	0	0.021	-0.021	0	0	0	
AC	0	0	0	0.039	0.016	+0.023	
BB	0.220	0.171	+0.049	0.167	0.334	-0.167	
BC	0	0	0	0.034	0.016	+0.018	
β -Lg							
AA	0.153	0.093	+0.060	0.402	0.158	+0.244	
AB	0.537	0.466	+0.071	0.426	0.474	-0.048	
AD	0.006	0	+0.006	0.015	0.003	+0.012	
BB	0.299	0.440	-0.141	0.157	0.355	-0.198	
BD	0.006	0	+0.006	0	0.011	-0.011	

¹⁾ OSS = original Swiss Simmental

FV = original Simmental \times Red Holstein

OSB = original Swiss Brown

BV = original Swiss Brown \times American Brown Swiss

genes between different populations are mainly, if not entirely, the result of breeding and crossing.

Allele frequencies of κ -Cn

Allele frequencies in Table 1 show that κ -Cn A and B variants were predominant and that κ -Cn E and C were rare. The κ -Cn E variant was identified only in FV and κ -Cn C variant in OSB and BV.

In OSS the difference in frequencies between κ -Cn A (0.514) and κ -Cn B (0.486) was not as pronounced as in FV where the frequencies were 0.593 and 0.396, respectively. In OSB, the κ -Cn variants A, B and C were present with frequencies of 0.539, 0.424 and 0.037 and in BV with 0.409, 0.575 and 0.016, respectively. The allele frequencies of κ -Cn A and B in OSB and BV were different from those in OSS and FV. κ -Cn A was predominant in OSS, FV and OSB, and κ -Cn B in BV.

Table 3. *F*-ratios for the overall effect and least squares mean and standard error of a 305-day milk yield for κ -Cn by breed.

κ -Cn Overall (<i>F</i>)	Breed ¹⁾							
	OSS		FV		OSB		BV	
n =	177		193		204		380	
	3.04* ²⁾		0.43		0.16		0.08	
κ -Cn Genotype	LSM ³⁾	SE ⁴⁾	LSM	SE	LSM	SE	LSM	SE
AA	5999	272	7001	339	4978	138	6740	230
AB	5784	233	6879	351	4916	127	6804	173
BB	5233	302	6762	448	4882	192	6735	179

- 1): OSS = original Swiss Simmental
 FV = original Swiss Simmental \times Red Holstein
 OSB = original Swiss Brown
 BV = original Swiss Brown \times American Brown Swiss
 2): * = $p < 0.05$
 3): LSM = least square mean
 4): SE = standard error

The results concerning the frequencies of κ -Cn variants in the studied populations agreed in many respects with those reported for Italy and Germany. MARIANI (1987) found allele frequencies of κ -Cn A : B : C = 0.504 : 0.490 : 0.006 and ERHARDT (1989) κ -Cn A : B : C = 0.505 : 0.479 : 0.016 in the Brown cattle. LI and GAUNT (1972) reported the frequency 0.41 for κ -Cn A and 0.59 for κ -Cn B for Brown Swiss in the USA.

It was found that the highest κ -Cn B (favourable variant) frequency occurred in BV (0.575) followed by OSS (0.486), OSB (0.424) and FV (0.396). This might support the view that the frequency of κ -Cn B increases in the Swiss Brown cattle population due to crossing with American Brown Swiss and decreases in the Simmental cattle population due to crossing with American Red Holstein. A comparison of the allele frequencies of κ -Cn in Austrian FV, reported in 1975 (κ -Cn A 0.59 and κ -Cn B 0.41) by FOISSY and WINTERER and in 1991 (κ -Cn A 0.70 and κ -Cn B 0.30) by MAYER et al., showed that the frequencies of κ -Cn A had increased whereas the frequency of κ -Cn B had decreased during this period. The same result has also been observed in German dairy cattle by BUCHBERGER (1990) and in Danish dairy cattle by BECH and KRISTIANSEN (1990).

κ -Cn variants and their relation to milk yield

The results of the statistical analysis on the associations of κ -Cn variants with a 305-day lactation yield are presented in Table 3.

For the majority of the breeds (FV, OSB and BV), κ -Cn polymorphism was not significantly associated with the 305-day lactation yield. For OSS, however, a significant ($p < 0.05$) association was found between the κ -Cn locus and 305-day lactation yield.

When comparing the least squares means for the different κ -Cn genotypes, the FV cows with κ -Cn AA out produced those with AB and BB by 122 and 239 kg milk, respectively. For OSS, the differences were higher: cows with κ -Cn AA produced 215 and 766 kg milk more than those with κ -Cn AB and BB. For BV and OSB the differences were small. In a study by TAHA (1992) comprising the same animals as the present study but also including first-lactation cows and those with more than 10 lactations (11th, 12th and 13th lactation), the same tendencies were found but the differences between the κ -Cn genotypes were all non significant. Neither was there any significant overall effect of the κ -Cn locus on milk yield for any of the breeds.

Our results agree in some aspects with the works

of MCLEAN et al. (1984) and ALEANDRI et al. (1990), who failed to find any association between κ -Cn and milk yield. In contrast, NG-KWAI-HANG et al. (1986) reported that a higher test-day milk production was associated with κ -Cn AA. LIN et al. (1989) demonstrated, however, that the κ -Cn locus had a significant effect on fixed parity and on fixed age total milk yield and herd life, and that cows with κ -Cn BB produced more milk than those with κ -Cn AA and AB. He argued that first-lactation records alone should not be used when studying the association between κ -Cn variants and milk yield. We have reason to believe, moreover, that records

from more than one lactation are needed to determine such association.

Conclusion

Our study suggests that before genetic variants of milk proteins, in particular κ -Cn, are included in selection and breeding strategies, it is essential to account for the magnitude of both the effects of the different milk protein loci on quantitative traits such as milk yield as well as on traits of a more qualitative nature such as manufacturing properties.

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SELOSTUS

Maidon κ -kaseiini- ja β -laktoglobuliini -jakeiden geneettinen polymorfia sveitsiläisellä lypsykarjalla

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Maitovalkuaisjakeissa esiintyvää geneettistä muuntelua tutkittiin neljällä sveitsiläisellä lypsykarjarotutyypillä. Koeaineistona käytettiin kaikkiaan 208 Original Swiss Simmental (OSS) -rodun lehmää, 220 Swiss Simmental- ja American Red Holstein (RH) -rotujen risteytysjälkeläistä, 215 Swiss Brown (OSB) -rodun lehmää ja 390 Swiss Brown- ja American Brown Swiss (BS) -rotujen risteytysjälkeläistä. Kaseiinin ja β -laktoglobuliinien geneettisen muuntelun lisäksi selvitettiin κ -kaseiinin ja maidon tuotantomäärän välisiä vuorovaikutussuhteita.

Rotujen välillä havaittiin jonkin verran alleelimuuntelua. Risteytettäessä OSS-rotuisia lehmiä RH-rodun kanssa havaittiin α_{s1} -CnC, β -CnB ja κ -CnB alleelien esiintymistiheyden vähenevän verrattuna OSS-rodun yksilöihin. Toisaalta β -LgB-alleelin määrän havaittiin kasvavan. OSB- ja BS-rotujen risteytyksissä α_{s1} -CnC- ja β -CnB -alleelien määrä väheni ja κ -CnB- ja β -LgB -alleelien määrä kasvoi. Ainoastaan OSS-roduilla havaittiin merkittävä vuorovaikutussuhde κ -Cn- lokuksen ja maidon määrän välillä.