Estimation of Heritability and Genetic Correlations for the Major Fatty Acids in Bovine Milk

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ABSTRACT

The current cattle selection program for dairy cattle in the Walloon region of Belgium does not consider the relative content of the different fatty acids (FA) in milk. However, interest by the local dairy industry in differentiated milk products is increasing. Therefore, farmers may be interested in selecting their animals based on the fat composition. The aim of this study was to evaluate the feasibility of genetic selection to improve the nutritional quality of bovine milk fat. The heritabilities and correlations among milk yield, fat, protein, and major FA contents in milk were estimated. Heritabilities for FA in milk and fat ranged from 5 to 38%. The genetic correlations estimated among FA reflected the common origin of several groups of FA. Given these results, an index including FA contents with the similar metabolic process of production in the mammary gland could be used, for example, to increase the monounsaturated and conjugated fatty acids in milk. Moreover, the genetic correlations between the percentage of fat and the content of C14:0, C12:0, C16:0, and C18:0 in fat were -0.06 , 0.55 , 0.60 , and 0.84 , respectively. This result demonstrates that an increase in fat content is not directly correlated with undesirable changes in FA profile in milk for human health. Based on the obtained genetic parameters, a future selection program to improve the FA composition of milk fat could be initiated. **Key words:** heritability, genetic correlation, fatty acid, mid-infrared

INTRODUCTION

Interest in differentiated nutritional quality of dairy products is increasing in Belgium and around the world. Due to the negative reputation of milk fat for human health, the modification of milk composition presents

a real interest for the dairy industry. The fat contains mainly triglycerides (96%; Grummer, 1991; Jensen, 1995). They are composed of a glycerol linked with 3 esterified fatty acids (FA). Many previous studies have intensively examined the effect of FA on human health (Noakes et al., 1996; Hu et al., 1999; Parodi, 1999; Simopoulos, 2003). Based on these results, some studies have tried to modify the FA profile by feeding to obtain a fat composition more desirable for human health (Chilliard et al., 2000). Despite the large number of studies regarding the effect of nutrition on FA composition, the information about the effect of animal factors on the FA profile is very poor. However, few studies (Karijord et al., 1982; Palmquist et al., 1993; Soyeurt et al., 2006a) have suggested the possibility of genetically modifying the FA profile. Thus, it could be interesting for farmers to select cows that produce milk with a particular FA composition.

Selection for improved FA profiles would be feasible only if there is sufficient genetic variation in FA composition. Until now, very few studies have estimated genetic parameters for these traits. One of the first studies estimating heritabilities in bovine milk was by Edwards et al. (1973), who observed very high values that ranged from 0.64 to 0.98. However, these authors did not use an optimal model. They assumed that the environmental variance was the sum of variances within monozygotic twins and that the environmental variance added to the half of genetic variance was the sum of variances within dizygotic twins. Therefore, we can assume these heritability values were probably overestimated. Renner and Kosmack (1974a) obtained estimated heritabilities of 0.26, 0.06, and 0.04 for the content of FA with short (FA <C12:0) and medium carbon chains (C12:0 to C16:0) and for the C18 family in milk fat, respectively. They also obtained estimates of 0.26, 0.25, and 0.02 for contents of FA with short and medium carbon chain and for the C18 family in milk, respectively. From their estimates, it appeared that FA content in milk is more heritable than the content of FA in milk fat. The heritabilities estimated by Karijord et al. (1982) were

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different from those observed by Renner and Kosmack (1974a). They were on average 0.13, 0.14, and 0.10 for FA contents with short and medium carbon chains and for the C18 family in milk fat, respectively.

Renner and Kosmack (1974b) were among the first scientists to estimate the genetic correlations among different FA in milk or fat. Only the content of FA with short carbon chains in milk seemed to be positively correlated with milk yield (0.24). As expected, all studied classes of FA were positively correlated with milk fat except the correlation between the content of C18 family in fat and the content of fat (%FAT). Karijord et al. (1982) studied the genetic correlations between the content of FA in %FAT and the traditional production traits like the content of protein (%PROT), %FAT, and the milk yield (MILK). As found by Renner and Kosmack (1974b), the correlation with the C18 family and %FAT was also negative. However, the values estimated by Karijord et al. (1982) were greater than those obtained by Renner and Kosmack (1974b). The values of genetic correlations estimated among the contents for major FA were extremely variable and ranged from -0.68 to 0.97. Globally, the contents of FA of the same class [saturated (SAT), monounsaturated (MONO), or polyunsaturated fatty acids (POLY)] were positively correlated. On the other hand, MONO or POLY contents were negatively correlated with SAT. However, the results must be interpreted with caution, because the heritabilities estimated for MILK and %FAT were very low in this study (0.09 for these 2 traits), indicating potential data quantity and quality problems.

The estimation of heritability and genetic correlations requires sufficient data to obtain reliable estimates. Many studies have used the data from chromatography of FA to estimate the heritabilities of FA in milk and fat (Renner and Kosmack, 1974a; Karijord et al., 1982). This method to measure FA is accurate (Dorey et al., 1988; Collomb and Bühler, 2000) but requires a long time for analysis, expensive reagents, and well-skilled staff. Therefore, these studies have generally been restricted in the number of animals and samples available. Mid-infrared (MIR) spectrometry is a faster method to estimate different milk components (up to 500 samples/h; Foss, 2006). This technology is currently routinely used by milk recording agencies to measure different components as overall concentrations of %FAT and %PROT. A recent study (Soyeurt et al., 2006b) provided the first calibration equations to estimate the major FA contents in milk.

The results available for the heritabilities or genetic correlations for FA profile in bovine milk are very variable. Consequently, the aim of this study was to estimate the heritabilities and the genetic correlations among the major FA. This study used a simple test day

model and FA contents predicted by MIR spectrometry. Use of this type of data facilitates an increase in the number of records and should improve the reliability of estimates.

MATERIALS AND METHODS

Animal Population and Milk Samples

From April 2005 to May 2006, milk samples (7,700) were collected from 25 herds that represented 7 breeds (Brown Swiss, dual-purpose Belgian Blue, Holstein-Friesian, Jersey, Montbeliarde, Normande, and non-Holstein Meuse-Rhine-Yssel type Red and White breeds). These herds were selected using several criteria: their participation in Walloon milk recording, which was necessary to analyze samples with MIR, and the degree of pedigree completeness. The samples were taken from all cows during regular visits for milk recording and comprised equal numbers from morning and evening milkings. Due to technical issues, the number of test days was not constant for all herds. Also, some cows were dried off or calved during this study, meaning that numbers of test days per cow within herds also varied.

Predicted Contents of Fatty Acids in Milk and Milk Fat

All samples were analyzed by using a MIR spectrometer (Foss MilkoScan FT6000, Foss, Hillerød, Denmark). Calibration equations used to predict the contents of FA in milk (C12:0, C14:0, C16:0, C18:0, C18:1, C18:2 *cis*-9, *cis*-12, SAT, and MONO, g/dL of milk) were those developed by Soyeurt et al. (2006b). Using the density of milk (1.03 g/cm³), these FA contents were transformed to grams per 100 g of milk. Using the %FAT predicted by the MilkoScan FT6000, these FA contents in milk were then converted into content in milk fat expressed as grams per 100 g of fat. Table 1 gives the means and SD observed for all studied traits.

Additional Information About Milk History

To have additional data for MILK, %FAT, and %PROT, the historical records for these traits of cows and herds were added to the database. Complete records were added for all cows since March 2005, including those cows for which no FA were available. The final edited data set contained 40,007 records on 2,047 animals.

Breed composition was determined according to the known pedigrees of the animals. A certain proportion of genes were of unknown origin, however, and thus treated as though they were provided by another dis-

Table 1. Mean and standard deviation for each analyzed component of milk for the studied population

Trait	Milk (g/100 g of milk)		Milk fat (g/100 g of fat)	
	Mean	SD	Mean	SD
Milk ¹ (kg/d)	23.12	8.43		
Fat (%) ¹	4.13	0.79		
Protein ¹ (%)	3.47	0.40		
C12:0 ²	0.13	0.03	3.15	0.65
C14:0 ²	0.44	0.10	11.09	1.88
C16:0 ²	1.24	0.29	30.76	4.24
C18:0 ²	0.51	0.13	12.44	1.03
C18:1 ²	0.95	0.30	23.63	6.00
C18:2 <i>cis</i> -9, <i>cis</i> -12 ²	0.07	0.02	1.84	0.38
Saturated fatty acids ²	2.86	0.63	70.72	6.53
Monounsaturated fatty acids ²	1.02	0.32	25.35	5.69

¹n = 40,007 test-day records.²n = 7,700 test-day records.

tinct breed. Table 2 describes the average breed composition for the animals with records.

Model

Due to the computational challenges related to the number of traits, the final data set was divided into 5 runs that contained the following groups of traits, respectively:

- MILK, %FAT, %PROT, SAT, and MONO;
- SAT, MONO, and 6 major FA (C12:0, C14:0, C16:0, C18:0, C18:1, C18:2 *cis*-9, *cis*-12);
- MILK, %FAT, %PROT, and the 3 shortest FA (C12:0, C14:0, and C16:0);
- MILK, %FAT, %PROT, and the 3 18C FA (C18:0, C18:1, C18:2 *cis*-9, *cis*-12); and
- 6 FA (C12:0, C14:0, C16:0, C18:0, C18:1, C18:2 *cis*-9, *cis*-12).

For these 5 runs, the same simplified multitrait mixed repeatability test-day model with a constant genetic effect was used:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{W}\mathbf{l} + \mathbf{Z}\mathbf{p} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where $\mathbf{y}$ = the vector of observations (e.g., MILK, %FAT, %PROT, SAT, and MONO); β = the vector of fixed effects (herd $\times$ test day $\times$ class of parity number, stage of lactation $\times$ class of parity number, class of age $\times$ class of parity number, and regressions on the fractions of genes for every breed other than Holstein); $\mathbf{l}$ = the vector of permanent environment random effects within lactation; $\mathbf{p}$ = the vector of permanent environment random effects across lactations; $\mathbf{u}$ = the vector of animal effects; $\mathbf{X}$, $\mathbf{W}$, and $\mathbf{Z}$ = incidence matrices; and $\mathbf{e}$ = the vector of random residual effects.

Fixed effects were defined as follows. Stage of lactation was divided into 24 classes of 15 d each. Records with DIM <5 or >365 were deleted. Parities were grouped as first, second, and third or later lactation with 14,844, 10,132, and 15,031 records in each of the respective groups. Age at test day was defined as number of months from birth. There were 9 classes of age (for first lactation, age less than 29, 29 to 32, 33 and older; for second lactation, age less than 42, 42 to 46, 47 and older; and for the third or later lactation, age <54, 54 to 59, 60 and older).

Pedigree completeness was good, with 18,856 animals. Due to the informative pedigree, genetic and permanent environmental effects could be separated. Variance components were estimated using expectation maximization REML and average information REML (Miszta, 2007). Standard errors of estimates were obtained using average information REML (Miszta, 2007).

The variances reported are the average values measured from the results obtained by the 5 runs. Due to the separate estimation of correlations, the correlation matrices had to be banded by applying the weighted bending procedure presented by Jorjani et al. (2003). The weights were the number of observations used to estimate a given correlation.

RESULTS AND DISCUSSION

Heritability of MILK, %FAT, %PROT, and FA in Milk

The model used allowed the estimation of genetic, 2 permanent environmental, and residual effects. Table 3 summarizes the variance components for MILK, %FAT, %PROT, SAT, and MONO and for the major FA in bovine milk (g/100 g of milk). Heritability estimates for MILK were similar to those estimated by other authors (Veerkamp and Goddard, 1998; Lidauer and Mäntysaari, 1999; Bormann et al., 2003; Gengler et al., 2004). Few recent authors have reported daily %FAT and %PROT heritabilities. The results obtained in this

Table 2. Average breed composition of the studied animal population (%)

Breeds	Average breed composition
Dual-purpose Belgian Blue	12.31
Meuse-Rhine-Yssel type Red and White	4.31
Holstein-Friesian	45.39
Jersey	3.92
Brown Swiss	2.90
Montbeliarde	11.21
Normande	13.12
Unknown	6.85

Table 3. Average estimate and average standard error of variances (% of phenotypic variance) for each studied effect (genetic, 2 permanent environments, residual) with a multitrait model including the quantity of milk, the content of milk fat, the content of protein, and the content of fatty acids in milk (g/100 g of milk)

Trait	Permanent environment effects							
	Genetic						Residual	
	Estimate	SE	Within lactation		Across lactations		Estimate	SE
Milk	18	1.75	31	0.73	9	1.50	42	0.24
Fat (%)	32	1.78	5	0.25	5	1.20	58	0.15
Protein (%)	28	2.20	12	0.37	9	1.72	51	0.27
Saturated	36	2.13	7	0.51	6	1.43	51	0.35
Monounsaturated	15	0.98	16	0.96	1	0.36	68	0.52
C12:0	29	2.20	13	1.20	8	1.54	49	0.60
C14:0	31	2.48	12	1.24	10	1.95	48	0.53
C16:0	38	1.97	7	0.83	2	0.89	53	0.33
C18:0	30	1.86	8	0.77	4	1.08	57	0.35
C18:1	5	0.63	18	1.03	1	0.19	75	0.47
C18:2 <i>cis</i> -9, <i>cis</i> -12	20	1.50	12	1.13	3	0.78	66	0.63

study were lower than those mentioned by Druet et al. (2005). The average heritabilities obtained by those authors for the first 3 lactations were 33, 37, and 47% for MILK, %PROT, and %FAT, respectively. This difference could partially be explained by the type of model (random regression) and the eigenvalue approach used by Druet et al. (2005).

The content of SAT in milk was more heritable than MONO. The heritability of SAT was close to the value observed for %FAT. This result could be explained by the part-whole relationship among the various measures, because SAT was a major constituent of milk fat (Table 2). The heritability difference between SAT and MONO observed in this study is in line with estimates of animal-specific relative variances obtained earlier by Soyeurt et al. (2006a).

The greatest heritability was observed for the FA having the greatest content in milk (C16:0; Tables 2 and 3). The heritability for C18:1 was very low. One possible reason for this result could be that the simple model used is suboptimal for this trait, because it explained <25% of the variation of C18:1 in total (Table 3). Although the heritability for POLY was not studied due to the precision of the calibration equation, the principal FA of this class, C18:2 *cis*-9, *cis*-12, had a moderate estimated heritability (Table 3).

No relationship between the length of the carbon chain and heritability was observed in milk (Table 3). This result was in opposition to Renner and Kosmack (1974a), who reported a decreasing value of heritability as a function of FA length. Heritabilities estimated in this study [29, 31, and 38%, respectively, for C12:0, C14:0, and C16:0 (Table 3)] were moderate, as were the values found by Renner and Kosmack (1974a) for the FA with medium length chains (26%). The heritability estimated by Renner and Kosmack (1974a) for the C18

family was 2%. Although the complete family of C18 was not evaluated in this analysis, the values estimated for C18:2 *cis*-9, *cis*-12 and C18:1 were clearly greater (Table 3) than those for other FA.

Relative Environmental Variances of FA in Milk

For all traits, relative permanent environmental variance across lactations was smaller than relative permanent environmental variance within lactation (Table 3). The lowest within-lactation variance was observed for %FAT and the highest for MILK. Monounsaturated fatty acids seemed to be more variable within lactation than the content of SAT in milk, which showed the same trend as %FAT. Clear separation of both types of permanent environmental estimates would have required a larger number of repeated records within and across lactations than were available for FA in this study. The results should therefore be considered preliminary.

The estimates for the residual effects mentioned in Table 3 were important, in particular for MONO and for C18:1. This observation could be an indication that the model used missed some important source of variation in MONO content in milk.

Heritability of FA in Milk Fat

Estimates and SE of relative variances for each random effect for SAT, MONO, and the major FA in milk fat (g/100 g of fat) are given in Table 4. Heritability estimated for SAT in fat (Table 4) was smaller than that observed for the same component in milk (g/100 g of MILK; Table 3). This observation can be generalized for all studied saturated FA. The results obtained by Renner and Kosmack (1974a) showed the same trend.

Table 4. Average estimate and average standard error of variances (% of phenotypic variance) for each studied effect (genetic, 2 permanent environments, residual) with multitrait mixed models including in particular the saturated, monounsaturated, C12:0, C14:0, C16:0, C18:0, C18:1, and C18:2 *cis*-9, *cis*-12 fatty acid contents in milk fat (g/100 g of fat)

Trait	Genetic		Permanent environment effects				Residual	
			Within lactation		Across lactations			
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Saturated	14	1.46	27	1.50	3	0.68	55	0.43
Monounsaturated	24	2.27	25	1.70	8	1.62	43	0.37
C12:0	9	1.17	24	1.18	5	0.97	61	0.42
C14:0	19	1.75	20	1.32	7	1.64	52	0.36
C16:0	20	2.20	8	0.94	12	1.85	60	0.47
C18:0	28	2.35	14	1.40	9	2.01	50	0.57
C18:1	15	1.57	28	1.55	4	1.00	53	0.30
C18:2 <i>cis</i> -9, <i>cis</i> -12	15	1.79	15	1.56	6	1.43	64	0.82

However, the heritabilities for MONO and for C18:1 in fat were greater than that in milk (Table 3 and 4).

Relative Environmental Variances of FA in Milk Fat. Contents of SAT and MONO in fat were highly variable within lactation (Table 4). This could be linked to seasonal effects. Saturated fatty acids in fat are lowest during the grazing period. Lock and Garnsworthy (2003) suggested that a molecule contained in the grass could activate the enzymatic activity (especially Δ^9 -desaturase activity).

The residual variances in Table 4 were smaller than those shown in Table 3. This observation is an indirect indication that the model used in this study seems to be more appropriate to analyze the proportion of FA in milk fat than in milk.

Genetic Correlations Among MILK, %FAT, %PROT, and Different FA in Milk

Table 5 shows genetic and phenotypic correlations for SAT and MONO in milk and for traditional production traits (MILK, %FAT, and %PROT). The genetic correlations between MILK and %PROT or %FAT were nega-

tive and moderate, -0.35 and -0.48 , respectively. The genetic correlation between %FAT and %PROT was positive and tended to be greater in absolute value (0.63). These results are in agreement with Roman and Wilcox (2000), who estimated that the genetic correlation expressed on a lactation basis between MILK and %FAT was -0.21 and between MILK and %PROT was -0.56 . These same authors also found that the genetic correlation between %FAT and %PROT was 0.63 . The observed genetic correlations for these traditional production traits were also similar to those estimated by others (Othmane et al., 2004). Given these results, we think that this simplified model is still adapted for traditional traits; however, more research is needed to establish an optimal model for FA.

The genetic correlations between MILK and FA (Table 5) were all negative. This result is probably due to the effect of dilution. When the production of MILK increased, %FAT and FA contents seemed to decrease. Other scientists (Lock and Garnsworthy, 2003) have already observed this effect between MILK and %FAT.

As expected, the genetic correlations between SAT and all of the studied saturated FA and %FAT were

Table 5. Genetic (above the diagonal) and phenotypic correlations (below the diagonal) among each studied trait [milk yield, content of fat, content of protein, saturated (SAT), monounsaturated (MONO), C12:0, C14:0, C16:0, C18:0, C18:1, and C18:2 *cis*-9, *cis*-12 fatty acid contents in milk]

Trait	Milk	Fat	Protein	SAT	MONO	C12:0	C14:0	C16:0	C18:0	C18:1	C18:2
Milk (kg/d)		-0.35	-0.48	-0.26	-0.21	-0.36	-0.29	-0.25	-0.28	-0.39	-0.28
Fat (%)	-0.18		0.63	0.97	0.74	0.91	0.80	0.95	0.97	0.75	0.75
Protein (%)	-0.32	0.39		0.62	0.44	0.73	0.60	0.55	0.60	0.45	0.62
SAT (g/100 g of milk)	-0.13	0.90	0.40		0.66	0.91	0.83	0.94	0.94	0.60	0.67
MONO (g/100 g of milk)	-0.17	0.72	0.15	0.49		0.44	0.21	0.61	0.63	0.86	0.81
C12:0 (g/100 g of milk)	-0.11	0.61	0.52	0.81	0.02		0.94	0.89	0.93	0.53	0.61
C14:0 (g/100 g of milk)	-0.07	0.67	0.39	0.83	0.07	0.93		0.83	0.85	0.34	0.38
C16:0 (g/100 g of milk)	-0.16	0.88	0.34	0.91	0.60	0.67	0.72		0.97	0.67	0.72
C18:0 (g/100 g of milk)	-0.13	0.94	0.34	0.91	0.67	0.67	0.74	0.92		0.73	0.75
C18:1 (g/100 g of milk)	-0.15	0.66	0.08	0.38	0.93	-0.02	0.10	0.51	0.64		0.84
C18:2 (g/100 g of milk)	-0.22	0.66	0.46	0.48	0.80	0.21	0.18	0.57	0.67	0.77	

Table 6. Genetic (above the diagonal) and phenotypic correlations (below the diagonal) among each studied trait [milk yield, content of fat, content of protein, saturated (SAT), monounsaturated (MONO), C12:0, C14:0, C16:0, C18:0, C18:1, and C18:2 *cis*-9, *cis*-12 fatty acid contents in milk fat]

Trait	Milk	Fat	Protein	SAT	MONO	C12:0	C14:0	C16:0	C18:0	C18:1	C18:2
Milk (kg/d)		-0.35	-0.48	-0.09	0.22	-0.34	-0.22	0.01	-0.15	0.11	-0.01
Fat (%)	-0.18		0.63	0.76	-0.22	0.55	-0.06	0.60	0.84	-0.78	-0.37
Protein (%)	-0.32	0.38		0.51	-0.34	0.77	0.15	0.20	0.52	-0.59	-0.02
SAT (g/100 g of fat)	0.04	0.13	0.21		-0.44	0.67	0.37	0.55	0.66	-0.90	-0.66
MONO (g/100 g of fat)	-0.06	0.03	-0.18	-0.73		-0.70	-0.84	-0.34	-0.44	0.67	0.67
C12:0 (g/100 g of fat)	0.00	-0.03	0.37	0.75	-0.84		0.60	0.20	0.52	-0.78	-0.54
C14:0 (g/100 g of fat)	0.09	-0.19	0.11	0.65	-0.90	0.84		0.00	0.10	-0.46	-0.68
C16:0 (g/100 g of fat)	-0.03	0.10	0.05	0.44	-0.23	0.16	0.12		0.61	-0.62	-0.28
C18:0 (g/100 g of fat)	0.00	0.65	0.23	0.30	-0.24	0.11	0.01	0.29		-0.78	-0.38
C18:1 (g/100 g of fat)	-0.03	-0.13	-0.27	-0.93	0.83	-0.85	-0.73	-0.47	-0.33		0.70
C18:2 (g/100 g of fat)	-0.10	-0.23	0.21	-0.50	0.53	-0.34	-0.50	-0.23	-0.32	0.53	

greater than those estimated with MONO or all of the studied unsaturated fatty acids (Table 5). In the same way, the genetic correlations estimated between MONO and unsaturated FA were greater than those that involved saturated FA (Table 5).

The genetic correlations reflect the physiological processes involved in the production of FA in milk. Consequently, the values of genetic correlations can be interpreted biologically. Bobe et al. (1999) have already analyzed the corrected correlations existing among the FA contents. Three groups can be isolated from Table 5. The first group contains C12:0, C14:0, C16:0, and C18:0. The high genetic correlations observed among these FA could be explained by similarities in their origin. These FA are synthesized *de novo* in the mammary gland and are regulated by only 2 enzymes, acetyl-coenzyme A carboxylase and fatty acid synthase (Chilliard et al., 2001). The second group is composed of C18:1, C18:2 *cis*-9, *cis*-12, C16:0, and C18:0. These FA are extracted from the blood. The presence of C16:0 and C18:0 in 2 groups can be explained by their double origin. These FA are partially extracted from the blood and partially synthesized *de novo* by the mammary gland (Chilliard et al., 2001). Finally, the third group contains only C18:1 and C18:2 *cis*-9, *cis*-12. These FA are extracted from the blood, and the biohydrogenation acts little on them (Bobe et al., 1999).

Genetic Correlations Among MILK, %FAT, %PROT, and Different FA in Milk Fat

Table 6 has the genetic and phenotypic correlations estimated for each studied traits in milk fat. Results among MILK, %FAT, and %PROT were slightly different from those reported in Table 5, because they came from different analyses, and a bending procedure was applied.

Table 6 shows low to moderate negative or positive genetic correlations between MILK and the different

FA in fat. In general, SAT and saturated FA tended to be negatively correlated with MILK and MONO, and C18:1 was positively correlated. Given these results, genetic selection for MILK would be expected to increase the content of MONO in fat. For C18:2, the correlation was close to zero. The genetic correlation estimated between SAT and %FAT is also given in Table 6. Greater %FAT was genetically linked to lower MONO, higher SAT, and lower C18:2 and C18:1. Genetic selection for greater %FAT content would increase nearly all SAT and decrease MONO and C18:2. However, all saturated FA did not seem to show the same response to the increase of fat. The genetic correlation between C18:0 and %FAT was high (0.84), and the genetic correlation between C12:0 and %FAT was lower (0.55). These observations could be explained by the variation of Δ^9 desaturase activity in cows observed by Lock and Garnsworthy (2003) and Soyeurt et al. (2006a). In the same way, the results involving the content of myristic acid (C14:0) in milk fat are interesting, because Table 6 shows a genetic correlation between C14:0 and %FAT that is close to 0 and also a low phenotypic correlation (-0.19). Also, C14:0 is highly negatively correlated with MONO (-0.84). Given its negative effects on human health (Hu et al., 1999), genetic selection to increase MONO should have a beneficial effect of reducing the C14:0 content in fat. In the same way, the greatest genetic correlations with %FAT were observed for C16:0 (0.60) and C18:0 (0.84) compared with the 0.37 estimated for C14:0. Hu et al. (1999) found that C16:0 and C18:0 are known for their low to nonexistent effects on human health; therefore, the increase of %FAT in bovine milk does not seem to involve an undesirable milk fat composition for human health.

The negative genetic correlation between SAT and MONO shows the logical opposition of these 2 types of FA (Table 6). If the content of SAT in fat increases, the content of POLY or MONO will obviously decrease.

As mentioned, the genetic correlations reflect the origin of FA. As in Table 5, the results indicated in Table 6 show the links which could exist between C12:0 and C14:0, C18:1 and C18:0, or C18:2 *cis*-9, *cis*-12. The genetic correlations between C16:0 or C18:0 with C12:0, C14:0, C18:1, or C18:2 *cis*-9, *cis*-12 were lower than those in Table 5. This latter result did not confirm the previous observation regarding the two possibilities of production for C16:0 and C18:0.

CONCLUSIONS

The interest of consumers for the nutritional quality of dairy products is increasing. It is thus interesting to study the genetic variation of FA composition to evaluate the feasibility of selecting animals to alter the relative proportions of FA and improve the nutritional quality of the milk fat. The current study shows that the genetic variation in FA exists. The heritabilities for the major FA in milk ranged from 19 to 38% in milk with the exception of C18:1 (5.39%). Similarly, the heritabilities of FA in milk fat ranged from 15 to 28% with the exception of C12:0 (9.11%).

The genetic correlations estimated among each FA reflected the common origin of several groups of FA. Given these results, information about each distinct FA is not necessary. An index could be created to include the groups of FA with similar metabolic origins in the mammary gland. For example, it could be interesting to use an index including the FA for which the Δ^9 desaturase is needed (e.g., C14:1, C16:1, C18:1). Based on such an index, selection could be used in the future to increase MONO and conjugated FA in bovine milk.

The nearly zero genetic correlation between %FAT and the percentage of C14:0 and the greater genetic correlations between %FAT and the contents of C12:0, C16:0, and C18:0 in fat showed that the increase of %FAT is not directly associated with undesirable milk fat composition for human health.

In conclusion, genetic variability seems to exist in milk FA content. Based on the obtained estimates of genetic parameters, selection programs could be implemented in the future to improve the nutritional quality of fat in bovine milk by altering relative amounts of the various FA.

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