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Genetic Parameters of Saturated and Monounsaturated Fatty Acid Content and the Ratio of Saturated to Unsaturated Fatty Acids in Bovine Milk

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ABSTRACT

Fatty acid composition influences the nutritional quality of milk and the technological properties of butter. Using a prediction of fatty acid (FA) contents by mid-infrared (MIR) spectrometry, a large amount of data concerning the FA profile in bovine milk was collected. The large number of records permitted consideration of more complex models than those used in previous studies. The aim of the current study was to estimate the effects of season and stage of lactation as well as genetic parameters of saturated (SAT) and monounsaturated (MONO) fatty acid contents in bovine milk and milk fat, and the ratio of SAT to unsaturated fatty acids (UNSAT) that reflect the hardness of butter (SAT:UNSAT), using 7 multiple-trait, random-regression test-day models. The relationship between these FA traits with common production traits was also studied. The data set contained 100,841 test-day records of 11,626 Holstein primiparous cows. The seasonal effect was studied based on unadjusted means. These results confirmed that milk fat produced during spring and summer had greater UNSAT content compared with winter (63.13 vs. 68.94% of SAT in fat, on average). The effect of stage of lactation on FA profile was studied using the same methodology. Holstein cows in early first lactation produced a lower content of SAT in their milk fat. Variance components were estimated using a Bayesian method via Gibbs sampling. Heritability of SAT in milk (0.42) was greater than heritability of SAT in milk fat (0.24). Estimates of heritability for MONO were also different in milk and fat (0.14 vs. 0.27). Heritability of SAT:UNSAT was moderate (0.27). For all of these traits, the heritability estimates and the genetic and phenotypic correlations varied through the lactation.
Key words: genetic parameter, milk, fatty acid, fat, mid-infrared

INTRODUCTION

The World Health Organization points out that unhealthy nutrition contributes to some chronic diseases such as diabetes, cardiovascular diseases, and cancer (World Health Organization, 2006). One of the 5 proposals formulated by this organization is to decrease the energy intake and endorse a diet with a greater proportion of unsaturated fatty acids (**UNSAT**) for humans. This statement is related to the results obtained by several studies that mention the hypercholesterolemic effect of saturated fatty acids (**SAT**), especially C12:0, C14:0, and C16:0 (e.g., Hu et al., 1999; Fernandez and West, 2005). In comparison with SAT, the intake of UNSAT seems to decrease the level of cholesterol in blood (Ulbricht and Southgate, 1991; Noakes et al., 1996; Hu et al., 2001; Fernandez and West, 2005) and thus, reduces the risk of cardiovascular diseases.

Besides these effects on human health, increasing the proportion of UNSAT in bovine milk fat has a positive impact on the technological properties of butter. Butter spreadability is improved by increasing the contents of UNSAT and short-chain fatty acids (**FA**) in milk fat (Bobe et al., 2007). In accordance with Bobe et al. (2003), the textural properties of butterfat could be modified by using the phenotypic variation of fatty acid composition observed by those authors from cows fed the same diet. This variation could be partly genetic. Initial results obtained by Soyeurt et al. (2007b) confirmed this hypothesis.

A few researchers such as Renner and Kosmack (1974), Karijord et al. (1982), Soyeurt et al. (2006, 2007, and 2008), and Stoop et al. (2008) have studied the individual variability of FA. The results obtained by those authors suggested the presence of significant genetic variability of the FA profile in bovine milk and fat. Generally, the contents of individual SAT were more heritable than individual UNSAT. This genetic variability of FA should be sufficient to implement a selection program based on the improvement of FA composition. The previous studies had some limitations. Renner and Kosmack (1974) as well as Karijord et al.

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Table 1. Descriptive statistics calculated for the 2 calibration equations used in this study and established from 114 milk samples[1]

Fatty acid (g/dL of milk)	Mean	SD	SEC	R^2c	SECV	R^2cv	RPD
Saturated	3.20	0.85	0.09	0.99	0.15	0.97	5.78
Monounsaturated	1.40	0.43	0.08	0.97	0.12	0.93	3.65

[1]SEC = standard error of calibration; R^2c = calibration coefficient of determination; SECV = standard error of cross-validation; R^2cv = cross-validation coefficient of determination; RPD = the ratio of SD to SECV.

(1982) and Stoop et al. (2008) analyzed a limited number of samples without repeated measures on the same animals. This was true even for the study of Karijord et al. (1982) in which 7,000 milk samples were analyzed. Limiting the number of samples was likely due to the expensive cost of gas chromatographic analysis needed to measure the FA contents in milk fat. Renner and Kosmack (1974) and Karijord et al. (1982) estimated the genetic parameters of FA contents in bovine milk fat using a sire model. Stoop et al. (2008) used a single-trait animal model. With the development of calibration equations to predict FA contents in bovine milk by mid-infrared (**MIR**) spectrometry (Soyeurt et al., 2006b), Soyeurt et al. (2007) estimated the genetic parameters of FA using a multiple-trait (**MT**) test-day (**TD**) animal model on a larger number of samples including repeated measurements of FA composition. The use of an MT-TD model presents major advantages: 1) more efficient use of collected data, 2) a genetic model that better accounts for the biology of dairy cows, 3) better accounting for short-term environmental effects at each test-day milk recording, and 4) more accurate estimation of cow indices (Schaeffer et al., 2000; Mayeres et al., 2004; Muir et al., 2007). Parametric curves, such as the Ali-Schaeffer curve (Ali and Schaeffer, 1987), the Wilmink curve (Wilmink, 1987), or orthogonal polynomials have been used to model the random regressions (Druet et al., 2003). The disadvantage of TD models is their computation time, cost, or both (Druet et al., 2003). The amount of FA content data is generally small. Thus, the computational cost for a TD model using a limited database remains acceptable. The TD model used by Soyeurt et al. (2007, 2008) did not include random regressions (**RR**) to model the shape of lactation curve, assuming that the genetic parameters of FA were constant throughout the lactation. Karijord et al. (1982) and Soyeurt et al. (2008) showed a phenotypic variation of FA contents within lactation. In accordance with Karijord et al. (1982), the contents of each individual SAT increased until the fourth month of lactation and then decreased slowly; the opposite trend was observed for UNSAT. Soyeurt et al. (2008) found that the lowest content of monounsaturated FA (**MONO**) in fat was reached around 100 DIM. Soyeurt et al. (2007b) showed that the ratio of SAT to UNSAT (SAT:UNSAT), approximating the hardness of butter, also varied throughout the lactation. The values of SAT:UNSAT increased rapidly until 100 DIM, when the ratio was near 2; then, the ratio decreased slowly to 1.5 at 365 DIM. All FA traits seem to be influenced by stage of lactation.

The aims of this study were to 1) examine the effects of season and stage of lactation on the contents of SAT and MONO, and SAT:UNSAT, 2) estimate their genetic parameters, and 3) study the relationship of these FA traits with production traits [milk yield, percentage of fat (**%FAT**), and protein content (**%PROT**)].

MATERIALS AND METHODS

Animal Population and Milk Samples

Following the standard procedures of the International Committee for Animal Recording (2007), 27,959 composite milk samples consisting of approximately 50% from morning milking and 50% from evening

Table 2. Descriptive statistics of saturated and monounsaturated fatty acid contents in milk fat (g/100 g of fat) observed from the chromatographic and spectral analysis of 14 milk samples collected randomly from the 1,060 samples collected previously

Fatty acid, g/100 g of fat	Mean	SD	Minimum	Maximum
Chromatographic analysis				
Saturated fatty acids	67.98	4.69	61.69	77.89
Monounsaturated fatty acids	27.33	4.26	19.14	33.03
Mid-infrared spectrometry				
Saturated fatty acids	67.81	5.27	58.67	77.44
Monounsaturated fatty acids	27.44	5.10	19.54	38.44

Table 3. Mean, SD, skewness, and kurtosis for milk yield, the percentages of fat and protein (100,799 test-day records), the contents of saturated and monounsaturated fatty acids in milk and milk fat, and the ratio of saturated to unsaturated fatty acids approximating the hardness of butter (4,666 test-day records).

Item	Mean	SD	Skewness	Kurtosis
Milk (kg/d)	22.54	6.13	0.17	0.08
Fat (g/100 g of milk)	4.05	0.68	0.59	1.70
Protein (g/100 g of milk)	3.32	0.34	0.64	2.16
Saturated (g/100 g of milk)	2.63	0.54	0.57	1.89
Monounsaturated (g/100 g of milk)	1.08	0.26	1.85	7.46
Saturated (g/100 g of fat)	66.26	6.15	−0.60	0.31
Monounsaturated (g/100 g of fat)	27.55	4.80	0.65	0.47
Saturated:unsaturated	2.06	0.55	0.39	0.26

milking were collected from April 2005 through July 2007 from 96 herds during the Walloon milk recording. Herds were selected based on completeness of pedigrees of cows, number of dairy breeds on the farm, and geographical location. Eight herds were followed from April 2005, 18 herds were included after November 2005, and the remaining herds were included after January 2007. Because of technical issues, the number of TD was not constant for all herds. Also, some cows were dried off or calved during this experiment. Percentage of fat and %PROT were measured using a Foss MilkoScan FT6000 spectrometer (Foss, Hillerød, Denmark). The spectra generated during this infrared analysis were recorded for all analyzed milk samples. For this study, only cows with greater than 84% Holstein breed composition were studied and represented 1,167 cows. To increase the number of contemporaries, milk yield, %FAT, and %PROT known for all studied primiparous cows and herds were added. Test-day records with DIM <5 and >365 were deleted. The final edited data file contained 100,799 TD records of 11,626 first-parity Holstein cows (Holstein genes >84%) recorded from 1991 to 2007. Pedigree contained 18,573 animals including 1,895 sires.

Predicted Contents of FA in Milk and Milk Fat

Soyeurt et al. (2006b) developed 42 calibration equations to predict the FA composition in bovine milk by MIR spectrometry. New calibration equations were built from FA concentrations of 114 samples measured using a gas chromatograph (model 6890N; Agilent Technologies Inc., Palo Alto, CA) and a CPSIL-88 capillary column (length: 100 m; internal diameter: 0.25 mm; film thickness: 0.20 μm; Varian Inc., Palo Alto, CA).

A total of 78 samples were selected using principal components analysis (**PCA**) (Palm, 1998) from the 1,609 frozen milk samples collected between March 2005 and May 2006 from 475 cows representing 6 dairy breeds: dual-purpose Belgian Blue, Holstein Friesian, Jersey, Normande, Montbeliarde, and non-Holstein Meuse-Rhine-Yssel–type Red and White. To increase the spectral variability of calibration set, 36 milk samples were also chosen based on the results of successive PCA conducted during the routine Walloon milk spectral analysis.

The methodology used to measure the FA contents was the one described previously by Soyeurt et al. (2008). The milk fat of these selected samples was extracted according to ISO Standard 14156:2001 (International Organization for Standardization, 2001). Preparation of FA methyl esters was made following the ISO 15884:2002 standard (International Organization for Standardization, 2002). These milk fat samples were analyzed using gas chromatography as described above. The conditions for the chromatographic analyses were as follows: carrier gas, helium; average velocity, 19 cm/s; cold on-column injector; flame-ionization detector at 255°C; and a temperature program from 60°C (5 min) to 165°C (at 14°C/min) for 1 min, and then 165 to 225°C (at 2°C/min) for 17 min. The volume injected was 0.5 μL. The FA concentrations were measured according to the method developed by Collomb and Bühler (2000). An anhydrous milk fat with a certified FA composition (reference material BCR-164, obtained from the Commission of the European Communities, Brussels, Belgium) was used to determine the FA methyl esters response factors, the repeatability, and the accuracy of this method.

The methodology used to develop the calibration equations was identical to that mentioned previously by Soyeurt et al. (2006b, 2008). More details about the calibration procedure are available in Williams (2007). The calibration equations were built from chromatographic and spectral data using a specific program for multivariate calibration (WINISI III; http://www.winisi.com/) and partial least squares regressions. No treatment was applied beforehand on the spectral data. Because overfitting can occur through the use of partial least squares regressions technique, cross-validation of the developed calibration equations was used to pre-

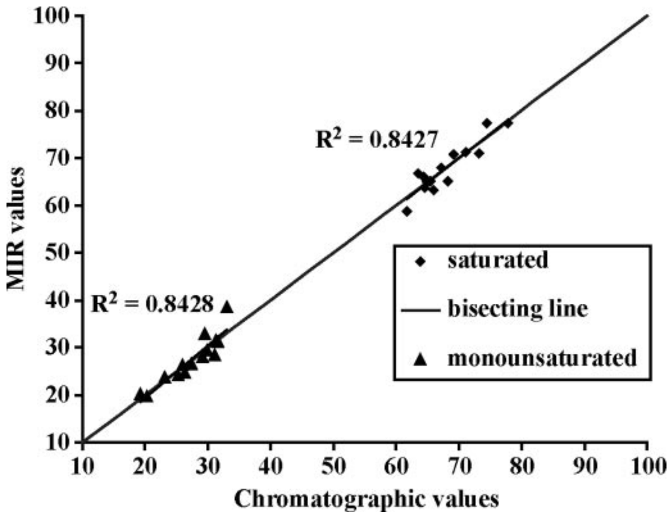

Figure 1. Relationship between the contents of saturated and monounsaturated fatty acids measured by gas chromatography and predicted by mid-infrared (MIR) spectrometry from 14 milk samples.

vent this. Cross-validation was applied to validate the number of factors used in the different equations and to estimate the validation errors of the obtained equations. These errors were calculated by partitioning the calibration set into several groups. In this study, a full cross-validation was used. Thus, a calibration was performed for each sample, until every sample had been predicted once. Validation errors were combined into a standard error of cross-validation (**SECV**). To assess the robustness of the developed calibration equations, several statistical parameters were calculated: mean and SD measured from reference concentrations of FA, standard error of calibration (**SEC**), calibration coefficient of determination (**R^2_C**), SECV, cross-validation coefficient of determination (**R^2_{CV}**), and the ratio of SD to SECV (**RPD**). The calibration equations predicting the contents of SAT and MONO in milk (g/dL of milk) were applied to the recorded spectra. Using the density of milk, these FA contents were converted into grams per 100 g of milk. Using the %FAT measured by the Foss MilkoScan FT6000 (Foss), these FA contents were converted into grams per 100 g of fat. The hardness of butter was defined as SAT:UNSAT in fat. The content of UNSAT was estimated by: 100 – the percentage of SAT in fat.

The ability of established calibration equations to predict the contents of SAT and MONO in bovine milk was also assessed by analyzing 14 independent samples. An additional larger validation is planned in a parallel study. These samples were taken randomly in the 1,609 frozen milk samples collected previously.

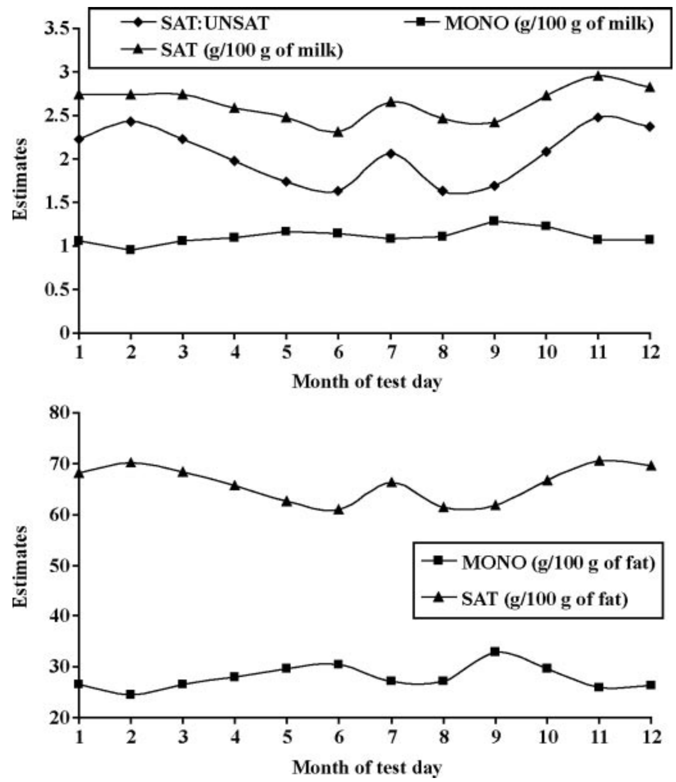

Figure 2. Effect of season on the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk (g/100 g of milk) and milk fat (g/100g of fat) and the ratio of saturated to unsaturated fatty acids (SAT:UNSAT). The SD ranged between 0.21 and 0.59 for SAT and MONO in bovine milk, and the ratio of saturated to unsaturated fatty acids. The SD ranged from 3.72 to 5.70 for SAT and MONO in milk fat.

Statistical Model

Variance components were estimated by Bayesian method with Gibbs sampling (Misztal, 2007) using 7 MT-TD-RR models:

$$\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Q}(\mathbf{WI} + \mathbf{Zp} + \mathbf{Zu}) + \mathbf{e},$$

where **Y** was the vector of observations (milk yield, %FAT, %PROT, and SAT in milk and fat; milk yield, %FAT, %PROT, and MONO in milk and fat; milk yield, %FAT, %PROT, and SAT:UNSAT; SAT:UNSAT, SAT, and MONO in milk and fat); $\boldsymbol{\beta}$ was the vector of fixed effects [herd × test day, stage of lactation (24 classes of 15 DIM), age (3 classes: <29 mo, 29–32 mo, >32 mo)]; **Q** as the covariate matrix of second-order Legendre polynomials; **I** was the vector of random herd × date of calving effects; **p** was the vector of random permanent environmental effects; **u** was the vector of animal effects; **X**, **W**, and **Z** were incidence matrices; and **e** corresponded to the vector of random residual effects.

Table 4. Variance estimates and posterior standard deviation (in parentheses) of random effects for each trait[1]

	Genetic			Herd			Permanent			
Trait	i_0	i_1	i_2	i_0	i_1	i_2	i_0	i_1	i_2	Residual
Milk (kg^2/d^2)	3.15	1.23	0.49	0.42	0.69	0.30	6.19	0.67	0.42	4.20
	(0.11)	(0.06)	(0.02)	(0.06)	(0.07)	(0.03)	(0.16)	(0.07)	(0.04)	(0.02)
%Fat [g^2/(10 g of milk)^2]	11.22	11.38	0.77	0.37	0.45	0.72	4.29	1.57	0.96	13.52
	(0.38)	(0.08)	(0.03)	(0.05)	(0.08)	(0.07)	(0.26)	(0.12)	(0.06)	(0.08)
%Protein [g^2/(10 g of milk)^2]	2.54	0.44	0.24	0.33	0.20	0.23	0.64	0.37	0.22	19.36
	(0.07)	(0.03)	(0.02)	(0.04)	(0.02)	(0.02)	(0.04)	(0.03)	(0.02)	(0.01)
SAT [g^2/(10 g of milk)^2]	7.51	1.19	0.50	0.34	0.02	0.69	2.74	1.55	0.87	6.42
	(0.20)	(0.12)	(0.07)	(0.09)	(0.00)	(0.09)	(0.13)	(0.15)	(0.11)	(0.16)
MONO [g^2/(10 g of milk)^2]	0.33	0.04	0.21	0.33	0.74	0.16	0.45	0.50	0.41	2.06
	(0.02)	(0.00)	(0.02)	(0.00)	(0.00)	(0.03)	(0.03)	(0.04)	(0.06)	(0.05)
SAT [g^2/(100 g of fat)^2]	1.03	1.85	1.05	0.98	0.26	0.33	1.45	0.44	0.85	8.32
	(0.05)	(0.15)	(0.14)	(0.16)	(0.04)	(0.02)	(0.24)	(0.07)	(0.13)	(0.22)
MONO [g^2/(100 g of fat)^2]	1.15	0.83	1.18	0.51	0.47	0.12	0.9	0.68	0.67	0.54
	(0.04)	(0.06)	(0.06)	(0.12)	(0.03)	(0.04)	(0.10)	(0.14)	(0.06)	(0.15)
SAT:UNSAT ($\times 10^2$)	2.20	1.70	1.25	0.62	0.42	0.23	1.75	0.25	0.68	9.89
	(0.06)	(0.11)	(0.12)	(0.13)	(0.07)	(0.05)	(0.17)	(0.04)	(0.26)	(0.28)

[1]SAT = saturated fatty acids; MONO = monounsaturated fatty acids; SAT:UNSAT = the ratio of saturated to unsaturated fatty acids; Herd = herd × date of calving random effect. Values of estimates and posterior SD for milk yield and percentages of fat and protein were the average values calculated from the 5 runs, $i_0 = 1$; $i_1 = \sqrt{3} \cdot x$; $i_2 = \sqrt{\frac{5}{4}} \cdot (3x^2 - 1)$, where $x = -1 + 2 \cdot \left(\frac{DIM - 1}{365 - 1}\right)$.

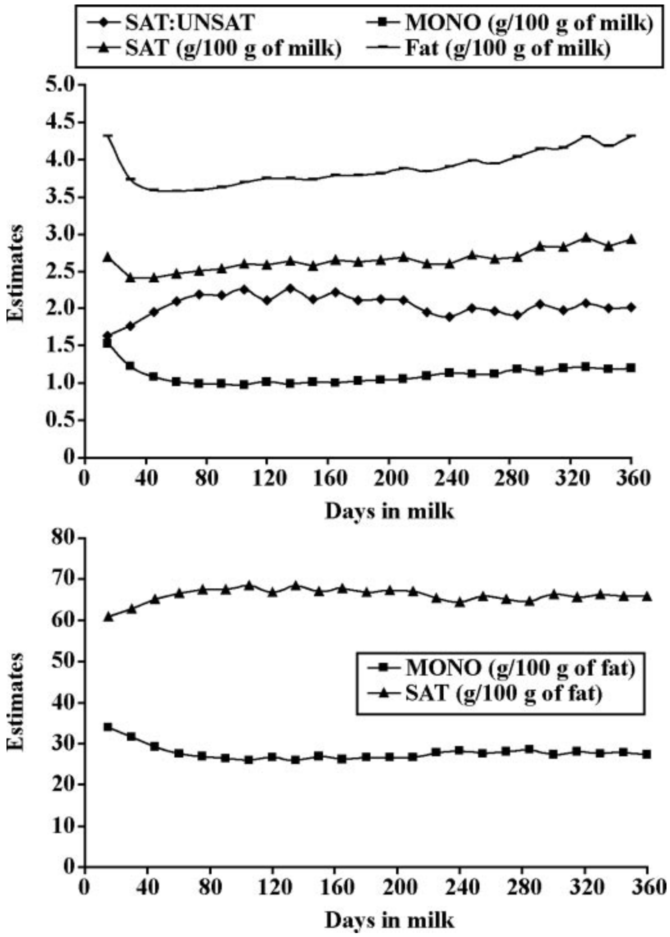

Figure 3. Effect of days in milk on the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk (g/100 g of milk) and milk fat (g/100 g of fat), and the ratio of saturated to unsaturated fatty acids (SAT:UNSAT). The SD ranged between 0.17 and 0.66 for SAT and MONO in bovine milk, and the ratio of saturated to unsaturated fatty acids. The SD ranged from 3.81 to 6.56 for SAT and MONO in milk fat.

Coefficients of Legendre polynomials were calculated as:

$$i_0 = 1,$$

$$i_1 = \sqrt{3} \cdot x,$$

$$i_2 = \sqrt{\frac{5}{4}} \cdot (3x^2 - 1),$$

where $x = -1 + 2 \cdot \left(\frac{DIM - 1}{365 - 1}\right)$.

Priors of variance components were estimated using expectation maximization REML (Misztal, 2007) using 12 MT-TD models (4 each for milk yield and SAT or MONO in milk and fat; %FAT and SAT or MONO in milk and fat, %PROT and SAT or MONO in milk and fat). The fixed and random effects included in these models were the same as those mentioned previously. Priors of variance components for SAT:UNSAT were those obtained previously by Soyeurt et al. (2007b). Residual variances were assumed to be independent. Posterior means of (co)variance components were calculated using 90,000 samples after a burn-in of 10,000 samples.

Average daily heritability values were defined as a ratio of average genetic variance to the average sum of genetic, herd × date of calving, permanent environment, and residual variances for each DIM from 1 to 365. The same method was used to calculate the estimates of herd × date of calving random effect, permanent environment, and residual effect expressed in percentage of phenotypic variances. These values showed in the current study for milk yield, %FAT, and %PROT were the average of values obtained from the 5 MT-TD-RR models including these traits. Daily phenotypic and genetic correlations between trait a and trait b at DIM i were calculated as:

$$r_{a_i,b_i} = \frac{t\Sigma_{a,b}t'}{\sqrt{\left(t_i\Sigma_a t_i'\right) \cdot \left(t_i\Sigma_b t_i'\right)}},$$

where t was the vector created by summing coefficients of Legendre polynomials for DIM 1 to 365; $\mathbf{\Sigma_{a,b}}$ was the matrix including the genetic or phenotypic covariances between trait a and trait b; and $\mathbf{\Sigma}_a$ and $\mathbf{\Sigma}_b$ were the genetic or phenotypic variance matrices for traits a and b, respectively. Heritability values for milk yield, %FAT, and %PROT and correlations among these traits shown in the current study were the average of values obtained from the 5 MT-TD-RR models including these traits.

To test the fit of the proposed model, the residuals were estimated by difference between the observed and estimated values for all studied traits and for each test-day observed from all studied cows. The estimated values were obtained using the solutions provided by the BLUPf90 program (Misztal, 2007).

RESULTS AND DISCUSSION

Calibration Equations

Table 1 gives the results obtained during the calibration procedure for the mean, SD, SEC, R^2c, SECV,

R^2cv, and RPD. The values of RPD were 5.78 and 3.75 for SAT and MONO, respectively. If RPD is ≥2, the infrared predicted value is considered to be a good indicator of the studied trait (Sinnaeve et al., 1994). In the same way, the estimates of R^2cv were 0.97 for SAT and 0.93 for MONO. If R^2cv ranged between 92 and 96%, Williams (2007) noted that the predicted values could be used in most applications, including quality assurance.

To confirm the ability of established calibration equations to predict the contents of SAT and MONO in bovine milk, a validation with 14 independent milk samples chosen randomly was conducted. Table 2 presents descriptive statistics obtained from chromatographic and spectral analysis of these 14 selected samples. The variation of FA composition for these samples was relatively large. The concentrations of SAT and MONO in milk fat ranged from 61.69 to 77.89% and from 19.14 to 33.03%, respectively (Table 2). Based on the values shown in Table 2, bias corresponding to the mean difference between MIR and chromatographic data were calculated and were 0.17% for SAT and −0.11% for MONO. Because of the low estimates of bias, the predicted values of SAT and MONO in milk obtained from the developed calibration equations can be considered as good indicator of these FA. Figure 1 illustrates the reference contents of SAT and MONO measured by gas chromatography on the x-axis and the infrared-predicted values for these same FA on the y-axis. This figure confirms the linear relationship between these 2 methods. The validation coefficients of determination (**R^2v**) were 84.27% (R = 91.80%) and 84.28% (R = 91.80%) for SAT and MONO, respectively. The values of R^2v were inferior to those estimated from the cross-validation. In accordance with Williams (2007), these values of R^2v are sufficient to be considered in some research applications. By using successive PCA during the Walloon milk recording, our group is continuing to select new samples to increase the robustness of the developed calibration equations.

Seasonal Effect

The variation for the contents of SAT (66.26%, SD = 6.15) and MONO (27.55%, SD = 4.80) was large (Table 3). Based on SAT:UNSAT, the milk fat contained twice as much SAT as UNSAT (2.06, SD = 0.55). Stoop et al. (2008) calculated a mean value for SAT:UNSAT of 2.80 from 1,918 samples. Those researchers mentioned that this value was overestimated because the UNSAT content (denominator) included only the major UNSAT fatty acids in milk. The coefficient of variation for this trait observed in the current study (26.70%) was greater than that observed by Stoop et al. (2008) probably because of the difference in the number of analyzed samples.

Figure 2 illustrates the seasonal effect on the contents of SAT and MONO in bovine milk (g/100 g of milk) and milk fat (g/100 g of fat), and SAT:UNSAT. This effect was estimated from unadjusted means. These means calculated for July, August, and September were different than the estimates normally expected based on the trend of the curve drawn in Figure 2. These differences can be explained by the month of TD and the number of observations. During the summer, there is one month without infrared analysis for the routine Walloon milk recording. The number of observations used to calculate these average values for July, August, and September were low (52 for July, 61 for August, and 58 for September). For the other months, the minimum and maximum numbers of observations were equal to 103 and 799. Without considering the means obtained for July, August, and September, Figure 2 suggests that the content of SAT decreased until the summer and then increased (63.13 vs. 68.94%). The opposite relationship was observed for MONO. Karijord et al. (1982) and Lock and Garnsworthy (2003) have observed a similar seasonal effect for these 2 traits. Gallacier et al. (1974) observed the lowest concentrations of SAT (C4 to C16) and the greatest contents of C18:0 and C18:1 at the end of summer.

The values of SAT:UNSAT decreased until summer and then increased. As expected, these results confirmed that the butter is more spreadable at the end of spring and during the summer. This seasonal effect is explained mainly by changes in feeding (Chilliard et al., 2001), especially during the grazing period. Taking into account the date of test in the model was important for all studied traits.

Stage of Lactation Effect

Figure 3 describes the effect of DIM on the contents of SAT and MONO in bovine milk and fat, and SAT:UNSAT. This figure shows unadjusted means. The numbers of observations for each class of 15 DIM ranged from 76 to 274. A strong decrease in %FAT in bovine milk was observed until 60 DIM when %FAT was the lowest. de Vries and Veerkamp (2000) obtained the same curve. The greatest %FAT value observed at the beginning of lactation could be explained, in part, by the negative energy balance of cows in early lactation. To sustain high milk production, cows mobilize their lipids from adipose tissue. For example, cows (which produced an average 30 kg of milk/d) secreted 1.5 kg of fat from mobilization of 1 kg of adipose tissue lipids per day (Barber et al., 1997). The FA stored in the form of triacylglycerols in adipose tissue were mainly C16:0,

Table 5. Average daily estimate for random effects (genetic, herd × test day, permanent environment, residual) expressed in percentage of phenotypic variation for the quantity of milk, the percentage of milk fat and protein, the contents of saturated and monounsaturated fatty acids in bovine milk (g/100 g of milk) and milk fat (g/100 g of fat) and the ratio of saturated to unsaturated fatty acids[1]

Item	Heritability	Herd	Permanent environment	Residual
Milk (kg/d)	0.27	0.08	0.41	0.24
Fat (g/100 g of milk)	0.37	0.05	0.19	0.39
Protein (g/100 g of milk)	0.45	0.11	0.17	0.27
Saturated (g/100 g of milk)	0.42	0.05	0.24	0.29
Monounsaturated (g/100 g of milk)	0.14	0.04	0.33	0.49
Saturated (g/100 g of fat)	0.24	0.09	0.17	0.50
Monounsaturated (g/100 g of fat)	0.27	0.09	0.19	0.45
Saturated:unsaturated	0.27	0.07	0.14	0.52

[1]Herd = herd × date of calving random effect. Values of estimates for milk yield and percentages of fat and protein were the average values calculated from the 5 runs.

C18:0, and C18:1 *cis-9* (Barber et al., 1997; Chilliard et al., 2001). This unbalanced energy status involves some changes in milk composition to sustain the milk production. The contents of SAT and MONO in milk decreased rapidly until the peak of lactation and then increased slowly (Figure 3).

The content of MONO in milk fat followed the same trend as %FAT. The content of SAT in fat increased until the peak of lactation and then decreased. The same trend was observed by Karijord et al. (1982) for the major saturated FA in bovine milk fat, except for C18:0. The ratio SAT:UNSAT varied through the lactation following the same trend as that observed for the content of SAT in fat. The peak for this trait occurred around 80 DIM.

Heritability

Based on the results of skewness and kurtosis shown in Table 3, the distribution of studied traits approached normality. Table 4 gives the variance estimates for all coefficients of Legendre polynomials and their corresponding posterior SD. Average daily estimates expressed as a percentage of phenotypic variance for each studied random effect are in Table 5. Figure 4 depicts the changes of heritability values throughout the lactation. Average daily heritability for milk yield of 0.27 (Table 5) obtained in this study was lower than that estimated for Holstein cows in Belgium (0.48; Interbull, 2007). This value was also lower than that (0.52) observed by Miglior et al. (2007). Heritability values for milk yield decreased until the lactation peak and then increased slightly (Figure 4); the values ranged from 0.25 to 0.33. Muir et al. (2007) observed a similar trend for Italian Holstein cows. Other studies such as those of Veerkamp and Goddard (1998), Gengler et al. (2004), Mayeres et al. (2004), and Druet et al. (2005) found the greatest heritability at mid-lactation.

Average daily heritability estimates observed for %FAT and %PROT were 0.37 and 0.46, respectively (Table 5). These values were similar to those obtained previously by Soyeurt et al. (2007b) with the same model but a smaller number of records. Miglior et al. (2007) obtained greater estimates for first-lactation Holstein cows (0.55 and 0.58 for %FAT and %PROT, respectively). The changes of heritability estimates through the lactation were similar for %FAT and %PROT with greater values for %PROT (Figure 4). The heritability values ranged from 0.23 to 0.44 for %FAT, and from 0.30 to 0.51 for %PROT. The greatest heritability values were reached in mid-lactation. Druet et al. (2005) observed similar trends for these 2 traits

Table 6. Mean, standard deviation, minimum, and maximum values for the residual variances estimated for milk yield, the percentages of fat and protein, the contents of saturated and monounsaturated fatty acids in milk and milk fat, and the ratio of saturated to unsaturated fatty acids

Item	n	Mean	SD	Minimum	Maximum
Milk (kg/d)	100,799	0.00	1.68	−18.50	16.25
Fat (g/100 g of milk)	100,799	0.00	0.31	−3.82	4.00
Protein (g/100 g of milk)	100,799	0.00	0.11	−1.43	2.57
Saturated (g/100 g of milk)	4,666	0.00	0.22	−1.13	2.03
Monounsaturated (g/100 g of milk)	4,666	0.00	0.12	−0.56	1.57
Saturated (g/100 g of fat)	4,666	0.00	2.38	−13.24	15.42
Monounsaturated (g/100 g of fat)	4,666	0.00	1.89	−7.46	11.58
Saturated:unsaturated	4,666	0.00	0.26	−1.33	1.73

even though heritability values for %FAT were greater compared with %PROT.

Average daily estimates of heritability were 0.42 and 0.14 for SAT and MONO in milk, respectively. A lower value (0.24) was obtained for heritability of SAT expressed in milk fat than for the heritability of SAT in milk. The greatest heritability was found for MONO in fat (0.24) compared with the heritability of MONO in milk (Table 5). Soyeurt et al. (2007) also observed this difference in SAT heritability values between the contents expressed in milk and milk fat, although this difference is slightly greater in the current study. These

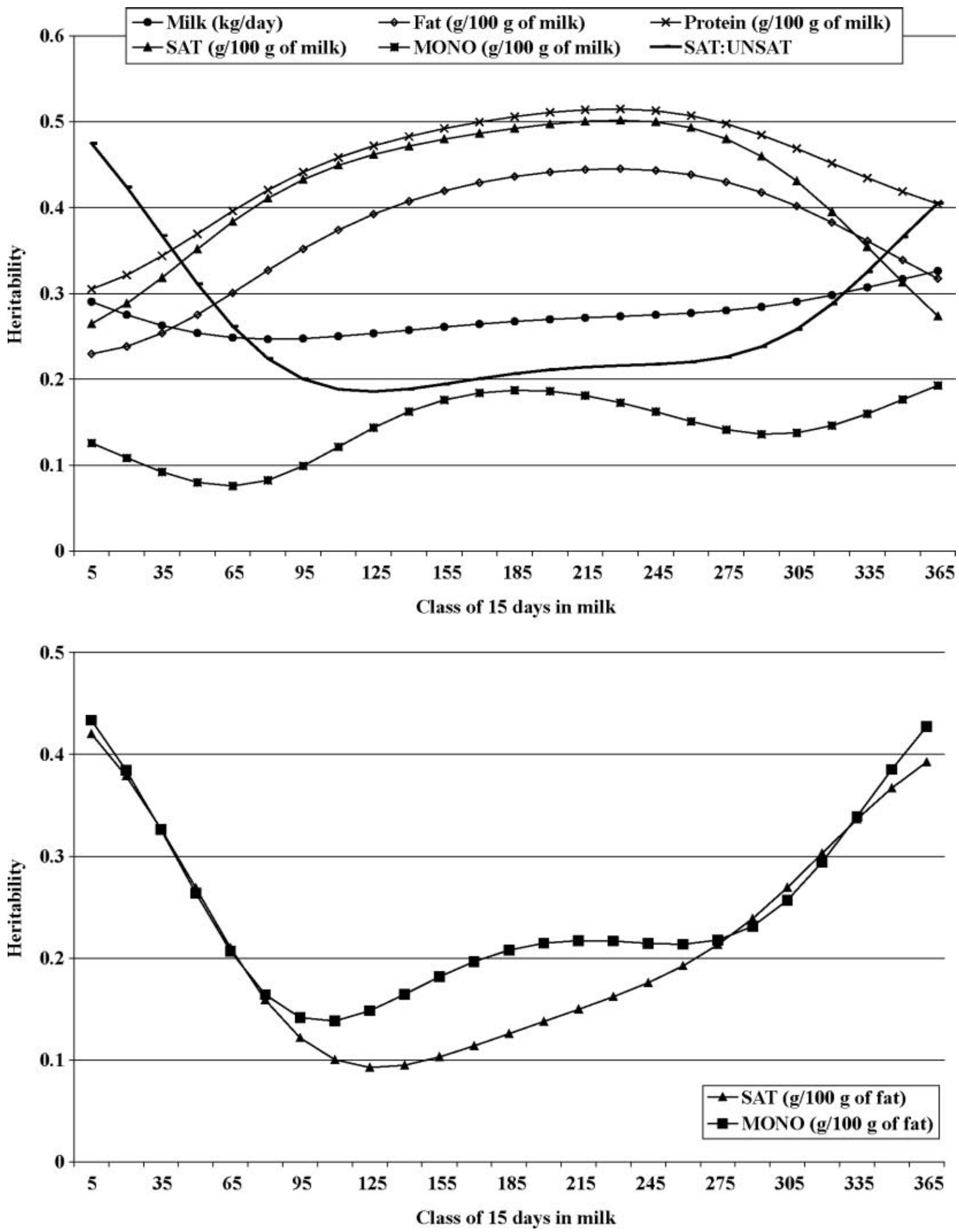

Figure 4. Changes of heritability value through the lactation for milk yield, percentages of fat and protein, the ratio of saturated to unsaturated fatty acids (SAT:UNSAT), and the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk (g/100 g of milk) and milk fat (g/100 g of fat).

differences in heritability values between Soyeurt et al. (2007) and the current study can be explained by the methodology used to estimate the heritabilities. Soyeurt et al. (2007, 2008) assumed constant genetic variation throughout the lactation. By the introduction of orthogonal regressions in the model, this study takes into account fluctuations of genetic variation throughout the lactation. The heritability estimates mentioned in Table 5 represent the means of values obtained for 1 to 365 DIM. As the differences between the extremes and the middle of lactation shown in Figure 4 were high, the average values for SAT and MONO in fat (g/100 g of fat) shown in the study were greater than those estimated without modeling the lactation curve.

The trend of heritability values for SAT in bovine milk was similar to that observed for %FAT and %PROT. This could be explained by the highly positive genetic correlations existing between SAT and %FAT (Karijord et al., 1982; Soyeurt et al., 2007; Figure 5) and the positive genetic correlation between SAT and %PROT (Soyeurt et al., 2007). The heritability values for this trait ranged from 0.26 to 0.50 for SAT in milk.

The changes of heritability values for SAT and MONO in fat were extremely large across the lactation (Figure 4). Heritability values ranged from 0.09 to 0.42 for SAT, and from 0.14 to 0.43 for %MONO. The greatest heritability values were observed at the beginning and the end of lactation. The greatest heritability estimates observed at the early stage of lactation could be explained by the energy status of cows. As the energy balance of cows at early stage of lactation is negative, cows mobilize their lipid reserves from adipose tissue. This mobilization requires some internal mechanisms genetically regulated. The part of genetics compared with the total variation at the early stages of lactation could be expected to be greater. The greater heritability estimates observed at the end of lactation could be related to the persistency of lactation. Fluctuation of heritability for SAT in milk and milk fat was similar to the one observed for the additive genetic variance of SAT in milk and milk fat (Figure 5).

Figure 4 and Table 5 have the heritability values observed for SAT:UNSAT. Average daily heritability observed for this trait was 0.27 (Table 5). This value was greater compared with that found previously by Soyeurt et al. (2007b; 0.11) but in agreement with the value obtained by Stoop et al. (2008; 0.20). This value confirmed the suggestion of Bobe et al. (2003) concerning the possible influence of genetics on the technological properties of butter. As expected, the curve of variation for heritability of this ratio followed the same trend as that observed for SAT in bovine milk fat (Figure 4). The heritability values ranged from 0.19 to 0.47. The greatest values were observed at the beginning and at the end of lactation.

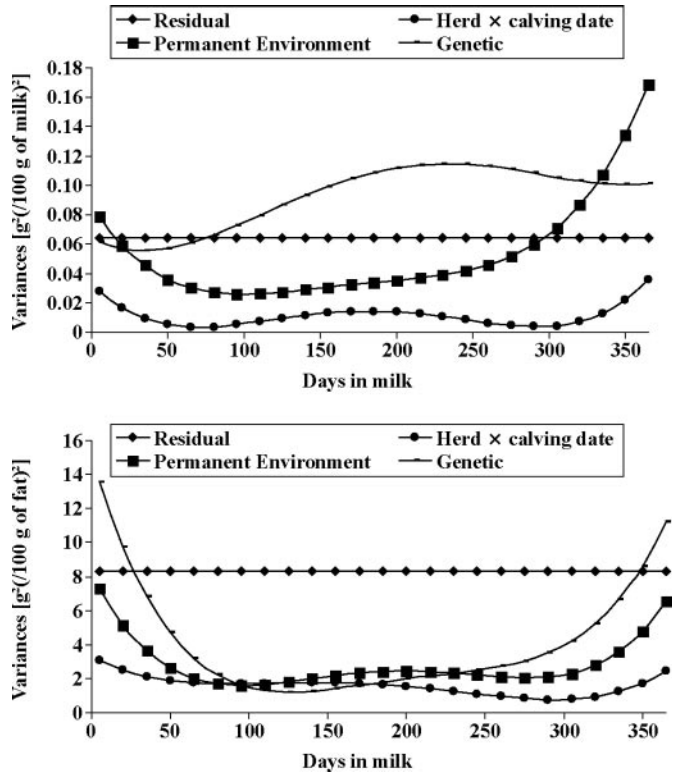

Figure 5. Changes of additive genetic, herd × calving date, permanent environment, and residual variances through the lactation for the contents of saturated (SAT) fatty acids in bovine milk (g/100 g of milk) and milk fat (g/100 g of fat).

Correlations

Figures 6, 7, and 8 depict the trend of daily genetic and phenotypic correlations among traits throughout the lactation. Generally, the genetic correlations of milk yield with the studied milk components (%FAT, %PROT, SAT, and MONO in milk, and SAT:UNSAT) were negative. These correlations were lower at the beginning of lactation. Changes of genetic correlation between milk yield and MONO in milk were more accentuated. The lowest correlations were observed at the beginning and end of lactation. The phenotypic correlations observed between milk yield and milk components (Figure 7) were relatively stable throughout the lactation, except for MONO. The phenotypic correlations between milk yield and MONO decreased over the lactation.

The curves of variation obtained for genetic correlations of milk yield with the fatty acid composition traits (SAT and MONO in fat) presented a trend opposite to that observed for SAT and MONO. The greatest genetic correlations were observed at the beginning of lactation and were positive for SAT and negative for MONO in fat. As the genetic correlation between SAT and MONO in fat was negative (Soyeurt et al., 2007; Figure 6), it was expected that the curves observed for SAT and MONO in milk fat would be in opposite trend. The phenotypic correlations between these FA traits and milk yield remained stable as the lactation progressed (Figure 8).

The genetic correlations of %FAT with SAT or MONO in milk (g/100 g of milk) were positive and high

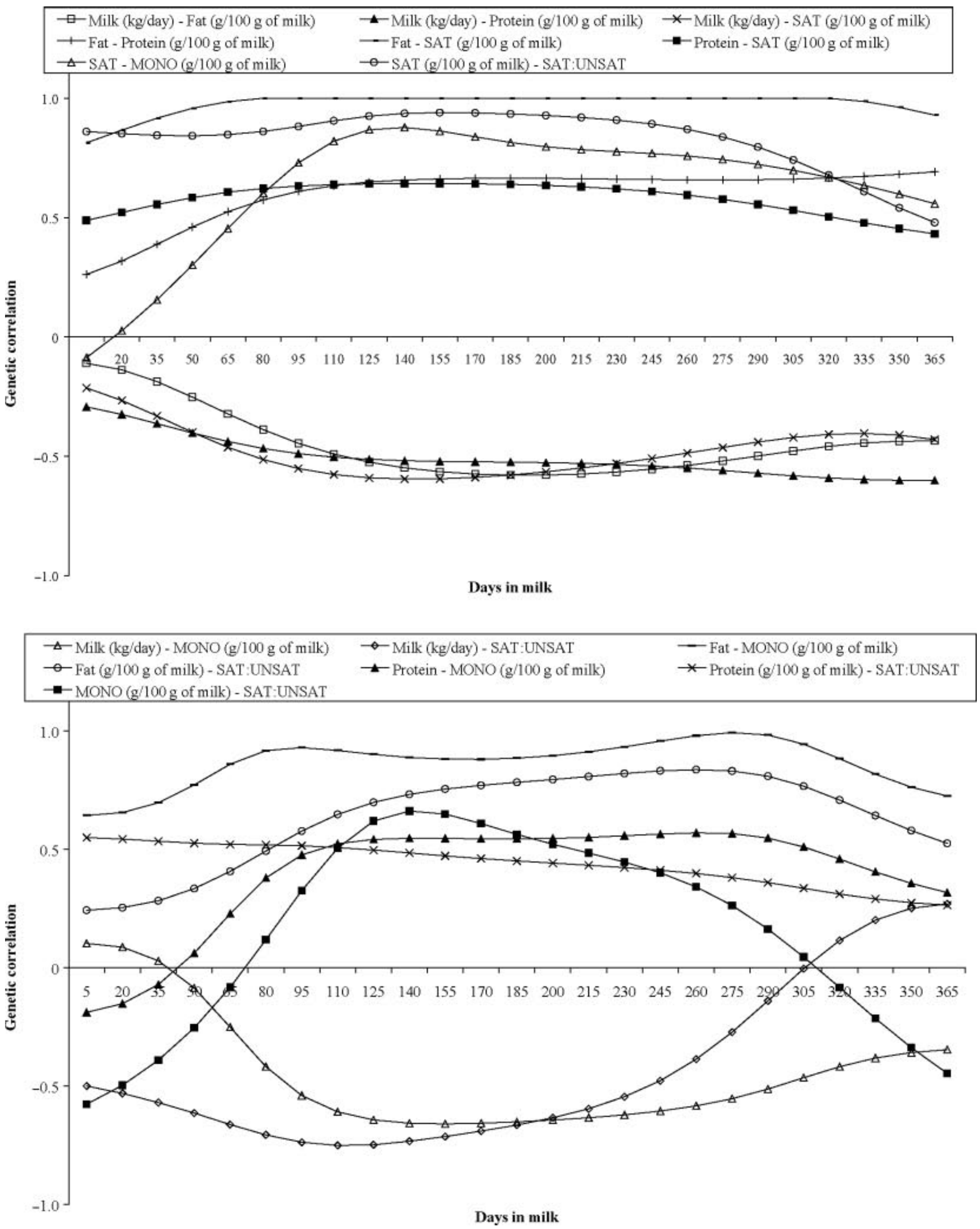

Figure 6. Changes of genetic correlation through the lactation among milk yield, percentages of fat and protein, the ratio of saturated to unsaturated fatty acids (SAT:UNSAT), and the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk (g/100 g of milk).

throughout the lactation (Figure 6). The changes for genetic correlations between %FAT and SAT:UNSAT were greater. These values were lowest at the beginning of lactation. Phenotypic correlations between %FAT and SAT were stable within lactation (Figure 7). The phenotypic correlations observed between %FAT and MONO or SAT:UNSAT changed through the lactation. As for genetic correlations, the phenotypic correlations between %FAT and the hardness of butter were lower at the beginning of lactation (Figure 7). Similar results were obtained previously (Soyeurt et al., 2007b). A nadir was observed around 80 DIM for the curve of

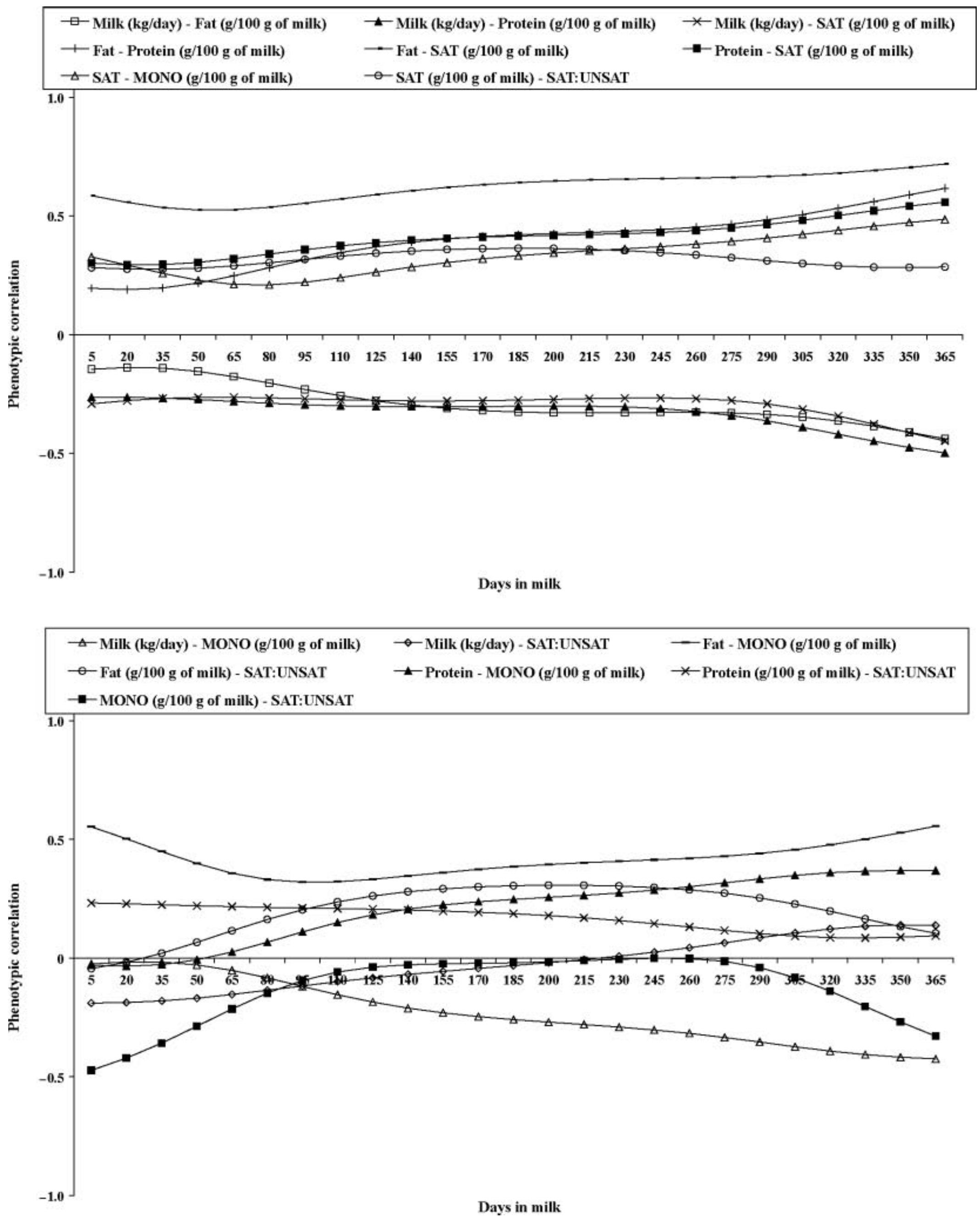

Figure 7. Changes of phenotypic correlation through the lactation among milk yield, percentages of fat and protein, the ratio of saturated to unsaturated fatty acids reflecting the hardness of butter and the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk (g/100 g of milk).

phenotypic correlations between %FAT and MONO in milk (Figure 7).

The genetic correlations between %FAT and SAT in milk fat (g/100 g of fat) increased positively after the first part of the lactation, remained relatively stable, and then decreased slightly. These values ranged from 0.23 to 0.62 (Figure 8). The same trend was observed for the phenotypic correlations between these 2 traits

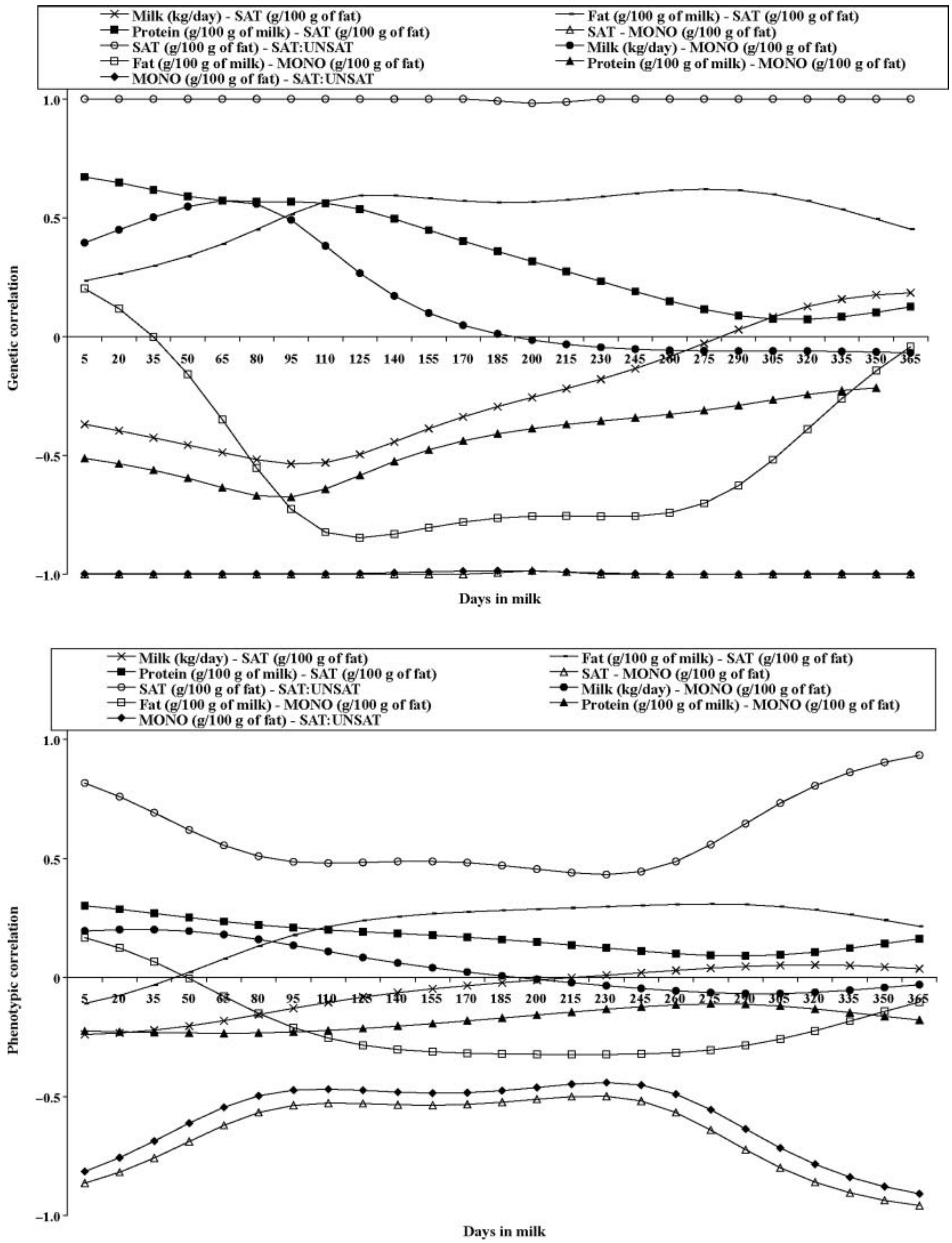

Figure 8. Changes of genetic and phenotypic correlations through the lactation among milk yield, percentages of fat and protein, the ratio of saturated to unsaturated fatty acids reflecting the hardness of butter and the contents of saturated (SAT) and monounsaturated (MONO) fatty acids in bovine milk fat (g/100 g of fat).

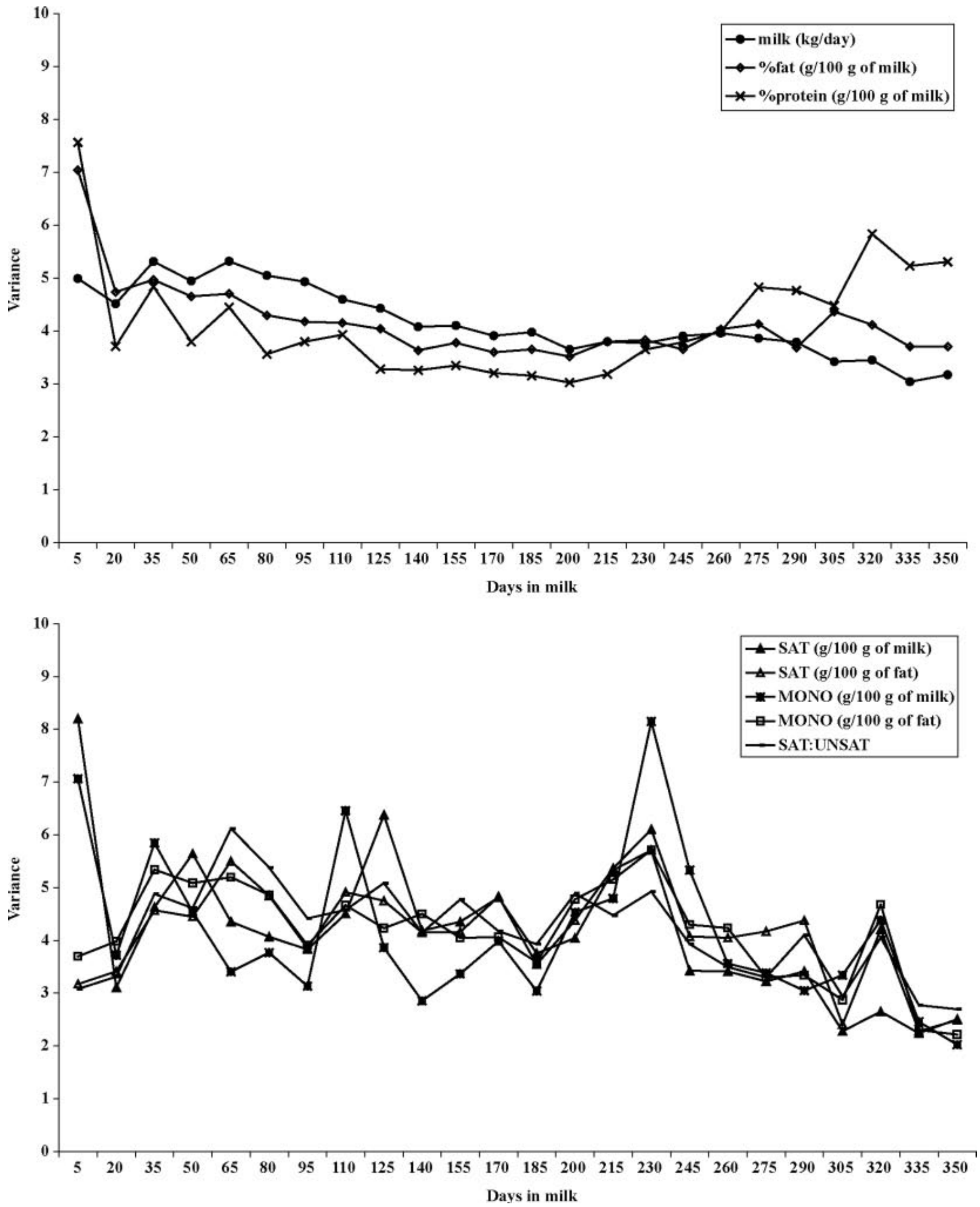

Figure 9. Changes of relative residual variances (% of the total residual variance) throughout the lactation for milk yield, percentages of fat and protein, contents of saturated (SAT) and monounsaturated fatty acids (MONO) in milk and fat, and the ratio of saturated to unsaturated fatty acids (SAT:UNSAT).

but the values were lowest compared with the corresponding genetic correlations. The negative energy balance of cows at the beginning of lactation could partly explain the lowest correlations being observed then. A strong opposite trend was observed for the genetic and phenotypic correlations between %FAT and MONO in milk fat (Figure 8).

The changes of genetic and phenotypic correlations between %FAT and SAT:UNSAT (Figure 6) within the lactation were the same as those observed between %FAT and %SAT (Figure 8).

Residuals

The general means of residuals calculated for all studied traits were equal to zero (Table 6). In the same way, the means of residuals for the 24 classes of DIM were also equal to zero (data not shown). These results reinforced the fit of the proposed model. However, the values of residuals varied slightly (Table 6 and Figure 9). The residuals for milk yield and the percentages of fat and protein were more stable as the lactation progressed compared with other studied traits (Figure 9). The relative residual variances for FA traits ranged globally between 3 and 6% of the total residual variance, showing a slight heterogeneity. Based on the observed means of residuals and the low values of relative residual variances, the assumption to keep constant the residual variances seems to be justified.

CONCLUSIONS

The seasonal effect on FA composition was studied based on unadjusted means. As expected, the contents of SAT in milk fat were smaller during the spring and summer while the contents of MONO decreased. Some changes were observed for the contents of %MONO in milk fat. The greatest contents of %MONO were observed during the spring and summer. The hardness of butter was influenced by stage of lactation. The milk fat produced by cows in first parity at early stage of lactation had lower contents of SAT. Therefore, butter from milk produced by cows at the beginning of lactation should be more spreadable and softer. For all traits studied, the estimates of heritability were moderate to high and changed during the lactation. The %FAT and SAT content in milk were less heritable at the beginning of lactation. A more fluctuating curve of heritability was observed for MONO. It was interesting to observe that the contents of SAT and MONO in milk fat were strongly heritable at the beginning and at the end of lactation. In conclusion, this study confirms that genetic variability of FA exists and varies throughout the lactation.

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