Variation of Δ^9 -Desaturase Activity in Dairy Cattle

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ABSTRACT

The endogenous production of unsaturated fatty acids (FA), particularly some monounsaturated FA (%MONO) and nearly all conjugated linoleic acids, is regulated by the Δ^9 -desaturase activity. The aims of this study were to assess the variation of this enzymatic activity within lactation, across dairy breeds, and to estimate its genetic parameters. The ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis* to C18:0 were calculated from FA contents predicted by mid-infrared spectrometry. Variance components and standard errors were estimated using average information REML. The multitrait mixed model included as fixed effects herd $\times$ test date $\times$ class of lactation number, class of days in milk $\times$ class of lactation number, class of age $\times$ class of lactation number, and regressions on breed composition. Four random effects were also included: animal genetic effect, 2 permanent environments (within and across lactations), and residual effect. Under the assumption that the calculated ratios are an approximate measurement of Δ^9 -desaturase activity, this study showed different sources of variation for this enzymatic activity. A slight difference was observed within lactation. The ratios of C14:1 *cis*-9 to C14:0 and C16:1 *cis*-9 to C16:0 increased as a function of days in milk. Differences across 7 dairy breeds were observed. The values of Δ^9 -desaturase indices observed for Jersey and Brown-Swiss cows were lower compared with Holstein. The opposite was observed for dual-purpose Belgian Blue cows. Values of heritability for the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis* to C18:0 were 20, 20, and 3%, respectively. Negative genetic correlations observed between fat or protein contents and the 3 indices suggested that an increased activity of Δ^9 -desaturase could inhibit the synthesis of fat and protein in bovine milk. Negative

correlations were also observed between fat or protein contents and the contents of 3 studied unsaturated FA in milk fat (C14:1 *cis*-9, C16:1 *cis*-9, and C18:1 *cis*). The positive genetic correlations observed between %MONO and the ratios of C14:1 *cis*-9 to C14:0 (0.72), C16:1 *cis*-9 to C16:0 (0.62), and C18:1 *cis* to C18:0 (0.97) showed that %MONO is linked to the Δ^9 -desaturase activity.

Key words: Δ^9 -desaturase, fatty acid, genetic parameter, cattle

INTRODUCTION

Milk fat is considered hypercholesterolemic because of its high saturated fatty acid (FA) contents (Ulbricht and Southgate, 1991), in particular for C12:0, C14:0, and C16:0 (Hu et al., 1999; Fernandez and West, 2005). In contrast, the intake of polyunsaturated and monounsaturated FA reduces the plasma cholesterol concentrations (Ulbricht and Southgate, 1991; Noakes et al., 1996; Hu et al., 2001; Fernandez and West, 2005). Beside its positive effect on cardiovascular diseases, the intake of conjugated linoleic acids (CLA), particularly C18:2 *cis*-9, *trans*-11 and C18:2 *trans*-10, *cis*-12, is also beneficial for the prevention of cancer (Ip et al., 1994; Belury, 1995; Parodi, 1999) and obesity (Park et al., 1997). Average milk fat contains 70% of saturated FA, 25% of monounsaturated FA (%MONO), and 5% of polyunsaturated FA (Grummer, 1991). Some researchers studied different possibilities to modify the FA profile, especially to increase the proportion of unsaturated FA. The sources of variation such as feed, breed, or animal genetics can be used to improve the nutritional quality of fat (Palmquist et al., 1993; DePeters et al., 1995). Detailed information about the feeding effect on the FA profile in bovine milk is available (Chilliard et al., 2000); information about the genetic effect on milk FA composition is limited (Renner and Kosmack, 1974a; Karijord et al., 1982; Soyeurt et al., 2006a, 2007).

The introduction of a *cis* double bond between carbon 9 and 10 of saturated FA with a chain length of 10 to 18 carbons is an important step in the synthesis of

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unsaturated FA (Ntambi, 1995; Bauman et al., 1999; Thomson et al., 2003; Ntambi and Miyazaki, 2004). The iron attached to the Δ^9 -desaturase enzyme, also named stearyl-coenzyme A desaturase (**SCD**), catalyzes this desaturation together with NADPH, cytochrome b5 reductase, cytochrome b5, and oxygen (Ntambi, 1995; Yahyaoui et al., 2002). The Δ^9 -desaturase activity regulates the production of the major isomer of CLA by converting C18:1 *trans*-11 into C18:2 *cis*-9, *cis*-12 (Kinsella, 1972; Bauman et al., 1999). Corl et al. (2001) observed that 78% of the total of C18:2 *cis*-9, *trans*-11 secreted in milk fat was endogenously synthesized. The conversions of C10:0 into C10:1 *cis*-9, C12:0 into C12:1 *cis*-9 (Thomson et al., 2003), and, mainly, the conversions of C14:0 into C14:1 *cis*-9, C16:0 into C16:1 *cis*-9, and C18:0 into C18:1 *cis*-9 (Ntambi, 1995; Bauman et al., 1999) are also regulated by this enzyme in the mammary cells. Chilliard et al. (2001) reported that, on average, 40% of C18:0 taken by the mammary gland from the circulating plasma lipids is converted into C18:1 *cis*-9. This Δ^9 desaturation contributes to more than 50% of C18:1 *cis*-9 secreted in bovine milk. The effect of this enzyme on the cited FA is not equal, the favorite substrates being C18:0 and C16:0 (Ntambi and Miyazaki, 2004).

Bovine SCD gene contains 5,331 bp and is localized on chromosome 26 (Campbell et al., 2001; Taniguchi et al., 2004). Its opening reading frame includes 1,080 nucleotides and codes for 359 amino acids (Taniguchi et al., 2004). The exact number of SCD genes in bovine is currently unknown (Campbell et al., 2001). Ward et al. (1998) reported that the ovine SCD gene was widely expressed. Kinsella (1972) reported that the Δ^9 -desaturase activity and mRNA abundance were greater in the mammary gland for lactating ruminants. Taniguchi et al. (2004) studied the full length of the bovine SCD from 20 Japanese Black steers and observed 8 single-nucleotide polymorphisms (**SNP**). One of these SNP is the site of an amino acid replacement, substitution of valine (V) for alanine (A). Mele et al. (2007) suggested that this locus could be a candidate gene to explain the variability of FA profile in bovine milk. They observed that the relative frequencies of bovine SCD genotypes were 27% for AA, 60% for AV, and 13% for VV. Generally, the A allele was associated with higher %MONO and greater values of FA indices of C14. Moioli et al. (2007) studied the SNP on exon 5 and observed an influence of this SNP on the C14 and C16 indices.

Previous studies estimated specific FA indices to approximate the measurement of the Δ^9 -desaturase activity. These indices were defined as ratios of FA dependent on the activity of this enzyme: product/substrate (Lock and Garnsworthy, 2003; Thomson et al., 2003), substrate/product (Chouinard et al., 1999), or product/

(substrate + product) (Kelsey et al., 2003; Royal and Garnsworthy, 2005). These ratios are affected by lipid supplementation (Chouinard et al., 1999), season (Lock and Garnsworthy, 2003), and breed (Kelsey et al., 2003; Soyeurt et al., 2006a). Consequently, a cow of a specific breed with a higher Δ^9 -desaturase activity should produce higher contents of %MONO and CLA in milk fat. Peterson et al. (2002) suggested that the variation of CLA content in milk fat among individuals was related to the rumen biohydrogenation and the Δ^9 -desaturase activity. Due to the price and the time needed by the gas chromatography to measure FA contents in milk fat, the major part of these studies was limited to a small number of cows and samples. Recently, several calibration equations have been developed by our group (Soyeurt et al., 2006b) to predict the FA contents from mid-infrared (**MIR**) spectrum. Thanks to the low cost of this infrared analysis, the number of cows and samples analyzed can be large. The objective of the current research was to study, in a large cow population, the variation of the Δ^9 -desaturase indices within and across lactations, the differences among dairy breeds, and to estimate their genetic parameters.

MATERIALS AND METHODS

Animal Population and Milk Samples

Between April 2005 and December 2006, as part of the standard farm recording activities in the Walloon region of Belgium, 10,401 milk samples were collected once a month from 1,918 cows in 26 herds. Several criteria were used to select herds, such as their participation in Walloon milk recording and their degree of pedigree completeness. A total of 8 herds were followed since April 2005. The remaining herds were studied since November 2005. The number of lactating cows per herd ranged from 25 to 100. Herds were also chosen to have a mixed breed structure representing a diversity of breeds. There were 7 main dairy breeds with Holstein (**HOL**) being the most common (47.27%). The remaining breeds in decreasing order of abundance were as follows: dual-purpose Belgian Blue (**DPB**), 15.95%; Montbeliarde (**MON**), 12.93%; Normande (**NOR**), 8.51%; unknown, 5.59%; Meuse-Rhine-Yssel type Red and White (**RED**), 4.11%; Jersey (**JER**), 3.43%; and Brown-Swiss (**BSW**), 2.21%. Following standard procedures (International Committee for Animal Recording, 2007), milk samples were representative of the 24-h milking period (50% of morning milk and 50% of evening milk). The Milk Committee of Battice (Belgium) analyzed these samples on a Foss MilkoScan FT6000 spectrometer (Foss, Hillerød, Denmark) during the regular milk analysis. All of the MIR milk spectra generated by this infrared analysis were recorded. Due

to different time frames and technical issues, the number of test days was not constant for all herds. Some cows were also dried off or calved during this experiment.

Due to the limited size of the spectral database, milk yields and the percentages of fat (%FAT) and protein (%PROT) measured by MIR spectrometry were added. To increase the number of contemporaries, the historic milk records were also added for all studied herds and represented records from 1995 to 2007. The edited data set contained 52,950 records from 3,217 cows.

Predicted Concentrations of FA in Milk and Milk Fat

Recently, our group developed calibration equations useful to predict the FA contents in bovine milk (Soyeurt et al., 2006b). The reference FA concentrations were measured by gas chromatography with a capillary column of 50-m length. This column showed a poor chromatographic resolution for C18:1 isomers. Therefore, in this study, improved calibration equations were developed.

Between March 2005 and May 2006, 1,609 milk samples were collected in 8 herds from 475 cows representing 6 dairy breeds (DPB, HOL, JER, NOR, MON, and RED). From their spectral variability, 78 milk samples were selected using a principal components approach. The milk fat of these samples was extracted according to ISO Standard 14156:2001 (ISO, 2001). Preparation of FA methyl esters was made following the ISO 15884:2002 (ISO, 2002). These milk fat samples were analyzed using gas chromatography from the method developed by Collomb and Bühler (2000). The gas chromatograph (model 6890N, Agilent Technologies Inc., Palo Alto, CA) was equipped with a CPSil-88 capillary column (Varian Inc., Palo Alto, CA) with a length of 100 m, an internal diameter of 0.25 mm, and a film thickness of 0.20 μ m. 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) during 1 min, then 165 to 225°C (at 2°C/min) during 17 min. The volume injected was 0.5 μ L. 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 ester response factors, the repeatability, and the accuracy of this method.

The methodology used to develop the calibration equations was similar to the one used previously (Soyeurt et al., 2006b). These equations were established from chromatographic and spectral data using a specific program for multivariate calibration (WINISI III;

<http://www.winisi.com/>) and partial least squares regressions. No treatments were 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 prevent 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; Sinnaeve et al., 1994). To assess the robustness of the developed calibration equations, several statistical parameters were calculated: mean and standard deviation measured from reference concentrations of FA, standard error of calibration, calibration coefficient of determination, SECV, cross-validation coefficient of determination, and the ratio of SECV to standard deviation (RPD). For the interested readers, Williams (2007) explains in details the calibration procedure.

The calibration equations predicting the contents of monounsaturated FA, C14:0, C14:1 *cis*-9, C16:0, C16:1 *cis*-9, C18:0, and the total C18:1 *cis* in milk (g/dL of milk) were applied to the recorded spectra. All predicted FA contents were converted into grams per 100 grams of fat using %FAT measured by the MilkoScan FT6000. From these predictions, the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis* to C18:0 were calculated. Lock and Garnsworthy (2003) estimated these ratios to approximate the measurement of the Δ^9 -desaturase activity. From the 78 calibration samples, canonical correlations were calculated using PROC CANCORR (SAS Institute, 1999). These correlations were used to study the similarities between the Δ^9 -desaturase indices calculated from FA contents measured by gas chromatography and MIR spectrometry.

Statistical Model

The division of permanent environment into 2 distinct parts (within and across lactations) was based on the model used by Bormann et al. (2003). A total of 3,024 cows had repeated records within lactation, and 1,838 cows had repeated records across lactations. All traits were studied with 8 separate runs using the same multitrait mixed animal model:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{WI} + \mathbf{Zp} + \mathbf{Zu} + \mathbf{e}$$

where $\mathbf{y}$ = the vector of observations for each of the 8 runs (milk yield, %FAT, %PROT, and %MONO; milk

yield, %FAT, %PROT, and the ratio of C14:1 *cis*-9 to C14:0; milk yield, %FAT, %PROT, and the ratio of C16:1 *cis*-9 to C16:0; milk yield, %FAT, %PROT, and the ratio of C18:1 *cis* to C18:0; %MONO, the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis* to C18:0; milk yield, %FAT, %PROT, C14:1 *cis*-9, and C14:0; milk yield, %FAT, %PROT, C16:1 *cis*-9, and C16:0; milk yield, %FAT, %PROT, C18:1 *cis*, and C18:0); β = the vector of fixed effects (herd $\times$ test day $\times$ class of lactation number, stage of lactation $\times$ class of lactation number, class of age $\times$ class of lactation number, regressions on breed composition because many animals were cross-bred); $\mathbf{I}$ = 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 chosen from the sources of variation known for the traditional production traits as milk yield, %FAT, and %PROT. Stage of lactation was divided in 24 classes of 15 DIM. Records with DIM lower than 5 and greater than 365 were deleted. Parities were grouped as first, second, and third or later lactation (18,733 records for cows in first lactation, 12,857 in second lactation, and 21,359 in third or later lactation). Age at test day was defined as the number of months from birth. A total of 9 classes of age were created: for first lactation, age below 29 mo (3.62% of test day records), 29 to 32 mo (6.65%), and 33 mo and older (25.11%); for second lactation, age below 42 mo (2.72%), 42 to 46 mo (5.52%), and 47 mo and older (16.04%); and for the third or later lactation, age below 54 mo (1.52%), 54 to 59 mo (4.28%), and 60 mo and older (34.54%). Significance of the fixed effects was tested using PROC GLM (SAS Institute, 1999).

Pedigree contained 9,174 animals including 1,666 sires and 7,508 dams. Only animals born after 1980 were considered. In this context, a maximum of 6 generations per animal were covered. Breed composition was determined according to the known pedigrees of animals. A certain proportion of this breed composition was of unknown origin. To optimize the comparison between breeds, these proportions were assumed to correspond to another breed (unknown breed). Variance components were estimated using expectation maximization REML and average information REML (Misztal, 2007). Covariance components were considered converged when the relative squared differences were equal to 10^{-11} . Variance components were assumed to be identical across breeds, lactation number, and stages of lactation. Standard errors of estimates were obtained using average information REML (Misztal, 2007). Heritability was calculated as the ratio of genetic variance ($\sigma^2_{\text{genetic}}$) to the sum of variances obtained for the genetic

effect, the permanent environment within lactation (σ^2_{PEWL}) and across lactations (σ^2_{PEAL}), and the residual effect ($\sigma^2_{\text{residual}}$):

$$\text{heritability} = \frac{\sigma^2_{\text{genetic}}}{\sigma^2_{\text{genetic}} + \sigma^2_{\text{PEWL}} + \sigma^2_{\text{PEAL}} + \sigma^2_{\text{residual}}}.$$

Genetic or phenotypic correlations were calculated using the ratio of genetic or phenotypic covariance between 2 traits to the product of the genetic or phenotypic standard deviations estimated for these 2 traits. Heritability values and correlations for milk yield, %FAT, and %PROT were the means of the estimates obtained from the 8 computations. The genetic and phenotypic correlations among the studied FA were estimated from the variance components using the same mixed model than the one exposed previously including milk yield, %FAT, %PROT, and the 6 studied FA (C14:1 *cis*-9, C14:0, C16:1 *cis*-9, C16:0, C18:1 *cis*, and C18:0). Due to the large number of traits, covariance components for this calculation were considered converged when the relative squared differences were equal to 10^{-10} .

RESULTS AND DISCUSSION

Calibration Equations

If RPD is equal to or greater than 2, the MIR predicted value is considered to be a good indicator of the studied trait (Sinnaeve et al., 1994). The calibration equations predicting the contents of monounsaturated FA, C14:0, C16:0, C18:0, and C18:1 *cis* in milk (g/dL of milk) showed a RPD >2 (Table 1). The lowest values of RPD observed for C14:1 *cis*-9 and C16:1 *cis*-9 can be explained by the lower concentrations of these FA in bovine milk. The means and standard deviations observed for their respective Δ^9 -desaturase indices calculated from FA contents measured by gas chromatography and MIR spectrometry were similar (Table 2). This suggests that predictors covered a similar range. The differences between the studied indices were relatively small (Table 2). Skewness for these traits was close to 0 except for the ratio of C18:1 *cis* to C18:0 (Table 2). This value was not extremely large (-1.405). Consequently, the differences were approximately normally distributed.

A canonical correlation of 0.86 was observed between the first canonical variable calculated from the Δ^9 -desaturase indices estimated from the FA contents measured by gas chromatography and MIR spectrometry. This first principal component explained 78.25% of the variability. The second principal component described 13.60% of the variability and the canonical correlation was 0.58. The last principal component explained 0.08% of the variability and had a canonical correlation equal

Table 1. Mean, standard deviation, standard error of calibration (SEC), calibration coefficient of determination (R^2_c), standard error of cross-validation (SECV), cross-validation coefficient of determination (R^2_{cv}), and the ratio of standard deviation to SECV (RPD) calculated for the 7 calibration equations used in this study and established from 78 milk samples¹

Fatty acid (g/dL of milk)	Mean	SD	SEC	R^2_c	SECV	R^2_{cv}	RPD
%MONO	1.43	0.45	0.06	0.98	0.12	0.93	3.76
C14:0	0.50	0.15	0.02	0.97	0.05	0.90	3.22
C14:1 <i>cis</i> -9	0.04	0.01	0.01	0.58	0.01	0.53	1.45
C16:0	1.39	0.42	0.12	0.92	0.17	0.84	2.50
C16:1 <i>cis</i> -9	0.08	0.03	0.02	0.64	0.03	0.28	1.17
C18:0	0.58	0.26	0.06	0.94	0.10	0.85	2.54
C18:1 <i>cis</i>	1.08	0.39	0.06	0.97	0.12	0.91	3.25

¹%MONO = content of monounsaturated fatty acids in milk fat.

to 0.48. Figure 1 illustrates the position of the indices calculated from chromatographic and spectral data on a graph representing the first and the second principal components of the chromatographic data. The positions for each pair of indices were close. Results indicated the existence of a strong relationship between the Δ^9 -desaturase indices calculated from chromatographic and spectral data. This suggests, therefore, a potential use of the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0 predicted by MIR.

Skewness values observed in Table 3 for each studied trait were <1 except for the Δ^9 -desaturase indices. Consequently, the distribution of these traits was close to normality. Skewness values for the ratios of C14:1 *cis*-9 to C14:0 (2.49) and C16:1 *cis*-9 and C16:0 (1.04) were not high. The same comment can be made for kurtosis (Table 3). Even if the distributions of the ratios of C14:1 *cis*-9 to C14:0 and C16:1 *cis*-9 to C16:0 cannot be considered having a normal distribution, they are close enough to normality to be used in this study. The ratio of C18:1 *cis* to C18:0 had a very high value of skewness and kurtosis. The distribution of this trait was not normal. This ratio was also included in this study, but the results obtained have to be interpreted cautiously.

Variation Within and Across Lactations

As expected, the herd $\times$ test day $\times$ class of lactation number fixed effect explained the major part of the

variability (49.6 to 97.6%; Table 4). The percentage of total variation explained by the second fixed effect, stage of lactation $\times$ class of lactation number, ranged from 2.4 to 50.4%. This effect was also significant for all traits. The class of age $\times$ class of lactation number fixed effect was significant except for %PROT, %MONO, the ratio of C16:1 *cis*-9 to C16:0, C14:0, C16:0, C18:1 *cis*, and C18:0. Because this effect was significant for some studied traits, it was included in the used statistical model.

The lactation curves for milk yield and %FAT were better fitted than the curve for %MONO (Figure 2), which can be explained by a larger number of observations used to trace the lactation curve of milk yield and %FAT (52,950 records). The lactation curve for %MONO represented 10,401 spectral records. The variation of %MONO within lactation was similar to the curve observed for %FAT. The lowest contents of %FAT and %MONO were observed at around 50 DIM for %FAT and at around 100 DIM for %MONO. As observed for %FAT, the differences between the first, second, and third class of lactation number were not large. Karijod et al. (1982) observed a similar curve for C18:1. A slight increase of the values for the studied indices was observed within lactation, especially for the ratios of C14:1 *cis*-9 to C14:0 and C16:1 *cis*-9 to C16:0 (Figure 3). The differences across lactations were small. An outlier appeared in Figure 3c. The contents of all FA in fat (g/100 g of fat) were influenced by the days in

Table 2. Mean and standard deviation for the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis* to C18:0 estimated from the contents of fatty acid measured by GC and predicted by mid-infrared spectrometry from 78 milk samples¹

Trait (g/dL of milk)	GC		Mid-infrared spectrometry		Difference				
	Mean	SD	Mean	SD	Mean	SD	Range	IQR	Skewness
C14:1 <i>cis</i> -9/C14:0	0.081	0.024	0.083	0.019	-0.011	0.020	0.091	0.026	0.292
C16:1 <i>cis</i> -9/C16:0	0.057	0.021	0.058	0.018	-0.001	0.014	0.88	0.017	-0.67
C18:1 <i>cis</i> /C18:0	2.004	0.572	2.011	0.597	-0.007	0.361	2.549	0.291	-1.405

¹IQR = interquartile range.

Figure 1. Circle of correlations for the canonical variables representing C14:1 *cis*-9/C14:0, C16:1 *cis*-9/C16:0, and C18:1 *cis*/C18:0 estimated from the contents of fatty acid measured by GC (reference analysis) and predicted by mid-infrared (MIR) spectrometry. The axis represented the first and second principal components estimated from chromatographic data.

milk (Figures 4 and 5). The effect of lactation number was small. The curves observed for all studied FA were similar to those mentioned by Karijord et al. (1982). Therefore, the effect of lactation number was small. Days in milk affected the content of %MONO and studied FA and, more slightly, the values of Δ^9 -desaturase indices.

Heritability

Heritability for daily milk yields was 20%. This value was rather low compared with the 305-d heritability estimates used by the majority of countries in their genetic evaluations (Interbull, 2007). Average daily milk yield was modeled. Therefore, the model used in this study provided an average heritability. Logically, average heritability observed for a test date is low compared with a figure representing the whole lactation, because test-day specific measurement errors are still included. Our model did also not model genetic or non-genetic variations of milk yield as a function of DIM

for individual cows. Still, it is similar to daily estimates reported by some other authors like Veerkamp and Goddard (1998), Lidauer and Mäntysaari (1999), Bormann et al. (2003), and Gengler et al. (2004). Heritability values were 33% for %FAT and 36% for %PROT and little higher than those estimated for HOL by Welper and Freeman (1992), Ikonen et al. (1999), and Miglior et al. (2007). Our model also included several breeds. The cited publications studied only HOL cows.

Milk FA composition results from the production of FA by 2 distinct metabolic processes: de novo synthesis in the mammary gland (40% of FA secreted in milk; Chilliard et al., 2001) and extraction from the circulating plasma lipids (60%; Chilliard et al., 2001). It has been found that C4:0 to C12:0, most of C14:0, and, on average, 50% of C16:0 are produced by the de novo synthesis. All of C18 and longer-chain FA are extracted from blood (Givens and Shingfield, 2004; Palmquist, 2006). Effect of dietary fat on FA profile has been extensively studied, such as the effect of dietary unsaturated FA on milk fat depression (Bauman et al., 2006; Palm-

Table 3. Number of samples (n), mean, standard deviation, mode, interquartile range (IQR), CV, skewness, and kurtosis of the milk components in the studied Walloon cattle populations¹

Trait	n	Mean	SD	Mode	IQR	CV	Skewness	Kurtosis
Milk yield (in kg)	52,950	22.54	8.56	20.00	11.6	37.95	0.47	0.24
% Fat (g/100 g of milk)	52,950	4.02	0.76	3.85	0.91	18.85	0.91	2.52
% Protein (g/100 g of milk)	52,950	3.44	0.40	3.18	0.50	11.59	0.74	2.63
%MONO (g/100 g of fat)	10,401	28.42	5.05	28.32	6.80	18.16	0.84	2.22
C14:1 <i>cis</i> -9/C14:0	10,401	0.10	0.02	1.00	0.27	24.39	2.49	29.34
C16:1 <i>cis</i> -9/C16:0	10,401	0.07	0.02	0.67	0.20	26.59	1.04	4.09
C18:1 <i>cis</i> /C18:0	10,401	2.14	1.32	1.92	0.65	61.58	27.72	1,212.81
C14:1 <i>cis</i> -9 (g/100 g of fat)	10,401	1.03	0.22	1.01	0.30	21.66	0.37	2.97
C14:0 (g/100 g of fat)	10,401	10.62	1.88	11.40	2.50	17.72	-0.57	0.42
C16:1 <i>cis</i> -9 (g/100 g of fat)	10,401	1.88	0.40	2.02	0.51	21.18	-0.14	7.91
C16:0 (g/100 g of fat)	10,401	28.72	4.60	30.30	6.80	15.98	-0.40	1.21
C18:1 <i>cis</i> (g/100 g of fat)	10,401	22.31	4.48	20.30	5.90	20.08	0.63	0.51
C18:0 (g/100 g of fat)	10,401	11.00	2.58	10.38	3.10	23.46	-0.11	1.81

¹%MONO = content of monounsaturated fatty acids in milk fat; fatty acid ratios were calculated from fatty acid concentrations (expressed in g/dL of milk).

quist, 2006). To circumvent the dietary effect, a fixed effect including herd $\times$ test day $\times$ class of lactation number was included in the statistical model used. The model assumed that all cows present in the same herd received the same feeding. If this hypothesis is verified, which was largely the case in this study, the herd fixed effect includes the main effect of feeding on milk FA composition. Consequently, the genetic variance obtained, for instance for %MONO, reflected more the endogenous production of monounsaturated FA.

Heritability for %MONO was equal to 17% (Table 5). This value is lower than the one observed for %MONO with the same model developed by Soyeurt et al. (2007; 24% with SE = 2.3%) on a smaller data set. Two reasons can explain these differences. First, a larger spectral database was used. In this study, many cows were studied at least during 1 yr. Second, the calibration equation

used previously to estimate the percentage of monounsaturated FA in bovine milk (g/dL of milk) was established from FA contents measured using gas chromatography with a capillary column of 50-m length (RPD = 2.54). Based on the results given in Table 1, the new calibration equation used in this study can be considered more accurate (RPD = 3.76). Overall, the genetic parameter estimates of both studies are similar and suggest a moderate heritability of %MONO. Heritability of unsaturated C18 obtained by Renner and Kosmack (1974a) and Karijord et al. (1982) was close to 0. The sire model and the small number of samples used by these authors could explain this extremely low value.

Heritability observed for the ratio of C14:1 *cis*-9 to C14:0 was similar to the one found for %MONO (20%). This similarity between %MONO and this Δ^9 -desaturase index is partially explained by their link with the

Table 4. Percentage of variation measured on total fixed effects explained by each separate studied fixed effect after their introduction in the model and their significance¹

Trait	Total variation explained by studied effect (%)		
	Herd	DIM	Age
Milk yield (in kg)	68.81 (***)	31.11 (***)	0.08 (**)
% Fat (g/100 g of milk)	84.80 (***)	14.52 (***)	0.68 (***)
% Protein (g/100 g of milk)	49.59 (***)	50.35 (***)	0.06 (NS)
%MONO (g/100 g of fat)	89.53 (***)	10.43 (***)	0.04 (NS)
C14:1 <i>cis</i> -9/C14:0	95.79 (***)	3.95 (***)	0.26 (***)
C16:1 <i>cis</i> -9/C16:0	97.55 (***)	2.38 (***)	0.07 (NS)
C18:1 <i>cis</i> /C18:0	94.45 (***)	4.68 (***)	0.87 (***)
C14:1 <i>cis</i> -9 (g/100 g of fat)	87.40 (***)	12.38 (***)	0.22 (***)
C14:0 (g/100 g of fat)	91.01 (***)	8.96 (***)	0.03 (NS)
C16:1 <i>cis</i> -9 (g/100 g of fat)	94.17 (***)	5.76 (***)	0.07 (*)
C16:0 (g/100 g of fat)	95.92 (***)	4.06 (***)	0.02 (NS)
C18:1 <i>cis</i> (g/100 g of fat)	83.89 (***)	16.09 (***)	0.02 (NS)
C18:0 (g/100 g of fat)	91.94 (***)	8.00 (***)	0.05 (NS)

¹%MONO = the content of monounsaturated fatty acids in milk fat; herd = herd $\times$ test date $\times$ lactation number; DIM = class of DIM $\times$ class of lactation number; age = class of age $\times$ class of lactation number.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 2. Variation of unadjusted means for milk yield, % fat, and % monounsaturated fatty acids (%MONO) in fat in function of class of 15 DIM and lactation number. Number of samples used for estimating the value of each data point ranged from 193 to 1,250.

Δ^9 -desaturase activity; %MONO includes several FA whose production is partially catalyzed by the Δ^9 -desaturase (Chilliard et al., 2001). The ratio of C14:1 *cis*-9 showed a similar heritability. This result was expected because of the origin of this FA. Nearly all C14:0 in milk fat is produced by de novo synthesis in the mammary gland. Consequently, the desaturation should be

Figure 3. Variation of unadjusted means for the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1 *cis*-9 to C18:0 in function of class of 15 DIM and lactation number. Number of samples used for estimating the value of each data point ranged from 45 to 268.

the main source of C14:1 *cis*-9 (Lock and Garnsworthy, 2003). Mosley and McGuire (2007) observed that 90% of C14:1 *cis*-9 was the result of Δ^9 desaturation. Heritability observed for C14:0 was a little lower (15%; Table 5). Due to the endogenous production of C14:0 and C14:1, the effect of feeding on these FA contents is low. This effect could explain the low values of residue observed in Table 5 for the C14 ratio compared with the 2 other Δ^9 -desaturase indices. Heritability estimated by Royal and Garnsworthy (2005), from 1,520 cows and 1 analyzed sample per cow, for the ratio of C14:1 *cis*-9 to the sum of C14:0 and C14:1 *cis*-9 was equal to 30%.

Figure 4. Variation of unadjusted means for the 3 studied saturated fatty acids in function of class of 15 DIM and lactation number. Number of samples used for estimating the value of each data point ranged from 45 to 268.

Karijord et al. (1982) obtained heritability values equal to 7% for C14:0 and 26% for C14:1.

The ratio of C16:1 *cis*-9 to C16:0 had a heritability equal to 20%. Palmitic acid is synthesized *de novo* in the mammary gland and is also extracted from blood. Mosley and McGuire (2007) showed that 50% of the C16:1 *cis*-9 came from the Δ^9 desaturation. The herita-

Figure 5. Variation of unadjusted means for the 3 studied unsaturated fatty acids in function of class of 15 DIM and lactation number. Number of samples used for estimating the value of each data point ranged from 45 to 268.

bility for this ratio was more similar to that observed for the ratio of C14:1 *cis*-9 to C14:0. Our result was different from the one obtained by Royal and Garnsworthy (2005), who found the lowest heritability for the ratio of C16:1 *cis*-9 to the sum of C16:0 and C16:1 *cis*-9. Similar heritability values to those observed for

Table 5. Estimate and SE of variances (in % of phenotypic variance) for genetic, 2 permanent environmental, residual random effects estimated for daily milk yield, fat content, protein content, percentage of monounsaturated fatty acids in fat (%MONO), and the 3 Δ^9 -desaturase indices (C14:1 *cis*-9/C14:0, C16:1 *cis*-9/C16:0, and C18:1 *cis*/C18:0)¹

Trait	Permanent environments							
	Heritability						Residual	
	Estimate	SE	Within lactation		Across lactations		Estimate	SE
			Estimate	SE	Estimate	SE		
Milk yield (in kg)	20	1.8	27	0.6	15	1.5	38	0.2
% Fat	33	1.7	4	0.2	5	1.2	57	0.2
% Protein	36	1.8	10	0.3	5	1.2	49	0.4
%MONO	17	1.4	12	1.1	4	0.8	67	0.8
C14:1 <i>cis</i> -9/C14:0	20	1.8	25	1.4	4	0.9	51	0.6
C16:1 <i>cis</i> -9/C16:0	20	2.3	6	1.0	6	2.2	69	0.8
C18:1 <i>cis</i> /C18:0	3	0.2	2	0.4	0	0.0	95	1.0
C14:1 <i>cis</i> -9	20	2.1	8	0.8	10	1.8	62	0.7
C14:0	15	1.3	11	1.1	3	0.8	71	0.8
C16:1 <i>cis</i> -9	22	1.6	12	1.1	3	0.7	63	0.6
C16:0	15	1.8	10	1.1	8	1.7	66	0.8
C18:1 <i>cis</i>	17	1.3	10	1.0	5	0.7	68	0.6
C18:0	16	1.8	3	0.7	7	1.6	73	0.7

¹Sample number = 52,950; cow number = 3,217; sire number = 1,666.

C14:0 and C14:1 *cis*-9 were estimated for C16:0 (15%) and C16:1 *cis*-9 (22%). Heritability values obtained by Karijord et al. (1982) were 15% for C16:0 and 12% for C16:1 *cis*-9.

The heritability estimates for C18:1 *cis* to C18:0, C18:1 *cis*, and C18:0 were 3, 16, and 17%, respectively (Table 5), which are lower than for the ratio of C18:1 *cis*-9 to the sum of C18:0 and C18:1 *cis*-9 by Royal and Garnsworthy (2005). The low heritability can be explained partly by the fact that these FA are primarily extracted from blood (Bobe et al., 1999; Chilliard et al., 2001; Mosley and McGuire, 2007).

Correlations

Genetic correlations between milk yield and %FAT, %PROT were -0.36 and -0.50, respectively. Genetic correlation between %FAT and %PROT was 0.68 (Table 6). These values were in agreement with the ones found in the literature (Roman and Wilcox, 2000). Genetic correlation between %FAT and %MONO was -0.70.

This value was higher than the one obtained by Soyeurt et al. (2007; $r = -0.22$), which can be explained by similar reasons as the differences in heritabilities. Karijord et al. (1982) and Renner and Kosmack (1974b) found a similar genetic correlation. The positive genetic correlation between milk yield and %MONO (0.23) was similar to the one found by Soyeurt et al. (2007) but differed from results obtained by Karijord et al. (1982) and Renner and Kosmack (1974b). Genetic correlations between %MONO and the C14, C16, and C18 ratios were 0.72, 0.62, and 0.97, respectively (Table 6). This observation is explained, because the major part of monounsaturated FA produced endogenously is catalyzed by the Δ^9 -desaturase. The higher genetic correlation between the ratio of C18:1 *cis* to C18:0 and %MONO is explained by the large content of C18:1 present in %MONO (Mosley and McGuire, 2007).

A negative genetic correlation observed between the ratio of C14:1 *cis*-9 to C14:0 and %FAT was equal to -0.66. Negative genetic correlations were also observed for the 2 other studied indices (Table 6). Genetic correla-

Table 6. Genetic (above the diagonal) and phenotypic correlations (below the diagonal) among milk yield, content of fat and protein, percentage of monounsaturated fatty acids in fat (%MONO), and the 3 Δ^9 -desaturase indices¹

Trait	Milk	% Fat	% Protein	%MONO	C14:1/C14:0	C16:1/C16:0	C18:1/C18:0
Milk yield (in kg)		-0.36	-0.50	0.23	0.27	0.10	0.39
% Fat	-0.19		0.68	-0.70	-0.66	-0.43	-0.80
% Protein	-0.32	0.40		-0.48	-0.56	-0.38	-0.29
%MONO	0.02	-0.17	-0.17		0.72	0.62	0.97
C14:1 <i>cis</i> -9/C14:0	0.01	-0.36	-0.20	0.55		0.51	0.82
C16:1 <i>cis</i> -9/C16:0	0.04	-0.14	-0.15	0.65	0.32		0.64
C18:1 <i>cis</i> /C18:0	0.03	-0.15	-0.01	0.21	0.22	0.14	

¹Sample number = 52,950; cow number = 3,217; sire number = 1,666.

Table 7. Genetic (above the diagonal) and phenotypic correlations (below the diagonal) among milk yield, content of fat and protein, and percentage of C14:1 *cis*-9, C14:0, C16:1 *cis*-9, C16:0, C18:1 *cis*, and C18:0¹

Trait	Milk	% Fat	% Protein	C14:1	C14:0	C16:1	C16:0	C18:1	C18:0
Milk		-0.36	-0.50	0.21	-0.18	0.14	-0.04	0.32	-0.25
% Fat	-0.19		0.68	-0.48	0.40	-0.24	0.52	-0.73	0.36
% Protein	-0.32	0.40		-0.34	0.43	-0.24	0.42	-0.56	0.05
C14:1	0.08	-0.55	-0.10		-0.05	0.40	-0.16	0.40	-0.60
C14:0	0.05	-0.12	0.19	0.34		-0.26	0.36	-0.75	-0.22
C16:1	0.05	-0.09	-0.09	0.09	-0.28		-0.18	0.41	-0.13
C16:0	0.00	0.15	0.14	0.10	0.41	-0.03		-0.72	0.03
C18:1	0.02	-0.13	-0.20	-0.06	-0.78	0.39	-0.64		-0.29
C18:0	-0.09	0.30	-0.15	-0.53	-0.41	-0.11	-0.31	0.14	

¹Sample number = 52,950; cow number = 3,217; sire number = 1,666.

tions obtained for the studied indices could suggest the inhibition of milk fat synthesis when a higher Δ^9 -desaturase activity is observed. This enzyme catalyzes the production of CLA (Bauman et al., 1999). Some previous studies indicated that some isomers of CLA inhibit milk fat synthesis. For instance, Chouinard et al. (1999) and Perfield et al. (2007) suggested that CLA altered milk FA composition and inhibited milk fat synthesis. This observation is confirmed by the genetic correlations obtained between %FAT and each individual studied monounsaturated FA (Table 7).

Similarly, genetic correlations for the 3 Δ^9 -desaturase indices and %PROT were similar, lower than those observed between these ratios and %FAT. The reason could be that some products resulting from the Δ^9 desaturation could also inhibit the percentage of protein in bovine milk. No studies were found to corroborate this hypothesis. The genetic correlation between %FAT and %PROT was positive due to their similar biological pathways (Barber et al., 1997; Rosen et al., 1999). Consequently, some molecules produced by the desaturation, which inhibit the synthesis of milk fat, could also inhibit the synthesis of protein. The genetic correlations obtained between %PROT and each individual monounsaturated FA studied were also all negative, confirming this possible inhibition of protein synthesis by the Δ^9 -desaturase products (Table 7). The effect of a higher Δ^9 -desaturase activity on the synthesis of milk fat and protein was also observed from the values of phenotypic correlations between %FAT or %PROT and the 3 Δ^9 -desaturase indices (Table 6) and between %FAT or %PROT and the studied individual monounsaturated FA (Table 7).

Genetic correlations among the 3 Δ^9 -desaturase indices were positive. The values of correlations observed in Table 6, especially between the ratio of C14:1 *cis*-9 to C14:0 and C16:1 *cis*-9 to C16:0 or the ratios of C16:1 *cis*-9 to C16:0 and C18:1 *cis* to C18:0, were lower than expected. Genetic correlations observed between the ratio of C14:1 *cis*-9 to C14:0 and C18:1 *cis* to C18:0 were

high (0.82). The ratio of C14:1 *cis*-9 to C14:0 was more related to this last desaturase index than to the ratio of C16:1 *cis*-9 to C16:0. Based on the results indicated by Mosley and McGuire (2007), a higher content of oleic acid compared with palmitic acid (59 vs. 50%) resulted from the Δ^9 desaturation. This slight difference could be explained by the higher genetic correlation observed between the ratio of C14:1 *cis*-9 to C14:0 and C18:1 *cis* to C18:0. Indeed, because 90% of myristoleic acid is converted via the action of Δ^9 -desaturase (Mosley and McGuire, 2007), these FA are more influenced by the Δ^9 -desaturase activity. The phenotypic correlation between these 2 indices was low (0.22).

If the genetic parameters estimated in this study reflect mainly the endogenous production of FA via the Δ^9 -desaturase activity, the phenotypic correlation is also influenced by the permanent environments relative to a specific animal and other factors of variation not explained by the statistical model used (for example, some specific diet effects). Consequently, the lower phenotypic correlation observed between the ratio of C14:1 *cis*-9 to C14:0 and C18:1 *cis* to C18:0 was expected, because C18:0 and C18:1 *cis*-9 are more influenced by feeding. In the same way, the higher phenotypic correlations between the ratio of C14:1 *cis*-9 to C14:0 and C16:1 *cis*-9 to C16:0 (0.32) compared with the observed genetic correlation between these 2 indexes was expected.

Phenotypic correlations between milk yield and the 3 Δ^9 -desaturase indices were close to 0 (Table 6). So, in contrast with %FAT and %PROT, the products secreted by the action of Δ^9 -desaturase did not seem to influence milk production. Perfield et al. (2007) observed that the different treatments of CLA made by these authors did not influence the milk yield of studied cows.

Differences Across Breeds

The difference in %MONO produced by DPB compared with HOL cows was highly significant (Table 8).

Table 8. Differences for milk yield, percentage fat, percentage protein, the content of monounsaturated fatty acids in fat (%MONO), and the 3 Δ^9 -desaturase indices (C14:1 *cis*-9/C14:0; C16:1 *cis*-9/C16:0, and C18:1 *cis*/C18:0) between studied breeds and Holsteins¹

Trait	Dual-purpose Belgian Blue (n = 275)	Red and White (n = 35)	Jersey (n = 46)	Brown-Swiss (n = 61)	Montbeliarde (n = 85)	Normande (n = 162)
Milk yield	-5.13 (***)	-1.77 (**)	-5.54 (***)	-1.90 (**)	-3.42 (***)	-7.05 (***)
% Fat	-0.23 (**)	0.04 (NS)	1.15 (***)	0.40 (***)	0.05 (NS)	0.10 (NS)
% Protein	0.04 (NS)	0.05 (NS)	0.40 (***)	0.28 (***)	0.20 (***)	0.20 (***)
%MONO	1.34 (**)	0.03 (NS)	-1.93 (***)	-1.56 (***)	0.08 (NS)	0.23 (NS)
C14:1 <i>cis</i> -9/C14:0	0.0021 (NS)	-0.0068 (**)	-0.0160 (***)	-0.0130 (***)	-0.0030 (NS)	-0.0031 (NS)
C16:1 <i>cis</i> -9/C16:0	0.0026 (NS)	0.0010 (NS)	-0.0044 (**)	-0.0031 (*)	0.0023 (NS)	0.0030 (**)
C18:1 <i>cis</i> /C18:0	0.03 (NS)	-0.14 (NS)	-0.38 (***)	-0.22 (*)	0.03 (NS)	-0.19 (**)

¹The level of significance is added in parentheses. n = number of pure breed cows. Number of crossbred cows = 1,311; number of pure breed Holstein cows = 1,242.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The DPB cows had a higher content of %MONO in milk fat. The low %FAT synthesized by these cows was in line with the negative value of genetic correlation observed between %FAT and %MONO. This breed showed a Δ^9 activity similar (or slightly higher) to that estimated for HOL cows. The difference of Δ^9 -desaturase activity for the C18:1 *cis*/C18:0 was close to significance, as was previously observed by Soyeurt et al. (2006a).

In the contrast to DPB, JER produced more fat content than HOL cows. The %MONO in JER milk fat was lower than the one observed for HOL. The low activity of Δ^9 -desaturase indices observed for these cows could explain the significant differences observed in fat composition. This result was in agreement with Soyeurt et al. (2006a). Generally, the breed effects were studied using the phenotypic differences observed on a limited number of cows fed with the same diet. Consequently, although the obtained results did not represent exactly the breed differences excluding individual cow differences, these publications gave some indications. Many studies observed the same difference between JER and HOL: Stull and Brown (1964) on 40 to 50 for HOL and 10 to 15 for JER, White et al. (2001) on 18 JER and 19 HOL cows, Drackley et al. (2001) on 4 JER and 4 HOL, and Beaulieu and Palmquist (1995), DePeters et al. (1995), and Morales et al. (2000) on 12 JER and 12 HOL. These last authors found that differences disappeared when cows were fed with soybean.

Similar to JER, BSW cows produced a greater content of %MONO essentially because of the low Δ^9 -desaturase activity observed for this breed. The differences between BSW and HOL shown in Table 8 were significant for %MONO and the 3 Δ^9 -desaturase indices. Kelsey et al. (2003) found a significant difference between BSW and HOL for the activity of Δ^9 -desaturase indices calculated from 113 HOL and 106 BSW. The value for the ratio of C16:1 *cis*-9/(C16:1 *cis*-9 + C16:0) measured by these authors for BSW was lower than that calculated for HOL. The ratio of C18:1/C18:0 calculated by DePe-

ters et al. (1995) from 16 HOL and 29 BSW was larger for BSW than HOL cows. The ratio of C16:1 *cis* to C16:0 calculated from the results mentioned by these authors was similar.

The MON cows did not produce a different %MONO in milk fat. Consequently, Table 8 shows that this breed had Δ^9 -desaturase indices similar to the ones observed for HOL cows. The ratio of C14:1 to C14:0 calculated from FA contents measured by Lawless et al. (1999) from 23 HOL and 29 MON was lower for MON than HOL, whereas the C18 ratio was similar. Soyeurt et al. (2007) have found a significant difference between HOL and MON. This difference could be explained by a larger number of MON cows in this study. Even if the value observed for the ratio of C14:1 *cis*-9 to C14:0 was lower than the one observed from HOL cows, %MONO produced by RED cows was not significantly different. The 2 other Δ^9 -desaturase indices were not different from the ones observed in HOL cows. The %MONO produced by NOR cows was not significantly different from the one observed for HOL cows. The values observed for the ratios of C16:1 *cis*-9 to C16:0 and C18:1 *cis* to C18:0 were different between HOL and NOR (Table 8). The ratios of C14:1 to C14:0 and the total C18:1 to C18:0 calculated from the results obtained by Lawless et al. (1999) showed smaller values for NOR than HOL cows.

CONCLUSIONS

Under the assumption that Δ^9 -desaturase activity can be approximated by the ratio of product to substrate, this study showed different sources of variation for this enzyme. The effect of DIM was significant for all studied traits. A slight increase within lactation was observed for the Δ^9 -desaturase indices. The variation of these indices did not explain completely the variation of monounsaturated FA observed in this study within the lactation. Heritability values obtained for the ratios of C14:1 *cis*-9 to C14:0, C16:1 *cis*-9 to C16:0, and C18:1

cis to C18:0 were 20, 20 and 3%, respectively. The low heritability observed for the third ratio could be explained by the influence of feeding in the production of C18:0 and C18:1 *cis* in milk. However, the distribution of this ratio was not normal. Consequently, the results obtained for the ratio of C18:1 *cis* to C18:0 have to be interpreted cautiously. Negative genetic correlations observed between %FAT or %PROT and the studied indices suggested that an increase of Δ^9 -desaturase activity by some of its products could inhibit the synthesis of milk fat or protein in the mammary gland. Some previous studies observed that some isomers of CLA altered milk FA composition. The implication of Δ^9 -desaturase in the endogenous production of %MONO in milk fat was suggested by the positive genetic correlations observed between %MONO and the 3 Δ^9 -desaturase indices. The values of indices differed between the studied dairy breeds. Particularly, JER cows had lower values compared with HOL and, consequently, had lower content of %MONO in milk fat. The same observation was made for the BSW cows. In contrast, DPB cows produced a higher content of %MONO in milk fat and had slightly higher values. Based on the estimated heritability values, the selection of animals based on their Δ^9 -desaturase indices is feasible. This potential selection program should increase the content of monounsaturated FA and CLA in bovine milk.

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