Short communication: Genetic parameters of individual fatty acids in milk of Canadian Holsteins

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ABSTRACT

The objective of the present study was to estimate heritabilities of milk fatty acids (FA) and genetic and phenotypic correlations among milk FA and milk production traits in Canadian Holsteins. One morning milk sample was collected from each of 3,185 dairy cows between February and June 2010 from 52 commercial herds enrolled in Valacta (Ste-Anne-de-Bellevue, Quebec, Canada). Individual FA percentages (g/100 g of total FA) were determined for each sample by gas chromatography. After editing the data, 2,573 cows from 46 herds remained. Genetic parameters were estimated using multitrait animal models fitted under REML. The model included fixed effects of age at calving and stage of lactation each nested within parity and random effects of herd-year-season of calving, animal, and residual. The pedigree of animals with data was traced back 5 generations on both the male and female sides to account for relationships among animals. The estimates of heritability for individual FA ranged from 0.01 to 0.39, with standard errors ranging from 0.01 to 0.06. Generally, monounsaturated FA (MUFA) and saturated FA (SFA) showed higher heritability estimates than polyunsaturated FA (PUFA). Overall, SFA were negatively genetically correlated with MUFA and PUFA, whereas genetic correlations between MUFA and PUFA were positive. The SFA showed positive associations with fat yield and fat percentage, whereas unsaturated FA were negatively associated with fat yield and fat percentage. Bovine milk FA composition could be improved through genetic selection, and selection for MUFA or against SFA could alter the bovine milk fat profile in a desirable direction.

Key words: cow milk fatty acid, milk production, heritability, genetic correlation

Short Communication

Milk fat provides energy, fat-soluble nutrients, and bioactive lipids such as triacylglycerides, diacylglycerides, SFA, MUFA, PUFA, and phospholipids (German and Dillard, 2006). From a human health point of view, minimal intake of saturated and *trans* FA and an increased intake of n-3 PUFA is desirable; therefore, the American Dietetic Association and the Dietitians of Canada have suggested using low-fat dairy products (Kris-Etherton and Innis, 2007). During the past 20 yr, consumption of bovine milk with a higher fat percentage in Canada has followed a downward trend. The per capita consumption of fluid milk with 3.25% fat (whole milk), milk with 2% fat, and ice cream decreased, whereas that of milk with 1% fat, skim milk, and yogurt increased from 1990 to 2011 in Canada (<http://www.dairyinfo.gc.ca>). This decrease in the consumption of dairy products with higher fat percentage may be due in part to the human health concerns of the FA composition of milk fat. Milk fat has been criticized because of its higher concentration of SFA and low concentrations of MUFA and PUFA. In dairy cows, typical milk fat contains about 70% SFA, 25% MUFA, and 5% PUFA, which is considerably different from the ideal (from a human health perspective) milk fat containing 8% SFA, 82% MUFA, and 10% PUFA (Grummer, 1991). About 60% of the total SFA in bovine milk fat is C14:0 and C16:0 (Mansson, 2008). These SFA are associated with increased levels of cholesterol and an increased risk of cardiovascular diseases (Astrup et al., 2011). Desirable changes in milk FA in regard to human health are to increase the amounts of MUFA and PUFA, particularly conjugated linoleic acid (CLA) *cis*-9,*trans*-11 and n-3 FA, and to decrease in the amounts of SFA, particularly C12:0, C14:0, and C16:0.

The milk FA profile can be improved through changes in the production system (Ashes et al., 1997; Butler et al., 2011) or via genetic selection (Bobe et al., 2008; Stoop et al., 2008). Genetic selection can provide a more permanent solution compared with management-related approaches. Recent studies have focused on estimating genetic parameters of individual FA and have

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found that genetic variability exists among cows with respect to individual FA percentages (Bobe et al., 2008; Stoop et al., 2008; Mele et al., 2009; Garnsworthy et al., 2010). In a previous study, we reported on the genetic parameters of milk FA unsaturation indices in Canadian Holsteins (Bilal et al., 2012). However, no reports are available on the genetic parameters of individual FA in milk fat of Canadian Holsteins. Therefore, the current study was designed to estimate heritabilities of and genetic and phenotypic correlations among individual FA, groups of FA, and their associations with milk production traits in Canadian Holsteins.

The present study was conducted on 3,185 lactating dairy cows from 52 commercial herds enrolled in Valacta (Ste-Anne de Bellevue, Quebec, Canada), between February and June 2010. One morning milk sample was collected from each cow, placed in a vial containing preservative, cooled, and transported to the Crampton Nutrition Laboratory of the Department of Animal Science (McGill University, Macdonald Campus, Sainte-Anne-de-Bellevue, Quebec, Canada) for FA analysis. Fat was extracted from milk samples according to the method described by Hara and Radin (1978) and methyl esters of milk FA were prepared according to Christie (1982) as modified by Chouinard et al. (1999). Fatty acid composition was determined by gas chromatography. After edits (registration status, breed and country of the cow; cow, sire and dam identification; age at calving; DIM; herd-year-season of calving) were applied, the data set included 2,573 cows representing 46 herds that calved during 2009 and 2010. The parity of cows ranged from 1 to 8 and DIM ranged from 3 to 450 d. Heritabilities were estimated for all 33 FA identified. However, only 18 FA were chosen for the estimation of genetic and phenotypic correlations among individual FA and for correlations with production traits in the present study because they accounted for 88.25% of the total FA content and have been cited most often in relation to human health (Palmquist and Griinari, 2006). The test-day milk yield, fat yield, and fat percentage data were obtained on the same day as milk FA data. The fat yield and percentage data were obtained from mixed (morning + evening) milk samples from Valacta.

The MIXED procedure of SAS Institute (2008) was used for preliminary statistical analysis of individual FA to establish the final model for estimation of genetic parameters. The final mixed linear multivariate animal model used for the analysis of all traits considered in the present study was

$$Y_{ijklm} = \mu + P_i + A_{j(i)} + S_{k(i)} + HYS_l \\ + Animal_m + E_{ijklm},$$

where Y_{ijklm} is a measurement of a trait on a milk sample of the m th cow in the l th herd-year-season (HYS) class, k th stage of lactation class in the i th parity and j th age at calving class in the i th parity; μ is the overall population mean; P_i is the fixed effect of the i th parity (3 levels: parity 1, 2, and ≥ 3); $A_{j(i)}$ is the fixed effect of the j th age at calving nested within the i th parity (57 levels); $S_{k(i)}$ is the fixed effect of the k th stage of lactation nested within the i th parity (107 levels); HYS_l refers to the random effect of the l th herd-year-season of calving (115 levels), assumed to be distributed as $N \sim (0, \mathbf{I}\sigma_{hys}^2)$, where $\mathbf{I}$ is the identity matrix and σ_{hys}^2 is herd-year-season variance; $Animal_m$ is the random additive genetic effect of the m th animal, assumed to be distributed as $N \sim (0, \mathbf{A}\sigma_a^2)$, where $\mathbf{A}$ is the additive genetic relationship matrix among animals and σ_a^2 is additive genetic variance; and E_{ijklm} is the random residual associated with each record, assumed to be distributed as $N \sim (0, \mathbf{I}\sigma_e^2)$, where $\mathbf{I}$ is the identity matrix and σ_e^2 is residual variance. The details on various classes related to parity, age at calving, stage of lactation, and HYS are given in Bilal et al. (2012). The pedigree of cows with data was traced back 5 generations on both the male and female sides to account for relationships among animals. The final pedigree file contained 13,102 animals. In total, 580 sires and 2,177 dams had progeny with phenotypes in the data. Estimates of heritabilities of FA percentages and genetic and phenotypic correlations among individual milk FA percentages, FA groups, and production traits were obtained by fitting the above model under REML using Wombat software (Meyer, 2007).

Means, standard deviations, and the proportions of variance explained by HYS for each of the 33 FA are provided in Table 1. The 33 FA reported in the present study accounted for approximately 96.61% of the total FA in milk fat. On average, the total amounts of SFA, MUFA, and PUFA in milk fat were 68.10, 25.23, and 3.27%, respectively. These values are close to the typical bovine milk fat composition reported in the literature, of approximately 70% SFA, 25% MUFA, and 5% PUFA (Grummer, 1991). In accordance with earlier literature estimates, C14:0, C16:0, and C18:1 *cis*-9 (oleic acid) were the most abundant FA in milk fat. These 3 FA constituted 66.73% of the total FA in bovine milk fat.

The proportion of variance related to HYS ranged from 10 to 75%, being lowest for C4:0 and highest for CLA *cis*-9, *trans*-11 (Table 1). For de novo synthesized FA (C4:0 to C14:0), the proportion of variance explained by HYS was less (10 to 20%), possibly because their production is less dependent on diet. The proportion of HYS variance for C16:0 was higher (42%),

Table 1. Means, standard deviations, heritability estimates (h^2) with standard errors of individual FA (measured as g/100 g of total FA), production traits, and proportion of variance explained by herd-year-season of calving (HYS) based on milk samples obtained from each of 2,573 Canadian Holsteins

Item	Mean	SD	HYS variance	h^2	SE
SFA	68.11	4.54	0.34	0.20	0.04
C4:0	0.82	0.15	0.10	0.08	0.03
C6:0	1.04	0.16	0.10	0.14	0.04
C8:0	0.92	0.15	0.13	0.24	0.05
C10:0	2.69	0.52	0.16	0.34	0.05
C11:0	0.23	0.06	0.21	0.25	0.05
C12:0	3.49	0.72	0.20	0.31	0.05
C13:0	0.44	0.26	0.03	0.02	0.02
C14:0	12.34	1.63	0.19	0.19	0.04
C15:0	1.13	0.27	0.30	0.16	0.04
C16:0	34.06	3.95	0.42	0.18	0.04
C17:0	0.65	0.08	0.40	0.21	0.04
C18:0	10.05	2.18	0.35	0.16	0.04
C20:0	0.12	0.03	0.42	0.08	0.03
C22:0	0.05	0.01	0.36	0.07	0.03
C23:0	0.03	0.03	0.39	0.03	0.02
C24:0	0.04	0.03	0.26	0.06	0.04
MUFA	25.23	4.05	0.31	0.21	0.04
C14:1 <i>trans</i> -9	0.26	0.10	0.73	0.02	0.01
C14:1 <i>cis</i> -9	0.99	0.31	0.16	0.39	0.06
C16:1 <i>trans</i> -9	0.32	0.06	0.56	0.05	0.02
C16:1 <i>cis</i> -9	1.77	0.39	0.21	0.30	0.05
C18:1 <i>cis</i> -9	20.33	3.80	0.26	0.20	0.04
C18:1 <i>trans</i> -9	0.27	0.12	0.59	0.01	0.01
C18:1 <i>trans</i> -11	1.29	0.61	0.72	0.03	0.01
PUFA	3.27	0.61	0.51	0.15	0.03
C18:2 <i>trans</i> -9,12	0.17	0.05	0.27	0.02	0.02
C18:2 <i>cis</i> -9,12 (n-6)	1.80	0.39	0.51	0.15	0.03
CLA ¹ <i>cis</i> -9, <i>trans</i> -11	0.43	0.18	0.75	0.07	0.02
CLA <i>trans</i> -10, <i>cis</i> -12	0.02	0.01	0.64	0.01	0.01
C18:3 <i>trans</i> -9, <i>cis</i> -12,15	0.10	0.02	0.31	0.17	0.03
C18:3 <i>cis</i> -9,12,15 (n-3)	0.40	0.14	0.71	0.06	0.02
C20:3n-6	0.09	0.03	0.25	0.21	0.04
C20:4n-6	0.12	0.04	0.32	0.09	0.03
C20:5n-3	0.03	0.02	0.25	0.04	0.02
C22:5n-3	0.10	0.13	0.43	0.01	0.01
Production traits					
Test-day milk yield (kg)	33.73	9.55	0.19	0.22	0.05
Test-day fat yield (kg)	1.28	0.35	0.19	0.18	0.05
Test-day fat percentage (%)	3.86	0.62	0.08	0.34	0.06

¹Conjugated linoleic acid.

which may be explained by the mixed origin of the C16:0 FA; about half of the C16:0 excreted in bovine milk is produced de novo in the mammary gland of cows, whereas the remainder comes through uptake of preformed FA in the diet (Bauman and Grinari, 2003). The proportion of variance attributable to HYS for preformed FA (C18:0 and FA with >18 carbon atoms) was greater (25 to 75%) because these are mainly of dietary origin. The HYS variances for test-day milk and fat yields were similar (19%) but higher than that for test-day fat percentage (8%).

Estimates of heritabilities with standard errors for percentages of individual FA in milk fat, FA groups, and milk production traits are reported in Table 1. Heritability estimates of total SFA, total MUFA, and total PUFA (groups of FA) were 0.20, 0.21, and 0.15,

respectively. The heritability estimates for individual FA ranged from 0.01 to 0.39, with standard errors ranging from 0.01 to 0.06. Among the SFA (C4:0 to C24:0), C10:0 had the highest heritability estimate (0.34) followed by C12:0 (0.31), C14:0 (0.19), C16:0 (0.18), and C18:0 (0.16). Oleic acid (C18:1 *cis*-9) is the main MUFA and constitutes about 80% of the total unsaturated FA in milk of dairy cows (Haug et al., 2007). The heritability estimates of oleic acid (C18:1 *cis*-9), C16:1 *cis*-9, and C14:1 *cis*-9 were 0.20, 0.30, and 0.39, respectively. Heritability estimates of 3 major MUFA were higher than those of their corresponding SFA in the present study: C14:1 *cis*-9 (0.39) and C14:0 (0.19); C16:1 *cis*-9 (0.30) and C16:0 (0.18); C18:1 *cis*-9 (0.20) and C18:0 (0.16). A similar trend was observed by Mele et al. (2009) for all 3 MUFA and by Karijord

et al. (1982) for C14:1 *cis*-9 only. The genetic standard deviations of major FA were also taken into account because a FA with relatively high heritability but a low genetic standard deviation cannot contribute greatly to modifying the whole category. The estimates of genetic standard deviation of C16:0 (1.59) and oleic acid (1.40) were high, followed by C18:0 (0.79), C16:1 *cis*-9 (0.65), C14:0 (0.56), and C14:1 *cis*-9 (0.50). Among the groups of FA, SFA (1.75) had higher estimates of genetic standard deviation, followed by MUFA (1.56) and PUFA (0.70). Furthermore, SFA and MUFA groups as a whole had about the same heritability estimates and genetic variability; therefore, selections in favor of MUFA or against SFA are likely to yield similar results. Heritability estimates for PUFA were generally lower than those of SFA and MUFA and ranged from 0.01 to 0.21. The CLA *cis*-9,*trans*-11 had a low heritability estimate (0.07) in the present study, which is lower than those reported by Mele et al. (2009; 0.12) and Stoop et al. (2008; 0.21) but higher than that reported by Garnsworthy et al. (2010; 0.02). The n-3 FA and CLA *cis*-9,*trans*-11 are the most desirable FA from a human health point of view. The lower heritability estimates for n-3 FA and CLA *cis*-9,*trans*-11 in the present study suggest that the variation among cows in n-3 FA and CLA *cis*-9,*trans*-11 is mainly due to environmental differences.

A possible physiological explanation of the heritability estimates of individual FA can be found in their mode of synthesis. Bovine milk FA originate from 2 main sources: de novo synthesis and dietary uptake of preformed FA. Almost all of C4:0 to C14:0 and about half of C16:0 are synthesized de novo in the mammary gland of cows, whereas the remaining half of C16:0 and C18 or higher carbon chain FA are mainly derived from the diet (Bauman and Griinari, 2003). The C14:1 *cis*-9 had the highest heritability estimate among the FA under study. The C14:0 in milk fat is produced almost exclusively from de novo synthesis in the mammary gland and, therefore, almost all the C14:1 *cis*-9 is synthesized from C14:0 by stearoyl-CoA desaturase enzyme (SCD) activity (Bauman and Griinari, 2003). Consequently, C14:1 *cis*-9 is likely to be under stronger genetic control than the other FA (Mele et al., 2009), followed by C16:1 *cis*-9 and C18:1 *cis*-9.

Overall, heritability estimates of individual FA in the present study are consistent with earlier studies, at least for major FA (Soyeurt et al., 2007; Stoop et al., 2008; Mele et al., 2009; Garnsworthy et al., 2010). A pooled sample of morning and evening milk may give a more accurate FA profile of milk fat of dairy cows compared with only morning milk samples used in the present study. However, previous research has found high correlations for proportions of FA between evening

and morning milk (Morris et al., 2005; Garnsworthy et al., 2010).

Heritability estimates of test-day milk yield, fat yield, and fat percentage were 0.22, 0.18, and 0.34, respectively. Heritability estimates of the majority of important individual FA and groups of FA are close to or higher than the heritability estimates of milk yield, fat yield, and fat percentage, indicating that genetic selection can be effectively used to alter milk fat composition in a desirable direction.

Estimates of genetic and phenotypic correlations among 18 important human health-related individual FA are reported in Table 2. Overall, the phenotypic correlation estimates had the same direction of variation (negative or positive) as the corresponding genetic correlation estimates. The 2 important SFA, C12:0 and C14:0, were strongly positively genetically correlated with each other (0.74) probably because of a common mode of synthesis (i.e., de novo synthesis in mammary gland). The C16:0, which is of mixed origin, had a moderate negative genetic correlation (−0.42) with C14:0. The SFA C18:0, which is of dietary origin, showed negative genetic and phenotypic correlations with C12:0, C14:0 (de novo synthesized), and C16:0 (mixed origin), possibly because of different modes of synthesis. The MUFA with *cis*-9 configuration (C14:1, C16:1, and C18:1) were positively genetically correlated with each other (0.10 to 0.32) and with CLA *cis*-9,*trans*-11. In particular, oleic acid (C18:1 *cis*-9) showed a strong positive genetic correlation (0.62) with CLA *cis*-9,*trans*-11. The possible explanation of positive genetic correlations among the 3 MUFA and between MUFA and CLA *cis*-9,*trans*-11 lies in their common mode of synthesis. Oleic acid (C18:1 *cis*-9), which is the main MUFA and which constitutes about 20 to 25% of the total milk fat, is predominantly synthesized by mammary uptake of C18:0 and its conversion to oleic acid by the enzymatic activity of SCD (Bauman et al., 2006). The C14:1 *cis*-9, C16:1 *cis*-9, and CLA *cis*-9,*trans*-11 are also produced endogenously by the activity of SCD in the mammary gland (Kay et al., 2004). Oleic acid (C18:1 *cis*-9) was negatively genetically correlated with C12:0 (−0.64), C14:0 (−0.28), and C16:0 (−0.65). Oleic acid showed moderate positive genetic correlations with linoleic acid (C18:2 *cis*-9,12; 0.40) and α-linolenic acid (C18:3 *cis*-9,12,15; 0.34). Linoleic acid showed strong positive genetic correlations with α-linolenic acid (0.92) and CLA *cis*-9,*trans*-11 (0.63). It should be noted that a small negative autocorrelation is always present between components in studies where components are expressed as a percentage of the total, especially when there are few components; this negative autocorrelation is expected to be very small in the present study with as many as 33 fatty acids comprising the total.

In general, most of the genetic correlation estimates between SFA and MUFA and between SFA and PUFA were negative, whereas they were positive between MUFA and PUFA. Genetic and phenotypic correlation estimates among 3 FA groups (total SFA, total MUFA, and total PUFA) were also estimated (data not shown). The SFA had strong negative genetic correlation with MUFA (−0.99) and PUFA (−0.71), whereas MUFA and PUFA were positively genetically correlated with each other (0.60), implying that either selection for MUFA or selection against SFA could have a positive effect on milk fat composition.

Estimates of genetic and phenotypic correlations of the 18 individual FA and 3 FA groups with milk production traits are shown in Table 3. Genetic and phenotypic correlations between C16:0 and production traits were positive, particularly with fat yield (0.57) and fat percentage (0.72). In contrast, the more desirable oleic acid and CLA *cis*-9,*trans*-11 showed negative genetic and phenotypic correlations with fat yield and fat percentage. These correlation estimates suggest that selection for increased fat yield and fat percentage is likely to increase the concentration of C16:0, a saturated and potentially harmful FA, and decrease the concentrations of the more desirable oleic acid and CLA *cis*-9,*trans*-11 in milk of dairy cows. Furthermore, a positive association between total SFA and fat yield and fat percentage and negative associations of total MUFA and total PUFA with fat yield and fat percentage reinforce the concept that selection for increased fat yield and fat percentage may have undesirable effects on milk fat composition. Although the standard errors of the genetic correlations were high, the estimates of genetic correlations among FA and between FA and milk production traits reported in the present study are generally comparable with those of earlier studies (Karijord et al., 1982; Stoop et al., 2008; Mele et al., 2009).

Although the more desirable FA (such as oleic acid) were negatively correlated with less desirable ones (such as C16:0), the less desirable FA were positively correlated with test-day fat yield and fat percentage, and the more desirable FA were negatively correlated with fat yield and fat percentage. This presents a challenge for selection as we tend to select for higher production, and milk producers in Canada and many other countries are paid for their milk on the basis of kilograms of fat and protein produced by the cow. The potential application of these results on FA research would require changes in the current dairy industry structure. A payment system based on milk FA profile may be initiated, as suggested by Stoop et al. (2008), to encourage the farmers to produce healthier milk. Furthermore, more reliable genetic parameter estimates

Table 2. Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations¹ among individual FA based on milk samples obtained from each of 2,573 Canadian Holsteins

Item	Fatty acid	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	C4:0																		
2	C12:0	−0.08																	
3	C14:0	−0.03	0.74																
4	C16:0	−0.05	−0.06	−0.42															
5	C18:0	0.34	−0.14	−0.08	−0.36														
6	C20:0	0.29	0.03	−0.14	−0.30	0.97													
7	C14:1 <i>cis</i> -9	−0.33	−0.16	−0.25	0.09	−0.34	−0.44												
8	C16:1 <i>cis</i> -9	−0.20	−0.27	−0.31	0.40	−0.57	−0.35	0.32											
9	C18:1 <i>cis</i> -9	0.01	−0.64	−0.28	−0.65	−0.03	0.06	0.11	0.10										
10	C18:1 <i>trans</i> -11	−0.10	0.05	0.21	−0.54	0.20	0.08	−0.20	−0.28	0.28									
11	C18:2 <i>cis</i> -9,12 (n-6)	−0.15	−0.17	0.03	−0.34	−0.30	−0.46	0.08	−0.07	0.40	0.41								
12	CLA ² <i>cis</i> -9, <i>trans</i> -11	−0.05	−0.22	0.10	−0.27	−0.57	−0.60	0.16	0.14	0.62	0.66	0.63							
13	CLA <i>trans</i> -10, <i>cis</i> -12	0.29	0.62	0.32	−0.32	0.38	−0.08	−0.38	−0.32	−0.24	0.75	0.20	0.02						
14	C18:3 <i>cis</i> -9,12,15 (n-3)	−0.07	−0.00	0.17	−0.40	−0.35	−0.44	0.14	−0.07	0.34	0.53	0.92	0.64	0.26					
15	C20:3n-6	−0.02	0.19	0.05	−0.22	0.25	0.13	−0.03	−0.33	−0.03	−0.04	0.09	−0.14	0.05	0.13				
16	C20:4n-6	−0.34	0.22	0.01	−0.01	−0.30	−0.40	0.08	0.17	−0.03	−0.11	0.13	−0.24	0.26	−0.09	0.35			
17	C20:5n-3	0.09	−0.55	0.04	−0.18	−0.04	0.50	0.22	0.06	−0.20	−0.40	−0.03	−0.11	−0.38	−0.07	0.22	−0.17		
18	C22:5n-3	−0.72	−0.08	−0.27	−0.12	−0.17	0.14	−0.28	0.24	0.34	−0.39	0.05	−0.14	−0.24	−0.07	0.21	0.48	0.72	

¹Standard errors of phenotypic correlations ranged from 0.00 to 0.07 and standard errors of genetic correlations mostly ranged from 0.04 to 0.27.

²Conjugated linoleic acid.

Table 3. Estimates of phenotypic and genetic correlations (SE in parentheses) of important individual FA and groups of FA (expressed as g/100 g of total FA) with milk production traits based on milk samples from each of 2,573 Canadian Holstein cows

Item	Test-day milk yield (kg)		Test-day fat yield (kg)		Test-day fat percentage (%)	
	Phenotypic	Genetic	Phenotypic	Genetic	Phenotypic	Genetic
C4:0	0.02 (0.02)	0.05 (0.22)	0.04 (0.02)	0.24 (0.23)	0.01 (0.02)	0.03 (0.22)
C12:0	−0.02 (0.03)	−0.26 (0.14)	0.06 (0.03)	0.04 (0.16)	0.13 (0.03)	0.43 (0.13)
C14:0	0.13 (0.03)	−0.09 (0.17)	0.06 (0.03)	−0.09 (0.18)	−0.11 (0.03)	0.04 (0.16)
C16:0	0.15 (0.03)	0.10 (0.15)	0.31 (0.03)	0.57 (0.13)	0.26 (0.03)	0.72 (0.10)
C18:0	−0.19 (0.03)	−0.20 (0.17)	−0.12 (0.03)	−0.28 (0.18)	0.07 (0.03)	−0.10 (0.17)
C20:0	−0.13 (0.04)	−0.42 (0.19)	−0.08 (0.04)	−0.26 (0.21)	0.06 (0.03)	0.25 (0.20)
C14:1 <i>cis</i> -9	0.06 (0.03)	0.05 (0.14)	−0.01 (0.03)	−0.01 (0.13)	−0.11 (0.03)	−0.05 (0.13)
C16:1 <i>cis</i> -9	−0.05 (0.03)	0.09 (0.15)	0.02 (0.03)	0.31 (0.15)	0.11 (0.03)	0.24 (0.13)
C18:1 <i>cis</i> -9	−0.11 (0.03)	0.13 (0.16)	−0.24 (0.03)	−0.42 (0.15)	−0.22 (0.02)	−0.85 (0.08)
C18:1 <i>trans</i> -11	−0.01 (0.04)	−0.07 (0.22)	−0.12 (0.04)	−0.44 (0.21)	−0.18 (0.03)	−0.66 (0.18)
C18:2 <i>cis</i> -9,12 (n-6)	0.10 (0.04)	0.24 (0.15)	−0.11 (0.04)	−0.25 (0.16)	−0.29 (0.03)	−0.69 (0.10)
CLA ¹ <i>cis</i> -9, <i>trans</i> -11	0.03 (0.04)	0.35 (0.15)	−0.15 (0.04)	−0.06 (0.17)	−0.29 (0.03)	−0.68 (0.11)
CLA <i>trans</i> -10, <i>cis</i> -12	−0.11 (0.04)	0.40 (0.55)	−0.15 (0.04)	0.29 (0.53)	−0.07 (0.03)	0.04 (0.56)
C18:3 <i>cis</i> -9,12,15 (n-3)	0.02 (0.04)	0.15 (0.17)	−0.06 (0.04)	−0.25 (0.18)	−0.13 (0.03)	−0.55 (0.14)
C20:3n-6	−0.05 (0.03)	−0.10 (0.15)	−0.11 (0.03)	−0.24 (0.15)	−0.09 (0.03)	−0.18 (0.14)
C20:4n-6	−0.15 (0.03)	−0.37 (0.18)	−0.18 (0.03)	−0.40 (0.19)	−0.05 (0.03)	0.05 (0.20)
C20:5n-3	−0.09 (0.03)	−0.52 (0.29)	−0.07 (0.03)	−0.32 (0.32)	0.01 (0.03)	0.18 (0.31)
C22:5n-3	−0.04 (0.04)	−0.77 (0.20)	−0.06 (0.04)	−0.95 (0.21)	−0.03 (0.03)	−0.01 (0.27)
SFA ²	0.09 (0.03)	−0.16 (0.15)	0.29 (0.03)	0.56 (0.12)	0.30 (0.02)	0.94 (0.06)
MUFA ³	−0.10 (0.03)	0.15 (0.15)	−0.27 (0.03)	−0.54 (0.12)	−0.25 (0.03)	−0.89 (0.07)
PUFA ⁴	0.06 (0.04)	0.19 (0.14)	−0.18 (0.04)	−0.41 (0.14)	−0.35 (0.03)	−0.80 (0.08)

¹Conjugated linoleic acid.²SFA includes C4:0; C6:0; C8:0; C10:0; C11:0; C12:0; C13:0; C14:0; C15:0; C16:0; C17:0; C18:0; C20:0; C22:0; C23:0; C24:0.³MUFA includes C14:1 *trans*-9; C14:1 *cis*-9; C16:1 *trans*-9; C16:1 *cis*-9; C18:1 *trans*-9; C18:1 *trans*-11; C18:1 *cis*-9.⁴PUFA includes C18:2 *trans*-9,12; C18:2 *cis*-9,12 (n-6); CLA *cis*-9,*trans*-11; CLA *trans*-10,*cis*-12; C18:3 *trans*-9,*cis*-12,15; C18:3 *cis*-9,12,15 (n-3); C20:3n-6; C20:4n-6; C20:5n-3; C22:5n-3.

of milk FA could be obtained by increasing the number of milk fat samples. Although milk FA analysis using GC gives accurate and more detailed information on major and minor FA in milk fat, it is an expensive and time-consuming option for routine FA analyses of large numbers of milk samples (Soyeurt et al., 2011). A possible alternative could be mid-infrared spectrometry (Soyeurt et al., 2006), which is nondestructive, more efficient, and cheaper than GC. However, Soyeurt et al. (2011) observed that mid-infrared spectrometry is less accurate in determining the FA content in milk fat than that in milk. Moreover, genetic correlations of milk FA with traits other than production (e.g., durability traits and health and fertility traits) will be required before including fat composition in the breeding objective of dairy cattle.

In conclusion, most of the important milk FA displayed reasonable heritability estimates (close to or higher than heritabilities of milk production traits), suggesting that milk fat composition of cows could be changed by genetic selection. Based on the results from the present study, selection for MUFA or against SFA would seem to be an effective and simple way to change the FA composition of bovine milk in a desirable direction, although such a selection objective may somewhat reduce the current industry emphasis on selection for total fat.

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