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Review article

Genetic variability of milk fatty acids

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Abstract. The milk fatty acid (FA) profile is far from the optimal fat composition in regards to human health. The natural sources of variation, such as feeding or genetics, could be used to increase the concentrations of unsaturated fatty acids. The impact of feeding is well described. However, genetic effects on the milk FA composition begin to be extensively studied. This paper summarizes the available information about the genetic variability of FAs. The greatest breed differences in FA composition are observed between Holstein and Jersey milk. Milk fat of the latter breed contains higher concentrations of saturated FAs, especially short-chain FAs. The variation of the delta-9 desaturase activity estimated from specific FA ratios could explain partly these breed differences. The choice of a specific breed seems to be a possibility to improve the nutritional quality of milk fat. Generally, the proportions of FAs in milk are more heritable than the proportions of these same FAs in fat. Heritability estimates range from 0.00 to 0.54. The presence of some single nucleotide polymorphisms could explain partly the observed individual genetic variability. The polymorphisms detected on *SCD1* and *DGAT1* genes influence the milk FA composition. The *SCD1* V allele increases the unsaturation of C16 and C18. The *DGAT1* A allele is related to the unsaturation of C18. So, a combination of the molecular and quantitative approaches should be used to develop tools helping farmers in the selection of their animals to improve the nutritional quality of the produced milk fat.

Keywords: delta-9 desaturase, diacylglycerol O-acyltransferase and genetic, milk fatty acids.

Introduction

Milk fat is a complex mix of tri- and diglycerides, complex lipids, and liposoluble substances (Debry 2001). On average, 96% of milk fat is composed of triglycerides (Jensen 1995), each made up of glycerol esterified with 3 fatty acids (FAs). These are carboxylic acids with aliphatic chains, whose length and degree of saturation vary. According to the saturation, the FAs are divided into 3 classes: saturated FAs (SFAs), monounsaturated FAs (MUFAs), and polyunsaturated FAs (PUFAs).

Dairy products account approximately for 15–25% of fat intake and for 25–35% of SFA intake in human nutrition. Due to the negative effects of some SFAs on human health, milk fat has a bad reputation, because it is composed of 65–75% of SFAs (Debry 2001). Diets rich in SFAs, such as the lauric (C12:0), myristic (C14:0), and palmitic acids (C16:0), are highly related to an increased risk of atherosclerosis, obesity, and coronary heart diseases (e.g. Ulbricht and Southgate 1991; Cox et al. 1995; Hu et al. 1999; Haug et al. 2007). However, not all SFAs increase the cholesterol level in blood with the same proportion. According to Mensink et al. (2003), C12:0 markedly increases the total cholesterol content but decreases the ratio of total cholesterol to HDL cholesterol. This last property is favourable and more marked for C12:0 than for C14:0 and stearic acid (C18:0). C16:0 increases this ratio. The risk of cardiovascular diseases is not influenced by C18:0 (Hu et al. 1999). So, judging the nutritional quality of milk fat only basing on their total SFA content seems to be too generalist.

The unsaturated FAs are usually called 'healthy fats', especially for their impact on the level of cholesterol in blood (Ward et al. 1998;

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Haug et al. 2007). PUFAs decrease the cholesterol content more strongly than MUFAs (Williams et al. 2000). Oleic acid (C18:1 *cis-9*) and linolenic acid (C18:3 *cis-9, cis-12, cis-15*), belonging to the ω-3 family, have anticancer and antiatherogenic properties (et al. 2000; Haug et al. 2007). Besides its effect on cholesterol level, linoleic acid (C18:2 *cis-9, cis-12*), the most important in the ω-6 family, improves the sensibility to insulin and thus reduces the incidences of type 2 diabetes (Hu et al. 2001). This FA has also bactericidal impact on *Lysteria monocytogenes* (Petrone et al. 1998). Western diets are known to be deficient in ω-3 and excessive in ω-6. This disequilibrium promotes many diseases, such as cardiovascular diseases, cancer, and inflammatory or autoimmune diseases (Simopoulos 2002). So, reaching and keeping a lower ratio of ω-6 to ω-3 is important. This ratio is usually higher than 12 in industrialized societies. Current dietary recommendations propose dietary ω-6:ω-3 lower than 5 to reduce the risk of cardiovascular diseases, cancer, autoimmune disorders, allergies, obesity, some mental disorders, etc. (Sabikhi 2004). Excess of ω-6 can lead to disruption of the biosynthesis of prostaglandins and consequently to inflammation, obesity, high blood pressure, irritation of the digestive tract, depressed immune function, and other disorders. Deficiency in ω-3 can also lead to other physiologic disorders, such as asthma and heart diseases (Sabikhi 2004). This ratio is naturally low in milk products (1.6; Haug et al. 2007). Dairy and beef products are rich sources of conjugated linoleic acid (CLA) (2.5–18.0 mg g^{-1} of fat in bovine milk), which is a mixture of positional and geometric isomers of C18:2 *cis-9, cis-12*. This structural variability explains the several functions, sometimes contradictory, attributable to CLA (Lock and Bauman 2004; Parodi 1997; Whale et al. 2004). The most important isomers are the rumenic acid, C18:2 *cis-9, trans-11,* which represents about 75–90% of the total CLA (2004), and C18:2 *trans-10, cis-12*. According to several animal models, CLA exhibits antiatherogenic, antiobesity, and anticarcinogenic proprieties (e.g. Corl et al. 2001, MacDonald 2000; McGuire and McGuire 2000, Parodi 1997). CLA are also able to modulate the immune response and bone growth, to promote cell growth, etc. (e.g. Keating et al. 2005; Lock and Bauman 2004; MacDonald 2000; Tanaka 2005; Whale et al. 2004). More details can be found in many reviews about the effects of FAs on human health (e.g., Hu et al. 2001; Chilliard et al. 2000).

Basing on these health aspects, it would be interesting to modulate the quality of milk fat, and then to promote the production of some FAs in relation to the others. Even if the consumption of dairy products is lower than recommended [450–600 mL of milk and 20–40 g of cheese (Devriese et al. 2006)], the improvement of nutritional quality of milk could have a significant impact only in the context of a balanced diet. Numerous investigations described the feeding effects on milk fat composition (e.g., Chilliard et al. 2000), but information about genetic effects on the FA profile of bovine milk is scarce in the literature. The aim of this paper was to review the impact of genetic factors on the FA composition of bovine milk fat.

Quantitative approach

Breed differences

Several authors observed breed differences in the milk FA profile. Table 1 summarizes the breed differences in FA concentrations in milk fat, observed in various studies and expressed in comparison with Holstein (Soyeurt et al. 2008a). The papers referenced in Table 1 are some examples of available studies on breed differences in FAs. Holstein and Jersey milk fats present the greatest differences. Higher concentrations of SFAs, especially of FAs with short and medium carbon chains, are observed in Jersey milk fat (e.g., Hermansen and Lund 1990; Beaulieu and Palmquist 1995; White et al. 2001; Table 1). However, DePeters et al. (1995) reported that the concentrations of FAs with short and medium chains did not differ. Moreover, the proportion of C16:0 did not differ significantly between Holstein and Jersey milk fat. According to Lawless et al. (1999), Normande and Montbeliarde produce milk fat with the highest proportions of C18:0. In contrast to Normande, however, Montbeliarde milk fat has higher CLA content, as compared to Dutch Holstein milk fat (Table 1).

Unfortunately, the studies focussing on the breed differences in FA composition analysed generally small numbers of milk samples and cows (Table 1). This is related to the cost of the gas chromatographic analysis needed to measure FA concentrations in bovine milk. Recently, Soyeurt et al. (2006a) showed the possibility to estimate the FA concentrations by mid-infrared spectrometry. This technology is faster and cheaper than the reference chemical analysis. Thanks to these estimations of FAs by infrared, Soyeurt et al. (2006b and 2008b) studied the differences across dairy

Table 1. Breed differences in the fatty acid profile of bovine milk fat obtained in various studies of a limited number of cows (N) fed with the same diet (et al. 2008)

Fatty acids	Differences in fatty acid content compared to Holstein (%) within each respective study								
	Guernsey	Jersey				Brown-Swiss		Montbeliarde	Normande
	Stull[1]	Stull[1]	Beaulieu[2]	DePeters[3]	White[6]	DePeters[3]	Kelsey[4]	Lawless[5]	Lawless[5]
	N = 25	N = 10	N = 8	N = 23	N = 18	N = 29	N = 106	N = 29	N = 27
C4:0			–2.43*	–4.90	+3.81(**)	–1.47	+12.36(***)	–5.50	–2.75
C6:0	+20.73	+8.54	+16.67(*)	+3.32(*)	+16.33(**)	+2.21	+7.32 (**)	–2.54	+0.85
C8:0	+13.16	+15.79	+38.46(**)	+7.55(**)	+27.17(**)	+5.03(**)	+13.13(***)	+1.02	+5.10
C10:0	+14.29(**)	+34.10(**)	+43.33(***)	+13.59(**)	+34.00(**)	+4.08(**)	+14.22(***)	+6.98	+9.30
C10:1	+12.5	+70.83						–16.67	0.00
C12:0	+7.59(**)	+36.90(**)	+42.86(***)	+16.90(**)	+34.19(**)	+6.34(**)	+14.41(***)	+6.46	+10.77
C14:0	+5.64	+9.26	+8.62(*)	+2.36	+10.71(**)	+2.14	+4.66 (*)	+2.61	+1.87
C14:1 *cis*	–11.31	–4.76			+1.69		–1.64	–28.09	–10.11
C15:0	–6.80	–2.04					–6.76(**)		
C16:0	+7.20(**)	+5.63(**)	–6.79(*)	–1.24	–1.11	–1.70	+0.96	–11.49	–8.15
C16:1 *9-cis*	–7.14(**)	–16.67(**)		–9.55	–10.71(**)	–1.51	–13.08(***)		
C18:0	+4.64	+1.12	+12.50	+6.61(**)	+0.72	–6.83(**)	–3.42	+10.89	+14.93
C18:1 *9-cis*	–11.15(**)	–12.92(**)	–12.72(**)	–9.51	–10.35(**)	+3.91	–1.96(***)	+5.37 *	+1.37 *
C18:2	–4.92	–4.64	0.00	+1.58	0.00	–4.74	–5.80(***)	+5.94	+3.96
CLA					–21.95(**)		–6.82(***)	+13.07	–5.11
C18:3	–19.79	–32.29	–16.67	+15.50(*)	–2.63	–6.98	–2.56	+1.22	–6.10

[1]Stull et al. (1964); [2]Beaulieu and Palmquist (1995); [3]DePeters (1995); [4]Kelsey et al. (2003); [5]Lawless et al. (1999); [6]White et al. (2001); * = P<0.05; ** = P < 0.01; *** = P < 0.001

breeds on a large dataset using mixed models. The obtained results for Jersey, Montbeliarde, and Normande breeds were generally in agreement with those mentioned in Table 1. Those authors also observed that the milk fat produced by dual-purpose Belgian Blue cows had the highest concentrations of unsaturated FAs. The observed breed differences were partly explained by the values of C14:1 *cis-9*/C14:0, C16:1 *cis-9*/C16:0, and C18:1/C18:0, reflecting the activity of delta-9 desaturase.

Delta-9 desaturase (SCD), also named stearoyl coenzyme-A desaturase (E.C. 1.14.19.1), catalyses the introduction of a *cis*-double bond between carbons 9 and 10 of SFAs with a chain length of 10-18 carbons (Bauman et al. 1999; Thomson et al. 2003). So, it converts specific medium- and long-chain SFAs into the corresponding MUFAs (Reh et al. 2004). This last activity is an essential step in the synthesis of unsaturated FAs. Up to 90% of the CLA in bovine milk is formed due to the activity of this enzyme in the mammary gland (Keating et al. 2005). According to Feng et al. (2007) and Lock and Garnsworthy (2003), the C14 desaturase index is considered as the best indicator of desaturase activity. In fact, 90% of C14:1 *cis-9* is the result of SCD activity (Mosley and McGuire 2007). The total concentrations of MUFAs and CLA should increase in fat if SCD activity rises, improving in this way the nutritional quality of milk. Some studies estimated SCD activity by specific FA indices, defined as ratios of FAs dependent on this enzymatic activity: product/substrate (e.g., Lock and Garnsworthy 2003), substrate/product (e.g., Chouinard et al. 1999) or product/(substrate + product) (e.g., Kelsey et al. 2003). Kelsey et al. (2003) observed that Holstein cows showed higher FA indices compared to Brown-Swiss cows, except for CLA index. The greatest concentrations of MUFAs and CLA observed by those authors for Holstein breed could be explained by this enzymatic activity (Table 1). Soyeurt et al. (2008b) observed the greatest FA indices for the dual-purpose Belgian Blue, explaining partially the greatest concentrations of unsaturated FAs observed for this breed. In the same way, the FA indices of Jersey cows were lower, compared to Holstein cows, explaining partly the high SFA content observed in this breed.

Individual genetic variability

The effects of feeding on FA composition of bovine milk are well known. For a few years, some Belgian and Dutch breeders used specific feeding to increase the concentrations of unsaturated FAs in their milk, especially of ω-3 and CLA. Although this method is efficient, the effects are not durable. If the feeding supplementation stops, the improvement of FA composition disappears. So, animal selection using the genetic variability of FAs should transmit from generation to generation this nutritional improvement. For this purpose, a selection index needs to be developed. The estimation of genetic parameters for FA concentrations in bovine milk is the first step.

The heritability values mentioned in Table 2 differ between the cited studies. The number of analysed samples and the methodology used for estimating the genetic parameters could explain these differences. This section presents the heritability values obtained in various studies, describes the particularities of each study, and discusses all the obtained results.

To our knowledge, Edwards et al. (1973) were the first authors who estimated the genetic parameters of FA concentrations in bovine milk fat. They expressed FA concentrations as molar percentage. The genetic parameters were calculated from 50 winter milk samples (2 × 10 samples from Ayrshire monozygotic twins and 2 × 15 samples from Ayrshire dizygotic twins). Heritabilities were high and ranged between 0.64 and 0.98 (Table 2). This may be partly due to the specific unit, but these values can also be considered as overestimated because of the low number of analysed samples and the biased hypothesis used to calculate the variance components. Environmental variance was estimated from the variance component within monozygotic pairs. The variance components within dizygotic pairs represented the environmental variance and half of the genetic variance. In spite of these overestimated values, this study was the first one showing high heritability for each FA in milk fat.

One year later, Renner and Kosmack (1974a) estimated the genetic parameters of various groups of FAs based on 2082 milk samples collected from the progeny of 10 AI sires by using a sire model. They obtained some heritability estimates of 0.26, 0.06 and 0.04 for the concentrations of FA classes with short and medium carbon chains and of C18 family in milk fat, respectively. Heritability values were 0.26, 0.25 and 0.02 for the same classes of FAs in milk, respectively. From these estimates, it appears that the FA concentrations in milk seem to be more heritable than the concentrations of FAs in milk fat.

Table 2. Heritability of fat content and fatty acid composition of bovine milk and milk fat

Fat or fatty acids	Heritability estimates of fat content and fatty acid content							
	Edwards[1] N = 50	Karijord[2] N = 7000	Soyeurt[3] N = 40 007		Soyeurt[4] N = 52 950	Stoop[5] N = 1918	Bobe[6] N = 592	
	mol %	g/100g fat	g/100g milk	g/100g fat	g/100g fat	%wt	g/l milk	%wt
%Fat	nd	0.09	0.32	0.32	0.33	0.47	nd	nd
C4:0	0.82	nd	nd	nd	nd	0.35	0.01	0.00
C6:0	0.88	0.11	nd	nd	nd	0.39	0.19	0.00
C14:0	0.89	0.07	0.31	0.19	0.15	0.49	0.18	0.00
C14:1	0.98	0.26	nd	nd	0.20	nd	nd	nd
C16:0	0.95	0.15	0.38	0.20	0.15	0.31	0.20	0.09
C16:1	0.92	0.12	nd	nd	0.22	nd	0.34	0.49
C18:0	0.88	0.15	0.30	0.28	0.16	0.19	nd	0.24
C18:1	nd	0.06	0.05	0.15	0.17	0.18	0.25	0.06
C18:2	nd	0.11	0.20	0.15	nd	0.13	0.27	0.00
CLA	nd	nd	nd	nd	nd	0.21	nd	nd
C18:3	0.72	0.09	nd	nd	nd	0.09	nd	nd
SFAs	nd	nd	0.36	0.14	nd	nd	0.27	0.05
MUFAs	nd	nd	0.15	0.24	0.17	nd	0.09	0.08
PUFAs	nd	nd	nd	nd	nd	nd	0.25	0.00

[1]Edwards et al. (1973); [2]Karijord et al. (1982); [3]Soyeurt et al. (2007a); [4]Soyeurt et al. (2008b); [5]Stoop et al. (2008); [6]Bobe et al. (2008); %wt = fatty acid (FA) weight as a proportion of total fat weight; CLA = conjugated linoleic acid; MUFAs = monounsaturated FAs; PUFAs = polyunsaturated FAs; SFAs = saturated FAs; nd = no data

Renner and Kosmack (1974a), Karijord et al. (1982) used also a sire model to estimate the genetic parameters but they calculated the heritability values for the major individual FAs. A total of 7000 milk samples collected from about 30 daughters of each of the 114 selected AI test bulls between January 1979 and August 1979 were used in this study. As in the previous studies, concentrations of FAs were measured by gas chromatography. The heritability values of the FA concentrations in fat (g/100g of fat) ranged from 0.06 to 0.26 (Table 2). The comparison of the studies conducted by Renner and Kosmack (1974) and Karijord et al. (1982) with the one of Edwards et al. (1973) is impossible because the methods and units used were clearly different. Compared to the methodology used by Edwards et al. (1982), the sire model used by Renner and Kosmack (1974) and Karijord et al. (1982) gave more accurate variance components.

Using an animal model instead of a sire model permits to estimate directly the genetic effects of all relatives. Further, this model permits to take into account the performances of ancestors, descendants and collateral relatives, and thus improves the accuracy of the estimation. More recent studies, such as Soyeurt et al. (2007a and 2008b), Stoop et al. (2008) and Bobe et al. (2008), used an animal model to estimate the genetic parameters of FAs.

The previous studies used gas chromatography to measure FA concentrations in milk fat. Although this method is efficient, it requires skilled staff, expensive reagents, and takes time, so only small numbers of samples were analysed. The estimation of the genetic parameters needs a large amount of data, hence Soyeurt et al. (2006a) proposed to use mid-infrared spectrometry to predict the FA concentrations directly in bovine milk. Thanks to the large data set including the spectral data and, thus, the FA concentrations estimated by applying the developed calibration equations on these collected spectra, Soyeurt et al. (2007a) estimated the genetic parameters of FAs by using a multi-trait test-day animal mixed model. A total of 7700 milk samples were collected in 25 herds between April 2005 and May 2006, and analysed by mid-infrared spectrometry. The generated spectra were recorded. To increase the number of contemporaries, milk history of studied animals and herds was added. The final edited data set contained 40 007 records on 2047 cows. Heritability estimates ranged from 0.05 to 0.38 for the individual FA concentrations in milk (g $100g^{-1}$ of milk) and from 0.09 to 0.32 for FA concentrations in fat (g $100g^{-1}$ of fat) (Table 2). One year later, the same authors (Soyeurt et al. 2008b) used the same model but with a larger data set containing 52 950 records (including 10 401 spectral data collected from April 2005 to December 2006) from 3217 cows. Only FA concentrations (g $100g^{-1}$ of fat) related to the delta-9 activity were estimated (C14:0 to C18:1 and MUFAs). Heritability values ranged from 0.15 to 0.33. The results were slightly lower than those estimated previously by the same authors except for C18:1. These differences could be explained mainly by the data (the second data set contained spectral data from a larger number of winter milk samples) and partly by the improvements of the calibration equations (78 reference milk samples used to build the calibration equations instead of 49 used in the previous study).

Stoop et al. (2008) used a single-trait animal mixed model to calculate the heritability of the individual FA measured by gas chromatography and expressed as %wt (FA weight as a proportion of total fat weight), based on 1918 milk samples collected from 1918 cows between February and March 2005. The benefit of using gas chromatography instead of mid-infrared spectrometry is a more accurate measurement of FAs with low concentrations in bovine milk fat. In fact, if the concentration of an individual FA in bovine milk decreases, the accuracy of its prediction by mid-infrared spectrometry decreases (Soyeurt et al. 2006a). Stoop et al. (2008) studied a large number of various FAs, especially of several isomers of C18:1. The various studied isomers showed similar heritabilities, ranging between 0.11 and 0.18. Heritability values for the major FAs ranged from 0.09 to 0.54 (Table 2).

Bobe et al. (2008) calculated the genetic parameters of FAs measured by gas chromatography, using single-trait mixed animal models based on 592 milk samples collected between August 1993 and July 1994 from 233 cows. Heritability values ranged between 0.01 and 0.40 in milk (g L^{-1} of milk) and between 0.00 and 0.49 in fat (%wt) (Table 2).

The comparison of results among the cited studies is difficult because of the diversity of the units used to express the concentrations of FAs, the model used, and the amount of data available. However, some observations made by various authors can be compared. All of these studies confirmed the existence of the genetic variability of the FA concentrations in bovine milk and fat, sug-

gesting a potential future animal selection. Results obtained by Soyeurt et al. (2007a) and Bobe et al. (2008) and presented in Table 2 suggest that the concentrations of FAs in milk (expressed as g $100g^{-1}$ of milk and g $L^{-1}$of milk) are generally more heritable than the concentrations of FAs in milk fat (expressed as g $100g^{-1}$ of fat and %wt). Renner and Kosmack (1974a) also observed this trend. This observation was expected because the fat content of bovine milk is strongly heritable. Heritability of fat percentage ranged from 0.32 to 0.47 (Table 2). Karijord et al. (1982) found a lower value, equal to 0.09. Stoop et al. (2008) as Renner and Kosmack (1974a) suggested a relation between FA length and the heritability estimates. The other cited studies did not observe the same trend.

The improvement of models used to describe the variability of FAs is related to the facilities needed to obtain the FA data. Gas chromatography is too expensive to be used on a large scale to develop the tools needed for the implementation of animal selection based on FA concentrations. The use of mid-infrared spectrometry to predict the FA concentrations in bovine milk is a good alternative method, even if the prediction of FAs with low concentrations in milk is not accurate enough. The implementation of this methodology in the different milk labs used to collect the data for the routine milk recording is a crucial point before thinking about developing a selection programme based on the FA profile. Currently, the Walloon and Luxembourg milk recordings are, to our knowledge, the only ones that record the spectral data during the routine milk infrared analysis used to measure the concentrations of fat, protein, lactose, and urea. However, recently, Foss (Hillerod, Denmark) proposed different calibration equations to predict the FA concentrations in milk. All this suggests that in the near future a larger number of labs could predict the FA concentrations needed for a selection program. Thanks to a larger data set, a test-day animal mixed model could be used to describe the variability of FAs, as done by Soyeurt et al. (2007a, 2007b, 2008b). The use of this type of model presents some advantages, such as a more efficient use of the collected data, a genetic model that accounts better for the biology of dairy cows, a better accounting for short-term environmental effects at each test-day milk recording, and finally, more accurate estimations of cow indices (Schaeffer et al. 2000; Mayeres et al. 2004; Muir et al. 2007). Also due to the availability of data, the model could be improved by the addition of some regressions, to take into account the variation of genetic parameters throughout the lactation. So, parametric curves, such as the Ali-Schaeffer curve, the Wilmink curve, or orthogonal polynomials, could be used to model the random regressions. However, the disadvantage of the test-day model is the computation time, cost, or both (Druet et al. 2003).

The number of FAs is very large: 406 registered currently (Debry 2001). Consequently, it could be interesting to find an indicator that reflects the most important information contained in the FA variability, especially to decrease the computation cost and time. By its implication in the production of MUFAs and CLA, the FA indices could reflect the nutritional quality of bovine milk fat. Royal and Garnsworthy (2005) reported heritability values of 0.30, 0.19, and 0.29 for C14:1/(C14:0+C14:1), C18:1 *cis-9*/(C18:1 *cis-9*+C18:0), and C18:2 *cis-9, trans-11*/(C18:2 *cis-9, trans-11*+C18:1 *trans-11*), respectively. Only C16:1/(C16:0+C16:1) showed a heritability equal to 0.01. Heritability for C14:1 *cis-9*/C14:0, C16:1 *cis-9*/C16:0, and C18:1 *cis*/C18:0 obtained by Soyeurt et al. (2008b) were equal to 0.20, 0.20, and 0.03, respectively. These results showed the individual genetic variability of the FA indices.

The FA composition influences the nutritional quality of milk fat but also the technological properties of butter (Soyeurt et al. 2007b). Increasing the concentrations of unsaturated FAs and short-chain FA improves butter spreadability (Bobe et al. 2007). Bobe et al. (2003) suggested that the phenotypic variation of FA composition was sufficient to modify the textural properties of butterfat. One of the indicators used to determine the hardness of butterfat is the ratio of SFAs to unsaturated FAs. Heritability of this ratio estimated by Soyeurt et al. (2007b) was equal to 0.22. Stoop et al. (2008) found a heritability of 0.20. As expected, the genetic variability of the ratio of SFAs to unsaturated FAs exists.

Molecular approach

Few authors pointed out the *SCD* gene level expression as one of the possible origins of FA variation in milk (e.g., Baumgard et al. 2002; Keating et al. 2005). The bovine *SCD* mRNA, completely cloned and sequenced, spans 5.1 kb and codes for a 355-amino-acid enzyme. The *SCD* gene is identified in various species (e.g., Tabor et al. 1998, Kuchel et al. 2004). Currently, two *SCD* genes are

identified on BTA6 and BTA26 (Campbell et al. 2001; Lengi and Corl 2007). The first *SCD* gene is expressed in several tissues and organs, principally in mammary glands and adipose tissue, but also in the liver, muscle, lung, brain, heart, etc. The second one is principally expressed in the brain (Ward et al. 1998; Yahyaoui et al. 2001). Medrano et al. (1999) identified 8 single-nucleotide polymorphisms (**SNP**) in various bovine breeds (Holstein, Jersey, and Brown-Swiss): 3 SNPs were detected on exon 5 and the others in the 3' UTR of the *SCD* gene. Keating et al. (2005) have characterized the bovine *SCD* gene promoter and studied its regulation on 9 Holstein cows having high and low concentrations of CLA and on 10 cows of various dairy breeds. According to their results, no polymorphic sites between the bovine *SCD* promoters of these 19 cows were shown by the sequence comparison. Keating et al. (2005) concluded that the variations in the levels of CLA in milk could not be explained by polymorphisms of the *SCD* promoter regions. However, these variations could be explained by other hypotheses, such as differences in ruminant synthesis of CLA (or CLA precursors), differences in the regulatory proteins themselves, or by polymorphisms in the coding sequences of the bovine *SCD* gene (Keating et al. 2005). Moioli et al. (2007) and Mele et al. (2006) studied the effect of the SNP (C/T) located on exon 5 of the *SCD* gene from 79 cows belonging to 3 breeds (27 Piedmontese, 27 Valdostana, and 25 Jersey) and from 297 Holstein Italian Friesian cows, respectively. They concluded to a higher enzymatic activity of SCD polymorphism essentially on C14:0 and caproleic acid (C10:1). Recently, Schennink et al. (2008) observed that the *SCD1* V allele was related to higher concentrations of C10:0, C12:0, C14:0, C16:1 *cis-9* and CLA in milk fat.

The diacylglycerol O-acyltransferase (**DGAT-1**) is also implied in the FA composition of bovine milk (Schennink et al. 2007). DGAT-1 is considered as a microsomal enzyme (E.C. 2.3.1.20) able to catalyse the only committed step in triacylglycerol synthesis by using diacylglycerol and fatty acyl CoA as substrates (Cases et al. 1998). Situated on BTA14, the *DGAT1* gene encodes 489 amino acids and comprises 17 exons. By sequencing the bovine *DGAT1* gene, a non-conservative lysine to alanine substitution was observed at position 232 (K232A) and seems to influence the major milk production traits, such as milk yield and milk composition (Grisart et al. 2004; Thaller et al. 2003; Winter et al. 2002). Winter et al. (2002) observed that the lysine variant is associated with greater milk fat content than the alanine variant. According to results of Schennink et al. (2007), K232A led to a larger fraction of C16:0 in milk fat but less C14:0, less unsaturated C18 and less CLA. Further, K232A had a positive effect on the ratio of SFAs to unsaturated FA. This could be explained by the fact that the presence of alanine residue at position 232 could inhibit the acyl-CoA-binding capacity of this enzyme, and this leads to a greater activity or an alteration of specificity of DGAT-1 (Schennink et al. 2007; Winter et al. 2002)

Impact on animal selection

As mentioned previously, thanks to the development of FA calibration equations (Soyeurt et al. 2006a) and the possibility to record all spectra generated during the infrared analysis executed during the milk recording, the creation of a large database including the FA profile is now possible. This data set should permit the development of selection indexes to improve the nutritional quality of milk fat. Which FA should be included in this selection index? The answer to this question is not easy. The genetic correlations among some FAs are high (Soyeurt et al. 2007a; Stoop et al. 2008). This relationship is explained by the similarities in their metabolic production processes. For instance, it will be impossible to increase the concentrations of C18:2 *cis-9, cis-12* without increasing the concentrations of C18:3 *cis-9, cis-12, cis-15*. Besides the relationships among FAs, these milk components are also related to the traditional production traits, such as milk yields, fat or protein contents, and fat or protein yields. The FA composition of milk fat is influenced by fat and protein contents. Negative genetic correlations were observed between the unsaturated FAs and the fat and protein contents (Karijord et al. 1982; Soyeurt et al. 2007a; Stoop et al. 2008). Consequently, as the fat and protein contents influence positively the milk payment, increasing the concentrations of unsaturated FAs should have negative economic impacts for farmers. A new procedure of milk payment needs to be developed, basing on, e.g. the concentrations of some FAs. Thanks to that, many farmers should be interested in improving the nutritional quality of their milk fat, and thus a large selection program could be developed, basing on the genetic variability of FA concentrations in dairy cattle.

During the last few decades, quantitative genetics permitted important genetic progress without knowing the genes responsible for livestock performance. Even if molecular approach is expensive, it permits to identify these genes, so it complements the quantitative approach. For instance, molecular approach permits the quality control of selection, the major gene identification, and development of new methods enabling better estimates of animal performance. Currently, several genetic marker maps are available for many species, and various QTL regions have been identified. Marker-assisted selection is useful in many situations, especially when the accuracy of conventional selection is low, e.g. when studied traits have low heritability or are measured late in life. Some SNPs have been identified on *DGAT1* and *SCD* genes, permitting early selection of animals. Molecular analyses are interesting for the testing animals. For global animal selection on FA composition, the molecular and quantitative approaches should be associated.

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