Review

Animal factors affecting fatty acid composition of cow milk fat: A review

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Abstract

The review summarizes literature dealing with the effects of animal factors (breed, cow individuality, parity and stage of lactation) on fatty acid (FA) composition of milk fat. Genetic parameters affecting the composition of the FAs in milk are reviewed and the possibilities for altering milk fat composition are discussed. Cow individuality and the stage of lactation appear to be the main animal factors affecting milk fat composition. Breed and parity affect the variability in FA composition to a limited extent. Some of these factors can be used effectively to alter milk fat composition. Polymorphism of the enzymes, stearoyl-CoA desaturase (SCD) and acyl-CoA-diacylglycerol acyltransferase (DGAT) can explain to some extent the variability among cows. The great individual differences, probably given by varying SCD activities, may be used in breeding programmes, supported by the heritability estimates determined for individual FAs. Effective results can also be achieved through the combined effect of several factors. For instance, the level of conjugated linoleic acid could be increased not only by feed factors, but also through thorough knowledge of rumen biohydrogenation or by cow selection using information on SCD and DGAT polymorphism. The animal factors that are discussed are closely related to milk yield, particularly fat content. Both parameters can change FA composition. Thus, it is necessary in breeding programmes to take these relationships into consideration, along with known genetic correlations.

Keywords: Breed, genetic correlations, heritability, milk and fat yield, parity, single nucleotide polymorphism, stage of lactation
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Introduction

Interest in the chemical composition of animal fats has increased steadily since the first scientific reports were published on the negative effects of these fats on human health. The consumption of milk and often of other milk products has decreased owing to widespread reports on the hypercholesterolaemic effects of certain fatty acids (FAs) in humans. Such a situation has stimulated interest in research into altering milk fat (MF) composition.

Fatty acids, the most important component of MF, constitute about 90% of its weight. Over 95% of the FAs are bound in triacylglycerols, the remainder in mono- and diacylglycerols, phospholipids and cholesterol esters. Free FAs are present in small proportions. Fatty acids differ in chain length and degree of unsaturation, position and orientation of double bonds. Among the hundreds of FAs that have been identified in MF, only 15 occur at concentrations of 10 g per kg and higher. Saturated and unsaturated FAs constitute about 65% and 35% of the FAs, respectively (Jensen, 2002; Parodi, 2004).

The FAs in ruminant milk are synthesized (i) in the mammary gland (so-called *de novo* synthesis) from acetate and to a lesser extent from β-hydroxybutyrate. The precursors are produced in the rumen from dietary polysaccharides. This is the origin of the FAs with shorter carbon chains (≤C15 and a portion of

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C16), while (ii) about one half of the FAs (a portion of C16 and ≥C17; so-called preformed FAs) are synthesized from dietary lipids and adipose tissue reserves (Bauman *et al.*, 2006; Nafikov & Beitz, 2007; Harvatine *et al.*, 2009).

Trans-isomers of unsaturated FAs (TFA) originate from rumen bacterial biohydrogenation of cis-polyunsaturated FAs obtained from the diet. They constitute up to 5% of all FAs (Precht & Molkentin, 2000; Glasser *et al.*, 2008). Within this group, FAs designated cis-9, trans-11-C18:2, with the trivial name, rumenic acid (Kramer *et al.*, 1998), and trans-10, cis-12-C18:2 are two main isoforms of the group of conjugated linoleic acids (CLAs). The CLAs are considered highly beneficial to human health (Gnädig *et al.*, 2001) and thus desirable in milk products (Dhiman *et al.*, 2005). Nevertheless, these two isoforms can have different effects on metabolism and cell functions. The majority of scientific reports attribute the beneficial properties of the CLA for human health without differentiation of the individual isoforms. However, few investigations have studied the effects of individual isoforms on human health, though some researchers (Rajakangas *et al.*, 2003) have attributed negative effects such as pro-carcinogenic effects (especially colon and prostate cancer) to the trans-10, cis-12 isomer in animals. Furthermore, most of these studies have been conducted on animal models, and recent studies have indicated that some effects observed in animals do not pertain to humans (Gebauer *et al.*, 2007).

Similarly, the odd- and branched-chain FAs (up to 4% of all FAs) in MF have been synthesized predominantly by specific rumen bacteria. The interest in these FAs lies in better understanding of rumen function, their anticarcinogenic activity, as well as their influence on the melting point of MF (for more information see Vlaeminck *et al.*, 2006).

Fatty acid composition, their position in the molecules of triacylglycerols, as well as the proportion of saturated and unsaturated FAs, affect nutritional, sensory and technological properties of MF extensively. However, the perception of optimal FA composition can vary among nutritionists and dairy technologists. A high proportion of saturated FAs can improve fat stability against oxidation and thus diminish a potential for sensory defects. Nevertheless, such a composition has been perceived as undesirable from a nutritional point of view. Saturated FAs, particularly lauric, myristic and palmitic, and TFA have been assessed negatively as risk factors for cholesterolaemia, which, in turn, is considered a risk factor for cardiovascular diseases in humans (Mensink, 2005; Gebauer *et al.*, 2007). However, generalized recommendations to reduce the consumption of fatty dairy foods because of their high content of saturated FAs should be made with caution. Short-chain FAs reduce low-density lipoprotein (LDL)-cholesterol concentration, and the negative effects of ruminant TFA in comparison with industrial TFA are ambiguous (see review by German *et al.*, 2009). Unlike other saturated FAs, stearic acid lowered LDL-cholesterol levels (Hunter *et al.*, 2010). Some mono- (oleic acid) and polyunsaturated FAs (long-chain n-3 FAs) are known to possess substantial antiatherogenic and further positive health properties (Kris-Etherton *et al.*, 2009; Lopez-Huertas, 2010; Siri-Tarino *et al.*, 2010).

The proportion of nutritionally desirable FAs to detrimental ones can be altered, utilizing factors that effectively change MF composition. These factors are usually classified in two or three groups: feed, animal and environmental (Palmquist *et al.*, 1993; Perdrix *et al.*, 1996; Jensen, 2002). To date, the greatest attention has been focused on feed factors. Their application has enabled important essential changes in MF composition, especially following the feeding of oil seeds, and plant and fish oils. A more desirable composition of MF has also been reported for milk from cows on pasture (Chilliard *et al.*, 2001; 2008; Kalač & Samková, 2010).

Over the past few years, numerous reports have been published on the effects of environmental conditions, especially heat stress (e.g. O'Brien *et al.*, 2007; Wang *et al.*, 2010).

In comparison with the abundance of studies on the effect of cow nutrition on FA composition, information on the effect of animal factors is considerably limited. Breed, stage of lactation and cow individuality are the most frequently studied animal factors affecting MF composition. These are assessed alone or in combination with other factors (Kelsey *et al.*, 2003; Secchiari *et al.*, 2003; Soyeurt *et al.*, 2006a; Samková, 2008; Stoop *et al.*, 2009a).

The aim of this article is to review current knowledge of animal factors that can alter the FA composition of MF of cows.

2. Genetic parameters

In comparison with other milk constituents, FA composition is most amenable to change. Goddard (2001) reported that knowledge of genetics could be useful in altering MF composition. Methods to achieve this include choice of breed, traditional breeding programmes, including progeny testing, selection of bulls and cows based on specific genes, and transgenesis.

The application of animal factors to change in fat composition is dependent on genetic variability of individual FAs and their groups. Of special interest is the focus on genetic and phenotypic correlations related to milk production and proportion/production of FAs, as well as relations between individual FAs (see 'Milk and fat yield').

The results reviewed by Gibson (1991) showed that the coefficient of genetic variation was in the range of 0.05 – 0.2 for molar proportion of individual FAs in MF, and heritability estimates were moderate (*ca*. 0.3). These values were calculated from the results obtained from 254 dairy cows, daughters of 10 bulls (Renner & Kosmack, 1974). Higher heritability estimates (0.8 - 0.98) were observed in 25 twins, 15 dizygotic and 10 monozygotic twin pairs (Edwards *et al.*, 1973). Recently the results of genetic research have prompted increasing interest in genetic parameters dealing with FAs (Soyeurt *et al.*, 2007; Bobe *et al.*, 2008; Schennink *et al.*, 2008; Soyeurt *et al.*, 2008a; b; Arnould & Soyeurt, 2009; Mele *et al.*, 2009). These authors proved the existence of genetic variability and determined moderate heritability coefficients based on the results from various countries and breeds, and of numerous animal populations and milk samples.

Stoop *et al.* (2008) estimated genetic parameters for individual FAs, expressed in g/100 g of fat. The data were derived from 1 918 cows (all over 87.5% Holstein-Friesian) and 101 bulls from 398 commercial herds in the Netherlands (Table 1). It was shown that estimates of heritability for the individual FAs and their groups are correlated with the length of the carbon chain: *"de novo"* synthetized FA (C4:0 to C14:0 and half of C16:0) had higher heritability estimates (0.31 - 0.54) than FAs originating from the diet and from body fat mobilization (LCFA and PUFA) (0.09 - 0.21) (Gibson, 1991; Stoop *et al.*, 2008; Bastin *et al*., 2011).

However, heritability estimates for FAs expressed as g/100 g fat have different, mainly higher values than the heritabilities for FAs expressed as g/100 g milk. This suggests a considerable effect of milk yield, similar to the different values of heritability for FAs when expressed in g/day (Soyeurt *et al.*, 2007; Bobe *et al.*, 2008).

Some research groups (Schennink *et al.*, 2008; Mele *et al.*, 2009) have studied genetic variability of unsaturation indices (Table 1). These indices approximate the measurement of stearoyl-CoA desaturase (SCD, also known as Δ^9-desaturase) activity. Several methods may be used to estimate SCD activity. The indices of unsaturation are defined as ratios of FAs dependent on this enzymatic activity: product of Δ^9-desaturase to substrate Δ^9-desaturase (e.g. Soyeurt *et al.*, 2008b), substrate to product (e.g. Chouinard *et al.*, 1999) and product to substrate + product (e.g. Kelsey *et al*. 2003; Schennink *et al.*, 2008). Thus, the interpretation of indices had to be carried out with caution. For instance, although CLA is produced as an intermediate in the rumen biohydrogenation of linoleic acid, its major source in MF is endogenous synthesis by SCD in the mammary gland and other tissues from trans-11-C18:1 acid (vaccenic acid). In fact, vaccenic acid is produced as a rumen biohydrogenation intermediate from both linoleic and linolenic acids. Thus, knowledge on mammary synthesis of MF, rumen fermentation and dietary supply of lipids can be applied to alter MF composition (Lock & Garnsworthy, 2002; Lock & Bauman, 2004; Mosley *et al.*, 2006).

The initial reported relationships indicate a need for further research, which could elucidate the genetics of milk FA unsaturation level and clarify the interaction between genetics and feeding.

3. Breed

Most published papers dealing with the effect of cow breed have evaluated the response in FA composition following a change in feed composition (Carroll *et al.*, 2006; Kliem *et al.*, 2009; Ferlay *et al.*, 2010). Some authors found inter-breed differences in MF composition, resulting in different technological properties with the potential to produce unique milk products (Auldist *et al.*, 2004; De Marchi *et al.*, 2008).

Two breeds, Holstein (Friesian) and Jersey, have been tested most frequently (Morales *et al.*, 2000; White *et al.*, 2001; Croissant *et al.*, 2007). Nevertheless, inter-breed differences in MF composition were reported in other breeds, such as Belgian Blue, Brown Swiss, Montbéliarde, Salers and Simmental (Agabriel *et al.*, 2001; Moore *et al.*, 2005; Soyeurt *et al.*, 2006a; Barłowska *et al.*, 2009), particularly in comparison with the Holstein. Numerous studies compared MF composition of indigenous and universally used breeds,

including their crossbreds (Malacarne *et al.*, 2001; Żegarska *et al.*, 2001; Pešek *et al.*, 2005; Talpur *et al.*, 2006; Moioli *et al.*, 2007; Palladino *et al.*, 2010).

Table 1 Mean, relative standard deviation (RSD), genetic variation (σ^2_a), herd effect (h_{herd})* and heritability estimates (h^2, h^2_{IH})** for milk production, individual fatty acids (FA), groups of FA and FA unsaturation indices measured morning milk of first lactation cows

Traits [1]	Mean	RSD (%)	σ^2_a	h_{herd}	h^2	h^2_{IH}
Milk production						
Milk yield (kg/day)	13.5	20	2.04	0.28	0.29	0.41
Fat content (%)	4.36	16	0.24	0.07	0.47	0.51
Protein content (%)	3.51	9	0.05	0.19	0.53	0.65
Individual FA (g/100 g fat)						
C4:0	3.50	8	0.03	0.17	0.35	0.42
C6:0	2.23	7	0.01	0.16	0.39	0.46
C8:0	1.37	10	0.01	0.20	0.48	0.61
C10:0	3.03	14	0.11	0.24	0.54	0.71
C12:0	4.11	17	0.18	0.43	0.35	0.63
C14:0	11.62	8	0.43	0.18	0.49	0.59
C16:0	32.61	9	2.46	0.29	0.31	0.43
C18:0	8.73	16	0.37	0.19	0.19	0.23
*c*9-C18:1	18.02	12	0.77	0.18	0.18	0.25
*t*11-C18:1	0.77	26	0.01	0.55	0.12	0.28
*c*9,12-C18:2	1.20	24	0.01	0.51	0.13	0.26
*c*9,*t*11-C18:2 (CLA)	0.39	28	<0.01	0.49	0.21	0.42
*c*9,12,15-C18:3	0.41	27	<0.01	0.64	0.09	0.26
Groups of FA (g/100 g fat)[2]						
C6–C12	10.74	11	0.79	0.27	0.49	0.67
C14–C16	44.24	6	0.81	0.35	0.11	0.16
>C18	21.58	11	1.05	0.31	0.18	0.26
S/U	2.80	13	0.03	0.28	0.20	0.28
Indices of Δ^9-desaturases[3]						
C12:1 index	0.027	20	0.09	0.06	-	0.37
C14:1 index	0.105	17	1.35	0.06	-	0.45
C16:1 index	0.042	19	0.30	0.07	-	0.46
C18:1 index	0.676	6	4.36	0.06	-	0.33
CLA index	0.337	12	3.49	0.09	-	0.23

* $h_{herd} = \sigma^2_{herd}/(\sigma^2_a + \sigma^2_{herd} + \sigma^2_e)$, where σ^2_{herd} = herd variation, and σ^2_e = residual variation.
** $h^2 = \sigma^2_a/(\sigma^2_a + \sigma^2_{herd} + \sigma^2_e)$; $h^2_{IH} = \sigma^2_a/(\sigma^2_a + \sigma^2_e)$.
[1] Adapted from Stoop *et al.* (2008) – milk yield, n = 1,783; fat and protein content, individual FA, groups of FA, n = 1,918; and Schennink *et al.* (2008) – indices of Δ^9-desaturases, n = 1 933.
[2] C6 – C12 = sum of C6:0, C8:0, C10:0, and C12:0; C14 – C16 = sum of C14:0 and C16:0; >C18 = sum of *t*4-8-C18:1, *t*9-C18:1, *t*11-C18:1, *c*9-C18:1, *c*11-C18:1, *c*9,12-C18:2, and *c*9,12,15-C18:3.
CLA – conjugated linoleic acid.
S/U = ratio of saturated FA to unsaturated FA.
[3] Indices of Δ^9-desaturases were calculated according to the following example:
C14:1 index = *c*9-C14:1/*c*9-C14:1 + C14:0; CLA index = *c*9,*t*11-C18:2/*c*9,*t*11-C18:2 + *t*11-C18:1.

Comparative studies seem to indicate that dairy breeds with a high milk fat content often have a less desirable MF composition (higher levels of saturated and hypercholesterolaemic FAs, and a lower proportion of polyunsaturated FAs) than breeds with a lower milk yield or fat content. The fat composition produced by indigenous breeds, dual-purpose breeds and crossbreds appears to have a more desirable profile than imported dairy breeds (mostly Holstein). Such differences are apparent from Table 2. The proportions of FA groups that are important from a technological or nutritional point of view (including values of Δ^9-desaturase indices) were calculated from mean proportions of the individual FAs, reported in the cited works.

To select these works, we took into consideration parameters of the experiments (e.g. number of cows, number of analysed samples, number of determined FAs, and type of diets) to ensure maximum comparability of the results. Cow nutrition was the most variable factor in these experiments. The diets varied in forage type (pasture, silage, hay) and in ratio of forage to concentrates. Thus, meta-analysis of data is problematic as various factors are involved in the experiments and the experimental conditions are often described incompletely.

Table 2 Milk production, groups of fatty acids (FA) (means; g/100 g FA), and indices of Δ^9-desaturases in cow milk fat of Holstein (H), Jersey (J), Brown Swiss (BS), Ayrshire (A) and Montbéliarde (M)

	H	J	BS	A	M
n [1]	3/177/177	2/43/93	2/124/142	2/40/80	1/28/64
Milk production					
Milk yield (kg/day)	27.5–38.0	23.6–24.8	21.7–31.5	27.9–34.0	16.9–17.8
Fat content (%)	3.2–3.4	3.7–4.4	3.9–4.4	4.0–4.6	3.6–3.8
Protein content (%)	2.9–3.0	3.4–3.8	3.0–3.5	3.4–3.6	3.1–3.2
Groups of FA [2]					
VFA	5.4–9.6	6.7–12.0	8.6–11.2	9.6–12.0	-
SFA	55.5–64.4	67.0–72.4	57.4–68.7	69.3–74.7	62.8–69.0
HFA	34.5–44.1	44.9–48.7	36.0–47.8	43.9–51.9	-
MUFA	25.0–39.9	20.9–22.5	20.9–29.7	21.5–24.8	16.1–22.0
PUFA	3.3–4.9	3.2–3.5	2.8–4.7	2.5–4.3	2.6–3.2
UFA	28.3–43.8	24.4–25.7	23.9–33.9	24.9–30.6	18.7–25.2
H/U [3]	0.8–1.6	1.8–2.0	1.1–2.0	1.5–2.1	-
S/U [4]	1.3–2.3	2.6–3.0	1.7–2.9	2.3–3.0	2.5–3.7
Indices of Δ^9-desaturases [5]					
C14:1 index	0.059–0.091	0.054–0.075	-	0.078–0.086	0.067–0.072
C16:1 index	0.034–0.067	0.031–0.038	-	0.049–0.059	0.045–0.058
C18:1 index	0.602–0.721	0.574–0.650	0.638–0.682	0.592–0.659	0.662–0.689
CLA index	0.278–0.316	-	0.291–0.430	-	0.329–0.341

[1] n = number of papers/cows/milk samples; adapted from/with number and breed of tested cows:
White *et al.* (2001) – 19 H, 18 J; Kelsey *et al.* (2003) – 113 H, 106 BS; Leiber *et al.* (2005) – 18 BS; Shingfield *et al.* (2005) – 16 A; Bargo *et al.* (2006) – 45 H; Ferlay *et al.* (2006) – 28 M; Mäntysaari *et al.* (2007) – 24 A; Moioli *et al.* (2007) – 25 J.
[2] VFA – volatile FA; SFA – saturated FA; HFA – hypercholesterolaemic FA (sum of C12:0, C14:0, and C16:0); MUFA – monounsaturated FA; PUFA – polyunsaturated FA; UFA – unsaturated FA.
[3] H/U – ratio of HFA to UFA.
[4] S/U – ratio of SFA to UFA.
[5] Indices of Δ^9-desaturases were calculated according to the following example:
C14:1 index = *c*9-C14:1/*c*9-C14:1 + C14:0,
CLA (conjugated linoleic acid) index = *c*9,*t*11-C18:2/*c*9,*t*11-C18:2 + *t*11-C18:1.

Although the collected data were not all available in some cited publications, it is evident from Table 2 that the highest levels of hypercholesterolaemic and saturated FAs were observed in breeds characterized by a high milk fat content, such as the Ayrshire (51.9% and 74.7%) and Jersey (48.7% and 72.4%).

Data on statistically evaluated inter-breed differences in the proportions of individual FAs are presented in Table 3. It may seem somewhat surprising that differences between Holstein and Jersey breeds from several independent investigations are ambiguous for most of the FA profiles. Similar differences in statistical significance are apparent in two studies comparing the Holstein and Brown Swiss breeds.

Table 3 Statistical significance [1] of differences between Holstein (H), and Jersey (J) or Brown Swiss (BS) breeds in proportions of fatty acids (FA), and indices of Δ^9-desaturases in cow milk fat

References [2]	A	B	C	D	E
	Breed differences				
	H vs. J	H vs. J	H vs. J	H vs. BS	H vs. BS
Number of cows	12/12	4/4	19/18	113/106	8/5
Individual FA					
C4:0	*	***	ns	***	ns
C6:0	*	ns	**	**	ns
C8:0	*	ns	**	***	ns
C10:0	*	**	**	***	ns
C12:0	*	***	**	***	ns
C14:0	*	*	**	*	ns
*c*9–C14:1	ns	*	ns	ns	ns
C16:0	ns	*	ns	ns	ns
*c*9–C16:1	*	ns	**	***	ns
C18:0	*	ns	ns	ns	*
*c*9–C18:1	*	**	**	ns	ns
*t*11–C18:1	-	-	-	***	***
*c*9,12–C18:2	ns	ns	ns	***	ns
*c*9,*t*11–C18:2 (CLA) [3]	ns	-	*	**	***
*c*9,12,15–C18:3	ns	*	ns	ns	ns
Indices of Δ^9–desaturases [4]					
C14:1 index	-	-	-	*	ns
C16:1 index	-	-	-	***	ns
C18:1 index	-	-	-	ns	ns
CLA index	-	-	-	***	ns

[1] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.
[2] A – Morales *et al.* (2000); B – Drackley *et al.* (2001); C – White *et al.* (2001); D – Kelsey *et al.* (2003) E – Moore *et al.* (2005).
[3] CLA – conjugated linoleic acid.
[4] Indices of Δ^9–desaturases were calculated according to the following example:
C14:1 index = *c*9–C14:1/*c*9–C14:1 +. C14:0.
CLA index = *c*9,*t*11–C18:2/*c*9,*t*11–C18:2 + *t*11–C18:1.

These results support the opinion that the effect of breed explains only a limited proportion of the variability (Kelsey *et al.*, 2003; Soyeurt *et al.*, 2006a; Samková, 2008). Further reasons for inter-breed differences may be the low number of cows used in these experiments, resulting in different responses of cows on different diets. This suggestion is supported by the results of Ferlay *et al.* (2006). In three experiments with numerically nearly equal groups of Montbéliarde and Tarentaise cows they observed statistical significance differences in the proportion of certain FAs.

Mele *et al.* (2007) and Schennink *et al.* (2008) attributed differences in MF composition among breeds to varying activity of SCD (see Section 4).

4. Cow Individuality

Several papers have reported that the proportion of individual FAs in MF varied among dairy cows within a breed to a greater extent than inter-breed differences (Kelsey *et al.*, 2003; Soyeurt *et al.*, 2006a).

High variability in the composition of MF from cows fed the same diet enabled Bobe *et al.* (2003) to select animals with widely different FA compositions. The authors were successful in obtaining butter with a higher proportion of unsaturated FAs, resulting in better texture parameters: more spreadable, softer, and less adhesive. A further improvement was obtained from a combination of dairy cow selection and change in diet (Bobe *et al.*, 2007b).

Table 4 Range of milk production and fatty acid (FA) composition (g/100 g FA) in cow milk fat of Holstein (H), Brown Swiss (BS), Jersey (J), Friesian (F), and Czech Pied (C) breeds

References [1]	Kelsey *et al.* (2003)		Auldist *et al.* (2004) [2]		Pešek *et al.* (2006)
	Breed				
	H	BS	J	F	C
Number of milk samples	113	106	29	29	55
Milk production					
Milk yield (kg/day)	16.5–61.5	11.2–57.4	-	-	6.6–36.8
Fat content (%)	2.0–6.1	1.9–5.7	4.8–6.8	3.6–5.4	2.7–6.0
Protein content (%)	2.5–3.8	2.6–4.1	3.7–4.6	3.1–4.1	2.8–4.4
Individual FA					
C4:0	2.7–9.4	3.1–7.7	4.2–5.8	4.2–5.4	0.5–3.7
C6:0	1.3–2.6	0.7–2.7	2.7–3.4	2.6–3.3	0.7–2.3
C8:0	0.5–1.3	0.2–1.5	1.5–2.1	1.6–1.9	0.7–1.7
C10:0	0.9–2.9	0.4–3.5	3.1–4.7	3.0–4.2	1.9–4.4
C12:0	0.9–3.2	0.4–3.8	3.0–5.2	3.1–4.4	2.3–5.4
C14:0	4.2–10.9	2.5–10.5	9.6–12.6	8.9–12.6	8.1–15.2
*c*9–C14:1	0.1–1.2	0.2–1.1	0.5–1.1	0.5–1.4	0.4–1.6
C16:0	25.0–33.4	24.4–32.6	23.6–30.3	22.1–32.9	22.5–39.1
*c*9–C16:1	0.8–2.4	0.7–1.8	0.7–1.4	0.9–1.5	1.2–2.8
C18:0	6.6–18.3	8.4–20.7	10.0–14.1	8.7–13.4	5.5–16.1
C18:1	19.6–30.4 [3]	19.4–32.3 [3]	17.6–25.0	17.7–28.1	19.3–30.8
*t*11–C18:1	0.7–2.4	0.6–1.8	-	-	-
*c*9,12–C18:2	2.5–4.4	2.6–4.5	0.9–1.9	1.4–2.3	1.3–3.9
CLA [4]	0.2–0.7 [5]	0.2–0.7 [5]	0.6–1.5	1.0–2.4	-
*c*9,12,15–C18:3	0.2–0.5	0.3–0.5	0.5–0.9	0.6–1.1	0.3–1.0

[1] Different diets were used in the individual papers; the same rations were fed in Kelsey *et al.* (2003) and Auldist *et al.* (2004). [2] Data given in g/100 g fat; [3] *c*9–C18:1; [4] CLA = conjugated linoleic acid; [5] *c*9,*t*11–C18:2 (CLA).

The importance of the effect of cow individuality on MF composition was confirmed by Elgersma *et al.* (2006), who tested the responses of individual cows to changes in diets. They found that even if the patterns in response to the diet changes were similar, the concentration of CLA differed among cows.

The existence of great individual variability in several breeds, characterized by minimum and maximum values in FA composition, is apparent from Table 4. Ranges in nutritionally important FAs such as CLA, hypercholesterolaemic and monounsaturated FAs could be a major factor in altering the proportion of desirable and undesirable FAs.

Lock & Garnsworthy (2002) and Kelsey *et al.* (2003) explained the differences in CLA and monounsaturated FA proportions among individual cows by different SCD activity, similar to inter-breed variability. The SCD, as the key enzyme of mammary lipid metabolism, participates in the formation of the double bond in the cis-Δ^9- position in a large spectrum of medium- and long-chain FAs. Variability in SCD activity is explained by single nucleotide polymorphism (SNP) in the SCD gene located on chromosome 26 (exon 5) (Mele *et al.*, 2007; Schennink *et al.*, 2008). SNP causes substitution (A293V) of valine (allele *V*) with alanine (allele *A*). Thus, there are three genotypes *(VV, VA,* and *AA)* with different distributions in breeds. The SCD allele *A* was associated with a higher proportion of monounsaturated FAs.

Kgwatalala *et al.* (2007) hypothesized that SNP in the SCD gene accounts for some differences between Canadian Holstein and Jersey cattle. While three SNPs (A702G, T762C, C878T) were identified in both breeds (44 and 48 cows, respectively), only one SNP (G435A) was unique to Holsteins. Thus, SNPs characterized four genetic variants in Holsteins, with only two variants in Jerseys.

Single nucleotide polymorphism (A293V) has been associated with some milk FAs in Italian Holstein-Friesian (Mele *et al.*, 2007), Italian Brown (Conte *et al.*, 2010), Piedmontese and Valdostana cattle (Moioli *et al.*, 2007). The distribution of the SCD genotype in 297 Italian Holsteins was 0.27, 0.60, and 0.13 for *AA*, *VA*, and *VV*, respectively. The frequencies of alleles *A* and *V* were 0.57 and 0.43, respectively. Conte *et al.* (2010) found that the allele frequencies in 351 Italian Brown cows were 0.18 and 0.82, respectively. Moioli *et al.* (2007) found frequencies of allele *A* of 0.42 in 27 Piedmontese and 0.65 in 27 Valdostana cows. Schennink *et al.* (2008) reported a high frequency (0.73) of allele *A* in 1725 Dutch Holstein-Friesian cows.

Moreover, Milanesi *et al.* (2008) reported SNPs (A702G, T762C, C878T) in the SCD gene in 11 cattle breeds (in total, 336 animals), studied in Italy. High variability and differences across breeds showed an association to different selection goals (milk, meat, dual-purpose). Such results support the opinion (see Section 3) about milk production, for example milk yield and milk fat, of the individual breeds.

Acyl-CoA-diacylglycerol acyltransferase (DGAT), a key enzyme in triacylglycerol synthesis, may also play a significant role in changing saturated FAs into unsaturated ones. The gene polymorphism in the DGAT gene located on chromosome 14 (exon 8) may explain genetic variation in fat content, milk and fat yields (Hradecká *et al.*, 2008) and it has also a strong effect on milk FA composition (Schennink *et al.*, 2008). Dinucleotide polymorphism (K232A) causes replacement of lysine (allele *K*) with alanine (allele *A*). In comparison with allele *K*, the allele *A* of DGAT was associated with significantly lower indices of C10, C12, C14 and C16 acids and with significantly higher indices of C18 and CLA. The frequencies of allele *A* were 0.6 in 1713 Dutch Holstein-Friesian cows (Schennink *et al.*, 2008) and 0.98 in 351 Italian Brown cows (Conte *et al.*, 2010).

As reported by Schennink *et al.* (2008), genetic variance explained by DGAT polymorphism is lower (3% - 15%) than SCD polymorphism (6% - 52%). Genetic variance due to SCD polymorphism is higher (34% - 2%) for Δ^9-desaturase indices of C10-C14 acids than for Δ^9-desaturase indices of C18 acids (12% - 15%). Relatively high genetic variance explained by SCD and DGAT polymorphism (31% and 14%, respectively) for index C16 can be caused by the two above mentioned ways of C16-FAs formation (*de novo* and preformed).

Similarly, as in the inter-breed differences, varying enzymatic activities in individual cows may be affected by SCD and DGAT polymorphism. Thus, the selection of dairy cows could increase the proportion of nutritionally required FAs.

Stoop *et al.* (2009b) reported that quantitative trait loci (QTL) might also participate in the FA phenotypic variance. QTL is a locus with genes controlling quantitative properties, linked for example with milk composition. However, more genes can be responsible for genetic variation in milk production traits (Goddard, 2001; Ordovas *et al.*, 2008). Phenotypic variance explained by QTL was 3% - 8% and 4% - 13% for short- and medium-chain FAs, respectively, and 4% - 10% for FAs with long carbon chain and 3% - 8% for Δ^9-desaturase indices (Schennink *et al.*, 2009; Stoop *et al.*, 2009b).

As evident from the last two sections, inter- and within-breed differences in MF composition do exist. Based on the recent state of knowledge, several factors may be involved, for example different milk (fat or protein) yields of the individual breeds, different activity of desaturases and genetic polymorphism. The expected discoveries of genetic polymorphism could hold great promise for future explanation of the principles of inter-breed differences and differences in FA formation.

Future knowledge on gene identification and genetic polymorphism can contribute to the elucidation of genetic variance and the process of FA biosynthesis.

5. Parity

Although data in the literature on the effect of parity (or age) on MF composition are limited, it is indisputable that this factor affects MF composition (Kelsey *et al.*, 2003; Craninx *et al.*, 2008; Samková, 2008; Soyeurt *et al.*, 2008b). Most papers categorize cows into two groups, primiparous and multiparous. In experiments, which did not evaluate the factor of parity separately, both groups were present to balance the experimental design (Bargo *et al.*, 2006; Ferlay *et al.*, 2006; Mäntysaari *et al.*, 2007).

As the available data seem to indicate, primiparous cows produce MF with a higher proportion of unsaturated FAs and lower proportion of saturated FAs than cows in second and further lactations. For instance, Thomson *et al.* (2000) reported higher proportions of oleic acid and total unsaturated FAs in the fat of primiparous cows compared with multiparous ones. In a similar comparison, Craninx *et al.* (2008) observed significantly lower levels of palmitic acid and higher levels of stearic acid, oleic acid, VA and CLA in MF of primiparous cows.

The different MF composition from primiparous and multiparous cows can be partially explained by changing milk production and fat content during the individual lactations (Bradford & Allen, 2004). Miller *et al.* (2006) reported that the content of FA synthase in the mammary gland, participating in FA biosynthesis, was very low during the initial third of lactation and then gradually increased in primiparous cows. In multiparous animals the level of FA synthase in the early lactation was the same as that in the primiparous cows at the end of lactation.

Wathes *et al.* (2007) suggested that there are differences between primiparous and multiparous cows in the control of tissue mobilization that may promote nutrient partitioning into growth, as well as milk during the first lactation. Metabolic demands for milk production limit the deposition of preformed FAs to adipose tissue during the initial 90 days of lactation (Lake *et al.*, 2007).

6. Stage of Lactation

The effect of stage of lactation was studied more extensively than the role of parity. Lactation has often been divided into three periods: early (<100 days in milk), mid (100 - 200 days in milk) and late (>200 days in milk).

Milk sampled during these three periods (usually one sample per cow) was used for comparison of differences in FA composition during lactation (Barłowska *et al.*, 2005; Garnsworthy *et al.*, 2006; Mele *et al.*, 2007; 2009). Commonly, the highest sampling frequency has been during the early period (Kay *et al.*, 2005; Komprda *et al.*, 2005; Lake *et al.*, 2007), the period with the most significant changes in FA composition. Some authors took more than five samples during a lactation (Bernal-Santos *et al.*, 2003; Secchiari *et al.*, 2003; Craninx *et al.*, 2008; Samková, 2008).

The most extensive changes in MF composition within early lactation occur during the initial weeks and become less extensive from the eight week of lactation (Bernal-Santos *et al.*, 2003; Secchiari *et al.*, 2003; Kay *et al.*, 2005; Lake *et al.*, 2007). Nevertheless, Fearon *et al.* (2004) reported that during late-lactation cows produced MF containing a significantly higher proportion of unsaturated FAs than during mid-lactation.

Depending on the fat sources (*de novo* synthesis or preformed FAs) the changes in MF composition during the lactation may follow different patterns. As lactation progresses, the relative proportions of most *de novo* FAs (short- and medium-chain FAs) increase, whereas proportions of most preformed FAs (long-chain FAs) decrease (Palmquist *et al.*, 1993; Secchiari *et al.*, 2003; Kay *et al.*, 2005; Komprda *et al.*, 2005; Garnsworthy *et al.*, 2006; Kgwatalala *et al.*, 2009). In the case of C16:0, where only one half originates from *de novo* synthesis, the relationship follows the same pattern as that seen for the FA's synthesised completely *de novo* (Figure 1). Its content is the lowest during the initial days of lactation, while for C18:1 (Figure 2) it

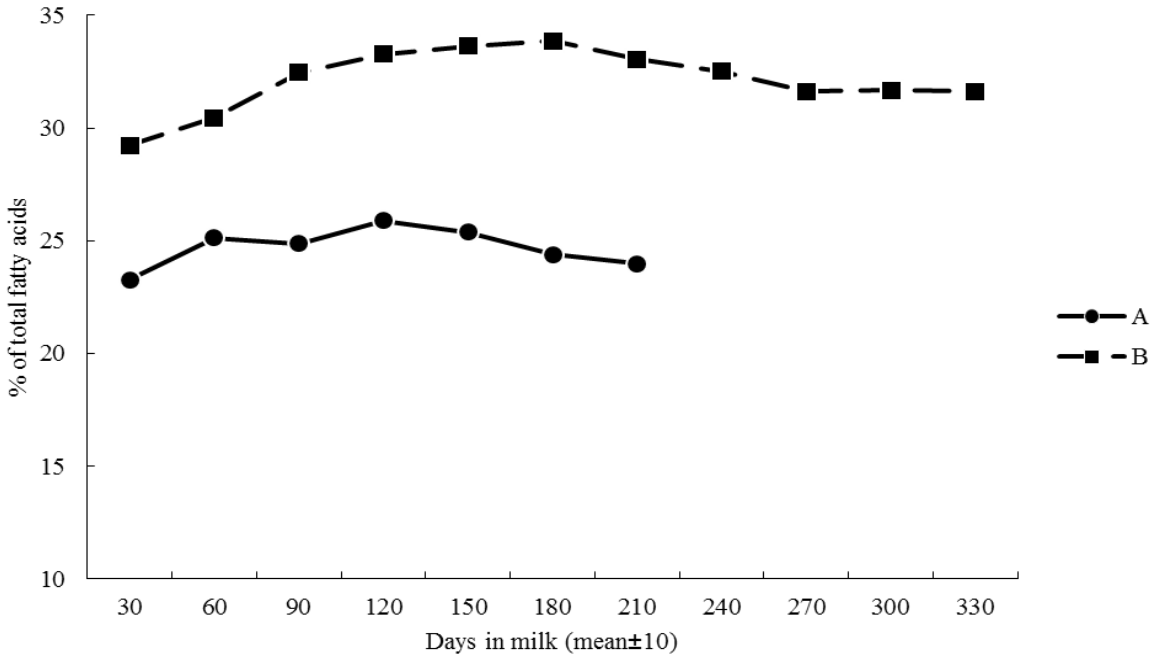

Figure 1 The effect of stage of lactation on the proportion of C16:0 in cow milk fat; adapted from A = Secchiari *et al*. (2003) – g/100 g of fat; B = Samková (2008) – g/100 g of fatty acids.

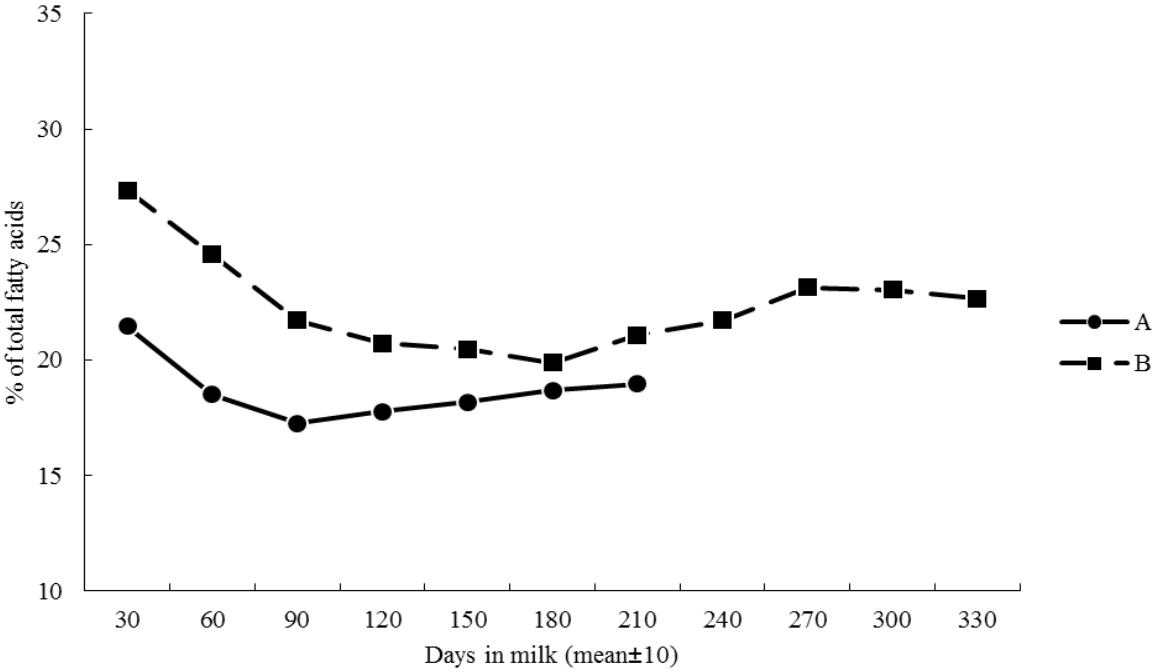

Figure 2. The effect of stage of lactation on the proportion of C18:1 in cow milk fat; adapted from A = Secchiari *et al*. (2003) – g/100 g of fat; B = Samková (2008) – g/100 g of fatty acids.

is at the highest level during this period. This is explained by the negative energy balance in dairy cows with an increased mobilization of long-chain FAs from adipose tissue reserves. Lake *et al.* (2007) reported that cows have a significant energy deficit during the initial 30 days of lactation in particular. The significant role

of energy balance is emphasized by Stoop *et al.* (2009a). According to Bauman & Griinari (2003), the contribution of preformed FAs can vary from about 5% (when cows are in a good physiological state) to 20%.

The odd- and branched-chain FAs with chain lengths of 14 and 15 carbon atoms followed the lactation curves of the short- and medium-chain FAs (increase in early lactation). In contrast, odd- and branched-chain FAs with a chain length of 17 carbon atoms follow the pattern of long-chain FAs, and showed a decrease during the early lactation period (Craninx *et al.*, 2008). Levels of trans isomers of unsaturated FAs, including VA and CLA, were the lowest at early lactation and increased gradually (Figure 3). The highest proportions of VA and CLA were observed at the end of the lactation (Secchiari *et al.*, 2003; Barłowska *et al.*, 2005; Kay *et al.*, 2005; Mele *et al.*, 2007; Samková, 2008; Mele *et al.*, 2009).

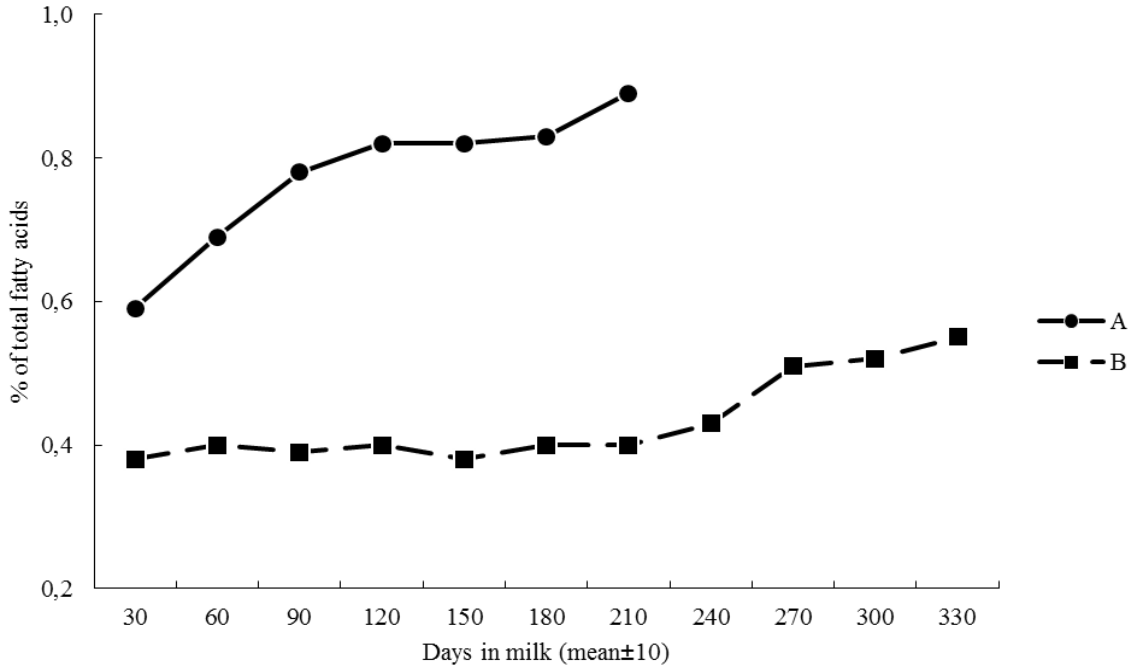

Figure 3 The effect of stage of lactation on the proportion of conjugated linoleic acid (CLA, *c*9,*t*11-C18:2) in cow milk fat; adapted from A = Secchiari *et al.* (2003) – g/100 g of fat; B = Samková (2008) – g/100 g of fatty acids.

7. Milk and Fat Yield

Fatty acid composition has been related to milk production. Milk and fat yields are affected by individual animal factors such as breeds, individuality, parity, stage of lactation and milk production level. The relationships between the parameters of milk production (fat or protein contents, milk yield as well as fat and protein yields) and the FA proportion or FA yield appears to determine the understanding of the animal factor effects. Such relationships have been studied by numerous authors (e.g. Soyeurt *et al.*, 2007; 2008b; Craninx *et al.*, 2008; Schennink *et al.*, 2008; Stoop *et al.*, 2008).

An association between fat content and FA composition has been proven by Åkerlind *et al.* (1999). They tested 48 Swedish Red and White cows selected for high or low milk fat content. Statistically significant differences were found mainly in proportions of FAs with carbon chains ≥C16, including palmitic (higher proportion in cows selected for high fat content), oleic, linoleic, linolenic acids and CLA (higher proportions in cows selected for low fat content). On the other hand, selection for milk yield decreased contents of milk protein and fat but had little effect on milk FA composition (Kay *et al.*, 2005; Bobe *et al.*, 2007b).

Table 5 Genetic correlations between milk yield, fat content, fat yield, and milk fatty acids (FA), groups of FA (g/100 g of fat), and indices of Δ^9-desaturases

References [1]	A	B	A	B	B
	Milk yield (kg/day)		Fat (%)		Fat yield (kg/day)
Individual FA					
C16:0	0.01	-0.50	0.60	0.65	0.18
C18:0	-0.15	0.15	0.84	0.01	0.18
C18:1	0.11	0.32 [2]	-0.78	-0.63 [2]	-0.36 [2]
*t*11-C18:1	-	0.34	-	-0.43	-0.13
*c*9,12-C18:2	-0.01	0.77	-0.37	-0.70	0.04
*c*9,*t*11-C18:2 (CLA) [3]	-	0.33	-	-0.58	-0.30
*c*9,12,15-C18:3	-	0.53	-	-0.75	-0.28
Groups of FA [4]					
C6 – C12	-	0.06	-	0.14	0.26
C14 – C16	-	-0.57	-	0.65	0.13
>C18	-	0.43	-	-0.72	-0.35
SFA	-0.09	-	0.76	-	-
MUFA	0.22	-	-0.22	-	-
S/U [5]	-	-0.23	-	0.56	0.37
Indices of Δ^9-desaturases [6]					
C10:1 index	-	-0.22	-	0.25	-0.05
C12:1 index	-	-0.39	-	0.26	-0.21
C14:1 index	-	-0.39	-	0.31	-0.13
C16:1 index	-	-0.37	-	0.17	-0.21
C18:1 index	-	0.01	-	-0.35	-0.36
CLA index	-	0.05	-	-0.48	-0.44

[1] A = Soyeurt *et al.* (2007) – FA were analyzed by Mid-IR spectrometry; B = Stoop *et al.* (2008) – FA were analyzed by GLC; Indices of Δ^9-desaturases were used from Schennink *et al.* (2008).
[2] *c*9-C18:1.
[3] CLA = conjugated linoleic acid.
[4] C6 – C12 = sum of C6:0, C8:0, C10:0, and C12:0; C14 – C16 = sum of C14:0 and C16:0; >C18 = sum of *t*4-8-C18:1, *t*9-C18:1, *t*11-C18:1, *c*9-C18:1, *c*11-C18:1, *c*9,12-C18:2, and *c*9,12,15-C18:3; SFA = saturated FA; MUFA = monounsaturated FA.
[5] S/U = ratio of saturated FA to unsaturated FA.
[6] Indices of Δ^9-desaturases were calculated according to the following example: C14:1 index = *c*9-C14:1/*c*9-C14:1 + C14:0, CLA index = *c*9,*t*11-C18:2/*c*9,*t*11-C18:2 + *t*11-C18:1.

Soyeurt *et al.* (2007) and Stoop *et al.* (2008) tested genetic correlations between milk yield, fat content, fat yield and FA composition and reported lower correlation between milk/fat yields and FA composition than between fat content and FAs (Table 5). However, Stoop *et al.* (2008) reported a relatively high correlation between milk yield and C16:0 (-0.50) and a moderate one between milk yield and C18:1 (+0.32). Nearly identical genetic correlations were reported in both the papers between fat content and FAs with the highest proportions of acids C16:0 (+0.60 and +0.65, respectively) and C18:1 (-0.78 and -0.63, respectively), supporting the perception that milk from breeds or individual cows with a high milk fat content have a nutritionally less desirable FA composition. The higher fat content was associated with a lower proportion of FAs >C18 and monounsaturated FAs as indicated by correlations of -0.72 and -0.22,

respectively. Genetic correlations of fat content with C10 to C16 Δ^9-desaturase indices were low but positive, whereas with C18 and CLA the indices were negative (Schennink *et al.*, 2008).

The positive genetic correlations observed by Soyeurt *et al.* (2008b) between the indices of C14, C16 and C18 (0.72; 0.62 and 0.97, respectively) and monounsaturated FAs showed that a proportion of the monounsaturated FAs is linked to SCD activity.

Several factors probably explain why the selection for milk production resulted in an increased proportion of *de novo* FAs to preformed FAs. For instance, relatively high genetic correlations were reported between individual FAs (Soyeurt *et al.*, 2007; Stoop *et al.*, 2008). Moderate genetic correlation coefficients were determined between milk yield and FAs and also between fat content and proportion of short- and medium-chain FAs. Furthermore, heritability estimates for these FAs seem to be higher than that for long-chain FAs.

Thus, it is important to pay attention to selection criteria because of their potential effects on various physiological processes (Veerkamp *et al.*, 2003; Martin & Sauvant, 2007). Breeder associations usually use health and other parameters rather than milk yield (kg/d). It would be useful to take into consideration not only the main compositional parameters, fat and protein, but also FA composition or usage of gene-assisted selection as useful selection criteria. Furthermore, association with traits of other dairy cows, such as fertility and longevity, should be considered in the selection process.

The selection of individual cows according to their specific MF composition for particular milk products could be feasible if analytical methods to determine FA composition were available and cheaper than gas chromatography. Mid-infrared spectrometry analysis (Soyeurt *et al.*, 2006b; Kaylegian *et al.*, 2009) seems to be promising in this context. If FA composition could be used in a breeding programme, the ratio of saturated to unsaturated FAs or ratio of hypercholesterolaemic to unsaturated FAs seem to be acceptable selection criteria, though the use of the individual FAs would be too complicated.

Conclusions

Composition of cows' milk fat is influenced by numerous factors, including animal factors. Some of them can be utilized to improve the technological and nutritional properties of milk. It has been shown that FA composition can be affected to a large degree by cow individuality and stage of lactation, while breed and parity are factors of lower significance. Thus, desirable changes in fat composition can be achieved mainly through the factors of cow individuality and, to a lesser extent, breed. The utilization of these factors could be possible owing to the genetic variability in FA composition. The availability of data on genetic parameters (heritability, correlations) for the individual FAs and polymorphism of key enzymes SCD and DGAT can be used to achieve increased levels of nutritionally desirable FAs. Moreover, cows with increased SCD activity in the mammary gland could be selected for an increased production of monounsaturated FAs and CLA.

As the literature data indicate, processes in the rumen have extraordinary effects on FAs' proportion of milk fat. Thus, biochemical changes, especially biohydrogenation, should be studied in more detail.

It is necessary to keep in mind relationships of animal factor effects with milk production, resulting from genetic correlations between milk yield, fat content and proportions of FAs. Selection of cows for low fat content can result in a more desirable milk fat composition for human health, while selection for milk yield can affect the proportion of most individual FAs to a limited extent.

The results of the genetic research seem to hold promise for future efforts aimed at alteration of milk fat composition. Significant advances can be made by utilizing all available knowledge of genetic parameters and heritability concerning short- and medium-chain FAs and genetic polymorphism in medium-chain and unsaturated FAs.

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