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Genetic, physiological and nutritive factors affecting the fatty acid profile in cows' milk – a review

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Fatty Acids (FAs) are a group of compounds with complex structure and different effects on the human organism. There are over 400 FAs in cows milk, many of them as trace amounts. In well fed cows, 95% of milk fat originate from feed and from synthesis in mammary gland, while about 5% come from body fat reserves. There are two ways of FAs formation within the mammary gland. Long-chain FAs originate from triacylglicerols of blood serum, while *de novo* synthesis of FAs (no longer that 16 carbon atoms in mammary gland cells) is a multi-step process, requiring the activity of numerous enzymes (among others Acetyl-CoA Carboxylase, Fatty Acid Synthase, Stearoyl-CoA Desaturase, Diglyceride Acyltransferase). Every enzyme participating in this synthesis is encoded by a different gene: Acetyl-CoA Carboxylase α – ACACA gene, Fatty Acid Synthase – FASN gene, Stearoyl-CoA Desaturase – SCD1 gene, Diglyceride Acyltransferase 1 – DGAT1 gene. Several research show a significant relation between presence of Single Nucleotide Polymorphisms (SNPs) in these genes and FAs profile of cows' milk. Similarly, different non-genetic factors alter the FAs content of milk, one of the most important is nutrition. The FAs profile is affected not only by the type of feed ration (pasture / green forage / silage), but also by plant species offered, concentrates share in feed, supplementation with fat or oilseeds, use of vitamin-mineral complements. Moreover, it changes during lactation and according to body energy status. The aim of this review is to present the recent research concerning genetic, physiological and nutritive factors affecting the FAs profile of cows' milk.

KEY WORDS: cows / fatty acids / milk / non-genetic factors / polymorphism

The Fatty Acids (FAs) are a group of compounds with complex structure and different effects on human organism, divided into FAs with short chain (4-10 carbon atoms) and with long chain (more than 11 carbon atoms), as well as into Saturated

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(SFA) and Unsaturated (Monounsaturated – MUFA and Polyunsaturated – PUFA) Fatty Acids, according to the presence of double bonds. In the UFA group, two families are distinguished: the ω-3 and the ω-6. Depending on the position of hydrogen atoms beside the double bond, two forms of FAs can be distinguished: *cis* (on the same side) and *trans* (on the opposite side). The properties of FAs depend on the chain length plus the number and shape of the double bonds. They serve primarily as energetic material in the form of triglycerides, which are characterized by a high content of fatty acids with chain length from 4 to 14 carbon atoms. Triglycerides are synthesized *de novo* in mammary gland cells. Furthermore, FAs play an essential role in many biological processes in the body, *i.e.* in the synthesis of glycerophospholipids and sphingolipids – important compounds of cell membrane [Hames and Hooper 2012]. There are over 400 fatty acids in milk, many of them in trace amounts [Barłowska and Litwińczuk 2009]. In well-fed cows, 95% of milk fat originate from feed and from synthesis in the mammary gland, only about 5% from body fat reserves. In case of energy deficiency in feed ration, this latter contribution can raise up to 20% or more [Bauman and Lock 2010].

Some groups of FAs have very beneficial properties and a broad spectrum of activity on human organism [Nowakowski *et al.* 2012, Poławska *et al*. 2011]. The most beneficial fatty acids for humans are the PUFAs group, which represents 4-5% of cows' milk fat. Among them are the Essential Fatty Acids (EFA), which are not synthesized by the human body, but must be supplied in the diet (like linoleic and linolenic acid). The EFA group protects against heart disease, by the fact that they have antiarrhythmic, anticoagulant, anti-inflammatory and anti-arteriosclerosis capacities, and also improve endothelial function and reduce blood pressure [Masson *et al*. 2013]. The isomer *cis*-9 *trans*-11 of linoleic acid (CLA – Conjugated Linoleic Acid) is especially important for health, because of its anti-tumor, anti-diabetic and anti-atherosclerotic abilities [Corl *et al*. 2003]. The ω-3 family is also vital, not only due to its significance in growth and development of nurslings, but also because of its beneficial properties for human health. The ω-3 PUFAs have positive effects on reproduction and endocrine system [Gulliver *et al*. 2012]. The content of ω-3 fatty acids of milk is quite low, about 0.5% of total FAs. They are present mostly in the form of linoleic acid. Two derivatives of this fatty acid, eicosapentaenoic acid **(**EPA) and docosahexaenoic acid (DHA), are essential as well [Bauman and Lock 2010]. Moreover, the ratio of ω-3 and ω-6 is also important; it should be around 1:4 [Rustan and Drevon 2005].

Transformations and *de novo* synthesis of FAs

There are two ways of FAs formation inside mammary gland. The long-chain FAs (more than 16 carbon atoms) are supplied by triacylglicerols of blood serum. These triacylglicerols come from three different sources: feed, energetic reserves and *de novo* synthesis in the rumen. The activity of rumen microflora, bacteria (*Butyrivibrio fibrisolvens, Eubacterium spp., Ruminococcus album, Borrelia, Micrococcus, Fusocillus spp.*) and protozoa *Epidinium spp*., causes FAs hydrolysis to esters and in consequence

the release of free FAs plus biohydrogenation of UFA [Palmquist 2005, Elgersma *et al*. 2006, Bauman and Lock 2010]. The level of biohydrogenation of PUFAs depends on their content of feed, on the speed of food passage trough digestive system and on the pH of rumen fluid [Qiu *et al*. 2004]. The UFA C18:2 ω-6 (linoleic) and C18:3 ω-3 (linolenic) are hydrogenated into stearic acid (C18:0). During this process other FAs are formed, like C18:2 *cis*-9 *trans*-11 (CLA) with isomers absorbed in the small intestine and C18:1 *trans*-11 (vaccenic acid). Rumen bacteria produce mostly long-chain FAs from acetic acid [Wu and Palmquist 1991]. The content of FAs in rumen bacteria (mostly C16:0, C18:0, C18:1) range from 50 to 150 g/kg dry matter [Elgersma *et al*. 2006].

Whereas, short-chain FAs (C4-C16) are formed inside mammary gland cells from acetates and 3-hydroxybutanoate. Moreover, the conversion of SFAs (C10:0-C18:0) to their MUFA equivalents in mammary gland can occur [Conte *et al*. 2010].

De novo synthesis of fatty acids in mammary gland cells is a multi-step process, requiring the activity of numerous enzymes. The preliminary stage is transportation of acetyl-CoA (formed from pyruvate) from mitochondria to cytosol, where the synthesis occurs. This process is complex, because the acetyl-CoA molecule must be condensed with oxaloacetate to a citrate form. The citrate is transposed trough mitochondria membrane to cytosol, where it is split by ATP citrate lyase into acetyl-CoA and oxaloacetate, which returns to mitochondria after transformation to pyruvate. During this stage NADPH is produced – an energy but insufficient source for the synthesis. Remaining NADPH required by the synthesis comes from pentose phosphate pathway [Hames and Hooper 2012].

The first phase of FAs synthesis itself is the carboxylation of acetyl-CoA into malonyl-CoA with the use of carbon dioxide. This reaction is catalysed by one enzyme, Acetyl-CoA Carboxylase (ACC). The carboxylation of acetyl-CoA is an example of control on key-step of metabolic pathway. This regulation runs in three ways, through: phosphorylation of ACC, hormonal and allosteric regulation. Thus, it is the step that determines the amount of synthesized FAs [Moioli *et al*. 2005].

The second phase is an elongation of the carbon chain catalysed by multi-functional enzymatic complex – Fatty Acid Synthase (FAS). The chain is built of malonyl-CoA and acetyl-CoA in presence of NADPH [Matsumoto *et al*. 2012a]. The elongation proceeds in four phases: condensation, reduction, dehydration, rereduction. In every elongation phase two new carbon atoms are added to the chain. During this process only SFAs with a chain no longer than 16 carbon atoms are produced. Hence, the longest FA synthesized *de novo* is palmitic acid [Hames and Hooper 2012].

Subsequently, the process of unsaturation in the position *cis*-9 can occur, or an addition of one double bond in the chain between carbon atom 9 and 10 [Schennink *et al*. 2008]. This concerns both FAs derived from blood and synthesised *de novo*. The unsaturation is catalysed by Stearoyl-CoA Desaturase (SCD).

The next step is creation of triglycerides by estrification of acyl-CoA in *sn*-3 position of diacylglicerol [Schennink *et al*. 2008]. This is the last stage of FAs synthesis, as they

are transposed from mammary gland cell to milk in triglyceride form. This process has numerous phases catalysed by several families of enzymes, which ends with a triglyceride formation catalysed by Diglyceride Acyltransferase (DGAT) – Takeuchi and Reue [2009].

Genetic factors affecting fatty acids *de novo* synthesis in mammary gland

Every enzyme participating in this synthesis is encoded by a different gene. In cattle the ACACA gene, encoding Acetyl-CoA Carboxylase α, is located on chromosome 19. Its expression occurs mainly in tissues associated with lipogenesis (liver, kidneys, mammary gland and other) and is linked with four promoters depending on tissue and species. The promoters PI (human) and PIA (rodents and ruminants) are responsible for expression in nervous system and white adipose tissue. The PII is ubiquitous in mammals and is recognized as a house-keeping gene. Whereas the PIII is observed in humans and ruminants and is responsible for the gene expression in the mammary gland during lactation [Matsumoto *et al.* 2012b].

The FASN gene, encoding fatty acid synthase, is also located on the chromosome 19. Its expression in cattle is observed in all tissues and is linked to two promoters. Wherein, the promoter FAS-1 is found exclusively in ruminants, in tissues with the highest FAs production [Laliotis *et al.* 2010].

The SCD gene, encoding Stearoyl-CoA Desaturase, is located on chromosome 26. It has two isoforms in cattle: SCD1 and SCD2. The former is expressed in adipose and mammary tissue while the latter in brain [Schennink *et al.* 2008].

The DGAT1 gene, encoding Diglyceride Acyltransferase 1, is located on chromosome 14, on which a milk fat QTL is positioned. Several authors described its polymorphism with lysine to alanine substitution [Conte *et al.* 2010, Demeter *et al.* 2009, Näslund *et al.* 2008].

The ACACA, FASN, SCD1 and DGAT1 genes polymorphisms in cattle

Matsumoto *et al.* [2012b] analysed the associations of 6 Single Nucleotide Polymorphisms (SNP) of the ACACA gene with Holstein-Friesian (HF) and Japanese Black (JB) cattle. Four of them showed a significant effect on the FAs profile of HF cows' milk, among others on C18:0. The TT genotype of a SNP detected on Coding DNA Sequence (CDS) was associated with a higher percentage of C18:0 comparing to genotype TC. While CCT/CCT type (2 SNP from PIII and 1 SNP of PIA) were linked with a higher percentage of C14:0 comparing to CCT/GTC, with GTC/GTC showing no significant differences. Concerning C16:0, differences were observed in case of GTC/GTC and CCT/CCT types, but not in CCT/GTC type. Moreover, the GTC type indicated a higher percentage of C18:0 comparing to other types. Other authors, analysing this gene, studied the effect of its polymorphism on beef [Shin *et*

al. 2011, Zhang *et al.* 2009] or other species like sheep or goats [Moioli *et al.* 2013, Signorelli *et al.* 2009a, Badaoui *et al.* 2007, Moioli *et al.* 2005].

Several SNPs were detected on FASN gene as well. Matsumoto *et al.* [2012a] found 13 SNPs, among them five were nonsynonymous mutations. Two of them: T1950A and W1955R, described also by Roy *et al.* [2006] affected productive traits of HF cows. The AR/AR type of both SNP was associated with a significantly higher percentage of fat and C14 indices (C14:1/C14:0+C14:1), plus SFAs/MUFAs ratio, comparing to TW/AR type. The research of Matsumoto *et al.* [2012b] and Roy *et al.* [2006] alike, showed that the genotype AA of T1950A was associated with a higher content of milk fat. Whereas Schennink *et al.* [2009] demonstrated that this genotype was linked to a higher content of C14:0 and lower of C18:2 *cis*-9, 12. The second SNP analysed (FASNg.17924A>G), influenced the C14:0, C18:1 *cis*-9 and total unsaturation index. Ciecierska *et al.* [2013] found that cows with AA genotype of this SNP had a higher milk and fat yield, comparing to cows with AG genotype.

The SCD1 is one of well known genes. A nonsynonymous mutation (A293V) consisting of substitution of T to C and causing change of valine to alanine was described by several authors. Schennink *et al.* [2008] studied the effects of this polymorphism on unsaturation indices of FA in HF cows' milk. They showed that allele V was associated with a higher content of C10:0, C12:0, C14:0, C16:1 and CLA, plus a lower content of C10:1, C12:1, C14:1, C18:0 and C18:1 *trans*-11. Moreover, this SNP had a significant influence on the unsaturation indices of different FA ([UFA / UFA + SFA]*100). In the case of allele V, the unsaturation indices were lower for C10, C12 and C14, plus higher for C16, C18 and CLA. Authors suggested that the activity of the enzyme can be changed by this polymorphism, because the SNP causes a substitution of valine to alanine in position 293, located on region 3 rich in histidine of the enzyme. This type of regions have a strong catalytic activity [Shanklin *et al.* 1994]. Conte *et al.* [2010] affirmed that, but they suggested that the SCD1 gene is not the only factor controlling FA unsaturation. They also confirmed that VV genotype is associated with a higher content of C14:1 *cis*-9 and saturation index of C14. A similar relation was found in Canadian Jersey cattle by Kgwatalala *et al.* [2009], who demonstrated that allele A of SCD1 polymorphism affects positively the unsaturation of C10, C12 and C14, but not unsaturation of C16 and C18. Furthermore, they suggested that this polymorphism can be used as a genetic marker in selection of Jersey cattle aiming at amelioration C10, C12 and C14 FA unsaturation. Bouwman *et al.* [2011], analysing genotypes of Dutch population of HF cattle, found that allele A of this SNP was associated with a higher content of C10:1, C12:1 and C14:1, plus a lower content of C10:0, C14:0 and C16:1. A similar relation was observed for C12:0 and C12:1, but the effect of the SNP on C12:0 turn out to be statistically insignificant. Authors noticed that this SNP influence on medium-chain UFAs and their SFA analogues is consistent with the function of encoded enzyme. Macciotta *et al.* [2008] showed that cows with VV genotype had a higher daily milk yield comparing to cows of AA genotype. They did not observe any influence of genotype on fat yield. Signorelli *et al.* [2009b] analysed the A293V

polymorphism in four cattle breeds (HF, Jersey, Piemontese and Valdosana). They showed that this substitution has a slight, insignificant effect on production traits – it affects negatively milk yield and positively fat content. However, Mao *et al.* [2012] were studying Chinese HF cattle and obtained dissimilar results. Cows with AA genotype had a higher test-day, milk yield and fat corrected milk, but a lower fat content of milk, comparing to VV and VA genotypes.

Another well known polymorphism which affects the fat composition of milk and has a significant effect on FAs profile, is K232A mutation in DGAT1 gene. This mutation is responsible for variability of FAs profile in milk at 50% level [Schennink *et al.* 2008]. It consists of a nonsynonymous non-conservative substitution of lysine to alanine [Cardoso *et al.* 2011]. Bouwman *et al.* [2011] detected both alleles (A and K) and found the allele K was associated with a higher content of C6:0, C8:0, C16:0 and C16:1 fractions, plus a lower content of C14:0, C18:1 and CLA fractions. Whereas, Conte *et al.* [2010] showed that AK genotype was linked to a higher content of C14:1 *cis*-9, C16:1 *cis*-9, C18:1 *trans*-6-8, C18:1 *trans*-10, C18:2 *cis*-9 *trans*-11, plus lower content of C10:0, C16:0 *iso*, C18:0, C20:0 and C24:0, comparing to AA genotype. The frequency of KK genotype was too low to be considered in statistical analysis. Schennink *et al.* [2008] demonstrated that allele A was associated with lower unsaturation indices for C10, C12, C14 and C16, plus higher indices for C18, CLA and total unsaturation index. Schennink *et al.* [2007] suggested that the influence of DGAT1 genotype on FAs composition and unsaturation may have two causes: an enhancement of enzyme activity or a change in substrate specificity. Molee *et al.* [2012] detected both alleles in HF crossbred cattle in Thailand. The KK genotype had a stronger influence on milk composition, including fat, rather than AA genotype which influenced more milk yield. Authors supposed that this polymorphism can be used as genetic marker in the selection of crossbred HF cattle. Mao *et al.* [2012] analysed Chinese population of HF cattle. Cows with KK genotype had a lower daily milk yield, but a higher milk fat content, comparing to cows with KA and AA genotypes. Moreover, animals with KA genotype had a higher 305-days milk yield. The substitution of A to K was also associated with a significantly higher fat yield. Cardoso *et al.* [2011] showed that in Girlando cattle allele K was related to a higher daily milk yield and milk production in total. Similar results were obtained in Signorelli's *et al.* [2009b] research on HF and Jersey cattle. Näslund *et al.* [2008] investigated Swedish Red (SRB) and Swedish HF (SLB) cattle genotypes. They showed that the KK genotype was related to a higher fat yield in SRB cows. Moreover, significant differences were shown between genotypes AK and KK concerning the percentage of fat in SLB cattle. Similar results were obtained in Irish HF population [Berry *et al.* 2010]. Authors showed that allele K was associated with a lower milk yield and a higher fat yield. Whereas, Strzałkowska *et al.* [2005] did not observe a significant influence of genotype on daily milk yield in Polish HF cattle. They found a tendency to higher milk yield in cows with AA genotype and a significantly higher fat yield in cows with KA genotype.

Non-genetic factors affecting the fatty acid composition of milk

Milk fat is composed by various types of fat, among them triacylglicerols are the major fraction (96-99%) – Barłowska and Litwińczuk [2009]. The SFAs fraction in cattle stands for 65-75%, while the MUFAs are around 30% of milk fat [Szulc 2012]. The FAs content of milk is mostly conditioned by feeding. It is affected not only by the type of feed (pasture / green forage / silage – Strzałkowska *et al*. [2009a]), but also by plant species, concentrates part in feed ration, supplementation with fat or oilseeds, use of vitamin-mineral complements. Jacobs *et al.* [2011] analysed influence of different types of feed supplements (rapeseed oil, soybean oil, linseed oil, oils mixture 1:1:1) on FAs profile of milk. They showed that in milk from cows fed with the oils mixture, SFA content was significantly lower comparing to the milk from cows fed with rapeseed or linseed oil supplement. Furthermore, the content of PUFAs fraction was higher with use of linseed oil or oils mixture, comparing to rapeseed oil complement. Total content of *trans* FAs tended to increase with oils mixture and rapeseed oil addition. The unsaturation indices were lower with the use of soybean oil and highest with that of the use of oils mixture. The content of C18:2 *cis*-9, 12 in blood serum did not differ significantly in particular groups. Contrary to milk, where a significantly higher content of this FA was detected in the group supplemented with soybean oil, comparing to rapeseed or linseed oil. It may be an evidence for its higher absorption from blood with use of this complement, which is important, because the transfer of PUFAs from feed to milk is usually low in cows. Kupczyński *et al.* [2011] analysed the effect of fish oil with mineral supplementation on milk fat composition. They observed that after 4 weeks of using the supplement, the content of PUFAs fraction increased, similar to CLA *cis*-9 *trans*-11, DHA and EPA content. Comparing to the control group, a decrease of C18:2 *cis*-9 *cis*-12 was observed in experimental group. Nowakowski *et al.* [2012] studied the effect of lipid preparatio,ns based on a bioactive plant-fish complex in cattle feeding. They found that using this preparation the content of CLA, EPA, DHA and vaccenic acid in milk fat increased. O'Donnell-Megaro *et al.* [2012] tested the influence of soybean oil with vitamin E on the FA profile in milk. They demonstrated that this complement increased twice the vaccenic acid and C18:2 *cis*-9 *trans*-11 content.

Also system of production (biological / extensive / intensive) affects the profile of FAs with health-promoting effects. A greater use of pasture and a major part of forage in cows' daily ration is the reason of a higher content of UFAs in milk in the biological and extensive production systems [Dewhurst *et al.* 2003, Nałęcz-Tarwacka *et al.* 2009].

Stoop *et al.* [2009] showed that both, phase of lactation and body energy status, significantly affect the variations of milk fat composition. They proved that lactation phase influenced significantly FA profile in milk, except C5-C15 and CLA *trans*-10 *cis*-12. The C16 content increased between 80th and 150th day of lactation, and then stayed relatively constant. Meanwhile the percentage of C18 decreased. The SFAs level varied significantly during lactation, increasing in the first half, and after that decreasing from 71.5 to 69.7%. In milk from cows with negative energy balance, lower content of C5-C15 and higher content of C16:0 and C18:0 were found. This

may suggest a possible lack of energy and change of C3 compounds allocation during *de novo* synthesis, plus a mobilization of body fat reserves.

The influence of non-genetic factors on milk fat content was also analysed in other species: in the sheep [Bodkowski *et al.* 2008] and goats [Strzałkowska *et al.* 2009b, Jóźwik *et al.* 2010, D'Urso *et al.* 2008]. The effect of feeding system on beef and lamb FAs composition was studied as well by Angulo *et al.* [2011], Bodkowski and Patkowska-Sokoła [2013a,b].

The review presented here shows a significant relation between the presence of SNP in ACACA. FASN, SCD1 and DGAT1 genes and the FAs profile in cows milk. The best known are described by several authors, is the DGAT1 gene. A better knowledge of the others, with understanding of non-genetic factors influence like feeding, will probably allow to design selection of cattle basing on genetic markers with purpose of functional food production.

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