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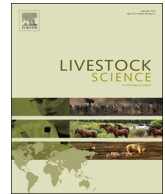
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Genetic and phenotypic trends for milk fatty acids in a Holstein cattle population reared under tropical conditions

Eula Regina Carrara^{a,1}, Leila de Genova Gaya^{a,*}, Juliana Petrini^{b,2}, José Teodoro de Paiva^{a,1}, Mayara Salvian^b, Gregori Alberto Rovadoski^b, Paulo Fernando Machado^b, Gerson Barreto Mourão^b

^a Department of Animal Science, Federal University of São João del-Rei, São João del-Rei, Minas Gerais, Brazil

^b Department of Animal Science, University of São Paulo, Piracicaba, São Paulo, Brazil

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ABSTRACT

Evaluation of genetic and phenotypic trends is important to monitor the evolution of dairy cattle breeding programs. Traits that are not commonly included as selection goals should also be monitored, especially when they have some effect on consumer health, such as milk fatty acids profile. Thus, the aim was to evaluate the genetic and phenotypic trends of the milk fatty acids composition on a Holstein dairy cattle population, from three farms, reared in a tropical environment. Monthly records of palmitic (C16:0), stearic (C18:0), oleic (C18:1), total saturated (SFA), unsaturated (UFA), monounsaturated (MUFA), and polyunsaturated (PUFA) fatty acids content in milk (g/100 g of milk), were collected of 2047 Holstein cows from three Brazilian farms between May and December of 2012. The pedigree file contained 7963 animals of seven generations. Genetic and phenotypic trends were obtained by linear regression of breeding values or phenotypic values, respectively, over generations. Single-trait analyses were performed and the breeding values were estimated using Bayesian approach. All traits showed negative phenotype trend (−0.02723 g/100 g of milk to −0.00395 g/100 g of milk), indicating reduction of the phenotypic value over generations. According to the genetic trends for MUFA and PUFA (−0.00023 and −0.00005, respectively, in g/100 g of milk) the breeding values of the animals were reduced throughout the generations, while for SFA, C16:0 and C18:0 the genetic trends (0.00134, 0.00052 and 0.00013, respectively, in g/100 g of milk) showed an increase in breeding values, possibly due to correlated effects originated from selection protocols applied to the herd. The linear regression coefficients of the genetic values in the generations were not significant for UFA and C18:1 (p -value > 0.6226 and p -value > 0.9708, respectively). Significant genetic and phenotypic trends of small magnitude were obtained, which may be a consequence of the absence of direct selection for these traits in these populations. Genetic and phenotypic gains for fatty acids profile in milk should be monitored to guide breeding programs in their selection objectives. It is suggested to investigate the causes of possible correlated response in the studied populations.

1. Introduction

Milk fat is characterized by the predominance of saturated fatty acids (70%), usually associated with an increase in blood cholesterol and, consequently, an increased in the risk of atherosclerosis and coronary artery diseases in humans. However, only lauric, myristic and palmitic acids have been related to this effect, whereas other saturated fatty acids have positive or neutral effects (Kromhout et al., 2002; Mensink et al., 2003). Likewise some saturated fatty acids, several

unsaturated fatty acids also have potential beneficial effects on human health (Moraes and Colla, 2006). Oleic fatty acid (prevalent in this group), for example, has been associated with effects against metabolic disorders and it is anticarcinogenic (Sales-Campos et al., 2013). In addition, the increase in the proportion of unsaturated fatty acids in bovine milk fat also has a positive impact on the technological properties of dairy products, such as butter (Soyeurt et al., 2008).

Interest in fatty acids profile is increasing given its importance for milk nutritional value as well as its impact on technological properties

* Corresponding author.

E-mail address: genova@ufs.br (L.d.G. Gaya).

¹ Present address: Department of Animal Science, Federal University of Viçosa, Viçosa, Minas Gerais, Brazil.

² Present address: Institute of Exact Sciences, Federal University of Alfenas, Alfenas, Minas Gerais, Brazil.

of milk and dairy products. There is genetic variation in fatty acid profile in milk fat (Bastin et al., 2013; Kelsey et al., 2003; Soyeurt et al., 2006). Therefore, it is possible to use this profile as a selection criterion in animal breeding programs. Moderate and high heritability coefficients for many fatty acids in Holstein cows' milk were reported, suggesting direct selection as a feasible tool to genetically manipulate some of these components. Heritabilities varying from 0.01 to 0.15 were estimated for UFA, PUFA and C18:1; ranging from 0.07 to 0.21 were reported for MUFA, whereas for SFA, C16:0 and C18:0, heritabilities ranging from 0.14 to 0.26 were obtained (Bilal et al., 2014; Penasa et al., 2015; Petrini et al., 2016). These studies also showed the existence of genetic correlation between the percentage of fatty acids and other production and milk quality traits. For example, Penasa et al. (2015) and Petrini et al. (2016) reported genetic correlations between groups of fatty acids (SFA, UFA, MUFA and PUFA) ranging from -0.28 to -0.47 . In addition, with fat percentage, the correlations varied from 0.47 to 0.99 and with protein percentage, the values were between 0.33 to 0.69. Thus, the indirect selection for fatty acid content in bovine milk, especially for those with low heritability coefficients, is possible.

Although the fatty acid profile is not yet a selection criterion in animal breeding programs, genetic and phenotypic trends for these traits may be an opportunity to evaluate the impact of selection decisions based on other traits (such as milk yield) on fatty acid profile due to indirect selection. However, there is a lack in literature of studies reporting genetic and phenotypic trends for milk fatty acid composition in cattle, which highlights the importance of investigating them.

Therefore, the aim of this study was to evaluate the genetic and phenotypic trends for palmitic (C16:0), stearic (C18:0), oleic (C18:1), total saturated (SFA), unsaturated (UFA), monounsaturated (MUFA), and polyunsaturated (PUFA) fatty acids content in milk (g/100 g of milk) in a Holstein cows population raised in a tropical condition.

2. Material studied, area descriptions, methods, techniques

All experimental procedures related to animal in this study were performed in agreement with the protocol number 2017.5.1197.11.3 approved by Institutional Animal Care and Use Committee Guidelines from “Luiz de Queiroz” College of Agriculture, University of São Paulo to ensure compliance with international guidelines for animal welfare.

2.1. Animals and data

Data were obtained from milk samples collected in first milking of the test day from May to December 2012, in three Brazilian farms located in São Paulo state. Holstein cows were milked three times a day with an automatic milking system, maintained in freestall barns, and they were fed a total mixed ration. The main components of the ration were corn silage, grass hay, cotton seed, soybean meal, soybean hulls, corn meal, citrus pulp, minerals and vitamins (Petrini et al., 2016). Only proven sires (progeny testing or genomic evaluation) are used for breeding, considering as selection criteria: milk yield, udder conformation, and legs and feet conformation, in that order.

Each milk sample were analyzed by Fourier transform mid-infrared spectroscopy method (Delta Instruments CombiScope™ Filter; Advanced Instruments, Inc., Norwood, MA, USA), as described by Rodriguez et al. (2014), to measure palmitic (C16:0), stearic (C18:0), oleic (C18:1), total saturated (SFA), unsaturated (UFA), monounsaturated (MUFA), and polyunsaturated (PUFA) fatty acids content in milk (g/100 g of milk).

Data from animals without valid measurements or with measurements outside the acceptable range (mean \pm three standard deviations); without calving date, lactation order and age information were deleted. Animal records with days in milk (DIM) lower than five or higher than 305, age higher than 10 years, and lactation order higher than seven were also excluded. The final number of cows per farm was

Table 1

Frequency of animals with records analyzed by interval generation.

Interval generation	Frequency
1 F 2	3
2 F 3	58
3 F 4	1248
4 F 5	458
5 F 6	278
6 F 7	2

Table 2

Number of observations (N), observed mean (Mean), standard deviation (SD), coefficient of variation (CV,%), and minimum (MIN) and maximum (MAX) values of milk fatty acids.

Fatty acid ^a (%)	N	Mean	SD	CV (%)	MIN	MAX
SFA	7407	2.16	0.456	21.08	0.71	3.66
UFA	7386	1.12	0.295	26.47	0.11	2.15
MUFA	7492	0.94	0.256	27.32	0.11	1.83
PUFA	7418	0.17	0.046	26.71	0.02	0.33
C16:0	7413	0.80	0.186	23.28	0.20	1.40
C18:0	7365	0.64	0.157	24.55	0.10	1.19
C18:1	7385	0.71	0.215	30.23	0.04	1.45

^a SFA = total saturated fatty acid; UFA = total unsaturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid; C16:0 = palmitic fatty acid; C18:0 = stearic fatty acid; C18:1 = oleic fatty acid.

Table 3

Linear regression coefficients (intercept μ and genetic trend b) and their p -value obtained from the regression of breeding values in function of generations for milk fatty acids.

Fatty acid ^a (%)	μ (p-value)	b (p-value)
SFA	-0.00366 (<0.0001)*	0.00134 (<0.0001)*
UFA	-0.00002 (0.9428) ^{NS}	-0.00004 (0.6226) ^{NS}
MUFA	0.00238 (<0.0001)*	-0.00023 (0.0259)*
PUFA	0.00031 (<0.0001)*	-0.00005 (0.0044)*
C16:0	-0.00089 (0.0212)*	0.00052 (<0.0001)*
C18:0	-0.00090 (<0.0001)*	0.00013 (0.0260)*
C18:1	0.00024 (0.2697) ^{NS}	-0.000002 (0.9708) ^{NS}

^a SFA = total saturated fatty acid; UFA = total unsaturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid; C16:0 = palmitic fatty acid; C18:0 = stearic fatty acid; C18:1 = oleic fatty acid.

* Significant to 0.05.

^{NS} Not significant to 0.05.

1668, 258 and 121, totaling 2047 cows with records, from first to seventh parity, and ranging from five to 305 DIM at the test day. Additionally, the pedigree was composed by 7963 animals, 3758 dams and 535 sires from 7 generations, considering the first generation as one. The number of generations in the pedigree file was calculate by the CALGERA software (Mourão et al., 2004), based on Brinks et al. (1961). From the first to the seventh generation, there were 389 fractional generations (two decimal digits). The number of cows with records analyzed per generation interval can be visualized in Table 1. The descriptive statistics of the data are presented in Table 2.

2.2. Genetic analyses

Breeding values were predicted using Bayesian approach under an animal model: $y = Xb + Za + Sc + e$, in which y is the vector of phenotypes; b is the vector of systematic effects of contemporary group and the cubic effect of DIM; a is the vector of random additive genetic effects; c is the vector of random permanent environment effects; X , Z and

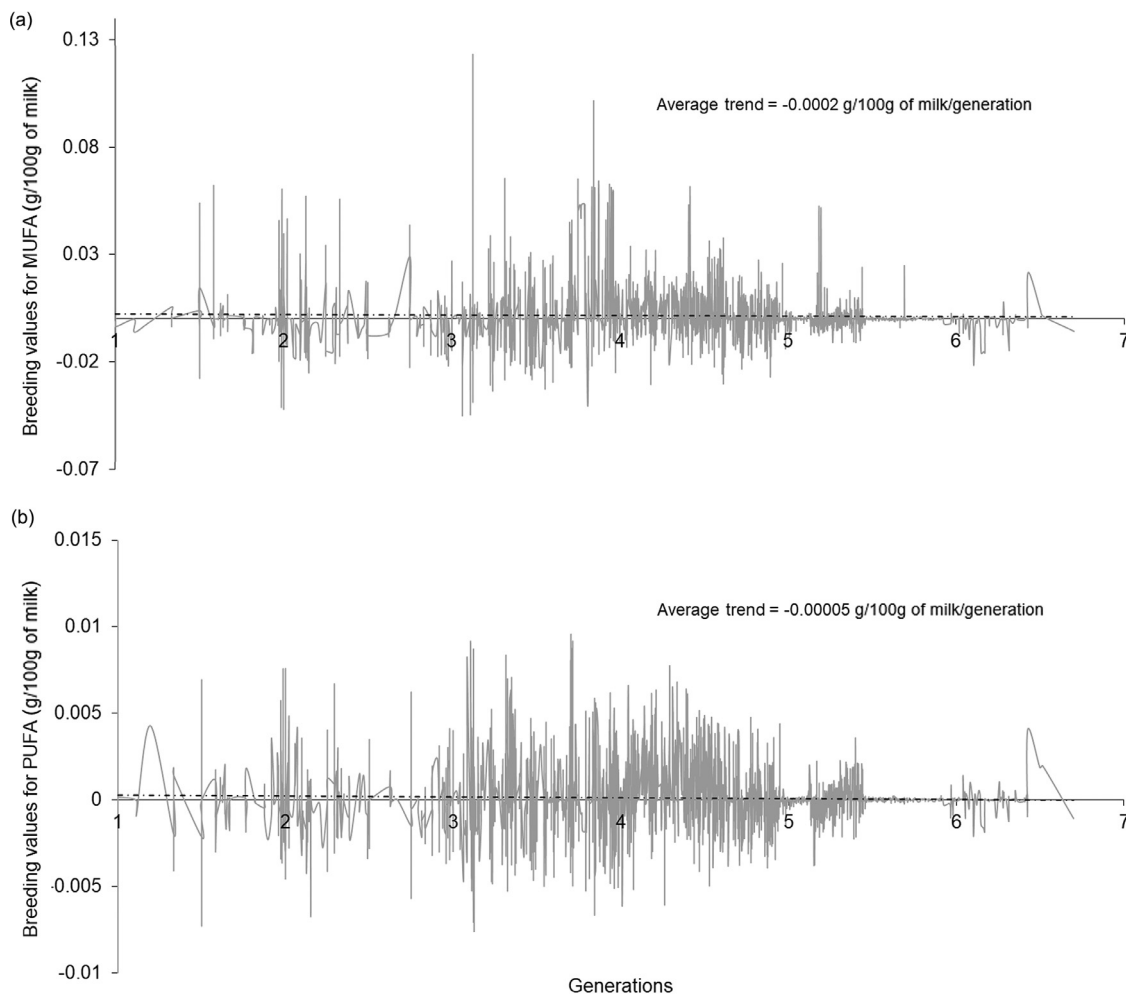


Fig. 1. Genetic trend for (a) monounsaturated (MUFA) and (b) polyunsaturated (PUFA) fatty acids over the generations studied estimated by regression analysis.

\mathbf{S} are the incidence matrices associating \mathbf{b} , \mathbf{a} and \mathbf{c} to \mathbf{y} ; \mathbf{e} is the vector of residual random effects. The following distributions were adopted: $\mathbf{y}|\mathbf{b}, \mathbf{a}, \mathbf{c}, \mathbf{e} \sim N(\mathbf{Xb} + \mathbf{Za} + \mathbf{Sc}, \mathbf{I}\sigma_e^2)$; $\mathbf{b} \sim N(0, \Sigma_b)$; $\mathbf{a}|\sigma_a^2 \sim N(0, \mathbf{A}\sigma_a^2)$; $\mathbf{c}|\sigma_c^2 \sim N(0, \mathbf{I}\sigma_c^2)$; $\mathbf{e}|\sigma_e^2 \sim N(0, \mathbf{I}\sigma_e^2)$; $\sigma_a^2|S_a, n_a \sim \chi^2-(S_a, n_a)$; $\sigma_c^2|S_c, n_c \sim \chi^2-(S_c, n_c)$; $\sigma_e^2|S_e, n_e \sim \chi^2-(S_e, n_e)$, in which Σ_b is a diagonal matrix with high values for the variances to represent a non-informative prior; σ_a^2 , σ_c^2 and σ_e^2 are the components of direct additive genetic variance, permanent environment variance and residual variance, respectively; \mathbf{A} is the numerator relationship matrix, \mathbf{I} is the identity matrix of order equal to the number of animals with observations; χ^2- represents inverted chi-square distribution; S_a , S_c and S_e are the hyperparameters values of the variances; n_a , n_c and n_e are their corresponding prior “degrees of belief”.

Contemporary groups (CG) for SFA, UFA, PUFA, C16:0, C18:0 and C18:1 were formed by combination of farm, parity, calving season [dry (April to September) or rainy (October to March)] and month of analysis information (106 CG with 6 to 167 animals). For MUFA, contemporary groups were formed by combination of farm, calving season [dry (April to September) or rainy (October to March)] and month of analysis information (36 CG, with 7 to 417 animals each).

The evaluation of the CG formation and systematic effects of the model associated with the traits studied was performed using the GLM (General Linear Models) procedure from SAS software (Statistical Analysis System; SAS Institute, 2018), considering as significant those with p -value < 0.05 . Different CG for traits were expected, since they were registered at different experimental stages, which should affect their variability.

The breeding values were predicted by Bayesian approach through Markov Chain Monte Carlo method (MCMC) and algorithm Gibbs Sampler using GIBBS3F90 software (Misztal et al., 2002). A total of 1200,000 cycles after discarding the 120,000 initial samples used for burn-in were considered for genetic analyses in order to minimize the effects of initial samples. A total of 100 cycles sampling interval was kept to ensure the independence of samples and avoid autocorrelation. Thus, a total of 10,800 samples of marginal posterior distributions of breeding values were recorded for each animal per trait. The chain convergence diagnosis provided by Gibbs Sampler was monitored visually (density, trace and mean graphs) and tested by Geweke (1992), Heidelberger and Welch (1983) and Raftery and Lewis (1992) convergence criteria, using the Bayesian Output Analysis (BOA; Smith, 2005) package from the R software (R Core Team, 2018).

2.3. Genetic and phenotypic trends

Genetic and phenotypic trends of milk fatty acids were estimated by linear regression of the breeding values or phenotypic values, as a function of generations using the PROC GLM procedure from SAS software (Statistical Analysis System; SAS Institute, 2018) and the coefficients were considered significant when p -value < 0.05 . The regression equation used was: $y_{ij} = \mu + b(x_{ij} - \bar{x}) + e_{ij}$, in which y_{ij} is the predicted breeding value or the phenotypic value for the j th animal of the i th generation, μ is the intercept, b is the angular coefficient associated with generation (genetic or phenotypic trend, in g/100 g of milk), x_{ij} is the i th generation of the j th animal, \bar{x} is a generation

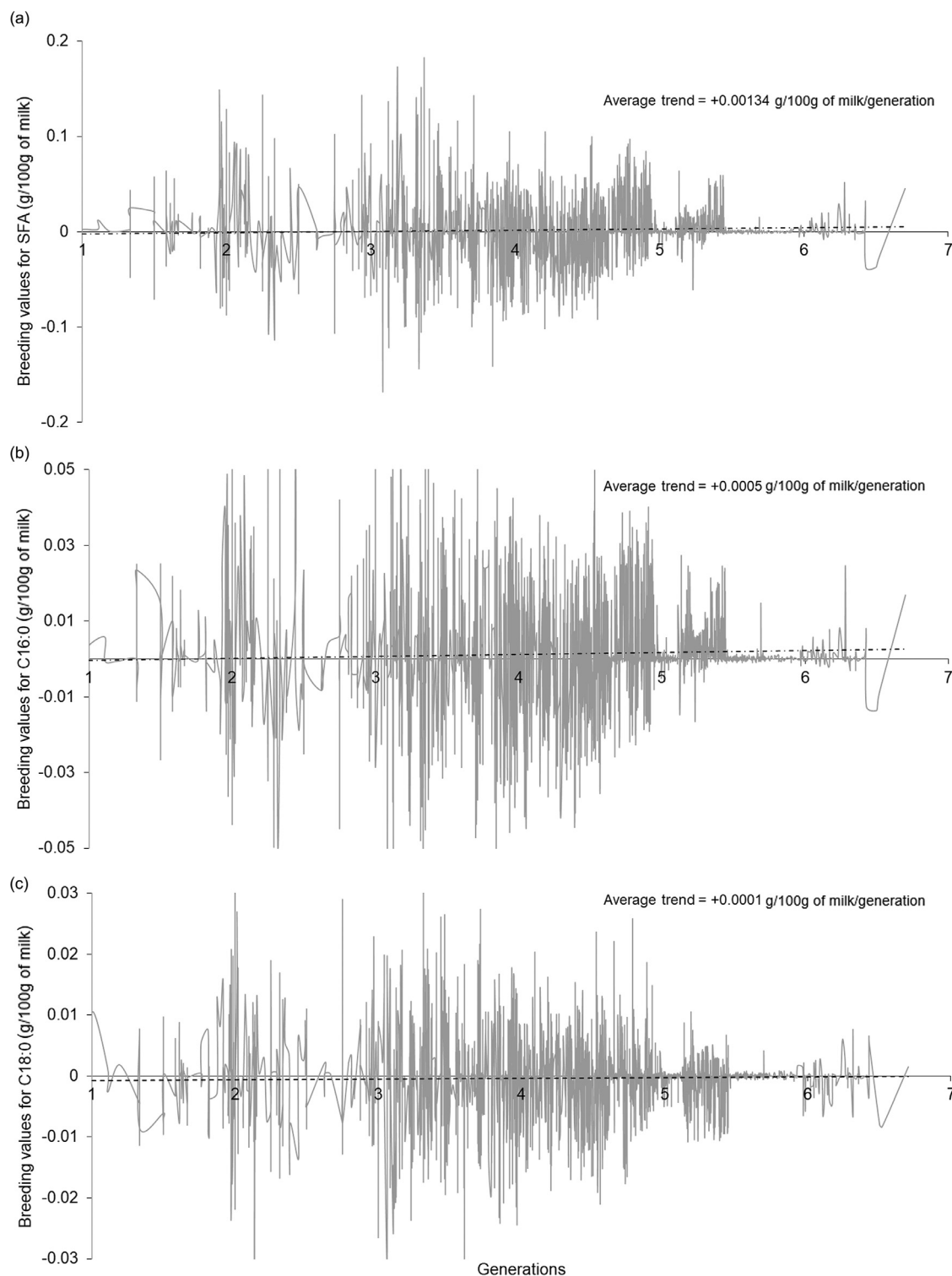


Fig. 2. Genetic trend for (a) saturated (SFA), (b) palmitic (C16:0) and (c) stearic (C18:0) fatty acids over the generations studied estimated by regression analysis.

average, and e_{ij} is the residue, $NID(0, \sigma^2)$.

3. Results

3.1. Genetic trends

The regression coefficients for each trait studied, and their respective p -values, are shown in Table 3.

For SFA, MUFA, PUFA, C16:0 and C18:0 the regression coefficients

were significant (p -value < 0.05) and for UFA and C18:1 they were not significant (p -value > 0.05).

Genetic trends for the MUFA and PUFA were negative, demonstrating that the breeding values of animals for these traits reduced throughout the generations. There was a decrease of 0.00023 g/100 g of milk and 0.00005 g/100 g of milk per generation, for MUFA and PUFA respectively (Fig. 1). These decreases corresponded to 0.02% and 0.03% of the phenotypic mean of MUFA and PUFA, respectively. For the SFA, C16:0 and C18:0, the genetic trends were positive,

Table 4

Linear regression coefficients (intercept μ and phenotypic trend b) and their p -value obtained in the regression of phenotypic values in function of generations for milk fatty acids.

Fatty acid ^a (%)	μ (p-value)	b (p-value)
SFA	2.27035 (<0.0001)*	-0.02723 (0.0002)*
UFA	1.19584 (<0.0001)*	-0.02063 (<0.0001)*
MUFA	1.00446 (<0.0001)*	-0.01689 (<0.0001)*
PUFA	0.18913 (<0.0001)*	-0.00395 (<0.0001)*
C16:0	0.82752 (<0.0001)*	-0.00769 (0.01)*
C18:0	0.66404 (<0.0001)*	-0.00652 (0.01)*
C18:1	0.76629 (<0.0001)*	-0.01441 (<0.0001)*

^a SFA = total saturated fatty acid; UFA = total unsaturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid; C16:0 = palmitic fatty acid; C18:0 = stearic fatty acid; C18:1 = oleic fatty acid.

* Significant to 0.05.

demonstrating that the breeding values of the animals for these traits increased throughout the selection generations. There was an increase of 0.00134 g/100 g of milk, 0.00052 g/100 g of milk and 0.00013 g/100 g of milk by generation for SFA, C16:0 and C18:0 respectively (Fig. 2). These increases represented to 0.06%, 0.07% and 0.02% of the phenotypic mean of SFA, C16:0 and C18:0, respectively.

3.2. Phenotypic trends

The regression coefficients for each trait studied, with their respective p -values, are shown in Table 4. The regression coefficients for all traits, MUFA, PUFA, SFA, UFA, C16:0, C18:0 and C18:1, were significant (p -value < 0.05).

All phenotypic trends for the studied traits were negative, demonstrating that the phenotypic value of the milk fatty acids has decreased throughout the generations. The reduction in phenotypic values, in g/100 g of milk, was 0.01689, 0.00395, 0.02723, 0.02063, 0.00769, 0.00652 and 0.01441 by generation for MUFA, PUFA, SFA, UFA, C16:0, C18:0 and C18:1, respectively (Figs. 3–5) and represented 1.80, 2.32, 1.26, 1.84, 0.96, 1.02 and 2.03 percent of phenotypic mean, respectively.

4. Discussion

The genetic and phenotypic trends for the evaluated fatty acids were of small magnitude. A possible cause for this fact is the absence of direct selection for these traits in the studied population. However, despite the small magnitudes, genetic and phenotypic trends indicated changes throughout the generations in most of the milk fatty acids evaluated. This possibly occurred due to a correlated response through indirect selection, since there is genetic correlation between milk yield and fatty acid profile as reported by Penasa et al. (2015) and Petrini et al. (2016).

In traits of economic interest, indirect selection may be a resource to increase the efficiency of selection process in dairy cattle

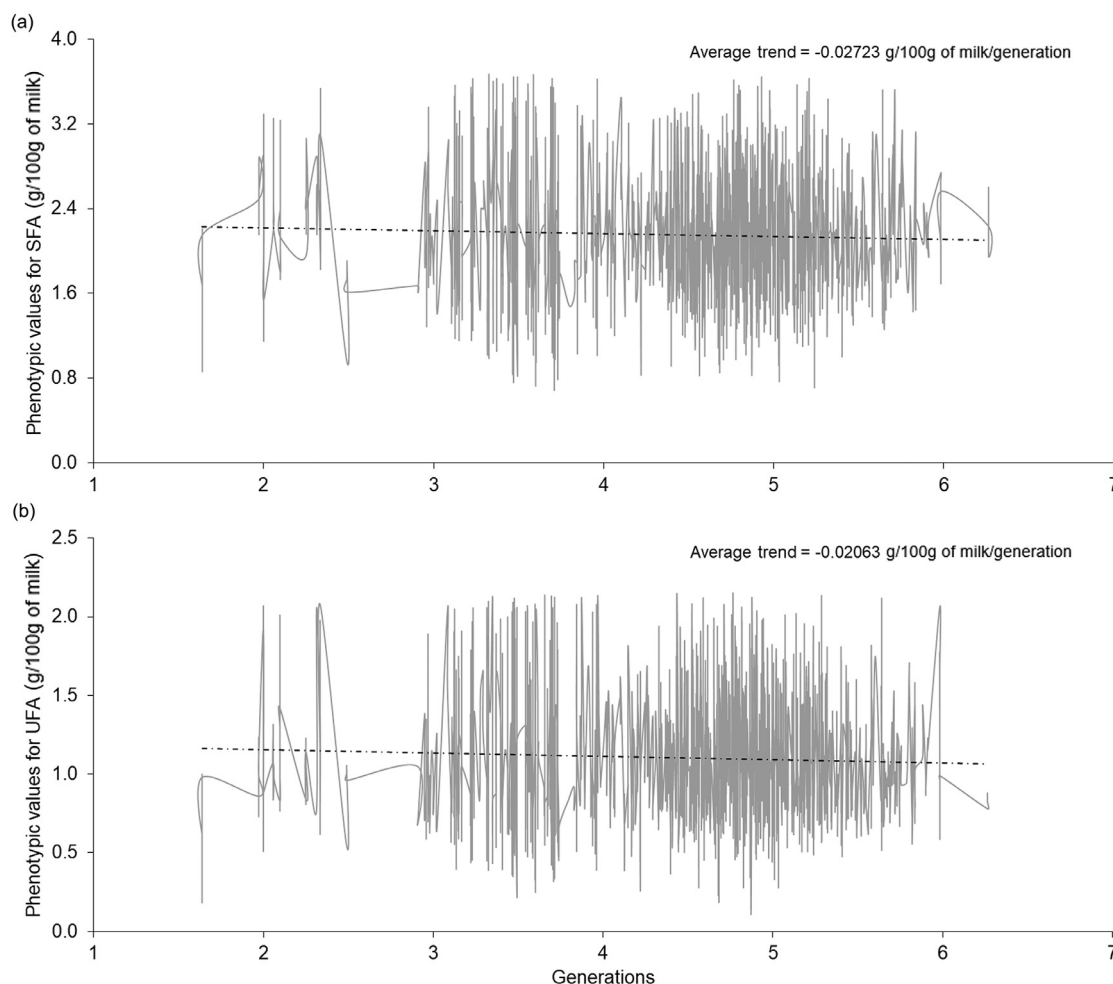


Fig. 3. Phenotypic trend for (a) saturated (SFA) e (b) insaturated (UFA) fatty acids over the generations studied estimated by regression analysis.

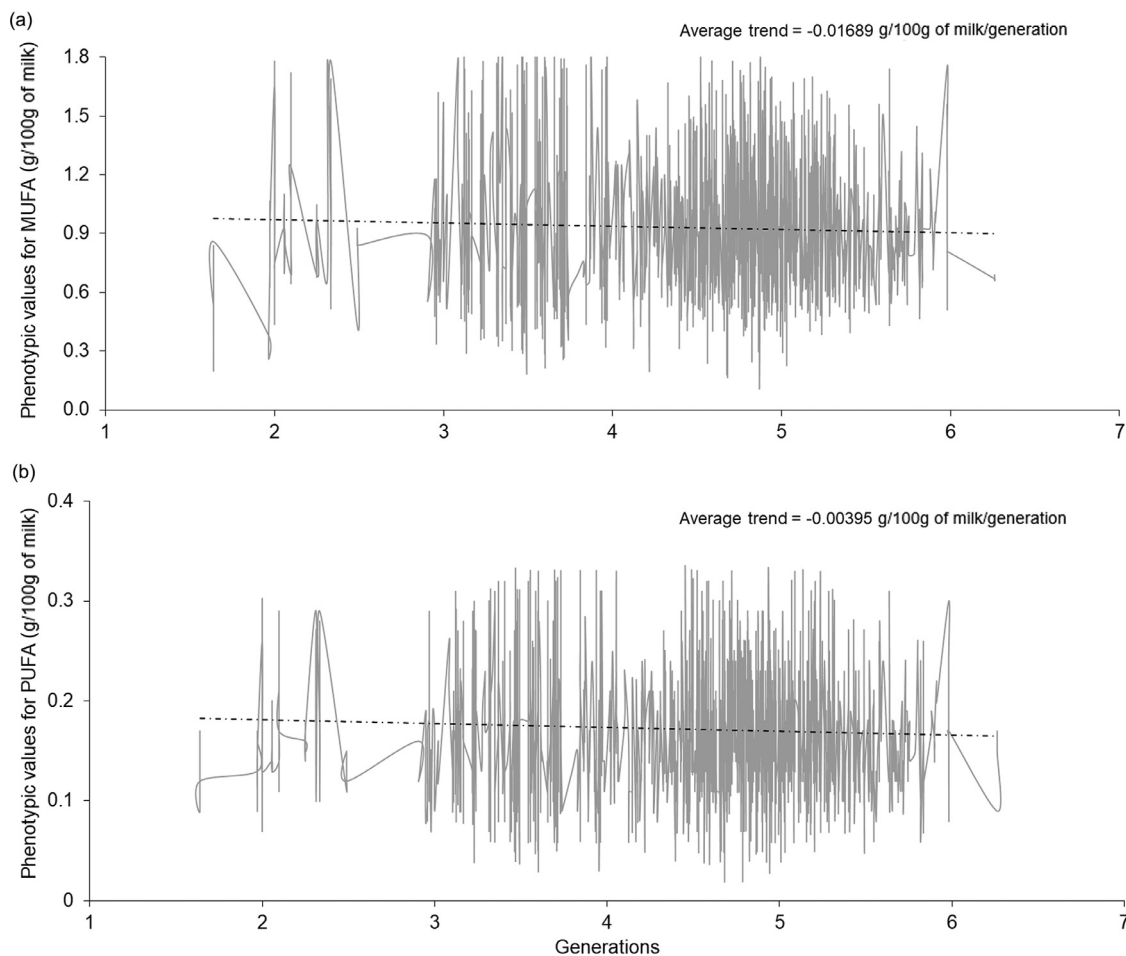


Fig. 4. Phenotypic trend for (a) monounsaturated (MUFA) and (b) polyunsaturated (PUFA) fatty acids over the generations studied estimated by regression analysis.

(Pantelic et al., 2011), since a smaller number of traits is used as selection criteria. For example, direct selection for milk yield in Holstein cattle can cause a favorable correlated response for resistance to bovine tuberculosis, in other words, it is possible to obtain animals that produce more milk and that are less prone to bovine tuberculosis even without including this disease as a selection criterion (Brotherstone et al., 2010). Likewise, direct selection for fat percentage in milk can indirectly improve the protein content of Holstein cows (Zamani et al., 2011). However, indirect selection can also result in unfavorable gains. In a review of 14 genetic studies regarding the relationship between milk yield and health in dairy cattle, Ingvarsten et al. (2003) reported that continuous selection for an increase in milk yield could also increase the incidence of diseases related to production, such as mastitis, ketosis, ovarian cyst and claudication, reducing not only productive values but also the cows' welfare (Oltenacu and Broom, 2010). In fact, the continuing decline in genetic merit for reproductive and health traits demanded from dairy breeding programs the inclusion of non-production traits in selection indexes (Pryce et al., 2004).

In this sense, the antagonistic relationship between total milk yield and various fatty acids can be detrimental when the main selection criterion is milk yield. This is the case of Brazil, where the payment to the farmer is made mostly based on the total volume of milk delivered, directing the selection objectives mainly for milk yield (Petrini et al., 2016), and causing indirect genetic modification on fatty acids content in milk. It is expected that with the genetic selection for increased milk yield, there will be a reduction in the contents of several fatty acids, both by the dilution effect and by the existence of a negative genetic correlation between milk yield and these fatty acids, such as SFA, UFA,

MUFA, PUFA, C16:0, C18:0 and C18:1 (Bilal et al., 2014; Penasa et al., 2015; Petrini et al., 2016). This may justify the decrease of breeding values and, consequently, phenotypic values for fatty acids, possibly as a result of the correlated response due to the direct selection for milk yield, which can be observed through the genetic and phenotypic trends.

According to the genetic trends, breeding values for MUFA and PUFA decrease along of generations, which can be harmful because these groups of fatty acids have been generally associated with beneficial effects to human health. Several PUFA are involved in the induction of protective effects against cardiovascular diseases, such as linoleic acid and alpha-linoleic acid (Sun et al., 2007). Other PUFA have been associated with a reduced risk of Alzheimer's disease (Ruxton et al., 2004). Furthermore, MUFA, including C18:1, have also been associated with the prevention of cardiovascular diseases (Mente et al., 2009), and to effects against metabolic and carcinogenic disorders (Sales-Campos et al., 2013). However, there are also reports of an increased risk of coronary events caused by increased MUFA intake (Jakobsen et al., 2009).

Note that for SFA, C16:0 and C18:0, the genetic trends obtained indicated an increase in the genetic merit of the animals during the generations. However, a decrease in the phenotypic average of these traits by generation was also verified and possibly this occurred due to environmental interference. Nutritional factors may influence the pH and microbial population of the rumen, causing alteration in the extent and rate of ruminal biohydrogenation of dietary fatty acids (Kargar et al., 2017). The modification of the biohydrogenation of ruminal fatty acids can alter the duodenal flow of fatty acids and, consequently, the milk fatty acids composition (Loor et al., 2005).

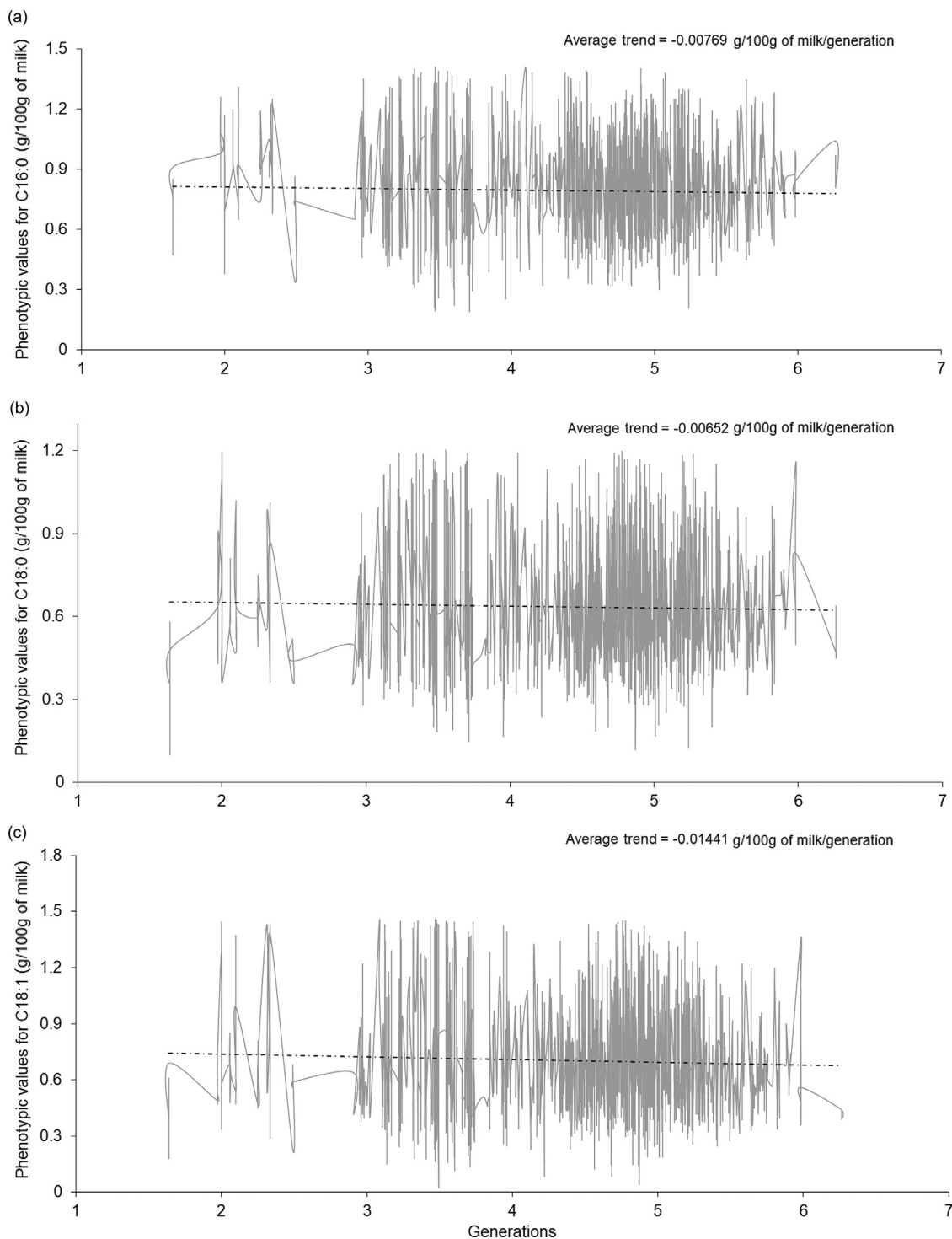


Fig. 5. Phenotypic trend for (a) palmitic (C16:0), (b) stearic (C18:0) and (c) oleic (C18:1) fatty acids over the generations studied estimated by regression analysis.

The increase obtained for the breeding values for SFA and C16:0 over the generations is not desirable, since it is known that the SFA, mainly myristic fatty acid (C14:0) and palmitic fatty acid (C16:0), act in proportions of LDL and HDL cholesterol in the blood. Although some studies point to other effects (Lemaitre et al., 2010; Wu et al., 2011), the presence of high levels of SFA in blood has been widely related to potential negative effects on human health (Hu et al., 2001), increasing the risk of cardiovascular diseases, for example. However, the increase in the genetic merit of animals for C18:0 may be favorable, since this fatty acid was not associated with coronary events (Lemaitre et al.,

2010; Wu et al., 2011). In addition, about 40% of C18:0 is desaturated by $\Delta 9$ desaturase in the mammary gland, contributing with more than 50% of C18:1 secreted in milk fat (Chilliard et al., 2000; Enjalbert et al., 1998), which is a beneficial fatty acid to human health, as mentioned above.

The fatty acids constitute about 98% of milk fat and therefore are important components for the industry, since fat is used for the manufacture of by products such as cheese and butter. Simultaneously, there is a growing interest of consumers for healthy foods, with less fat and an ideal combination of fatty acids composition.

Despite the possibility of changing the fatty acid profile of milk, their economic value is still uncertain, mainly because most dairy producers do not receive differentiated payment according to this profile (Bastin et al., 2013; Petrini et al., 2016). However, the physical, nutritional and organoleptic properties of milk are related to milk fat composition (Chilliard et al., 2000). The fatty acid profile can also provide information on the environmental impact of dairy cows (Dijkstra et al., 2011) and on the health status of these animals (Van Haelst et al., 2008). According to Bastin et al. (2013), even if fatty acids have undefined monetary value, a better overall economic efficiency could be achieved if these traits were included in the selection objectives. Therefore, the definition of the desirable direction of change in milk fatty acids profile should take into account all aspects related to fatty acids to choose which ones are important (Bastin et al., 2013).

The monitoring of genetic and phenotypic trends in dairy cattle breeding programs is important not only for the traits previously included as selection objectives, but also for traits that may be affected indirectly, mainly due to the growing interest of researchers, consumers and producers in special traits such as fatty acids. The ideal profile of fatty acids in milk fat should be better defined so these components can be appropriately included as selection objectives. Thus, selection strategies can be determined to work together with nutritional, sanitation and milking management, aiming to improve the quality of the milk and providing higher revenues for the farmers.

5. Conclusion

A slightly change in the milk fatty acid profile in the bovine population studied over the generations was observed, possibly due to the indirect selection process. The ideal fatty acids profile in milk fat is still not well defined, which makes it difficult to design selection strategies for these traits. However, due to the effects caused by these fatty acids on human health, as well as their involvement in physical, nutritional and organoleptic properties of milk, it is suggested to monitor the genetic and phenotypic gains of the fatty acid profile and to investigate the causes of the possible occurrence of a correlated response in this population.

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.livsci.2019.08.006.

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