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Abstract

Semimembranosus muscle samples from 795 Large White heavy pigs were used to determine their intramuscular fatty acid composition and to estimate the heritability and the genetic correlations of these traits. Muscle fatty acids showed heritability estimates of low-to-moderate magnitude, ranging from 0.157 for total fatty acids to 0.237 for docosahexaenoic acid. Only small differences in heritability appeared among fatty acids based on their chain length, saturation and double bond position. Omega-6 polyunsaturated fatty acids showed positive genetic correlations with carcass lean % (0.563 ± 0.005) and loin thickness (0.438 ± 0.005) while being negatively related to backfat thickness measured both by calibre (-0.225 ± 0.008) and Fat-O-Meat'er (FOM) apparatus (-0.603 ± 0.004). Interestingly, the monounsaturated fatty acid class was not correlated with carcass measures

and presented only a weak positive genetic correlation with intramuscular fat (0.145 ± 0.002). This result suggests that in heavy pig breeds monounsaturated fatty acids in muscle could be selected for without interfering with carcass traits.

Keywords: heritability; genetic correlation; *Semimembranosus* muscle; pork; meat quality; fat.

1 Introduction

Over the last decades, the swine industry has mainly prioritised production efficiency and increased lean mass growth, with a consistent decrease in the fat depots stored in carcass and muscle (Wood et al., 2008). In this scenario, the heavy pig industry has shaped distinct selection goals in Mediterranean countries such as Spain and Italy to develop selection schemes more suitable for the production of high-value seasoned meat products, such as high-quality dry-cured hams and salamis. The breeding objectives in these countries combine carcass conformation traits (ham and loin weights and conformations) with the maintenance of suitable amounts of subcutaneous and intramuscular fat (Silió, 2000; Bosi & Russo, 2004). Indeed, fat thickness strongly affects dry-cured ham quality, since an appropriate fat layer prevents hams from excessive seasoning losses and the worsening of organoleptic characteristics (Bosi & Russo, 2004). In addition to fat thickness, seasoning losses in dry-cured hams also depend on the amount of fat stored in muscles, since the presence of more intermuscular and intramuscular fat were proven to increase the seasoning yields (Bosi & Russo, 2004). The amount and composition of intramuscular fat are important factors determining meat quality and therefore consumers' acceptance (Wood et al., 2008). Even though an increase in the degree of lipid unsaturation in meat could be beneficial for human health (Caggiula & Mustad, 1997; Kritchevsky, 1998; Simopoulos, 2008), unsaturated (and in particular polyunsaturated) fatty acids (FA) are more likely to incur in oxidative phenomena, especially in

seasoned products such as Parma ham (Lo Fiego, Santoro, Macchioni, & De Leonibus, 2005). Therefore, the seasoning industry technological requirements and the consumers' dietary demands do not completely match. These contrasting demands raise the necessity to elucidate the factors underlying meat traits and qualitative characteristics, in order to find a balance between what is important for the consumer and what for the industry. So far, efforts have been made to improve pork meat quality and an extensive body of literature focuses on aspects affecting the qualitative characteristics and FA composition of the final meat products (Wood et al., 2008; Kim et al., 2018). The relevance of pig diet in modulating muscle and carcass fat deposition and composition has been extensively reported in literature (Lo Fiego, Macchioni, Santoro, Pastorelli, & Corino, 2005; Minelli, Macchioni, Ielo, Santoro, & Lo Fiego, 2013; Jasińska & Kurek, 2017; Minelli et al., 2019), but also breed and genetics affect the animal adipogenic potential (Wood et al., 2004; Wood et al., 2008). Several authors have determined the heritability of intramuscular fat deposition and composition in pigs, showing heritability values (h^2) ranking from 0.15 to 0.55 (Ntawubizi et al., 2010; Ibáñez-Escriche, Magallón, Gonzalez, Tejeda, & Noguera, 2016). The high h^2 estimates reported by these authors strongly support a direct role for genetics in influencing the intramuscular fat composition. However, these estimates may vary considerably among pig populations and breeds, as reported by Zhang et al. (2018). The lack of agreement among different studies may also depend on the statistical methods used, on the type of information used to calculate genetic parameters (whether the authors have genomic data or only pedigree-based information; Song, Zhang, Zhang, & Ding, 2019) and/or the phenotypic and genetic features of the studied population. The latter point is also strongly dependent on the structure of the population and on the distinct breeding goals pursued across countries since these differences can affect the estimation of the genetic parameters (Robertson, 1977). In this scenario, the peculiar selection objectives of Italian pig breeding programs have shaped the genetics of the purebred pigs reared for the production of heavy carcasses. In our previous study (Davoli et al., 2019) we investigated the genetic parameters of the backfat FA profile in the Italian Large White pig population and, to the best of our

knowledge, no study exists giving estimates of the genetic parameters of muscle FA composition in this breed. Subcutaneous and intramuscular fat (IMF) show specific development and metabolism (Mourot, Kouba & Peiniau, 1995) and several studies have reported considerable anatomical variation in FA composition in the pig adipose tissues (Ros-Freixedes, Reixach, Bosch, Tor & Estany, 2014; Popova, Nakev & Marchev, 2015; Jiang et al., 2018). The aim of the present research is to estimate the heritability and genetic correlations of the *Semimembranosus* muscle (SM) IMF FA composition in a sample of Sib tested Italian Large White pigs bred for heavy pig production. The pedigree-based heritability values obtained for muscle FA composition were furthermore compared with the estimates based on genomic data available from a previous study for the same pig population, in order to compare the reliability of the heritability values estimated using the two approaches.

2 Material and methods

2.1 Animals and phenotypes

This study was carried out on a sample of 795 Italian Large White (ILW) pigs belonging to the population described by Davoli et al. (2019). Briefly, the pigs were from the national sib testing selection program of the Italian National Association of Pig Breeders (Associazione Nazionale Allevatori Suini, ANAS, http://www.anas.it). During the testing period, siblings were kept separated, fed the same finishing diet at a *quasi ad libitum* feeding level until an average final live weight of about 150 kg. Pigs were slaughtered in 27 different days between 2011 and 2012 at the same commercial abattoir. During Sib-Test, each litter made by three full-sibs females and castrated males was slaughtered in at least two different dates. The animals used in this study belonged to 324 litters: 48 litters were made by one pig, 81 litters comprised two full-sibs, and the remaining 195 litters were constituted by three full-sibs. Animal care and slaughter of the animals used in this

study were performed in compliance with the European rules (Council Regulation (EC) No. 1/2005 and Council Regulation (EC) No. 1 099/2009) on the protection of animals during transport and related operations and at the time of the killing. All slaughter procedures were monitored by the veterinary team appointed by the Italian Ministry of Health. Sampling occurred with the ANAS permission. SM samples were taken on the trimming line from the thigh of the left carcass side, at the same point in all carcasses, and were then wrapped in aluminium foil, immediately put in vacuum-sealed bags and frozen in liquid nitrogen. The samples were kept at -20°C for further use.

At slaughtering, hot carcass weight (kg) and backfat thickness (BFT) measured in mm by a calibre at the level of *Gluteus medius* muscle were measured. Furthermore, optical measures (in mm) of loin and backfat were taken by Fat-O-Meat'er (FOM - CrometecGmbh, Lünen, Germany) between the third and fourth last ribs, 8 cm off the carcass midline were recorded, together with the estimated percentage of lean meat. The high carcass weight (118.61 ± 8.66 kg) of the animals considered in the present study approaches the weight of typical heavy pigs grown for the production of heavy carcasses and high quality dry-cured hams, such as Parma and San Daniele, in compliance with official guidelines for the production of Parma and San Daniele hams (Commission Regulation (EC) No 1 107/96 of 12 June, 1996).

The SM content of IMF was determined by extraction with petroleum ether from 1 g of fresh tissue by means of an XT15 Ankom apparatus (Macedon, NY, USA), according to Official procedure AOCS Am 5-04 (AOAC, 2005). IMF was reported as g of IMF per 100 g of tissue (%).

2.2 Genotyping and quality control

The DNA of 795 ILW pigs was genotyped using the PorcineSNP60 v2 BeadChip (Illumina Inc., San Diego, CA, USA), which contains 61,565 SNP markers across the whole genome.

Quality control of the genomic data was performed using PLINK (Purcell et al., 2007), and the markers that did not satisfy the following criteria were excluded: call rate for SNP > 95%, minor allele frequency (MAF) ≥ 0.01 and Hardy-Weinberg equilibrium with *P*-value ≥ 0.001. The call rate was also computed and individuals with more than 10% of missing data were removed. After quality control, 783 pigs and 40,115 SNPs were retained.

2.3 Lipids extraction and Gas-Chromatographic analysis

The total IMF destined to the gas-chromatographic analysis were extracted from SM by chloroform:methanol mixture (2:1, v/v) (Carlo Erba Reagents, MI, Italy) according to the method of Folch, Lees, & Sloane Stanley (1957).

The extracted lipids were submitted to methylation before the gas-chromatographic (GC) analysis. Two mL of Hexane (for UV, IR, HPLC, ACS Reag. Ph. Eur., Carlo Erba reagents, MI, Italy) and 200 µL of methanolic solution of 2N-potassium hydroxide (Carlo Erba reagents, MI, Italy) were added to 25 mg of sample. As an internal standard, tridecanoic acid (Larodan AB, Solna, Sweden) was used according to Ficarra et al. (2010). The fatty acid methyl esters (FAMEs) were analyzed using TRACE^{TM}GC Ultra (Thermo Electron Corporation, Rodano, MI, Italy) equipped with a Flame Ionization Detector, a PVT injector, and a TR-FAME Column 30m x 0.25 mm i.d., 0.2 µm film thickness (Thermo Scientific, Rodano, MI, Italy). Helium was used as a carrier gas and it had a flow rate of 1 mL/min. The injection of FAME sample (1 µL) was performed in split mode with a split flow of 10 mL/min, and operating in a constant condition of carrier gas. Injector and detector were kept at 240°C and the initial oven temperature was 140°C. After the first two minutes, the temperature increased by 4°C/min to reach the final temperature of 250°C, and this was kept for 5 min. The Chrom-Card software (vers.2.3.3, Thermo Electron Corporation, Rodano, MI, Italy) was used to record and integrate the peaks of FAMEs. Each FA was identified by comparing the

obtained retention times with the retention times of standard solutions with known quantities of each methyl esters (Larodan AB, Solna, Sweden). The response factor was calculated and the method of internal standard was used for quantification purposes. The FA and FA classes were expressed as mg/g of IMF and the complete list of FA is reported in Supplementary Table S1.

2.4 Statistical analysis

Experimental data included information on a three-generation pedigree, with animals showing an average inbreeding coefficient of 4.38%, as reported in Davoli et al. (2019). Given its low level, inbreeding was not considered in the model any further. The influence of the level of fattening of the carcass on the acidic composition of the intramuscular fat was evaluated both for each single FA and for the classes of FA (Saturated FA-SFA, monounsaturated FA- MUFA, polyunsaturated FA-PUFA, *n*-3 and *n*-6 PUFA).

Data were analysed with the procedure PROC GLM of the SAS 9.4 software by linear models as described below:

Model 1: $y = M + SLAU + SEX + CLASS + AGE + litter + error$

where *y* is the observation vector for the ith trait; *SLAU* is the slaughter day (27 levels); *SEX*: two levels for barrows and gilts; *CLASS* is the thickness of the backfat measured with calibre: 4 levels (see below for a detailed description); *AGE* at slaughtering (covariate: 1 level); *litter* has been modeled as random factor (324 levels); *error* represents random effects of residues.

The four classes of subcutaneous fat thickness were defined based on the quartile values estimated with the UNIVARIATE procedure of the SAS software. It turned out that this character follows a normal distribution and the Shapiro-Wilk test has a *P*-value of 0.0002. The distribution was divided into quartiles: the first has a value of 23 mm and it includes the 25% leaner carcasses; the second

(26 mm) corresponds to the median and it includes one-half of carcasses, the third quartile (30 mm) the 75% of carcasses. The four classes were defined accordingly: the first includes all the values less than 23 mm (n = 163); the second from 23 to 26 (n = 213); the third from 27 to 30 (n = 214); the fourth all values greater than 30 mm (n = 175).

The same data set was used to estimate genetic parameters, such as variance components, heritability and the genetic correlations among FA components. Estimates were calculated by restricted maximum likelihood methodology using the VCE software system version 6 (Groeneveld, Kovač, & Mielenz, 2010) and were carried out by two multiple trait animal models: one involving the measures recorded at slaughtering added with individual FA, the other involving the same measurements at slaughtering added with FA classes. The multiple trait animal models are mixed infinitesimal models where all the individual FA or FA classes were fitted together. The used models are the following:

Model 2: $y = M + SLAU + SEX + AGE + litter + animal + error$

where *y* is the observation vector for the ith trait; *SLAU* is the fixed factor of the slaughter day (27 levels); *SEX* is the fixed factor of sex with two levels for barrows and gilts; *AGE* at slaughtering is the covariate effect (1 level); *litter* has been modeled as random factor (324 levels); *animal* includes the random additive genetic effect of the animals with and without records (795 level); *error* represents random effects of residues.

The estimate of genomic heritability was performed with GenABEL package in R environment (Aulchenko, Ripke, Isaacs, & van Duijn, 2007) using a univariate model with a genomic kinship matrix instead of the classical pedigree-based kinship matrix. The model was fitted using as fixed effects the slaughter day (27 levels), the sex (2 levels), the litter (324 levels) and the covariate on age at slaughtering.

3 Results and Discussion

3.1 *Semimembranosus* muscle fatty acid composition in Italian Large White heavy pigs

Descriptive statistics for the recorded phenotypes are reported in Table 1. The most abundant FA are oleic (C18:1 *cis*-9), palmitic (C16:0), stearic (C18:0) and linoleic (C18:2 *cis*-9, *cis*-12) acids. The amounts observed in our sample for these FA are in agreement with the values reported in previous researches on pigs slaughtered at an average live weight of 145 kg (Lo Fiego, Macchioni, Minelli, & Santoro, 2010), where oleic, palmitic, stearic and linoleic acids accounted in *Longissimus lumborum* muscle for about 42.2%, 23.7%, 12.4% and 11.2% of the total IMF FA, respectively. The *n*-6/*n*-3 ratio noticed in the studied pig population was higher than reported by Minelli et al. (2019) for immunocastrated medium-heavy pigs slaughtered at about 142 kg live weight (22.9 in the present study *vs.* 15.9 in Minelli et al., 2019). These differences may be ascribed to the different muscles considered (SM in the present study *vs*. *Longissimus lumborum* in Minelli et al., 2019), to the different genetic types used (pure breed *vs.* crossbreed) and/or to immunocastration, which may affect the *n*-6/*n*-3 ratio (Grela, Kowalczuk-Vasilev & Klebaniuk, 2013). Similarly, the *n*-6/*n*-3 ratios described by Corino, Musella, & Mourot (2008) and Enser, Richardson, Wood, Gill, & Sheard (2000) were consistently lower (12.2 and 8.8, respectively) than the value reported in the present research. These differences, however, may also depend on the different slaughter weight of the considered animals. Indeed, while the pigs investigated in Corino, Musella, & Mourot (2008) and Enser, Richardson, Wood, Gill, & Sheard (2000) were slaughtered at about 110 kg and 98 kg live weight, respectively, the ILW pigs considered for the present study were slaughtered at higher weights. For Parma and San Daniele ham productions, high values of PUFA, and in particular *n*-3 PUFA, are undesirable because they increase ham oxidability (Bosi & Russo, 2004). On the contrary, SFA and MUFA are less likely to incur in oxidative and lipolytic processes and thus are better regarded as desirable FA by the ham processing industry. In this trial

MUFA and SFA represented the main FA classes noticed in SM, accounting for 313.71 ± 68.02 and 239.66 ± 44.77 respectively.

FA composition in muscle showed to depend on sex and overall carcass fatness (Table 2). According to literature, sex of animals is an important source of variation, influencing the majority of the FA amounts in meat (Juárez et al., 2017). As compared to gilts, barrows showed higher contents in IMF and significantly higher contents of several SFA and MUFA, namely palmitic, stearic, oleic, vaccenic (C18:1 *cis*-11), arachidic (C20:0) and gadoleic (C20:1 *cis*-11) acids. On the contrary, gilts showed higher contents of PUFA in the SM, thus exhibiting greater amounts of *n*-6 and *n*-3 PUFA, linoleic, α-linolenic (C18:3 *n*-3), eicosadienoic (C20:2 *n*-6), arachidonic (C20:4 *n*-6), docosapentaenoic (C22:5 *n*-3) and docosahexaenoic (C22:6 *n*-3) FA. In this trial, the estimated effect of sex on IMF content and FA composition is in agreement with previous results, where castrated males had higher total fat content and increased amounts of some FA compared to gilts (Barton-Gade, 1987; Bertol et al., 2013; Juárez et al., 2011; Lo Fiego, Macchioni, Minelli, & Santoro, 2010; Minelli, Macchioni, Ielo, Santoro, & Lo Fiego, 2013; Stupka et al., 2008). These results are also consistent with the direct proportionality expected between the amount of fat stored and the proportion of PUFA (Wood et al., 2008). Therefore, the lower SFA content observed in gilt muscle could be explained by the lower IMF deposition in their SM (1.91 ± 0.08 % in gilts *vs.* 2.09 ± 0.09 % in barrows). Beyond different adipogenic potentials, sex seems to be related also to a distinct deposition of some specific FA, as reported by Geri, Franci, Poli, Campodoni, & Zappa (1990) and Juárez et al. (2017). In agreement with our results, previous studies showed that, compared to barrows, gilts tends to store more PUFA and linoleic acid, and less oleic and SFA, in subcutaneous fat (Geri, Franci, Poli, Campodoni, & Zappa, 1990; Lo Fiego, Macchioni, Minelli, & Santoro, 2010) and muscle (Juárez et al., 2017; Lo Fiego, Macchioni, Minelli, & Santoro, 2010). This difference could find a functional explanation insofar PUFA are more readily available for supporting reproductive and nursing purposes (Raclot & Groscolas, 1994).

Together with sex, also the grade of carcass fatness showed to affect SM fat deposition and composition. Considering the four quartile categories obtained for backfat thickness and reported in Table 2, it is possible to observe that backfat thickness is associated with both IMF and the level of several muscle FA. The animals belonging to the first backfat thickness class (less than 23 mm) showed the lowest % of IMF (1.84%), significantly different from the IMF in the thickest group, the fourth (2.153%). This result is in agreement with previous studies (Wood, Enser, Whittington, Moncrieff, & Kempster, 1989) and with the commonly accepted view that IMF and subcutaneous fat share, at least in part, a common genetic basis, as reviewed in Pena, Ros-Freixedes, Tor, & Estany (2016) and reported in our previous study (Davoli et al., 2019). Together with IMF, a thicker backfat layer is also associated with increased contents of SFA in SM, namely capric (C10:0), myristic (C14:0), palmitic and oleic acids. Together with them, also palmitoleic (C16:1 *cis*-9) and vaccenic acids had higher contents in the muscle of pigs with high adipogenic potential.

An opposite trend was observed for most of the *n*-6 and *n*-3 FA and for PUFA, *n*-6 PUFA, and *n*-3 PUFA classes, which showed higher contents in the muscle of pigs with a thinner backfat layer. The only exceptions were the SFA heptadecenoic acid (C17:0), showing greater amounts in leaner pigs, and eicosapentaenoic acid (C20:5 *n*-3), which, despite being an *n*-3 PUFA, was higher in animals with high subcutaneous fat thickness. The essential FA, namely linoleic (C18:2 *cis*-9, *cis*-12) and α-linolenic (C18:3 *n*-3) acids were higher in animals with lower fat deposition. This trend is in agreement with the results in the literature showing that lower amounts of stored fat are associated with higher proportions of PUFA (Matthews, 2011). UFA are essential components of cell membranes, and while the storage of energy through SFA may change among individuals and over time, in individuals fed the same diet the amount of UFA remains stable due to their important roles in membrane flexibility, inflammation control, eicosanoid production, plasma triacylglycerol synthesis and gene expression (reviewed in Fernandez & West, 2005). Furthermore the observed negative relation occurring between PUFA and backfat thickness may also be related to the role of

several PUFA (in particular *n*-3 PUFA) in influencing blood-circulating Low Density Lipoprotein (LDL) level, fat deposition and fat-related chronic inflammation processes (reviewed in Fernandez & West, 2005; Wang & Huang, 2015).

3.2 Heritability estimates for *Semimembranosus* muscle fatty acid composition

Estimated variance components and heritability values of individual FA and FA classes are reported in Table 3 and Table 4, respectively. On the whole, the heritability values estimated for muscle FA were moderate, ranging from 0.177 ± 0.004 to 0.237 ± 0.001 for capric and docosahexaenoic acid (DHA; C22:6 *n*-3), respectively. Similarly, FA classes showed heritability estimates of low-to-moderate magnitude, varying little from 0.209 ± 0.002 for *n*-6 PUFA to 0.226 ± 0.001 for PUFA.

Only small differences in heritability appeared among FA based on their chain length, saturation and double bond position. The linoleic and α-linolenic essential FA showed a moderate level of heritability (0.219 ± 0.001 and 0.223 ± 0.001, respectively), suggesting partial genetic control of digestion, absorption and utilisation mechanisms regulating their storage in muscle. Interestingly, also *n*-6/*n*-3 ratio resulted to be moderately heritable (h^2 = 0.228). Despite this trait being largely affected by feeding factors (De Smet, Raes, & Demeyer, 2004), the heritability found for the *n*-6/*n*-3 ratio suggests a genetic basis for its variability does exist. The heritabilities observed in the present work are on the whole less variable and lower than those reported in the literature for the IMF content and for muscle FA composition (Sellier, Maignel, & Bidanel, 2010; Ibáñez-Escriche, Magallón, Gonzalez, Tejeda, & Noguera, 2016; Zhang et al., 2016). These differences may be caused by the different statistical models used to estimate the heritabilities in the studies in literature, and by the phenotypic and genetic features of the studied population (Robertson, 1977; Zhang et al., 2018). Indeed, the structure of the populations and the different breeding goals pursued across countries may have affected the differences observed among the results of this work and the

literature. The Italian pig breeding system has shaped the genetics of its purebred pigs reared for the production of heavy carcasses, differentiating these animals from those selected for fresh meat production. Pedigree-based heritability values were on the whole consistent with genomic h^2 coefficients obtained integrating molecular marker information (Supplementary Table S2), as shown in Figure 1. Genomic heritability estimates showed greater variability between the different FA than pedigree-based h^2 coefficients, possibly because the first were estimates from univariate analyses and the latter from multivariate analysis. However, the average values from the two types of estimates were on the whole similar (0.237 and 0.222 for genomic and pedigree-based coefficients, respectively). Genomic and pedigree heritabilities were most different for palmitoleic, heptadecenoic (C17:1 *cis*-9), vaccenic, γ-linolenic acid (C18:3 *n*-6), eicosatrienoic (C20:3 *n*-3), docosahexaenoic, and, to a less extent, for eicosapentaenoic acid. In particular, palmitoleic, vaccenic, eicosatrienoic and docosahexaenoic acids showed higher genomic heritability values than the corresponding pedigree-based h^2 coefficients. The higher genomic heritability can be explained either by a greater genetic control over these traits or by an overestimation of the genetic variance due to the presence of an imperfect linkage disequilibrium existing between the DNA markers and the Quantitative Trait Loci (QTLs) controlling the traits (de los Campos, Sorensen & Gianola, 2015).

3.3 Genetic correlations between *Semimembranosus* muscle fatty acid composition and carcass traits

Examining the genetic correlations occurring between FA and carcass traits it is possible to identify some recursive correlation patterns. In Table 5 only a few significant correlations (heptadecenoic and linoleic acids) are reported between single FA and hot carcass weight, suggesting that in our samples the SM FA content is not related to the weight of the animals. The same behaviour can be

observed also for the correlations between single FA and BFT measured by calibre. Only three FA are genetically correlated with subcutaneous fat depots: in particular, capric acid shows a weak positive correlation while heptadecenoic and linoleic acids are negatively correlated with BFT. Considering now the measures obtained by the FOM apparatus, we can observe that the majority of analysed FA is related to those measures. Indeed, several MUFA and PUFA are positively associated with lean % and loin thickness while being negatively correlated with BFT measured by FOM. A significant negative correlation between lean meat content and the content of some FA, namely capric and palmitoleic acids, was also found. The correlation between FA and IMF is positive and highly significant for C10 to C20 SFA and for the MUFA oleic, vaccenic and C20:1 *cis*-11. These results are in agreement with the fact that triacylglycerols, the main neutral lipids used to store energy in muscle, mainly consists of SFA and MUFA (De Smet, Raes, & Demeyer, 2004). On the contrary, the correlation is negative and highly significant for many PUFA. From Table 6, it is possible to note that the FA classes of PUFA, *n*-6 PUFA, and *n*-3 PUFA were positively correlated with measures related to lean mass deposition (hot carcass weight, lean % and loin thickness) and negatively related to BFT measured with the calibre and FOM, in agreement with the general view that PUFA amounts on total FA are negatively related to fat depository (De Smet, Raes, & Demeyer, 2004; Matthews, 2011). Interestingly, the MUFA class did not show to be correlated with carcass measures and presented only a weak positive correlation with IMF (0.145 ± 0.002). This result is in agreement with the evidence reported in Davoli et al. (2019) for the amount of MUFA in backfat. Indeed, also in that previous work, hardly any genetic correlation was observed both for BFT and loin thickness with MUFA (Davoli et al., 2019), suggesting that in heavy pig breeds MUFA could be selected for with no direct effects on carcass traits. This result could be relevant considering that a growing number of studies have pointed out the importance of dietary MUFA for consumers' health. Indeed MUFA such as C16 positional isomers and oleic acid, seem to display desirable effects (Terés et al., 2008; Calder, 2015), while they have hardly any impact on the organoleptic quality of seasoned pork products. However, further studies are

necessary to elucidate the possible direct response of selection for MUFA on PUFA and SFA and the correlated combined effects of the last two classes on carcass characteristics.

3.4 Genetic correlations among *Semimembranosus* muscle fatty acids

The genetic correlations between muscle FA classes and the relative standard errors are reported in Table 7. In this study, all genetic correlations among FA classes showed to be positive, except for the muscle *n*-6/*n*-3 ratio, which showed negative correlations with all of the other FA categories and with muscle total lipids. The positive correlations found between SFA, MUFA and PUFA and the apparent discrepancy with other results reported in literature (Ntawubizi et al., 2010) can be explained because the SM FA composition considered in the present research is reported as absolute value (mg/g of IMF) and not as percentage on the total FA.

The complete matrix of estimated genetic correlations among FA is reported in Supplementary Table S3. The highest genetic correlations were between the essential FA linoleic and α-linolenic acids with the other muscle FA. Linoleic and α-linolenic acids were positively correlated with eicosadienoic acid (C20:2 *n*-6), eicosatrienoic acid and docosapentaenoic acid (C20:5 *n*-3). Essential FA play an important functional role in monogastric mammals since they need to be supplied by the diet. Indeed, monogastric mammals are not able to synthesize the enzymes responsible for introducing double bonds beyond carbons 9 and 10 (Sprecher, Luthria, Mohammed, & Baykousheva, 1995), therefore they are not able to synthesize *de novo* significant amounts of essential FA. Anyway, monogastric mammals can successfully elongate and desaturate linoleic and α-linolenic acids into longer chain PUFA (Brenner, 1974). This biosynthetic pathway linking essential FA with longer chain PUFA, such as eicosadienoic, eicosatrienoic and docosapentaenoic acids, may explain the positive genetic correlations noticed among these FA. Furthermore, high positive correlations were also found among SFA with a number of carbon atoms comprised

between 10 and 16. This result may be associated with the fact that these medium-chain FA are mainly de novo synthesized through subsequent elongation steps by the Fatty acid synthase (FASN) enzyme. FASN has a complex homodimeric structure with the major role of regulating the *de novo* synthesis of long-chain FA in mammals through the formation of 16-carbon FA from acetyl-CoA and malonyl-CoA (Chakravarty, Gu, Chirala, Wakil, & Quiocho, 2004). This synthesis involves a cyclic-step elongation of the precursors by 2 carbon units (Smith, 1994) and the growing FA is generally released when the chain reaches 16 carbon atoms in length.

4 Conclusions

On the whole, SM FA composition showed to be a moderately heritable trait and thus it could be directly modified through genetic selection. Interestingly, genomic and pedigree-based heritabilities estimated for muscle FA were on the whole similar. Palmitoleic, vaccenic, eicosatrienoic and docosahexaenoic acids showed higher genomic heritabilities compared with the corresponding pedigree-based h^2 coefficients. This evidence may suggest that these FA are under greater genetic control than others or, alternatively, the presence of DNA markers in imperfect linkage disequilibrium with the QTLs controlling these FA. Finally, while muscle contents of PUFA were highly correlated with carcass traits, MUFA amounts showed low (or null) genetic correlations with lean and subcutaneous fat measures. In agreement with our previous work on the backfat FA composition, this result seems to indicate that MUFA could be selected for without interfering with carcass traits. However, this hypothesis would require further verification.

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Table 1. Descriptive statistics for the studied traits in *Semimembranosus* muscle with the number of considered pigs (N), the minimum and maximum values, the mean value and the standard deviation (SD).

Traits	N	Minimum	Maximum	Mean	SD
Hot carcass weigth (kg)	715	89.000	137.000	118.613	8.658
BFT (mm)[1]	795	13.000	45.000	26.616	5.091
Lean (%)[2]	715	40.700	59.100	48.982	2.808
BFT FOM (mm)[3]	713	13.000	47.000	27.282	5.240
Loin thickness (mm)[4]	713	26.000	80.000	63.203	6.915
IMF (%)[5]	784	0.590	8.640	2.054	1.107
C10:0 (mg/g IMF)	795	0.209	1.698	0.834	0.212
C12:0 (mg/g IMF)	795	0.201	1.340	0.670	0.181
C14:0 (mg/g IMF)	795	2.718	14.120	8.786	2.046
C16:0 (mg/g IMF)	795	67.900	235.531	151.291	28.953
C16:1 *cis-9* (mg/g IMF)	795	4.643	36.268	18.895	4.840
C17:0 (mg/g IMF)	795	0.510	1.864	0.983	0.208
C17:1 *cis-9* (mg/g IMF)	795	0.719	2.773	1.468	0.335
C18:0 (mg/g IMF)	795	38.144	136.904	76.094	14.510
C18:1 *cis-9* (mg/g IMF)	795	100.206	419.702	263.630	58.830
C18:1 *cis-11* (mg/g IMF)	795	11.339	44.131	25.155	4.770
C18:2 *cis-9, cis-12* (mg/g IMF)	795	35.079	128.232	68.394	12.984
C18:3 *n-6* (mg/g IMF)	795	0.093	1.410	0.708	0.195
C18:3 *n-3* (mg/g IMF)	795	0.109	5.140	2.400	0.698
C20:0 (mg/g IMF)	795	0.080	1.998	1.003	0.265
C20:1 (mg/g IMF)	795	0.168	9.000	4.443	1.191

C20:2 *n-6* (mg/g IMF)	795	1.446	5.108	2.863	0.593
C20:3 *n-6* (mg/g IMF)	759	0.630	3.846	1.455	0.397
C20:4 *n-6* (mg/g IMF)	795	3.155	42.286	11.287	4.265
C20:3 *n-3* (mg/g IMF)	795	0.013	1.945	0.563	0.129
C20:5 *n-3* (mg/g IMF)	795	0.003	0.258	0.080	0.025
C22:1 (mg/g IMF)	759	0.006	0.581	0.123	0.049
C22:2 *n-6* (mg/g IMF)	795	0.006	1.697	0.571	0.294
C22:4 *n-6* (mg/g IMF)	795	0.644	4.835	1.766	0.513
C22:5 *n-3* (mg/g IMF)	795	0.166	3.340	0.674	0.239
C22:6 *n-3* (mg/g IMF)	795	0.007	1.240	0.178	0.084
Total lipids (mg/g IMF)	795	315.941	918.311	644.242	112.414
SFA (mg/g IMF)[6]	795	120.820	384.152	239.661	44.766
MUFA (mg/g IMF)[7]	795	118.789	492.681	313.708	68.018
PUFA (mg/g IMF)[8]	795	48.354	177.158	90.872	16.279
n-3 PUFA (mg/g IMF)[9]	795	1.356	7.304	3.894	0.904
n-6 PUFA (mg/g IMF)[10]	795	46.322	170.020	86.978	15.535
n-6/*n*-3 ratio	795	12.530	53.270	22.856	3.555

[1]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.

[2]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.

[3]Backfat thickness (including rind) measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[4]Loin thickness measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[5]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official procedure AOCS Am 5-04.

[6]Saturated fatty acids.

[7]Monounsaturated fatty acids.

[8]Polyunsaturated fatty acids.

[9]Omega-3 polyunsaturated fatty acids.

[10]Omega-6 polyunsaturated fatty acids.

Table 2. Estimated means and standard deviations (SD) of the *Semimembranosus* muscle fatty acids for the fixed effects of sex and classes of backfat thickness.

	Sex		Backfat thickness classes			
	Barrow	Gilt	1	2	3	4
Traits[1]	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
IMF[2]	2.090 ± 0.093[a]	1.913 ± 0.077[b]	1.840 ± 0.114[b]	2.011 ± 0.094[ab]	2.002 ± 0.097[ab]	2.153 ± 0.104[a]
C10:0	0.812 ± 0.018	0.805 ± 0.015	0.78 ± 0.022[b]	0.804 ± 0.018[ab]	0.810 ± 0.019[ab]	0.840 ± 0.020[a]
C12:0	0.646 ± 0.015	0.654 ± 0.012	0.646 ± 0.018	0.663 ± 0.015	0.641 ± 0.016	0.650 ± 0.017
C14:0	8.570 ± 0.171	8.486 ± 0.142	8.254 ± 0.211[b]	8.573 ± 0.171[ab]	8.503 ± 0.178[ab]	8.780 ± 0.190[a]
C16:0	151.329 ± 2.410[a]	146.810 ± 1.995[b]	144.18 ± 2.963[b]	149.892 ± 2.411[a]	148.803 ± 2.505[ab]	153.401 ± 2.674[a]
C16:1 *cis*-9	18.706 ± 0.405	18.185 ± 0.335	17.307 ± 0.498[c]	18.331 ± 0.405[bc]	18.698 ± 0.421[ab]	19.445 ± 0.449[a]
C17:0	0.966 ± 0.017	0.978 ± 0.014	1.025 ± 0.021[a]	0.981 ± 0.017[b]	0.935 ± 0.018[c]	0.946 ± 0.019[bc]
C17:1 *cis*-9	1.446 ± 0.028	1.441 ± 0.023	1.485 ± 0.034	1.443 ± 0.028	1.425 ± 0.029	1.421 ± 0.031
C18:0	76.935 ± 1.222[a]	73.433 ± 1.011[b]	72.976 ± 1.502[b]	75.852 ± 1.223[a]	74.753 ± 1.27[ab]	77.157 ± 1.356[a]
C18:1 *cis*-9	265.680 ± 4.845[a]	250.866 ± 4.01[b]	253.427 ± 5.955	259.873 ± 4.847	257.561 ± 5.035	262.231 ± 5.375
C18:1 *cis*-11	25.280 ± 0.397[a]	24.252 ± 0.329[b]	24.010 ± 0.488[b]	24.714 ± 0.397[a]	25.076 ± 0.413[a]	25.263 ± 0.44[a]

C18:2 *cis*-9, *cis*-12	66.062 ± 0.989^{b}	71.472 ± 0.819^{a}	74.151 ± 1.216^{a}	70.766 ± 0.989^{b}	66.244 ± 1.028^{c}	63.907 ± 1.097^{d}
C18:3 *n*-6	0.714 ± 0.015	0.734 ± 0.013	0.755 ± 0.019^{a}	0.730 ± 0.015^{ab}	0.707 ± 0.016^{b}	0.706 ± 0.017^{b}
C18:3 *n*-3	2.243 ± 0.057^{b}	2.445 ± 0.047^{a}	2.557 ± 0.07^{a}	2.422 ± 0.057^{b}	2.227 ± 0.059^{c}	2.170 ± 0.063^{c}
C20:0	1.044 ± 0.021^{a}	0.935 ± 0.017^{b}	0.943 ± 0.026^{b}	1.006 ± 0.021^{a}	0.992 ± 0.022^{ab}	1.016 ± 0.023^{a}
C20:1 *cis*-11	4.574 ± 0.097^{a}	4.123 ± 0.08^{b}	4.196 ± 0.119	4.395 ± 0.097	4.384 ± 0.101	4.420 ± 0.108
C20:2 *n*-6	2.749 ± 0.048^{b}	2.836 ± 0.04^{a}	3.026 ± 0.059^{a}	2.896 ± 0.048^{b}	2.686 ± 0.05^{c}	2.562 ± 0.053^{d}
C20:3 *n*-6	1.430 ± 0.029	1.584 ± 0.024	1.562 ± 0.035^{a}	1.537 ± 0.029^{a}	1.499 ± 0.03^{a}	1.429 ± 0.033^{b}
C20:4 *n*-6	11.392 ± 0.328^{b}	12.898 ± 0.271^{a}	12.785 ± 0.403^{a}	12.170 ± 0.328^{ab}	12.185 ± 0.34^{ab}	11.440 ± 0.363^{b}
C20:3 *n*-3	0.546 ± 0.011	0.560 ± 0.009	0.592 ± 0.013^{a}	0.565 ± 0.011^{b}	0.532 ± 0.011^{c}	0.524 ± 0.012^{c}
C20:5 *n*-3	0.087 ± 0.002^{a}	0.077 ± 0.002^{b}	0.078 ± 0.003^{b}	0.084 ± 0.002^{a}	0.083 ± 0.002^{a}	0.084 ± 0.002^{a}
C22:1	0.129 ± 0.004^{b}	0.143 ± 0.003^{a}	0.143 ± 0.005^{a}	0.137 ± 0.004^{ab}	0.135 ± 0.004^{ab}	0.128 ± 0.004^{b}
C22:2 *n*-6	0.519 ± 0.024	0.551 ± 0.020	0.543 ± 0.029	0.545 ± 0.024	0.541 ± 0.025	0.512 ± 0.026
C22:4 *n*-6	1.847 ± 0.040	1.900 ± 0.033	2.006 ± 0.050^{a}	1.896 ± 0.040^{b}	1.842 ± 0.042^{bc}	1.751 ± 0.045^{c}
C22:5 *n*-3	0.725 ± 0.017^{b}	0.787 ± 0.014^{a}	0.811 ± 0.021^{a}	0.769 ± 0.017^{b}	0.746 ± 0.018^{b}	0.699 ± 0.019^{c}
C22:6 *n*-3	0.189 ± 0.006^{b}	0.227 ± 0.005^{a}	0.237 ± 0.007^{a}	0.209 ± 0.006^{b}	0.198 ± 0.006^{bc}	0.189 ± 0.007^{c}

SFA[3]	240.301 ± 3.739[a]	232.1 ± 3.094[b]	228.804 ± 4.596[b]	237.77 ± 3.74[a]	235.438 ± 3.886[ab]	242.79 ± 4.148[a]
MUFA[4]	315.803 ± 5.604[a]	298.997 ± 4.638[b]	300.557 ± 6.889	308.882 ± 5.607	307.268 ± 5.824	312.894 ± 6.217
PUFA[5]	88.356 ± 1.194[b]	95.934 ± 0.988[a]	98.97 ± 1.468[a]	94.453 ± 1.195[b]	89.355 ± 1.241[c]	85.802 ± 1.325[d]
n-6 PUFA[6]	84.566 ± 1.135[b]	91.838 ± 0.939[a]	94.697 ± 1.395[a]	90.405 ± 1.135[b]	85.569 ± 1.180[c]	82.136 ± 1.259[d]
n-3 PUFA[7]	3.790 ± 0.071[b]	4.096 ± 0.059[a]	4.273 ± 0.087[a]	4.048 ± 0.071[b]	3.786 ± 0.074[c]	3.666 ± 0.079[c]
n-6/*n*-3 ratio	22.860 ± 0.283	22.904 ± 0.234	22.586 ± 0.348	22.837 ± 0.283	23.218 ± 0.294	22.886 ± 0.314

[1]Fatty acids were expressed as mg/g of *Semimembranosus* muscle intramuscular fat, while intramuscular fat (IMF) was expressed as %.

[2]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official procedure AOCS Am 5-04 (expressed as %).

[3]Saturated fatty acids.

[4]Monounsaturated fatty acids.

[5]Polyunsaturated fatty acids.

[6]Omega-6 polyunsaturated fatty acids.

[7]Omega-3 polyunsaturated fatty acids.

Table 3. Genetic variance (σ_a^2), litter variance (σ_f^2), error variance (σ_e^2), total variance (σ_t^2), heritability (h^2) and heritability standard error (SE) for *Semimembranosus* muscle fatty acid composition.

Traits[1]	σ_a^2	σ_f^2	σ_e^2	σ_t^2	h^2	SE
C10:0	6.480E+02	2.422E+02	2.775E+03	3.666E+03	0.177	0.004
C12:0	2.328E+03	4.620E+02	7.745E+03	1.053E+04	0.221	0.002
C14:0	6.964E+05	1.147E+05	2.186E+06	2.997E+06	0.232	0.001
C16:0	1.936E+08	3.071E+07	6.109E+08	8.352E+08	0.232	0.001
C16:1 *cis*-9	5.146E+06	8.736E+05	1.595E+07	2.197E+07	0.234	0.001
C17:0	4.343E+03	5.081E+02	1.520E+04	2.005E+04	0.217	0.002
C17:1 *cis*-9	1.090E+04	1.861E+03	3.836E+04	5.112E+04	0.213	0.002
C18:0	6.799E+07	8.911E+06	2.189E+08	2.958E+08	0.230	0.001
C18:1 *cis*-9	1.637E+09	2.211E+08	5.322E+09	7.181E+09	0.228	0.001
C18:1 *cis*-11	9.631E+06	1.425E+06	3.041E+07	4.146E+07	0.232	0.001
C18:2 *cis*-9, *cis*-12	3.631E+07	3.799E+06	1.256E+08	1.657E+08	0.219	0.001
C18:3 *n*-6	5.453E+03	6.439E+02	1.967E+04	2.576E+04	0.212	0.001
C18:3 *n*-3	2.500E+05	2.283E+04	8.461E+05	1.119E+06	0.223	0.001
C20:0	2.021E+04	2.809E+03	6.615E+04	8.917E+04	0.227	0.001

C20:1 *cis*-11	7.248E+05	1.006E+05	2.325E+06	3.150E+06	0.230	0.001
C20:2 *n*-6	1.880E+05	1.822E+04	6.246E+05	8.309E+05	0.226	0.001
C20:3 *n*-6	2.395E+04	5.956E+03	7.423E+04	1.041E+05	0.230	0.001
C20:4 *n*-6	6.354E+06	1.249E+06	1.977E+07	2.737E+07	0.232	0.001
C20:3 *n*-3	6.176E+03	8.584E+02	1.939E+04	2.642E+04	0.234	0.001
C20:5 *n*-3	8.593E+01	1.297E+01	3.072E+02	4.061E+02	0.212	0.001
C22:1	4.743E+02	1.080E+02	1.436E+03	2.019E+03	0.235	0.001
C22:2 *n*-6	4.599E+04	7.655E+03	1.452E+05	1.988E+05	0.231	0.001
C22:4 *n*-6	9.938E+04	1.855E+04	3.057E+05	4.236E+05	0.235	0.001
C22:5 *n*-3	1.655E+04	3.182E+03	5.073E+04	7.046E+04	0.235	0.001
C22:6 *n*-3	1.386E+03	3.086E+02	4.147E+03	5.842E+03	0.237	0.001

[1]Fatty acids were expressed as mg/g of *Semimembranosus* muscle intramuscular fat.

Table 4. Genetic variance (σ_a^2), litter variance (σ_f^2), error variance (σ_e^2), total variance (σ_t^2), heritability (h^2) and heritability standard error (SE) for the fatty acid classes in *Semimembranosus* muscle.

Traits[1]	σ_a^2	σ_f^2	σ_e^2	σ_t^2	h^2	SE
IMF[2]	2.562E+04	1.716E+04	1.488E+05	1.916E+05	0.134	0.002
Total lipids	3.681E+08	1.952E+08	1.783E+09	2.347E+09	0.157	0.002
SFA[3]	9.983E+08	1.353E+08	3.296E+09	4.430E+09	0.225	0.001
MUFA[4]	3.274E+09	4.446E+08	1.079E+10	1.451E+10	0.226	0.001
PUFA[5]	1.466E+08	1.697E+07	4.837E+08	6.473E+08	0.226	0.001
n-6 PUFA[6]	1.937E+07	6.523E+06	6.698E+07	9.288E+07	0.209	0.002
n-3 PUFA[7]	2.876E+05	3.543E+04	9.743E+05	1.297E+06	0.222	0.002
n-6/*n*-3 ratio	3.896E+06	5.409E+05	1.266E+07	1.709E+07	0.228	0.001

[1]Fatty acids were expressed as mg/g of *Semimembranosus* muscle intramuscular fat, while intramuscular fat (IMF) was expressed as %.

[2]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official procedure AOCS Am 5-04 (expressed as %).

[3]Saturated fatty acids.

[4]Monounsaturated fatty acids.

[5]Polyunsaturated fatty acids.

[6]Omega-6 polyunsaturated fatty acids.

[7]Omega-3 polyunsaturated fatty acids.

Table 5. Genetic correlation coefficients (r_g) ± the relative standard errors between *Semimembranosus* muscle fatty acid composition and carcass traits.

Traits[1]	Hot carcass weight (kg)	BFT[2] (mm)	Lean[3] (%)	BFT FOM[4] (mm)	Loin thickness[5] (mm)	IMF[6] (%)
C10:0	-0.062 ± 0.012	0.076 ± 0.013*	-0.282 ± 0.012***	0.367 ± 0.011***	-0.319 ± 0.011	0.768 ± 0.009***
C12:0	-0.031 ± 0.005	0.030 ± 0.005	0.020 ± 0.005	0.001 ± 0.005	0.009 ± 0.005	0.301 ± 0.005***
C14:0	-0.037 ± 0.003	0.039 ± 0.004	-0.051 ± 0.004	0.067 ± 0.003	-0.043 ± 0.004	0.241 ± 0.003***
C16:0	-0.028 ± 0.003	0.031 ± 0.003	-0.056 ± 0.003	0.079 ± 0.003*	-0.064 ± 0.003	0.206 ± 0.003***
C16:1 *cis*-9	-0.038 ± 0.003	0.042 ± 0.003	-0.089 ± 0.003*	0.101 ± 0.003**	-0.061 ± 0.003	0.176 ± 0.003***
C17:0	0.099 ± 0.004**	-0.107 ± 0.005**	0.174 ± 0.005***	-0.169 ± 0.004***	0.088 ± 0.005*	0.023 ± 0.006
C17:1 *cis*-9	0.032 ± 0.005	-0.037 ± 0.005	0.107 ± 0.005**	-0.119 ± 0.005***	0.101 ± 0.005**	-0.042 ± 0.005
C18:0	-0.022 ± 0.002	0.024 ± 0.003	-0.045 ± 0.003	0.078 ± 0.003*	-0.084 ± 0.003*	0.167 ± 0.003***
C18:1 *cis*-9	-0.015 ± 0.002	0.016 ± 0.002	-0.014 ± 0.002	0.022 ± 0.002	-0.011 ± 0.002	0.117 ± 0.002***
C18:1 *cis*-11	-0.023 ± 0.002	0.025 ± 0.002	-0.038 ± 0.002	0.049 ± 0.002	-0.028 ± 0.002	0.123 ± 0.002***
C18:2 *cis*-9, *cis*-12	0.078 ± 0.003**	-0.088 ± 0.005*	0.217 ± 0.003***	-0.237 ± 0.003***	0.171 ± 0.003***	-0.067 ± 0.005

C18:3 *n*-6	0.032 ± 0.004	-0.037 ± 0.004	0.099 ± 0.004**	-0.127 ± 0.004***	0.11 ± 0.004**	-0.073 ± 0.004*
C18:3 *n*-3	0.030 ± 0.002	-0.035 ± 0.003	0.109 ± 0.002**	-0.122 ± 0.002***	0.096 ± 0.002**	0.001 ± 0.003
C20:0	-0.009 ± 0.003	0.01 ± 0.003	-0.029 ± 0.003	0.057 ± 0.003	-0.068 ± 0.003	0.084 ± 0.003*
C20:1 *cis*-11	-0.024 ± 0.002	0.025 ± 0.002	-0.018 ± 0.002	0.028 ± 0.002	-0.014 ± 0.002	0.108 ± 0.002**
C20:2 *n*-6	0.048 ± 0.002	-0.054 ± 0.003	0.139 ± 0.002***	-0.149 ± 0.002***	0.106 ± 0.002**	-0.025 ± 0.004
C20:3 *n*-6	0.024 ± 0.004	-0.029 ± 0.004	0.098 ± 0.004**	-0.099 ± 0.004**	0.067 ± 0.004	-0.133 ± 0.004***
C20:4 *n*-6	0.018 ± 0.002	-0.021 ± 0.003	0.054 ± 0.002	-0.062 ± 0.002	0.045 ± 0.002	-0.115 ± 0.002**
C20:3 *n*-3	0.019 ± 0.002	-0.025 ± 0.003	0.108 ± 0.003**	-0.137 ± 0.002***	0.132 ± 0.002***	-0.010 ± 0.004
C20:5 *n*-3	0.001 ± 0.004	0.001 ± 0.004	-0.037 ± 0.004	0.021 ± 0.004	-0.008 ± 0.004	0.067 ± 0.004
C22:1	0.011 ± 0.003	-0.015 ± 0.003	0.074 ± 0.003*	-0.088 ± 0.003*	0.075 ± 0.003*	-0.089 ± 0.003*
C22:2 *n*-6	0.022 ± 0.002	-0.023 ± 0.002	0.026 ± 0.002	-0.014 ± 0.002	-0.017 ± 0.002	-0.078 ± 0.002*
C22:4 *n*-6	0.032 ± 0.002	-0.037 ± 0.003	0.090 ± 0.002*	-0.094 ± 0.002**	0.066 ± 0.002	-0.118 ± 0.003***
C22:5 *n*-3	0.033 ± 0.003	-0.037 ± 0.003	0.092 ± 0.003**	-0.102 ± 0.003**	0.078 ± 0.003*	-0.075 ± 0.003*
C22:6 *n*-3	0.058 ± 0.003	-0.065 ± 0.004	0.132 ± 0.003***	-0.178 ± 0.003***	0.146 ± 0.003***	-0.098 ± 0.004**

* *P*-value ≤ 0.05; ** *P*-value ≤ 0.01; *** *P*-value ≤ 0.001.

[1]Fatty acids were expressed as mg/g of *Semimembranosus* muscle intramuscular fat.

[2]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.

[3]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.

[4]Backfat thickness (including rind) measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[5]Loin thickness measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[6]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official procedure AOCS Am 5-04.

Table 6. Genetic correlation coefficients (r_g) ± the relative standard errors between the fatty acid classes in *Semimembranosus* muscle and carcass traits.

Traits[1]	Hot carcass weight (kg)	BFT[2] (mm)	Lean[3] (%)	BFT FOM[4] (mm)	Loin thickness[5] (mm)	IMF[6] (%)
Total lipids	-0.048 ± 0.008	0.048 ± 0.008	-0.018 ± 0.008	0.093 ± 0.008**	-0.089 ± 0.008**	0.731 ± 0.006***
n-6 PUFA[7]	0.203 ± 0.005***	-0.225 ± 0.008***	0.563 ± 0.005***	-0.603 ± 0.004***	0.438 ± 0.005***	-0.267 ± 0.009***
n-3 PUFA[8]	0.07 ± 0.002*	-0.079 ± 0.004*	0.236 ± 0.003***	-0.265 ± 0.002***	0.216 ± 0.003***	-0.035 ± 0.004
n-6/*n*-3 ratio	0.014 ± 0.003	-0.012 ± 0.003	-0.048 ± 0.003	0.076 ± 0.003*	-0.107 ± 0.003**	-0.134 ± 0.003***
SFA[9]	-0.025 ± 0.002	0.027 ± 0.002	-0.054 ± 0.002	0.086 ± 0.002*	-0.084 ± 0.002*	0.214 ± 0.002***
MUFA[10]	-0.017 ± 0.002	0.018 ± 0.002	-0.021 ± 0.002	0.033 ± 0.002	-0.021 ± 0.002	0.145 ± 0.002***
PUFA[11]	0.077 ± 0.002*	-0.085 ± 0.003*	0.215 ± 0.002***	-0.231 ± 0.002***	0.169 ± 0.002***	-0.099 ± 0.003**

* *P*-value ≤ 0.05; ** *P*-value ≤ 0.01; *** *P*-value ≤ 0.001.

[1] Fatty acid classes were expressed as mg/g of *Semimembranosus* muscle intramuscular fat.

[2]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.

[3]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.

[4]Backfat thickness (including rind) measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[5]Loin thickness measured with Fat-O-Meat'er (FOM) instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.

[6]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official procedure AOCS Am 5-04.

[7]Omega-6 polyunsaturated fatty acids.

[8]Omega-3 polyunsaturated fatty acids.

[9]Saturated fatty acids.

[10]Monounsaturated fatty acids.

[11]Polyunsaturated fatty acids.

Table 7. Genetic correlations (above diagonal), standard errors (below diagonal) and heritabilities (diagonal, in bold) for the fatty acid classes in *Semimembranosus* muscle.

Traits[1]	Total lipids	*n*-6 PUFA[2]	*n*-3 PUFA[3]	*n*-6/*n*-3	SFA[4]	MUFA[5]	PUFA[6]
Total lipids	**0.157**	0.313***	0.392***	-0.554***	0.635***	0.515***	0.131***
n-6 PUFA[2]	0.009	**0.209**	0.716***	-0.517***	0.398***	0.367***	0.477***
n-3 PUFA[3]	0.005	0.004	**0.222**	-0.691***	0.583***	0.471***	0.812***
n-6/*n*-3 ratio	0.004	0.003	0.002	**0.228**	-0.878***	-0.722***	-0.753***
SFA[4]	0.004	0.004	0.002	0.002	**0.225**	0.883***	0.591***
MUFA[5]	0.003	0.003	0.002	0.002	0.001	**0.226**	0.562***
PUFA[6]	0.004	0.003	0.002	0.002	0.002	0.002	**0.226**

*** *P*-value ≤ 0.001.

[1]Fatty acid classes were expressed as mg/g of *Semimembranosus* muscle intramuscular fat.

[2]Omega-6 polyunsaturated fatty acids.

[3]Omega-3 polyunsaturated fatty acids.

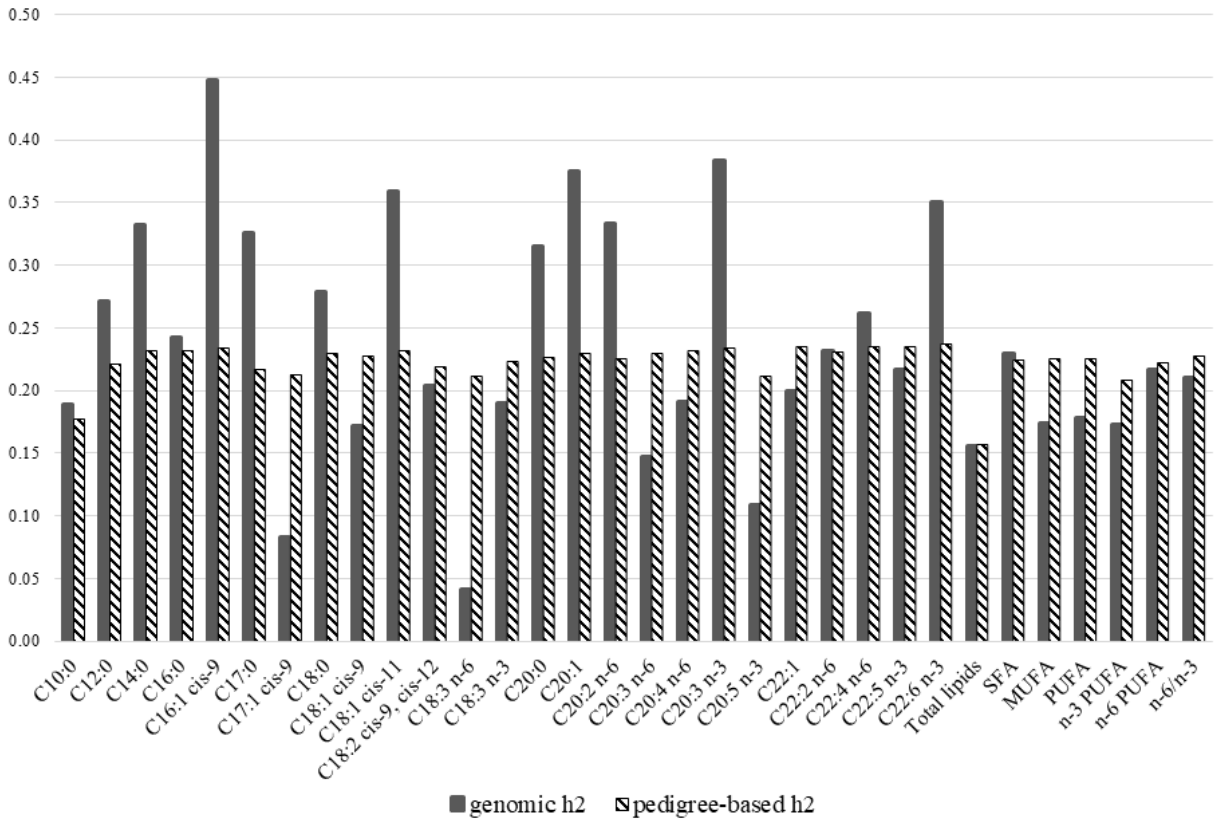
[4]Saturated fatty acids.

[5]Monounsaturated fatty acids.

[6]Polyunsaturated fatty acids

Figure captions

Figure 1. Histogram showing the estimates of the genomic and pedigree-based heritabilities (h^2) for *Semimembranosus* muscle fatty acid composition.



Supplementary Material

Supplementary Table S1. List of the analysed fatty acids and fatty acid categories with shorthand notation, IUPAC and common nomenclature.

Supplementary Table S2. Estimates of the genomic and pedigree-based heritabilities for *Semimembranosus* muscle fatty acid composition.

Supplementary Table S3. Genetic correlations (above diagonal), standard errors (below diagonal) and heritabilities (diagonal, in bold) for *Semimembranosus* muscle fatty acid composition.

Supplementary Table S1. List of the analysed fatty acids and fatty acid categories with shorthand notation, IUPAC and common nomenclature.

Shorthand notation	IUPAC nomenclature	Common nomenclature
C10:0	Decanoic acid	Capric acid
C12:0	Dodecanoic acid	Lauric acid
C14:0	Tetradecanoic acid	Myristic acid
C16:0	Hexadecanoic acid	Palmitic acid
C16:1 *cis*-9	(9Z)-Hexadec-9-enoic acid	Palmitoleic acid
C17:0	Heptadecanoic acid	Margaric acid
C17:1 *cis*-9	Heptadecenoic acid	Heptadecenoic acid
C18:0	Octadecanoic acid	Stearic acid
C18:1 *cis*-9	(9Z)-Octadec-9-enoic acid	Oleic acid
C18:1 *cis*-11	(E)-Octadec-11-enoic acid	Vaccenic acid
C18:2 *cis*-9, *cis*-12	(9Z,12Z)-9,12-Octadecadienoic acid	Linoleic acid
C18:3 *n*-6	(6Z,9Z,12Z)-octadeca-6,9,12-trienoic acid	γ-Linolenic acid
C18:3 *n*-3	(9Z,12Z,15Z)-9,12,15-Octadecatrienoic acid	α-Linolenic acid
C20:0	Eicosanoic acid	Arachidic acid
C20:1	(9Z)-9-Icosenoic acid	Gadoleic acid
C20:2 *n*-6	(11Z,14Z)-Icosa-11,14-dienoic acid	Eicosadienoic acid
C20:3 *n*-6	(8Z,11Z,14Z)-Icosa-8,11,14-trienoic acid	Dihomo-gamma-linolenic acid
C20:4 *n*-6	(5Z,8Z,11Z,14Z)-Icosa-5,8,11,14-tetraenoic acid	Arachidonic acid
C20:3 *n*-3	(Z,Z,Z)-11,14,17-Eicosatrienoic acid	Eicosatrienoic acid (ETE)
C20:5 *n*-3	(5Z,8Z,11Z,14Z,17Z)-icosa-5,8,11,14,17-pentaenoic acid	Eicosapentaenoic acid (EPA)
C22:1	(Z)-Docos-13-enoic acid	Erucic acid
C22:2 *n*-6	(13Z,16Z)-Docosa-13,16-dienoic acid	Docosadienoic acid

C22:4 *n*-6	(7Z,10Z,13Z,16Z)-Docosa-7,10,13,16-tetraenoic acid	Adrenic acid
C22:5 *n*-3	(7Z,10Z,13Z,16Z,19Z)-docosa-7,10,13,16,19-pentaenoic acid	Docosapentaenoic acid (DPA)
C22:6 *n*-3	(4Z,7Z,10Z,13Z,16Z,19Z)-Docosa-4,7,10,13,16,19-hexaenoic acid	Docosahexaenoic acid (DHA)

Supplementary Table S2. Estimates of the genomic and pedigree-based heritabilities for *Semimembranosus* muscle fatty acid composition.

Traits[1]	Genomic heritability	Pedigree-based heritability
C10:0	0.189	0.177
C12:0	0.271	0.221
C14:0	0.332	0.232
C16:0	0.242	0.232
C16:1 *cis*-9	0.448	0.234
C17:0	0.326	0.217
C17:1 *cis*-9	0.083	0.213
C18:0	0.279	0.230
C18:1 *cis*-9	0.172	0.228
C18:1 *cis*-11	0.359	0.232
C18:2 *cis*-9, *cis*-12	0.204	0.219
C18:3 *n*-6	0.041	0.212
C18:3 *n*-3	0.190	0.223
C20:0	0.315	0.227
C20:1	0.375	0.230
C20:2 *n*-6	0.333	0.226
C20:3 *n*-6	0.147	0.230
C20:4 *n*-6	0.191	0.232
C20:3 *n*-3	0.384	0.234
C20:5 *n*-3	0.109	0.212
C22:1	0.200	0.235
C22:2 *n*-6	0.232	0.231

C22:4 *n*-6	0.262	0.235
C22:5 *n*-3	0.217	0.235
C22:6 *n*-3	0.350	0.237
Total lipids	0.156	0.157
SFA[2]	0.230	0.225
MUFA[3]	0.174	0.226
PUFA[4]	0.178	0.226
n-3 PUFA[5]	0.173	0.209
n-6 PUFA[6]	0.217	0.222
n-6/*n*-3 ratio	0.210	0.228

[1]Fatty acids and fatty acid classes were measured as mg/g of *Semimembranosus* muscle intramuscular fat.

[2]Saturated fatty acids.

[3]Monounsaturated fatty acids.

[4]Polyunsaturated fatty acids.

[5]Omega-3 polyunsaturated fatty acids.

[6]Omega-6 polyunsaturated fatty acids.