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Genetic parameters of backfat fatty acids and carcass traits in Large White pigs

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Subcutaneous fat thickness and fatty acid composition (FAC) play an important role on seasoning loss and organoleptic characteristics of seasoned hams. Dry-cured ham industry prefers meats with low contents of polyunsaturated fatty acids (PUFA) because these negatively affect fat firmness and ham quality, whereas consumers require higher contents in those fatty acids (FA) for their positive effect on human health. A population of 950 Italian Large White pigs from the Italian National Sib Test Selection Programme was investigated with the aim to estimate heritabilities, genetic and phenotypic correlations of backfat FAC, Semimembranosus *muscle intramuscular fat (IMF) content and other carcass traits. The pigs were reared in controlled environmental condition at the same central testing station and were slaughtered at reaching 150 kg live weight. Backfat samples were collected to analyze FAC by gas chromatography. Carcass traits showed heritability levels from 0.087 for estimated carcass lean percentage to 0.361 for hot carcass weight. Heritability values of FA classes were low-to-moderate, all in the range 0.245 for n-3 PUFA to 0.264 for monounsaturated FA (MUFA). Polyunsaturated fatty acids showed a significant genetic correlation with loin thickness (0.128), backfat thickness (−0.124 for backfat measured by Fat-O-Meat'er and −0.175 for backfat measured by calibre) and IMF (−0.102). Obviously, C18:2(n-6) shows similar genetic correlations with the same traits (0.211 with loin thickness, −0.206 with backfat measured by Fat-O-Meat'er, −0.291 with backfat measured by calibre and −0.171 with IMF). Monounsaturated FA, except with the backfat measured by calibre (0.068;* $P < 0.01$*), do not show genetic correlations with carcass characteristics, whereas a negative genetic correlation was found between MUFA and saturated FA (SFA; −0.339;* $P < 0.001$*). These results suggest that MUFA/SFA ratio could be increased without interfering with carcass traits. The level of genetic correlations between FA and carcass traits should be taken into account in dealing with the development of selection schemes addressed to modify carcass composition and/or backfat FAC.*

Keywords: swine, heritability, correlations, selection, fat quality

Implications

Backfat fatty acid composition (FAC) is a heritable trait and could be changed through genetic selection. Moreover, the results show that selection aimed to change carcass traits would affect backfat FAC and fat quality.

Introduction

Subcutaneous and intramuscular fat (IMF) content and composition strongly contribute to the nutritional and technological values of fresh and seasoned pork products and therefore they are of significant economic interest. The relative amount of saturated fatty acids (SFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) in pig carcass and meat is extremely important both for the food processing industry and for consumers. In particular, thickness and FAC of subcutaneous fat play an important role in dry-cured hams during seasoning period, as backfat prevents excessive seasoning loss and worsening of organoleptic characteristics (Bosi and Russo, 2004). Due to the distinct melting points shown by different fatty acids (FA), variation in lipid composition also plays an important effect on fat firmness (Suzuki *et al.*, 2006).

However, technological requirement by the seasoning industry and dietary demands by consumers do not completely match. Dry-cured ham industry requires meat with a limited amount of PUFA (Bosi and Russo, 2004) as they are

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more likely to incur in lipolytic and oxidative processes, causing rancidity, abnormal flavours, fat softness and altered organoleptic properties of dry-cured hams (Wood *et al*., 2004; Juárez *et al*., 2011). However, consumers are interested in products with improved nutritional quality and enriched in PUFA. Polyunsaturated fatty acids are essential for life, as they represent a structural component of cell membrane and take part in the synthesis of a wide variety of molecules with key biological functions (Wallis *et al*., 2002).

On the contrary, high percentage of SFA has positive effects on fat firmness and oxidative stability (Wood *et al*., 2004), but is generally thought to have a negative impact on human health (Mensink *et al*., 2003).

Fatty acids composition is influenced by breed, diet, age, sex, fatness and genotype (Pena *et al*., 2016). So far, efforts to change FAC of pig fat depots have mainly been concerned with the integration of unsaturated FA sources in pig diets (Raes *et al*., 2004; Dugan *et al*., 2015), and little research has been performed on the genetic variability of FAC. A limited number of studies are available both on the genetic basis of backfat FAC and on the genetic connections between backfat FAC and other carcass traits.

This work aims to estimate the heritability of backfat FAC, *Semimembranosus* muscle (SM) IMF content and other carcass traits in a population of Italian Large White heavy pigs. Genetic and phenotypic correlations among these traits will be also estimated.

Material and methods

Sampling

A purebred population of 950 Italian Large White pigs included in the national sib-testing selection programme of Italian National Association of Pig Breeders (Associazione Nazionale Allevatori Suini (ANAS), http://www.anas.it) was investigated in this study. The sib-testing programme is based on the performances of triplets of full sibs (two females and one castrated male) in the testing station. The experimental population came from 393 litters by 87 boars and 371 sows. Each group of siblings entered the central testing station at the age of 30 to 45 days and kept together in the same box for the following 6 weeks. The actual testing period lasted a maximum of 145 days to an average final live weight of about 150 kg. During the testing period siblings were kept separated, fed the same finishing diet at a *quasi ad libitum* feeding level. All animals were kept and slaughtered according to Italian and European laws on pig welfare as reported in the 'Ethics statement' section. Pigs were slaughtered in 27 different days between 2011 and 2012 at the same commercial abattoir. Each litter was slaughtered in at least two different dates.

Backfat tissue (including both inner and outer layers) and SM samples were taken on the trimming line from the left carcass side, wrapped in aluminium foil, immediately put in vacuum-sealed bags and frozen in liquid nitrogen. The samples were kept at −80°C for further use. Samples of backfat tissue were collected at the level of its maximum thickness. Samples of SM were collected from the thigh, at the same point in all carcasses.

Phenotypes

At slaughtering hot carcass weight (kg), backfat thickness (BFT) measured in mm by a calibre at the level of *Gluteus medius* muscle, ultrasonic measures (in mm) taken by Fat-O-Meat'er (FOM, Frontmatec A/S, Kolding, Denmark) between the third and fourth last ribs, 8 cm of the carcass midline of loin and backfat and estimated percentage of lean cuts on carcass were recorded.

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

Backfat lipids were extracted according to Serra *et al*. (2014). Backfat samples (10 g) were finely minced, then for each sample 15 mg were collected, dissolved in 30 ml of chloroform/methanol 2/1 vol/vol, homogenated by using a T-25 Ultra Turrax homogenizer (Janke & Kunkel, Staufen, Germany) and filtered through paper filter to remove the residue of tissues. Solvent was removed by a Büchi 461 rotavapor apparatus (Büchi, Flavil, Switzerland). The sample was trans-esterified with 0.5 ml of a sodium methoxydemethanolic solution (0.5 N); the reaction was achieved at room temperature and was completed in few minutes. Fatty acid methyl-esters were extracted with 1 ml of hexane and injected in a Gas-Chromatograph apparatus (GC 2010 plus, Shimadzu, Columbia, MD, USA) equipped with a flame ionization detector and with a high polar capillary column (SP 2560 100 m × 0.25 mm; Supelco, Bellefonte, PA, USA).

Fatty acids methyl-esters were identified by comparison with commercial standard mix of FA methyl-esters (GLC-674; Nuchek, Elysian, MN, USA) addicted with single FA (Nuchek; Larodan, Malmö, Sweden) obtaining a complete standard of 105 FA methyl-esters. For each FA methyl-ester, response factors to flame ionization detector and inter- and intra-assay CV were calculated by using a reference standard butter (CRM 164; Community Bureau of Reference, Brussels, Belgium). Results were expressed as g of FA on 100 g of total FA after the conversion of FA methyl-esters into FA.

The analyzed backfat FA and FA classes are listed in Supplementary Table S1.

Overall, the initial sample size reduced to 881 pigs because classes of factor litter with only one individual were excluded. Moreover, the number of recorded animals was different among phenotypes: with data on different traits recorded on a minimum of 838 to a maximum of 871 animals. Some data were missing because of the unavailability of the online measurement at a slaughterhouse or because some samples were not available or insufficient in size.

Heritability and genetic correlation estimation

Experimental data included information on a three-generation pedigree for a total of 2318 animals, 623 males

and 1695 females. The inbreeding coefficient was calculated for all tested animals by the inbreed procedure of SAS software 9.4. Out of the 881 pigs, 401 were inbred with an average inbreeding coefficient of 4.38%. Given this low level of inbreeding it was not considered in the model subsequently.

The components of variance and heritability for a number of traits grouped in the three classes of subcutaneous FAC, carcass quality and meat quality, and the genetic correlations among them, were estimated by restricted maximum likelihood methodology using the VCE software system version 6 (Groeneveld *et al.*, 2010).

Genetic analyses were carried out by two multiple trait animal models in two different steps: one involving the measures recorded at slaughtering added with individual FA, the other involving the same measurements at slaughtering added with classes of FA.

The model of analysis adopted was:

$$Y_i = X_i + W_i f_i + Z_i a_i + e_i$$

where Y_i is the observation vector for the ith trait; β_i the vector of fixed effects for ith trait (sex: two levels for barrows and gilts; slaughtering date: 27 levels; age at slaughtering as covariate: 1 level); f_i the vector of random effect of litter for traits ith (324 levels of litter); a_i the vector of additive genetic values of the animals with and without records; e_i the vector of residues; X the matrix of incidence of $n \times p$ order associating each observation (n) to the pertinent level of sex and slaughter day (p); W the matrix of incidence of $n \times q$ order associating each observation (n) to the pertaining litter level (q); Z the matrix of incidence of $n \times s$ order associating each observation (n) to each animal (s).

It was assumed that:

$$\mathrm{Var}\begin{pmatrix} a \\ f \\ e \end{pmatrix} = \begin{pmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & F & 0 \\ 0 & 0 & R \end{pmatrix}$$

in which A is the relationship matrix between all animals; F the variance of litter ($F = I\sigma_f^2$); and R the residual variance ($R = I\sigma_e^2$).

The equation of mixed models under the animal model have the following matrix form:

$$\begin{pmatrix} X'X & X'W & X'Z \\ W'X & W'W & W'Z \\ Z'X & Z'W & Z'Z + A^{-1}\lambda \end{pmatrix} \begin{pmatrix} \beta \\ f \\ a \end{pmatrix} = \begin{pmatrix} X'y \\ W'y \\ Z'y \end{pmatrix}$$

where λ is the ratio between σ_e^2 and σ_a^2 that can also be expressed as $(1 - h^2)/h^2$ (h^2 is the heritability for the trait).

The use of multiple trait model allowed to compute genetic correlation among traits; whereas, phenotypic correlation was estimated using the procedure Proc Corr of software SAS 9.4.

Results and discussion

Sample description and heritability estimates

Table 1 reports minimum, maximum, mean values and standard deviations for the recorded phenotypes. The high carcass weight (119.236 ± 8.525 kg) approaches the weight of typical heavy pigs grown for the production of 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). Phenotypes are the results of selection performed over many years by ANAS with the aim of producing pigs with suitable subcutaneous fat thickness while maintaining some genetic progress for average daily gain and feed conversion ratio. The limited variability observed for the carcass weight is the result of the testing

Table 1 *Descriptive statistics for the studied traits with the number of considered pigs (n), the minimum and maximum values, the mean value and the standard deviation*

Traits	*n*[a]	Minimum	Maximum	Mean	SD
Hot carcass weight (kg)	840	89.000	137.000	119.236	8.525
Lean (%)[b]	840	40.600	59.100	48.885	2.728
BFT FOM (mm)[c]	838	13.000	47.000	27.490	5.099
Loin thickness (mm)[d]	838	25.000	80.000	63.331	6.933
BFT (mm)[e]	878	13.000	45.000	26.864	5.044
IMF (%)[f]	878	0.590	8.640	2.044	1.112
SFA	871	30.120	44.378	37.599	2.581
MUFA	871	34.048	49.140	43.703	1.804
PUFA	871	13.295	26.248	18.263	2.123
n-6 PUFA	871	11.565	23.729	16.328	1.980
n-3 PUFA	871	0.424	1.747	0.812	0.177
C12:0[g]	871	0.046	0.249	0.105	0.033
C14:0[g]	871	0.800	1.823	1.228	0.162
C16:0[g]	871	18.120	27.004	22.500	1.304
C16:1 *cis*-7(n-9)[g]	871	0.209	0.627	0.342	0.059
C16:1 *cis*-9(n-7)[g]	871	0.813	2.736	1.455	0.260
C18:0[g]	871	8.498	18.828	13.210	1.757
C18:1 *cis*-9(n-9)[g]	871	30.105	43.311	38.435	1.564
C18:2(n-6)[g]	871	11.464	23.593	16.213	1.971
C18:3(n-3)[g]	871	0.380	1.704	0.745	0.172
C20:0[g]	871	0.039	0.373	0.185	0.042
C20:2(n-6)[g]	871	0.443	1.228	0.781	0.102
C20:3(n-6)[g]	871	0.045	0.170	0.084	0.016
C20:4(n-6)[g]	871	0.083	0.487	0.223	0.046
C22:4(n-6)[g]	871	0.048	0.378	0.094	0.020
C22:5(n-3)[g]	871	0.008	0.099	0.053	0.011
C22:6(n-3)[g]	871	0.003	0.110	0.013	0.006

SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.
[a]Number of considered samples.
[b]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.
[c]Backfat thickness (BFT) (including rind) measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[d]Loin thickness measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[e]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.
[f]Intramuscular fat content (IMF) measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official Procedure AOCS Am 5-04.
[g]Fatty acids are expressed as percentage on the total fatty acids. The reported fatty acids account for the 96% of the total fatty acids. The remaining fatty acids, such as C14:1 *cis*-9, C15:0, C17:0, C18:1 *cis*-11, C20:1 *cis*-11, C21:1 and C22:1 *cis*-12, were excluded due to their low quantities in backfat tissue.

station controlled environment. Similar variations were also reported by Virgili *et al*. (2003) and Lo Fiego *et al*. (2010). Lean percentage (48.885 ± 2.728%) and loin thickness (63.331 ± 6.933 mm) indicated a moderate lean mass deposition. These phenotypic measures are in line with the 40% to 54.9% (U, R and O classes of EUROP grid for carcass classification) of carcass lean meat content required for high quality protected designation of origin ham production.

Backfat thickness measured with FOM were similar and consistent with data obtained by other authors with the same instrument (Lo Fiego *et al*., 2010). Among the observed phenotypes, both BFT measures obtained by FOM and calibre showed higher variability than the other carcass traits. Average IMF content was lower (2.044 ± 1.112%) than the 2.87% found in Italian crossbred pigs by Virgili *et al*. (2003).

In agreement with literature, the most abundant FA classes in backfat were MUFA and SFA (43.703% and 37.599% of the total FA content, respectively; Table 1). In addition, the most represented FA were C18:1 *cis*-9(n-9) (38.435 ± 1.564%), C16:0 (mean value 22.500 ± 1.304%) and C18:0 (13.210 ± 1.757%).

Carcass traits showed heritability levels from 0.087 ± 0.008 for estimated lean percentage to 0.361 ± 0.022 for hot carcass weight (Table 2). Loin thickness heritability (0.213 ± 0.002) is in agreement with the results reported by Miar *et al*. (2014) in Landrace × White and Duroc crossbred pigs for loin muscle area ($h^2 = 0.22 \pm 0.08$), an estimate based on loin thickness value. Among carcass traits, hot carcass weight showed the highest estimated heritability (0.361 ± 0.022), supporting the values reported in literature for the same trait (Miar *et al*., 2014).

Heritability values of FA classes were low-to-moderate (Table 3), varying little from 0.245 ± 0.029 for n-3 PUFA to 0.264 ± 0.029 for MUFA. As reported in Table 3, the FA with the lowest heritability was C12:0 (0.106 ± 0.006), whereas all other considered FA showed heritabilities within the range of 0.233 ± 0.030 for C22:6(n-3) and 0.255 ± 0.003 for C14:0. No clear differences in heritability appeared among FA based on their length, saturation and double bound position. The essential FA C18:2(n-6) and C18:3(n-3) showed a moderate level of heritability (0.242 ± 0.001 and 0.235 ± 0.008, respectively), suggesting partial genetic control of digestion, absorption and utilization mechanisms regulating these PUFA deposition. The FA C16:1 *cis*-7(n-9), C16:1 *cis*-9(n-7); C18:0, C20:0, C20:2(n-6) and C20:3(n-6) showed a level of heritability roughly ranging from 0.24 to 0.25. Heritabilities found in the present investigation for backfat FA were on average lower than those reported by Sellier *et al*. (2010), possibly due to differences in the experimental populations and in the environmental conditions.

Genetic and phenotypic correlations between carcass traits

The genetic and phenotypic correlations among carcass traits and the relative standard error are reported in Table 4. Carcass lean percentage showed a significant negative genetic correlation (r_g) with BFT measured both by FOM and a calibre (−0.401 ± 0.032 and −0.428 ± 0.031, respectively), but hardly any correlation with loin thickness measured by FOM (−0.020 ± 0.035). As expected, phenotypic correlations (r_p) between lean percentage and BFT measured by FOM and calibre, and loin thickness measured by FOM were high (−0.918 ± 0.014; −0.617 ± 0.027 and 0.558 ± 0.029, respectively). The negative genetic correlation between lean percentage and carcass fat coverage is well known and it represents a limit to the simultaneous selection for meatiness and backfat depth maintenance. Thus, this issue has always been a limitation for the concurrent improvement of pig performances and carcass quality for seasoning, and the results of this trial confirm that an excessive increase in lean meat content would hinder both subcutaneous and muscle fat deposition at the expense of seasoned pig product quality.

Moreover, IMF shows positive genetic correlation with both BFT measures (0.167 ± 0.034 measured by FOM and 0.242 ± 0.034 by calibre). These evidences suggest that selection schemes aimed at maintaining BFT may also have an indirect effect in keeping an adequate percentage of IMF, an important indicator of meat quality. Besides, this result indicates that a specific partial genetic control on IMF, independent from BFT, exists as already reported by Tyra *et al*. (2013).This implies that the identification of different genes and genetic markers associated with IMF and BFT could allow for independent selection and improvement of these two traits.

Table 2 *Carcass phenotypic measurements of the studied pig population: genetic variance (σ^2_a), litter variance (σ^2_f), error variance (σ^2_e), total variance (σ^2_t), heritability (h^2) and standard error (SE) of heritability*

Traits	σ^2_a	σ^2_f	σ^2_e	σ^2_t	h^2	SE
Hot carcass weight (kg)	98 572.146	47 039.336	127 708.339	273 319.821	0.361	0.022
Lean (%)[a]	6739.344	26 203.855	44 958.478	77 901.677	0.087	0.008
BFT FOM (mm)[b]	2 060 712.754	586 657.861	5 548 433.557	8 195 804.172	0.251	0.002
Loin thickness (mm)[c]	3 083 297.228	642 109.578	10 754 933.916	14 480 340.722	0.213	0.002
BFT (mm)[d]	1 780 159.150	559 148.309	4 750 858.060	7 090 165.520	0.251	0.002
IMF (%)[e]	8603.326	4242.403	41 708.115	54 553.843	0.158	0.005

[a]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.
[b]Backfat thickness (BFT) (including rind) measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[c]Loin thickness measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[d]BFT manually measured with a calibre at the level of *Gluteus medius* muscle.
[e]Intramuscular fat (IMF) content measured in semimembranosus muscle by means of a XT15 Ankom apparatus according to Official Procedure AOCS Am 5-04.

Table 3 *Backfat fatty acid composition of the studied pig population: genetic variance (σ^2_a), litter variance (σ^2_f), error variance (σ^2_e), total variance (σ^2_t), heritability (h^2) and standard error (SE) of heritability*

Traits[a]	σ^2_a	σ^2_f	σ^2_e	σ^2_t	h^2	SE
SFA	5 587 083.625	800 235.771	15 840 723.280	22 228 042.676	0.251	0.091
MUFA	730 478.088	167 405.132	1 874 298.622	2 772 181.843	0.264	0.029
PUFA	4 394 190.612	619 100.909	12 879 282.330	17 892 573.850	0.246	0.031
n-6 PUFA	4 373 412.752	623 229.826	12 798 479.629	17 795 122.206	0.246	0.040
n-3 PUFA	10 967.347	1679.411	32 104.382	44 751.139	0.245	0.029
C12:0	2.369	10.994	8.960	22.322	0.106	0.006
C14:0	1471.200	508.785	3792.318	5772.303	0.255	0.003
C16:0	65 489.729	20 834.595	185 057.307	271 381.631	0.241	0.003
C16:1 *cis*-7(n-9)	384.830	87.657	1119.808	1592.296	0.242	0.002
C16:1 *cis*-9(n-7)	4531.649	969.813	13 521.190	19 022.652	0.238	0.002
C18:0	857 672.698	131 217.133	2 463 810.326	3 452 700.158	0.248	0.001
C18:1 *cis*-9(n-9)	112 947.820	36 071.900	311 517.869	460 537.590	0.245	0.003
C18:2(n-6)	1 374 180.134	220 962.120	4 078 439.471	5 673 581.725	0.242	0.001
C18:3(n-3)	2115.670	451.839	6434.553	9002.062	0.235	0.008
C20:0	499.132	73.996	1478.939	2052.067	0.243	0.002
C20:2(n-6)	637.377	225.173	1674.331	2536.880	0.251	0.006
C20:3(n-6)	74.448	9.745	220.319	304.512	0.244	0.002
C20:4(n-6)	1167.342	148.268	3426.390	4742.000	0.246	0.057
C22:4(n-6)	67.628	9.101	194.191	270.920	0.250	0.038
C22:5(n-3)	51.850	6.610	152.345	210.804	0.246	0.056
C22:6(n-3)	4.337	0.915	13.384	18.637	0.233	0.030

SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.
[a]Fatty acids are expressed as percentage on the total fatty acids. The reported fatty acids account for the 96% of the total fatty acids. The remaining fatty acids, such as C14:1 *cis*-9, C15:0, C17:0, C18:1 *cis*-11, C20:1 *cis*-11, C21:1 and C22:1 *cis*-12, were excluded due to their low quantities in backfat tissue.

Table 4 *Estimates of genetic (above diagonal), phenotypic (below diagonal) correlations and heritabilities values (diagonal, in bold) for carcass phenotypic measurements ± the relative standard errors for the studied pig population*

Traits	Hot carcass weight (kg)	Lean (%)[a]	BFT FOM (mm)[b]	Loin thickness (mm)[c]	BFT (mm)[d]	IMF (%)[e]
Hot carcass weight (kg)	**0.361 ± 0.022**	0.981*** ± 0.007	− 0.217*** ± 0.034	− 0.182*** ± 0.034	− 0.310*** ± 0.033	− 0.276*** ± 0.033
Lean (%)[a]	− 0.141*** ± 0.034	**0.087 ± 0.008**	− 0.401*** ± 0.032	− 0.020 ± 0.035	− 0.428*** ± 0.031	− 0.292*** ± 0.033
BFT FOM (mm)[b]	0.270*** ± 0.033	− 0.918*** ± 0.014	**0.251 ± 0.002**	− 0.756*** ± 0.023	0.678*** ± 0.025	0.167*** ± 0.034
Loin thickness (mm)[c]	0.163*** ± 0.034	0.558*** ± 0.029	− 0.244*** ± 0.034	**0.213 ± 0.002**	− 0.724*** ± 0.024	− 0.089* ± 0.034
BFT (mm)[d]	0.295*** ± 0.033	− 0.617*** ± 0.027	0.677*** ± 0.025	− 0.121*** ± 0.034	**0.251 ± 0.002**	0.242*** ± 0.034
IMF (%)[e]	0.055 ± 0.034	− 0.074* ± 0.034	0.070 ± 0.034	− 0.052 ± 0.034	0.111** ± 0.034	**0.158 ± 0.005**

[a]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.
[b]Backfat thickness (BFT) (including rind) measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[c]Loin thickness measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[d]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.
[e]Intramuscular fat (IMF) content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official Procedure AOCS Am 5-04.
*$P \leqslant 0.05$; **$P \leqslant 0.01$; ***$P \leqslant 0.001$.

Genetic and phenotypic correlations between backfat fatty acids and between fatty acids and carcass traits

All the FA classes showed to be highly correlated, with the strongest negative correlations found between SFA and the other FA classes (Table 5). These findings are consistent with the biochemical processes involved in FA *de novo* synthesis, where SFA are the substrate for subsequent elongation and desaturation steps leading to the formation of MUFA and PUFA. C16:0 and C18:0 SFA are among the preferred substrates for the *de novo* synthesis of MUFA species. The balance among MUFA C16:1 *cis*-7(n-9), C16:1 *cis*-9(n-7) and C18:1 *cis*-9(n-9) is reported to be essential for cell functions (Green *et al*., 2010) and depends on the coordinated regulation of elongases (belonging to ELOVL family) and desaturases such as stearoyl-CoA desaturase (SCD) Δ9. The biosynthesis of C18:1 *cis*-9(n-9), the most abundant MUFA, requires either the direct elongation of C16:1 *cis*-9(n-7), catalyzed by the enzyme ELOVL elongase 6 (ELOVL6), or a first elongation step of C16:0 to C18:0 performed by ELOVL6, followed by the desaturation of C18:0 to C18:1 *cis*-9(n-9) catalysed by SCD. Polymorphisms of the genes coding for the enzymes SCD and ELOVL6 have been reported as markers for fat quality, as variants in their sequence have been associated with C18:1 *cis*-9(n-9) content in *Gluteus medius*

muscle (Estany *et al*., 2014; Ros-Freixedes *et al*., 2016) and to C16:1 *cis*-9(n-7) and C16:0 contents in *Longissimus dorsi* and adipose tissue (Corominas *et al*., 2015), respectively.

In Supplementary Tables S2 and S3, the genetic and phenotypic correlations between individual FA in backfat are reported. The two main saturated FA, C16:0 and C18:0, are positively correlated ($r_g = 0.364 \pm 0.032$ and $r_p = 0.419 \pm 0.031$). C16:0 is negatively correlated with C16:1 *cis*-7(n-9) and with C18:1 *cis*-9(n-9) acids ($r_p = -0.453 \pm 0.030$ and $r_g = -0.378 \pm 0.031$, respectively). Both C16:1 positional isomers show negative genetic correlations with C16:0 (-0.722 ± 0.023 with $P < 0.001$ for C16:1 *cis*-7(n-9) and -0.254 ± 0.033 with $P < 0.001$ for C16:1*cis*-9(n-7), respectively) but interestingly the two correlations are very different in size. Literature suggests different roles for these two positional isomers (Guijas *et al*., 2016) and, although the molecular processes controlling FA biosynthesis are still partly unknown, it is possible to hypothesize that distinct regulation patterns affect C16:1 *cis*-9(n-7) and C16:1 *cis*-7(n-9) biosynthesis. In particular, C16:1 *cis*-7(n-9) originates from Δ9 desaturation of C16:0, whereas C16:1 *cis*-9(n-7) derives from the partial β-oxidation of C18:1 *cis*-9(n-9) (Guijas *et al*., 2016). This may partly explain why the isomer C16:1 *cis*-7(n-9) is negatively correlated with C18:0 and marginally with C18:1 *cis*-9(n-9) as well ($r_g = -0.624 \pm 0.027$ and -0.065 ± 0.034, respectively). C18:0 also showed a positive genetic correlation with C20:0 content ($r_g = 0.779 \pm 0.021$, $P < 0.001$): this outcome is related to the origin of C20:0, mainly derived from the elongation of C18:0 (Marinetti, 2012). Another cluster of correlated FA is composed of C18:2 (n-6), C18:3(n-3), C20:3(n-6), C20:4(n-6), C22:4(n-6), C22:5 (n-3) and C22:6(n-3). These FA show highly positive genetic correlations among themselves because they are synthesized through subsequent elongation steps from linoleic and α-linolenic essential FA (Leonard *et al*., 2002). C18:2(n-6) and C18:3(n-3) are essential for mammals and are particularly

Table 5 *Estimates of genetic (above diagonal), phenotypic (below diagonal) correlations and heritabilities values (diagonal, in bold) for backfat fatty acid categories ± the relative standard errors for the studied pig population*

Traits[a]	SFA	MUFA	PUFA	n-6 PUFA	n-3 PUFA
SFA	**0.251 ± 0.091**	−0.339*** ± 0.032	−0.911*** ± 0.014	−0.841*** ± 0.018	−0.711*** ± 0.024
MUFA	−0.556*** ± 0.028	**0.264 ± 0.029**	0.098*** ± 0.034	0.085*** ± 0.034	0.011** ± 0.034
PUFA	−0.710*** ± 0.024	−0.174*** ± 0.033	**0.246 ± 0.031**	0.949*** ± 0.011	0.811*** ± 0.020
n-6 PUFA	−0.693*** ± 0.024	−0.190*** ± 0.033	0.995*** ± 0.003	**0.246 ± 0.040**	0.849*** ± 0.018
n-3 PUFA	−0.290*** ± 0.032	−0.113** ± 0.034	0.433*** ± 0.031	0.356*** ± 0.032	**0.245 ± 0.029**

SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.
[a]Fatty acids are expressed as percentage on the total fatty acids.
**$P \leq 0.01$; ***$P \leq 0.001$.

Table 6 *Genetic and phenotypic correlation values ± the relative standard errors between carcass traits and backfat fatty acid classes for the studied pig population: genetic correlation values are in the top part of the table, whereas the phenotypic correlation values are reported in the bottom part*

Traits	SFA	MUFA	PUFA	n-6 PUFA	n-3 PUFA
Genetic correlations					
Hot carcass weight (kg)	−0.048 ± 0.035	−0.043 ± 0.035	0.073* ± 0.034	0.069* ± 0.034	0.055 ± 0.034
Lean (%)[a]	−0.065 ± 0.034	−0.049 ± 0.035	0.093** ± 0.034	0.088** ± 0.034	0.068* ± 0.034
BFT FOM (mm)[b]	0.101** ± 0.034	0.040 ± 0.035	−0.124*** ± 0.034	−0.116*** ± 0.034	−0.081* ± 0.034
Loin thickness (mm)[c]	−0.109** ± 0.034	−0.041 ± 0.035	0.128*** ± 0.034	0.119*** ± 0.034	0.080* ± 0.034
BFT (mm)[d]	0.138*** ± 0.034	0.068* ± 0.034	−0.175*** ± 0.034	−0.163*** ± 0.034	−0.118*** ± 0.034
IMF (%)[e]	0.082* ± 0.034	0.019 ± 0.035	−0.102** ± 0.034	−0.096** ± 0.034	−0.055 ± 0.034
Phenotypic correlations					
Hot carcass weight (kg)	0.099** ± 0.034	0.079* ± 0.034	−0.190 ± 0.034	−0.203*** ± 0.034	0.045 ± 0.035
Lean (%)[a]	−0.291*** ± 0.033	−0.028 ± 0.035	0.383*** ± 0.032	0.398*** ± 0.032	−0.039 ± 0.035
BFT FOM (mm)[b]	0.288*** ± 0.033	0.046 ± 0.035	−0.392*** ± 0.032	−0.406*** ± 0.032	0.037 ± 0.035
Loin thickness (mm)[c]	−0.072* ± 0.034	−0.037 ± 0.035	0.119*** ± 0.034	0.129*** ± 0.034	−0.031 ± 0.035
BFT (mm)[d]	0.298*** ± 0.033	0.098** ± 0.034	−0.452*** ± 0.031	−0.460*** ± 0.031	−0.061 ± 0.034
IMF (%)[e]	0.011 ± 0.035	0.072* ± 0.034	−0.077* ± 0.034	−0.082* ± 0.034	−0.033 ± 0.035

SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.
[a]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.
[b]Backfat thickness (BFT) (including rind) measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[c]Loin thickness measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[d]BFT manually measured with a calibre at the level of *Gluteus medius* muscle.
[e]Intramuscular fat (IMF) content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official Procedure AOCS Am 5-04.
*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

desirable in human nutrition, but extremely undesirable in pork processing and seasoning because of their susceptibility to oxidation and rancidity. In addition, MUFA, such as C16 positional isomers and C18:1 *cis*-9(n-9), display desirable effects on consumers' health (Terés *et al*., 2008), whereas they have hardly any impact on the organoleptic quality of seasoned pork products. Thus, selecting pigs with increased proportions of MUFA would improve the nutritional quality of products and reduce the problems of fat oxidation and rancidity (Estany *et al*., 2014; Pena *et al*., 2016). Genetic correlations between backfat FAC and carcass traits and the relative low standard error are reported in Tables 6 and 7. These results suggest that selection for carcass lean percentage and against BFT may increase backfat content of PUFA ($r_g = 0.128 \pm 0.034$; -0.124 ± 0.034; -0.175 ± 0.034, respectively, for loin thickness, BFT measured by FOM and calibre). The same three carcass traits are unfavourably correlated with C18:2(n-6) ($r_g = 0.211 \pm 0.033$; -0.206 ± 0.033; -0.291 ± 0.032, respectively, for loin thickness, BFT measured by FOM and calibre). Both PUFA and C18:2(n-6) (linoleic acid) are unfavourable to the technological quality of fat. Conversely, selection schemes for Italian heavy pigs aimed at maintaining a backfat level suitable for high quality seasoned products may have the indirect effects of preserving the content of C18:1 *cis*-9(n-9) ($r_g = 0.120 \pm 0.034$ and $r_g = 0.193 \pm 0.033$ between C18:1 *cis*-9(n-9) and BFT measured by FOM and calibre, respectively) while reducing PUFA. Backfat depth is furthermore associated with n-6 PUFA with

Table 7 *Genetic and phenotypic correlation values ± the relative standard errors between carcass traits and backfat fatty acids for the studied pig population: genetic correlation values are in the top part of the table, whereas the phenotypic correlation values are reported in the bottom part*

Traits[a]	Hot carcass weight (kg)	Lean (%)[b]	BFT FOM (mm)[c]	Loin thickness (mm)[d]	BFT (mm)[e]	IMF (%)[f]
Genetic correlations						
C12:0	0.075 ± 0.034	0.147*** ± 0.034	−0.383*** ± 0.031	0.509*** ± 0.029	−0.432*** ± 0.031	−0.733*** ± 0.023
C14:0	−0.007 ± 0.034	−0.023 ± 0.034	0.080* ± 0.034	−0.115** ± 0.034	0.120*** ± 0.034	−0.012 ± 0.034
C16:0	−0.172*** ± 0.033	−0.253*** ± 0.033	0.458*** ± 0.030	−0.526*** ± 0.029	0.633*** ± 0.026	0.306*** ± 0.032
C16:1 *cis*-7(n-9)	0.235*** ± 0.033	0.297*** ± 0.032	−0.383*** ± 0.031	0.377*** ± 0.031	−0.547*** ± 0.028	−0.283*** ± 0.033
C16:1 *cis*-9(n-7)	0.104** ± 0.034	0.098** ± 0.034	−0.005 ± 0.034	−0.061 ± 0.034	−0.009 ± 0.034	−0.113** ± 0.034
C18:0	−0.075* ± 0.034	−0.096** ± 0.034	0.130*** ± 0.034	−0.131*** ± 0.034	0.176*** ± 0.033	0.126*** ± 0.034
C18:1 *cis*-9(n-9)	−0.131*** ± 0.034	−0.147*** ± 0.034	0.120*** ± 0.034	−0.110** ± 0.034	0.193*** ± 0.033	0.088* ± 0.034
C18:2(n-6)	0.122*** ± 0.034	0.156*** ± 0.034	−0.206*** ± 0.033	0.211*** ± 0.033	−0.291*** ± 0.032	−0.171*** ± 0.033
C18:3(n-3)	0.113** ± 0.034	0.141*** ± 0.034	−0.172*** ± 0.033	0.172*** ± 0.033	−0.250*** ± 0.033	−0.114** ± 0.034
C20:0	−0.069* ± 0.034	−0.082* ± 0.034	0.085* ± 0.034	−0.079* ± 0.034	0.112** ± 0.034	0.098** ± 0.034
C20:2(n-6)	−0.008 ± 0.034	0.028 ± 0.034	−0.175*** ± 0.033	0.222*** ± 0.033	−0.250*** ± 0.033	−0.073* ± 0.034
C20:3(n-6)	0.082* ± 0.034	0.098** ± 0.034	−0.109** ± 0.034	0.101** ± 0.034	−0.156*** ± 0.034	−0.077* ± 0.034
C20:4(n-6)	0.081* ± 0.034	0.098** ± 0.034	−0.112** ± 0.034	0.112** ± 0.034	−0.155*** ± 0.034	−0.106** ± 0.034
C22:4(n-6)	0.051 ± 0.034	0.052 ± 0.034	−0.020 ± 0.034	0.013 ± 0.034	−0.033 ± 0.034	−0.062 ± 0.034
C22:5(n-3)	0.055 ± 0.034	0.062 ± 0.034	−0.053 ± 0.034	0.036 ± 0.034	−0.077* ± 0.034	−0.060 ± 0.034
C22:6(n-3)	0.097** ± 0.034	0.113** ± 0.034	−0.107** ± 0.034	0.079* ± 0.034	−0.153*** ± 0.034	−0.060 ± 0.034
Phenotypic correlations						
C12:0	0.090** ± 0.034	0.020 ± 0.034	0.009 ± 0.034	0.081* ± 0.034	0.052 ± 0.034	−0.088** ± 0.034
C14:0	0.130*** ± 0.034	−0.128*** ± 0.034	0.160*** ± 0.033	0.031 ± 0.034	0.212*** ± 0.033	−0.062 ± 0.034
C16:0	0.130*** ± 0.034	−0.285*** ± 0.033	0.302*** ± 0.032	−0.034 ± 0.034	0.355*** ± 0.032	−0.009 ± 0.034
C16:1 *cis*-7(n-9)	−0.209*** ± 0.033	0.445*** ± 0.030	−0.462*** ± 0.030	0.120*** ± 0.034	−0.458*** ± 0.030	−0.098** ± 0.034
C16:1 *cis*-9(n-7)	0.001 ± 0.034	−0.031 ± 0.034	0.053 ± 0.034	0.021 ± 0.034	0.074* ± 0.034	−0.040 ± 0.034
C18:0	0.039 ± 0.034	−0.205*** ± 0.033	0.186*** ± 0.033	−0.082* ± 0.034	0.154*** ± 0.034	0.027 ± 0.034
C18:1 *cis*-9(n-9)	0.097** ± 0.034	−0.054 ± 0.034	0.069* ± 0.034	−0.044 ± 0.034	0.123*** ± 0.034	0.072* ± 0.034
C18:2(n-6)	−0.203*** ± 0.033	0.400*** ± 0.031	−0.408*** ± 0.031	0.129*** ± 0.034	−0.461*** ± 0.030	−0.083* ± 0.034
C18:3(n-3)	0.055 ± 0.034	−0.050 ± 0.034	0.050 ± 0.034	−0.031 ± 0.034	−0.045 ± 0.034	−0.037 ± 0.034
C20:0	0.047 ± 0.034	−0.202*** ± 0.033	0.169*** ± 0.033	−0.132*** ± 0.034	0.158*** ± 0.033	0.081* ± 0.034
C20:2(n-6)	0.001 ± 0.034	0.164*** ± 0.033	−0.186*** ± 0.033	−0.019 ± 0.034	−0.219*** ± 0.033	0.076* ± 0.034
C20:3(n-6)	−0.090** ± 0.034	0.157*** ± 0.034	−0.169*** ± 0.033	0.027 ± 0.034	−0.217*** ± 0.033	0.031 ± 0.034
C20:4(n-6)	−0.184*** ± 0.033	0.269*** ± 0.033	−0.272*** ± 0.033	0.091** ± 0.034	−0.301*** ± 0.032	−0.064 ± 0.034
C22:4(n-6)	−0.047 ± 0.034	−0.006 ± 0.034	0.006 ± 0.034	−0.006 ± 0.034	−0.050 ± 0.034	0.016 ± 0.034
C22:5(n-3)	−0.095** ± 0.034	0.101** ± 0.034	−0.119*** ± 0.034	−0.004 ± 0.034	−0.190*** ± 0.033	0.025 ± 0.034
C22:6(n-3)	−0.065 ± 0.034	0.095** ± 0.034	−0.111** ± 0.034	−0.021 ± 0.034	−0.145*** ± 0.034	0.028 ± 0.034

[a]Fatty acids are expressed as percentage on the total fatty acids.
[b]Percentage of carcass lean meat content estimated using Fat-O-Meat'er (FOM) instrument.
[c]Backfat thickness (BFT) (including rind)measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[d]Loin thickness measured with FOM instrument on the back between the third and fourth last ribs at 8 cm off the carcass midline.
[e]Backfat thickness manually measured with a calibre at the level of *Gluteus medius* muscle.
[f]Intramuscular fat content measured in *Semimembranosus* muscle by means of a XT15 Ankom apparatus according to Official Procedure AOCS Am 5-04.
*$P \leqslant 0.05$; **$P \leqslant 0.01$; ***$P \leqslant 0.001$.

low-to-moderate negative genetic and phenotypic correlations, whereas correlations with n-3 PUFA are weaker (Table 6). These data suggest that selecting in favour of subcutaneous fat would reduce more n-6 PUFA than n-3 PUFA. Interestingly, MUFA are not genetically correlated with BFT and loin thickness, suggesting that a selection for a better MUFA/SFA ratio would not interfere with carcass traits selection.

An exception to the correlations between fat deposition and MUFA stored in backfat is represented by C16:1 *cis*-7 (n-9), which showed negative genetic correlations with BFT measured by both FOM and calibre (-0.383 ± 0.031 and -0.547 ± 0.028, respectively, Table 7). At the same time, C16:1 *cis*-9(n-7) showed hardly any correlation with backfat, and this difference appears to reinforce the hypothesis that C16:1 *cis*-7(n-9) synthesis could be controlled by distinct regulation patterns than C16:1 *cis*-9(n-7) and other MUFA, in agreement with the hypothesis reported by Guijas *et al*. (2016). Despite C16:1 *cis*-7(n-9) representing <1% of the total content in FA in pig backfat, the behaviour of this FA could be of practical interest as marker of specific pathways of lipid metabolism such as β-oxidation of FA or lipid droplet accumulation (Guijas *et al*., 2016).

On the whole, backfat FAC showed to be a moderately heritable trait and thus it could be directly modified through genetic selection. The results obtained pointed out the existence of complex genetic and phenotypic correlations between backfat FAC and carcass traits, such as backfat thickness, loin thickness, lean percentage and IMF. Backfat thickness showed a negative genetic correlation with PUFA and a positive one with SFA, whereas loin thickness showed the opposite trend. Hardly any genetic correlation could be observed both for BFT and loin thickness with MUFA, whereas a negative genetic correlation was found between MUFA and SFA. This is probably the most promising result, as MUFA could be selected for without interfering with carcass traits, while decreasing the content of SFA. Although pig meat quality was relevant to the selection goals, these direct and correlated effects should be taken into account in dealing with the development of selection schemes addressed to modify carcass composition and/or backfat FAC.

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Declaration of interest

The authors declare that they have no competing interests.

Ethics statement

Sampling occurred with the permission of the Italian National Association of Pig Breeders (ANAS). 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 killing. All slaughter procedures were monitored by the veterinary team appointed by the Italian Ministry of Health.

Software and data repository resources

The data analyzed in the current study and the produced outputs are available by request from the corresponding author.

Supplementary material

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