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Meat Science 131 (2017) 1–8

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Genetic analysis of meat quality traits in maternal lines of rabbit and their diallel cross☆

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ARTICLE INFO

Chemical compounds studied in this article:
Myristic Acid (PubChem CID: 11005)
Palmitic Acid (PubChem CID: 985)
Palmitoleic Acid (PubChem CID: 445638)
Stearic Acid (PubChem CID: 5281)
Vaccenic Acid (PubChem CID: 5281127)
Oleic Acid (PubChem CID: 445639)
Linoleic Acid (PubChem CID: 5280450)
Arachidomic Acid (PubChem CID: 444899)
Docosatetraenoic Acid (PubChem CID: 5282844)
Docosahexanoic Acid (PubChem CID: 445580)

Keywords:
Crossbreeding parameters
Diallel cross
Meat quality
Maternal lines
Rabbit

ABSTRACT

Young rabbits, the dams of which came from a full diallel cross among four maternal lines (A, V, H and LP) and the sires from a single paternal line (R), that produce sixteen genetic groups, was carried out to evaluate the genetic groups and to estimate the crossbreeding genetic parameters of meat quality. The meat quality traits were recorded by NIRS from a sample of 285 *longissimus lumborum* muscles. Crossbreeding parameters were estimated according to Dickerson model. No differences in protein were found. The line A had significant differences with V line for intramuscular fat, and fatty acids groups. Significant differences for these traits appeared between the crossbred AH and VV (in favor of AH). As conclusion, the significant contrasts between genetic types for chemical composition of the meat are mainly consequence of direct-maternal genetic effects, having grandmaternal and maternal heterosis effects a less relevant role.

1. Introduction

Meat rabbit selection programs improves, between other traits, litter size in dam lines and growth rate in sire lines (Baselga, 2004; Rochambeau, 1988). Maximizing growth potential of sire lines is important to ensure the economic viability of rabbits producers (Cartuche, Pascual, Gómez, & Blasco, 2014); however, it can produce an undesirable effect on meat and carcass qualities because the degree of maturity at market weight is reduced (Pascual, 2007). Meat quality is a generic term used to describe properties and perceptions of meat: sensory characteristics, nutritional properties, healthiness, technological factors, microbiological and chemical safety and ethical and environment aspects. Rabbit meat has good nutritive properties because it has lower fat and higher polyunsaturated fatty acid (PUFA) content than other meats (Hernández & Gondret, 2006). The most ubiquitous fatty acids (FA) are palmitic (C16:0), oleic (C18:1 n-9) and linoleic (C18:2 n-6) acids, showing percentages higher than 20% of total FA. Rabbit meat also contains high protein content and high levels of essential amino acids (Hernández & Dalle Zotte, 2010).

Traditional methods used to determine meat chemical composition are laborious, expensive, time-consuming and destructive. New methods for meat quality evaluation were used by researchers, as e.g. ultrasound, electric nose, tastes sensing, NIRS, TOBEC and Video Image Analysis (Cross & Belk, 1992). NIRS (near infrared reflectance spectroscopy) is a fast, accurate and cheap analytical technique and rabbit is a good experimental model to measure meat quality. NIRS had been used in some studies in meat quality traits in rabbits, for example, Masoero, Xiccato, Zotte, Parigi-Bini, and Bergoglio (1994) to predicte chemical composition, Pla (2007) to discriminate between conventional and organic production, Pascual and Pla (2007) to evaluate changes in meat

☆ This work was supported by the Spanish project AGL2011-30170-C02-01 from the Spanish National Research Plan. C. Mínguez acknowledges a Formación de Personal Investigador (FPI) grant from the Ministerio de Economía y Competitividad (MEC), Spain.

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http://dx.doi.org/10.1016/j.meatsci.2017.04.005
Received 9 September 2016; Received in revised form 4 April 2017; Accepted 5 April 2017
Available online 10 April 2017
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quality when selecting rabbits for growth rate or Zomeño, Blasco, and Hernández (2013) and Martínez-Álvaro, Hernández, and Blasco (2016) to predict fatty acid content in rabbit selection programs.

Some studies were made to describe the effects of genotype and crossbreeding parameters on chemical composition of meat in other species as in pigs (Larzul et al., 1997; Sellier & Monin, 1994), beef cattle (Gregory, Cundiff, & Koch, 1994), sheep (Hopkins, Fogarty, & Mortimer, 2011), chicken (Liu, Dunnington, & Siegel, 1993) or ducks (Wołoszyn et al., 2011). In rabbits, there are studies on these topics in pure lines (Hernández, Ariño, Grimal, & Blasco, 2006; Hernández, Cesari, & Blasco, 2008) but there are few studies estimating crossbreeding parameters on meat quality traits.

The objective of this work was to estimate differences and crossbreeding parameters for some meat quality traits based on NIRS measurements in rabbits, the dams of which come from a full diallel-cross among four maternal lines and the sires from a paternal line; trying to evaluate the impact of a large genetic improvement program in meat rabbit on meat quality.

2. Material and methods

2.1. Animals

The rabbit lines and the animals used for this study were the same rabbits used in Mínguez et al. (2015a) and Mínguez, Sáchez, Ragab, El Nagar, and Baselga (2015b) to measure growth and carcass traits, respectively. The genetic groups involved in the study were four pure lines (AA, VV, HH and LL) and 12 single crosses: AV, VA, AH, HA, AL, LA, VH, HV, VL, LV, HL and LH (a total of 16 genetic groups) and involved four different farms, located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain), Valencia (Spain) and Sant Carles de la Rápita (Tarragona, Spain). The genetic group VV was present on all farms allowing data connection between farms. The pure line HH was only presented in Tarragona. For this reason, pure line HH does not share the farm with A and LP lines.

2.2. Crossbreeding design and management

The crossbreeding design and the procedure of slaughter were described in Mínguez et al. (2015a, 2015b)). After slaughtering, the carcasses were stored at 4 °C during 24 h and then, in the meat laboratory of the Department of Animal Science of the Universidad Politécnica de Valencia (UPV), the *longissimus lumborum* muscles (LL) were excised from the carcasses.

2.2.1. Meat quality traits

Muscle pH at 24 h. post mortem was obtained in the LL muscle at the level of the fifth lumbar vertebra of the left side and recorded with a Crison pH-meter Basic 20 + (Crison Instruments, Barcelona, Spain). Meat colour (lightness, L*; redness, a*; and yellowness, b*) was measured at the seventh lumbar vertebra in a transversal section of the right LL. Meat obtained from the LL was ground, freeze-dried and stored at − 80 °C until analyses. Meat was scanned with near infrared reflectance spectroscopy (NIRS) (model 5000, FOSS NIRSystems INC., Hilleroed, Denmark). Protein content and fatty acid (FA) composition of the LL were determined applying calibration equations previously developed (Zomeño, Juste, & Hernández, 2012).

2.3. Data recording and statistical model

The pH was measured in a total of 950 LL which came from carcasses that were used by Mínguez et al. (2015b) and the other meat quality traits were recorded in a sample of 285 LL of these animals.

The model used in the analysis was:

$$Y_{jkl} = GG_j + F_k + S_l + e_{jkl}$$

where: Y_{jkl} is a record of the trait; GG_j is the effect of genetic group (16 levels); F_k is the effect of the farm (4 levels, one level for each farm); S_l is the effect of the sex and e_{jkl} is the residual effect.

Estimates of the differences between all the genetics groups and VV animals, crossbreeding parameters (proposed by Dickerson (1969)) and the estimable functions of the crossbreeding parameters were calculate according to Mínguez et al. (2015a).

Table 1
Descriptive statistics of pH, colour, intramuscular fat (IMF), protein, fatty acid groups and fatty acid ratios of the *Longissimus lumborum* muscle (LL).

Trait	N[a]	Mean	SD[b]	Minimum	Maximum
pH	950	5.66	0.17	5.05	6.20
L*	285	51.52	3.37	39.07	59.89
a*	285	4.69	1.44	1.97	9.72
b*	285	1.61	1.44	− 1.80	6.97
Groups (g/100 g muscle)					
IMF	285	1.21	0.22	0.80	2.09
Protein	285	22	0.40	20	23
Groups (mg/100 g muscle)					
SFA	285	308	66	173	546
MUFA	285	232	70	99	491
PUFA	285	331	36	243	449
n-3 PUFA	285	54	3	47	66
n-6 PUFA	285	277	35	208	409
Ratios					
n-6/n-3	285	5.10	0.47	3.94	7.95
PUFA/SFA	285	1.09	0.08	0.84	1.29

[a] N = number of LL.
[b] SD = standard deviation.

3. Results and discussion

3.1. Descriptive statistics

Tables 1 and 2 show descriptive for the traits measured. The value for pH was similar to those obtained in previous studies (Hernández, Aliaga, Pla, & Blasco, 2004; Hernández & Gondret, 2006; Zomeño, 2013) and is in the optimum range to avoid potentials problems related with meat pH. In rabbit, pH ranges between 5.4 and 6.4 depending on muscle location (Hulot & Ouhayoun, 1999) and it does not look like a potential problem for meat quality. Our results, jointly with previous

Table 2
Descriptive statistics of individual fatty acid composition (mg/100 g muscle) of the *Longissimus lumborum* muscle (LL).

Trait	N[a]	Mean	SD[b]	Min[c]	Max[d]
C14:0	285	14.2	5.2	1.0	32.0
C15:0	285	4.3	0.9	2.6	7.8
C16:0	285	200	45	119	387
C16:1	285	15.8	9.7	3.3	56.7
C17:0	285	6.0	1.1	3.6	10.5
C18:0	285	70	9	52	108
C18:1 n-7	285	14.1	2.3	9.4	23.4
C18:1 n-9	285	192	54	90	402
C18:2 n-6	285	196	36	124	326
C18:3 n-3	285	14.0	4.4	4.6	30.1
C20:2 n-6	285	2.6	0.6	1.9	4.2
C20:3 n-6	285	4.2	0.4	3.3	7.7
C20:4 n-6	285	45.9	2.5	29.3	51.7
C20:5 n-3	285	12.4	1.5	7.4	16.2
C22:4 n-6	285	16.5	0.4	15.4	19.3
C22:5 n-3	285	6.4	0.8	1.8	10.0
C22:6 n-3	285	21.0	2.5	4.6	27.5

[a] N = number of LL.
[b] SD = standard deviation.
[c] Min = minimum.
[d] Max = maximum.

finds, support that rabbit meat cannot be said to be subject to any abnormal post-mortem acidification kinetics (Hernández & Dalle Zotte, 2010). Colour variables were also in the range of that reported by Hernández et al. (2004), Combes and Dalle Zotte (2005), Hernández and Gondret (2006) and Zomeño (2013). Rabbit meat has a high lightness (L*) because it has a high capacity to reflect the light and due to its low myoglobin content it has a low red index (a*).

Intramuscular fat (IMF) showed a low value because LL is the leanest muscle of the carcass (Pla, Pascual, & Ariño, 2004). Fat and protein values are in the ranges already reported by Metzger et al. (2003), Pla et al. (2004), Hernández and Dalle Zotte (2010) and Zomeño (2013). Polyunsaturated (PUFA) and saturated (SFA) FA are the most important FA groups in rabbit LL, 37% and 36%, respectively. The percentage of monounsaturated (MUFA) FA is lower (27%). With regard to PUFA, the most abundant group is n-6 (32%), while n-3 only had a percentage of 6%. These values are in the same magnitude of those by Hernández and Dalle Zotte (2010), Dalle Zotte and Szendrõ (2011) and Zomeño et al. (2012). PUFA/SFA and n-6/n-3 ratios, used to evaluate quality of fat, showed values close to the nutritional recommendations (reviewed by Hernández & Dalle Zotte, 2010).

In Table 2 is shown that the most abundant FA in LL were palmitic (C16:0), oleic (C18:1 n-9) and linoleic (C18:2 n-6) acids, showing percentages of 24%, 23% and 23%, respectively. Stearic (C18:0) and arachidonic acids (C20:4 n-6) were also important with percentages around 8% and 5%, respectively. Linolenic acid (C18:3 n-3) and some long chain PUFA (i.e. C20:5 n-3, C22:4 n-6 and C22:6 n-3) were also present in rabbit meat although at a lower content. The FA composition in LL observed was similar to that reported in previous studies (reviewed by Hernández & Gondret, 2006; Zomeño et al., 2012).

3.2. Differences between genetic groups

In Table 3 the contrasts between the dam effects of the lines for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the LL can be observed. Table 4 shows the same contrasts for individual fatty acid composition (mg/100 g muscle). Notice that, when the lines involved in the contrast do not share the farm (H line with A and LP lines) have higher standard errors. Muscle pH exerts a high influence on the technological and eating quality of meat. The post-mortem evolution of pH and the pH measured at 24 h post-mortem affect the brightness of meat, its water holding capacity and toughness (Lawrie, 1998) and an abnormal postmortem acidification can produce PSE or DFD meat. A significant difference was observed between A and LP lines. However, this difference was not relevant, and all lines were in the range of an appropriate pH. Meat colour affects consumer acceptance and purchasing decisions (Hernández & Dalle Zotte, 2010). Significant differences were not observed in the contrasts between lines for L*, a* and b*. IMF plays an essential role in meat quality, largely determining eating quality and the nutritional value of the meat (Wood et al., 2008). Regarding IMF, the line A had the higher content, being significant the difference with respect to line V. Rabbit meat is rich in proteins compared to other meats, and contains high levels of essential amino acids with an easy digestibility (Hernández & Dalle Zotte, 2010). Non-significant differences were found for the content of protein between the lines. One of the main aims of meat researchers is to produce dietetic and healthy meat to reduce the SFA and increase the unsaturated FA (Dalle Zotte, 2002). Thus, it is important to measure the possible differences between lines for these traits. Significant differences in the contrast A-V were found for all fatty acid groups (in favor of the A line), and despite non-significant differences with the other lines, it seems that the line A had the highest content for fatty acid groups (SFA, MUFA and PUFA) in agreement with its highest value for IMF observed in Table 3. Among PUFA, significant differences were shown between A-V for n-3 PUFA and between A-V and A-LP for n-6 PUFA (in favor of the A line). Although, no other contrasts for fatty acid groups content involving line A were significant, it seems that this line has the highest values. The Department of Health and Social Security (1994) recommended a ratio of 0.45 or higher for PUFA/SFA and a maximum of 4.0 for the n-6/n-3 ratio. However, diets in developed countries seem to have much higher n-6/n-3 ratios fatty acids than in n-3 fatty acids, and the PUFA/SFA ratios are far from the recommended value. For ratios n-6/n-3 and PUFA/SFA no significant differences were found between the lines, and the four lines have correct values for the first ratio and a light excess of n-6 in the second (Table 1). Table 4 shows significant differences in the contrast A-V, in favor of the A line, for SFA (C14:0, C15:0, C16:0, C17:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:2 n-6, C18:3 n-3 and C20:2 n-6. Significant differences were not found between the A line and the other lines, but it seems that this line had the highest values for all traits, as commented before for IMF, and fatty acid groups (Table 3).

In commercial farms, crossbred does are the most common type of females and, consequently, some differences in meat quality traits in dam effects might have importance. As Mínguez et al. (2015b) and Mínguez et al. (2015a) made for growth traits and carcass traits, respectively; we consider first the different crossbred groups (the average of a cross and its reciprocal) with respect to the V line. In Table 5 the contrasts between the dam effects of the lines for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the LL can be observed. In general, no significant differences were found in the contrast All-VV. Only for a*, this contrast was significant in favor of V line. Also for a*, the contrasts AH-VV and AL-VV were significantly superior for the line V. Table 5 shows that the crossbreds

Table 3
Contrasts (standard error) between the lines for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum* muscle.

Trait	A-H	A-LP	A-V	H-V	LP-H	LP-V
pH	0(0.03)	0.05(0.02)*	0.04(0.02)	0.04(0.02)	− 0.06(0.03)	− 0.02(0.02)
L*	− 0.78(1.50)	− 0.44(1.07)	− 0.14(1.09)	0.64(1.03)	− 0.34(1.47)	0.30(1.05)
a*	0.79(0.66)	0(0.47)	− 0.20(0.48)	− 1.00(0.45)	0.78(0.65)	− 0.21(0.46)
b*	0.03(0.55)	− 0.12(0.40)	0.08(0.41)	0.05(0.40)	0.15(0.56)	0.20(0.40)
IMF	0.15(0.11)	0.14(0.08)	0.23(0.08)*	0.08(0.08)	0.01(0.11)	0.09(0.08)
Protein	− 0.10(0.20)	0.05(0.14)	0.17(0.15)	0.27(0.14)	− 0.15(0.20)	0.13(0.15)
SFA	49(33)	38(23)	67(24)*	19(23)	10(33)	29(24)
MUFA	58(33)	41(23)	66(24)*	8(23)	17(33)	25(24)
PUFA	26(18)	24(13)	34(13)*	7(13)	3(18)	10(13)
n-3 PUFA	2.4(1.6)	2.1(1.1)	3.1(1.1)*	0.7(1.1)	0.2(1.6)	0.9(1.1)
n-6 PUFA	26(18)	25(13)*	31(13)*	4(12)	1(13)	5(12)
n-6/n-3	0.41(0.24)	0.22(0.16)	0.25(0.16)	− 0.16(0.16)	0.19(0.24)	0.03(0.16)
PUFA/SFA	− 0.05(0.04)	− 0.02(0.02)	− 0.05(0.03)	0(0.02)	− 0.02(0.04)	− 0.02(0.03)

* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 4
Contrasts (standard error) between the lines for individual fatty acid composition (mg/100 g muscle) of the *Longissimus lumborum* muscle.

Trait	A-H	A-LP	A-V	H-V	LP-H	LP-V
C14:0	3.0(2.6)	2.5(1.8)	5.6(1.9)*	2.5(1.8)	0.5(2.6)	3.1(1.9)
C15:0	0.7(0.4)	0.5(0.3)	0.9(0.3)*	0.2(0.3)	0.1(0.4)	0.3(0.3)
C16:0	31(22)	22(15)	41(16)*	10(15)	9(22)	19(16)
C16:1	7.1(4.7)	7.4(3.2)	10.0(3.3)*	2.7(3.2)	2.6(4.7)	5.4(3.3)
C17:0	0.9(0.6)	0.7(0.4)	0.9(0.4)*	0.0(0.4)	0.3(0.6)	0.2(0.4)
C18:0	6.9(4.7)	6.2(3.3)	9.4(3.4)*	2.6(3.3)	0.7(4.7)	3.3(3.4)
C18:1 n-7	1.6(1.2)	1.5(0.8)	2.3(0.8)*	0.6(0.8)	0.2(1.2)	0.8(0.8)
C18:1 n-9	47(27)	33(19)	53(19)*	6(19)	13(27)	19(19)
C18:2 n-6	33(18)	24(13)	32(13)*	− 1(13)	9(18)	8(13)
C18:3 n-3	4.3(2.2)	2.7(1.5)	4.0(1.6)*	− 0.3(1.5)	1.6(2.2)	1.3(1.6)
C20:2 n-6	0.3(0.2)	0.2(0.1)	0.3(0.1)*	0.0(0.1)	0.1(0.2)	0.1(0.1)
C20:3 n-6	0.2(0.2)	0(0.1)	0(0.1)	− 0.2(0.1)	0.2(0.2)	0.1(0.1)
C20:4 n-6	− 1(1)	0.7(1)	0(1)	1(1)	− 1(1)	0(1)
C20:5 n-3	− 0.3(0.6)	− 0.3(0.4)	− 0.1(0.4)	0.2(0.4)	0.0(0.6)	0.2(0.4)
C22:4 n-6	− 0.1(0.2)	− 0.1(0.1)	− 0.2(0.1)	0.2(0.1)	0(0.2)	0.2(0.1)
C22:5 n-3	0.0(0.4)	0.5(0.3)	0.1(0.3)	0.2(0.3)	− 0.1(0.4)	0.1(0.3)
C22:6 n-3	− 1.6(1.5)	0.1(1.0)	0.3(1.0)	1.9(1.1)	− 1.7(1.5)	0.2(1.0)

* $P < 0.05$ (significant difference at $\alpha = 0.05$).

involving A line had the higher content for IMF, SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA respect to purebred V animals (significant differences between AH and VV). This agrees with the result commented before in the Table 3. Table 6 shows no significant differences for individual fatty acids in the contrast All-VV. In agreement with Table 5 and Table 4, Table 6 indicated that the contrast AH-VV was significant for SFA (C14:0, C15:0, C16:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:3 n-3 in favor of the crossbred AH. However, C22:4 n-6 was higher for animals from purebred V dams than for animals from AH dams.

The importance of using a particular line either as sire or dam in a cross was assessed by testing the differences between a particular cross and its reciprocal (Tables 7 and 8). In Table 7, a significant difference was found in the contrast HV-VV for a* in favor of the line V as sire. For the contrast AV-VA the significant difference in SFA was favorable to the A acting as sire, because the crossbred AV had lower value of SFA than VA animals, and, as commented before, one desirable feature would be to reduce the level of SFA.

Table 8 shows significant differences for C16:0 and C16:1 in the contrast AV-VA (higher values for VA). The higher value of C16:0 in the cross VA fully agree the results in Table 7 of this cross having higher level of SFA. In addition to this, Table 8 also shows significant differences in the contrast AH-HA for C20:5n-3 (in favor of H as sire) and for C22:5n-3 (in favor of A as sire). These results and the rest of the contrasts between the reciprocal crosses, the situation is not clear to decide if one cross or its reciprocal is the best because, in general, the reciprocal effects are infrequent, do not follow neither pattern and made difficult to decide which crossbred is optimal.

3.3. Direct-maternal effects

Differences between direct-maternal effects are shown in Tables 9 and 10. The results of the contrasts between lines (Tables 2 and 3) are in close agreement with the results for direct-maternal differences between lines. For pH, significant differences were found for G_{A-V}^{I}, G_{L-H}^{I} and G_{L-V}^{I} (negative values). These indicate direct-maternal effects of the LP line are the lowest.

The concordance for the significant differences between Tables 3 and 9 is complete for IMF, SFA, MUFA, PUFA, n-3 PUFA and n-6 PUFA. Thus, G_{A-V}^{I} was significant for these traits. According to the Table 3, here G_{A-H}^{I} and G_{A-L}^{I} had positive values (no significant difference) and there were indications that the direct-maternal effects of the A line were the highest. In Table 10, significant differences were found in G_{A-V}^{I} for C14:0, C15:0, C16:1, C17:0, C18:0 C18:1n-7, C18:1n-9, C18:2n-6 and C18:3 n-3 in favor of the A line. These agree with the results commented from Table 4. For C16:0, C17:0, C18:1n-7 and C20:2n-6, no significant differences were found regarding G_{A-V}^{I}, these results do not agree with those from Table 4 but they show the same pattern. For G_{A-H}^{I} and G_{A-L}^{I}, there are not significant differences but, as happened before in Table 4, there are indications that the direct-

Table 5
Contrasts (standard error) between crossbred genetic groups[a] and V line for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum* muscle.

Trait	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
pH	0.04(0.02)	0.03(0.02)	0(0.02)	0(0.02)	0(0.02)	0(0.02)	0.01(0.01)
L*	0.41(0.69)	− 0.31(0.70)	0.44(0.70)	0.14(0.71)	− 0.52(0.71)	− 0.32(0.70)	− 0.02(0.53)
a*	− 0.64(0.30)*	− 0.61(0.31)*	− 0.44(0.31)	− 0.55(0.31)	− 0.40(0.31)	− 0.19(0.31)	− 0.47(0.23)*
b*	− 0.40(0.26)	− 0.58(0.27)	− 0.21(0.27)	− 0.03(0.27)	− 0.26(0.27)	− 0.18(0.27)	− 0.27(0.20)
IMF	0.15(0.05)*	0.05(0.05)	0.2(0.05)	0.06(0.05)	0.07(0.05)	− 0.06(0.05)	0.05(0.04)
Protein	0.1(0.1)	0(0.1)	0(0.1)	0(0.1)	0(0.1)	0.1(0.1)	0(0.1)
SFA	47(16)*	17(16)	8(16)	19(16)	24(16)	− 18(16)	16(12)
MUFA	40(16)*	13(16)	2(16)	16(16)	16(16)	− 18(16)	11(12)
PUFA	20(9)*	4(9)	0(9)	7(9)	6(9)	− 10(9)	4(6)
n-3 PUFA	2.1(0.8)*	0.7(0.8)	0.2(0.8)	0.7(0.8)	1.0(0.8)	− 0.8(0.8)	0.6(0.6)
n-6 PUFA	19(9)*	6(9)	− 1(9)	10(9)	12(9)	− 4(9)	6(7)
n-6/n-3	0.1(0.1)	0(0.1)	− 0.1(0.1)	0(0.1)	0(0.1)	− 0.1(0.1)	0(0.1)
PUFA/SFA	− 0.03(0.02)	0(0.02)	− 0.02(0.02)	− 0.01(0.02)	− 0.01(0.02)	0.02(0.02)	− 0.01(0.01)

[a] One cross and its reciprocal are considered together.
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 6
Contrasts (standard error) between crossbred genetic groups[a] and V line for individual fatty acid composition (mg/100 g muscle) of the *Longissimus lumborum* muscle.

Trait	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
C14:0	3.71(1.28)*	1.74(1.29)	0.29(1.29)	1.36(1.30)	1.86(1.31)	− 1.21(1.30)	1.28(0.99)
C15:0	0.51(0.21)*	0.14(0.21)	0.03(0.21)	0.23(0.21)	0.20(0.21)	− 0.23(0.21)	0.15(0.16)
C16:0	26(10)*	11(10)	8(10)	13(10)	19(10)	− 12(10)	11(8)
C16:1	6.7(2.3)*	2.9(2.3)	1.1(2.3)	3.2(2.3)	4.1(2.3)	− 2.0(2.3)	2.6(1.7)
C17:0	0.4(0.3)	0.1(0.3)	− 0.1(0.3)	0.1(0.3)	0.2(0.3)	− 0.3(0.3)	0.1(0.2)
C18:0	5.6(2.3)*	1.5(2.3)	0.0(2.3)	1.7(2.3)	2.0(2.3)	− 2.6(2.3)	1.5(1.7)
C18:1 n-7	1.4(0.6)*	0.4(0.6)	0.0(0.6)	0.7(0.6)	0.5(0.6)	− 0.6(0.6)	0.4(0.4)
C18:1 n-9	32(13)*	10(13)	1(13)	12(13)	13(13)	− 15(13)	9(10)
C18:2 n-6	16(9)	7(9)	− 1(9)	6(9)	11(9)	− 7(9)	5(7)
C18:3 n-3	2.1(1.1)*	1.0(1.1)	0.1(1.1)	0.9(1.1)	1.5(1.1)	− 0.8(1.1)	0.8(0.8)
C20:2 n-6	0.1(0.1)	0.1(0.1)	0.0(0.1)	0.0(0.1)	0.1(0.1)	− 0.1(0.1)	0.1(0.1)
C20:3 n-6	0.0(0.1)	0.1(0.1)	− 0.1(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)
C20:4 n-6	0.3(0.6)	− 0.2(0.6)	− 0.2(0.6)	− 0.8(0.6)	− 0.3(0.6)	− 1.0(0.6)	0.3(0.4)
C20:5 n-3	0.0(0.3)	− 0.1(0.3)	0.0(0.3)	0.1(0.3)	− 0.1(0.3)	0.2(0.3)	0.1(0.2)
C22:4 n-6	− 0.3(0.1)*	− 0.2(0.1)	− 0.1(0.1)	− 0.1(0.1)	− 0.3(0.1)*	− 0.1(0.1)	− 0.2(0.1)
C22:5 n-3	− 0.1(0.2)	− 0.1(0.2)	0.1(0.2)	− 0.1(0.2)	− 0.2(0.2)	− 0.3(0.2)	− 0.1(0.2)
C22:6 n-3	− 0.2(0.7)	− 0.5(0.7)	− 0.1(0.7)	− 0.8(0.7)	− 1.0(0.7)	− 1.0(0.7)	− 0.6(0.6)

[a] One cross and its reciprocal are considered together.
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 7
Contrasts (standard error) between reciprocal crosses for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum* muscle.

Trait	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
pH	0.04(0.03)	− 0.02(0.03)	− 0.01(0.03)	− 0.02(0.03)	− 0.06(0.03)	− 0.04(0.03)
L*	− 1.6(1.4)	1.4(1.4)	0.4(1.4)	2.0(1.4)	2.4(1.4)	0.3(1.4)
a*	− 0.2(0.6)	0.2(0.6)	0.1(0.6)	− 1.3(0.6)*	− 0.4(0.6)	0.5(0.6)
b*	− 0.8(0.05)	0.5(0.05)	0.4(0.05)	0.5(0.05)	− 0.3(0.05)	0.3(0.05)
IMF	0.1(0.1)	− 0.1(0.1)	− 0.2(0.1)	0.1(0.1)	0.1(0.1)	0.0(0.1)
Protein	0.1(0.2)	0.1(0.2)	0(0.2)	− 0.2(0.2)	0.2(0.2)	0.1(0.2)
SFA	46(32)	− 18(32)	− 70(32)*	41(32)	25(32)	− 8(32)
MUFA	40(33)	− 17(33)	− 58(33)	32(33)	22(33)	− 3(33)
PUFA	17(18)	− 8(18)	− 29(18)	15(18)	10(18)	− 3(18)
n-3 PUFA	2.5(1.6)	− 1.3(1.6)	− 2.9(1.6)	1.4(1.6)	1.1(1.6)	− 1.0(1.6)
n-6 PUFA	15(17)	0(17)	− 25(17)	19(17)	6(17)	− 1(17)
n-6/n-3	0(0.2)	0(0.2)	− 0.1(0.2)	0.1(0.2)	0.1(0.2)	0.2(0.2)
PUFA/SFA	− 0.06(0.04)	0.03(0.04)	0.06(0.04)	− 0.03(0.04)	− 0.02(0.04)	0.00(0.04)

* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 8
Contrasts (standard error) between reciprocal crosses for individual fatty acid composition (mg/100 g muscle) of the *longissimus lumborum* muscle.

Trait	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
C14:0	2.9(2.6)	− 1.5(2.6)	− 4.9(2.6)	2.5(2.6)	1.8(2.6)	0.0(2.6)
C15:0	0.5(0.4)	− 0.2(0.4)	− 0.7(0.4)	0.4(0.4)	0.6(0.4)	− 0.3(0.4)
C16:0	32(21)	− 13(21)	− 45(21)*	26(21)	8(21)	− 9(21)
C16:1	6.8(4.6)	− 3.3(4.6)	− 9.7(4.6)*	4.3(4.6)	3.0(4.6)	− 3.1(4.6)
C17:0	0.6(0.6)	− 0.2(0.6)	− 0.8(0.6)	0.7(0.6)	0.2(0.6)	0.0(0.6)
C18:0	5.0(4.6)	− 2.5(4.6)	− 8.0(4.6)	4.5(4.6)	2.7(4.6)	− 0.6(4.6)
C18:1 n-7	1.0(1.2)	− 0.5(1.2)	− 1.9(1.2)	1.1(1.2)	0.6(1.2)	− 0.3(1.2)
C18:1 n-9	− 33(26)	− 14(26)	− 48(26)	27(26)	18(26)	− 2(26)
C18:2 n-6	15(18)	− 3(18)	− 25(18)	18(18)	5(18)	− 2(18)
C18:3 n-3	2.0(2.2)	− 0.4(2.2)	− 3.3(2.2)	2.3(2.2)	0.7(2.2)	− 0.6(2.2)
C20:2 n-6	0.1(0.2)	0.1(0.2)	− 0.2(0.2)	0.1(0.2)	− 0.1(0.2)	− 0.1(0.2)
C20:3 n-6	− 0.2(0.2)	0.2(0.2)	0.0(0.2)	0.1(0.2)	− 0.1(0.2)	0.3(0.2)
C20:4 n-6	2.2(1.2)	− 1.6(1.2)	− 1.3(1.2)	− 0.1(1.2)	0.6(1.2)	− 0.3(1.2)
C20:5 n-3	− 1.6(0.5)*	0.4(0.5)	0.3(0.5)	0.0(0.5)	0.2(0.5)	0.0(0.5)
C22:4 n-6	0.1(0.2)	− 0.2(0.2)	0.1(0.2)	0.1(0.2)	0.1(0.2)	0.0(0.2)
C22:5 n-3	1.00(0.4)*	− 0.2(0.4)	− 0.5(0.4)	0.0(0.4)	0.3(0.4)	− 0.6(0.4)
C22:6 n-3	1.0(1.5)	− 1.0(1.5)	0.0(1.5)	− 0.2(1.5)	− 0.1(1.5)	− 0.4(1.5)

* $P < 0.05$ (significant difference at $\alpha = 0.05$).

maternal effects of the A line were the highest.

3.4. Grand-maternal effects

Tables 11 and 12 show grand-maternal effect differences between lines. As Mínguez et al. (2015a) and Mínguez et al. (2015b) reported, it can be observed that the errors for the latter are smaller than those for the former, showing that our data structure is better suited to estimate grand-maternal effects than direct-maternal effects. Contrary for direct-maternal effects, no significant contrast were found for grand maternal

Table 9
Direct-maternal effect differences between lines[a] (standard error) for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	[a]G_{A-H}^{I}	G_{A-L}^{I}	G_{A-V}^{I}	G_{H-V}^{I}	G_{L-H}^{I}	G_{L-V}^{I}
pH	0.00(0.04)	0.08(0.03)*	0.02(0.03)	0.02(0.03)	−0.08(0.04)*	−0.06(0.03)*
L*	−1.35(1.6)	−0.82(1.3)	0.22(1.3)	1.58(1.3)	−0.53(1.6)	1.05(1.3)
a*	1.20(0.72)	−0.06(0.56)	−0.19(0.56)	−1.39(0.56)*	1.26(0.72)	−0.13(0.56)
b*	−0.39(0.63)	−0.10(0.48)	0.31(0.48)	0.71(0.48)	−0.29(0.63)	0.41(0.48)
IMF	0.14(0.12)	0.11(0.10)	0.20(0.10)*	0.06(0.10)	0.03(0.12)	0.09(0.10)
Protein	−0.01(0.23)	−0.05(0.18)	0.11(0.18)	0.13(0.18)	−0.04(0.23)	0.17(0.18)
SFA	45(37)	33(29)	63(29)*	17(29)	12(37)	30(29)
MUFA	56(37)	34(29)	61(29)*	4(29)	22(37)	26(29)
PUFA	24(20)	20(16)	33(16)*	5(16)	4(20)	9(16)
n-3 PUFA	2.4(1.8)	2.2(1.4)	2.9(1.4)*	0.2(1.4)	0.4(1.8)	0.6(1.4)
n-6 PUFA	24(20)	26(15)	31(15)*	7(15)	−2(20)	5(15)
n-6/n-3	0.4(0.3)	0.1(0.2)	0.3(0.2)	−0.1(0.2)	0.3(0.3)	0.2(0.2)
PUFA/SFA	−0.06(0.04)	−0.02(0.03)	−0.05(0.03)	0.00(0.03)	−0.04(0.04)	−0.03(0.03)

[a] G_{i-j}^{I} = direct-maternal differences between lines i and j (see text for a complete explanation.
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 10
Direct-maternal effect differences between lines[a] (standard error) for individual fatty acid composition (mg/100 g muscle) of the *longissimus lumborum* muscle.

Trait	[a]G_{A-H}^{I}	G_{A-L}^{I}	G_{A-V}^{I}	G_{H-V}^{I}	G_{L-H}^{I}	G_{L-V}^{I}
C14:0	2.7(2.9)	1.6(2.3)	5.0(2.3)*	2.3(2.3)	1.0(2.9)	3.3(2.3)
C15:0	0.6(0.5)	0.5(0.4)	0.8(0.4)*	0.1(0.4)	0.1(0.5)	0.3(0.4)
C16:0	28(25)	22(20)	37(20)	9(20)	6(25)	15(20)
C16:1	6.9(5.2)	4.1(4.1)	8.2(4.1)*	1.3(4.1)	2.7(5.2)	4.1(4.1)
C17:0	0.8(0.6)	0.6(0.5)	0.9(0.5)	0.1(0.5)	0.2(0.6)	0.3(0.5)
C18:0	6.2(5.2)	5.1(4.1)	8.6(4.1)*	2.3(4.1)	1.1(5.2)	3.4(4.1)
C18:1 n-7	1.3(1.3)	1.2(1.0)	1.9(1.0)	0.6(1.0)	0.1(1.3)	0.7(1.0)
C18:1 n-9	46(30)	28(24)	50(24)*	3(24)	17(30)	21(24)
C18:2 n-6	30(20)	24(16)	32(16)*	1(16)	6(20)	7(16)
C18:3 n-3	4.0(2.5)	2.8(1.9)	3.9(1.9)*	−0.1(1.9)	1.2(2.5)	1.1(1.9)
C20:2 n-6	0.2(0.3)	0.3(0.2)	0.3(0.2)	0.0(0.2)	−0.1(0.2)	0(0.2)
C20:3 n-6	0.1(0.2)	−0.1(0.2)	0.1(0.2)	0.0(0.2)	0.2(0.2)	0.2(0.2)
C20:4 n-6	0.4(1.3)	0.3(1.0)	−0.1(1.0)	−0.4(1.0)	0.7(1.3)	−0.2(1.0)
C20:5 n-3	−0.7(0.6)	−0.5(0.5)	−0.2(0.5)	0.4(0.5)	−0.1(0.6)	0.3(0.5)
C22:4 n-6	−0.1(0.3)	−0.2(0.2)	−0.2(0.2)	−0.1(0.2)	0.1(0.3)	−0.1(0.2)
C22:5 n-3	0.4(0.5)	0.3(0.4)	0.1(0.4)	−0.3(0.4)	0.0(0.5)	−0.2(0.4)
C22:6 n-3	−1.1(1.6)	0.2(1.3)	0.4(1.3)	1.6(1.3)	−1.4(1.6)	0.2(1.3)

[a] G_{i-j}^{I} = direct-maternal differences between lines i and j (see text for a complete explanation).
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 11
[a]Grand-maternal effect differences between lines (standard error) for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	[a]$G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
pH	0.03(0.02)	0.01(0.02)	0.02(0.02)*	−0.02(0.02)	0.02(0.02)	0.00(0.02)
L*	−0.99(0.88)	−0.59(1.10)	−0.44(1.16)	0.55(0.88)	−0.40(0.88)	0.15(1.02)
a*	−0.05(0.39)	−0.35(0.44)	−0.42(0.51)	−0.37(0.39)	0.31(0.39)	−0.06(0.45)
b*	−0.48(0.33)	−0.27(0.38)	−0.74(0.44)	−0.26(0.33)	−0.21(0.33)	−0.47(0.39)
IMF	−0.02(0.07)	−0.10(0.08)	−0.11(0.09)	−0.09(0.07)	−0.09(0.07)	0.00(0.08)
Protein	0.08(0.12)	0.05(0.14)	−0.17(0.16)	−0.09(0.12)	0.03(0.12)	−0.12(0.14)
SFA	−5(20)	−34(23)	−30(26)	−25(20)	28(20)	2(23)
MUFA	−1(20)	−35(23)	−32(26)	−30(20)	34(20)	3(23)
PUFA	−1(11)	−17(12)	−17(14)	−16(11)	16(11)	0(12)
n-3 PUFA	0.0(1.0)	−1.5(1.1)	−1.2(1.2)	−1.3(1.0)	1.5(1.0)	0.2(1.1)
n-6 PUFA	4(10)	−10(12)	−11(14)	−15(10)	15(10)	0(12)
n-6/n-3	0.07(0.15)	−0.19(0.17)	−0.13(0.19)	−0.20(0.15)	0.03(0.15)	0.05(0.17)
PUFA/SFA	0.03(0.02)	0.04(0.03)	0.03(0.03)	0.00(0.02)	−0.01(0.02)	0.00(0.03)

[a] $G_{i-j}^{M'}$ = grand-maternal differences between lines i and j (see text for a more complete explanation).
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

effects, clearly indicating that the importance of the latter should be lower than the importance of the former.

3.5. Maternal heterosis

Estimates of maternal heterosis effects are shown in Tables 13 and 14. No significant differences were found. Many results of positive heterosis, regarding litter size, have been reported (Brun & Saleil, 1994;

Table 12
[a]Grand-maternal effect differences between lines (standard error) for individual fatty acid composition (mg/100 g muscle) of the l*ongissimus lumborum* muscle.

Trait	[a]$G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
C14:0	− 0.1(1.6)	− 2.1(1.8)	− 2.6(2.1)	− 2.5(1.6)	2.1(1.6)	− 0.4(1.8)
C15:0	0.0(0.3)	− 0.4(0.3)	− 0.4(0.3)	− 0.4(0.3)	0.4(0.3)	0.0(0.3)
C16:0	− 6(13)*	− 19(15)	− 18(17)	− 12(13)	12(13)	1(15)
C16:1	− 1.0(2.8)	− 5.1(3.2)	− 4.7(3.7)	− 3.7(2.8)	4.1(2.8)	0.4(3.2)
C17:0	0.0(0.3)	− 0.4(0.4)	− 0.5(0.5)	− 0.5(0.3)	0.4(0.3)	− 0.1(0.4)
C18:0	− 0.1(2.9)	− 4.4(3.3)	− 4.8(3.7)	− 4.6(2.9)	4.2(2.9)	− 0.4(3.3)
C18:1 n-7	0.1(0.7)	− 1.0(0.8)	− 1.1(0.9)	− 1.1(0.7)	1.1(0.7)	0.0(0.8)
C18:1 n-9	− 1(16)	− 28(18)	− 26(21)	− 25(16)	27(16)	2(18)
C18:2 n-6	4(11)	− 13(12)	− 13(14)	− 17(11)	17(11)	0(12)
C18:3 n-3	0.2(1.3)	− 1.8(1.5)	− 1.6(1.7)	1.8(1.3)	2.1(1.3)	0.2(1.5)
C20:2 n-6	0.05(0.10)	− 0.05(0.10)	− 0.01(0.10)	− 0.14(0.10)	0.10(0.10)	0.00(0.10)
C20:3 n-6	0.10(0.10)	− 0.01(0.12)	0.02(0.14)	− 0.08(0.10)	0.12(0.10)	0.04(0.12)
C20:4 n-6	0.17(0.73)	0.31(0.83)	− 0.17(0.96)	− 0.34(0.73)	− 0.14(0.73)	− 0.48(0.83)
C20:5 n-3	− 0.19(0.33)	− 0.09(0.38)	− 0.13(0.44)	0.06(0.33)	− 0.10(0.33)	− 0.04(0.38)
C22:4 n-6	0.01(0.12)	0.04(0.14)	0.03(0.16)	0.02(0.12)	0.03(0.12)	− 0.01(0.14)
C22:5 n-3	− 0.28(0.25)	0.03(0.28)	− 0.20(0.32)	0.08(0.25)	− 0.31(0.25)	− 0.23(0.28)
C22:6 n-3	− 0.5(0.9)	0.5(1.0)	− 0.8(1.2)	− 0.2(0.9)	− 1.1(0.9)	− 1.3(1.0)

[a] $G_{i-j}^{M'}$ = grand-maternal differences between lines i and j (see text for a more complete explanation).
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 13
[a]Maternal heterosis (standard error) for pH, colour, intramuscular fat (IMF, g/100 g muscle), protein (g/100 g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	[a]H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
pH	0.00(0.02)	0.00(0.02)	− 0.01(0.02)	0.01(0.02)	0.01(0.02)	0.04(0.02)*
L*	− 0.44(0.87)	− 0.86(1.02)	− 0.12(0.87)	− 0.92(0.72)	− 0.37(0.72)	− 0.74(0.72)
a*	− 0.10(0.38)	0.16(0.44)	− 0.09(0.38)	0.39(0.32)	0.00(0.32)	− 0.08(0.32)
b*	− 0.29(0.33)	− 0.38(0.38)	− 0.06(33)	− 0.26(0.27)	− 0.23(0.27)	− 0.21(0.27)
IMF	− 0.11(0.07)	− 0.02(0.07)	0.02(0.07)	0.02(0.05)	0.03(0.05)	0.01(0.05)
Protein	0.02(0.12)	− 0.18(0.14)	− 0.08(0.12)	− 0.05(0.10)	− 0.04(0.10)	− 0.12(0.10)
SFA	− 32(20)	0(23)	9(20)	2(17)	4(17)	0(17)
MUFA	− 30(20)	0(23)	12(19)	3(16)	5(16)	-1(16)
PUFA	− 15(11)	− 2(12)	4(11)	1(9)	3(9)	0(9)
n-3 PUFA	1.2(1.0)	0.2(1.1)	0.4(1.0)	0.4(0.8)	0.4(0.8)	0.3(0.8)
n-6 PUFA	− 7(10)	7(12)	7(10)	− 2(9)	− 1(9)	1(9)
n-6/n-3	− 0.09(0.14)	0.04(0.17)	0.06(0.14)	− 0.05(0.12)	− 0.04(0.12)	− 0.12(0.12)
PUFA/SFA	0.03(0.02)	0.00(0.02)	0.00(0.02)	− 0.01(0.02)	0.00(0.02)	0.00(0.02)

[a] H_{ij}^{M} = maternal heterosis between lines i and j.
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Table 14
[a]Maternal heterosis (standard error) for individual fatty acid composition (mg/100 g muscle) of the *longissimus lumborum* muscle.

Trait	[a]H_{AH}^{M}	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
C14:0	− 2.7(1.6)	− 1.0(1.8)	0.1(1.6)	− 0.3(1.3)	0.5(1.3)	− 0.2(1.3)
C15:0	− 0.37(0.3)	− 0.03(0.3)	0.14(0.3)	0.04(0.3)*	0.08(0.3)	0.01(0.3)
C16:0	− 21(13)	5(15)	8(13)	1(11)	3(11)	3(11)
C16:1	− 4(3)	0(3)	2(3)	1(2)	1(2)	1(2)
C17:0	− 0.43(0.35)	0.08(0.40)	0.16(0.35)	− 0.11(0.29)	− 0.03(0.29)	− 0.07(0.29)
C18:0	− 4.1(2.8)	− 0.9(3.3)	1.4(2.8)	0.2(2.3)	0.8(2.3)	− 0.1(2.3)
C18:1 n-7	− 0.96(0.7)	− 0.17(0.8)	0.39(0.7)	0.05(0.6)	0.29(0.6)	0.10(0.6)
C18:1 n-9	− 25(16)	0(18)	9(16)	2(13)	3(13)	− 1(13)
C18:2 n-6	− 11(11)	7(13)	6(11)	− 2(9)	0(9)	1(9)
C18:3 n-3	− 1.4(1.3)	1.0(1.5)	1.1(1.3)	− 0.2(1.1)	0.1(1.1)	0.2(1.1)
C20:2 n-6	− 0.10(0.10)	0.10(0.12)	0.03(0.10)	− 0.03(0.09)	0(0.09)	0.10(0.09)
C20:3 n-6	0.02(0.10)	0.03(0.12)	0.06(0.10)	− 0.16(0.9)	− 0.12(0.09)	− 0.07(0.09)
C20:4 n-6	− 0.8(0.73)	− 0.80(0.84)	− 1.23(0.73)	0.81(0.60)	0.21(0.60)	− 0.08(0.60)
C20:5 n-3	0.16(0.33)	− 0.23(0.39)	0.07(0.33)	− 0.30(0.28)	− 0.08(0.28)	0.13(0.28)
C22:4 n-6	0.04(0.12)	− 0.08(0.14)	0.03(0.12)	− 0.05(0.10)	− 0.08(0.10)	− 0.11(0.10)
C22:5 n-3	− 0.39(0.25)	− 0.34(0.28)	− 0.19(0.25)	0.40(0.21)	0.03(0.21)	0.29(0.21)
C22:6 n-3	− 1.1(0.9)	− 1.9(1.1)	− 1.7(0.9)	0.3(0.7)	− 0.1(0.7)	0.0(0.7)

[a] H_{ij}^{M} = maternal heterosis between lines i and j.
* $P < 0.05$ (significant difference at $\alpha = 0.05$).

Khalil and Afifi (2000); Baselga, Garcia, Sanchez, Vicente, & Lavara, 2003; Brun & Baselga, 2005; Youssef et al., 2008). Mínguez et al. (2015a) and Mínguez et al. (2015b) reported that maternal heterosis estimates on the majority of growth and carcass traits in crosses involving lines with high prolificacy (H and LP lines) were significantly negative. However, our results did not found this negative heterosis estimates in meat quality traits, perhaps because these traits are less dependent on litter size that growth and carcass traits. Also, Sellier (1988) indicated that heterosis for quality of pork does not exist in most breed crosses.

4. Conclusions

It can be concluded that the observed significant contrasts are mainly consequence of direct-maternal genetic effects, playing grand-maternal and heterotic effects a much lower role in the control of the chemical composition of the meat of the studies lines and their crosses.

Acknowledgements

The authors are grateful to Ph.D. Cristina Zomeño and Ms. Veronica Juste for their laboratory work, advice, comments and suggestions.

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