Available online at www.sciencedirect.com
SCIENCE DIRECT®
Food Chemistry 100 (2007) 1639–1648
Food Chemistry
www.elsevier.com/locate/foodchem

Effect of increasing amounts of a linoleic-rich dietary fat on the fat composition of four pig breeds. Part II: Fatty acid composition in muscle and fat tissues

J.V. Pascual [a], M. Rafecas [a], M.A. Canela [b], J. Boatella [a], R. Bou [a], A.C. Barroeta [c], R. Codony [a,*]

[a] Department of Nutrition and Food Science-CeRTA, Faculty of Pharmacy, University of Barcelona, Av. Joan XXIII s/n, 08028 Barcelona, Spain
[b] Department of Applied Mathematics and Analysis, University of Barcelona, Gran Via Corts Catalanes 585, 08007 Barcelona, Spain
[c] Department of Nutrition and Animal Feeding, Faculty of Veterinary, Universitat Autònoma of Barcelona, 08193 Bellaterra-Cerdanyola, Spain

Received 22 November 2005; received in revised form 15 December 2005; accepted 15 December 2005

Abstract

This paper studies the change of fatty acid profile in four different tissues of the pig (backfat, abdominal fat, and the muscles *trapezius* and *longissimus thoracis et lumborum*) in response to four diets containing increasing amounts (0%, 2%, 4% and 8%) of a high linoleic acid fat blend, in a sample of 48 pigs of four different breeds (Landrace, Large White, Duroc and a crossbreed Landrace × Duroc). The effects of dietary fat and breed on this profile have been separately tested for each tissue. The diet effect (increasing % of linoleic acid intake) was positive on linoleic acid deposit in all tissues, meanwhile it was negative on palmitic and stearic levels, as well as for the oleic acid. However, this effect was clear in the four tissues for the linoleic acid, while the differences did not follow the same pattern for the saturated fatty acids in trapezius muscle and abdominal fat. Although the levels of arachidonic acid in muscle tissues were higher than those found in adipose tissues, the increasing effect of the diet was stronger, in relative terms, in adipose tissues. The breed effect was, in general, lower than the diet effect. Landrace showed the higher ability to increase linoleic acid levels, particularly in the loin (*longissimus thoracis et lumborum*), whereas Duroc pigs seemed to be the most resistant to change of fatty acid composition according to the diet.

Keywords: Pig tissues; Fatty acids; Dietary fat; Breed; Metabolic markers

1. Introduction

The fatty acid (FA) composition and the total amount of saturated fatty acids (SFA) have been identified as dietary risk factors, related to cardiovascular diseases (Katan, Zock, & Mensink, 1994). In the developed countries, animal fats contribute substantially to the total fat intake and are the major sources of SFA. However, the compositions of these animal fats (i.e., pork tissues' fat) can be modified by the nature of feeding fat, which can affect their metabolic pathways in different ways. For example, when pigs have a restricted feeding (low energy), fat synthesis is reduced and the muscular lean production is enhanced (Henry, 1977). It is also known that, under isocaloric conditions, the fat added to animal feed can induce a diminution of endogenous fat synthesis, probably due to a parallel reduction of carbohydrates utilization, which is the main source of the lipogenesis (Allee, Baker, & Leveille, 1971; Enser, 1984). It seems that this affects only the endogenous synthesis, but not the total amount of fat, which is mainly due to the diet. Besides, the dietary FA profile seems to affect the metabolic pathways. In this sense, an increase

Abbreviations: FA, fatty acids; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; FAME, fatty acid methyl esters; LW, Large White; D, Duroc; L, Landrace; F1, crossbreed Landrace × Duroc; LTL, *longissimus thoracis et lumborum*.

* Corresponding author. Tel.: +34 934024514; fax: +34 934035931.
E-mail address: rafaelcodony@ub.edu (R. Codony).

0308-8146/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.foodchem.2005.12.045

of unsaturated and long chain FA can reduce the lipogenesis enzymatic activity (Mourot, Aumaitre, Mounier, Peiniau, & François, 1994). Finally, the enzyme regulation mechanisms in the pig for the desaturases and the elongases are not well known, even though their activities are crucial for FA tissue composition. Δ-9 desaturase activities can be modulated by the dietary FA composition, so a diet rich in SFA can enhance these activities, whereas one rich in oleic acid (Klingenberg, Knabe, & Smith, 1995) or in PUFA (Kouba, Enser, Whittington, Nute, & Wood, 2003) can decrease them. There are several papers dealing with the effects of dietary fats on the FA composition of pork adipose and muscle tissues, and with the interactions between these effects and other factors, such as breed and feed energy level (Averette Gatlin, See, Hansen, Sutton, & Odle, 2002; Bee, Geert, & Messikommer, 2002; Eder, Nonn, & Kluge, 2001; Fontanillas, Barroeta, Baucells, & Codony, 1997; Wood, Buxton, Whittington, & Enser, 1986). Some authors (Ahn, Lutz, & Sim, 1996; Eder et al., 2001; Scheeder, Gläser, Eichenberger, & Wenk, 2000) have observed that increasing the linoleic acid in the diet leads to a higher content of linoleic acid in the loin, but not to a significant increase in arachidonic acid. Fewer data are available on the parallel increase of linoleic and arachidonic acids in fat tissues in response to increased linoleic acid in the diet (D'Arrigo et al., 2002). Other authors have also attempted to study a nutritional model of the FA distribution within pig tissues (Lizardo, van Milgen, Mourot, Noblet, & Bonneau, 2002). Such a model described the interactions between dietetic FA intake and the different lipid metabolic pathways. Moreover, this study concluded that the available models for predicting the FA composition of pork tissues were still too simple, and more knowledge is needed with regard to some metabolic processes. These authors called for studies that might provide more information on FA composition, taking into account different factors to improve the accuracy of the predictions. We have examined, in this paper, the effect of the addition of increasing amounts of a polyunsaturated fat in the diet on the FA composition of muscle and adipose tissues of pork. We also assess the differences between various breeds related to these dietary changes. This information could be of great interest from a productive point of view, and could be used for enhancing some aspects of pork fat quality.

2. Materials and methods

2.1. Samples and experimental design

The experimental work was based on a 4×4 complete factorial design of two factors, diet and breed, with four levels per factor. The sample size was 48, with three animals for each of the 16 diet–breed combinations. Castrated male pigs of four breeds were used: Large White, Duroc, Landrace and a commercial crossbreed Landrace × Duroc (F1). Animals of each breed were distributed uniformly according to their weight and original litter (avoiding littermates inside the same group) and they were fed a conventional adaptation diet during a 7-d period, before the start of the experiment. The control animal feeding (diet 1) was a mixture whose main ingredients were wheat, barley and soya meal. The three other diets were obtained by adding increasing amounts of fat as follows: 2%, 4% and 8%, respectively, for diets 2, 3 and 4. The fat added to the feed was a commercial mixture of 50% of a soy/sunflower acid oil and 50% of animal fat. Diets were formulated to achieve minimal differences in energy and protein content. A complete description of the ingredients and the composition of the four diets is given in Table 1. The experiment was carried out under controlled conditions of temperature, light, and ventilation. Animals were given ad libitum access to feed throughout the experiment, and animal weight and feed consumption were recorded each 15 days, until the end of the experiment. Also, *daily feed intake* (kg feed/day), *average daily gain* (kg live weight/day) and *feed conversion ratio* were calculated. After slaughter, which took place at a live weight of 85–90 kg, the following carcass measurements were taken: *carcass weight*, *carcass yield*,

Table 1
Ingredients and composition, including FA, of the four experimental diets

	Diet 1	Diet 2	Diet 3	Diet 4
Ingredients (g/100 g)				
Wheat	61.86	48.06	27.76	10.00
Barley	20.00	25.00	34.00	45.94
Wheat bran	3.00	5.12	15.00	15.00
47% soy meal	9.50	14.50	13.94	15.44
50% meat meal	2.00	2.00	2.00	2.00
Added fat[a]	0.00	2.00	4.00	8.00
Salt	0.50	0.50	0.50	0.58
Calcium carbonate	0.88	0.78	0.74	0.94
Bicalcium carbonate	1.10	1.16	1.20	1.28
78% methionine	0.04	0.02	0.02	0.01
78% lysine	0.40	0.24	0.22	0.18
Vit-mineral premix	0.07	0.07	0.63	0.63
Composition (g/100 g)				
Digestible energy[b] (kcal/kg)	3579	3579	3579	3734
Dry matter	88.48	88.82	89.51	90.55
Crude protein	16.4	17.5	17.9	17.5
Ash	4.78	5.56	6.18	6.88
Ether extract	2.71	4.34	7.35	10.56
Crude fibre	3.50	3.40	4.26	4.17
Fatty acids (mg/100 g)				
C14:0	16	38	66	133
C16:0	334	668	946	1729
C18:0	101	286	470	848
C16:1 $n-7$	12	36	59	128
C18:1 $n-9$ *cis*	392	917	1454	2575
C18:1 *trans*[c]	18	61	105	202
C18:2 $n-6$	897	1526	2140	3208
C20:4 $n-6$	2	4	5	12
C18:3 $n-3$	79	117	189	199
C20:5 $n-3$	5	11	13	25

[a] 50% acid oil (soy and sunflower) and 50% animal fat.
[b] Estimated values.
[c] Total C18:1 *trans* isomers.

backfat thickness measured at the 4th and last ribs (Fat-O-Meter, SFK Ltd., Denmark), and *percentage of lean*, calculated as proposed by Oliver, Gispert, Tibau, and Diestre (1991). After slaughter, samples of four tissues were taken from each subject: two adipose tissues, backfat and abdominal fat, and two muscle tissues, *longissimus thoracis et lumborum* (*muscle LTL*) and *trapezius*. Backfat and longissimus samples were taken at the level of the 10th rib. Samples were then vacuum stored in plastic bags, frozen and kept at −20 °C, until analysis.

2.2. Reagents

All solvents were ACS grade. Chloroform, methanol and diethyl ether were from Panreac (Montplet & Esteban, Barcelona, Spain) and *n*-hexane from E. Merck (Darmstadt, Germany). The other reagents were anhydrous sodium sulphate and sodium chloride (both for analysis) from Panreac and sodium (for synthesis), phenolphthalein (ACS) and boron trifluoride in methanol (14% p/v for synthesis) from E. Merck. All the standards of fatty acid methyl esters (FAME) were supplied by Sigma Chemical Co. (St. Louis, MO), except the dodecanoic acid methyl ester from Altech Associates Inc. (Deerfield, IL). A mixture of some FAME (PUFA-2) was supplied by Supelco Inc. (Bellefonte, PA). Except for the C20:2 $n-6$ methyl ester (98%), all the standards were of 99% purity.

2.3. Fatty acids determination

Lipids were obtained by extraction, following the method of Folch, Lees, and Stanley (1957), but with a few modifications. Five gramme of muscle tissue or 0.5 g of adipose tissue were weighed and homogenised with 30 ml of chloroform/methanol mixture (2:1 v/v) by using a Polytron (PT 2000, Kinematica AG, Lucerne, Switzerland), at 20,000 rpm, during 30 s. The solid residue was re-extracted with 30 ml of the solvent mixture, and the combined organic fractions were washed with a NaCl aqueous solution (0.58%). The chloroform phase was then filtered through anhydrous sodium sulphate and evaporated to dryness. The fatty acids were determined in this fat extract according to the method proposed by Guardiola, Codony, Rafecas, Boatella, and López (1994), by obtaining their methyl esters (FAME) and by gas chromatographic analysis. The FA were quantified by applying relative response factors and the results were expressed as compensated area normalisation. The repeatability and intermediate precision of the FA analysis were evaluated. In the repeatability assessment, six aliquots of a sample were extracted, and their FAME were injected in triplicate on the same day, following the design: 1 day × 6 samples × 3 replicates. In the intermediate precision determination, 12 aliquots of a sample were used, following the design: 4 days × 3 samples × 3 replicates. The repeatability and intermediate precision estimates for the six selected FA, expressed as % RSD (relative standard deviations in percentage scale) ranged between 0.89% and 7.18% for the repeatability, and between 0.52% and 6.73% for the intermediate precision. Values were similar for muscle and adipose tissues. For the non-reported FA, the results were similar.

2.4. Selection of FA markers

For this purpose, we classified the FA according to their accumulation pattern in different tissues, which allowed us to reduce the number of variables to be studied. So, in this study, we determined 22 FA in all tissues, but the presentation of the results is restricted to six selected FA (α-linoleic, palmitic, oleic, arachidonic, palmitoleic and eicosatrienoic acids). A previous study on these samples (Pascual, 2000), based on correlations and on principal components analysis, showed that the rest of the FA are highly correlated to one of the six markers. The six FA selected are sufficient to understand the effects of the diet on FA profile, and the strong correlations observed support the extrapolation to the rest of FA. Table 2 summarises the classification of the 22 FA, based on these correlations. The first group of FA showed a deposit from a dietary origin, not from endogenous metabolism, and it consisted of the $n-3$ and $n-6$ PUFA located at the head of these two series, the *trans* FA, C15:0 and C16:1 $n-9$. From this group we selected linoleic acid (C18:2 $n-6$), as it shows the highest level in all tissues. This is due to the composition of the fat added to the feed. If a fat rich in $n-3$ PUFA were to be added to the feed, then C18:3 $n-3$ would also be useful as a marker of this group. And if a hydrogenated fat or tallow were used in feed, then *trans* C18: isomers could also be good markers. The second group consists of FA whose

Table 2
Classification of fatty acids in the pork as markers of different metabolic processes (bold letters indicates the markers selected)

Effect	Fatty acid markers
Markers of dietary supply	**C18:2 *n* − 6**, C18:3 *n* − 6, C20:2 *n* − 6 C18:3 *n* − 3, C18:1 *n* − 9 *trans*, C18:2 *n* − 6 *trans*, C15:0, C16:1 *n* − 9
Markers of the de novo synthesis	**C16:0**, C18:0, C20:0, C20:1 *n* − 9
Markers of the Δ-9 desaturase activity	**C18:1 *n* − 9**
Markers of the Δ-6 desaturase activity	**C20:4 *n* − 6**, C20:5 *n* − 3, C22:5 *n* − 3
Markers of competition for the Δ-9 desaturase	**C16:1 *n* − 7**, C18:1 *n* − 7, C10:0, C12:0, C14:0
Markers of competition for the Δ-6 desaturase between *n* − 3 and *n* − 6 PUFA	**C20:3 *n* − 3**

deposit is mainly the result of de novo synthesis. Within this group, palmitic (C16:0) is the most abundant FA and, as a consequence, it would be the most reliable marker of a predominant de novo FA synthesis in pork tissues. Oleic acid is the only FA classified in the group of markers of the Δ-9 desaturase activity. The fourth group consists of $n-3$ and $n-6$ PUFA located at the end of these two series, and a higher level of these FA in the fat depots is a result of a higher activity of the Δ-6 desaturase. Within this group, arachidonic acid (C20:4 $n-6$) shows the highest content in all tissues, while the $n-3$ metabolites are minor components. When a fat source rich in linolenic acid (i.e., linseed oil) was used, C20:5 $n-3$ could also be useful as a marker of this activity. In the fifth group we find the medium chain saturated fatty acids leading to the synthesis of palmitic acid (C10:0, C12:0 and C14:0), as well as palmitoleic acid (C16:1 $n-7$). Therefore, these FA can be markers of the competition of FA for the enzyme Δ-9 desaturase. Among them, we have selected palmitoleic acid, since it shows the highest levels in pork fat tissues, although C14:0 could also be a good marker. Finally, we have selected eicosatrienoic acid (C20:3 $n-3$), since it shows an ability to indicate a priority activity in the $n-3$ PUFA synthesis at the expense of the $n-6$ PUFA synthesis.

2.5. Statistical methods

Two-factor analysis of variance (ANOVA) was used for testing the significance of the diet and breed effects. F tests were used to test the overall significance, and Bonferroni tests for pair-wise comparisons. The analysis was carried out with the SPSS 11.0 statistical package (2001).

3. Results and discussion

3.1. General

No significant differences were observed for any of the productive parameters evaluated, with respect to the factor diet. In contrast, significant differences were observed related to the breed, but only for two parameters. So, mean values of *daily feed intake* were significantly lower for LW (1.72 kg feed/day) and D (1.58) than for L (1.88) and F1 (1.89), and values of *average daily gain* were also lower for LW (0.58 kg weight/day) and D (0.56) than for L (0.67) and F1 (0.67). However, *feed conversion ratio* did not show significant differences at the end of the experiment. No significant differences were observed for any of the carcass measurements. Similar results are described by other authors comparing different diets and breeds. So, Coutron-Gambotti, Gandemer, and Casabianca (1998) reported that, comparing a concentrated diet versus a chestnut diet (rich in oleic and linoleic acids), no differences were found in carcass fatness, live-weight or carcass weight at slaughter. However, significant differences were found when Corsican pigs were compared with Corsican × Large White pigs.

3.2. Effect of the breed on the fatty acid composition

3.2.1. General

Breed differences were, in relative terms, lower than those induced by the diet. Differences in linoleic acid content between breeds changed from tissue to tissue (Table 3), being significant only in *muscle LTL* ($p = 0.019$), while the diet–breed interaction effect was not significant. Palmitic acid levels showed significant differences only in abdominal fat (Table 4), although they were quite small in relative terms. The interaction effect was not significant, so the diet effect was quite similar in the four breeds for palmitic acid levels. As opposed to linoleic and palmitic acids, the breed effect was significant in all tissues for oleic acid (Table 5), although it was higher in adipose ($p < 0.003$) than in muscle tissues (*muscle LTL* $p = 0.022$ and *trapezius* $p = 0.012$). Except in the *muscle LTL*, Landrace pigs always had the highest and Large White the lowest levels of oleic acid. The interaction effect was not significant, so diet effects on oleic acid content were similar for all breeds. The greater differences, with respect to the breed, were found for arachidonic acid whose levels showed very significant differences in muscle tissues and abdominal fat ($p < 0.001$), while they were less significant in backfat ($p = 0.031$). Landrace pig tissues always showed the highest arachidonic acid levels (Table 6). In addition, the interaction effect of breed and diet was significant for arachidonic acid only in fat tissues, where the diet effect was not uniform across breeds. Finally, there was also a

Table 3
Linoleic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	11.7	15.0	17.9	20.5	16.3
Duroc	10.3	12.1	16.5	21.7	15.1
F1	10.5	15.6	17.3	20.8	16.1
Landrace	11.9	14.9	20.7	20.8	17.1
Mean	11.1[a]	14.4[b]	18.1[c]	20.9[d]	16.1
Backfat					
Large White	11.2	14.0	14.6	20.4	15.0
Duroc	9.91	13.3	19.6	22.6	16.4
F1	9.28	14.2	16.1	21.7	15.3
Landrace	10.8	12.2	17.1	19.1	14.8
Mean	10.3[a]	13.4[b]	16.8[c]	21.0[d]	15.4
Longissimus thoracis et lumborum					
Large White	9.87	11.1	13.7	16.9	12.9[a]
Duroc	6.99	10.2	12.9	17.3	11.9[a]
F1	7.49	10.7	13.6	18.5	12.6[a]
Landrace	9.91	13.5	15.1	19.6	14.5[b]
Mean	8.57[a]	11.4[b]	13.4[c]	18.1[d]	13.0
Trapezius					
Large White	8.07	12.9	14.9	19.3	13.8
Duroc	7.71	9.04	15.4	19.2	12.8
F1	7.86	10.9	15.9	19.7	13.6
Landrace	8.47	11.2	15.0	19.9	13.6
Mean	8.03[a]	11.0[b]	15.3[c]	19.5[d]	13.5

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

Table 4
Palmitic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	26.2	24.0	23.3	20.9	23.6[b]
Duroc	26.8	26.0	23.6	20.9	24.3[b]
F1	25.9	24.1	23.4	20.9	23.5[b]
Landrace	24.8	23.0	20.2	20.6	22.2[a]
Mean	25.9[d]	24.3[c]	22.6[b]	20.8[a]	23.4
Backfat					
Large White	24.4	22.6	23.4	19.6	22.5
Duroc	25.5	23.3	21.5	19.1	22.4
F1	24.5	23.0	22.3	20.1	22.4
Landrace	24.1	22.7	20.7	19.5	21.7
Mean	24.6[c]	22.9[b]	21.9[b]	19.6[a]	22.3
Longissimus thoracis et lumborum					
Large White	24.3	23.3	22.9	21.3	22.9
Duroc	24.3	23.4	23.3	20.3	22.8
F1	24.2	23.5	22.6	20.7	22.8
Landrace	24.0	21.8	21.3	20.8	22.0
Mean	24.2[c]	23.0[b]	22.5[b]	20.8[a]	22.6
Trapezius					
Large White	24.6	22.4	22.5	19.8	22.3
Duroc	24.0	23.9	22.4	20.1	22.6
F1	23.5	23.2	21.4	19.9	22
Landrace	23.5	22.1	20.2	19.4	21.3
Mean	23.9[d]	22.9[c]	21.6[b]	19.8[a]	22.0

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

very significant breed effect on the palmitoleic acid level ($p < 0.01$) in all tissues, except in *trapezius* muscle where it was less significant ($p = 0.044$), while the interaction effect was not significant for this FA. For palmitoleic acid, the higher levels were found in muscle tissues and in the Duroc breed (Table 7). Eicosatrienoic acid levels showed significant differences only in backfat related to the breed. The most relevant characteristics of each breed, related to the modification of the FA composition according to a linoleic acid-rich diet, can be further categorised.

3.2.2. Large White

Results corresponding to this breed show a good ability to change their FA composition in different tissues, according to increasing % on intake of this FA. But LW pigs showed very small differences with respect to the other three breeds. Palmitic, palmitoleic and oleic acid levels showed no relevant differences. Only arachidonic acid levels showed small differences, which can be summarised in a significant lower level in backfat with respect to the other three breeds, and in abdominal fat with respect to LD and F1.

3.2.3. F1 crossbreed

No relevant linoleic acid differences were observed for F1 pigs, while some interesting differences were noted for arachidonic acid. So, significantly higher levels were observed in adipose tissues with respect to the other three breeds, while significantly lower levels in muscle tissues

Table 5
Oleic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	34.2	34.2	32.9	33.4	33.7[a]
Duroc	35.7	33.9	35.2	33.5	34.6[a]
F1	36.4	34.1	33.9	34.5	34.7[a]
Landrace	38.6	37.4	35.7	35.1	36.7[b]
Mean	36.2	34.9	34.4	34.1	34.9
Backfat					
Large White	37.7	37.2	37.2	36.3	37.1[a]
Duroc	38.7	38.5	36.6	35.8	37.4[a]
F1	41.0	37.7	36.8	34.8	37.6[a]
Landrace	39.6	40.1	38.7	39.4	39.4[b]
Mean	39.2[c]	38.4b[c]	37.3[ab]	36.6[a]	37.9
Longissimus thoracis et lumborum					
Large White	38.3	38.3	36.6	35.8	37.2[ab]
Duroc	41.9	39.4	37.6	38.1	39.3[c]
F1	41.8	39.4	37.8	35.4	38.6[bc]
Landrace	39.1	37.6	37.5	33.7	37.0[a]
Mean	40.3[c]	38.7[b]	37.4[b]	35.8[a]	38.0
Trapezius					
Large White	38.8	37.2	36.2	35.8	37.0[a]
Duroc	41.5	39.9	36.6	35.7	38.4[ab]
F1	42.5	39.2	37.1	35.1	38.5[ab]
Landrace	41.3	40.2	39.7	36.1	39.3[b]
Mean	41.0[d]	39.1[c]	37.4[b]	35.7[a]	38.3

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

Table 6
Arachidonic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	0.22	0.23	0.29	0.37	0.28[a]
Duroc	0.18	0.21	0.3	0.39	0.27[a]
F1	0.2	0.3	0.28	0.43	0.30[b]
Landrace	0.25	0.3	0.39	0.38	0.33[c]
Mean	0.21[a]	0.26[b]	0.32[c]	0.39[d]	0.29
Backfat					
Large White	0.19	0.23	0.25	0.31	0.24[a]
Duroc	0.18	0.22	0.35	0.38	0.28[b]
F1	0.18	0.26	0.26	0.44	0.29[b]
Landrace	0.22	0.24	0.32	0.35	0.28[b]
Mean	0.19[a]	0.24[b]	0.29[c]	0.37[d]	0.27
Longissimus thoracis et lumborum					
Large White	1.32	1.42	1.21	1.7	1.41[a]
Duroc	0.69	0.84	1.22	1.31	1.02[a]
F1	0.98	1.17	1.07	1.4	1.15[a]
Landrace	1.51	2.15	1.75	2.7	2.03[b]
Mean	1.12[a]	1.39[ab]	1.31[a]	1.78[b]	1.4
Trapezius					
Large White	0.54	0.98	0.9	1.04	0.86[a]
Duroc	0.61	0.6	0.75	1	0.74[a]
F1	0.57	0.95	0.78	1.02	0.83[a]
Landrace	1.07	1.18	1.33	1.04	1.15[b]
Mean	0.69[a]	0.92[b]	0.94[b]	1.03[b]	0.9

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

Table 7
Palmitoleic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	2.09	1.7	1.68	1.49	1.76[a]
Duroc	2.31	2.14	2.3	1.83	2.15[c]
F1	1.93	1.78	1.7	1.9	1.82[ab]
Landrace	2.36	2.11	1.83	1.71	2.00[bc]
Mean	2.17[b]	1.93[a]	1.88[a]	1.73[a]	1.93
Backfat					
Large White	2.04	1.71	1.91	1.48	1.79[a]
Duroc	2.21	2.32	2.29	1.72	2.15[b]
F1	2.04	1.87	1.67	1.79	1.84[a]
Landrace	1.97	2	1.76	1.87	1.90[a]
Mean	2.07[b]	1.97[b]	1.91[ab]	1.73[a]	1.92
Longissimus thoracis et lumborum					
Large White	2.52	2.36	2.51	2.18	2.38[a]
Duroc	3.13	2.77	3.24	2.38	2.88[b]
F1	2.89	2.28	2.31	2.09	2.48[a]
Landrace	2.67	2.36	2.29	2.48	2.45[a]
Mean	2.79[b]	2.54[b]	2.58[ab]	2.28[a]	2.55
Trapezius					
Large White	2.32	1.94	2.15	1.89	2.08
Duroc	2.61	2.57	2.43	1.91	2.38
F1	2.39	2.2	1.9	1.78	2.07
Landrace	2.45	2.16	2.07	1.91	2.15
Mean	2.44[c]	2.22[bc]	2.14[b]	1.87[a]	2.17

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

were only found with respect to LD pigs. This differences suggest a clear different activation pattern of the Δ-6 desaturase, depending on the type of tissue. More complex is the analysis of the differences for palmitoleic and oleic acids, but in general there is not a particular pattern for F1 pigs.

3.2.4. Landrace

Pigs of this breed only showed linoleic acid differences in the loin (*muscle LTL*), where the levels of these FA are significantly higher than those of the other three breeds ($p = 0{,}019$). Also, Landrace pigs showed arachidonic acid levels much higher in muscle tissues than LW, D and F1 pigs, while differences in adipose tissues were minimum or zero with respect to the other breeds. In contrast, levels of the other FA markers were scarcely different with respect to the other breeds. So, palmitic acid showed only significantly lower levels for Landrace pigs in the abdominal fat, but not in the other three tissues. Moreover, oleic acid levels, corresponding to Landrace pigs, were similar to those of LW in *muscle LTL*, and similar to those of D and F1 in *trapezius*. Palmitoleic acid levels in Landrace were only significantly higher than those of LW in abdominal fat, and significantly lower than those of Duroc in backfat and *muscle LTL*.

3.2.5. Duroc

In contrast to the results corresponding to the other three breeds, the FA profile of Duroc pigs seemed to be the least affected by the fat content of the diet. This breed showed only particular differences for oleic acid levels in loin, which were significantly higher levels than in LW and LD pigs, but similar to F1 pigs. Duroc pigs also showed significantly higher levels of palmitoleic acid in backfat and loin, with respect to the other breeds. These differences suggest a lower inhibition of the Δ-9 desaturase in Duroc, with respect to the other breeds, when linoleic-rich fat was added to the feed.

Our results agree with those reported by some authors, who also observed that D pigs showed a lower capacity to deposit linoleic acid when increasing amounts of polyunsaturated fats were added to the feed (Wood et al., 1996). Most of the works dealing with breed differences in pork FA composition show that D carcasses are less polyunsaturated than those of L (Cameron & Enser, 1991), those of Landrace crossbreeds (Honkavaara, 1989), and those of LW (Bout, Girard, Sellier, & Runavot, 1990). Only Cameron, Warris, Porter, and Enser (1990) found that L backfat was more polyunsaturated than D, at the expense of stearic acid levels. The fact that *muscle LTL* shows a lower linoleic acid accumulation rate than the corresponding backfat was also reported by some authors in D carcasses (Bout et al., 1990; Cameron et al., 1990). This could be explained by the results reported in a study (van Laack & Spencer, 1999), showing that D pigs have lower PUFA deposits in the muscle phospholipid fraction than other breeds fed identical diets. However, all of this effects cannot be taken as a whole, since the type of experimental diet can change some patterns of increase or decrease of certain FA. So, we now consider the influence of the factor diet (% increase of the linoleic acid supply) on the FA composition in muscle and adipose tissues, focusing on the FA markers selected.

3.3. Effect of the diet on the fatty acid composition

3.3.1. General

The results for fatty acid composition in the four tissues are shown in Tables 3–8. FA content is expressed as mean values. We do not report the usual measures of dispersion, which have been used in testing the significance of the diet and breed effects, in order to simplify the Tables. As a global conclusion, the diet effect can be seen as a shift toward the FA of the dietary supply. The increase in the levels of this group (represented by linoleic acid in this paper) and in the levels of those FA metabolised from them, represented here by arachidonic acid, must be compensated mainly by a decrease in palmitic, stearic and oleic acids. However, these differences seem to be tissue-dependent. Therefore, palmitic and stearic levels significantly decreased in all tissues when linoleic acid levels increased, but oleic acid levels showed only a clear decrease in muscle tissues, a slight decrease in backfat, and no significant differences in abdominal fat. The most notable pattern of deposit corresponded to arachidonic acid (Table 6), indicating a higher dietary linoleic effect on the Δ-6 desaturase activity in fat tissues than in muscle tissues, although levels were much higher in muscle than in adipose tissues.

Table 8
Eicosatrienoic acid contents, expressed as compensated area normalization (%) (means of three animals)

	Diet 1	Diet 2	Diet 3	Diet 4	Mean
Abdominal fat					
Large White	0.12	0.13	0.14	0.13	0.13
Duroc	0.12	0.12	0.13	0.12	0.12
F1	0.11	0.13	0.13	0.10	0.12
Landrace	0.11	0.11	0.14	0.11	0.12
Mean	0.12[a]	0.12[ab]	0.14[b]	0.12[a]	0.12
Backfat					
Large White	0.14	0.15	0.14	0.15	0.14[bc]
Duroc	0.13	0.15	0.17	0.15	0.15[c]
F1	0.11	0.13	0.16	0.12	0.13[ab]
Landrace	0.12	0.11	0.14	0.13	0.13[a]
Mean	0.13[a]	0.14[ab]	0.15[b]	0.13[a]	0.14
Longissimus thoracis et lumborum					
Large White	0.11	0.11	0.12	0.10	0.11
Duroc	0.09	0.10	0.11	0.11	0.10
F1	0.08	0.10	0.12	0.10	0.10
Landrace	0.08	0.09	0.11	0.11	0.10
Mean	0.09	0.10	0.11	0.10	0.10
Trapezius					
Large White	0.11	0.14	0.15	0.14	0.13
Duroc	0.10	0.11	0.15	0.13	0.12
F1	0.09	0.11	0.15	0.12	0.12
Landrace	0.10	0.09	0.12	0.14	0.11
Mean	0.10[a]	0.11[a]	0.14[b]	0.13[b]	0.12

[a–d] Mean values with different letters are significantly different ($p < 0.05$).

3.3.2. Linoleic acid content

A large positive diet effect was evident (about a 100% increase in relative terms) for linoleic acid in the four tissues ($p < 0.001$). All the pair-wise comparisons between diets gave significant differences (Table 3). The linoleic acid levels were higher in fat than in muscle tissues, but the rate of increase from diet to diet was similar in both types of tissue. These effects can be extrapolated to a group of FA having a high correlation with linoleic acid in the four tissues, which are C15:0 (minimum correlation 0.760 in *muscle LTL*, and maximum 0.934 in *trapezius*), C16:1 $n-9$ (min. 0.756 in *muscle LTL*, and max. 0.809 in backfat), C18:1 $n-9$ *trans* (min. 0.874 in *muscle LTL*, and max. 0.942 in *trapezius*), C18:2 $n-6$ *trans* (min. 0.819 in abdominal fat, and max. 0.921 in *trapezius*), C18:3 $n-3$ (min. 0.640 in *muscle LTL*, and max. 0.838 in backfat), C18:3 $n-6$ (min. 0.786 in *muscle LTL*, and max. 0.936 in *trapezius*) and C20:2 $n-6$ (min. 0.820 in *muscle LTL*, and max. 0.927 in *trapezius*). Our results, showing linoleic acid as a good marker of the influence of the dietary fat agree with those found in other studies (Irie & Sakimoto, 1992; Morgan, Noble, Cocchi, & McCartney, 1992; Wiseman, Redshaw, Jagger, Nute, & Wood, 2000), with diets rich in linoleic, linolenic, and long chain PUFA (EPA and DHA, in fish oil diets). In all cases, a high positive correlation existed between levels in the diet and levels in fat and muscle tissues for these FA, usually at the expense of palmitic and oleic levels in these tissues. In contrast, some authors (Cava et al., 1997; Coutron-Gambotti et al., 1998) found, in Iberian pigs and Corsican pigs respectively, that "montanera" diets (based on acorns) and chestnut diets, both rich in oleic acid, led to higher linoleic deposits in intramuscular fats than other diets containing more linoleic acid. These authors propose that rustic breeds may possess a different lipid metabolism, from commercial breeds which are genetically more fatty.

3.3.3. Palmitic acid content

In contrast, the diet effect for palmitic acid was negative (about a 25% of decrease in relative terms, between diet 1 and 4), but weaker than the positive effect for linoleic acid,. The overall significance level was less than 0.001 in all tissues, but the diet effect was slightly stronger in the adipose than in the muscle tissue (Table 4). However, only in abdominal fat and muscle *trapezius* were the differences significant for the four tissues. In contrast, in backfat and *muscle LTL*, diets 2 and 3 gave no differences in palmitic acid levels. The majority of remarks made for palmitic also apply to stearic acid, since their levels were well correlated in all tissues (0.70–0.75). Other studies, which yielded similar conclusions for linoleic and linolenic acids, did not find significant decreases in palmitic acid (Averette Gatlin et al., 2002; Cherian & Sim, 1995; Warnants, Van Oeckel, & Boucqué, 1999). However, the variety of experimental designs and dietary treatments tested in those studies should be taken into account, since they show the additional influence of other dietary factors. The level of energy of feed, the simultaneous presence of high linoleic and linolenic acid levels, and the length of the treatment were able to modify the rate of incorporation of linoleic, linolenic and palmitic acids into pig tissues.

3.3.4. Oleic acid content

The diet effect on oleic acid tissue content was also negative, showing a decrease between 2 and 5 points, which is stronger and more significant in muscle tissues ($p < 0.001$) than in backfat ($p = 0.008$), while for abdominal fat there was no significant differences (Table 5). An interesting effect is that oleic acid levels were higher in muscle than in adipose tissues when there was no fat added to the feed (diet 1), but this pattern was changed by the diet, so that the differences between the tissues were reduced when the amount of added dietary fat increased. In contrast, other studies, working with diets rich in PUFA, did not find significant decreases in oleic acid levels (Bee et al., 2002; Bryhni, Kjos, Ofstad, & Hunt, 2002; Enser, Richardson, Wood, Gill, & Sheard, 2000; Øverland, Taugbøl, Haug, & Sundstøl, 1996).

3.3.5. Arachidonic acid content

Arachidonic acid content in the four tissues increased as a function of the fat enrichment of the diets, more than 50% in relative terms (Table 6). But, whereas in adipose tissues the pattern of increase was the same as for the linoleic acid, an unclear fluctuating pattern appeared in muscle tissues, where the level of arachidonic acid was much higher.

The overall significance level for the diet effect was $p < 0.001$ in fat tissues and around $p = 0.03$ in muscle tissues. Except for muscle tissues, due to the fluctuations mentioned above, all the pair-wise comparisons among diets showed significant differences. In *muscle LTL*, only diet 4 showed significantly higher values of arachidonic acid whereas, in *trapezius*, only diet 1 showed significantly lower values. These effects can be extrapolated, at least, to C22:5 $n-3$, since the correlation between its levels and those of arachidonic acid range from 0.59 in abdominal fat to 0.86 in *muscle LTL*. Table 6 shows very clear differences in arachidonic acid content in the four tissues and the pattern of variation of the arachidonic acid deposit between the different muscles was clearly related to the linoleic acid deposit, although the correlation was stronger in adipose tissues than in muscle (Table 9). Similar, but negative, correlations were also found between arachidonic and palmitic acids. This suggests that the Δ-6 desaturase in pigs was more activated in adipose than in muscle tissues by the increasing addition of a polyunsaturated fat in the diet. Different authors (Ahn et al., 1996; Eder et al., 2001; Scheeder et al., 2000) observed that diets with a high content of linoleic acid lead to a high linoleic deposit in the loin (*muscle LTL*), but not to significant increases in arachidonic acid. Only one study (Wood et al., 1986) reported a slight but significant increase. More data is available on the parallel increase of linoleic and arachidonic acids in fat tissues when linoleic acid increases in the diet (D'Arrigo et al., 2002; Warnants et al., 1999). Other authors (Bout et al., 1990; Enser et al., 2000; Fontanillas et al., 1997; Leskanich, Matthews, Warkup, Noble, & Hazzledine, 1997), giving dietary fats rich in linolenic acid, observed that C20:5 and C22:6 levels in pig fat and muscle tissues were good markers of the activity of Δ-6 desaturase, instead of arachidonic acid, although the rate of increase was clearly higher for C20:5 than for C22:6.

Table 9
Correlation matrix between the levels of the selected fatty acid markers, in the four tissues (from left to right and from top to bottom: abdominal fat, backfat, *longissimus thoracis et lumborum*, and *trapezius*)

Linoleic		Palmitic		Oleic		Arachidonic	
Palmitic							
−0.864	−0.876						
−0.867	−0.858						
Oleic							
−0.316	−0.617	−0.156	0.230				
−0.789	−0.793	0.429	0.411				
Arachidonic							
0.891	0.883	−0.893	−0.819	−0.039	−0.467		
0.497	0.365	−0.409	−0.455	−0.614	−0.221		
Palmitoleic							
−0.416	−0.239	0.420	0.414	0.317	0.135	−0.296	−0.172
−0.518	−0.567	0.607	0.743	0.338	0.281	−0.171	−0.125

3.3.6. Palmitoleic acid content

An overall negative diet effect for palmitoleic acid was clear ($p < 0.02$), in spite of the fluctuations observed when comparing different tissues. The overall significance level was below 0.05 for all tissues, but pair wise comparisons (Table 7) revealed different patterns among the four tissues. So, significant differences were observed only between diet 1 and diet 4 in backfat and *muscle LTL*, whereas in abdominal fat diets 2, 3 and 4 showed no differences, and in trapezius there were differences only between diets 1 and 3, and between diet 4 and the other three. These conclusion on palmitoleic acid could be extrapolated to another FA, since we found a good correlation between palmitoleic acid and C18:1 $n-7$ (around 0.8) and C14:0 (around 0.6), and lower, but worth mentioning, with C10:0 and C12:0 (around 0.5).

3.3.7. Eicosatrienoic acid content

As regards eicosatrienoic acid levels, only the *trapezius* muscle showed a certain pattern of accumulation, dependent on the dietary treatment (Table 8). This could suggest that competition for Δ-6 desaturase favours the synthesis of $n-3$ PUFA at the expense of $n-6$ PUFA, mainly in this tissue. Eicosatrienoic acid is the marker that shows less significant differences, which is easy to understand since the fat added to the diet was poor in linolenic acid. However, our results agree with those obtained by other authors (D'Arrigo et al., 2002; Fontanillas et al., 1997), who found a large increase in linolenic acid and total $n-3$ PUFA in the backfat of pigs fed linseed oil, as opposed to pigs fed olive or sunflower oils. But they also observed that C20:3 $n-3$ showed a higher rate of increase than the other $n-3$ PUFA (EPA and DHA). This confirms that this FA could be the best marker to indicate a synthesis favouring $n-3$ PUFA at the expense of $n-6$ PUFA.

3.3.8. Correlation matrix between FA markers

Finally, interesting changes between selected FA across tissues need to be considered. Table 9 shows the 4-fold correlation matrix for the FA selected as markers (except eicosatrienoic acid). The main points are: (a) the negative correlation between linoleic and palmitic acids in terms of the opposition between the dietary supply and the de novo synthesis, and (b) the differences between fat and muscle tissues, in the accumulation patterns of oleic and arachidonic acids. Oleic acid and arachidonic acid correlations with the pair linoleic/palmitic changed from adipose to muscle tissues. The pattern is clear for arachidonic acid levels, which showed positive correlation with linoleic acid levels and negative correlation with palmitic acid levels, the correlation being stronger for adipose than for muscle tissues. In contrast, the oleic acid levels were negatively correlated with linoleic acid levels in all tissues, the correlation being weaker in adipose tissues (particularly in abdominal fat). However, the correlation between oleic acid and palmitic acid levels is controversial. Our results suggest that there is a weak positive correlation in muscle, but no correlation in adipose tissues. This can be due to the fact that oleic acid supply

increased a lot from diet 1 to 4 (Table 1), compared to the increase of palmitic acid supply. So, levels of palmitic acid would be more dependent on the activity of the de novo synthesis, whereas oleic acid levels would also be dependent on the diet. Finally, the correlation between palmitoleic and palmitic acids was higher in muscle than in adipose tissues. This could be attributed to a preferential activity of the Δ-9 desaturase in muscle tissues for palmitoleic synthesis, at the expense of oleic synthesis.

Acknowledgement

This work was supported by research grants from the *Comissió Interdepartamental de Recerca i Innovació Tecnològica* (CIRIT) and the *Comisión Interministerial de Ciencia y Tecnología* (CICYT). Salgot S.A. and Marta Roca de Viñals provided technical support.

References

Ahn, D. U., Lutz, S., & Sim, J. S. (1996). Effects of dietary α-linolenic acid on the fatty acid composition, storage stability and sensory characteristics of pork loin. *Meat Science, 43*, 291–299.

Allee, G. L., Baker, D. H., & Leveille, G. A. (1971). Influence of level of dietary fat on adipose tissue lipogenesis and enzymatic activity in the pig. *Journal of Animal Science, 33*, 1248–1254.

Averette Gatlin, L., See, M. T., Hansen, J. A., Sutton, D., & Odle, J. (2002). The effects of dietary fat sources, levels, and feeding intervals on pork fatty acid composition. *Journal of Animal Science, 80*, 1606–1615.

Bee, G., Geert, S., & Messikommer, R. (2002). Effect of dietary energy supply and fat source on the fatty acid pattern of adipose tissues and lipogenesis in the pig. *Journal of Animal Science, 80*, 1564–1574.

Bout, J., Girard, J. P., Sellier, P., & Runavot, J. P. (1990). Comparaison de porcs Duroc et Large White pour la composition chimique du gras de bardière et du muscle long dorsal. *Journées de la Recherche Porcine en France, 22*, 29–34.

Bryhni, E. A., Kjos, N. P., Ofstad, R., & Hunt, M. (2002). Polyunsaturated fat and fish oil in diets for growing-finishing pigs: Effects on fatty acid composition and meat, fat, and sausage quality. *Meat Science, 62*, 1–8.

Cameron, N. D., & Enser, M. B. (1991). Fatty acid composition of lipid in Longissimus dorsi muscle of Duroc and British Landrace pigs and its relationship with eating quality. *Meat Science, 29*, 295–307.

Cameron, N. D., Warris, P. D., Porter, S. J., & Enser, M. B. (1990). Comparison of Duroc and British Landrace pigs for meat and eating quality. *Meat Science, 27*, 227–247.

Cava, R., Ruiz, J., López-Bote, C., Martín, L., García, C., Ventanas, J., et al. (1997). Influence of finishing diet on fatty acid profiles of intramuscular lipids, triglycerides and phospholipids in muscles of the Iberian pig. *Meat Science, 45*, 263–270.

Cherian, G., & Sim, J. S. (1995). Dietary α-linolenic acid alters the fatty acid composition of lipid classes in swine tissues. *Journal of Agricultural and Food Chemistry, 43*, 2911–2916.

Coutron-Gambotti, C., Gandemer, G., & Casabianca, F. (1998). Effects of substituting a concentrated diet for chestnuts on the lipid traits of muscle and adipose tissues in Corsican and Corsican × Large White pigs reared in a sylvo-pastoral system in Corsica. *Meat Science, 50*, 163–174.

D'Arrigo, M., Hoz, L., López-Bote, C. J., Cambero, I., Pin, C., Rey, A. I., et al. (2002). Effect of dietary linseed oil and α-tocopherol on selected properties of pig fat. *Canadian Journal of Animal Science, 82*, 339–346.

Eder, K., Nonn, H., & Kluge, H. (2001). The fatty acid composition of lipids from muscle and adipose tissues of pigs fed various oil mixtures differing in their ratio between oleic acid and linoleic acid. *European Journal of Lipid Science and Technology, 103*, 668–676.

Enser, M. (1984). The relationship between the composition and consistency of pig backfat. In: *Fat quality in lean pigs* (pp. 53–57). Meat Research Institute, Special Report No. 2. Brussels: Commission of EC.

Enser, M., Richardson, R. I., Wood, J. D., Gill, B. P., & Sheard, P. R. (2000). Feeding linseed to increase the $n-3$ PUFA of pork: Fatty acid composition of muscle, adipose tissue, liver and sausages. *Meat Science, 55*, 201–212.

Folch, J., Lees, M., & Stanley, G. H. S. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry, 226*, 497–509.

Fontanillas, R., Barroeta, A., Baucells, M. D., & Codony, R. (1997). Effect of feeding highly *cis*-monounsaturated, *trans* or $n-3$ fats on lipid composition of muscle and adipose tissue of pigs. *Journal of Agricultural and Food Chemistry, 45*, 3070–3075.

Guardiola, F., Codony, R., Rafecas, M., Boatella, J., & López, A. (1994). Fatty acid composition and nutritional value of fresh eggs, from large- and small-scale farms. *Journal of Food Composition and Analysis, 7*, 171–178.

Henry, Y. (1977). Development morphologique et metabolique du tissue adipeux chez le porc: influence de la selection, de la alimentation et du mode d'elevage. *Annales de Biologie Animale Biochimie Biophysique, 17*, 923–952.

Honkavaara, M. (1989). Influence of porcine stress and breed on the fatty acid profiles of subcutaneous and intramuscular total lipids. *Fleischwirtsch, 69*, 1429–1432.

Irie, M., & Sakimoto, M. (1992). Fat characteristics of pigs fed fish oil containing eicosapentaenoic and docosahexaenoic acids. *Journal of Animal Science, 70*, 470–477.

Katan, M. B., Zock, P. L., & Mensink, R. P. (1994). Effects of fats and fatty acids on blood lipids in humans: an overview. *American Journal of Clinical Nutrition, 60*, 1017S–1022S.

Klingenberg, I. L., Knabe, D. A., & Smith, S. B. (1995). Lipid metabolism in pigs fed beef tallow or high oleic sunflower oil. *Comparative Biochemistry and Physiology., 110*, 183–192.

Kouba, M., Enser, M., Whittington, F. M., Nute, G. R., & Wood, J. D. (2003). Effect of a high linoleic acid diet on lipogenic enzyme activities, fatty acid composition, and meat quality in the growing pig. *Journal of Animal Science, 81*, 1967–1979.

Leskanich, C. O., Matthews, K. R., Warkup, C. C., Noble, R. C., & Hazzledine, M. (1997). The effect of dietary oil containing ($n-3$) fatty acids on the fatty acid, physicochemical, and organoleptic characteristics of pig meat and fat. *Journal of Animal Science, 75*, 673–683.

Lizardo, R., van Milgen, J., Mourot, J., Noblet, J., & Bonneau, M. (2002). A nutritional model of fatty acid composition in the growing-finishing pig. *Livestock Production Science, 75*, 167–182.

Morgan, C. A., Noble, R. C., Cocchi, M., & McCartney, R. (1992). Manipulation of the fatty acid composition of pig meat lipids by dietary means. *Journal of the Science of Food and Agriculture, 58*, 357–368.

Mourot, J., Aumaitre, A., Mounier, A., Peiniau, P., & François, A. C. (1994). Nutritional and physiological effects of dietary glycerol in the growing pig: Consequences on adipose tissues and post mortem muscle parameters. *Livestock Production Science, 98*, 237–244.

Oliver, M. A., Gispert, M., Tibau, J., & Diestre, A. (1991). The measurement of light scattering and electrical conductivity for the prediction of PSE pig meat at various times post mortem. *Meat Science, 29*, 141–151.

Øverland, M., Taugbøl, O., Haug, A., & Sundstøl, E. (1996). Effect of fish oil on growth performance, carcass characteristics, sensory parameters, and fatty acid composition of pigs. *Acta Agriculturae Scandinavica Section A-Animal Science, 46*, 11–17.

Pascual, J. (2000) PhD thesis, University of Barcelona.

Scheeder, M. R. L., Gläser, K. R., Eichenberger, B., & Wenk, C. (2000). Influence of different fats in pig feed on fatty acid composition of

phospholipids and physical meat quality. *European Journal of Lipid Science and Technology, 102*, 391–401.

SPSS 11.0 (2001). Chicago, IL, USA.

Laack, R. L. J. M., & Spencer, E. (1999). van Influence of swine genotype on fatty acid composition of phospholipids in longissimus muscle. *Journal of Animal Science, 77*, 1742–1745.

Warnants, N., Van Oeckel, M. J., & Boucqué, C. V. (1999). Incorporation of dietary polyunsaturated fatty acids into pork fatty tissues. *Journal of Animal Science, 77*, 2478–2490.

Wiseman, J., Redshaw, M. S., Jagger, S., Nute, G. R., & Wood, J. D. (2000). Influence of type and dietary rate of inclusion of oil on meat quality of finishing pigs. *Animal Science, 70*, 307–315.

Wood, J. D., Brown, S. N., Nute, G. R., Whittington, F. M., Perry, A. M., Johnson, S. P., et al. (1996). Effects of breed, feed level and conditioning time on the tenderness of pork. *Meat Science, 44*, 105–112.

Wood, J. D., Buxton, P. S., Whittington, F. M, & Enser, M. (1986). The chemical composition of fat tissues in the pig: effect of castration and feeding treatment. *Livestock Production Science, 15*, 73–82.