Combining pig genetic and feeding strategies improves the sensory, nutritional and technological quality of pork in the context of relocation of feed resources

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Abstract

Genetic and feeding factors were combined to improve various quality attributes of pork. Thirty Duroc (D) and thirty Pietrain NN (P) female crossbreeds received a control (C) or an R diet including extruded faba bean and linseed, from 30 to 115 kg. Growth, feed efficiency and slaughter weight were higher for P vs. D pigs and for R vs. C pigs. D pigs had fatter carcasses than P, whereas feeding did not affect carcass fatness. Compared with P, loin meat from D pigs had lower drip, higher ultimate pH and lipid content, and higher marbling, tenderness and juiciness scores ($P < 0.05$). R feeding did not modify sensory traits but improved pork nutritional value by markedly reducing n-6:n-3 and saturated:n-3 fatty acid ratios ($P < 0.001$). Combining D genotype and R diet is a favorable strategy for sensory, nutritional, technological properties and societal image of pork through relocation of feed resources, but requires a better market valorization to be implemented.

Highlights

- Pork sensory and technological traits are higher in Duroc than Pietrain crossbreeds
- Dietary faba bean and linseed improves growth traits and pork nutritional value
- Faba bean and linseed diet participates to relocation of feed resources in Europe
- Combining genetics and feeding factors improves intrinsic quality and image of pork

Keywords: genotype; faba bean; linseed; carcass composition; carcass value; meat quality

1. Introduction

Pork is the first meat consumed in Asia and Europe and the second meat consumed worldwide (OECD, 2022). Over the last two decades, pork consumption per capita has been declining slightly but continuously in some EU countries like France (-10% since 2000; IFIP, 2021). At the same time, there has been a large increase in the volumes of fresh pork and pork products sold in France with official quality labels or trademarks, highlighting the consumer demand for high quality products (IFIP, 2021). Quality of pork and pork products covers a wide range of properties. A recent work proposed to define quality by a set of various attributes. They included carcass commercial value and meat organoleptic, nutritional and technological properties (i.e. suitability for processing and storage), that all correspond to the 'intrinsic' quality of meat. Quality attributes also included convenience, and societal image which corresponds to the product's extrinsic cues, encompassing the credibility, ethical, cultural and environmental dimensions related to the way food is produced, and its geographical origin (Lebret & Čandek-Potokar, 2022). The ranking of quality attributes varies according to the chain actor, e.g. the pork producer, slaughterhouse, processor, consumer, or citizen. To better fulfill a variety of pork quality demands, the French pork sector has declared a new segmentation of the pork market as priority. At the European level, as part of the EU Green Deal, the Commission supports the ''Farm to Fork Strategy for a fair, healthy and environmentally friendly food system" which includes the objective of reducing dependency on critical feed materials (e.g. soya grown on deforested land) by fostering EU-grown plant proteins (EC, 2020). More generally, pork quality attributes are required in several countries or world regions, even though there are differences in ranking (Murphy et al., 2015). In this context, proposing pork production strategies to simultaneously improve various quality attributes is of great interest to pork chain stakeholders, including consumers.

The effects of pig genotypes and feeding practices on intrinsic qualities of pork are relatively

well established, but the interactions between these factors are less documented (review by Lebret & Čandek-Potokar, 2022). Regarding genetics, the Duroc breed is favorable for sensory and technological quality in comparison with other selected breeds used in conventional production. Both purebred (Plastow et al., 2005; Ciobanu, Lonergan, & Huff-Lonergan, 2011) and crossbred (Edwards, Bates, & Osburn, 2003; Morales et al., 2013) Duroc pigs generally exhibit higher intramuscular fat (IMF) content, meat pH and water-holding capacity, while maintaining their growth performance. Regarding feeding, the adjustment of protein and energy intakes to pigs' nutritional requirements determines growth and body composition while limiting the excretion of components with environmental impacts (Andretta et al., 2014). Furthermore, the nature of dietary lipids strongly affects the fatty acid (FA) composition and nutritional value of pork (Wood et al., 2008; Huang, Chiba, & Bergen, 2021). Therefore, we hypothesized that combining genetic and feeding factors could jointly improve the sensory, nutritional and technological quality of pork, while the use of domestic protein resources improves the image attribute of pork by reducing feed material imports and reinforcing the link between pig rearing and land. We set up an experiment involving two pig genotypes: Duroc and Pietrain NN crossbreeds, and two feeding regimen: a diet including faba bean as a protein source and extruded linseed as source of n-3 FA, and a control diet based on soybean meal. The aim was to evaluate the effects of genotype, feeding and genotype x feeding interaction on growth performance, carcass composition and economic value, and technological, sensory and nutritional attributes of pork. The final goal was to provide a proof of concept that the combination of genetic and feeding factors is a relevant strategy to jointly improve various intrinsic and extrinsic quality attributes of pork.

2. Material and methods

The experiment was performed in the INRAE experimental facilities (UE3P, 35590 Saint-

Gilles, France doi.org/10.15454/1.5573932732039927E12) in compliance with EU directive 2010/63/EU for animal experiments and French legislation. The technical and scientific staffs had individual accreditation from the French Minister to experiment on living animals. The methods for animal experiment were approved by the local Committee on Ethics in animal experimentation and the present animal experimentation was authorized by the French Ministry of Higher Education, Research and Innovation (APAFiS #19388-2019022208529883-v2).

2.1 Animals, experimental design and feeding strategy

The experiment included 60 female crossbred pigs. Animals originated from Large White × Landrace sows (INRAE herd) inseminated with semen from either 3 Duroc boars (Genesus herd (22400 Lamballe, France) issued from males' herd selected by the breeding company for growth rate, feed intake and IMF content), or semen from 3 Pietrain NN boars (Nucleus herd (35650 Le Rheu, France), non-carriers of the hal mutation at the RYR1 gene and issued from males' herd selected by the breeding company for growth rate, feed efficiency and pork technological quality). The Duroc crossbred pigs (D, n=30) were issued from 7 litters and the Pietrain crossbred pigs (P, n=30) were issued from 9 litters. For each genotype, 15 pairs of female littermates were chosen few days before the end of post-weaning (approximately 31 kg of body weight, BW) on the basis of their BW and growth rate from birth, so that the average BW of these 30 female pigs was similar to those of all female pigs available for the experiment. These 15 pairs of littermates were distributed in two groups with similar average and SD of BW. They were allocated to one of two different feeding regimen: Relocation of feed resources (R) or control (C). Thus, the experiment was based on a 2 × 2 factorial design with 4 experimental groups (n=15 female pigs per group); DR, DC, PR and PC. All pigs were housed in individual pens (85 x 265 cm) on concrete floor with individual drinking bowl and

feeding. This allowed to implement precisely the feeding strategy according to the nutritional requirements of each pig and to measure their individual feed intake. Pigs were placed in the same room during the whole growing-finishing period, i.e. from 33. 7 + 2.0 kg BW until slaughter at around 115.0 kg BW.

DC and PC pigs received a control diet based on oilseed meal (imported soybean, rapeseed and shelled sunflower) as protein resources. DR and PR pigs received the R diet including extruded faba bean (French origin) as main protein resource and extruded linseed (Valorex, France) as source of n-3 poly-unsaturated fatty acids (PUFA) and contained 0.2% of antioxidants from plant origin (including vitamin E) to prevent PUFA oxidation. The high n-3 PUFA content of the R diet was in accordance with the specifications of the "Bleu Blanc Coeur" (BBC) trademark for high nutritional quality.

In each group, the nutritional intakes i.e. the digestible lysine (LysD)/net energy (NE) ratio were adjusted weekly to the pigs' requirements, so that growth of pigs was driven by protein supply in order to properly evaluate the different protein resources. Pig nutritional requirements were determined for each genotype as described previously (Furbeyre, Guillevic, Chesneau, & Labussière, 2020) and calculated according to the average per group of individual BW which was determined every two weeks. For the DC and PC pigs, and for the DR and PR pigs, the diet was prepared each week as a blend of two experimental C and R formulae, respectively, and containing either high or low protein and lysine levels. The respective amounts of the high and low protein formulae constitutive of the blend were calculated weekly per genotype to fit their average LysD/NE requirements according to their average BW and associated amino acid and energy requirements. The ingredients and chemical composition of the four experimental formulae are presented in Table 1. The LysD/NE ratio thus varied progressively along the growing-finishing period from 1 to 0.70 in the DC and DR groups, and from 0.95 to 0.68 in the PC and PR groups. All other amino acids

were given to meet or slightly exceed requirements. All pigs had free access to feed and water until the end of the experiment.

2.2 Growth performance

Pigs were weighed individually at the start of the experiment, every two weeks during the experiment (growing-finishing period), and the day before slaughter. Individual feed consumption was measured weekly (feed offered minus refusals) during the experimental period. Average daily feed intake, average daily gain and feed efficiency were calculated per pig over the experimental period.

2.3 Slaughter and carcass measurements

Pigs were slaughtered at the INRAE experimental slaughterhouse (35590 Saint-Gilles, France) on three different slaughtering days spread over 2 weeks, including the same number of pigs from each experimental group on each slaughtering day. All pigs were fasted for 24 hours before slaughter. The day before slaughter, pigs from the same experimental group (n = 6 from each group for the first and for the second slaughtering days, and n = 3 from each group for the third slaughtering day) were loaded onto the truck, transported together to the slaughterhouse (5 min) and kept in lairage in the same pen without mixing them with the other groups. All pigs had free access to water. The next day, pigs were taken alternately from each group and slaughtered by electrical head-stunning (320 V, 6 A, 10 s duration) followed by jugular exsanguination in compliance with the current national regulations applied in slaughterhouses.

Just after slaughter, the hot carcass (trimmed of digestive, reproductive, and respiratory tracts and of perirenal fat) was weighed. Carcass dressing was calculated as the ratio of hot carcass weight to final BW. Backfat (G2) and muscle (M2) depths were measured on one dorsal spot

between the third and fourth last ribs at 6 cm of the spinal canal axis, using the Lean Fat Sensor (CGM, Capteur Gras Maigre) device (Fives Syleps, Lorient, France). Carcass lean meat content was calculated using the G2 and M2 measurements according to the equation developed by Daumas, Causeur, & Predin (2010): Lean meat content (%) = 62.19 − 0.729 × G2 + 0.144 × M2. After 24 h of chilling at 4°C, the weight of the cold carcass and of wholesale cuts from the right carcass side (ham, loin, backfat, shoulder and belly) were recorded, and the proportion (relative percentage) of each carcass cut to the cold right carcass side was calculated.

2.4 Tissue sampling and measurements of meat quality traits in the slaughterhouse

Thirty minutes after slaughter, samples of *Longissimus thoracis et lumborum* muscle (LTL) were taken from the carcass's right side at the level of the first lumbar vertebra, cut into small pieces and immediately frozen in liquid nitrogen. Samples were stored at -76°C until determination of glycolytic potential, lipid oxidation, metabolic enzyme activities and pH at 30 min p.m. The latter was assessed with a pH meter equipped with a specific meat electrode (HI98163, Hanna Instruments, Smithfields, RI, USA) after homogenization of 2 g of muscle in 18 mL of 5 mM Na iodoacetate (Lebret, Batonon-Alavo, Perruchot, Mercier, & Gondret (2018).

Twenty-four hours after slaughter, on the right carcass side, pH was measured directly in the LTL (between 13^{th} and 14^{th} ribs) and in the ham muscles, namely *Semimembranosus* (SM), *Gluteus medius* (GM), *Gluteus superficialis* (GS) and *Adductor* (AD), using the same apparatus as above and with an automatic temperature compensation. The same day, a transversal section of LTL muscle (last and second to last ribs) was taken, trimmed of external fat, minced and homogenized. A sub-sample was freeze dried and powdered before determination of protein and water contents. The remaining part was vacuum packaged and

stored at -20°C before determination of IMF and FA contents. Another transversal section of LTL muscle (1.5 cm depth) was taken consecutively (cranial part) and bloomed for 15 min at 4°C under artificial light before measurement of color coordinates CIE *L**: lightness, *a**: redness, *b**: yellowness, *C**: saturation (chroma) and *h*°: hue (average values of 3 different determinations) using a chromameter Minolta CR 400 (Osaka, Japan) with a D65 illuminant, a 1-cm diameter aperture and a 2° observer angle. A third slice of LTL muscle (100 ± 10 g, consecutive to the previous one) was taken to determine drip loss at 4 days p.m. (plastic bag method; Lebret et al., 2018). Last, a piece of deboned loin (1.0 kg of LTL muscle) was taken consecutive to the previous samples and between the 5^{th} and 12^{th} dorsal vertebrae, vacuum packaged, kept at 4°C and shipped to the sensory laboratory (IDELE, Villers-Bocage, France).

On the right ham of each carcass, the day after slaughter, color coordinates were also measured at one site of the GM and GS muscles, as described above. A slice of SM was taken on surface of the muscle, trimmed of external fat, minced and homogenized. A sub-sample was freeze dried and powdered before determination of protein and water contents and the remaining part was vacuum-packed and stored at -20°C before determination of IMF content.

2.5 Muscle biochemical analyses

Protein (= 6.25 × nitrogen) and water contents were determined from freeze-dried LTL and SM samples as previously described (Lebret et al., 2018), and expressed as percentage of fresh muscle considering water loss of each muscle sample during freeze-drying. Lipid (IMF) content was determined on LTL and SM samples kept at -20°C by chloroform-methanol (2:1 v/v) extraction (Lefaucheur & Lebret, 2020). Fatty acid contents of LTL muscle lipids were determined after FA methylation with boron trifluoride methanol, as described by Lebret et al. (2021). Analyses were performed with a gas chromatograph (Agilent Technologies 7890A,

Santa Clara, CA, USA) equipped with an injector, a capillary column (30 m × 0.25 mm internal diameter) filled with a stationary phase containing 50% cyanopropylphenyl and 50% dimethylpolysiloxane (Agilent technologies) and a flame ionization detector (280°C). The carrier gas was hydrogen. The column temperature was increased from 150°C up to 220°C (+ 4°C/min) and reached a plateau after 10.5 min. Heptadecanoic acid (C17:0) was used as the internal standard. Retention times and peak areas were determined for all samples. The identities of the peaks were determined by comparing them to the retention times of standard FA methyl esters. The amount of each FA was calculated as a function of the internal standard (heptadecanoic acid, C17:0), and was expressed in mg per 100 g of muscle by considering the LTL lipid content.

Glycolytic potential, defined as GP = 2 * [(glycogen) + (glucose) + (glucose-6-phosphate)] + (lactate) and expressed as µmole equivalent lactate/g of fresh tissue, was determined in LTL muscle sampled 30 min p.m., as previously described (Lebret et al. 2018). On the same samples, activities of lactate dehydrogenase (LDH), citrate synthase (CS) and β-hydroxy-acyl-CoA dehydrogenase (HAD) were determined as markers of glycolytic metabolism, oxidative capacity (tricarboxylic acid cycle) and lipid β-oxidation potential, respectively, as detailed by Lefaucheur & Lebret (2020). Thiobarbituric acid reactive substances (TBARS) content was determined in the LTL muscle samples taken 30 min p.m., after forced chemical oxidation induced by iron trichloride and sodium ascorbate for 0, 60, 120, 180 and 240 min to assess lipid oxidative stability, as detailed by Lebret et al. (2018).

2.6 Sensory analyses and texture measurements of loin

The sensory analyses were undertaken by a panel of 13 selected, qualified and trained members for pork assessment (NF ISO 8586-1 and 8586-2) with the same 13 panelists all along the experiment. On the week before the first slaughtering, the 13 panelists participated

in two training sessions with commercial pork. Then, for the first and second slaughtering, loin samples were assessed over 3 sessions: 2 sessions taking place after 7 days of ageing and 1 session after 8 d of ageing in vacuum at 4°C. For the third slaughtering, loin samples were assessed over 2 sessions, after 7 d of ageing in vacuum at 4°C. Each session included 8 meat samples, i.e. 2 per experimental group, except the last session which included 4 meat samples (1 per experimental group), to reach a total of 60 samples tested.

At each session, on the 8 meat samples tested, a transversal slice of LTL muscle was taken at the level of the 10^{th} dorsal vertebrae for the assessment of raw meat. The remaining cranial part of this loin sample was cut into cubic pieces (25 $\pm$ 1 g) and cooked in an oven at 250°C during 5 min 30 s to reach a core temperature of 70°C (determined from previous tests). Samples were served one by one following a random distribution between the 4 experimental groups, with the 4 first and 4 last samples from each session representing the 4 experimental groups. Panelists assessed the appearance of raw meat (red color, marbling, homogeneity of marbling, odor) and the eating traits of cooked meat (odor, flavor, tenderness, juiciness) on a continuous scale from 0 (absence) to 10 (high intensity). The average of individual panelist scores for each sensory trait were calculated per pig and used for statistical analyses.

On the same day, a 200 g part of each of the LTL meat pieces (at the level of 11^{th} and 12^{th} dorsal vertebrae) was cut into two similar pieces of 100 g which were cooked in an oven (250°C up to a core temperature of 70°C) and cooled. Then, a 1 cm thick slice was removed from the 6 sides of each meat piece and core pieces were used to prepare 10 rectangular cut stripes of 1 cm^2 parallel to fiber axis per pig. Shear force was determined perpendicularly to muscle fibers with a Warner-Bratlzer cell fitted on a texturometer Instron 3343 (Norwood, MA, USA). The average of shear force measurements were calculated per pig and used for statistical analyses.

2.7 Economic indicators

Economic parameters were assessed by calculating the feed costs and revenues per pig, on the basis of the market situation at the time of the trial. The feed cost per pig was calculated considering their total intakes of high and low protein diets (either C or R) calculated from their weekly feed intake and the relative proportion of each diet in the distributed blend feed. Price per ton for the control diets (i.e. global context and prices) were 245 € and 202 € for high and low protein diets, respectively. Price per ton for the R diets (no GMO soybean meal and sunflower from French origin) were 280 € and 205 € for high and low protein diets, respectively. Feed cost per kg of cold carcass weight was also calculated.

The output price per kilogram of cold carcass was calculated as the average reference price over the month all experimental pigs were slaughtered (1.69 €) plus premiums and discounts based on carcass weight and lean meat content, according to the payment scale of the French pig market. Moreover, according to the practices of the BBC chain actors, a premium of 4 cts/kg was added for the R pigs which all fit the BBC specifications for high nutritional quality. Output price per pig was calculated as output price per kilogram × cold carcass weight of the pig. The added value was calculated as output price minus feed cost, and expressed per pig and per kg of cold carcass.

2.8 Statistics

Statistical Analysis System software (version 9.4; SAS Institute, Cary, NC, USA) was used to analyze the data. The pig was considered as the statistical unit for all traits. First, data were analyzed by an analysis of variance (ANOVA, proc GLM) with the genotype and feeding regimen as fixed effects to calculate residues. The normality of residues was checked (Kolmogorov-Smirnov, $P \geq 0.05$). When necessary, data were log-transformed and tested again to assess the normality of their residues. Then, raw or log-transformed data were

analyzed by ANOVA (proc GLM) with the genotype (G), the feeding regimen (F) and their interaction (G×F) as fixed effects in the model. Slaughtering day (n = 3) was included in the model as random effect for data analysis of meat quality traits and muscle biochemical traits. For data analyses of TBARS, the model included the fixed effects of G, F, incubation time (T) and their interaction (G×F×T). For data analysis of sensory traits, session (n = 8) was included in the model as random effect. Least-square means were calculated by experimental group and included in the Tables and Figure, and were compared (pdiff) in case of significant G×F or G×F×T interactions ($P < 0.05$).

3. Results and discussion

3.1 Growth performance and carcass traits

Genotype and feeding regimen influenced growth performance of female pigs with no significant G×F interaction on these traits (Table 2). The D pigs tended to have a higher average daily feed intake ($P < 0.10$) but had lower feed efficiency than P pigs, leading to a lower average growth rate and slaughter BW. These findings differ from previous studies reporting higher average growth rate due to higher average daily feed intake but similar feed efficiency in D compared to P(NN) female and castrated male crossbred pigs (Morales et al., 2013; Kowalski et al., 2020). Higher growth performance for D than P (NN) crossbred pigs was also found by Edwards, Tempelman & Bates (2006) even though genotype differences were lower for females than castrated males in their study. The discrepancies among studies may be due to differences between Duroc and also between Pietrain sire lines, as highlighted by Kowalski et al. (2020).

The effect of feeding regimen on growth performance was significant but with much less magnitude compared to genotype. Pigs fed the R feeding regimen had higher ($P < 0.05$) average daily feed intake and feed efficiency, leading to higher ($P < 0.01$) growth rate and

final BW compared with C pigs. This was more marked among the D crossbreeds with a trend for higher final BW for DR compared to DC pigs, whereas difference between PR and PC pigs was smaller (G×F, $P = 0.053$). In agreement with our results, Sun, Yun, & Kim (2020) reported linear increase in average feed intake and growth rate and a trend for higher feed efficiency with decreasing dietary n-6:n-3 ratio (17:1 to 5:1, isoenergetic and isoproteic diets) in growing-finishing pigs. Belmonte et al. (2021) also found a greater feed efficiency in pigs fed a diet including 5% linseed instead of barley meal (C18:2 n-6:C18:3 n-3 ratio of 1.2 vs. 9.4, respectively), but without variation in growth rate or daily feed intake. It can be hypothesized that a potential difference in palatability between the two regimens could contribute to explain these results. However, feeding behavior was not assessed in our experiment. Conversely, other studies reported no differences in growth performance parameters following the increase in dietary n-3 PUFA content obtained by replacing part of soybean meal by crushed linseed (C18:2 n-6:C18:3 n-3 ratio varying from 7.0 to 1.1; Kouba, Enser, Whittington, Nute, & Wood, 2003), palm and sunflower oil by extruded linseed (C18:2 n-6:C18:3 n-3 ratio varying from 13.7 to 1.5; Guillevic, Kouba, & Mourot, 2009) or soybean oil with linseed oil (n-6:n-3 PUFA ratio varying from 15:1 to 5:1, Liu & Kim 2018). In our experiment, the measurement of growth performance from pigs individually housed may have affected their voluntary feed intake and feeding behavior. However, such housing conditions were more adequate to reach the objective of the study than group housing with automatic feeders that enhance competition between animals and/or lead to consumption of a diet of inadequate composition in relation to individual BW.

Carcass traits were mostly affected by pig genotype whereas feeding regimen and the G×F interaction had much less effects and affected only one trait each (Table 2). Carcass dressing was lower in D pigs than in P pigs and tended to be higher for R pigs compared with C pigs. The differences in final BW and carcass dressing between groups led to a higher carcass

weight in DR pigs than in DC pigs, whereas PR and PC pigs did not differ for this trait (G×F interaction, $P < 0.05$) and had the heaviest carcasses. There was no other significant G×F interaction on carcass traits. Compared with P pigs, carcasses from D pigs had lower lean meat content (-1.5 point on average, $P < 0.01$) due to lower muscle depth. The relative proportions of wholesale cuts also differed between genotypes, with lower loin and ham, and higher backfat and belly proportions in D than P carcasses. These results agree with previous studies based on the comparison of Duroc vs. Pietrain NN female and castrated male crossbreeds for carcass fatness (Edwards et al., 2006) and composition (Edwards et al., 2003; Morales et al., 2013; Kowalski et al., 2020) and with studies comparing pure breeds (Plastow et al., 2005; Ciobanu et al., 2011). Except slightly higher loin and lower shoulder percentages in R than in C pigs ($P < 0.05$), the feeding regimen did not influence carcass lean meat content, muscle depth, backfat thickness and proportions of wholesale cuts. These results are consistent with previous studies reporting that variation in dietary n-6:n-3 PUFA ratio had no significant effect on carcass lean meat percentage, backfat thickness or on lean and fat proportions in loin (Kouba et al., 2003; Liu & Kim, 2018; Sun et al., 2020; Belmonte et al., 2021). These results also validate that locally produced protein sources can be valuable resources for pigs at the expense of soybean meal.

3.2 Meat quality traits

Several meat quality traits determined in the LTL and ham muscles were affected ($P < 0.05$) by pig genotype whereas feeding regimen had no significant effect, with only two traits that tended to differ between R and C pigs (Table 3). Besides, a G×F interaction ($P < 0.05$) was found for only one trait. In LTL muscle, the pH 30 min p.m., an indicator of the rate of p.m. pH decline, was similar in the four experimental groups. This suggests an overall similar response of pigs to pre-slaughter stress (Terlouw et al., 2021). In contrast, the pH 24 h p.m.

was higher ($P = 0.031$) in the LTL of D than in P pigs. A similar result ($P < 0.05$) was found in the GS muscle, whereas genotype differences did not reach significance ($P > 0.1$) in the SM, AD and GM muscles.

Compared with P pigs, loin (LTL) meat from D pigs had lower ($P < 0.05$) drip loss and shear force of cooked meat. Meat from D pigs had also lower ($P < 0.05$) a^* and b^* color coordinate values leading to lower C^* (saturation) but non-different $h°$ and L^* values. For meat color of other muscles, genotype differences were more marked in the GS muscle with lower ($P < 0.01$) L^*, a^*, b^*, C^* and $h°$ values for D than P pigs. In the GS, compared with C, the R feeding regimen tended to decrease b^* and $h°$ values especially for the DR pigs which exhibited lower $h°$ (i.e. redder color) than the three other groups (G×F interaction, $P \leq 0.05$). A similar trend for lower $h°$ in the GM of the D and especially DR pigs was found, whereas the other color coordinates did not differ according to genotype or feeding regimen.

The lower drip, higher pH 24 h, similar pH 30 min and lightness and slightly reduced color coordinates found in the meat from D vs. P pigs are all in agreement with previous studies comparing the technological quality and color of pork from D vs. P NN crossbreeds (Edwards et al., 2003; Morales et al., 1023; Lowell et al., 2018; Kowalski et al., 2020). The lower shear force of meat from D pigs contrasts with results obtained by Lowell et al. (2018) who reported slightly higher shear force of loin aged 13 d for D vs. P NN crossbred pigs. In two other studies, shear force of loin was similar in D and P NN crossbred pigs (Edwards et al., 2003; Kowalski et al., 2020). The use of meat samples taken and frozen one day after slaughter may explain the lack of texture differences in these studies.

Altogether, our results indicate that D crossbreds exhibited a superior technological and textural quality of pork than P NN crossbreds, as reported for pure D compared with P NN breeds (Ciobanu et al., 2011). The lack of effect of feeding regimen on loin and ham quality traits agrees with studies evaluating the effect of reducing n-6:n-3 ratio on loin meat quality of

Duroc crossbreeds (Liu & Kim, 2018; Sun et al., 2020; Belmonte et al., 2021). Interestingly, the R feeding regimen had a specific effect on meat color of ham from D pigs, with lower hue angle indicating of a redder color in the DR pigs than in the three other groups, which could be associated with the trend for higher pH 24 h of the formers.

3.3 Muscle biochemical and metabolic properties

Muscle biochemical composition was markedly affected by genotype and to a lesser extent by feeding regimen (Table 4). Water content in LTL and SM and protein content in LTL were lower ($P < 0.05$) in D pigs than in P pigs, even though genotype differences remain low. Present results found on LTL muscle agree with those of Morales et al. (2013). As expected, IMF content in LTL was higher in D than in P pigs (average of 1.87 vs. 1.37%, respectively, $P < 0.001$) and the same trend was found in SM (average of 3.14 vs. 2.72%, respectively, $P = 0.076$). Indeed, higher IMF contents in D compared to P NN pigs have been reported in both crossbreeds (Morales et al., 2013; Lowell et al., 2018; Kowalski et al., 2020) and pure breeds (Ciobanu et al., 2011; Warner, Dunshea, & Channon, 2017). However, and despite the fact that feed was provided ad libitum, the average IMF content found in the LTL of D pigs in our study was in the low range of values reported by other authors in pure or crossbreed D pigs with values ranging from 1.80 % (Plastow et al., 2005) to around 4.0 % (Morales et al., 2013). In this latter study, the IMF content reaches on average 3.5% in females. With this finding, and due to the well described lower IMF content in females compared to castrated males (Schwob, Lebret, & Louveau, 2020), we cannot argue that the use of females in the present study may explain the observed differences. Our findings rather illustrate the high diversity between Duroc lines for this trait (Redifer, Beever, Stahl, Boler, & Dilger, 2020; Schwob et al., 2020). The R feeding regimen did not affect muscle protein and water contents as observed in growing-finishing Large White pigs with increasing dietary intake of n-3 PUFA

(Belmonte et al., 2021). This R diet decreased IMF content in the LTL, and tended to decrease IMF content in the SM, in accordance with results reported by Kouba et al. (2003) in LTL of Duroc crossbreeds.

Glycolytic potential (GP) in LTL was lower ($P = 0.029$) in D pigs than in P pigs and this was especially the case for the DR pigs which tended to have a lower GP than the three other experimental groups (G×F interaction, $P = 0.049$). Among the GP components (lactate, free glucose and glycogen), glycogen was the main contributor to these differences with lower values in the LTL of D and especially the DR pigs (G×F, $P = 0.050$, data not shown). These results can explain the higher pH 24 h found in the meat from D and in particular the DR pigs (Terlouw et al., 2021). The GP differences were not associated with variations in activities of enzymes involved in glycolytic (LDH) and oxidative (CS) energy metabolism in the LTL in the four experimental groups (Table 4). However, HAD activity, an indicator of a lipid β-oxidation, was lower ($P = 0.033$) in D than in P pigs, which could contribute to their higher IMF content. Variations in GP without differences in LDH and CS activities between experimental groups agree with a previous study evaluating pig LTL metabolic traits according to finishing season in extensive system (Lebret et al., 2021). This suggests that muscle glycogen balance may be controlled by other metabolic pathways at the tissue and/or body level.

3.4 Muscle fatty acid contents and lipid oxidation

Muscle FA contents were strongly affected by both genotype and feeding regimen (Table 5). Contents of all individual saturated (SFA) and mono-unsaturated fatty acids (MUFA) (except the minor C14:1, C15:0, C22:0, C22:1 and C24:0) were higher ($P < 0.001$) in D than in P pigs. D pigs also had higher ($P \leq 0.01$) contents of n-6 (including the linoleic acid LA, C18:2 n-6) and of n-3 PUFA (including the linolenic acid ALA, C18:3 n-3) to lesser extent than P

pigs, whereas the C20:5 n-3 (eicosapentaenoic acid, EPA) and C22:6 n-3 (docosahexaenoic acid, DHA) contents did not vary between genotypes. These effects led to lower ratios of C18:2 n-6:C18:3 n-3 and PUFA:SFA and higher SFA:n-3 ratio, whereas n-6:n-3 ratio did not differ between D and P pigs. The present results agree with those of Alonso, Campo, Espanol, Roncales, & Beltran (2009) reporting similar differences in FA composition between Duroc and Pietrain crossbred pigs (even though genotype differences for PUFA content did not reach significance in their study). Our results could be explained by a higher lipid synthesis (i.e. SFA and MUFA, especially the oleic acid C18:1, the major FA in pig tissues) in D pigs than in P pigs that could at least partly result from their higher feed intake (Lebret & Čandek-Potokar, 2022). Thus, the higher IMF content in D than in P pigs contributes to their differences in FA profile.

The R feeding regimen reduced ($P < 0.05$) the total SFA, MUFA and PUFA contents due to lower contents of the individual major FA within each of these classes in both genotypes, thus explaining the overall lower IMF content in R vs. C pigs. The reduced MUFA content with R feeding regimen is largely due to a lower content of the C18:1 ($P < 0.001$), which may be explained by the inhibition of the activity of the Δ-9 desaturase enzyme, responsible for the synthesis of C18:1 following diet enrichment in ALA, as demonstrated by Kouba et al. (2003). Above all, the R feeding strongly modified the muscle PUFA content with a marked increase in n-3 PUFA content especially in DR pigs (G×F interaction, $P = 0.032$). Among the n-3 PUFA, ALA was 2.4-fold higher in R vs. C pigs in both genotypes. Conversely, the n-6 PUFA and especially LA contents were markedly reduced in DR vs. DC pigs, the difference being less important between PR and PC pigs. This lead to a strong decrease by a factor of 2.7 (P pigs) up to 3.6 (D pigs) in the n-6:n-3 ratio of the LTL muscle of pigs receiving the R feeding regimen (G×F interaction, $P < 0.001$). These results confirm our hypotheses and are consistent with the abundant literature on the influence of dietary fat composition on the FA

455 composition of pork (Kouba et al., 2003; Guillevic et al., 2009; Belmonte et al., 2021; reviews
456 by Wood et al., 2008; Lebret & Čandek-Potokar, 2022; meta-analysis by Corino, Rossi,
457 Cannata, & Ratti, 2014). Among the n-3 PUFA, the amounts of EPA were also higher in the
458 LTL of R vs. C pigs. Because diets did not contain EPA (data not shown), this demonstrates
459 that EPA in the LTL muscle of DR and PR pigs resulted from a conversion of ALA by a
460 succession of desaturations (by Δ5 and Δ6 desaturases) and elongations (Sprecher, 2000). By
461 contrast, DHA content was not significantly modified by the feeding regimen, in agreement
462 with other studies (Kouba et al. 2003; Guillevic et al., 2009; Belmonte et al., 2021) and
463 review by Huang et al. (2021). Accordingly, Corino et al. (2014) calculated in their meta-
464 analysis that DHA content is only slightly increased compared to ALA (average of +12% vs.
465 + 137%, respectively) in the LTL muscle of pigs fed linseed enriched diets. The pathway for
466 DHA synthesis from EPA includes an elongation to C24:5, desaturation to 22:5, and β-
467 oxidation in peroxisomes to C22:6, which can be further degraded in C20:4 and C22:4
468 (Sprecher, 2000). Moreover, in case of high dietary intake of ALA, a competition for Δ6
469 desaturase activity between ALA and the C24:5 precursor for DHA may occur (Corino et al.,
470 2014). Therefore, DHA content in pig muscle is generally not affected by dietary
471 supplementation with ALA. Differences in muscle FA contents in response to feeding
472 regimen resulted in a 3 fold lower LA:ALA ratio in the meat of DR and PR pigs compared
473 with DC and PC pigs, and very close to the nutritional recommendation of LA:ALA ≤ 5 in
474 human diet, established by the French health agency (ANSES, 2011). In addition, pork from
475 DR and PR pigs met the BBC specification criteria for high nutritional quality, i.e. target
476 values in the meat of ALA ≥ 1.8% (when expressed in percentage of total FA) and of ratios of
477 n-6:n-3 ≤ 4 and SFA:n-3 ≤ 12.
478 The risk for lipid oxidation in loin meat was influenced by pig genotype, feeding regimen and
479 incubation time in oxidizing conditions, with a significant G×F×T interaction ($P < 0.01$)

(Figure 1). On average, and for each experimental group, the TBARS content significantly increased with time, from start (t = 0 min) until 180 min then remained constant until 240 min. No differences between experimental groups were found at start, corresponding to lipid oxidation level in muscle just after slaughter. After 60 and 120 min incubation, muscle TBARS content was higher in DC pigs than in the 3 other groups. From 180 min onwards, PR pigs had the lowest TBAR content without significant differences between the 3 other experimental groups. These results suggest that muscle lipid oxidation occurred faster in DC pigs than in DR and PC pigs, and could at least partly be explained by their higher IMF content. The lowest oxidation level in meat from PR pigs may result from the supplementation in vitamin E provided in the R diets to prevent from lipid oxidation (Warner et al., 2017; Lebret & Čandek-Potokar, 2022). In DR pigs, compared with DC pigs, this antioxidant supplementation seemed to protect from oxidation after intermediate (60 and 120 min) but not long incubation in oxidized conditions. This suggests that dietary antioxidant supplementation should be increased to reduce risk of lipid oxidation in meat with average IMF content above 1.5-1.7%.

3.5 Meat sensory quality

The appearance and eating quality of loin was significantly affected by pig genotype but not by the feeding regimen (Table 6). Meat from D pigs had higher ($P < 0.001$) marbling intensity and homogeneity scores than meat from P pigs, in agreement with the higher IMF content of D pigs. Red color did not differ between genotypes, in accordance with the lack of difference in $h°$ determined by colorimetry. Odor intensity of raw and cooked meat was similar in the two genotypes, but meat from D pigs was found more tender and juicier than meat from P pigs ($P < 0.01$). The higher tenderness of meat from D pigs agrees with the lower shear force value, compared with meat from P pigs. Meat flavor was slightly lower ($P < 0.05$) for D

505 compared with P pigs. No difference was observed between genotypes for meat odor. The
506 higher pH 24 h and IMF content of D vs. P pigs may partly explain genotype differences
507 found for meat tenderness and juiciness, in agreement with the positive role of these muscle
508 biochemical properties in the determination of pork sensory traits reported in the literature
509 (Listrat et al., 2016). Higher sensory quality of pork from D vs. P crossbreeds or pure breeds
510 is often reported but is not systematic (reviews by Ngapo & Gariepy, 2008; Warner et al.,
511 2017), especially when considering NN Pietrain pigs. Kowalski et al. (2020) reported no
512 significant genotype differences in tenderness, toughness, odors or flavors intensity of loin
513 chops assessed either by a trained sensory or a consumer panel, but only a consumer
514 preference (based on ranking) for meat from D pigs. In the current study, one can assume that
515 the long ageing duration (8 days) could have highlighted genotype sensory differences
516 (Warner et al., 2017). Differences in meat flavor scores between D and P pigs could result
517 from different contents of neutral and polar lipid fractions, a higher IMF content being
518 associated with higher neutral (triglycerides) lipids whereas content in polar lipids remains
519 almost constant (Listrat et al., 2016). The polar lipid fraction plays an important role on pork
520 flavor attributes (Tikk et al., 2007). One can hypothesized that the higher content of neutral
521 lipids but similar content of polar lipids in meat from D pigs may have 'diluted' flavor
522 components, resulting in a slightly lower pork flavor for D vs. P pigs. Compared with C, the
523 R feeding regimen had no significant effect on the sensory profile of loin. Thus, the marked
524 differences in loin PUFA contents between R and C pigs did not affect pork flavor intensity.
525 In agreement, Guillevic et al. (2009) found no difference in overall appreciation by consumers
526 of sausages from pigs fed a linseed enriched vs. a control diet.
527

528 ***3.6 Economic evaluation***

529 Cold carcass (CC) weight differed according to genotype and feeding regimen, with lower

weights in D than in P pigs and among the formers for DC vs. DR pigs ($P < 0.05$). Therefore, economic indicators were calculated per kg CC and per pig (Table 7). The output price per kg CC was higher for P compared with D pigs and for R compared with C pigs because of their differences in carcass lean meat content. When calculated per pig, the output price differed significantly between the four groups, with the highest price for the PR pigs followed by PC pigs, then DR pigs, and the lowest price for the DC pigs (G×F interaction, $P < 0.05$). These group differences resulted from differences in CC weight combined with differences in carcass lean meat content and BBC qualification, due to the higher price for leaner carcasses and the BBC premium for high nutritional quality. Feed cost per kg CC was higher for D vs. P pigs, as a result of the lower feed efficiency of the D pigs, and for R vs. C pigs, due to the higher cost of R diets despite the slightly higher feed efficiency of the R pigs. When expressed per pig, feed costs tended to be lower in D than in P pigs due to their lighter final BW, and was higher (+ 5 to 6 €) for R vs. C pigs.

The added value calculated per kg of CC was lower ($P < 0.001$) for D than P pigs and tended to be higher for R vs. C pigs ($P = 0.087$). Results expressed per pig showed a lower ($P < 0.001$) added value for D compared with P pigs, and higher ($P < 0.01$) for R compared to C pigs, but with a greater effect of the R feeding regimen within the Duroc (+ 13 €/pig) than within the Pietrain crossbreeds (+ 4 €/pig) in our conditions (G×F interaction, $P = 0.062$). Altogether, these data indicate that, in the current experimental conditions (individual housing and gilts) and context prices, the R feeding strategy would be more profitable with Duroc than Pietrain crossbred pigs. Nevertheless, Pietrain crossbred pigs are still more profitable with market prices for pork carcasses largely determined by their lean meat content and not by other pork quality dimensions.

4. Conclusion

The Duroc female crossbred pigs produced meat with superior sensory and technological quality but had lower, even though satisfactory growth performance and carcass leanness, compared with Pietrain NN female crossbred pigs. Compared to C, the R feeding regimen slightly improved growth performance and markedly modified the FA contents of pork towards improved nutritional value, without affecting carcass composition or meat technological and sensory quality. Economic evaluation in the context prices of the experiment shows that R feeding strategy would be more profitable in Duroc than in Pietrain crossbred pigs. Altogether, our results show that the production of Duroc crossbred pigs fed a faba bean based diet enriched with extruded linseed is a favorable strategy to jointly improve the sensory and nutritional properties of pork, while meeting the challenge of relocating protein resources to reduce dependence on third countries for animal feeding. A validation of these results in commercial farming conditions (group housing, several sexes, simplification of multiphase feeding) is needed before the transposition of these breeding strategies to the pig production sector. Also, under the current price scheme based on carcass composition, it is less profitable to raise Duroc compared with Pietrain crossbred pigs. A further valuation of sensory and 'image' properties of DR pork, presently valued only for nutritional properties, would allow pork producers to implement this win-win strategy.

Declarations of interest

None.

Author contributions

B. Lebret: conceptualization, formal analysis, funding acquisition, supervision, validation, writing of original draft, review and editing; S. Lhuisset: data curation, investigation, writing of original draft; E Labussiere: conceptualization, methodology; I. Louveau:

conceptualization, methodology. All authors discussed the data, commented on the draft versions of the manuscript, and read, commented and approved the submitted and revised versions.

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728 **Table 1. Composition and nutritional value of the experimental formulae used in the R**

729 **(relocation of feed resources) and Control feeding strategies**

	R		Control	
	High protein	Low protein	High protein	Low protein
Ingredients, % (as fed basis)				
Wheat	17.41	21.03	22.13	20.98
Maize	17.41	21.03	22.13	20.98
Barley	17.41	21.03	22.13	20.98
Wheat bran	3.22	18.63	4.00	19.92
Dehydrated beet pulp	1.61	9.32	2.00	9.96
Soybean meal 48	4.75	-	14.28	0.94
Rapeseed meal	-	-	3.10	-
Shelled sunflower meal	-	-	3.10	-
Extruded linseed + extruded faba bean	3.52	3.52	-	-
Faba bean[1]	29.28	-	-	-
Cane molasses	2.00	2.00	2.00	2.00
Rapeseed oil	-	0.50	-	-
Sunflower oil	-	-	1.81	1.50
L-Lysine HCl	0.23	0.27	0.43	0.28
Mineral-vitamin mix[2]	0.50	0.50	0.50	0.50
Antioxidants (Sevefarm®)[3]	0.20	0.20	-	-
Analyzed chemical composition, % [4]				
Dry matter	88.39	87.92	87.36	87.64
Crude protein	17.60	12.11	16.32	12.00
Crude fat	3.24	3.59	3.73	3.86
Crude fiber	4.23	4.44	3.87	3.87
Starch	42.18	41.39	40.75	41.71
Ash	4.96	4.96	4.84	4.74
Gross energy, MJ/kg	16.21	15.90	16.43	16.08
Fatty acid (FA) composition, % of identified FA[5]				
Saturated	15.6	15.2	14.8	15.7
Monounsaturated	22.3	27.3	29.0	27.1
Polyunsaturated (PUFA)	62.1	57.6	56.2	57.1
C18:3 n-3 (ALA)[6]	18.9	15.3	2.30	2.66
n-6:n-3 PUFA	2.29	2.77	23.6	20.5
Calculated composition[7]				
Digestible lysine, %	0.97	0.52	0.97	0.52
Net energy, MJ/kg	9.71	9.35	9.67	9.21
LysD/EN	1.00	0.55	1.00	0.57

Vitamin E, mg/100g	60	60	20	20

[1] 90% faba beans + 10% soy beans extruded together.
[2] Contains 4 000 mg/kg vitamin E.
[3] Contains 20 000 mg/kg vitamin E, 50 000 mg/kg vitamin C, and aromatic substances
[4] Analyzed as described by Lebret et al. (2021) and expressed relative to fresh feed for dry matter, and to standardized dry matter of 88.0 % for all other components within each diet.
[5] Fatty acid (FA) composition of diets analyzed by gas chromatography after chloroform-methanol extraction of lipids as described for FA contents of intramuscular fat.
[6] ALA: Alpha linoleic acid.
[7] Calculated values as described by Furbeyre et al. (2020) and expressed on a fresh feed basis, except vitamin E that was calculated from its concentration in the ingredients of each diet.

740 **Table 2. Growth performance and carcass traits in Duroc (D) and Pietrain (P) crossbred**

741 **pigs fed a R or a control (C) diet**

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	15	15	15				
Growth performance								
Initial body weight (BW), kg	33.9	33.5	33.9	33.5	2.08	0.96	0.46	1.00
Final (slaughter) BW, kg	116.6	108.6	122.0	119.0	4.79	**<0.001**	**<0.001**	0.053
Average daily gain, g/d	989	898	1052	1002	0.77	**<0.001**	**0.003**	0.14
Average daily feed intake, g/d	2879	2727	2744	2713	0.16	0.072	**0.026**	0.14
Feed efficiency	0.34	0.33	0.38	0.37	0.02	**<0.001**	**0.019**	0.41
Carcass traits								
Hot carcass weight, kg	89.4^{b}	82.2^{a}	96.7^{c}	93.8^{c}	4.07	**<0.001**	**<0.001**	**0.045**
Carcass dressing, %	76.6	75.7	79.2	78.3	1.39	**<0.001**	0.060	0.42
Backfat thickness G2, mm[3]	14.1	13.3	13.4	13.7	1.86	0.70	0.66	0.23
Muscle depth M2, mm[3]	57.7	55.9	64.6	64.4	4.98	**<0.001**	0.43	0.55
Lean meat content, %[4]	60.2	60.5	61.9	61.5	1.32	**0.003**	0.85	0.26
Carcass composition, %[5]								
Ham	25.1	25.5	26.0	25.9	0.69	**<0.001**	0.33	0.19
Loin	28.0	27.8	29.3	28.5	0.99	**<0.001**	**0.043**	0.19
Shoulder	23.8	24.2	23.6	24.2	0.73	0.39	**0.015**	0.62
Belly	13.3	13.0	12.6	12.7	0.75	**0.019**	0.70	0.41
Backfat	6.6	6.3	5.8	6.0	0.71	**0.003**	0.65	0.25

742 [1] Least-square means calculated from raw data.

743 [2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and
744 RMSE obtained from the ANOVA. a, b, c : differences between experimental groups ($P <$
745 0.05).

746 [3] Measured using the Lean Fat Sensor (CGM, capteur gras maigre) device.

747 [4] Calculated using the CGM measurements according to the equation developed by Daumas et
748 al. (2010).

749 [5] Calculated as relative percentage of the cold right carcass side.

750 **Table 3. Meat quality traits of the loin and ham muscles in Duroc (D) and Pietrain (P)**

751 **crossbred pigs fed a R or a control (C) diet**

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	14	15	15				
Loin : Longissimus thoracis et lumborum muscle								
pH 30 min p.m.	6.33	6.24	6.32	6.29	0.15	0.69	0.099	0.42
pH 24 h p.m.	5.94	5.89	5.80	5.83	0.18	**0.031**	0.84	0.31
Drip loss 1 - 4 d p.m., %	3.24	3.68	4.69	4.73	1.60	**0.005**	0.57	0.64
Color								
*L**	48.3	50.2	50.9	50.2	3.15	0.12	0.45	0.11
*a**	6.02	6.54	6.87	7.09	1.04	**0.013**	0.18	0.57
*b**	4.34	4.85	5.54	5.36	1.17	**0.007**	0.59	0.26
*C**	7.47	8.20	8.87	8.92	1.40	**0.005**	0.30	0.36
h°	35.3	36.3	38.2	36.9	4.80	0.16	0.88	0.35
Shear force of cooked meat, N	40.2	40.8	43.3	47.5	0.19	**0.017**	0.23	0.56
Ham muscles								
pH 24 h p. m., Semimembranosus	5.95	5.82	5.82	5.88	0.21	0.51	0.53	0.10
pH 24 h p.m., Adductor	6.10	5.91	5.96	5.97	0.26	0.49	0.17	0.14
pH 24 h p.m., Gluteus medius (GM)	5.82	5.78	5.71	5.77	0.18	0.18	0.88	0.26
pH 24 h p.m., Gluteus superficialis (GS)	5.98	5.87	5.79	5.86	0.20	**0.048**	0.71	0.082
Color, GS								
*L**	42.6	45.2	47.5	47.4	3.19	**<0.001**	0.14	0.11
*a**	9.51	9.69	10.29	10.82	1.32	**0.007**	0.31	0.61
*b**	5.32	6.32	7.10	7.41	1.32	**<0.001**	0.063	0.32
*C**	10.92	11.58	12.51	13.14	1.68	**<0.001**	0.15	0.96
h°	28.9[a]	32.8[b]	34.8[b]	34.2[b]	3.88	**<0.001**	0.10	**0.030**
Color, GM								
*L**	46.8	48.1	49.5	48.0	3.83	0.19	0.92	0.17
*a**	9.64	9.96	9.57	9.89	1.46	0.85	0.40	0.99
*b**	6.18	7.12	7.35	7.23	1.49	0.10	0.30	0.18
*C**	11.50	12.28	12.09	12.28	1.86	0.54	0.32	0.54
h°	32.2	35.6	37.2	35.8	4.86	**0.046**	0.43	0.070

752 [1] Least-square means calculated from raw data.

753 [2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and

754 RMSE obtained from the ANOVA applied to raw data (all traits except shear force) or to log-

755 transformed values (shear force) to fit a normal distribution. a, b : differences between
756 experimental groups ($P < 0.05$).

Table 4. Biochemical composition and energy metabolism of the Longissimus thoracis et lumborum (LTL) and Semimembranosus muscles in Duroc (D) and Pietrain (P) crossbred pigs fed a R or a control (C) diet

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	14	15	15				
LTL muscle								
Water, %	75.4	75.2	75.6	75.6	0.49	**0.013**	0.30	0.39
Proteins, %	22.3	22.1	22.5	22.4	0.34	**0.013**	0.12	0.87
Lipids, %	1.69	2.05	1.32	1.41	0.31	**<0.001**	**0.008**	0.10
Glycolytic potential, µmol eq lactate/g	122	147	151	149	27.03	**0.029**	0.10	**0.049**
Metabolic enzyme activities[3]								
Lactate dehydrogenase	2121	2172	2267	2166	246	0.28	0.70	0.24
β-hydroxy-acyl-CoA dehydrogenase	3.70	3.60	3.84	4.07	0.54	**0.033**	0.67	0.25
Citrate synthase	5.94	6.26	5.94	6.64	1.60	0.64	0.22	0.64
Semimembranosus muscle								
Water, %	74.5	74.4	75.3	75.3	0.01	**0.015**	0.86	0.91
Proteins, %	21.4	21.2	21.5	21.4	0.02	0.56	0.38	0.91
Lipids, %	2.94	3.33	2.48	2.96	0.14	0.076	0.072	0.83

[1] Least-square means calculated from raw data.

[2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and RMSE obtained from the ANOVA applied to raw data for all traits, except water, protein and lipids of the Semimembranosus muscle, for which ANOVA was applied to log-transformed values to fit a normal distribution. a, b, c, d: differences between experimental groups ($P < 0.05$).

[3] Expressed as micromole of substrate per min per g of fresh muscle.

767 **Table 5. Fatty acid (FA) contents of the Longissimus thoracis et lumborum muscle in**

768 **Duroc (D) and Pietrain (P) crossbred pigs fed a R or a control (C) diet**

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	14	15	15				
FA, mg/100 g muscle								
C10:0	2.10	2.40	1.32	1.48	0.50	**<0.001**	0.084	0.61
C12:0	1.32	1.44	0.82	0.89	0.35	**<0.001**	0.32	0.79
C14:0	15.86	20.08	10.37	11.50	4.44	**<0.001**	**0.024**	0.19
C14:1	0.16	0.09	0.10	0.06	0.20	0.41	0.32	0.77
C15:0	0.69	0.83	0.74	0.72	0.29	0.73	0.41	0.29
C16:0	309.91	395.04	210.07	229.98	77.11	**<0.001**	**0.011**	0.11
C16:1 n-9	3.22[a]	4.69[b]	2.82[a]	3.12[a]	0.97	**<0.001**	**<0.001**	**0.024**
C16:1 n-7	35.17	46.86	25.53	26.88	10.12	**<0.001**	**0.017**	0.055
C18:0	179.63	222.99	111.53	124.10	47.03	**<0.001**	**0.026**	0.21
C18:1 n-9	503.36	663.30	331.42	373.47	134.47	**<0.001**	**0.006**	0.098
C18:1 n-7	45.33	59.40	33.10	35.71	11.10	**<0.001**	**0.006**	0.053
C18:2 n-6 (LA)	132.89[a]	179.70[b]	127.95[a]	143.69[a]	23.02	**0.001**	**<0.001**	**0.012**
C18:3 n-6	1.19	0.98	1.66	2.12	1.12	**0.008**	0.66	0.25
C18:3 n-3 (ALA)[4]	21.66	9.04	16.35	6.88	3.45	**<0.001**	**<0.001**	0.085
C18:4 n-3	0.57	0.84	0.48	0.88	0.56	0.84	**0.024**	0.68
C20:0	3.16	3.82	1.60	2.05	1.67	**<0.001**	0.21	0.80
C20:1 n-9	7.92	10.30	5.28	6.40	2.30	**<0.001**	**0.005**	0.30
C20:2	3.88[a]	6.43[b]	3.25[a]	3.89[a]	1.48	**<0.001**	**<0.001**	**0.016**
C20:3 n-6	3.74	4.82	3.83	4.29	1.05	0.42	**0.007**	0.26
C20:4 n-6	21.48	32.36	24.94	34.70	5.76	0.059	**<0.001**	0.71
C20:3 n-3	3.89	1.78	2.97	1.28	1.41	0.057	**<0.001**	0.57
C20:4 n-3	0.24	0.01	0.39	0.10	0.29	0.10	**0.001**	0.71
C20:5 n-3 (EPA)[4]	8.06	0.85	6.30	1.93	3.27	0.69	**<0.001**	0.11
C22:0	1.03	0.29	0.01	0.33	1.62	0.25	0.63	0.21
C22:1 n-11	0.73	0.01	0.33	0.22	0.76	0.65	**0.039**	0.12
C22:1 n-9	0.09	0.01	0.13	0.19	0.39	0.28	0.88	0.44
C22:4 n-6	2.87	6.49	2.63	5.75	2.11	0.37	**<0.001**	0.65
C22:5 n-6	3.44	2.47	0.74	1.55	4.28	0.11	0.94	0.43
C22:5 n-3	9.44	4.17	9.47	4.96	1.87	0.41	**<0.001**	0.44
C22:6 n-3 (DHA)[4]	1.24	0.82	0.69	0.59	1.59	0.35	0.53	0.70
C24:0	0.59	0.10	0.00	0.00	1.06	0.22	0.38	0.38
C24:1	0.63	0.33	0.00	0.00	0.84	**0.031**	0.49	0.49
SFA[3]	514.28	646.98	336.45	371.06	128.58	**<0.001**	**0.016**	0.15
MUFA[3]	596.62	784.96	398.71	446.06	157.60	**<0.001**	**0.006**	0.092

PUFA[3]	214.60	250.78	201.65	212.61	32.79	**0.004**	**0.008**	0.15
n-6	165.62[a]	226.84[c]	161.74[a]	192.11[b]	28.10	**0.011**	**<0.001**	**0.040**
n-3	45.10[c]	17.52[a]	36.66[b]	16.61[a]	6.55	**0.008**	**<0.001**	**0.032**
n-6: n-3	3.75[a]	13.32[c]	4.43[a]	11.80[b]	0.06	0.43	**<0.001**	**<0.001**
C18:2 n-6: C18:3 n-3	6.28	20.62	7.92	21.84	0.08	**0.002**	**<0.001**	0.072
SFA:n-3	11.47[b]	38.87[d]	9.09[a]	22.33[c]	0.11	**<0.001**	**<0.001**	**0.018**
PUFA:SFA	0.46	0.40	0.62	0.60	0.12	**<0.001**	0.19	0.64

[1] Least-square means calculated from raw data.

[2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and RMSE obtained from the ANOVA applied to raw data for all traits, except n-6:n-3, C18:2 n-6: C18:3 n-3, and SFA:n-3 ratios, for which ANOVA was applied to log-transformed values to fit a normal distribution. a, b, c, d: differences between experimental groups ($P < 0.05$).

[3] SFA: Saturated, MUFA: Monounsaturated, PUFA: Polyunsaturated FA.

[4] LA: linoleic acid, ALA: alpha-linolenic acid, EPA: ecosapentaenoic acid, DHA: docosahexaenoic acid.

Table 6. Sensory quality traits (scored on a discrete scale from 0: absent to 10: high) of loin (Longissimus thoracis et lumborum muscle) in Duroc (D) and Pietrain (P) crossbred pigs fed a R or a control (C) diet

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	14	15	15				
Appearance of raw meat								
Red color	5.9	5.3	5.8	5.9	0.85	0.35	0.27	0.097
Marbling	3.8	3.3	2.6	2.7	0.71	**<0.001**	0.23	0.077
Homogeneity of marbling	4.4	4.0	3.4	3.4	0.66	**<0.001**	0.24	0.22
Odor	3.0	3.1	3.1	3.1	0.26	0.31	0.80	0.73
Eating traits of cooked meat (roast)								
Odor	5.5	5.7	5.7	5.6	0.26	0.28	0.94	0.082
Flavor	5.6	5.7	5.7	5.8	0.20	**0.023**	0.14	0.15
Tenderness	6.2	6.1	5.4	5.3	0.87	**<0.001**	0.61	0.93
Juiciness	5.4	5.6	5.2	5.2	0.33	**0.002**	0.24	0.14

[1] Least-square means of raw data (data used were the average per pig of individual panelist scores for each sensory descriptor, and of shear force measurements).

[2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and RMSE obtained from the ANOVA applied to raw data.

784 **Table 7. Economic indicators of pork production in Duroc (D) and Pietrain (P) crossbred**

785 **pigs fed a R or a control (C) diet**

	Experimental groups[1]				RMSE	Significance[2]		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	15	15	15				
Cold Carcass (CC) weight, kg	87.4[b]	80.3[a]	94.5[c]	91.7[c]	4.00	**<0.001**	**<0.001**	**0.048**
Output price/kg CC, €	1.86	1.79	1.92	1.87	0.05	**<0.001**	**<0.001**	0.17
Output price/pig, €	163.0[b]	143.7[a]	181.1[d]	171.8[c]	0.07	**<0.001**	**<0.001**	**0.044**
Feed cost/kg CC, €	0.64	0.62	0.60	0.56	0.03	**<0.001**	**<0.001**	0.33
Feed cost/pig, €	55.8	49.6	56.6	51.5	0.05	0.057	**<0.001**	0.42
Added value (output - feed cost)/kg CC, €	1.22	1.17	1.32	1.31	0.06	**<0.001**	0.087	0.15
Added value (output - feed cost)/pig, €	107.2	94.2	124.5	120.3	0.09	**<0.001**	**0.002**	0.062

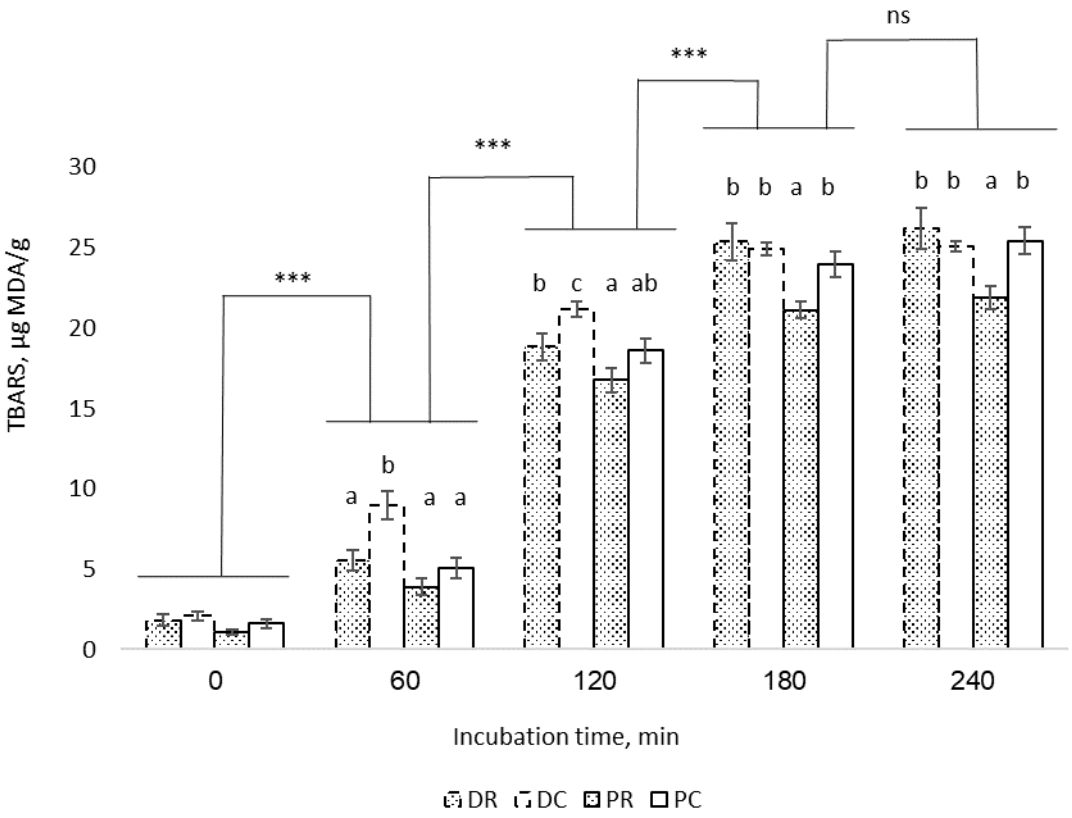
786 [1] Least-square means calculated from raw data.

787 [2] P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and
788 RMSE obtained from the ANOVA applied to raw data (all traits except output price/pig, feed
789 cost/pig and added-value/pig) or to log-transformed values (output price/pig, feed cost/pig and
790 added value/pig) to fit a normal distribution. a, b, c, d: differences between experimental
791 groups ($P < 0.05$).

792 **Figure 1. Lipid oxidation in *Longissimus lumborum et thoracis* muscle in Duroc (D) and**

793 **Pietrain (P) crossbred pigs fed a R or a control (C) diet**

794



795

796

797 Thiobarbituric acid reactive substances (TBARS) were assessed after 0, 60, 120, 180 or 240
798 minutes of incubation in oxidizing conditions, and values were expressed in µg of
799 malondialdehyde (MDA) per g of muscle. Data are lsmeans ± standard errors calculated from
800 raw data.
801 Pigs were either from Duroc × (Large White × Landrace) (D) or Pietrain × (Large White ×
802 Landrace) (P) genotype and were fed either a control (C) or a R feeding regimen (F). ANOVA
803 applied to raw data showed significant effects of genotype ($P < 0.001$), feeding regimen ($P <$
804 0.001), incubation time ($P < 0.001$) and their interaction genotype×feeding regimen×
805 incubation time ($P < 0.01$). a, b, c : differences between experimental groups ($P < 0.05$) within
806 incubation time. Differences on average MDA content between incubation times (*** : $P <$
807 0.001). Within each experimental group, differences between incubation times were all
808 significant ($P < 0.001$) except between 180 and 240 min ($P > 0.05$).
809