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► To cite this version:

Bénédicte Lebret, Sihem Lhuisset, Etienne Labussière, Isabelle Louveau. Combining pig genetic and feeding strategies improves the sensory, nutritional and technological quality of pork in the context of relocation of feed resources. *Meat Science*, 2023, 197, pp.109074. 10.1016/j.meatsci.2022.109074 . hal-03920179

HAL Id: hal-03920179

<https://hal.inrae.fr/hal-03920179v1>

Submitted on 3 Jan 2023

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

3

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POST PRINT

9 **Abstract**

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

22 **Highlights**

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

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

29

30 **1. Introduction**

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

55 well established, but the interactions between these factors are less documented (review by
56 Lebret & Čandek-Potokar, 2022). Regarding genetics, the Duroc breed is favorable for
57 sensory and technological quality in comparison with other selected breeds used in
58 conventional production. Both purebred (Plastow et al., 2005; Ciobanu, Lonergan, & Huff-
59 Lonergan, 2011) and crossbred (Edwards, Bates, & Osburn, 2003; Morales et al., 2013) Duroc
60 pigs generally exhibit higher intramuscular fat (IMF) content, meat pH and water-holding
61 capacity, while maintaining their growth performance. Regarding feeding, the adjustment of
62 protein and energy intakes to pigs' nutritional requirements determines growth and body
63 composition while limiting the excretion of components with environmental impacts
64 (Andretta et al., 2014). Furthermore, the nature of dietary lipids strongly affects the fatty acid
65 (FA) composition and nutritional value of pork (Wood et al., 2008; Huang, Chiba, & Bergen,
66 2021). Therefore, we hypothesized that combining genetic and feeding factors could jointly
67 improve the sensory, nutritional and technological quality of pork, while the use of domestic
68 protein resources improves the image attribute of pork by reducing feed material imports and
69 reinforcing the link between pig rearing and land. We set up an experiment involving two pig
70 genotypes: Duroc and Pietrain NN crossbreeds, and two feeding regimen: a diet including
71 faba bean as a protein source and extruded linseed as source of n-3 FA, and a control diet
72 based on soybean meal. The aim was to evaluate the effects of genotype, feeding and
73 genotype x feeding interaction on growth performance, carcass composition and economic
74 value, and technological, sensory and nutritional attributes of pork. The final goal was to
75 provide a proof of concept that the combination of genetic and feeding factors is a relevant
76 strategy to jointly improve various intrinsic and extrinsic quality attributes of pork.

77

78 **2. Material and methods**

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

80 Gilles, France doi.org/10.15454/1.5573932732039927E12) in compliance with EU directive
81 2010/63/EU for animal experiments and French legislation. The technical and scientific staffs
82 had individual accreditation from the French Minister to experiment on living animals. The
83 methods for animal experiment were approved by the local Committee on Ethics in animal
84 experimentation and the present animal experimentation was authorized by the French
85 Ministry of Higher Education, Research and Innovation (APAFiS #19388-
86 2019022208529883-v2).

87

88 ***2.1 Animals, experimental design and feeding strategy***

89 The experiment included 60 female crossbred pigs. Animals originated from Large White ×
90 Landrace sows (INRAE herd) inseminated with semen from either 3 Duroc boars (Genesus
91 herd (22400 Lamballe, France) issued from males' herd selected by the breeding company for
92 growth rate, feed intake and IMF content), or semen from 3 Pietrain NN boars (Nucleus herd
93 (35650 Le Rheu, France), non-carriers of the hal mutation at the RYR1 gene and issued from
94 males' herd selected by the breeding company for growth rate, feed efficiency and pork
95 technological quality). The Duroc crossbred pigs (D, n=30) were issued from 7 litters and the
96 Pietrain crossbred pigs (P, n=30) were issued from 9 litters. For each genotype, 15 pairs of
97 female littermates were chosen few days before the end of post-weaning (approximately 31 kg
98 of body weight, BW) on the basis of their BW and growth rate from birth, so that the average
99 BW of these 30 female pigs was similar to those of all female pigs available for the
100 experiment. These 15 pairs of littermates were distributed in two groups with similar average
101 and SD of BW. They were allocated to one of two different feeding regimen: Relocation of
102 feed resources (R) or control (C). Thus, the experiment was based on a 2 × 2 factorial design
103 with 4 experimental groups (n=15 female pigs per group); DR, DC, PR and PC. All pigs were
104 housed in individual pens (85 x 265 cm) on concrete floor with individual drinking bowl and

105 feeding. This allowed to implement precisely the feeding strategy according to the nutritional
106 requirements of each pig and to measure their individual feed intake. Pigs were placed in the
107 same room during the whole growing-finishing period, i.e. from 33.7 ± 2.0 kg BW until
108 slaughter at around 115.0 kg BW.

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

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

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

132

133 ***2.2 Growth performance***

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

139

140 ***2.3 Slaughter and carcass measurements***

141 Pigs were slaughtered at the INRAE experimental slaughterhouse (35590 Saint-Gilles,
142 France) on three different slaughtering days spread over 2 weeks, including the same number
143 of pigs from each experimental group on each slaughtering day. All pigs were fasted for 24
144 hours before slaughter. The day before slaughter, pigs from the same experimental group (n =
145 6 from each group for the first and for the second slaughtering days, and n = 3 from each
146 group for the third slaughtering day) were loaded onto the truck, transported together to the
147 slaughterhouse (5 min) and kept in lairage in the same pen without mixing them with the
148 other groups. All pigs had free access to water. The next day, pigs were taken alternately from
149 each group and slaughtered by electrical head-stunning (320 V, 6 A, 10 s duration) followed
150 by jugular exsanguination in compliance with the current national regulations applied in
151 slaughterhouses.

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

155 between the third and fourth last ribs at 6 cm of the spinal canal axis, using the Lean Fat
156 Sensor (CGM, Capteur Gras Maigre) device (Fives Syleps, Lorient, France). Carcass lean
157 meat content was calculated using the G2 and M2 measurements according to the equation
158 developed by Daumas, Causeur, & Predin (2010): Lean meat content (%) = $62.19 - 0.729 \times$
159 $G2 + 0.144 \times M2$. After 24 h of chilling at 4°C, the weight of the cold carcass and of
160 wholesale cuts from the right carcass side (ham, loin, backfat, shoulder and belly) were
161 recorded, and the proportion (relative percentage) of each carcass cut to the cold right carcass
162 side was calculated.

163

164 ***2.4 Tissue sampling and measurements of meat quality traits in the slaughterhouse***

165 Thirty minutes after slaughter, samples of *Longissimus thoracis et lumborum* muscle (LTL)
166 were taken from the carcass's right side at the level of the first lumbar vertebra, cut into small
167 pieces and immediately frozen in liquid nitrogen. Samples were stored at -76°C until
168 determination of glycolytic potential, lipid oxidation, metabolic enzyme activities and pH at
169 30 min p.m. The latter was assessed with a pH meter equipped with a specific meat electrode
170 (HI98163, Hanna Instruments, Smithfields, RI, USA) after homogenization of 2 g of muscle
171 in 18 mL of 5 mM Na iodoacetate (Lebret, Batonon-Alavo, Perruchot, Mercier, & Gondret
172 (2018)).

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

180 stored at -20°C before determination of IMF and FA contents. Another transversal section of
181 LTL muscle (1.5 cm depth) was taken consecutively (cranial part) and bloomed for 15 min at
182 4°C under artificial light before measurement of color coordinates CIE L^* : lightness, a^* :
183 redness, b^* : yellowness, C^* : saturation (chroma) and h° : hue (average values of 3 different
184 determinations) using a chromameter Minolta CR 400 (Osaka, Japan) with a D65 illuminant,
185 a 1-cm diameter aperture and a 2° observer angle. A third slice of LTL muscle (100 ± 10 g,
186 consecutive to the previous one) was taken to determine drip loss at 4 days p.m. (plastic bag
187 method; Lebret et al., 2018). Last, a piece of deboned loin (1.0 kg of LTL muscle) was taken
188 consecutive to the previous samples and between the 5th and 12th dorsal vertebrae, vacuum
189 packaged, kept at 4°C and shipped to the sensory laboratory (IDELE, Villers-Bocage,
190 France).

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

197 **2.5 Muscle biochemical analyses**

198 Protein ($= 6.25 \times$ nitrogen) and water contents were determined from freeze-dried LTL and
199 SM samples as previously described (Lebret et al., 2018), and expressed as percentage of
200 fresh muscle considering water loss of each muscle sample during freeze-drying. Lipid (IMF)
201 content was determined on LTL and SM samples kept at -20°C by chloroform-methanol (2:1
202 v/v) extraction (Lefaucheur & Lebret, 2020). Fatty acid contents of LTL muscle lipids were
203 determined after FA methylation with boron trifluoride methanol, as described by Lebret et al.
204 (2021). Analyses were performed with a gas chromatograph (Agilent Technologies 7890A,

205 Santa Clara, CA, USA) equipped with an injector, a capillary column (30 m × 0.25 mm
206 internal diameter) filled with a stationary phase containing 50% cyanopropylphenyl and 50%
207 dimethylpolysiloxane (Agilent technologies) and a flame ionization detector (280°C). The
208 carrier gas was hydrogen. The column temperature was increased from 150°C up to 220°C (+
209 4°C/min) and reached a plateau after 10.5 min. Heptadecanoic acid (C17:0) was used as the
210 internal standard. Retention times and peak areas were determined for all samples. The
211 identities of the peaks were determined by comparing them to the retention times of standard
212 FA methyl esters. The amount of each FA was calculated as a function of the internal standard
213 (heptadecanoic acid, C17:0), and was expressed in mg per 100 g of muscle by considering the
214 LTL lipid content.

215 Glycolytic potential, defined as $GP = 2 * [(glycogen) + (glucose) + (glucose-6-phosphate)] +$
216 $(lactate)$ and expressed as $\mu\text{mole equivalent lactate/g}$ of fresh tissue, was determined in LTL
217 muscle sampled 30 min p.m., as previously described (Lebret et al. 2018). On the same
218 samples, activities of lactate dehydrogenase (LDH), citrate synthase (CS) and β -hydroxy-acyl-
219 CoA dehydrogenase (HAD) were determined as markers of glycolytic metabolism, oxidative
220 capacity (tricarboxylic acid cycle) and lipid β -oxidation potential, respectively, as detailed by
221 Lefaucheur & Lebret (2020). Thiobarbituric acid reactive substances (TBARS) content was
222 determined in the LTL muscle samples taken 30 min p.m., after forced chemical oxidation
223 induced by iron trichloride and sodium ascorbate for 0, 60, 120, 180 and 240 min to assess
224 lipid oxidative stability, as detailed by Lebret et al. (2018).

225

226 ***2.6 Sensory analyses and texture measurements of loin***

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

230 in two training sessions with commercial pork. Then, for the first and second slaughtering,
231 loin samples were assessed over 3 sessions: 2 sessions taking place after 7 days of ageing and
232 1 session after 8 d of ageing in vacuum at 4°C. For the third slaughtering, loin samples were
233 assessed over 2 sessions, after 7 d of ageing in vacuum at 4°C. Each session included 8 meat
234 samples, i.e. 2 per experimental group, except the last session which included 4 meat samples
235 (1 per experimental group), to reach a total of 60 samples tested.

236 At each session, on the 8 meat samples tested, a transversal slice of LTL muscle was taken at
237 the level of the 10th dorsal vertebrae for the assessment of raw meat. The remaining cranial
238 part of this loin sample was cut into cubic pieces (25 ± 1 g) and cooked in an oven at 250°C
239 during 5 min 30 s to reach a core temperature of 70°C (determined from previous tests).

240 Samples were served one by one following a random distribution between the 4 experimental
241 groups, with the 4 first and 4 last samples from each session representing the 4 experimental
242 groups. Panelists assessed the appearance of raw meat (red color, marbling, homogeneity of
243 marbling, odor) and the eating traits of cooked meat (odor, flavor, tenderness, juiciness) on a
244 continuous scale from 0 (absence) to 10 (high intensity). The average of individual panelist
245 scores for each sensory trait were calculated per pig and used for statistical analyses.

246 On the same day, a 200 g part of each of the LTL meat pieces (at the level of 11th and 12th
247 dorsal vertebrae) was cut into two similar pieces of 100 g which were cooked in an oven
248 (250°C up to a core temperature of 70°C) and cooled. Then, a 1 cm thick slice was removed
249 from the 6 sides of each meat piece and core pieces were used to prepare 10 rectangular cut
250 stripes of 1 cm² parallel to fiber axis per pig. Shear force was determined perpendicularly to
251 muscle fibers with a Warner-Bratzler cell fitted on a texturometer Instron 3343 (Norwood,
252 MA, USA). The average of shear force measurements were calculated per pig and used for
253 statistical analyses.

254

255 **2.7 Economic indicators**

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

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

272

273 **2.8 Statistics**

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

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

288

289 **3. Results and discussion**

290 ***3.1 Growth performance and carcass traits***

291 Genotype and feeding regimen influenced growth performance of female pigs with no
292 significant G×F interaction on these traits (Table 2). The D pigs tended to have a higher
293 average daily feed intake ($P < 0.10$) but had lower feed efficiency than P pigs, leading to a
294 lower average growth rate and slaughter BW. These findings differ from previous studies
295 reporting higher average growth rate due to higher average daily feed intake but similar feed
296 efficiency in D compared to P(NN) female and castrated male crossbred pigs (Morales et al.,
297 2013; Kowalski et al., 2020). Higher growth performance for D than P (NN) crossbred pigs
298 was also found by Edwards, Tempelman & Bates (2006) even though genotype differences
299 were lower for females than castrated males in their study. The discrepancies among studies
300 may be due to differences between Duroc and also between Pietrain sire lines, as highlighted
301 by Kowalski et al. (2020).

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

305 final BW compared with C pigs. This was more marked among the D crossbreeds with a trend
306 for higher final BW for DR compared to DC pigs, whereas difference between PR and PC
307 pigs was smaller ($G \times F$, $P = 0.053$). In agreement with our results, Sun, Yun, & Kim (2020)
308 reported linear increase in average feed intake and growth rate and a trend for higher feed
309 efficiency with decreasing dietary n-6:n-3 ratio (17:1 to 5:1, isoenergetic and isoproteic diets)
310 in growing-finishing pigs. Belmonte et al. (2021) also found a greater feed efficiency in pigs
311 fed a diet including 5% linseed instead of barley meal (C18:2 n-6:C18:3 n-3 ratio of 1.2 vs.
312 9.4, respectively), but without variation in growth rate or daily feed intake. It can be
313 hypothesized that a potential difference in palatability between the two regimens could
314 contribute to explain these results. However, feeding behavior was not assessed in our
315 experiment. Conversely, other studies reported no differences in growth performance
316 parameters following the increase in dietary n-3 PUFA content obtained by replacing part of
317 soybean meal by crushed linseed (C18:2 n-6:C18:3 n-3 ratio varying from 7.0 to 1.1; Kouba,
318 Enser, Whittington, Nute, & Wood, 2003), palm and sunflower oil by extruded linseed (C18:2
319 n-6:C18:3 n-3 ratio varying from 13.7 to 1.5; Guillevic, Kouba, & Mourot, 2009) or soybean
320 oil with linseed oil (n-6:n-3 PUFA ratio varying from 15:1 to 5:1, Liu & Kim 2018). In our
321 experiment, the measurement of growth performance from pigs individually housed may have
322 affected their voluntary feed intake and feeding behavior. However, such housing conditions
323 were more adequate to reach the objective of the study than group housing with automatic
324 feeders that enhance competition between animals and/or lead to consumption of a diet of
325 inadequate composition in relation to individual BW.

326 Carcass traits were mostly affected by pig genotype whereas feeding regimen and the $G \times F$
327 interaction had much less effects and affected only one trait each (Table 2). Carcass dressing
328 was lower in D pigs than in P pigs and tended to be higher for R pigs compared with C pigs.
329 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.

347

348 **3.2 Meat quality traits**

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

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

358 Compared with P pigs, loin (LTL) meat from D pigs had lower ($P < 0.05$) drip loss and shear
359 force of cooked meat. Meat from D pigs had also lower ($P < 0.05$) a^* and b^* color coordinate
360 values leading to lower C^* (saturation) but non-different h° and L^* values. For meat color of
361 other muscles, genotype differences were more marked in the GS muscle with lower ($P <$
362 0.01) L^* , a^* , b^* , C^* and h° values for D than P pigs. In the GS, compared with C, the R
363 feeding regimen tended to decrease b^* and h° values especially for the DR pigs which
364 exhibited lower h° (i.e. redder color) than the three other groups ($G \times F$ interaction, $P \leq 0.05$).
365 A similar trend for lower h° in the GM of the D and especially DR pigs was found, whereas
366 the other color coordinates did not differ according to genotype or feeding regimen.

367 The lower drip, higher pH 24 h, similar pH 30 min and lightness and slightly reduced color
368 coordinates found in the meat from D vs. P pigs are all in agreement with previous studies
369 comparing the technological quality and color of pork from D vs. P NN crossbreeds (Edwards
370 et al., 2003; Morales et al., 2023; Lowell et al., 2018; Kowalski et al., 2020). The lower shear
371 force of meat from D pigs contrasts with results obtained by Lowell et al. (2018) who reported
372 slightly higher shear force of loin aged 13 d for D vs. P NN crossbred pigs. In two other
373 studies, shear force of loin was similar in D and P NN crossbred pigs (Edwards et al., 2003;
374 Kowalski et al., 2020). The use of meat samples taken and frozen one day after slaughter may
375 explain the lack of texture differences in these studies.

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

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

384

385 ***3.3 Muscle biochemical and metabolic properties***

386 Muscle biochemical composition was markedly affected by genotype and to a lesser extent by
387 feeding regimen (Table 4). Water content in LTL and SM and protein content in LTL were
388 lower ($P < 0.05$) in D pigs than in P pigs, even though genotype differences remain low.

389 Present results found on LTL muscle agree with those of Morales et al. (2013). As expected,
390 IMF content in LTL was higher in D than in P pigs (average of 1.87 vs. 1.37%, respectively,
391 $P < 0.001$) and the same trend was found in SM (average of 3.14 vs. 2.72%, respectively, $P =$
392 0.076). Indeed, higher IMF contents in D compared to P NN pigs have been reported in both
393 crossbreeds (Morales et al., 2013; Lowell et al., 2018; Kowalski et al., 2020) and pure breeds
394 (Ciobanu et al., 2011; Warner, Dunshea, & Channon, 2017). However, and despite the fact
395 that feed was provided ad libitum, the average IMF content found in the LTL of D pigs in our
396 study was in the low range of values reported by other authors in pure or crossbreed D pigs
397 with values ranging from 1.80 % (Plastow et al., 2005) to around 4.0 % (Morales et al., 2013).
398 In this latter study, the IMF content reaches on average 3.5% in females. With this finding,
399 and due to the well described lower IMF content in females compared to castrated males
400 (Schwob, Le Bret, & Louveau, 2020), we cannot argue that the use of females in the present
401 study may explain the observed differences. Our findings rather illustrate the high diversity
402 between Duroc lines for this trait (Redifer, Beever, Stahl, Boler, & Dilger, 2020; Schwob et
403 al., 2020). The R feeding regimen did not affect muscle protein and water contents as
404 observed in growing-finishing Large White pigs with increasing dietary intake of n-3 PUFA

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

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

423

424 ***3.4 Muscle fatty acid contents and lipid oxidation***

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

430 pigs, whereas the C20:5 n-3 (eicosapentaenoic acid, EPA) and C22:6 n-3 (docosahexaenoic
431 acid, DHA) contents did not vary between genotypes. These effects led to lower ratios of
432 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
433 differ between D and P pigs. The present results agree with those of Alonso, Campo, Espanol,
434 Roncales, & Beltran (2009) reporting similar differences in FA composition between Duroc
435 and Pietrain crossbred pigs (even though genotype differences for PUFA content did not reach
436 significance in their study). Our results could be explained by a higher lipid synthesis (i.e.
437 SFA and MUFA, especially the oleic acid C18:1, the major FA in pig tissues) in D pigs than
438 in P pigs that could at least partly result from their higher feed intake (Lebret & Čandek-
439 Potokar, 2022). Thus, the higher IMF content in D than in P pigs contributes to their
440 differences in FA profile.

441 The R feeding regimen reduced ($P < 0.05$) the total SFA, MUFA and PUFA contents due to
442 lower contents of the individual major FA within each of these classes in both genotypes, thus
443 explaining the overall lower IMF content in R vs. C pigs. The reduced MUFA content with R
444 feeding regimen is largely due to a lower content of the C18:1 ($P < 0.001$), which may be
445 explained by the inhibition of the activity of the Δ -9 desaturase enzyme, responsible for the
446 synthesis of C18:1 following diet enrichment in ALA, as demonstrated by Kouba et al.
447 (2003). Above all, the R feeding strongly modified the muscle PUFA content with a marked
448 increase in n-3 PUFA content especially in DR pigs (G×F interaction, $P = 0.032$). Among the
449 n-3 PUFA, ALA was 2.4-fold higher in R vs. C pigs in both genotypes. Conversely, the n-6
450 PUFA and especially LA contents were markedly reduced in DR vs. DC pigs, the difference
451 being less important between PR and PC pigs. This led to a strong decrease by a factor of 2.7
452 (P pigs) up to 3.6 (D pigs) in the n-6:n-3 ratio of the LTL muscle of pigs receiving the R
453 feeding regimen (G×F interaction, $P < 0.001$). These results confirm our hypotheses and are
454 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 $\Delta 5$ and $\Delta 6$ 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 $\Delta 6$
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 $\geq 1.8\%$ (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 ($P < 0.01$)

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

495

496 ***3.5 Meat sensory quality***

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

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

543 The added value calculated per kg of CC was lower ($P < 0.001$) for D than P pigs and tended
544 to be higher for R vs. C pigs ($P = 0.087$). Results expressed per pig showed a lower ($P <$
545 0.001) added value for D compared with P pigs, and higher ($P < 0.01$) for R compared to C
546 pigs, but with a greater effect of the R feeding regimen within the Duroc (+ 13 €/pig) than
547 within the Pietrain crossbreeds (+ 4 €/pig) in our conditions ($G \times F$ interaction, $P = 0.062$).

548 Altogether, these data indicate that, in the current experimental conditions (individual housing
549 and gilts) and context prices, the R feeding strategy would be more profitable with Duroc than
550 Pietrain crossbred pigs. Nevertheless, Pietrain crossbred pigs are still more profitable with
551 market prices for pork carcasses largely determined by their lean meat content and not by
552 other pork quality dimensions.

553

554 4. Conclusion

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

572

573 **Declarations of interest**

574 None.

575

576 **Author contributions**

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

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

583

584 **Funding**

585 This work is part of the ROC+ regional project (2018-2021) and was supported by Région
586 Bretagne and Rennes Métropole. The funding sources were not involved in the conduct of the
587 research, interpretation of data, or writing of the manuscript.

588

589 **Acknowledgements**

590 The authors thank the staff of INRAE experimental farm, feed mill and slaughterhouse (H.
591 Demay, P. Roger, M. H. Lohat, G. Guillemois, J. F. Rouault, J. Liger; UE3P, 35590 Saint-
592 Gilles, France). They are also grateful to PEGASE laboratory staff (S. Daré-Michelot, S.
593 Tacher, F. Mayeur-Nickel, N. Bonhomme) for their excellent technical assistance. The
594 authors acknowledge P. Malletroit (Genesis) for his help to set up experimentation with
595 crossbreed pigs from Duroc boars, A. Minetto (Valorex, France) for his contribution to diet
596 formulations, F. Garcia-Launay (INRAE PEGASE) for her valuable help on calculations of
597 economic indicators, and the Valorex company for providing feed ingredients.

598

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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
730	¹ 90% faba beans + 10% soy beans extruded together.				
731	² Contains 4 000 mg/kg vitamin E.				
732	³ Contains 20 000 mg/kg vitamin E, 50 000 mg/kg vitamin C, and aromatic substances				
733	⁴ Analyzed as described by Lebret et al. (2021) and expressed relative to fresh feed for dry				
734	matter, and to standardized dry matter of 88.0 % for all other components within each diet.				
735	⁵ Fatty acid (FA) composition of diets analyzed by gas chromatography after chloroform-				
736	methanol extraction of lipids as described for FA contents of intramuscular fat.				
737	⁶ ALA: Alpha linoleic acid.				
738	⁷ Calculated values as described by Furbeyre et al. (2020) and expressed on a fresh feed basis,				
739	except vitamin E that was calculated from its concentration in the ingredients of each diet.				

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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								
<i>L</i> *	48.3	50.2	50.9	50.2	3.15	0.12	0.45	0.11
<i>a</i> *	6.02	6.54	6.87	7.09	1.04	0.013	0.18	0.57
<i>b</i> *	4.34	4.85	5.54	5.36	1.17	0.007	0.59	0.26
<i>C</i> *	7.47	8.20	8.87	8.92	1.40	0.005	0.30	0.36
<i>h</i> ^o	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								
<i>L</i> *	42.6	45.2	47.5	47.4	3.19	<0.001	0.14	0.11
<i>a</i> *	9.51	9.69	10.29	10.82	1.32	0.007	0.31	0.61
<i>b</i> *	5.32	6.32	7.10	7.41	1.32	<0.001	0.063	0.32
<i>C</i> *	10.92	11.58	12.51	13.14	1.68	<0.001	0.15	0.96
<i>h</i> ^o	28.9 ^a	32.8 ^b	34.8 ^b	34.2 ^b	3.88	<0.001	0.10	0.030
Color, GM								
<i>L</i> *	46.8	48.1	49.5	48.0	3.83	0.19	0.92	0.17
<i>a</i> *	9.64	9.96	9.57	9.89	1.46	0.85	0.40	0.99
<i>b</i> *	6.18	7.12	7.35	7.23	1.49	0.10	0.30	0.18
<i>C</i> *	11.50	12.28	12.09	12.28	1.86	0.54	0.32	0.54
<i>h</i> ^o	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 ($P < 0.05$).

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757 **Table 4. Biochemical composition and energy metabolism of the Longissimus thoracis et**
 758 **lumborum (LTL) and Semimembranosus muscles in Duroc (D) and Pietrain (P) crossbred**
 759 **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

760 ¹ Least-square means calculated from raw data.

761 ² P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and
 762 RMSE obtained from the ANOVA applied to raw data for all traits, except water, protein and
 763 lipids of the Semimembranosus muscle, for which ANOVA was applied to log-transformed
 764 values to fit a normal distribution. a, b, c, d: differences between experimental groups ($P <$
 765 0.05).

766 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

769 ¹ Least-square means calculated from raw data.

770 ² P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and
 771 RMSE obtained from the ANOVA applied to raw data for all traits, except n-6:n-3, C18:2 n-
 772 6: C18:3 n-3, and SFA:n-3 ratios, for which ANOVA was applied to log-transformed values
 773 to fit a normal distribution. a, b, c, d: differences between experimental groups ($P < 0.05$).

774 ³ SFA: Saturated, MUFA: Monounsaturated, PUFA: Polyunsaturated FA.

775 ⁴ LA: linoleic acid, ALA: alpha-linolenic acid, EPA: ecosapentaenoic acid, DHA:
 776 docosahexaenoic acid.

777 **Table 6. Sensory quality traits (scored on a discrete scale from 0: absent to 10: high) of**
 778 **loin (Longissimus thoracis et lumborum muscle) in Duroc (D) and Pietrain (P) crossbred**
 779 **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

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

782 ² P-values of effects of genotype (G), feeding regimen (F) and their interaction (G×F) and
 783 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**

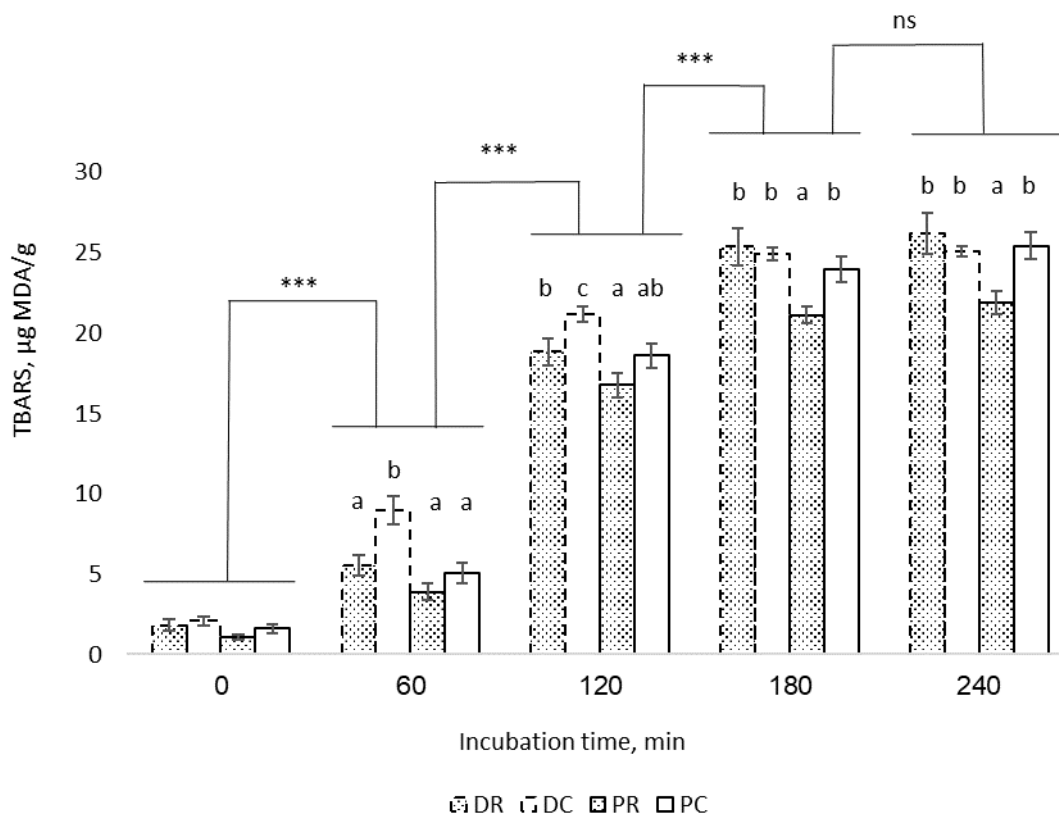
	Experimental groups ¹				RMSE	Significance ²		
	DR	DC	PR	PC		G	F	G×F
Number of animals	15	15	15	15				
Cold Carcass (CC) weight, kg	87.4 ^b	80.3 ^a	94.5 ^c	91.7 ^c	4.00	<0.001	<0.001	0.048
Output price/kg CC, €	1.86	1.79	1.92	1.87	0.05	<0.001	<0.001	0.17
Output price/pig, €	163.0 ^b	143.7 ^a	181.1 ^d	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 lumbarum et thoracis* muscle in Duroc (D) and**
 793 **Pietrain (P) crossbred pigs fed a R or a control (C) diet**

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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