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Estimation of genetic trends in French Large White pigs from 1977 to 1998 for growth and carcass traits using frozen semen^{1,2}

T. Tribout,*^{†3} J. C. Caritez,[‡] J. Gruand,[‡] M. Bouffaud,[§] P. Guillouet,[#] Y. Billon,[‡] C. Péry,^{||} E. Laville,[¶] and J. P. Bidanel*[†]

*INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78350 Jouy-en-Josas, France; †AgroParisTech, UMR1313 Génétique Animale et Biologie Intégrative, F-75231 Paris, France; ‡INRA, UE967 Génétique et Expérimentation en Productions Animales, F-17700 Surgères, France; §INRA, UE450 Testage-Porc, F-35653 Le Rheu, France; #INRA, UE88 Insémination Caprine et Porcine, F-86480 Rouillé, France; ||INRA, UE332 Domaine de Galle, F-18520 Avord, France; and ¶INRA, UMR792 Laboratoire d'Ingénierie des Systèmes Biologiques et des Procédés, F-31077 Toulouse, France

ABSTRACT: Genetic trends for growth, feed efficiency, composition, and morphometry of carcasses were estimated in a French Large White (LW) pig population using frozen semen. Two groups of pigs were produced by inseminating LW sows with either stored, frozen semen from 17 LW boars born in 1977 or with semen from 23 LW boars born in 1998. In each group, 15 males and 90 females were randomly chosen and mated to produce approximately 1,000 pigs/group. These pigs were performance tested with individual ADFI and serial BW and backfat thickness measurements, slaughtered at 105 kg of BW, and measured for carcass traits. The data were analyzed using mixed linear animal models, including the fixed effect of the experimental group (offspring of 1977 or 1998 boars), the random effect of the additive genetic value of each animal, and, when significant, the fixed effects of sex, fattening batch, and slaughterhouse, the linear regression on BW, and the random effect of the common environment of birth litter. For each trait, the genetic

trend was estimated as twice the difference between the 2 experimental groups. Results showed moderately favorable trends for on-test ADG (3.7 ± 1.3 g/d per year) and feed conversion ratio (-0.014 ± 0.005 kg/kg per year) in spite of a tendency toward an increase in ADFI (7.6 ± 4.7 g/yr). A strong reduction in carcass fatness (-0.35 ± 0.07 mm/yr for carcass average backfat thickness) and a large improvement in carcass leanness (0.31 ± 0.10 mm²/yr and $0.41 \pm 0.08\%$ /yr for loin eye area and carcass muscle content, respectively) were observed. Carcass shape measurements (back and leg length, back width, muscle thickness of hind limbs) were not affected by selection. Serial measurements of BW and backfat thickness showed that the major part of the genetic gains occurred during late growth and that the reduction in the backfat layer was more pronounced in the rear than in the front part of the carcass. The use of frozen semen appears to be a powerful practice to thoroughly investigate changes attributable to selection.

Key words: carcass, frozen semen, genetic trend, growth, swine

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INTRODUCTION

The major pig populations have been selected for decades to improve growth efficiency, carcass quality,

and, over the last 15 yr, prolificacy in maternal lines (Ollivier, 1998; Tribout et al., 1998). Large improvements have generally been obtained for the main selected traits (e.g., Ducos and Bidanel, 1993; Chen et al., 2002). Genetic trends for these traits, in particular selection criteria that are routinely measured, can easily be estimated using BLUP genetic evaluation systems, provided that all the information pertaining to the selection process is included in the analyses (Im et al., 1989). However, selection is likely to affect a much larger number of traits that are genetically correlated with those used as selection criteria, but genetic trends for these traits cannot be estimated because of a lack of data. As suggested by Smith (1977), this difficulty can

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³Corresponding author: thierry.tribout@jouy.inra.fr

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be circumvented by storing gametes or embryos and using them after some time to produce groups of pigs that can be compared with more recent populations and that can provide estimates of genetic trends for a large number of traits.

A stock of frozen semen of Large White (LW) boars born in 1977 was collected for this purpose at the end of the 1970s. A part of the stock was used to estimate genetic trends for performance and meat quality traits after 5 and 10 yr of selection (Molénat et al., 1986; Ollivier et al., 1991). Twelve years later, it was decided to repeat the experiment in the LW breed so as to estimate genetics trends after 21 yr of selection for a wider range of production, lean and fat tissue quality, and reproduction traits. This paper presents the experimental design and the results for growth and carcass traits.

MATERIALS AND METHODS

Animals used in this study were raised and slaughtered in accredited slaughterhouses according to the protection of animals rules defined in the French law (Code Rural, articles R214-64 to R214-71; <http://www.legifrance.gouv.fr>).

Brief History of Selection in the French LW Breed from 1977 to 1998

As with most commercial pig populations, the breeding goal of the French LW population has evolved several times in recent decades. Until the mid-1980s, pigs were selected for growth rate, feed efficiency, and carcass leanness using a simple individual selection index (Ollivier et al., 1986). In 1985, a meat quality index, built as a predictor of the technological yield of cooked ham processing and computed as a linear combination of pH of the adductor femoris muscle, water-holding capacity, and reflectance of the biceps femoris muscle (Jacquet et al., 1984), was introduced in the breeding goal. Candidates for selection were selected on a combined selection index based on their own performance and those of slaughtered siblings, with a restriction on meat quality index. At the end of the 1980s, a strong emphasis was placed on improving the litter size through the generalization of so-called “hyperprolific” breeding schemes. Finally, in the mid-1990s, standard selection indexes were replaced by more accurate predictors of breeding values based on multiple-trait BLUP animal model methodology (Tribout et al., 1998). Management and other environmental conditions have improved progressively over the 21-yr period considered, with, for instance, an increasing knowledge of nutritional requirements of the growing pig and the generalization of AI.

Animals and Data Recording

First-Generation Animals and Phenotypes. The design of the experiment is shown schematically in

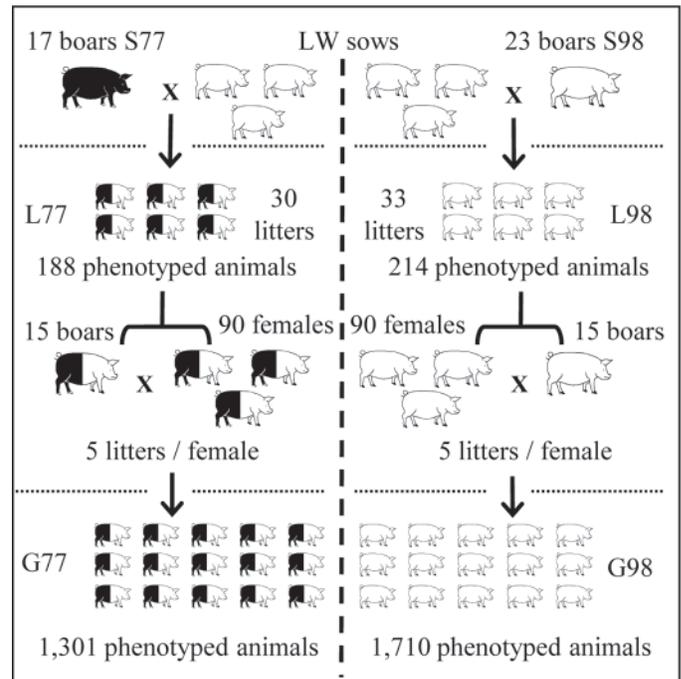


Figure 1. Experimental design. S77 = boars born in 1977; S98 = boars born in 1998; L77 and L98 = first generation of the design; G77 and G98 = second generation of the design; LW = French Large White.

Figure 1. Two groups of LW pigs were produced in one of the INRA GEPA experimental units (Le Magneraud, Surgères, referred to as *Le Magneraud* hereafter) by inseminating 104 contemporary LW sows with frozen semen from LW boars born in 1977 (S77 sires) or with fresh semen of boars born in 1998 (S98 sires). Both S77 and S98 sires were chosen so as to be minimally related and as representative as possible of the population of AI boars in 1977 and 1998, respectively. Moreover, S77 and S98 boars were chosen to have a similar average superiority (i.e., a similar difference in average breeding value) for production traits over their contemporaries. Sows were randomly inseminated with either S77 or S98 semen, but particular attention was paid to having the same average parity number for each group of sows and to avoid inbreeding. Boars were all genotyped for the ryanodine receptor locus responsible for halothane sensitivity (HAL locus). All S98 boar and female founders were found to be free from the halothane sensitivity allele (Hal^S), but 3 of the 17 S77 sires were heterozygous at this same locus. Because studies on the frequency of halothane-sensitive pigs carried out in 1975 and 1976 had shown that the LW population could be regarded as free from the Hal^S allele (Ollivier et al., 1978), the heterozygous progeny of these 3 boars was not considered representative of the 1977 LW population. As a consequence, all progeny of these 3 boars were also genotyped for the HAL locus, and heterozygous pigs were removed from the study (see discussion section). All experimental pigs considered in this study were hence negative for the HAL locus.

A total of 30 litters from 17 S77 sires and 33 litters from 23 S98 sires (L77 and L98 litters, respectively) were produced. The sow herd was managed under a batch farrowing system, with a 3-wk interval between consecutive batches. These batches then became postweaning and performance-test batches of their progeny. Male L77 and L98 piglets were not castrated. At weaning (4 wk of age), one-half of the male and female piglets from each litter were randomly sampled and transferred to the INRA experimental unit at Bourges (Avord, referred to as *Bourges* hereafter), with the other one-half remaining in *Le Magneraud* unit.

In both herds, L77 and L98 male and female piglets were raised in pens of 12 animals and fed ad libitum from 10 until 22 wk of age. Animals were individually weighed at 10, 14, 18, and 22 wk of age and measured for backfat thickness at 14, 18, and 22 wk of age at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib, and the hip joint, respectively) using a real-time ultrasound Aloka SSD-500 device (Ecotro Aloka, Tokyo, Japan).

Second-Generation Animals and Phenotypes. After puberty, 90 L77 females, 90 L98 females, 15 L77 males, and 15 L98 males were randomly chosen from a maximum number of litters and kept to produce a second generation of animals. Matings were performed within each experimental group (L77 and L98), and each female was kept to produce 5 successive litters to estimate realized genetic trends for reproduction and maternal ability traits (results not presented here). The piglets born in these litters are referred to hereafter as G77 and G98 animals. To disentangle direct and maternal effects on early piglet growth, cross-fostering was practiced within the first hours after birth. The objective was to have an equivalent number of G77 and G98 piglets raised by either L77 or L98 nursing sows and to standardize litters to either 7 or 13 piglets. This objective was difficult to achieve in practice, so the number of piglets ranged from 5 to 19, with 2 peaks around 7 and 13. Similarly, the proportions of G77 and G98 piglets in each litter were, on average, close to 50%, but with extreme values of 0 and 100%.

All male piglets were castrated within the first week after birth. At weaning (4 wk of age), a random sample of 298 piglets born in *Le Magneraud* was transferred to the other GEPA experimental herd (Rouillé, referred to as *Rouillé* hereafter). Moreover, 63 randomly sampled piglets born in the *Bourges* unit and 119 randomly sampled piglets born in *Le Magneraud* unit were sent to a fourth INRA experimental unit (Le Rheu, referred to as *Le Rheu* hereafter). All remaining pigs were fattened in their herd of origin (*Le Magneraud* or *Bourges*). In the 4 herds, animals were raised in discontinuous batches (each batch including G77 and G98 individuals of both sexes) and grouped in pens of 12 animals (except in *Le Rheu*, where each pen was made up of 2 animals) of the same sex and experimental group. They were given ad libitum access to water and to a standard pelleted diet formulated to contain 3,200 kcal of DE/kg and 17%

CP from 10 wk of age until the day before slaughter, considered as the end of the test period. The pens in the *Rouillé* herd were equipped with Acema 64 electronic feeders (Acemo, Pontivy, France), allowing the recording of individual food consumption (Labroue et al., 1993). Slaughters occurred once per week on a fixed day, when pig BW reached approximately 105 kg [the average BW at the end of the test period was 106 kg (SD = 6.1 kg)].

Pigs were individually weighed at 10 and 20 wk of age and also the day before slaughter (23rd wk of age, on average, varying from 135 to 199 d of age in both the G77 and G98 groups). Backfat thickness was ultrasonically measured at 20 wk of age at the same 6 locations as for L77 and L98 animals. At the end of the test period, 2 samples of 120 animals fattened in the *Bourges* and *Rouillé* herds, balanced for experimental group and sex, were slaughtered in the INRA experimental slaughterhouses at Jouy-en-Josas and Saint-Gilles, respectively. The remaining pigs were slaughtered in different commercial slaughterhouses [i.e., Montfort-sur-Meu (Cooperl-Hunaudaye, Montfort-sur-Meu, France), Celles-sur-Belle (Socopa, Celles sur Belle, France), and Orléans Viande (Fleury les Aubrais, France) for pigs from the *Le Rheu*, GEPA, and *Bourges* units, respectively]. The same measurement protocol was applied in the different slaughterhouses. Carcass weight was recorded after evisceration on the day of slaughter. The day after slaughter, the length of the carcass from the pubis to the atlas, as well as the backfat thickness at the shoulder, last rib, and hip joint at the sectioned edge of the carcass were recorded. After chilling, the medial and dorsal faces of the right side of the hung carcass were photographed, following the protocol described by Laville et al. (1996) for carcass shape comparison purposes (pigs slaughtered at Montfort-sur-Meu, Jouy-en-Josas, and Saint-Gilles only). Additional measurements used for carcass grading [i.e., backfat thickness between the third and fourth lumbar vertebrae (G1) and between the third and fourth last ribs (G2), as well as loin eye depth between the third and fourth last ribs (M2)] were taken using a CGM probe (Sydel, Lorient, France; Daumas et al., 1998). Finally, a standardized cutting of the right half carcass was performed (Ministère de l'Agriculture et de la Forêt, 1990). Ham, loin, backfat, shoulder, belly, head, foot, leaf fat, and diaphragm were weighed. An additional measurement (i.e., loin eye area) was determined from the outline of the loin eye muscle at the seventh rib (traced on tracing paper). The number of pigs measured per herd and experimental group, as well as the number of fattening batches and slaughter groups per herd are shown in Table 1.

Power of the Design

The power of the actual design (i.e., the probability of detecting a trend if it exists) can be computed as the power of a 2-sided test (i.e., hypothesis 1, $\mu_{98} \neq \mu_{77}$ vs. null hypothesis, $\mu_{98} = \mu_{77}$). If the test statistic T is nor-

Table 1. Numbers of pigs measured per herd and experimental group, and number of fattening batches and slaughter groups per herd in the first and second generations of the design¹

Herd	First generation, ² No.			Second generation, ³ No.			
	Animals		Fattening batches	Animals		Fattening batches	Slaughter groups
	L77	L98		G77	G98		
<i>Le Magneraud</i>	88	95	7	228	450	13	12
<i>Bourges</i>	100	119	7	886	1,027	24	54
<i>Rouillé</i>				122	124	7	17
<i>Le Rheu</i>				65	109	1	5
Total	188	214	14	1,301	1,710	45	88

¹The number of records varies for the different traits.

²First generation = offspring of boars born in 1977 (L77 animals) and in 1998 (L98 animals).

³Second generation = offspring of L77 boars and L77 females (G77 animals) and of L98 boars and L98 females (G98 animals).

mally distributed with variance σ^2 and mean 0 under the null hypothesis and $(\mu_{98} - \mu_{77})$ under hypothesis 1, the power can be computed as

$$\Pr[T > T_c(\alpha)] = \Pr\left[U < \frac{\mu_{77} - \mu_{98}}{\sigma} - z_{(1-\alpha/2)}\right] + \Pr\left[U > \frac{\mu_{77} - \mu_{98}}{\sigma} + z_{(1-\alpha/2)}\right],$$

where α is the significance level of the test, $T_c(\alpha)$ is the α -level critical value, $U = (T - \mu_{98} - \mu_{77})/\sigma \sim N(0, 1)$ and $z_{(1-\alpha/2)}$ is the $(1 - \alpha/2)$ -level critical value of U . Ignoring covariances between experimental groups attributable to female founders, the variance σ^2 is the sum of the sampling variance of the mean of each experimental group, calculated as $V = [1 + (n-1)t_1 + n(d-1)t_2]/nds$ (Smith, 1976), where s is the number of sires, d is the number of dams per sire, n is the number of offspring per dam, and t_1 and t_2 are, respectively, the phenotypic correlations between full-sibs ($t_1 = h^2/2 + c^2$, where h^2 is the heritability of the trait and c^2 is the proportion of phenotypic variance from birth litter environmental origin), and half-sibs ($t_2 = h^2/4$) (Falconer, 1981). Four cases were considered, according to the size of the G77 and G98 samples and their familial structure in the present design: A) $nds = 1,000$ pigs, $ds = 75$ dams, and $s = 18$ boars; B) $nds = 500$ animals, $ds = 75$ dams, and $s = 18$ boars; C) $nds = 180$ animals, $ds = 56$ dams, and $s = 18$ boars; D) $nds = 120$ animals, $ds = 48$ dams, and $s = 17$ boars. Three heritabilities ($h^2 = 0.2, 0.5, \text{ and } 0.7$), corresponding to the range of heritability values for the traits investigated, were considered for each of the 4 cases. The power of the corresponding designs is shown in Figure 2, assuming a value of 5% for α .

Traits Analyzed

Growth traits analyzed included ADG from the beginning to the end of the test period (i.e., from 10

22 wk of age in first-generation pigs, and from 10 wk of age to slaughter in second-generation pigs), as well as between successive BW measurements (i.e., from 10 to 14 wk, 14 to 18 wk, and 18 to 22 wk of age in first-generation pigs, and from 10 to 20 wk of age in second-generation pigs). Body weight at 20 wk of age was not measured on first-generation pigs, but was derived by interpolating BW at 18 and 22 wk of age to compute ADG from 10 to 20 wk of age for L77 and L98 pigs.

Individual cumulative feed consumption was computed as the sum of the amounts of food ingested by an animal at each of its feed intakes during the whole test period (10 to 20 wk of age) and divided by either the BW increase or the length of the test period to compute feed conversion ratio (**FCR**) and ADFI, respectively.

Carcass composition traits included average backfat thickness (computed as the mean of the 6 ultrasonic measurements) at 14, 18, and 22 wk of age in generation 1 and at 20 wk of age in generation 2; dressing percentage; pubis-atlas length; backfat thickness measured at the sectioned edge of the carcass at the levels of the shoulder, the last rib, and the hip joint; G1 and G2 fat depth; M2 loin eye depth; and loin eye area as well as ham, loin, backfat, shoulder, belly, head, feet, leaf fat, and diaphragm weights. An estimated carcass lean content was computed from primal cut weights, expressed as a percentage of half-carcass weight (Métayer and Daumas, 1998):

$$\text{Estimated carcass lean content} = 5.684$$

$$+ 1.197\% \text{ ham} + 1.076\% \text{ loin} - 1.059\% \text{ backfat.}$$

To investigate changes in carcass shape, 10 measurements were taken on carcass numeric images (Figure 3) using Optimas image analysis software (Media Cybernetics, Silver Spring, MD). On the dorsal face, measurements included back dorsal width at the pelvis and 2 angles reflecting the thickness of ham muscles (i.e., the angle between the vertical and a line set down the medial hind leg plumb and the angle between the vertical and a line set down the lateral hind leg plumb). On

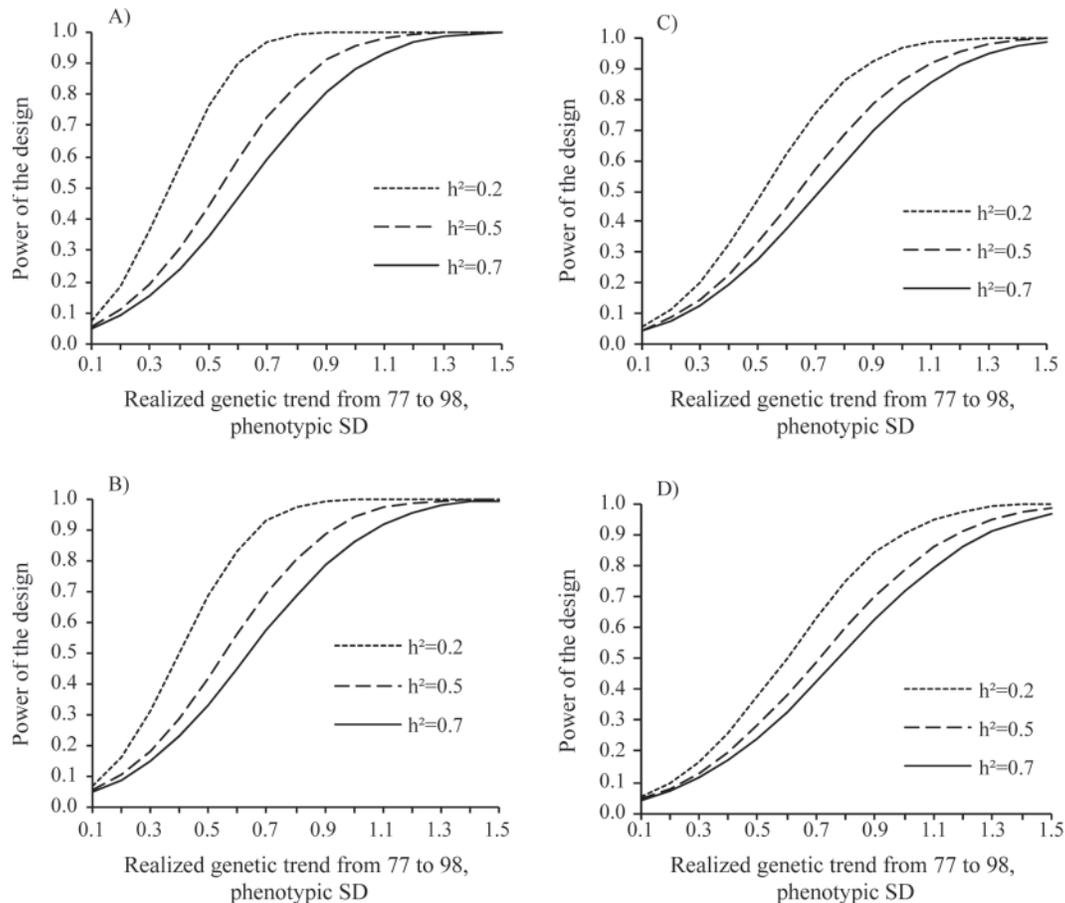


Figure 2. Power of the design for different sample sizes and heritability (h^2) values, as a function of the realized genetic trend from 1977 to 1998 (in phenotypic SD units), assuming a 5% type I error. A) Offspring ($n = 1,000$) from 18 boars and 75 dams measured in each experimental group. B) Offspring ($n = 500$) from 18 boars and 75 dams measured in each experimental group. C) Offspring ($n = 180$) from 18 boars and 56 dams measured in each experimental group. D) Offspring ($n = 120$) from 17 boars and 48 dams measured in each experimental group

the medial face, measurements included a third angle related to the ham muscle thickness (i.e., the angle between the vertical and a line set down the posterior hind leg plumb), 2 indicators of hind leg length (i.e., the distances between the calcaneal tip and the cranial edge of the pubic symphysis and between insertion of the tendon on the toes and the cranial edge of the pubic symphysis). The length of the back was assessed by 3 measurements (i.e., the distances between the cranial edge of the pubic symphysis and the last lumbar vertebra, between the last lumbar vertebra and the last thoracic vertebra, and between the last thoracic vertebra and the first thoracic vertebra). Finally, the depth of the thoracic cavity was estimated by the dorso-ventral height at the level of the thorax. Descriptive statistics for the 44 traits analyzed are presented in Supplemental Table 1 (<http://jas.fass.org/content/vol88/issue9/>).

Statistical Analyses

The data were analyzed using a mixed linear model, taking into account relationships within each of the 2 groups of pigs. With the exception of ADG from 10 to 20 wk of age, traits differed between generations and were consequently analyzed on a within-generation

basis. The model used for each trait was determined using a 2-step procedure. First, the fixed effects and covariates to be included in the final analyses were determined using a fixed linear model with the GLM procedure (SAS Inst. Inc., Cary, NC). The fixed effects investigated were the experimental group (L77 vs. L98, or G77 vs. G98 pigs), the sex (males or females in the first generation; castrates or females in the second generation), the fattening batch (defined as the pigs born during the same week and fattened in the same building), and the abattoir (for traits measured after slaughter). The covariates tested were BW at 10 wk of age (for ADG from 10 to 14 wk of age in first-generation pigs, ADG from 10 to 20 wk of age in both generations of pigs, ADG from 10 wk of age to slaughter in second-generation pigs, FCR, and ADFI), at 14 wk of age (for ADG from 14 to 18 wk of age and ultrasonic backfat thickness at 14 wk of age in first-generation pigs), at 18 wk of age (for ADG from 18 to 22 wk of age and ultrasonic backfat thickness at 18 wk of age in first-generation pigs), at 20 wk of age (for ultrasonic backfat thickness at 20 wk of age in second-generation pigs), at 22 wk of age (for ultrasonic backfat thickness at 22 wk of age in first-generation pigs), and at the end of the test period (for FCR, ADFI, and all the traits mea-

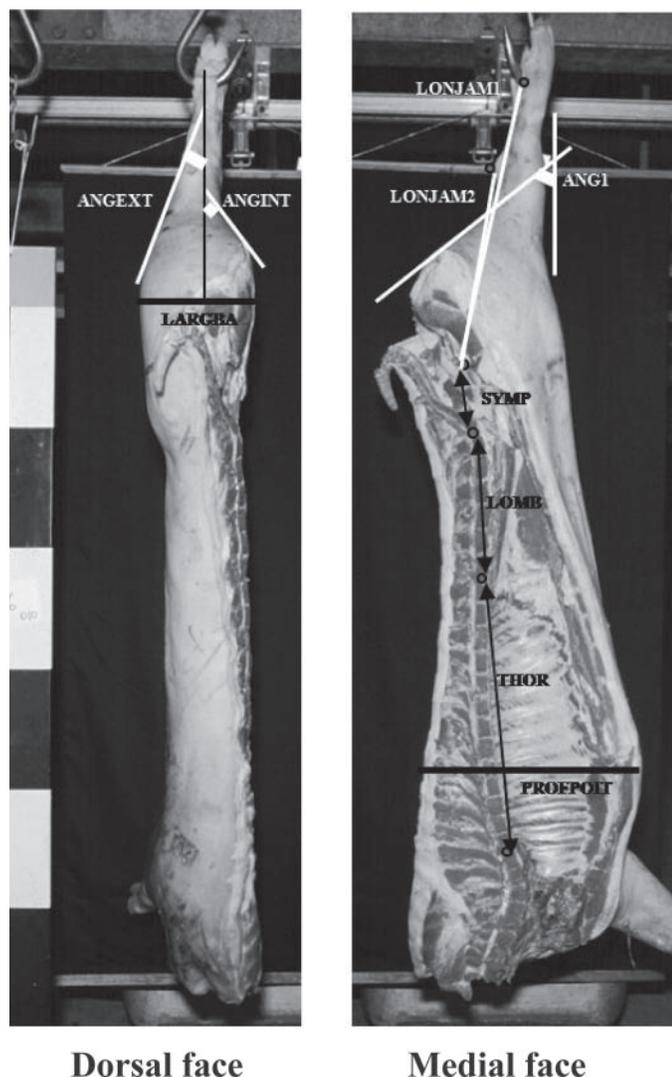


Figure 3. Carcass shape measurements: LONJAM1 = hind leg length between insertion of tendon on toes and the cranial edge of pubic symphysis; LONJAM2 = hind leg length between the calcaneal tip and the cranial edge of pubic symphysis; SYMP = distance between cranial edge of pubic symphysis and the last lumbar vertebra; LOMB = distance between the last lumbar vertebra and the last thoracic vertebra; THOR = distance between the last thoracic vertebra and the first thoracic vertebra; PROFPOIT = dorso-ventral height at thorax; ANG1 = angle between the vertical and a line set down the posterior hind leg plumb; ANGINT = angle between the vertical and a line set down the medial hind leg plumb; ANGEXT = angle between the vertical and a line set down the lateral hind leg plumb; LARGBA = back dorsal width at pelvic.

sured after slaughter). The effects of cross-fostering, of the number of piglets nursed by the nursing sow, and interactions between fixed effects as well as between fixed effects and covariates were tested in preliminary analyses. With very few exceptions, they were found to be nonsignificant ($P > 0.15$) and had no effect on estimates of contrasts between genetic types. They were consequently removed from the final analyses. A joint analysis of the 2 generations was also performed for ADG from 10 to 20 wk of age by adding a generation effect and its interaction with the experimental group in the model. Once the fixed part of the model was established, it was included in a mixed linear model

including the additive genetic value of each animal and the common effect of birth litter as random effects. The fraction of the phenotypic variance attributable to random effects was then estimated using REML methodology applied to the single-trait individual animal model described above with VCE software (Neumaier and Groeneveld, 1998). The effects considered and the estimates of heritability and common litter effect (when significant) for each trait analyzed are given in Supplemental Table 2 (<http://jas.fass.org/content/vol88/issue9/>).

These REML estimates were then introduced as priors in the same mixed models to compute best linear unbiased estimates of the contrasts between genetic groups and to test their significance. The analyses were performed with PEST software (Groeneveld et al., 1990). Finally, contrasts between genetic groups (D_{98-77}) and their SE (seD_{98-77}) were used to estimate genetic trends from 1977 to 1998 (ΔG) and their SE (Smith, 1976) as $\Delta G = (2 \times D_{98-77})$ and $SE = (2 \times seD_{98-77})$.

RESULTS

Performance Traits

Results for growth traits are given in Table 2. Positive estimates of genetic trends for ADG over the whole test period were obtained in both generations, but with a smaller and nonsignificant ($P \geq 0.15$) estimate in the first generation ($+45 \pm 31$ g/d for ADG from 10 to 22 wk of age) and a larger, highly significant ($P = 0.0043$) estimate in second-generation pigs ($+77 \pm 27$ g/d for ADG from 10 wk of age to slaughter). The improvement mainly occurred during late growth: no significant trend was obtained in first-generation pigs from 10 to 14 wk or from 14 to 18 wk of age, whereas ADG significantly increased over the period from 18 to 22 wk of age in first-generation pigs ($+116 \pm 56$ g/d for ADG from 18 to 22 wk of age). Similarly, the contrast between G77 and G98 animals did not reach significance ($P \geq 0.14$) for ADG from 10 to 20 wk of age but became significant ($P = 0.0043$) when considering the whole test period (ADG from 10 wk of age to slaughter in second-generation pigs). Finally, the joint analysis of ADG from 10 to 20 wk of age in second-generation pigs did not reveal any difference between estimated genetic trends in the 2 generations, with a significance level for the generation \times experimental group interaction test of $P = 0.75$ (results not presented).

Although only measured on a limited subsample of second-generation pigs, estimated genetic trends for ADFI and FCR showed a tendency toward an increase ($P = 0.09$) in ADFI (0.16 ± 0.10 kg) and a significant ($P = 0.006$) improvement in FCR (-0.30 ± 0.11 kg/kg). The estimated genetic trends for ultrasonic backfat thickness are given in Table 3. They showed a strong and consistent decrease in carcass adiposity (all P -values < 0.0001) in both generations. The relative reduction in backfat thickness tended to increase with age

Table 2. Estimated genetic trends from 1977 to 1998 for ADG and feed efficiency

Trait ¹	Observations ²		Mean performance ³	σ^4	$\Delta G \pm SE^5$	Pr > f for H0: $\Delta G = 0^6$
	L77	L98				
ADG from 10 to 22 wk of age, g/d	187	214	872	94	45 ± 31	0.15
ADG from 10 to 20 wk of age, ⁷ g/d	187	214	838	91	29 ± 30	0.34
ADG from 10 to 14 wk of age, g/d	187	214	690	106	-15 ± 37	0.69
ADG from 14 to 18 wk of age, g/d	188	214	870	129	17 ± 46	0.71
ADG from 18 to 22 wk of age, g/d	188	214	1,032	170	116 ± 56	0.038
Trait ⁸	G77	G98				
ADG from 10 wk of age to slaughter, g/d	1,287	1,610	883	85	77 ± 27	0.0043
ADG from 10 to 20 wk of age, ⁷ g/d	988	1,213	858	103	36 ± 24	0.14
FCR from 10 to 20 wk of age, kg/kg	104	117	2.76	0.22	-0.30 ± 0.11	0.006
ADFI from 10 to 20 wk of age, kg	104	117	2.07	0.17	0.16 ± 0.10	0.09

¹First generation = offspring of boars born in 1977 (L77 animals) and offspring of boars born in 1998 (L98 animals).

²Number of L77 and L98 (first-generation) or G77 and G98 (second-generation) measurements.

³Average performance of phenotyped animals.

⁴REML estimate of phenotypic SD.

⁵Estimated realized genetic trend from 1977 to 1998 (ΔG) and its SE.

⁶Probability associated with the null hypothesis (H0): $\Delta G = 0$ (P -value) for each trait.

⁷Results obtained by analyzing the data of the first and second generations independently.

⁸Second generation = offspring of L77 boars and L77 sows (G77 animals) and offspring of L98 boars and L98 sows (G98 animals). FCR = feed conversion ratio.

[-2.7 phenotypic SD (σ_{ph}) and -2.8 σ_{ph} at 18 and 22 wk of age, respectively, vs. -1.9 σ_{ph} at 14 wk of age]. It also varied according to the measurement site (Figure 4), with a stronger decrease at the level of the hip joint (-5.9 mm, or -2.7 σ_{ph}) and of the last rib (-4.9 mm, or -2.6 σ_{ph}) than at the shoulder level (-4.7, or -1.9 σ_{ph}).

Carcass Traits

Estimated genetic trends for carcass traits are shown in Tables 4 and 5. Selection did not significantly affect dressing percentage or carcass length ($P > 0.2$).

Similarly, none of the 10 measurements of carcass shape showed any significant change between 1977 and 1998 ($P > 0.3$; Table 5). Conversely, results showed a highly significant increase in loin thickness (loin eye depth and loin eye area; $P < 0.006$). Estimated genetic trends for backfat thickness measured on the sectioned edge of the carcass showed a highly significant decrease ($P < 0.001$). They were consistent with the estimated trends for ultrasonic backfat measurements, with stronger reductions at the hip joint (-7.9 mm, or -2.0 σ_{ph}) and last rib (-7.3 mm, or -2.0 σ_{ph}) than at the shoulder (-7.0 mm, or -1.4 σ_{ph}). However, it should be emphasized that the relative increases in loin eye depth and

Table 3. Estimated genetic trends from 1977 to 1998 for ultrasonic backfat thickness (UBT)

Trait ¹	Observations ²		Mean performance ³	σ^4	$\Delta G \pm SE^5$	Pr > f for H0: $\Delta G = 0^6$
	L77	L98				
Average UBT at 14 wk of age, mm	188	214	9.0	1.0	-1.9 ± 0.4	<0.0001
Average UBT at 18 wk of age, mm	187	214	11.1	1.5	-4.1 ± 0.6	<0.0001
Average UBT at 22 wk of age, mm	188	212	14.8	2.0	-5.6 ± 0.8	<0.0001
Trait ⁷	G77	G98				
UBT at 20 wk of age at hip joint, mm	988	1,213	12.9	2.20	-5.9 ± 0.9	<0.0001
UBT at 20 wk of age at last rib, mm	988	1,213	10.7	1.86	-4.9 ± 0.7	<0.0001
UBT at 20 wk of age at shoulder, mm	988	1,213	17.0	2.42	-4.7 ± 0.8	<0.0001
Average UBT at 20 wk of age, mm	988	1,213	13.5	1.86	-5.2 ± 0.7	<0.0001

¹First generation = offspring of boars born in 1977 (L77 animals) and offspring of boars born in 1998 (L98 animals).

²Number of L77 and L98 (first-generation) or G77 and G98 (second-generation) measurements.

³Average performance of phenotyped animals.

⁴REML estimate of phenotypic SD.

⁵Estimated realized genetic trend from 1977 to 1998 (ΔG) and its SE.

⁶Probability associated with the null hypothesis (H0): $\Delta G = 0$ (P -value) for each trait.

⁷Second generation = offspring of L77 boars and L77 sows (G77 animals) and offspring of L98 boars and L98 sows (G98 animals).

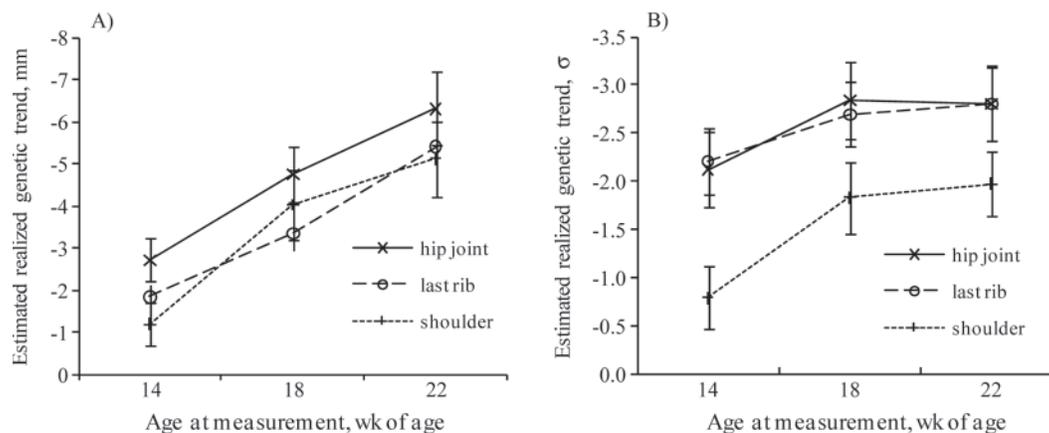


Figure 4. Estimated genetic trends (\pm SE) for ultrasonic backfat thickness at the hip joint, last rib, and shoulder recorded at 14, 18, and 22 wk of age on first-generation pigs. A) Estimated genetic trends, expressed in millimeters. B) Estimated genetic trends, expressed in phenotypic SD (σ) units.

loin eye area were much less (1.1 and 1.2 σ_{ph} , respectively) than the decrease in backfat thickness.

The estimated genetic trend pattern was similar when considering primal cut weights. An important decrease in backfat thickness and a strong increase in loin and ham weights were obtained, resulting in a large

improvement in estimated carcass lean content (+8.6 percentage points, or 2.5 σ_{ph}). When expressed in SD units, the improvement in backfat weight ($-2.4 \sigma_{ph}$) was twice as large as that of loin and ham weights (1.2 and 1.1 σ_{ph} , respectively). Selection also affected internal fat with a significant reduction in leaf fat weight

Table 4. Estimated genetic trends from 1977 to 1998 for carcass traits

Trait ¹	Observations ²		Mean performance ³	σ^4	$\Delta G \pm SE^5$	Pr > f for H0: $\Delta G = 0^6$
	G77 ⁷	G98 ⁸				
Dressing percentage	852	996	77.6	1.80	-0.7 ± 0.6	0.26
Pubis-atlas length, mm	579	673	991.9	27.1	-6.6 ± 10.8	0.54
BTSEC, mm						
At hip joint	553	649	18.6	3.9	-7.9 ± 1.6	<0.0001
At last rib	553	649	19.2	3.3	-7.3 ± 1.2	<0.0001
At shoulder	553	649	30.6	4.6	-7.0 ± 1.5	<0.0001
CGM ⁹ measurements, mm						
G1	857	1,032	19.7	3.8	-10.0 ± 1.5	<0.0001
G2	857	1,032	17.0	3.5	-8.9 ± 1.3	<0.0001
M2	857	1,032	52.1	5.4	6.0 ± 2.1	0.0054
Loin eye area at 7th rib, cm ²	170	167	43.3	5.4	6.6 ± 2.1	0.002
Primal cut wt, kg						
Ham	506	559	9.67	0.50	0.56 ± 0.20	0.005
Loin	504	560	10.45	0.68	0.85 ± 0.30	0.004
Shoulder	506	559	8.32	0.51	-0.17 ± 0.16	0.27
Backfat	504	559	3.04	0.60	-1.41 ± 0.28	<0.0001
Belly	506	560	5.30	0.45	-0.25 ± 0.14	0.07
Feet	482	549	0.97	0.07	0.05 ± 0.03	0.08
Head	320	403	4.72	0.34	0.18 ± 0.14	0.18
Leaf fat	116	120	0.96	0.27	-0.33 ± 0.14	0.02
Diaphragm	116	120	0.31	0.03	0.03 ± 0.02	0.06
ECLC, %	481	550	55.7	3.5	8.6 ± 1.7	<0.0001

¹BTSEC = backfat thickness measured at the sectioned edge of the carcass; G1 = backfat thickness at the third and fourth lumbar vertebrae; G2 = backfat thickness at the third and fourth last ribs; M2 = loin eye depth at the third and fourth last ribs; ECLC = estimated carcass lean content.

²Number of observations per population.

³Average performance of phenotyped animals.

⁴REML estimate of phenotypic SD.

⁵Estimated realized genetic trend from 1977 to 1998 (ΔG) and its SE.

⁶Probability associated with the null hypothesis (H0): $\Delta G = 0$ (P -value) for each trait.

⁷Second-generation intercross of boars born in 1977 and base females.

⁸Second-generation intercross of boars born in 1998 and base females.

⁹CGM (Sydel, Lorient, France).

Table 5. Estimated realized genetic trends from 1977 to 1998 for carcass shape measurements

Trait ¹	Observations ²		Mean performance ³	σ^4	$\Delta G \pm SE^5$	Pr > f for H0: $\Delta G = 0^6$
	G77 ⁷	G98 ⁸				
LONJAM1, cm	151	146	48.8	2.1	0.86 ± 0.98	0.38
LONJAM2, cm	156	158	31.9	1.3	0.44 ± 0.62	0.48
SYMP, cm	156	158	10.9	1.0	-0.10 ± 0.30	0.71
LOMB, cm	156	158	28.0	1.6	-0.08 ± 0.68	0.90
THOR, cm	156	158	47.9	2.5	1.32 ± 1.26	0.30
PROFPOIT, cm	156	158	31.7	1.4	0.72 ± 0.70	0.31
ANG1, degrees	156	158	50.4	4.6	-1.40 ± 2.02	0.49
ANGINT, degrees	100	79	46.1	6.2	-2.10 ± 3.62	0.56
ANGEXT, degrees	100	79	24.9	3.3	0.88 ± 1.42	0.53
LARGBA, cm	100	79	20.0	0.8	0.12 ± 0.38	0.74

¹LONJAM1 = hind leg length between insertion of tendon on toes and the cranial edge of pubic symphysis; LONJAM2 = hind leg length between the calcaneal tip and the cranial edge of pubic symphysis; SYMP = distance between cranial edge of pubic symphysis and the last lumbar vertebra; LOMB = distance between the last lumbar vertebra and the last thoracic vertebra; THOR = distance between the last thoracic vertebra and the first thoracic vertebra; PROFPOIT = dorso-ventral height at thorax; ANG1 = angle between the vertical and a line set down the posterior hind leg plumb; ANGINT = angle between the vertical and a line set down the medial hind leg plumb; ANGEXT = angle between the vertical and a line set down the lateral hind leg plumb; LARGBA = back dorsal width at pelvis.

²Number of observations per population.

³Average performance of phenotyped animals.

⁴REML estimate of phenotypic SD.

⁵Estimated realized genetic trend from 1977 to 1998 (ΔG) and its SE.

⁶Probability associated to the null hypothesis (H0): $\Delta G = 0$ (P -value) for each trait.

⁷Second-generation intercross of boars born in 1977 and base females.

⁸Second-generation intercross of boars born in 1998 and base females.

(-0.33 kg, or $-1.2 \sigma_{ph}$; $P = 0.02$), tended to reduce belly weight ($P = 0.07$) and to increase feet weight ($P = 0.08$). Conversely, no significant trend was observed for head and shoulder weights.

DISCUSSION

The use of frozen semen is a simple and efficient way to estimate realized genetic trends in a population (Smith, 1976). Indeed, it allows genetic trends to be estimated on a large number of traits that are not routinely recorded. This is particularly attractive for phenotypes that are difficult or expensive to measure on a large number of animals, such as quality, behavioral, or physiological components of traits of interest. Genetic trends can also be estimated in various environments (e.g., feeding regimens) to check for potential genotype \times environment interactions. Finally, the estimated genetic trends are basically contrasts between the 2 levels of a fixed effect in a linear model, and are therefore much more robust than annual averages of BLUP EBV, which are known to be sensitive to the data modeling and to the genetic parameters used as priors. Because some of the animals tested in the present design were related (siblings, offspring of related parents), it was decided to model the data with an animal model to take these relationships into account and not to overestimate the significance of the estimated differences between the offspring of S77 and S98 boars. This does not imply that the results are prior dependent because best linear unbiased estimates are more robust than BLUP to bad priors. Indeed, a sensitivity analysis of our results performed by increasing and decreasing the

heritabilities used in PEST by 30% gave results that remained unchanged.

In spite of its interest, frozen semen has seldom been used to estimate genetic trends in livestock. In pigs, besides the above-mentioned French studies (Molénat et al., 1986; Ollivier et al., 1991), the only study was that of Schwab et al. (2007), who estimated genetic trends from 1985 to 2002 for growth, backfat, loin muscle area, and intramuscular fat in American Durocs. This situation is presumably because such an experiment is rather complex to set up. Indeed, semen has to be collected on a random sample of males many years before the implementation of the design, which requires long-term planning of the experiment. Substantial financial support is also required for semen collection and long-term storage, and to compensate for the reduced conception rates attributable to the use of frozen semen, the reduced commercial value of unselected animals, and the measurement costs of numerous traits of interest.

Another limitation of frozen semen designs is that, by construction, they allow comparison of the population genetic levels only at the beginning and at the end of the period considered, without providing the actual shape of the genetic trends. It is rather likely that trends have not been linear in French LW because the relatively simple breeding goal from the late 1970s based on growth, feed efficiency, and carcass merit (Ollivier et al., 1986) has progressively become more complex with the inclusion of meat quality since the mid-1980s and, above all, the emergence of litter size at birth as the major trait of interest in dam populations since the early 1990s. Selection on these new traits has reduced selection pressure on the formerly selected traits, so

trends computed over the 21 yr are inevitably less than those computed over a shorter period of time corresponding to a single breeding goal. This at least partly explains the smaller yearly trends obtained in the current study as compared with those previously obtained in the same population by Molénat et al. (1986) and Ollivier et al. (1991) over the 1977 to 1982 and 1977 to 1987 time periods, respectively (the most striking difference being for ADG, with yearly trends of 24.5 ± 5.9 g/d and 12.8 ± 3.2 g/d, respectively, vs. 3.7 ± 1.3 g/d in the current study). Moreover, the studies by Molénat et al. (1986) and Ollivier et al. (1991) were conducted on smaller numbers of animals (203 and 269 animals, respectively), so the limited accuracy of their estimates of genetic trends can also explain the differences from current results.

The fact that animals are generally compared under current management conditions that would favor modern genotypes and lead to biased results is often put forward as another limitation of frozen semen designs. The latter can address genotype \times environment interactions by comparing experimental groups under different management conditions, but at the expense of an increasing size of the design. Investigation of the genotype \times feeding regimen interaction was one of the initial goals of the project, but this could not be addressed because of both financial and experimental limitations.

Contrary to the above-mentioned experiments, the current study also aimed at estimating genetic trends for reproductive traits, which offered the opportunity to set up a 2-generation design. This extension of the design had several advantages. First, it allowed the size and, consequently, the power of the experiment to be increased. Second, the potential bias attributable to the smaller size of the litters resulting from frozen semen no longer exists in second-generation pigs. Finally, the S77 boars and the "modern" sows can be considered as belonging to 2 different populations, given the large number of generations separating them; consequently, the potential heterosis effects that could have appeared when mating S77 boars to "modern" sows would be divided by 2 in the second generation of the design (Falconer, 1981). This latter hypothesis could be addressed for only 1 trait (i.e., ADG from 10 to 20 wk of age), which is one of the most likely to exhibit heterosis effects. The lack of a generation \times genotype interaction suggests that heterosis effects are absent, or at least very limited, in first-generation pigs.

As mentioned above, 3 of the 17 S77 sires were found heterozygous at the ryanodine receptor locus. This was unexpected because tests for malignant hyperthermia syndrome susceptibility performed on samples of the LW population in 1975 and 1976 showed that the French LW population could be considered free from the Hal^S allele (Ollivier et al., 1978). The presence of 3 heterozygous boars in the S77 sample showed that the Hal^S allele was still present in the population in the

late 1970s, but at a very low frequency, and was due to a greater probability of heterozygotes being selected, given the strong favorable effects of HAL on carcass lean content. It has to be added that the use of AI was minimal at the end of the 1970s, so the diffusion of the Hal^S allele on a large scale was limited, as shown by the results of Ollivier et al. (1978). As a consequence, it was decided that all progeny of the 3 heterozygous S77 boars be removed from the study, to have a sample of pigs that was as representative as possible of the 1977 French LW population. The consequences of these eliminations on the estimated genetic trends were nevertheless very small because fewer than 7% of the piglets produced were likely to be heterozygous for the ryanodine receptor locus.

The significant, favorable trends obtained in the present study for growth rate, feed efficiency, and carcass composition tended to be larger than those previously obtained in the same population by Tixier and Sellier (1986) between 1970 and 1981 and by Ducos and Bidanel (1993) between 1977 and 1990. Indeed, yearly trends for ADG, backfat thickness, and FCR amounted to, respectively, 4.3, -9.0 to -13.3 (depending on the measurement period), and -6.5% of the σ_{ph} in the current study vs. 3.5, -13.7 , and -4.6% of the σ_{ph} by Tixier and Sellier (1986) and 0.8, -6.2 , and -3.6% of the σ_{ph} by Ducos and Bidanel (1993). Both studies estimated genetic trends using mixed model methodology, but used only data from test stations without considering on-farm data, which may have resulted in some underestimation of actual genetic trends.

Yearly trends are also rather comparable with those obtained in other populations. Indeed, similar moderate trends were obtained for growth rate by Kennedy et al. (1996) on 4 Canadian breeds (2.9 to 4.1% of the σ_{ph} for days to 100 kg) and by Chen et al. (2002) on American Yorkshires, Landraces, and Durocs (2.3, 3.1, and 3.2% of the σ_{ph} for age at 113 kg, respectively). Trends for average backfat thickness were much larger and somewhat more variable between populations. Results from the current study were slightly larger than the estimates reported by Chen et al. (2002) in 4 American breeds (-6.4 to -9.2% of the σ_{ph}) and by Kennedy et al. (1996) in 4 Canadian breeds (-4.4 to -9.4% of the σ_{ph}). Differences in the amount of response to selection mean that more emphasis was placed on the reduction of backfat thickness and on the improvement of carcass lean content than on the improvement of growth rate. It should also be emphasized that estimates of genetic trends are generally less than the maximum improvement that is theoretically possible in the pig population (e.g., Smith, 1984). Reasons for these discrepancies are numerous, but are at least partly related to the fact that breeding goals in pig dam lines include additional major objective traits that are independent of (litter size) or unfavorably related to (meat quality) performance traits and reduce the selection pressure on those traits.

This study also provides additional information on the way genetic improvement has acted in the French LW population. In particular, it should be emphasized that the effects of selection on growth and backfat deposition were much larger at the end of the test period. Schwab et al. (2007) also reported differences in daily accretion of backfat between pigs sired by current vs. old-time period Duroc boars, but without any difference in growth rate. Numerous hypotheses can be proposed to explain these differences; the 2 populations may differ in terms of food intake, protein, and fat accretion curves, which would result in differences in the amount and the partitioning of energy to maintenance or to protein and fat deposition during the growth period. It may, for instance, be hypothesized that food intake is a limiting factor in the French LW breed at the beginning of the growth period, which might restrict genetic improvement during early growth. Such questions could be addressed using suitable growth models (e.g., Knap, 1996; Schinckel, 1999) but require specific experiments to estimate the parameters associated with these models.

Furthermore, selection has altered the distribution of lean and fat tissues, as well as loin muscle thickness, without any change in carcass dimensions (i.e., without affecting the size of the skeletal frame). The amounts of both backfat and internal fat tissues have been strongly reduced in favor of lean tissues in both the loin and the ham. The reduction has not been homogeneous all along the carcass because the reduction has been larger at the back of the carcass in spite of a large fat depth at the shoulder. This result is consistent with the result of Legault et al. (1985), who showed in a breed comparison that the profile of the backfat layer differs between lean and fat genotypes. The gradient between fat depths at the levels of the rump and of the back is clearly positive in fat genotypes, such as the Meishan breed, but reduces in leaner genotypes and becomes negative in very lean breeds, such as the Pietrain. A reduction of intramuscular fat content can also be expected based on genetic correlation estimates with carcass composition traits (e.g., Sellier, 1998) and on the results of Schwab et al. (2007), who reported a decrease in intramuscular fat content when comparing current vs. old-time Duroc boars.

In conclusion, this study has demonstrated that the use of frozen semen is a useful practice for investigating the consequences of selection in animal populations. It has been shown that large improvements have been achieved in the French LW population for growth, feed efficiency, and carcass lean content. Additional studies are necessary to investigate the effects of selection on other economically important traits, such as reproduction or meat quality. The use of growth models would be useful to better understand the impact of selection on the different components of pig growth to optimize food utilization, lean tissue growth, and quality while minimizing the environmental impact of pig production.

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Supplementary Material

Supplementary material can be found at:

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