Original article

Genetic parameters of backfat thickness, age at 100 kg and meat quality traits in Pietrain pigs

JP Bidanel [1], A Ducos [2], F Labroue [2], R Guéblez [2], C Gasnier [3]

[1] INRA, Station de Génétique Quantitative et Appliquée, Centre de Recherche de Jouy-en-Josas,
78352 Jouy-en-Josas Cedex;
[2] Institut Technique du Porc, Pôle Amélioration de l'Animal, BP 3, 35650 Le Rheu;
[3] UCAGENOF, Erin, 62134 Anvin, France

Summary — Genetic parameters were estimated for Pietrain pigs using a derivative-free restricted maximum likelihood procedure applied to a multiple trait individual animal model. Two production traits, ie age (AGE) and average backfat thickness (ABT) adjusted to 100 kg liveweight, and 4 meat quality traits, pH of Semispinalis muscle at 45 min *post mortem* (pH_1), ultimate pH (pH_u), drip loss (DL) and cooking loss (CL) of a sample of Semimembranosus muscle, were considered. The data consisted of 5 464 boars tested for AGE and ABT in a single station between 1986 and 1992, of which 1 276 were measured for meat quality traits. The heritabilities of AGE, ABT, pH_1, pH_u, DL and CL are 0.30, 0.45, 0.04, 0.07, 0.04 and 0.24, respectively, with standard errors ranging from 0.02 to 0.03. AGE and ABT exhibit an unfavourable genetic correlation (−0.44 ± 0.05). The genetic correlations between the meat quality traits are high, with the exception of pH_1 which is almost independent of DL and CL. Both pH_1 and pHu show positive, ie unfavourable, genetic correlations with ABT (0.26 ± 0.15 and 0.22 ± 0.12, respectively) and AGE (0.15 ± 0.28 and 0.60 ± 0.21, respectively). DL tends to be unfavourably correlated with ABT (−0.20 ± 0.17), but shows favourable genetic correlations with AGE (0.77 ± 0.19). CL is almost independent of both AGE (0.07 ± 0.12) and ABT (−0.04 ± 0.08).

pigs / genetic parameters / growth / backfat / meat quality

Résumé — **Paramètres génétiques de l'épaisseur de lard dorsal, de l'âge à 100 kg et de caractères de qualité de la viande chez des porcs Piétrain.** *Les paramètres génétiques de caractères de production et de qualité de la viande ont été estimés chez des porcs Piétrain à l'aide d'une procédure du maximum de vraisemblance restreinte sans dérivation appliquée à un modèle animal multicaractères. Les caractères considérés sont, d'une part, l'âge (AGE) et l'épaisseur de lard dorsal (ELD) à 100 kg, d'autre part, le pH du muscle Semispinalis mesuré 40 mn post mortem (pH_1), le pH ultime (pH_u), les pourcentages de perte d'exsudat (PR) et à la cuisson (PC) d'un échantillon de muscle Semimembranosus. L'analyse a porté sur un total de 5 464 verrats contrôlés pour AGE et ELD dans une station unique entre 1986 et 1992, parmi lesquels 1 276 ont fait l'objet de mesures de qualité de la viande. Les valeurs d'héritabilité de AGE, ELD, pH_1, pH_u, PR et PC s'élèvent respectivement à 0,30 ; 0,45; 0,04 ; 0,07 ; 0,04 et 0,24, avec des erreurs standard de 0,02 à 0,03. Une corrélation génétique défavorable (−0,44 ± 0,05) est obtenue entre AGE et ELD.*

Les caractères de qualité de la viande sont fortement corrélés entre eux, à l'exception de pH$_1$, qui est pratiquement indépendant de PR et de PC. pH$_1$ et pH$_u$ présentent des corrélations génétiques défavorables avec AGE (respectivement 0,26 ± 0,15 et 0,22 ± 0,12) et ELD (respectivement 0,15 ± 0,28 et 0,60 ± 0,21). PR tend à être lié de façon défavorable avec ELD (−0,20 ± 0,17), mais est génétiquement lié de façon favorable avec AGE (0,77 ± 0,19). CL est pratiquement indépendant de AGE (0,07 ± 0,12) et de ELD (−0,04 ± 0,08).

porcin / paramètres génétiques / croissance / épaisseur de lard dorsal / qualité de la viande

INTRODUCTION

Accurate estimates of genetic parameters are essential for predicting breeding values and evaluating alternative breeding plans. Numerous estimates of genetic parameters for growth, carcass and to a lesser extent meat quality traits in the Large White (or Yorkshire) and Landrace breeds are available in the literature (see reviews by Ollivier and Sellier, 1982; Sellier, 1988; Stewart and Schinckel, 1988; Hovenier *et al*, 1993; Ducos, 1994). Conversely, estimates of genetic parameters in the Pietrain breed are scarce and generally based on relatively limited numbers of animals. More-over, with the exception of Sönnichsen *et al* (1984a,b), they only deal with growth and carcass traits (Hanset and Van Snick, 1972; Kintaba *et al*, 1981; Lagrange, 1982; Schirvel and Hanset, 1988). Meat quality is becoming increasingly important in pig production. The processing quality of meat has been included in the selection goal and the selection criteria for several years in France. Predictors of the technological yield of cured-cooked ham processing, *ie* pH, reflectance and water-holding capacity (Jacquet *et al*, 1984), are measured on pig carcasses 24 h *post mortem*. However, some abattoirs cannot keep carcasses for 24 h. In such cases, the measurement of the curing cooking yield on a small sample of meat has been suggested (*eg*, Naveau *et al*, 1985). The purpose of this study was to estimate genetic parameters in a Pietrain population for growth rate, backfat thickness and meat quality traits measured on a sample of *Semimembrano-* *sus* muscle using a restricted maximum likelihood (REML) procedure (Patterson and Thompson, 1971) applied to a multiple trait individual animal model.

MATERIALS AND METHODS

Data

The data were obtained from a Pietrain testing station located in the north of France (Erin, Pas-de-Calais) belonging to the Ucagenof selection scheme. The performance data of 5 464 male pigs tested between 1986 and 1992 were used in the analysis. The meat quality measurements began in 1989, and only 1 276 of the pigs were slaughtered and measured for meat quality traits. The pigs originated from 3 Pietrain selection herds with synchronized batch farrowing. Hence, the pigs were tested in batches, which systematically included animals from all 3 herds. All the male pigs from the 3 herds were tested. The structure of the data is shown in table I.

Piglets from each batch entered the testing station at around 35 d of age. They were kept in a postweaning unit until 75 d of age and then allotted to fattening pens of 15–18 animals, where they stayed until the end of the test at 100 kg liveweight. They were fed *ad libitum* during the whole test period with a commercial diet formulated to contain 3 100 kcal of digestibility energy and 17–18% crude protein. At the end of the test, pigs were weighed and backfat thickness was measured ultrasonically on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint. Age (AGE) and average backfat thickness (ABT = mean of the 6 ultrasonic measurements) were adjusted to 100 kg liveweight using the equations established by Jourdain *et al* (1989). The pigs chosen for the meat

Table I. Structure of the data set analysed.

	Traits measured	
	Production	Meat quality
Pigs tested	5 464	1 276
No of sires	175	43
No of dams	651	141
No of batches	40	–
No of tested pigs/batch	136.6	–
No of slaughter dates	–	60
No of tested pigs / slaughter date	–	21.27
No of litters	1 579	619
No of tested pigs/litter	3.46	2.06

quality study were litter-mates of pigs selected for breeding. They were slaughtered at a commercial abattoir 40 km away. Pigs were killed by electrostunning and severing of the *vena cava*. About 45 min after slaughter, the pH of the *Semispinalis* muscle (pH_1) was measured and a sample of about 100 g of *Semimembranosus* muscle was taken from the right-hand side of the carcass. The sample were weighed and hung for 48 h in a plastic bag at 0–4°C. The meat sample was not allowed to touch the bottom of the bag in order to ensure a correct drip. It was then weighed again, measured for pH (pH_u), placed inside another plastic bag in water at 75°C and cooked for 30 minutes. After cooking, the sample was finally wiped and weighed. Drip loss (DL) and cooking loss (CL) were computed as:

$$DL = 100 \times (X_1 - X_2) / X_1$$
$$CL = 100 \times (X_2 - X_3) / X_2$$

where X_1 and X_2 are the weights of the fresh sample at 45 min and 48 h after slaughter, respectively, and X_3 is the weight of the cooked sample.

Model

Genetic effects, common litter environmental effects and residual variance and covariance components were estimated using a derivative-free REML algorithm (Graser *et al*, 1987) applied to a multiple trait individual animal model (IAM). The model for each trait was as follows:

$$y_{ijkl} = \mu + H_i + B_j + bx_{ijkl} + c_{jk} + a_{ijkl} + e_{ijkl}$$

where y_{ijkl} = observation of the *ijkl* th pig; μ = over-all mean; H_i = fixed effect of the *i* th herd of origin (for AGE and ABT only); B_j = fixed effect of the *j* th batch (or slaughter date for meat quality traits); b = regression of y_{ijkl} on weight at slaughter x_{ijkl} (for meat quality traits only); c_{jk} = random effect of the *k* th litter in the *j* th batch; a_{ijkl} = random additive genetic effect of the *l* th pig of the *i* th sex in the *jk* th litter; and e_{ijkl} = random residual associated with the *ijkl* th observation. Location and dispersion parameters for the random effects have the same structure as in Ducos *et al* (1993). The analyses were performed using the derivative-free multiple trait REML procedure described by Groeneveld (1991). For computational reasons, the calculations were done pairwise. Approximate standard errors of variance components and genetic parameters were obtained from an approximation of the Hessian matrix as described by Ducos (1994).

RESULTS

Means and phenotypic standard deviations for the 6 traits studied are shown in table II. Preliminary univariate analyses indicated that common litter effects (c^2) were close to zero (less than 1% of phenotypic standard deviation) for pH_1, pH_u and DL. As a consequence, the common litter variance for these 3 traits was set to zero in multivariate analyses. The litter covariance was also set to zero for all pairs of traits. The herd of origin had a significant effect on AGE and ABT (about 0.2 phenotypic standard deviations between the extremes for both traits). Conversely, the herd of origin effect did not significantly affect meat quality traits and was hence excluded from final analyses for these traits.

Estimates of heritability and common litter effect are shown in table III. Heritability estimates are 0.30 and 0.45, for AGE and ABT respectively. Meat quality traits have

Table II. Means and phenotypic standard deviations (σ_P) for the 6 traits studied.

Trait	Mean	σ_P
Age at 100 kg (d)	177.1	12.2
Average backfat thickness at 100 kg (mm)	6.4	1.2
pH_1 of *Semispinalis* muscle [a]	6.22	0.23
Ultimate pH (pH_u) [b]	5.42	0.11
Drip loss (DL) (%) [b]	2.1	0.7
Cooking loss (CL) (%) [b]	22.2	2.6

[a] Measurement 45 min *post mortem;* [b] measured on a sample of *Semimembranosus* muscle.

low heritability (0.04–0.07), with the exception of CL, which has a medium heritability value (0.24 ± 0.03). Significant common litter effects are found for AGE and ABT (12 and 9% of phenotypic variance respectively). Conversely, the c^2 value for CL is low and non-significant (0.02 ± 0.02).

Estimates of genetic and phenotypic correlations are shown in table IV. AGE and ABT exhibit a rather marked genetic antagonism (–0.44 ± 0.05). The phenotypic correlations between meat quality traits are rather low. The genetic correlations are higher, with the exception of pH_1, which is genetically almost independent from DL and CL. DL and CL are positively correlated (0.75 ± 0.19) and show negative genetic correlations with pH_u (respectively, –0.99 ± 0.15 and –0.72 ± 0.18). The two pH measurements exhibit moderately positive correlations (0.49 ± 0.29). Unfavourable genetic correlations are found between ABT and the 4 meat quality traits. AGE also shows positive, *ie* unfavourable, genetic correlations with pH measurements, particularly pH_u (0.60 ± 0.21), but is favourably related to DL (0.77 ± 0.19).

DISCUSSION

Methodology

The REML procedure using an animal model is now regarded as the method of choice to estimate genetic parameters for traits that can be described by linear models in animal breeding. The growing interest in this methodology is due to its desirable statistical and genetic properties (Harville, 1977). In particular, REML appears to be rather robust to the effects of selection, provided that all the information describing the selection process is included in the analysis

Table III. Estimates of heritability and common environmental effects.

Trait	$h^2 \pm se$ [a]	$c^2 \pm se$ [a]
Age at 100 kg	0.30 ± 0.02	0.12 ± 0.01
Average backfat thickness	0.45 ± 0.02	0.09 ± 0.01
pH_1 of *Semispinalis* muscle [b]	0.04 ± 0.03	–
Ultimate pH (pH_u) [c]	0.07 ± 0.03	–
Drip loss (DL) [c]	0.04 ± 0.03	–
Cooking loss (CL) [c]	0.24 ± 0.03	0.02 ± 0.02

[a] Heritability (h^2) and common environmental effect (c^2) ± standard error; [b] measured 45 min *post mortem*; [c] measured on a sample of *Semimembranosus* muscle.

Table IV. Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations in the Pietrain breed.

Trait	Age at 100 kg	Average backfat thickness	pH_1 of Semispinalis muscle	Ultimate pH (pH_u) [a]	Drip loss (DL) [a]	Cooking loss (CL) [a]
Age at 100 kg	–	-0.44 ± 0.05	0.15 ± 0.28	0.60 ± 0.21	0.77 ± 0.19	0.07 ± 0.12
Average backfat thickness	-0.22 ± 0.03	–	0.26 ± 0.15	0.22 ± 0.12	-0.20 ± 0.17	-0.04 ± 0.08
pH_1 of Semispinalis	-0.05 ± 0.05	0.00 ± 0.03	–	0.49 ± 0.29	0.01 ± 0.24	0.04 ± 0.20
Ultimate pH (pH_u) [a]	0.26 ± 0.05	0.03 ± 0.03	0.01 ± 0.02	–	-0.99 ± 0.15	-0.72 ± 0.18
Drip loss (DL) [a]	0.17 ± 0.05	-0.01 ± 0.03	-0.10 ± 0.02	0.00 ± 0.03	–	0.75 ± 0.19
Cooking loss (CL) [a]	-0.22 ± 0.05	-0.06 ± 0.03	-0.10 ± 0.03	-0.20 ± 0.03	0.34 ± 0.03	–

[a] Measured on a sample of Semimembranosus muscle.

(Meyer, 1990). In pigs, this implies the use of multivariate models, as selection is generally based on several traits. In the present case, the animals were selected using an index involving AGE and ABT. Hence, the fact that pigs slaughtered for meat quality measurements were not chosen at random could be taken into account by 3-trait IAM-REML models including AGE and ABT. In fact, only 2-trait analyses could be performed, due to the huge computational requirements of IAM-REML procedures. As a consequence, the effects of selection were fully accounted for in the analysis of AGE and ABT, but were only partly treated in the other analyses. However, the lack of variability between estimates of variance components obtained from the different 2-trait analyses suggests that the bias should be very limited.

An important assumption usually made when estimating variance components is that the traits analysed exhibit purely polygenic variation. This is probably not true in the present case, as the halothane sensitivity gene (Hal^n) is known to be segregating in most Pietrain populations, with a very high frequency of the halothane sensitivity allele. A segregating major gene in a population generally affects the heritability and the genetic correlations (Smith and Webb, 1981). The effect of the gene on genetic parameters depends on the polygenic variability, the additive and dominance effects and the allele frequency at the corresponding locus. The Hal^n gene is known to affect lean yield, feed efficiency, appetite, survival and meat quality traits such as pH_1, DL and to a lesser extent CL (Webb et al, 1985; Sellier, 1988). However, due to the very high frequency of the halothane sensitivity allele in the French Pietrain population (more than 95% according to first estimations using a molecular test; Sellier, personal communication) the impact of the gene on genetic parameters is likely to be small, except if the halothane sensitivity allele is recessive.

For instance, consider 2 traits with a polygenic heritability of 0.3, a genetic correlation of zero and an additive genetic effect of the gene of 0.5 standard deviation (ie a difference of 1 standard deviation between homozygotes). With no dominance, the overall heritability would be 0.22 and a genetic correlation of 0.11 would be generated by the major gene. The corresponding values would be 0.26 and 0.30 in the case of complete dominance. The REML-animal model methodology used in the present study only estimates the genetic variability due to the combined effects of the major gene and the polygenes. Segregation analysis methods would allow the separation of genetic variation related to a major gene from polygenic variation (Le Roy et al, 1989, Knott et al, 1992). These methods are unfortunately computationally very demanding, so that their use is currently limited to simple pedigrees. Their use becomes unnecessary if the genotype of the animals at the Hal^n gene is known, which has become possible with the recent identification of the ryanodine receptor gene and the elaboration of a molecular test (Fujii et al, 1991).

Genetic parameters

The heritability estimates for AGE and ABT are slightly larger than average literature values for age at 100 kg and backfat thickness in pigs (Stewart and Schinckel, 1988; Ducos, 1994). There was apparently no published heritability value for age at 100 kg in the Pietrain breed. The only comparable estimate concerns lifetime daily gain: Sönnichsen et al (1984a) reported heritability values of 0.16–0.24 in a joint analysis of Pietrain and Belgian Landrace data. The heritability of ABT is larger than the only previously available estimate for ultrasonic backfat thickness in the Pietrain breed (0.20 ± 0.06, Lagrange, 1982). Hanset and Van Snick (1972) and Kintaba et al (1981)

obtained similar heritability estimates for carcass backfat thickness in centrally tested Pietrain pigs. Conversely, a larger value (0.61 ± 0.08) was reported by Schirvel and Hanset (1988).

The heritability values are also larger than (for AGE) or comparable to (for ABT) values obtained in on-farm tested Large White and Landrace pigs in France (Bidanel et al, 1994). Moreover, compared with the values obtained in Large White and Landrace breeds, the phenotypic variance was almost twice as large for AGE and 50% lower for ABT (Bidanel et al, 1994). Hence, the genetic variability in the French Pietrain population appears to be more important for growth rate and less important for backfat thickness than in French Large White or Landrace populations.

The heritability estimate for CL is comparable to average literature values (Sellier, 1988; Ducos, 1994) and shows that an important genetic variation for meat quality exists in the Pietrain breed. Conversely, heritability estimates of pH_1, pH_u and DL are lower than usual values. These low values may indicate a low genetic variation for these traits, but could also be due to insufficiently standardized slaughter, sample collection or measurement conditions. The choice of a 'red' muscle, ie the Semispinalis muscle, which exhibits a much lower pH fall after slaughter, might also be associated with a lower genetic variation of pH_1.

The genetic antagonism between AGE and ABT tends to be more pronounced than indicated by average literature values (around −0.20, Stewart and Schinckel, 1988; Ducos, 1994) and the estimates of Kintaba et al (1981) and Schirvel and Hanset (1988) in the Pietrain breed. This unfavourable relationship tends to decrease the efficiency of selection for growth rate and carcass lean content in the Pietrain breed. The sign and the extent of the genetic correlations between production and meat quality traits are still debated. The recent reviews of Hovenier

et al (1993) and Ducos (1994) show that growth rate or backfat thickness are on average genetically independent from the ultimate pH of the meat, but unfavourably related to meat colour and water-holding capacity. However, large variations exist between individual estimates, which are probably partly due to the population studied and, in particular, to the frequency of alleles at the Hal^n locus in the population. As emphasized by Sellier (1988), growth rate is unfavourably related to meat quality traits in the Large White, but not in the Landrace breed. On the other hand, the antagonism between meat quality and carcass lean content is stronger in highly muscular breeds, as shown by Sönnichsen et al (1984b) and Cole et al (1988). The antagonism between ABT and meat quality traits obtained in the present study is in agreement with these results, even if the most heritable meat quality trait, ie CL, exhibits a rather low genetic correlation with ABT. The genetic relationships between AGE and meat quality traits are more unusual, particularly the large positive correlations with pH_u and DL. The very low phenotypic and genetic correlations between pH_1 and DL are also rather unexpected. However, these results may be due to the relatively low precision of estimates of genetic correlations or to the low additive genetic variance for pH_u and DL, which tends to enlarge any variation of genetic covariances.

CONCLUSION

This study supports previous results from other breeds indicating that meat quality traits show unfavourable genetic correlations with performance traits. As a consequence, any attempt to prevent further deterioration of meat quality in the Pietrain breed will require the inclusion of meat quality measurements in the selection criterion. However, it is necessary to accurately quan-

tify genetic variation due to the halothane sensitivity gene and residual polygenic variability to be able to define optimal selection strategies.

ACKNOWLEDGMENTS

REFERENCES

Bidanel JP, Ducos A, Guéblez R, Labroue F (1994) Genetic parameters of backfat thickness, age at 100 kg and ultimate pH in on-farm tested Large White and French Landrace pigs. *Livest Prod Sci* (in press)

Cole G, Le Henaff G, Sellier P (1988) Paramètres génétiques de quelques caractères de qualité de la viande dans les races porcines Large White, Landrace Français et Landrace Belge. *In: 20es Journées de la Recherche Porcine en France,* Paris, 2–4 February, 1988; Institut Technique du Porc, Paris, 249-254

Ducos A (1994) Évaluation génétique des porcs contrôlés dans les stations publiques à l'aide d'un modèle animal multicaractère. Doctoral Thesis, Inst Nat Agron Paris-Grigon, France, 222 p

Ducos A, Bidanel JP, Ducrocq V, Boichard D, Groeneveld E (1993) Multivariate restricted maximum likelihood estimation of genetic parameters for growth, carcass and meat quality traits in French Large White and French Landrace pigs. *Genet Sel Evol* 25, 475-493

Fujii J, Otsu K, Zorzato F, de Leon S, Khanna VK, Weiler JE, O'Brien PJ, MacLennan DH (1991) Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. *Science* 253, 448-451

Graser HU, Smith SP, Tier B (1987) A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J Anim Sci* 64, 1362-1370

Groeneveld E (1991) Simultaneous REML estimation of 60 covariance components in an animal model with missing values using the Downhill Simplex algorithm. *In: 42nd Annual Meeting of the EAAP*, Berlin, Germany, September 1991, Commission on animal genetics

Hanset R, Van Snick G (1972) Les paramètres génétiques des caractères d'engraissement et de carcasse chez le porc de Piétrain. *Ann Genet Sel Anim* 4, 451-467

Harville DA (1977) Maximum likelihood approaches to variance component estimation and to related problems. *J Amer Stat Assoc* 72, 320-338

Hovenier R, Kanis E, Van Asseldonk T, Westerink NG (1993) Breeding for pig meat quality in halothane negative populations – a review. *Pig News and Information* 14, 17N-25N

Jacquet B, Sellier P, Runavot JP, Brault D, Houix Y, Perrocheau C, Gogué J, Boulard J (1984) Prédiction du rendement technologique de la fabrication du 'Jambon de Paris' à l'aide de mesures prises à l'abattoir. *In: 16es Journées de la Recherche Porcine en France.* 1–3 February, 1984, Institut Technique du Porc, Paris, 49-58

Jourdain C, Guéblez R, Le Hénaff G (1989) Ajustement, à poids vif constant, des critères de contrôle en ferme chez le Large White et le Landrace Français. *In: 21es Journées de la Recherche Porcine en France.* 31 January-2 February, 1989, Institut Technique du Porc, Paris, 399-404

Kintaba KN, Hanset R, Leroy P, Michaux C (1981) Paramètres génétiques des caractères d'engraissement et de carcasse chez le porc de Piétrain et le porc Landrace Belge. *Ann Med Vet* 125, 123-142

Knott SA, Haley CS, Thompson R (1992) Methods of segregation analysis for animal breeding data: a comparison of power. *Heredity* 68, 299-311

Lagrange S (1982) Étude génétique d'une note visuelle de développement musculaire chez le porc de Piétrain en relation avec la sensibilité à l'halothane. Mémoire de DEA, Université de Paris-Sud, 40 p

Le Roy P, Elsen JM, Knott S (1989) Comparison of four statistical methods for detection of a major gene in a progeny test design. *Genet Sel Evol* 21, 341-357

Meyer K (1990) Present status of knowledge about statistical procedures and algorithms to estimate variance and covariance components. *In: 4th World Congress on Genetics Applied to Livestock Production,* Edinburgh, UK, Vol XIII, 407-418

Naveau J, Pommeret P, Lechaux P (1985) Proposition d'une méthode de mesure du rendement technologique : 'la méthode NAPOLE'. *Techni-porc* 8 (6), 7-13

Olliver L, Sellier P (1982) Pig genetics: a review. *Ann Genet Sel Anim* 14, 481-544

Patterson HD, Thompson R (1971) Recovery of inter-block information when block sizes are unequal. *Biometrika* 58, 545-554

Schirvel C, Hanset R (1988) Paramètres génétiques et phénotypiques des caractères d'engraissement et de carcasse des porcs de Piétrain testés à la station de sélection porcine de Wavre (Belgique) de 1982 à 1986. *Ann Med Vet* 132, 401-414

Sellier P (1988) Aspects génétiques des qualités organoleptiques et technologiques des viandes de porc. *In: 20es Journées de la Recherche Porcine en France.* 2–4 February, 1988, Institut Technique du Porc, Paris, 227-242

Smith C, Webb AJ (1981) Effect of major genes on animal breeding strategies. *Z Tierz Zuechtungsbiol* 98, 161-169

Sönnichsen ML, Claus J, Kalm E (1984a) Parameterschätzung und Indexkonstruktion für die Populationen Deutsche Landrasse B und Piétrain in Schleswig-Holstein. 1. Mitteilung: Schätzung von Heritabilitäten. *Zuechtungskunde* 56, 238-248

Sönnichsen ML, Claus J, Kalm E (1984b) Parameterschätzung und Indexkonstruktion für die Populationen Deutsche Landrasse B und Piétrain in Schleswig-Holstein. 2. Mitteilung: Schätzung von genetische und phänotypischen Korrelationen. *Zuechtungskunde* 56, 249-261

Stewart TS, Schinckel AP (1988) Genetic parameters for swine growth and carcass traits. *In: Genetics of Swine* (LD Young, ed) Roman L. Hruska Meat Animal Research Center, Clay Center, Nebraska, 77-79

Webb AJ, Southwood OI, Simpson SP, Carden AE (1985) Genetics of porcine stress syndrome. *In: Stress Susceptibility and Meat Quality in Pigs* (JB Ludvigsen, ed), EAAP Publication n° 33, 9-30