Original article

Estimation of crossbreeding parameters between *Large White* and *Meishan* porcine breeds. I. Reproductive performance

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Summary – A crossbreeding experiment using *Large White* (LW) and *Meishan* (MS) pig strains was conducted. Direct, maternal and grand-maternal additive genetic effects along with direct, maternal and paternal heterosis effects were estimated for litter productivity traits: total number born (TNB), number born alive (NBA), number weaned (NW), litter weight at birth (WB) and at 21 days (W21), either adjusted or not for litter size, and survival rate from birth to weaning (SR). Direct, maternal additive and direct heterosis effects were also estimated for sow traits: weight before farrowing (SWF) and at weaning (SWW), weight loss (SWL) and feed consumption (SFC) during lactation. Data from 267 litters farrowed by 117 sows were analysed. Between breeds additive differences in prolificacy are mainly maternal (3.7 ± 0.9, 4.2 ± 0.8 and 2.8 ± 0.8 piglets/litter in favour of MS for TNB, NBA and NW respectively). Maternal effects are also important, but in favour of LW, for adjusted litter weights. However, due to litter size differences, they are non-significant for unadjusted litter weights. Direct and grand-maternal differences are non-significant for all litter traits, except SR where grand-maternal effects are in favour of MS ($4.1 \pm 1.5\%$). Large additive differences also exist in sow traits: LW dams are heavier (57 ± 8 and 56 ± 6 kg for SWF and SWW respectively) and consume more feed per female (22 ± 7 kg) or per piglet weaned (4.7 ± 0.6 kg) than MS dams. On the other hand, LW and MS dams do not differ for SWL and SFC per unit of litter growth rate. Extremely high non-additive effects are obtained for all traits except SR. Maternal heterosis estimates amount to 2.4 ± 0.4 (TNB), 2.6 ± 0.3 (NBA) and 2.5 ± 0.3 (NW) for litter size, 3.8 ± 0.4 kg (WB) and 20.6 ± 1.5 kg (W21) for unadjusted litter weights, 1.7 ± 0.3 kg (WB) and 11.3 ± 1.0 kg (W21) for adjusted litter weights. High direct heterosis values are also obtained in unadjusted and adjusted litter weights (respectively 2.6 ± 0.6 and 1.9 ± 0.5 kg for WB; 7.9 ± 2.5 and 2.9 ± 1.8 kg for W21), sow weights (respectively 34 ± 4 and 19 ± 3 kg for SWF and SWW) and feed consumption (16 ± 3 kg per female and -0.35 ± 0.07 kg per unit of litter growth rate). On the other hand, none of the traits exhibits any paternal heterosis effect. Some hypotheses are proposed and discussed to explain these high heterosis values.

pigs – crossbreeding parameters – Chinese breeds – reproductive traits

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Résumé − **Estimation des paramètres du croisement entre les races porcines *Large White* et *Meishan*. 1. Performances de reproduction.** *Une expérience de croisement entre des lignées Large White (LW) et Meishan (MS) a été réalisée. Les effets génétiques additifs directs, maternels, grand-maternels ainsi que les effets d'hétérosis directs, maternels et paternels ont été estimés pour les caractères de productivité de la portée: nombre de porcelets nés totaux (NT), nés vivants (NV), sevrés (NS), poids de la portée à la naissance (PPN) et à 21 jours (PP21) ajustés ou non pour la taille de la portée, taux de survie de la naissance au sevrage (TS). Les effets additifs directs et maternels et les effets d'hétérosis direct ont été également estimés pour différents caractères de la truie: poids avant la mise bas (PTN) et au sevrage (PTS), perte de poids (PPT) et consommation alimentaire (CAT) pendant la lactation. Les analyses portent sur 267 portées issues de 117 truies. Les différences additives entre races sont essentiellement maternelles (3, 7 ± 0, 9; 4, 2 ± 0, 8 et 2, 8±0, 8 porcelets/portée en faveur de MS pour NT, NV et NS respectivement). Des effets maternels importants, mais en faveur du LW, existent également pour les poids de portée ajustés. Ils sont par contre non significatifs pour les poids de portée non ajustés du fait des différences de taille de portée. Les effets directs et grand-maternels sont non significatifs pour l'ensemble des caractères de la portée, sauf pour TS où un effet grand-maternel favorable au MS est obtenu (4, 1 ± 1, 5%). Des différences additives importantes existent également pour les caractéristiques des truies: les mères LW sont plus lourdes (57 ± 8 et 56 ± 6 kg pour PTN et PTS respectivement) et consomment davantage d'aliment par femelle (22±7 kg) ou par porcelet sevré (4, 7±0, 6 kg) que les mères MS. A l'inverse, aucun écart significatif entre races n'est observé pour PPT et CAT exprimée par unité de gain de poids de la portée. Les différences additives entre races sont de moindre importance et non significatives pour les autres caractères. Des effets non additifs extrêmement élevés sont obtenus sur l'ensemble des caractères, à l'exception de TS. Les estimations de l'hétérosis maternel atteignent 2, 4±0, 4 (NT), 2, 6±0, 3 kg (NV) et 2, 5±0, 3 (NS) pour la prolificité, 3, 8 ± 0, 4 kg (PPN) et 20, 6 ± 1, 5 kg (PP21) pour les poids de portée non ajustés, 1, 7±0, 3 kg (PPN) et 11, 3±1, 0 kg (PP21) pour les poids de portée ajustés. Des valeurs d'hétérosis direct élevées sont également obtenues pour les poids de portée non ajustés et ajustés (respectivement 2, 6 ± 0, 6 et 1, 9 ± 0, 5 kg pour PPN; 7, 9 ± 2, 5 et 2, 9 ± 1, 8 kg pour PP21), les poids des truies (respectivement 34 ± 4 et 19 ± 3 kg pour PTN et PTS) et la consommation alimentaire (16 ± 3 kg par femelle et −0, 35 ± 0, 07 kg par unité de gain de poids de la portée). Par contre, aucun des caractères étudiés ne présente d'effet d'hétérosis paternel significatif. Des hypothèses sont avancées et discutées pour expliquer ces valeurs d'hétérosis élevées.*

porcins − paramètres du croisement − races chinoises − caractères de reproduction

INTRODUCTION

Improving sow productivity is a major way to increase the economic efficiency of pig production systems in the future (Tess *et al.*, 1983; Legault, 1985). Due to their exceptional reproductive ability, some Chinese pig breeds could play a prominent role in achieving this goal. Comparing the reproductive performance of 3 Chinese breeds (*Meishan, Jiaxing* and *Jinhua*) with that of 2 French breeds (*Large White* and *Landrace*), Legault and Caritez (1983) have indeed shown that the use of half − *Meishan* and half − *Jiaxing* dams leads to a significant increase in sow prolificacy. Unfortunately, these breeds exhibit very poor productive performance, so that the economic value of half − Chinese sows under intensive European production systems is questionable (Legault *et al.*, 1985).

Several other crossbreeding systems can be proposed for taking advantage of the high prolificacy of Chinese breeds (see for instance Sellier and Legault, 1986). However, the high number of possible systems makes any exhaustive experimental evaluation almost impracticable. In this context, the analytical approach developed

by Dickerson (1969, 1973), based on the knowledge of a limited number of cross-breeding parameters (*i.e.* direct, maternal and grand-maternal breed effects, direct, maternal and paternal heterosis effects, and the corresponding epistatic recombination loss effects) is a useful tool for predicting and comparing the relative merit of various crossbreeding schemes.

Accordingly, an experiment was designed to estimate crossbreeding parameters relative to the cross between the most promising Chinese breed, the *Meishan*, and the most widely used French breed, the *Large White*, for the main traits of economic interest. The purpose of the present article is to evaluate breed additive differences and heterosis effects in reproductive traits.

MATERIALS AND METHODS

A. Animals and experimental design

The experiment was carried out at the INRA Experimental Station "Le Magneraud" (Surgères, Charente-Maritime) between 1983 and 1988. Founder animals of the *Meishan* (MS) breed (29 sows and 11 boars) originate from 2 herds (one of them is situated in Le Magneraud and the other one belongs to the French breeding company SELPA). They are derived from 6 animals and are therefore related, but not inbred. Founder animals of the *Large White* (LW) breed (25 sows and 8 boars) partly come from a closed herd (INRA – Station de Recherches Porcines, Saint-Gilles, Ille-et-Vilaine) and partly are sired by A.I. boars, so that there are also some relationships among them, but no inbreeding. Later, some inbreeding occured in MS purebreds, but matings were planned in order to keep inbreeding level at a minimum.

The general "3-step" design of the experiment is shown in Fig. 1. The first step is a 2-breed diallel whose main objective is to produce the 4 genetic types of females (MS, LW×MS, MS×LW, LW) and the 3 genetic types of males (MS, F1, LW) used as parents in the second step. Data from this first step have not been analysed because LW founder animals were selected on an index including average daily gain and backfat thickness and selection rates differed according to the sex, so that results would have been biased. The second step is a complete quadrallel; 12–21 boars from the 3 genetic types MS, F1 and LW are mated to the 4 above-mentioned genetic types of females (22–45 sows per group), leading to the production of 12 genetic types of litters. Sows are normally kept to produce 3 litters, each one with a different genetic type of boar. In the third step, females from these 12 genetic types are mated to boars from a third breed (*Pietrain*) and are kept to produce 5 litters. Breeding animals in the second and third steps were chosen at random within the greatest number of litters after unthrifty animals were culled.

Data analysed in this article originate from the second step of the experiment. The distribution of the 267 litters produced according to sire and dam genetic types is presented in Table I.

B. Herd management

The sow herd has been managed under a batch farrowing system. Each batch included a maximum number of 24 sows. With the exception of some LW gilts

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1st STEP

2nd STEP

3rd STEP   SLAUGHTER
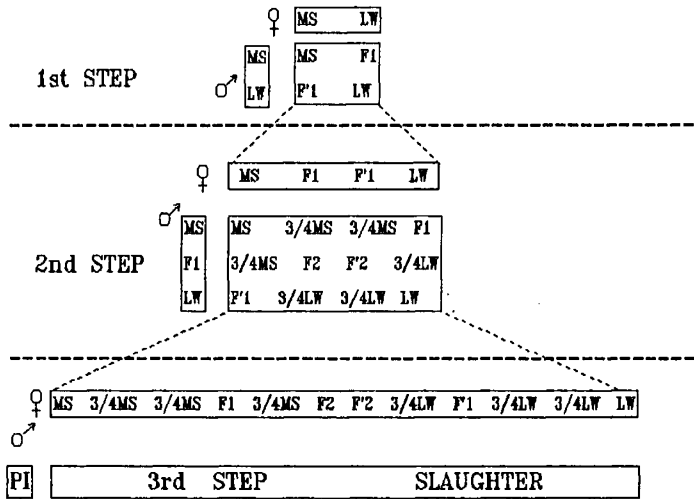
Fig. 1. General design of the crossbreeding experiment between *Large White* and *Meishan* breeds of pigs: LW = *Large White*; MS = *Meishan*; PI = *Pietrain*.

Table I. Distribution of litters by sire and dam genetic types

Sire genetic type (number of sires)	Dam genetic type (number of dams)			
	MS (45)	LW×MS (26)	MS×LW (24)	LW (22)
MS (21)	44	21	21	11
F1 (12)	23	23	23	17
LW (12)	27	21	24	18

MS: *Meishan*; LW: *Large White*. F1: LW×MS or MS×LW (breed of sire given first).

showing delayed puberty, young females were bred at the age of 32 weeks, after a synchronisation treatment with a progestagen. In order to avoid any effect of this treatment on prolificacy, matings were not made on the induced oestrus, but on the following natural one. Natural service was used during the first 2 steps, while artificial insemination was employed in the third one. All females that did not conceive at first mating joined the subsequent farrowing batch where they had the opportunity to be mated once more.

Litters were born in individual farrowing crates. When necessary, some piglets could be moved to another crate within the first few hours after farrowing. With very few exceptions, these procedures were practised within each genetic type. Creep feed was provided to piglets at about 5 days of age. Weaning occurred at around 28 days post-farrowing.

A 16% crude protein and 3100 kcal DE/kg diet was fed to all sows, *ad libitum* during lactation and at the rate of 2–2.2 kg for MS, 2.2–2.5 kg for crossbred and 2.5–2.7 kg for LW during gestation. A 3–4 kg forage complement (Beatruts or alfalfa) was also given during gestation.

C. Traits measured

Fourteen traits have been measured and analysed:
- total number of fully formed piglets born per litter (TNB);
- number of piglets born alive per litter (NBA);
- number of piglets weaned per litter (NW); when adoption occurred, piglets were assigned to their birth litter;
- survival rate from birth to weaning (SR), computed as the number of piglets weaned divided by the number of piglets born alive;
- unadjusted litter weight at birth (UWB). Piglets born alive were individually weighed within the first 12h after farrowing;
- litter weight at birth adjusted for litter size (AWB);
- unadjusted litter weight at 21 days (UW21);
- litter weight at 21 days adjusted for litter size (AW21);
- sow feed consumption during a 30-day lactation period (SFC). Consumption was measured daily during this period. Adjustment to 30 days was computed by truncating long lactations and adding the following quantity (Q) for short lactations: $Q = N \times CL$, where N is the number of missing days and CL the consumption on the day before weaning.
- sow weight before farrowing (SWF);
- sow weight at weaning (SWW);
- total weight loss of the sow between farrowing and weaning (SWL), computed as the difference between SWF and SWW;
- the ratio of sow feed consumption to number weaned during lactation (SFC/NW);
- the ratio of sow feed consumption to litter weight gain during the first 3 weeks of lactation (SFC/LWG).

The latter 2 traits were considered for evaluating feed efficiency of the lactating sow.

Following Matheron and Mauleon (1979), the traits which depended on both sire and dam genetic types were regarded as litter traits. The others were considered as dam traits.

D. Statistical analyses

A 2-step procedure has been used to estimate crossbreeding genetic parameters; they have been computed from genetic type effects using a generalized least-squares method (Fimland, 1983).

1. Estimation of genetic type effects. Genetic type effects were obtained from a mixed model analysis (Henderson, 1984) for all traits except survival rate. The assumed model was as follows:

$$Y_{ijklmn} = \mu + b_i + p_j + d_k + s_p + (ds)_{k_p} + (pd)_{jk} + T_{km} + E_{ijklmn}$$

where Y_{ijklmn} = an observable random variable; μ = an unknown constant; b_i = fixed effect of the ith farrowing batch ($i = 1 \ldots 27$); p_j = fixed effect of the jth parity ($j = 1, 2, 3$); d_k = fixed effect of the kth dam genetic type ($k = 1 \ldots 4$); s_ℓ = fixed effect of the lth sire genetic type ($l = 1, 2, 3$); $(ds)_{kl}$ = interaction effect between dam and sire genetic types; $(pd)_{jk}$ = interaction effect between dam genetic type and parity; T_{km} = random effect of the mth female nested within the kth dam genetic type with mean O and variance σ_t^2; E_{ijklmn} = random residual effect associated with the $ijklmn^{th}$ record, with mean O and variance σ_e^2;

Age at measurement and litter size at birth or at weaning were added as covariables to the model to analyse litter weights.

Preliminary analyses indicated that interactions between genetic type and farrowing batch effects, sire genetic type and individual dam effects, genetic type and age at measurement or litter size were small and not significant. Therefore, these interactions were not considered in the final analyses. The SAS Harvey procedure (SAS Institute, 1986) was used. The individual dam effect was treated as random by including the estimated ratios of residual to sow variances. Equations for sows were then absorbed. Sow variances were estimated from the data with a Restricted Maximum Likelihood method (Patterson and Thompson, 1971) using the same model as above. The SAS Varcomp procedure (SAS Institute, 1985) was used for this estimation. This model does not describe the data quite adequately because the relationships between animals are not taken into account. Estimates of fixed effects remain unbiased, but are not actually best linear unbiased estimates.

Survival rates were analysed with a Maximum Likelihood method (Bishop *et al.*, 1975), using the SAS Catmod procedure (SAS Institute, 1985). The assumed model is the same as above, except that the random individual dam effect is ignored.

2. Estimation of crossbreeding parameters. Crossbreeding parameters were obtained by generalized least-squares analyses of litter or dam genetic type effects. The assumed genetic model was as follows:

$$\boldsymbol{y} = \boldsymbol{Kb} + \boldsymbol{e} \text{ with } \mathrm{Var}(\boldsymbol{y}) = \boldsymbol{V}$$

where $\boldsymbol{y}$ is 12×1 or 4×1 vector of estimates of litter genetic type effects;
$\boldsymbol{b}$ is a 11×1 or 6×1 vector of crossbreeding genetic parameters;
$\boldsymbol{b}' = (\mu \ g_{MS}^o \ g_{LW}^o \ g_{MS}^m \ g_{LW}^m \ g_{MS}^n \ g_{LW}^n \ h^o \ h^m \ h^p \ r^o)$ for litter traits;
$\boldsymbol{b}' = (\mu \ g_{MS}^o \ g_{LW}^o \ g_{ns}^n + g_{ns}^n \ g_{LW}^m + g_{LW}^n \ h^o)$ for dam traits;
where μ is an unknown constant; g_x^o, g_x^m, g_x^n are direct, maternal and grand-maternal effects for breed x (x =LW or MS); h^o, h^m, h^p are direct, maternal and paternal heterosis effects for the MS×LW cross; and r^o is the direct epistatic recombination loss effect. $\boldsymbol{K}$ is a 12×11 or 4×6 matrix relating $\boldsymbol{y}$ to $\boldsymbol{b}$. An example of a $\boldsymbol{K}$ matrix (for litter traits) is shown in Table II; $\boldsymbol{e}$ is a vector of residual errors; $\boldsymbol{V}$ is a 12×12 or 4×4 variance-covariance matrix of $\boldsymbol{y}$.

The generalized least-squares estimate of $\boldsymbol{b}$ is

$$\boldsymbol{b} = (\boldsymbol{K}'\boldsymbol{V}^{-1}\boldsymbol{K})^- \boldsymbol{K}'\boldsymbol{V}^{-1}\boldsymbol{y}$$

$(\boldsymbol{K}'\boldsymbol{V}^{-1}\boldsymbol{K})^-$ being the generalized inverse of $(\boldsymbol{K}'\boldsymbol{V}^{-1}\boldsymbol{K})$.

Table II. Decomposition of litter genetic type means according to Dickerson's crossbreeding parameters (1969).

Litter genetic type[1]		g^o		g^m		g^n		h^o	h^m	h^p	r^o
		LW	MS	LW	MS	LW	MS				
MS	1	0	1	0	1	0	1	0	0	0	0
F1×MS	1	1/4	3/4	0	1	0	1	1/2	0	1	1/4
LW×MS	1	1/2	1/2	0	1	0	1	1	0	0	0
MS×(LW×MS)	1	1/4	3/4	1/2	1/2	0	1	1/2	1	0	1/4
F1×(LW×MS)	1	1/2	1/2	1/2	1/2	0	1	1/2	1	1	1/2
LW×(LW×MS)	1	3/4	1/4	1/2	1/2	0	1	1/2	1	0	1/4
MS×(MS×LW)	1	1/4	3/4	1/2	1/2	1	0	1/2	1	0	1/4
F1×(MS×LW)	1	1/2	1/2	1/2	1/2	1	0	1/2	1	1	1/2
LW×(MS×LW)	1	3/4	1/4	1/2	1/2	1	0	1/2	1	0	1/4
MS×LW	1	1/2	1/2	1	0	1	0	1	0	0	0
F1×LW	1	3/4	1/4	1	0	1	0	1/2	0	1	1/4
LW×LW	1	1	0	1	0	1	0	0	0	0	0

[1] LW = *Large White*; MS = *Meishan*. F1 = LW×MS or MS×LW. The sire breed is mentioned first.
[2] g_x^o, g_x^m, g_x^n = direct, maternal and grand-maternal effects respectively of breed x (x = LW or MS).
h^o, h^m, h^p = direct, maternal and paternal heterosis effects respectively of the MS×LW cross
r^o = direct epistatic recombination loss of the MS×LW cross.

This genetic model is not of full-rank, but can be reparameterized in order to estimate contrasts between the additive effects $g_{MS}^o - g_{LW}^o$, $g_{MS}^m - g_{LW}^m$, $g_{MS}^n - g_{LW}^n$, the direct heterosis effect h^o, and the following linear combinations: $h^m + 1/4\ r^o$, $h^p + 1/4\ r^o$. These 2 latter quantities are most generally referred to as maternal and paternal heterosis effects. Although this terminology is not rigorously true, we shall comply with it on grounds of simplicity.

RESULTS

A. Analyses of variance

Mean squares (or chi-squares for survival rate) and significance of Fisher statistics (or Wald statistics for survival rate) are given in Tables III and IV.

The farrowing batch effect is significant for all traits except litter weight at birth, but examination of batch means suggests that these effects are not related to any seasonal influence.

The parity effect is significant for litter size and unadjusted litter weights, but not for AWB and AW21. This tends to indicate that parity effects on litter weights

Table III. Analyses of variance for litter productivity traits.

source of variation[1]	df	Litter size			Survival rate[3] (%)	Means squares[2]			
						Litter weight (kg)			
						at birth		at 21 days	
		Total number born	Number born alive	Number weaned		unadjusted	adjusted[4]	unadjusted	adjusted[4]
Farrowing batch	27	12.17*	10.41*	7.34**	52.77**	7.02	1.76	118*	51***
Parity	2	81.00***	59.47***	29.75***	11.86***	26.38*	1.93	276*	16
Dam genetic type	3	97.04***	108.28***	85.39***	7.93*	178.96***	37.51***	2827***	1502***
Sire genetic type	2	10.56	7.45	1.89	18.37***	4.90	3.40	92	42
Sire × dam genetic types	6	13.99*	12.36*	10.24*	15.58*	22.61**	9.54***	1877***	41
Parity × dam genetic type	6	2.06	1.31	2.19	14.32*	5.43	1.93	57	47+
Regression on age at measurement	1	–	–	–	–	–	–	4726***	2343***
Regression on litter | linear	1	–	–	–	–	–	444.41***	–	15295***
size[4] | quadratic	1	–	–	–	–	–	24.99***	–	78+
Repeatability[1]		0.31	0.31	0.23	–	0.43	0.49	0.38	0.51
Residual	212 to 221	7.94	7.20	6.95	–	8.08	2.40	106	32

[1] Equations for dams, treated as random effects in the model, were absorbed. Repeatability = ratio of dam to total variance.

[2] $+ : P < 0.10$; $* : P < 0.05$; $** : P < 0.01$; $*** : P < 0.001$.

[3] Chi-squares instead of means squares.

[4] Litter weight is adjusted for number born alive at birth and number weaned at 21 days.

Table IV. Analyses of variance for sow traits.

Source of variation[1]	df	Sow weight (kg)		Sow weight loss during lactation (kg)	Sow feed consumption during lactation (kg)	Feed conversion ratio during lactation[3]	
		at farrowing	at weaning			SFC/LWG	SFC/NW
Farrowing batch	27	383***	209***	381***	782***	0.336*	6.62*
Parity	2	2012***	932***	221	158	0.081	9.22+
Sow genetic type	3	18875***	11305***	2490***	5345***	1.796***	102.28***
Boar genetic type	2	195	70	5	251	0.043	3.53
Sow × boar genetic types	6	164	108	279+	323	0.227	4.07
Parity × sow genetic type	6	161	172+	168	193	0.105	2.02
Repeatability[1]	1	0.49	0.73	0.28	0.22	0.06	0.04
Residual	209	201	132	168	282	0.197	3.96

[1] Equations for sows, treated as random effects in the model, were absorbed. Repeatability = ratio of sow to total variance.

[2] + : $P < 0.10$; * : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$.

[3] SFC/LWG = ratio of sow feed consumption (kg) to litter weight gain (kg). SFC/NW = ratio of sow feed consumption (kg) to number weaned.

are due to differences in litter size. This is, however, not entirely true, for parity tends to influence litter size and weight according to different patterns. Prolificacy remains stable during the 2 first parities and increases steadily in the third one (+3.3 and +2.8 piglets/litter at birth; +1.6 piglet/litter at weaning). On the other hand, litter weights increase linearly with parity, owing to much lower piglet weights in the first litters than in the second and third. Parity also affects sow weight before farrowing (27±6 and 17±8 kg between subsequent parities) and at weaning (18±5 and 10±6 kg between subsequent parities), but has no influence on sow weight loss, feed consumption and efficiency during lactation. These trends are similar for the different genetic types of sows, as indicated by the absence of interaction between parity and dam genetic type. The only exception concerns piglet survival rate from birth to weaning, but this interaction has a complicated structure and is difficult to interpret.

None of the traits except survival rate exhibits any additive variation due to sire genetic type. On the other hand, all traits are greatly affected by dam genetic type. F1 sows have the largest litters at birth and at weaning, with little difference between reciprocal crosses. They farrow about 1 piglet more per litter than MS sows (15.3 vs. 14.2 for TNB; 14.7 vs. 13.7 for NBA) and 4 piglets more per litter than LW sows, whose mean litter size reaches 11.4 (TNB) and 10.3 (NBA). Differences are of similar magnitude at weaning: NW is on average 13.4, 12.2 and 9.4 piglets/litter for F1, MS and LW sows respectively. Litter weight differences follow a somewhat different pattern. Litters from F1 sows are on average much heavier (17.5 kg at birth; 72.0 kg at 21 days) than litters from MS or LW sows (14.0 and 13.0 kg at birth; 50.7 and 50.9 kg at 21 days, respectively). Differences between adjusted litter weights are less important, but litters from crossbred dams remain higher than litters from LW and especially MS sows (+0.9 and +2.8 kg at birth; +3.6 and +16.5 kg at 21 days respectively).

A significant interaction between sire and dam genetic types is obtained for all litter size and weight traits except AW21. Least-squares means for litter genetic types are presented in Table V. This interaction is partly due to an inversion of the ranking of sire genetic types in litters farrowed by purebred dams. Crossbred litters are larger and heavier than purebred ones, indicating the presence of some heterosis effects. Low performance of F1×MS litters also greatly contributes to this interaction.

On the other hand, weight, feed consumption and efficiency of sows during lactation mainly depend on their own genotype. Least-squares means for sow genetic types are presented in Table VI. LW and crossbred females have similar weights before farrowing and are much heavier (around 65 kg) than MS sows. Crossbred females are lighter at weaning, due to higher weight loss at farrowing and during lactation than purebred sows which are comparable from this standpoint. Crossbred sows also tend to consume more feed during lactation than LW (+6 kg) and above all MS (+26 kg). But, in spite of their high feed consumption, crossbred females have a much better feed efficiency (expressed as SFC/LWG) during lactation than purebred. On the other hand, MS sows consume less feed/piglet weaned than LW, F1 being intermediate.

Table V. Least-squares means for litter productivity traits

Litter genetic type[1]		No. of litters	Litter size			Survival rate (%)	Litter weight (kg)			
							at birth		at 21 days	
sire	dam[2]		Total number born	Number born alive	Number weaned		unadjusted	adjusted	unadjusted	adjusted
MS	MS	44	14.3 ± 0.5	13.5 ± 0.5	12.0 ± 0.5	88.0 ± 1.4	13.0 ± 0.5	13.0 ± 0.3	48.6 ± 2.2	51.5 ± 1.3
F1	MS	22	13.2 ± 0.7	12.9 ± 0.7	11.7 ± 0.6	89.7 ± 2.0	13.5 ± 0.7	14.2 ± 0.4	48.4 ± 2.9	51.5 ± 1.6
LW	MS	27	14.9 ± 0.6	14.5 ± 0.6	13.0 ± 0.6	89.2 ± 1.9	16.0 ± 0.6	15.2 ± 0.4	55.8 ± 2.6	53.6 ± 1.5
MS	LW×MS	21	14.0 ± 0.7	13.6 ± 0.7	13.0 ± 0.6	96.6 ± 2.0	17.1 ± 0.7	17.0 ± 0.5	69.4 ± 3.0	68.6 ± 1.8
F1	LW×MS	23	16.1 ± 0.7	15.1 ± 0.6	13.5 ± 0.6	91.9 ± 1.7	18.1 ± 0.7	17.0 ± 0.5	73.4 ± 2.8	68.9 ± 1.7
LW	LW×MS	21	15.1 ± 0.7	14.7 ± 0.7	13.4 ± 0.6	92.1 ± 1.8	18.1 ± 0.7	17.4 ± 0.5	74.6 ± 2.9	72.2 ± 1.7
MS	MS×LW	21	14.6 ± 0.7	13.8 ± 0.7	12.7 ± 0.6	91.3 ± 2.2	16.6 ± 0.7	16.4 ± 0.5	67.2 ± 2.9	66.4 ± 1.7
F1	MS×LW	23	16.3 ± 0.7	15.8 ± 0.7	13.7 ± 0.6	85.0 ± 1.8	17.4 ± 0.7	15.7 ± 0.5	73.0 ± 2.9	67.6 ± 1.7
LW	MS×LW	24	15.5 ± 0.7	15.0 ± 0.6	13.6 ± 0.6	91.2 ± 1.7	17.8 ± 0.7	16.6 ± 0.4	73.8 ± 2.7	68.9 ± 1.6
MS	LW	11	11.4 ± 1.0	11.0 ± 1.0	10.3 ± 0.9	96.7 ± 4.1	14.2 ± 0.9	16.4 ± 0.7	57.4 ± 4.1	67.8 ± 2.5
F1	LW	17	12.0 ± 0.8	10.8 ± 0.8	10.0 ± 0.7	95.3 ± 2.7	13.7 ± 0.8	15.9 ± 0.5	53.0 ± 3.3	63.7 ± 2.0
LW	LW	16	10.6 ± 0.8	9.3 ± 0.8	8.2 ± 0.8	90.1 ± 3.8	11.4 ± 0.9	15.1 ± 0.6	44.2 ± 3.5	63.8 ± 2.1

[1] LW = *Large White*; MS = *Meishan*; F1 = LW×MS or MS×LW.
[2] The sire breed is mentioned first.

Table VI. Least-squares means for sow weight and feed consumption.

Sow genetic type[1]	Number of measurements	Sow weight (kg)		Sow total weight loss during lactation (kg)	Sow feed consumption during lactation (kg)	Feed conversion ratio during lactation[2]	
		at farrowing	at weaning			SFC/LWG	SFC/NW
MS	90	192 ± 3	152 ± 3	40 ± 2	109 ± 3	2.03 ± 0.06	8.94 ± 0.29
LW×MS	62	254 ± 4	198 ± 3	55 ± 3	136 ± 3	1.79 ± 0.07	10.88 ± 0.32
MS×LW	63	260 ± 4	201 ± 3	59 ± 3	134 ± 3	1.69 ± 0.07	10.35 ± 0.31
LW	39	255 ± 5	210 ± 4	45 ± 3	129 ± 4	2.14 ± 0.09	13.11 ± 0.43

[1] LW = *Large White*; MS = *Meishan*. The sire breed is mentioned first.
[2] SFC/LWG = ratio of sow feed consumption to litter weight gain.
SFC/NW = ratio of sow feed consumption to number weaned.

B. Crossbreeding parameters

Because of the significant interaction between dam and sire genetic types, cross-breeding parameters have been estimated regarding prolificacy and litter weights as litter traits. On the other hand, sow weights, feed consumption and efficiency have been considered as dam traits.

Crossbreeding parameters for litter traits are given in Table VII. Additive differences between breeds for prolificacy are mainly of maternal origin. These maternal effects are in favour of MS sows and tend to decrease from birth to weaning (respectively 3.7 ± 0.9; 4.2 ± 0.8 and 2.8 ± 0.8 for TNB, NBA and NW). They are accordingly negative on piglet survival ($-11.8 \pm 3.2\%$). Direct and grand-maternal effects are never significant, except for survival rate where grand-maternal effects are in favour of MS ($4.1 \pm 1.5\%$). Estimates are close to 0 at weaning, but are not negligible at birth. Unfortunately, due to the large sampling errors of the estimates, it is not possible to know whether they reflect real differences. Additive differences between breeds are less important for unadjusted litter weights so that none of the estimated contrasts approaches significance. In general, the MS breed tends to have higher maternal effects and lower direct effects, but both contrasts are quite imprecisely estimated. On the other hand, adjusted litter weights are quite similar to prolificacy, with large maternal effects (but in favour of LW) and non-significant direct and grand-maternal effects.

Direct heterosis effects are quite small for TNB and AW21, but higher for the other traits. Significant estimates are obtained for survival rate (4.7 ± 2.2 percentage points; 5%) litter size at weaning (1.2 ± 0.6; 12%), unadjusted litter weights (2.6 ± 0.6 kg; 21% at birth and 7.9 ± 2.5 kg; 17% at weaning) and AWB (1.9 ± 0.5 kg; 14%). Maternal heterosis effects are highly significant for all traits except survival rate from birth to weaning. These estimates range from 16% (TNB) to 19% (NBA and NW) of parental means for prolificacy and from 11% (AWB) to 36% (UW21) for litter weights. On the other hand, none of paternal heterosis estimates approaches significance.

Crossbreeding parameters for dam traits are given in Table VIII. Sow weights and feed consumption, either expressed on a sow or on a weaned piglet basis, exhibit important additive breed differences, mainly of direct origin. LW sows are much heavier and consume more feed than MS. On the contrary, no additive breed effect appears for weight loss and efficiency of piglet growth during lactation. All traits except feed conversion ratio per piglet present high heterosis effects, with estimates ranging from 10% (SWW) to 35% (SWL) of parental means.

IV. DISCUSSION

First of all, it must be kept in mind that the MS pigs used in this experiment originate from a very limited sample of animals, so that any extrapolation to the MS breed as a whole is unadvisable. Generally, results of MS and crossbred litters are consistent with those previously obtained in France (Legault and Caritez, 1983) and, for MS sows, with results obtained in China (Cheng, 1983; Zhang et al., 1983; Zhang et al., 1986). One exception concerns feed consumption of lactating

Table VII. Crossbreeding parameters for litter productivity traits.

| Parameter[1] | Litter size | | | Survival rate (%) | Litter weight (kg) | | | |
| | Total number born | Number born alive | Number weaned | | at birth | | at 21 days | |
					unadjusted	adjusted	unadjusted	adjusted
g^o	-0.7±0.9	-0.7±0.8	-0.1±0.8	5.1±3.0	-1.2±0.9	-0.7±0.7	-3.1±3.6	-3.6±2.6
g^m	3.7±0.9 ***	4.2±0.8 ***	2.8±0.8 ***	-11.8±3.2 ***	1.3±0.9	-2.2±0.7 **	0.9±3.5	-9.9±2.5 ***
g^n	-0.4±0.5	-0.4±0.5	-0.1±0.5	4.1±1.5 **	0.5±0.5	0.9±0.4 *	1.0±2.0	0.9±1.4
h^o	0.3±0.6	0.9±0.6	1.2±0.6 *	4.7±2.2 *	2.6±0.6 ***	1.9±0.5 ***	7.9±2.5 **	2.9±1.8
$h^m + 1/4 r^o$	2.5±0.4 ***	2.6±0.3 ***	2.5±0.3 ***	-0.0±1.2	3.8±0.4 ***	1.7±0.3 ***	20.6±1.5 ***	11.3±1.0 ***
$h^p + 1/4 r^o$	0.5±0.4	0.4±0.4	0.3±0.3	-2.0±1.2	0.0±0.4	-0.2±0.3	0.3±1.5	-0.4±1.1

[1] g^o, g^m, g^n = contrasts (*Meishan–Large White*) for direct, maternal and grand-maternal effects respectively.
h^o, h^m, h^p = direct, maternal and paternal heterosis.
r^o = direct epistatic recombination loss.
$+: P < 0.10; *: P < 0.05; **: P < 0.01; ***: P < 0.001$

Table VIII. Crossbreeding parameters for sow traits (estimate ± standard error).

Parameter[1]	Sow weight (kg)		Sow total weight loss during lactation (kg)	Sow feed consumption during lactation (kg)	Feed conversion ratio during lactation[2]	
	at farrowing	at weaning			SFC/LWG	SFC/NW
g^o	-57 ± 8 ***	-56 ± 6 ***	-3 ± 5	-22 ± 7 ***	-0.20 ± 0.14	-4.70 ± 0.64 ***
$g^m + g^n$	-6 ± 5	-3 ± 4	-3 ± 4	1 ± 5	0.10 ± 0.10	0.52 ± 0.42
h^o	34 ± 4 ***	19 ± 3 ***	15 ± 3 ***	16 ± 3 ***	-0.35 ± 0.07 ***	0.41 ± 0.31

[1] g^o, g^m, g^n = contrasts (Meishan–Large White) for direct, maternal and grand-maternal effects respectively.
h^o = direct heterosis.

[2] SFC/LWG = ratio of sow feed consumption (kg) to litter weight gain (kg).
SFC/NW = ratio of sow feed consumption (kg) to number weaned.

***: $P < 0.001$.

LW sows, which is much less important than previously reported by Legault and Caritez (1983). In addition, LW purebred matings lead to somewhat lower litter sizes at birth (NBA) and at weaning (NW) than figures usually obtained in France for that breed (*e.g.* Benoit *et al.*, 1987). This could have led to some overestimation of direct heterosis effects and inversely to some underestimation of direct additive effects on prolificacy and litter weights.

The effect of parity on prolificacy is somewhat different from the usual literature results, which generally indicate a linear increase in litter size between first and third parities. A similar trend (*i.e.* a lower than expected performance of second parity females) had already been found by Legault and Caritez (1983). However, this effect is not specific for sows derived from Chinese breeds, as several authors have recently reported similar results (see Clark and Leman, 1986). A common explanation is that high first parity litter size would increase sow weight losses during lactation and affect their subsequent litter size (Hillyer, 1979; Clark and Leman, 1986). This could be the case in the present study; parity does not affect total weight loss of sows but, as first parity litter weights are lighter, net weight loss of gilts during lactation is probably higher than weight loss of sows. Otherwise, the increase of litter weight with parity is a well-known result (see for instance Schneider *et al.*, 1982; Buchanan and Johnson (1984) or Gaugler *et al.* (1984). However, none of these studies investigated the part taken by prolificacy in litter weight variability.

Contrary to parity differences, variation in litter weights between genetic types cannot be entirely explained through litter size. Indeed, adjusted litter weight means indicate an important additive and non-additive variability of individual piglet weight, which will be analysed in the next article of this series.

The analysis of litter and sow weights and of sow feed consumption provides some information on the respective nursing abilities of LW, MS and crossbred females. So, a comparison of the growth of crossbred litters fostered by LW and MS sows shows a significant superiority of LW females over MS. This indicates a better energy supply to piglets and accordingly a better production and/or composition of milk for LW sows. This superiority is likely to come from their greater appetite. Indeed, milk energy originates either from feed consumption of the sow or from the mobilization of the sow's body reserves. The above results seem to indicate that net weight losses of MS and LW sows fostering crossbred litters are comparable. Therefore, the higher milk energy amount provided by LW dams comes from a better energy availability of their body reserves or more likely from a higher feed energy supply related to their greater appetite. This also explains why feed efficiency per unit of piglet growth does not vary among purebreeds. Similar comparisons between LW and crossbred sows indicate a much better milk production and/or composition for F1 females. But, contrary to the former case, the superiority of crossbred dams comes to a large extent from a higher mobilization of their body reserves. The consequence is a better feed efficiency of piglet growth during lactation.

The estimation of genetic parameters has led to some unusual results. The main feature concerns maternal heterosis effects on litter size and weight. Estimates are from 2 to 4 times higher than usual values (from 14 to 36% of the parental means vs. 6-10% for average literature results (Sellier, 1976; Johnson, 1981; Bidanel, 1988). Litter weights also exhibit surprisingly high direct heterosis effects (21% and 17% v.s. 5% and 4% for average literature values on UWB and UW21, respectively).

The large differences in litter size partly explain the high values obtained for litter weights, as shown by adjusting data for litter size. However, even so, estimates remain larger than usual values (14% and 11% at birth; 5% and 19% at 21 days for direct and maternal heterosis respectively).

Obtaining significant heterosis for sow weight is not surprising, as nulliparous and primiparous females are still growing actively and growth traits exhibit important non-additive variations. However, estimates are much larger than usual values. Moreover, heterosis values should reduce with parity, as sows approach their mature size and weight, which are known to be mainly additive. This is not the case here, as estimates do not vary much with parity (35 ± 2, 31 ± 3, 36 ± 4 kg respectively before farrowing; 16 ± 2, 17 ± 3, 23 ± 4 kg at weaning). A partial explanation could be a possible earlier maturity of MS (and maybe crossbred) females, which seem to reach their adult size earlier than LW (Bidanel, Caritez and Legault, unpublished data). The third step of the present experiment will provide more detailed information on this problem. Heterosis for sow feed consumption and efficiency results from complex interactions between body size, appetite, milk production and litter weight gain. More precise studies are necessary to elucidate the respective part played by each of these components.

Several general hypotheses can be proposed to explain the high heterosis values obtained in the present study:

1) The great genetic distance between LW and MS breeds. Heterosis level is related to between-breed genetic distance (Glodek, 1982; Lefort-Buson, 1986). This distance can be characterized through the comparison of allelic frequency distribution at marker loci in each breed (Glodek, 1982; Brunel, 1985). Unfortunately, the low number of founder animals of the French MS line makes it difficult to check this hypothesis. The only noticeable indication concerns the highly polymorphic swine major histocompatibility complex (SLA): among the 5 haplotypes found in the French MS line, 2 also exist in the French LW breed (Christine Renard, personal communication).

2) The existence of some inbreeding in the MS line. Crossbreeding involving inbred lines generally leads to high heterosis values (Sellier, 1970). Yet, this hypothesis is quite unlikely. As stated above, the experimental design has kept inbreeding at a low level ($< 5\%$) so that its effect should be negligible on the basis of average literature values (Hill and Webb, 1982). On the other hand, the existence of some prior inbreeding could not be verified. However, it should not be very high, as parents of founder animals were not closely related.

3) The existence of a dominant major gene for prolificacy in the MS breed. Due to the complexity and the high coefficient of variation of litter size, testing this hypothesis requires considerable experimental work. The existence of a major gene for embryo survival can theoretically be tested from the data analysed in this study through the analysis of F2 and backcross litters distribution. Unfortunately, our present data set is insufficient to draw conclusions.

The other genetic parameters are more consistent with literature results. The lack of paternal heterosis observed in this study seems to be a general fact, as pointed out by recent reviews of Buchanan (1987) and Bidanel (1988). Pani *et al.* (1963) first reported significant grand-maternal effects on litter size at weaning. Since then, several other estimates have been reported by Smith and King (1964), Legault *et*

al. (1975), Nelson and Robison (1976) and Johnson *et al.* (1978). They are all non-significant, in agreement with present results, but are generally estimated with very low precision and do not indicate any consistent trend with respect to the influence of the size of the birth litter of a female on its own reproductive performance. Direct and maternal effects were also estimated with low accuracy. However, the estimates confirm the prominent part played by the dam in the determination of litter size.

CONCLUSION

The first estimation of crossbreeding parameters for *Large White* and *Meishan* is of great interest for studying strategies of economic use in crossbreeding of the *Meishan* breed under intensive European management systems. Because of important maternal heterosis effects on prolificacy, the use of discontinuous crossbreeding plans involving crossbred females *a priori* constitutes the best short-term solution for using the *Meishan* breed. However, as shown by Legault *et al.* (1985) and Gueblez *et al.* (1987), the economic value of such systems also depends on the extent of the deterioration of production performance in Chinese crossbreds. This deterioration can be predicted from the knowledge of appropriate crossbreeding parameters. Estimation of these parameters for growth traits will be presented in the second article of this series.

Moreover, as pointed out by Hill (1971), short-term analysis is not entirely satisfactory for comparing the merit of various crossbreeding plans. Long-term results can differ widely from short-term conclusions, particularly for composite lines or continuous crossbreeding schemes. The value of these latter strategies greatly depends on the proportion of heterosis retained in advanced generations of crossing, *i.e.* on the amount of the epistatic recombination loss effects. The third step of this experiment will provide data for estimating these parameters.

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