Theor Appl Genet (1991) 81:720–728

Crossbreeding effects after long-term selection for purebred performance: a model experiment with mice

1. Performance of F_1 crosses

K.-U. Götz [1,*], P. Glodek [1] and K. Rapp [2]

[1] Institute of Animal Breeding and Genetics, University of Göttingen, Albrecht-Thaer-Weg 1, W-3400 Göttingen, FRG
[2] Institute of Laboratory Animals, Lettow-Vorbeck Allee 57, W-3000 Hannover, FRG

Received August 25, 1990; Accepted November 16, 1990
Communicated by E. J. Eisen

Summary. The influence of purebred selection on the combining abilities of five lines of mice was examined. Two replicated testcross diallels were made after 10 and 20 generations of purebred selection for litter size, weaning weight, weight gain, and feed efficiency. Average direct genetic effects were of major importance, followed by average maternal genetic effects. In all of the replications, between two and four out of ten crosses showed significant heterosis. Heterosis ranged from 0 to 38% in litter size, from 0 to 20% in weaning weight, from −11 to 11% in weight gain, and from −8 to 17% in feed efficiency. For litter size and weaning weight, heterosis estimates increased between 80 and 100% from generation 10 to 20. Weight gain and feed efficiency showed decreasing heterosis with partly negative estimates in the second diallel. Combinations exhibiting significant heterosis varied between replicates and between the two diallels.

Key words: Diallel cross – Heterosis – Maternal effects – Mice

Introduction

Crossbreeding has proven to be an effective way of improving the performance of production in poultry, pigs, and other species with high reproductive rates. Because the degree of heterosis varies between different crosses due to previous selection and inbreeding in the lines, diallel crosses are needed for a final determination of optimal line combinations. Despite this need, methods for the systematic improvement of combining abilities of lines, such as reciprocal recurrent selection (RRS), have not been used in commercial breeding programs except for poultry. The major argument against applying these methods is that selection for purebred performances in different lines will also lead to an improvement of non-additive genetic effects, since different selection criteria will lead to larger genetic distances between lines, so that the costs of RRS schemes are not justified. In commercial crossbreeding programs, most lines are elimininated after the best crossbred combination is chosen from a diallel cross. Therefore, a repeat of the diallel after several generations of purebred selection in the lines cannot be made to check whether the combining ability of the lines has improved or decreased.

The aim of the present experiment was to obtain estimates of the change in crossbreeding parameters after several generations of purebred selection in closed populations. To obtain these estimates, two testcross diallels with mice were made after 10 and 20 generations of selection for purebred performance.

* To whom correspondence should be addressed: Quantitative and Applied Genetics Station, Domaine de Vilvert, F-78350 Jouy-en-Josas, France

Materials and methods

Design

The experiment was carried out from 1976 to 1981 at the Institute of Laboratory Animals, Hannover. From a HAN:NMRI outbred line, six lines were formed by random sampling. Five of these lines were selected for different traits in closed populations for 20 generations. The sixth line was an unselected control. The population size was 50 pairs per line and generation. The selection criteria of the six lines were as follows:

LS: large litter size at birth (number born alive, first parity);
WW: high average weaning weight of young at the age of 4 weeks;
WG: high average weight gain from 4 to 6 weeks;
FE: low average feed efficiency from 4 to 6 weeks (g feed/g gain);
FT: low body fat percentage;
C: unselected control.

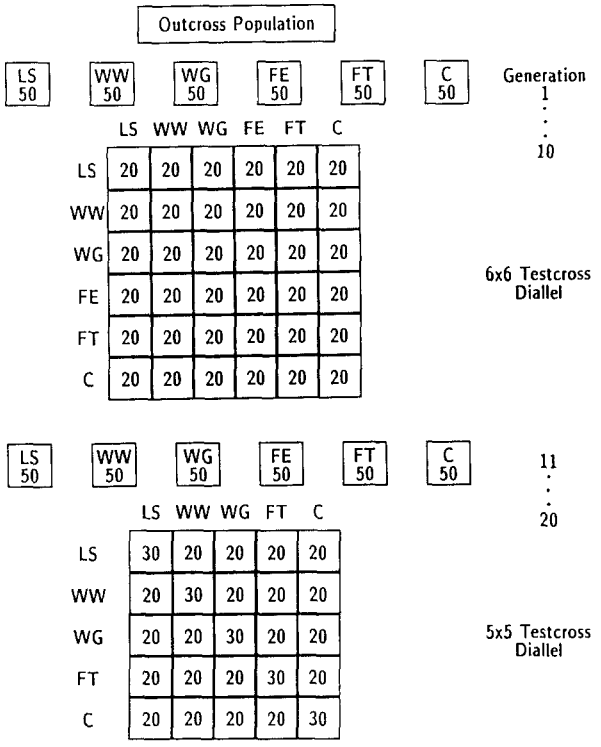

Fig. 1. Design of the experiment (no. of pairs)

Animals in the lines were selected according to an among-family selection scheme. Whenever feasible, complete litters were selected as parents of the next generation. Depending on the fertility rates in the different lines, from 20 to 30% of the litters was selected for replacement. A generation interval of 13 weeks was strictly maintained to avoid seasonal effects. Under this regimen, infertile matings could not be repeated, resulting in different selection intensities for the five lines. The whole experiment was repeated simultaneously in a second room.

After ten generations of purebred selection, a complete 6×6 diallel of testcrosses with 20 matings/subcell was done. The parents in the diallel were taken at random from all litters of the tenth generation. The five lines were then selected for another ten generations. In generation 20, a second testcross diallel was made in the same way as the first one. One of the lines could not be included for lack of capacity. It was decided to drop the FE line because it was similar to line FT. Figure 1 shows the design of the experiment.

One male was caged with one female for 2 weeks, after which females were housed singly and checked daily for litters beginning on day 19. In the first diallel cross, litters were standardized to ten pups on the day of parturition, whereas there was no standardization of litters in the second diallel cross. Mice were weaned at 4 weeks of age and the two sexes were housed in different cages. Weight and feed intake were recorded at 6 weeks of age. Mice were fed ad libitum with "Herilan HAN MR5." The laboratory was maintained at 22 ± 1 °C and 55 ± 5% Rel. Hum.

Statistical analysis

Data were analyzed according to the model proposed by Eisen et al. (1983). Komender (1987, 1988) showed that this model is equivalent to those of Henderson (1948, 1977) and Griffing (1956); i.e., that transformation matrices exist for the conversion of the parameters among these models. The model of Eisen et al. (1983) was chosen because it allows for genetic interpretation of its parameters in terms of gene frequencies, additive and dominance effects.

Because line FE had to be omitted in the second diallel, this line was also omitted in the analysis of the first diallel to ensure the comparability of parameter estimates. Due to an error in the design of the experiment, no data of body fat content were available for the first diallel. Therefore, results are presented only for the traits LS, WW, WG, and FE. The statistical model was as follows:

$$Y_{ijk} = \mu + 1/2\,(l_i + l_j) + m_j + \delta\,(\bar{h} + h_i + h_j + s_{ij} + r^*_{ij}) + e_{ijk}\ ,$$

where

Y_{ijk} = average performance of the k^{th} litter of sire line i and dam line j ($i, j = 1 \ldots 5$);
μ = mean of all purebred animals;
l_i = average direct genetic effect of line i;
m_j = average maternal genetic effect of line j;
δ = 0 for purebred and 1 for crossbred litters;
$\bar{h}$ = average direct heterosis;
h_i = direct heterosis of line i as a deviation from overall direct heterosis;
s_{ij} = specific combining ability of the ij^{th} cross (specific heterosis);
r^*_{ij} = specific reciprocal difference between lines i and j;
e_{ijk} = random error.

For the analysis of the second diallel cross, the covariate litter size was added to the model for traits WW, WG, and FE. The trait LS was analyzed as "number of pups born alive per mating", to include the different levels of female fertility in the lines. Preliminary studies showed no significant interactions between sex of the progeny and crossbreeding parameters. Therefore, females were linearly adjusted to the level of males and both sexes were analyzed together. However, the two replications (rooms) of each diallel were analyzed separately, because the analyses showed highly significant interactions between rooms and group means in both diallels.

Parameter estimation was carried out using weighted least squares in a one-step procedure, as described in Komender (1987) and Komender and Fewson (1987). Weighting factors were the reciprocals of the variances of full-sib means. Using this method, the components of heterosis ($\bar{h}$, h_i, and s_{ij}) as defined by Gardner and Eberhart (1966) can be estimated directly.

Additionally, the parameters $\bar{z}$ and z_i were calculated using the formulae given by Eisen et al. (1983):

$$z_i = \frac{1}{2p}\left[(p-1)\,(\bar{y}^*_{i.} + \bar{y}^*_{.i} - \bar{y}_c) - (p-2)\,\bar{y}_{ii} - \bar{y}_a\right]$$

and

$$\bar{z} = \frac{1}{p}\sum_i z_i\ ,$$

where $\bar{y}^*_{i.}$ ($\bar{y}^*_{.i}$) is the mean of sire (dam) line i averaged over crosses with all other lines, excluding parental lines, $\bar{y}_c$ is the mean of all crosses, $\bar{y}_a$ the mean of all purebreds, and p is the number of lines in the diallel.

Results and discussion

Table 1 shows the significance (F-test) of the different crossbreeding parameters in the analysis of variance. Sig-

Table 1. Significance (F-test) of the parameters of the model of Eisen et al. (1983) by traits and replications (rooms)

Trait	Room	Line direct (l_i)	Direct maternal (m_i)	Average heterosis ($\bar{h}$)	Line heterosis (h_i)	Specific heterosis (s_{ij})	Reciprocal effects (r^*_{ij})	Direct heterosis (h_{ij})	n
First diallel									
LS	1	*	NS	NS	NS	NS	NS	NS	499
	2	NS	***	NS	o	NS	NS	o	500
WW	1	NS	***	o	NS	NS	NS	NS	424
	2	NS	***	NS	NS	***	*	***	439
WG	1	***	***	NS	***	NS	NS	**	418
	2	***	NS	NS	NS	NS	NS	NS	432
FE	1	***	***	NS	*	NS	o	NS	418
	2	**	o	NS	o	NS	NS	NS	428
Second diallel									
LS	1	**	o	NS	NS	NS	NS	NS	527
	2	**	**	*	NS	NS	NS	NS	548
WW	1	o	***	***	o	*	NS	***	385
	2	o	***	o	o	NS	**	NS	374
WG	1	***	**	NS	***	**	NS	***	383
	2	***	NS	NS	**	NS	NS	**	373
FE	1	***	***	NS	NS	NS	NS	NS	381
	2	***	NS	NS	*	NS	NS	NS	369

NS = Not significant
o = $P<0.1$
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$

nificance levels of average direct genetic effects for litter size and weaning weight increased from the first to the second diallel. However, weaning weight did not meet the 5% level of significance, even in the second diallel. Weight gain and feed efficiency showed highly significant direct genetic effects in both diallels. Maternal genetic effects were significant for weaning weight and litter size. For weight gain and feed efficiency, statistical significance occurred only in the first room.

Significance levels for the components of heterosis showed an erratic fluctuation between rooms, as well as between the two diallels. Line direct heterosis (h_i) was significant mainly for the traits WG and FE, whereas specific heterosis (s_{ij}) and specific reciprocal effects (r^*_{ij}) were only occasionally significant.

Estimates of the crossbreeding parameters will be discussed according to the order of the effects in the model, since the main objective of this paper is to compare the development of the crossbreeding parameters in the different stages of the experiment. Two additional parameters are introduced to facilitate comparison between different replications for the same trait, as well as between different traits: (i) the correlation (r) of parameter estimates within diallels and within replicates, respectively; (ii) the coefficient of variation of estimates (CV). Because of the usual restrictions, the estimates have mean zero so that the least-squares mean was used to compute the CV.

Average direct genetic and average maternal genetic effects

Direct and maternal genetic effects for *litter size* showed the highest variation of all traits (Table 2). Coefficients of variation ranged from 4.5 to 38%. For both effects the variation increased between the two diallels. However, the direction of responses in line LS for the two effects was different. In both rooms there was a decrease in direct genetic effects for line LS compared with the control line between the two diallels, while maternal genetic effects increased.

In *weaning weight* there was only a slight influence of direct genetic effects (Table 3). In the second diallel, direct genetic effects reached the 10% significance level. Maternal genetic effects were significant in both diallels, mainly because of their lower standard errors. For both effects, line WW showed the highest estimates if the effect was significant. In both rooms the magnitude of maternal effects increased between diallels. The correlation of the estimates between diallels was high, with those for the second room tending to be higher than for the first room.

Table 2. Average direct and maternal genetic effects, standard errors, coefficients of variation (CV), and correlations between rooms and between diallels (r) in *litter size*

Line	Average direct				Maternal			
	Diallel 1		Diallel 2		Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2
LS	3.11	−0.18	2.74	0.62	0.36	1.75	2.04	1.27
WW	−1.93	−1.45	−1.93	1.39	0.40	0.52	−0.49	0.00
WG	−1.01	−0.13	−2.86	−3.69	−0.42	0.70	−0.65	1.92
FT	0.30	0.17	0.29	−2.02	0.22	−1.90	−0.05	−0.68
C	−0.47	1.59	1.76	3.70	−0.56	−1.07	−0.85	−2.51
SE	1.04	1.00	1.12	1.23	0.56	0.54	0.69	0.75
CV	19.3	10.9	29.9	38.7	4.5	14.8	14.8	23.3
r	0.20		0.56		0.27		0.43	
	0.31				0.74			
	0.79				0.60			

Table 3. Average direct and maternal genetic effects, standard errors, coefficients of variation (CV), and correlations between rooms and between diallels (r) in *weaning weight* (g)

Line	Average direct				Maternal			
	Diallel 1		Diallel 2		Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2
LS	0.55	0.58	0.44	0.80	1.07	0.43	0.58	−0.32
WW	0.22	0.64	2.24	1.77	1.01	1.72	2.13	2.86
WG	−1.50	−0.91	−1.77	−1.09	−1.59	−1.11	−1.67	−1.64
FT	0.18	−0.69	−0.38	−0.53	−0.43	−1.12	−2.65	−1.13
C	0.55	0.39	−0.53	−0.96	−0.06	0.08	1.61	0.23
SE	0.46–0.61	0.52–0.65	0.67–0.89	0.70–0.89	0.25–0.31	0.26–0.29	0.42–0.50	0.41–0.45
CV	3.7	3.3	7.0	5.7	4.8	5.3	9.9	8.1
r	0.60		0.70		0.85		0.82	
	0.95				0.95			
	0.75				0.71			

For *weight gain* and *feed efficiency*, line WG showed the highest direct response (Tables 4 and 5). Correlated responses for weight gain in line FT were negative, as was expected from the results of Hörstgen (1978). CV for this trait ranged from 16 to 26%. Correlations for the estimates were between 0.63 and 0.99, with those between diallels tending to be somewhat higher than those between rooms within diallels. Maternal effects were of a much lower magnitude. Their influence decreased between the two diallels.

The responses in average direct genetic effects reflect the direction of the selection applied. Correlated responses often showed inconsistencies. For example, in weight gain the deviations of the estimates for lines LS, WW, and FT from the control were negative in room 2 and positive in room 1. However, many of the estimates were not significantly different from zero, so that the differences between rooms may be due to different levels of the control line.

In comparison to the direct genetic effects, the variation in maternal genetic effects was lower. Only in weaning weight was the impact of maternal effects higher than that of average direct genetic effects. The highest variation of estimates was observed in litter size, followed by

Table 4. Average direct and maternal genetic effects, standard errors, coefficients of variation (CV), and correlations between rooms and between diallels (r) in *weight gain* (g)

Line	Average direct				Maternal			
	Diallel 1		Diallel 2		Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2
LS	−0.86	−1.47	−0.68	−2.29	−0.97	−0.10	−0.01	0.25
WW	−0.69	−0.92	0.30	−1.09	−0.77	0.14	−0.66	−0.20
WG	4.52	3.36	4.83	5.50	1.17	0.14	0.81	−0.02
FT	−0.93	−0.81	−2.35	−1.97	−0.16	−0.04	0.26	−0.38
C	−2.04	−0.17	−2.10	−0.14	0.72	−0.14	−0.40	0.36
SE	0.38–0.46	0.32–0.42	0.33–0.45	0.36–0.51	0.22–0.25	0.22–0.25	0.21–0.26	0.23–0.26
CV	22.9	16.1	23.1	26.5	8.3	1.1	4.5	2.6
r	0.91		0.88		0.11		−0.19	
		0.99				−0.54		
	0.95				0.53			

Table 5. Average direct and maternal genetic effects, standard errors, coefficients of variation (CV), and correlations between rooms and between diallels (r) in *feed efficiency*

Line	Average direct				Maternal			
	Diallel 1		Diallel 2		Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2	Room 1	Room 2
LS	−0.17	0.62	0.19	0.97	0.72	0.05	0.18	−0.01
WW	0.85	0.37	0.40	0.63	0.41	0.18	0.58	0.35
WG	−1.85	−0.90	−1.89	−1.77	−0.65	−0.38	−0.45	−0.31
FT	0.14	0.10	0.66	0.45	−0.12	0.14	−0.74	−0.03
C	1.03	−0.19	0.64	−0.28	−0.35	0.01	0.43	−0.06
SE	0.24–0.35	0.25–0.31	0.25–0.36	0.27–0.39	0.15–0.18	0.14–0.16	0.17–0.20	0.17–0.22
CV	14.5	8.1	16.2	15.6	6.8	3.1	8.6	3.4
r	0.63		0.83		0.68		0.54	
		0.99				0.62		
	0.92				0.47			

weaning weight and feed efficiency. Correlations of the estimates between rooms and between diallels were lower than for direct genetic effects. The relatively low correlations between direct genetic and maternal genetic effects (with the exception of weaning weight) confirm that selection affects primarily the direct genetic effects (Table 6). Hörstgen-Schwark et al. (1984a) and Eisen et al. (1984) also found only negligible or negative correlations between direct and maternal genetic effects. While in the present investigation the variation of maternal genetic effects was between 20 and 50% of that of the direct genetic effects, Hörstgen-Schwark et al. (1984a, b) and Eisen et al. (1984) found a substantially greater difference in line variation for these two effects. From this result, it may be concluded that there is little agreement with the results in the literature. But the present results are consistent insofar as directional changes were found only for the lines that were selected for the respective trait.

Average direct heterosis and line direct heterosis

Average direct heterosis is a measure of the variation of gene frequencies between *all* lines in the diallel and of the

Table 6. Correlations between average direct and average maternal genetic effects within rooms or diallels for traits litter size (LS), weaning weight (WW), weight gain (WG), and feed efficiency (FE)

Trait	Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2
LS	0.32	−0.50	0.61	−0.70
WW	0.82	0.90	0.66	0.80
WG	0.56	0.53	0.59	0.06
FE	0.41	0.86	0.37	0.77

Table 7. Average direct heterosis for traits litter size (LS), weaning weight (WW), weight gain (WG), and feed efficiency (FE) (standard error in brackets)

Trait	Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2
LS	0.276	0.757	0.523	1.323
	(0.491)	(0.475)	(0.527)	(0.569)
	NS	NS	NS	*
WW (g)	0.472	0.393	1.285	0.668
	(0.264)	(0.273)	(0.374)	(0.383)
	o	NS	***	o
WG (g)	0.096	−0.145	−0.034	−0.196
	(0.212)	(0.208)	(0.177)	(0.194)
	NS	NS	NS	NS
FE	−0.159	0.0	0.214	0.199
	(0.146)	(0.140)	(0.142)	(0.152)
	NS	NS	NS	NS

NS = Not significant
o = $P<0.1$
* = $P<0.05$
*** = $P<0.001$

Table 8. Estimates for z_i and $\bar{z}$ for traits litter size (LS), weaning weight (WW), weight gain (WG), and feed efficiency (FE)

Trait	Line	Diallel 1		Diallel 2	
		Room 1	Room 2	Room 1	Room 2
LS	LS	−0.43	0.98**	−0.05	1.26**
	WW	0.49	0.56	0.50	0.53
	WG	−0.02	−0.48	0.26	0.26
	FT	−0.29	0.30	0.46	0.25
	C	0.79*	0.15	−0.12	0.34
	$\bar{z}$	0.11	0.30	0.21	0.53
WW (g)	LS	−0.08	0.02	0.27	−0.18
	WW	0.16	0.22	0.34	0.05
	WG	0.54*	0.27	1.26**	0.99**
	FT	0.12	−0.08	0.52	0.08
	C	0.20	0.36	0.18	0.39
	$\bar{z}$	0.19	0.15	0.51	0.27
WG (g)	LS	0.33**	0.01	0.26	0.24
	WW	0.38*	0.02	0.12	0.23
	WG	−0.34	−0.13	−0.10	−0.32
	FT	−0.32*	0.08	−0.51**	−0.42**
	C	0.14	−0.27	0.16	−0.12
	$\bar{z}$	0.04	−0.06	−0.01	−0.08
FE	LS	−0.18	0.01	−0.05	−0.19
	WW	−0.31*	0.12	0.08	0.00
	WG	0.06	−0.14	0.17	0.27*
	FT	0.19	−0.18	0.23*	0.23
	C	−0.08	0.19	−0.01	0.08
	$\bar{z}$	−0.06	0.00	0.08	0.08

* = $P<0.05$
** = $P<0.01$

importance of dominance effects for the trait. Line direct heterosis is useful for computing the relative contribution of dominance effects to general combining ability. But this parameter depends on the squared difference of the gene frequencies of the examined line, as well as on the variance of gene frequency between all lines (Eisen et al. 1983). Therefore, significant line direct heterosis will be found if the variance of gene frequencies is low, but one line deviates in gene frequency from the others. With increasing differentiation in gene frequencies, line direct heterosis will be "absorbed" into average direct heterosis and specific heterosis. However, the parameter z_i proposed by Casas and Wellhausen (1968) depends only on the sum of squared deviations of the gene frequencies of line i from average gene frequency, and therefore has the most meaningful genetic interpretation (Eisen et al. 1984).

Table 1 shows that levels of significance for the components of heterosis (average, line direct, specific) were more often observed in the second diallel. While litter size and weaning weight showed significant average and specific heterosis, for weight gain and feed efficiency, only line direct heterosis was significant. Table 7 presents the estimates of average direct heterosis for *litter size* and *weaning weight*. In the first diallel, average heterosis was not significant. In the second diallel, significant average heterosis for weaning weight could be observed in room 1 and for litter size in room 2.

Results for line direct heterosis are presented as estimates for z_i and $\bar{z}$ (Table 8). In most of the room-diallel-subcells, only one of the lines showed a significant estimate for z_i. In room 2, line LS showed the highest estimate of z_i for *litter size* in both diallels. However, in room 1, neither value for line LS was significantly different from zero. The weighted variance of the gene frequencies at loci with dominance ($\bar{z}$) is twice as great in room 2 than in room 1. This factor increases the number of significant estimates for total heterosis, as will be seen later. In *weaning weight*, only line WG showed significant estimates of z_i.

In *weight gain*, line FT deviated most in its gene frequencies, but LS and WW were of importance for room 1

Table 9. Specific heterosis (s_{ij}), standard errors, and coefficients of variation (CV) between rooms and diallels (r) for traits *weaning weight and weight gain* ($s_{ij}=s_{ji}$)

Combination	Diallel 1		Diallel 2	
	Room 1	Room 2	Room 1	Room 2
	Weaning weight (g)			
LS × WW	0.18	−0.50	0.95	−0.16
LS × WG	−0.23	0.51	−0.26	0.42
LS × FT	0.16	0.28	−0.35	−0.12
LS × C	−0.11	−0.28	−0.34	−0.13
WW × WG	0.19	−0.81	−0.60	0.20
WW × FT	−0.48	0.51	−0.87	0.05
WW × C	0.11	0.81	0.52	−0.08
WG × FT	0.18	0.02	1.14	−0.38
WG × C	−0.14	0.28	−0.27	−0.24
FT × C	0.14	−0.81	0.09	0.45
SE	0.23–0.31	0.22–0.30	0.38–0.55	0.36–0.44
CV	1.0	2.5	3.1	1.3
	Weight gain (g)			
LS × WW	−0.28	0.05	−0.58	0.14
LS × WG	0.29	0.27	0.23	−0.33
LS × FT	0.23	−0.32	0.24	0.11
LS × C	−0.25	0.00	0.11	0.08
WW × WG	0.07	0.01	0.24	0.18
WW × FT	−0.05	−0.05	0.54	0.18
WW × C	0.26	−0.02	−0.19	−0.50
WG × FT	−0.26	0.03	−0.66	−0.28
WG × C	−0.10	−0.31	0.20	0.44
FT × C	0.08	0.33	−0.11	−0.02
SE	0.19–0.24	0.19–0.26	0.19–0.27	0.20–0.25
CV	2.0	1.7	3.0	2.4

in the first diallel. For this trait and for feed efficiency, no increase in $\bar{z}$ between the two diallels could be observed. In *feed efficiency* there was no definite trend, but the agreement of the estimates for lines WG and FT should be noted.

It is obvious that for the second room in the first diallel, the differentiation of gene frequencies as measured by z_i was developed only for litter size. However, in the second diallel this was no longer true, and estimates of z_i agreed well for weight gain and feed efficiency.

Specific heterosis

Specific heterosis was significant only in a few cases for weaning weight and weight gain (Table 1). Table 9 gives the results for these traits. For *weaning weight*, the CVs of the two significant cases (columns 2 and 3) were 2.5 and 3.1%, respectively, about 1/3 of the variation of average direct and maternal genetic effects. An increase of the variation could only be observed in the first room.

For *weight gain*, significant estimates were reached for room 1 in the second diallel. For this subcell combination, WW × FT showed the highest (+0.54 g) and combination WG × FT the lowest estimate (−0.66 g) for specific heterosis. The variation of the parameters is of the same magnitude as for weaning weight (3%).

Direct heterosis of a cross

The magnitude of the different components of heterosis ($\bar{h}$, h_i, and s_{ij}) depends on the difference in gene frequencies at loci exhibiting dominance effects, as well as on the variance of gene frequencies at these loci as already mentioned. Therefore, a discussion of the single components is not fruitful unless the estimates for direct heterosis (h_{ij}) are known. The significant estimates for direct heterosis are summarized in Table 10. In all of the room-diallel-subcells, between one and four crosses gave significant estimates for direct heterosis. These results agree well with the findings for z_i in Table 8. In the first room, combinations WW × K and WW × FT showed significant heterosis for *litter size* in diallels 1 and 2. In the second room, only combinations with line LS gave significant estimates. This line also showed the highest estimates for z_i. There was a tendency for higher heterosis estimates in the second diallel, but the differences were statistically not significant.

Heterosis for *weaning weight* ranged from 1.13 to 3.68 g. Certain crosses (e.g., WG × FT and WG × C) gave significant estimates in both diallels. As for litter size, heterosis was higher in the second diallel, but at different levels in the two rooms. For *weight gain* and *feed efficiency*, the results differed from those in litter size and weaning weight. While all significant estimates of direct heterosis for the latter were in the desired direction, weight gain and feed efficiency partly showed undesired heterosis effects, especially in the second diallel; WG × FT showed undesirable heterosis in six out of seven cases (Table 7). It might be assumed that there is a connection between the positive heterosis of combination WG × FT in weaning weight and the negative estimates for weight gain and feed efficiency.

An increase in the amount of heterosis can only be stated for litter size and weaning weight. This corresponds with the findings for average direct heterosis. The frequency of significant heterosis estimates varied for the different combinations. Most frequently, significant estimates were found for WG × FT followed by LS × WW, LS × WG, and WG × C. Line WG was involved in 17 out of 33 combinations showing significant estimates. On average, WG showed a higher change in z_i values than the other lines. Selection for weight gain resulted in a different growth curve for this line. The superiority of line WG for weight gain is achieved by a low weaning weight in conjunction with a slightly superior 6-week body weight. Presumably, genes causing a slow preweaning growth had higher frequencies in WG than in the

Table 10. Significant estimates for *direct heterosis* (h_{ij}) absolute values and percent of parental line means (in brackets)

Trait	Diallel 1				Diallel 2			
	Room 1		Room 2		Room 1		Room 2	
LS	WW × C	2.25	LS × FT	2.42	WW × FT	2.73	LS × WG	2.89
	(26.0)		(14.7)		(39.7)		(38.3)	
			LS × WW	1.80			LS × WW	2.43
			(17.6)				(26.6)	
WW (g)	WG × FT	1.19	WW × C	1.64	WG × FT	3.68	WG × C	1.84
	(5.3)		(6.8)		(20.6)		(9.2)	
	WW × WG	1.13	WG × C	1.20	LS × WG	1.86	LS × WG	1.55
	(5.2)		(5.5)		(9.4)		(7.5)	
					WG × C	1.69	WW × WG	1.71
					(8.5)		(7.5)	
					LS × WW	1.54		
					(6.4)			
WG (g)	WW × C	1.11	WG × C	−0.93	LS × C	0.82	LS × WW	0.99
	(11.2)		(−6.8)		(7.4)		(9.5)	
	LS × WW	0.88			WG × FT	−1.66	FT × C	−0.86
	(9.1)				(−11.5)		(−7.8)	
	WG × FT	−1.41					WG × FT	−1.45
	(−10.4)						(−10.7)	
FE	LS × WW	−0.73	WG × FT	−0.56	WG × FT	0.96	WG × FT	1.05
	(−8.2)		(−8.4)		(17.6)		(16.9)	
	WW × C	−0.64	WW × C	0.60				
	(−7.2)		(8.2)					
	WG × FT	0.61						
	(9.1)							

Table 11. Correlations of heterosis estimates (h_{ij}) between rooms and diallels for traits litter size (LS), weaning weight (WW), weight gain (WG), and feed efficiency (FE)

Trait	Between rooms		Between diallels	
	Diallel 1	Diallel 2	Room 1	Room 2
LS	0.15	−0.22	−0.27	0.60
WW	0.06	0.53	0.75	0.24
WG	0.02	0.72	0.73	−0.04
FE	−0.74	0.79	0.59	−0.51

other lines. With these loci showing dominance, the frequent occurrence of heterosis in crosses with WG could be explained.

Direct heterosis in litter size was higher than previously reported. Van den Nieuwenhuizen et al. (1982) found 3.1% heterosis and Eisen et al. (1983) found a maximum of 14%, with an average heterosis of 5.4%. For weaning weight, the magnitude of heterosis is similar to that reported by Hörstgen-Schwark et al. (1984a) and Aumann (1986). The present findings for weight gain and feed efficiency agree with Hörstgen-Schwark et al. (1984a), who found estimates in the range of −8 to +10% and −11 to +7%, respectively. However, Bakker et al. (1976) reported only 3.4% direct heterosis for weight gain.

Litter size and weaning weight showed the expected increase in the amount of average heterosis through long-term selection. Particularly in weaning weight, more crosses gave significant heterosis estimates in the second diallel. However, the comparison of rooms and diallels points out that the occurrence of heterosis showed erratic fluctuations in the different subcells. The results for the two rooms were not in agreement, especially as regards litter size (Table 11). In room 2 the direct response to selection for line LS was negative, but the estimates of heterosis were in agreement for the two diallels (r of the estimates = 0.6). On the other hand, room 1 showed a consistent development in purebred performance, with a negative correlation of the heterosis estimates for the two diallels ($r = -0.27$). Heterosis estimates for the other traits were in agreement for the second diallel. The same was true for the correlation between diallels in room 1. Taking into account the values of z_i in Table 8, these results lead to the conclusion that the differentiation of gene frequencies at loci with dominance effects was insufficient for room 2 in the first diallel. This insufficiency may be due to different selection intensities in the two rooms.

Conclusions

Selection for purebred performance led to an increase of average direct genetic effects for the selected lines (WW and WG) in weaning weight, weight gain, and feed efficiency between the two diallels. In litter size, the estimates for line LS decreased as compared with C. Heritability of litter size is low, and selection was for the performance of the mother of the litter. These factors may explain the low response in direct effects, whereas in maternal effects an increase could be expected. In weaning weight, maternal effects for line WG also increased between the diallels.

In litter size, the increase in maternal effects compensated for the decrease in direct genetic effects of line LS. Thus, maternal effects were more important in the second than in the first diallel. In weaning weight, the increase in average direct genetic effects of line WW was higher than in maternal effects. In weight gain and feed efficiency, direct effects clearly dominated maternal genetic effects, even in the second diallel.

Nonadditive effects became more important in the second diallel. Average heterosis in litter size and weaning weight increased. However, levels of significance occurred only for weaning weight in room 1 and for litter size in room 2. The estimates of z_i for lines WG and FT often changed between diallels. This result caused frequent heterosis in combinations of these lines, especially in diallel 2. In the second diallel, heterosis estimates partly showed an undesired direction.

The combinations exhibiting significant heterosis estimates varied between replications. It is concluded that selection for purebred performance does not naturally improve combining abilities. There were several examples where heterosis of certain combinations disappeared in the second diallel. This disappearance agrees with the findings of Bell et al. (1955), where two or three of the nine inbred lines of *Drosophila* in the experiment showed very different combining abilities between replicated testcrosses.

Finally, in no case were nonadditive effects crucial for the absolute performance of the best combination. In litter size and weaning weight, crosses had the best absolute performance in each of the four groups. However, these crosses gave only intermediate heterosis estimates. The importance of maternal effects for these two traits can be seen from the fact that in each case lines LS and WW, respectively, were the dam of the best cross. However, in weight gain and feed efficiency, a purebred line (WG) was superior to all crosses.

Acknowledgements. The director of the Institute of Laboratory Animals in Hannover supplied the facilities and personnel for the experiment, for which the authors are grateful. Drs. Gabriele Hörstgen-Schwark and H. Swalve helped in the collection and preparation of the original data.

References

Aumann J (1986) Modellversuch mit Mäusen zur Schätzung von Kreuzungswirkungen unter Berücksichtigung der Epistasie. PhD, University of Munich, Germany

Bakker H, Nagai J, Eisen EJ (1976) Average genetic and heterotic effects on growth in mice selected for large 6-week body weight or rapid postweaning gain. J Anim Sci 43:1145–1155

Bell AE, Moore CH, Warren DC (1955) The evaluation of new methods for the improvement of quantitative characteristics. Cold Spring Harbor Symp Quant Biol 20:197–212

Casas DE, Wellhausen ET (1968) Diveridad genetica y heterosis. Cited in: Eisen et al. (1983)

Eisen EJ, Hörstgen-Schwark G, Saxton AM, Bandy TR (1983) Genetic interpretation and analysis of diallel crosses with animals. Theor Appl Genet 65:17–23

Eisen EJ, Hörstgen-Schwark G, Bandy TR, Saxton AM (1984) Postpartum performance in a diallel cross among lines of mice selected for litter size and body weight. J Anim Sci 58:863–877

Gardner CO, Eberhart SA (1966) Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439–451

Griffing B (1956) Concept of general and specific combining ability in relation ot diallel crossing systems. Aust J Biol Sci 9:463–493

Harvey WR (1975) Least squares analysis of data with unequal subclass numbers. USDA-ARS, H-4

Henderson CR (1948) Estimation of general, specific, and maternal abilities in crosses among inbred lines of swine. PhD thesis, Iowa State University, Ames/IA (Cited in: Harvey 1975)

Henderson CR (1977) Prediction of the merits of single crosses. Theor Appl Genet 49:273–282

Hörstgen G (1978) Modellversuch mit Mäusen zur genetischen Differenzierung von Zuchtlinien durch Selektion für quantitative Merkmale. PhD thesis, University of Göttingen, Germany

Hörstgen-Schwark G, Eisen EJ, Saxton AM, Bandy TR (1984a) Diallel cross among lines of mice selected for litter size and body weight: growth traits. J Anim Breed Genet 101:96–111

Hörstgen-Schwark G, Eisen EJ, Saxton AM, Bandy TR (1984b) Reproductive performance in a diallel cross among lines of mice selected for litter size and body weight. J Anim Sci 58:846–862

Komender P (1987) Auswertung von diallelen Kreuzungsversuchen zur Schätzung von Kreuzungsparametern ergänzt durch ein Beispiel aus der Schweinezucht. PhD thesis, University of Hohenheim, Germany

Komender P (1988) Crossbreeding in farm animals. III. A general method of comparing models to estimate crossbreeding parameters with an application to diallel crossbreeding experiments. J Anim Breed Genet 105:362–371

Komender P, Fewson D (1987) Estimation of crossbreeding parameters in a full-diallel experiment with selected lines of swine. In: Proc 38th Ann Meeting EAAP, Lisbon, pp I:218–219

van den Nieuwenhuizen J, Bakker H, Buis RC (1982) Genetic differences in reproduction and growth rate between two lines of mice selected for litter size. J Anim Breed Genet 99:292–307