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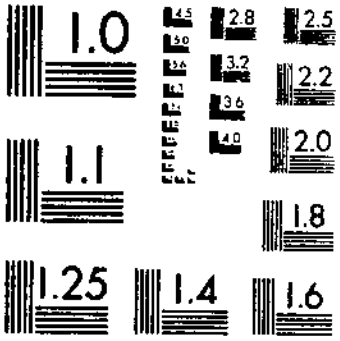

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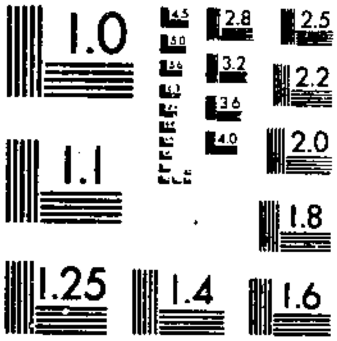

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Combining Abilities in Crosses Among

SIX INBRED LINES OF SWINE

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Numerous studies on the effects of crossbreeding swine have made use of inbred lines both in crosses with other inbred lines and in crosses with noninbreds (Dickerson et al., 1946; Chambers and Whatley, 1951; Bradford et al., 1958).[3] While the results of these studies generally show an advantage in the performance of crosses over that of their parents, little information is available in the literature concerning the general combining ability of different lines or the relative merit of specific crosses. If inbred lines are to be used to best advantage by producers of market hogs, some effort must be made in obtaining such information.

The primary purpose of this study was to obtain estimates of general and specific combining abilities and maternal effects from single crosses among six inbred lines of swine maintained at the Agricultural Research Center, Beltsville, Md. Results comparing the performance of the single crosses with that of their inbred parent lines have been reported by Hetzer et al. (1951) and are not included here. In general, both prenatal and postnatal mortality were lower among crosses than among inbreds, crosses exceeding inbreds by 1.2 pigs, or 14 percent, in litter size at birth and by 1.7 pigs, or 29 percent, at 56 days. Crosses differed little from inbreds in individual pig weight at birth, but crosses grew faster until they exceeded inbreds by 2.7 pounds, or 10 percent, at 56 days and by 9.3 pounds, or 6 percent, at 140 days. In total litter weight at 56 days the advantage for crosses was 64 pounds, or 40 percent. Carcass data showed that crosses tended to have a slightly higher dressing percentage, a slightly lower yield of lean cuts, and more fat than did inbreds.

REVIEW OF LITERATURE

Combining ability, as used by plant and animal breeders, is usually subdivided into general and specific combining ability. According to Sprague and Tatum (1942), general combining ability refers to the average performance of a line in hybrid combinations, while specific combining ability applies to crosses that do relatively better or worse than would be expected on the basis of the average performance of the lines involved. In crosses among unselected lines

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[2] The authors are indebted to J. X. King and W. H. Peters for assistance with the calculations.

[3] References to literature cited (p. 25) are indicated by the names of the author (or authors) followed by the year of publication.

of corn, these workers found general combining ability to be more important than specific combining ability, an indication that in such lines genes with additive effects on yield are either more common or produce greater effects than dominant genes or genes with epistatic effects. In contrast, in crosses among inbred lines previously selected for general combining ability, the variance for specific combining ability, attributable largely to dominance and epistatic effects, was generally greater than that for additive effects.

Henderson (1948, 1953) developed mathematical models and formulas for estimating and testing general, maternal, specific, and sex-linkage effects in swine crosses involving multiple classifications with disproportionate subclass numbers. In studies of 8 litter characteristics in single crosses among 12 inbred lines of Poland China swine, he found that differences in general combining ability at most accounted for only 5 percent of the variability among crosses, whereas from 5 to 15 percent of the variation could be ascribed to specific effects. Neither sex linkage nor possible line differences in mothering abilities contributed to the variability among crosses. Henderson also investigated the relative efficiency of linecross and topcross tests for estimating combining abilities and concluded that linecross tests not only estimate general combining ability more efficiently but also furnish information concerning maternal, specific, and sex-linkage effects.

In a study of single crosses among nine highly inbred strains of mice, Eaton et al. (1950) found that line differences in transmitted influence or general combining ability were important for individual weight but not for litter size or litter weight. Maternal effects were important for both litter size and individual weight, while specific linecross effects were important only for viability and total litter weight. Glazener and Blow (1951), studying topcrosses involving eight inbred lines of chickens, reported significant positive regressions of topcross performance on inbred performance for broiler weight and for feathering and concluded that a large portion of the line variance of these traits was the result of genes which act in an additive manner. In contrast, Wyatt (1953), also working with chickens, found little relation between topcross performance and inbred performance for body weight at 8 weeks. He concluded that differences between his lines were due primarily to factors other than additive genes. Craig and Chapman (1953) correlated the average body weight of eight inbred lines of rats with those of their single crosses and topcrosses to an outbred control strain and found the lines' own performance to be as reliable as topcrossing for predicting the relative value of inbred lines in other crosses. Specific combining ability appeared to be relatively unimportant in their experiment.

Durham et al. (1952) compared the performance of topcross pigs sired by boars from eight inbred lines with pigs sired by noninbred boars in 44 Wisconsin farm herds. Collectively, topcrosses and straight breeds did not differ significantly in weight at 154 days, but there was some evidence that the lines differed in their general combining ability both for this trait and for sow productivity. Hetzer, Comstock, and Zeller (1953), in summarizing some of the results from crossing noninbred Berkshire, Chester White, Hampshire, and Poland China boars with sows of the six inbred lines represented in the present study and with inbred Danish Landrace sows, gave constants representing breed differences in transmitted influence and line differences in direct maternal and transmitted influence for litter weight at 56 days of age. Although both breed and line differences in the constants obtained were fairly large, ranging from 14.5 to −12.9 pounds for breeds and from 21.6 to −16.8 pounds for lines, only differences for litter weight at birth between lines were statistically significant. Substantial but nonsignificant differences in specific effects were indicated for all traits studied.

Recently, Cobb (1958) studied the results from topcrossing boars of the same seven inbred lines used by Hetzer et al. (1953) on purebred Berkshire, Chester White, Hampshire, and Poland China sows on Pennsylvania farms. Topcross and purebred litters were farrowed and raised on the same farms, and on some farms data were also available on the productivity of topcross and purebred gilts. Differences between breeds were significant for litter size and litter weight, but topcross groups did not differ significantly for either trait. However, the topcross groups differed significantly for pig weight at 140 days, daily gain to market weight and certain carcass characteristics, indicating that the lines differed in their ability to combine with purebreds for these traits.

Dinkel (1955) studied the value of a line's own performance for predicting single and multiple cross performance with respect to individual pig weight at 154 days, and reported a correlation of 0.57 between line average and average of all single crosses involving that line. The correlation between inbred line performance and multiple cross performance was slightly lower, 0.50, while the correlation between single cross and multiple cross was 0.38. Dinkel's results were based on 3,541 inbred pigs and 1,399 single cross pigs from crosses among the 12 inbred Poland China lines previously used by Henderson (1948). Dinkel concluded that an inbred line's own performance is useful in predicting single and multiple cross performance. He added that differences in mothering ability seemed important enough to be considered in the planning of single and multiple crosses. Magee and Hazel (1959) studied the 154-day weights of three-line cross pigs involving the same 12 inbred lines of Poland China swine. They reported differences in general combining ability to be the most important genetic source of variation, accounting for 4 percent of the variation among pigs of the same season-farm group. Neither maternal effects nor specific combining effects were statistically significant in their data.

MATERIAL AND METHODS

The data used in this study came from 218 litters representing all the possible reciprocal crosses among six inbred lines that had been developed by the U.S. Department of Agriculture from crosses of the Danish Landrace with six other breeds of swine. Of the 218 litters, 82 were farrowed in the fall of 1947, 102 in the fall of 1948, and 34 in the fall of 1950.

The inbred lines were the Landrace–Chester White (L–CW), Landrace-Duroc (L–D), Landrace-Poland China (L-PC), Landrace–Large Black (L–LB), Landrace–Duroc–Hamphire (L–D–H), and Yorkshire-Duroc-Landrace-Hampshire (Y–D–L–H). The first four lines were formed from crosses made from 1934 through 1936, while the latter two lines were established in 1939 by crossing stock from a Landrace × Hampshire cross made at Miles City, Mont., with stock from each of the L–D lines and a line that had been started in 1935 from a Danish Yorkshire × Duroc cross. Except for certain generations in the early years in which the individual's coat color constituted the primary criterion of selection in five of the six lines, selection was primarily based on such traits as prolificacy, pig viability, rate of growth, and carcass quality as reflected by the meat type conformation of the Landrace. Because of differences in the number of introduced Landrace animals following the initial crosses, the proportion of Landrace germ plasm possessed by the lines when they were closed to outside blood in 1943 and 1944 varied considerably, ranging from about 75 percent in the L–D, L–LB, L–PC, and L–D–H lines to about 15 percent in the L–CW line and 5 percent in the Y–D–L–H line. All Landrace animals used in developing the lines came from a single group of 7 boars and 16 sows imported from Denmark in 1934. However, some of the lines had no common Landrace ancestors and, hence, were considered to be unrelated. The average coefficients of relationship between the various pairs of lines are given in table 1, together with the average inbreeding (Wright, 1922) of the females used to produce the single cross litters.

TABLE 1.—*Average coefficients of inbreeding and relationship among inbred lines, for the 3 years 1947, 1948, and 1950*[1]

Line	Inbreeding coefficient	Relationship coefficient				
		L–D	L–LB	L–PC	L–D–H	Y–D–L–H
L–CW	0.411	0.012	0.018	0.014	0.020	0.000
L–D	.198		.140	.135	.246	.018
L–LB	.187			.123	.121	.000
L–PC	.248				.108	.000
L–D–H	.263					.031
Y–D–L–H	.283					

[1] See p. 3 for meaning of line symbols.

In 1947 and 1948, litters were obtained from each of the 30 possible single cross combinations, but in 1950 only 28 combinations were represented. One boar was used from each line to sire litters in 1947 and 1950, while in 1948 two boars were used from each line. Only one boar sired litters in 2 years. A total of 23 boars were used as sires in the 3 years. The number of females used as dams varied from 23 to 35 between lines. There were 182 females in all, including 146 that produced one litter each and 36 that produced two litters each. The number of litters produced per cross ranged from 5 to 9 (table 2).

The traits studied were litter size, litter weight, and individual pig weight at birth and at 21 and 56 days of age; individual pig weight at 98 and 140 days of age; daily gain from weaning to a final weight of about 225 pounds; and six carcass yields and measurements. The carcass traits were: (1) total carcass yield or dressing percentage, (2) yield of lean cuts (sum of trimmed hams, loins, picnic shoulders, and shoulder butts), (3) yield of trimmed belly or bacon, (4) yield of preferred cuts (sum of lean cuts and bacon), (5) yield of fat cuts (sum of fat back, leaf fat, plates, and cutting fat), and (6) average backfat thickness based on measurements at five locations. All cuts were weighed to the nearest one-tenth pound and each was expressed as a percentage of live weight at slaughter. Slaughter weight averaged 211.0±0.35 pounds.

TABLE 2.—*Distribution of litters by line of sire and line of dam* [1]

Line of dam	Line of sire						Total
	L-CW	L-D	L-LB	L-PC	L-D-H	Y-D-L-H	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	
L-CW	--------	6	5	6	6	6	29
L-D	8	--------	8	7	8	7	38
L-LB	8	8	--------	8	7	8	39
L-PC	9	7	6	--------	8	8	38
L-D-H	7	7	9	5	--------	7	35
Y-D-L-H	7	7	9	8	8	--------	39
Total	39	35	37	34	37	36	218

[1] See p. 3 for meaning of line symbols.

Post-weaning growth and carcass data were obtained only for pigs farrowed in 1947 and 1948. The plan here was to have each of the 30 different crosses represented by one barrow and one gilt from each of two litters in each of the 2 years and to self-feed these pigs in groups of four each under record-of-performance conditions. Actually, three of the crosses were represented by 7 instead of 8 pigs, giving 237 pigs from 118 litters for which rate of growth data were obtained after weaning. Since the pigs were grouped so as to have all pigs in a pen as nearly the same age as possible, information on feed requirements was not obtained for each cross separately and hence is not included here. Carcass data were obtained on 234 pigs, including 24 crosses represented by 8 pigs each and 6 by 7 pigs each. Feeding and management practices were as uniform as it was possible to keep them, and they compared favorably with those used in good commercial herds. Data on the carcass traits were obtained in accordance with slaughtering and cutting procedures as described by Hankins and Hiner (1937).

The least squares method of fitting constants for multiple classifications with disproportionate subclass numbers was used to obtain estimates of the line characteristics for the birth, 21-day, and 56-day data. The line characteristics studied were the general and specific combining ability effects of the lines and line differences in maternal effects. To eliminate any bias due to possible confounding effects caused by year of birth, age of dam, inbreeding of dam, and inbreeding of litter, constants were fitted simultaneously for the effects of these variables. In order that the same set of equations could be used in analyzing the litter and pig weights at the three ages, the analyses pertaining to individual pig weight were accomplished by dividing the weight of each litter at a given age by the number of pigs at the same age.

While linear regressions appeared to be adequate for measuring the effects of inbreeding of dam and inbreeding of litter, examination of the data, as well as results reported by other workers (Lush and Molln, 1942; Henderson, 1948) indicated the regressions of litter size and litter weight on age of dam to be curvilinear. Since the age-of-dam effect was most pronounced at younger ages, the sows were classified into the following four age groups: first litter, from 10 to 11.5 months; first litter, from 11.6 to 13.5 months; second litter, from 17 to 19 months; and third or later litter, from 22 to 48 months.

The following mathematical model was used to describe the effects of the variables studied:

$$y_{ijkln}=\mu+g_i+g_j+s_{ij}+m_i+z_k+a_l+b_1X_1+b_2X_2+e_{ijkln}$$

where

$i, j=1, 2, \ldots, 6$ lines
$k=1, 2, 3$ years of birth
$l=1, 2, 3, 4$ ages of dam
$n=1, 2, \ldots$ litters per cross-year-age-of-dam class

y_{ijkln} is the record of the n-*th* litter of a cross between the i-*th* and j-*th* lines produced in the k-*th* year by a sow in the l-*th* age class. The g's are the general combining ability effects of the i-*th* and j-*th* lines in any cross and s_{ij} represents the specific combining ability of the i-*th* and j-*th* lines. The m_i's are maternal effects that are common to all litters having the i-*th* line as female parent, the z_k's are effects associated with year of birth of litter, the a_l's are age-of-dam effects and b_1 and b_2 are partial regressions of the litter or pig trait on the dam's inbreeding (X_1) and litter's inbreeding (X_2), respectively. The population mean that is represented in the records of all litters is designated by μ; and the residual or error variation that is peculiar to litters within a particular cross, year, and age-of-dam class by e_{ijkln}. The relations among the g_i's, s_{ij}'s, m_i's z_k's and a_l's are such that

$$\Sigma_i g_i=\Sigma_{ij} s_{ij}=\Sigma_i m_i=\Sigma_k z_k=\Sigma_l a_l=0.$$

Letting S_{ij} equal $\mu+g_i+g_j+s_{ij}$, the total reduction in sum of squares due to fitting all constants included in the model was obtained by first absorbing the $15S_{ij}$ equations into the equations for the other variables, fitting constants for all variables including the S_{ij}'s, multiplying the right-hand side of the equations by their appropriate constants, and summing the products over all equations.

Preliminary tests of significance of year-of-birth effects, age-of-dam effects, line differences in maternal effects, and differences in inbreeding of dam and inbreeding of litter were next carried out. Sums of squares for these effects were obtained from the equation $SS=C'DC$, where SS refers to a specific sum of squares, C' is the transpose of the column vector (C) of constants for a particular class of effects, and D is the matrix inverse of the section of the variance-covariance inverse pertaining to the corresponding class of effects. The sums of squares associated with the general and specific combining ability effects were then obtained by subtracting the reductions in sums of squares when these variables were ignored from the reduction in sum of squares with all variables included. Since the results of these latter analyses, as indicated in the discussion of table 5, strongly suggested that specific combining ability effects contributed very little, if any, to the variation in the litter and pig data at the three ages, analysis of these data was completed by ignoring specific effects and obtaining constants and sums of squares for the remaining variables as outlined for the preliminary tests of significance mentioned above

The error term used for carrying out tests of significance in each case was the residual mean square remaining after the fitting of constants for all variables included in the original model. It includes mostly the variance due to individual differences between sows and other effects peculiar to each litter within a particular cross, year of birth, and age class of dam.

Since almost identical numbers of pigs were fed and slaughtered from the various crosses each year, the methods used to analyze the post-weaning growth and carcass data were essentially those given by Henderson (1948) for balanced single cross experiments. Thus, the 30 different crosses were considered to include eight pigs each; this greatly reduced the computations required for estimating genetic parameters and for testing hypotheses.

Because of differences in sex ratio, estimates of the effects of sex were first obtained for each character. All litters represented by equal numbers of barrows and gilts were used, and the data were adjusted for all characters showing a significant sex difference to the mean of the two sexes. In addition, the 98- and 140-day weights were adjusted to a mean age of dam of 20.4 months and the daily gain data to a mean initial weight of 32.0 pounds, by means of simple intra-year-and-cross regressions computed from the original data. Backfat thickness—the only carcass trait that showed a significant regression on slaughter weight—was also adjusted to a mean slaughter weight of 211.0 pounds. While larger bodies of data or more refined methods may have provided more appropriate adjustment of the data than those used here, the use of adjustment factors developed from the same data to which they are applied should not of itself introduce any systematic errors. Hence, adjustment of the data as indicated here appeared justified in view of the time saved in analyzing them on the assumption of a completely balanced design.

The mathematical model used for the post-weaning growth and carcass data was

$$y_{ijklm}=\mu+g_i+g_j+s_{ij}+m_i+z_k+f_{ijkl}+e_{ijklm}$$

where the constants designated by g, s, m, and z are as defined under the model for the litter traits, f_{ijkl} is the effect of the l-*th* litter in the ij-*th* cross and k-*th* year, and the e_{ijklm} are pig effects within litter. Inbreeding of dam and inbreeding of litter were ignored largely because inbreeding effects were found to be essentially nil in the pre-weaning data. Estimates of the effects of years, on the other hand, were obtained directly since the various crosses were represented by essentially equal numbers in the 2 years for which post-weaning growth and carcass data were available. While it was not feasible to obtain expected values of the least squares mean squares for the pre-weaning data, estimates of the relative importance of line differences in maternal effects and of general and specific combining effects were obtained for the post-weaning growth and carcass data as described by Henderson (1948) for completely balanced designs.

RESULTS AND DISCUSSION

LITTER SIZE AND PIG WEIGHT AT THREE AGES

The constants fitted for the effects of years, age of dam, line differences in maternal influence, and the regressions for litter size, litter weight, and pig weight on inbreeding of dam and inbreeding of litter are presented in table 3 along with the number of litters for each

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classification. Estimates of the constants representing the general and specific combining abilities of the lines are shown in table 4. All estimates are given as deviations from their respective means except for the regressions that represent average changes in the dependent variables for each unit change in each of the independent variables. The mean squares associated with the several variables are shown in table 5.

Year-of-Birth Effects

Year-of-birth effects were significant or highly significant for litter weight at each of the three ages and for pig weight at birth and at 56 days, but they lacked significance for litter size at each age and for pig weight at 21 days. However, all of the litter and pig traits averaged lower in 1948 than in either of the other 2 years, indicating that yearly fluctuations in weather conditions and yearly differences in the incidence of disease and parasites that affected the herd's general state of health had similar effects on all traits studied. Annual changes in the genetic merit of the lines may also have contributed to the differences between years, but it is doubtful that such changes were very important in these data.

Age-of-Dam Effects

Age-of-dam effects were highly significant for all litter and pig traits. No adjustment was made for the upward bias which presumably was introduced in the estimates of age effects for older sows because of selection practiced on the basis of their previous record. The importance of this bias is not known, but it should not be large because of the relatively low repeatability generally reported for these traits. The effect of age of dam was most pronounced in sows farrowing their first litter at approximately 1 year of age. Thus, gilts farrowing between 10 and 11.5 months of age produced an average of 1.03 pigs less at birth and raised 0.93 pig less to weaning than did gilts between 11.6 and 13.5 months. Litter size at the three ages continued to increase with age of dam until the oldest group averaged approximately 2.5 years. Sows in this age group produced litters that had 0.71 pig more at birth, 1.03 pigs more at 21 days, and 1.15 pigs more at 56 days than litters from 1.5-year-old sows.

The estimates of the age-of-dam effects on litter size and litter weight agree rather well with those obtained by other workers. For example, Olbrycht (1943), Stewart (1945), and Henderson (1948) reported that gilts farrowing their first litter at or under 1 year of age produced from 1.1 to 1.5 pigs less at birth than those over 1 year of age. Johannson (1929) also found that the number of pigs in the first litter increased with age of sow at farrowing to about 15 months. Squires et al. (1952) studied ovulation rates and embryonic mortality in gilts, and found that for each increase of 10 days in age of gilt when bred, 0.5 more embryo was present 25 days after conception. The increase of 19 pounds in litter weight at weaning, reported by Henderson (1948) for gilts farrowing their first litter over 1 year of age, is identical with the increase of 19.0 pounds found in this study. Also, the increase of 31 pounds which Lush and Molln (1942) found in litter weight at weaning from the first to the second litter coincides almost exactly with the 29.9-pound increase found here for litters from 1.5-year-old sows compared with those from gilts between 11.6 and 13.5 months of age.

TABLE 3.—*Least squares estimates of the effects of year of birth, age of dam, line differences in maternal influences, and inbreeding of dam and litter on litter and pig traits at three ages* [1]

Effects studied	Litters	Litter size at—			Litter weight at—			Pig weight at—		
		Birth	21 days	56 days	Birth	21 days	56 days	Birth	21 days	56 days
	Number	*Number*	*Number*	*Number*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
General mean	218	10. 40	7. 89	7. 93	28. 2	85. 8	245. 4	2. 82	10. 99	31. 34
Year of birth:										
1947	82	. 10	—. 04	—. 04	. 6	2. 3	—. 2	—. 01	. 30	. 06
1948	102	—. 07	—. 42	—. 52	—1. 7	—6. 6	—24. 7	—. 13	—. 31	—1. 33
1950	34	—. 03	. 46	. 56	1. 1	4. 3	24. 9	. 14	. 01	1. 27
Age of dam:										
10.0–11.5 months	20	—1. 53	—1. 18	—1. 15	—4. 8	—16. 1	—41. 7	—. 08	—. 62	—1. 10
11.6–13.5 do	27	—. 50	—. 25	—. 22	—3. 1	—10. 7	—22. 7	—. 17	—. 99	—2. 27
17.0–19.0 do	86	. 66	. 20	. 11	1. 9	4. 4	7. 2	. 03	. 31	. 42
22.0–48.0 do	85	1. 37	1. 23	1. 26	6. 0	22. 4	57. 2	. 22	1. 30	2. 95
Line differences in direct maternal effects: [2]										
L–CW	29	—1. 17	—1. 08	—1. 04	—2. 0	—8. 5	—27. 6	. 18	. 39	. 57
L–D	38	—. 03	. 07	—. 10	—2. 4	—7. 0	—29. 8	—. 23	—1. 02	—3. 34
L–LB	39	. 12	. 47	. 49	1. 8	4. 9	15. 8	. 08	—. 37	—. 68
L–PC	38	. 23	. 15	. 26	—. 1	4. 1	18. 4	—. 05	. 47	1. 53
L–D-H	35	—. 03	. 26	. 21	—. 0	2. 6	4. 1	—. 02	. 03	—. 13
Y–D-L-H	39	. 88	. 13	. 18	2. 7	3. 9	19. 1	. 04	. 50	2. 05
Regression on inbreeding of dam:										
Linear percent	218	—. 04	—. 00	—. 01	—. 1	—. 2	—. 7	—. 01	—. 02	—. 06
Regression on inbreeding of litter:										
Linear percent	218	. 01	—. 00	—. 03	—. 0	—. 6	—1. 7	—. 00	—. 08	—. 14

[1] Computed by ignoring specific combining ability effects among lines.
[2] See p. 3 for meaning of line symbols.

TABLE 4.—*Least squares estimates of the general and specific combining effects of lines on litter and pig traits at three ages*

Effects studied [1]	Litter size at—			Litter weight at—			Pig weight at—		
	Birth	21 days	56 days	Birth	21 days	56 days	Birth	21 days	56 days
General combining effects: [2]	*Number*	*Number*	*Number*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*	*Pounds*
L–CW	0.33	0.59	0.56	2.1	3.6	13.3	0.10	−0.46	−0.87
L–D	.23	.48	.52	1.4	10.0	29.5	.03	.62	1.89
L–LB	−.26	−.37	−.34	−1.8	−5.8	−12.3	−.08	.16	.62
L–PC	.44	.08	.04	−.2	−3.1	−9.8	−.13	−.51	−1.41
L–D–H	−.26	−.31	−.15	−.6	−.6	−5.5	.05	.24	−.25
Y–D–L–H	−.48	−.47	−.63	−.9	−4.1	−15.2	.03	−.05	.02
Specific combining effects:									
L–CW × L–D	.66	−.46	−.32	.4	−.9	−8.7	−.16	.38	−.40
L–CW × L–LB	−.27	−.41	−.31	−.1	−2.4	−2.3	.05	.35	1.15
L–CW × L–PC	−.21	−.12	−.28	.1	2.5	4.4	.04	.49	1.60
L–CW × L–D–H	.64	.65	.69	1.4	5.0	10.6	−.09	−.25	−1.66
L–CW × Y–D–L–H	−.83	.35	.21	−1.8	−4.1	−4.0	.16	−.97	−.70
L–D × L–LB	.10	−.27	−.32	.0	−3.4	−8.1	.00	−.18	.02
L–D × L–PC	.44	1.03	1.09	1.4	6.8	26.9	.01	−.42	−.82
L–D × L–D–H	−1.30	−.09	−.35	−1.5	−1.8	−6.4	.21	−.02	1.18
L–D × Y–D–L–H	.10	−.21	−.11	−.3	−.8	−3.7	−.07	.24	.02
L–LB × L–PC	−.45	.42	.32	−1.2	.1	−2.6	−.01	−.56	−1.28
L–LB × L–D–H	.50	.51	.53	1.1	5.8	12.9	−.02	−.08	−.69
L–LB × Y–D–L–H	.11	−.24	−.22	.2	−.0	.1	−.02	.46	.79
L–PC × L–D–H	−.12	−1.25	−1.07	−1.5	−11.7	−26.7	−.04	.28	.89
L–PC × Y–D–L–H	.34	−.08	−.08	1.2	2.2	−1.9	−.01	.20	−.40
L–D–H × Y–D–L–H	.28	.18	.19	.6	2.7	9.6	−.06	.06	.29

[1] See p. 3 for meaning of line symbols.
[2] Computed by ignoring specific combining ability effects among lines.

TABLE 5.—*Mean squares from least squares analyses for birth, 21-day, and 56-day data*[1]

Source of variation	Degrees of freedom	Pigs per litter at—			Litter weight at—			Pig weight at—		
		Birth	21 days	56 days	Birth	21 days	56 days	Birth	21 days	56 days
Years	2	0. 5	7. 6	12. 0	122. 5*	1, 867*	25, 812**	0. 75*	5. 9	73. 9*
Age of dam	3	41. 0**	29. 2**	30. 4**	696. 1**	9, 341**	60, 084**	. 95**	33. 7**	175. 1**
Inbreeding of dam	1	8. 8	. 1	. 4	147. 2	451	3, 703	. 30	4. 1	26. 6
Inbreeding of litter	1	. 0	. 0	1. 1	. 2	322	2, 879	. 03	6. 6	20. 5
Maternal line effects	5	7. 2	3. 7	3. 9	84. 8	680	10, 112*	. 31	6. 0	69. 1*
General combining effects	5	5. 1	7. 5	7. 9	79. 5	1, 134	10, 423*	. 25	4. 5	39. 3
Specific combining effects	9	1. 8	6. 1	5. 8	16. 3	433	3, 071	. 00	2. 7	19. 6
Error	191	6. 9	4. 8	4. 7	38. 8	514	4, 421	. 22	3. 0	24. 2

[1] All mean squares except those for specific combining effects computed on assumption of zero differences in specific effects.
*=Significant at 5-percent level.
**=Significant at 1-percent level.

Influence of Inbreeding of Dam and Inbreeding of Litter

The average inbreeding coefficients of dams varied from 12.6 to 45.1 percent, while those of litters varied from 0 to 17.3 percent between crosses and years. The corresponding intra-cross-and-year standard deviations were 6.3 and 0.7 percent, which showed that inbreeding of litters within crosses differed little compared with that of dams.

None of the regression coefficients for the litter and pig traits on inbreeding of dams and inbreeding of litters were significant, except the regression of litter weight at birth on inbreeding of dam which was on the borderline of significance at the 5-percent level of probability. However, all but one of the regressions were negative—an indication that both inbreeding of dams and inbreeding of litters tended to cause a decline in performance. The small positive regression of litter size at birth on inbreeding of litter does not agree with earlier findings of Hetzer et al. (1940), Comstock and Winters (1944), and Blunn and Baker (1949), but agrees with Stewart's (1945) conclusions that the inbreeding of the litter has little or no adverse effect on prolificacy. Results of regression analyses by Blunn and Baker (1949), on the other hand, suggest that the inbreeding of litters is more important than the inbreeding of dams in influencing litter performance after birth. The declines per 10 percent inbreeding of litters and dams reported by these workers were 0.38 and 0.27 pig, respectively, for litter size at 21 days, 0.36 and 0.30 pig for litter size at 56 days, and 14.4 and 12.4 pounds for litter weight at 56 days.

Line Differences in Maternal Effects

Since the six lines were crossed reciprocally, the data provided an opportunity for obtaining estimates of line differences in maternal abilities. Although acting directly through the environment a sow provides for her offspring, maternal effects as used here were probably largely genetically determined, since all sows and pigs were kept under essentially the same environmental conditions each year.

Line differences in maternal effects were significant or approached significance at the 5-percent level only for litter weight at birth and for litter and pig weight at 56 days. However, except for litter size at 21 and 56 days, the mean squares for the remaining litter and pig traits were all large enough, compared with their error mean squares, to suggest that line differences in maternal effects were real in these data. As shown in table 3, the differences between the best and poorest lines averaged 2.05 pigs for number farrowed, 1.55 pigs for number alive at 21 days, and 1.53 pigs for number weaned at 56 days. For litter weight the range in line of dam influence was 5.1 pounds at birth and 13.4 and 48.9 pounds at 21 and 56 days. The corresponding ranges for pig weight were 0.41, 1.52, and 5.4 pounds. The Y–D–L–H and L–PC sows ranked highest for litter size at birth and L–CW sows lowest. Y–D–L–H and L–PC sows were also superior to sows of the other lines in litter and pig weight at weaning. Since inbreeding has been shown to have a rather marked deleterious effect on sow productivity (Dickerson et al., 1946; Hetzer et al., 1951), it appears that the relatively poor maternal abilities of the L–CW line for litter size were largely due to the fact that it was the most highly inbred line, as shown in table 1.

The ranking of the lines for litter weight corresponds more closely with that for litter size than for pig weight, which indicates that line differences in litter weight were more largely determined by line differences in prolificacy and pig viability than by differences in individual pig weight. This agrees with results reported by Cobb (1958), who found that breed differences in litter weight at weaning are largely due to differences in pig survival.

Previous studies of maternal effects in crosses involving inbred lines of swine include those of Henderson (1948) on preweaning performance, of Magee and Hazel (1959) on body weight at 154 days, of Squiers et al. (1952) on ovulation rate, of Warren and Dickerson (1952) on preweaning performance, feed lot performance, and carcass quality, and of Bradford et al. (1958) on body weight at 56 days and 5 months of age. Neither Henderson nor Magee and Hazel found line differences in maternal influence to be significant sources of variation in their data. Warren and Dickerson, on the other hand, found rather large and significant differences in maternal influence on body weight at weaning and at 154 days, on daily gain to market weight, and on backfat thickness.

General and Specific Combining Ability

As shown in table 5, none of the mean squares for general combining ability were significant, except the one for litter weight at weaning which was significant at the 5-percent level and those for litter weight at birth and 21 days which bordered on significance at this level. However, all except the mean square for litter size at birth were larger than their corresponding error mean squares. Although not definitely conclusive, this would indicate that some of the variation in these traits can probably be ascribed to additive genetic effects.

Line differences in general combining effects between the best and poorest lines averaged 0.92 pig for litter size at birth, 1.06 pigs for litter size at 21 days, and 1.19 pigs for litter size at 56 days. For litter weight the range was 3.9 pounds at birth, 15.8 pounds at 21 days, and 44.7 pounds at 56 days, while for pig weight at the same ages the ranges were 0.2, 1.1, and 3.3 pounds, respectively. The L–CW and L–D lines generally were best or second best in general combining ability for litter size and litter weight at the three ages while the L–LB and Y–D–L–H lines were poorest or next to the poorest for these traits. In individual pig weight at weaning, the L–D line was best, followed by the L–LB, Y–D–L–H, L–D–H, L–CW, and L–PC in that order. While differences in rank of the lines for individual pig weight and litter size may reflect differences in the genetic makeup between the lines for the two traits, if significant, the observed discordance in rank probably was exaggerated by the fact that pig weights were not adjusted for differences in litter size.

The constants for the lines' general combining effects on litter size and litter weight at weaning can be compared with those reported by Cobb (1958) from crosses involving boars of the same six lines used in the present study with outbred sows of four breeds on Pennsylvania farms. Both the correlations between the two set of constants for litter size and those for litter weight were small but positive—0.32 and 0.10, respectively—which suggests that the ranking of the lines did not differ significantly between locations.

Specific combining effects were not significant for any of the litter or pig traits at the three ages. Only the mean squares for litter size at 21 and 56 days were larger than their corresponding error mean squares, but both were substantially smaller than the mean squares pertaining to the general combining effects for these traits. The same was true for the specific combining variances for all of the other traits, indicating that specific combining effects did not exist or, if present at all, that they were negligibly small. The small differences in specific combining effects on the litter and pig traits studied here is rather surprising in view of the marked heterosis effects exhibited by the same traits in the various crosses as a whole, as indicated earlier in this report. Additional data would seem to be necessary to resolve the apparent inconsistency between the two sets of results.

POST-WEANING GROWTH AND CARCASS DATA

While least squares procedures as described by Henderson (1948) for balanced single cross designs were used to obtain estimates of line characteristics for the post-weaning growth and carcass traits, tests for the effects of year of birth, sex, and sex linkage were carried out by analysis of variance methods given by Snedecor (1956).

Test for Sex Linkage

The results of the analyses of variance for testing for the presence of sex-linked genes are shown in table 6. Comparison of the interaction mean squares for sex among reciprocals within pairs of crosses with those for error is of primary interest in this connection. When adjusted values for the traits previously found to exhibit a significant sex difference were used, none of the interaction variances were large enough for significance, most of them actually being much smaller than those for error. Thus, the results provide no evidence for the presence of sex linkage.

Year-of-Birth Effects

As shown in the upper part of table 7, year-of-birth effects were not significant for pig weight at 98 or 140 days of age, but they were significant for daily gain. They were also significant at the 5 or 1 percent level for all carcass traits, except percentage yield of lean cuts. Fluctuations in weather conditions appear to be the most likely cause of the year effect on daily gain, although changes in average genetic merit may have been partly responsible.

Effect of Sex

Barrows were 0.2 and 3.2 pounds heavier at 98 and 140 days of age and gained 0.02 pound more per day than gilts, but these differences were not significant and were much smaller than the differences of 5.4 pounds in weight at 140 days and 0.06 pound in daily gain reported by Cobb (1958) for topcrosses involving the same lines on Pennsylvania farms. Sex differences, on the other hand, were highly significant for all carcass traits except percentage yield of total carcass. Gilts dressed out slightly lighter and averaged 0.4 percent less bacon, 1.0 percent less fat cuts, and 0.4 centimeter less backfat, but yielded 1.2 percent more lean cuts than barrows. These results agree rather closely with those reported by Hetzer et al. (1950, 1956), Freeden (1953), Anderson (1955), Cobb (1958), and others.

TABLE 6.—*Analysis of variance for testing for sex linkage in post-weaning growth and carcass traits*[1]

Source of variation	Degrees of freedom	Mean squares								
		Weight and gain items			Carcass items					
		Weight at—		Daily gain to 225 pounds	Yield as percent of slaughter weight					Backfat thickness
		98 days	140 days		Total carcass	Preferred cuts			Fat cuts	
						Lean	Bacon	Total		
Pairs of crosses	14	103. 3	158. 9	0. 009	1. 06	2. 44	0. 15	2. 62	1. 38	0. 56
Reciprocals in crosses	15	64. 7	87. 2	. 008	1. 11	. 44	. 28	. 25	1. 62	. 92
Sex	1	. 7	148. 8	. 013	. 51	. 00	. 00	. 00	. 00	. 00
Pairs of crosses × sex	14	30. 8	48. 3	. 002	. 55	. 19	. 08	. 25	. 78	. 37
Reciprocals in pairs × sex	15	42. 8	77. 4	. 004	. 46	. 12	. 07	. 18	. 37	. 21
Error [2]	98	47. 3	97. 1	. 007	. 46	. 46	. 12	. 43	. 54	. 50

[1] Based on litters represented by equal numbers of males and females, using unweighted means adjusted to zero sex difference for items showing significant sex difference.

[2] Obtained by multiplying within sex, cross, and year mean squares by reciprocal of harmonic mean of subclass numbers. NOTE: Error mean squares for carcass data based on 92 degrees of freedom.

TABLE 7.—*Estimates of effects of year of birth, sex, line differences in maternal influences and of various other factors on post-weaning growth and carcass traits*

Effects studied	Weight and gain items				Carcass items						
	Pigs fed	Weight at—		Daily gain	Pigs slaughtered	Yield as percent of slaughter weight					Backfat thickness
		98 days	140 days			Total carcass	Preferred cuts			Fat cuts	
							Lean	Bacon	Total		
	number	*Pounds*	*Pounds*	*Pounds*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Cm.*
General mean [1]	237	83.7	158.7	1.65	234	80.1	38.8	10.6	49.4	15.3	4.4
Year of birth:											
1947	119	−1.1	−.2	−.03*	117	−.4**	.1	−.5**	−.4**	.2*	.1**
1948	118	1.1	.2	.03*	117	.4**	−.1	.5**	.4**	−.2*	−.1**
Sex:											
Barrows	116	.1	1.6	.01	113	.1	−.6**	.2**	−.4**	.5**	.2**
Gilts	121	−.1	−1.6	−.01	121	−.1	.6	−.2**	.4	−.5**	−.2**
Line differences in direct maternal influences: [2]											
L-CW	39	−5.0	−9.0	−.06	39	.4	−.6	.4	−.2	.8	.04
L-D	39	−3.2	−4.0	−.02	39	−.7	−.0	.0	−.1	−.9	−.16
L-LB	40	−1.6	−2.0	.02	39	.2	.4	.2	.6	−.4	−.10
L-PC	40	.7	2.7	−.02	38	.0	.3	.2	.6	−.4	−.10
L-D-H	40	4.0	3.9	.02	40	.3	.3	−.4	−.1	−.1	.14
Y-D-L-H	39	5.1	8.4	.06	39	.4	−.2	.1	−.1	.6	.16
Regression on [3]—											
Age of dam..months	[4] 57	.55**	.82**	------	------	------	------	------	------	------	------
Weight at 56 days pounds	[4] 116	------	------	.006*	------	------	------	------	------	------	------
Slaughter weight pounds	------	------	------	------	[4] 113	.002	−.014	.005	−.009	.035	.017**

[1] Adjusted to a mean age of dam of 20.3 months, except daily gain adjusted to a mean initial weight of 32.0 pounds and carcass items adjusted to a mean slaughter weight of 211.0 pounds, and zero sex differences.

[2] See p. 3 for meaning of line symbols.

[3] Regressions for weight items were computed on a between litters within cross and year basis, while regressions for daily gain and carcass items were computed on a between pigs within sex, cross and year basis.

[4] Numbers represent degrees of freedom for corresponding regressions.

*=Significant at 5-percent level. **=Significant at 1-percent level.

Regressions

The regression coefficients used to adjust the 98- and 140-day pig weights for differences in age of dam are shown in the lower part of table 7, together with those for daily gain on weight at 56 days, and those for the various carcass traits on slaughter weight. The regressions for both 98-day weight and 140-day weight as well as those for daily gain were positive and significant or highly significant. They show that an increase of 1 month in the dams' age resulted in 0.55 $\pm$0.167 pound increase in weight at 98 days and 0.82$\pm$0.235 pound increase in weight at 140 days, while each pound increase in weight at 56 days resulted in 0.006$\pm$0.0023 pound increase in daily gain. For the carcass traits, only the regression for backfat thickness was large enough for significance at the 1-percent level. It indicates that for each 1-pound increase in slaughter weight backfat thickness increased 0.017$\pm$0.0064 centimeter.

Line Characteristics

The constants derived from the least square analyses are presented in table 7 for maternal line effects while those for general and specific combining effects are presented in table 8. The mean squares associated with the three sets of effects are given in table 9 along with those for litter within crosses and years and those between littermates. Litter differences for weight at 98 and 140 days of age, for daily gain, for yield of total carcass, for yield of lean cuts, and for yield of five preferred cuts and fat cuts were all significant or highly significant. Although the mean squares for yield of bacon and backfat thickness were not significant, both were larger than those within litters, which suggests that litter differences were real in these data. Consequently, the litter mean squares were used as error terms in testing the significance of the other effects.

Line Differences in Maternal Effects.—The mean squares for line differences in maternal effects were significant or highly significant for weight at 140 days, yield of total carcass, yield of bacon, and yield of fat cuts. The lack of significance of maternal effects for daily gain is not surprising because daily gain was adjusted for differences in 56-day weight and hence would not be expected to show maternal effects. The existence of maternal effects for 140-day weight, on the other hand, can be interpreted as reflecting maternal line effects on weaning weight because both 98-day and 140-day weights are partly made up of pig weight at 56 days. The positive correlation of 0.51 obtained between the estimates of maternal effects for 56- and 140-day weight is in agreement with this explanation. However, the existence of maternal effects for total yield of carcass, yield of bacon, and yield of fat cuts cannot be explained on the same basis since none of these traits can be considered as having been subject to direct maternal effects that could reasonably be attributed to differences in lactation or mothering ability. While sex linkage or factors acting through the cytoplasm of the egg might be invoked as a possible explanation, the results provide no critical evidence for sex-linked genes or cytoplasmic inheritance in these data. On the other hand, estimates of maternal line effects for pig weight at 56 days gave rather large positive correlations with those for total yield of carcass (0.82), yield of fat cuts (0.79), and backfat thickness (0.92), thereby suggesting that

TABLE 8.—*Estimates of general and specific combining effects of lines on post-weaning growth and carcass traits*

Effects studied [1]	Weight and gain items			Carcass items					
	Weight at—		Daily gain to 225 pounds	Yield as percent of slaughter weight					Backfat thickness
	98 days	140 days		Total carcass	Preferred cuts: Lean	Preferred cuts: Bacon	Preferred cuts: Total	Fat cuts	
General combining effects:	*Pounds*	*Pounds*	*Pounds*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Cm.*
L-CW	3. 6	8. 5	0. 06	0. 2	0. 9	−0. 3	0. 6	−0. 6	−0. 13
L-D	4. 4	3. 6	−. 00	. 5	−. 1	. 0	−. 1	. 9	. 12
L-LB	−. 0	−2. 9	−. 06	−. 0	−. 2	−. 2	−. 4	. 4	. 10
L-PC	−3. 3	−3. 3	. 02	. 1	. 4	. 2	. 6	−. 4	−. 16
L-D-H	−5. 6	−7. 4	−. 03	−. 4	−1. 0	. 2	−. 8	. 4	. 12
Y-D-L-H	. 9	1. 6	. 00	−. 3	−. 0	. 1	. 1	−. 6	−. 04
Specific combining effects:									
L-CW × L-D	4. 0	4. 5	. 02	. 2	−. 2	−. 1	−. 3	. 3	−. 00
L-CW × L-LB	. 6	−. 6	−. 01	−. 6	−. 2	−. 0	−. 2	−. 3	−. 01
L-CW × L-PC	3. 5	1. 2	−. 01	. 0	. 5	−. 2	. 4	−. 3	−. 17
L-CW × L-D-H	−2. 1	. 7	. 03	. 1	−. 3	. 1	−. 3	. 3	. 18
L-CW × Y-D-L-H	−6. 0	−5. 8	−. 03	. 3	. 2	. 2	. 4	−. 0	. 00
L-D × L-LB	−3. 3	−1. 9	−. 01	. 1	. 0	−. 0	. 0	. 1	−. 00
L-D × L-PC	−. 6	−. 1	. 03	−. 2	−. 3	. 1	−. 2	−. 0	. 06
L-D × L-D-H	−3. 6	−7. 4	−. 04	−. 0	. 6	−. 2	. 4	−. 3	−. 02
L-D × Y-D-L-H	3. 5	4. 9	. 00	−. 1	−. 2	. 2	. 1	−. 1	−. 03
L-LB × L-PC	−. 6	. 0	. 01	. 5	. 5	. 1	. 6	−. 0	. 10
L-LB × L-D-H	1. 9	4. 0	−. 00	. 0	−. 2	−. 0	−. 2	. 0	−. 09
L-LB × Y-D-L-H	1. 4	−1. 6	. 01	. 0	−. 1	−. 0	−. 1	. 2	−. 00
L-PC × L-D-H	. 2	−. 4	−. 01	−. 1	−. 4	. 2	−. 2	. 2	−. 05
L-PC × Y-D-L-H	−2. 5	−. 7	−. 01	−. 2	−. 3	−. 3	−. 6	. 2	. 06
L-D-H × Y-D-L-H	3. 6	3. 2	. 03	−. 0	. 3	−. 1	. 2	−. 3	−. 03

[1] See p. 3 for meaning of line symbols.

TABLE 9.—*Mean squares for maternal and general and specific combining effects of lines on post-weaning growth and carcass traits*

Source of variation	Degrees of freedom	Weight and gain items			Carcass items					
		Weight at—		Daily gain to 225 pounds	Yield as percent of slaughter weight					Backfat thickness
		98 days	140 days		Total carcass	Preferred cuts			Fat cuts	
						Lean	Bacon	Total		
Maternal line effects	5	388. 9	938. 1*	0. 047	4. 41*	2. 73	2. 36**	2. 84	9. 32**	0. 419
General combining effects	5	587. 4**	1, 251. 6**	. 069*	3. 61	15. 98**	1. 79**	11. 98**	16. 32**	. 642**
Specific combining effects	9	232. 4	296. 0	. 012	1. 55	2. 94	. 64*	3. 28	1. 21	. 167
Litters within crosses and years [1]	57	171. 3*	338. 3*	. 026**	1. 75*	2. 63**	. 31	2. 93**	2. 55**	. 187
Within litters [1]	119	104. 2	237. 0	. 013	1. 15	1. 00	. 23	1. 52	1. 30	. 137

[1] Adjusted for linear regression on age of dam, except mean squares for daily gain adjusted for regression on 56-day weight, and those for carcass items adjusted for linear regression on slaughter weight, using data adjusted to zero sex difference for items showing significant sex difference. NOTE: Within litter mean squares for daily gain and carcass items are based on 118 and 116 degrees of freedom, respectively.

*=Significant at 5-percent level.

**=Significant at 1-percent level.

line differences in maternal effects on these traits were largely due to differences in pig weight at 56 days rather than to direct maternal effects.

This interpretation agrees with the positive correlations reported by Dickerson (1947) and other workers between rate of gain in the feed lot and thickness of backfat. On the other hand, McMeekan (1940), by controlling the plane of nutrition, found that pigs on a low plane during the early stages of growth were significantly fatter when slaughtered at 200 pounds weight, than pigs that were started on a high plane of nutrition. Based on results from reciprocal crosses of inbred Poland China lines with other inbred and noninbred stocks, Warren and Dickerson (1952) also reported significant line-of-dam effects on a number of post-weaning traits, including pig weight at 154 days of age, daily gain from weaning to market weight, and thickness of backfat.

As shown in table 7, the differences between the best and poorest lines averaged 10.1 pounds for weight at 98 days, 17.4 pounds for weight at 140 days, and 0.12 pound for daily gain. For carcass traits, the range in line-of-dam effects averaged 1.1 percent for yield of total carcass, 1.0 percent for yield of lean cuts, 0.8 percent for yield of bacon, 0.8 percent for yield of five preferred cuts, 1.7 percent for yield of fat cuts, and 0.32 centimeter for backfat thickness. The Y–D–L–H line ranked highest for weight both at 98 and 140 days of age and for daily gain, while the L–CW line ranked lowest for these traits. The L–CW also ranked lowest in maternal effects for yield of lean cuts, but exceeded all other lines for yield of bacon and yield of fat cuts.

General and Specific Combining Ability.—Line differences in general combining ability for weights at 98 and 140 days of age and for daily gain were all significant or highly significant. They were also highly significant for all carcass traits except total carcass yield, which did not differ significantly between lines. As shown in table 8, the range in general combining effects between the best and poorest lines was 10.0 pounds for weight at 98 days, 15.9 pounds for weight at 140 days, and 0.12 pound for daily gain. For carcass traits, the range in general combining effects between lines was 0.9 percent for total yield for carcass, 1.9 percent for yield of lean cuts, 0.5 percent for yield of bacon, 1.4 percent for sum of preferred cuts, 1.5 percent for yield of fat cuts, and 0.28 centimeter for backfat thickness. The L–CW line ranked highest in general combining ability for daily gain, followed by the L–PC, Y–D–L–H, L–D, L–D–H, and L–LB lines in that order. The L–CW line also ranked highest for yield of lean cuts and for sum of five preferred cuts, and was followed in order by the L–PC, Y–D–L–H, L–D, L–LB, and L–D–H lines. The L–D, L–LB, and L–D–H lines were the least desirable in general combining ability for carcass quality, both as indicated by the relatively low yields of lean cuts and the relatively high yields of fat cuts exhibited by their progeny.

Results reported by Cobb (1958) from topcrosses involving boars of the same six lines on Pennsylvania farms show that Y–D–L–H and L–D–H topcrosses were the two best groups in both 140-day weight and daily gain, and L–D topcrosses were the poorest. In this study, the same three lines ranked third, sixth, and second for 140-day weight and third, fifth, and fourth for daily gain. In percentage of lean cuts L–CW and L–PC crosses were the most desirable while the

L-D-H crosses were the least desirable in both studies. The results for the other carcass traits showed similar agreement between the two studies. The fact that the constants for line effects in Cobb's study contained some farm effects may explain the apparent discordance in rank between lines, although sampling errors due to the relatively small number of animals tested from each line probably were partly responsible.

Differences in specific combining abilities were large enough for significance at the 5-percent level only for yield of bacon. Most of the mean squares for specific effects for the other post-weaning growth and carcass traits were actually smaller than their corresponding error terms, indicating that in these data, specific combining effects were very small, if present at all. The absence of any indication of differences in specific effects for these traits thus agrees with the results obtained for the preweaning litter and pig traits.

Variance Components.—Estimates of the relative importance of differences in maternal effects and in general and specific combining ability effects, compared with the variances due to litter and intra-litter differences, were obtained from variance component analyses as suggested by Henderson (1948) for balanced single cross designs and are illustrated in table 10. The results of these analyses are presented in table 11. Intra-litter differences appeared to be the most important single source of variation for all traits, accounting for slightly less than one-half of the variance in yield of lean cuts to nearly three-fourths of the variances in 140-day weight and backfat thickness. Litter effects generally were small compared with intra-litter variation but, except for yield of bacon, they were nearly two to six times larger than those associated with any of the next most important source of variation. The litter variance actually varied from less than one-tenth for yield of bacon to nearly two-fifths for yield of lean cuts.

TABLE 10.—*Analysis of variance model for estimating variance components for post-weaning growth and carcass traits*

Source of variation	Degrees of freedom	Theoretical composition of mean squares
Maternal line effects	5	E+2D+24M
General combining effects	5	E+2D+9.6S+38.4G
Specific combining effects	9	E+2D+16S
Litters within crosses and years	57	E+2D
Pigs within litters	118	E

Maternal effects appeared to be absent for both yields of lean cuts and for total yield of preferred cuts, but accounted for about one-fifth of the variance in yield of bacon. For the remaining traits, estimates of maternal effects accounted from about one twenty-fifth of the variance in daily gain to about one-tenth of the variance in yield of fat cuts. General combining effects appeared to be small compared with maternal effects for total yield of carcass and yield of bacon but they were the most important genetic source of variation for yield of lean cuts, yield of fat cuts, and total yield of preferred cuts, accounting from about one-tenth to nearly one-sixth of the variance in

TABLE 11.—*Estimates of variance components (V.C.) and percentage of variance due to maternal line effects (M), general combining effects (G), specific combining effects (S), differences between litters within crosses and years (L), and differences between littermates (E).*

Observation	Maternal effects (M)		General combining effects (G)		Specific combining effects (S)		Litters (L)		Litter mates (E)	
	V.C.	Percent	V.C.	Percent	V.C.	Percent	V.C.	Percent	V.C.	Percent
Weight at—										
98 days ....pounds..	9. 1	5	9. 9	7	3. 8	2	33. 5	21	104. 2	65
140 days ....do....	25. 0	8	23. 8	7	0. 0	0	50. 6	15	237. 0	70
Daily gain ....do....	. 0009	4	. 0011	5	. 0000	0	. 0066	30	. 0131	61
Yield as percent of slaughter weight:										
Total carcass................	. 111	7	. 048	3	. 000	0	. 298	18	1. 152	72
Preferred cuts:										
Lean cuts................	. 004	0	. 343	16	. 020	1	. 816	37	. 998	46
Bacon................	. 085	21	. 033	8	. 021	5	. 037	9	. 233	57
Total................	. 000	0	. 230	10	. 022	1	. 706	28	1. 516	61
Fat cuts................	. 282	11	. 358	14	. 000	0	. 628	24	1. 298	51
Backfat thickness ....cm..	. 097	5	. 118	6	. 000	0	. 248	14	1. 370	75

these traits. For 98-day weight, 140-day weight, daily gain, and backfat thickness general combining effects differed little from maternal effects, the portions of the variances due to general effects varying from about one-twentieth to nearly one-fifteenth for these traits.

The apparent absence of differences in specific combining ability suggested by the tests of significance in table 9 is reflected by the results in table 11, which show that specific effects at best accounted for only about one-twentieth of the variability in any of the traits. Thus only in yield of bacon was there a suggestion that differences in specific combining ability existed in these data. These results are in distinct contrast with those of other workers, notably Henderson (1948) who reported differences in specific combining ability to be more important in his data than differences in general combining ability or in maternal effects.

CORRELATIONS

The correlations between the average inbreeding coefficients of the lines and the estimates of the general and maternal abilities of the lines are shown in table 12. The correlations between the calculated inbreeding of the lines and the estimates of maternal effects were negative for all litter traits, ranging from -0.27 for litter weight at birth to -0.91 for litter size at 56 days. In contrast, the correlations

TABLE 12.—*Correlations relating estimates of line differences in maternal effects and general combining ability effects with inbreeding coefficients of lines* [1]

Observation	r_{IM}	r_{IG}
Birth to weaning:		
Litter size at—		
Birth	−0. 62	0. 23
21 days	−. 90*	. 40
56 days	−. 91*	. 32
Litter weight at—		
Birth	−. 27	. 58
21 days	−. 47	. 12
56 days	−. 35	. 12
Pig weight at—		
Birth	. 66	. 37
21 days	. 64	−. 51
56 days	. 48	−. 59
Weaning to 225 pounds:		
Pig weight at—		
98 days	−. 20	. 20
140 days	−. 32	. 58
Daily gain	−. 42	. 82
Carcass Data:		
Yield as percent of slaughter weight:		
Total carcass	. 56	−. 08
Preferred cuts:		
Lean	−. 87*	. 58
Bacon	. 42	−. 36
Total	−. 56	. 53
Fat cuts	. 87*	−. 72
Backfat thickness	. 47	−. 64

[1] Computed by using zero for line with largest negative constant for M and G and expressing constants for other lines as deviations from zero.
* = Significant at 5-percent level.

with maternal effects were positive for all preweaning measures of pig weight but negative for the three post-weaning growth measures. The difference in signs between these two sets of correlations presumably is partly due to the fact that individual pig weights to weaning are negatively correlated with litter size and that the data were not adjusted for these correlations. For the carcass data, estimates of maternal effects were positively correlated with inbreeding of the lines for total yield of carcass, for yield of bacon, for yield of fat cuts, and for backfat thickness. The correlation between the two variables, on the other hand, was negative for yield of lean and for total yield of preferred cuts.

Interestingly enough, all of the correlations between the calculated inbreeding of the lines and the estimates of general combining abilities were of opposite sign from the corresponding correlations with the estimates of maternal effects, except for pig weight at birth which gave a positive correlation of inbreeding with both the estimates of general combining ability and those of maternal effects. However, this rather consistent difference in signs between the corresponding correlations probably is largely automatic, because of the negative correlations that one would expect between estimates of general and maternal effects where, as in this study, the two sets of estimates were calculated from the same sets of equations. Thus, with the probable exception of litter size and yields of lean and fat cuts, which gave significant correlations between inbreeding of lines and estimates of maternal effects, the results provide no convincing evidence that the inbreeding practiced in developing the lines affected either their maternal or general combining abilities.

SUMMARY AND CONCLUSIONS

The results of single crosses among six inbred lines of swine developed at the Agricultural Research Center, Beltsville, Md., were studied to obtain estimates of the general and specific combining abilities and maternal abilities of the six lines. The data were also analyzed to estimate the effects of certain environmental factors. A total of 218 litters farrowed during the fall of 1947, 1948, and 1950, and representing all of the 30 possible reciprocal crosses were available for study. The characteristics studied were litter size, litter weight and individual pig weight at birth and at 21 and 56 days of age, individual pig weight at 98 and 140 days of age, daily gain from weaning to a final weight of about 225 pounds, and six carcass yields and measurements.

Differences in year of birth were significant or highly significant for all traits, except litter size at the three ages, individual pig weight at 21, 98, and 140 days, and yield of lean cuts. Age of dam had a highly significant effect on both litter size and litter weight as well as on all measurements of individual pig weight. In agreement with estimates obtained by other workers, age-of-dam effects were most pronounced among sows farrowing their first litter at approximately 1 year of age. Intra-cross-and-year differences in inbreeding of dam bordered on significance at the 5-percent level only for litter weight at birth, although most of the regressions on inbreeding of dam and inbreeding of litter were negative. Sex had no significant effect on post-weaning growth rate or on total carcass yield but had a highly significant effect on all other carcass traits studied. Gilts averaged 0.4 percent less bacon, 1.0 percent less fat cuts, and 0.4 centimeter less backfat, but yielded 1.2 percent more lean cuts than barrows. There was no evidence that sex-linked genes contributed to the variation in the post-weaning growth and carcass traits.

Line differences in maternal abilities had no demonstrable effect on litter size, but they were statistically significant for litter weight and pig weight at 56 days. Maternal influences were also significant for individual pig weight at 140 days, total yield of carcass, yield of bacon, and yield of fat cuts, accounting for 7 to 21 percent of the variation in these characteristics. The mean squares associated with line differences in general combining abilities were larger than their corresponding error terms for most litter traits, although only for litter weight at 56 days were these differences significant. However, general combining effects were significant or highly significant sources of variation in all post-weaning growth measures as well as in all carcass traits except total yield of carcass. They accounted for 5 to 7 percent of the variation in the three rate-of-growth measures and for 3 to 16 percent of the variation in the six carcass traits. There was no evidence of differences in specific combining effects for any of the traits except yield of bacon. The results thus suggest that differences in specific effects were unimportant in these data. The results also suggest that differences in general combining effects and maternal influences were about equally important in their contribution to the variation of most of the traits for which variance component estimates were obtained.

Correlations of least squares estimates of general combining effects and maternal effects with average inbreeding coefficients of the lines suggested that the inbreeding practiced when the lines were being developed affected adversely maternal abilities for large litter size and high yields of lean cuts, while it had the opposite effect on yields of fat cuts.

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