RESEARCH BULLETIN 689 FEBRUARY, 1959

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
J. H. LONGWELL, *Director*

Heritabilities and Heterosis of Some Economic Traits in Swine

V. B. REDDY, J. F. LASLEY AND L. F. TRIBBLE

In cooperation with the
Regional Swine Breeding Laboratory,
A.H.R.D., A.R.S., U. S. Department of Agriculture.

(Publication authorized February 5, 1959)

COLUMBIA, MISSOURI

ABSTRACT

Rate of gain and backfat thickness in the live hog were studied in 436 Landrace x Poland pigs from reciprocal crosses farrowed in two seasons. Seasons, sex, and type of feeding (pasture or dry lot) were found to significantly influence both of these characteristics and corrections were made on the original data before heritability estimates and correlations between relatives were determined.

Heritability estimates for rate of gain calculated by means of the intra-sire regression of off-spring on dam were only 2 percent for spring pigs, 16 percent for fall pigs, and 4 percent for pigs from both seasons combined.

Heritability estimates determined by the regression of offspring on the mean of the sire and dam gave values of 31, 20 and 21 percent, respectively, for spring, fall, and both seasons combined.

Heritability estimates for backfat thickness obtained on the basis of the intra-sire regression of offspring on dam were 49 percent, 18 percent and 35 percent, respectively, for pigs farrowed during spring, fall and both seasons combined.

Heritability estimates for backfat thickness based on the regression of the offspring on the mean of the parents were 16, 18 and 10 percent respectively for pigs farrowed in the spring, fall, and both seasons.

Of the several family relationships studied for both traits, the correlations between the progeny and the average of the dam and her litter mates were fairly high and consistent. A positive association was found between rate of gain and backfat thickness ($P < .05$) in the spring-farrowed pigs, whereas a negative correlation was observed between the same traits ($P < .05$) for pigs farrowed in the fall. The expression and the extent of heterosis in body length, heart girth, flank girth, shoulder fat, hip fat and ham fat were also investigated.

TABLE OF CONTENTS

Heritabilities and Heterosis of Some Economic Traits in Swine

V. B. Reddy, J. F. Lasley and L. F. Tribble

INTRODUCTION

Selection has been the tool most widely used by animal breeders in the past for the improvement of their animals. Over a period of time selection has been quite effective as evidenced by the definite phenotypic differences that now exist between breeds and types of farm animals. These differences exist in qualitative traits such as coat color and in certain important quantitative traits such as milk and meat production and rate of gain in the feed lot.

Although selection has been effective in the past, more needs to be learned about how it may be used to the best advantage in improving quantitative traits. The testing of different methods of selection in farm animals is an expensive and slow process but studies of this kind are now in progress at various experiment stations. Small laboratory animals and insects in which the generation interval is much shorter and which are relatively cheap to produce and maintain are also being used in selection experiments. The results of these studies should serve as guides for future selection experiments with farm animals.

Heritability estimates have been calculated for many economic traits in farm animals. Heritability estimates may serve as a guide for the kind of selection to practice and as to the amount of progress that one should expect to make in selection. High heritability estimates indicate that additive gene effects are large and that mass selection, or the mating of the best to the best, should be effective. Low heritability estimates, on the other hand, indicate that progress through mass selection may be slow and that selection for the improved performance of crosses of two or more lines might be more effective. Selection for this combining ability is also indicated when a trait, or traits, are affected by heterosis.

Heritability estimates are usually calculated from the resemblance between parents and their offspring or between half sibs and full sibs. Little information is available in which heritability estimates have been calculated by other means. In this study, one of the objectives was to compare regression coefficients of offspring on the parents with those of the offspring on various combinations of the parents and the parent's close relatives. If higher regression coefficients (and heritability estimates) could be obtained in such a study, the selection of breeding stock based on a combination of their own phenotype and that of their full brothers and sisters might be more effective than when based on the individual's phenotype alone.

Two important economic traits in swine, rate of gain and backfat thickness in the live animal, were studied. In addition, a study was made of the degree of association between rate of gain and backfat thickness in the same animals since a negative correlation between them could slow or complicate selection. The amount of heterosis expressed for certain body measurements in swine when inbred Landrace and inbred Polands were crossed was also investigated.

REVIEW OF LITERATURE

Heritability Estimates for Some Quantitative Traits in Swine

Quantitative traits, by definition, relate to measurable differences in degree rather than in kind. In their inheritance they usually exhibit a continuous range of variability in segregating populations. Quantitative traits are particularly susceptible to environmental influences, and it should be understood that it is the manner of reaction under particular conditions that is inherited and not the character itself (Hayes and Immer, 1942; Yarnell, 1942). Dobzhansky and Holz (1943) stated that "genes produce not characters but physiological states which, through interactions with the physiological states induced by all other genes of the organism and with the environmental influences cause the development to assume a definite course and the individual to display certain characters at a given stage of the developmental process."

Heritability may be defined as the portion of the total phenotypic variation which is due to additive gene action. Heritability may also be defined as the portion of the total phenotypic variation that is due to hereditary differences between individuals. The former definition gives an estimate of what we can hope to achieve by selection, whereas, the latter includes some genetic variation due to epistasis, dominance and other genetic interactions on which selection may not act effectively. The larger the additively genetic portion of the phenotypic variance, the more accurately the genotype can be identified by means of estimates of heritability.

Heritability of Rate of Gain: Lush (1936), by employing different methods of estimating heritabilities, obtained values of 0.48, –0.19 and 0.24 for rate of gain in swine. He referred to these figures as maximum, minimum, and optimum values for the portion of the individual variance in average daily gain which can be ascribed to additive gene effects. Smith and Donald (1937) stated that at least $^1/_5$ of the individual variance in growth rate is due to additive genetic factors. Whatley (1942) conducted a study of 180-day weights in Poland China pigs. He obtained heritability estimates of 0.204, 0.304, 0.620, and 0.300. These figures were calculated from paternal half sib correlations, correlations between non-litter mate full sibs, by intra-sire regression of offspring on dam and regression of variance on genetic relationship.

Whatley and Nelson (1942) employed half sib correlations and the regression of offspring on the parents to determine the heritability of 180-day weight in swine. They observed correlations of 0.107 for paternal half sibs, 0.146 for maternal half sibs, and 0.380 for litter mates. The intra-sire regression of offspring on dam was -0.159 and the intra-dam regression of offspring on sire was 0.111. They indicated that 23 percent of the individual differences in 180-day weight and 33 percent in individual scores were hereditary. Comstock, *et al.* (1942) estimated the influence of heredity on weaning weight, 180-day weight and the post-weaning growth rate in several inbred lines of pigs. They believed that the real value of the heritability of weaning weight was low possibly as a result of sub-optimum nutrition of the suckling pigs. They further pointed out that since 180-day weight included weaning weight, it was probably subjected to greater environmental variation than measures of post-weaning growth rate. They obtained a heritability value of 0.14 for 180-day weight.

Baker, *et al.* (1943), using the analysis of variance technique, obtained estimates of heritability of weight at different ages that varied from 0.00 at birth to a maximum of 0.28 at 112 days and then declined to 0.25 at 168 days of age. From these results they stated that it appears possible to select animals with heredity for rapid growth at the relatively young age of about 112 days. They also pointed out that sire effects on rate of growth of his progeny became increasingly important with the advancement on age; the dam's influence decreased in importance.

Hazel, *et al.* (1943) determined the heritability of three 56-day periods of gain from birth to 168 days and the correlations between these periods. They found that the genetic variance constituted only a small fraction of the observed variance in each of the three periods (15, 28 and 17 percent, respectively). However, the genetic correlations were larger than the corresponding environmental correlations, indicating that genes with persistent effects were responsible for much of the genetic variation. Consequently, heredity has a less important but more constant influence upon growth rate than either of the environmental sources. They stated that genetic correlations between the gains in adjacent periods were considerably larger than those for the two periods separated by 56 days. In their study, five possible measures of hereditary growth rate for the 168 day period were compared. A multiple regression equation based on gain in each 56-day period was about 4 percent more accurate than the gain from 56 to 112 days or gain from birth to 168 days. Gains from birth to 56 days and from 112 to 168 days were not efficient measures of hereditary growth rate. They suggested the possibility of using gain from 56 to 112 days as a measure of hereditary growth rate in selecting boar pigs.

Krider, *et al.* (1948) reported on data gathered on 749 Hampshire pigs from 98 litters sired by 41 boars. They obtained a heritability estimate of about 0.18 for 180-day weight from actual separation between lines selected for rapid and for slow growth. Dickerson and Grimes (1947) found that doubling the intra-sire regression of progeny on dam overestimates actual heritability. Doubling the regression of progeny on sire underestimates the heritability to the same degree that regression on dam overestimated it. Thus, one would expect regression on dam to be larger than regression on sire for characters influenced greatly by the maternal environment if the correlation between the dam's transmitted and environmental influences is small or positive. From the regression of progeny on the parental mean, they arrived at a heritability estimate of 0.43 for the average daily gain.

Heritability of Backfat

The estimates of heritability of backfat thickness vary considerably but the average of about 40 percent would offer some hope of improvement in selecting for less backfat in swine. Lush (1936) obtained heritability values in Danish hogs for backfat thickness of 0.80, 0.23 and 0.47 which he referred to as maximum, minimum and average values.

Blunn and Baker (1947), from data on Duroc pigs, found a heritability of backfat thickness of 12.3 percent. They stated that 24.7 percent of the variability of backfat thickness was due to litter environment and 63 percent to environmental factors peculiar to pigs within litters. Dickerson (1947) reported a heritability value of 54.0 percent for the same trait.

Stothard (1947) studied the correlations between the individual and average parental full sibs, parental half-sibs and progeny, in maturity index, carcass score, length, backfat and area of loin with Canadian bacon hogs. By means of regression of progeny on the average of sire and dam sibs he indicated that backfat thickness was 37 percent heritable. Johansson and Korkman (1950) obtained a value of 54.0 percent for the same trait.

MATERIALS AND METHODS

Experimental Animals

The animals employed in the study of heritability were obtained from reciprocal crosses between the Landrace and Poland China breeds, maintained at the Missouri Agricultural Experiment Station in cooperation with the Regional Swine Breeding Laboratory. A total of 436 pigs were used in this study. Two hundred fifty-seven of these pigs were farrowed in the spring of 1954 and 179 were farrowed during the fall of the same year. These pigs were obtained from 15 Landrace and 22 Poland sows and from six Landrace and six Poland boars. In addition, data collected on 138 Landrace x Poland, 45 Poland, and 41 Landrace gilts were employed for the study of heterosis.

Feeding and Management

The sows and litters were kept on dry lot from the time the pigs were farrowed until they reached three weeks of age. After three weeks they were shifted to pasture. They were maintained on pasture until 56 days of age when the pigs were weaned. The male pigs were castrated at about 21 days of age and all pigs were vaccinated for hog cholera and erysipelas at about 56 days of age. A creep ration (Table 1) was fed to the pigs from the fourteenth day after farrowing until they reached 56 days of age. The pigs farrowed in the spring of 1954 were fed with the ration shown in Table 2 after weaning and the ration given in Table 3 was fed to pigs farrowed in the fall of 1954.

TABLE 1--STARTER RATION AND CREEP RATION FED AT THE MISSOURI STATION

	Starter	Creep
Corn	4.5	68.5
Rolled oats	10.0	---
Wheat shorts	4.5	---
Dried skim milk	40.0	---
Soybean oil meal	10.0	16.0
Tankage	---	8.0
Fish meal	3.0	3.0
Alfalfa meal	---	2.5
Salt[3]	0.63	0.5
Limestone	0.5	0.2
Bonemeal	1.0	---
Blood flour	5.0	---
Corn distiller solubles	5.0	---
Dextrose	9.0	---
Lard	5.0	---
Antibiotics[1]	+	+
Vitamins[2]	+	+

[1] Terramycin or aureomycin 20 mg./lb. in creep ration and 40 mg./lb in starter ration

[2] Vitamins A, D, B_2, B_{12}, pantothenic acid and nicotinic acid in creep ration and all known vitamins in starter ration.

[3] Trace mineralized (Fe, Mn, Cu, Zn, and Co).

TABLE 2--RATION FED EXPERIMENTAL ANIMALS FARROWED IN THE SPRING OF 1954

Shelled corn	Free choice
Protein supplement	Free choice
Soybean oil meal	200
Tankage	300
Shorts	100
Vit. A & D	5
Fortafeed	8
Aurofac 2A	5
Salt	12

TABLE 3--RATION FED EXPERIMENTAL ANIMALS FARROWED IN THE FALL OF 1954

Corn*	432
Wheat*	435
Tankage	80
Linseed oil meal	40
Salt	5
Lime	3
Aurofac (antibiotic supplement)	1.5
Fortafeed (B vitamin supplement)	1.0
Vitamins A & D	2.5

* Corn was substituted for wheat about January 1, 1955.

Live Animal Measurements

The pigs were restrained by looping the upper maxilla with a hog catcher. They were also controlled in some instances by means of a specially equipped holding crate which provided an easier way of controlling hogs. Incisions about ¼ inch deep and ½ inch long were made with a scalpel through the skin. A narrow metal ruler was pressed through the soft fat to the firm tissue underneath. When resistance due to the firm tissue was felt, the ruler was assumed to have passed through the fat. Pressure on the ruler was a little relaxed and the reading marked at skin level with a sliding metal clip on the ruler. The three sites of backfat measurements were chosen about 1½ inches on either side of midline of the body above the longissimus dorsi muscle. The first of these was located immediately behind the shoulder; the second was in the middle of the back, while the third was midway between the hipbone and tail head on the ham.

All the pigs used in this study were weighed at weekly intervals from 56 days of age until they reached 200 pounds body weight. The mean rates of gain per day are employed in this study.

Heritability estimates were calculated on the basis of analysis of covariance technique as described by Snedecor (1946).

RESULTS AND DISCUSSION

Factors Affecting Rate of Gain

In this study several factors were found to influence the rate of gain in swine. The relative roles of heredity and environment manifested in differences of weights has considerable practical importance because of the extent to which the rate of gain indicates general health, economy of feed utilization and carcass composition. Rate of gain was found to be influenced mainly by season, sex and the type of feeding (pasture or dry lot).

Influence of Season: The mean values of rate of gain in spring and fall along with the analysis of variance are presented in Table 4. The spring farrowed pigs averaged .14 pounds higher in the daily gain than the fall farrowed pigs which was

TABLE 4--MEANS AND ANALYSIS OF VARIANCE OF RATE OF GAIN OF FALL PIGS AND A COMPARISON WITH SPRING PIGS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F. Value
	Influence of sex (fall pigs) barrows (mean) = 1.52 lbs. gilts (mean) = 1.42 lbs.			
Total	239	5.11		
Between sexes	1	0.51	0.51	26.42**
Error	238	4.60	0.0193	
	Influence of season spring (mean) = 1.67 lbs. fall (mean) = 1.53 lbs.			
Total	505	54.99		
Between seasons	1	42.30	42.30	1685.25**
Within seasons	504	12.69	0.0251	

** Highly significant with $P < .01$

highly significant ($P < .01$). This seasonal influence might be either due to a direct effect of light and temperature on the physiological and endocrine mechanisms of the body or due to the interaction between genes and environment. The spring pigs were grown and fattened during a period of long daylight hours with higher temperatures as contrasted to a period of shorter daylight with cooler temperatures under which the fall pigs were reared. It is now well understood that both increasing light and temperature depress the secretion of thyrotropic hormone from the pituitary gland. Lesser thyrotropic output from the pituitary gland would in turn lead to a decreased thyroxine secretion rate, consequently resulting in a reduced basal metabolism. When the metabolism is lowered, the subcutaneous and the intramuscular deposition of fat tends to become greater.

Influence of Sex: Of the 506 pigs employed in this study, 272 were gilts and 234 were barrows. The differences between sexes were analyzed separately for the spring and fall seasons. Barrows gained 1.52 pounds per day in the spring, compared to an average gain of 1.46 pounds by gilts (Table 5). The difference in the fall pigs was also in favor of the barrows (Table 4.) These differences were highly significant in both seasons ($P < .01$). Sex hormones influence the expression of hereditary potentialities in farm animals. Males usually are found to grow faster than females and the females are somewhat smaller than the males at maturity. The higher rate of gain of barrows might have been due to the deposition of fat rather than any kind of growth. These results agree with observations of Bennett and Cole (1946), who found that rate of gain was significantly greater in barrows than in gilts.

Influence of Dry Lot and Pasture: Pigs fed in dry lot during the summer averaged 0.24 pounds more in the daily rate of gain than pigs on pasture (Table 5). Pigs on pasture naturally expend more energy on exercise than dry lot pigs. Dry lot

TABLE 5--MEANS AND ANALYSIS OF VARIANCE OF RATE OF GAIN OF THE PIGS FARROWED DURING THE SPRING, 1954

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F Values
	Influence of sex barrows (mean) = 1.52 lbs. gilts (mean) = 1.46 lbs.			
Total	265	7.57		
Between sexes	1	.22	.22	7.91**
Error	264	7.35	.0278	
	Influence of dry lot and pasture dry lot (mean) = 1.64 lbs. pasture (mean) = 1.40 lbs.			
Total	265	7.57		
Between treatments	1	3.42	3.42	217.83**
Error	264	4.15	.0157	

** Highly significant with $P < .01$.

pigs conserve considerable energy which may subsequently lead to increased body weight. Also, it is possible that dry lot pigs were more comfortably housed whereas the pigs out on the pasture were exposed to a less comfortable environment. Fluctuations of the environment induce physiological stress which might in turn reduce the feed intake. These factors might explain the higher rate of gain in dry lot pigs when compared to pigs on pasture.

Factors Affecting Backfat Thickness

Apart from the genetic variations affecting the degree of fat deposition in hogs, nutrition, season, and sex also influence the amount of backfat to a considerable extent.

Influence of Season: The mean values of backfat thickness and the mean squares tested for significance are shown in Table 6. The fall farrowed pigs averaged 0.43 mm. higher in backfat than the spring farrowed pigs but this difference was not significant.

Influence of Sex: Sex was found to have considerable effect on the amount of fat deposition. Barrows averaged 3.8 mm. and 4.08 mm. more than gilts during the spring (Table 7) and fall seasons (Table 6), respectively. These differences were found to be highly significant ($P < .01$) in both seasons. The results obtained in this study as well as the earlier findings recorded in the literature seem to suggest that the male hormones cause greater bone growth and greater development of muscle and less deposition of fat. Since castration removes the primary source of androgens, the lack of male hormone in barrows could be responsible for a greater deposition of fat. .

Influence of Dry Lot and Pasture: The pigs reared on pasture in the summer averaged 1.56 mm. greater backfat thickness than those in dry lot (Table 7). This higher backfat thickness in the pigs on pasture may be explained by the fact that

TABLE 6--MEANS AND ANALYSIS OF VARIANCE OF BACKFAT THICKNESS OF FALL PIGS AND A COMPARISON WITH SPRING PIGS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Value
	Influence of sex (fall pigs) barrows (mean) = 41.14 m.m. gilts (mean) = 37.07 m.m.			
Total	239	5894.14		
Between sexes	1	983.63	983.63	48.17**
Error	238	4860.51	20.42	
	Influence of season spring (mean) = 38.42 m.m. fall (mean) = 38.86 m.m.			
Total	492	13874.28		
Between seasons	1	22.76	22.76	.813n
Error	491	13851.52	28.01	

** Highly significant with $P < .01$.
n = F. value is not significant.

TABLE 7--MEANS AND ANALYSIS OF VARIANCE OF BACKFAT THICKNESS OF THE PIGS FARROWED DURING THE SPRING, 1954

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F. Value
	Influence of sex barrows (mean) = 40.14 m.m. gilts (mean) = 39.96 m.m.			
Total	252	8007.38		
Between sexes	1	634.46	634.46	21.602**
Error	251	7372.92	29.37	
	Influence of dry lot and pasture dry lot (mean) = 37.46 m.m. pasture (mean) = 39.02 m.m.			
Total	252	8007.38		
Between treatments	1	145.98	145.98	4.66*
Error	251	7861.40	31.32	

** Highly significant with $P < .01$.
* Significant with $P < .05$.

these pigs had a slower rate of gain than the pigs in dry lot, hence they were considerably older when they reached 200 pounds body weight. It is known that there is a tendency for the gains to be proportionately more of fat and less of muscle and bone as the pigs grow older.

Heritability Estimates

As is evident from the preceding discussion, the season, sex, and treatment (pasture or dry lot) influenced both rate of gain and backfat thickness to a considerable degree. Therefore, appropriate correction factors were used before subjecting the data to further statistical treatment for the purpose of computing heritabilities and family relationships.

All the fall pigs employed in this investigation were corrected to a spring basis by adding 0.14 pounds to their observed rate of gain. No such correction factor was used for backfat thickness because the difference between the two seasons was found to be very little and was not statistically significant. Similarly, all the gilts used in this study were corrected to a barrow basis; correction factors of 0.06 and 0.10 pounds were added to the daily rates of gain of the gilts farrowed during spring and fall seasons, respectively. In the same way, correction factors of 3.18 and 4.08 mm. were added to the backfat thickness of spring and fall gilts. Average daily gains of spring farrowed pigs reared on pasture were adjusted to dry lot basis by adding 0.24 pounds to their daily gains. Since fall-farrowed pigs were all reared on dry lot, no corrections for pasture were made for them.

Heritability Estimates for Rate of Gain: The technique of computing the regression of progeny on dam was employed in this study. The average change in performance of offspring per unit change in the performance of the parents is a direct measure of heritability. Of course, this would apply strictly if environmental influences on progeny and parents are independent. The regressions for spring and fall seasons were computed separately. The values for both seasons combined were also calculated. The coefficients of correlations and regression and the heritability values for the spring are in Table 8. A total of 257 pigs sired by 12 different boars were used. The heritability value for rate of gain, which was obtained by doubling the intra-sire regression of progeny on dam, was only 0.02 for the spring pigs while the heritability value computed from the fall-farrowed pigs was 0.16 (Table 9). The heritability value when computed for both seasons together (Table 10) dropped to 0.04. The regression of offspring on the mean of the sire and dam gave values of 0.31, 0.20 and 0.22 for the spring, fall and for both seasons, respectively.

TABLE 8--CORRELATION AND REGRESSION COEFFICIENTS FOR RATE OF GAIN OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; SPRING

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression "r"	"b"	"2b"
Intra-sire regression of offspring on dam	245	.0103	.0099	.0198
Regression of offspring on the average of sire and dam	256	.1924**	.3087	
Intra-sire regression of offspring on dam's brothers	245	.2178**	.3013	
Intra-sire regression of offspring on dam's sisters	245	-.0399	-.0630	
Intra-sire regression of offspring on dam's littermates	245	.4980	.6031	

** Highly significant with $P < .01$.

TABLE 9--CORRELATION AND REGRESSION COEFFICIENTS FOR RATE OF GAIN OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; FALL

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression		
		"r"	"b"	"2b"
Intra-sire regression of offspring on dam	169	.0682	.0808	.1616
Regression of offspring on the average of sire and dam	178	.1200	.2000	
Intra-sire regression of offspring on dam's brothers	169	-.1992*	-.3888	
Intra-sire regression of offspring on dam's sisters	169	.0823	.1555	
Intra-sire regression of offspring on dam's littermates	169	-.2171**	-.4583	

* Significant with $P < .05$.
** Highly significant with $P < .01$.

TABLE 10--CORRELATION AND REGRESSION COEFFICIENTS FOR RATE OF GAIN OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; TWO SEASONS COMBINED

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression		
		"r"	"b"	"2b"
Intra-sire regression of offspring on dam	424	.0221	.0222	.0444
Regression of offspring on the average of sire and dam	435	.1315**	.2147	
Intra-sire regression of offspring on dam's brothers	424	.0241	.0370	
Intra-sire regression of offspring on dam's sisters	424	.0027	.0045	
Intra-sire regression of offspring on dam's littermates	424	.1600*	.2835	

* Significant with $P < .05$.
** Highly significant with $P < .01$.

Results indicated that the gains from weaning to 200 pounds body weight in this test were subjected to greater environmental variation than were the measures of earlier growth rates for which higher values have been reported in the literature. Since heritability studies are based on different populations of pigs under different environments, differences are to be expected in both the relative amounts of genetic variation present in each herd and the relative influence of environmental factors. It is probable that there could be much "interaction" between heredity and environment. Heredity good in one environment might become poor in another environment. These interactions will vary from population to population and might cause the size of heritability estimates to vary in different populations from various areas of the country. Differences in age of dams is an important source of variation. However, the obvious and perhaps the most reasonable way would be to ascribe these differences to sampling errors or to the selection of parents, which biases the estimates of heritability.

Heritability Estimates for Backfat Thickness: Little emphasis was given to the backfat measurements in the earlier work in swine breeding. But in recent years attention, second only to that in rate of gain and possibly body length, is being paid to the backfat thickness in hogs. In some cases, thickness of backfat seems to receive even more attention than length of body, since it has more to do with the market classification of the carcass.

By doubling the intra-sire regression of progeny on dam, heritability for backfat thickness was estimated as 49 percent from the spring farrowed pigs (Table 11). The heritability estimate for the same trait dropped to 18 percent when computed from the fall-farrowed pigs (Table 12); it was 35 percent for spring and fall seasons combined (Table 13). Also, the heritability for backfat thickness was estimated at 16 percent from the spring-farrowed pigs as shown by the regression of progeny on the mean of the parents (Table 11). Values of 18 percent for fall and 10 percent for both seasons were obtained, when calculated on a similar basis.

The regression of the progeny on the mean performance of the two parents is biased only to the extent that the change in the offspring, due to non-additive effects of certain genetic combinations transmitted by the immediate parents, will be lost as these combinations break up in later generations. Of course, another variation which will be of great importance, if heritabilities were calculated at an earlier age, is the environmental variation in the dam's own performance that affects the environment she provides for her pigs. This variation cannot be said to

TABLE 11--CORRELATION AND REGRESSION COEFFICIENTS FOR BACKFAT THICKNESS OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; SPRING

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression "r"	"b"	"2b"
Intra-sire regression of offspring on dam	245	.1986**	.2444	.4888
Regression of offspring on the average of sire and dam	256	.1163	.1627	
Intra-sire regression of offspring on dam's brothers	245	.0863	.1588	
Intra-sire regression of offspring on dam's sisters	245	.2819**	.5462	
Intra-sire regression of offspring on dam's littermates	245	.1283*	.2014	

* Significant with $P < .05$.

** Highly significant with $P < .01$.

TABLE 12--CORRELATION AND REGRESSION COEFFICIENTS FOR BACKFAT THICKNESS OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; FALL

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression		
		"r"	"b"	"2b"
Intra-sire regression of offspring on dam	170	.0686	.0917	.1834
Regression of offspring on the average of sire and dam	179	.2735**	.1793	
Intra-sire regression of offspring on dam's brother	170	-.2689**	-.3593	
Intra-sire regression of offspring on dam's sisters	170	-.0691	-.1030	
Intra-sire regression of offspring on dam's littermates	170	.0144	.0191	

* Significant with P < .05.
** Highly significant with P < .01.

TABLE 13--CORRELATION AND REGRESSION COEFFICIENTS FOR BACKFAT THICKNESS OF PROGENY WITH DAM, MEAN OF SIRE AND DAM, AND THE DAM'S RELATIVES; SP. & F.

Method of Analysis	Degrees of Freedom	Coefficients of Correlation and Regression		
		"r"	"b"	"2b"
Intra-sire regression of offspring on dam	425	.1511**	.1757	.3514
Regression of offspring on the average of sire and dam	436	.0838	.1004	.2008
Intra-sire regression of offspring on dam's brothers	425	.0617	.0928	
Intra-sire regression of offspring on dam's sisters	425	.1338**	.2083	
Intra-sire regression of offspring on dam's littermates	425	.0784	.1455	

* Significant with P < .05.
** Highly significant with P < .01.

have much influence in this study except that the dam's performance was important to the extent of conditioning her pigs at the time of weaning.

The heritability estimates for backfat thickness, based on intra-sire regression of offspring on dams, agree with the results reported in the literature. Lush (1936) obtained a heritability value of 47 percent which he indicated as an average value. Dickerson (1947), Johansson and Korkman (1950) reported 54 percent heritability. Even though some lower heritability estimates are found in the literature, on the average 40 percent heritability for backfat thickness as obtained in this investigation appears to be consistent.

Correlations Between Family and Offspring: Correlations and regressions were calculated between the progeny and (1) the dam's brothers (2) the dam's sisters, and (3) the dam and all of her litter mates. All the correlations and regressions for rate of gain between the progeny and the relatives are presented for spring, fall and for both seasons in Tables 8, 9 and 10, respectively. The correlations for the spring were generally higher than those for the fall. As was reported in the earlier part of this study, a highly significant difference in rate of gain was found between seasons, with superior gains during the spring. Since the heritability values for rate of gain were low, these variations must be due to environmental influences.

The correlation between dams and progeny farrowed in the spring logically should be higher than when the dam was farrowed in the spring and her progency in the fall because environmental conditions such as temperature and forage would be more similar. A highly significant correlation of 0.498 was noted between the progeny and the dam's litter mates with respect to rate of gain during the spring. Some of the negative correlations and regressions obtained might be due to complicated interactions between heredity and environment. The size of the correlation coefficients between the progeny and the dam's litter mates may provide valuable information for selection of breeding stock.

Similar corrélations and regressions between progeny and family were derived for backfat thickness (Tables 11, 12 and 13). Here again the correlations for spring-farrowed pigs are generally higher than for the fall-farrowed pigs.

The intra-sire correlations between rate of gain and backfat thickness were computed from the data on 257 pigs farrowed during the spring of 1954 (Table 14). The gross correlation coefficient between rate of gain and backfat thickness was highly significant ($P < .01$). However, when the influence of the sires was removed by the covariance technique the correlation was still positive but not significant. Table 15 shows the intra-dam correlations between the same two traits. It is interesting to note that the intra-dam correlation was significant ($P < .05$). A similar analysis of the data was made on 179 pigs farrowed during the fall of

TABLE 14--INTRA-SIRE CORRELATIONS OF PROGENY'S BACKFAT WITH PROGENY'S RATE OF GAIN

Source of Variation	Degrees of Freedom	Coefficients of Correlation and Regression	
		r	b
	Spring, 1954		
Total for all sires	256	.2077**	.0041
Between sires	11	.5405	.0311
Within sires	245	.0767	.0019
	Fall, 1954		
Total for all sires	178	-.0877	-.0054
Between sires	9	-.1078	-.0051
Within sires	169	-.0855	-.0055

* Significant with $P < .05$.
** Highly significant with $P < .01$.

TABLE 15--INTRA-DAM CORRELATIONS OF PROGENY'S BACKFAT WITH PROGENY'S RATE OF GAIN

Source of Variation	Degrees of Freedom	Coefficients of Correlation and Regression	
		r	b
	Spring, 1954		
Total for all dams	256	.2077**	.0041
Between dams	36	.2787	.0066
Within dams	220	.1505*	.0039
	Fall, 1954		
Total for all dams	178	-.0877	-.0054
Between dams	26	-.1078	-.0011
Within dams	152	-.1675*	-.0110

* Significant with $P < .05$.
** Highly significant with $P < .01$.

1954. The intra-sire correlation between these two traits was negative but not significant. When the analysis was made on an intra-dam basis, the rate of gain was significantly and negatively correlated ($P < .05$) with backfat thickness (Table 15). It may be said that backfat thickness and rate of gain are physiologically correlated with each other because these two characteristics partly result from the same body functions and probably because they might result from manifold effects and expressions of the same genes.

According to the results of this investigation, selection for faster gains would be less effective than selection for thinner backfat thickness. When family selection is practiced along with selection for individuality, however, the results of this study suggest that progress could be made in selecting for either or both traits.

Influence of Sire on the Performance of His Progeny: Mean values of rate of gain along with variations for the 1954 spring pigs are shown in Table 16. Six Poland

TABLE 16--MEANS AND RELATIVE VARIATION IN RATE OF GAIN AND BACKFAT THICKNESS OF PROGENY FROM DIFFERENT SIRES; SPRING, 1954

Sire	Number of Progeny from Each Sire	Rate of Gain			Backfat Thickness		
		Mean Lb.	S.D.	C.V. %	Mean mm.	S.D.	C.V. %
P. 93	16	1.66	.0682	4.10	37.95	4.18	11.01
P. 296	20	1.69	.1414	8.37	40.36	3.65	9.04
P. 175	34	1.68	.0852	5.07	43.44	4.55	10.47
P. 295	34	1.55	.0758	4.89	38.08	3.23	8.48
P. 305	25	1.58	.1135	7.18	39.85	3.04	7.63
P. 92	34	1.74	.1044	6.00	43.85	5.09	11.61
L. 5	11	1.71	.1483	8.67	40.27	5.60	13.91
L. 105	11	1.68	.0632	3.76	37.85	4.99	13.18
L. 3	13	1.74	.1322	7.60	39.08	3.97	10.16
L. 8	15	1.76	.1690	9.60	38.72	4.86	12.55
L. 149	21	1.62	.1000	6.17	36.41	4.47	12.28
L. 333	23	1.71	.0878	5.13	44.16	3.48	7.88
All Sires	257	1.67	.1229	7.36	40.47	4.91	12.13

and six Landrace boars sired a total of 257 pigs. Large differences were found to exist between progeny from different sires in rate of gain and also in the variation as expressed by standard deviations and coefficients of variation among the progeny by the same sires. The coefficients of variation varied from 3.76 to 9.60 percent. There was a tendency for greater variation within the sire groups among the fall pigs (Table 18).

The analysis of variance showed that the differences between sires were less significant ($P<.05$) among the fall-farrowed pigs than among the spring-farrowed pigs ($P<.01$; Table 17). In other words, sire differences were not as great in the fall as in the spring. This observation agrees with the earlier find-

TABLE 17--VARIANCE ANALYSIS OF RATE OF GAIN OF PROGENY FROM DIFFERENT SIRES (CORRECT FOR SEASON, SEX AND PASTURE OR DRY LOT WHERE APPROPRIATE)

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Value
		Spring, 1954		
Total	256	3.87		
Between sires	11	1.07	.0973	8.54**
Within sires	245	2.80	.0114	
		Fall, 1954		
Total	178	3.74		
Between sires	9	0.43	.0478	2.44*
Within sires	169	3.31	.0196	
		Both seasons together		
Total	435	7.64		
Between sires	11	1.20	.1091	7.18**
Within sires	424	6.44	.0152	

* Significant with $P < .05$.
** Highly significant with $P < .01$.

TABLE 18--MEANS AND RELATIVE VARIATION IN RATE OF GAIN AND BACKFAT THICKNESS OF PROGENY FROM DIFFERENT SIRES; FALL, 1954

Sire	Number of Progeny from Each Sire	Rate of Gain Mean Lb.	S.D.	C.V. %	Backfat Thickness Mean mm.	S.D.	C.V. %
P. 93	11	1.56	.0836	5.36	38.95	2.95	7.59
P. 296	14	1.51	.0919	6.09	40.93	1.94	4.74
P. 175	32	1.51	.1204	7.97	39.47	3.31	8.38
P. 295	23	1.42	.0797	5.61	40.13	3.72	9.27
P. 305	24	1.56	.1641	10.52	39.88	2.92	7.32
P. 92	23	1.57	.1126	7.17	41.61	3.28	7.88
P. 105	5	1.53	.2120	13.86	41.40	2.91	7.03
L. 8	22	1.58	.2104	13.32	38.95	2.93	7.52
L. 149	12	1.61	.1612	10.01	39.17	3.93	10.03
L. 333	14	1.54	.1175	7.63	41.93	3.71	8.85
All Sires	180	1.53	.1449	9.47	40.12	3.32	8.28

ings of Foley and Lasley (1956). It is interesting to note that the variation in backfat thickness was greater among spring pigs (Table 16) while fall pigs showed greater variation in rate of gain (Table 19). Also note that the differences in backfat thickness due to sires were highly significant ($P<.01$) among the spring-farrowed pigs.

TABLE 19--VARIANCE ANALYSIS OF BACKFAT THICKNESS OF PROGENY FROM DIFFERENT SIRES (CORRECTED FOR SEASON, SEX AND PASTURE OR DRY LOT WHERE APPROPRIATE)

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Value
		Spring, 1954		
Total	256	6176.00		
Between sires	11	1801.88	163.81	9.18**
Within sires	245	4374.22	17.85	
		Fall, 1954		
Total	179	1971.31		
Between sires	9	186.04	20.67	1.97*
Within sires	170	1785.27	10.50	
		Both seasons together		
Total	436	7160.40		
Between sires	11	1460.14	132.74	9.9**
Within sires	425	5700.26	13.41	

* Significant with $P < .05$.
** Highly significant with $P < .01$.

The coefficients of correlation for rate of gain and backfat thickness between paternal half-sibs farrowed during spring and fall seasons of 1954 are presented in Table 20. The non-significant correlations seem to suggest that there was considerable variation in the performance of the progeny of individual sires between the spring and fall seasons. The possible modification of the expression of the genes by seasonal influences was demonstrated by the failure of progeny of different sires to repeat their performance during both spring and fall seasons. There was always the possibility of segregation and re-combination of genes transmitted by the sire, which holds good for both the seasons. Another source of variation was that the spring and fall pigs sired by the same boar were from different dams.

TABLE 20--COEFFICIENTS OF CORRELATION AND REGRESSION BETWEEN SPRING AND FALL PIGS BY THE SAME SIRE BASED ON AVERAGES FOR EACH SIRE EACH SEASON

Trait	Degree of Freedom	Coefficient of Correlation and Regression: r	b
Rate of gain	8	.533[n]	.533
Backfat thickness	8	.548[n]	.223

[n] Not statistically significant.

Expression of Heterosis in Certain Body and Backfat Measurements

Heterosis or increased vigor of the progeny which results from the cross of two inbred strains of corn is an established fact. Similar results have been observed in the various species of farm animals for certain traits. In swine, heterosis is usually observed in the number of pigs saved per litter and to a lesser extent in the rate of gain or weight at a certain age. It would be of considerable value if the expression of heterosis could be determined for other traits in swine.

In this study the influence of heterosis on (1) body length, (2) heart girth, (3) flank girth, (4) shoulder fat, (5) hip fat, and (6) ham fat as measured in the live hog was investigated. A total of 224 female pigs were used; 41 were inbred Landrace, 45 were inbred Poland China and 138 were the F_1 crosses of these two breeds. Data were obtained only on females to avoid variations due to sex.

Table 21 presents the means for all of the traits studied in each of the two breeds and their F_1 cross. Body length, heart girth, flank girth, shoulder fat, hip fat and ham fat varied significantly between the two breeds and the cross (Tables 22 and 23). There was a tendency for heart girth and flank girth to vary more between breeds than the body length. Similarly, shoulder fat exhibited more variance than hip and ham fat measurements.

The percentage of heterosis was calculated as the percentage increase of the F_1 cross over the mean of the parental breeds. The data showing the mean of the two parental lines and that of the F_1 cross for the various measurements are given in Table 21 together with the percent of heterosis for each trait. All body measurements showed some heterosis although the amount was not large, varying from 1.12 percent for body length to 6.51 percent for shoulder fat. The three body measurements in the F_1 cross were equal to or superior to that of the superior parent, but this was not true for backfat measured at various sites. Each of the fat measurements in the F_1 cross pigs ranged somewhere between that of the lower and the higher parent with a tendency to be closer, on the average, to that of the parent with the most fat.

Perhaps the most significant fact from these data is that body length in pigs is not increased merely by crossing two different breeds. In fact, if one is to obtain longer bodies in crossbred pigs it appears that the length must be present in either one or both of the parental breeds. A similar statement could be made about the amount of heterosis involved in backfat thickness. Crossing the two inbred lines resulted in crossbred pigs which were fatter, not thinner, in backfat than the average of the parental breeds. Thus, heterosis, in this study at least, expressed itself in the laying down of more fat in the crossbreds. Here, too, we could say that if crossbreds with thin backfat are to be produced, the parental lines also must possess inherently thinner backfat.

TABLE 21--MEANS OF PUREBRED LANDRACE, PUREBRED POLAND AND THE MEANS AND THE DEGREE OF HETEROSIS OF THE F_1 OF THOSE TWO BREEDS FOR CERTAIN TRAITS

	Mean* Landrace	Mean* Poland	Mean* L x P	Per Cent of** Heterosis
Body length	1058.88	1041.3	1061.85	1.12
Heart girth	962.50	1006.02	1006.04	2.21
Flank girth	951.93	997.80	1008.57	3.46
Shoulder fat	35.10	45.72	43.04	6.51
Hip fat	27.50	34.06	31.24	1.49
Ham fat	28.52	32.58	32.15	5.24

* These figures are in millimeters.

** Per cent of F_1 cross as compared to the mean of the two parental breeds.

TABLE 22--VARIANCE ANALYSIS OF BODY LENGTH, HEART GIRTH AND FLANK GIRTH FOR SIGNIFICANT DIFFERENCES BETWEEN BREEDS

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Value
		Body length		
Total	223	218699		
Between breeds	2	14488	7244	7.84**
Within breeds	221	204211	924.03	
		Heart girth		
Total	223	180858		
Between breeds	2	63600	31800	59.93**
Within breeds	221	117258	530.58	
		Flank girth		
Total	223	368661		
Between breeds	2	91606	45803	36.54**
Within breeds	221	277055	1253.6	

** Highly significant with $P < .01$.

TABLE 23--VARIANCE ANALYSIS OF SHOULDER, HIP AND HAM FAT FOR SIGNIFICANT DIFFERENCES BETWEEN BREEDS

Sources of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F Value
		Shoulder fat		
Total	223	8155.97		
Between breeds	2	2723.46	1361.72	55.4 **
Within breeds	221	5432.51	24.58	
		Hip fat		
Total	223	5774.61		
Between breeds	2	927.22	463.61	21.14**
Within breeds	221	4847.39	21.93	
		Ham fat		
Total	223	5212.28		
Between breeds	2	471.73	235.87	11.00**
Within breeds	221	4740.55	21.45	

** Highly significant with $P < .01$.

SUMMARY AND CONCLUSIONS

Heritability estimates for rate of gain and backfat thickness were computed. The degree of association of the progeny with the dam's relatives with respect to those two economically important traits was studied. Manifestations of heterosis for body length, heart girth, flank girth and backfat thickness in the F_1 cross of the purebred Landrace and purebred Poland China breeds were also investigated.

Rate of gain and backfat thickness were influenced significantly by season, sex and method of feeding. Heritability values for rate of gain were obtained by the intra-sire regression of offspring on dam. Values were only 2 percent in spring pigs, 16 percent in the fall pigs, and 4 percent for the two seasons combined. Heritability estimates based on the regression of offspring on the mean of the sire and dam gave values of 31 percent, 20 percent and 21 percent for the spring, fall, and combined seasons, respectively. The heritabilities for backfat thickness based on the intra-sire regression of offspring on dam were 49 percent, 18 percent, and 35 percent for spring, fall, and the two seasons combined. When based on regression of the offspring on the mean of the sire and dam the values were 16 percent in the spring, 18 percent in the fall and 10 percent for the two seasons together.

In this study, correlation and regression coefficients were calculated between the progeny and (1) the average of the dam's brothers, (2) the average of the dam's sisters, and (3) the average of the dam and all of the litter mates of the dam. These relationships gave some additional information. The correlations for spring pigs were generally higher than those for the fall pigs. Only the correlations between the progeny and dam's litter mates were fairly high and consistent; so this measure might be of greater value for the selection of breeding stock than individuality alone.

The correlation between the rate of gain and backfat thickness was calculated for each group of pigs. The rate of gain was found to be positively correlated ($P < .01$) with backfat thickness during the spring months. When the influence of the sires was removed by covariance, the correlation was still positive, but not significant statistically. Intra-dam correlations were higher than intra-sire correlations which could be due to maternal influence.

This study indicated that the percentage progress actually made in selecting for rate of gain would be smaller than the progress made in selecting against backfat thickness. But there seems to be enough additive genetic variation to permit improvement in both traits, if selection is constantly practiced in a given direction.

The expression of heterosis was investigated for body length, heart girth, flank girth, shoulder fat, hip fat and ham fat. Differences between the breeds and crosses for all the traits studied were highly significant ($P < .01$). There was a tendency for heart and flank girth to vary more than the body length between the breeds. Similarly, shoulder fat exhibited more variance than hip fat and ham fat between the breeds. In the case of backfat thickness, the F_1 cross had mean values intermediate between the 2 parental breeds. This was unlike the observed values for body length, heart girth and flank girth where the mean of the offspring exceeded that of either parent. However, the percentages of heterosis in this study varied from a low value of 1.12 percent for body length to a high value of 6.51 percent for shoulder fat. Other values of 1.49 percent, 2.21 percent, 3.46 percent and 5.24 percent were obtained as degrees of heterosis for hip fat, heart girth, flank girth and ham fat, respectively.

Heterosis resulted in a small, desirable increase in body length, but it also resulted in an undesirable increase in such traits as backfat thickness. Therefore, combining only favorable genes or facilitating a preponderance of favorable genes into one line, strain, breed or population may not be an easy task for the animal breeder.

PRACTICAL APPLICATION OF RESULTS

In this study it was found that rate of gain and backfat thickness were affected significantly by season of the year, sex of the pig, and whether the pigs were fed on dry lot or on pasture. In the selection of breeding stock, it would be important to adjust the records of all pigs for such factors so they could be compared on a more equal basis. Thus, the more desirable animals would be more likely to be superior because of genes and not because of a more favorable environment.

Selection of breeding stock for improvement of rate of gain on the basis of individuality would not seem to be effective. If selection for rate of gain included records on the individuals as well as the entire litter, more progress should be made in selecting for this trait. The same is probably true of backfat thickness except that selection for this trait on the basis of individuality should be more effective than in the case of rate of gain. From a practical standpoint, the selection of outstanding individuals from outstanding litters is indicated.

Body length and backfat thickness were affected only slightly by heterosis. Both traits in the offspring were approximately the same as the average of the two parental breeds. Thus, to produce market pigs with greater body length and thinner backfat, both parental breeds should possess these traits. It does seem true, however, that crossing of a short, fat breed or strain with a long lean one will improve the progeny over that of the less desirable strain or breed. The boar or the sow, however, supplies only ½ of the inheritance of the pigs and both parents must possess the trait if more desirable offspring are to be produced.

BIBLIOGRAPHY

Baker, M. L., L. N. Hazel and C. F. Reinmiller (1943)
The Relative Importance of Heredity and Environment in the Growth of Pigs of Different Ages.
J. An. Sci. 2:3-13.

Bennett, J. A. and J. H. Cole (1946).
A Comparative Study of Certain Performance and Carcass Characteristics of Yorkshire Barrows and Gilts.
Sci. Agric. 26:265-270.

Blunn, C. T. and M. L. Baker (1947).
The Relation Between Average Daily Gain and Some Carcass Measurements.
J. An. Sci. 6:424-431.

Comstock, R. E., L. M. Winters, P. S. Jordan and O. M. Kiser (1942).
Measures of Growth Rate for Use in Swine Selection.
J. Agric. Res. 65:379-389.

Dickerson, G. E. (1947).
Composition of Hog Carcass as Influenced by Heritable Differences in Rate and Economy of Gain.
Iowa Exp. Sta. Res. Bull. 354.

Dickerson, G. E. and J. C. Grimes (1947).
Effectiveness of Selection for Efficiency of Gain in Duroc Swine.
J. An. Sci. 6:265-287.

Dobzhansky, R. and A. M. Holz (1943).
A Re-examination of the Problem of Manifold Effects of Genes in Drosophila Melanogaster.
Genetics 28:295-303.

Foley, C. W. and J. F. Lasley (1956).
Influence of the Sire on the Performance of His Progeny. Unpublished data; research, University of Missouri, Columbia.

Hayes, H. K. and F. R. Immer (1942).
Methods of Plant Breeding, p. 432.

Hazel, L. N., M. L. Baker and C. F. Reinmiller (1943).
Genetic and Environmental Correlations Between the Growth Rates of Pigs at Different Ages.
J. An. Sci. 2:118.

Johansson, Ivar and Niles Korkman (1950).
A Study of the Variation in Production Traits of Bacon Pigs.
Acta Agriculturae Scandinavica 1:62-94.

Krider, J. L., B. W. Fairbanks, W. E. Carrell and E. Roberts (1946).
Effectiveness of Selecting for Rapid and for Slow Growth Rate in Hampshire Swine.
J. An. Sci. 5:3-15.

Lush, J. L. (1936).
Genetic Aspects of the Danish System of Progeny-Testing Swine.
Iowa State College Res. Bull. 204.

Smith, A. D. B. and H. P. Donald (1937).
Weaning Weight of Pigs and Litter Sampling with Reference to Litter Size.
J. Agric. Sci. 28:485-502.

Snecedor, G. W. (1956).
Statistical Method
Fifth Edition, Iowa State College Press.

Stothard, J. G. (1947).
A Study of Parental-Progeny Correlation with Canadian Bacon Hogs.
Sci. Agr. 27:354-363.

Whatley, J. A., Jr. (1942).
Influence of Heredity and Other Factors on 180 Day Weight in Poland China Swine.
J. Agr. Res. 65:249-264.

Whatley, J. A., Jr. and R. H. Nelson (1942).
Heritability of Differences in 180 Day Weight and Market Score in Duroc Swine.
(Abstract) *J. An. Sci.* 1:70.

Yarnell, S. H. (1942).
Influence of the Environment on the Expression of Hereditary Factors in Relation to Plant Breeding.
Am. Soc. Hort. Sci. Proc. 41:398-411.