A STUDY OF SELECTION INTENSITY IN THE INITIAL STAGES OF A SWINE RECIPROCAL RECURRENT SELECTION PROGRAM.

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TABLE OF CONTENTS

INTRODUCTION

In breeding work with both plants and animals we try to improve a population by selecting such individuals for parents, which we believe are capable of producing improved offspring. When selection is continued over many generations, we use some kind of a selection program, and this program is based on our knowledge and conception of heredity. The key to our present knowledge of heredity is the rediscovery of Gregor Mendel's work about 50 years ago. Mendel's principles of heredity were later confirmed in numerous experiments and were accepted over nearly the whole world. When later work by cytogeneticists identified Mendel's factors as genes carried by the chromosomes, a new door was opened for further discoveries. We now consider, that the characters of plants and animals are the result of actions, reactions, and interactions of countless number of genes. What is inherited, however, is not the character itself but the manner of gene actions, which under conditions of environment express themselves as the character (Hayes 1952). If, for example, the environment changes, the character may also change, but the genes do not.

Because we cannot select the genes themselves but only for or against them after the effects their actions and interactions express in a given environment, we have to base selection programs on our conceptions of these actions. Different ideas and theories of the genetic mechanism therefore create different selection programs. This is especially the case if the genetic mechanism is complicated, as for quantitative characters, where many genes are involved. Most economically important characters exhibit quantitative type of inheritance. It is also known from experiments with both plants and animals, that such characters often are expressed in a superior way in crosses. This phenomena is called heterosis or hybrid vigor. Much experimental work with animals and cross pollinated plants is characterized by efforts to take advantage of these heterosis effects.

Two main ideas of heterosis have been developed. Therefore, the selection programs for hybrid vigor can be classified into two main groups: (1) Selection programs for general combining ability are based on the dominance theory of heterosis (Crow, 1952). Here the heterosis effect is believed to be caused by an increased number of dominant favorable genes in the crosses. The selection goal is therefore to create homozygous populations which are able to complement each other, i.e. combine with each other in crosses so that a maximum number of dominant favorable genes may be present. (2) Selection programs for specific combining ability are based on the overdominance theory of heterosis (Crow, 1952). According to this theory heterosis is caused by such an interaction between allelic genes that the heterozygote is superior to either homozygote. The selection goal is therefore to produce in a cross as many of such heterozygous gene pairs as possible, which are believed to have overdominance effect.

In 1949 Comstock *et al.* proposed a reciprocal recurrent selection program for corn to take advantage of the heterosis effect from both dominant and overdominant effects of genes at different loci.

The effectiveness of a selection program depends, however, not only upon how well adapted the program is in taking advantage of the actions, reactions and interactions of genes, but also upon how intensive the selection can be made in each generation. The maximal selection intensity is determined by the fraction required for breeding purposes in a population stationary in number (Lush, 1947). The selection intensity practiced therefore depends upon the decision of which individuals are to be in that selected fraction. When many characteristics must be considered at the same time, the selection is based on the overall merit, a selection index, of the individuals in the population subject for selection.[1] The accuracy of such a selection index may be checked in advanced stages of a selection program by comparing the expected gain from selection with actual gain reached. The expected gain of a trait is the product of the heritability and the selection intensity of the trait. The selection intensity in a trait is expressed by the selection differential, which is the difference between the mean of the individuals saved for parents and the mean of the generation in which they were born (Lush, 1947).

The selection intensity may, however, give some information also in the initial stages of a selection program, where the actual gain cannot be measured. It can give a measure of the selection pressure used. If the heritability of the trait is known or can be computed, the expected

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[1] Jay L. Lush, Animal Breeding Plans, (Ames, Iowa, 1947). pp. 161-167, when many characteristics must be considered at the same time, there are three basic methods of selection: (1) the tandem method, (2) the total score method, and (3) the independent culling method. The total score method is the most effective and most commonly used. Each characteristic is given a score based on its economical value and in one or another way corrected for its heritability. The separate scores are then summarized to a total score or a selection index.

gain from selection can also be computed, and in that way indicate, if reasonable results are to be expected from the selection. Thus, the selection intensity in the initial stages of a selection program may indicate if sufficient selection pressure is being applied to permit maximum hereditary change.

REVIEW OF LITERATURE

Plant breeders have greater opportunities than animal breeders in experiments with inbred lines and crosses between them. In plants the lines can be made highly homozygous by self fertilization and adequate numbers can easily be employed in tests. Therefore, plant breeders and expecially corn breeders were early involved in extensive programs of inbreeding and hybridization. The results of these plant breeding experiments with inbred lines are useful to animal breeders as indications of possible applications to animals.

The concept of a stimulating effect of hybridization began independently with Shull (1908, 1910) and East (1908). The heterosis effect was explained by a stimulus of the uniting gametes, which increased with heterozygosis, (East and Hayes, 1912). There was, however, at that time no evidence of any loci, at which the heterozygote exceeded either homozygote. "For a number of years, overdominance as an explanation of heterosis largely was given up because of failure to find such loci" (Crow, 1952). Sprague (1952) says that the method of selection within and among inbred lines and the evaluation of the lines in crosses was extensively established at various stations in the early 1920's and is still the most commonly used procedure in corn breeding. According to Crow (1952) the dominance theory of heterosis was the basis for these programs.

Hull (1945) proposed a recurrent selection program for specific combining ability in corn. The procedure and the overdominance theory was further discussed by Hull (1952). Specific combinability is described as: "that part of the genetic superiority of specific F_1 crosses of homozygous lines, which is not transmitted into or through general combinations". The concurrent definition of general combinability is: "that part which is transmitted into or through general combinations". Sprague (1952) states that the recurrent selection method is an outgrowth of the work on early testing, in which lines are tested in crosses with a common tester line in the early stages of inbreeding. Only the lines which show the best combining ability with the tester line are saved for further inbreeding and testing. In that way considerable time is saved in the development of lines. Hull modified the early testing program by abandoning inbreeding, except to produce selfed seed from the progeny tested parents. In his program plants in a crossbred population are tested with a common tester. The tested plants are self pollinated at the same time as they are topcrossed on the tester stock. Selfed seed from the best parents in the top crosses are planted next season. These plants are then intercrossed to produce the crossbred stock for testing similarly the next generation. The interbreeding phase is characteristic of the program and repeated selection in successive generations within the crossbred group for specific combinability with a permanent unrelated tester is the proposed plan. For field corn the tester usually is an F_1 cross between inbred lines. For sweet corn an inbred line tester is normally used. For livestock the tester should be an inbred line with 50 percent inbreeding for equal efficiency with the single cross of homozygous lines employed as the corn tester.

Hull (1952) agrees with Crow, that the guiding principle for developing superior hybrids of corn, other crops and livestock has been "selection within and among inbred lines to improve frequencies of dominant factors" - selection for general combinability. Hull does not mean that overdominance is the only explanation for heterosis and says that "the first proposal with the recurrent selection method was to determine with direct tests, if higher levels of specific combinability could be accumulated by recurrent selection".

Most breeders nowadays believe that heterosis effects probably are caused by both dominant and overdominant actions of genes. Henderson (1952) says: "those wishing to employ crosses among inbred lines for commercial use select for a combination of general, maternal and specific effects".

A selection program designed to take maximal use of both general and specific combinability was proposed by Comstock _et al_. in 1949. The program is called a reciprocal recurrent selection program and is in principle the same as the recurrent selection program for specific combinability, proposed by Hull, except that two crossbred segregating populations are used instead of one crossbred population and one stable tester. Here two varieties, synthetic lines, F_2-groups or other kinds of genetically divergent material are tested in crosses with each other. The program is therefore especially attractive for work with livestock, because it does not require a highly homozygous inbred line as a tester.

No results are yet available from a reciprocal recurrent selection program with corn. However, Comstock _et al_. (1949) made theoretical comparisons of the limits of improvement and improvement rates to be expected from (1) this method, (2) from selection for general combining ability and (3) from the recurrent selection method, proposed by Hull. The comparisons indicate that under no circumstances would reciprocal recurrent selection be more than slightly inferior to the better of the other two. However, reciprocal recurrent selection would be definitely superior to selection for general combining ability for loci, at which there is overdominance, or if a situation analogous to that with overdominance exists due to linkage. It would also be definitely superior to the recurrent selection method proposed by Hull for loci at which there is partial dominance. Because heterosis is believed to be partly due to dominance and partly due to overdominance, the reciprocal recurrent selection program is believed to be generally more effective than the other two programs.

The only report found on results from a reciprocal recurrent program is an abstract by Bell _et al._ (1952). Such a program was tested with Drosophila and was compared with three other selection programs: (1) Selection within a closed population on the basis of individual or family merit, (2) recurrent selection for specific combining ability with an inbred tester, and (3) inbreeding and hybridization. Selection was based on an index giving about equal weight to two quantitative characters, egg production and egg size. Egg production has low heritability and shows considerable heterosis in crosses. In the first experiment comparisons were made over 16 generations. Another experiment is still continuing and has advanced to the 13th generation in 1952. In both experiments selection within a closed population proved to be the most effective for the four methods, and reciprocal recurrent selection showed no superiority.

Breeding work for hybrid vigor in swine has been based primarily on the dominance theory of heterosis, and has been characterized by the developing of inbred lines and testing for combinability in crosses. Previous to this work with inbred lines increased vigor was reported in crosses between breeds of swine. This increased vigor may be regarded as an expression of heterosis, even if no special selection was made for such effects. Winters et al. (1935) reported results from a six years' study of crossbreeding swine. Two-breed crosses, three--breed crosses and back crosses were made between Duroc, Poland China, Yorkshire and Chester White swine. The various kinds of crossbred litters contained up to two more pigs and weighed 39-96 pounds more at weaning than the purebred litters. The crossbred pigs reached market weight 17-22 days earlier than the purebred pigs and required 27-36 pounds less feed during that time. The three-way crosses performed best. The two-way crosses and back crosses were about equal in superiority to the purebreds. Similiar results were reported by Hutton and Russell (1939) from crossbreeding experiments with Yorkshire and Chester White swine, and by Lush et al. (1939) from crosses of other breeds at the Iowa experiment station.

In 1936 the Regional swine breeding laboratory was established as a co-operative organ between the different state experiment stations, and the Bureau of Animal Industry working with swine breeding problems. A few of the reports from some of these stations concerning inbreeding and line crosses for hybrid vigor will be cited.

Winters et al. (1944) reported from the Minnesota station that crosses between inbred lines of the same breed showed less hybrid vigor than crosses between lines from different breeds. Differences between intra-breed line crosses and inter-breed line crosses were of about the same degree as differences between conventional purebreds and crossbreds. Superior lines appeared to produce superior crossbreds. Hybrid vigor was also reported in single crosses between lines of the same breed at the Iowa station by Dickerson et al. (1946). The average inbreeding was 42 per cent for inbred litters and 6 per cent for line--cross litters. Hybrid vigor was larger for viability than for rate of growth. Line-cross litters had at 5 months of age 1.4 or 42 per cent more pigs than inbred litters. Line-cross pigs were heavier than inbred pigs at farrowing and at later ages. At 56 days of age they were 12 per cent heavier and at 154 days 21 per cent heavier. The authors therefore suggested a careful selection within lines to maintain litter size and viability. Slaughter data suggested but did not establish that crosses had a lower dressing percentage than inbreds. From a summary of results at four stations Dickerson et al. (1947) reported a comparison between inbred litters and line-cross litters from 14 lines of Duroc and 17 lines of Poland China swine. Average inbreeding of lines varied from 23 to 40 per cent. For each 10 per cent increase in litter inbreeding, independent of age and inbreeding of dam, the average decline in litter size was: 0.2 of a pig at farrowing, 0.4 of a pig at 21 days, and 0.5 of a pig at 56 and 154 days. In pig weight there was no decline up to 56 days, but a decline of 3.6 pounds at 154 days. The decline from inbreeding was greater in the Duroc lines than in the Poland China lines, especially for litter size.

Sierk and Winters (1951 a) described the development of 5 inbred lines of Poland China swine and two lines developed from crossbred foundations. These latter two lines were the Minnesota No. 1 (Danish Landrace x Tamworth) and Minnesota No. 2 (Canadian Yorkshire x inbred Poland China), now present at the Minnesota station. The selection for breeding stock was strictly on performance basis and the predominant philosophy in the Minnesota project was to measure the true worth or performance of a line by its value in crossing. The inbreeding program was described as a flexible one which was not advanced at any fixed rate. Sometimes new genetic material was introduced, but the basic plan was to advance the inbreeding as rapidly as possible without sacrificing performance.

In another report the same year Sierk and Winters (1951 b) compared line crosses between Poland China lines and crosses of Poland China lines with the Minnesota No. 1 and 2 lines. Average inbreeding of the lines ranged from 22 to 75 per cent. An overall estimate of hybrid vigor was determined by averaging the advantage in percent of: (1) weaning weight, (2) rate of gain, and (3) efficiency of food-utilization of the crossbred pigs over the average of the parental lines. Crosses of inbred lines within the Poland China breed showed less heterosis than crosses of Minnesota No. 1 and No. 2, or crosses of the Poland China lines with either Minnesota No. 1 and No. 2. This was taken as an indication of the importance of genetic diversity in relation to heterosis. Two unrelated Poland China lines seemed to be similar in their genetic composition on the basis of the performance of crosses involving them. The relationship between genetic purity (homozygosis) and heterosis can be indicated from the progenies. As measured by the coefficient of inbreeding one of the lines was nearly two times as homozygous as the other, but the two lines performed essentially the same in crosses.

At the Indiana station crosses of inbred lines from different breeds had a higher growth rate but only a slight superiority for other traits in comparison with conventional purebred and crossbred hogs (Warwick and Wiley, 1950). The inbred lines were a Chester White line, the White King line, and a Landroc line (Landrace x Duroc). Both the lines were considered to have good growth rates. The White King line performed well in crosses with other lines and had no important defects. The Landroc line, however, was described as being low in sow productivity and having a high incidence of sterility.

Similiar results were reported from the Missouri station by Dickerson et al. (1950). Two lines of Poland China and one line of Hampshire swine were topcrossed on an inbred Duroc line and also crossed with each other. Crossline pigs showed marked superiority in rate and economy of gain, when compared with the parental inbred pigs. However, topcrossed pigs showed no marked advantage over outbred Durocs in rate and economy of gain.

Chambers and Whatley (1951) reported results from the inbreeding and line crossing program at the Oklahoma station. From 1938 to 1949 seven inbred lines of Duroc swine were developed. Two-line-cross litters were compared with: (1) inbred litters within line of dam, (2) the average of the two parental inbred lines, (3) three-line crosses and (4) with outbred Durocs. Three-line crosses were also compared with outbred Durocs. Characters studied were: litter weight at birth, 21, 56 and 180 days of age and of number of pigs per litter at these same ages. The three-line crosses performed best. When initial weights of pigs were the same, the advantage of two-line-cross pigs over inbreds with the same line of dam in post weaning rate of gain and efficiency of gain were relatively small and inconsistent. Because heterosis was expressed both in number of pigs which survived and in the growth rate of the individual pig, total weight of litter seemed to be the best over all measure of performance for comparison of lines or crosses.

At the same station Whatley et al. (1951) compared 21 outbred Duroc gilts with 29 two-line-cross gilts of the same breed. The cross gilts farrowed 1.7 and weaned 1.4 more pigs per litter than the outbreds. Rate and efficiency of gain was higher in the crosses. Cross litters weighed 21 pounds more than outbred litters at 56 days of age. In carcass merit there was very little difference. Selection for carcass merit had, however, not been possible in the development of the lines. Sow productivity and rate of gain were the traits for which strongest selection was made. These traits also showed to best advantage in the crosses.

Dickerson and Lasley (1951 a) described the first steps taken in a reciprocal recurrent selection program for developing complimentary lines of swine at the Missouri station. The two Poland China lines mentioned earlier were tested in reciprocal crosses with each of nine other stocks of five breeds in the spring and fall of 1950. On the basis of litter size, rate and efficiency of gains and carcass desirability of these crosses, four lines were saved from three of the breeds as foundation stocks. Within each of these strains continued selection is planned on basis of progeny performance of individual boars and gilts in test cross matings. The two Poland China tester lines showed such a similarity in their respective crosses that they are to be combined into a single Poland China line. Besides the heterosis effects in the F_1 in prolificacy, viability and rate and economy of gain, the potential prolificacy and suckling ability of the F_1 gilts were also studied. Gilts from the breed crosses generally produced more ova and carried larger litters when sacrificed about 25 days after service, than did the gilts from line crosses within the Poland China breed. Number of teats varied in the different crosses. Largest teat numbers were found in crosses with Landrace lines.

As a summary of the breeding work for heterosis effects mentioned above, a study by Dickerson (1951 b) may be cited in which time trends in litter size and growth rate within strains in data from five of the projects of the Regional Swine Breeding Laboratory (49 strains with an average of 9 seasons each) were studied. On the average no general improvement in the litter size and growth rate were found from selection within these closed strains, unless nutrition, disease or management factors have been steadily deteriorating in these herds. Time trends in feed utilization and carcass composition were not studied. Inbreeding has, however, shown little effect on these characters and selection for efficient feed utilization and for desirable carcasses has largely been indirect through selection for conformation of live animals. From the few comparisons made between line crosses and representative purebreds no major improvement was achieved from selection during the development of the lines.

The average annual selection differentials for the traits was generally high: 0.8 for pigs farrowed per litter, 1.2 for pigs weaned per litter, 4 pounds for individual weaning weight and 16 pounds for the weight at 154 days of age. The genetic variability was considered to account for 1/10 to 1/6 of the variation in litter size at weaning and 1/5 to 1/4 of the variation in weight of pigs at 154 days of age. The heritability for body dimensions and carcass quality were higher and steady changes in these traits had been produced by selection. The selection for these traits had, however, been mild and the direction of the selection had changed frequently.

On the basis of these studies Dickerson discusses the recurrent selection program as a means to improve the effectiveness of selection for economically important traits in swine. Dickerson (1952) discusses the same problem later and suggests heterozygote advantage (overdominance) for net desirability in prolificacy, suckling ability and growth rate. He further says, that some sort of negative relationship between components of total performance is indicated by lower heritability for total performance than for its component characters, and by direct estimates of correlation. This would correspond to heterozygote superiority (overdominance). Reciprocal recurrent selection program is proposed and the use of a partially inbred line as one of the populations in such a program is considered to greatly increase progress in early cycles.

Reciprocal recurrent selection program for swine was also discussed in the 1951 report from the Regional Swine Breeding Laboratory. Dickerson (1951 c) presented a summary of selection differentials at 8 stations in the laboratory and compared the expected gains and the actual gains reached for different traits. Though the tests clearly indicated the usefulness of hybrid vigor in swine, it was thought that inbreeding and crossing do not take the maximal advantage of heterosis. "Some degree of heterozygote advantage (overdominance) is compatable with: (a) the relative ineffectiveness of ordinary selection, (b) the inability of selection to control the decline in performance from mild inbreeding, (c) the rather high heritabilities for individual traits and (d) negative correlations between traits. Recurrent cycles of selection for maximum performance in crosses between specific strains offers a possible means of exploiting this sort of genetic variability".

Material and Methods

In 1951 a reciprocal recurrent selection program with hogs was initiated at the Oklahoma Agricultural Experiment Station to investigate the usefulness of such a program for developing lines for specific combining ability. Two sets of tests were included in the program. One test was with two unrelated lines within the same breed, Duroc lines T and 3, and the other test was with two unrelated lines from different breeds, Duroc line 8 and Landrace Poland line 9. The testing and breeding program with each pair of lines was as follows: Five or six young boars of each line were each to be mated to three or four gilts of the other line for a progeny test. One third of the 18-20 gilts tested in each line were to be culled on their production record at the time of weaning their first crossbred litters. Litters from the remaining gilts were to be placed on a standard feeding test from weaning to 210 pounds final weight. This would give 24-28 test litters from the two reciprocal crosses. A minimum of two litters from each boar were to be placed on the feeding test.

As a result of these progeny tests, two boars and 8-10 gilts were to be selected for replacements in their respective lines. In the spring season one year after the reciprocal test crosses were made, 8-10 litters would be farrowed in each line from the mating of gilts and boars which performed best in the reciprocal test crosses. From these 8-10 line litters, the new set of gilts and boars would be selected to be tested in reciprocal crosses in the spring season of the following year. This makes the generation interval in this program two years in length.

In order to broaden the genetic base for selection, at least for the first two or three generations, new stock would be brought into the project and tested along with the line stock. Any of this new material which showed evidence of good combining ability, would be introduced into the line opposite that with which it crossed best. This procedure would prevent a rapid rise in inbreeding in the lines and introduce more genetic variability, thus permitting more effective selection for combining ability.

The items to be considered in the selection program were:

a. Sow productivity: About one third of the gilts would be culled on a productivity score. This score is based on the number of pigs farrowed and weaned in the cross litters and the weight of these litters at 56 days of age.

b. Rate and efficiency of gain: Litters from the 12-14 gilts of each line, selected on productivity and so that at least two litters represented each boar on test, would be tested for performance after weaning. Litter samples of four pigs would be placed on a standard feeding test from weaning to 210 pounds final weight. Rate of gain was to be expressed by the average daily gain in pounds, and efficiency of gain by the pounds of feed required to produce 100 pounds of gain.

c. Carcass merit: Two pigs, one barrow and one gilt, would be selected at random from each test litter for a slaughter test. These pigs would be slaughtered and carcass measurements and cut-out data would be obtained in the College Meats Laboratory. Carcass merit was to be measured by a Carcass Index in which the yield of the various cuts was weighted by the relative value of the individual cuts.

For boars the rate of gain, efficiency of gain, and carcass index of the progeny were to be given equal weight and summarized into a total score*, or a selection index. In the gilts' selection index the gilts' own productivity score would be included in addition to the items on their cross progeny performance.

The selection of young boars and gilts from the progeny tested parents was to be on the following items:

a. Life time productivity score of their dams.

b. Individual and litter weight at 154 days of age.

c. Conformation and backfat thickness of the individuals at 210 pounds weight. The backfat thickness was measured by a probe as suggested by Hazel and Kline (1952).

The program was followed as closely as possible. For the spring farrow of 1951, 17 gilts in line 8 were mated to four boars from line 9, and four sows and 12 gilts in line 9 were mated to five boars from line 8. In the fall of 1951, nine sows and three boars in line 8 were selected on their cross progeny tests, and eight sows and two boars in line 9 were selected on the same basis. These selected individuals were mated within their lines and gave a progeny in the spring of 1952 of 66 pigs weaned in line 8 and 63 pigs weaned in line 9. Of these pigs, 18 gilts and six boars were selected for reciprocal test crosses in each line in the spring of 1953.

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*The scoring system was based on the mean and the standard deviation of each trait. The minimum base for a trait would be roughly one standard deviation less than the mean, and one point score would be given for each 1/10 of the standard deviation above that minimum base.

In the spring of 1952, 17 gilts in line T were mated to six boars from line 3, and 13 gilts plus four sows in line 3 were mated to five boars from line T. The four sows in line 3 were introduced from three other Duroc lines (lines 10, 11, 12). At the conclusion of the progeny test in the fall of 1952, nine sows and two boars were selected in line T, and nine sows and two boars in line 3. One of the selected sows in line 3 was from line 12. These selected sows and boars were then mated within their respective lines. In line T only seven of the nine sows produced litters in the spring of 1953. In line 3 all the selected sows produced litters. The 1953 spring progeny consisted of 46 pigs in line T and 42 pigs in line 3 at two weeks of age.

Selection differentials were computed separately for sows and boars in each of the four lines on the following items: (1) number of pigs farrowed, (2) number of pigs weaned, (3) litter weight at 56 days of age, (4) sow productivity score, (5) progeny's average daily gain, (6) feed per hundred weight gain of progeny, and (7) progeny's carcass index. The selection differentials for the sow productivity items (1 through 4 above) were calculated by subtracting the mean performance of all the sows farrowing in a particular line from the mean performance of the sows selected on their progeny tests for breeding within their lines. The performance of the selected sows was weighted by the number of pigs weaned in their line litters one year after the cross matings were made. This weights the performance of selected sows by the number of line progeny they contribute for testing and selection the next generation, i.e. their contribution to the next generation.

For the progeny items (average daily gain, feed per hundred weight gain and carcass index), the mean of all litters tested in a reciprocal cross was subtracted from the mean of the progeny of the selected sires or dams, weighted by the number of pigs subsequently weaned by these selected parents in their line litters. The differences between these means are the selection differentials.

In addition to these selection differentials for sow productivity and progeny performance, selection differentials were also computed for the line 8 and 9 boars and gilts selected for testing in the first generation from progeny tested parents. The items included were productivity score of dam, individual's 56 day weight, 154 day weight and backfat thickness. The average of the gilt and boar pigs selected for testing were compared to the averages of all their contemporaries in these four items.

Standard deviations were calculated for comparison with the selection differentials. The selection differentials were then expressed as percentages of the standard deviations in order to get the selection differentials for different items on a similar basis for comparison.

Results

Selection differentials for the line 8 sows are presented in Table I. Selected sows produced line-cross litters that were 1.17 and 0.70 pigs above the average of all tested line 8 sows in number of pigs per litter farrowed and weaned. The selection differential for litter 56 day weight was 38.5 pounds. In computing the sows' productivity score twice as much weight was given to the number of pigs weaned and litter weaning weight as to the number of pigs farrowed per litter. The selection differential of seven points for sow productivity score was about two thirds as large as the standard deviation in that trait. With normal variation in sow productivity this would be equivalent to culling the poorest 40 per cent of the sows on productivity alone.[1] Actually, 47 per cent of the line 8 sows were culled so that the opportunity for selection on sow productivity was almost fully utilized.

Selection for average daily gain and carcass index was very weak as indicated by selection differentials equivalent to only seven to eight per cent of a standard deviation in these items. Selection for feed efficiency, on the other hand, was very good. The litters from selected sows required 11 pounds less feed for each hundred pounds of gain than the litters from all tested line 8 sows. This selection differential was equivalent to about two thirds of the standard deviation in this trait and was equal to the selection differential for sow productivity score.

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[1]Jay L. Lush, Animal Breeding Plans, Ames, Iowa. 1947 p. 148 Table 12.

Table 1.

Selection differentials for line 8 sows.

	Sow's own performance				Progeny performance		
	No. farrow.	No. wean.	Litter 56 day wt. lbs.	Productivity score	Ave. da. gain lbs.	Feed/cwt. gain.lbs.	Carcass index
Means of selected sows	10.82	9.05	326.2	69.4	1.73	316.9	45.47
Means of all sows	9.65	8.35	287.7	62.4	1.72	328.0	45.41
Selection differentials	+1.17	+.70	+38.5	+7.0	+.01	-11.1	+.06
Standard deviations	2.91	1.99	64.8	10.5	.14	17.1	.78
Sel. dif. in per cent of stand. dev.	40	35	59	66	7	65	8

Table 2.

Selection differentials for line 8 boars.

	Progeny performance		
	Ave. da. gain, lbs.	Feed/Cwt gain, lbs.	Carcass index
Means of selected boars	1.69	328.4	46.38
Means of all boars	1.63	333.6	46.18
Selection differentials	+.06	-5.2	+.20
Standard deviations	.13	11.5	1.28
Sel. dif. in per cent of Stand. dev.	47	45	16

The selection data for line 8 boars are given in Table 2. Two to three litters were tested from each boar. In general, the selection differentials in the three items of progeny performance were higher than for similar items for the line 8 sows. There was seven times as much selection pressure for average daily gain and twice as much selection pressure for carcass indexes for boars as for sows. The selection pressure for efficiency of gain was not as high for the boars as for the sows (45 per cent of a standard deviation compared to 65 per cent for the sows). This selection differential on boars would equal a culling rate of about 25 per cent of the boars if selection was made only on feed per hundred weight of gain. The actual culling rate for line 8 boars was 40 per cent.

In Table 3 the selection data for the line 9 sows are presented. The standard deviations of the items are the same in Tables 1 and 3 because they were calculated on the litter averages of all litters from both line 8 and line 9 sows. As for the line 8 sows the largest selection differential for the line 9 sows was in sow productivity score. This selection differential was nearly two thirds of the standard deviation of the productivity score. Line 9 sows, however, were selected more intensively than line 8 sows on number of pigs weaned. The selection differential was 1.23 pigs and was equivalent to 62 per cent of the standard deviation , which was nearly twice as much as for the line 8 sows.

The selection differentials for average daily gain were the same for both groups of sows. The selection differential for carcass index was 0.38 points for the line 9 sows, or 48 per cent of the standard deviation. This would be equivalent to a culling rate of 30 per cent

Table 3.

Selection differentials for line 9 sows.

	Sow's own performance				Progeny performance		
	No. farrow.	No. wean.	Litter 56 day wt. lbs.	Productivity score	Ave. da. gain. lbs.	Feed/ Cwt. gain,lbs	Carcass index
Means of selected sows	10.09	8.05	289.3	64.5	1.65	328.5	46.53
Means of all sows	8.87	6.82	255.2	58.2	1.64	331.8	46.15
Selection differentials	+1.22	+1.23	+34.1	+6.3	+.01	-3.3	+.38
Standard deviations	2.91	1.99	64.8	10.5	.14	17.1	.78
Sel. dif. in per cent of stand. dev.	42	62	53	60	7	19	48

Table 4.

Selection differentials for line 9 boars.

	Progeny performance		
	Ave. da. gain lbs.	Feed/Cwt. gain lbs.	Carcass index
Means of selected boars	1.84	313.2	45.28
Means of all boars	1.76	326.5	45.34
Selection differentials	+.08	-13.2	-.06
Standard deviations	.13	11.5	1.28
Sel. dif. in per cent of Stand. dev.	63	116	5

on this trait only. The actual culling rate for the line 9 sows was 50 per cent. The high selection on carcass index had evidently caused a low selection for feed required per hundred weight gain. The litters from selected sows in line 9 required only 3 pounds less feed for each hundred pound gain than the litters from all the tested sows in this line.

Selection differentials for line 9 boars are shown in Table 4. In this table and in Table 2 the standard deviations were calculated on sire progeny averages of both line 8 and line 9 boars. A very high selection was made on feed efficiency. Litters from the selected boars required 13 pounds less feed to gain hundred pounds than litters from all the line 9 boars. This selection differential was 16 per cent larger than one standard deviation for this trait, and would be equivalent to culling 60 per cent of the boars on this trait only. The actual culling rate of the line 9 boars was 50 per cent. The selection differential for average daily gain of 0.08 of a pound per day, was also rather high. This was equal to 63 per cent of the standard deviation, or culling the poorest 40 per cent of the boars on their progeny performance in this trait. Accompanying the high positive selections for rate and efficiency of gain was a negative selection of 0.06 for carcass index.

Table 5.

Selection differentials for line T sows.

	Sow's own performance				Progeny performance		
	No. farrow.	No. wean.	Litter 56 day wt. lbs.	Productivity score	Ave. da. gain lbs.	Feed/ Cwt. gain lbs.	Carcass index
Means of selected sows	9.61	7.28	213.4	56.1	1.59	330.3	44.57
Means of all sows	8.47	5.71	164.0	46.9	1.61	333.6	44.62
Selection differentials	+1.14	+1.57	+49.4	+9.2	-.02	-3.3	-.05
Standard deviations	2.61	2.47	82.2	13.7	.30	19.4	1.02
Sel. dif. in per cent of Stand. dev.	44	64	60	68	7	17	5

Table 6.

Selection differentials for line T boars.

	Progeny performance		
	Ave. da. gain lbs.	Feed/Cwt. gain lbs.	Carcass index
Means of selected boars	1.68	347.4	44.00
Means of all boars	1.60	350.4	43.96
Selection differentials	+.08	-3.0	+.04
Standard deviations	.07	18.3	.84
Sel. dif. in per cent of Stand. dev.	108	16	5

The selection differentials on line T sows are given in Table 5. As was true with the lines 8 and 9 sows, the most intensively selected trait for line T sows was in productivity score. The selected sows were nine points over the average which was equivalent to culling the poorest 40 per cent of the sows on that trait only. The actual culling per cent was 47 for the line T sows. The selection intensities for number of weaned pigs and 56 day litter weight were fairly high, or about 60 per cent of the respective standard deviations, while the selection differentials for number of pigs farrowed was lower, 44 per cent of its standard deviation.

Selection on progeny performance of line T sows was negative, except for feed efficiency, and the selection differential for this trait was very small, corresponding to only 17 per cent of its standard deviation. This situation may be explained by the failure of two of the selected line T sows to farrow litters in the line after the sows were selected. One of these sows had rather high records for nearly all the traits, and the other was a little above average. This failure of these sows to contribute to the line after they were selected greatly reduced the effective selection in the line.

Among the line T boars (Table 6) most of the selection was on average daily gain as indicated by the very high selection differential in this trait. The value was over one standard deviation and equivalent to a culling rate of about 60 per cent on this trait. This was also the actual culling per cent practiced for line T boars. The strong selection on average daily gain may have been due to the relatively low mean for all-boars in this trait. Selection on carcass merit and feed efficiency was low.

In Table 7 the data for the line 3 sows are given. The most striking figures in this table were the low selection differential for the productivity score and the relatively high selection differential for carcass index. The low figure for the productivity score is predominantly caused by the negative selection practiced for number of pigs farrowed. The selected sows farrowed on the average 1.18 pigs less than the average of all the sows. The other productivity traits had positive, but very small selection differentials, and the selection intensity for the productivity score in that way was only 12 per cent of its standard deviation. The selection intensity for the carcass index, on the other hand, was 30 per cent of its standard deviation. The selection differentials for the other two traits of progeny performance were higher than for the line T sows, but still low. The selection for line 3 sows was therefore mainly based on carcass quality.

The selection differentials for line 3 boars are shown in Table 8. Selection differentials for average daily gain and for carcass index were high and were equivalent to about 70 per cent of their standard deviations. The selection on feed efficiency, on the other hand, was negative. The litters from the selected boars required six pounds more feed per hundred pounds gain than the litters from all the boars.

Sow selection differentials from the four lines, are summarized in Table 9. The first four rows of the table contain the selection differentials from the sow-tables discussed above. In row five are the averages of these selection differentials. Selection differentials for the items of sow productivity ranged from 21 to 44 per cent of a standard deviation. The average selection differential for sow productivity score in all four lines was almost one-half of a standard devi-

Table 7.

Selection differentials for line 3 sows.

	Sow's own performance				Progeny performance		
	No. farrow.	No. wean.	Litter 56 day wt. lbs.	Productivity score	Ave. da. gain lbs.	Feed/ Cwt. gain lbs.	Carcass index
Means of selected sows	7.73	6.71	228.9	55.3	1.66	345.4	44.22
Means of all sows	8.91	6.38	198.9	53.6	1.62	349.4	43.92
Selection differentials	-1.18	+.33	+30.0	+1.7	+.04	-4.0	+.30
Standard deviations	2.61	2.47	82.2	13.7	.30	19.4	1.02
Sel. dif. in per cent of Stand. dev.	45	13	36	12	13	21	30

Table 8.

Selection differentials for line 3 boars.

	Progeny performance		
	Ave. da. gain lbs.	Feed/Cwt. gain lbs.	Carcass index
Means of selected boars	1.66	338.2	45.06
Means of all boars	1.61	332.7	44.47
Selection differentials	+.05	+5.5	+.59
Standard deviations	.07	18.3	.84
Sel. dif. in per cent of Stand. dev.	68	30	70

ation. This is equivalent to the selection of approximately the best 70 per cent of the sows on productivity score. Actually about 56 per cent of the tested sows were selected. This indicates that a large portion of the selection opportunity for sow productivity was utilized.

Selection differentials for the items of progeny performance were generally lower than for productivity items and ranged from eight to 28 per cent of the standard deviations. The greatest amount of selection was for feed efficiency, but line 8 was the only line of sows in which there was very high selection in that trait. Selection on carcass index was highest in line 9 sows, followed by that in line 3 sows. The facts that only about 11 sows per line had litters being progeny tested, and that eight or nine sows were selected from them, left little opportunity to do much culling of sows on the three items of progeny performance. The larger numbers of sows tested on production gave more opportunity for selection in those items than in the progeny performance items.

The average selection differentials on boars from all lines are summarized in Table 10. The average selection differentials of the three items of progeny performance ranged from one seventh to two thirds of a standard deviation. Selection was highest for average daily gain and lowest for carcass index. Roughly, the average for all three traits was about one third of a standard deviation, or the equivalent of culling the poorest 20 per cent of the boars. Actually 55 per cent of the tested boars were culled. Therefore, the opportunity for selection of boars in these traits were far from being fully utilized, except with regard to average daily gain. In spite of the much smaller percentage of tested individuals selected in boars than in sows and

Table 9.

Summary of selection differentials of sows in the four lines.

Selection differentials on:	Sow's own performance No. farrow.	No. wean.	Litter 56 day wt. lbs.	Productivity score	Progeny performance Ave. da. gain lbs.	Feed/ Cwt. gain lbs.	Carcass index
Line 8 sows	+1.17	+ .70	+38.5	+7.0	+.01	-11.1	+.06
Line 9 sows	+1.22	+1.23	+34.1	+6.3	+.01	- 3.3	+.38
Line T sows	+1.14	+1.57	+49.4	+9.2	-.02	- 3.3	-.05
Line 3 sows	-1.18	+ .33	+30.0	+1.7	+.04	- 4.0	+.30
Average of all sows	+ .59	+ .96	+38.0	+6.0	+.01	- 5.5	+.17
Standard deviations	2.78	2.36	86.6	13.2	.12	19.2	1.14
Selection differentials in per cent of standard deviation	21	41	44	46	8	28	15

Table 10.

Summary of selection differentials of boars in the four lines.

Selection differentials on:	Av. daily gain, lbs.	Feed/Cvt, lbs.	Carcass index
Line 8 boars	+ .06	- 5.2	+ .20
Line 9 boars	+ .08	-13.2	- .06
Line T boars	+ .08	- 2.9	+ .04
Line 3 boars	+ .05	+ 5.5	+ .59
Average for all boars	+ .07	- 4.0	+ .19
Standard deviations	.11	16.1	1.27
Selection differentials in per cent of standard deviation	66	25	15

presumably the greater opportunity for selection of boars, this was not realized, except for average daily gain.

The individual selection differentials for gilts and boar pigs from selected boars and sows give information of the selection in the line-breeding phase of the program. In line 8 (Table 11) there was a negative selection on dam's productivity score for both gilts and boar pigs. This probably occured because dam's productivity was generally ignored in the selection of the young boars and gilts, because all of their dams had been previously selected on the basis of their productivity scores when raising line-cross litters. Most of the selection for the individual's performance was for weight at weaning and 154 days, and for probe backfat thickness. The selected gilts weighed seven pounds more than the average of all the gilt pigs at 154 days, which is equivalent to 37 per cent of the standard deviation for this trait. The selection pressure was only 16 per cent of the standard deviation for gilts' probe backfat.

The boar pigs had higher selection differentials than the gilts. Strongest selection was made on weaning weight, where the four pounds' selection differential was about two thirds of the standard deviation. The figure for probe backfat was four times as large as for the gilts, or 0.08 of an inch.

Corresponding data for line 9 gilts and boar pigs are presented in Table 12. The selection on dams productivity was positive, but very low for the gilts. Also here the strongest selection for gilts was made on the 154 day weight. The selection differential was nearly the same as for line 8 gilts, or seven pounds. Selection on gilts' probe backfat was the same in both the lines, but was equi-

Table 11.

Individual selection differentials for gilt and boar pigs in line 8

	Dam's product. score	Weaning wt.,lbs.	154 day wt., lbs.	Probe back fat, inch.
Gilts				
Means of selected gilts	71.8	41.7	151.3	1.81
Means of all gilts	73.9	39.5	144.1	1.83
Selection differentials	-2.1	+2.2	+ 7.2	-.02
Standard deviations	11.5	8.1	19.4	.13
Sel. dif. in per cent of stand. dev.	18	28	37	16
Boars				
Means of selected boars	71.7	43.8	147.2	1.58
Means of all boars	74.9	39.6	138.6	1.66
Selection differentials	-3.2	+4.2	+ 8.6	-.08
Standard deviations	9.2	6.6	19.5	.14
Sel. dif. in per cent of stand. dev.	35	64	44	56

Table 12.

Individual selection differentials for gilt and boar pigs in line 9

	Dam's product. score	Weaning wt., lbs.	154 day wt., lbs.	Probe back fat, inch.
Gilts				
Means of selected gilts	73.4	41.6	163.0	1.32
Means of all gilts	72.9	39.0	155.6	1.34
Selection differentials	+ .5	+2.6	+ 7.4	-.02
Standard deviations	12.9	8.8	20.1	.19
Sel. dif. in per cent of stand. dev.	4	30	36	10
Boars				
Means of selected boars	69.8	46.0	173.3	1.18
Means of all boars	66.7	40.7	160.2	1.23
Selection differentials	+3.1	+5.3	+13.1	-.05
Standard deviations	11.7	10.7	23.9	.11
Sel. dif. in per cent of stand. dev.	27	50	55	46

alent to only 10 per cent of the standard deviation in line 9.

The boar pigs in line 9 were selected mainly on 154 day weight. The selection differential was 13 pounds. The selection pressure on probe backfat was four times as large as for the gilts, or 46 per cent of the standard deviation.

The average selection differentials for the boars and gilts in both lines are given in Table 13. In both sexes the greatest amount of selection was in weight at weaning and at 154 days. There was very little selection for dam's productivity and very little more for probe backfat thickness. The selection differentials were higher for boars than for gilts due to a higher culling rate in the boars. This was especially true for probe backfat, as the selection intensity was three times greater for the boars in this trait.

Table 13.

Summary for selection differentials
for line 8 and 9 gilt and boar pigs.

Av. select. dif.	Dam's product. score	Weaning wt., lbs.	154 day wt., lbs.	Probe back fat, inch.
Boars	-.05	+4.8	+10.8	-.06
Gilts	-.8	+2.4	+ 7.2	-.02
All pigs	-.4	+3.6	+ 9.0	-.04
Standard deviations	14.5	8.6	22.0	.30
Selection differentials in per cent of standard deviation	3	43	41	13

Discussion

In a selection program, where the selection is based on a selection index, the maximum selection differential for each of the traits can seldom be reached. Many of the individuals selected by the index will not rate very high on certain individual traits. However, the index, if properly prepared, should give a reasonably reliable measure of the average merit of the individual, when taking all traits into consideration. In a measure, then, a selection index is a phenotypic evaluation used as an estimate of the breeding value of an individual. Although it may be the best estimate available of breeding value, it will not be completely accurate. Its accuracy will depend on the heritability of the selection index. The effectiveness of the selection index and the selection practiced can be measured by determining the actual gains made in the progeny of selected parents. This experiment had not been underway long enough to measure the effectiveness of the selection practiced, but it was possible to measure the intensity of selection for certain items of sow productivity and progeny performance. This permits some partial evaluation of the probable success of the program and may indicate that certain changes are desirable to permit more intense selection.

Opportunities for selection for sow productivity were utilized to a high degree. The amount of selection practiced for this trait appeared to be sufficient to be effective in a long range breeding program. The experimental procedure of farrowing about 30 per cent more gilts than can be progeny tested permits good opportunity for selection in sow productivity and this opportunity was utilized to a high degree.

With reference to the selection opportunities for the sow progeny performance items, it is clear that there was little opportunity for selection in these items and the actual selection differentials were low. An increase in the number of sows progeny tested is essential if selection is to be improved in the progeny performance traits.

Among the boars the full selection opportunities in progeny performance were far from realized. This may result from death losses, sterility, disease or the necessity of culling certain individuals for reasons other than the items considered in this study. A certain amount of the available selection opportunity normally must be expended for some of these things. Furthermore, there may be negative genetic correlations among the three items being selected. This would reduce the amount of selection below the maximum for the individual items. A properly constructed selection index would be helpful if such negative correlations exist.

An increase in the number of boars tested with perhaps an increase in the accuracy of the boar progeny test by testing several more litters from each boar seems to be indicated from the present results. This would increase the accuracy of the boar progeny test and also afford more opportunity to cull a higher percentage of the tested boars. Consequently the selection intensity would be increased and also be more effective.

Summary

The selection intensity in the first generation of a swine reciprocal recurrent selection program was studied in two parallel trials with two different pairs of lines. One pair of unrelated lines were lines T and 3 of the same (Duroc) breed and the other pair of lines were of different breeds. Line 8 was from the Duroc breed and line 9 was from the Beltsville No. 1 breed.

The selection intensity on line-cross progeny performance was generally weak, especially for sows where the selection differentials for rate and efficiency of gain and for carcass index were small. For boars the selection differential for rate of gain was good, but for efficiency of gain and for carcass index the selection differentials were as small as for the sows.

The selection intensity for sow productivity was reasonably good, because of the opportunity to cull one third of the tested sows on their production records.

The limited number of sows progeny tested for rate of gain, efficiency of gain and carcass merit left little opportunity for culling many sows after the progeny test was completed.

Failure of certain selected animals to produce offspring within their line after they had been tested reduced the amount of selection below that originally planned. Also deaths of certain selected individuals and the necessity of culling some individuals with certain defects not measured in the progeny test, as shown in the tables, further reduced the amount of selection that could be attained.

The results indicate that an increase in the number of boars and sows tested and a higher culling rate on basis of the progeny test will be necessary in order to test this breeding program effectively.

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