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CONTENTS

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INTRODUCTION

NEARLY ALL of our breeds of livestock, with the exception of the Arabian Horse, probably originated from a crossbred foundation. The development of these breeds has been slow and was accomplished chiefly by selection.

The Minnesota No. 1 line of swine was started in 1937 from a crossbred foundation of Landrace and Tamworth, with the distinct objective of developing a superior line of hogs for crossbreeding. On August 24, 1946, the Inbred Livestock Registry Association was formed—one of its functions being the registration of the Minnesota No. 1 line of swine.

The application of genetics, the reshuffling of the genes, selection based on actual performance, and the immediate use of inbreeding made it possible to develop this breed in 10 years, a much shorter time than was required for any other breed to date. It is, therefore, timely that the breeding methods by which this work was accomplished should be analyzed.

METHODS OF ANALYSIS

Since the rediscovery of Mendel's Laws in 1900, a real science of breeding based on the Mendelian principles of heredity has been developed. By applying these principles, the hereditary characteristics of many plants and of some rapid-breeding laboratory animals can be controlled with some precision. The larger farm animals breed more slowly, resulting in relatively smaller populations and the slowing down of genetic analysis.

Genetics has made an important contribution by explaining the results of the well-established methods of breeding, such as inbreeding, crossbreeding, culling, etc.

Studies made by Miss Helen King *(4)*[2] at the Wistar Institute of inbreeding and selection of rats show the effects of continued brother-sister

[1] The data on which this study is based were gathered in a project being conducted by the University of Minnesota in cooperation with the Regional Swine Breeding Lab., Ames, Iowa, Bureau of Animal Industry, U.S.D.A. This publication has been condensed from a thesis submitted by the senior author to the Graduate Faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Italic figures in parentheses refer to corresponding references in Literature Cited.

matings for 25 generations and of rigorous selection.

Sewall Wright's *(19)* report on the experiments of the Bureau of Animal Industry with 23 different inbred lines of guinea pigs points out that after 25 generations of brother-sister matings, some degeneration was usually encountered. Although several families showed no apparent degeneration, there was a full recovery of vigor when crosses were made between inbred families or lines. In other words, the lines had good combining ability; the favorable genes lacking in one line were supplied by the other.

Wright *(17, 18, 20, 21)* analyzed the Duchess family of Shorthorns as bred by Thomas Bates, who used measures of inbreeding and relationship.

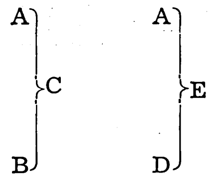
McPhee and Wright *(7, 8)* made another study of the history of the Shorthorns on the basis of the values of certain Mendelian coefficients (Wright *17, 18*).

Relationship

During the last part of the 19th century, Sir Francis Galton made the first scientific attempt to determine the degree of likeness between individuals related by descent. He expressed the degree of resemblance as the correlation coefficient.

An offspring will resemble its parents because it receives one-half of its genes from the male and the other half from the female parent. This is the basis of all relationships. All other relationships are combinations of chains of parent-offspring relationships. If the parents are A and B and the offspring is C, C's relationship to A is .50, and to B, .50, providing there is no inbreeding. Sex-linkage can affect this relationship slightly. Two individuals of the same population usually, perhaps always, carry some like genes. Thus, the two parents, even though not related by the general understanding of the term "related," may transmit some like-genes to their offspring. If the parents are closely related, the probability that they will transmit similar genes is increased, and if they have been inbred, the chances of transmitting similar genes are further increased.

Relationship is thus the probability that two individuals related by descent will carry more like genes than individuals which are not related within the same population. For example, the relationship of half-sibs C and E is 25 per cent. (This is based on the assumption that one-half of A's genes are in a homozygous state.) C has half its



genes in common with A, the other half with B. The same is true of E. Thus on the average, C and E will have 25 per cent of the genes of A in common. It must be remembered that this is on the average. The most the genes could be in common is 50 per cent, that is, if C and E each received the same genes from A. The least the genes could be in common is zero, that is, if C has received one-half of the genes of A, and E the other half, but an entirely different half. These would be extreme cases. The standard deviation of the mean would be the expected average in per cent divided by the square root of the independent pair of genes involved. Thus animals with different calculated relationship figures may be noticeably more alike in their genes than those having the same figure.

The effect of an ancestor in an outbred population is halved each time the individual becomes an additional generation removed from that ancestor. When five generations removed, the contribution of the ancestor to the individual is $\frac{1}{2}^5 = 1/32$. Therefore, any ancestor more than three generations removed from the individual contributes very little. In general, the relationship in any one line between two animals is $\frac{1}{2}^n$ where "n" is the number of Mendelian segregations between the two animals in that line or path. Lush *(6)* shows that linkage makes "n" larger than the linkage groups involved, but smaller than the number of genes. With 20 to 30 pairs of chromosomes involved, an effective "n" of 25-100 appears reasonable. The total relationship is the sum of all these paths, as reported by Wright *(18)*.

Base from Which to Measure Relationship

The foundation stock, chosen at random from the population, which is used as the basis from which the relationship is figured, would have many like genes, because these genes would be widespread in the population. The distribution of pairs of allelic genes chosen at random is as follows: q^2 will be AA, $2q(1-q)$Aa and $(1-q)^2$aa. The relationship between two animals is established because they have a more common ancestry than the rest of the animals in the same population. The two animals, therefore, are more likely to possess more genes in common. In the application of relationship figures to an animal, or herd, it is necessary to first determine what population to use as a base. It is impossible to carry the analysis beyond the origin of pedigrees and, in many cases, it adds little to the study to go even that far. It is essential, however, to clearly define the base.

The processes of calculating relationship do not take into consideration mutations or selection which might bring about a change in gene frequency. Mutations apparently do not play a great part unless the calculations involve many generations. Intense selection on the other hand, especially for genes with major effects, will have an important bearing on the gene frequency in as few as five to six generations back.

The further one goes back in a pedigree, the more opportunity there is for chance to have altered the inheritance, on the average, of the genes considered collectively.

The most practical use of the coefficient of relationship is in estimating the merits of relatives of animals whose merit is known. This estimate is the basis for using pedigree or progeny in making selection more effective, and in so doing the effects of environment, the degree of heritability, dominance, and selection are neglected. Many practical difficulties and necessary precautions harass the use of relationship coefficients with respect to evaluating the prepotency of an animal.

Dominance and epistasis may make the individuals appear more alike than the actual calculated coefficients of relationship indicate. The coefficients of relationship can also be used to make a genetic analysis of a breed. They can be used to establish how much inbreeding was practiced. The measurement of relationship is closely related to measurement of inbreeding. Wright *(17)* gives the following formula for the coefficient of inbreeding:

$$F_x = \Sigma[(\tfrac{1}{2})^{n+n^1+1}(1 + F_A)]$$

and the coefficient of relationship between x and y:

$$R_{xy} = \frac{\Sigma[(\tfrac{1}{2})^n(1 + F_A)]}{\sqrt{(1 + F_x)(1 + F_y)}}$$

and the formula for the coefficient of relationship between sire and dam:

$$R_{SD} = \frac{2F_O}{\sqrt{(1 + F_S)(1 + F_D)}}$$

where:

F_S = the inbreeding coefficient of the sire

F_D = the inbreeding coefficient of the dam

F_x and F_y = the inbreeding coefficient of the individuals

F_O = the inbreeding coefficient of the offspring

n = number of generations between the common ancestor and the sire

n^1 = number of generations between the common ancestor and the dam

F_A = the inbreeding coefficient of the common ancestor

A = common ancestor

x and y are the two individuals whose relationship we wish to measure

From the formulas it follows that the inbreeding coefficient would be one-half the coefficient of relationship:

$$F_O = \frac{R_{SD}}{2} \times \sqrt{(1+F_S)\,(1+F_D)}^{\,*}$$

These formulas were derived by Wright *(17)* for use in calculating the respective coefficients from pedigrees for each line or path from the sire back to a common ancestor and then forward to the dam.

The method used to obtain the relationship coefficients in this study, however, is somewhat different from Wright's method in tracing pedigrees and calculating the individual path and summing them. All the animals in the breeding herd were used in the calculations; in other words, sampling was not resorted to. Further, the relationship figures were calculated starting from the foundation stock and working up year by year until the final year was reached. For example: If there are two litter mates A♀ and D♂ from sire B and female C, their pedigree being:

$$A♀, D♂ \begin{cases} B♂ \\ C♀ \end{cases}$$

then the relationship on the basis of Mendelian segregation will be on the average:

A or D to B is .50
A or D to C is .50

If the two litter mates A and D are mated the next year, then the pedigree becomes:

$$E \begin{cases} A \begin{cases} B \\ C \end{cases} \\ D \begin{cases} B \\ C \end{cases} \end{cases}$$

A and D will have on the average one-quarter of the genes of B, and one-quarter of the genes of C in common. The relationship between A and D is then .25 + .25 = .50.

A will transmit half of its genes to E, but half of this amount (or .25 of the total genes of A) are in common with D. This is the same for D. Therefore E will have lost 25 per cent of its heterozygosity, or be inbred 25 per cent, which is half of the relationship between the parents A and D.

By establishing the coefficients of relationship, it is possible to obtain an approximate measure of the effect of certain individuals on the herd or on another individual.

An analysis based on such data is a valuable guide when developing a new breed.

ANALYSIS

To trace the development of the Minnesota No. 1 line of swine, this study is divided in the following sections:

I. How rigid was selection? How many males and females were selected for the breeding herd from the males

* $\sqrt{(1+F_S)\,(1+F_D)}$ is the correction factor for inbreeding of sire and dam.

and females available? How many years did noncontributors or their offspring remain in the herd before dropping out?

II. (a) The average distribution of genes of the six contributing foundation animals among the contributors by years, including the total 1947 breeding herd.

(b) The average distribution of the genes of each year's contributors (1938 through 1946) in the 1947 herd, and how important individual animals (male and female) have been in the development of the breed as a whole.

III. What is the inter-se relationship by years and the inbreeding which would be expected in a closed herd on the basis of the number of males and females used?

IV. What is the average length of time between generations?

V. What is the average performance by years, considering the factors: fertility, survival, rate of gain, and economy of gain?

I. How rigid was selection?

Figure 5 shows the geneology of the foundation herd for the Minnesota No. 1 line. The heavy lines indicate the contributors, and the dotted lines the noncontributors. This line of swine is based on a crossbred foundation of the Tamworth and Danish Landrace breeds. Winters *et al. (15)* outline the source of the breeding stock and the nature of the matings made during the first five years of the experiment.

1937 Farrow—The Danish Landrace boar 18-2 was used on six Tamworth gilts. Offspring of five of the six gilts were used for breeding stock for the 1938 farrow. None of the offspring of the 3-36 Tamworth gilt were used. This animal was carried over for one more year, but again none of the offspring were kept, and she was eliminated from the herd. Offspring of the Tamworth gilts 6-70P and 6-72P carried on in the herd for 3 years and 5 years respectively before dropping out. Only 3 of the Tamworth gilts, 12-79, 9-36, and 1-36, and the Landrace boar 18-2 contribute directly to the present breeding herd (figure 7). Thus 57.1 per cent of the 1937 breeding stock contributed to the 1947 breeding herd (figure 8).

Litters—All of the six litters farrowed in 1937 were tested. Of the animals weaned and tested, 13 gilts and three boars, or 33.3 per cent, were selected for breeding, eight of which, or 16.7 per cent, contribute to the present herd.

1938 Farrow—Winters *et al. (14)* give the breeding program for 1938 as follows:

13 F_1 gilts bred to 3 F_1 boars
5 Tamworth females to F_1 boars for backcross litters
4 Landrace females bred to F_1 boars for backcross litters
2 Tamworth females, one bred to the Landrace boar 18-2, the other to Landrace boar 6.7.

All the purebred animals and all the F_1 breeding stock farrowed in 1937 were marketed, and selection of breeding stock to produce the 1939 farrow was thus restricted to the 1938 crop.

The 13 F_1 gilts farrowed in 1938 represented 50 per cent of the gilts available for selection into the breeding herd, and the boar pigs 23.1 per cent of the available boar pigs, or 13.6 per cent

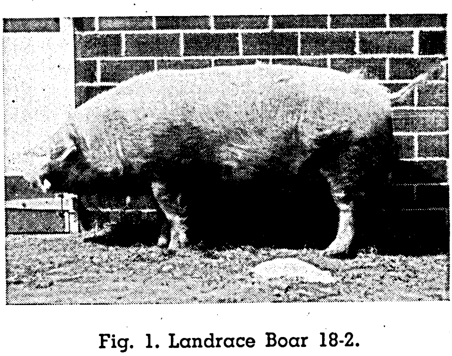


Fig. 1. Landrace Boar 18-2.

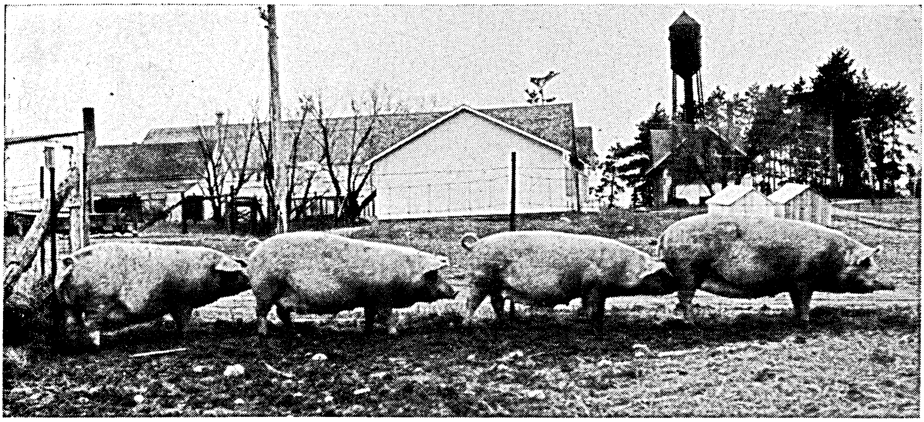


Fig. 2. Landrace gilts.

of the total males (boar pigs and barrows). All of the boar pigs and 38.7 per cent of the gilts are contributors. All litters were tested, therefore numbers weaned, tested, and available are the same (table 4).

Of the stock brought into the herd in 1937, only one Tamworth gilt and one Landrace gilt contributed. The 6 sows and the aged boar of the 1937 breeding stock were kept over into the 1938 breeding herd, but none of the offspring from these matings contributed.

The 1938 breeding stock contains 14 foundation animals (figure 6), and 66.7 per cent did not contribute (figure 8). Seven animals remained in the herd for 1 year, six for 2 years, two for 3 years, four for 4 years, and one for 5 years. Three boar pigs, five gilts, one Tamworth female, and one Landrace female have contributed. It is to be remembered that foundation stock was brought in in 1936 and 1937. Four of the seven foundation animals in 1936 and two of the seven which were added in 1937 contributed, making a total of six contributors.

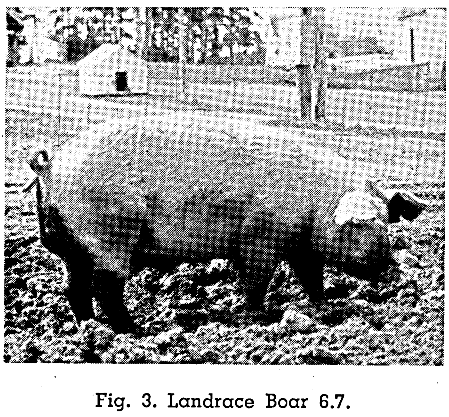


Fig. 3. Landrace Boar 6.7.

Table 1 indicates the number of years between 1939 and 1947, inclusive, that animals or their offspring remained in the breeding herd before being eliminated. Table 2 shows the litter summary. Table 3 summarizes the composition of the breeding stock, and table 4 shows the per cent of breeding stock, by years, which contributed to the 1947 breeding herd. Figures 5 and 7 show the geneology of the Minnesota No. 1 breeding herd. Figure 5 includes all the breeding animals and figure 7 includes contributors only. Figure 6 shows by years the number of foundation animals to which the University of Minnesota breeding herd at Grand Rapids traces back. Figure 8 indicates by years the proportion of animals in the University of Minnesota breeding herd which did not contribute to the 1947 breeding herd.

Table 1. Number of years animals or their offspring remained in the herd before being elimiated.

	Year of farrow									
	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946
Animals remaining 1 year		7	24	25	24	22	19	15	26	21
2 years	1	6	3	6	5	3	9	5	4	
3 years	1	2	5	2		2	3	2		
4 years		4	1			1	2			
5 years	1	1								
Total animals	3	20	33	33	29	28	33	22	30	21
Noncontributing Breeding Stock per cent	42.9	66.7	76.7	70.2	58.0	57.1	57.9	47.8	49.2	35.6

Table 2. Litter Summary.

	Year of farrow										
	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	Ave.
Total litters farrowed	6	24	39	42	45	43	49	41	52	46	387
Litters tested in per cent	100.0	100.0	53.8	64.3	53.3	60.5	53.1	56.1	48.1	43.5	57.4
On the basis of animals weaned											
Per cent of animals tested	100.0	96.7	45.5	71.7	63.1	70.6	75.3	41.5	63.0	46.0	63.2
Per cent of animals selected for breeding stock	33.3	23.6	14.5	12.3	10.8	12.9	7.3	14.7	10.8	17.9	13.7
Per cent of animals which contributed	16.7	5.5	4.0	4.8	3.6	5.3	4.2	6.8	6.7	20.4	6.8
On the basis of animals tested											
Per cent of animals selected for breeding stock	33.3	24.4	32.0	17.1	17.1	18.2	9.7	35.5	17.1	38.9	21.5
Per cent of animals which contributed	16.7	5.7	8.8	6.7	5.7	7.9	5.5	16.4	10.6	14.6	10.9

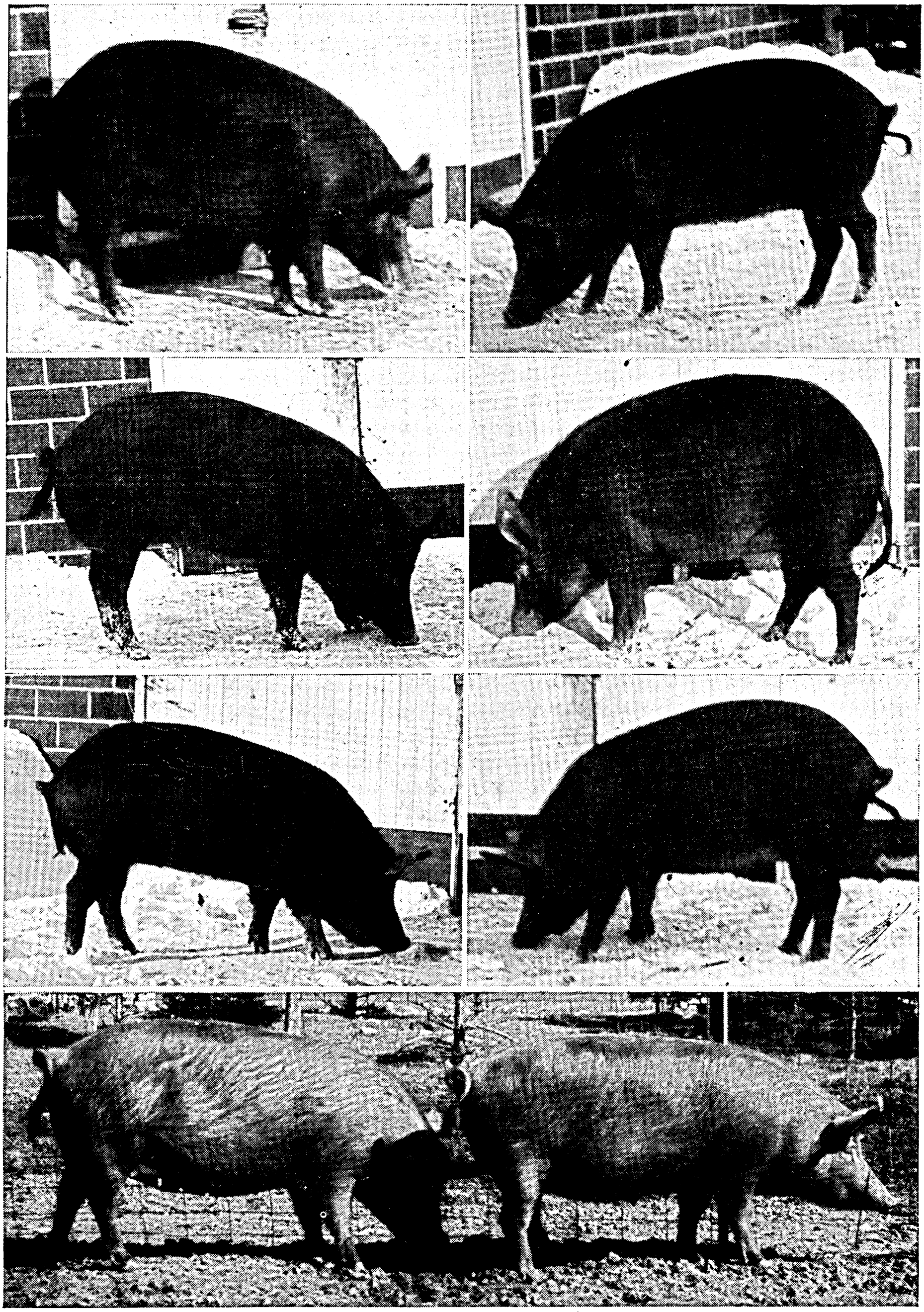


Fig. 4. Foundation stock of Tamworth gilts.

Table 3. Composition of Breeding Stock

	To produce farrow in											
	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	Ave.
Total females	6	24	39	43	45	45	50	40	54	46	68	
Per cent gilts			100.0	88.4	73.3	66.7	70.0	47.5	63.0	58.7	70.6	
Per cent sows			0.0	11.6	26.7	33.3	30.0	52.5	37.0	41.3	29.4	
Total males	1	4	4	4	5	5	7	6	7	13	10	
Per cent boar pigs			100.0	50.0	60.0	60.0	57.2	50.0	71.4	76.9		
Per cent aged boars			0.0	50.0	40.0	40.0	42.8	50.0	28.6	23.1		
Per cent gilts from available gilts*		50.0	44.8	58.5	32.7	30.3	34.0	19.0	38.6	23.5	59.3	36.5
Per cent sows from available sows		100.0	0.0	12.8	27.9	33.3	33.3	42.0	50.0	35.2	43.5	33.9
Per cent boar pigs from available boar pigs*		23.1	21.1	10.5	7.3	10.3	3.6	2.6	22.7	9.9	12.7	8.4
Per cent aged boars from available aged boars		100.0	0.0	50.0	50.0	40.0	60.0	42.8	40.0	42.8	15.4	36.4
Per cent boar pigs from available boar pigs and barrows		18.2	4.5	3.3	2.8	3.2	3.6	1.7	22.7	9.9	12.7	5.7
Per cent females from available sows and gilts			35.1	41.3	31.3	31.3	33.8	24.0	42.2	27.9	53.5	35.7
Per cent males from available aged boars, boar pigs and barrows			4.3	6.3	4.4	5.0	6.1	4.0	5.4	12.0	13.1	7.7

* Tested

Table 4. Per Cent of the Breeding Stock which Contributed to the 1947 Breeding Herd (Gilts and Boar Pigs Only)

	Breeding stock which produced the farrow in										
	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947
No. of boar pigs selected	1	3	4	2	3	3	4	2	5	10	8
Per cent boar pigs which contributed	100.0	100.0	100.0	100.0	66.0	100.0	100.0	66.7	60.0	70.0	
No. of gilts selected	6	13	39	38	33	30	35	19	34	27	48
Per cent gilts which contributed	50.0	38.7	15.4	23.7	36.4	26.7	34.3	52.6	44.1	29.3	

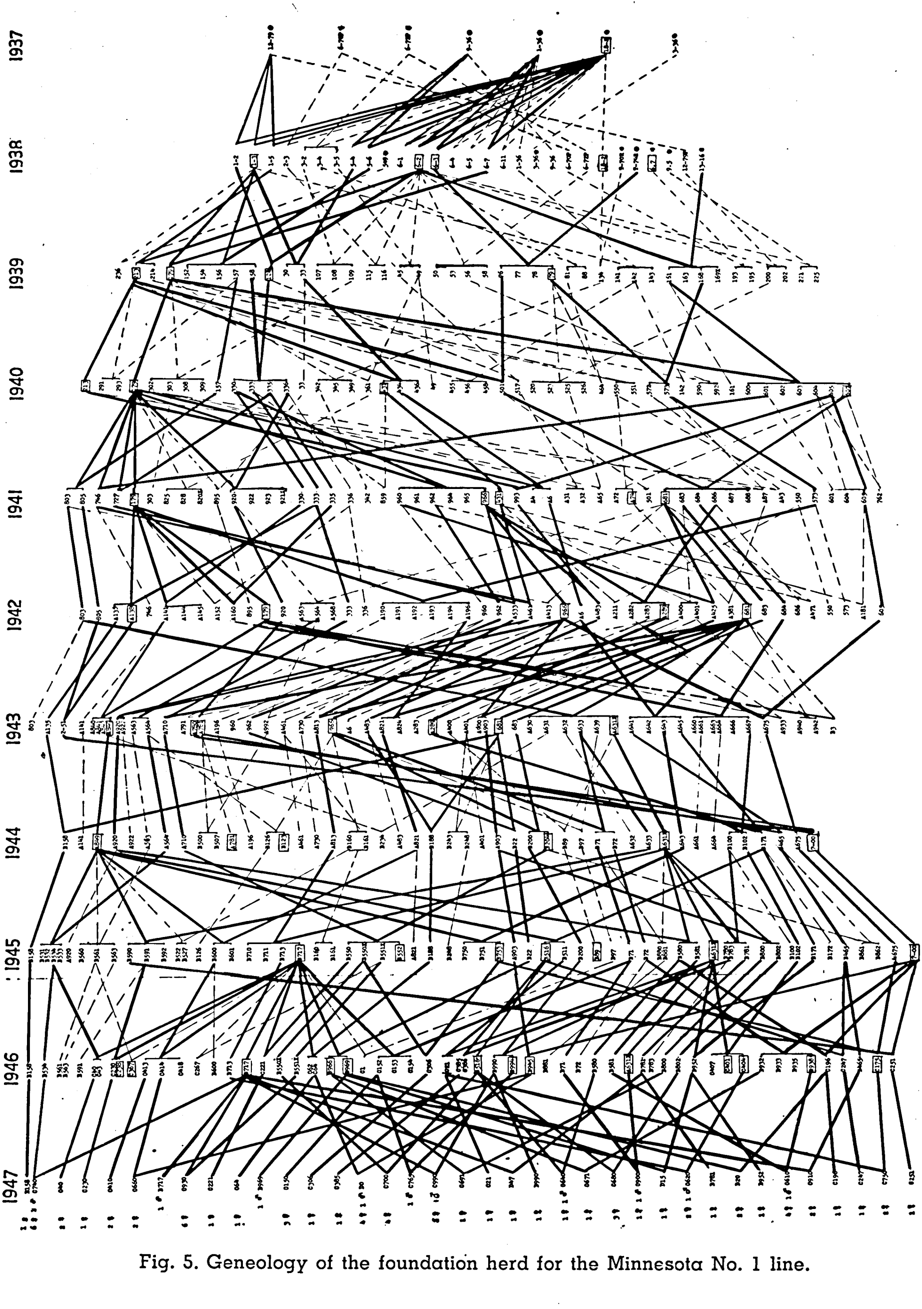


Fig. 5. Geneology of the foundation herd for the Minnesota No. 1 line.

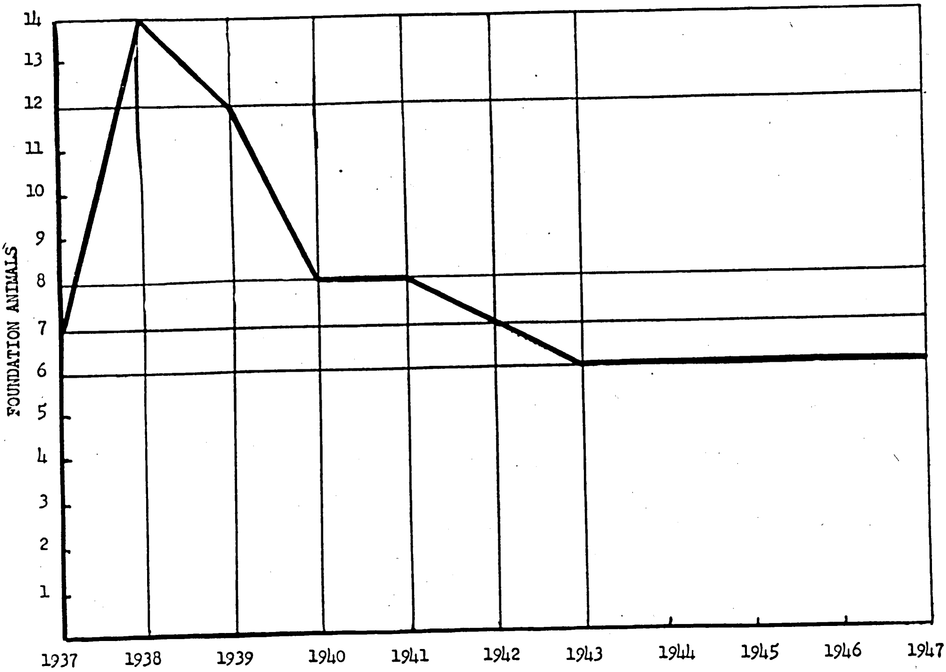


Fig. 6. Number of foundation animals to which the breeding herd of the Minnesota No. 1 line at Grand Rapids trace back, by years.

II. (a) The average distribution of genes of the six contributing foundation animals among the contributors by years, including the total 1947 breeding herd.

The graph in figure 9 represents the distribution of the genes, based on the collateral relationship of the animals (corrected for inbreeding), of the six foundation animals to the contributors in each year's breeding herd, through 1946, and to all the animals in the 1947 breeding herd.

The Landrace boar 18-2 has contributed the most genes to the line; he is responsible, on the average, for having 52 per cent in 1938 and 39 per cent in 1947 of the genes in common with the herd. The Tamworth female T74 has contributed the least in any year—from 5 to 10 per cent. The Landrace female 13-16 has the second lowest and the Tamworth female 1-36 the highest percentage of genes of all the Tamworths in common in all years.

The actual collateral relationship[3] of an animal in the 1947 herd to the foundation animals is on the average as follows:

18-2	.47	9-36	.15
1-36	.23	13-16	.11
12-79	.20	T74R	.05

II. (b) The average distribution of the genes of each year's contributors (1938 through 1946) in the 1947 herd, and how important individual animals (male and female) have been in the development of the breed as a whole.

Gene distribution of the 1938 contributors:

[3] Corrected for inbreeding period.

The three boars 1-3, 6-2, and 6-3 have on the average contributed 15.4, 13.8, and 12.5 per cent respectively to the 1947 herd (table 5). Their effect has a tendency to be somewhat equal—none of the three boars made any outstanding contribution (figure 7).

The effect of the boars 1-3 and 6-2 has been declining, but that of 6-3 is on the increase (see table 5).

Four females, 1-2, 1-5, 5-6, and 6-7, contribute 11.6, 11.8, 11.5 and 14.7 per cent of the heredity, which again has no outstanding effect. The three re-

Table 5. Expected Average Distribution of Genes of the more Prominent Boars in One Year among the Contributors in the Following Years, if Chance Prevails.

Year	Boars	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947*
1938	1-3		21.6	23.6	20.6	21.1	16.7	16.4	16.0	15.9	15.4
	6-2		19.9	24.5	20.3	17.7	17.1	15.2	14.8	13.9	13.8
	6-3		8.6	3.6	4.9	5.1	9.9	11.6	12.1	12.3	12.5
1939	179			17.0	19.8	20.8	24.7	25.0	25.5	24.8	24.2
	124			15.9	19.3	21.2	15.3	15.4	16.0	15.4	15.7
	213			17.6	12.8	12.2	16.7	17.0	16.3	16.2	16.3
1940	179				28.2	33.7	27.3	25.8	25.7	22.7	20.2
	213				2.5	2.1	1.4	1.1	0.7	0.5	1.1
	607				9.3	11.6	23.1	24.1	23.5	20.6	17.8
1941	179					14.3	15.1	15.6	22.9	24.5	18.9
	431					2.7	3.2	3.4	3.5	2.7	3.0
	681					9.2	13.1	12.1	6.6	4.5	4.3
	966					13.1	18.6	19.0	19.6	20.0	24.9
1942	179						5.1	8.2	12.9	11.2	9.3
	681						25.3	26.5	26.1	24.6	19.7
	966						11.1	9.0	7.8	4.7	6.0
	A138						2.6	2.4	1.2	3.0	3.8
1943	681							6.9	7.6	7.3	8.1
	966							9.9	14.8	16.5	18.0
	A289							7.9	15.3	11.5	12.0
	A781							2.7	3.0	4.0	2.0
	A780							2.5	2.8	8.6	10.0
1944	A631X								17.1	26.2	29.6
	A849								13.4	18.5	13.8
	B204								5.3	5.2	5.0
1945	A631X									8.9	13.3
	B717									16.1	21.8
	B754									2.9	2.4
	7-00									7.3	12.5
	B516									5.1	1.8
1946	A631X										1.6
	B516										7.2
	B717										16.1
	B938										4.1
	B945										5.6
	B966										1.7
	B969										3.7
	B994										.8
	C175										1.6
	C404										2.6

* All animals in this year's breeding herd and contributors only in the other years.

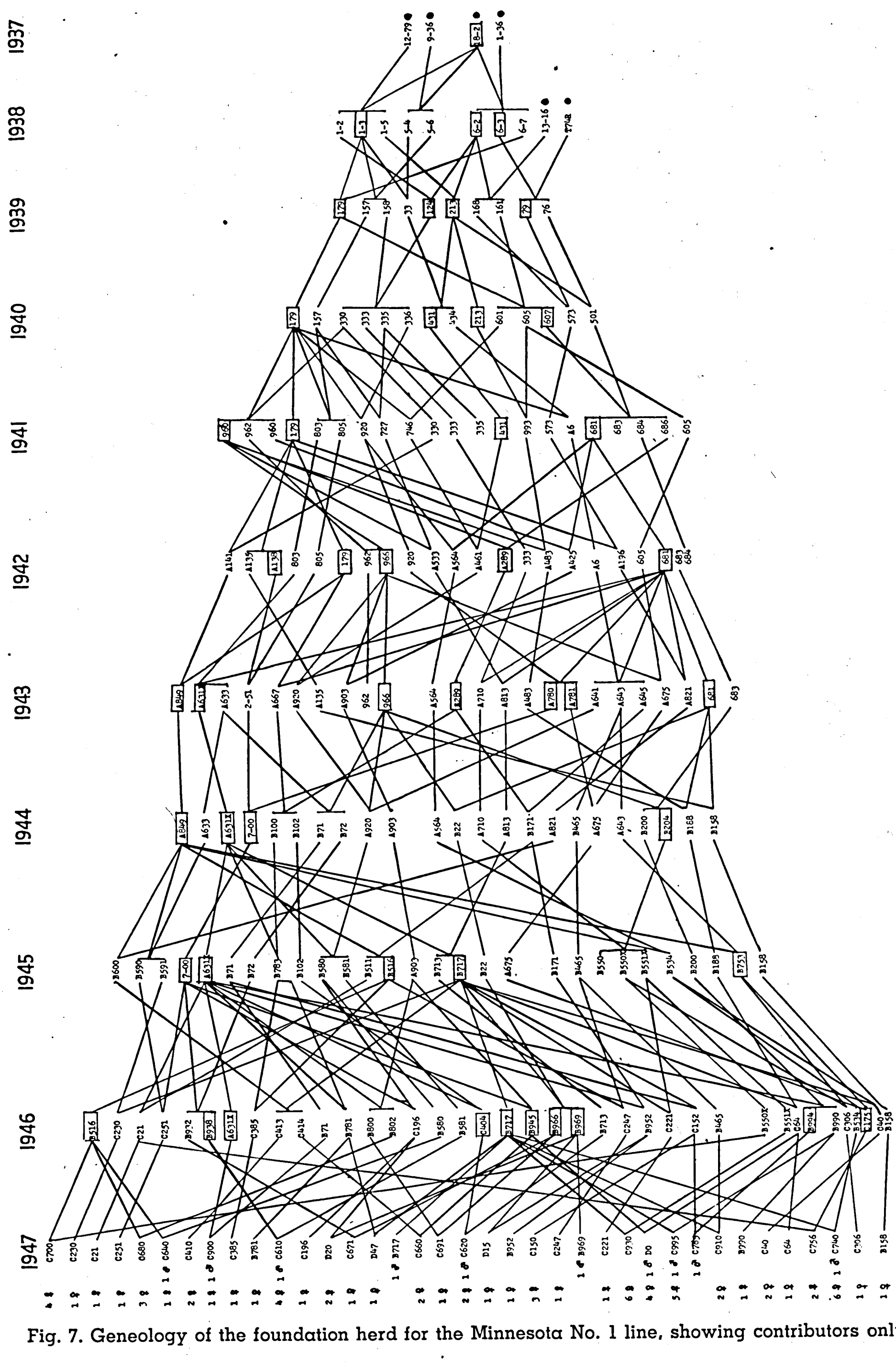


Fig. 7. Geneology of the foundation herd for the Minnesota No. 1 line, showing contributors only.

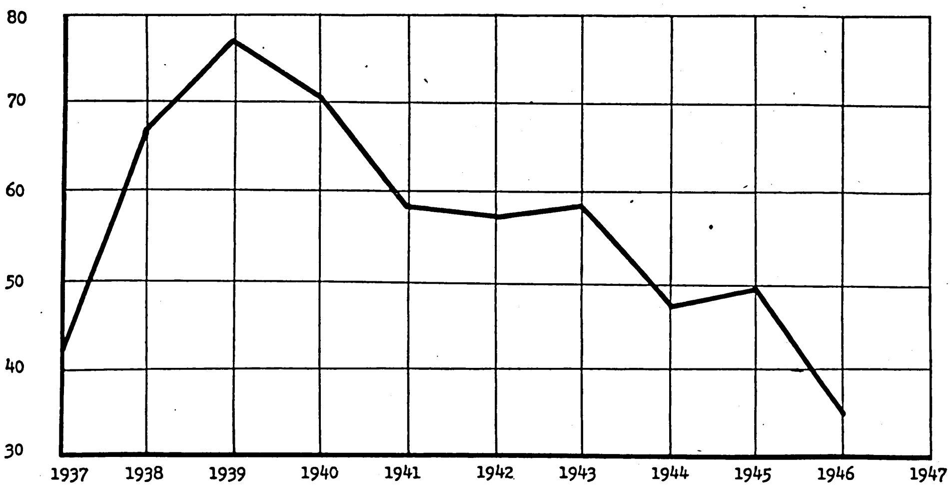


Fig. 8. Proportion of animals in the breeding herd of the Minnesota No. 1 line at Grand Rapids which did not contribute to the 1947 breeding herd.

maining females, however, contribute less than 10 per cent, two of which, 13-16 and T74R, are foundation animals.

All the animals but 5-4 appear in the pedigree of **each** animal of the 1947 herd.

The expected average distribution of genes of the more prominent boars in one year among the contributors in the following years, if chance prevails, for the remaining period of 1939 to 1947, inclusive, is summarized in table 5. Figure 7 gives additional information as to the effect of contributors on the development of the line.

III. Inter-se relationship and inbreeding expected on the basis of number of males and females used in a closed herd (assuming random matings).

In a population closed to outside breeding, about $\frac{1}{8 \times M} + \frac{1}{8 \times F}$ of the remaining heterozygosity will be lost per generation (M = number of males, and F = number of females reaching breeding age in each generation). Sows and boars are weighted according to their age, e.g., eight boar pigs, and two 2-year-old boars would amount to $8 + (2 \times 2) = 12$ males. The fraction then becomes $\frac{1}{8 \times 12} = \frac{1}{96}$.

The graph in figure 6 shows the two curves as calculated for the Minnesota No. 1 line of swine. The expected F_x tends to fall below the actual F_x. Except in 1943 they are the same, and in 1946 the actual F_x falls below the expected F_x.

The coefficients have been summarized in table 6.

In the years 1940, 1941, 1944, and 1947, the difference between the actual F_x and expected F_x exceeds twice the standard error.

Table 6. Inbreeding Coefficients

	Actual F_x	Expected F_x
1937	....	......
1938	....	......
1939	.07 ± .001	......
1940	**.14 ± .005	.10
1941	**.19 ± .005	.16
1942	.22 ± .005	.21
1943	.24 ± .005	.24
1944	**.27 ± .005	.25
1945	.29 ± .005	.28
1946	.29 ± .005	.30
1947	**.32 ± .005	.30

** Highly significant difference.

The standard error of the inbreeding coefficients was calculated by using the ordinary formula for the standard deviation of a fraction. The inbreeding coefficient, F_x, is the fraction of the heterozygotes, each pair of genes considered by itself, which are expected to have disappeared because of inbreeding. The sampling variance of the F_x calculated from the pedigrees would be $\frac{F_x(1-F_x)}{n}$ where n represents the number of independent loci. The standard error will then be $\sqrt{\frac{F_x(1-F_x)}{(N)n}}$ N will represent the number of animals in question, and this is multiplied by n, the number of independent loci or pairs of genes.

Swine have been credited 19 pairs of chromosomes, but linkage makes n larger than the number of linkage groups and smaller than the total number of genes involved.

IV. The average length of time between generations.

The length of time which elapses between one generation and the next can be determined by noting the birth date of the foundation animal and the animal at the end of an ancestral line, and calculating the number of generations which intervene.

In the breeding herd of the Minnesota No. 1 line enough sows and aged boars were kept to raise the average age of the parents to 1.56 years, instead of a minimum of 1 year.

V. The average performance by years.

The graph in figure 11 and table 7 represent a summary of the performance of the Minnesota No. 1 herd. Data through weaning are on all the pigs farrowed, and the remaining data are on test lots only.

The F_x increased from 0 in 1937 to 34 per cent in 1947. The increase was more rapid the first four years, partly because the breeding herds were smaller.

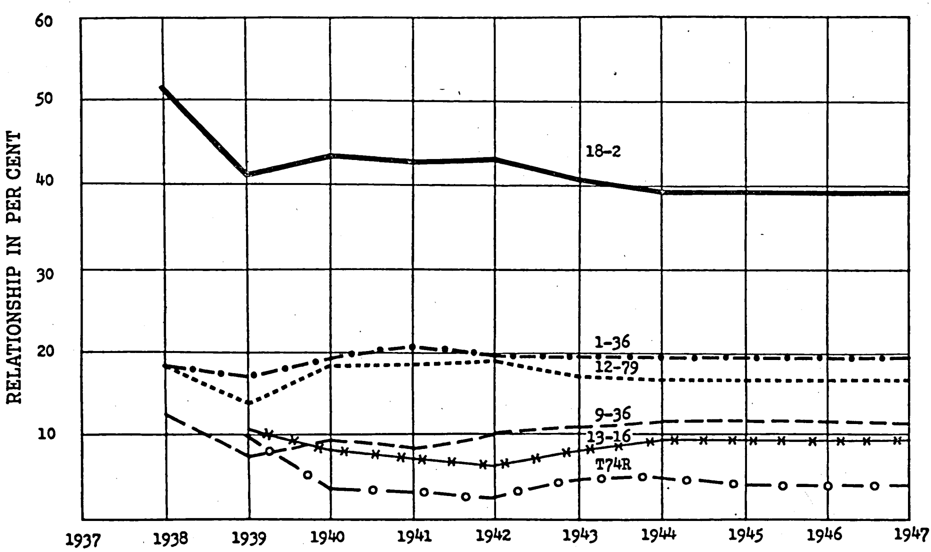


Fig. 9. Average relationship of the six foundation animals to the contributing breeding stock, by years.

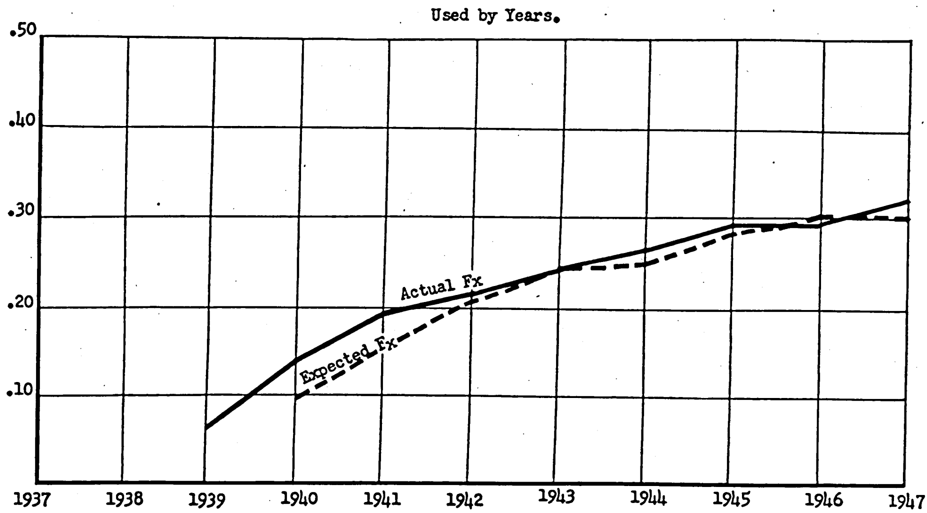


Fig. 10. Inbreeding of the breeding herd of the Minnesota No. 1 line at Grand Rapids, and the expected inbreeding on the basis of the number of males and females used, by years.

Management and feeding practices have been standardized as much as possible, but even at that, yearly environmental differences occur.

On the average, the number of pigs born alive, 154-day weights, rate of gain, and feed per 100 pounds gain tend to remain the same for the 10-year period. Number of pigs weaned tend to be somewhat lower, which can be partly explained by the losses from baby pig disease. Weaning weights have declined somewhat, but, as reported by Nordskog *(10)*, the heritability of weaning weights is low. Furthermore, the baby pig disease apparently was responsible for some of the decline in weaning weight.

DISCUSSION

Winters *(13)* points out that the animal breeder has three "tools" at his disposal: selection, inbreeding, and crossbreeding. Crossbreeding was used to form the basis of the Minnesota No. 1 line. A line developed from such a cross may be expected at the outset to be in a more highly heterozygous condition than one started from a single breed. By practicing mild inbreeding following such a cross, many new gene combinations not found in either of the foundation breeds can be produced. In an experiment of this kind certain precautions should be taken, and Winters *et al. (15)* list the following three reasons for most of the failures of inbreeding experiments:

"1. Most of the early experiments were of necessity conducted on a small scale. It does not appear that an experiment of this kind is as likely to be highly successful if conducted with small numbers.

"2. In some cases, at least, it appears that performance was not given special consideration in the selection of breeding stock. Waters and Lambert (experiment with fowl) make a special point to mention that, in the conduct of their experiment, selection was most exacting for the factors affecting performance.

"3. In most of the early experiments attempts were made to follow definite

Table 7. Performance of Minnesota No. 1 Line by Years

	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947*	1948*
F_x of litters	.00	.07	.14	.19	.22	.24	.27	.29	.29	.32	.34	.36
Ave. No. of pigs born alive	9.2	9.5	8.8	9.3	8.6	8.8	9.8	10.2	9.6	9.65	8.26	9.20
Ave. No. of pigs weaned	8.0	7.7	7.1	7.0	6.8	7.1	7.0	7.0	6.6	6.8	3.97	6.80
Weaning weight	44	34	30	29	35	33	30	31	31	25	26.44	27.52
154 day weight	191†	178†	181†	195†	184†	194†	166	174	186	184	170	157
Rate of gain	1.53	1.51	1.57	1.67	1.50	1.64	1.36	1.46	1.58	1.55	1.43	1.31
Feed‡ per 100 lbs. of gain	308	358	315	302	307	306	313	308	311	308	284	294

* Data from years 1947 and 1948 were not available at the time the calculations were made for other tables and graphs.
† Corrected from 180 day weights.
‡ On pasture which varied from year to year. 1938 was very dry hence practically no pasture.

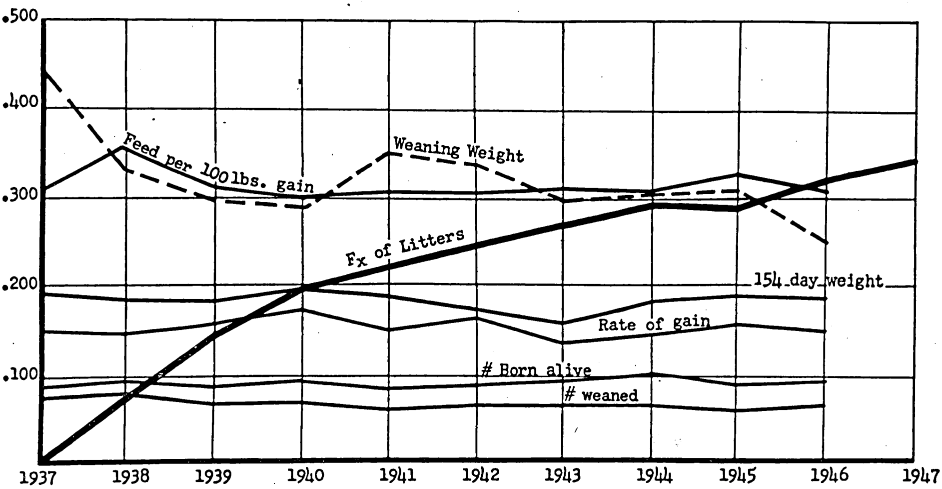


Fig. 11. Inbreeding of the litters and performance of the herd of the Minnesota No. 1 line at Grand Rapids, by years.

experimental patterns, such as continuous full-sib matings or half-sib matings. A fixed pattern of procedure restricts the use of superior animals to an extent that will conform with this pattern. It appears that when superior breeding animals are uncovered they should be used to a maximum."

It is also essential that the best foundation stock obtainable should be used. This stock should be as genetically diverse as possible and yet possess the desirable characteristics. Each strain should have a maximum of desirable characters which are to be combined in a single strain which, in this case, were the length of body, plumpness of ham, and prolificacy of the Landrace, and the color, prolificacy, and milking ability of the Tamworth.

Breeding stock was selected on the basis of: (1) fertility, (2) survival, (3) rate of gain, (4) economy of gain, (5) quality of the finished carcass and type.

I. Effect of selection

Average breeding procedures for the years 1937 to 1947, inclusive, (unless otherwise specified) are as follows:

Of the four classes of gilts (tested), sows, boar pigs (tested), and aged boars which were available for breeding purposes, 36.5 per cent of the gilts (tested), 33.9 per cent of the sows, 8.4 per cent of the boar pigs (tested), and 36.4 per cent of the aged boars were selected (table 3).

Of the total number of sows and gilts and the total number of males (boar pigs, barrows, and aged boars) available for breeding purposes, 35.7 and 7.7 per cent, respectively, were selected into the breeding herd.

A total of 141 gilt and 38 boar pigs, excluding foundation animals, contributed in 1938-1947, inclusive.

Litters—A total of 387 litters were farrowed, and 57.4 per cent were tested.

Two thousand, six hundred and sixteen animals were weaned, and 1,653 or 63.2 per cent were tested. This includes the year 1946.

On the basis of animals weaned, 13.7 per cent were selected for breeding stock and 6.8 per cent contributed. On the basis of animals tested, 18.5 per cent were selected for breeding and 10.9 per cent contributed.

In order to be able to put greater emphasis on selection for fertility, more litters were farrowed from 1939 on than could be tested. Animals were selected first of all on the basis of litter size. This is reflected in the fact that a higher percentage of animals than percentage of litters was tested. The test litters were larger. Thus 46.8 per cent of the animals were eliminated in the first culling. The breeding stock selected from the animals tested was 21.7 per cent. Almost four-fifths were eliminated in the second culling, mostly on feed lot performance—e.g., economy of feed utilization and rate of gain—and some on type. Of the animals tested only 10.9 per cent contributed. In this third culling the breeding stock which did not perform was eliminated. It took as long as five years in the case of two animals (table 1) before their offspring finally dropped from the herd. Offspring of seven animals remained four years, but most of them were eliminated by the end of two years.

There was a tendency, on the average, to select a similar percentage of the available gilts and sows for the breeding herd (36.5 and 33.9 per cent, respectively). This also held true for the aged boars (36.4 per cent). However, only 8.4 per cent of the available boar pigs were selected into the breeding herd. This low figure is due to the fact that fewer boar pigs were required, for on the average the sexes are about equal. There is thus more opportunity to practice selection for boar pigs than gilts.

The percentage of boar pigs which contributed was larger than that of the gilts. This is mainly because of the smaller number of boar pigs as compared to gilts.

Starting in 1946 the number of boars used was expanded. In 1946, 13 boars were used and in 1947, 10. Before this, from three to seven boars were used. Increasing the number of boars tends to retard inbreeding.

II. Gene distribution and important contributors

From 1944 on, the distribution of the genes of the foundation stock has been constant. It will remain so from now on, because all of the animals in the 1947 breeding herd have all the six contributing foundation animals appearing in their pedigree and each animal in the herd carries, on the average, the genes of the foundation animal in the same ratio.

The present day herd carries, on the average if chance prevails, 39.0 per cent of the genes of the Landrace boar 18-2 and 9.0 per cent of the genes of the Landrace female 13-16, or a total of 48 per cent Landrace genes and 52 per cent Tamworth genes.

Table 8. Proportion of Genes Which the Most Important Ancestors Contributed Relative to Their Base or Ancestral Year, and Average Relationship of Animals in the 1947 Herd to These Ancestors.

Individual	Per cent contribution	Base year	Average relationship
Boars			
18-2	39.0	1937	.47
A631X	29.6	1944	.77
966	24.9	1941	.63
179 (figure 12)	24.2	1939	.67
B717	21.8	1945	.90
681	19.7	1942	.65
607 (figure 13)	17.8	1940	.59
213	16.3	1939	.45
124	15.7	1939	.43
1-3	15.4	1938	.47
6-2	13.8	1938	.42
6-3	12.5	1938	.38
7-00	12.5	1944	.76
A289	12.0	1943	.65
Gilts			
813	23.4	1944	.73
803	17.2	1942	.63
727	17.0	1941	.56
158	16.7	1939	.46
330	14.9	1940	.49
501	13.7	1940	.45
A533	11.8	1942	.64
161	11.7	1939	.32
683	10.3	1943	.59
76	9.6	1939	.26
2-51	9.5	1943	.64
A645	9.3	1943	.66

Three animals, 18-2, 12-79, and 1-36, represent about three-fourths (74.5 per cent) of the heredity of the 1947 herd.

Some animals had a greater effect on the development of the breed than others. Table 8 represents the proportion of the genes which the most important ancestors contributed relative to their base year or ancestral year, and the average relationship of the animals in the 1947 herd to these ancestors.

The most important boar contributor in any one year is A631X, and he carries the highest relationship of any of the 1944 animals to the 1947 herd.

All pedigrees will show boar 18-2 as the foundation boar, and the relationship and per cent distribution has been

Table 9. Animals in B717 and B938 Pedigrees, "Per Cent Blood," and Relationship of Each Animal to B717 and B938.

B717	Per cent Blood	Relationship
FOUNDATION ANIMALS		
12-79	.19	.19
9-36	.05	.15
18-2 (b)	.43	.46
1-36	.20	.23
13-16	.06	.12
T74R	.06	.06
1938		
1-2	.03	.34
1-3 (a) (b)	.28	.44
1-5	.06	.35
5-6	.09	.35
6-2 (a) (b)	.16	.42
6-3 (a) (b)	.03	.37
6-7	.19	.43
1939		
179 (a) (b)	.13	.64
158 (a)	.06	.44
124 (a) (b)	.06	.41
213 (a) (b)	.06	.45
161 (a)	.13	.33
76 (a)	.13	.28
1940		
179 (a) (b)	.25	.64
607 (a) (b)	.25	.60
157	.13	.47
330 (a)	.06	.45
335	.06	.48
501 (a)	.25	.48
1941		
966 (a) (b)	.13	.60
727 (a)	.13	.60
1942		
681 (a) (b)	.5	.77
920		.70
803 (a)	.25	.66
A533 (a)	.25	.70
1943		
....	....	....
....	....	....
....	....	....
....	....	....
1944		
A631X (a) (b)	.5	.92
A813 (a)	.5	.92

B938	Per cent Blood	Relationship
FOUNDATION ANIMALS		
12-79	.20	.22
9-36	.05	.16
18-2 (b)	.45	.49
1-36	.20	.22
13-16	.05	.09
T74R	.05	.03
1938		
1-2	.05	.38
1-3 (a) (b)	.32	.52
1-5	.05	.37
5-6	.11	.38
6-2 (a) (b)	.14	.42
6-3 (a) (b)	.05	.37
6-7	.20	.46
1939		
179 (a) (b)	.09	.71
158 (a)	.09	.52
124 (a) (b)	.09	.46
213 (a) (b)	.09	.42
161 (a)	.09	.28
76 (a)	.09	.23
1940		
179 (a) (b)	.31	.71
607 (a) (b)	.13	.55
157	.13	.52
330 (a)	.13	.60
336	.06	.60
501 (a)	.13	.39
1941		
179 (a) (b)	.06	.71
333	.06	.50
1942		
681 (a) (b)	.25	.58
A138	.13	.61
803 (a)	.13	.67
920	.13	.65
805	.13	.67
1943		
966 (a) (b)	.25	.72
A780 (b)	.25	.72
A633	.25	.73
2-51 (a)	.25	.74
1944		
....	....	....
....	....	....
1945		
7-00 (a) (b)	.50	.92
B-72	.50	.72

(a) Animals in the group which had the greatest effect on the development of the breed. (b) Boars.

the same since 1944 and will remain so. (This is the same for all foundation animals.)

Table 9 shows the animals which appear in the pedigrees of B717 and B938 (by years), the "per cent blood", and relationship of each animal to B717 and B938. B717 has had a great effect on the development of the breed, and B938 has had only a small effect, contributing 4.1 per cent of the genes in 1946, as compared with 21.8 per cent for B717 in 1945. The six original animals appear in the pedigrees of both B717 and B938.

The per cent of blood gives a relative idea of how often an individual appears in the pedigree when compared with the parent-offspring relationship of .50 (assuming random matings). In other words, if an individual four generations back shows a percentage of blood of 50 to the offspring, then that individual must appear $50 \div 6.25 = 8$ times in the pedigree, as the percentage of blood under random mating between that individual and the offspring will be only $\frac{1}{2}^4 = .0625$, or 6.25 per cent. A percentage of 50 indicates the matings to be the equivalent of a parent-offspring relationship.

The Minnesota No. 1 swine are an inbred and highly related line of hogs. As the inbreeding increases each year, the differences between relationship and per cent blood increase and the number of genes which the offspring will have in common with its parent or ancestor will be greater than the per cent blood will indicate. However, the per cent blood will always be lower than the collateral relationship between two animals in a highly related and inbred population, because the latter is corrected for inbreeding of the animals in question. If the animals are not inbred or related, the per cent blood will be equal to the relationship figure.

The average distribution of the genes based on relationship and on per cent blood of the 1944 ancestors into the 1947 breeding herd is summarized in table 10. The per cent blood and relationship fol-

Table 10. Average Distribution of the Genes Based on Relationship and Per Cent Blood of the 1944 Ancestors in the 1947 Breeding Herd.

Animals	Per cent Blood	Relationship
A631X	28.8	29.6
A849	16.1	13.8
B204	6.2	5.0
A920	4.7	4.0
A813	17.9	23.4
B100	2.1	1.5
A903	2.1	2.0
B171	7.3	6.5
A564	4.7	4.3
A821	1.0	1.7
A643	1.0	1.4
A710	1.0	5.2
A633	6.2	0.9
B158	1.0	0.7

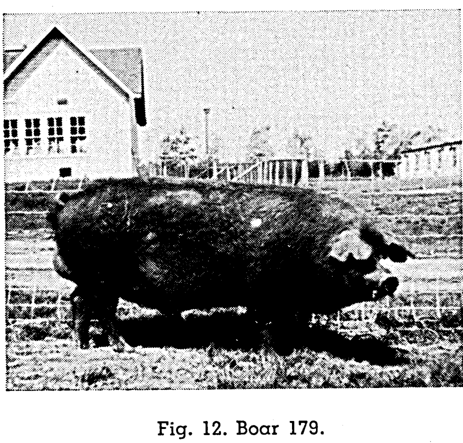


Fig. 12. Boar 179.

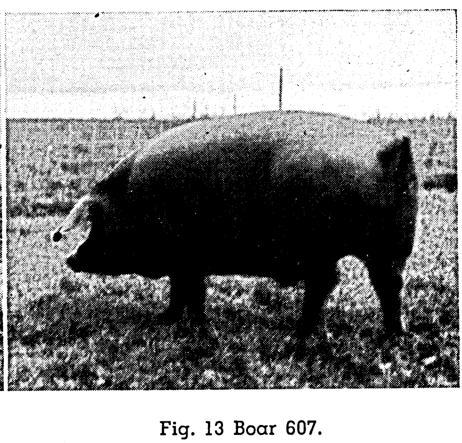


Fig. 13 Boar 607.

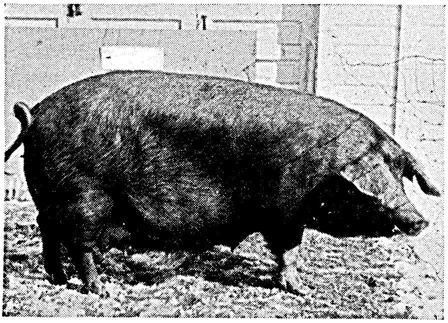


Fig. 14. Sow 601.

low the same trend in actual values as well as in distribution. In other words, when per cent blood is high, relationship will be high, although sometimes one and sometimes the other might be higher. This is mainly because the animals vary somewhat in inbreeding—not a great deal, but enough to cause this difference to be noticeable. Relationship can be shown to exist between the breed and an animal which did not appear in the pedigree, but the relationship exists because a relative of the animal in question occurs in the pedigree and therefore it has no genetic effect on the breed. If a percentage of blood can be shown, the animal is a direct contributor. Thus the genetic relationship of an animal to the breed can be more precisely expressed in terms of relationship than in terms of per cent blood.

III. Actual and expected F_X

The percentage of genes which an animal in any one year contributes to a herd in some future year will depend on the number of males and females present in that year's herd. If there are a large number of males and females used, this might reduce the effect of any one individual which in turn is affected by whatever effect the balance of the individuals exerted.

The collateral relationship is affected by the number of generations intervening between the two animals and the amount of inbreeding of each animal. The fewer generations intervening and the higher the inbreeding, the higher the collateral relationship will be.

The actual amount of inbreeding increases more rapidly in the first few years, then levels off to a more slowly but steadily increasing rate. The system of breeding has been such that about 32 per cent of the heterozygosity which was in the foundation animals had been lost by 1947. This is about equal to three generations of half brother and sister mating.

The number of males and females (M and F) as used in the formula are the numbers which are expected to have offspring. This is not always the case, however, and the formula tends to underestimate the amount of F_x in a closed population. In 1946, 13 boars were used, but only 10 contributed. In 1947 the difference between the actual inbreeding and the expected is 4 times the standard error or a highly significant difference, which can be attributed partly to the fact that almost one-fourth of the boars did not contribute. The difference also exceeded twice the standard error in 1940, 1941, and 1944.

The actual and expected inbreeding coefficients tend to follow the same general direction.

IV. Generation interval

The length of time between generations was found to be 1.56 years. Sows and boars usually produce their first litters when they are about one year old, but some breeding stock is kept longer than this. If only gilts and boar pigs were used, inbreeding would go up much faster, but at the same time this would sacrifice some of the opportunity to practice selection. Desirable breeding stock would not have a chance to produce additional progeny. The generation interval can be as short as one year, and if a breeder wishes to increase the inbreeding as fast as possible, he could breed from gilts and boar pigs only, and thus accomplish five years of inbreeding in five years. But under the system of breeding followed in the development of the Minnesota No. 1, it would take 7.8 years to obtain the same amount of inbreeding.

Lush *et al. (5)* found that the generation interval of the Poland China breed is 2.5 years, considerably longer than that of the Minnesota No. 1

V. Performance

The greater the heritability of a factor the more effective selection for that factor will be. Rigorous selection and an increase of the inbreeding at the same time appears to be a desirable method for producing good performing inbred lines. The estimate of heritability for daily gains was found by Nordskog *(9)* to be .21 and .40, from birth and weaning, respectively, to 200 pounds weight. Selection for this trait should have some effect.

Cummings *et al. (3)* report the heritablity of size of litter at weaning to be 32 per cent.

Winters *et al. (16)* report that selection has been effective in holding survival at a relatively high level in the Minnesota No. 1 line of swine. This has been the case with all other traits, except probably weaning weight. Although this recovered somewhat in 1941, the tendency has been in a downward direction. The heritability of this trait is rather low.

Comstock *et al. (1)* state that the selection differentials can be increased by putting less emphasis on other less important characters. Craft *(2)* reports that in general, as inbreeding is advanced, a slight decrease in fertility, vitality, and rate of growth is encountered. However, it usually is not serious in the better lines. In stock which is genetically superior, the rate of inbreeding can be increased probably five to 10 times as fast as that being practiced by the breeders of the pure breeds, without any serious decline of the factors mentioned above.

Stewart *(12)* found that the heritability of pigs born alive is approximately 17 per cent on the basis of an outbred population. Cummings *et al. (3)* found 22 per cent. Selection for fertility in an outbred population low in fertility is certain to be slow, and it appears that best results would be obtained by developing fertile inbred lines and by outcrossing these throughout the breed.

The heritability of post-weaning weight, as reported by Nordskog *(10)*, is approximately 45 per cent for 112 days post-weaning, and an average heritability from birth to 200 pounds of 21 per cent. Selection for this trait can be effective.

Attention to unimportant characteristics was cut to a minimum in the development of the Minnesota No. 1 line of swine. Selection has been rigorous enough to offset the undesirable effects usually encountered in an inbreeding experiment.

VI. Appearance or type of the animals

The color of the Landrace breed is white, which is dominant over the red color of the Tamworth breed. Therefore, all F_1 pigs and some F_2 and F_3 were white (figure 15, Sow 335). In 1938 about three-fourths of the pigs were white. Since a colored pig was desired, selection was made in that direction, and all pigs are now red (figure 17). Spasmodically some animals may show some black patches or spots, but this now occurs only rarely.

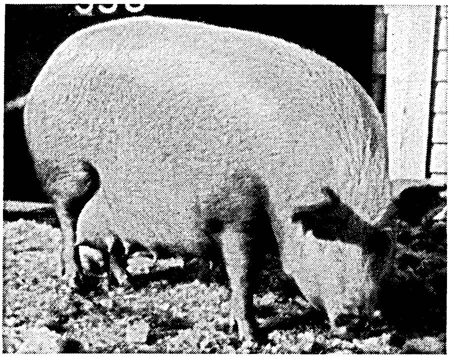


Fig. 15. Sow 335.

The bone structure of the Minnesota No. 1 is finer than that of the Landrace; it is probably more like the Tamworth.

In the early segregating generations, a great deal of variation in body length and length of legs was encountered. Extreme types were culled, but the culls always brought normal market price.

The Minnesota No. 1 hog yields a longer carcass, a lean bacon and ham, and has an excellent flavor, if it is provided an adequate ration.

The line performs extremely well in crosses with other breeds, as pointed out in the 11th Annual Report of the Regional Swine Breeding Laboratory *(11)*.

SUMMARY

Analysis was made of the breeding stock of the University of Minnesota

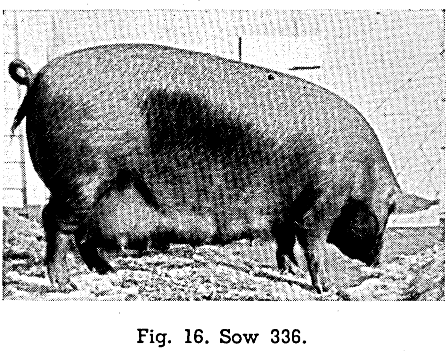


Fig. 16. Sow 336.

No 1 line of swine at Grand Rapids, Minnesota, for the years 1937 to 1947 inclusive.

I. The Minnesota No. 1 line of swine has been developed from a cross of Landrace and Tamworth breeds of swine, and has been further developed by rigorous selection and inbreeding. Fourteen animals entered into the foundation stock, but only one Landrace boar, one Landrace female, and four Tamworth females contribute to the present herd. On the average, for the 10 years, about 36.5 per cent of the gilts, 33.9 per cent of the sows, 8.4 per cent of the boar pigs, and 36.4 per cent of the aged boars which were available for breeding purposes were selected into the breeding herds.

Of the litters farrowed, 57.4 per cent were tested; of the 2,616 animals weaned, 1,653, or 63.2 per cent, were tested. Of the animals weaned, 13.7 per cent were selected for breeding stock, and 6.8 per cent contributed to the herd. A total of 141 gilts and 38 boar pigs have contributed to the herd from 1937 to 1947 inclusive (excluding foundation animals). Rigorous selection for performance has been practiced throughout the development of the line.

II. (a) Noncontributors or their offspring remained in the herd not longer than five years, and most of them were eliminated at the end of two years.

The 1947 breeding herd should carry, on the average according to chance, 48 per cent Landrace genes and 52 per cent Tamworth genes. From 1944 on, the gene distribution of the foundation animals has become fixed and will remain as such. Three animals, 18-2, 12-79, and 1-36, represent about three-fourths (74.5 per cent) of the heredity of the 1947 herd.

II. (b) The six contributing foundation animals appear in the pedigree of every animal since 1944. The six boars and six gilts which had the most important effect on the development of

the breed are in order of their importance:

	Per cent Contribution	Base year	Average Relationship to 1947 herd
Boars			
18-2	39.0	1937	.47
A631X	29.6	1944	.77
966	24.9	1941	.63
179 (figure 12)	24.2	1939	.67
B717	21.8	1945	.90
681	19.7	1942	.65
Females			
813	23.4	1944	.73
803	17.2	1942	.63
727	17.0	1941	.56
158	16.7	1939	.46
330	14.9	1940	.49
501	13.7	1940	.45

III. Inbreeding of the breeding stock increased from 0 in 1937 to .32 in 1947. The expected F_x tends to be lower than the actual except in 1946, when it is higher, and in 1943, when it is the same. The difference between the actual and expected F_x is significant in 1940, 1941, 1944, and 1947. Part of the difference is because not all animals (especially males) contribute, and in that case the expected F_x tends to underestimate the actual F_x.

IV. The interval between generations was found to be 1.56 years.

V. Performance by years has been maintained in spite of the increase of the inbreeding coefficient of the litters from 0 to .34. This has been accomplished by putting more emphasis on selection for performance and very little on less important factors.

The advance in inbreeding has been more rapid and the breed has been developed in a much shorter time than any other breed known to date.

All F_1 pigs were white, but the present day animal is red.

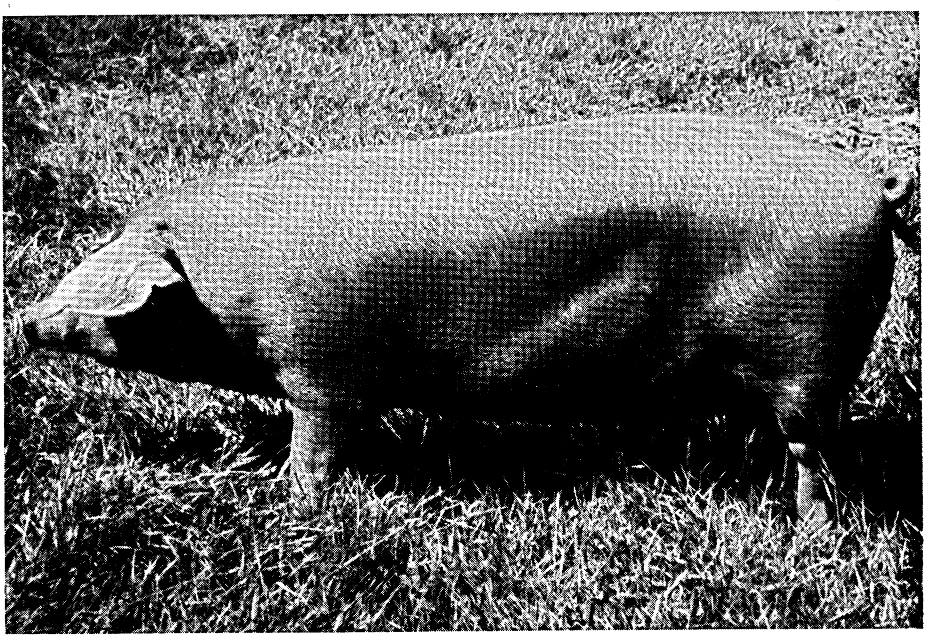


Fig. 17. Minnesota No. 1 Hog (1946)

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