Preliminary Studies on Reciprocal Recurrent Selection in Sugar Beets¹

LEROY POWERS, R. E. FINKNER, C. W. DOXTATOR, and J. F. SWINK²

Comstock, Robinson, and Harvey (1) a proposed reciprocal recurrent selection as a breeding procedure designed to make maximum use of both specific and general combining ability. Preliminary studies on reciprocal recurrent selections with sugar beets provide information pertaining to the solution of problems arising from the application of this method of breeding.

Some of these problems are as follows: 1. determining the proportion of progeny resulting from fertilization by the opposite source; 2. designing planting arrangements that give the desired amount of fertilization between plants of different sources and between plants within a given source; 3. obtaining precision in selection; 4. obtaining sufficient amounts of seed from each mother beet to provide adequate yield tests of the respective progeny; and 5. perpetuation of the genotypic complex of the mother beet whose progeny are being tested.

Certain formulas and procedures not previously available aid in the solution of these problems. The purpose of this article is to present such formulas and procedures together with other information pertaining to their solution.

Materials and Methods

The plant material consisted of 600 roots selected from the variety American Crystal 3S. Those beets having green hypocotyls were designated as source A and those having red hypocotyls as source B. These 600 roots were quartered to provide for planting three different isolation plots.

Two isolation plots, one of the A source and one of the B source, were planted near Salida, Colorado, two quarters from each beet of the respective source being planted in each isolation plot. The purpose of these plots was to obtain seed resulting from self fertilization. As many of the flowering branches as time and facilities would permit were bagged to control pollination.

²Geneticist, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Manager Research Station, Plant Breeder, and Station Superintendent, American Crystal Sugar Company, Rocky Ford, Colorado, respectively.

³ Numbers in parentheses refer to literature cited.

¹ Cooperative investigations of the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, the Colorado Agricultural Experiment Station, the Beet Sugar Development Foundation, and the American Crystal Sugar Company. Approved by the Colorado Agricultural Experiment Station for publication as Scientific Series Article No. 523.

Diagram 1.—Sectional Portion of the Planting Arrangement for Sources A and B Showing the Position in the Isolation Plot of the Two Quarters of Each Beet, Grown in 1955 at Fort Collins, Colorado.

Al	B2	A3	134	A5	*			B30
A1	B2	A3	B4	A5			•	B30
B60	A59	B58	A57	B56		9		A31
B60	A59	B58	A57	B56			(20)	A31
A61	B62	A63	B64	A65	8			B90
A61	B62	A63	B64	A65				B90
B120	A119	B118	A117	B116	*		300	A91
B120	A119	B118	A117	B116	50		120	A91
A121	B122	A123	B124	A125	2)	:	140	B150
A121	B122	A123	B124	A125	200			B150
*							V*/:	
			•				240	
		5.0				×		
B600	A599	B598	A597	B596			0,50	A571

The two remaining quarters of each beet were planted on the Agronomy Farm of Colorado State University at Fort Collins, Colorado. The planting arrangement of the two sources are shown in Diagram 1. Actually only 170 of the 600 selected beets had green hypocotyls. In planting, the two quarters of each of these 170 beets were alternated with two quarters from source B as shown in Diagram 1. They were planted in the middle of the isolation plot. The spacing was 3 feet between rows and 3 feet between beets within a row.

Of the 170 mother beet selections having green hypocotyls 166 produced sufficient seed to warrant their being included in the study. Only 136 of the green hypocotyl selections were surrounded by source B and other source A plants as indicated by the solid line in Diagram 1. Only the progeny of these 136 mother beets were employed in calculating the proportion of the offspring resulting from fertilization by source B gametes. However, the entire 166 selections of source A and 170 selections of source B should be (according to Diagram 1) and were used in the calculation of the relative proportions of the two-genotypic gametes fertilizing the ovules of the source A plants.

Of the 600 plants in the isolation plot at Fort Collins, 490 produced sufficient open-pollinated seed and seed from self pollination to warrant including open-pollinated seed in progeny yield of roots and percentage sucrose tests. The design of the experiment was a modified randomized complete block with five blocks (replications). The 490 progenies were divided into

49 groups of 10 progenies each. The groups for each of the five replications were determined at random. That is, the 490 progenies were randomized within replications and then the two checks were randomized within each of the 49 groups of 10 progenies. This procedure was followed for each of the five replications. The checks were American Crystal 3S and US 401. Hence, there were 49 cultures of American Crystal 3S and 49 cultures of US 401 per replication. In this study the 49 groups within each replication composed of 12 populations each are designated as series. The plot consisted of one row 20 feet long and the beets within the row were thinned to a 10-inch spacing. Four replications were grown at Mason City, Iowa, and one was grown at Waseca, Minnesota. Excellent stands were obtained in all five replications.

The checks were used to estimate the environmental variance. The F value of an analysis of variance of the two checks for all replications revealed that the probability of the variance of the first order interaction of populations X series being significantly different from the variance of populations X replications X series was exceedingly small for both weight of roots per plot and percentage sucrose. Hence, the variance of populations X replications X series was used as an estimate of the environmental variance and applied as described below to detect superior performing progenies.

Fisher's (2) Table 1 was used to obtain the value of P. The value of x (see Fisher, 2, Table 1) is $(X-\overline{C}) \div [Vprs + (Vprs/2)]$. The symbol designations are as follows:

X = the value for any given progeny within a series

 \overline{C} = the average of the two checks in the same series as the

progeny being evaluated

Vprs = the variance of populations X replications X series In selection experiments based on progeny performance, as are these, the P values for only the most promising progenies need be calculated. The final selection is based on the performance of such progenies in all five replications.

Results

Formula for and Determination of Percentage of Fertilization of Source A Female Gametes (rr) by Source B Male Gametes (RR and Rr)

In determining the percentage of fertilization of source A female gametes by source B male gametes the formulas for predicting gene frequency as given by Li (5) are employed. These formulas are based on those used by Hardy and Weinberg in

developing the Hardy-Weinberg law (see Hardy, 4 and Weinberg,

8). They are:
$$p=\frac{D+\frac{1}{2}H}{N}$$
 and $q=\frac{\frac{1}{2}H+R}{N}.$

The letter designations have the following connotations in this article:

p = the proportion of male gametes carrying R genes

q = the proportion of male gametes carrying r genes

D = the number of plants of the RR genotype in the mother beet population

H = the number of plants of the Rr genotype in the mother beet population

R = the number of plants of the rr genotype in the mother beet population

N = the total number of individuals in the mother beet population

The values for these designations are:

$$D = 73$$
 $H = 97$ $R = 166$ $N = 336$

Substituting these values in the formula we have

$$p = \frac{73 + 48.5}{336} = 0.3616$$
, and $q = \frac{48.5 + 166}{336} = 0.6384$.

The progeny of 136 of the rr mother beets were classified for hypocotyl color. There were 24,121 plants in these 136 progenies, 11,796 of which had red hypocotyl color and 12,325 of which had green hypocotyls. The proportions are red hypocotyl color 0.4890 and green 0.5110. The theoretical expected on the basis that the population is panmictic and that there is random union of gametes is 0.3616 red hypocotyl plants and 0.6384 green hypocotyl plants. Since these progenies are from the rr plants, the male gametic output as regards the genes conditioning hypocotyl color is measured directly. Hence, of the 24,121 plants of these 136 progenies from rr plants, 8,722 would be expected to have red hypocotyls and 15,399 would be expected to have green hypocotyls. Comparing these with the obtained given above, without further statistical analysis, it is apparent that there is a greater proportion of the A source plants being fertilized by R gametes which come only from the B source than expected on the basis of panmixia and random union of gametes. The percentage of the progeny resulting from fertilization by the B source is important, because the percentage of fertilization of source A ovules with the gametes from source B provides a measure for determining the extent to which tests conducted with resulting progeny measure the combining ability of source A fertilized by source B.

The estimation of the percentage of the progeny resulting from ovules of source A fertilized with gametes from source B requires formulas which are readily developed from those given by Li (5). Let p' equal the proportion of the source A ovules (rr plants) fertilized by male gametes carrying the R gene. Then p' equals $\frac{D' + H'}{N'}$ in which D' + H' is the number of plants among the progeny of source A plants having red hypocotyls and N' is the total number of plants in this progeny. Let x equal the proportion of the progeny of A source plants resulting from fertilization by B source. Then the formula for determining the proportion of the progeny of source A resulting from fertilization by source B gametes is $x = \frac{(D+H)p'}{D+1/2H}$. One of the functions of this formula is to take into consideration r gametes from source B plants.

By substituting in the formula, $x = \frac{(73 + 97) \cdot 0.4890}{73 + 48.5} = 0.6842$. Hence the percent of the progeny of source A resulting from fertilization by source B gametes is 68.42. Hence 68.42 percent of the progeny of source A plants had source B as the male parent and 31.58 percent (100.00 - 68.42) resulted from fertilization between plants within the A source. This 31.58 percent of the progeny includes those resulting from self fertilization.

Since 68.42 percent of the progeny had source B as the pollen parent, it seems that probably there was comparatively little self fertilization of plants within the A strain and hence most of the 31.58 percent of the progeny resulting from fertilization within the A strain would be expected to have resulted from fertilization between plants within the source.

Formulas for Determining the Percentage of Fertilization by Source A Male Gametes of Source B Female Gametes Produced by Rr Mother Beets

Since, in this study, the only difference between sources A and B was hypocotyl color the findings for source A as to the percentage of the progeny having source B plants as the male parent should apply equally well to the percentage of the progeny of source B plants having source A plants as the male parent. It does not seem appropriate to pursue the inquiry as to the actual amount of cross fertilization between plants of different sources further because the material under study is of extremely limited interest. However, the formulas for determining the percentage of fertilization by source A male gametes of those source B female gametes produced by Rr mother beets

have wide application in breeding sugar beets and other crops. Hence, the formulas are given and their applications are illustrated.

As before, gene frequencies for the male plants are calculated from the formulas given by Li (5). Again D = 73, H = 97, and R = 166. Only the progeny of the source B plants having the genotype Rr will be considered because all the progeny of the RR genotypic plants would have red hypocotyls. Let D' equal the proportion of the progeny of Rr plants having the genotype RR, H' equal the proportion of the progeny of Rr plants having the genotype Rr, and R' equal the proportion of the progeny of Rr plants having the rr genotype. It follows from Li's (5) formula that $D' = \frac{1}{2}p$, $H' = \frac{1}{2}(p+q)$ and $R' = \frac{1}{2}q$. Hence the theoretical proportion of the progeny of Rr plants having red hypocotyls is p + 1/9 and the theoretical proportion having green hypocotyls is 1/9q.

With the above formulas in mind formulas are readily developed for determining the proportion of progeny of Rr source B plants resulting from fertilization of source A gametes. Let 1/2q' be the proportion of green hypocotyl plants among the progeny of Rr source B plants. Then using the same symbol designations as before p' = 1 - q', and the formula for determining the proportion of the progeny of source B (Rr plants) that result from fertilization by source A gametes is $x = 1 - \frac{(D + H) p'}{D + \frac{1}{2}H}$

$$x = 1 - \frac{(D + H) p'}{D + \frac{1}{2}H}$$

Accepting the results based on the studies with the A source plants (rr genotype) 1/2q' = 0.387150. By substituting the values in the formula, p' = 1 - 2(0.387150) = 0.2257 and x = 1 - $(73 + 97) \cdot 0.2257 = 1 - 0.3158 = 0.6842$. It must be kept in 73 + 48.5mind that the value of 0.6842 is obtained by accepting the results of the study of the progeny of source A plants and the value of 0.387150 based on 0.6842 is used solely to illustrate the application of the formula for determining the proportion of the progeny of source B plants resulting from fertilization by source A gametes.

> Proposed Planting Arrangement Designed to Result in a Higher Proportion of the Progeny Having Been Fertilized by Male Gametes from the Opposite Source

In some breeding programs it may be desirable to have a higher proportion of the progeny result from fertilization by

Diagram 2.—Sectional Portion of a Planting Arrangement Providing that a Higher Proportion of the Progeny from Source B Result from Fertilization by Gametes from Source A.

AI	A3	B2	A5	A7	B4	
В8	.A15	A13	В6	A11	A9	
A17	A19	B10	A29	A23	B12	
B16	Al	A3	B14	A5	A7	
A15	A13	B18	A11	A9	B20	
B24	A17	A19	B22	A21	· A23	
					A THURS	EUE

male gametes of the opposite source. Diagram 2 presents a sectional portion of a planting arrangement providing that a higher proportion of the progeny from source B results from fertilization by gametes from source A. In this planting arrangement there are two source A plants to one source B plant. In the planting arrangement depicted in Diagram 1 the ratio is one source A plant to one source B plant. This latter planting arrangement resulted in 68.42 percent of the progeny having arisen from fertilization by the opposite source.

In the planting arrangement shown in Diagram 2 two quarters of A are used to one quarter of B. Thus, considerably more than 68.42 percent of the progeny grown from noncontrolled-pollinated seed of source B plants would be expected to have source A plants as the male parent. That such is probable can be seen by examining the areas in Diagram 2 blocked out by the solid line. Conversely, the noncontrolled-pollinated seed from source A plants would be expected to have a higher proportion of the progeny resulting from fertilization between plants within source A. To complete the plantings for the reciprocal recurrent selection method another isolation plot is required in which two quarters of A are planted and one quarter of B for each mother beet. Thus three of the four quarters of each beet would be used in the two seed plots to obtain cross-fertilized seed for progeny tests. The mother beet genotypes would be maintained by planting the fourth quarter under controlled temperature and light in an endeavor to cause reversion to the vegetative condition, or in the event the physiological conditions necessary to seed production had not been induced, to maintain it in the vegetative condition.

Preserving the Genotypic Complex of the Mother Beets Whose Progeny Are Being Tested

In a planting arrangement such as shown in Diagram 2 self-pollinated seed of the A source is obtained and in the second isolation plot in which source B plants predominate self-pollinated seed is obtained from source B plants. Bagging is employed to obtain this self-pollinated seed. If sufficient self-pollinated seed were obtained, this would be an effective means of preserving the genotype of the mother beets. However, such is not always the case, and therefore another method of preserving the genotype of the mother beets is needed.

Owen and others (6) tested vernalization techniques with sugar beet seed and found it a practical measure for hastening reproduction under greenhouse conditions. Gaskill (3) demonstrated that a combination of continuous light and low temperature exposure to seedlings can be used to bring about two gen-

erations a year of biennial sugar beets.

Hence, these experiments on inducing reproduction indicate that it might be possible to preserve the genotype of each mother beet by causing reversion of one or more quarters to the vegetative condition or by maintaining them in the vegetative condition.

Figure 1 illustrates the results from studies to asexually preserve the genotype of 32 mother beets selected from approximately 10,000 plants of G. W. 359-52R. Figure 1A shows the seed stocks grown from ½ of each beet. These plants were kept under continuous light until the flower buds were well established and the night temperatures ranged from 45 to 55 degrees F., the day temperatures from 65 to 75 degrees F. Figure 1B shows two quarters of each mother beet under a light period occurring during the day and under temperatures ranging from 60 to 65 degrees F. during the night, and ranging from 75 to 85 degrees F. during the day. These beets had been placed in the root cellar on October 5 and transplanted into the greenhouse on November 27, 1956.

As Figure 1A shows, the plants under continuous light and comparatively low temperatures produced seed, whereas those under the short light period and comparatively higher temperatures remained vegetative or reverted, whichever the case may be. Figure 1B shows that the plants given a period of light normal during the days from November 27 remained in the vegetative condition. These together with the self-pollinated seed should be sufficient to preserve the genotype of those mother beets whose progeny may prove to be superior, and hence desired for further genetic and breeding studies.



Figure 1.—(A) Seed and seed stocks produced on plants grown from one-half of each mother beet. (B) Plants in the vegetative condition grown from two quarters of each mother beet.

Probabilities of Certain Progenies from Mother Beets Selected from American Crystal 3S Being Superior to the Checks

The probabilities of certain progenies of mother beets selected from American Crystal 3S being superior to the average of the two checks are given in Table 1. The characters considered are weight per plot and percentage sucrose. The data shown are for only eight of the progeny of the 490 mother beets. It will be remembered that the two checks were American Crystal 3S and US 401. The F values obtained from an application of analysis of variance showed that the two checks did not differ significantly in weight of beets per plot but that American Crystal averaged 0.4 percent more sucrose than US 401. The odds against this value of 0.4 percent being a chance deviation were extremely great.

Table 1.—The Probability of Certain Progeny (Indicated by 1955 Culture Number) Falling Outside —x to +x (See Fisher, 2, Table 1) for Weight Per Root and Percentage Sucrose, the Probability (P) Being Based on the Difference Between Any Given Progeny and the Average of the Two Checks.

1955 Culture Number	Weight Per Plot					Percentage Sucrose					
	Replication					1.70	Replication				
	1	2	3	4	5	1	2	3	4	5	
	P	P	P	P	P	P	P	P	P	P	
6148	0.36	0.06	0.27	0.75	0.12	0.21	0.72	0.19			
6221	0.08	0.48	0.60	0.11	0.44	0.52	*****		0.05		
6440	0.02	0.09	0.15	0.43	-	0.81	0.05	0.67	0.44	0.01	
6444	0.08	0.67	0.46	0.06	0.70	0.34	* 100	0.95	0.56		
6506	0.06	0.49	0.03	0.14	0.83	*****	0.86		0.34	0.63	
6551		0.90	0.33	0.20	-	0.00	0.32	0.60	0.11	0.72	
6585	0.03	3200	bertana	0.42	0.96	0.04	0.48	0.81	0.21	0.02	
6590	0.14	0.45		0.71	0.74	0.14	0.72	0.34	0.28	0.95	

..... Values less than the average of the two checks.

A study of Table 1 reveals that none of the progenies exceeded the checks in all the replications for both weight per plot and percentage sucrose. Four of the eight progeny exceeded the check in weight per plot in all five replications and four exceeded the average of the checks for percentage sucrose in all five replications. The selfed seed from 25 of the mother beets whose progeny showed the most promise are being grown for the purpose of producing a synthetic variety. It remains to be determined whether such a synthetic variety will be superior to

American Crystal 3S in yield of beets per acre, percentage sucrose, or both characters. This procedure of producing a synthetic variety from the self-pollinated plants of the 25 mother beets whose progeny showed the most promise is essentially the polycross method of breeding.

If the plant breeder desired to follow the reciprocal recurrent selection method of breeding with this material the procedure would be as follows: Seed produced from self-pollination of mother beets of source A having the most promise, as shown by the progeny test, would be planted to produce mother beets that in turn would be intercrossed to give source A for the second cycle of breeding. Likewise seed produced from self-pollinated mother beets of source B having the most promise, as shown by the progeny test, would be planted to produce mother beets for intercrossing to give source B for the second cycle of breeding. Since it was found that crossing between sources that yielded the seed planted in the progeny test was 68.42 percent, differentiation of the two sources would have started. In other words, due to the greater preponderance of the progeny having resulted from fertilization by gametes of the opposite source the accumulation of genes in each source that combined well with genes of the opposite source would be under way.

Discussion and Conclusions

Two planting arrangements given differ in the amount of crossing that would be expected between sources. It was found from the planting arrangement given in Diagram 1 that 68.42 percent of the progeny of source A had source B plants as the male parent. Since the only difference between sources was hypocotyl color this same percentage of the progeny from the source B mother beets would be expected to have had source A plants as the pollen parent. Hence only 31.58 percent of the progeny of the two sources would be expected to have resulted from self fertilization and fertilization between plants within sources. The comparatively high percentage of crossing between sources indicates that very little self fertilization is occurring in this material. Hence, most of the 31.58 percent resulting from either self fertilization or fertilization between gametes within sources would be expected to have resulted from the latter type of fertilization.

Diagram 2 presents a suggested planting arrangement that should result in a higher proportion than 68.42 percent of the progeny resulting from fertilization between gametes of the opposite sources. The question arises whether more than 68.42

percent of the progeny resulting from fertilization between gametes of different sources is necessary or desirable. The 31.58 percent of progeny resulting from fertilization by gametes of different plants within sources would tend to keep the two sources in a more heterozygous condition and hence to avoid a too rapid approach towards homozygosity. This is important as improvement in the further cycles of reciprocal recurrent selection is dependent upon heterozygosity and heterogeneity within sources.

In the planting arrangements depicted by Diagrams 1 and 2, if facilities are ample and the breeder so desires, the following methods of breeding designed to take advantage of any beneficial heterosis may be practiced from each planting arrangement. From the isolation plot of source A and the isolation plot of source B (in this study grown near Salida, Colorado,) open pollinated seed saved from each plant would provide for polycross tests (or recurrent selection tests) and hence allow employing this method of breeding. Seed saved from the open pollinated plants in the isolation plot depicted in Diagram 1 (in this study grown at Fort Collins, Colorado,) would allow practicing the reciprocal recurrent selection method of breeding. As pointed out by Comstock, Robinson, and Harvey (1) inbreeding within sources to establish inbred lines could be started at any time. However, it seems that the number of inbred lines that it would be necessary to produce and test for combining ability could be materially reduced by doing the inbreeding within sources after at least two or three cycles of reciprocal recurrent selection had been completed.

Following the planting arrangement depicted in Diagram 2, seed resulting from open pollination and saved from A source plants would allow practicing the polycross method of breeding; and seed saved from the B plants would allow following the reciprocal recurrent selection method of breeding. In the corresponding isolation plot in which B plants predominated, the polycross method of breeding could be followed by saving seed resulting from open pollinated B plants; and the reciprocal recurrent selection method could be practiced by saving seed resulting from open pollinated A plants.

The findings from the studies with 600 mother beets as regards the amount of cross fertilization are of further interest in connection with the extent to which the progeny tests measure general and specific combining ability. On the average 68.42 percent of the progeny from any given mother beet resulted from fertilization between plants of different sources, and 31.58 percent from fertilization between plants within sources and from

self fertilization. The data indicated that the amount of self fertilization was negligible. Hence, in this material, on the average the performance of 68.42 percent of the progeny from any given mother beet measures general and specific combining ability between sources and the performance of 31.58 percent of the progeny from any given mother beet predominantly measures general combining ability within the respective source. However, as the program employing reciprocal recurrent selection progresses the 68.42 percent of the progeny resulting from fertilization between plants of different sources tends more and more to emphasize specific combining ability. For definition and usage of the terms, general and specific combining ability, see Sprague and Tatum (7) and Comstock, Robinson, and Harvey (1).

It seems probable from the studies reported herein, that the genotypes of each mother beet in the tests for combining ability could be retained by a combination of self pollination and maintaining in the vegetative condition, or bringing about reversion to the vegetative condition one quarter of each mother beet. In following such a procedure in the planting arrangement depicted in Diagram 1, bagging of flowering branches should be practiced in all isolation plantings; that is, in the planting in which plants of sources A and B are grown together and in the plantings in which sources A and B are grown separately. In the planting arrangement depicted in Diagram 2 flowering branches of the A plants should be bagged in an attempt to bring about self fertilization, and source B plants should be similarly treated in the corresponding isolation plot in which B plants predominate. In this latter planting arrangement it seems that all the seed from those plants of the source in the minority should be saved for progeny tests. Hence, bagging to bring about self fertilization and propagation of a quarter of each beet in the vegetative condition should make it possible to retain the genotype of each mother beet whose progeny are being tested.

Another point of interest is the effect that reciprocal recurrent selection would have on progressive changes in the amount of cross fertilization as compared with self fertilization. It can be seen that, if heterosis is playing an important part in conditioning favorable economic characters, as the program progresses those individuals having any appreciable amount of self fertilization would be less desirable and hence would be eliminated. Then, as the breeding program progressed a greater proportion of the progeny would result from cross fertilization and finally

a very high proportion of the progeny would result from this type of fertilization. The reciprocal recurrent selection program would be particularly effective in bringing about a higher percentage of cross ferilization when either sources A or B, or both, at the beginning of the breeding program were low in this respect.

One of the most important aspects of the reciprocal recurrent selection program is precision of tesing the progeny for the characters sought. In order to make the selections within a small area and thus lower the environmental effect on selection each replication of 588 populations was divided into 49 series with two checks in each series. The 49 checks of each variety per each of five replications provided a measure of the environmental variance. Any given progeny was evaluated on the basis of the average of the two checks in the series in which it occurred. Since any given progeny occurs in each replication, five such determinations (see Table 1) are available for evaluating any one of the 490 progeny. Growing the five replications at a single location might result in a hybrid that would have limited adaptation. However, if the five replications were distributed over the area in which the hybrid is to be grown the probability of such happening would be reduced materially. In the present experiment the progeny were grown at two locations, Mason City, Iowa, and Waseca, Minnesota. Further studies are necessary to determine the effectiveness of this method of evaluating the progeny.

Summary

1. The formulas developed for determining the proportion of the progeny resulting from fertilization by male gametes of the opposite source are:

(A) Progeny from source A mothers (rr genotypic plants) $x = \frac{(D + H) p'}{D + \frac{1}{2}H}$

(B) Progeny from source B mothers (Rr genotypic plants) $x = 1 - \frac{(D + H) p'}{D + \frac{1}{2}H}$

The applications of these formulas are illustrated.

- 2. Two different planting arrangements are proposed that should provide different amounts of cross fertilization between plants of opposite sources. Others not presented that are obvious may prove superior.
- 3. Self pollination and maintaining in or causing reversion of quarters of each mother beet to the vegetative condition were found effective in preserving the genotype of each mother beet whose progeny was under test.

- 4. The method employed in testing the progeny of the 490 mother beets proved satisfactory in the present study. However further studies are needed to determine precision of selection based on this method of testing the progeny.
- 5. The planting arrangement described in Diagram 1 provided sufficient seed to test the progeny of 490 of the 600 mother beets with which the research was started.
- 6. Under "Discussion and Conclusions" applications of the findings to a plant breeding program are presented.

Literature Cited

- (1) Comstock, R. E., Robinson, H. F., and Harvey, P. H. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. Jour. 41:360-367.
- (2) Fisher, R. A. 1934. Statistical methods for research workers. Oliver and Boyd, Ed. 5, 319 pp. Edinburgh and London.
- (3) GASKILL, J. O. 1952. Induction of reproductive development in sugar beets by photothermal treatment of young seedlings. Proc. Amer. Soc. Sug. Beet Tech. 112-120.
- (4) HARDY, G. H. 1908. Mendelian proportions in a mixed population. Science 28:49-50.
- LI, C. C. 1955. Population genetics. Univ. Chicago Press, 366 pp. Chicago, Ill.
- (6) OWEN, F. V., CARSNER, E., and STOUT, M. 1940. Photothermal induction of flowering in sugar beets. Jour. Agr. Res. 61:101-124.
- (7) Sprague, G. F., and Tatum, L. A. 1942. General vs. specific combining ability in single crosses of corn. Jour. Amer. Soc. Agron. 34:923-932.
- (8) Weinberg, W. 1908. Uber den Nachweis der Vererbung beim Menchen. Jahreshefte Verein Naturk. Wurttemberg 64:368-382.