CONTRIBUTION OF INBRED LINES TO THE RESISTANCE OF HYBRID DENT CORN TO LARVAE OF THE EARLY SUMMER GENERATION OF THE EUROPEAN CORN BORER[1]

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INTRODUCTION

In a previous publication[3] certain inbred lines of dent corn (*Zea mays* L.) were shown to be resistant, partially resistant, or susceptible to the survival of larvae of the early summer generation of the European corn borer (*Pyrausta nubilalis* (Hbn.)), and to be able to transmit this resistance or susceptibility to their hybrids. Since there were fewer borers from eggs that hatched on corn in a less advanced stage of growth than from eggs that hatched on corn in a more advanced stage, the population of borers to be expected in each strain was predicted on the basis of the regression of number of borers per plant on silking date.

The inbred lines or corn hybrids that consistently contained fewer than the predicted number of borers were classed as inherently borer-resistant. One experiment involved different combinations of these lines in single-cross hybrids. From borer populations in resistant single crosses averaging 39 percent less than the predicted number of borers, the populations increased to 2 percent more than the predicted number in single crosses made up entirely of partially resistant lines, and to 58 percent more than the predicted number in single crosses involving only susceptible lines. The cumulative effect of multiple factors in inbred lines on borer resistance in hybrids was clearly indicated.

The purpose of the work herein described was to determine whether or not the quantitative effects of the inbred lines in the single crosses were the same as those with double-cross hybrids involving, with two exceptions, the same lines used in the single crosses. Incidental to this study, the possibility of complementary or modifying factors for borer resistance was considered.

STRAINS TESTED

Single-cross hybrids were tested in 1939 and double crosses in 1941, at Toledo, Ohio. The 6 possible single-cross combinations of resistant, partially resistant, and susceptible inbred lines were each

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[3] PATCH, L. H., HOLBERT, J. R., and EVERLY, R. T. STRAINS OF FIELD CORN RESISTANT TO THE SURVIVAL OF THE EUROPEAN CORN BORER. U. S. Dept. Agr. Tech. Bul. 823, 22 pp. 1942.

represented by 3 to 10 crosses. The crosses involved the resistant lines Ia. L317, Ill. R4, Mich. 77, and Mich. 106, the partially resistant lines Ill. Hy, Ind. TR, Ia. I205, and U. S. 540, and the susceptible lines Ill. A, Ill. 90, Ind. WF9, and U. S. 187–2. Lines L317, R4, Hy, and A in all combinations and crosses on lines TR, I205, 540, 90, WF9, and 187–2 were tested. . In addition, line R4 crosses on 77 and 106, 77 on 106, and 540 on 77, 106, and I205 were tested, making a total of 36 single crosses.

Each of the 15 possible double-cross combinations of resistant, partially resistant, and susceptible inbred lines was represented, with one exception, by 4 double crosses. In order that the combinations made up entirely of resistant or partially resistant lines be represented by more than one double cross, it was necessary to use at least 1 inbred line in addition to the 4 lines involved in the resistant and partially resistant groups of the single crosses. Hence, resistant Wis. CC5 and partially resistant Wis. CC1 were also used in the pedigree of the double crosses. In earlier experiments [4] these lines had about the same effect on borer survival as the other lines in their respective groups, and, as shown in figure 1, a comparison of the single crosses with the double crosses disclosed no significant changes resulting from the use of these lines in the pedigrees of the double crosses. In the combinations made up entirely of susceptible lines, however, another line showing consistent susceptibility to the borer was not available at the time of the experiment. Hence, double cross (A×90) × (WF9×187–2) was entered 4 times under that combination.

The pedigrees of the 60 double crosses involved the following single crosses: 16 made up entirely of single crosses used in the foregoing test of single crosses; 13 made up with only 1 of the 2 single crosses involving either CC1 crossed on R4, Hy, or A, or CC5 crossed on R4 or A; and 31 made up of 2 single crosses, at least 1 of which was not used in the test of single crosses although they involved the same inbred lines as those crosses. The 31 double crosses involved single crosses of 106 on L317, Hy, and A, of TR on I205, 540, and 90, of WF9 on TR, I205, 540, 90, and 187–2, and of 187–2 on I205 and 540.

The hybrids were designated according to the borer reaction of the inbreds involved. For example, a single cross involving 1 resistant, no partially resistant, and 1 susceptible inbred was designated as a 1–0–1 hybrid combination; and a cross made up of no resistant, 1 partially resistant, and 1 susceptible inbred as a 0–1–1 combination. In double crosses a cross involving 2 resistant, 1 partially resistant, and 1 susceptible inbred was designated as a 2–1–1 hybrid combination.

METHODS AND ANALYSIS OF DATA

The single crosses were grown in 2-hill plots of 3 plants per hill with 7 replications, and the double crosses in 1-hill plots of 3 plants per hill with 8 replications. The hills were 42 inches apart each way. Each plant was infested by hand with 4 egg masses, or about 80 eggs, before the tassels became a factor in borer survival, and each was tagged with the date of silking. All plants were dissected during the last 2 weeks of August to determine the number of borers surviving. The differences in the number of eggs laid naturally on the different hybrids were so small that they were not considered as a factor in the study.

[4] See footnote 3, p. 257.

The first step in the analysis of the data was to eliminate the effect of differences in maturity among the hybrids on the mean number of borers per plant in each hybrid, by use of a regression coefficient determined from previous experiments. The decrease in the mean

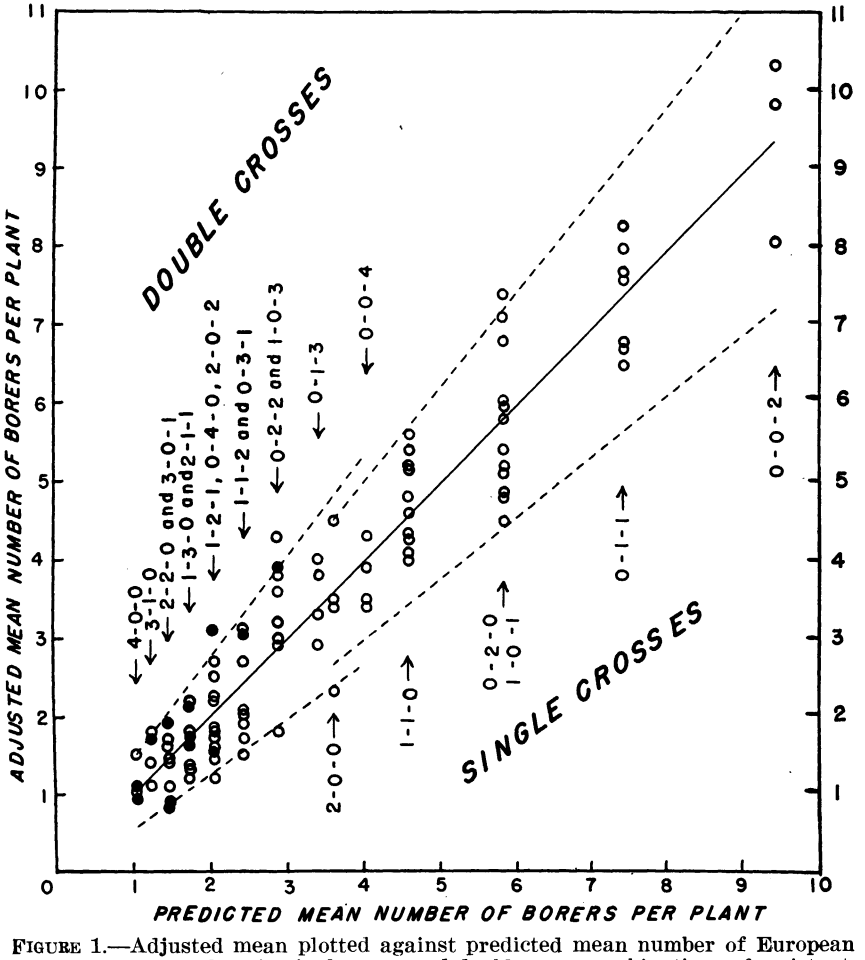

FIGURE 1.—Adjusted mean plotted against predicted mean number of European corn borers per plant in single-cross and double-cross combinations of resistant, partially resistant, and susceptible inbred lines of dent corn. The first, second, and third figures in each set indicate, respectively, the number of resistant, partially resistant, and susceptible inbreds in the different crosses. Open circles indicate different combinations of these lines. Solid circles indicate double crosses in which Wis. CC5 and Wis. CC1 were used. After variability due to replication is removed, 95 percent of the hybrids would be expected to fall within the dotted lines.

number of borers for each day later in silking may be closely estimated by multiplying the mean number of borers per plant in the experiment by 0.043.[5] For each day earlier or later than July 23, the average

[5] PATCH, L. H., and EVERLY, R. T. RESISTANCE OF DENT CORN INBRED LINES TO SURVIVAL OF FIRST-GENERATION EUROPEAN CORN BORER LARVAE. U. S. Dept. Agr. Tech. Bul. 893, 10 pp., illus. 1945.

silking date of the single crosses averaging 6.06 borers per plant, 0.26 was added to or subtracted from the number of borers observed per plant to obtain the adjusted mean. In a similar manner the means of the double crosses that averaged 2.20 borers per plant were adjusted.

The second step was to determine the decrease in borer population in hybrids involving different combinations of resistant, partially resistant, and susceptible lines, as compared with hybrids made up entirely of susceptible lines. In the single crosses the borer populations in combinations 0–0–2, 0–1–1, 0–2–0, 1–1–0, and 2–0–0, were known to decrease from a high to successively lower levels.[6] In the double crosses the borer populations in combinations 0–0–4, 0–1–3, 0–2–2, 0–3–1, 0–4–0, 1–3–0, 2–2–0, 3–1–0, and 4–0–0 would be expected to decrease from a high to successively lower levels if the effects of the inbred lines in double crosses were similar to their effects in single crosses. Certain balanced combinations, such as 1–2–1, 0–4–0, and 2–0–2, would be expected to contain the same level of borers except for the variation due to sampling errors.

TABLE 1.—*Adjusted and predicted mean numbers of European corn borers in groups of single-cross and double-cross combinations of borer-resistant, partially resistant, and susceptible inbred lines of dent corn*

SINGLE-CROSS COMBINATIONS, 1939

1	2	3	4	5	6	7
Prediction group No.	Combination [1]	Number of hybrids in combination	Adjusted mean of borers per plant	Predicted number of borers per plant		
				Arithmetical progression	Geometrical progression	
					Empirical estimates [2]	By method of least squares [3]
1	2-0-0	4	3.43	3.57	3.522	3.611
2	1-1-0	10	4.73	4.67	4.508	4.590
3	1-0-1	8	5.81	5.77	5.77	5.834
	0-2-0	4	5.55	5.77	5.77	5.834
4	0-1-1	7	7.46	6.87	7.386	7.415
5	0-0-2	3	9.38	7.97	9.454	9.424

DOUBLE-CROSS COMBINATIONS, 1941

1	4-0-0	4	1.13	0.97	1.013	1.040
2	3-1-0	4	1.50	1.22	1.196	1.232
3	2-2-0	4	1.58	1.47	1.412	1.460
	3-0-1	4	1.13	1.47	1.412	1.460
4	1-3-0	4	1.55	1.72	1.668	1.730
	2-1-1	4	1.75	1.72	1.668	1.730
5	0-4-0	4	2.23	1.97	1.97	2.050
	1-2-1	4	1.77	1.97	1.97	2.050
	2-0-2	4	1.90	1.97	1.97	2.050
6	0-3-1	4	2.35	2.22	2.327	2.429
	1-1-2	4	2.13	2.22	2.327	2.429
7	0-2-2	4	3.63	2.47	2.748	2.878
	1-0-3	4	3.00	2.47	2.748	2.878
8	0-1-3	4	3.50	2.72	3.245	3.410
9	0-0-4	[4] 4	3.78	2.97	3.832	4.041

[1] Respective numerals indicate the number of resistant, partially resistant, and susceptible inbred lines involved.
[2] The progression ratio is 1.280 and 1.181 for the single and double crosses, respectively.
[3] The progression ratio is 1.271 and 1.185 for the single and double crosses, respectively.
[4] The hybrid (A × 90) × (WF9 × 187-2) was entered 4 times under combination 0-0-4.

[6] See table 11 of reference cited in footnote 3, p. 257.

Column 5 of table 1 shows an arithmetical progression with values that closely approximate the adjusted mean numbers of borers (column 4) of the low-numbered prediction groups, but diverge rather widely from the means of the high-numbered groups. On the other hand, the geometrical progression (column 6) closely approximates the numbers of borers in all the groups. Both the arithmetical and geometrical progressions were determined empirically as giving the best fit to the adjusted data.

For a more accurate determination of the geometrical progression giving the best fit to the data, the method of least squares was employed. The adjusted mean number of borers, Y, in each hybrid was used. With the empirical values of the geometrical progression given in column 6 designated as X, a value of Y' was estimated for each value of X on the basis of the regression of Y on X. The values of Y were paired with the value of X for the group in which they occurred. The values of Y' gave the geometrical progression shown in column 7 of the table. The regression of Y on Y' gave a coefficient of 1.0 borer in each case.

The third step in the analysis of the data was to plot (fig. 1) the adjusted mean number of borers per plant, Y, dissected from the individual hybrids against Y', the number predicted for the group in which they occurred. The regression line was drawn through the plotted points. Then, after the variability due to replication was deducted, the variability from plot to plot within hybrids was determined for 26 levels of borer population by grouping hybrids according to borer level. The data from the double and single crosses fell so closely along the same regression line that both lots were considered as one set. The standard error of the mean of samples of 24 plants containing an average of 1 borer per plant was found to be 0.24, and this value increased by linear regression to 1.46 for samples averaging 9.5 borers per plant. With twice the standard error of the mean of 42 plants for the single crosses and of 24 plants for the double crosses, limits were set off above and below the regression line in figure 1 within which 95 percent of the plotted points would be expected to lie.

EFFECTS OF INBRED LINES IN HYBRID COMBINATION

The combinations of single crosses made up entirely of susceptible, partially resistant, and resistant lines contained estimated averages of 9.42, 5.83, and 3.61 borers per plant, respectively, as compared with 4.04, 2.05, and 1.04 borers in the same combinations of double crosses. There were 61.9 percent as many borers in the partially resistant as in the susceptible combinations of single crosses compared with 50.7 percent in the double crosses. There were also 61.9 and 50.7 percent as many borers in the resistant as in the partially resistant combinations of single and double crosses, and 38.3 and 25.7 percent as many borers in the resistant as in the susceptible combinations of single and double crosses, respectively.

The difference between partially resistant and susceptible, and between resistant and partially resistant, combinations in each case was equal on a percentage basis rather than by an absolute amount.[7] The genes multiply the traits of each other instead of combining additively.

[7] SINNOTT, E. W., and DUNN, L. C. PRINCIPLES OF GENETICS. Ed. 3, 408 pp., illus. New York and London. 1939. See p. 134.

COMPLEMENTARY OR MODIFYING FACTORS

In tests for complementary or modifying factors for borer resistance in an inbred line when used in single crosses, the average reaction to borer survival in single-cross combination with several other lines must be known before it can be determined whether or not that line deviates significantly from the average when in combination with some particular inbred line. For this purpose the data plotted in figure 1 were used. It may be noted that only 2 of the 36 single crosses were outside the limits set by the dotted lines. Five percent, or 2 crosses, would be expected to deviate this much from the prediction line through chance alone. Therefore, whatever complementary or modifying action of factors for borer resistance the inbred lines in combinations may have had was not enough to prove important in 1939 when the variability of the data is considered.

Other tests of the possible effect of complementary or modifying factors for borer resistance were provided by data obtained in 1940 and 1941. In 1940 inbred lines Ia. L317, Ill. M14 and 408, Ind. 38–11, Kan. K226 and K230, Mich. MS1, Minn. A340 and A392, Ohio 02, 07, 51A, and 3113, and Wis. CC5, 3922, and 4308 were tested in single-cross combinations on the common parent lines—susceptible A, partially resistant Hy, and resistant R4. In 1941 the following lines were tested in single-cross combination with Hy and R4: Ia. 159, 289, L304A, L317, BL339, and OS420; Ill. A, Pr, 90, and 5120; Ind. P8, WF9, and 38–11; Kan. K226 and K230; Mich. MS1 and 898; Minn. 49, 50, and 374; Ohio 07, 28, 28A, 33, 40B, 51, 51A, 61–67, and 67A; U. S. 4–8, 153, and 187–2; and Wis. CC2, CC4, CC6, CC7, CC8, and CC11. Single crosses made up of susceptible lines were also included in 1941 as standards for comparison.

In 1940 the number of borers in the 2–0–0, 1–1–0, 1–0–1, 0–1–1, and 0–0–2 combinations averaged 3.886, 4.768, 5.850, 7.178, and 8.807 per plant, respectively, on the basis of a geometrical progression with a ratio of 1.227. In 1941 these combinations averaged 1.664, 2.237, 3.006, 4.040, and 5.430 borers per plant, respectively, on the basis of a geometrical progression with a ratio of 1.344. In 1940 crosses A×51A, A×K226, R4×K230, R4×A340, and R4×CC5 contained significantly fewer borers than the predicted averages of their respective combinations. However, two of these crosses, R4×K230 and R4×CC5, were retested in 1941, and they deviated only slightly, one negatively and the other positively, from the averages predicted. Crosses A×51A, A×K226, and R4×A340 contained 5.5, 5.1, and 2.8 borers per plant, while the average numbers predicted for these respective combinations were 7.18, 7.18, and 3.89 borers. The differences were not more than 0.6 borer greater than those expected on the basis of the within-strain variability. In 1941 single cross Minn. 49×R4 was slightly below the lower limit set up on the basis of the within-strain variability as compared with the expected number. It is concluded that whatever complementary or modifying action of factors for borer resistance the inbred lines might have had in combination with lines A, Hy, or R4, in 1940, or with Hy or R4 in 1941, it was not enough to prove important when the variability of the data is considered.

SUMMARY

The average effect of parent inbred lines of dent corn on the survival of larvae of the early summer generation of the European corn borer in single-cross combinations in 1939 was compared quantitatively with their effect in double-cross combinations in 1941 involving, with two exceptions, the same lines used in the single crosses. The lines used had previously been rated as resistant, partially resistant, or susceptible to larval survival. The tests were conducted by infesting each plant by hand with an average of 80 eggs in addition to the natural infestation, and dissecting the plants later to count the mature borers. From a low population of borers in single crosses or double crosses involving resistant lines, the number of borers per plant increased by geometrical progression in the crosses involving successively more susceptible combinations. On the basis of the progressions there were 38.3 percent as many borers in the resistant as in the susceptible combinations of single crosses, as compared with 25.7 percent as many in the resistant as in the susceptible double crosses. A smaller reduction of borers occurred in the presence of a higher infestation in the single crosses than in the double crosses.

A graphical method for determining the possibility of complementary or modifying action of factors for resistance to borer survival is described. One experiment involving 12 inbred lines indicated no effect of complementary or modifying factors in the 36 single crosses tested. From another experiment in which 16 lines were crossed on susceptible line Ill. A, partially resistant Ill. Hy, and resistant Ill. R4 as the common parents, and from still another experiment in which 39 lines were crossed on Hy and R4, it was concluded that whatever complementary or modifying action of factors for borer resistance the inbred lines may have had was not sufficient to be of importance when the variability of the data is considered.