AMERICAN BREEDERS ASSOCIATION

VOLUME VI

Report of the Meeting held at Omaha, Neb., December [illegible], 9, and 10, 1909, and for the Year ending December 31, 1909

WASHINGTON, D. C.
AMERICAN BREEDERS ASSOCIATION
1911

between types ought to be greater under such conditions, thus affording an opportunity to isolate the more promising forms. It is not advisable to manure the land heavily prior to setting with grass, but some care must be exercised in choosing an area of uniform fertility.

PLANTING THE INCREASE PLAT.

After growing the nursery stock in the manner indicated for one or two seasons, it will be possible to reach some conclusion with reference to the rows which have made the strongest growth and contain plants that correspond in a measure with our ideal. Roots from these rows can be transplanted in larger plats, where they can be further compared with each other and with the parent varieties, and from this area material will be available for the general field planting.

HYBRIDIZATION METHODS IN CORN BREEDING.

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The simultaneous preparation of papers by three different authors about a year ago, advocating the use of more or less definite hybridization in the breeding of Indian corn in lieu of the methods of selection and partial isolation now in general use, probably marks an important step in the improvement of this exceedingly valuable American crop; for the appearance of these papers indicates a growing appreciation of the real biological nature of Indian corn and the requirements necessary to the attainment of the highest and most permanent success in corn breeding.

The three papers to which I refer are, "The distinction between development and heredity in inbreeding," by Dr. E. M. East, in the *American Naturalist* for March, 1909; a circular of the U. S. Department of Agriculture on "The importance of broad breeding in corn," by Mr. G. N. Collins, issued in June, 1909; and my own paper on "A pure-line method in corn breeding," read before this Association at its last meeting at Columbia, Mo., in January, 1909, and published in its last Annual Report. These three papers are in some particulars fundamentally alike, but as they approach the subject from somewhat different points of view it will be interesting to compare them briefly.

The suggestion for a hybridization method in corn breeding is not entirely new. A very clear outline of such a method, with experimental results sufficient to warrant the suggestion, was presented by Morrow and Gardner in Bulletins 25 and 31 of the Illinois Agricultural Experiment Station in 1893 and 1894. These bulletins were evidently unknown to two of the three writers above mentioned,[a] and the third, Mr. Collins, while referring to Morrow and Gardner's bulletins, makes no statement of the fact that they had devised an adequate hybridization method for the practical utilization of the advantage shown by them to be sometimes attainable by crossing two distinct varieties.

In my paper on "The composition of a field of maize," read before the American Breeders Association in Washington two years ago, I pointed out the fundamental defect of the method now in general use, which simulates to a degree the isolation methods so successfully used in the improvement of small grains, and I suggested there that "continuous hybridization is perhaps the proper aim of the corn breeder." The conceptions which formed the basis of that paper were the complex hybridity of corn as ordinarily grown and the stimulating effect to heterozygosis or hybridity. It was shown that this stimulating effect comes into play in corn breeding because self-fertilizations result in the partial or complete isolation of many quite distinct strains, and that cross-fertilization must therefore result in the production of hybrid combinations of these pure strains.

My suggestion for a pure-line method in corn breeding was a direct logical sequel of this original paper on "The composition of a field of maize." Dr. East's article on inbreeding above mentioned is also a sequel to the same paper, as shown by his references to it and also by his excellent discussion of the stimulation which results from hybridity, in regard to which he has arrived at views identical with those entertained by me at the time my original corn paper was written. It may be said, therefore, that Dr. East's paper and my

[a] I am indebted to Prof. W. J. Spillman for calling my attention to these bulletins. Dr. East has informed me since this was written and read at Omaha, that he, too, knew of the existence of Morrow and Gardner's bulletins on corn, but was not aware that these authors had described a method for continuous hybridization in the culture of this crop.—G. H. S.

own have grown out of the conception, first presented by myself two years ago, that what may appear to be a uniform variety of Indian corn is really a series of very complex hybrids involving numerous distinct biotypes,[b] which may be isolated from their hybrid combinations by self-fertilization and which owe their smaller size and inferior yielding qualities, not to any injurious effect of inbreeding as such, but to the fact that self-fertilization gradually results in their reduction to a pure homozygous state. They are thus deprived of the stimulus which had been derived from crossing with other biotypes.

It appears that my paper of two years ago was unknown to Mr. Collins, although it was read in Washington and published in the Annual Report of the American Breeders Association in 1908. As Dr. East and I have both performed many experiments which have led us to place great confidence in the practical importance of the discoveries of Mendel, De Vries, and Johannsen, it is interesting to read in Mr. Collins's paper that these new results from the scientific side are "particularly dangerous" when applied to corn breeding. As Dr. East and I by the application of the newer biological conceptions have arrived at practically the same method which Mr. Collins recognizes as necessary for the best results in corn breeding, it should become evident to him that there is no such danger as he fears in the application of the latest scientific results to practical work.

The crossing of relatively homozygous strains or of distinct biotypes in corn in order to secure the stimulus of hybridity, as advocated by Dr. East and myself, involves a much more definite conception, however, than that suggested by the term "broad breeding." The idea of hybridization between distinct strains or between biotypes calls for the use each year of those two parental strains or biotypes which careful tests have shown to result in the greatest capacity for yielding an excellent F_1 (first generation hybrid) progeny. Although Mr. Collins advocates a method which is essentially identical with that proposed by Morrow and Gardner fifteen years ago and which has been invented anew by Dr. East, the idea of broad breeding would logically require the working in of a new variety or strain each year, instead of going back to the same relatively inbred strains for each successive crop. In other words, while Mr. Collins has suggested a splendid method of corn breeding, it is not one which corresponds

[b] A biotype is a group of individuals which do not differ from one another in any hereditary quality, and which therefore constitute a pure race.

well with the theory upon which he bases his suggestion. If the "broad breeding" idea is taken as a basis and a new variety is brought into the combination every year, it is plain that it must be done blindly, since the influence which this new variety will have upon either the quality or quantity of the crop cannot be known. However, the method advocated by Mr. Williams,[c] of the Ohio Agricultural Experiment Station, would overcome to a certain extent the blindness of this "introduction of new blood" by first testing its influence.

In the method of Morrow and Gardner, which, as we have seen, has been endorsed by East and Collins, involving the use of strains that, according to my experiments, are already complexly hybrid, there must be more or less resolution of characters in the resultant cross-bred plants, since the crop would not consist of F_1 plants with respect to all the numerous characters in which the two chosen parental strains differed, but would be, with respect to many of them, the F_2 (second generation hybrid) in which splitting up of characters occurs. The method which I described last year under the name of a "pure-line method" is the only one yet suggested in which all the plants in the resultant progeny would be first generation hybrids in regard to all the qualities which served to distinguish the parents. This does not prove, however, that my pure-line method is better than the method of Morrow and Gardner. It may be true, as Dr. East says, that the pure-line method is "more correct theoretically but less practical" than the method of Morrow and Gardner which he describes. It is conceivable that the method of using highly developed strains which have been produced by line-breeding and continual selection of the best and most vigorous ears may produce such high yields when crossed together that the expense and trouble of isolating pure biotypes will not be justified; but such a conclusion can be properly reached only as the result of extensive experimentation; and this experimentation, if undertaken in earnest by our State experiment stations, must result in the discovery of the best possible method for the breeding of Indian corn. My anxiety is not for the success of the pure-line method outlined by myself, but that serious experimentation shall be undertaken by every station within the corn-growing region for the purpose of discovering what is the best method. I feel quite

[c] Williams, C. G., Corn Breeding and Registration. Report American Breeders Association, 3: 110-122, 1907.

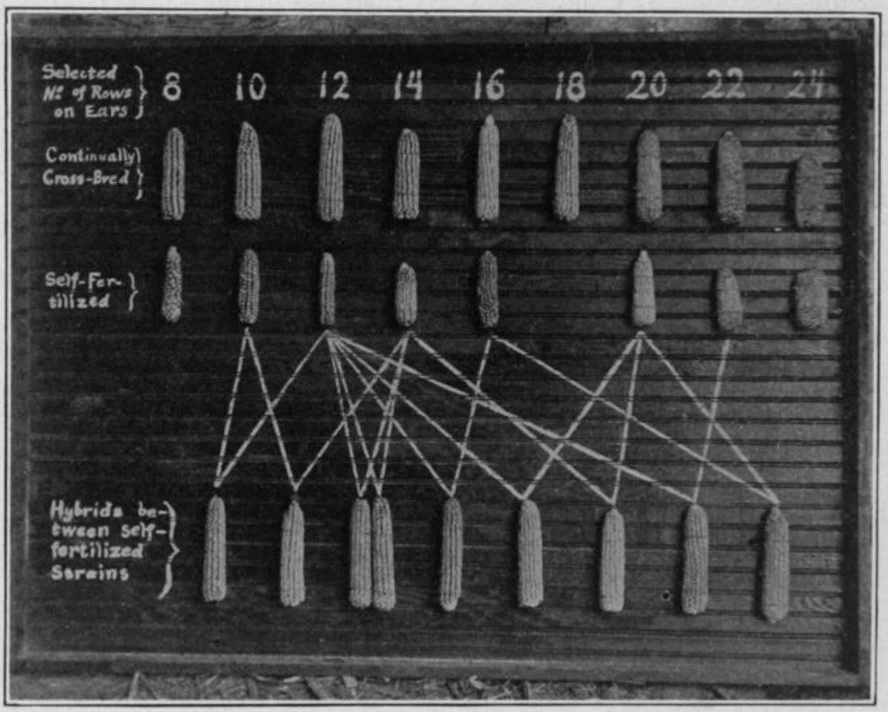
sure that the results of su h investigations will lead to the adoption of some hybridization method in the breeding of this crop.

My experiments with corn during the last year have again given the fullest confirmation of my theories regarding the complex hybridity of the plants which compose an ordinary field of corn as grown at the present time; and data have also been secured having a direct bearing upon the applicability and importance of hybridization methods in corn breeding. Last year I presented the results of a single pair of reciprocal crosses between two self-fertilized strains which I called strain *A* and strain *B*. Those strains in hybrid combination produced a yield a little larger than the average of those families which had not been self-fertilized, but the difference was very slight. As strains *A* and *B* had been essentially unselected, being the first two self-fertilized strains which had become nearly pure-bred, it was anticipated that a larger number of crosses would discover some strains much superior to *A* and *B* as parents of a high-yielding F_1 hybrid progeny, as well, perhaps, as some which are inferior. This belief has been fully supported by the results secured in 1909, for in eight different hybrid combinations which were tested during the past season three have proved better than the combination between strains *A* and *B;* one other combination, also having strain *A* as one of the parents, gave a result about equal to that of *A* and *B,* and three combinations produced somewhat less than those of strains *A* and *B*. Not all of these hybrid families produced higher yields than the corresponding cultures which had never been self-fertilzed, but the three highest yields produced in all my cultures were the result of hybridizing self-fertilized strains which had been, no doubt, reduced nearly to a homozygous (pure-bred) state. The average of all the hybrids when compared with the average of all the corresponding cross-bred[d] families shows the yield of the former to be only significantly lower than that of the latter, these averages being respectively 78.9 bushels per acre from the hybrids, and 79.4 bushels per acre from the cross-breds. This shows how effectively the cumulative "injurious effects" of five years of self-fertilization may disappear in a single year as the result of crossing.

The large yield of two of my hybrid strains as compared with the product of the best cross-bred families is not a mere chance relation, but is a specific function of the particular hybrid combination

[d] I use the term "cross-bred" here to denote those families in which all self-fertilization has been prevented during the five years these investigations have been in progress.

which produced them, as may be shown by two series of facts. In the first place, the hybrids between strains *A* and *B* which were reported last year as producing from 74.4 to 78.6 bushels per acre have this year yielded 79.8 bushels per acre. A slight increase in the other cultures for 1909 as compared with those for 1908 makes this slight increase in yield of the hybrid between strains *A* and *B* simply a measure of the better climatic conditions of 1909 as compared with



CROSS-FERTILIZED, SELF-FERTILIZED, AND HYBRIDIZED CORN.

The lines between self-fertilized and hybridized series indicate the parentages of the latter.

1908. The important feature of this result is that the F_1 hybrids between strains *A* and *B* maintain essentially the same yielding capacity in successive years, while other hybrid strains produce quite different yields, varying from 61.5 bushels per acre to 98.4 bushels per acre. This fact, therefore, speaks for the view that the yield is a result of the particular hybrid combination. The second fact which supports this view is that reciprocal hybrids[e] give essentially equal results. Thus, strains *A* and *B*, between which reciprocal hybrids were reported last year as yielding 74.4 and 78.6 bushels per acre, respectively, produced this year, in reciprocal hybrid families, exactly equal yields, namely, 79.8 bushels per acre. More conclusive still is the result from my best hybrid combination of the past season which has also been tested in reciprocal crosses; see figure. These crosses were made between a self-fertilized strain which had been selected continually to 16 rows and another which had been continually selected to 20 rows of grains on the ear. When the 16-rowed type was used as the mother, a yield of 98.4 bushels per acre was produced; when the 20-rowed type was used as the mother, a yield of 96.1 bushels per acre was produced. If the production of 98.4 bushels per acre had been purely a chance result which might by equal chance have appeared in any other strain, it is scarcely conceivable that the reciprocal should have so nearly approached the same extreme yield. The lower of these two yields, namely, 96.1 bushels, is 8 bushels per acre above the best yield produced during the same season by any continually cross-bred family of corn in my cultures. From all the results reported in this paragraph, it may be safely concluded that the production of the highest yield requires simply the finding of the best combination of parents and then repeating this combination year after year.

Several new evidences of the correctness of my view regarding the hybrid character of any ordinary vigorous corn plant have resulted from the past season's work. The assumption that self-fertilization results in the isolation of pure homozygous strains or biotypes and that the real purpose of cross-breeding is to secure the stimulus which comes from the heterozygous[f] association of alternative qualities from the two parents, requires that the first generation of the cross between two pure self-fertilized strains be relatively uniform, and that the second generation, in which these various hybrid qualities are rearranged in every possible combination, shall show greater diversity. I have now reared two families representing the second generation of such a cross between strains *A* and *B*. The variation in the number of rows in self-fertilized strains, in F_1 hybrids, and in F_2 hybrids, are shown in the following table:

[e] Formed by using one variety as the male parent in one cross and in another cross between the same varieties using the other variety as the male parent; thus *A* x *B* and *B* x *A* are reciprocal crosses, and their progenies are reciprocal hybrids.

[f] Having each separate characteristic derived from only one of the two parents.

TABLE 1.—*Variations in number of rows of grains in self-fertilized strains, and in F_1 and F_2 hybrids.*

Strain	Number of plants having ears with—						Yield—bushels per acre
	8 rows	10 rows	12 rows	14 rows	16 rows	18 rows	
Pure strain *A*.	66	5	3				14.2
Pure strain *B*.			10	18	12		12.1
A × *B* (F_1)..		2	18	9	2		79.8
B × *A* (F_1)..		19	58	9			79.8
A × *B* (F_2)..	3	32	57	16	2	3	61.0
B × *A* (F_2)		1	26	10	15	2	78.0

It is clearly seen that the F_2 ears show a greater range of variation in number of rows on the ear than those of the F_1. Since the empirical range of variation is capricious, and therefore is not a satisfactory measure of variability, I have calculated the mean, standard deviation, and coefficient of variation, for the numbers of rows on the ears of each of these six families. The constants thus derived are arranged for comparison in the following table:

TABLE 2.—*Mean, standard deviation, and coefficient of variation for number of rows on ear.*

Strain	Mean	Standard deviation	Coefficient of variation
Pure strain *A*....	8.297 ±0.055	0.705 ±0.039	8.498 ±0.474
Pure strain *B*....	14.100 ± .145	1.363 ± .103	9.664 ± .736
A × *B* (F_1)	12.710 ± .154	1.271 ± .109	9.998 ± .865
B × *A* (F_1)	11.767 ± .070	.956 ± .049	8.128 ± .421
A × *B* (F_2)	11.841 ± .110	1.733 ± .078	14.638 ± .671
B × *A* (F_2)	13.786 ± .108	1.464 ± .076	10.623 ± .559

It will be seen by noting the numbers in the last column that the inferences as to the relative variability of F_1 and F_2, drawn from the range of variation in the several families, were correct. This fact will be even more obvious if the coefficients of variation are averaged in pairs. In this way it may be found that these pure strains had an average variability of 9.081 per cent; their F_1 hybrids had an average variability of 9.063 per cent; and the F_2 hybrids an average variability of 12.63 per cent. My hypothesis requires that in the fertilization of the pure homozygous strains and in the production of the F_1 hybrids between them equal sperms meet equal eggs, so that in each case the resultant offspring should be exactly equivalent in all their hereditary qualities and the coefficients 9.081 per cent and 9.063 per cent must be measures of the non-hereditary variations or "fluctuations," while the coefficient 12.63 per cent in the F_2 is the result of the concurrence of hereditary and non-hereditary variations.

The number of rows on the ear, which is used here as a measure of the variability, is not in itself of great practical importance, of course, but the general question of variability, which is illustrated by this character, is of very great practical value. The possibility of attaining a fair degree of uniformity in the several desirable qualities will favor a more definite specialization of the crop to meet particular desired ends. Besides, any diversity in the qualities of the crop necessarily means a lower value in regard to each desirable quality than would be attainable if all individuals were brought up to a uniformly high standard.

Another very practical point in regard to this second generation and which emphasizes the importance of utilizing the F_1 plants for the crop each year, is seen by a comparison of the yields per acre (see Table 1) produced by the F_2 as compared with F_1. In both of the F_2 families the yield is less than the corresponding yield of the F_1 families, and when taken together this difference amounts to 8 bushels per acre. When considered in connection with the increased variability, this serves to further illustrate the point made in the last paragraph, namely, that the increased range of variation means a decreased yield.

The results of all my investigations to the present time, which seem to demonstrate that there are many distinct biotypes of corn continually mingled together in complex hybrid combinations, and that there is a stimulating effect of heterozygosis, may be summarized in the following statements. The first four of these propositions were demonstrated by data presented in my paper on "The composition of a field of maize"; the next four in "A pure-line method of corn breeding"; and the present paper gives further proof of the correctness of (6), (7) and (8), and adds the last four.

(1) The progeny of every self-fertilized corn plant is of inferior size, vigor and productiveness, as compared with the progeny of a normally cross-bred plant derived from the same source. This is true when the chosen parent is above the average conditions as well as when below it.

(2) The decrease in size and vigor which accompanies self-fertilization is greatest in the first generation, and becomes less and less in each succeeding generation until a condition is reached in which there is (presumably) no more loss of vigor.

(3) Self-fertilized families from a common origin differ from one another in definite hereditary morphological characters.

(4) Regression of fluctuating characters has been observed to take place away from the common mean or average of the several families instead of toward it.

(5) A cross between sibs[a] within a self-fertilized family shows little or no improvement over self-fertilization in the same family.

(6) A cross between plants belonging to two self-fertilized families results in a progeny of as great vigor, size, and productiveness, as are possessed by families which had never been self-fertilized.

(7) The reciprocal crosses between two distinct self-fertilized families are equal, and possess the characters of the original corn with which the experiments were started.

(8) The F_1 from a combination of plants belonging to certain self-fertilized families produces a yield superior to that of the original cross-bred stock.

(9) The yield and the quality of the crop produced are functions of the particular combination of self-fertilized parental types, and these qualities remain the same whenever the cross is repeated.

(10) The F_1 hybrids are no more variable than the pure strains which enter into them.

(11) The F_2 shows much greater variation than the F_1.

(12) The yield per acre of the F_2 is less than that of the F_1.

[Presented by Committee on Breeding Corn.]

A NEW ZEBRA HYBRID.

E. H. RILEY.

During the past few years investigations relative to the production of new and useful zebra-hybrids have been in progress at the Experiment Station (Bethesda, Maryland) of the Bureau of Animal Industry of the United States Department of Agriculture.

[a] Sibs are brothers or sisters or both brothers and sisters, *i. e.*, they are the offspring of one pair of parents, without reference to sex.