

# AMERICAN BREEDERS' ASSOCIATION

## VOLUME IV

Report of the Meeting Held at  
Washington, D. C., January 28-30, 1908,  
and for the year ending January 12,  
1908

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W. M. HAYS  
Secretary

H. H. MOWRY  
Assistant Secretary

WASHINGTON, D. C.

me to this opinion have been conducted also in other directions. Although I have published the trials in my book on plant breeding two years ago, I may be allowed to give the results here briefly: One cluster of alfalfa (*Medicago sativa*) enclosed did not give any seed; one cluster enclosed with honey bees in a large cage produced 19.2 per cent of seeds and a cluster on an undisturbed plant showed in the mean 68.8 per cent of seeds. The pollen of one flower can work on the stigma of the same flower. This has been shown by several experiments. In these the stigma has been rubbed and pollen of the same flower has been distributed by pinching the keel in accordance with Burkill's methods.

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### THE COMPOSITION OF A FIELD OF MAIZE.

By GEORGE H. SHULL, *Cold Spring Harbor, N. Y.*

While most of the newer scientific results show the theoretical importance of isolation methods, and practical breeders have demonstrated the value of the same in the improvement of many varieties, the attempt to employ them in the breeding of Indian corn has met with peculiar difficulties, owing to the fact that self-fertilization, or even inbreeding between much wider than individual limits, results in deterioration.

The cause of such a result is wholly unknown at present. The old hypothesis which sought an explanation of the deleterious effects of inbreeding in the inharmonious or unbalanced constitution produced by the accumulation of disadvantageous individual variations, can hardly stand in the face of the fact that a very large number of plants normally self-fertilize and a noteworthy few have even given up sexual reproduction entirely, without in the least degree lessening their physiological vigor and evident chances of success in competition with sexually produced plants. The dandelion is propagated parthenogenetically, i. e., its seeds are produced without fertilization, but only the advocate of an unwarrantable theory will maintain that this plant is on that account undergoing a process of deterioration which threatens it with summary extinction. Many species of violets produce most of their seeds from flowers that never open, and one of the most vigorous forms of the small-petaled evening primrose (*Oenothera cruciata*) does the same. In the breeding of tobacco, it is now well known that cross pollination within the limits of a single strain produces inferior offspring and only self-fertilization gives offspring of the highest degree of vigor, though hybrids between distinct strains of tobacco often display a vigor superior to that of either parental strain. Examples could be continued indefinitely, but even one instance in which long-continued inbreeding results in no injurious effects would be sufficient to discredit the old hypothesis.<sup>a</sup>

<sup>a</sup> For a good discussion of inbreeding see A. D. Shamel, on "The effect of inbreeding in plants," Yearbook U. S. D. A., 1905, pp. 377-392.

Some results of the pedigree-breeding of maize at the Cold Springs Harbor Station for Experimental Evolution have suggested a different explanation of the deterioration which has been universally observed in self-fertilized maize. For several years a series of investigations on Indian corn has been in progress at the Station, which involved parallel cultures of cross-pollinated and self-fertilized lines of as nearly equivalent parentage as possible. Although a study of the injurious effects of self-fertilization was not the aim of the investigation, it was immediately apparent in the smaller, weaker stalks, fewer and smaller ears, and the much greater susceptibility to the attacks of the corn-smut (*Ustilago maydis*). These results were almost as marked when the chosen parents were above the average quality as when they were below it, which in itself refutes the idea that the injurious effect is due to the accumulation of deficiencies possessed by the chosen parents.

All the cross-bred rows were similar in structure, vigor, variability, etc., but each self-fertilized row could be seen to differ from other self-fertilized rows in ways capable of description in fairly definite terms. Without entering into a description of all the different self-fertilized rows, a comparison between the two rows showing the greatest contrast will suffice to illustrate and serve as a basis for the conclusion to be arrived at. Following the method everywhere known among breeders as the "ear-row test," I planted parallel rows from ears having given numbers of rows of grains, one self-fertilized and one cross-fertilized ear from each row-class, i. e., one row was planted from a self-fertilized ear and beside it a row from a cross-fertilized ear having 10 rows of grains each; one row each was planted from two ears having 12 rows of grains; and so on.

Taking for comparison the row produced from a self-fertilized ear having 12 rows of grains, and the row produced from a self-fertilized ear having 14 rows of grains, the following differences were observed. In each row the variability was slight and the different qualities noted were characteristic of the entire row. The characters are given in contrasted pairs (designated as a and b), the qualities of the row originating from a 12-rowed ear (a) being given first in each pair: (a) Average height,  $6\frac{1}{4}$  feet, (b) average height,  $8\frac{1}{2}$  feet; (a) stalks moderately stocky, (b) stalks slender; (a) strong tendency to sucker near the ground, (b) no suckers; (a) leaves broad, dark green, and spreading, (b) leaves rather narrow, light green, not strongly spreading; (a) ears rather strongly diverging on long shanks, the latter usually as long as the internodes or longer, (b) ears erect on short shanks which are usually not over half the length of the internode; (a) husks with well-marked leafy appendages, (b) husks without appendages; (a) grains flinty, (b) grains starchy; (a) most common number of rows to the ear, 10, (b) most common number of rows, 14.

Most of the features here contrasted differ more or less in both cases from the cross-fertilized rows derived from the same original

stock. If self-fertilization is assumed to be the direct cause of any of the above characteristics of the one row, it is obviously illogical to attribute the opposite characteristic possessed by the other row to self-fertilization as a direct result. We come to the conclusion therefore that the observed differences between these rows are not *directly* attributable to self-fertilization, but must be due to an indirect effect. The distinguishing characters of these two rows are permanent inheritable qualities and each therefore represents what is known as an elementary species or biotype, as Johannsen has appropriately named the elementary form-group. Self-fertilization has simply isolated the two described forms by separating them from their hybrid combinations with other elementary species.

By rearing under different conditions or by selecting in different directions, it is possible to get a number of somewhat different strains within the same biotype; but, if we do not distinguish clearly between biotypes and these strains which differ only because of the different treatment they have received, only confusion can result. The difference between biotypes and the different strains of a single biotype lies in the nature of the characters which they possess as regards their heritability. Two biotypes will remain distinct from each other without resort to selection as long as they are kept pure-bred and are grown under like conditions, provided those conditions are sufficiently favorable generally to allow such characters as each possesses to develop normally. Two strains within the same biotype may be just as distinct from each other as some biotypes are, but when they are grown under the same conditions, constant selection will be required to keep them distinct, and if selection is omitted the distinguishing characteristics quickly disappear, usually within several generations. Such characters as can only be retained in a pure-bred race by constant selection or by culture under a particular set of external conditions are called fluctuating characters. Now, the inheritance of the fluctuations in any character follow a well-known law, usually known as Galton's law, whose essential feature is the lagging of the average value of single characters of the offspring behind the average of the parents with respect to the same characters. In other words, the average condition of children with respect to any fluctuating character, stands between the average condition of the parents and the average condition of the biotype to which they belong.

It follows from this law that when a given degree of a fluctuating condition is continuously selected under fairly constant cultural conditions, the ideal which is followed in the selection marks the theoretical limit of progress which will take place in the direction of that ideal, and there will always be some lagging back of the average condition, which lagging becomes less and less, the longer the selection is continued. To be specific, in the strain of maize with which I started the most frequent number of rows of grains per ear was 14. According to theory, if we are dealing here with a fluctuating character of a single biotype, we should never expect to be able

to exceed 20 rows on the average, by continuously selecting 20-rowed ears for seed, and in like manner we could never hope to get a strain whose average number of rows is less than 12, by continuously selecting 12, provided no change in the conditions of the culture tended to increase the number of rows generally in the former instance or to decrease them generally in the latter. Not the least significant contrast therefore between the two self-fertilized strains above described is that which deals with the number of rows of grains on the ears. In the case of the selection to 14 rows, the result shows a considerable predominance of 14 among the ears of this year's (1907) crop, nearly 40 per cent falling into that single class as compared with 38 per cent in the same class among the unselected population with which the experiments were begun four years ago. As 14 rows was the original prevailing class or "modal" class as it is called, it is quite what we would expect, to find that continued selection of this modal number has simply increased the relative value of class 14. In the case of selection to 12 rows on the other hand we are met with a surprise, for instead of the average number of rows being between 12 and 14 as the supposition that we are dealing with the fluctuations of a single elementary species whose normal mode is 14 rows, would lead us to expect on theoretical grounds, we find the prevailing class to be 10, with nearly 39 per cent in that class. Knowing that this row was the result of continued selection of 12-rowed ears, one would infer from the data of this year's crop that the original condition of the population—the normal condition for the race to which this row belongs—is probably 10 rows or possibly even 8 rows as the modal class, instead of the 14 rows possessed by the original stock from which all my cultures came. It is demonstrated therefore that these two rows belong to distinct races or elementary species of corn, though the original stock appeared to be fairly homogeneous. Most of the other self-fertilized rows showed by various marks that they were likewise to be considered members of distinct biotypes, instead of fluctuant parts of a single biotype as I believed they were when I began my investigation.

✓ } The obvious conclusion to be reached is that an ordinary corn-field is a series of very complex hybrids produced by the combination of numerous elementary species. Self-fertilization soon eliminates the hybrid elements and reduces the strain to its elementary components. In the comparison between a self-fertilized strain and a cross-fertilized strain of the same origin, we are not dealing, then, with the effects of cross and self-fertilization *as such*, but with the relative vigor of biotypes and their hybrids. The greater vigor of the cross-fertilized rows is thus immediately brought into harmony with the almost universal observation that hybrids between nearly related forms are more vigorous than either parent.

The components of a hybrid strain may be separated by means of cross-fertilization just as surely as by self-fertilization, if the parents of the cross are rigidly selected, generation after generation,

for definite characteristics; but the process of segregation will be in this case much slower, because in each cross some of the elements which were eliminated from the mother will be reintroduced by the father, and *vice versa*. For this reason the deterioration which comes from close inbreeding coupled with cross-fertilization should not be as rapid though just as sure as by self-fertilization. This again is in accord with such observations as are on record.

As most of the important characteristics for which the corn breeder strives are closely related to the question of physiological vigor the fundamental problem in breeding this plant is the development and maintenance of that *hybrid combination* which possesses the greatest vigor. Up to a certain point the common empirical method of selection will mostly eliminate only those components which do not contribute to the best possible result, and the more rigid the selection during this period the more rapid will be the improvement of the selected strain; but if the selection is continued in the same rigid manner after these inferior components are eliminated, it may lead to the loss of one after another of the component biotypes which had added to the physiological vigor of the strain and there will then be a resultant deterioration, especially if among the characteristics which guide the selection are some which are unrelated to vigorous growth. The fundamental defect in every empirical scheme of corn-breeding which simulates the isolation methods of the breeder of small grains, lies in the fact that there is no intelligent attempt in these methods to determine the relative value of the several biotypes *in hybrid combination*, but only in the pure state.

In the present state of our knowledge it is impossible to predict from a study of two pure strains what will be the relative vigor of their hybrid offspring. That is an important relation which future investigations must unlock for us. The problem of getting the seed-corn that shall produce the record crop, or which shall have any specific desirable characteristic combined with the greatest vigor, may possibly find a solution, at least in certain cases, similar to that reached by Mr. Q. I. Simpson in the breeding of hogs by the combination of two strains which are only at the highest quality in the first generation, thus making it necessary to go back each year to the original combination, instead of selecting from among the hybrid offspring the stock for continued breeding. That is, it may be found that the desirable combination of elementary species of Indian corn will be best attained by separating and recombining in some definite manner the different elementary species, or on the other hand it may be found that selection according to the empirical methods now most approved can be carried to a point at which the most efficient combination has been isolated from the less efficient components and may then be maintained only by a relaxation of the rigid selection.

Such questions as these cannot be settled in the study, but only in the field by means of carefully conducted experimentation.

I hope that those experiment stations which are dealing with the problems of the improvement of maize will undertake the solution of these fundamental problems and that as a consequence the technique of corn-breeding will find a basis in scientific knowledge quite different from the present more or less blind conflict between empirical selection and the little understood injurious effects of inbreeding. ✓

In conclusion I wish to say that the idea that in breeding maize we are dealing with a large number of distinct elementary species or biotypes is not presented here as a new idea, for De Vries, in his little book on "Plant breeding" presents this view, and Dr. East in a recent bulletin from the Connecticut Station has indicated the great complexity of the corn breeder's problems owing to the concurrence of these elementary species and fluctuating variations. I have aimed simply to point out how my own experience in corn-breeding supports the same view. I think, however, that the suggestion here made, that continuous hybridization instead of the isolation of pure strains is perhaps the proper aim of the corn breeder, is new and it is this view that I wish to submit for your consideration. NB

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## REPORT OF THE COMMITTEE ON ANIMAL AND PLANT INTRODUCTION.

DAVID G. FAIRCHILD, *Washington, D. C., Chairman,*  
 DR. A. D. MELVIN, *Washington, D. C.,*      PROF. W. N. HUTT, *Raleigh, N. C.,*  
 PROF. T. L. LYON, *Ithaca, N. Y.,*      PROF. A. G. McCALL, *Columbus, Ohio,*  
 PROF. N. E. HANSEN, *Brookings, S. Dak.*

OBJECTS: To investigate and report on ways and means of finding, securing and introducing new and valuable strains of animals and plants into the various localities and conditions for which they give promise of value.

(Report submitted by the Chairman.)

### THE DANGERS OF PLANT AND ANIMAL INTRODUCTION AND THE NEEDS OF RESEARCH QUARANTINE WORK.

The following report of the Committee, though prepared by the chairman, is endorsed through correspondence by the entire membership of the Committee.

Plant and animal introduction, or the exchange of plants and animals over the earth's surface, brought about by human beings, is increasing at a rate which corresponds with the increasing speed and decreasing cost of transportation.

The time is fast approaching when certain plants or animals can be sent around the world for a 6-cent stamp. Frogs, queen bees, fishes, and almost any of the ordinary plants grown can be shipped now by sample post. The Office of Seed and Plant Introduction of the Department of Agriculture has trees now growing in its greenhouses which came in as plants in a 12-ounce package