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THE SOURCES OF EFFECTIVE GERM-PLASM IN HYBRID MAIZE

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The last twenty years have seen a complete change in the corn-breeding methods of the U. S. corn belt. Since 1924, when "Copper Cross" was first offered for sale in Iowa[1], hybrid corn has almost entirely supplanted open-pollinated varieties in that area. In the summer of 1944 one could drive across the state without seeing a single field of open-pollinated corn, and in order to find one of any size for study it was necessary to make an intensive search. The total annual yield of hybrid corn in the United States is now about two billion bushels, and the sale of the hybrid seed grosses well over fifty million dollars annually. These are matters of common knowledge to corn breeders but they need to be discussed in terms of population genetics, since the problems they raise are of theoretical as well as practical importance.

In terms of gene combinations and their distributions, the whole genetic pattern of *Zea Mays* in the United States has been catastrophically overhauled in the last two decades. To describe precisely what has happened to the maize germplasm of the U. S. corn belt and to predict its probable effects is a gigantic problem in population genetics. This paper is an attempt to look at the problem as a whole and to give it a preliminary discussion; to estimate some of the facts and to put them on record. Some of these facts are every-day matters to those in the seed-corn business, and it may seem trivial to record them. For some of the others even the estimates must necessarily be so controversial as to be scarcely more than one man's opinion. In gathering the information and discussing its significance I have relied almost wholly upon the staff of the Pioneer Hi-Bred Corn Company. Mr. Raymond Baker, the manager of the breeding department, and his assistants (Messrs. Karl Jarvis, Sam Goodsell, and James Weatherspoon) have put their knowledge and records at my disposal. They also took the trouble to locate Mr. Hershey and obtain the interviews reproduced below. I have done no more than to phrase the problem and to write the paper. If the conclusions, however, are out of line with the actual facts, the fault is entirely my own.

Before discussing gene-pattern distributions it will be necessary to describe the method of producing and marketing modern hybrid seed corn for those unfamiliar with the process. Maize is normally open-pollinated and the plants under such conditions are highly heterozygous. In producing hybrid corn, uniform inbred lines are produced by controlled self-pollinations or sib-pollinations until practical homozygosity has been reached (usually six or more generations). Most of the inbreds produced in this way are discarded or eliminate themselves by their sterility. The few which remain are tested in crosses with each other until sets

[1] Iowa Seed Co. Catalogue. 1924, p. 30.

of four inbreds are obtained which make an effective "four-way" cross. (Single crosses and top-crosses are also produced but the bulk of the business is now in four-way crosses.) Let us designate the four in any one cross as 'A', 'B', 'C', and 'D'. 'A' and 'B' are crossed together the first year in one plot (by detasseling, i. e., removing the male inflorescence from one parent) and 'C' and 'D' in another. The following year hybrid 'AB' is interplanted with hybrid 'CD'. The present practice is usually to have this done under contract by skilled farmers, who detassel either 'AB' or 'CD', as the case may be, and the resulting crop ('AB' x 'CD') is marketed as seed corn. A large part of the effort in modern corn breeding is spent in maintaining and improving the inbred lines upon which the business is based. In addition to the purely negative effort of roguing, the development of "Convergent Improvement" by Richey and Sprague[2] has resulted in what are termed in the trade as "second cycle" and "third cycle" inbreds. These are produced as follows: Let us suppose that inbred 'XYZ' is useful in a particular set of crosses except that it has certain obvious faults. It might, for example, have such weak roots or short ears that even its hybrid offspring are affected; or it might, on the other hand, be so weak as to be difficult to raise in quantity year after year. In a convergent improvement program 'XYZ' is therefore crossed with a series of other inbreds (or with an open-pollinated variety) and the resulting hybrids are backcrossed to 'XYZ' again. From these three-quarter bloods, by inbreeding and selection, a series of second-cycle inbreds is obtained, and if the work has been well done at least one of them may have most of the advantages of 'XYZ' without all of its defects.

Such is the present system. By it, effective gene combinations are discovered in the breeding plots of the experiment stations and corn-breeding companies and are propagated for sale to the actual farmer. Where did these gene combinations come from on the whole? Do they trace back to many open-pollinated varieties or to a few, and how does the present process of obtaining effective gene combinations compare with that in vogue before the hybrid-corn business came into being? To obtain an approximate answer to these questions 6 widely sold four-way hybrids of known composition were listed. They are all outstanding commercial successes and have been very widely planted. They might, in one year or another, have accounted for one-quarter of the total corn crop in central Iowa. Since all are four-way crosses we might have expected as many as 24 inbred lines; actually only 18 are involved, the inbreds known as Ill A, Iowa 205, R-4, Wf-9, and Ill-HY having entered into two or more crosses. When the 18 inbreds are tabulated according to the open-pollinated variety from which they were derived, we find the whole group came from only 3 open-pollinated varieties! Twelve are from some strain of Reid Yellow Dent, 3 from Krug, and 3 are from Lancaster Surecropper, as follows:

[2] Richey, Frederick D., and George F. Sprague. Experiments on hybrid vigor and convergent improvement in corn. U. S. Dept. Agr., Tech. Bull. 267:1-22. 1931.

REID YELLOW DENT: HY, 38-11, WF-9, Os 420, Os-426, Ia 205, R-4, Ill A, Idt, Ind Fe, TEA, LE-773.

KRUG: K-77, K-187, K-159.

LANCASTER SURECROPPER: L-317, L-289, LDG.

The way in which the inbreds are combined is also significant. The six four-way hybrids under consideration were combined as follows:

3 hybrids: 3 Reid inbreds and 1 Lancaster inbred.
1 hybrid: 2 Reid inbreds, 1 Lancaster inbred and 1 Krug inbred.
1 hybrid: 2 Reid inbreds and 2 Krug inbreds.
1 hybrid: 4 Reid inbreds.

The above estimate is from only one section of the corn belt but it is in line with what is generally known. The bulk of the inbreds now being most widely used were derived from very few open-pollinated varieties. In the above sample only 3 open-pollinated varieties were represented—Reid Yellow Dent, Lancaster Surecropper, and Krug. The last of these is little more than a sub-strain of Reid. According to Wallace and Bressman[3], it was originated by George Krug of Woodford, Illinois, who crossed Gold Mine with a Nebraska strain of Reid and selected for a smoother rather small-eared utility corn.

We are faced with the remarkable fact therefore that much of the corn now being grown traces back mainly to two open-pollinated varieties. It is not surprising to find Reid inbreds high on the list since that variety in one sub-strain or another dominated the corn belt when hybrid corn was being evolved. Popularity might also help to explain the prevalence of Krug inbreds, this variety having been very extensively grown in the central corn belt immediately before the advent of hybrid corn on a commercial scale. However, these were by no means the only varieties grown commercially at that time. As late as 1906, when E. M. East was just starting his work with inbreeding, 11 varieties of yellow dent corn were offered for sale by the Iowa Seed Co. in Des Moines. The standard authorities on corn growing, Wallace and Bressman[3], in 1937 listed the following open-pollinated yellow dents as commercially important in the central corn belt: Reliance, Leaming, Gold Mine, Ioleaming, Golden King, in addition, of course, to Reid and Krug. Some of these are known to have been inbred fairly extensively, yet only the Reid and Krug inbreds have held up under commercial competition. Popularity of the open-pollinated variety certainly would not explain the success of Lancaster Surecropper inbreds. This variety was of such minor importance in the corn belt that Wallace and Bressman merely list it among the "also-rans" without any further comment. It was not until its inbreds demonstrated their usefulness that it became a real factor there. Its excellence as a source of good inbreds is well known among corn-breeders. In addition to the inbreds listed above a number of other excellent ones have been derived in whole or in part from

[3] Wallace, Henry A., and Earl N. Bressman. Corn and corn growing. New York. 4th ed. 1937 (see p. 208).
[3] *loc. cit.*

this variety, and Dr. F. D. Richey informs me that at least three well-known inbred lines came from a single open-pollinated ear of Lancaster Surecropper. It is also generally appreciated that the inclusion of a Lancaster inbred in a four-way hybrid steps up productivity, and it will be noted that half of the hybrids listed above were so constituted.

It is apparently true therefore that the inbred strains in use at the present time are far from a random sample of the open-pollinated varieties which immediately preceded them. Many of the minor varieties of yellow dent are not represented by inbreds derived from them. The germ-plasm of two open-pollinated varieties predominates in modern inbreds, and one of these varieties, Lancaster Surecropper, is represented out of all proportion to its previous importance in this region. If these phenomena are general and not merely a chance result, they raise a number of interesting questions. A few of these can be suggested here: (1) If Lancaster Surecropper is really an especially effective source of good inbreds is there anything in its history to suggest why this might be so? (2) How do the frequency and the pattern of effective gene combinations in hybrid maize compare to those in the open-pollinated varieties? How much of the apparent progress is merely the uncovering of progress already achieved by the originators of Reid, Krug, and Lancaster Surecropper? Is potentially effective germ-plasm being lost under the present system?

To question number 1 we can give a partial answer. Lancaster Surecropper was originated in Pennsylvania by Mr. Isaac Hershey and his father. The former is still living, and Mr. Karl Jarvis and Mr. James Weatherspoon of the Pioneer Hi-Bred Corn Company visited him in September of this year and have kindly prepared accounts of the interview. Mr. Jarvis's is printed in its entirety; supplementary and confirmatory evidence from Weatherspoon's report is given in brackets:

> In 1860 (when Isaac Hershey was eight years old) a neighbor, Henry High of Byerstown, Lancaster Co., Pa., received a packet of a variety of corn from the Patent Office. Mr. High and several of the neighbors liked this new variety and some of them, especially Jacob Hershey (Isaac Hershey's father) and Jacob's brothers, began to depend on it for their main crop. It was described as a rather small, rather slender-eared corn, very variable in type [but a good yielder]. In general, it was rather smooth, mainly one-eared, and rather early. From Mr. Hershey's description I got the impression that it must have been either a semi-flint or else a flint-dent hybrid which was still segregating. One of the common segregates was a "lilac colored" ear, which caused one of Isaac Hershey's uncles to nickname it "Lilac corn."
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> The common corn of the community was a large, late, rather coarse type with medium to rough kernels, rather resembling Golden Queen according to Mr. Hershey. The new variety, "Lilac corn," was such a contrast and looked so much smaller, even though very productive, that most farmers laughed at it and called it "popcorn." The Hersheys began selecting later strains and blending in a little seed from a few selected ears of the larger, later and rougher local varieties. This blending process, which Isaac Hershey called "dipping," was repeated a number of times [by his father] before Isaac started farming, but he does not know just how many times. Isaac estimated that he himself had "dipped" Lancaster Surecropper six or eight times with various varieties including once with some white corn. "Dipping" consisted of taking two or three selected, high-yielding ears, shelling them, and then mixing the seed thoroughly throughout his pile of shelled seed corn. The last dip was about 1910.

One year, Isaac Hershey planted a field to Golden Queen. The stand was very poor so he replanted with Lancaster Surecropper. Since he saved some seed corn from this field, he undoubtedly introduced considerable Golden Queen into his variety. In addition, after his neighbors began to get seed from him and then grow their own strains, Isaac Hershey would watch their fields and when a strain had been carried on for eight to ten years and seemed to be desirable, he would buy back about one-half bushel of selected seed and blend it into his own.

At first there was no attempt to make the variety uniform. In fact, if anything, they (Isaac and Jacob, and Noah, son of Isaac) preferred to keep it "mongrelized." In seed selection, in general, he preferred a medium-length ear, but would save any ear irrespective of type which was, as he said, "a good business ear that would put lots of pork on a hog." He insisted on well-matured, sound ears with clean shanks and no mold or "silk cut." He said he could recognize the latter by slightly protruding kernels. This insistence on a sound, well-matured ear earned it the name of "Surecropper," since it always matured while other later, softer varieties did not. [He did pick ears with good solid, clean shanks, evidently ears with a reasonable amount of length. In regard to length, he did say this—that he kept an ear for seed if it was somewhat short, provided that the kernels were not filled out clear over the end. He seemed to think if there was still bare cob sticking out at the end the ear still had considerable chance to develop more length. However, if it was a short ear and filled out to the end, he believed there wasn't any possibility of getting any length out of it.] No plant type selection was made because, "I never saw a good ear of corn on a poor corn plant." His only regret was that this type of selection had given a weak-rooted variety. However, his son, Noah Hershey, had later selected for a larger ear and a better root system by making field selections.

When Lancaster Surecropper became popular and seedmen began buying seed from Mr. Hershey, they continually put pressure on him to select for uniformity and a longer, more showy ear type. He refused at first, but finally gave in, and, as he said, "spoiled Surecropper and cut off about 10 to 15 bushels per acre at least." This "spoiling" occurred about 30 years ago. Some years ago Pennsylvania State College asked him to select a sample of Lancaster Surecropper representing the original range of types as he originally grew the variety, before he "spoiled" it. This was done and sent to them and may possibly still be stored somewhere at State College. [In the early days with the development of Lancaster Surecrop, Hershey didn't go in for selling seed very much. He was mostly interested in a high-yielding corn. However, as the fame of his corn spread seedmen wanted to sell Lancaster Surecropper, but they, of course, insisted that he dress the corn up—that is, select for uniformity of ear type. So, along about 1910, he began to sell quite a bit of seed and he stopped "dipping" his corn and began to select for uniformity. He feels very strongly himself that at this stage he began spoiling his corn. In fact, he said that he wrote to a worker in the U. S. D. A. and told him how he spoiled Lancaster Surecrop, and that was by selecting for uniformity as to ear type and dressing it up to suit the seedsmen.]

Incidentally, Mr. and Mrs. Hershey mentioned as a very profitable year one in which they sold 1,000 bushels of seed at $3.00 per bushel. For super-select seed such as he himself would plant, the charge was $5.00 per bushel. Since ordinary corn was bringing 50 to 60 cents per bushel at that time, they were very glad to get such prices. At various times Lancaster Surecropper was shipped to Europe, China and frequently to South America so its germ-plasm may well be scattered throughout the world.

Mr. Hershey's opinion of the bad effects of selection for uniformity is interesting because it parallels conclusions reached from a morphological study of recombination in species crosses[4]. From both theoretical and experimental considerations it was shown that the achievement of optimum recombinations in crosses between species or races is a difficult and long-time affair. Relatively little progress can be made in any one generation. The practical problem involved is to be able to work towards the desired end, generation by generation, without losing potentially valuable genes before they are incorporated with the other superior ones. In the paper referred to, it was suggested that simultaneous selection for performance and for morphological diversity might solve this dilemma. It is interesting to find that a family of successful corn-breeders has come to

[4] Anderson, Edgar. Recombination in species crosses. Genetics **24**:668-698. 1939.

rather similar conclusions on the basis of practical experience. It should be possible to test these conclusions experimentally. Parallel convergent improvement experiments[5] could be set up with and without selection for morphological diversity during the generations of selection and inbreeding. If Mr. Hershey and I are right a more complete synthesis of desirable genes could be achieved by considering the general morphology of the plants chosen as parents in each generation as well as their performance. (See Anderson, *loc. cit.*, pp. 694-695, for a more complete discussion.)

The second set of questions (concerning the pattern of gene combinations) cannot be answered at the present time, nor have I found any general unanimity of opinion among maize breeders or maize geneticists. We know virtually nothing about the breeding structure (or, to put it in other words, the population genetics) of a field of maize. On this fundamental subject almost nothing has been written. The title of Shull's pioneer paper[6] defined the problem but his discoveries helped to initiate four decades of more pressingly practical research. Jones and others have shown that mating is not at random in open-pollinated fields[7]. One can scarcely visit a maize-breeding farm without noticing a number of very suggestive phenomena which bear on the problem, yet at present we are almost without facts. We do not even have a simple plant-by-plant description of a single field of any open-pollinated variety, let alone an estimate of how the individuals of one generation are related genetically to those of the next. Yet before we can give reasoned answers to such questions as those raised above, we must have fairly reliable estimates on these matters.

To achieve optimum results with hybrid-corn breeding we must understand at least approximately the population genetics of a field of open-pollinated maize. We shall have to move swiftly if the desired information is to be recorded; open-pollinated fields are almost a thing of the past. It may be necessary for breeders of hybrid corn to subsidize highly skilled farmers as raisers of open-pollinated corn until we have at least an estimate of when, where, and how the majority of the useful gene combinations in hybrid corn were accomplished.

SUMMARY

1. An attempt was made to determine which open-pollinated varieties of maize have contributed most germ-plasm to modern four-way hybrids.

2. For central Iowa it was shown that one group of highly successful hybrids was made up wholly of inbreds from three open-pollinated varieties, Reid, Krug, and Lancaster Surecropper.

3. Evidence is given for the particular excellence of this latter variety as a source of hybrid germ-plasm. The history of the variety was obtained from Isaac

[5] Richey and Sprague, *loc. cit.*

[6] Shull, George H. The composition of a field of maize. Amer. Breed. Assoc. Rept. 4:296-301. 1908.

[7] Jones, D. F. Selective fertilization. 163 pp. Chicago. 1938.

Hershey, one of the originators, and his methods of selection are described.

4. Two questions are discussed in the light of the above information: (a) the possible advantages of selecting simultaneously for performance and morphological diversity; (b) the need of more exact information on population structure in *Zea Mays*. It is concluded that, for the sake of understanding and improving modern hybrid maize, it will be necessary to investigate the breeding structure of representative open-pollinated varieties.