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Chapter 2

Beginnings of the Heterosis Concept

The heterosis concept was first definitely recognized in the work with hybrid corn. Before attempting to define this concept, however, we will take a brief look at some of the observations of early workers which indicated the probable presence of heterosis, and where recognition of heterosis as an important biological principle might have been expected.

The first hybridizer of plants, Dr. J. G. Koelreuter, noted some impressive examples of excessive luxuriance in his Nicotiana hybrids. These were isolated observations which suggested no theory as to why these hybrids should exceed their parents in size and general vigor. Koelreuter cannot be said to have had a heterosis concept. Probably every conscious producer of hybrids since Koelreuter's time has made similar observations of the excessive vigor of some hybrids over their parents, so that such hybrid vigor has ceased to cause surprise. But the general acceptance of hybrid vigor as a normal phenomenon did not establish a heterosis concept. It was merely the summational effect of oft-repeated experience.

Thomas Andrew Knight noted the deterioration of some of the old standard horticultural varieties, and concluded that such varieties have a natural life-span and gradually decline as the result of advancing senility. He saw that such decline makes it necessary to develop new varieties which will start off with the vigor of youth. Although Knight himself produced many such new varieties, some of which were produced by hybridization, it is not apparent that he thought of hybridization as an agency for the production of such new vigor. Although he advanced a theory concerning physiological vigor and its decline, he did not recognize the heterosis concept.

Luther Burbank also produced numerous varieties, often following intentional hybridizations, and it is easy to recognize heterosis as a potent factor in the remarkable values displayed by many of these new varieties. But while Burbank made great use of hybridizations in his plant breeding work, he did not recognize hybridization, as such, as the source of the large size and remarkable vigor of his new varieties. For him the role of hybridization, aside from the bringing together of desirable qualities possessed separately by the two chosen parents, was merely the "breaking of the types." In this way the variability in subsequent generations was greatly increased, thus enlarging the range of forms from among which to select the most desirable for recognition as *New Creations*.

There are many other important observations and philosophical considerations that bear a close relationship to our current understanding of heterosis, and which antedated the recognition of heterosis. It would take us too far afield, however, to discuss these related observations at length. We can make only this passing reference to the highly significant work of Charles Darwin in demonstrating that cross-fertilization results, in many cases, in increased size, vigor, and productiveness as compared with self-fertilization or with other close inbreeding within the same species.

Darwin did not recognize this increased vigor as identical with *hybrid vigor*, nor specifically attribute it to the differences between the uniting gametes. To him it only demonstrated a method which would inevitably preserve by natural selection any variation that might occur—whether mechanical or physiological—which would make cross-fertilization more likely or even an obligate method of reproduction. With heterosis established as a recognized pattern of behavior, or type of explanation, we can now interpret Darwin's demonstrated superiority of crossbreds as examples of the occurrence of heterosis. We may go even further and include the whole field of sexual reproduction in showing the advantages of heterosis. These result from the union of two cells—the egg and the sperm—extremely differentiated physiologically, and in all dioecious organisms also differentiated genetically.

Let us briefly consider several investigations which foreshadowed the procedures now used in growing hybrid corn—for somewhere in the course of this work with corn the heterosis principle was first definitely recognized.

Two techniques are characteristically associated with the work of the "hybrid-corn makers." Uncritical commentators have mistakenly considered these techniques synonymous with the development of the hybrid-corn program itself. These are (*a*) cross-pollination by interplanting two different lines or varieties, and the detasseling of one of these lines which then supplies the seed to be planted; and (*b*) controlled self-pollination.

In deciding what part these two methods played in the development of the heterosis concept, we must first consider why these methods were used by various workers and how their use affected the experimental conclusions.

Dr. William J. Beal, of Michigan Agricultural College, apparently was the first to make extensive use of controlled cross-pollination in the breeding of corn. Beal was a student of Asa Gray from 1862 to 1865, when the latter was in active correspondence with Charles Darwin. Darwin was beginning the studies on cross- and self-fertilization, which were reported in 1877 in an important book on the subject. It has been thought that Darwin's views on the significance of crossbreeding may have been instrumental in inciting and guiding Beal's experiments in the crossing of corn. There seems to be no supporting evidence, however, for such a surmise.

Beal's lectures before various farmers' institutes stressed the importance of being able to control the source of the pollen, so that the choice of good ears in the breeding program would not be nullified by pollen from barren stalks and other plants of inferior yielding capacity. On this point Professor Perry Greeley Holden, for several years assistant to Dr. Beal, has stated that controlled parentage, not heterosis, was the aim of the corn breeding program at Michigan and at Illinois before 1900.

In 1895 Holden was invited by Eugene Davenport to become professor of agricultural physics at the University of Illinois. Davenport also had served for several years as assistant to Dr. Beal at Michigan. Like Holden, he was very enthusiastic about the importance of Beal's program, so it was natural that Davenport and Holden should agree that corn improvement be a major undertaking of Holden's new department at the University of Illinois. On initiating this work at the University of Illinois, they learned that Morrow and Gardner already had tested Beal's variety crossing at Illinois before they got there, and with confirmatory results. Concerning the motivation of all this early work, both at Michigan and at Illinois, Holden says:

> 1. Hybrid corn [as we know it today] was unknown, not even dreamed of, previous to 1900. 2. *Controlled parentage* was the dominant purpose or object of this early corn improvement work.

Holden thus makes it clear that while heterosis was at play in all of this early work, it was not the result of, nor did it result in, a *heterosis concept.*

I refer next to the matter of inbreeding, which some writers have confused with the crossing that has brought the benefits of heterosis. Enough selfing had been done with corn prior to 1900 to convince all of those who had had experience with it that it resulted in notable *deterioration.* The results of these early observations are aptly summed up by Holden in the statement that "Inbreeding proved to be disastrous—the enemy of vigor and yield." Nowhere, so far as I have been able to determine, did any of the early inbreeders discover or conceive of the establishment of permanently viable pure lines as even a secondary effect of inbreeding.

In 1898 A. D. Shamel, then a Junior in the University of Illinois, offered himself to Holden as a volunteer assistant without pay. He did so well that when Holden severed his connection with the University in 1900, Shamel was appointed his successor, and continued in this capacity until 1902. He then transferred to the United States Department of Agriculture and did no further work with corn. In Shamel's final report of his own corn experiments (1905), he laid no stress on the positive gains which resulted from crossbreeding, but only on the injurious effects of inbreeding. His "frame of reference" was the normally vigorous crossbred (open-pollinated) corn, and the relation between self-fertilized and cross-fertilized corn was that of something *subtracted* from the crossbred level, not something *added* to the inbred level. The prime objective in a breeding program, he said, "is the prevention of the injurious effects of cross-fertilization between nearly related plants or inbreeding." In summing up the whole matter he said:

> In general, . . . it would seem that the improvement of our crops can be most rapidly effected with permanent beneficial results by following the practice of inbreeding, or crossing, to the degree in which these methods of fertilization are found to exist naturally in the kind of plant under consideration.

This means, for corn, practically no self-fertilization at all, and makes it obvious that, at least for Shamel, the heterosis concept had not yet arrived.

Edward Murray East was associated with the corn work at the University of Illinois, off and on, from 1900 to 1905. He worked mainly in the role of analytical chemist in connection with the breeding program of C. G. Hopkins and L. H. Smith. He must have been familiar with the inbreeding work of Shamel, if not with that of Holden. It is generally understood that he did no self-fertilizing of corn himself, until after he transferred to the Connecticut Agricultural Experiment Station in 1905. Some of his inbred lines at Connecticut may have had the inbreeding work at Illinois back of them, as he secured samples of seeds of the Illinois inbreds sent to him by Dr. H. H. Love, who assisted him for one year and succeeded him at Illinois. But according to his subsequently published records these older inbred lines did not enter to any important extent into his studies in Connecticut.

As reported in *Inbreeding and Outbreeding* (East and Jones, pp. 123, 124), "The original experiment began with four individual plants obtained from seed of a commercial variety grown in Illinois known as Leaming Dent." Table III (p. 124) presents the data for these four lines for the successive years from 1905 to 1917, and clearly indicates that the selfing was first made in 1905. East's work is so adequately presented in this excellent book that it seems unnecessary to comment on it further here except to recall that, as shown by his own specific statements, my paper on "The composition of a field of maize" gave him the viewpoint that made just the difference between repeated observations of heterosis and the heterosis concept. In proof of this we have not only his letter to me, dated February 12, 1908, in which he says: "Since studying your paper, I agree entirely with your conclusion, and wonder why I have been so stupid as not to see the fact myself"; but we also have the published statements of his views just before and just after the publication of my paper. Thus, we read in his Conn. Agr. Exp. Sta. Bull. 158, "The relation of certain biological principles to plant breeding," which was published in 1907, only a few months before I read my paper in his presence in Washington, D.C., what seems like an echo of the final conclusion of Shamel, above cited. In this bulletin East urged that "corn breeders should discard the idea of forcing improvement along paths where nothing has been provided by nature," specifically rejecting a program of isolation of uniform types because of a "fear of the dangers of inbreeding," adding that he was "not able to give a reason for this belief beyond the common credence of the detrimental effects of inbreeding." He returned to this problem of the deterioration due to inbreeding in his Annual Report to the Conn. Agr. Exp. Sta. for 1907–8, prepared in 1908, with my paper before him. In this report he says:

> I thought that this deterioration was generally due to the establishment and enhancement of poor qualities common to the strain. . . . A recent paper by Dr. George H. Shull ("The composition of a field of maize") has given, I believe, the correct interpretation of this vexed question. His idea, although clearly and reasonably developed, was supported by few data; but as my own experience and experiments of many others are most logically interpreted in accordance with his conclusions, I wish here to discuss some corroboratory evidence.

We have thus far failed to recognize the existence of a general heterosis concept among plant breeders, prior to the reading of my paper on "The composition of a field of maize" in January, 1908, even when they were using the methods of inbreeding and controlled crossing in which such a concept could have developed. I must mention, however, a near approach to such a concept from the side of the animal breeders. Before the American Breeders' Association, meeting in Columbus, Ohio, 1907, Quintus I. Simpson, an animal breeder from Bear Creek Farm, Palmer, Illinois, read a paper which definitely recognized hybridization as a potent source of major economic gains beyond what could be secured from the pure breeds. The title of his paper, "Rejuvenation by hybridization," is more suggestive of the views of Thomas Andrew Knight than of the current students of heterosis, but the distinction seems to me to be very tenuous indeed.

Although I listened with great interest to Simpson's paper, I do not think that I recognized any direct applications of his views to my results with maize. I was working within the material of a single strain of a single species, and not with the hybridizations between different well established breeds to the superiority of whose hybrids Simpson called attention.

Students may make varying estimates as to how closely the work of men to whom I have referred approached the heterosis concept as we understand it today. But there can be no doubt that there was a *beginning* of this concept in the course of my own experiments with corn. At the beginning of 1907 I had not the slightest inkling of such a concept. By the end of 1907 I had written the paper that brought such concept clearly into recognition. At that time I knew nothing of the work of Beal, Holden, Morrow and Gardner, McCluer, Shamel or East, in the selfing and crossing of the maize plant. This will become obvious as I explain the motivation and plan of procedure of my corn experiments.

Upon arriving at the Station for Experimental Evolution at Cold Spring Harbor on May 2, 1904, I found the laboratory building unfinished. It was in fact not ready for occupation until the following November. The potentially arable portion of the grounds was in part a swampy area in need of effective provision for drainage. The rest had been at one time used as a garden. But it had lain fallow for an unknown number of years, and was covered with a heavy sod that would need a considerable period of disintegration before it could be used satisfactorily as an experimental garden. The total area available was about an acre.

In the middle of this small garden plot was a group of lusty young spruce trees. These had to be removed in order to use the area for experimental planting the following spring. The ground was plowed, disked, and planted as soon as possible to potatoes, corn, sorghum, buckwheat, sugar beets, turnip beets, and many kinds of ordinary garden vegetables. None of them were designed as the beginning of a genetical experiment, but only as an excuse for keeping the ground properly tilled so it would be in best possible condition for use as an experimental garden later. Due to this fact, no adequate record was made of the origin of the several lots of seeds which were planted. This is unfortunate in the several cases in which some of these cultures did provide material for later experimental use.

There were two cultures of corn, one a white dent, the other a Corry sweet corn. These two varieties were planted at the special request of Dr. Davenport, who wished to have available for display to visitors the striking illustrations of Mendelian segregation of starchy and sugary grains on the single ears of the crossbred plants. I planted the white dent corn with my own hands on May 14, 1904, and must have known at the time that the grains came from a single ear. Although I have found no contemporary record to that effect, I am now convinced from a well-remembered conversation with Mrs. Davenport, that this ear of white dent corn came from the farm of her father, Mr. Crotty, who lived near Topeka, Kansas.

When I was last in Ames, after almost forty years of devotion to other lines of genetical experimentation, my memory played me false when Professor J. C. Cunningham asked me about the source of the foundation stock for my experimental work with corn, and I told him that my studies on corn began with some corn I had purchased in the local market as horse feed. I repeated the same unfortunate misstatement to several other highly reputable historians of science. I deeply regret this error because these men were trying so hard to get the record straight. My recollection was restored by finding the statement at the very beginning of the record of my formal corn studies under date Nov. 7, 1904: "Counted the rows on the ears of White dent corn raised in Carnegie garden this year." In fact, as I think of it now, I doubt that I could have bought white dent corn in the feed market of Long Island at that time.

I planted the Corry sweet corn on May 17. On July 18 I bagged the corn preparatory to making crosses between the two varieties. This crossing was carried out on the Corry sweet on July 25, and the crosses for the reciprocal combination were made on July 27 and 28. These were the first controlled pollinations I ever made in corn, and they were not part of a scientific experiment.

My interest in investigating the effects of cross- and self-fertilization in maize arose incidentally in connection with a projected experiment with evening primroses (Oenothera) to determine the effect, if any, of these two types of breeding on the kinds and the frequencies of occurrence of mutations. A critic of De Vries's mutation theory had urged that the mutations discovered by De Vries in *Oenothera lamarckiana* were artifacts produced by selfing a species which, in a natural state, had been always cross-fertilized. I developed a program to put this question to a crucial test. Then, it occurred to me that it would be interesting to run a parallel experiment to test the effects of crossing and selfing on the expressions of a purely fluctuating character. Since I had available this culture of white dent maize, I chose the grain-row numbers on the ears of corn as appropriate material for such a study. The Oenothera problems thus begun, continued to be a major interest throughout my genetical career, but it is not expedient to pursue them further here. It is important, however, to keep them in mind as a key to my motivation in launching my studies with maize.

In this double-barreled exploration of the genetical effects of cross-fertilization *versus* self-fertilization, I had no preconception as to what the outcome of these studies would be in either the mutational or the fluctuational field. Certainly they involved no plan for the demonstration of distinctive new biotypes, nor any thought of the possible economic advantages of either method of breeding. I was a faithful advocate of the early biometricians' slogan: *Ignoramus, in hoc signo laboremus.* Until the middle of summer of 1907, certainly, I had no premonition of the possible existence of a heterosis principle which would have important significance either scientifically or economically. I was forced to recognize this principle by direct observations of manifestations in my cultures which had not been anticipated, and therefore could not have been planned for.

Let us proceed then to a description of my experiments with corn which forced the recognition of this important phenomenon. The culture of white dent corn which we had growing, almost incidentally, on the Station grounds that first year, showed no variations that seemed to indicate the presence of any segregating characteristics. It appeared to be ideal material for the study of fluctuations of so definite and easily observed a quantitative character as the number of the rows of grains on the ears. The crop was carefully harvested and placed in a crib. On November 7, 1904, I counted the rows of grains on every ear, with the result shown in figure 2.1. The 524 ears ranged over the seven classes from 10-rowed to 22-rowed. The most populous classes were the 14-rowed with a frequency of 201, and 16-rowed with 153 individual ears. The mean was 14.85 ± .06.

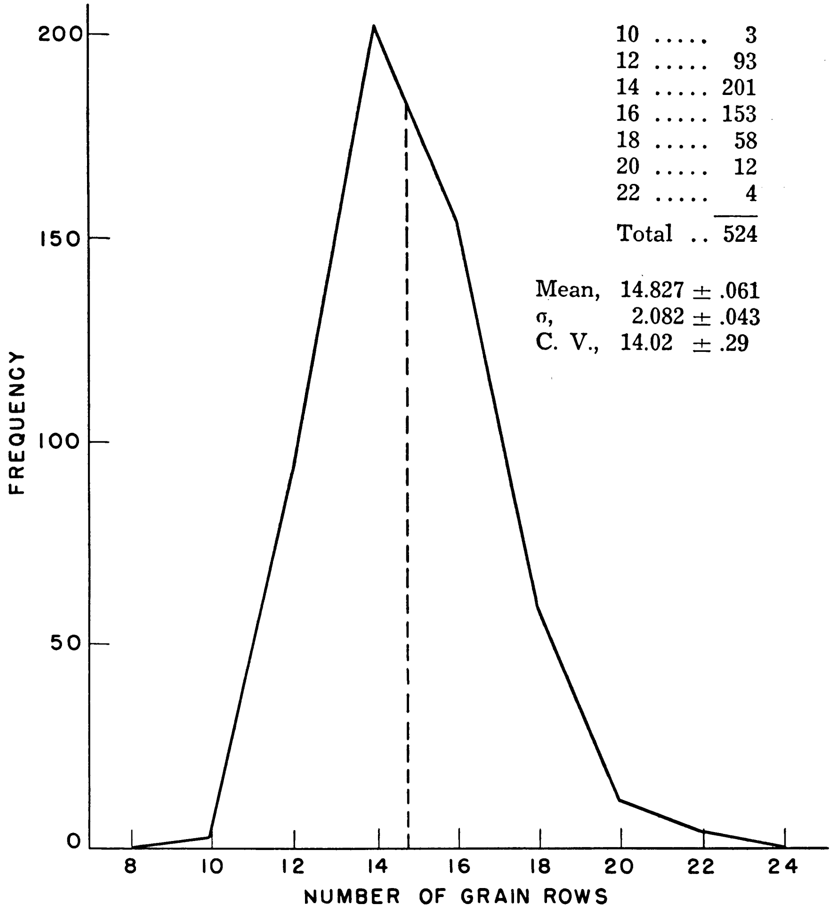

FIG. 2.1—Frequency curve of grain-rows of 524 ears of white dent corn. The total progeny of presumably a single ear of corn received from the Crotty farm near Topeka, Kansas, and grown at the Station for Experimental Evolution in 1904.

No photograph nor verbal description was made of the parent ear, since there was no intention at the time of its planting to use it in a breeding experiment. But its characteristics must have been accurately duplicated in all of the crossbred families subsequently grown, as well as in most of the F_1 hybrids between the several selfed lines. From each of the grain-row classes, several good ears were saved for planting in the spring of 1905, and the rest was used as horse feed.

The plantings from this material were made on May 25, 26, 27, 1905, again with my own hands, in the form of an ear-row planting. Two ears from each grain-row class of the 1904 crop were used. The seeds were taken from the mid-region of each seed ear. An additional row was planted from grains of each of the two parent ears with 16 grain-rows. Only modified basal grains and modified distal grains for the two halves of the same row in the field were used. In Table 2.1 these cultures from modified grains are indicated by A_b and B_b for the basal grains, and A_p and B_p for the modified "point" grains. A second row was planted from each of the two chosen ears having 16 grain-rows, and these additional rows (A8 and A10) were detasseled, beginning July 24, 1905, and received pollen from the intact plants in the corresponding rows (A7 and A9) beside them.

TABLE 2.1

GRAIN-ROW COUNTS OF PROGENIES GROWN IN 1905 FROM PARENT EARS SELECTED FOR DIFFERENT NUMBERS OF GRAIN-ROWS IN NOVEMBER, 1904

Culture Numbers	Parental Grain-Rows	Frequencies of Progeny Grain-Row Numbers									
		10	12	14	16	18	20	22	24	26	Totals
A1	10 *A**	8	55	47	16	3	.....	.....	.....	.....	129
A2	10 *B**	11	50	57	15	1	1	.....	.....	.....	135
A3	12 *A*	12	36	45	10	1	.....	.....	.....	.....	104
A4	12 *B*	3	30	43	28	4	.....	.....	.....	.....	108
A5	14 *A*	7	32	58	13	5	.....	.....	.....	.....	115
A6	14 *B*	1	11	47	26	13	1	1	.....	.....	100
A7 and 8	16 *A*	3	62	81	44	10	.....	.....	.....	.....	200
A9 and 10	16 *B*	4	31	79	66	14	1	.....	.....	.....	195
A11$_1$	16 A_b†	3	7	19	7	2	.....	.....	.....	.....	38
A11$_2$	16 A_p†	2	19	18	16	4	.....	.....	.....	.....	59
A12$_1$	16 B_b	3	3	5	8	4	.....	.....	.....	.....	23
A12$_2$	16 B_p	3	5	18	12	11	.....	.....	.....	.....	49
A13	18 *A*	.....	12	36	39	17	3	1	.....	.....	108
A14	18 *B*	.....	20	33	29	7	.....	.....	.....	.....	89
A15	20 *A*	.....	3	28	38	14	2	1	.....	.....	86
A16	20 *B*	1	10	14	28	14	10	2	.....	.....	79
A17	22 *A*	.....	2	9	21	27	19	7	.....	.....	85
A18	22 *B*	.....	3	9	20	28	18	.....	2	1	81
A19	22 *C*‡	.....	2	12	32	24	16	3	1	1	91
Totals	....	61	393	658	468	203	71	15	3	2	1,874

* The significance of the *A* and *B* in this column involved the plan to use the *A* rows for selfing and the *B* rows to be crossed with mixed pollen of plants in the corresponding *A* rows.

† The subscript *b* signifies the use for planting of only the modified basal grains of the given ear; and the subscript *p* refers to the planting only of modified grains at the "point" or distal end of the ear.

‡ *C* represents an added row grown to increase the probability of finding ears with still higher numbers of grain-rows.

In harvesting these two pairs of rows, one detasseled, the other intact, the two rows from the same parent ear, through an oversight, were not kept separate. No further detasseling was done. Since the self-fertilized plants could not be detasseled and still utilized for selfing, the method of controlling cross-fertilization by detasseling would prove a distorting factor in comparing the effects of selfing and crossing.

Consequently, no detasseling was practiced in any of my subsequent experimental work with corn, but every pollination was controlled by bagging with glassine bags and manipulation by hand. The bags were tied in place by ordinary white wrapping-cord passed once around and tied with a loop for easy detachment. Each plant was labeled at the time of crossing with a wired tree-label attached to the stalk at the height of the operator's eyes, and marked with the exact identification of the plant to which it was attached and the source of the pollen which had been applied. On harvesting these hand-pollinated ears, the label was removed from the plant and attached securely to the ear, thus assuring that the ear and its label would remain permanently associated. A third row (A 19) from an ear having 22 grain-rows was added to improve the chances of finding ears with still higher numbers of grain-rows.

In November, 1905, these 19 pedigree cultures were carefully harvested by my own hands and the grain-rows counted, with the results tabulated in Table 2.1.

The only observation noted on these 1905 cultures was that there was no clear indication of mutations or segregations of any kind, but the aspect of the field was that of any ordinarily uniform field of corn. Row counts did show the expected indication of Galtonian regression, in that the parents with low numbers of grain-rows produced progenies having lower numbers of grain-rows than did the ears having higher than average numbers of grain-rows. Thus, the two ears with 10 rows of grains each had the average of 13.2 rows of grains on their progeny ears. The two 20-rowed ears showed an average of 15.5 rows of grains on their progeny ears. The three 22-rowed parent ears produced progenies with an average of 17.5 rows of grains.

The same general plan was followed in 1906, except that the pollen for the crossbred cultures was no longer taken from the plants set aside for selfing. The reason for this change, as specifically stated in my notes written at the end of the 1906 season, being "to avoid the deleterious effects of self-fertilization in the cross-fertilized series." This indicated that at the end of 1906 I had only the concept held by Holden, Shamel, East, and all other corn breeders who had had experience with the selfing of maize—that selfing has deleterious effects, not that crossing has advantageous effects other than the simple avoidance of the deleterious effects of selfing.

The new method of handling the crossbred cultures was to divide each such culture by a marker set at the midpoint of the row. All the plants in these rows were bagged. Mixed pollen from the plants in the first half of the row was collected and applied at the appropriate time to the silks of all the plants in the second half of the row. Then the mixed pollen from the plants in the second half of the row was applied in turn to the silks of all the plants in the first half of the row. It was realized that this still involved a considerable degree of inbreeding, but it seemed about the only way of carrying on a continuing program of crossing while still keeping the breeding completely under the operator's control.

Two major observations made on the 1906 crop were: (1) that every one of the seven families from selfed parents could be readily detected by their less height, more slender stalks, and greater susceptibility to the attack of *Ustilago maydis*. When the ears were harvested each lot was weighed and it was found that cross-fertilized rows produced on an average about three times as much grain as the self-fertilized. (2) The family A3, from a self-fertilized ear having 12 grain-rows, was practically all flint corn, showing that to be probably recessive. This occurrence of a rather obvious segregation in the 1906 crop remained at the end of the season only an isolated observation which led to no generalization. From the fall of 1905 until his retirement in 1943, Charles Leo Macy assisted me in many of the technical details of my experimental cultures. While I handled the planning and breeding operations as well as the actual pollinations, Macy prepared the plants for selfing and crossing, and counted the grain-rows and weighed the ear corn. The results of these counts for the 1906 crop are given in Table 2.2.

The following quotation from my notebook seems justified here, since it includes the first formulation of the considerations and conclusions which appeared in my report to the American Breeders' Association in 1908, on "The composition of a field of maize":

> The same plan was continued, (in 1907 as in 1906), namely each self-fertilized row was the offspring of a single self-fertilized ear, and each cross-fertilized row was divided in half, each half coming from a single cross-fertilized ear, one ear in each such case coming from the first half of the corresponding row of the preceding year, the other ear coming from the second half. . . .
>
> The obvious results were the same as in 1906, the self-fertilized rows being invariably smaller and weaker than the corresponding cross-fertilized. Ustilago is again much more in evidence on the self-fertilized. A very different explanation of the facts is forced upon me by the fact that the several self-fertilized rows differ from each other in a number of striking morphological characteristics, thus indicating that they belong to distinct elementary strains. The same point appeared last year in the case of the 12-row class which came almost a uniform flint corn, but the significance of this was not recognized at that time. It now appears that self-fertilization simply serves to purify the strains, and that my comparisons are not properly between cross- and self-fertilization, but between pure strains and their hybrids; and that a well regulated field of corn is a mass of very complex hybrids.
>
> It may also be assumed that correct field practice in the breeding of corn must have as its object the maintenance of such hybrid combinations as prove to be most vigorous and productive and give all desirable qualities of ear and grain.

The ideas in this quotation represent a discovery in complete disagreement with my preconception that my white dent foundation stock, which had been the progeny of a single ear, was essentially a genetically pure strain. I had before me seven distinct biotypes, clearly distinguishable in their several morphological characteristics. They had been derived from seven separate self-pollinations of sibs in a family which I had reason to think was genetically homogeneous. This could not fail to make a great impression. Had these several pure-bred self-fertilized strains come from different breeders and from more or less disconnected experiments, as did the selfed lines available to Dr. East, the observation that they showed themselves to be genetically distinguishable biotypes would have given no cause for the special conclusions I drew from them. It would have been strange, indeed, if strains thus derived from heterogeneous sources had not been genetically different, one from another.

TABLE 2.2

GRAIN-ROW COUNTS AND YIELDS OF EAR CORN IN CULTURES OF WHITE DENT MAIZE GROWN AT THE STATION FOR EXPERIMENTAL EVOLUTION IN 1906

Culture Numbers	Parental Grain-Rows	Frequencies of Progeny Grain-Row Numbers													To-tals	Weights Lbs. Av.	Yield Bu./A.
		8	10	12	14	16	18	20	22	24	26	28	30	32			
A1.1	10 selfed	4	36	62	14	1	...	...	...	...	...	...	...	...	117	...	...
A2.2$_1$	10 crossed	...	3	32	25	7	1	...	...	...	...	...	...	...	68	...	...
A2.2$_2$	10 crossed	...	2	26	29	11	1	...	...	...	...	...	...	...	69	...	...
A3.3	12 selfed	5	13	40	19	4	1	...	...	...	...	...	...	...	82	21.6	37.7
A4.4$_1$	12 crossed	...	...	13	26	12	6	1	...	...	...	...	...	...	58	65.8	78.9
A4.4$_2$	12 crossed	...	1	16	34	9	1	...	...	...	...	...	...	...	61		
A5.5	14 selfed	...	...	12	41	34	15	4	1	...	...	...	...	...	107	33.6	44.9
A6.6$_1$	14 crossed	...	...	6	28	18	7	...	...	...	...	...	...	...	59	61.3	74.5
A6.6$_2$	14 crossed	...	...	6	17	19	12	4	...	...	...	...	...	...	58		
A7.7	16 selfed	...	...	8	17	28	17	4	...	...	...	...	...	...	74	29.6	59.1
A9.8$_1$	16 crossed	...	...	14	16	15	1	1	...	...	...	...	...	...	47	58.3	77.1
A9.8$_2$	16 crossed	...	...	5	16	28	11	1	...	...	...	...	...	...	61		
A19.9	16(22)×10	...	...	8	23	22	11	5	1	1	...	...	...	...	71	22.1	44.5
A12$_1$.10$_1$	16$_b$ crossed	...	...	9	28	20	3	...	...	...	...	...	...	...	60	...	...
A12$_2$.10$_2$	16$_p$ crossed	...	1	20	23	15	4	...	...	...	...	...	...	...	63	...	...
A11$_1$ A12$_1$ 11$_1$	16$_p$ crossed	...	...	7	39	18	9	1	...	...	...	...	...	...	74	...	...
A11$_1$ A12$_2$ 11$_2$	16$_b$ crossed	...	...	10	22	18	5	2	...	...	...	...	...	...	57	...	...
A13.12	18 selfed	...	...	2	8	6	5	3	2	...	...	...	...	...	26	9.6	52.9
A14.13	18 open-pol.	...	...	...	16	29	18	19	9	1	1	1	...	...	94	58.3	88.5
A15.14	20 selfed	...	...	6	11	23	18	10	4	...	...	...	...	...	72	23.6	46.9
A16.15$_1$	20 crossed	...	...	...	2	8	21	13	5	1	...	...	...	...	50	56.3	75.1
A16.15$_2$	20 crossed	...	...	...	3	17	20	13	4	...	...	...	...	...	57		
A17.16	22 selfed	...	...	1	4	10	17	13	7	3	...	...	...	...	55	24.1	62.4
A18.17	24 crossed	...	...	...	4	11	25	24	18	3	4	1	...	...	91	57.3	89.9
A19.18	24 open-pol.	...	1	3	12	14	17	11	6	2	...	...	...	...	66	32.6	70.6
A19.19	26 open-pol.	...	...	...	1	8	11	17	6	10	7	...	...	...	60	34.6	82.4
A18.20	26 open-pol.	...	...	...	...	5	9	14	19	13	5	1	1	1	68	40.6	85.4
A16.21	18 crossed	...	...	1	5	17	25	21	7	2	...	...	...	...	78	...	...
A19.22	18(22)×10	...	...	16	29	20	6	1	...	...	...	...	...	...	72	...	...
A19.23	14(22)×10	...	1	11	31	22	26	1	...	...	...	...	...	...	92	46.1	71.6
Totals	...	9	58	334	543	469	323	183	89	36	17	3	2	1	2,067	...	...

Comparison of the results for 1907, presented in Table 2.3, with those for 1906 in Table 2.2, shows a heavy accentuation of grain-row classes 8 and 10 and a marked decrease in classes 18 to 20, inclusive. There was also a significant increase in all higher classes, with further extension of the range from a maximum of 32 to about 40. The increase in the frequencies of the low grain-row classes was attributed in part to the fact that the 1907 season had seemed less favorable in general than 1906.

It was also noted, as a possible contributory condition, that this was the third season in which this corn was grown on the same area north of the laboratory building, and that "the yield may have been lessened by the gradual accumulation of injurious substances in the soil." The fact that the average grain-row numbers were not significantly different in the two years—15.8 in 1906, 16.0 in 1907—in fact a trifle higher in what was thought to have been the poorer year, does not seem to support these suggested explanations of the observed differences of distribution in the two years.

FIG. 2.2—Young corn cultures growing in East Garden of the Station for Experimental Evolution in 1911, illustrating that no two were alike despite their descent from a single ear of 1904 by meticulously controlled pollinations that precluded the introduction of pollen from any other strain of corn.

My contemporaneous notes proposed an additional explanation, namely, that "each successive generation of close inbreeding still further reduces the strains to their simple constituent biotypes, and as these are weaker than hybrid combinations, this too would tend to lessen the vigor, and this lessened vigor might readily be evidenced by a decrease in the average number of [grain-]rows and the total number of ears in the crop."

If we accept this latter suggestion as valid, it is clear that the occurrence of essentially the same average numbers of grain-rows in the two years gives only a specious indication of the relative climatic and soil effectiveness in these two seasons. It must mean simply that the diminution of grain-row numbers produced by increasing homozygosity happened to be balanced by the increased frequencies in the higher classes, produced by the gradual accumulation by selection of more potent hybrid combinations.

TABLE 2.3

GRAIN-ROW COUNTS AND HEIGHTS OF PLANTS IN THE CULTURES OF 1907

PEDIGREE NUMBERS	GRAIN-ROWS OF PARENTS	FREQUENCIES OF PROGENY GRAIN-ROW NUMBERS																	TOTALS	AV. HT. IN FT.
		8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40		
B1.1	10 selfed	20	25	20	2	1	...	...	...	...	...	...	...	...	...	...	...	...	68	7.25
B2$_1$.2$_1$	10 crossed	2	22	21	5	...	...	...	...	...	...	...	...	...	...	...	...	...	50	9.00
B2$_2$.2$_2$	10 crossed	6	28	18	5	...	...	...	...	...	...	...	...	...	...	...	...	...	57	
B1.3	8 selfed	23	48	17	...	...	...	...	...	...	...	...	...	...	...	...	...	...	88	7.63
B3.4	12 selfed	10	21	18	4	1	...	...	...	...	...	...	...	...	...	...	...	...	54	6.25
B4$_1$.5$_1$	12 crossed	...	1	16	19	13	3	...	...	...	...	...	...	...	...	...	...	...	52	8.00
B4$_2$.5$_2$	12 crossed	1	...	7	14	14	7	1	...	...	...	...	...	...	...	...	...	...	44	.....
B5.6	14 selfed	...	4	23	29	15	1	1	...	...	...	...	...	...	...	...	...	...	73	8.50
B6$_1$.7$_1$	14 crossed	...	...	5	15	19	7	1	1	...	...	...	...	...	...	...	...	...	48	9.67
B6$_2$.7$_2$	14 crossed	...	...	5	18	19	7	1	1	...	...	...	...	...	...	...	...	...	43	
B7.8	16 selfed	...	1	19	26	9	...	...	...	...	...	...	...	...	...	...	...	...	55	8.25
B8$_1$.9$_1$	16 crossed	...	...	2	8	14	7	3	3	...	...	...	...	...	...	...	...	...	37	8.75
B8$_2$.9$_2$	16 crossed	...	...	...	9	15	9	3	...	...	...	...	...	...	...	...	...	...	36	
B10$_2$.10$_1$	16$_p$ crossed	...	...	6	13	10	1	1	...	...	...	...	...	...	...	...	...	...	31	8.67
B10$_1$.10$_2$	16$_b$ crossed	...	...	11	15	9	1	1	...	...	...	...	...	...	...	...	...	...	37	
B12.11	18 selfed	...	...	...	...	5	7	1	2	...	...	...	...	...	...	...	...	...	15	7.00
B13.12	18 open-pol.	...	...	9	21	22	15	3	1	...	...	...	...	...	...	...	...	...	71	8.33
B14.13	20 selfed	...	...	5	8	21	11	6	1	...	...	...	...	...	...	...	...	...	52	7.25
B15$_1$.14$_1$	20 crossed	...	...	1	3	16	18	13	10	2	...	...	...	...	...	...	...	...	63	8.83
B15$_2$.14$_2$	20 crossed	...	...	...	4	10	13	16	8	1	...	...	...	...	...	...	...	...	52	
B16.15	22 selfed	...	...	...	...	6	9	17	8	5	...	...	...	...	...	...	...	...	45	7.00
B17.16	22 crossed	...	...	...	1	9	17	17	11	4	3	1	...	...	...	...	...	...	63	8.67
B15.17	20 crossed	...	...	...	1	7	22	17	11	4	...	...	...	...	...	...	...	...	62	8.83
B19.18	24 crossed	...	...	...	...	1	7	16	14	5	4	3	...	...	...	...	...	...	50	9.50
B20.19	32 open-pol.	...	...	...	...	3	6	8	8	7	4	2	2	...	1	...	...	...	41	9.50
B?.20	Branched ear	...	...	1	6	9	13	8	1	1	...	...	...	...	...	...	...	...	58	8.33
B17.21	30 open-pol.	...	...	...	2	5	12	17	11	9	1	...	...	1	...	...	...	...	58	8.33
B?.22	Branched ear	...	...	...	3	14	17	12	3	...	...	...	...	...	...	...	...	...	49	.....
B15.23	16 crossed	...	...	...	5	14	15	17	6	3	4	...	...	...	...	...	...	...	64	.....
B20.24	24 selfed	...	...	...	...	5	5	7	7	6	6	...	...	...	...	...	...	...	36	8.00
B20.25	26 selfed	...	...	...	...	...	...	3	2	2	...	...	1	2	...	1	...	1	12	7.83
Totals	....	62	150	204	236	282	228	189	108	49	22	6	3	3	1	1	...	1	1,545	.....

A truer measure of the relative favorableness of the two seasons for growth and productiveness of these cultures can be derived from a study of the middle classes with 12, 14, 16, and 18 grain-rows. These grain-row classes making up 80 per cent of the 1906 crop and 61.5 per cent of the 1907 crop, must be relatively free from most of the distortion assumed to be produced either by increasing homozygosity or by the accumulation of the more potent hybrid combinations. If we average these four grain-row classes by themselves for the two years, we find that in 1906 their average was 15.5 grain-rows, and for 1907 only 15.0, thus agreeing with my general impression that 1907 was the less favorable year.

With the fundamental change in my understanding of the nature of my corn population came a reorientation of the experiment. I found myself at the end of 1907 only ready to make a beginning on the problems of the relationship between pure lines and their hybrids, which I now saw was the crucial field that needed exploration.

As a first step in that direction, but without as yet a full comprehension of its importance, I made in July, 1907, pollinations between plants of C4, which I later designated "Strain A," and a plant of C6, which later became my "Strain B." I also made two sib crosses within these two strains. The cross of Strain A × Strain B, which gave rise in 1908 to F_1 family, D9, involved an 8-rowed ear of the former strain (from an original selection for 12 grain-rows) and a 12-rowed ear of Strain B which had originated in a selection for 14 grain-rows. The near-reciprocal cross (F_1 family, D13) resulted from the application of pollen from a 12-rowed plant of Strain A to silks of the same plant of Strain B, which supplied the pollen for the near-reciprocal cross.

At the time when these two near-reciprocal crosses were made between Strains A and B, the truth had not yet dawned upon me that I should do the same with all of my other selfed families. Aside from these two sets of crosses, the handling of the cultures was the same as in previous years. The results of the grain-row counts are given in Table 2.4. Unfortunately, there was considerable damage from crows, and failures to germinate for unknown reasons. The missing hills were replanted on June 8, 1908, and all of the new plantings made on this date seem to have reached maturity. To overcome the suggested deteriorating effect of soil depletion, the cultures were grown this year on the area east of the laboratory building (occasionally referred to in subsequent notes as "East Garden").

In summarizing the results for the year 1908, it may be noted first that the tendency to concentrate the frequencies of the grain-rows in the extremes of the range, at the expense of those in the middle, has continued strongly. As before, the most noteworthy concentration is at the lower extreme. All classes below 16 are considerably stronger in 1908 than in 1907 and the maximum frequency is now on 12 instead of 16. This is in part due to the fact that several of the lower-class families were grown in duplicate. Between classes 14 and 26 the relative strength of the classes was lessened in 1908. Above class 24 the frequencies were increased, there being 84 ears above class 24 in 1908 and only the equivalent of about 50 in the same region in 1907, when raised to the same total number. The highest number of grain-rows noted was 42.

The important new features brought in by the near-reciprocal crosses between Strain A and Strain B and a sib cross in Strain A are presented in my report to the American Breeders' Association at Columbia, Mo., in January, 1909, on "A pure line method in corn breeding." I find a discrepancy in that the 78 ears produced by the sib cross weighed only 16.25 pounds instead of 16.5, as stated in my 1909 paper. Whether by an oversight or intentionally, I cannot now determine, the corresponding sib crosses in Strain B were not included in my 1909 report. The results were essentially the same as were reported for the sib cross in Strain A. Selfed Strain B (see Table 2.4, family C6.11) showed average heights of plants 2.3 meters, and yielded 66 ears weighing 13.0 pounds. The two sib crosses produced plants 2.5 meters tall and yielded 89 ears weighing 28.5 pounds. Distribution of the grain-row frequencies was closely similar in selfed and in sib-crossed Strain B, but significantly higher in the latter:

Grain-rows	10	12	14	16	18	Totals	Averages
Selfed	2	20	26	17	1	66	13.8
Sib-crossed	3	15	45	18	8	89	14.2

There was abundant evidence that the sib crosses showed a greatly restricted advantage over self-fertilization. It was also clearly indicated that

TABLE 2.4

GRAIN-ROW COUNTS, HEIGHTS, AND YIELDS OF WHITE DENT MAIZE GROWN IN 1908

Pedigree Numbers	Grain-Rows of Parents	Frequencies of Progeny Grain-Row Numbers																		To-tals	Av. Hts. in Dm.	Wts. in Lbs.	Yield Bu./A.
		8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42				
C3.1	10 selfed	52	39	13	...	...	...	...	...	...	...	...	..	..	..	..	..	..	..	104	19.5	31.5	43.3
C1.2	8 selfed	51	41	2	...	...	...	...	...	...	...	...	..	..	..	..	..	..	..	94	19.7	22.0	33.4
$C2_1.3_1$	8 crossed	6	29	14	2	...	...	...	...	...	...	...	..	..	..	..	..	..	..	51	23.4	25.0	70.7
$C2_2.3_2$	8 crossed	6	22	12	1	1	...	...	...	...	...	...	..	..	..	..	..	..	..	42	.....	21.0	
C1.4	10 selfed	28	48	12	2	...	...	...	...	...	...	...	..	..	..	..	..	..	..	90	18.0	22.0	30.5
$C2_1.5_1$	10 crossed	9	32	9	...	...	...	...	...	...	...	...	..	..	..	..	..	..	..	50	21.5	20.8	59.8
$C2_2.5_2$	10 crossed	12	18	3	...	...	...	...	...	...	...	...	..	..	..	..	..	..	..	33	.....	14.0	
C4.6	12 selfed	11	41	32	5	...	...	...	...	...	...	...	..	..	..	..	..	..	..	89	17.0	28.0	44.9
C4.7	10×sib	8	50	19	1	...	...	...	...	...	...	...	..	..	..	..	..	..	..	78	16.5	16.3	29.8
C4.8	8 selfed	65	6	2	...	...	...	...	...	...	...	...	..	..	..	..	..	..	..	73	16.5	12.0	23.5
C4.9	8×12	...	19	64	9	...	...	...	...	...	...	...	..	..	..	..	..	..	..	92	24.0	48.0	74.5
$C5_1.10_1$	12 crossed	2	9	31	15	1	1	...	...	...	...	...	..	..	..	..	..	..	..	59	24.5	34.8	84.1
$C5_2.10_2$	14 crossed	1	9	17	14	1	...	...	...	...	...	...	..	..	..	..	..	..	..	42	22.5	23.3	79.1
C6.11	14 selfed	...	2	20	26	17	1	...	...	...	...	...	..	..	..	..	..	..	..	66	23.0	13.0	28.1
$C6.12_1$	16×sib	...	2	4	25	11	5	...	...	...	...	...	..	..	..	..	..	..	..	47	25.0	16.8	50.9
$C6.12_2$	12×sib	...	1	11	20	7	3	...	...	...	...	...	..	..	..	..	..	..	..	42	25.0	11.8	40.0
C6.13	12×12	1	5	56	31	6	1	...	...	...	...	...	..	..	..	..	..	..	..	100	26.0	55.0	78.6
$C7_1.14_1$	14 crossed	...	...	18	28	11	2	...	...	...	...	...	..	..	..	..	..	..	..	59	25.0	30.0	72.6
$C7_2.14_2$	14 crossed	...	11	9	18	3	2	...	...	...	...	...	..	..	..	..	..	..	..	43	27.0	19.3	64.0
C8.15	16 selfed	...	1	31	32	28	1	1	...	...	...	...	..	..	..	..	..	..	..	94	24.4	31.5	47.9
$C9_1.16_1$	16 crossed	...	...	4	14	25	11	...	1	...	...	...	..	..	..	..	..	..	..	55	26.8	31.5	80.8
$C9_2.16_2$	16 crossed	...	...	6	18	13	4	...	...	...	...	...	..	..	..	..	..	..	..	41	25.2	20.0	69.7
C13.17	18 selfed	...	...	6	10	34	21	6	...	...	...	...	..	..	..	..	..	..	..	77	19.3	16.5	30.6
$C12_2.18_1$	18 crossed	...	1	6	20	16	12	1	...	...	...	...	..	..	..	..	..	..	..	56	23.5	31.3	79.7
$C12_2.18_2$	18 crossed	...	1	8	19	14	4	...	...	...	...	...	..	..	..	..	..	..	..	46	25.5	28.3	87.7
C13.19	20 selfed	...	...	2	15	39	23	6	...	...	...	...	..	..	..	..	..	..	..	85	21.6	23.0	38.7
$C14_1.20_1$	20 crossed	...	...	...	3	4	15	19	7	8	2	...	..	..	..	..	..	..	..	58	....*	31.0	76.4
$C14_2.20_2$	20 crossed	...	...	...	2	6	17	10	11	...	...	...	..	..	..	..	..	..	..	46	.....	24.5	79.2
C15.21	20 selfed	...	...	...	13	17	19	18	3	...	...	...	..	..	..	..	..	..	..	70	.....	20.5	41.8
$C16_1.22$	22 crossed	...	...	...	3	9	20	24	13	10	4	1	..	..	..	..	..	..	..	84	.....	48.3	82.1
C24.23	22 selfed	...	...	2	9	22	26	25	19	21	...	...	..	..	..	..	..	..	..	92	.....	33.8	52.4
C18.24	28 crossed	...	...	...	...	3	4	21	16	24	7	3	1	3	1	..	..	..	..	83	.....	43.3	74.4
C25.25	36? selfed	Grain-rows too difficult to count; silks shorter than husks.																					
C19.26	28(?)×26(?)	...	...	...	...	1	2	5	10	10	16	18	5	6	9	3	..	..	1	86	.....	50.5	83.9
C22.27	Branched ear open-pol.	...	...	1	11	14	19	16	14	4	2	2	..	..	..	..	..	..	..	83	.....	50.0	86.2
C22.28	20 open-pol.†	...	...	1	9	20	31	22	7	3	...	...	..	..	..	..	..	..	..	93	.....	51.8	79.5
Totals	....	252	387	415	375	323	244	172	91	60	31	24	6	9	10	3	..	..	1	2,403	.....	.....	......

* The remaining nine rows were not measured and described, "for lack of time."

† This plant carried four ears with 14, 14,16, and 20 rows of grains, of which only the twenty-rowed ear was used for planting.

FIG. 2.3—Vegetative habits of Strain A (*right*) and Strain B, drawn by J. Marion Shull from a photograph taken in the summer of 1908. At upper right typical ears of these two strains (*Strain A at right*) and between them their reciprocal F_1 hybrids, each hybrid standing nearest to its mother type.

if the advantage consisted solely of the effects of heterozygosity, both Strain A and Strain B were still a good way from being homozygous, Strain B being as yet more effectively heterozygous than Strain A.

In the reciprocal crosses between these nearly homozygous strains A and B, we have our first opportunity to arrive at an approximation to the actual amount of heterosis. The most important new discoveries these crosses made possible were: (1) As a result of such a cross it is possible to completely cancel in a single year the accumulated deterioration which had gradually accrued, although with lessening annual increments, over a period of several years; and (2) the approximate identity of the results of the reciprocal crosses gave assurance that the amount of heterosis resulting from a given hybridization is a specific function of the particular genetical combination involved in the cross.

Several new cultures of yellow- and red-grained corn were added to my experimental field in 1908, but these will not be followed here. They are mentioned only because they were included in my numbered pedigrees, and their omission in the following tables leaves a break in the series of numbered families which might lead to some question as to the reason for the apparent vacancies. The data from the 1909 cultures of white dent corn are presented in Table 2.5.

The families grown in 1909, as tabulated in Table 2.5, fall into three major classes: (1) Twelve families involve continuations of the original self-fertilized lines, whose average yields range from 18.8 to 41.2 bushels per acre, with the average for all twelve at 32.8 bushels per acre; (2) Twelve are continuations of crossbred families in which strictly controlled cross-fertilizations were made with mixtures of pollen taken from the other plants in the same crossbred strain. These yielded from 58.1 to 83.3 bushels per acre with the average of all at 73.3 bushels per acre; and (3) there were fourteen F_1 hybrid families from crosses between pairs of individuals representing two different selfed lines. The yields of these range from 60.3 to 87.5 bushels per acre, the average for all fourteen being 78.6 bushels per acre. As stated in my 1910 paper, the three highest yields of any of these cultures were from the families produced by crossing representatives of different selfed strains (see D8.13, D8.16, and D11.21).

Besides these, there were two cousin crosses involving matings between different families of the same selfed line. These produced, respectively, 27.1 and 44.6 bushels per acre. One cross between two sibs in Strain A gave 26.0 bushels per acre. The other cross was two F_2 families, each from crosses with mixed pollen within one of the F_1 families of my 1908 cultures. These F_2 families yielded 54.2 bushels per acre from the $(A \times B)F_2$, and 70.6 from the $(B \times A)F_2$. These yields should be compared with those of the corresponding F_1 families grown in the same season, in which $(A \times B)F_1$ yielded 74.9 and 83.5 bushels in two different families, and $(B \times A)F_1$ produced 82.6 bushels per acre.

In 1910 I was absent from the Station for Experimental Evolution during the entire summer and my experiments with corn, evening primroses, Lychnis, etc., were continued by an assistant, R. Catlin Rose, assisted by Mr. Macy, who carried out the operations meticulously described by myself in more than one thousand typewritten lines of detailed instructions.

The data on the white dent corn grown in 1910 are presented here in

TABLE 2.5

GRAIN-ROW COUNTS, HEIGHTS OF STALKS, AND YIELDS OF EARS OF WHITE DENT CORN IN 1909

Pedigree Numbers	Grain-Rows of Parents	Frequencies of Progeny Grain-Row Numbers																	Totals	Hts. in Dms.	Wts. in Lbs.	Yield Bu./A.
		8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40				
D1.1	8 selfed	21	51	30															102	18	24.0	53.0
D2.2	8 selfed	29	70	6															105	20	24.8	33.7
D3$_1$.3$_1$	8 crossed	18	25	12															55	21	21.0	59.2
D3$_2$.3$_2$	8 crossed	8	39	3															50	22	22.5	
D4.4	10×12	30	55	21															106	20	44.8	60.3
D4.5	10×14		8	44	11														63	24	35.3	80.0
D4.6	10×sib	10	53	32	1														96	17	17.5	26.0
D4.7	10 selfed	7	32	55	4														98	19	25.0	56.4
D5$_1$.8$_1$	10 crossed	3	23	17	1														44	24	17.3	59.7
D5$_2$.8$_2$	10 crossed	4	22	15															41	24	18.3	
D6.9	12 selfed	5	50	35	4														94	18	23.5	35.7
D7.10$_1$	12×cousins	1	31	18															50	19	9.5	27.1
D7.10$_2$	12×cousins	3	29	20	1														53	19	10.3	27.6
D8.11	A selfed	66	5	3															74	17	9.8	18.8
D8.12	A×20			4	40	45	9												96	24	54.0	80.4
D8.13	A×22		1	44	50	7													102	26	60.0	84.0
D8.14$_1$	A×B		2	18	9	2													31	24	16.3	74.9
D8.14$_2$	A×20			21	33	5	1												60	26	29.8	70.8
D8.15	A×16	1	1	74	32	7													115	28	61.3	76.2
D8.16	A×B	2	8	71	5														86	27	50.3	83.5
D9.17	(A×B)F$_1$ sibs	3	32	57	11	2	3												108	25	41.0	54.2
D10$_1$.18$_1$	12 crossed	2	5	28	16														51	25	29.5	......
D10$_2$.18$_2$	12 crossed		5	25	17	3	1												51	23	30.0	83.3
D11.19	B selfed			10	18	12													40	26	7.3	25.9
D11.20	B×A		19	58	9														86	28	49.8	82.6
D11.21	B×20			6	20	38	15	1											80	28	49.0	87.5
D13.22	(B×A)F$_1$ sibs		1	26	40	15	2												84	27	41.5	70.6
D14$_1$.23$_1$	14 crossed		2	13	23	10													48	28	23.8	71.4
D14$_2$.23$_2$	14 crossed			14	18	8	1												41	29	20.8	
D15.24	16 selfed		1	25	51	4													81	24	21.0	37.0
D16$_1$.25$_1$	16 crossed			2	11	9	8	4	1										35	25	22.5	80.0
D16$_2$.25$_2$	16 crossed			4	19	19	6												48	26	24.0	
D17.26	18 selfed			2	14	42	15												73	20	17.3	33.8
D17.27	20×16			1	4	27	43	18	3										96	27	53.8	80.0
D17.28	20×A	1		16	46	22													85	24	46.0	77.3
D17.29	16×cousin			3	9	19	4	1											36	23	11.3	44.6
D18$_1$.30$_1$	18 crossed			5	18	17	5	1		1									47	28	26.0	79.4
D18$_1$.30$_2$	18 crossed			5	18	23	4	1											51	28	28.5	
D19.31	20 selfed			2	14	36	27	8											87	24	20.3	33.3
D19.32	20×16			1	12	54	36	9	1										113	28	63.3	80.0
D20$_1$.33$_1$	20 crossed					2	12	23	8	5	2								52	30	29.0	76.5
D20$_2$.33$_2$	20 crossed					5	19	21	14	7	1								67	29	34.8	
D21.34	22 selfed					4	30	41	12	4									91	26	25.3	39.6
D22.35$_1$	22 crossed					5	12	11	4										32	25	17.5	83.2
D22.35$_2$	22 crossed				1	6	5	8	10	8	2	1	2	1					44	27	26.8	
D23.36	24 selfed					5	22	36	16	12	5	1							97	23	28.0	41.3
D24.37$_1$	24 crossed						2	10	7	11	3	1							34	27	14.8	71.4
D24.37$_2$	24 crossed							2	5	3	7	2	2						21	27	12.8	
D25.39	30 selfed							2	1	4	12	14	9	11	4	4	3	4	68	25	11.5	24.2
D26.40$_1$	28 crossed					3	4	5	5	3	5	8	5	1					39	29	14.3	58.1
D26.40$_2$	28 crossed					2	2	4	4	6	7	8	5	3	1	2			44	28	19.5	
D27.41	22 crossed				5	23	31	27	11	2		1							100	29	37.3	81.8
D28.42	24 crossed				3	18	22	28	21	7	4		1						104	29	53.5	73.5
Totals		214	570	846	588	497	341	261	123	73	48	36	24	16	5	6	3	4	3655	.....	.....	......

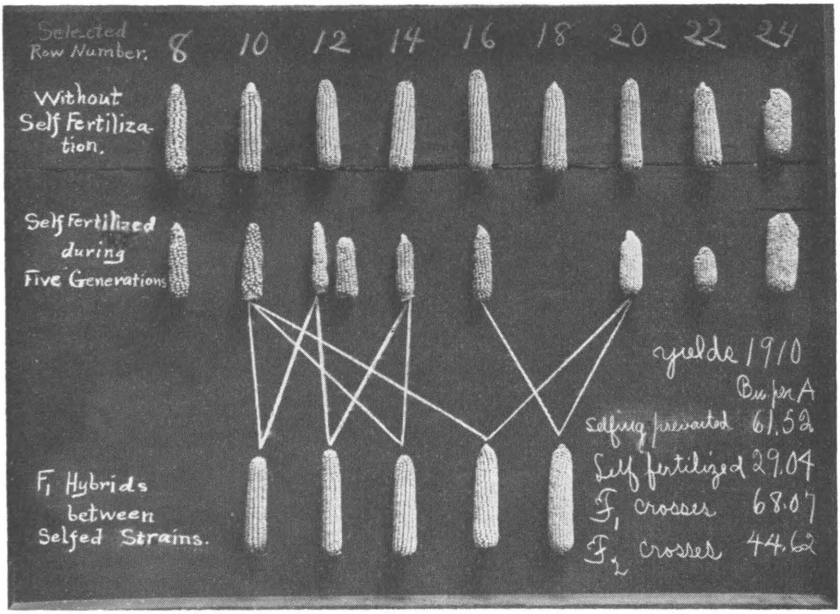

FIG. 2.4—An exhibit set up in the Genetics Department of Cornell University in 1910, displaying materials grown at the Station for Experimental Evolution in 1909.

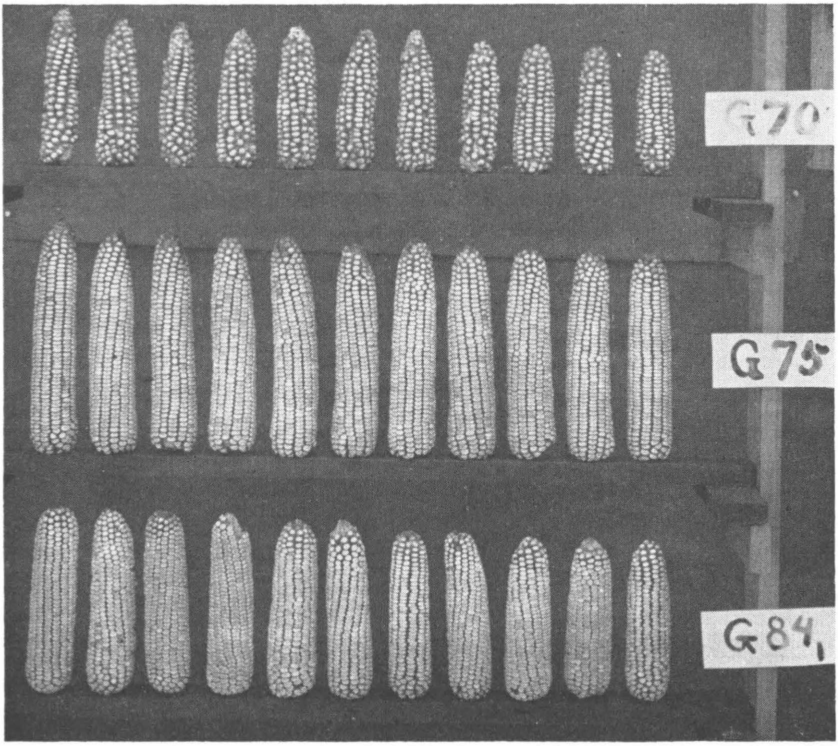

FIG. 2.5—The best eleven ears of the highest-yielding selfed line (F 29.70 in Table 2.7) grown in 1911 (*top row*); the best eleven ears of the best F_1 hybrid grown in the same year (F 32.75 in Table 2.7); and the best eleven ears of a crossbred strain (F 55.84 in Table 2.7) in which selfing was completely prevented during five years. This shows the relative variability which is characteristic of these three types of families, the F_1 being no more variable than the inbred, while the crossbred is quite noticeably more variable.

summary form. Some 73 ears were selected for planting, and 5,343 ears were harvested. The complete grain-row distribution was as follows:

Grain-rows	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	Total
Frequencies	401	812	1271	921	716	476	275	141	118	74	53	41	24	8	6	4	1	1	5343
Percentages	7.5	15.2	23.8	17.2	13.4	8.9	5.2	2.6	2.2	1.4	1.0	0.8	0.5	0.2	0.1	0.1	0.0	0.0	100.0

To save space and still indicate as completely as possible the significant results of these studies in 1910, the data from the several kinds of families of white dent corn grown at the Station for Experimental Evolution that year are presented in the form of averages in Table 2.6. The several quantitative indicators of physiological vigor, namely, the average number of grain-rows, heights of stalks, and bushels of ear-corn per acre, can be readily compared as follows:

Types of Families	No. of Families	Av. No. of Grain-Rows	Av. Heights in Dms.	Av. Yields in Bu./A.
Inbreds selfed	10	12.6	19.3	25.0
Inbreds × sibs	8	13.7	19.8	28.7
Crossbreds	11	16.9	23.5	63.5
F_1 between inbreds	6	15.2	25.7	71.4
F_2 from F_1 selfed	11	13.3	23.3	42.6
F_2 from F_1 × sibs	11	13.5	23.1	47.9

Six interesting comparisons can be made among these summaries: (1) comparisons between inbreds selfed and inbreds crossed with pollen from one or more of their sibs; (2) comparisons between inbreds and crossbreds in which selfing has been completely prevented, but which still represent a (fairly low) degree of inbreeding; (3) comparisons between inbreds and their F_1 hybrids; (4) comparisons between the crossbreds in which selfing has been prevented through six generations and the F_1 hybrids in which five successive generations of selfing have been succeeded by a single cross; (5) comparisons between the F_1 and the F_2 hybrids of the inbreds; and (6) comparisons between F_2 hybrid families produced by selfing the F_1 and those F_2 families produced by sibcrosses in the F_1.

On making these comparisons we see that the evidence for residual heterozygosity in the inbreds is indicated by excesses in the sibcrossed families of the inbreds over the selfed inbreds of 8.7 per cent in grain-row number, 2.8 per cent in heights of stalks, and 14.7 per cent in yield of ear-corn. In the F_2 families (sections E and F, of Table 2.6) those produced from sibcrosses in the F_1 surpass those families produced from selfings in the F_1 by 0.9 per cent in grain-row number and 12.5 per cent in yield.

The average heights of stalks reverse the expectation by showing an insignificantly less height from the sibcrossed matings than from the selfings, the difference being 0.9 per cent. The contrast between the results of six successive selfings and the continued prevention of selfing for the same six

TABLE 2.6

AVERAGE VALUES IN THE FAMILIES OF WHITE DENT MAIZE GROWN IN 1910, GROUPED ACCORDING TO THE TYPES OF MATING OF THE PARENTS

Pedigree Numbers	Parental Grain-Rows	Number of Stalks	Av. No. of Grain-Rows	Heights in Dms.	Wts. in Lbs. Av.	Yields Bu./A.
	(A) Families from Inbreds Selfed					
E1.16	8 selfed	57	10.0	17	9.8	24.4
E2.19	8 selfed	83	9.0	18	22.0	39.6
E7.29	10 selfed	79	11.1	20	18.3	33.9
E9.32	12 selfed	80	12.3	17	11.4	20.9
E11.34	A(8) selfed	75	8.8	16.5	9.1	18.1
E19.47	B(14) selfed	53	12.9	24	7.3	11.0
E24.54	14 selfed	66	13.8	23	16.3	25.8
E26.56	18 selfed	82	15.2	19	15.3	22.9
E34.67	22 selfed	62	17.9	19	11.0	19.2
E36.71	26, 28 selfed	72	15.2	19	17.5	34.2
	Unweighted averages	71	12.6	19.3	10.7	25.0
	(B) Families from Inbreds Pollinated by Sibs; Selfing Prevented					
E1.17	10×sibs	61	10.2	19	13.8	29.8
E2.20	10×sib	75	9.9	18	21.0	39.5
E7.30	12×sib	85	11.0	22	18.3	37.3
E11.35	A(8)×sib	55	9.5	16	7.5	16.0
E19.48	B(12)×sib	54	12.7	24	5.3	7.8
E26.57	18×sib	89	15.8	20	24.5	37.8
E34.68	20×sib	65	17.9	20	15.3	25.6
E36.72	?(fasc.)×sib	73	22.5	20	18.3	35.2
	Unweighted averages	61	13.7	19.8	15.5	28.7
	(C) Families from Parents Given Mixed Pollen in Each Generation; Selfing Prevented					
E3.23	8, 10 crossbred	88	9.5	22	30.8	49.9
E8.31	10 crossed	65	10.3	22	31.0	68.1
E18.46	12 crossed	91	13.2	24	51.0	80.1
E23.53	14 crossed	94	13.7	27	49.0	74.5
E25.55	16 crossed	95	14.9	28	48.8	73.3
E30.63	18 crossed	202	16.0	22.5	76.8	54.3
E33.66	20 crossed	100	18.5	23	35.8	51.1
E35.70	20, 22 crossed	45	20.0	21	26.3	83.3
E37.73	24, 20 crossed	69	24.2	22	24.5	50.7
E40.75	32 crossed	56	19.2	24	22.5	57.4
E40.76	32 crossed	99	26.2	23	39.0	56.3
	Unweighted averages	91.3	16.9	23.5	39.6	63.5

TABLE 2.6—*Continued*

Pedigree Numbers	Parental Grain-Rows	Number of Stalks	Av. No. of Grain-Rows	Heights in Dms.	Wts. in Lbs. Av.	Yields Bu./A.
	(D) F_1 Hybrids between Different Inbred Lines					
E2.21	A(10)×16	95	13.8	24	50.3	75.6
E2.22	A(10)×B	94	12.8	28	50.0	76.0
E11.36	A(8)×10	95	11.0	25	33.5	51.5
E11.37	A(8)×B	84	12.3	25	28.5	48.5
E26.58	18×14	109	17.8	27	60.8	79.6
E34.69	18×26±(fasc.)	92	23.3	25	62.5	97.1
	Unweighted averages	93	15.2	25.7	47.6	71.4
	(E) F_2 Families from F_1×Self					
E4.24	(10×A)F_1 selfed	86	10.6	21	30.8	51.1
E5.26	(10×14)F_1 selfed	86	12.1	22	29.8	49.4
E12.38	(A×20)F_1 selfed	76	13.9	19.5	20.5	38.5
E13.40	(A×22)F_1 selfed	83	12.8	24	18.8	31.4
E15.42	(A×16)F_1 selfed	94	12.8	25	33.5	50.9
E16.44	(A×B)F_1 selfed	96	12.0	25	24.0	35.7
E20.49	(B×A)F_1 selfed	95	11.7	24	25.3	38.0
E21.51	(B×20)F_1 selfed	92	15.1	25	28.0	43.5
E27.59	(20×16)F_1 selfed	97	16.6	25	35.3	51.9
E28.61	(20×A)F_1 selfed	95	13.0	22	22.0	33.1
E32.64	(20×16)F_1 selfed	93	15.9	24	29.5	45.3
	Unweighted averages	90.3	13.3	23.3	27.0	42.6
	(F) F_2 Families from F_1×Sibs					
E4.25	(10×12)F_1×sibs	85	10.7	21	31.3	52.5
E5.27	(10×14)F_1×sibs	83	12.2	22	35.0	60.2
E12.39	(A×20)F_1×sibs	80	14.2	21	28.8	51.3
E13.41	(A×22)F_1×sibs	96	13.4	25	27.0	40.2
E15.43	(A×16)F_1×sibs	95	12.3	23	37.3	56.0
E16.45	(A×B)F_1×sibs	93	11.8	24	21.0	32.3
E20.50	(B×A)F_1×sibs	80	11.6	24	23.5	42.0
E21.52	(B×20)F_1×sibs	93	15.5	25	31.8	48.8
E27.60	(20×16)F_1×sibs	89	17.2	25	37.3	59.8
E28.62	(20×A)F_1×sibs	92	13.7	23	30.0	46.6
E32.65	(20×16)F_1×sibs	97	15.4	21	25.3	37.6
	Unweighted averages	89.4	13.5	23.1	29.8	47.9

years (sections A and C, Table 2.6) shows the latter in excess of the former by 34.0 per cent in grain-row number, 22.1 per cent in height of stalks, and 154.2 per cent in per acre yields of ears. The superiority of the F_1 hybrids between different inbreds and the families in which selfing had been prevented during six generations of controlled breeding (sections D and C, Table 2.6), is indicated by an excess in heights of stalks of the F_1 families over the crossbreds, of 9.4 per cent, and in yields of ear-corn per acre of 12.3 per cent. But here there is a notable reversal in grain-row numbers. Notwithstanding these proofs of the superior vigor of the F_1's over the crossbreds, the latter exceed the former in grain-row number by 10.8 per cent.

The reason for this reversal is easily recognized when we consider that parents were selected in these studies for their grain-row numbers, with no noticeable selection for heights and yields. In section D of Table 2.6, we note that only one parent of any of the F_1 families had a grain-row number in excess of 18. The crossbred families ranged in parental grain-row numbers from 8 to 32. Five of the families came from parents having more than 18 rows of grains.

To make a fair comparison between the two types of breeding in their relation to grain-row number, it is necessary to use only the crossbred families having parents with no more than 18 grain-rows. When we make such a limitation, we find the average grain-row number for the remaining six crossbred families is only 12.9. The grain-row average for the six F_1 families, namely, 15.2, exceeds the crossbreds by 17.1 per cent. Limiting the other indicators of physiological vigor to the same six crossbred families, we find that the F_1's exceed the corresponding crossbreds on the average by 6.3 per cent in height of stalks and 7.0 per cent in yield of ear-corn.

In 1911 I was again in full personal charge of the corn experiments at the Station for Experimental Evolution, and was able to expand the work considerably, both quantitatively and in the types of matings studied. We planted 84 cultures in the white dent series as well as 25 cultures of other types of corn. The total number of white dent ears of which the grain-rows were counted was 6,508 which showed the following frequencies:

Grain-rows	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	Total
Frequencies	267	767	1725	1298	931	683	363	164	114	95	65	23	7	3	3	6508
Percentages	4.1	11.8	26.5	19.9	14.3	10.5	5.6	2.5	1.8	1.5	0.9	0.4	0.1	0.1	0.1	99.9

In Table 2.7 the 1911 results are presented in condensed form. Families are grouped in eleven sections representing fairly homogeneous groups, mostly based on the types of matings involved. Sections D and E are both made up of the same five families of F_2 hybrids produced by selfing the same number of different F_1's. For these families each seed ear was used to plant two rows. The one row of each such family was grown with the other cultures, as usual, in the East Garden. The second row of each of these families was

TABLE 2.7

AVERAGE GRAIN-ROW NUMBERS AND YIELDS PER ACRE OF WHITE DENT MAIZE GROWN IN 1911 GROUPED ACCORDING TO THE TYPES OF MATINGS OF THE PARENTS

Pedigree Numbers	Parental Strains Involved	Number of Stalks	Av. Number Grain-Rows	Weights in Lbs.	Yields Bu./A.
	(A) Families from Inbreds Selfed				
F16.68$_1$.	8 selfed	12	8.7	1.5	17.9
E2.68$_2$.	8 selfed	44	9.0	6.0	19.5
F29.70.	10 selfed	89	10.9	16.5	26.5
F32.73.	12 selfed	95	11.8	11.3	16.9
F34.76.	Strain A selfed	98	8.4	8.3	12.1
F0.77.	A from L. H. Smith	101	8.9	8.8	12.4
E19.79$_1$.	B selfed	3	Not counted nor weighed		
F47.79$_2$.	B selfed	46	Not counted nor weighed		
F0.80.	B from L. H. Smith	95	14.3	4.3	6.8
E24.82.	16 selfed	84	14.0	7.5	12.8
F56.85.	20 selfed	90	15.3	13.8	21.8
E36.92.	26, 28 selfed	79	22.7	11.5	20.8
F74.94.	*"Cobs" selfed	64	Not counted nor weighed		
	Unweighted averages (omitting the three uncounted families)	78.7	12.4	8.9	16.7
	(B) Families from Parents Given Mixed Pollen in Each Generation; Selfing Prevented				
F23.69.	8 crossed	71	10.4	30.3	60.2
F31.72.	10 crossed	95	10.7	30.3	45.5
F46.78.	12 crossed	92	12.2	44.5	69.1
F53.81.	14 crossed	97	13.7	40.8	60.0
F55.84.	16 crossed	101	15.2	33.0	46.7
F63$_2$.86.	18 crossed	105	18.2	42.5	51.8
F66.87.	20 crossed	99	19.4	40.0	57.7
F70$_1$.91.	22 crossed	63	22.3	20.8	45.9
F73.93.	24 crossed	68	23.8	34.5	72.5
F76.96.	32 crossed	94	25.2	50.5	60.4
	Unweighted averages	88.5	17.0	36.7	57.0
	(C) F$_1$ Hybrids between Different Inbreds				
F29.71.	(10×12)F$_1$	62	12.2	24.5	56.5
F32.74.	(10×B)F$_1$	106	12.8	65.3	87.9
F32.75.	(10×16)F$_1$	100	14.3	63.0	90.0
F54.83.	(16×20)F$_1$	100	18.4	58.2	83.2
	Unweighted averages	92	14.4	52.7	79.4

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* This was a slightly fasciated brevistylis type, with silks about half as long as the husks. Usually it produced no grains except when given artificial help.

TABLE 2.7—*Continue*

Pedigree Number	Parental Strains Involved	Number of Stalks	Av. Number Grain-Rows	Weights in Lbs.	Yields Bu./A.
	(D) F_2 Families from F_1 Selfed, Grown in Annex No. 1				
F21.24......	(8×20)F_1 selfed	69	13.8	23.0	47.6
F22.28......	(8×B)F_1 selfed	61	13.4	31.3	73.2
F36.31......	(A×10)F_1 selfed	99	11.3	33.3	48.0
F37.36......	(A×B)F_1 selfed	93	11.8	17.0	29.3
F58.54......	(20×16)F_1 selfed	103	16.2	54.3	47.5
	Unweighted averages	83	13.3	31.8	49.1
	(E) Same Families as in (D), but Grown in East Garden				
F21.24......	(8×20)F_1 selfed	98	13.4	36.0	52.5
F22.28......	(8×B)F_1 selfed	101	13.4	56.0	79.2
F36.31......	(A×10)F_1 selfed	98	11.1	31.3	45.9
F37.36......	(A×B)F_1 selfed	76	11.0	15.3	28.7
F58.54......	(20×16)F_1 selfed	97	16.8	34.3	50.8
	Unweighted averages	94	13.2	34.6	51.4
	(F) F_2 Families from F_1×sibs, All Grown in East Garden				
F21.25......	(8×20)F_1×sib	59	12.9	22.0	53.3
F22.29......	(8×B)F_1×sib	97	12.8	42.8	63.0
F36.34......	(A×10)F_1×sibs	93	10.8	26.3	40.3
F37.37......	(A×B)F_1×sib	71	11.3	18.5	37.2
F58.55......	(20×16)F_1×sib	110	16.0	35.0	45.5
	Unweighted averages	86	12.8	28.9	47.9
	(G) F_3 Families from F_2 Selfed				
F38.39......	(A×20)F_2 selfed	84	13.0	9.8	16.6
F40.42......	(A×22)F_2 selfed	108	11.6	19.3	25.5
F42.45......	(A×16)F_2 selfed	67	10.2	10.5	22.4
F44.46......	(A×B)F_2 selfed	92	11.0	6.0	9.3
F49.49......	(16×A)F_2 selfed	112	11.4	24.3	30.9
F51.52......	(16×20)F_2 selfed	95	15.0	23.8	35.7
F59.57†.....	(20×16)F_2 selfed	100	15.9	24.5	35.0
F59.57......	(20×16)F_2 selfed	100	16.4	25.5	36.4
F61.59......	(20×A)F_2 selfed	117	12.0	9.8	13.6
F64.62......	(B×16)F_2 selfed	107	17.0	12.5	16.7
	Unweighted averages	98.2	13.3	16.6	24.2

† This family was divided and this section was grown in the North Hill-field. All of the other families were grown, as usual, in East Garden.

TABLE 2.7—*Continued*

Pedigree Numbers	Parental Strains Involved	Number of Stalks	Av. Number Grain-Rows	Weights in Lbs.	Yields Bu./A.
	(H) F_3 Families from F_2×Sibs				
F38.40......	(A×20)F_2×sib	106	13.5	26.0	35.0
F40.43......	(A×22)F_2×sib	112	11.9	26.5	33.8
F44.47......	(A×B)F_2×sib	94	11.2	21.8	33.1
F49.50......	(16×A)F_2×sib	104	11.8	29.8	40.9
F59.58......	(20×16)F_2×sib	90	16.5	38.5	61.1
F61.60......	(20×A)F_2×sib	111	13.8	25.0	32.2
F64.63......	(B×16)F_2×sib	104	15.1	27.5	37.8
	Unweighted averages	103	13.4	27.9	39.1
	(I) Families from "Three-Way" and Iterative Crosses				
F58.56......	(20×16)F_1×22	114	18.9	61.8	77.4
F74.95......	"Cobs"×(20×16)F_1	29	20.6	23.3	114.5
F21.27......	(8×20)F_1×20	67	15.0	28.5	60.8
F22.30......	(8×B)F_1×B	103	14.3	37.8	52.4
F36.33......	(A×B)F_1×A	84	10.5	23.0	39.1
F27.38......	(A×B)F_1×B	79	12.8	23.5	29.8
F51.53......	(16×20)F_2×20	108	17.1	42.3	55.9
	Unweighted averages (three-way)	71.5	19.7	42.5	96.0
	Unweighted averages‡ (iterative)	83.3	13.1	28.2	45.5
	(K) Families from "Four-Way" Crosses, the So-called "Double-Cross"				
F21.26......	(8×20)F_1×(A×10)F_1	67	12.7	28.5	60.8
F36.35......	(A×10)F_1×(20×16)F_1	106	12.8	47.0	63.3
F69.66......	(22×"Cobs")F_1×(8×10)F_1	75	16.3	58.5	111.4
F36.32§.....	(A×10)F_1×(A×B)F_1	102	11.2	45.5	63.7
	Unweighted averages	87.5	14.3	44.9	74.8
	(L) F_3 Families from Four-Way F_2 Crosses, and Imperfect Iteratives of Same Form				
F61.61......	(20×A)F_2×(B×16)F_2	102	15.3	31.8	44.5
F38.41......	(A×20)F_2×(A×22)F_2	103	12.9	27.0	37.5
F40.44......	(A×22)F_2×(A×16)F_2	110	13.2	43.5	56.5
F44.48......	(A×B)F_2×(16×A)F_2	78	11.4	28.0	51.3
F49.51......	(16×A)F_2×(16×20)F_2	117	13.3	44.3	61.6
	Unweighted averages	102	13.2	34.9	50.3

‡ Does not include F51.53.

§ F36.32 is an imperfect 4-way, being partly iterative, involving only 3 inbreds.

planted in new plots of ground about one-fourth mile north of the original Station grounds.

The purpose of this replication was to determine the degree of consistency of results secured in these new locations with those recorded for the cultures grown in the different conditions of soil, drainage, exposure, lighting, etc., in the East Garden. Summaries of these two sections of Table 2.7 show the cultures grown in the new plot with average grain-row number 1.29 per cent higher than in the same families grown in the East Garden. However, the East Garden cultures produced a higher average yield of ear-corn by 4.70 per cent.

Comparison between selfing and sibcrossing was made a subject of special study in the inbred and F_1 families in 1910. This was not continued in 1911 in the inbreds, but was given a further test in the derivation of the F_2 families from the F_1, and was carried forward to the derivation of F_3 families from the F_2. These comparisons as they relate to F_1 families are given in sections E and F of Table 2.7. They show the F_2 families derived from selfing their F_1 parents slightly superior to those F_2 families produced from sibcrosses in the F_1. This is indicated by an average grain-row number 3.1 per cent higher and average yield 7.5 per cent higher in the F_2 families from selfed F_1 parents, thus reversing the indications from the 1910 cultures.

The comparison of selfing *versus* sibcrossing in the production of the F_3 by these two methods of breeding in F_2 can be derived from section G for selfings and section H for the sibcrosses. Summaries of these two sections show a superiority from sibcrosses of 0.4 per cent in average grain-row number and 61.6 per cent in yield. A part of this discrepancy is clearly due to the inclusion of families in the selfed group which had no direct counterpart in the sibcrossed group. If we limit the comparison to the families which are represented in both groups, we can avoid this cause of distortion. We then find the sibcrossed families superior to the selfed by 1.5 per cent in grain-row number, and 48.6 per cent in yields.

Comparative values between inbreds and crossbreds, as shown in sections A and B of Table 2.7, and between crossbreds and F_1 hybrids, are essentially the same as in 1910. The ratios of inbreds, crossbreds, and F_1 hybrids, with respect to yields, is 0.29 to 1.00 to 1.22. Again the average grain-row number is less in the F_1 than in the crossbreds, and for the same reason. This particular group of F_1 families came from parents with low average grain-row numbers, as compared with the broader parentage of the crossbreds.

The relationship of F_3 to F_2 can now be noted by comparing the results in sections G and H of Table 2.7, with sections D, E, and F. There are several ways in which such comparisons can be made. Perhaps as good a way as any is simply to combine all of the F_2's together, regardless of the considerations which led these to be tabulated in three separate sections, and compare the results with all the F_3 families of sections G and H likewise averaged in an undivided population. When treated in this way, we find that the F_2's have an average grain-row number of 13.1 and average yields of 49.5 bushels per acre, while the F_3 had an average of 13.4 grain-rows and produced an average of 30.4 bushels per acre. If we associate the average yield of the F_1 families, 79.0 with these values for F_2 and F_3, we see the beginning of the characteristic curve in which the loss of yield from one generation to the next is about twice as great as the loss for the next following generation.

It remains to consider the last three sections of Table 2.7, in which are included the results of more complicated crossing which had become possible through the accumulation of simpler crossing in preceding years. In section I are given two "three-way" crosses and four iterative crosses involving F_1 combinations and one iterative cross involving an F_2 combination, each representing a cross between a hybrid and an inbred. As might be expected, these seven families although similar in form show no special consistency, since they involve various combinations of five different inbreds and five different hybrids.

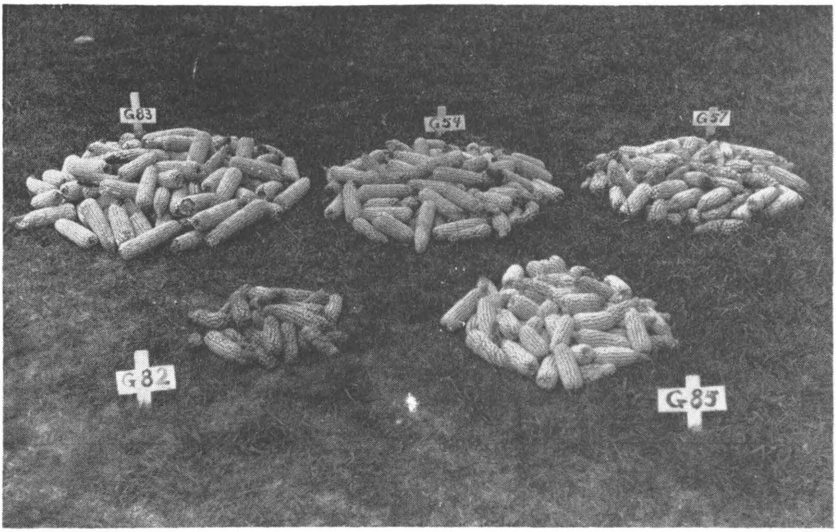

FIG. 2.6—Total yields of ear corn of two selfed strains, Strain 16 and Strain 20, in the foreground (exaggerated, of course, by foreshortening), and their F_1, F_2, and F_3 hybrids, left to right, successively, in the background. As may be seen in Table 2.7, these yields, calculated in terms of bushels per acre, are 12.76 and 21.82 for the two inbreds, and 83.21, 50.81, and 36.43 for the three hybrid families.

In Table 2.7, section K, are presented what I believe to be the first "four-way" or so-called "double crosses" ever made among inbreds. The elements of one of these double crosses are shown in Figure 2.7. These double crosses were made some five or six years before Dr. D. F. Jones pointed out the potentialities of such crosses in producing hybridized seed corn at a price

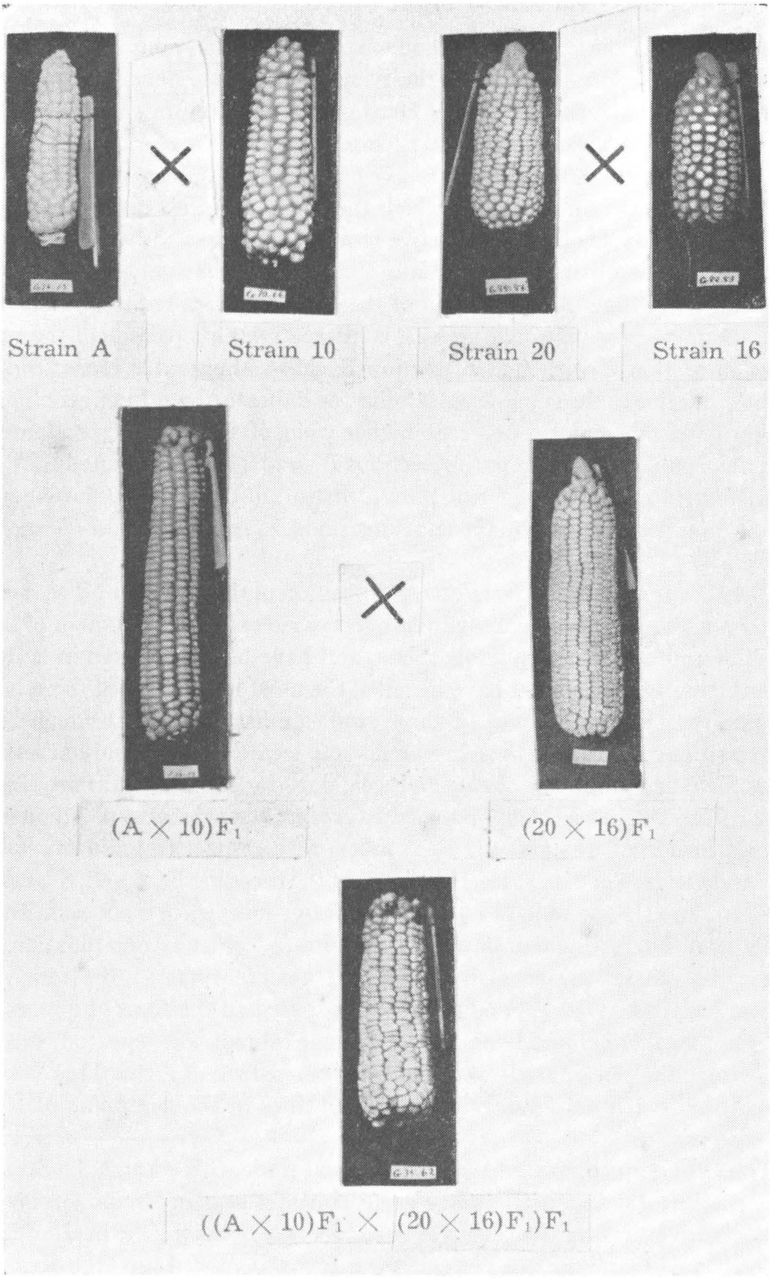

FIG. 2.7—One of the first *four-way* or *double crosses* ever grown from selfed strains of maize. The single crosses for this double cross were made in 1909, the cross between the F_1's was made in 1910, and the double-cross ear at bottom (G35.62) was grown in 1911 and grains from it were used for planting in 1912.

that could make the pure-line method of corn production practical. No credit is sought for the fact that I made these four-way crosses some years prior to the similar combinations made by Dr. Jones. They are presented here only because they belong in a historical account.

In the last section of Table 2.7 I have entered five families which have the form of four-way crosses, but in which the single crossings used were F_2 instead of F_1. Only the first of these five families actually involved four different inbreds, the others being partially iterative, in that only three inbreds contributed to each. A comparison of the double crosses both of F_1 and F_2, with the corresponding single crosses, is instructive. Comparison of the summary of section C with that of section K shows the double cross families slightly inferior to the single cross families, as indicated by a 1 per cent higher grain-row number and 6 per cent higher yield of the single cross families over the double cross. Comparing sections L and E, it is to be noted that the double cross retains the vigor of the F_2, instead of declining to the vigor of the F_3 families produced by the usual methods, as seen in sections G and H, Table 2.7.

In 1911 I realized that the effective exposition of the important discoveries we were making required photographs of prepared exhibits. A number of such exhibits were set up and photographed, and have been presented in lantern slides on many occasions. I have included the most instructive of these here.

Here the detailed account of these studies must end, for although they were continued in 1912, I have been unable to locate the field and harvesting notes including grain-row counts and weighings for the 1912 cultures. These 1912 cultures were especially designed to explore the evidences of Mendelian segregations in the F_2 and the F_3 families, with respect to grain-row numbers and yields. They included 11 families of the breeding $F_1 \times$ self, 8 families of $F_1 \times$ sib, 21 $F_2 \times$ self, 10 $F_2 \times$ sibs, and five families of $F_3 \times$ self. There was also an interesting pair of approximations to eight-way combinations or quadruple crosses produced by reciprocal combinations of the four-way crosses included in the 1911 cultures. While these had the form of quadruple crosses, they were imperfect in that one of the inbreds was repeated, so that only seven different inbreds were represented, instead of eight. This was inevitable since I initiated only seven inbred lines in the beginning of these experiments.

The 1912 crop completed the experimental work with corn at the Station for Experimental Evolution, and I spent the next year in Berlin, Germany. In a lecture I gave at Göttingen about three weeks before the beginning of the first World War the word *heterosis* was first proposed. I used the occasion to discuss the bearing of the results of these studies on the practical work of breeders of various classes of organisms, both plant and animal. I stressed the point that the breeder should not be content, as had long been the case, to seek merely to avoid the deterioration incident to inbreeding, but should

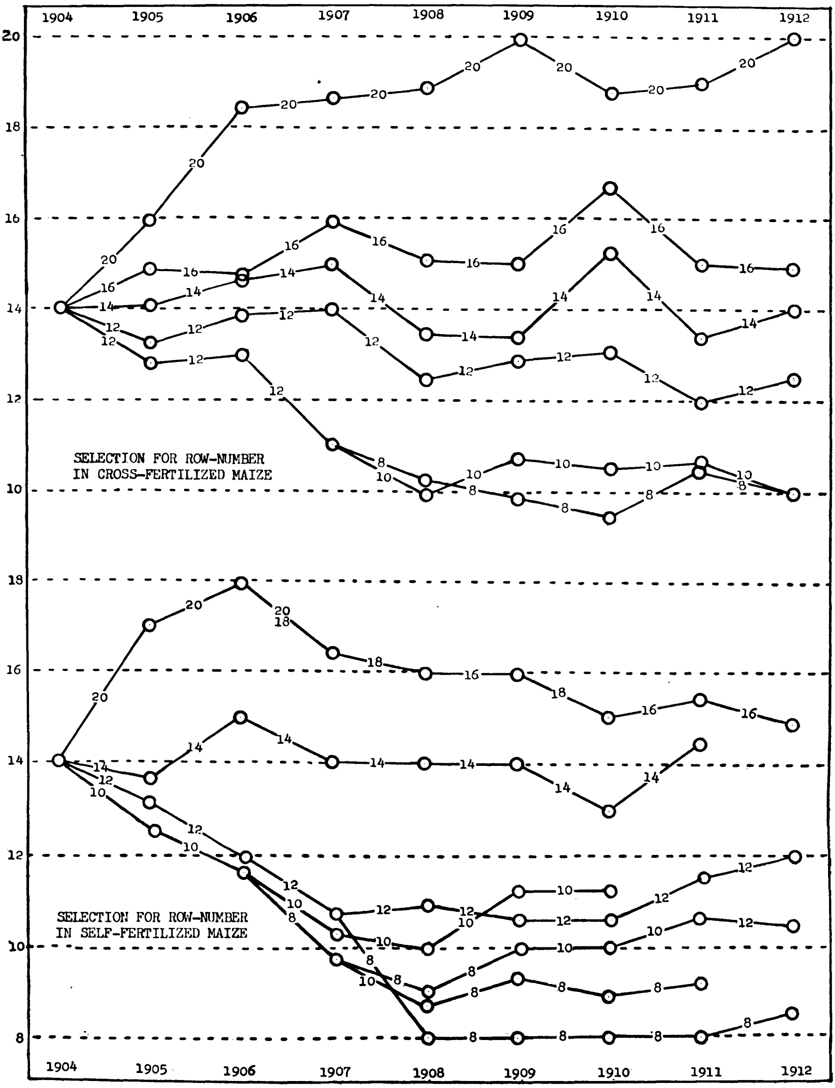

FIG. 2.8—Diagrams of the progressive results of selection for grain-row number under the two systems of breeding: selfing completely prevented in the upper diagram; selfing the sole method of breeding in the lower. The numbers on the lines indicate the numbers of rows of grains on the parent ears. The circles show by their position on the scale at left the average grain-row numbers of the resulting progenies.

recognize in heterosis a potent source of practical gains, to be investigated, understood, and utilized as a new tool in deriving from plant and animal life their maximum contributions in the service of man.

Although no further experimental work was done with corn at the Station for Experimental Evolution after 1912, I tried to resume the work in my first two years at Princeton University, by planting 77 cultures of pedigreed corn in 1916 and 65 in 1917. I used some of the materials from these cultures for laboratory studies in biometry in my classes in genetics. The interesting results shown in Figure 2.9 are from my 1916 crop at Princeton. The plantings at Princeton were made late and the young plants were decimated by pigeons and crows, so that some valuable connections were lost, and with them some of my interest in their continuation.

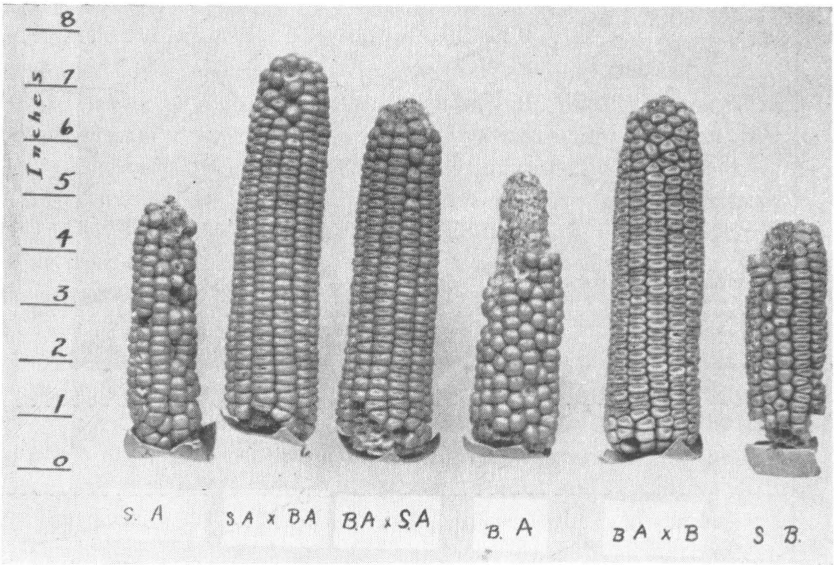

FIG. 2.9—Ears of my white dent "strain" of corn grown at Princeton University in 1916. The ears, each typical of the progeny to which it belonged, are from left to right: SA, Shull's Strain A; SA × BA, F_1 hybrid between Shull's Strain A and Blakeslee's "branch" of the same strain; BA × SA, reciprocal of the last; BA, Shull's Strain A, after two successive selfings by Dr. A. F. Blakeslee; BA × B, F_1 between Blakeslee's branch of Strain A and Shull's Strain B; and SB, Shull's Strain B. About as much heterosis is shown by a cross between two sub-lines of Strain A as between one of these sub-lines and Strain B, the implication being that something more specific may be involved in this example of heterosis than the mere number of genetic differences. (Photo by W. Ralph Singleton in 1945.)

As we all know, heterosis is not limited to corn, and my own interest in the matter was in no wise restricted to its manifestation in corn. There were examples presented in many other of my genetical experiments. I was particularly interested in the discovery of such special mechanisms as balanced lethal genes in the Oenotheras and self-sterility genes in *Capsella grandiflora* which, along with many types of asexual reproduction including parthenogenesis, specifically enable the organisms possessing these special mechanisms to maintain the full advantages of heterosis. On one occasion, one of my new hybrid combinations in Oenothera happened to be planted through an area in my experimental field where the soil had become so impoverished that none of my other cultures reached their normal growth. Many of the

FIG. 2.10—The F_1 hybrids between a cultivated form of *Helianthus annuus* and a wild form of the same species received from Kansas. This photograph, taken at the Station for Experimental Evolution in 1906, shows the author affixing a glassine bag to a head of one of the hybrid plants. The two parents of this hybrid averaged from 5 to 6 feet tall, while 51 of these F_1 hybrids, measured on August 28, 1906, ranged in height from 6.7 to 14.25 feet, the average being 10.46 feet. This may be considered my first experience with *hybrid vigor*.

plants remained rosettes or formed only weak depauperate stems. But this new hybrid became a vigorous upstanding form in this impoverished area as well as on better soil elsewhere. I recorded this as a notable example of making heterosis take the place of manure or commercial fertilizers.

Figure 2.10 is a notable hybrid, which represents my first direct personal contact with a recognized case of hybrid vigor. This hybrid resulted from a cross I made in 1905 between the so-called "Russian" sunflower and the wild *Helianthus annuus* of our western prairies. Both of these forms have been referred, botanically, to the same species. Both are of approximately equal height, scarcely as tall as the six-foot step-ladder shown in the figure. The tallest of these F_1 hybrids was 14.25 feet in height.

Returning now to the question which I sidestepped in the beginning—what we mean by the expression *the heterosis concept*—I suggest that it is the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind, manifested by crossbred organisms as compared with corresponding inbreds, as the specific results of unlikeness in the constitutions of the uniting parental gametes.

I think the first clear approach to this concept was involved in a statement which I have already quoted, that "a different explanation was forced upon me" (in my comparisons of cross-fertilized and self-fertilized strains of maize). That is, "that self-fertilization simply serves to purify the strains, and that my comparisons are not properly between cross- and self-fertilization, but between pure strains and their hybrids." Since heterosis is recognized as the result of the interaction of unlike gametes, it is closely related to the well known cases of complementary genes. It differs from such complementary genes, however, mainly in being a more "diffuse" phenomenon incapable of analysis into the interactions of specific individual genes, even though it may conceivably consist in whole or in part of such individual gene interactions.