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Chapter 3

Development of
the Heterosis Concept

Hybrid vigor in artificial plant hybrids was first studied by Koelreuter in 1763 (East and Hayes, 1912). The rediscovery of Mendel's Laws in 1900 focused the attention of the biological world on problems of heredity and led to renewed interest in hybrid vigor as one phase of quantitative inheritance.

Today it is accepted that the characters of plants, animals, and human beings are the result of the action, reaction, and interaction of countless numbers of genes. What is inherited, however, is not the character but the manner of reaction under conditions of environment. At this time, when variability is being expressed as genetic plus environmental variance, one may say that genetic variance is the expression of variability due to genotypic causes. It is that part of the total variance that remains after eliminating environmental variance, as estimated from studying the variances of homozygous lines and F_1 crosses between them.

Early in the present century, East, at the Connecticut Agricultural Experiment Station, and G. H. Shull at Cold Spring Harbor, started their studies of the effects of cross- and self-fertilization in maize. The writer has first-hand knowledge of East's work in this field as he became East's assistant in July, 1909, and continued to work with him through 1914. In 1909, East stated that studies of the effects of self- and cross-pollination in maize were started with the view that this type of information was essential to a sound method of maize breeding. In addition to studies of maize, which is normally cross-pollinated, East carried out studies in tobacco of crosses between varieties and species. This gave an opportunity of studying the effects of self- and cross-pollination with a self-pollinated plant. A 1912 publication of East and Hayes made the following statement:

> The decrease in vigor due to inbreeding naturally cross-fertilized species and the increase in vigor due to crossing naturally self-fertilized species are manifestations of one phenomenon. This phenomenon is heterozygosis. Crossing produces heterozygosis in all characters by which the parent plants differ. Inbreeding tends to produce homozygosis automatically.

Several photographs from this bulletin are of some interest. A picture of two inbred lines of maize and their F_1 cross was one of the first published field views of hybrid vigor from crossing inbred lines of maize. East told me that such a demonstration of hybrid vigor would create a sensation if the material had been grown in the corn belt.

Some F_1 crosses between species and sub-species in tobacco gave large increases in vigor. Some species crosses were sterile. Some varietal crosses within species showed little or no increase in vigor, other crosses gave an average increase of 25 per cent in height over the average of their parents. A few wide species crosses were very low in vigor. One such cross beween *Nicotiana tabacum* and *Nicotiana alata grandiflora* was sterile and very weak in growth. Photographs of the parents and hybrids bring out the fact that a lack of vigor in a few cases was known to accompany the heterozygous condition. Naturally such undesirable combinations had little importance either to the plant breeder or as a basis for evolution.

In 1910, G. H. Shull summarized the effects of inbreeding and crossbreeding in maize in a clear, concise, and definite manner. The student of heredity in this early period had little conception of the complexity of inheritance. Hybrid vigor was in many cases not clearly Mendelian. The term heterosis was coined by Shull and first proposed in 1914. He used the term to avoid the implication that hybrid vigor was entirely Mendelian in nature and to furnish a convenient term to take the place of such phrases as "the stimulus of heterozygosis."

At this time it was usually stated that increased vigor in hybrids was due to a more rapid cell division as stimulated by the heterozygous condition of the genotype. A. F. Shull in 1912 attributed the vigor "to the effect of a changed nucleus and a (relatively) unaltered cytoplasm upon each other."

The purpose of this chapter is to discuss some phases of the development of the heterosis concept since 1910. Three main topics will be presented covering utilization, breeding methods, and genetic concepts with particular reference to practical applications and to genetic explanations.

UTILIZATION OF HETEROSIS BY THE PRODUCER

The presentation of East and Hayes in 1912 emphasized the probable practical value of heterozygosis. A review of experiments with maize was made. In discussing Shull's (1909) plan for the use of single crosses between inbred lines, it was stated that the procedure was desirable in theory but difficult of application. At this early time the inbred lines of maize that were available seemed so lacking in vigor that the use of F_1 crosses between selfed lines in maize for the commercial crop seemed impractical. Both Shull and East believed that some method of direct utilization of hybrid vigor in maize would be found.

One is inclined to forget that the inbred lines of maize of today are marked-

ly superior, on the average, to those of 1910. Jones's discovery about 1917 of the double cross plan of producing hybrid seed in maize, and the subsequent proof by many workers that double crosses can be obtained that closely approach the vigor of F_1 crosses between selfed lines, furnished the basis for the utilization of hybrid vigor in field corn. With sweet corn, however, F_1 crosses between selfed lines are used very widely today for the commercial crop.

East and Hayes emphasized that F_1 crosses probably would be of commercial value in some truck crops where crossing was easy. Eggplants, tomatoes, pumpkins, and squashes were considered to offer promise for a practical use of such vigor. The writers also mentioned the fact that heterozygosis had been used in vegetatively propagated plants, though not purposely, and that it seemed feasible to make a practical application in the field of forestry.

The use of heterosis in practical plant and animal improvement has borne out and surpassed these early predictions as shown in Table 3.1.

TABLE 3.1

USE OF HETEROSIS IN CROP PLANTS AND LIVESTOCK

Farm crops:	Maize, sugar beets, sorghums, forage crops, and grasses
Horticultural crops:	Tomatoes, squashes, cucumbers, eggplants, onions, annual ornamentals
Silkworms	
Livestock:	Swine, poultry, beef and milk cattle
Vegetatively propagated plants	

In the corn belt of the United States nearly 100 per cent of all maize is hybrid. Hybrid corn is rapidly being developed in other countries of the world, and is one of the best illustrations of the practical utilization of modern genetics. Considerable evidence leads to the conclusion that heterosis can be used extensively in farm crops, including such widely different plants as sugar beets, sorghums, tobacco, forage crops, and grasses.

With horticultural plants, where the individual plant is of rather great value, planned heterosis has proven worth while. First generation crosses of tomatoes, onions, egg plants, cucumbers, and squashes have proven their value and are being grown extensively by home and truck gardeners. Similar use is being made of heterosis in some annual ornamentals.

Heterosis has become an important tool of the animal breeder. Its use in silkworm breeding is well known. Practical utilization of hybrid vigor has been made in swine and poultry, and applications are being studied with beef cattle, dairy cattle, and sheep. A somewhat better understanding of the effects of inbreeding and crossing by the breeder has aided in applications with livestock. As in plants, inbreeding makes controlled selection possible, while controlled crosses may be grown to utilize favorable gene combinations.

METHODS OF BREEDING FOR HETEROSIS

In general there is a much closer relation between the characters of parents and of their F_1 crosses in self-pollinated plants than between the characters of inbred lines of cross-pollinated plants and their F_1 crosses.

Characters of Parents and F_1 Crosses in Self-pollinated Plants

A recent study by Carnahan (1947) in flax, which is normally self-pollinated, may be used for illustrative purposes. Four varieties of flax were selected to represent desirable parental varieties. Each was crossed with four other varieties, of different genetic origin from the first group, to be used as testers. Sufficient seed for F_1 and F_2 progenies was produced so that all

TABLE 3.2
PARENT AND F_1 CROSSES, YIELD
IN BUSHELS PER ACRE*

Parent Varieties		Tester Varieties			
		5	6	7	8
		16	14	17	13
1	19	31	25	22	19
2	18	24	26	19	20
3	13	26	24	20	18
4	17	22	21	20	19

*Parent yields outside rectangle, F_1 crosses within.

progenies could be planted in replicated, 8-foot rows at the rate of 200 seeds per row. Combining ability was studied in F_1 and F_2 in comparison with the parents for yield of seed, number of seeds per boll, number of bolls per plant, weight of 1000 seeds, date of full bloom, and plant height.

As shown in Table 3.2, each F_1 cross yielded more than its highest yielding parent, although for one cross the difference was only slightly in favor of the F_1. For an average of all crosses, the F_1 yielded 40 per cent more than the average of the parents, and the F_2, 26 per cent more. The lowest yielding cross, 3 × 8, was produced from a cross of the two lowest yielding parents. The highest yielding cross, 1 × 5, however, could have been selected only by actual trial. It was obtained by crossing the highest yielding selected variety with the second highest yielding tester variety.

There was excellent agreement, on the average, for each of the characters studied between the average expression of the characters of the parents and their F_1 crosses. Carnahan concluded that for each character studied there appeared to be a good relationship between the performance of the parents and the average performance of their F_1 crosses. The characters of the parents in this study were as good or better indication of the combining ability of a parental variety as that obtained from a study of average combining ability in four crosses.

Powers (1945) obtained also relatively good agreement in tomatoes between the parental yield of 10 varieties and that of all possible F_1 crosses between the 10 varieties (see Table 3.3).

Moore and Currence (1950) in tomatoes made a somewhat comparable study to that of Carnahan with flax. They used two three-way crosses as testers for a preliminary evaluation of combining ability of 27 varieties. Based on this, eight varieties were selected that gave a wide range in average combining ability for several characters including early yield and total yield. These varieties were crossed in all combinations, and yield trials of the

TABLE 3.3

YIELD OF RIPE FRUIT IN GRAMS
IN TOMATOES (AFTER POWERS)

VARIETY OR INBRED	YIELD OF RIPE FRUITS (PER PLANT)	
	Variety or Inbred Grams	9 Crosses (av.) Grams
L. esculentum		
Bounty 4101.......	513 ± 39	1280 ± 53
4102.......	607 ± 86	1267 ± 46
4105.......	332 ± 64	1081 ± 33
4106.......	828 ± 108	1236 ± 45
Es. $\times$ *L. pim*		
4103.......	1066 ± 159	1597 ± 54
4104.......	808 ± 114	1340 ± 44
4107.......	801 ± 111	1181 ± 47
4108.......	857 ± 108	1192 ± 41
4109.......	1364 ± 151	1968 ± 46
4110.......	1868 ± 149	2231 ± 52

varieties and F_1 crosses were made. There was relatively good agreement between the early test for combining ability and the average yield of F_1 crosses, but the relationship did not seem superior to the varietal performance as a means of predicting combining ability in crosses. In the studies by Carnahan, Moore, Currence, and Powers the only means of selecting the most desirable F_1 cross was by actual trial.

Characters of Inbred Lines and Their F_1 Crosses in Maize

Numerous studies have been made with maize of the relation between characters of inbred lines and of their F_1 crosses. There usually have been indications of significant correlations for most characters of inbred lines and their F_1 crosses. In most cases, however, the relationship was not very large or highly important when one studied individual characters, or the more complex character—yield of grain. The studies have been reviewed by numerous workers (see Sprague, 1946b).

Hayes and Johnson (1939) in Minnesota studied the relation between the characters of 110 inbred lines of maize and their performance in top crosses. The characters studied in selfed lines in replicated yield trials are given in Table 3.4.

All possible correlations were made between the individual characters of the inbreds and of these characters and the yield of grain of top crosses. The

TABLE 3.4

CHARACTERS OF 110 INBRED LINES IN
CORN CORRELATED WITH INBRED-
VARIETY YIELDING ABILITY

1. Date silked	7. Stalk diameter
2. Plant height	8. Total brace roots
3. Ear height	9. Tassel index
4. Leaf area	10. Pollen yield
5. Pulling resistance	11. Grain yield
6. Root volume	12. Ear length

TABLE 3.5

TOTAL CORRELATIONS BETWEEN CHARACTERS OF 110 INBREDS,
LABELED 1 TO 12, AND YIELDING ABILITY OF INBRED-
VARIETY CROSSES DESIGNATED AS 15

	CHARACTERS CORRELATED											
	2	3	4	5	6	7	8	9	10	11	12	15
1	0.51	0.61	0.48	0.65	0.62	0.55	0.38	0.37	0.22	0.07	−0.06	0.47
2		0.76	0.44	0.48	0.43	0.40	0.26	0.19	0.36	0.25	0.08	0.27
3			0.43	0.54	0.50	0.41	0.35	0.33	0.22	0.15	−0.01	0.41
4				0.50	0.44	0.48	0.40	0.29	0.18	0.20	0.08	0.29
5					0.76	0.44	0.51	0.60	0.41	0.21	0.15	0.04	0.45
6						0.55	0.74	0.39	0.29	0.19	0.03	0.54
7							0.54	0.24	0.27	0.21	0.15	0.41
8	Multiple value of R							0.26	0.22	0.20	0.07	0.45
9	for inbred-variety yield								0.20	−0.00	0.03	0.19
10	and twelve characters of									0.35	0.32	0.26
11	inbred = 0.67										0.64	0.25
12												0.28

Significant value of r for P of .05 = 0.19.
Significant value of r for P of .01 = 0.25.

characters, in general, were those that were considered to evaluate the inbreds in developmental vigor.

The total correlations between characters are summarized in Table 3.5. Most correlations were significant at the 5 per cent or 1 per cent point except the relation between ear length and other characters of the inbreds. All relationships between the characters of the inbreds, including grain yield, and the yield of top crosses were significant at the 1 per cent point except for tassel index of the inbreds, and that was significant at the 5 per cent point. The multiple correlation coefficient of 0.67 indicated that under the conditions of the experiment about 45 per cent of the variability of inbred-variety

yield was directly related to characters of the inbreds. These relationships between the parents and their F_1 crosses were somewhat larger than those obtained by others with maize. Nevertheless, relationships were much smaller than has been obtained in similar studies with self-pollinated plants.

Richey (1945b) compared the yield of inbred parents in the S_3 and S_4 generations of selfing with the mean yield of their single crosses from data taken by Jenkins and Brunson. Similar comparisons were made between the yield in top crosses and the mean yield in single crosses (see Table 3.6).

Although for various reasons the r values are not strictly comparable, the yield of inbreds was as strongly correlated with the mean yield of their single crosses as the yield in top crosses was correlated with the mean yield of single crosses.

TABLE 3.6

CORRELATION COEFFICIENTS FOR YIELDS OF
INBRED PARENTS OR TOP CROSSES WITH
MEAN YIELDS OF SINGLE CROSSES*

HYBRIDS CORRELATED WITH	PREVIOUS GENERATIONS OF INBREEDING	
	S_3†	S_4
Inbred parents	.25, .64, .67	.41, .45
Top crosses	.53	.53

* After Richey, after Jenkins and Brunson.
† S_3 = three years selfed, etc.

Comparison of Methods with Self- and Cross-pollinated Plants

In self-pollinated plants it seems probable that the first natural step in the utilization of heterosis normally may consist of the selection of available parental varieties that in themselves produce the best combination of characters. It seems important to continue breeding for the best combination of genes that can be obtained in relatively homozygous varieties. Where hybrid seed can be produced cheaply enough, or new methods can be found to make crosses more easily, heterosis can be used to obtain from the hybrid an advance in productivity over the homozygous condition.

In cross-pollinated plants two general methods of breeding for heterosis are now being widely utilized. One consists, as in maize, of the selection within and between selfed lines and the use of single, three-way, or double crosses for the commercial crop. The second general method consists of selecting or breeding desirable clones of perennial crops. These are evaluated for combining ability by polycross, or other similar methods, and the desirable clones used to produce F_1 crosses, double crosses, or synthetic varieties.

There seems to be some difference of opinion regarding the selection process in its application to maize improvement. One school of thought practices a somewhat similar method of breeding selfed lines as is used in self-pollinated plants, with the viewpoint that controlled selection makes it possible to isolate in the inbred lines the genes for characters needed in the hybrids. Apparently the relationship between the characters of inbreds and their F_1 crosses will become greater as inbred lines themselves improve. The other extreme of viewpoint (Hull, 1945a) is that the greater part of hybrid vigor is due to interallelic interaction of genes to such an extent that selection based on appearance may be harmful. In a recurrent selection program Hull, therefore, does not recommend selection for vigor of growth, although he states that plants showing pest or weather damage should be avoided.

It is probable that differences between these two so-called schools may have been overstated. Both believe that the actual test for combining ability in hybrid combination is necessary. The stage in the breeding program when such test should be made will depend on the material worked with and the nature of the breeding program. In both cross- and self-pollinated plants an actual trial will be needed to determine the combination that excels in heterosis.

Where clonal lines can be propagated vegetatively, a method of selecting for heterosis in alfalfa was suggested by Tysdal, Kiesselbach, and Westover (1942), by means of polycross trials. The method is being used extensively today with perennial forage crops that normally are cross-pollinated. The writer is studying the method with early generation selfed lines of rye. With perennial crop plants, selection for combining ability is made for heterozygous parent clones. Where disease and insect resistance or winter hardiness are important, it may be essential to insure that the clones used in the polycross trials excel for these characters. Polycross seed is produced on selected clones under open-pollinated conditions where the clones are planted together at random under isolation.

In one study of progenies of eight clones by Tysdal and Crandall (1948) yields were determined from polycross seed in comparison with top cross seed when each of the clones was planted in isolation with Arizona common alfalfa (see Table 3.7). The agreement for combining ability was relatively good in the two trials.

An early suggestion of utilization of heterosis in alfalfa was by double crosses, from single crosses between vegetatively propagated clones, without entire control of cross-pollination. Synthetic varieties also have been suggested as a means of the partial utilization of heterosis. In one comparison the progeny of a synthetic combination of four clones of high combining ability yielded 11 per cent more forage than a similar combination of four clones of low yielding ability. A recent comparison of eight synthetics led Tysdal and Crandall to conclude that the first synthetic and second syn-

thetic seed progenies gave about the same forage yield. In this comparison, heterosis continued through the second seed increase of the high yielding synthetic.

Other Studies with Maize

Combining ability, that is ability to yield in hybrid combination, has been shown by various workers to be an inherited character (Hayes and Johnson, 1939), (Cowan, 1943), (Green, 1948). It seems feasible to breed for high combining ability as for other quantitative characters. In the breeding program

TABLE 3.7

FORAGE YIELDS OF POLY-
CROSSES COMPARED TO
TOP CROSSES OF THE
SAME CLONES*

CLONE No.	YIELD RELATIVE TO GRIMM AS 100	
	Polycross	Arizona Top Cross
1...........	121	130
2...........	111	122
3...........	101	117
4...........	99	103
5...........	97	105
6...........	96	101
7...........	89	101
8...........	76	101

* After Tysdal and Crandall.

for the production of improved inbred lines, it is often possible to select as parents of crosses, select lines having high combining ability as parents of crosses, in addition to selection for other characters that are desired. In breeding for heterosis, however, it seems evident that genetic diversity of parentage is equally as important as combining ability (see Hayes and Immer, 1942; Sprague, 1946b).

All relatively homozygous, inbred lines in maize are much less vigorous than the better F_1 crosses. It is apparent that heterosis is of great importance in crosses with inbred lines of maize.

Inbred lines that have undesirable characters may be easily improved by the application of any one of several methods of breeding. The breeder may select for each problem the method or methods that seem to him most applicable. In breeding selfed lines the selection of parents that have complementary characters that together include the characters desired in the improved inbred is a natural first step. Subsequent methods of breeding may

be used according to the viewpoint of the breeder and the particular problem to be solved.

While combining ability is an inherited character, it seems of special interest that single crosses of high × high combiners have not been greatly superior in yield, on the average, to crosses of high × low. Both, however, were clearly higher in yielding ability than low × low crosses (Johnson and Hayes, 1940), (Cowan, 1943), (Green, 1948). An illustration from Johnson and Hayes (Table 3.8) shows the type of results obtained. The crosses were classified for yielding ability in comparison with recommended double crosses of similar maturity.

Two recent studies in Minnesota may be used to illustrate other breeding problems. A further study was made by Johnson (1950) of the combining ability of F_4 lines that were studied in earlier generations by Payne and Hayes (1949). Yield relations in the double cross Min. 608 (A344 × A340) (A357 × A392) are illustrated in Table 3.9.

TABLE 3.8

FREQUENCY DISTRIBUTION FOR YIELD OF SINGLE CROSSES
OF SIMILAR MATURITY IN COMPARISON WITH
RECOMMENDED DOUBLE CROSSES AS 0

Type of Cross	Class Centers of -1 to -2, $+1$ to $+2$, etc. Times the S.E. of a Difference										
	-7 -8	-5 -6	-3 -4	-1 -2	0	$+1$ $+2$	$+3$ $+4$	$+5$ $+6$	$+7$ $+8$	Total	Mean
Low×low......	....	1	1	2	4	4	....	....	....	12	-0.5 ± 0.7
Low×high.....	1	3	....	11	6	16	9	5	1	52	$+1.1\pm0.4$
High×high....	....	1	5	12	8	33	20	4	....	83	$+1.1\pm0.2$

TABLE 3.9

YIELD RELATIONS IN MIN. 608
(A334×A340)(A357×A392)

	% M.	Yield (Bu.)
A334×A357 and A392.....	19.6	66.8
A340×A357 and A392.....	18.5	62.4
Average...............	19.0	64.6
A357×A334 and A340.....	19.5	66.0
A392×A334 and A340.....	18.6	63.2
Average...............	19.0	64.6
Min. 608..............	19.0	64.0

In these studies the usual method of predicting combining ability of a double cross gave excellent agreement between both predictions and the actual double cross yield.

The studies of the performance in early and later tests of F_2 to F_4 lines from L317 $\times$ A116 when crossed with (A334 $\times$ A340) in comparison with A357(A334 $\times$ A340) were carried out by Payne and Johnson. The methods of comparing combining ability in different generations were adapted by the writer, who alone is responsible for the conclusions drawn. The lines were first placed in $+1$, -1, etc. $\times$ L.S.D. at the 5 per cent point with the performance of A357(A334 $\times$ A340) as 0. Classes for performance of individual lines were made by adding the yield class of a line to its moisture class with the sign of the latter changed.

The F_2 and F_3 crosses were both grown the same year, the F_3 and F_4 were grown in different years, and the F_4 and the top crosses were grown the same year (see Tables 3.10, 3.11, 3.12).

In these studies no new lines seemed markedly superior to A357 in com-

TABLE 3.10

COMBINING ABILITY RELATION OF F_2 AND F_3 LINES
OF (L317$\times$A116) IN CROSSES WITH (A334$\times$A340)
GROWN IN SAME TRIAL IN 1947

F_3 crosses	+2	+1	0	−1	−2	−3	−4	−5	Total
+2			1						1
0			2		2	1	1		6
−1		1		2	1	1			5
−2					1	2	3		6
−3	1		1		1	3	1		7
−4					2	2			4
−5								2	2
−7								2	2
	+2	+1	0	−1	−2	−3	−4	−5	33

F_2 crosses, performance classes

TABLE 3.11

COMBINING ABILITY RELATION OF F_3 AND F_4 LINES
OF (L317$\times$A116) IN CROSSES WITH (A334$\times$A340)
F_3 GROWN IN 1947, F_4 IN 1949

F_3 crosses	+2	+1	0	−1	−2	−3	−4	−5	Total
+2			1						1
0	1		2		2	1			6
−1					5				5
−2			1	1	3	1			6
−3		1	1		2	3			7
−4			1		1	2			4
−5						1		1	2
−7							1	1	2
	+2	+1	0	−1	−2	−3	−4	−5	33

F_4 crosses, performance classes

bining ability with (A334 × A340). As A357 is rather outstanding in combining ability the result may not be so surprising. There was much greater relation between the combining ability of F_3 and F_4 lines and of F_4 with top crosses than between F_2 and F_3.

In an unpublished study of gamete selection, with a different but highly desirable double cross, there was an indication that a lower yielding inbred could be improved by an application of gamete selection (Stadler, 1944). The study is from one phase of a breeding program to improve Min. 406. The yield relations of inbreds in an average of single crosses are given in Table 3.13.

Approximately 60 F_1 plants of A25 × Golden King were selfed and top crossed with A73 × A375. Thirty-two of the more desirable plants were selected to study in yield trials. In this study both yield and moisture classes of plus 1, plus 2, etc. × L.S.D. at 5 per cent were used around the mean of

TABLE 3.12

COMBINING ABILITY RELATION OF F_4 LINES OF
(L317×A116) IN CROSSES WITH (A334×A340) AND
WITH GOLDEN KING. GROWN IN 1949

		+1	0	−1	−2	−3	−4	−5	Total
	+2		1						1
	+1		1						1
In	0	1	3	1	1				6
A334	−1					1			1
×	−2		9		1	3			13
A340	−3				3	4	1		8
Crosses	−4							1	1
	−5					1	1		2
		+1	0	−1	−2	−3	−4	−5	33

In Golden King Crosses

TABLE 3.13

GAMETE SELECTION IN THE IMPROVE-
MENT OF MINHYBRID 406
(A25×A334)(A73×A375)

	Av. of Crosses	
	%M.	Bu.
A25×A73, A375.......	24.6	76.2
A334×A73, A375......	24.7	79.4
A73×A25, A334.......	24.6	74.8
A375×A25, A334......	24.7	80.8

Proposal for improvement of A25 and A73:
A25×G. King gametes
A73×Murdock gametes

A25 $\times$ tester as 0. The results (see Table 3.14) indicate that gametes from Golden King are a desirable source of improvement of A25 in crosses with A73 $\times$ A375.

From this first trial three high and three low yielding lines were selected, and selfed progeny grown in S_1. Plants in each of the three S_1 high and three low combining lines were selected, selfed, and again top crossed on A73 $\times$ A375. The agreement for S_0 and S_1 lines was very good (see Table 3.15). It appears that gamete selection is an excellent breeding method for the early selection of material to improve the specific combining ability of a known inbred.

SOME GENETIC CONCEPTS OF HETEROSIS

It seems very evident to the writer that heterosis, the increased vigor of F_1 over the mean of the parents or over the better parent, whichever definition is used, is not due to any single genetic cause. A brief summary of various

TABLE 3.14

DISTRIBUTION OF % MOISTURE AND YIELD OF 32 S_0
PLANTS OF A25 $\times$ G. KING CROSSED TO A73 $\times$ A375.
CLASSES OF L.S.D. 5% AROUND MEAN OF A25 $\times$
TESTER

	$+2$		1		
% ear	$+1$		3	2	(mean of A25 $\times$
mois.					tester)
	-1	2	8	5	
	-2	3	5	3	
		-2	-1	$+1$ $+2$	

Yield
(mean of A25 $\times$ tester)

TABLE 3.15

PERFORMANCE INDICES OF S_0 AND S_1 LINES
FROM A25 $\times$ G. KING WHEN CROSSED TO
A73 $\times$ A375 TESTER AND COMPARED WITH
A25 $\times$ TESTER

GAMETE NUMBER	S_0		S_1	No. of S_1's
	1947	1949	1949	
19 H.....	$+11$	$+19$	$+25$	5
20 H.....	$+14$	$+9$	$+14$	7
36 H.....	$+9$	$+16$	$+11$	7
5 L.....	-11	-3	$+5$	7
29 L.....	-11	-1	-0	1
46 L.....	-5	$+1$	$+2$	7

theories advanced to explain heterosis seems desirable to set the stage for later discussions. Bruce (1910) explained heterosis on the combined action of favorable dominant or partially dominant factors, based as Richey (1945a) has emphasized on mathematical expectations.

Keeble and Pellew (1910) used a similar hypothesis on a di-hybrid basis to explain hybrid vigor in peas. East and G. H. Shull (1910–1914) believed vigor was dependent on heterozygosis on the basis that the stimulus of hybridity was not entirely Mendelian. A. F. Shull (1912) preferred the explanation that heterosis was due to a stimulus resulting from a changed nucleus on a relatively unaltered cytoplasm. Jones (1917) restated Bruce's concept and added the concept of linkage.

Collins (1921) and Richey (1945) have pointed out that where large numbers of factor pairs are involved it would be very difficult to recover all factors in a favorable condition in F_2, or in later segregating generations. With multiple factors involved, however, linkage must of necessity make the recombination of factors more difficult. East (1936) presented a Mendelian concept of the interaction of alleles at the same locus to explain heterosis, where two alleles of a particular gene pair had each developed a divergent physiological function. The writer believes he continued also to accept the previous explanation that heterosis was dependent on the cumulative effect of dominant or partially dominant linked genes.

Gustafsson (1947), Hull (1945a), Jones (1945), Castle (1946), and others have emphasized the importance of interallelic action in relation to heterosis. Castle has suggested also that the effect of interallelic action of a single pair of genes "is similar to that of the killer mutation of Sonneborn, except that the action induced in the dominant gene by its sensitized recessive, instead of being harmful, in this case is beneficial."

In certain cases a homozygous recessive pair of genes may completely modify the normal expression of either a homozygous or heterozygous organism. Homozygous dwarfs in maize condition such a result. A cross between two different dwarfs, however, releases the inhibition of each dwarf and results in marked heterosis. Both dominant factors, where two dwarfs are crossed, appear to be necessary to condition normal development. In this case the dominant conditions of both factor pairs act as complementary factors for normal growth.

It is evident that genes are greatly affected in their expression by differences in both external and internal environment. Cytoplasmic inheritance of male sterility may be used for illustrative purposes. Several cases of male sterility in sugar beets and onions, for example, are known that are due to maternal cytoplasmic inheritance which may be modified in expression by the dominant or recessive condition of one or more factor pairs.

Recently Hsu (1950) at Minnesota has studied the effect of two pairs of dwarf factors of maize in their homozygous dominant and recessive condi-

tions, and also when heterozygous in near isogenic, homozygous, and highly heterozygous backgrounds.

The factor pair for D_1d_1 was studied in the near isogenic background of inbred A188, that of D_xd_x in the near isogenic background of A95–344, and both factor pairs were studied in crosses between A188 × A95. Particular attention was given to total dry matter produced at various periods of growth under field conditions and to the growth in length of the coleoptile and mesocotyl under controlled laboratory conditions.

One comparison of the growth of the mesocotyl during a 12-day period for D_1D_1 and D_1d_1 on three different near isogenic backgrounds will be considered: the near isogenic background, A188, and the highly heterozygous backgrounds of A188 × A95 in the presence of D_xD_x and D_xd_x, respectively. While D_1 conditioned greater growth of mesocotyl in length than d_1, D_x conditioned less development of the mesocotyl in length than d_x.

The mesocotyl length of six strains consisting of comparisons of D_1D_1 with D_1d_1 on three different backgrounds was taken as 100. The comparisons are summarized in Table 3.16 and in Figure 3.1.

It is apparent that the superiority of D_1D_1 over D_1d_1 in mesocotyl length becomes less in the highly heterozygous background than in the homozygous background of A188. This may be more evident from the diagram in Figure 3.1.

TABLE 3.16

COMPARATIVE LENGTH OF MESOCOT-
YL FOR SIX STRAINS OF CORN

Background	Percentage Difference in Mesocotyl Length, D_1D_1 minus D_1d_1	Percentage Expression of Background
A188............	19	89
A188×A95 D_xD_x....	16	101
A188×A95 D_xd_x....	4	110

It seems of some interest that the differences between D_1D_1 and D_1d_1 were smaller in the highly heterozygous background than in the homozygous background, and that in the presence of D_xd_x that the differences were further reduced over those in the presence of D_xD_x. It may be well to recall that d_x conditioned greater length of mesocotyl than D_x.

Reference may be made to an explanation by Torssell (1948) of the decline in green weight or length of stem in alfalfa in different generations of inbreeding. It was not greatest in the first inbred generation. He suggests there was a surplus of vigor genes in a heterozygous condition in the early generations of selfing, and that great loss of vigor was not observed until about I_3
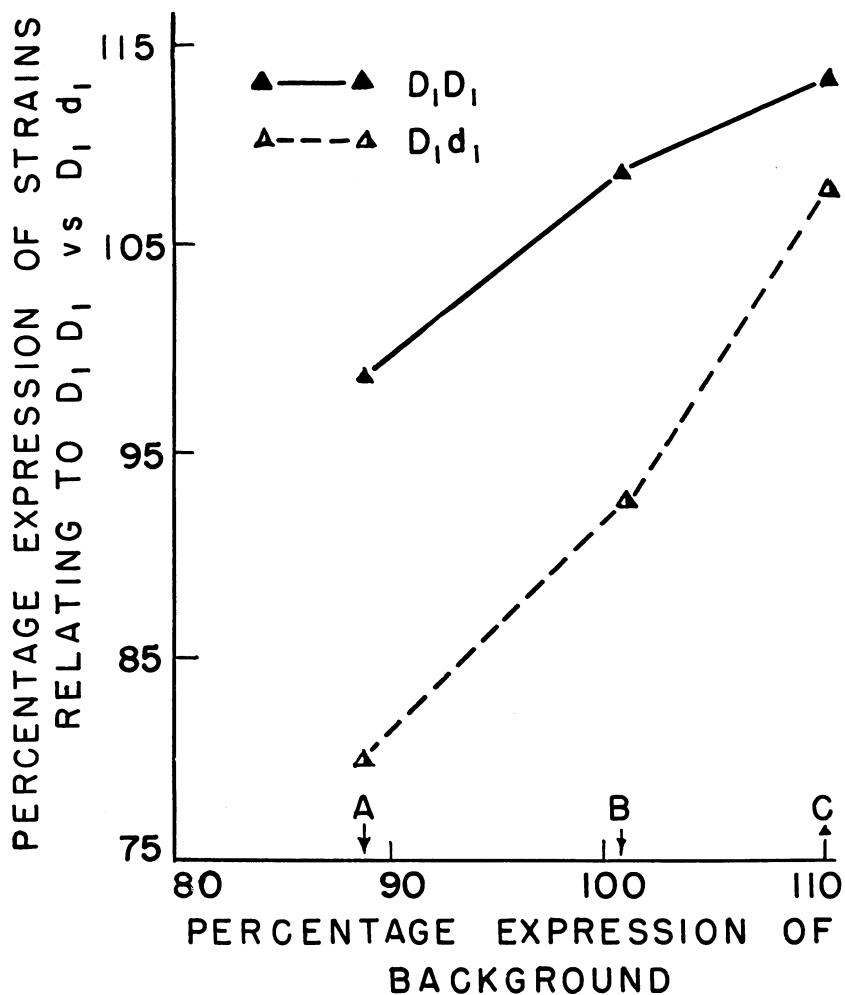
FIG. 3.1—Relative expression of D_1D_1 vs. D_1d_1 regarding final length of mesocotyl on various backgrounds: (A, A188; B, A188 × A95-344 carrying D_xD_x; C, A188 × A95-344 D_xd_x).

when selfing reduced the necessary genes below a stage needed by the organism. The following quotation from Thorssell emphasizes the viewpoint that the relative importance of genes controlling heterosis is greatly influenced by other factors of the organism:

> The cumulative effect of heritable characters, however, brings it about that development, that is to say green weight, does not stand in arithmetical proportion to the number of pairs of the dominant genes in question. From this it follows also that the said number can be reduced within a certain limit without perceptible or any great influence upon green weight. If this limit is exceeded, a considerable degeneration sets in.

The speaker has chosen to consider heterosis as the normal expression of a complex character when the genes concerned are in a highly heterozygous condition. As most normal characters are the end result of the action, reaction, and interaction of countless numbers of genes, and as gene mutation constantly occurs although relatively infrequently, it may be impossible to obtain all essential genes in the most favorable homozygous state. After selecting the best homozygous combinations, further vigor will be obtained due to heterozygous combinations of factors. Dominance or partial dominance seems of great importance as an explanation of hybrid vigor. In some cases there may be extra vigor correlated with the heterozygous condition of pairs of alleles. The types of response of inter and intra allelic factor interactions are without doubt dependent upon both external and internal environment.