

GENETIC BASIS OF HETEROSIS

By REINHARD KRUSE*

General Statements and Explanations of some Basic Genetic Principles.

The crossing of unrelated individuals often results in offspring with increased vigor. This is called heterosis or hybrid vigor, and the genetic background for it is not known with certainty.

There are two general modes in which heterosis is expressed. The first is an increase in size or number of parts. It is the result of greater cell activity or greater number of cells. The second way is by an increase in biological efficiency such as reproductive rate or survival ability. In addition to this, there may be a reduction of growth and/or survival rate, that is, hybrid weakness, reversed, or negative heterosis. This is not common, however, it does occur (18). Stern, 1948, has found one example of negative heterosis in *Drosophilla*, Hemizygotes and homozygotes for a series of position alleles R+ and +3 possess normal venation. However, the heterozygote R+/+3 exhibits various degrees of deficient venation. Thus the genotypic combination of the two, or the heterozygosity at a single locus decreases effectiveness (26).

Heterosis has been utilized for many plant and animal improvements.

Farm crops: Maize, sugar beets, sorghums, forage crops, and grasses.

Horticultural crops: Tomatoes, squashes, cucumbers, eggplants, onions, and annual ornaments.

Silkworms

Livestock: Swine, poultry, beef and milk cattle. Vegetatively propagated plants (13).

The greatest development of heterosis has been in *Zea Mays* (33). One hundred per cent of the corn now grown in the corn belt is hybrid corn (13). Commercially, hybrid corn seed is produced by the double-cross as follows:

Inbred	Inbred	Inbred	Inbred
A	B	C	D
(AxB)		(CxD)	
(AxB) x (CxD)			
(double-cross) (25)			

*

A paper presented in an Animal Breeding class at Louisiana Polytechnic Institute.

The expression of each character, as a rule, is independent of other characters. Thus, the plant will not be heterotic as a whole. Brieger, 1950, reports that the heterotic characters affected in maize, are: height, position of ear, size of leaves, chlorophyll formation, root system, resistance to disease, pests, and unfavorable conditions, size and number of kernels, width and length of ear, size and branching of tassel, and the amount

of pollen shed. Earliness, lateness, row number, plant and kernel color are not affected by heterosis (3). However, Leng reports that row number is affected in widely different degrees by heterosis, and that number of kernels per row (ear length) is the only primary yield component in which large positive effects of heterosis are manifested consistently (20).

Chambers, et al. (4), reported that in hogs, hybrid vigor is evident in number of pigs per litter, and litter weights at birth but it increases as the litter becomes less dependent upon the direct mothering ability of the dam. Vigor was expressed to a greater extent in the increased viability of pigs and productivity of two-line-cross gilts than in the increased growth rate of individual pigs. The extra number of pigs per litter in most cases was sufficient to account for a larger percentage of the increase in total litter weight. Therefore, since heterosis is expressed in both number of pigs survived and growth rate per pig, total weight of litter seems to be the one best over all measure of performance for comparison of lines or crosses (4).

When a heterozygote $A_1 A_2$ resembles in phenotype of the homozygotes $A_1 A_1$ or $A_2 A_2$ the allele A_1 is said to be dominant or recessive. Dominance is when $A_1 A_2$ resembles $A_1 A_1$. Dominance is absent when $A_1 A_2$ is exactly midway between $A_1 A_1$ and $A_2 A_2$. Dominance is incomplete when $A_1 A_2$ is intermediate between $A_1 A_1$ and $A_2 A_2$. Overdominance is when $A_1 A_2$ is more extreme—for example, larger—than either $A_1 A_1$ or $A_2 A_2$ (25).

Mutations constantly produce deleterious mutants. Natural selection quickly eliminates the dominant gene alleles but cannot eliminate recessive gene alleles because they are covered up or overpowered by good dominants. Thus in time the deleterious alleles build up in a population. Great loads of these deleterious recessive alleles are present in normally crossbred populations (25). This has been proven true by Dobzhansky in *Drosophila pseudoobscura* where a majority of the individuals carry heterozygous recessives. When these were inbred, the offspring were more highly homozygous but it resulted in a loss of vigor. This vigor was restored when the inbred lines were intercrossed (8).

Inbreeding increases the proportion of homozygotes in the population. For example the F_2 of a monohybrid cross $AA \times aa$ is $25AA : 50Aa : 25aa$. 50 percent are homozygous; 50 percent are heterozygous. Suppose all plants are selfed. The entire progeny of homozygous individuals remain homozygous, but only half of the heterozygous, individuals remain heterozygous, the other half become homozygous. This is illustrated in Table I.

The Effect of Selfing on Homozygosity.

F ₂	25	AA	50	Aa	25	aa
1st selfed generation	37.5	AA : 25		Aa : 37.5	aa	
2nd. selfed generation	43.75	AA : 12.5		Aa : 43.75	aa	
3rd. selfed generation	46.87	AA : 6.25		Aa : 46.87	aa	

Selfing thus cuts the proportion of heterozygotes to one-half of what this proportion was in the preceding generation. Even Mendel recognized this fact (25).

Selfing is the most extreme form of inbreeding. Mating between brothers and sisters, first cousins, and second cousins, also leads to progressive homozygosity, though at a much slower rate as shown in the following graph (25).

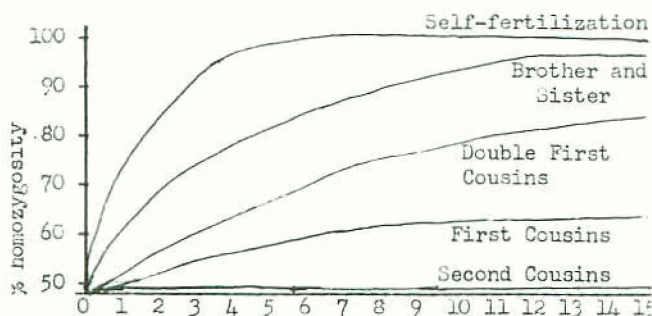


Fig 1. Generations of Inbreeding

It can be clearly seen that in self pollinated plants, deleterious recessive alleles are eliminated; but in crosspollinated varieties, they will accumulate readily. Thus heterosis is very important in corn, a normally cross-pollinated plant, but not in the tomato, a normally self-pollinated plant (32). It has been found that in plants where the flower is so constructed that self-fertilization takes place before the flower opens, there is no heterosis or no striking differences are obtained when they were forced to cross by artificial hybridization. Inbreeding of these hybrids leads to no deterioration. It is therefore questionable whether or not there is heterozygosity in normally self-pollinated plants (25). However, Jones points out several times that even though inbreeding does increase homozygosity, a family will still remain heterozygous even after many generations of inbreeding (18).

According to population selection, if $A_1 A_1 > A_1 A_2 > A_2 A_2$, then eventually the A_2 allele is eliminated to make the plant better adapted through A_1 . In heterosis this is different. If $A_1 A_1 > A_1 A_2 > A_2 A_2$, then selection is for an equilibrium of both A_1 and A_2 alleles. Biologically, this heterosis leads to a most interesting situation known as balanced polymorphism. The population will have all three present, since the homozygotes will always be produced in equal numbers (25).

If there is a hybrid superiority within a population, it is plausible to image that selection acts in favor of heterozygotes and so keeps their fre-

quency on a high level. But when hybrids between unrelated populations, natural or artificial, show an increased viability in comparison with the parental populations—as has been proved to be common in several species of *Drosophila*—then it can hardly be a question of selection (2).

In general, increased genetic diversity of crosses results in increased superiority of performance of these crosses over parental averages (10). This was shown to be true in swine by Sierk, et al, (24), where line crosses between breeds give greater increase in vigor than line crosses within the Poland China breed. The better performing inbred lines produced superior crossbreds (24).

The phenomenon termed heterosis or hybrid vigor is the direct result of achieving a high degree of heterozygosity in a hybrid (30). Bonnier (1961) found that there was a correlation between egg count and degree of heterozygosity in *Drosophila melanogaster* (2). Tantawy (1957) also using *D. melanogaster* found that the magnitude of heterosis is proportional to the degree of the inbreeding degeneration (29).

Early Ideas of Heterosis.

It is interesting to note how long it has been known to man that inbreeding will reduce vigor. Many savage tribes long ago tabooed marriage with close relatives probably because they saw the ill effects of inbreeding. The Greeks outlawed these marriages. However, much close marriage did occur especially in royal blood. The Pharaohs married their own sisters so that god-like blood would not be diluted. The pedigrees of Greek heroes show an amount of inbreeding similar to that of our modern stud books for race horses. A Grecian heiress was nearly always married by her kinsmen so that her property would not be lost to the family. However, endogamy seemed to have ended before bad effects were seen (33).

In 1716 Josef Gottlieb Koelreuter published a paper and described the first plant hybrid. Charles Darwin in 1876 wrote a 500 page book on hybrid vigor. It was titled **Cross and Self Fertilization in the Vegetable Kingdom** in which in his conclusion he said that the first and most important conclusion from his book was that cross-fertilization was generally beneficial and self-fertilization injurious. His work was of great importance on heterosis since he did careful and accurate work on it. W. J. Beal was influenced by Darwin's work and became the leader in American research designed to improve maize. He crossed the stocks of the same type of corn grown 100 miles apart and found that the hybrid seed exceeded in production as much as 151 to 100 (33).

At the beginning of the 19th century, much cattle breeding was begun. Prize bulls were bred to their own daughters. Breeders thought that selecting individuals and inbreeding was the quickest way to improve stock. However, sooner or later inbred stock seemed to go sterile, but

vigor was restored when outcrossed. They did not know what caused the sterility, but they did know the best corrective procedure. We owe our best stocks to this. They inbred to add up and get desirable qualities always selecting, then outcrossed to established vigor, repeating this process over and over (33).

Near the end of the 19th. century G. W. McClure published a paper (1892) in which he made the following observations on heterosis in corn.

- (1) Sterility and deformity often follow selfing.
- (2) Crossing imparts vigor.
- (3) It is impossible to tell in advance what varieties will produce corn of increased size when crossed.
- (4) The apparent best ears do not always produce the largest crops.
- (5) All hybrid corn grown the second year is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties (33).

It was not until 1907 that the idea of a heterosis concept came into being. Before that time, outcrossing was done only to restore vigor, but when the heterosis concept came into being, outcrossing was used to obtain better crops. George Harrison Shull, working with corn at the Station for Experimental Evolution at Cold Harbor, studied the effects of cross-breeding and summarized his results in 1910. He first coined the term "heterosis" in 1914 (23).

For over one-third of a century two main hypotheses have been accepted as the genetic basis of heterosis. One assumes that complementary dominant genes favorable for growth, and acting additively or synergistically, account for the phenomenon. The other postulates that heterozygosity *per se* is somehow responsible. The present trend, based on various lines of evidence, is believed that heterosis results from a combination of both types of gene action (1). The general interpretation of these two hypotheses is that the first is an accumulation of the effects of favorable dominant genes at different loci and is known as dominance. The other is the result of an interaction of different alleles at the same locus and is known as overdominance (19). The dominance hypothesis, stating that heterosis is due to the covering up of deleterious recessive alleles, is also called the dominance of linked genes. The overdominance hypothesis stating that heterosis is due to the fact that the heterozygote is superior to either homozygote, is also called the stimulation of heterozygosis, super-dominance, single gene heterosis, cumulative action of divergent alleles, and just simply as heterosis (7).

The Dominance Hypothesis.

In 1910, A.B. Bruce offered a Mendelian explanation of hybrid vigor in purely mathematical terms (21). He, and also Keeble and Pellew, explained heterosis as a mathematical expectation based on the combined action of favorable dominant or partially dominant factors (13). Thus,

it is postulated that the increase in vigor after crossing is the result of the combination of many different dominant alleles contributed by each parent. Inbreeding produces homozygosis for recessive alleles causing a loss of vigor (3).

An apparent objection to this hypothesis is that inbreeding should also be at least as likely to lead to homozygosity for vigorous dominant alleles as for weak recessive ones present. However, Jones in 1917 explained that several genes may be unked. For example, one chromosome may have *AbCdEf*, the other *aBcDeF*. To get an *ABCDEF* is highly unlikely (25). This hypothesis of Jones, or the theory of dominant unked growth factors, says that hybrid vigor is associated only indirectly with heterozygosity. The maximum degree of expression of vigor occurs in individuals that have a maximum number of loci with dominant favorable alleles and it is practically impossible to get all loci with dominant favorable alleles (15). Even though Jones formulated his hypothesis of linked dominant factors, assuming on the whole that dominant stimulating genes should be closely linked with recessive vigor-reducing factors, Brieger, (3), has suggested that such theory as proposed by Jones might represent an intermediate position between the dominance and the overdominance theory. If linkage between dominant and recessive genes become so close that practically no crossing over occurred, it would be difficult to distinguish experimentally between linkage and the heterosis theory. This would be dealing with heterozygosis of chromosome regions, instead of simple genes. If linkage is weak, the difference between the simple dominance and the linkage hypothesis would practically disappear (3).

Basically, the dominance hypothesis of hybrid vigor states that a cross-bred population contains numerous gene loci heterozygous for deleterious recessive factors and that heterosis is due to the result of dominant "beneficial" alleles masking the effects of recessive "deleterious" alleles in the hybrid. Inbreeding increases homozygosity and exposes recessive factors resulting in loss of vigor. The chances that the same deleterious alleles are made homozygous in two different strains are slim, thus when they are crossed many recessive genes will be covered by dominant genes in the hybrid. Since these genes are numerous and there is linkage between them it is highly improbable that an inbred line will become entirely homozygous for beneficial or recessive factors (6). (30).

Several experiments indicate that Heterosis is due to the dominance hypothesis. Straus, et al. 1943, has shown that two inbred strains of *Drosophila melanogaster* had egg production of almost 100 percent above the average of its parents. Genetic analysis demonstrated significant amounts of heterosis were contributed by each chromosome pair. Total heterotic increase equalled the sum of individual chromosome effects—that is, no interactions or combination effects could be detected. This relationship is therefore

definitely linear. Heterosis due to individual chromosome proved to be proportional to their "active" length as measured by band numbers in the salivary chromosomes and by crossover units. The physical length of the salivary and metaphase chromosomes and the percentage of visible loci showed significant but not equally close fit (28). Gowen reported another example of heterosis due to dominance, when *Drosophila melanogaster* were analyzed by degree of heterozygosity in relation to egg yield. Flies homozygous for all loci in chromosomes I, II, and III, or O heterozygous produced 38.2 eggs on the average. Those 1/3 heterozygous produced 51.5 eggs; those 2/3 heterozygous produced 62.6 eggs, and those all heterozygous produced 76.9 eggs. The differences are additive, about a 12.9 eggs increase for each 1/3 increase in heterozygosity. This suggests additivity of individual gene action on egg yield. This is an important point but does not necessarily follow, because the dominance or recessiveness or interallelic interaction could be balanced by the mass of gene pairs comprising one-third of the heterozygous loci (12). Sierk, et al. (24) found that some vigor in swine is caused by the fact that unfavorable genes in the parents were suppressed. This relationship of genetic diversity to heterosis tends to favor the "multiple allelic series" hypothesis (24).

Comstock and Robinson (1948) pointed out that nonallelic interaction or epistasis could inflate measures of interallelic interaction (dominance) and later suggested that epistasis might be partly responsible for the heterotic effects. Hayman. (14), tried to find a relation between epistasis and heterosis. He found that it appears that the relationship between epistasis, whether duplicate or complementary, and heterosis is a product of genotype, environment, and scalar representation and varies like any other character of an organism (14).

The dominance hypothesis, however, fails to explain everything. First of all, it will not explain the small increase in vigor that results when two already heterozygous strains are crossed. Furthermore, it cannot account for the increase in vigor followed by the crossing of artificially inbred strains much beyond the level of the equilibrium population from which the inbred strains were derived. It has also been formulated, assuming that all beneficial genes are completely dominant and all deleterious recessive, that the average decrease in selective value due to homozygous recessives is equal to the product of the number of gene loci and average mutation rate. Prevailing estimates show that this product is unlikely to be larger than .05. If one assumes that vigor is measurable in terms of selective value, then .05 would be the maximum possible increase in vigor under the dominance hypothesis. Thus any hybrid having a larger increase in vigor must be explained otherwise (6).

The Overdominance Hypothesis.

Overdominance is a situation where the heterozygote is more favorable for growth than

either homozygote (1). Shull, 1911, and East and Hayes, 1912, proposed this hypothesis in vague physiological language but it was put in modern genetic terminology by East in 1936. Different alleles combine in the heterozygote, to exert a complementary physiological action, resulting in hybrid vigor. Overdominance is essentially this (3). East 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 (13). Thus the excessive vigor of hybrids is due to the cumulative action of many loci of divergent nondefective alleles influencing vigor. $a_1 a_2$ is more vigorous than $a_1 a_1$ or $a_2 a_2$ due to the expression of the specific physiologic effect of a_1 plus a_2 (15). This hypothesis, based on the assumption that heterozygotes resulting from two alleles, for example a_1 and a_2 in combination is more "vigorous" than the respective homozygotes $A_1 A_1$ and $A_2 A_2$ is more than just an assumption. It has been noted that in certain allelic series, antimorphs will produce, in heterozygotes, phenotypes unexpected on the basis of their action when homozygous (30).

Overdominance may be produced in two ways. In the first place when two alleles function as complements together. They result in a better effect in the heterozygote than each of them in a homozygous state is able to produce. Secondly, one of the alleles may be without effect, may even be a deficiency, the other allele has an optimal effect when in single dose but is an overdose when in homozygous state (2).

Hull's original argument for over dominance is that the hybrid yields more than both parents combined. This would not be possible if dominant genes acted in a pure additive manner, but the validity of this argument depends on the unimportance of epistasis in corn yields. Evidence on this is incomplete and contradictory (7). The main reason for the reluctance to accept the heterozygosity hypothesis seems to have been the scarcity of recognized cases of such type of interaction; however, today many cases have been described. For example, flower color is often more intense in the heterozygote than in either homozygote. Several cases are known where monofactorial or even bifactorial segregations occurring in barley and *Drosophila* have a higher survival rate in the heterozygote than in either homozygote. (3)

In *Neurospora*, heterosis is evidently the result of the coexistence and interactions of two unlike whole nuclei operating in a common cytoplasmic mass. Increased activity may be the same as the result when two unlike nuclei fuse and rearrange their unlike elements in the organization of a single nucleus. In either case, the result is assumed to be due to the fact that elements of unlike constitution are brought into sufficiently close association that effective interactions can and do take place (22). Sometimes complementary gene action influences growth. In a number of these, for example in *Neurospora*,

(Continued on Page 12)

HUNTSVILLE Chair



HUNTSVILLE — Historical Huntsville is preparing a welcome-of-tomorrow for the annual meeting of two agricultural associations set for April 5-6-7.

While not in official sessions, the National Association of Colleges and Teachers of Agriculture and Delta Tau Alpha Honor Fraternity will have an opportunity for tours in an area that is fast becoming the leading tourist attraction in the great Southwest.

Meetings will be held in Sam Houston State Teachers College's glamorous new \$1.8 million Lowman Student Center.

Convention delegates will enjoy a tour of the historic campus. The Austin College Building, built in 1851, is the oldest building west of the Mississippi still in use for educational purposes. The newest of the college's many facilities is the Farrington Science building. Students study here under ideal conditions in well-equipped laboratories. Just one of the many advantages for study that the science students have is the planetarium.

The Graphic Arts Building houses the only complete graphic arts department in the world. Along with studies in journalism, photography, and photo-engraving, the complete Southwest School of Printing is housed in this building.

The modern new agriculture laboratory will be of interest to convention delegates. The 891-acre Country Campus offers agricultural students splendid opportunities to demonstrate and study in agronomy, horticulture, dairy, livestock, and poultry farming. Country Campus is also the home of Sam Houston's excellent 9-hole golf course in the rolling hills of Walker County.

Historic Huntsville is the home of the State Prison. The well-kept buildings of both the main unit and the farm units, are a clear reflection of Texas' advanced prison system. In tune with their striving for rehabilitation, the prisoners are entertained each October by well-known performers at the annual Prison Rodeo. This rodeo staged for the prisoners is visited by hundreds of rodeo lovers from the Lone Star state as well as other states.

Across from the prison, on the shortest highway in the state, is the grave of General Sam Houston, first president of the Republic of Texas.

Nestled in the tall pines of east Texas is Sam Houston Park. The serene park grounds feature a museum in Sam Houston's honor. Adjacent to the museum is the small home of the famous Texan, a vivid example of how the great man lived. A small log cabin houses the law books he used in his practice. Behind the white frame house is the newly built War and Peace House. A tribute to Texas' own soldiers is shown here in World War I and II relics.

W

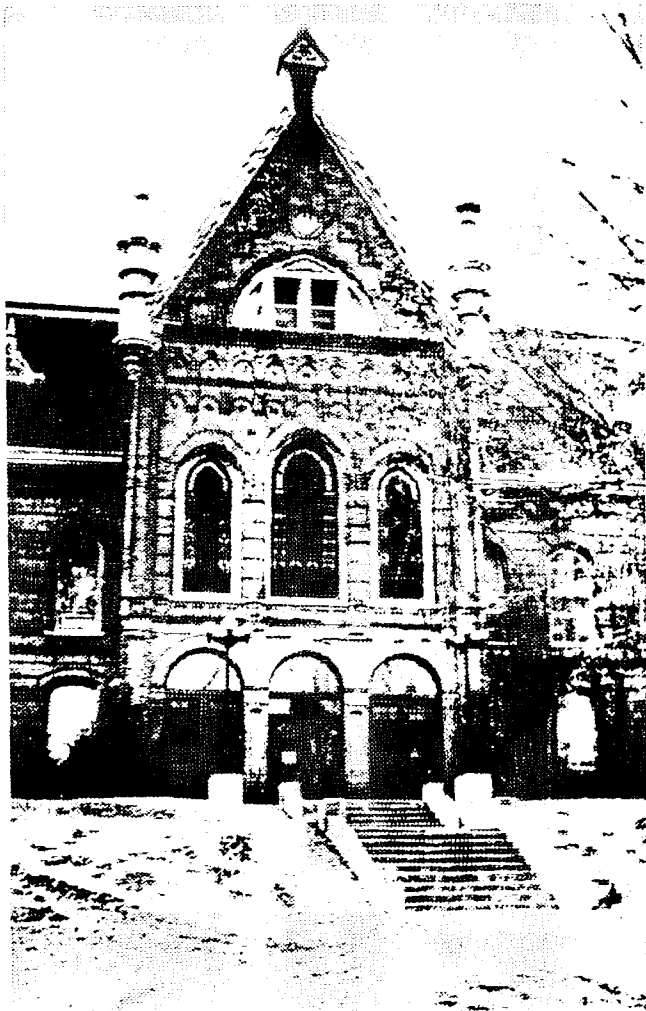
er of Commerce

Overlooking the park is the nostalgic Steamboat House, the two-story home fashioned after a Mississippi steamboat in which the Texas General spent his last days.

Only nine miles from the Sam Houston Park is Huntsville State Park. Thousands of Texans flock annually to the 21,000-acre recreational area. Pleasant holidays are spent fishing, camping, boating and skiing.

Driving back into scenic Huntsville, NACTA and DTA delegates travel through part of the 158,000 acre National Forest. Driving through this beautiful wooded area, they end up back on campus under the tall spires of Old Main.

News Bureau, Sam Houston State,
Huntsville, Texas



come

GENETIC BASIS . . .

(Continued From Page 9)

the interaction can be described in terms of the ability to synthesize specific metabolites. Emerson described this *Neurospora* heterocaryon (physiological approximation to a heterozygote in a diploid organism) with a one-gene difference between the component nuclei showing superior growth to either homocaryotic strain. Biochemically, it appears that one homocaryotic strain synthesizes too little vitamin para-amino benzoic acid, whereas the other produces an excess that promotes a reaction deleterious to growth. The heterocaryon achieves a proper balance that is enough for growth and not to the extent that it is deleterious (1).

Bonnier, (2), concluded that the single assumption of overdominance will make many accessory assumptions unnecessary. As long as there is not biochemical proof to the contrary, the assumption of overdominance seems to be the simplest explanation for heterosis (2).

Other Facts and Ideas on Heterosis.

The simplest kind of true heterosis—euheterosis—is the result of a superior dominant allele sheltering a deleterious recessive mutant (9). Thus heterosis proper or euheterosis is a product of mutation and selection pressures. Luxuriance of heterozygotes is an evolutionary accident (8). Luxuriance is observed in some hybrids between normally self-fertilized species, races, or strains. This luxuriance is not due to sheltering of deleterious genes nor due to overdominance. Luxuriance is from the evolutionary standpoint, an accidental condition brought about by complementary action of genes found in the parental form crossed. These cases do not seem to be better adaptable and also are more frequently found in domesticated species. Luxuriance is, really, pseudoheterosis (9).

It is interesting to note in the report of Wellhausen that Chalqueno corn, a hybrid of Conico and Tuxpeno: two distinct races of corn, will not outdo either parent in their respective location as measured by yield, yet in a new environment it has an excess of vigor. Certainly the genotype is no different. The difference in this case must be due to different interactions between over-all gene action and environment (31).

In *Drosophila pseudoobscura* both of the two kinds of heterosis are reasonably well known and understood. First, there is the presence of deleterious recessive mutant gene being sheltered by their normal dominant alleles in a population. Accumulation of these deleterious genes is a by-product of the mutation process. Secondly, there are complexes of linked polygenes which give specific "heterotic" interaction effects in heterozygotes (overdominance). This kind of heterosis is engendered by natural selection and a form of adaptation of species to its environment (8).

Hayman said that heterosis is a composite phenomena: possible causes are epistasis, overdominance, and accumulation of favorable dominants in the heterozygotes (14).

Many factors may influence hybrid vigor. Genes that have no dominance may be the ones

that have a major effect on heterosis. Then too, chromosomal deletions may occur which is the complete elimination of a normal locus. There are also dominant unfavorable genes present. In the homozygote, they are not completely lethal, but seldom produce seed or pollen. In the heterozygote there is a marked reduction in size, growth, and reproduction as compared with either parent (18).

In chromosomal rearrangements, such as inversions and translocations, genes without alteration are placed in different spatial relations with other genes. In altered position they have different effects (18). Dobzhansky and Rhodes in 1938 suggested a method of locating genes by paracentric inversions. In plants heterozygous for such inversions, the crossovers that occur within the inverted segments are only rarely recovered in viable gametes. Thus, the inverted segment is inherited as a unit and all genes contained within the segment are completely linked with very few exceptions. In plants without inversions, where crossing over breaks up favorable combinations of minor genes, the existence of them is difficult to demonstrate. Thus, if the same characteristics show up in all following generations, then it can be assumed that these characteristics were located in the inverted section. Sprague, 1941, used this method and found that plants with heterozygous inverted segments were superior to homozygous inverted segment in yield and kernel weight and the difference as significant. Chao, studying inbred lines of corn by this method, found that genes increasing ear height in most of these inbred lines were present in chromosome 6 of the 1n3a strain and in the long arm of chromosome 3. These genes did not show overdominance (5).

Loci are known that have different effects on the different parts of an organism. These genes may be so close together that they never show crossing over or they may be compound genes with multiple effects. That a chromosome is a linear arrangement of loci, each of which is a site of a single gene with a one-effect-function, is an over-simplification. There are also single genes with multiple effects. This has been proven to be especially true in growth production illustrated by chlorophyll formation (18). However the development of chlorophyll is affected by many genes, all, in this case, involved in the development of this heritable character. Each recessive allele when homozygous allows formation of partial or no pigmentation resulting in an albino. It is generally believed that the majority, if not all genes for albinism, affect different steps of chlorophyll production. Thus if one step fails to go to completion, albinism results (16).

It has also been suggested that heterosis may be the result of the interaction between genes and cytoplasm. Within species, differences in reciprocal crosses are rare; however, in two different flowering types of tobacco, crosses show a maternal effect (18). A. F. Shull preferred the explanation that heterosis was due to a stimulus resulting from a changed nucleus on a relatively unaltered cytoplasm.

Whaley reported that heterosis is associated with the ability of the hybrid to synthesize or to utilize one or several specific substances involved in fundamental growth processes of organisms. Much evidence indicates that primary heterosis effect is concerned with growth substances whose predominant activity is registered in the early part of the development cycle. Many hybrid plants gain their advantage a few hours after germination. The primary growth activities at this stage involves the unfolding of the enzymatic pattern. Here the hybrid has its advantage (32). Gartner, et al, (1953), found that the degree of heterosis in the experimental plants of *Antirrhinum majus* L. (snapdragon) was greatly influenced by the amount of solar radiation. Heterotic ability of the F1 to retain the indoleacetic acid has been demonstrated. The greater ability of the hybrids to retain and utilize growth substance under high light conditions permits greater expansion of plant tissue and thus gives the additional growth increment that can cumulatively result in heterosis (11).

Cases are reported where a deleterious recessive gene caused the heterozygote to be no better than the homozygous normal. These genes are lethal or nearly lethal. They are all unfavorable (17). Sernet al, (26), tested the viability of *Drosophila melanogaster* for 75 sex linked recessive lethals. It was found that on the average the viability of the heterozygote for lethals was .965. a decrease in viability of approximately 4 percent (27).

By way of a summary, it can be said that heterosis can involve only recombinations of already existing alleles, unless by rare chance mutation occurs. We are thus concerned with an interpretation limited to different types of recombinations, and to different kinds of gene action resulting from these recombinations (32). The basic principle of all explanations is that different gene combinations from the same restricted pool of genes will give many different phenotypes (30). In conclusion, heterosis is apparently not due to any single genetic cause.

1. Beadle, G. W., 1953, "Heterosis," *Journal of Heredity*, 44:88.
2. Bonnier, G., 1961 "Experiments on Hybrid Superiority in *Drosophila melanogaster*; Egg Laying Capacity and Larval Survival," *Genetics*, 46:9-24
3. Brieger, F. G., 1950, "Genetic Basic of Heterosis in Maize," *Genetics*, 35: 420-45.
4. Chambers, D. and Whatley, J. A., 1951, "Heterosis in Crosses of Inbred Lines of Duroc Swine," *Journal of Animal Science*, 10:505-15.
5. Chao, C. Y., 1959, "Heterotic Effects of a Chromosomal Segment in Maize," *Genetics*, 44:657-77.
6. Crow, J. F., 1948, "Alternative Hypothesis of Hybrid Vigor," *Genetics*, 33:477-87.
7. Crow, James F., "Dominance and Overdominance," edited by John W. Gowen, 1952 *Heterosis*, Iowa State College Press, Ames, Iowa.
8. Dobzhansky, T., 1950, "Genetics of National Populations: Origin of Heterosis Through Natural Selection in Population of *Drosophila pseudoobscura*," *Genetics*, 35:288-302.
9. Dobzhansky, T. H., "Nature and Origin of Heterosis," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
10. England, D. C. and L. M. Winters, 1953, "Effects of Genetic Diversity and Performance of Inbred Lines per se on Hybrid Vigor in Swine," *Journal of Animal Science*, 12: 836-47.
11. Gartner, J. B., and others, 1953, "Effect of Indoleacetic Acid and Amount of Solar Radiation on Heterosis in the Snapdragon," *Science*. 117:593-5.
12. Gowen, John W., "Hybrid Vigor in *Drosophila*," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
13. Hayes, H. K., "Development of the Heterosis Concept," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
14. Hayman, R. L., 1957 "Interaction, Heterosis, And Diallel Crosses." *Genetics*, 42:336-55
15. Henderson, M. T., 1949, "Consideration of the Genetic Explanations of Heterosis," *Agronomy Journal*, 41:123-6.
16. Irwin, M. R., "Specificity of Gene Effects," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
17. Jones, D. F., 1945, "Heterosis Resulting from Degenerative Changes," *Genetics*, 30:527-42.
18. Jones, Donald F., "Plasmagenes and Chromogenes in Heterosis," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
19. Jones, D. F., 1957, "Gene Action in Heterosis," *Genetics*, 42:92-103.
20. Leng, E. R., 1954, "Effects of Heterosis on the Major Components of Grain Yield in Corn," *Agronomy Journal*, 46:502-506.
21. Rickey, F. D., 1945, "Bruce's Explanation of Hybrid Vigor," *Journal of Heredity*, 36:243-4.
22. Shull, G. H., 1948, "What is Heterosis?" *Genetics*, 33:439-46.
23. Shull, George Harrison, "Beginning of the Heterosis Concept," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
24. Sierk, C. F., and L. M. Winters, 1951, "Study of Heterosis in Swine," *Journal of Animal Science*, 10:104-11.
25. Sinnott, Edmund W., Dunn, L. C., and Dobzhansky, Theodosius, 1958, *Principles of Genetics*, McGraw-Hill Book Company, Inc., New York, Chapter 19, Pages 254-268.
26. Stern, C., 1948, "Negative Heterosis and Decreased Effectiveness of Alleles in Heterozygotes," *Genetics*, 33:215-19.
27. Stern, C., and others, 1952, "Viability of Heterozygotes for Lethals." *Genetics*, 37:413-49.
28. Strauss, F. S., and J. W. Gowen, 1943, "Heterosis: Its Mechanism in Terms of Chromosomes Units in Egg Production of *Drosophila melanogaster*;" *Genetics*, 28:93.
29. Tantaway, A. O., 1957, "Heterosis and Genetic Variance in Hybrids Between Inbred Lines of *Drosophila melanogaster*, in Relation to the Level of Homozygosity," *Genetics*, 42:535-43.
30. Wagner, Robert P., and Mitchell, Herschell, 1955, *Genetics and Metabolism*, John Wiley & Sons, Inc., New York.
31. Wellhausen, E. J., "Heterosis in a New Population," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
32. Whaley, W. Gordon, "Physiology of Gene Action in Hybrids," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.
33. Zirkle, Conway, "Early Ideas on Inbreeding and Crossbreeding," edited by John W. Gowen, 1952, *Heterosis*, Iowa State College Press, Ames, Iowa.