DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS[1]

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A stimulation resulting from hybridization in both plants and animals has long been recognized. The increased growth as the result of crossing is so common an occurrence that it is probably familiar to everyone who has made any hybridization experiments.

This stimulation, variously spoken of as "hybrid vigor," stimulus due to heterozygosis, heterosis, etc., was clearly established as an organic phenomenon by the abundant cases cited by early investigators such as KÖLREUTER (1766), GÄRTNER (1849), DARWIN (1877) and FOCKE (1881), as well as a large number of other investigators at that time and an increasingly large number since then. The important investigations in recent times (EAST 1908, 1909; SHULL 1908, 1909, 1910, 1911; EAST and HAYES 1912) are so familiar that it is not necessary to do more than mention them.

Concrete explanations as to the cause of these results have not accompanied the accumulation of facts. Various hypotheses have attempted to account for the results, but they have been little more than outlines of the problem.

The valuable contributions of EAST (1908, 1909) and of SHULL (1908, 1909, 1910, 1911) established the fact that continued inbreeding is not a process of continuous degeneration but that the reduction in the amount of growth is due to the isolation of unlike biotypes differing in the amount of growth attained at normal maturity. Together with this isolation of biotypes there was a loss of a stimulation which was assumed to be derived in some way from crossing. This decrease of vigor becomes less after continued inbreeding and to all appearances ceases as complete homozygosis is approached. This stimulation has been shown to be correlated more or less closely with the degree of heterozygosity. The whole subject has been ably presented and discussed by EAST and

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HAYES (1912). A quotation from this paper (pp. 36 and 37) presents the matter as it stands at present:

> "The hypotheses in regard to the way by which the act of fertilization initiates development are numerous, but since they are entirely speculative it is not necessary to discuss them here. The only conclusion that seems justified is that they are not immediately psychological or vitalistic in nature. LOEB's remarkable researches prove this. But whatever may be the explanation of the means by which the process is carried out, the statement can be made unreservedly that the heterozygous condition carries with it the function of increasing this stimulus to development. It may be mechanical, chemical, or electrical. One can say that greater developmental energy is evolved when the mate to an allelomorphic pair is lacking than when both are present in the zygote. In other words, developmental stimulus is less when like genes are received from both parents. But it is clearly recognized that this is a statement and not an explanation. The explanation is awaited."

KEEBLE and PELLEW (1910) first suggested a concrete explanation to account for the results of this nature which they obtained with peas. Two varieties of garden peas, as grown by them, each averaged from 5 to 6 feet in height. The F_1 grown from this cross averaged from 7 to 8 feet in height, 2 feet taller than either parent. A result of this kind is comparable to heterosis. The F_2 was put into four classes: one class containing plants as tall as the F_1, two classes of semi-tall plants similar in height to the two parents, and one class of dwarfs shorter than either parent. The two classes of semi-tall plants, similar in height, were differentiated in the same manner as the two parents; one had thick stems and short internodes, the other had thin stems and long internodes. Other differences helped to distinguish the two classes of equal height. The number of plants falling into these four classes agreed closely with the expectation from a di-hybrid ratio where two factors showing dominance were concerned, giving a 9:3:3:1 ratio.

The writers assumed two factors to be concerned: one producing thick stems, the other long internodes. These factors they designated T and L. One of the parental varieties was medium in height because it possessed one of these factors, e.g., that for thick stems, but lacked the other. Such a plant had the formula $TTll$. The other variety was of medium height because it lacked this T factor but possessed the factor for long internodes, and was given the formula $ttLL$. Both of these factors showed dominance over the allelomorphic condition; hence the F_1 was taller than either parent because both factors were present together. Whether or not later investigations have justified the interpretation that KEEBLE and PELLEW have placed on the data as explaining height of their peas makes no material difference to the discussion here. Taken as it stands, it is a beautiful illustration of the way in which dominance may increase a character in F_1 over the condition of either parent.

Curiously enough, this explanation has never been considered an adequate one or in any way essentially related to the universal phenomenon of heterosis. This hypothesis of dominance accounting for heterosis, as outlined by KEEBLE and PELLEW, has two objections which have up to the present been considered insurmountable.

The chief objection has been that, if heterosis were due to the dominance of a greater or less number of factors governing the amount of development, it would be possible in generations subsequent to the F_2 to recombine in one homozygous race all of the factors resulting in large growth and, conversely, the negative condition in another homozygous race. In other words, it would be possible to obtain one strain having all of the dominant factors, and another with all of these dominant factors lacking. Both of these races should be homozygous, hence self-fertilization should not result in less vigorous progeny. The completely recessive race should be below the parents in its power for development, as the F_1 and the complete dominant were above the parents. That all of these supposedly necessary corollaries are not supported by the facts is well known.

Both SHULL (1911) and EAST and HAYES (1912) have considered this objection to be valid. A quotation (p. 39) from the latter makes their position on this point clear.

> "KEEBLE and PELLEW (1910) have recently suggested that 'the greater height and vigor which the F_1 generation of hybrids commonly exhibit may be due to the meeting in the zygote of dominant growth factors of more than one allelomorphic pair, one (or more) provided by the gametes of one parent, the other (or others) by the gametes of the other parent.' We do not believe this theory is correct. The 'tallness' and 'dwarfness' in peas which KEEBLE was investigating is a phenomenon apparently quite different from the ordinary transmissible size differences among plant varieties. Dwarf varieties exist among many cultivated plants, and in many known cases dwarfness is recessive to tallness. It acts as a monohybrid or possibly a dihybrid in inheritance, and tallness is fully dominant. Varietal size differences generally show no dominance, however, and are caused by several factors. Transmissible size differences are undoubtedly caused by certain genetic combinations (EAST 1911), but this has nothing to do with the increase of vigor which we are discussing. The latter is too universal a phenomenon among crosses to have any such explanation. Furthermore, such interpretation would not fitly explain the fact that all maize varieties lose vigor when inbred."

Another objection to the hypothesis of dominance has been raised by

EMERSON and EAST (1913). In this publication it is said that, if the effect of heterosis were due to dominance, the distribution of the F_2 individuals would be unsymmetrical in respect to characters in which heterosis was shown in F_1. This follows from the familiar Mendelian expectations where there is dominance and any number of factors is concerned. For the purpose of illustrating this point let us take the case of height of peas already cited. In the F_2 population a distribution of the individuals in respect to height is, theoretically, 9 tall plants (with both factors present), 6 medium-tall plants (3 with one factor + 3 with the other), and one short plant (with both factors lacking).

Similar asymmetrical distributions in F_2 would occur with any number of factors (if there were no other facts to be taken into consideration), as seen from the figures given in table 1 modified somewhat from those given by BAUR (1911, p. 63).

In any case of a size character similar to height of peas with any number of factors, the plotting of the number of individuals in F_2 occurring in the classes given in row B in table 1 would give an asymmetrical distribution. This is on the assumption that the individual having the greatest number of dominant factors present (whether in the simplex or duplex state) would attain the greatest development of the size character.

In the vast amount of data accumulated upon the inheritance of quantitative characters no such tendencies toward an asymmetrical distribution is evident in the majority of cases recorded. In EMERSON and EAST's paper, referred to, dealing with quantitative characters in maize, and in HAYES's publication (1912) dealing with the same type of characters in tobacco, the distributions in F_2, where heterosis is shown in F_1, are all considered to be of the type of normal frequency distributions. If any skewness is shown by any of these it is too slight to suggest the types of curves obtained by plotting the figures in table 1, B.

It is perfectly evident that the two objections raised against the hypothesis of dominance as a means of accounting for heterosis, as outlined by KEEBLE and PELLEW, and as it has been considered up to the present, are valid. But both these objections to dominance as an interpretation of heterosis have failed to take into consideration the fact of linkage.

Abundant evidence is fast being accumulated[2] to show that characters are inherited in groups. The different theories accounting for this link-

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[2] It is unnecessary to give references to the convincing results obtained by MORGAN, BATESON, and their collaborators, as well as to those obtained by many others whose work is of great importance if not so extensive.

TABLE 1

Distribution of F_2 individuals when each character shows complete dominance and each has a visible effect.

Number of factors in which the F_1 is heterozygous		Distribution of the individuals	Total number in the population
1	A	3 : 1	4
	B	3 : 1	
	C	1 : 0	
	D	1 : 1	
2	A	9 : 3 : 3 : 1	16
	B	9 : 6 : 1	
	C	2 : 1 : 0	
	D	1 : 2 : 1	
3	A	27 : 9 : 9 : 9 : 3 : 3 : 3 : 1	64
	B	27 : 27 : 9 : 1	
	C	3 : 2 : 1 : 0	
	D	1 : 3 : 3 : 1	
4	A	81 : 27 : 27 : 27 : 27 : 9 : 9 : 9 : 9 : 9 : 9 : 3 : 3 : 3 : 3 : 1	256
	B	81 : 108 : 54 : 12 : 1	
	C	4 : 3 : 2 : 1 : 0	
	D	1 : 4 : 6 : 4 : 1	
n	A	$3^n : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-2} : 3^{n-2}$: etc. .... : 1	$(2^n)^2$
	B	$1(3^n) : D(3^{n-1}) : D(3^{n-2})$: .... etc. .... : 1	
	C	$n : n-1 : n-2$: .... etc. ... $n-n$	
	D	1 : ... etc. = coefficients of the expanded binomial $(a+a)^n$ .... : 1	

A, The distribution into the visibly different categories. B, The distribution into categories with different numbers of dominant factors present (either in a homozygous or heterozygous condition). C, The number of dominant factors in which the categories differ. D, The number of visibly different categories with the same number of dominant factors present.

age of characters make no essential difference in the use to which these facts will be put here. It is only necessary to accept as an established fact that characters are inherited in groups and that it is these groups of factors which Mendelize. The chromosome view of heredity, as developed by MORGAN and others (1915), will be used because it gives a means of representation in a simple, graphical manner.

The increasing complexity of Mendelism points very strongly to the probability that the important characters of an organism are determined by factors represented in all or most of the chromosomes or linkage groups. This idea has been proposed by EAST (1915) and seems to be in accord with the facts. If this view is approximately correct, and if it may also be assumed that, in addition to the factors which differentiate varieties, many different factors may bring about the same visible effect, then it is possible to meet the two objections raised against dominance as a means of accounting for heterosis.

As an illustration of what is meant by different factors bringing about the same visible effect, an example may be taken in which one variety of plants grows to an average height of six feet because of one set of factors, and another variety grows to approximately the same average height but attains this height through the operation of a different set of factors. This is comprehensible when it is remembered that height is only an expression of a plant's power to develop. Hereditary factors which affect any part of the plant may indirectly determine height. Direct proof as to the essential correctness of this assumption, i.e., of different factors producing the same somatic effect, is at hand in the cases of duplicate genes producing the same morphological result in *Avena sativa* (NILSSON-EHLE 1909) and *Bursa bursa-pastoris* (SHULL 1914), as well as the other cases of duplicate genes reported by NILSSON-EHLE (1908) and EAST (1910).

The widespread occurrence of abnormalities and other characters detrimental to the organism's best development is well known in both the plant and animal kingdoms. This is especially true in naturally cross-pollinated species of plants. It may be taken for granted that no one variety has all of these unfavorable characters nor, on the other hand, has it all the favorable characters. For the most part each variety possesses a random sample of the favorable and unfavorable characters. There are differences between varieties in their power for development, however, just as there are differences in superficial characters. Some varieties of plants grow taller than others; some grow faster; some produce more seed. But, on the average, most of the varieties of a species tend to grow to about the same extent, however much they may differ in superficial characters.

If, for the most part, these favorable characters are dominant over the unfavorable (if normalities are dominant over abnormalities) it is not necessary to assume complete dominance in order to have a reasonable explanation of the increased development in F_1 over the average of the parents or any subsequent generation. It is in F_1, and in F_1 only, that the maximum number of different factors can be accumulated in any one individual.

Because of linkage it is impossible to recombine in any one individual in later generations any greater number of characters in the homozygous condition than were present in the parents if the factors were distributed uniformly in all of the chromosome pairs. Possible exceptions to this statement will be discussed later. This view of the situation explains why the effects of heterozygosis result in a greater development in F_1 than in the parents, and not less. Why should crossing not have resulted in a depressing or indifferent effect instead of a stimulating one, according to previous views?[3] It also makes it seem probable that the effects of heterozygosis remain throughout the life of the sporophyte, even through innumerable asexual generations. Furthermore, it will be shown that no skewness in the distribution of F_2 is expected.

Let me submit in the form of a concrete illustration the abstract view that I have tried to present in the preceding paragraphs. A purely hypothetical case will be assumed, in which two homozygous varieties of plants, having three pairs of chromosomes, both attain approximately the same development as represented by any measurable character. This development will be considered to amount to 6 units, 2 of which are contributed by each chromosome pair. One of these varieties, which will be called "X," attains this development because of factors distributed in the three pairs of chromosomes. Any number of factors may be chosen, but, for the sake of simplicity, only three in each chromosome will be employed. These are numbered 1, 3, 5; 7, 9, 11; and 13, 15, 17; in the following diagram, each different in its contribution to the plant's development. The other variety, "Y", develops to an equal extent in the character measured, and this development will also be considered to amount to 6 units. It attains this same development, however, by a different set of factors distributed in the three chromosomes, numbered 2, 4, 6; 8, 10, 12; and 14, 16, 18. It is also assumed that these 6 factors are fully as effective in the $1n$ condition as in the $2n$ condition, i.e., show perfect dominance. It will be seen from the diagram that the F_1 develops to twice the extent of either parent, because there are present here 18 different factors (in the $1n$ condition), whereas the parents have only 9 (in the $2n$ condition). In the diagram, any other factorial complex common to both varieties is ignored. The development of the parents of 6 units and of the F_1 of 12 units is additional to that afforded by this common factorial complex.

Following this hypothetical case into the F_2 generation by selfing or

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[3] Crosses between plants not closely related do result in no greater development than the parents and in many cases much less than the parents. This is because characters which are widely dissimilar are unfavorable to the organism's best development when acting together.

breeding together these F_1 plants, the theoretical results given in table 2 are obtained.

Summing up the results of this tabulation, it will be found that eight plants are homozygous and have the same development as either parent, i.e., of six units. Eight plants are heterozygous in all three chromosome pairs and have the same amount of growth as F_1, i.e., of twelve units. The remaining 48 plants fall into two equal-sized groups developing to eight and ten units respectively. In other words, the distribution is symmetrical, and this symmetry remains, however many chromosomes are concerned.

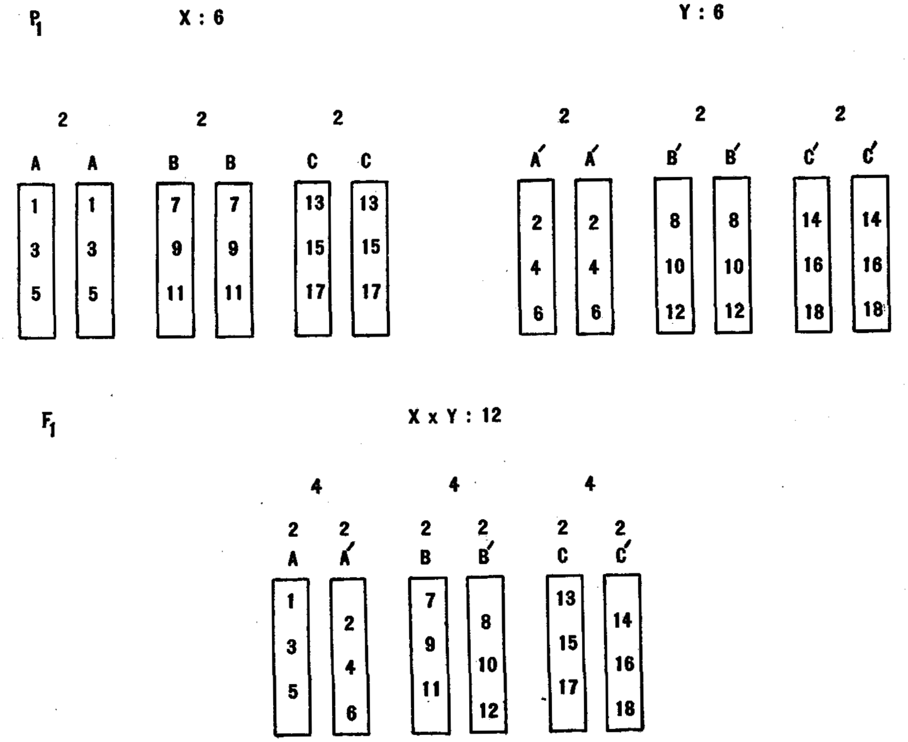

DIAGRAM I.—To show how factors contributed by each parent may enable the first generation of a cross to obtain a greater development than either parent.

Furthermore, it should be noted that the mean development of F_2 is nine units, which is an excess above the parents of just half of the excess of the F_1 over the parents. In other words, the extra growth derived by crossing the two varieties has diminished 50 percent. In F_3 from a random sample of F_2, it can be shown that this excess again diminishes 50 percent, so that the effect is only 25 percent as great in F_3 as in F_1,

TABLE 2

Composition of a tri-hybrid in F_2 according to Mendelism, and the development which each individual attains depending upon the number of heterozygous chromosomes contained and thereby the total number of different factors present.

Number of individuals in each category	Categories	Contribution of each chromosome pair	Total development
1	A A B B C C	2 + 2 + 2	6
2	A A′ B B C C	4 + 2 + 2	8
2	A A B B′ C C	2 + 4 + 2	8
2	A A B B C C′	2 + 2 + 4	8
4	A A′ B B′ C C	4 + 4 + 2	10
4	A A B B′ C C′	2 + 4 + 4	10
4	A A′ B B C C′	4 + 2 + 4	10
8	A A′ B B′ C C′	4 + 4 + 4	12
1	A A B B C′C′	2 + 2 + 2	6
2	A A B B′ C′C′	2 + 4 + 2	8
2	A A′ B B C′C′	4 + 2 + 2	8
4	A A′ B B′ C′C′	4 + 4 + 2	10
1	A A B′B′ C C	2 + 2 + 2	6
2	A A B′B′ C C′	2 + 2 + 4	8
2	A A′ B′B′ C C	4 + 2 + 2	8
4	A A′ B′B′ C C′	4 + 2 + 4	10
1	A′A′ B B C C	2 + 2 + 2	6
2	A′A′ B B′ C C	2 + 4 + 2	8
2	A′A′ B B C C′	2 + 2 + 4	8
4	A′A′ B B′ C C′	2 + 4 + 4	10
1	A′A′ B′B′ C C	2 + 2 + 2	6
2	A′A′ B′B′ C C′	2 + 2 + 4	8
1	A′A′ B B C′C′	2 + 2 + 2	6
2	A′A′ B B′ C′C′	2 + 4 + 2	8
1	A A B′B′ C′C′	2 + 2 + 2	6
2	A A′ B′B′ C′C′	4 + 2 + 2	8
1	A′A′ B′B′ C′C′	2 + 2 + 2	6
64 Total			

Distribution of the F_2 individuals according to the development attained.

Classes	6	8	10	12	= 4	Number of classes
Frequency	8	24	24	8	=64	Total population

and so on in subsequent generations. This is in accord with the mathematical prediction made by EAST and HAYES (1912), to which actual data obtained from maize roughly approximate, as shown by JONES (1916).

The development attained by any individual in table 2 is correlated with the number of heterozygous factors present. This has been maintained by all recent writers on the subject as a rough description of the facts as obtained in actual experiments.

When different numbers of chromosomes are concerned, according to this scheme, the number of individuals in the different classes making up the whole F_2 population is given in table 3.

In any F_2 distribution there are as many individuals heterozygous for all factors (duplicating F_1 individuals) as there are individuals homozygous for all factors concerned in the original cross (two duplicating the parents; the remaining forming new homozygous combinations). The remaining individuals fall into a symmetrical distribution between these two end classes. The theoretical figures for any F_2 distribution in which n Mendelizing units are concerned can be obtained by taking the coefficients of the expanded binomial $(a + a)^n$ and multiplying these by 2^n, as shown in table 3. Since the expanded binomial is used to illustrate a normal frequency distribution, there can be no question as to the symmetry of the F_2 distributions if the diagrammatic scheme outlined is, in this respect, a description of the actual facts.

TABLE 3

Distribution of the individuals in F_2 according to the number of heterozygous chromsomes pairs they contain.

Number of chromosome pairs in which the F_1 is heterozygous	Classes with different number of heterozygous chromosome pairs and the number and ratio of individuals in these classes						Total number of individuals in the population
	0	1	2	3	4	5	
1	2	2					4
	1	1					
2	4	8	4				16
	1	2	1				
3	8	24	24	8			64
	1	3	3	1			
4	16	64	96	64	16		256
	1	4	6	4	1		
5	32	160	320	320	160	32	1024
	1	5	10	10	5	1	
n	2^n	...... etc. ......$2^n \times$(coefficients)........2^n					$(2^n)^2$
	1	...... etc. ...... coefficients of the expanded binomial $(a + a)^n$............1					

In the preceding purely diagrammatic representation of the way in which dominance may account for the effects of heterozygosis, perfect dominance was assumed. Such an assumption is neither justified nor desirable. Many theoretical explanations of the inheritance of quantitative characters are based on exactly the converse assumption, i.e., that factors in the 1*n* condition have just half the effect that they have in the 2*n* condition.

In the development of an organism, however, all types of factors are concerned, both qualitative and quantitative. Partial dominance in qualitative characters is a normal occurrence. The concensus of opinion at the present time is that there may be, in reality, no cases of perfect dominance. In those cases in which the heterozygote cannot be distinguished from the pure dominant, it is assumed that the similarity is only apparent and not real. The heterozygote merely approaches the condition of the dominant type more or less closely. However much it may be true that perfect dominance rarely or never occurs, the fact and universality of partial dominance can hardly be denied.

In this connection it should be realized that the difference between the heterozygote and the recessive type in many cases is one of *kind,* while the difference between the heterozygote and the dominant type is one of *degree.* A good illustration of this point is found in the case of albinism in maize. Plants heterozygous for the factor (or factors) determining the production of chlorophyll cannot be distinguished from normal green plants—a case of apparently complete dominance. If there is in reality a difference between these heterozygous and homozygous normal green plants, although not apparent, that difference is very slight as compared with the difference between the heterozygote and the abnormal recessive. In the former case the difference, if there is any, is quantitative. The heterozygote may not have as much chlorophyll as the normal homozygote. In the second case the difference is qualitative. The heterozygote has chlorophyll; the recessive has none. This is a difference which determines the life or death of the organism.

All the evidence at hand leads to a seemingly logical conclusion, one necessary to the conception of dominance as an explanation of heterosis, which is, that *many factors in the 1n condition have more than one-half the effect that they have in the 2n condition.* Whether or not this is a logical conclusion and one that is justified by the facts remains to be seen. It certainly has the advantage of being more definite and comprehensible than the assumptions previously made (SHULL 1911; EAST and HAYES 1912), that factors in the heterozygous condition stimulate development by virtue of their being in that condition, without showing in any way why this should be so.

There is abundant evidence to show that many abnormal characters exist in a naturally cross-pollinated species and that they are recessive to the normal condition. In maize innumerable examples can be cited. In addition to the complete lack of chlorophyll already mentioned, there are also other chlorophyll factors which distinguish yellowish-green plants from normal green plants, just as there are cases of both conditions in other plants, e.g., Pelargonium (BAUR 1911). By inbreeding, strains of maize are isolated which are dwarf; some are sterile; some have contorted stems; some fasciated ears. Some are more susceptible to the bacterial wilt disease, and still others have brace roots so poorly developed that they cannot stand upright when the plants become heavy. It is unnecessary to mention more examples, because their occurrence in many kinds of material is familiar to everyone. All the characters cited are recessive, either completely or to a large degree, to the normal condition. More than one of these unfavorable characters may be present together in one inbred strain. No one strain so far known has them all.

Crossing many of these strains of maize together produces perfectly normal F_1 plants. They are normal because the factors which one strain lacks are supplied by the other, and conversely. Because more of the favorable characters are present when the strains are united in F_1 than in either parent, the F_1 is naturally able to attain a greater development. This effect is heterosis.

In the preceding diagrammatic illustration of the way in which heterosis may be brought about it was assumed that all factors had equal effects, that they were evenly distributed in the chromosomes, and that there were no crossovers. This is probably far from describing all the actual conditions. All deviations from this uniformity add to the complexity of the problem. It remains to be seen whether or not the assumption of dominance as an explanation of heterosis will not meet all or most of the requirements raised by all these complicating factors. It is only necessary to consider that a large number of factors is concerned, and that those factors are in most cases fairly evenly distributed among all the chromosomes, and that, in the main, crossovers in some places are balanced by crossovers in others.

Crossing over also provides a means of understanding why certain homozygous individuals (and varieties) may possess a greater number of desirable characters than others. Exceptionally good individuals might be formed by crossing over in heterozygotes occurring in such a manner that all, or a large number of, desirable characters would be combined together eventually in one individual. Such a condition, according to the laws of chance, would be exceedingly rare, which is well in accord with the facts.

Without going into all the possibilities which this viewpoint opens up, it is only necessary to say that a way is offered to meet the objections which have been raised against the conception of dominance as a means of accounting for the facts of heterosis as so far known.

There is still the possibility that there may be a stimulus derived from crossing quite apart from hereditary factors. The view presented here simply coördinates the existing knowledge of heredity so as to give a comprehensible view of the way in which heterosis may be brought about.

SUMMARY

1. The phenomenon of increased growth derived from crossing both plants and animals has long been known but never accounted for in a comprehensible manner by any hypothesis free from serious objections.

2. The conception of dominance, as outlined by KEEBLE and PELLEW in 1910 and illustrated by them in height of peas, has had two objections which were: *a*. If heterosis were due to dominance of factors it was thought possible to recombine in generations subsequent to the F_2 all of the dominant characters in some individuals and all of the recessive characters in others in a homozygous condition. These individuals could not be changed by inbreeding. *b*. If dominance were concerned it was considered that the F_2 population would show an asymmetrical distribution.

3. All hypotheses attempting to account for heterosis have failed to take into consideration the fact of linkage.

4. It is shown that, on account of linked factors, the complete dominant or complete recessive can never or rarely be obtained, and why the distributions in F_2 are symmetrical.

5. From the fact that partial dominance of qualitative characters is a universal phenomenon and that abnormalities are nearly always recessive to the normal conditions, it is possible to account for the increased growth in F_1 because the greatest number of different factors are combined at that time.

6. It is not necessary to assume perfect dominance. It is only necessary to accept the conclusion that many factors in the $1n$ condition have more than one-half the effect that they have in the $2n$ condition.

7. This view of dominance of linked factors as a means of accounting for heterosis makes it easier to understand: *a*, why heterozygosis should have a stimulating rather than a depressing or neutral effect; and *b*, why

the effects of heterozygosis should operate throughout the lifetime of the individual, even through many generations of asexual propagation.

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