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Additive and dominance effects

8. Components of means

With disomic inheritance, two alleles A-a can give rise to three genotypes AA, Aa and aa. Two parameters are required to describe the differences in phenotypic expression of these three genotypes in respect of any character which they affect. As the origin, we take the mid-point between the two homozygotes since this does not depend on the differences between the three genotypes, but on the rest of the genotype and the effects of the environment, and thus reflects the general circumstances of the observations. The two parameters measuring the differences between the genotypes may then be defined as $d$, measuring the departure of each homozygote from the mid-point, and $h$, measuring the departure of the heterozygote from it. Taking A as the allele which increases the expression of the character, AA will exceed the mid-point ($m$) by $d$, and so will have an expression $m + d$, while aa will equally fall short of the mid-point having an expression $m - d$, and Aa will deviate from $m$ by $h$ so having an expression $m + h$ (Fig. 6). If $h$ is 0 the heterozygote’s expression of the character will be midway between the expression of the two homozygotes and dominance is absent. If $h$ is positive, the heterozygote will be nearer to AA than to aa in its expression and A will be partially, or if $h = d$ completely, dominant. Similarly if $h$ is negative, a will be the dominant allele. If $h > d$ Aa will fall outside

![Fig. 6. The $d$ and $h$ increments of the gene difference A-a. Deviations are measured from the mid-parent, $m$, midway between the two homozygotes AA and aa. Aa may lie on either side of $m$ and the sign of $h$ will vary accordingly.](image-url)
the range delimited by AA and aa, and the gene may then be said to display over-dominance. It should be noted that here the capital letter A does not imply dominance of the allele so designated: A is the allele which increases the expression of the character whether it be dominant or not.

This characterization of the differences among the genotypes can be applied to any genes, whether their effects be large or small, leading to continuous variation or not, provided the expressions of the character in question can be expressed in quantitative terms. Thus the sex-linked mutant Bar-eye (B) reduces the number of facets in the eyes of *Drosophila melanogaster*, wild-type females (+/+) having an average number of 779.4 facets, heterozygotes (B/+) having an average of 358.4 facets and the homozygous mutant (B/B) having an average of 68.1 at 25°C (Sturtevant, 1925, quoted by Goldschmidt, 1938). Then \( m = \frac{1}{2}(779.4 + 68.1) = 423.75, \)
\( d = 779.4 - 423.75 = \frac{1}{2}(779.4 - 68.1) = 355.65 \)
and \( h = 358.4 - 423.75 = -65.35. \) Since \( h \) is negative the B mutant is partially dominant to wild-type and we may if we wish measure its degree of dominance by \( h/d = -65.35/355.65 = -0.184. \) We should note that the effect of the Bar-eye mutant is large, and leads to discontinuous variation, the phenotypes of B/B, B/+ and +/+ showing no overlap. No one would go to the trouble of counting the facets in classifying the three genotypes when Bar-eye is being used, and because its effect is sufficiently large for it to be recognized and followed individually in breeding experiments there would be no difficulty in disentangling it from other gene differences whose effects were sufficiently small to contribute only to the continuous variation in facet number that we can observe within the phenotypes associated with each of these genotypes for Bar-eye.

Confining ourselves now to continuous variation, we cannot distinguish individually the genes contributing to it. If we consider two homozygous lines the departure of each of them from their mid-point (or mid-parent as it is often called) will reflect the simultaneous action of all the genes affecting the character by which the lines differ. Assuming that the effects of these genes are simply additive, the departure from the mid-point will in fact be the sum of the \( d \)'s, one from each of the genes, taking sign into account. Where, for example, the lines differ at two loci, A-a and B-b, if one of them is AABB and the other aabb, the first will depart by \( d_a + d_b \) and the second by \(- (d_a + d_b) \). But if the lines are AAbb and aaBB, their departures will be \( d_a - d_b \) and \(- d_a + d_b \) respectively. Generalizing, where the homozygous lines differ at \( k \)