

4. Dominance

Once the data has been shorn to satisfy the hypotheses of section 2 or the awkward lines have been removed, the formulae of that section may be applied. If E is the environmental variation (assumed to be independent of the genotype) of an F_1 mean, the formulae may be written

$$V_p = D + E$$

$$V = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + ((n + 1)/2n)E$$

$$W = (\frac{1}{2})D - (\frac{1}{4})F + (1/n)E$$

$$V_M = (\frac{1}{4})D + (\frac{1}{4})H_1 - (\frac{1}{4})H_2 - (\frac{1}{4})F + (1/2n)E$$

where

$$D = \sum 4u_i v_i d_i^2$$

$$H_1 = \sum 4u_i v_i h_i^2$$

$$H_2 = \sum 16u_i^2 v_i^2 h_i^2$$

$$F = \sum 8u_i v_i (u_i - v_i) d_i h_i$$

and E is estimated from reciprocal differences or block differences if the experiment is replicated. The peculiar coefficients of E and its occurrence in W are caused by the use of means of reciprocals and by each array having an observation in common with the parental array.

H_1/D measures dominance since H_1 and D are weighted means of h_i^2 and d_i^2 respectively, the weighting being in favour of genes with both alleles represented equally in the parents. This ratio may be measured graphically. In the (Vr,Wr) graph let the line of unit slope through the mean point (V,W) cut the OW axis in A and let the parallel tangent to the limiting parabola cut this axis in B. Then (except for the correction for E), $AB/OB = H_1/D$.

$H_2/4H_1$ provides an estimate of the mean value of $u_i v_i$ (with maximum value 1/4 when $u_i = v_i = 1/2$) and so shows whether or not positive and negative alleles are present in equal proportions. Genes having the greatest values of h_i have the greatest weight in the estimator which thus provides no evidence about the distribution of allelic pairs exhibiting no dominance.

F is an indicator of the relative frequencies of dominant and recessive alleles and is positive if there is an excess of dominants.

The equations for F_2 may be derived from these as mentioned in section 3 and so provide independent estimates of dominance, etc. E in this case will contain a component due to genetic variation within F_2 families.

Maize yields These are from three different sources (see table). No estimate of E was given and it has been ignored in obtaining the results in the table. Interaction is present in all sets of data, but only that of Kinman and Sprague has been investigated fully. (Kinman and Sprague, Jour. Amer. Soc. Agron. 1945)

All the data show overdominance, an even distribution of positive and negative alleles, and equal frequencies of dominant and recessive alleles. Since the two lines removed from the F_1 of Kinman and Sprague correspond to points in the (Wr,Vr) graph on either side of the regression line, the dominance ratio has not been affected. (In our height data from *Nicotiana rustica* the removal of the progeny of 3 interacting lines out of the 8 used brought about the striking reduction of H_1/D from 2.2 to nearly zero.) The agreement between F_1 and F_2 is good enough considering that interaction is definitely present. k is the value of h/d obtained by Hull's method. It is about half our value of $\sqrt{(H_1/D)}$ except for F_2 when a zero result was obtained.

Order of dominance. The points in the (Wr,Vr) graph are in order of dominance along the straight line from the (possibly fictitious) complete dominant with minimum $Vr = \sum u_i v_i (d_i - h_i)^2 = V_D$ to the complete recessive with maximum $Vr = \sum u_i v_i (d_i + h_i)^2 = V_R$. It can be shown that unless h_i/d_i is constant these lie somewhat inside the limiting parabola. However assuming that (V_D, W_D) and (V_R, W_R) are at the intersection of the (Vr,Wr) line and the limiting parabola, we can find their values if necessary. Then an estimate of the ratio of the numbers of dominants to recessives in each parent under certain restrictions about equality of gene effects is

$$\frac{V_R - Vr}{V_r - V_D}$$

and over all parents is

$$\frac{V_R - V}{V - V_D} = \frac{\sqrt{(DH_1)} + F}{\sqrt{(DH_1)} - F}$$

This is close enough to unity in all the maize data.

If there is a strong correlation (p in the table) between the dominance order (given by $Vr + Wr$) and the parental order of magnitude, it is possible to predict the values of the complete dominant and recessive parents from the values of V_D and V_R . When this correlation is negative these are the values of the maximum and minimum parents possible, and vice versa for a positive correlation. (In K and S data, F_1 , these limits are 51.9 and 2.3) If there is little correlation between dominance order and parental magnitude (as in our Nicotiana data) no such prediction can be made.