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# The Degree Of Extramedial Response To Hybridity In The Growth Rates of Plant And Ear in a Series of Hybrids in Maize

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2. A reduced rate of cell elongation
3. No modification of cell divisions transverse to the mesocotyl
4. A greater amount of cell enlargement laterally.

The action of the gene $d_1$ in the homozygous recessive state, as evident from the growth of the mesocotyl, depresses the rate and reduces the number of cell divisions along the axis but does not affect the number transverse to the axis; inhibits cell enlargement along the axis and stimulates it transverse to the axis. The influence of the gene is not a simple one, but is complex, affecting both planes and rates of cell division and cell enlargement.

# THE DEGREE OF EXTRAMEDIAL RESPONSE TO HYBRIDITY IN THE GROWTH RATES OF PLANT AND EAR IN A SERIES OF HYBRIDS IN MAIZE

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Hybrid vigor in maize is a phenomenon not only of established economic importance but also of great scientific interest. Its existence has long been recognized, but its careful study began only relatively recently with the great developments in our knowledge of genetics and breeding. Hybrid vigor is commonly considered to be the increased development exhibited by a hybrid as compared with its parents. This often is also referred to as "heterosis." However, there is considerable ambiguity in the application of both the term "hybrid vigor" and of the term "heterosis," especially in quantitative studies. Because of this we will instead adopt the convention of referring the degree of expression of response to hybridity to the mean between the parents. This has elsewhere[1] been designated an extramedial response to hybridity.

The degree of extramedial response to hybridity is the extent by which the hybrid exceeds the mean between the parents. It may be expressed conveniently in the form of a quotient, the extramedial hybridity quotient, or med. H.Q., in which the quantitative feature of the hybrid is represented by AB, and in the parents by AA and BB:

$$\frac{AB}{\left(\frac{AA + BB}{2}\right)}.$$

[1] Abbe, E. C. 1944. Heterosis, Hybrid Vigor, and Hybridity Quotients. (in press).

If the hybrid exceeds the mean between the parents in a given quantitative characteristic, the med. H.Q. will be more than 1, if it is the same as the mean it will be 1, if less than the mean it will be less than 1. The use of a quotient has the advantage of rendering comparable the extent of the response to hybridity in characteristics measured in incomparable units, such as, bushels, millimeters, grams, etc.

A great variety of plant characteristics may exhibit extramedial responses to the state of hybridity. Examples of these are height of plant, width of leaf blade, yield in bushels per acre, and earliness of tasseling. It is of considerable theoretical interest to compare various manifestations of extramedial hybridity in a given hybrid to determine whether various organs and structures are affected to the same degree by the state of hybridity. To illustrate such a series of comparisons we have chosen certain developmental characteristics of the older plant which are of economic importance, namely, increase in dry weight of whole plant, increase in dry weight of ear, and increase in height of plant.

The strains used are four inbreds (A96, A116, A131 and A163) and the six hybrids between them. The inbreds and the facilities for growing the plants were kindly made available to us by the Division of Agronomy and Plant Genetics, University Farm. We are especially indebted to Prof. H. K. Hayes, Chief of the Division of Agronomy and Plant Genetics, who recommended these four inbreds on the basis of his knowledge of their combining ability with each other, which varies from good to poor.

The extramedial hybridity quotients for dry weight of plant, for the dry weight of ear, and for the height of plant for each of the six hybrids mentioned above are listed in the Table. We have listed in the Table the mean extramedial hybridity quotient during growth as well as the med. H.Q. at maturity, since it is thus possible to bring out some relationships of significance. The mean extramedial H.Q. during growth is the mean of the med. H.Q. as determined for each harvest during the growth period.

The observations upon which the med. H.Q.'s in the Table are based are presented graphically for two of the hybrids in figures 1, 2 and 3. In each graph the hybrid is represented by the cross-hatched circles, while the parents are represented by distinctive symbols (crosses, open circles, or triangles). The solid line in each graph connects the arithmetic mean of the values for the parents at each harvest. The broken line is drawn parallel to the solid line, and is equidistant from it by the mean value of the med. H.Q. for the hybrid concerned. The abscissa in each case represents days after planting and the ordinate the quantitative value of the characteristic under consideration. The values of the abscissa are plotted arithmetically and those on the ordinate logarithmically. Plotting the latter logarithmically has the advantage of presenting a

EXTRAMEDIAL HYBRIDITY QUOTIENTS (MED. H. Q.)

| | A96 x A116 | A96 x A131 | A96 x A163 | A131 x A116 | A116 x A163 | A131 x A163 |
|---|---|---|---|---|---|---|
| *Plant, dry weight* | | | | | | |
| 1. ....during growth | 1.7 | 2.4 | 2.2 | 1.2 | 2.3 | 2.9 |
| 2. ....at maturity | 1.3 | 1.5 | 1.6 | 1.2 | 1.6 | 1.7 |
| *Ear, dry weight* | | | | | | |
| 3. ....during growth | 3.0 | 3.9 | 3.7 | 2.1 | 2.8 | 4.8 |
| 4. ....at maturity | 1.9 | 2.2 | 2.4 | 1.5 | 2.2 | 2.7 |
| *Keight of Plant* | | | | | | |
| 5. ....during growth | 1.3 (2.2)[1] | 1.4 (2.7) | 1.4 (2.7) | 1.1 (1.3) | 1.4 (2.7) | 1.5 (3.4) |
| 6. ....at maturity | 1.2 (1.7) | 1.3 (2.2) | 1.3 (2.2) | 1.3 (2.2) | 1.2 (1.7) | 1.4 (2.7) |

[1] The cubed value of the med. H.Q. is given in parenthesis.

given med. H.Q. as of a fixed linear value (which is the reason for the broken line being parallel to the solid line in each case). The reader may thus detect immediately any deviation of the med. H.Q. of the hybrid at a given harvest period from the mean med. H.Q. for all periods of harvest by comparing the location of the point for the hybrid with the course of the broken line.

Increase in dry weight of the plant for the hybrids with the lowest and highest med. H.Q.'s is represented in Figure 1. On the left is A131 x A116 which has a mean med. H.Q. of 1.2 during growth, while on the right is A131 x A163 which has a value of 2.9. A131 x A116 shows so slight an extramedial response to hybridity during growth as well as at maturity as to barely surpass either the mean between the parents or the larger parent. On the other hand A131 x A163 not only exceeds the mean between the parents but also well exceeds the larger parent. By comparing in each hybrid the points for dry weight of hybrid with the curve (broken line) for the mean med. H.Q. it will immediately be seen that during the earlier stages of growth the hybrid grows more rapidly than do the parents, while in the later stages it begins to mature sooner. The earlier maturation of the hybrid is reflected in the fact that the med. H.Q. for mature dry weight is in practically each case lower than the med. H.Q. for the whole growth period covered in this study. That is to say, the parents make up some of the increasing discrepancy with the hybrid during the earlier part of the growth period by continuing to grow for a somewhat longer time; but as a corollary to this they reach maturity later.

If we now consider the dry weight of ear (Fig. 2) we again find that the same two hybrids are best or poorest (cf. Table) of the six hybrids both during development and at maturity. Within a given hybrid the value of the med. H.Q. for dry weight of ear does not invariably correspond closely to that for dry weight of plant, and in most of the hybrids the discrepancy is marked. There is the same tendency noted above for the hybrid to grow more rapidly than do its parents, and for the parents to mature at a later date, so that the med. H.Q. at maturity is lower for each hybrid than it averages during growth.

Rate of growth in plant height (Fig. 3) finds the same hybrids most and least responsive to the state of hybridity (cf. Table). There is also illustrated here the same tendency of the hybrid to grow more rapidly than do its parents and to mature sooner. The correlation for degree of extramedial response for rate of growth in length with the other characteristics mentioned is low.

Generalizing from the above it is evident that in the quantitative expressions of the characteristics chosen for illustration the same hybrid has in each case been either the best or the poorest, whether during growth or at maturity. Only the highest and lowest have maintained this relative position, the other four hybrids varying in order of the med. H.Q. from charactertistic to characteristic. This is brought out in Figures 4 and 5. Columns 1 through 6 in Figures 4 and 5 are numbered to correspond to the numbers of the lines in the Table. Thus the columns 1 and 2 indicate respectively the med. H.Q. during growth and at maturity. In Figure 4 the med. H.Q. is presented as an absolute value, and it is immediately evident upon comparing the first six columns for each of the hybrids that there is no marked quantitative correlation between the degree of expression of the individual characteristics studied. That is, the degree of response to the state of hybridity varies from characteristic to characteristic within the same hybrid. It may also be stated, then, that one may not predict with a great deal of accuracy from a given quantitative response in one characteristic what the quantitative response will be in another characteristic of the same hybrid. Several qualitative features are brought out in Figure 4. One is the fact that for each of the characteristics described the extramedial hybridity quotient is higher on the average during growth than it is at maturity, since each of the left hand columns for a given characteristic is higher than its right hand mate (with one exception). This state of affairs reflects the fact that the hybrid has a higher growth rate than its parents in each of the respects in which it was measured, and that it matures in that respect sooner than do the parents. Another qualitative feature brought out by Figure 4 is that for each of the characteristics described the hybrid exceeds the mean between the parents, since the med. H.Q. is above 1 throughout. A third qualitative feature which is suggested by Figure 4 is that A131 x A163 is consistently the highest and A131 x A116 is consistently the lowest in terms of med. H.Q. for each of the characteristics. This suggests that in some crosses there is a close agreement in the relative degree of extramedial response to hybridity for the various characters studied. This possibility is explored graphically in Figure 5, where the med. H.Q. is plotted for each characteristic as a percent of the largest med. H.Q. for that characteristic. Figure 5 brings out the fact that A131 x A163 is for each characteristic the best hybrid, but that the relative degree of response to hybridity varies markedly and without definite correlation in each of the other hybrids. We may therefore also conclude that there is no close correlation between characteristics of a given hybrid even in terms of the relative degree of expression of the extramedial response to hybridity. The point might be raised here that a comparison of med. H.Q.'s should be based on a reduction of the H.Q.'s to either cubes or cube roots of the linear or weight characteristics respectively. This is a valid suggestion, but it will not change the conclusions reached, if for example, the linear values are cubed for comparison with the dry weight characteristics. This is evident from the Table where the med. H.Q. for each linear value (lines 5 and 6) is converted to the cube in the parenthesis under the linear value.

The absence of a close quantitative correlation between the degree of expression of the response to the hybrid state within a given hybrid is of considerable interest, since it may be taken as axiomatic that the nuclei of all diploid cells in the soma of the hybrid have the same genetical constitution. This may be expressed in a slightly different way. In spite of the fact that within a given hybrid the genom is the same in each nucleus of each tissue and organ studied, the quantitative degree of response varied from organ to organ. It is evident that the quantitative influence of the genom varies from organ to organ. It may be assumed that one part of the genom controls a given organ during its development, while another part of the genom controls the development of another organ. Under such circumstances it would be not unreasonable to assume that the genes which control one character may be in a greater state of hybridity than for the genes controlling another and that the variation in response from organ to organ may be due primarily to this.

## SUMMARY

An extramedial response to the state of hybridity is defined for quantitative characteristics as the extent by which the hybrid departs from the mean between the parents. The extent of this extramedial response may be expressed in terms of a quotient which has the advantages accruing to a statistical constant. This quotient is here referred to as the extramedial hybridity quotient, or med. H.Q.

Four inbreds and their six hybrids form the basis for this study of the degree of response attained in three different characteristics of each hybrid.

The degree of the extramedial response in each of the hybrids is presented in terms of the med. H.Q. for each of three characteristics, namely, dry weight of plant, dry weight of ear, and plant height. Each characteristic is considered developmentally as well as at maturity. It is observed for these hybrids that:—

## LEGEND

FIGURE 1. Curves illustrating the rate of increase in dry weight of the two hybrids, A131 x A116 and A131 x A163, and of their parental inbreds. The solid line in each case represents the arithmetic mean between the parents, and the broken line represents the mean med. H.Q.

FIGURE 2. Curves illustrating the rate of increase in dry weight of ear.

FIGURE 3. Curves illustrating the rate of increase in height of plant.

FIGURE 4. Chart showing the degree of response to the state of hybridity achieved in dry weight of plant (columns 1 and 2), dry weight of ear (columns 3 and 4), and in height of plant (columns 5 and 6). The columns are numbered to correspond with the lines in the Table. The odd-numbered columns represent the med. H.Q. during growth, the even-numbered ones the med. H.Q. at maturity.

FIGURE 5 Chart showing the degree of med. H.Q. in per cent, the maximum med. H.Q. for each characteristic being reckoned as 100%.

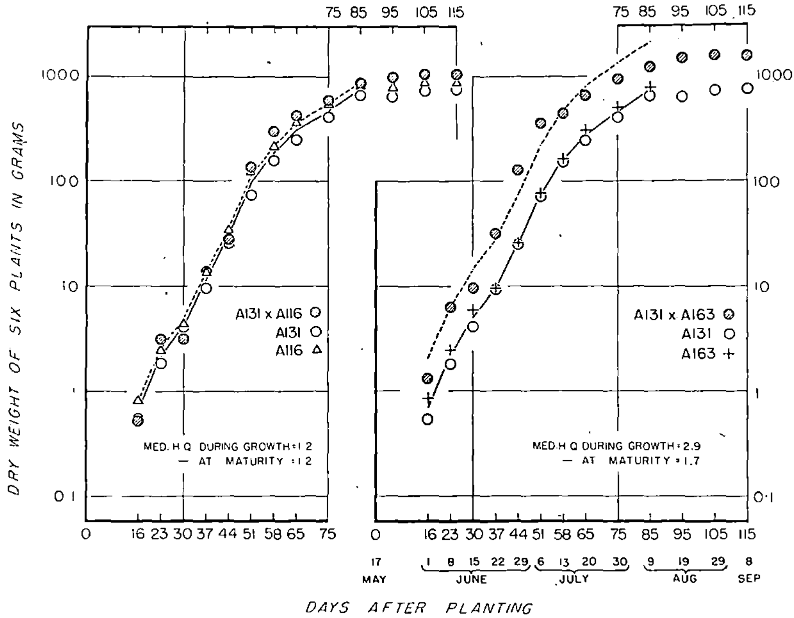


FIG. 1

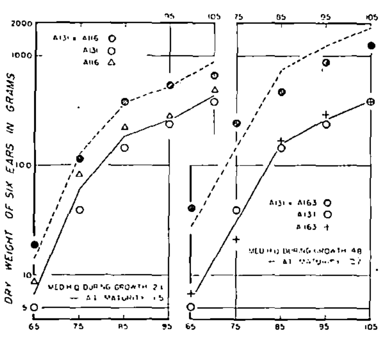


FIG 2

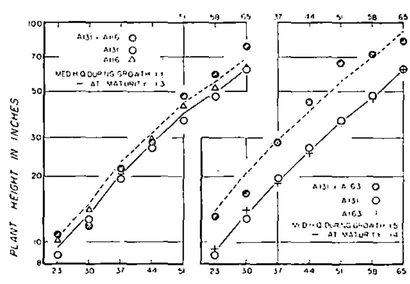


FIG 3

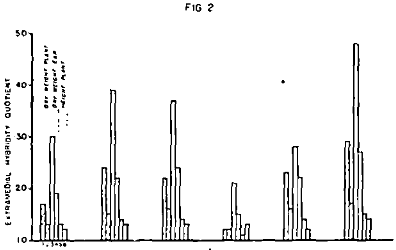


FIG. 4

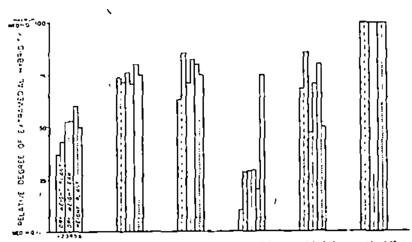

FIG. 5

1. The degree of response in any one characteristic is usually higher during the most active period of growth than it is at maturity. That is, the hybrids grow at a more rapid rate and mature sooner than do their parents.

2. The hybrid which is poorest (has the lowest med. H.Q.) in any one respect also tends to be so in other respects. Also the hybrid which has the highest med. H.Q. in a given respect also tends to have the highest one in other respects. The remaining hybrids vary considerably among themselves, but occupy intermediate positions between the best and poorest hybrids.

3. When the absolute med. H.Q.'s of the various hybrids are compared it becomes evident that:
   a. The correlation in the degree of the extramedial response for different characteristics of the same hybrid is not very great.
   b. Therefore the degree of response in one character may not be used for prediction of the degree of response in another characteristic of the same hybrid.

4. These observations suggest that each characteristic of a hybrid is controlled by certain genes that do not affect the development of the various characters to the same degree and that those genes which control one character may be in a greater state of hybridity than those which control another.

# THE DEGREE OF EXTRAMEDIAL RESPONSE TO HYBRIDITY IN THE GROWTH OF THE MESOCOTYL AND COLEOPTILE IN A SERIES OF HYBRIDS IN MAIZE

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If it were possible to predict the degree of extramedial response to hybridity as developed in commercially important characteristics of the mature plant from a study of the seedling characteristics of the same hybrid, the selection of crosses showing desirable characteristics would be greatly facilitated. With this in mind, a quantitative study of two seedling characters, mesocotyl length and coleoptile length, was made utilizing four inbreds and the six hybrids between them. These were the same strains as those reported on by Abbe and Wang[1], but one generation later in origin. Extramedial hybrid-

[1] Abbe, E. C. and K.-W. Wang. The degree of extramedial response to hybridity in the growth rates of plant and ear in a series of hybrids in maize. Proc. Minnesota Acad. Sci., vol. 11, pp. 51–58.