EVIDENCE FOR THE EXISTENCE OF GENES CONTROLLING SHAPE

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The increasing significance for genetics of the problems involved in growth, development, and differentiation has stimulated inquiry into the genetic basis of these processes. There is every reason to believe that size characters are amenable to genetic analysis, though the method of operation of the genes controlling them is by no means understood. Certain quantitative traits, such as total bulk or weight, lend themselves readily to the orthodox multiple-factor interpretation and may well be determined by genes affecting the various physiological processes concerned in growth. The case is by no means so clear for less generalized size traits such as the particular dimensions of a body or organ. Naturally these will be somewhat related to general size, but even in structures of the same volume there may be marked differences in individual dimensions. The question arises as to whether there are genes which control growth in particular directions or dimensions independently, with shape appearing as an incidental result of their combination, or whether genes with quite a different effect are concerned here which, through a control of growth correlation, govern shape directly.

The inheritance of dimensions has frequently been subjected to Mendelian analysis. The work of EMERSON and EAST (1913) on the length and diameter of maize ears; of KEEBLE and PELLEW (1910) on internode length and stem diameter in peas; of FREEMAN (1919) on plant height and leaf width in wheat; of TAVČAR (1925) on seed dimensions in *Phaseolus*; of DALE (1929) on fruit length in *Capsicum*, and of WRIEDT (1931) on beak length and leg length in pigeons come to mind as illustrations. Sometimes the existence of dimensional genes has been implied rather than directly postulated but in certain cases, such as the recent work of SIRKS (1932) on the inheritance of leaf traits in *Vicia*, genes for definite quantitative increments in length and width are assumed to be operative.

It is certainly conceivable, from what we know of the existence of specific gradients along various axes of the developing organ or organism, that genes controlling these gradients, and the resulting dimensions, may actually exist. If there are such genes, organic shapes must evidently be the results of interactions between them. If, on the contrary, there are genes directly controlling shapes or patterns, then any particular dimension will not be determined by specific "dimensional" genes but will,

instead, be the resultant of an interaction between genes for shape and genes which control the total volume or bulk of growth. No persistent attempt has been made to determine, in a given case, which of these alternatives is the correct one. Evidently one of the major problems in the relation of genetics to development is here involved.

The data which the author has gathered over a number of years on the heredity of fruit characters in *Cucurbita pepo* provide excellent material for such a study. Pure lines of this species differing markedly in the size and shape of their fruits have been crossed and the behavior of these traits investigated in more than 200 progenies. A study of this material has resulted in the establishment of five distinct lines of evidence supporting the hypothesis that genes are here operative which control shape directly and which are independent of others governing quantitative characters of volume or weight. These are as follows: (1) the fact that a simple, clearly segregating fruit-shape difference is inherited independently of fruit size; (2) the fact that there is rarely or never a significant correlation between fruit-size (weight) and fruit-shape index in the F_2 ; (3) the fact that shape indices segregate much more sharply than do dimensional traits; (4) the fact that there is a positive correlation between fruit length and width in pure lines and F_1 progenies and a negative correlation between these traits in the resulting F_2 progenies; and (5) the fact that the variability of length is twice as great as that of width in the F_2 generations from crosses between lines which differ appreciably in fruit-shape index, although length and width are essentially equal in their variability in both pure lines and F_1 progenies.

INDEPENDENT INHERITANCE OF SHAPE AND SIZE

The author has previously shown (1927) that in this species there are a number of fruit-shape differences which seem to be due to a single pair of genes, since they display simple monofactorial segregation in the F_2 . These differences often occur between pure lines which are also markedly different in fruit size (weight). In such cases, segregation for shape is independent of size, the latter behaving in typical multiple-factor fashion (1931). The simplest shape difference is between a line in which the fruits are essentially isodiametric ("spheres") and one in which the equatorial diameter is much greater than the polar one ("disks"). The latter type is completely dominant and the F_2 shows a sharp segregation into $\frac{3}{4}$ disks and $\frac{1}{4}$ spheres. A typical spherical line with a mean weight of 702 grams was crossed with a disk line weighing 1305 grams. The F_1 , displaying heterosis, weighed somewhat more than the heavier parent. The F_2 had a mean weight almost exactly intermediate between those of the two parental types, and a variability in weight markedly higher than that of the F_1 . The significant

fact, however, is that the segregating sphere and disk plants in the F_2 were almost identical in fruit weight, 1025 grams for the former and 1035 for the latter. Thus the spheres were about 300 grams heavier than the parental spheres and the disks about 300 grams lighter than the parental disks, differences which persisted in later generations. Evidently the single gene which presumably determines this shape difference is not dependent in any way upon the particular size of the fruit in which it expresses itself.

ABSENCE OF CORRELATION BETWEEN SHAPE AND WEIGHT IN F_2

If fruit shape is dependent in any way upon fruit size, there should evidently be a correlation between shape and weight in the F_2 . In a series of F_2 progenies from crosses between lines differing in both shape and weight, the coefficient of correlation was determined between fruit weight and fruit shape index. The results for 37 such progenies are presented in table 1. Most of these correlations are very small and few or none of them

TABLE 1

*Coefficients of correlation between fruit-shape index and fruit weight in various F_2 pedigrees.**

F_2	NUMBER OF INDIVIDUALS	CORRELATION COEFFICIENT	F_2	NUMBER OF INDIVIDUALS	CORRELATION COEFFICIENT
1-23	392	$-.04 \pm .06$	13-27	102	$-.21 \pm .10$
1-27	95	$-.20 \pm .10$	19-27	57	$+.02 \pm .13$
17-27	44	$+.07 \pm .15$	21-27	83	$-.13 \pm .11$
18-27	58	$-.04 \pm .13$	6-28	48	$-.01 \pm .15$
25-27	60	$+.17 \pm .13$	7-28	29	$+.11 \pm .18$
26-27	38	$+.18 \pm .16$	11-28	50	$+.30 \pm .13$
30-27	54	$+.03 \pm .14$	16-28	59	$-.36 \pm .11$
31-27	52	$-.01 \pm .14$	17-28	47	$+.16 \pm .14$
33-27	114	$-.27 \pm .09$			
12-28	57	$-.03 \pm .13$	3-27	44	$-.06 \pm .15$
33-28	50	$+.19 \pm .14$	6-27	39	$-.09 \pm .16$
			11-27	35	$-.10 \pm .17$
3-23	430	$-.05 \pm .05$	14-27	45	$+.05 \pm .15$
4-23	200	$+.08 \pm .07$	32-27	66	$+.06 \pm .12$
5-23	387	$-.19 \pm .05$	13-28	48	$+.31 \pm .13$
6-23	236	$+.16 \pm .06$	24-28	57	$-.23 \pm .13$
7-23	239	$+.10 \pm .06$	29-28	54	$-.07 \pm .14$
8-23	535	$+.17 \pm .04$	39-28	31	$+.10 \pm .18$
9-23	303	$-.19 \pm .06$	40-28	44	$+.02 \pm .15$
10-27	58	$+.01 \pm .13$			

* A positive sign indicates that increased weight is associated with increased flattening of the fruit shape; a negative sign, with a decreased flattening. In the first group of pedigrees (11), the heavier pure-line parent was the flatter; in the second group (16), the heavier was the more elongate; and in the third (10) the parents were not significantly different in weight, though they were in shape.

Standard errors are used throughout.

are significant. This is essentially the same type of evidence as was presented in the previous section, but in these pedigrees sharp segregation of shape is usually absent and Mendelian analysis difficult. Regardless of the complexity of the genetic basis for shape, however, it seems to be independent of that for size.

It is, of course, conceivable that genes affecting shape and others affecting weight may be present in the same chromosome and thus display genetic linkage with each other. Indeed, LINDSTROM (1932) has reported an instance of this sort in *Lycopersicum*. There is evidently little or none of such linkage in the material here investigated, since the particular com-

FIGURE 1.

binations of weight and shape which distinguish the parents are no more common than others in the F_2 progenies (table 1).

SHARPER SEGREGATION FOR SHAPE INDEX THAN FOR DIMENSIONS

That in such an F_2 pedigree as the one described previously there is a single "shape" gene rather than a series of "dimensional" ones is further indicated by comparing the segregation of shape index (the longer dimension divided by the shorter) with those for length and for width of fruit. In figure 1, the F_2 of a disk-sphere cross is plotted for these three characters, and it is obvious that shape index segregates far more sharply than either of the dimensions. Length, to be sure, shows a clear bimodality but is not separated into two classes. The curve for width is essentially a smooth one. On a hypothesis of "dimensional" genes we should be forced to assume that length is governed by a single pair of genes but width by

a series of multiple ones. Evidently the facts are to be explained most simply by assuming a single gene controlling shape directly, and which acts on fruits of widely varying sizes. The particular dimensions result here from the manner in which the total bulk of the fruit (presumably dependent on a series of general size factors) is molded by this single gene governing shape.

A similar result is obtained in the somewhat more complex F_2 resulting from the cross of two types of spheres, in which a ratio of 9/16 disks: 6/16 spheres : 1/16 elongates appears. This segregation is clearly evident in shape index but would hardly be guessed from length and is quite absent in width (figure 2).

FIGURE 2.

NEGATIVE CORRELATION BETWEEN LENGTH AND WIDTH IN F_2

Further evidence that genes determining shape rather than dimensions are here operative is provided by the marked reversal in the relation between length and width which is manifest in the F_2 as compared with pure lines and the F_1 . In both the latter there is, as might be expected, a positive correlation between length and width (table 2). Shape being essentially constant here, quantitative differences (due presumably to environmental causes only) involve all dimensions proportionally. If independent genes controlling dimensions exist, we should expect to find in the F_2 no correlation between length and width, or at most a small positive one. On the contrary, whenever the original parents differ at all markedly in shape index, there is a strong *negative* F_2 correlation. This necessarily follows if fruit size (volume or weight) is constant (or is independent of shape), for in that case the longer a fruit is, the narrower it must necessarily be, and *vice versa*. Segregating genes for shape, molding into various patterns a mass of material the total bulk of which is determined by other factors,

will explain this reversal of sign in the coefficients of correlation, which is inexplicable on a dimensional-factor hypothesis.

TABLE 2

Coefficients of correlation between fruit length and fruit width in six representative pure lines, and in the F₁ and F₂ progenies of fifteen crosses between pure lines differing in fruit shape.

PURE LINE	NUMBER OF INDIVIDUALS	CORRELATION COEFFICIENT	PURE LINE	NUMBER OF INDIVIDUALS	CORRELATION COEFFICIENT
103	156	$+.57 \pm .04$	438	83	$+.55 \pm .05$
125	84	$+.73 \pm .05$	C	136	$+.56 \pm .06$
391	193	$+.54 \pm .05$	M	105	$+.91 \pm .01$
F ₁			F ₂		
1-21	72	$+.48 \pm .10$	1-22	220	$-.44 \pm .06$
2-21	39	$+.52 \pm .12$	2-22	231	$-.37 \pm .06$
1-22	32	$+.41 \pm .15$	1-23	392	$-.32 \pm .05$
3-22	118	$+.62 \pm .05$	3-23	430	$-.41 \pm .04$
4-22	93	$+.61 \pm .07$	4-23	200	$-.71 \pm .04$
6-22	23	$+.25 \pm .11$	6-23	236	$-.12 \pm .06$
7-22	55	$+.39 \pm .12$	7-23	239	$-.45 \pm .05$
8-22	90	$+.26 \pm .10$	8-23	535	$-.33 \pm .04$
9-22	42	$+.13 \pm .15$	9-23	303	$-.19 \pm .05$
3-23	14	$+.58 \pm .18$	3-24	290	$-.40 \pm .05$
17-23	30	$+.53 \pm .13$	17-24	275	$-.47 \pm .05$
19-23	14	$+.30 \pm .24$	19-24	364	$-.43 \pm .05$
20-23	32	$+.32 \pm .16$	20-24	273	$-.36 \pm .05$
23-23	32	$+.59 \pm .12$	23-24	135	$-.22 \pm .07$
25-23	16	$+.72 \pm .12$	25-24	302	$-.30 \pm .05$

The correlation coefficients of the F₁ pedigrees tend to be somewhat smaller than those for the pure lines, indicating that the parents were not always completely homozygous and that a certain amount of segregation is sometimes occurring even in the F₁. In every case, however, there is a significant difference between the values for the F₁ and those for the F₂.

It may be suggested that linkage between dimensional genes might account for these facts. In this case, however, crossovers should occur. In the F₂ from a cross of a long, narrow squash with a short, wide one, for example, short, narrow fruits and long, wide ones should be found. It is significant that such extreme types seem never to appear. They would obviously increase the variability in size greatly, but in crosses between lines differing in shape but not in weight, the latter shows little increase in variability in size in F₂.

VARIABILITY IN LENGTH DOUBLE THAT OF WIDTH IN F₂

Not only does there appear a radical change in the character of the correlation between length and width in the F₂ from a cross of types differing in fruit shape, but an equally significant change in the relative varia-

bility of these two dimensions. In the various pure lines and in the F_1 there is no consistent difference between the variability of length and that of width (table 3). In the F_2 progenies, however, from crosses of types

TABLE 3

Coefficients of variability for fruit length and fruit width in six representative pure lines, and in the F_1 and F_2 progenies of twenty-one crosses between lines differing in fruit shape.

PURE LINE	NO. OF IND.	C.V. OF LENGTH	C.V. OF WIDTH	PURE LINE	NO. OF IND.	C.V. OF LENGTH	C.V. OF WIDTH
103	156	12.4±0.7	10.0±0.6	438	83	20.3±1.6	20.0±1.6
125	84	8.6±0.7	8.8±0.7	C	136	14.6±0.9	12.9±0.8
391	198	13.2±0.7	18.2±0.9	M	105	16.6±1.2	17.8±1.2
F_1				F_2			
1-21	72	13.0±1.1	14.2±1.2	1-22	220	35.7±1.7	16.6±0.8
2-21	39	12.0±1.4	12.4±1.4	2-22	231	27.5±1.3	14.7±0.7
1-22	32	11.1±1.4	8.8±1.1	1-23	392	34.2±1.2	17.9±0.7
3-22	118	13.5±0.8	11.4±0.8	3-23	430	36.0±1.2	19.7±0.7
4-22	93	12.3±0.9	10.6±0.8	4-23	200	44.4±2.2	24.6±1.2
5-22	59	9.6±0.8	11.0±1.0	5-23	387	30.2±1.1	14.3±0.5
6-22	23	8.0±1.2	14.5±2.2	6-23	236	34.0±1.6	15.8±0.7
7-22	55	8.5±0.8	10.6±1.0	7-23	239	36.8±1.7	15.5±0.7
8-22	90	8.2±0.6	6.6±0.5	8-23	535	31.9±1.0	14.9±0.5
9-22	42	7.5±0.8	7.2±0.8	9-23	303	34.8±1.4	15.8±0.6
3-23	14	11.4±2.1	6.0±1.1	3-24	290	34.9±1.5	16.6±0.7
14-23	31	14.0±1.8	7.4±0.9	14-24	158	30.4±1.7	14.5±0.8
15-23	30	10.8±1.4	10.3±1.3	15-24	248	44.2±2.0	22.8±1.0
16-23	31	7.7±1.0	6.9±0.9	16-24	150	35.6±2.1	22.8±1.3
17-23	30	6.6±0.9	7.3±0.9	17-24	275	31.2±1.3	18.5±0.8
19-23	14	7.8±1.5	8.2±1.6	19-24	364	35.1±1.3	18.6±0.7
20-23	32	8.4±1.1	9.5±1.2	20-24	273	34.3±1.5	16.8±0.7
23-23	32	9.3±1.2	7.7±1.0	23-24	135	29.0±1.8	14.0±0.9
25-23	16	11.3±2.0	9.9±1.8	25-24	302	37.5±1.5	19.4±0.8
3-24	47	7.6±0.8	8.0±0.8	3-25	157	50.7±2.9	19.4±1.1
9-27	21	8.7±1.4	9.1±1.4	9-28	220	33.2±1.6	16.0±0.8

differing at all widely in fruit shape the coefficient of variability for length is approximately *twice* as large as that for width (table 3); the average value of the former, for the 21 pedigrees listed, being 35.3 percent as compared with 17.6 percent for the latter. This relationship must necessarily follow if there are genes for shape which are independent of those for total volume. The volume of a radially symmetrical structure like the squash fruit is essentially length multiplied by the square of width, where length is the axis of symmetry (polar diameter) and width the diameter at right angles to this (equatorial diameter). Since width thus enters twice into the determination of volume ($v=lw^2$), it is evident that if volume is constant but shape (the ratio of length to width) is varying, a given change in width will produce a change (opposite in sign) in length which is pro-

portionally twice as great. This would cause the variability of length to be twice that of width. Such a difference, which is actually found to exist, is inexplicable on a hypothesis of dimensional factors and provides convincing evidence for the existence of genes governing shape independent of those for volume.

It is noteworthy that in F_2 pedigrees from crosses between lines of essentially the same fruit shape and showing no shape segregation, this difference in variability does not occur, even though the lines differ materially in fruit size.

DISCUSSION

These five groups of facts are mutually consistent in that they all necessarily follow if size and shape are independent in their inheritance. They provide evidence that there is a definite genetic basis for traits of shape and pattern, presumably consisting of a series of "shape" genes which are quite distinct from those which determine amount of growth. It is highly improbable that in this material there is any direct genic control over dimensions. The "size" genes of the orthodox multiple-factor conception apparently govern volume, bulk or weight, but affect dimensions only indirectly, through their interaction with genes determining shape or pattern.

Such a conclusion, if it is found to hold for other organisms, is not without certain important implications. A direct analysis of dimensional traits on the basis of multiple size factors would thus be very complicated where any shape or pattern difference was also involved. In such cases as height of stem in herbaceous plants, where the relation of length to diameter is very variable, a direct control of height by genes may be postulated for convenience; but even in such a loosely organized entity, extension in one dimension is probably not independent of that in others. This conception is especially helpful in the case of more determinate and highly organized structures. The study of such a complex dimensional analysis as that made by SIRKS (1932) of the leaf of *Vicia* leads one to wonder whether the facts could not be explained much more simply by assuming the operation of genes determining shape rather than dimensions. The inheritance of various aspects of bodily conformation in animals also suggests a similar treatment. The discussion over the occurrence and relative influence of general *vs.* local size factors loses much of its significance if we assume that total volume or weight is determined directly by "size" genes but that the manner in which this material is distributed is under the control of genes affecting relative growth rates and thus producing specific bodily shapes or patterns.

The nature and operation of such genes for shape are important biological

problems since they are concerned with one of the most distinctive features of all organisms—the tendency to assume a specific form. Whether they produce their effects by a control of growth localization, cell polarity, or other mechanisms are questions about which almost nothing is known at present. Their influence is evident in very early developmental stages and they clearly control the entire growth plan or schedule through which the organ or body passes in its development. When growth involves marked changes in shape as size increases (as in the development of elongate pepper fruits [SINNOTT and KAISER 1934]), there is obviously a relationship between size and shape, but this is a developmental rather than a genetic one. If gene mutations in size alone occur among organisms having such a type of development, there will be a definite relation between particular sizes and shapes at maturity; but this does not invalidate our conclusion, for it should be remembered that the genetic basis of shape controls the entire developmental plan or pattern (not the mature trait alone) and that this pattern is independent of the particular point along its course where growth happens to stop, this point being determined by genes which affect size differences alone. As ROBB has pointed out (1932), evolution may proceed by changes in size alone (which incidentally involve shape changes when the basic developmental plan is of this type), or by true shape mutations, when the plan itself is changed. In the former case, genes determining size are concerned; in the latter, genes determining shape, and the two seem to be quite distinct in their effects, as has here been maintained.

Genes governing shape evidently control *relative* growth rates. It is clear that a mere control of rates alone, suggestive as such a conception is proving to be in developmental genetics, will not suffice to explain development. Certain basic rates may be determined by what have here been called “size” genes, and thus influence total growth directly. Development, however, involves a series of *correlated* growth rates, and it is this correlation in growth, resulting in specific developmental patterns and finally in specific organic forms, with which the genes for shape, here postulated, are evidently concerned.

SUMMARY

From data on the inheritance of fruit characters in *Cucurbita pepo*, the following lines of evidence are presented which indicate that fruit shape is inherited independently of fruit size and thus presumably is directly determined by genes:

1. A simple, clearly segregating fruit shape difference is inherited independently of fruit weight.

2. There is rarely or never a significant correlation between fruit weight and fruit-shape index in the F_2 .

3. Shape indices segregate much more sharply than do dimensional traits.

4. There is a positive correlation between fruit length and width in pure lines and F_1 progenies, but a negative correlation between these traits in the resulting F_2 progenies.

5. Variability of length is twice as great as that of width in F_2 generations from crosses between lines which differ in fruit shape, although length and width are essentially equal in their variability in both pure lines and F_1 progenies.

The significance of this conclusion for problems of development and evolution is discussed.

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