

GENOTYPE \times ENVIRONMENT INTERACTIONS

IV. THE EFFECT OF THE BACKGROUND GENOTYPE

KENNETH MATHER and P. D. S. CALIGARI

Department of Genetics, University of Birmingham, Birmingham B15 2TT

Received 25.vii.75

SUMMARY

Experimental evidence from sternopleural chaeta number and yield of offspring in *Drosophila melanogaster* bears out the expectation (Mather, 1975) that the value of the regression of g , measuring genotype \times environment interaction, on e , measuring the overall effect of environmental change, depends on genes in which the contrasting genotypes are alike as well as on the genes in which they differ. With yield of offspring there is evidence of some genotypes reacting to the environmental changes in the opposite direction to others.

1. INTRODUCTION

Genotype \times environment interaction is the difference in response of two or more genotypes to a given change, or set of changes, in the environment. It is commonly represented and measured by the quantity g . Where the responses of the genotypes to the environmental change, instead of being differenced to reveal the interaction g , are summed or averaged they give another quantity e which measures the overall effect of the environment as revealed by the set of genotypes treated as a group. In other words e provides a biological measure of the environment and its changes, and it is commonly used as such especially where no simple or convenient means exist of defining the relevant environment and its changes in terms of external measurements such as temperature, humidity and so on.

Now g is frequently related in value to e , a relationship which is often conveniently represented by the regression of g on e (see, for example, Bucio Alanis, 1966; Perkins and Jinks, 1968). Since, however, g depends on differences in response between the genotypes it can reflect the properties of only those genes by which the genotypes differ, whereas e depends on the summed responses of the genotypes taken as a group and will reflect the properties not only of the genes by which the genotypes differ but also of those genes which affect response to the environment but for which all the genotypes are alike (see table 4). As Mather (1975) has therefore noted, the value of the regression coefficient, b , of g on e should be subject to change by alteration of the genetically uniform or background part of the genotypes, as well as by change in the genes by which the genotypes differ. An experiment reported by Caligari and Mather (1975) allows these effects of the background genes to be tested and examined further.

The experiment, for the details of which reference should be made to Caligari and Mather (*loc. cit.*), involved eight true breeding lines of *Drosophila melanogaster*, constructed as the eight possible homozygous combinations of the X, II and III chromosomes, taken as units, from the Wellington and Samarkand inbred stocks. Thus if we denote a Wellington chromosome by W and one from Samarkand by S, and writing the chromosomes in the order

X, II, III the eight lines can be denoted as WWW, WWS, WSW, WSS, SWW, SWS, SSW and SSS, the first and last of them being of course synonymous with the Wellington and Samarkand parent lines respectively. These eight lines were all raised simultaneously in nine environments, which were the nine combinations of three temperatures (18°, 21.5° and 25°C) and three culture container and food regimes (yeasted food in a $\frac{1}{2}$ -pint bottle, yeasted food in a 3" x 1" tube and unyeasted food in a 3" x 1" tube). The experiment was replicated and two characters were followed: number of sternopleural chaetae and yield of offspring. The results averaged over replicates are set out in table 1. The error variance based on the differences between replicates is given at the foot of table 3.

TABLE 1

Chaeta numbers and yields of offspring of the eight genotypes in nine environments

Environments	B			Y			U		
	25°C	21.5°C	18°C	25°C	21.5°C	18°C	25°C	21.5°C	18°C
<i>Genotypes</i>									
<i>Chaeta number</i>									
WWW	16.80	18.50	19.40	17.10	18.28	18.80	16.68	18.28	18.63
WWS	17.50	19.22	19.80	17.32	18.80	19.92	16.53	18.75	18.95
WSW	18.18	19.25	19.57	17.67	18.58	19.12	17.57	18.05	18.05
WSS	19.20	19.52	18.95	19.15	19.05	18.88	18.33	18.50	18.88
SWW	17.27	19.10	18.85	17.30	18.65	19.20	16.60	18.20	18.93
SWS	20.08	21.37	21.25	20.48	21.00	21.95	19.75	20.33	21.10
SSW	16.85	18.48	17.37	16.93	17.15	17.40	16.38	17.40	16.95
SSS	20.30	20.23	19.90	20.15	19.42	19.85	19.97	19.50	19.55
<i>Yield of offspring</i>									
WWW	327.5	495.0	300.5	136.5	161.5	138.0	105.0	52.0	43.5
WWS	276.5	356.0	121.5	119.0	194.5	107.5	84.5	49.0	30.5
WSW	80.0	57.0	89.5	56.0	63.0	65.5	29.0	34.5	35.5
WSS	117.0	127.5	94.5	75.0	91.0	70.0	71.0	31.5	24.0
SWW	391.5	385.5	153.5	116.0	183.0	80.0	55.0	63.0	46.5
SWS	130.0	119.0	180.5	127.5	97.5	106.0	66.5	43.0	48.5
SSW	198.5	253.0	111.5	47.5	84.0	105.0	19.5	111.0	30.5
SSS	190.0	153.5	47.5	131.5	150.5	37.5	25.5	29.0	11.5

B = $\frac{1}{2}$ pint bottles with yeasted medium. Y and U = 3" tubes with yeasted and unyeasted medium respectively.

With such a set of lines the genotype \times environment interactions associated with one pair of homologous chromosomes can be investigated against different backgrounds in respect of the other two. Thus, for example, we can examine the interactions with the environment of the genetic difference between the two X chromosomes by comparing the expressions of the characters of a pair of lines which differ in their X's but are alike in respect of chromosomes II and III. The eight lines yield four such comparisons: WWW *vs* SWW; WWS *vs* SWS; WSW *vs* SSW and WSS *vs* SSS. The subsequent analysis of the results yielded by these four different comparisons of the effects of the X chromosome differences over environments will reveal the effects of the changes in background genotype on the genotype \times environment interactions associated with the X chromosome.

2. HETEROGENEITY OF REGRESSIONS

The pairs of lines have been subjected to the two-line analysis of Bucio Alanis (1966), the regression of g (which depends solely on the chromosome in which the members of the pair differ) on e (which must also reflect the sensitivity to environmental change of the relevant genes in the other

TABLE 2a

Regressions of g on e for the three chromosomes, each on four backgrounds, in respect of chaeta number

Difference	Background	S.S. Sums	S.C.P.	S.S. Diffs.	b
X (W-S)	-WW	57.220	0.888	1.965	0.0155
	-WS	53.209	13.857	6.056	0.2604
	-SW	23.223	2.920	4.048	0.1257
	-SS	5.570	0.415	1.970	0.0745
II (W-S)	W-W	41.428	6.963	5.607	0.1681
	W-S	27.624	19.652	20.052	0.7114
	S-W	32.292	8.995	7.129	0.2786
	S-S	8.253	6.210	10.878	0.7525
III (W-S)	WW-	72.278	-6.505	1.693	-0.0900
	WS-	14.190	6.158	6.550	0.4359
	SW-	41.869	6.465	2.611	0.1544
	SS-	7.705	3.680	6.365	0.4776

TABLE 2b

Regressions of g on e for the three chromosomes, each on four backgrounds, in respect of yield of offspring

Difference	Background	S.S. Sums (in units of 1000)	S.C.P.	S.S. Diffs.	b
X (W-S)	-WW	613.56	31.54	35.68	0.0514
	-WS	144.93	77.23	71.63	0.5329
	-SW	63.07	-43.86	38.43	-0.6954
	-SS	77.41	-28.28	17.61	-0.3654
II (W-S)	W-W	211.20	174.64	151.86	0.8269
	W-S	156.93	83.14	47.81	0.5298
	S-W	341.48	99.23	46.21	0.2906
	S-S	75.84	-22.37	31.00	-0.2950
III (W-S)	WW-	504.20	85.33	37.48	0.1692
	WS-	20.76	-6.17	5.36	-0.2971
	SW-	209.62	131.01	114.50	0.6250
	SS-	136.94	9.41	33.46	0.0687

chromosomes) being found as the regression of the differences between the two lines in the nine environments on the corresponding sums of the two lines. The relevant data are given in table 2a in respect of chaeta number and in table 2b in respect of yield of offspring. The table shows the chromosome in which the two lines under comparison differed, the background chromosomes in which they were alike, the sum of squares (S.S.) of their sums, the S.S. of their differences, the sum of cross products (S.C.P.) of sum and difference and the regression of g on e (b), found of course as the ratio of S.C.P. to S.S. of sums.

The four regressions found for each chromosome difference have been compared by partitioning, in the usual way, the S.S. of differences into an

item for their joint regression (1 degree of freedom), an item for heterogeneity of regressions (3 d.f.) and one for the pooled departures from linearity of the four individual regressions ($7 \times 4 = 28$ d.f.). This analysis for each of the two characters is set out in table 3, together with the replicate error variances for the two characters. The first thing to note is that only in the case of the g/e regression for chromosome II in respect of chaeta number is

TABLE 3

Analyses of variance for the regression of g on e for the three chromosomes. The item for heterogeneity represents the effect of varying the background

Chromosome	Item	d.f.	Chaeta number		Yield of offspring	
			M.S.	P	M.S. (in units of 1000)	P
X	Joint reg.	1	2.348	0.02-0.01	1.49	n.s.
	Heterogeneity	3	0.558	n.s.	27.37	<0.001
	Remainder	28	0.358	n.s.	2.85	n.s.
II	Joint reg.	1	15.958	<0.001	142.57	<0.001
	Heterogeneity	3	2.124	0.05-0.02	27.10	<0.001
	Remainder	28	0.762	≈ 0.001	1.89	n.s.
III	Joint reg.	1	0.709	n.s.	55.32	<0.001
	Heterogeneity	3	1.776	0.01-0.001	14.49	≈ 0.02
	Remainder	28	0.399	n.s.	3.29	n.s.
	Replicate error	72	0.3835		4.491	

there any indication of significant residual variation round the regression lines. The replicate error variance can thus be used to test the heterogeneity of the regressions in all cases except perhaps that of chromosome II for chaeta number. In all three chromosomes in respect of yield of offspring the four regressions are heterogeneous: in other words the regressions clearly change with alteration of the background genotype. They are not demonstrably different for the X chromosome in respect of chaeta number, but they clearly differ for chromosome III and even when we use the remainder mean square as the estimate of error variance there is evidence of differences among the four regression lines for chromosome II. Clearly, as expected, the background genotype can and does affect the value obtained for the regression of g on e .

3. RELATION OF REGRESSIONS TO BACKGROUND GENOTYPE

The situation can be explored further. Table 4 sets out the phenotypic expressions in two environments of two lines differing in their X chromosomes, but with a uniform background B. The formulation is that used by Mather (1975), where d is the overall genetic difference between the X's, e_{xw} the measure of the change in expression of the Wellington X between the two environments, e_{x8} that of the Samarkand X, and e_B that of the background genotype. The contributions of e_{xw} , e_{x8} and e_B to the S.S. of sums, S.S. of differences, and S.C.P. are shown and the change in constitution of e_B with alteration of the background genotype is given at the bottom of the table. Now no matter what the background may be, the S.S. of differences (which depends on g) is constant but the S.S. for sums and the S.C.P. vary with e_B , as does of course the value of b , the regression of g on e . Thus the

TABLE 4
The effect of background on the expectations for *g* and *e*

Genotype	Environments			Mean
	1	2		
X_wB	$d_x - e_{xw} - e_B$	$d_x + e_{xw} + e_B$		d_x
X_sB	$-d_x - e_{xs} - e_B$	$-d_x + e_{xs} + e_B$		$-d_x$
Sum	$-(e_{xw} + e_{xs} + 2e_B)$	$(e_{xw} + e_{xs} + 2e_B)$		0
Difference	$2d_x - (e_{xw} - e_{xs})$	$2d_x + (e_{xw} - e_{xs})$		$2d_x$
S.S. Sum	$(e_{xw} + e_{xs} + 2e_B)^2$			
S.S. Diff.	$(e_{xw} - e_{xs})^2$			
S.C.P.	$(e_{xw} - e_{xs})(e_{xw} + e_{xs} + 2e_B)$			
<i>b</i>	$(e_{xw} - e_{xs}) / (e_{xw} + e_{xs} + 2e_B)$			
Background	-WW	-WS	-SW	-SS
e_B	$(e_{2w} + e_{3w})$	$(e_{2s} + e_{3s})$	$(e_{2s} + e_{3w})$	$(e_{2s} + e_{3s})$

In the subscripts 2 and 3 signify chromosomes II and III respectively. Thus e_{2w} is the *e* for chromosome II from Wellington.

variances of the differences should be homogeneous over the four backgrounds, but the variances of the sums should not. These variances have been subjected to Bartlett's test and the χ^2 's, each of which will have 3 d.f., are given in table 5 for the variances of sums and differences in relation to each chromosome for each character. For chaeta number the answers are clear: with all three chromosomes the variances of differences are homogeneous as

TABLE 5
The expression of varying the backgrounds on *e* (measured by the sum) and *g* (measured by the difference)

Chromosome		Chaeta number		Yield of offspring	
		Homogeneity of variances of sums	Homogeneity of variances of diffs.	Homogeneity of variances of sums	Homogeneity of variances of diffs.
X	$\chi^2_{[3]}$	10.00	3.57	13.47	3.61
	P	0.02-0.01	n.s.	0.01-0.001	n.s.
II	$\chi^2_{[3]}$	4.67	3.71	4.18	6.02
	P	n.s.	n.s.	n.s.	n.s.
III	$\chi^2_{[3]}$	10.62	4.73	15.32	14.49
	P	0.02-0.01	n.s.	0.01-0.001	0.01-0.001

expected, and in two cases the variances of sums are heterogeneous. The results thus accord quite well with expectation. The results are less clear with yield of offspring. Again in two of the three cases the variances of sums are heterogeneous as expected; but the variances of differences show a significant heterogeneity in one case (chromosome III) which clearly indicates some departure from simple expectation. It is in fact due particularly to the low S.S. of differences on the WS-background (table 2b) and one must suppose that this is due to some interaction between the genes of this background with those by which the IIIrd chromosomes differ. Such an interaction would perhaps not be surprising with a "fitness" character like yield of offspring. The data do not, however, allow us to test this point further.

If the background genotype as a whole is reacting to the environmental change in the same direction as the genes of the chromosome which is differing, e_B will have the same sign as $e_{xw} + e_{xs}$, to take the example set out in table 3. But if the background genotype is reacting in the opposite direction, *i.e.* reacting by a decrease in expression to a change which results in increased expression of the genes in the difference chromosome, e_B will be

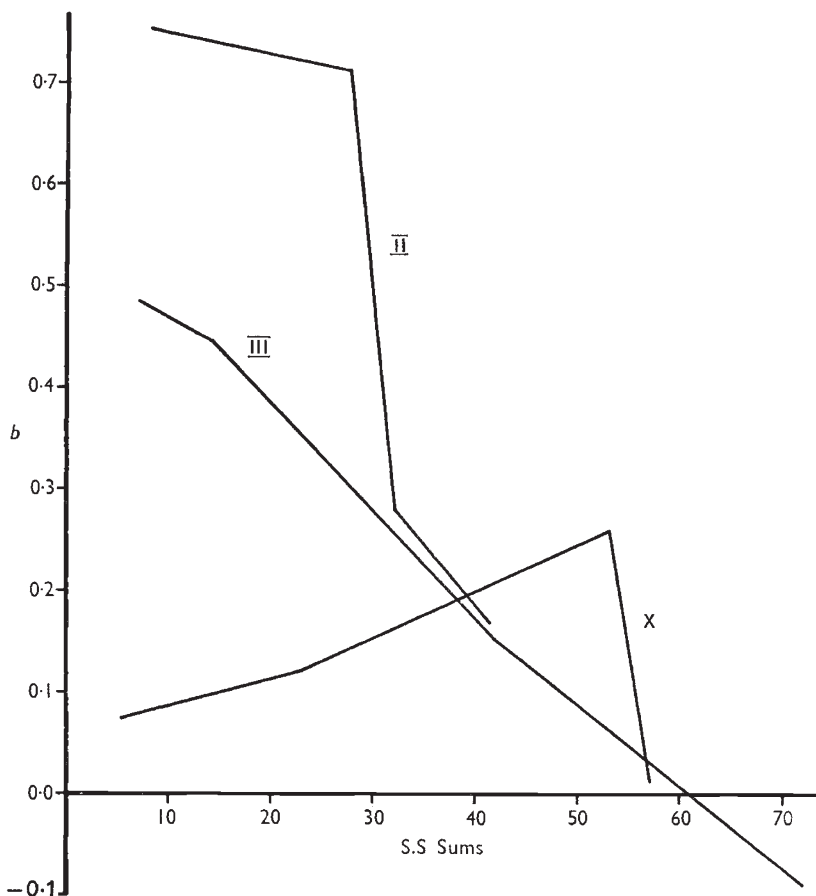


FIG. 1a.—The relation of b to variation in e , measured by the S.S. of sums, in respect of chaeta number. Data from table 1a.

of the opposite sign to $e_{xw} + e_{xs}$. Where e_B is of the same sign as $e_{xw} + e_{xs}$, the S.S. of sums will increase as e_B increases, but b will decrease since $(e_{xw} + e_{xs} + 2e_B)$ appears in its denominator. There will then be a negative correlation between S.S. sums and b and this is the pattern shown by chromosomes II and III for chaeta number (fig. 1a). b should not of course fall below zero, and the single small negative value for chromosome III can reasonably be attributed to sampling variation. The X chromosome fails to show this pattern, but as we have seen from table 3, there is no evidence of heterogeneity of the regressions for this chromosome in respect of chaeta number and no meaningful pattern can thus be expected. It should be noted

that if the difference between the lines had been taken the other way round, *i.e.* S-W, then, of course, the estimates of b would be identical in value but of opposite sign to those given, and consequently the relation between b and S.S. sums would be an exact mirror image.

Turning to yield of offspring (fig. 1b) we see in all three chromosomes this same fall of b with rise in S.S. sums, where the S.S. exceeds some 150-200;

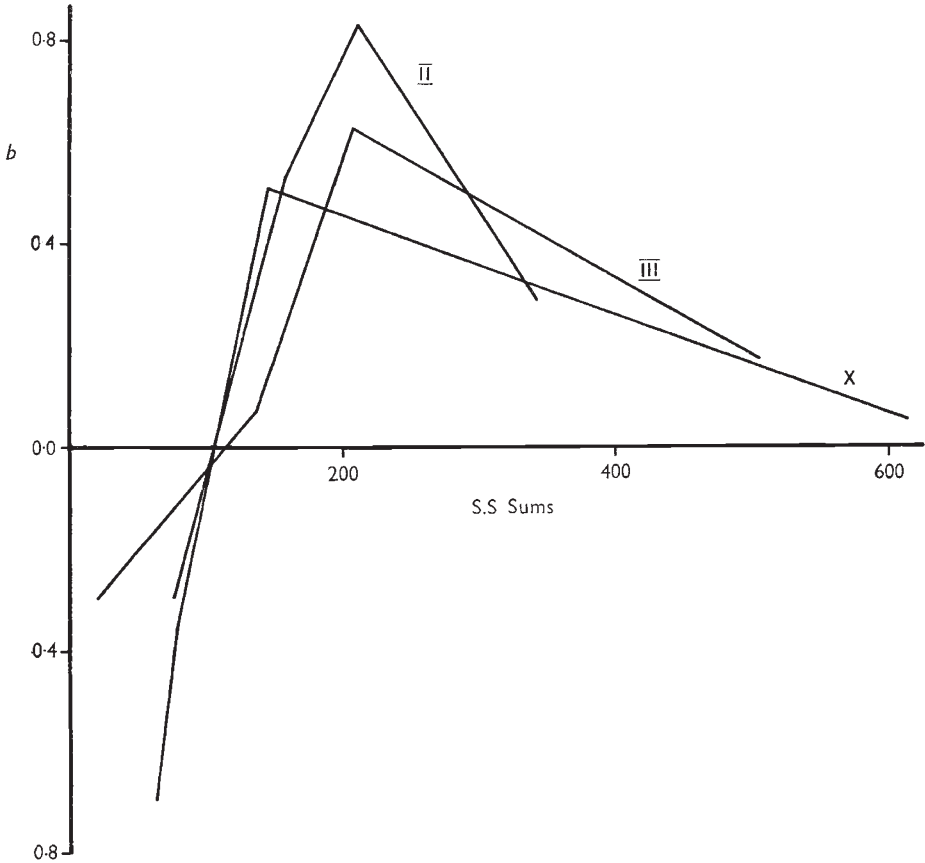


FIG. 1b.—The relation of b to variation in e , measured by the S.S. of sums, in respect of yield of offspring. Data from table 1b.

but below this value b falls sharply as the S.S. falls and indeed becomes negative. Such a pattern is to be expected where e_B is positive for some backgrounds, but negative for others. In the simple case of a single environmental difference set out in table 4, b will become negative when $e_{xw} + e_{xs} + 2e_B$ is less than 0, though of course S.S. sums, being quadratic, will still be positive albeit generally fairly small. With eight environmental comparisons, which there are of course between the nine environments, each of the S.S.'s and the S.C.P. will be the sum of eight terms of the kind set out in the table, and the S.S. will include also a non-heritable component. Since the relations of $e_{xw} + e_{xs}$ and e_B need not be the same for all comparisons (though the lack of residual variation round the regressions, as seen in table 3, suggests that they are broadly alike, even if not the same in detail) the detailed relations of

b to S.S. sums cannot be easily predicted. In broad outline, however, we expect just the features seen in fig. 1b: b falling gradually as S.S. sums increases above the turning point, but with it falling sharply to negative values as S.S. sums decreases below the turning-point. The turning-point value of S.S. sums will come where on average over all the environmental comparisons e_B is zero, *i.e.* where the S.S. sums reflects only the value of $e_{zw} + e_{zs}$.

4. CONCLUSION

Thus not only does this experiment confirm the expectation that the value of b , the regression of g on e , depends on the background genotype: the more detailed effects of alterations in the background genotype are as expected. The only anomaly is the heterogeneity of the S.S. of differences for chromosome III in respect of yield of offspring, and this is reasonably attributable to the genic interaction which is a common enough feature with "fitness" characters. Furthermore, we can see that in respect of yield of offspring, some background genotypes must be reacting to the environmental changes in the opposite direction to the others.

Acknowledgments.—We are indebted to the Agricultural Research Council and the Leverhulme Trust for financial assistance.

5. REFERENCES

- BUCIO ALANIS, L. 1966. Environmental and genotype-environmental components of variability. I. Inbred lines. *Heredity*, 21, 387-397.
- CALIGARI, P. D. S., AND MATHER, K. 1975. Genotype \times environment interactions. III. Interactions in *Drosophila melanogaster*. *Proc. Roy. Soc. B.* 191, 387-411.
- MATHER, K. 1975. Genotype \times environment interactions. II. Some genetical considerations. *Heredity*, 35, 31-53.
- PERKINS, J., AND JINKS, J. L. 1968. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. *Heredity*, 23, 339-356.