THE GENOTYPIC CONTROL OF LONGEVITY IN *DROSOPHILA MELANOGASTER* UNDER TWO ENVIRONMENTAL REGIMES

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Summary

Longevity in four inbred strains and their hybrids has been studied at two temperatures, 29·5 and 25°C. Heterosis was found at both temperatures but was more extreme at 29·5°C, which is a very unfavourable environment for *D. melanogaster*. This observation has its parallel in observations on various fitness factors in several organisms. At 29·5°C there was more variability of a genotypic nature between the hybrids than at 25°C, perhaps because the adaptation to this unfavourable environment depends on rather special gene combinations. Thus longevity varies between genotypes, but the pattern of variation depends in an intimate way on the environment.

I. Introduction

There is a great deal of information on longevity of different species, but rather limited data on genotypically controlled variations within species. In man a genetic component in longevity seems correct, but the evidence is confused by all kinds of environmental influences. Experimental animals are much more suitable for investigations on the genetic control of longevity; thus Grüneberg (1952) has given different survivorship curves for three inbred strains of mice. Variations between strains have also been found in other organisms, in particular certain species of *Drosophila*. Crossing inbred strains often leads to hybrids with greater longevity, i.e. they show hybrid vigour or heterosis (Clarke and Maynard Smith 1955; Comfort 1964).

To look in further detail into the possibility of longevity being controlled genotypically, the longevity of four inbred strains of *D. melanogaster* and their 12 possible hybrids will be discussed in this paper. The data can thus be arranged as a 4×4 diallel cross. Such an experimental design permits an assessment of the possibility of hybrid vigour, and based on hybrids themselves it is possible to gain an idea of the components of variance (additive, dominance, and environmental) controlling longevity using the methods of analysis of diallel crosses presented by Griffing (1956).

The experiment was carried out at 25 and 29·5°C, the latter temperature being a very extreme environment for *D. melanogaster*, so as to look for possible differences between temperatures.

II. Method

Two replicates of 25 virgin females and males separately were set up on the same day at each temperature in vials for each of the inbred strains and hybrids. A standard treacle–semolina medium was used. Twice a week the flies were transferred to fresh medium, at which stage the number of dead flies was scored. Scoring was continued until all the flies had died.

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III. Results

A preliminary assessment was made by taking the number of days on which 50% of the flies had died. In Table 1 the means of the F_1's (and their reciprocals) between the six possible pairs of inbred strains are given, with the means of the corresponding parental pairs for each sex and temperature separately.

Table 1

MEAN NUMBER OF DAYS AT WHICH 50% OF THE FLIES HAD DIED WITH A MEASURE OF HETEROSIS

	Temperature 25°C			Temperature 29·5°C		
Lines	$\bar{F}_1$	$\bar{P}$	Heterosis Measure*	$\bar{F}_1$	$\bar{P}$	Heterosis Measure*
			Females			
N_1,N_2	43·875	35·5	0·106	26·25	16·875	0·217
N_1,Y_1	40·5	30·875	0·135	24·5	16	0·210
N_1,Y_2	41·375	33·875	0·100	26	16·875	0·213
N_2,Y_1	45·25	32·625	0·162	26	16·875	0·213
N_2,Y_2	39·875	35·625	0·056	29	17·75	0·241
Y_1,Y_2	42·875	31	0·161	31	16·875	0·295
Means	42·292	33·25	0·120	27·125	16·875	0·233
			Males			
N_1,N_2	47.875	51·375	−0·035	24·25	15·875	0·209
N_1,Y_1	44·625	38·625	0·072	22·5	12·25	0·295
N_1,Y_2	47·25	48·125	−0·009	21	15	0·167
N_2,Y_1	52·25	41·25	0·118	27	14·125	0·313
N_2,Y_2	55·75	50·75	0·047	19·25	16·875	0·066
Y_1,Y_2	68	38	0·283	29·125	13·25	0·375
Means	52·625	44·688	0·082	23·854	14·563	0·242

* Measured by the ratio $(\bar{F}_1-\bar{P})/(\bar{F}_1+\bar{P})$.

At 29·5°C longevity is reduced greatly compared with that at 25°C as would be expected, since the flies would be under much more stress at this temperature than at 25°C (Comfort 1964). The percentage reduction in longevity at 29·5°C compared with 25°C is greater in males than in females, thus at 25°C males tend to live longer than females but at 29·5°C the reverse occurs. In general, in other studies on a variety of organisms the male sex is the shorter-lived (Comfort 1964), but many exceptions occur. The exact pattern may depend on the genes present (Maynard Smith 1959) or perhaps on a complex interaction between genotype and environment as the present results would indicate.

The possibility of heterosis is usually assessed by taking the mean value of the F_1's, $\bar{F}_1$, minus the mean of the two corresponding parents, $\bar{P}$. This was computed and was positive except for the $N_1 \times N_2$ and $N_1 \times Y_2$ crosses at 25°C for males, so indicating fairly general heterosis. This crude measure is, however, hardly appropriate when comparing temperatures because of the enormous differences in mean

longevity between temperatures. As a correction factor, this crude measure was divided by the sum of the F_1 and parental means ($\bar{F}_1+\bar{P}$) in a manner analogous to the method of assessing asymmetry between the left and right hand sides of flies for sternopleural chaeta number (Thoday 1955). Thus the ratio $[(\bar{F}_1-\bar{P})/(\bar{F}_1+\bar{P})]$ provides a measure of heterosis relative to the longevity of the constituent genotypes. Based on this measure it is clear that in all cases, heterosis is much more extreme at 29·5°C than at 25°C. The values for each sex show heterosis to be two to three times as great at 29·5°C as at 25°C.

An analysis of variance among the F_1's was then carried out using the methods of Griffing (1956) for each sex and temperature separately, to gain an idea of the components of variance controlling longevity. The analysis tests the significance of the general combining ability which provides an estimate of the additive genetic variance, the specific combining ability which provides an estimate of the dominance variance,

TABLE 2

F VALUES FROM COMBINING ABILITY ANALYSIS

Analysis	Degrees of Freedom	*F* Values at 25°C		*F* Values at 29·5°C	
		Females	Males	Females	Males
General combining ability (g.c.a.)†	3	0·09	3·33	15·22***	11·62***
Specific combining ability (s.c.a.)†	2	1·62	1·53	1·90	21·71***
Reciprocals†	6	1·74	0·98	8·09**	3·30*
Mean square (g.c.a.) / Mean square (s.c.a.)		0·06	2·18	1·56	0·54
No. dead (%)		27·5	31·5	28·6	31·7

* $P<0·05$. ** $P<0·01$. *** $P<0·001$.

† *F* values are based on the error mean square (12 d.f.).

and reciprocal differences. There are two ways of arranging the data. One is by taking a percentage death rate for the total data for each sex and temperature separately on a given day, and use the percentages for each hybrid on that day as the basis for an analysis of variance. Before carrying out the analysis the angular transformation (Fisher 1949) must be applied to the percentages so that their variances become independent of their means. The *F* values from such an analysis are given in Table 2 where the percentage deaths for each sex and temperature are close to 30%. At 25°C there are no significant effects, but at 29·5°C, relative to the error mean square, the general combining ability component is significant in both sexes, specific combining ability is significant in males only, and the reciprocal effects component is significant in both sexes. A strict test for general combining ability is the ratio of the mean squares for general and specific combining abilities, which in neither case was significant. Even so, the data show that there are more differences between genotypes at 29·5°C than at 25°C. Repeating the analysis for other percentage death rates confirmed this pattern of results in general, although when more than half the flies

had died, rather small but significant combining abilities tended to appear at 25°C. The second method of arranging the data is as in Table 1, where the number of days on which 50% of the flies had died is taken as the basic observation. Carrying out an analysis of variance on these data gave a similar picture to that given above. However, the error variances were extremely variable so the analysis is not presented here.

IV. Discussion

Heterosis is well-known for hybrids between inbred lines for many traits, and has been found in previous work on longevity (Clarke and Maynard Smith 1955). The extreme heterosis at 29·5°C, which is very near to the limit of tolerance for *D. melanogaster*, has its parallel in observations on various fitness factors in several organisms, for example larval survival in *D. melanogaster* (Parsons 1959), relative viability and mating speed in *D. pseudoobscura* (Dobzhansky *et al.* 1955; Parsons and Kaul 1966), and growth rates in *Arabidopsis thaliana* (Langridge 1962), and maize (McWilliam and Griffing 1965). In general it is perhaps true to say that the more severe the physical environment, the greater the level of heterosis developed.

The other feature of interest, on which work needs to be done, is the observation that there is more genotypic variability at 29·5°C than at the more optimal temperature of 25°C. This is perhaps reasonable, since under an extreme environment somewhat special gene combinations will be needed to adapt to it. It also emphasizes that the potentiality of a genotype must be assessed strictly in terms of the environments to which it has been exposed. We conclude then that there is a genotypic component in longevity in *D. melanogaster*, but that there may be large differences according to the exact environment.

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