Genet. Res., Camb. (1973), **22**, *pp.* 69–78
With 4 text-figures
Printed in Great Britain

Genetic differences between populations of *Drosophila melanogaster* for a quantitative trait

II. Wild and laboratory populations

By C. LÓPEZ-FANJUL† and W. G. HILL
Institute of Animal Genetics, Edinburgh EH9 3JN

(*Received* 18 *January* 1973)

SUMMARY

Crosses were made between four populations of *Drosophila melanogaster* – three of which were laboratory populations (Kaduna, Pacific and Canberra) and one recently captured (Stellenbosch) – and a line previously selected for low sternopleural bristle number for many generations from a Kaduna/Pacific source. In each of six replicate lines from each cross selection was practised for low sternopleural bristle number, and subsequently these replicates were intercrossed and reselected.

Initially, similar responses were made in each set of lines, but subsequently more variation between replicates was found in Stellenbosch, which was the primary source of lines which responded to a level below that of the original selected line.

It is concluded that this newly captured population contains genetic variability absent from the laboratory populations. Presumably variability has been lost from the latter populations, leaving essentially the same genes segregating in each.

1. INTRODUCTION

In the preceding paper we compared the rates and limits of response to selection in two laboratory populations of *Drosophila melanogaster*, and in synthetic populations formed from crosses between them (López-Fanjul & Hill, 1973). We concluded that the two populations (Kaduna and Pacific) were segregating for essentially the same alleles for the trait studied – sternopleural bristle number. Three possible explanations could be offered: either they were very similar when captured from different parts of the world many generations prior to the start of the experiment, or they became adapted to the same laboratory environment, or they had become contaminated with each other. The experiment described in this paper was designed to give some information on these alternatives.

Two further populations were used: a long-established cage population (Canberra) from a different laboratory, and a population (Stellenbosch) recently caught from the wild. These populations, together with our two original populations, were each crossed to a highly selected line from the first experiment, and selection con-

† Supported by Ministerio de Educación y Ciencia, Spain. Present address: Dept. Genética, I.N.I.A., Avda. de Puerta de Hierro, Madrid 3, Spain.

tinued from the cross. In this way it was possible to test whether new variation could be introduced into the selected line from the different populations, and a greater limit achieved. The experiment was similar to that conducted by Osman & Robertson (1968) except that they used only a single base population. Here, if Canberra or Stellenbosch contain favourable genes not present in either Kaduna or Pacific, we would expect the limit to be higher after selection of crosses to the new populations than to the two which formed the base of the highly selected line.

2. MATERIAL AND METHODS

The Canberra population was originally caught in Australia, and has been maintained in a cage for many years (Latter, 1964). In October 1970 a sample of about 100 flies of each sex was obtained from Dr J. S. F. Barker and used to establish a cage in this laboratory. The Stellenbosch population was caught in South Africa in early 1969, the initial sample comprising about 100 inseminated females, and a cage was established and maintained at 25 °C (J. H. Louw, personal communication). In November 1970 a sample of about 100 pairs was obtained from Dr J. H. Louw and used to establish a cage in this laboratory. The cages of Canberra and Stellenbosch in Edinburgh were maintained in the same way as the Kaduna and Pacific cages at 25 °C.

Table 1. *Plan of experiment, line designation and numbers of each sex scored and selected*

Generation	Population: Kaduna		Pacific		Canberra		Stellenbosch		
0	BK_1	BK_4	BP_1	BP_4	BC_1	BC_4	BSt_1	BSt_4	Initial lines (5/25)
	BK_2	BK_5	BP_2	BP_5	BC_2	BC_5	BSt_2	BSt_5	
	BK_3	BK_6	BP_3	BP_6	BC_3	BC_6	BSt_3	BSt_6	
7	BK_1^3	BK_2^3	BP_1^3	BP_2^3	BC_1^3	BC_2^3	BSt_1^3	BSt_2^3	Three-way crosses
11	BK^6		BP^6		BC^6		BSt^6		Final crosses (15/75)

The selected line, B, was denoted KP^6 in the previous experiment (López-Fanjul & Hill, 1973). It was established from a cross of three Kaduna and three Pacific lines which had been selected for ten generations for low bristle number with intensity 5/25 of each sex. After crossing, the line was selected for 21 generations with intensity 30/150, and with intensity 15/75 of each sex subsequently. Generation 0 of B in this experiment corresponds to generation 21 of selection in KP^6 (or 31 generations including selection in the parental replicates).

In March 1971 samples of eggs were collected from each of the four population cages, and reciprocal crosses made between the emerging flies from each and line B, using 150 flies of each sex as parents. The F_1 reciprocals of each cross were mixed, and selection started from the F_2 synthetics. The experimental design and

line designation are shown in Table 1. Selection was practised in six replicate lines of each of the four synthetics, and in each line five individuals of each sex were selected for low score on the two sternopleural plates from the 25 of each sex recorded. Selection was continued for seven generations when two three-way crosses (denoted by a superscript 3) were made between randomly chosen lines of each synthetic, and the cross lines selected for a further four generations with intensity 15/75. These two three-way crosses were themselves crossed at generation 11 and the new lines, based on all six original replicates (denoted superscript 6), were further selected with intensity 15/75. In the synthetics BK, BP and BC (of Kaduna, Pacific and Canberra, respectively) the six original lines were discarded after crossing, while selection was continued in these lines of BSt (Stellenbosch).

All flies were cultured in half-pint milk bottles at 25 °C, except in generations 4 and 15 which were reared at 18 °C.

3. RESULTS

(i) *Line B*

The selection response in the early generations of line B is given as line KP^6 in Fig. 5 of López-Fanjul & Hill (1973). It appeared to have reached a plateau when this experiment started (generation 21 of KP^6), but then showed a small but consistent response for most of this experiment. At generation 0 of this experiment its

Table 2. *The effect of relaxed and reversed selection in line B*

Generation when selection relaxed/ reversed†	Generations ...	Change in bristle score 5	10	13
		Relaxed selection		
10		0·96	1·36	—
15		1·13	1·37	—
20		0·99	1·07	—
25		0·80	1·22	—
32		1·34	1·66	—
		Reversed selection		
21		—	—	3·73

† Generation number of first experiment, generation 21 is generation 0 of the experiment on line B.

mean, about nine bristles, was more than eight bristles below the mean of the unselected Kaduna and Pacific populations. It subsequently responded another two bristles. However, the plateaux in the line were not stable. The mean increased by over a bristle if selection was relaxed, most of this occurring in five generations (Table 2). With reversed selection started at the same generation as this experiment, a more rapid increase resulted, reaching over three bristles before contamination from a marker stock was noted (Table 2).

(ii) *Base populations*

Estimates of the mean, variance and heritability, obtained by regression of offspring on mid-parent are given for each population in Table 3. Assortative mating (Reeve, 1961) of parents was practised in each case, together with selection of parents in Canberra (Hill, 1970). The estimates for Kaduna and Pacific are taken from López-Fanjul & Hill (1973). The means range from 18·1 to 19·4 bristles, the variance from 3·0 to 4·4. The estimates of variance and heritability in Canberra

Table 3. *Parameters of base populations*

Population	No. scored	Mean	Variance	Heritability ± S.E.†
Kaduna	200	18·07	3·69	0·39 ± 0·05
Pacific	200	18·29	4·04	0·40 ± 0·07
Canberra	250	19·41	3·02	0·16 ± 0·05
Stellenbosch	250	18·74	4·37	0·58 ± 0·12

† Based on about 500 progeny scored.

Table 4. *Parameters of the synthetic populations* (300 *scored each generation*)

		Type of line							
		Single replicates (mean)				Six-line crosses			
	Population ...	BK	BP	BC	BSt	BK[6]	BP[6]	BC[6]	BSt[6]
Generation									
0/1†	Mean	13·63	13·54	13·97	13·46	8·77	8·37	8·63	6·55
0	Deviation from mid-parent	0·06	−0·14	−0·27*	−0·44**	—	—	—	—
7/8‡	Mean	8·96	9·06	9·33	8·35	8·01	5·49	8·07	5·09
0/1	Variance	4·45	4·76	3·80	5·33	1·63	1·59	1·06	3·32
7/8	Variance	1·72	1·57	1·71	2·39	2·37	0·88	1·74	2·80
0/1	Coefficient of variation %	15·4	16·1	13·9	17·0	14·6	15·1	11·9	27·8
7/8	Coefficient of variation %	14·6	13·6	13·7	18·3	19·2	17·0	16·3	32·8
0–3	Realized heritability	0·51	0·56	0·57	0·51	—	—	—	—

* $P < 0·05$, ** $P < 0·01$ (deviation from mid-parent).

† (‡) Generation 0 (7) for single replicates, 1 (8) for six-line crosses, this latter equivalent to generations 12 (19) from the outset.

were lower than in the other populations. Heritability estimates have been made for the Canberra population previously. Latter (1964) obtained a realized heritability estimate of 0·40 from divergent selection. Sheridan *et al.* (1968) estimated heritability on a single plate (h_1^2). From their estimates and the phenotypic correlation between plates (r_p) given by Latter (1964), we have computed the heritability on two plates as $h_2^2 = 2h_1^2/(1+r_p)$. The estimates of h_2^2 from Sheridan *et al.* range from 0·25 to 0·35 – all of them higher than we obtained for Canberra, but still less than or equal to the estimates in our other populations (Table 3).

(iii) *Selected replicate lines*

The initial parameters of the crosses of the populations to line B are shown in Table 4. The Canberra and Stellenbosch crosses were slightly below mid-parent value. The patterns of response to selection in the initial small replicates and in the subsequent three-way and higher crosses are shown in Figs. 1–4. The responses

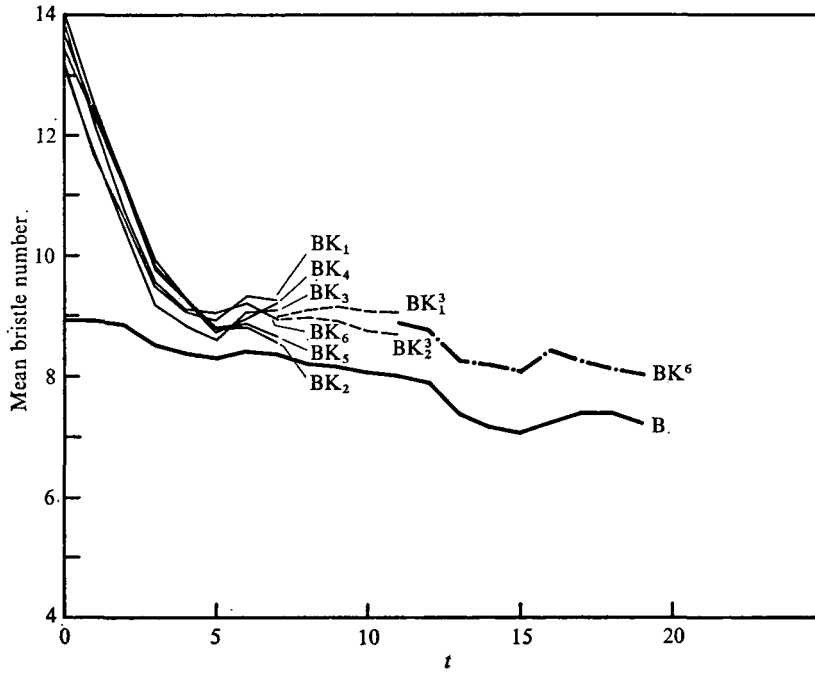

Fig. 1. Three-generation moving average scores for the BK replicates and their crosses.

in the first few generations were approximately the same for each set of replicates, as are the realized heritabilities (Table 4). The realized heritabilities were not found to differ significantly and were therefore pooled over replicates. Their standard errors were corrected for drift (Hill, 1972). However, by generation 5 there was more variation between the replicates of BC and BSt than between those of BK and BP, but the only small line to surpass line B substantially was a Stellenbosch line, BSt_6; two other BSt lines just passed B. Of the three-way crosses only those based on Stellenbosch exceeded line B, and of the final cross of these three-way cross lines, that of Stellenbosch (from its outset) and that of Pacific passed line B. The final means achieved in BSt^6 and BP^6 were almost two bristles below the level in B.

Overall fitness deteriorated in some of the initial BSt lines, two of which (BSt_3 and BSt_4) died out before the end of the experiment. No obvious reduction in fitness was observed in the initial replicates of the other synthetics, but line BP^6 became difficult to maintain after its period of rapid response.

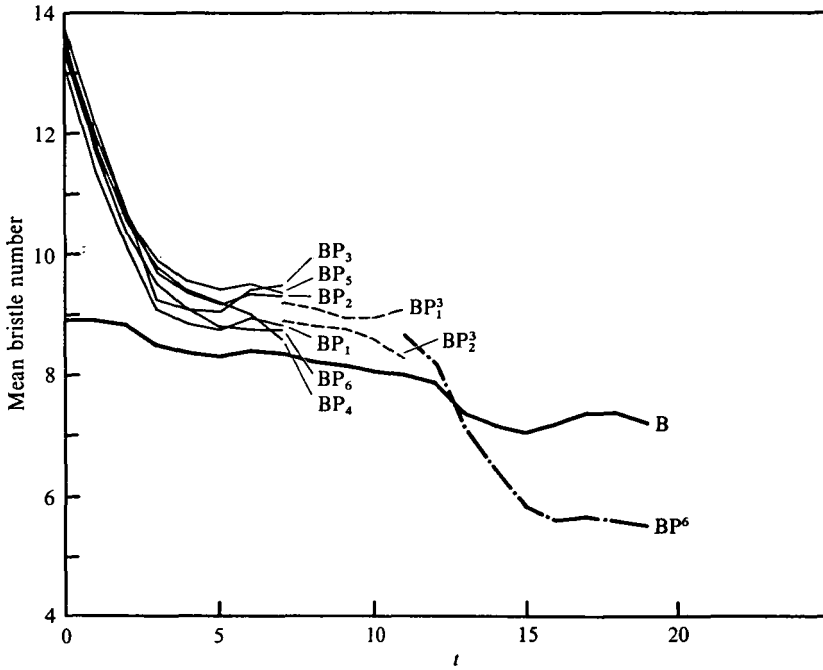

Fig. 2. Three-generation moving average scores for the BP replicates and their crosses.

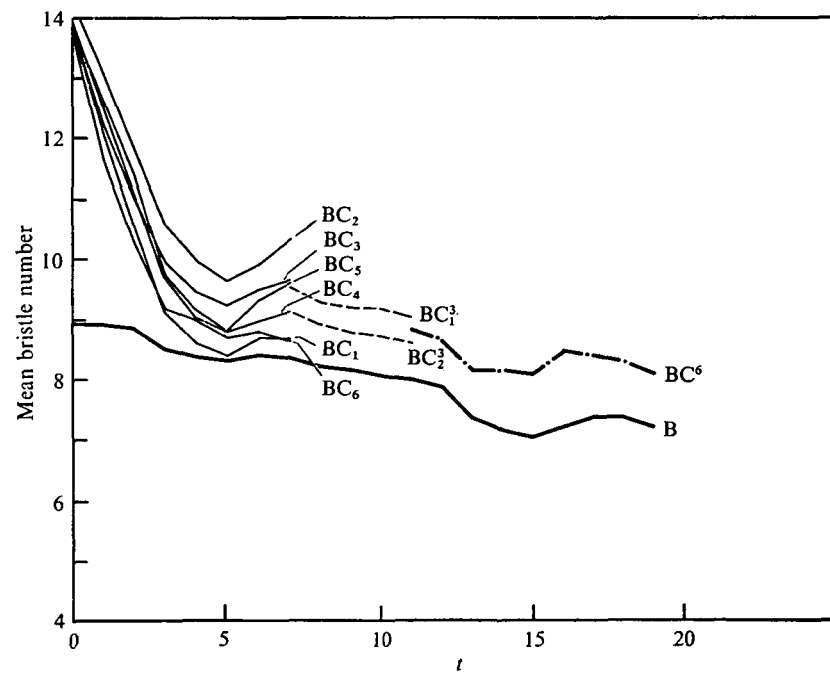

Fig. 3. Three-generation moving average scores for the BC replicates and their crosses.

https://doi.org/10.1017/S0016672300012842 Published online by Cambridge University Press

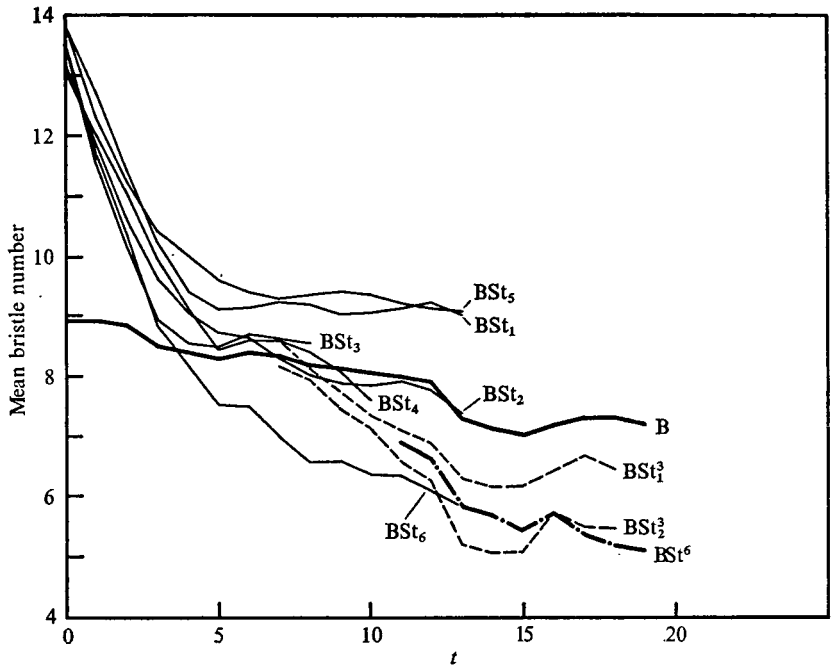

Fig. 4. Three-generation moving average scores for the BSt replicates and their crosses.

3. DISCUSSION

The similarities of the initial rapid responses in the four populations formed by crossing to the selected line may have been caused by a reselection of line B chromosomes in each case. Only one generation of random mating was allowed prior to selection, so little chance for recombination was permitted, especially in view of the evidence that genes affecting bristles appear to be concentrated on small regions of the chromosomes (Professor A. Robertson, personal communication). It is possible that a greater period of recombination should have been allowed prior to selection, but no advantages were found for this practice by Osman & Robertson (1968) in a similar type of experiment, and by Underwood (1971) using simulation techniques. Despite these initial similarities, the subsequent responses shown by the cross with Stellenbosch, the recently captured population, are strikingly different from those of the other populations, suggesting that the Stellenbosch population had genes absent from or rare in the other populations, for the plateau of line B was broken even in lines of size 5/25. Since the Stellenbosch population had a higher heritability and phenotypic variance than the other three populations one would expect it to have a larger response to selection. However, differences between heritabilities do not indicate presence or absence of particular alleles in the populations to be compared. The Canberra population, while not a constituent of line B, provided no useful variation to lower the limit. It initially

showed a rather low level of genetic variability, but appears to have been fixed for favourable alleles present in Kaduna, Pacific or both. As Osman & Robertson (1968) found, experiments such as this are subject to enormous sampling variation between replicates, and it must be noted that we used only one final large line from each population. It is quite possible that the behaviour of BP^6 was atypical.

With the resources used in this experiment introduction of genetic material from the Kaduna and Pacific populations into line B proved to be impossible or very difficult, respectively. Therefore we can consider the limits to selection reached in line B to be a property of the original base population. This finding provides additional support to the conclusion reached by López-Fanjul & Hill (1973) that essentially the same alleles controlling sternopleural bristle number were segregating in the Kaduna and Pacific populations.

Table 5. *Frequencies at seven enzyme loci in the four populations (from Malpica, 1972)*

Locus	Allelic form	Kaduna	Pacific	Canberra	Stellenbosch
Idh	A	1·00	1·00	1·00	1·00
Est6	A	0·31	0·74	0·76	0·35
	B	0·69	0·26	0·24	0·65
Pgm	A	0·00	0·00	0·08	0·03
	B	1·00	1·00	0·92	0·85
	C	0·00	0·00	0·00	0·12
EstC	A	0·00	0·00	0·00	0·19
	B	1·00	1·00	1·00	0·81
Odh	A	1·00	1·00	1·00	1·00
Xdh	A	1·00	1·00	1·00	1·00
Aldox	A	0·00	0·00	0·00	0·04
	B	0·00	0·00	0·00	0·18
	C	1·00	1·00	1·00	0·78
Proportion of polymorphic loci		0·14	0·14	0·29	0·57
Proportion of genome heterozygous per individual		0·061	0·055	0·073	0·197

Information on allelic frequencies at seven loci showing electrophoretic variation in the four original populations has been obtained by Malpica (1972). The results are shown in Table 5, and were obtained a few months after we sampled the populations to initiate this experiment. There are only small differences between any of the populations, but Stellenbosch shows a greater degree of heterozygosity and is segregating at three loci which are fixed in Kaduna and Pacific, and of these two are fixed in Canberra. As with the quantitative trait we examined, the Kaduna, Pacific and Canberra populations appear to be fixed for the same alleles, while Stellenbosch contains variants absent from the other three.

The similarities between Pacific and Kaduna found in the previous paper (López-Fanjul & Hill, 1973) could have been due to contamination of the two

populations during their many years in the laboratory in Edinburgh, although the esterase-6 frequencies are different (Table 5). However, significant contamination could not have occurred with Canberra or Stellenbosch which were brought to Edinburgh shortly before this experiment started and had not been in the same laboratory as Kaduna or Pacific previously. Therefore the three laboratory populations must have been segregating for similar genes when initially captured, or have become alike when maintained in cages. In view of the differences between each population and the recently captured Stellenbosch, the latter hypothesis seems more appropriate. Whether natural selection might have acted to produce the changes in the cages is difficult to predict. There is controversy about whether there is any selection on bristle numbers in cage populations. Some authors have claimed there is strong stabilizing selection for bristle number (Barnes, 1968; Linney, Barnes & Kearsey, 1971; McGill & Mather, 1972), while Robertson (1967) found that a population selected upwards from Kaduna for six generations and then relaxed regressed by only 20% over 40 generations in a cage. A reduction in the number of chromosomal inversions in two wild populations of *D. pseudoobscura* after they were transferred to, and maintained in, the laboratory was found by Anderson, Dobzhansky & Kastritis (1967) and Anderson, Dobzhansky and Pavlovsky (1972). A loss of the inversions originally present has also been reported in the Kaduna population (Latter and Robertson, 1962). Similar forces may have been acting on the loci controlling variation in sternopleural bristle number in our populations.

Variation present in the cage populations could be maintained by mutation, which would reach an equilibrium with the loss of variation by drift (Clayton & Robertson, 1955) without strong selective forces. However, a mutation/drift equilibrium does not imply equality of allele frequencies at any time in different populations, and increased variation on crossing, and thus higher rates of responses would be expected.

Similar studies to those reported here, but using several recently collected populations from different geographical regions might shed some light on the subject. The problem with studies such as this on quantitative traits compared with simple polymorphisms is that much more labour is required to obtain critical results. However, we do not feel that it will be sufficient just to look at biochemical polymorphisms and then draw inferences about quantitative traits.

REFERENCES

Anderson, W. W., Dobzhansky, T. & Kastritis, C. D. (1967). Selection and inversion polymorphisms in experimental populations of *Drosophila pseudoobscura* initiated with the chromosomal constitution of natural populations. *Evolution* **21**, 664–671.

Anderson, W. W., Dobzhansky, T. & Pavlovsky, O. (1972). A natural population of *Drosophila* transferred to a laboratory environment. *Heredity* **28**, 101–107.

Barnes, B. W. (1968). Stabilising selection in *Drosophila melanogaster*. *Heredity* **23**, 433–442.

Clayton, G. A. & Robertson, A. (1955). Mutation and quantitative variation. *American Naturalist* **89**, 151–158.

Hill, W. G. (1970). Design of experiments to estimate heritability by regression of offspring on selected parents. *Biometrics* **26**, 565–571.

Hill, W. G. (1972). Estimation of realised heritabilities from selection experiments. II. Selection in one direction. *Biometrics* **28**, 767–780.

Latter, B. D. H. (1964). Selection for a threshold character in *Drosophila*. I. An analysis of the phenotypic variance on the underlying scale. *Genetical Research* **5**, 198–210.

Latter, B. D. H. & Robertson, A. (1962). The effects of inbreeding and artificial selection on reproductive fitness. *Genetical Research* **3**, 110–138.

Linney, R., Barnes, B. W. & Kearsey, M. J. (1971). Variation for metrical characters in *Drosophila* populations. III. The nature of selection. *Heredity* **27**, 163–174.

Lopéz-Fanjul, C. & Hill, W. G. (1973). Genetic differences between populations of *Drosophila melanogaster* for a quantitative trait. I. Laboratory populations. *Genetical Research* **22**, 51–68.

Malpica, J. M. (1972). Enzyme polymorphisms in four populations of *D. melanogaster*. *Drosophila Information Service* **49**, 122–123.

McGill, A. & Mather, K. (1971). Competition in *Drosophila*. I. A case of stabilising selection. *Heredity* **27**, 473–478.

Osman, H. El Sayed & Robertson, A. (1968). The introduction of genetic material from inferior into superior strains. *Genetical Research* **12**, 221–236.

Reeve, E. C. R. (1961). A note on non-random mating in progeny tests. *Genetical Research* **2**, 195–203.

Robertson, A. (1967). The nature of quantitative genetic variation. In *Heritage from Mendel* (ed. R. A. Brink), pp. 265–280. Madison: University of Wisconsin Press.

Sheridan, A. K., Frankham, R., Jones, L. P., Rathie, K. A. & Barker, J. S. F. (1968). Partitioning of variance and estimation of genetic parameters for various bristle number characters of *Drosophila melanogaster*. *Theoretical and Applied Genetics* **38**, 179–187.

Underwood, S. (1971). Selection procedures in populations. Unpublished Ph.D. Thesis, University of Edinburgh.