COMPETITION IN *DROSOPHILA*

II. HOMOZYGOUS LINES

KENNETH MATHER* and ANNE McGILL†
University of Southampton

Received 8.i.72

1. Introduction

In an earlier report (McGill and Mather, 1971) an account was given of the behaviour of wild-type flies, derived from the F_2 of the cross between the Wellington (W) and Samarkand (S) inbred lines, in competition with individuals of the 6CL line. Wild-type flies with different number of chaetae also differed in their competitive abilities, at least in relation to 6CL, in such a way as to indicate that selection would be predominantly stabilising for sternopleural chaeta number though with a directional element in it too. The present report is concerned with the behaviour of the eight homozygous lines, which comprise all combinations of the three major chromosomes from W and S, taken as units, in similar mixed cultures with 6CL. The technique of setting up the mixed cultures was essentially like that of McGill and Mather (*loc. cit.*), using 1 in. × 3 in. glass tubes divided into two during mating and egg-laying by a cardboard partition which was withdrawn when the parent flies were removed.

2. The experiments

Three experiments were carried out. In the first the numbers of flies obtained from pure cultures (P) of the eight homozygous wild-type lines and of 6CL were compared with the yields of wild-type and 6CL flies from mixed cultures (M). The pure cultures were set up using two females and two males of the homozygous line, or of 6CL, placed on one side of the partition, the other compartment being left empty. In setting up the mixed cultures, two pairs of flies from the homozygous line were placed in one side of the partition and two pairs of 6CL on the other. Four replicates were set up of each line in pure culture and of each combination of homozygous line and 6CL in mixed culture, though in four cases one of the four replicates failed and in one case two of them did so. The average yields of either wild-type or 6CL flies from the pure cultures and of both wild-type and 6CL flies from the mixed cultures are shown in table 1, together with the average values of ϕ measuring the proportion of wild-type flies for the mixed cultures.

The second experiment was designed to test the effects of density. One half of it (A) consisted of cultures set up in just the same way and with the same four replicates, as the mixed in experiment 1. The second half (B) consisted of the same range and number of cultures, but with twice the

* Present address: Department of Genetics, University of Birmingham, Birmingham, B1 5 2TT.

† Present address: Unilever Ltd., Sharnbrook, Bedfordshire.

number of parents in each, *i.e.* 4 pairs of the homozygous line and 4 pairs of 6CL on the two sides of the partition, respectively. The yields of the A and B cultures are given in table 1 also.

TABLE 1

Average numbers of wild-type and 6CL flies yielded by pure (P) and mixed (M, A and B) cultures of the eight homozygous lines. The lines are designated by the origin, whether from Wellington (W) or Samarkand (S), of their major chromosomes listed in the order X, II and III. Each entry is the average of four replicates except for those marked with an asterisk, where one, or rarely two, replicates failed. Further details in the text

		Homozygous line									
Culture	Flies	WWW	WWS	WSW	WSS	SWW	SWS	SSW	SSS	Mean	
P	+	87·75	81·25	63·25	53·00*	52·67	*60·50	78·25	45·25	65·24	6CL 26·67*
M	+	61·00	50·75	64·67*	56·50	42·50	49·67*	30·33*	60·75	52·02	*Mean* ϕ
	6CL	27·25	32·50	27·00	31·75	15·00	21·33	18·00	12·50	23·17	56·23
A	+	52·50	54·75	60·33*	71·00	42·50*	38·00*	41·25	27·00*	48·42	55·31
	6CL	29·50	23·00	23·33	28·00	30·00	14·67	35·25	13·67	24·68	
B	+	85·50	105·50	76·25	112·25	58·33*	77·25	28·50	53·00	74·57	58·44
	6CL	30·25	31·00	13·00	48·25	25·00	11·75	27·50	31·50	27·28	

The third experiment, which will be reported more fully later, consisted of a diallel set of crosses among the eight homozygous lines. The offspring of these crosses were tested in mixed cultures with 6CL by the same technique as in the earlier experiment, two pairs of wild type and two pairs of 6CL being used in each. The diallel was carried out in triplicate. The leading diagonal consists of course, of the homozygous lines and the data (D) from this diagonal were extracted from the three replicates. It is summarised sufficiently for our present purpose in table 2, which also includes similar summaries of M, A and B.

TABLE 2

Mean yields of the wild-type and 6CL flies and mean ϕ from cultures with the Wellington (W) and Samarkand (S) X chromosomes in the various experiments. The experiment and chromosome means are shown in the margins denoted "Overall"

	Wild-type			6CL			ϕ		
Experiment	W	S	Overall	W	S	Overall	W	S	Overall
M	58·23	45·81	52·02	29·63	16·71	23·17	54·9	57·6	56·3
A	59·65	37·19	48·42	25·96	23·40	24·68	58·0	52·6	55·3
B	94·88	54·27	74·58	30·63	23·94	27·29	61·5	55·4	58·5
D-1	64·33	55·67	60·00	28·67	14·67	21·67	75·7	83·3	79·5
D-2	53·33	56·67	55·00	22·33	14·33	18·33	83·3	83·7	83·5
D-3	69·00	38·67	53·84	34·67	16·67	25·67	69·0	79·0	74·0
Overall	66·57	48·05	57·31	28·65	18·29	23·47	67·1	68·6	67·8

The first two experiments were carried out at much the same time and so will be analysed together. The third experiment was carried out on a different occasion and will not be included in the first analysis with the other experiments, though its inclusion would appear unlikely to make any material difference. First the yields of wild-type flies were compared in P, M and A in all of which they were from two pairs of parents. The yields were averaged over the available replicates and the averages, as set out in

table 1, used for analysis. The analysis of variance is set out in table 3. Two conclusions emerge: (*a*) the average yield of wild-type flies is lower in M and A than in P, with no evidence of difference between M and A; and (*b*) the average yield of wild-type flies is lower in cultures from homozygous lines carrying the S sex chromosomes than from those carrying the W sex chromosome, there being no evidence of any heterogeneity of this effect between P, M and A, and no evidence of either major autosome affecting the yield.

TABLE 3

Analysis of variance of average numbers of wild-type flies from P, M and A

Item	Degrees of freedom	Mean square	Variance ratio	P
Culture types	2	627·69	—	—
[M *v.* A	1	51·98	—	—]
[P *v.* M+A	1	1203·40	7·3	0·05-0·01]
Lines	7	230·88	—	—
[Effect of X chromosome	1	1473·92	8·9	0·01]
[Remainder	6	20·31	—	—]
C × L	14	165·53*	—	—
[Het. of X effect	2	69·07	—	—]

* This interaction mean square is significantly larger than the error variance of the replicates, and so is used as the error variance in testing the significance of the " P *v.* M+A " and " Effect of X chromosome " items.

Evidently, from (*a*), the presence of 6CL flies in the culture depresses the yield of wild type, as would be expected from a competitive situation. There is a suggestion from the overall averages of P, M and A that the yield of 6CL is depressed by the presence of wild-type flies again as we might perhaps expect, though it is a smaller depression, and the total yields of M and A are higher than that of P would suggest. A result not to be expected from simple considerations of competition emerges, however, when we compare the yields of 6CL from cultures with S and W sex chromosomes respectively. For this purpose the data from B in the second experiment are combined with M and A. The analyses of variance of both wild-type and 6CL numbers are given in table 4. We first note that the yield of wild

Table 4

Analysis of variance of average number of wild-type and 6CL flies from M, A and B

		Wild-type			6CL		
Item	*D.f.*	*M.S.*	*V.R.*	*P.*	*M.S.*	*V.R.*	*P.*
Culture types	2	1607·60	8·2	0·01-0·001	34·662	—	—
[M *v.* A	1	51·98	—	—]	—	—	—
[B *v.* M+A	1	3163·23	16·1	0·001]	—	—	—
Lines	7	697·35	3·6	0·20-0·05	123·42	2·0	0·20-0·05
[Effect of X chromosome	1	3798·15	19·4	<0·001	372·52	6·0	0·05-0·02]
[Remainder	6	180·55	—	—	82·48	—	—]
C × L	14	195·95	—	—	61·87	—	—
[Het. of X effect	2	408·23	2·5	0·20-0·10]	—	—	—

types is higher in B than in M and A, though not twice as high as the double number of parents might lead one to expect in the absence of some other (presumably competitive) limitation. Secondly, B shows the same effect of the X chromosome on the yield of wild-type flies as do M and A. Thirdly there is a suggestion that the yield of 6CL is similarly higher in B than in M and A, though the difference is not significant. Finally, however, the analysis of variance of the 6CL numbers shows that the yield of these flies is depressed like that of wild type by the S relative to the W sex chromosome (P between 0·05 and 0·01). If we take the average yields in the S-X and W-X parts of the three experiments there is a positive, though not fully significant ($P \simeq 0{\cdot}10$), regression of the 6CL numbers on the wild type, while there is no suggestion of such a regression within the groups into which the data are thus divided. Thus the 6CL numbers are affected by the substitution of the X chromosome in the same way as the wild type, not in the reverse direction as would be expected from a simple consideration of competition between wild type and 6CL.

This finding is confirmed by the data from the diallels in table 2. An analysis of variance (table 5) of the 6CL yields from all six sets of observations

TABLE 5

Analysis of variance of numbers of wild-type and 6CL flies, averaged over all lines with W and S sex chromosomes respectively, from all experiments

		Wild-type			6CL		
Item	D.f.	M.S.	V.R.	P.	M.S.	V.R.	P.
Effect of X chromosome	1	1029·34	8·2	0·05-0·01	322·09	20·37	0·01-0·001
Experiments	5	171·90	1·4	> 0·20	20·24	1·3	> 0·20
Interaction	5	125·52	—	—	15·81	—	—

in table 2 shows the S-X cultures to have a significantly lower yield of 6CL than the W-X (P between 0·01 and 0·001), the reduction being in fact more significant than that in the wild type (P between 0·05 and 0·01). The diallels gave a lower average yield of 6CL than did M, A and B and hence higher values of ϕ. The effects of the X chromosome on wild type and 6CL are, however, such as not to produce any consistent difference in ϕ within one experiment.

3. CONCLUSIONS

The results serve to emphasise the complexity of the processes that can appear in a prospectively competitive situation, especially when compared with the findings reported earlier (McGill and Mather, *loc. cit.*). There the number of 6CL flies rose as that of wild types fell, in accordance with simple competitive expectation, though one 6CL fly appeared to correspond to or compensate for nearly two wild-type flies. Here a genetic change, the substitution of the X chromosome, alters the yield of wild types and 6CL in the same direction. How can a change in the genotypes of the wild-type parents, which reduces their numbers of surviving offspring, also reduce the numbers of surviving offspring of 6CL parents mating and laying on the other side of a cardboard partition? An explanation in terms of competition is not impossible if it is made sufficiently complex; but one in terms of

deleterious materials excreted or secreted by the wild-type larvae into the food mass, as has been reported by Weisbrot (1966), would appear to be more likely. A possibly similar finding has been reported by Huang, Singh and Kojima (1971). One odd and perhaps no more than coincidental observation remains to be noted. In the data of table 3, the average reduction in wild-type yield brought about by substituting S-X for W-X is 18·52, and the corresponding reduction in 6CL is 10·36, a ratio of 1·79 wild type to 1 6CL, which is close to the ratio of 1·91 wild type corresponding to 1 6CL in the negatively correlated changes reported by McGill and Mather.

A further indication that a simple interpretation of the relationship between the wild-type and 6CL flies in terms of competition for a limiting supply of some requirement will not suffice, is the observation that while the number of wild type yielded by M and A is less than that from P, so suggesting competition from 6CL, the yield for B is higher than P, so that, one must suppose, the number in M and A is not limited by a restricted supply of some specific requirement. Yet there must be some limiting agent, for the yields in B were not twice those from M and A. The relations of flies in mixed cultures are clearly complex and competition by no means a simple, or single process.

4. Summary

1. The eight homozygous lines, comprising all combination of the three major chromosomes taken as units from the Wellington (W) and Samarkand (S) inbred lines, were tested for their yields of progeny in pure culture and in mixed cultures with 6CL.

2. The substitution of the X chromosome from S for that from W resulted in a reduction of the yield of offspring in both pure and mixed cultures.

3. In mixed cultures it also led to a reduction in the yield of 6CL flies —a result which cannot be interpreted in terms of simple competition.

Acknowledgment.—We gratefully acknowledge financial support from the Agricultural Research Council, which made this work possible.

5. References

HUANG, S. L., SINGH, M., AND KOJIMA, K. 1971. A study of frequency-dependent selection observed in the esterase-6 locus of *Drosophila melanogaster* using a conditioned media method. *Genetics*, *68*, 97-104.

MCGILL, A., AND MATHER, K. 1971. Competition in *Drosophila*. I. A case of stabilising selection. *Heredity*, *27*, 473-478.

WEISBROT, D. R. 1966. Genotypic interactions among competing strains and species of *Drosophila*. *Genetics*, *53*, 427-435.