THE ROLE OF RECOMBINATION IN ARTIFICIAL SELECTION

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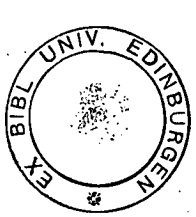

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I INTRODUCTION

Selection response

Mather (1941) was one of the first to draw attention to the association of genes governing quantitative characters in linkage groups and the consequences of this for selection response. His observations were based on the behaviour of his own population of *Drosophila* selected for high and low abdominal bristle number and those of Payne (1918) selected for high scutellar bristle number. In these experiments, periods of rapid advance alternated with those of stability under selection. Mather attributes the stable periods to the exhaustion of available genetic variation between chromosomes and the response periods to the release of new variation through recombination within linkage groups of genes. He hypothesises the accumulation under natural selection of complexes of such polygenes linked in internal and relational balance. This implies heterozygosity at individual loci and an excess of repulsion linkages among the loci (negative linkage disequilibrium). In a more detailed study of selection for abdominal bristle number Mather and Harrison (1949) reported further discontinuities in response and found that all four chromosomes contributed to response and their effects were additive. More recently similar discontinuities observed in lines selected for high sterno-pleural bristle number have been attributed to the same cause by Thoday and Boam (1961).

Although the behaviour of these lines under selection does provide some evidence for the existance of repulsion linkages of bristle genes, it provides none for an excess of such linkages in natural populations as proposed by Mather (1943). Wright (1952) has shown that the selective values of repulsion linkages have to be very high and linkage very tight/

/tight to maintain such a disequilibrium. Robertson (personal communication) agrees that such discontinuities observed may be due to recombination of repulsion linkagesbut the probability of their being observed was weighted in favour of these workers since their selection lines were derived from crosses between inbred lines. Under these conditions, there are initially relatively few gene arrangements each at about equal frequencies. Favoured coupling linkages are quickly fixed giving immediate selection response and repulsion heterozygotes of approximately equal effects persist and give rise to delayed response upon recombination.

Some doubt as to whether these discontinuities of response were due to recombinational events led Fraser (1957) to computer simulation studies with Monte Carlo techniques on the effects of linkage on selection response. Using a model of two groups of three linked loci with dominance and initial negative linkage disequilibrium, he was able to simulate discontinuous responses with tight linkage (0.005) and the same high selection intensity (4/40) as that used by Mather and Harrison (1949). Thus, the models of Fraser (1957) showed that Mather's polygene hypothesis was sufficient to explain the nature of the selection response.

Some of the response curves for the selection runs of Fraser also suggest a reduction in limit or total response to selection in populations with tightly linked loci and selected with high intensity. This effect appears to be greater for low initial frequency of the favoured alleles. However, from the data of Fraser (1957) it is not possible to find a quantitative relationship between degree of linkage and the selection limit. Also, it has not been satisfactorily established that his model of dominance and excess of repulsion linkages represents the true situation in nature. Martin and/

/and Cockerham (1960) enlarged upon the work of Fraser (1957) by studying the effect of linkage in models of five linked loci each with two alleles with additive effects and frequencies of 0.5. Under initial linkage equilibrium they found that response was reduced only with the tightest linkage (0.01) and the highest selection intensity (2/20). When they commenced selection from a population in negative linkage disequilibrium they found a more marked reduction in response due to linkage; in accordance with the observations of Fraser (1957). With these and other Monte Carlo studies of Qureshi (1963) a pattern of the effects of linkage on response to selection in polygenic characters began to appear. However, none of these workers attempted a general formulation of the inter-relationships among the factors, such as linkage and selection intensity, which were found in these computer runs to affect selection response.

Robertson (1960), developing the theory of Kimmura (1957) of the chance of fixation of genes under selection in small populations, was the first to formulate a prediction of total response to selection for a system of independent loci each with two alleles. By close examination of a gene at one of these loci he determined that its chance of fixation for a given initial frequency could be completely determined by $N\underline{i}\,a/6$ when N is the effective population size, $\underline{i}$ the selection differential in standard deviations and $\underline{a}/6$ the difference in mean between the two homozygotes at the locus. When the genetic variance $6g^2$ of all such additive genes affecting a character is small in relation to the total phenotypic variance 6^2, selection response can be simply represented by $Ni(2\,6g^2/6)$.

This approach to predicting response in a polygenic character through close examination of the behaviour of a single gene under selection was/

/was first used to elucidate the effects of linkage on selection limits by Latter (1965) Using Monte Carlo techniques, and a model of two loci of equal effect with alleles of equal frequency linked initially in equilibrium, he studied the chance of fixation of the favoured alleles under replicated selection runs with varying recombination frequencies. He found that linkage reduced response appreciably to long term selection only for pairs of loci of fairly large effect at recombination values of 0.10 or less. In a more recent study Latter (1966) observed the fate of the coupling and repulsion linkage phases under selection in a regime where linkage had a high depressing effect on response. Favoured coupling linkages were initially rare and a high proportion of total response was obtained from recombination among repulsion heterozygotes.

While these models of Latter considerably advanced the understanding of the effects of linkage on selection limits, they suffered from the limitations of equal effects and initial gene frequencies at the two loci under observation. These limitations were removed in the models studied by Hill and Robertson (1966). Using Monte Carlo techniques they observed the response to selection of a gene at one locus as affected by a gene segregating at a second linked locus. They found that the selection process for additive genes in initial linkage equilibrium could be completely specified by the parameters $N\,i\,a/\sqrt{6}$, $N\,i\,b/\sqrt{6}$ and $N\,c$ where N is the effective population size, i the standardised selection intensity, $a/\sqrt{6}$ and $b/\sqrt{6}$ the effects of the two loci on the selected character and c the linkage distance between them.

The chance of fixation of an observed gene was affected by linkage with a second locus to an extent which depended upon the frequency and/

/and effect of the favoured gene at the second locus. They found that the mean at the selection limit was most sensitive to changes in recombination frequency between the two loci when they had equal effects and when segregating independently, the favoured genes had chances of fixation of about 0.7. Thus, these studies of Hill and Robertson (1966) enabled the selection process to be adequately described for two linked loci from a knowledge of relatively few parameters. Whether or not this enables prediction of the selection process in natural populations where quantitative characters are likely to be influenced by more than two loci, is unknown.

Robertson (personal communication) has recently taken a more general approach to defining the effect of linkage on selection limits in a multi-locus system than the Monte Carlo studies reported above. He determined selection limits for a 'Normal' model of 2 N groups of $\underline{n}$ completely linked loci with equal effects $\underline{a}$ and initial gene frequencies $\underline{q}$. To establish selection lines these 2 N groups were sampled from a population in which they were normally distributed with a variance $6g^2$. They would correspond to the 40 chromosomes III needed to establish a selection line of 20 parents. He determined the relationship between advance under selection to the limit $(dg/6g)$ and N $\underline{i}$ $\underline{h}$ where $\underline{i}$ is the standardised selection differential and $\underline{h} = 6g/6$ where $6g$ and 6 are the genetic and phenotypic standard deviations. Limits for very low and very high values of N $\underline{i}$ $\underline{h}$ were obtained explicitly and those for intermediate values of N $\underline{i}$ $\underline{h}$ using Monte Carlo selection runs. By increasing the value of $\underline{i}$ $\underline{h}$ he found that with N = 10, limits rose rapidly from zero when N $\underline{i}$ $\underline{h}$ = 0 to reach about 3 $6g$ for high values of N $\underline{i}$ $\underline{h}$.

Selection limits were then calculated for the same N groups allowing free recombination among the $\underline{n}$ loci of which they were comprised. For/

/For each value of N i h the ratio R of the limit under free recombination to that under 'Normal' selection was obtained. Under this model of completely independent segregation and N = 10, values of R increased from one at very low values of N i h to $\sqrt{2/9\,(n(1-q)/q)}$ for high but finite values of N i h which allowed fixation of the best alleles at all n loci under free recombination. Some runs with recombination frequencies between 0 and 0.5 gave R values less than that for independent segregation.

This definition by Robertson of the interaction of linkage and selection limits for a multi-locus system using R estimable from a knowledge of population size, selection intensity and recombination frequency is analagous to the specification by Hill and Robertson (1966) of the response of two linked genes by similar parameters. It suffers only from the limitations of equality of gene effects, initial gene frequencies and distances between adjacent loci.

Reproductive fitness

Mather's (1943) balanced polygene hypothesis implies that a reduction in fitness is liable to result from unbalancing the combinations through an increase in coupling linkages under selection. Although reduction in fitness due to change in bristle score per se has not been demonstrated, a considerable variation in change of fitness among lines of Drosophila selected for bristle score, suggestive of bristle fitness gene linkage, has been found by Mather and Harrison (1949), Wigan and Mather (1942), Thoday and Boam (1961) and Clayton and Robertson (1957). Lines which do decline in fitness either die out or regain their fitness upon relaxation or back selection.

In a more definitive study of the change in fitness under selection for/

/for bristle score in Drosophila, Latter and Robertson (1962) established that most of the decline observed could be accounted for by inbreeding depression alone but in a few of the lines there was clear evidence of unfavourable bristle fitness linkages.

General

The experiments reported in this thesis are a check on the agreement between the simulation models presented above and the behaviour of Drosophila lines selected for sternopleural bristle number in which two degrees of recombination frequency of linked groups of genes affecting this character are contrived. From experiments carried out in this laboratory (Louw (1966), Osman Mousa (1963), Allan (1963),) sternopleural bristle number appears to fulfill the requirements of a character controlled by a number of additive genes at intermediate frequencies and occurring in linkage groups in initial equilibrium on all chromosomes.

Comparisons under the two regimes of recombination frequency are made of selection response as contributed by each of the four chromosomes and changes in reproductive fitness. In setting up the comparisons, use was made of the fact that crossing over does not occur in Drosophila males and crossover products occurring within inverted segments of chromosomes carried in females are inviable.

The control of recombination frequency was restricted to chromosomes II and III since they are responsible for a high proportion of the difference between lines selected for high and low bristle score (Louw (1966)).

II EXPERIMENTAL

ESTABLISHMENT OF RECOMBINATION REGIMES

For both high and low bristle score, one set of lines was selected in which recombination was suppressed by balancing wild chromosomes II and III in female parents against suppressor crossover chromosomes. This was compared with another set of lines where recombination occurred freely by using wild type female parents. Recombination referred to as Free in this study is that which is expected to occur between loci on chromosomes of normal order.

To be able to attribute with confidence differences in response to differences in recombination frequency, sets were equalised for other factors affecting response. For a gene with homozygous effect a above the homozygote of its alternate allele, it has already been shown that apart from its linkage relationship with other genes, its limit under selection is determined by its initial frequency and $N\,i\,a / 6\,p$ where N is the effective population size, i is the selection differential and 6 the phenotypic standard deviation.

To equalise initial gene frequencies, the chromosomes contributing to response in both sets were large samples from the same wild population. In addition, the chromosomes which were used to suppress recombination in the female parents were carried at the same frequency in male parents of the Free recombination set of lines. This balancing of the suppressor chromosome frequencies in both set of lines was necessitated by the effect which the presence of segregating suppressor chromosomes had on both N and $i\,a / 6$ and consequently the response of the wild chromosomes to selection. A comparison of the expected $i\,a / 6$ between selecting parents within/

/within heterozygous suppressor/wild and homozygous wild/wild genotypes is given in Appendix 2. It shows that $i\,a\,/\,\delta$ is slightly higher for the former than for the latter due to a reduction in the genetic component of δ. Also, the balancing of wild alleles by an invariate suppressor chromosome in one set of parents reduces the possible number of wild alleles segregating at a locus from 2N to $^3/_4(2N)$. Thus the sampling variances of such loci on chromosomes II and III are increased due to a reduction by $^1/_4$ in the effective population size N. The reduction in N through selection within suppressor heterozygotes is expected to more than compensate for the increase in $i\,a\,/\,\delta$.

CHROMOSOME AND MARKER STOCKS

Wild chromosomes These are the chromosomes which provided the response in the selection lines. They were sampled from the Kaduna cage population. This population of approximately 5,000 flies was described by Clayton, Morris and Robertson (1957) and has been maintained under constant conditions since. The mean sterno-pleural bristle score of the population was 17 at the samplings of both Experiments 1 and 2.

Crossover suppressors Approximate positions of chromosomal rearrangements and loci used in crossover tests are indicated in Fig. 1.

(i) Cy,pr (Curly). Chromosome II; homozygous lethal; carries inversions In (2L) Cy and In (2R) Cy; non-inverted pericentric region marked with pr (Abbreviated in this study to Cy).

(ii) Me, ca (Moiné). Chromosome III; homozygous lethal; carries inversions In (3L) P and In (3R) P. Non-inverted terminal region of right arm marked with ca (Abbrev. to Me).

(iii) Ubx 130 (Ultrabithorax). Chromosome III; homozygous lethal; carries a short inversion on the left arm, a long pericentric inversion and several translocations. Non-inverted terminal region marked with e. (Lewis 1952) (Abbrev. to Ubx).

Dominant markers These were used in chromosome substitution procedures.

(i) Pm Plum; chromosome II; homozygous lethal.

(ii) Sb Stubble; chromosome III; homozygous lethal.

(iii) ci^D Cubitus-interruptus dominant; chromosome IV; homozygous lethal.

(iv) ci^W Cubitus-interruptus of Wallace; chromosome IV; homozygous viable.

(v) Xa Xasta T(2:3) ; homozygous viable.

Recessive markers These were used in estimating recombination frequencies.

(i) scar Chromosome I; recessive markers in order are scute sc, echinus ec, crossveinless cv, cut ct, vermillion v, forked f and carnation car.

(ii) alsp Chromosome II; aristaless al, dumpy dp, black b, purple pr, curved c, plexus px and speck sp.

(iii) ruca Chromosome III; roughoid ru, hairy h, thread th, scarlet st, curled cu, stripe sr, ebony e and claret ca.

All of the above mutants except Ubx are listed by Bridges and Breheme (1944).

Background stock DF. The origin of this line and the inheritance of some of its body colour patterns has been described by Louw (1966). Mean sterno-pleural bristle score is 8 and has remained unchanged throughout 10 generations of selection in both directions. Multiple stocks of dominant markers and suppressor chromosomes were incorporated into DF backgrounds and maintained through males backcrossed to DF females each generation.

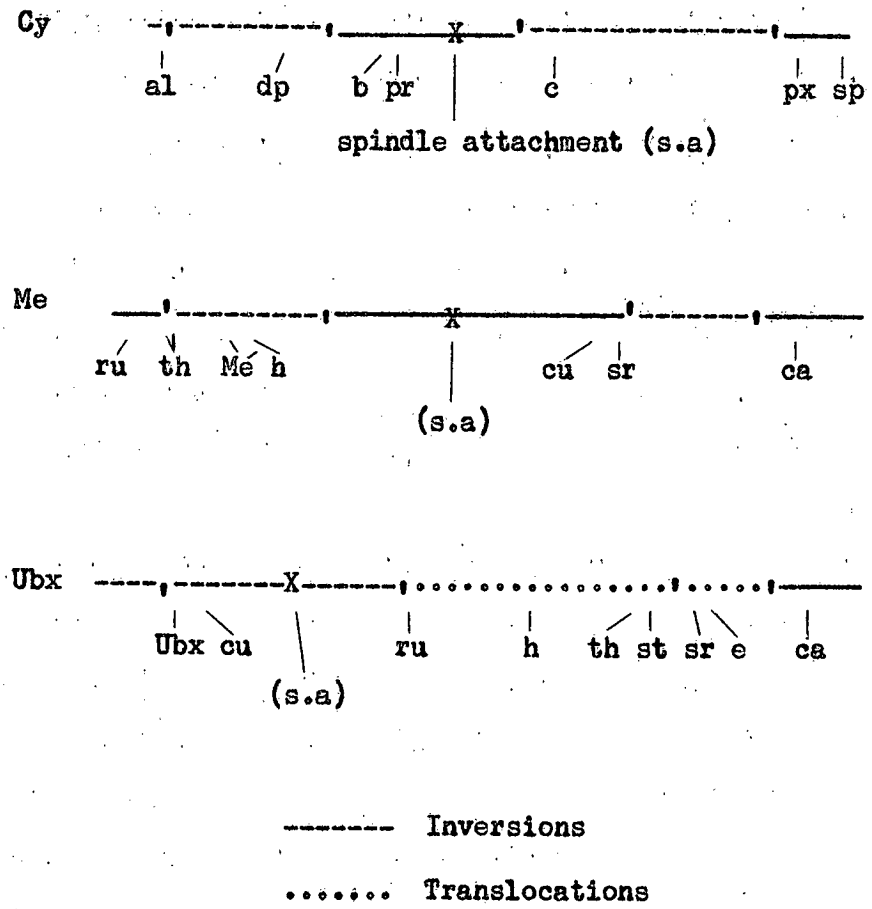


Figure 1. Structure of suppressor chromosomes and approximate positions of marker loci used in crossover tests. Bridges and Breheme (1944).

RECOMBINATION TESTS

In the first experiment Cy and Ubx were chosen to suppress recombination in the selection lines. This choice was based on recombination tests with marker chromosomes II alsp and III ruca when tested females had either one or other but not both suppressor chromosomes in their genomes. Also, Ubx was reported to have a better viability than Me (Louw (1966) personal communication). Subsequent difficulty in identifying Ubx and a breakdown in its ability to suppress recombination efficiently in the presence of Cy led to its replacement in a second experiment by Me.

Method

The following tests were carried out to determine the inter-chromosomal effects of suppressors on recombination within chromosomes I, II and III. Tester chromosomes used were I scar, II alsp and III ruca. The Cy, Me and Ubx chromosomes tested and used in establishing the selection lines were isogenic having been carried in stocks through males since their origin in a single male.

Chromosomes II and III Samples of 10 Cy Me and 10 Cy Ubx males were each mated to alsp and ruca tester females in separate bottle cultures. Collections were made of the following virgin females possessing one suppressor chromosome balanced with a tester chromosome: (i) Cy/alsp; (ii) Me/ru-e; (iii) Ubx/ruca. Also collected were virgin females with 2 suppressor chromosomes one of which was balanced with a tester. These were (i) Cy/alsp; Me; (ii) Cy; Me/ru-e; (iii) Cy/alsp; Ubx and (iv) Cy; Ubx/ruca. This enabled recombination testing of suppressor chromosomes II and III alone and in combination. For each of these genotypes, 3 bottle cultures each/

/each of 10 females were backcrossed to either alsp or ruca males according to whether chromosomes II or III was under test. Parents were removed after 4 days and offspring were scored each day for 5 days.

Chromosome I Males from a standard scar chromosome I stock were mated with females possessing the same Cy and Me chromosomes as used in establishing the selection lines of Experiment 2. From these matings Cy Me and + females heterozygous scar / + were backcrossed to scar males in 2 replicate bottle cultures. Females were allowed to lay for 2 successive periods of 4 days in separate cultures. Progeny were scored over the first 4 days of emergence from each culture. This gave 2 maternal genotypes X 2 maternal ages X 2 replicates.

RESULTS

Chromosomes II and III Table 1 summarises the backcross results. It shows that the Ubx, Me and Cy chromosomes are efficient suppressors of recombination when present alone in females. The only crossovers observed in Ubx and Me involved the ca locus at the end of the right arm of chromosome III. Cy was a less efficient suppressor than Ubx and Me. All single crossovers observed in chromosome II were between the left and right arms. Since pr was common to both Cy and the tester chromosome II alsp, crossovers occurring between b and c could not be identified as occurring either to the left or to the right of pr which is situated between b and c. The presence of 2 suppressor chromosomes in the same female produced a significant increase in the number of crossovers observed only when Cy and Ubx occurred together. Recombination in Ubx increased from 0.74% without Cy to 11.93% with Cy whereas it remained low in Me in the presence of Cy.

Ubx crossovers fell into 2 classes. These were (i) double crossovers involving the h, th and st loci and (ii) single crossovers involving the ca locus. According to the map in Figure 1 these loci occur in the non-inverted 61 A - C to 74 and the 96A to tip of 3R regions respectively of the Ubx chromosome. Recombination in Cy appeared independent of the status of chromosome III. All single crossovers were between the left and right arms and the 3 double crossovers were in the region of the centromere.

Chromosome 1 Table 2 presents the results of backcrossing scar/+ heterozygotes to scar males in the chromosome I recombination test. It shows the numbers of parental, single and multiple crossover types emerging from Cy Me and + females during the 2 time periods. A 3 x 2 X^2 contingency test was carried out on the 3 progeny and 2 maternal types within each maternal age. Older females produced a higher proportion of crossovers than younger ones. Cy Me females, particularly the older ones, produced more crossover progeny than + females. They also produced more multiple crossovers.

The distribution of crossover points over 6 regions of chromosome I for Cy Me and + females is shown in Table 3 with that of Bridges and Breheme (1944). As expected the total distance sc - car is greater for the Cy Me than for the + females. Both, however, were greater than that of Bridges and Breheme (1944). This may be explained by the relatively poor viability of scar genotypes in these cultures and their resultant low contribution to parental types. Despite differences in sc - car lengths, the distribution of crossover points does not differ markedly between the Cy Me and + females. The suggestion of enhanced crossing over in the f - car region in the presence/

Test chromosome	Non-homol genotype	Backcross genotypes				Total flies	% Crossovers
		Parental	Single	Double	Total		
Cy	+	303	6	0	6	309	1.9
"	Me	416	6	3	9	425	2.1
"	Ubx	368	6	0	6	374	1.6
Me	+	534	1	0	1	535	0.2
"	Cy	604	1	0	1	605	0.2
Ubx	+	675	5	0	5	680	0.7
"	Cy	753	74	28	102	855	11.9

Table 1. Frequency of recombination between tester chromosomes and suppressor chromosomes in the presence and absence of non-homologous suppressor chromosomes.

Age	Maternal genotype	Backcross phenotypes: Parental	Single	Multiple	Total scored	% Crossovers
1 *	Cy Me	186	223	32	441	57.8
"	+	192	193	34	419	54.2
2	Cy Me	118	203	58	379	68.9
"	+	182	243	30	455	60.0

* 1 4 day emergence from eggs laid immediately after mating

2 4 day emergence from eggs laid 4 days after mating

Table 2 Effect of maternal age and genotype on the frequency of recombination in chromosome I.

Maternal genotype	Chromosome I regions: sc - ec	ec - cu	cu - ct	ct - v	v - f	f - car	sc - car	No. scored
Cy Me	4.3	10.0	6.8	17.1	24.0	8.6	71.0	834
+	4.4	8.9	7.7	14.9	25.0	5.0	66.0	860
Bridges et al (1944)	5.5	8.2	6.3	13.0	23.7	5.8	62.5	

Table 3 Percentage distribution of crossover points in 6 regions of chromosome I carried in the 2 maternal genotypes Cy Me and +.

/presence of Cy Me reflects a much larger increase found in this region by Schultz and Redfield (1951) in the presence of Cy and the chromosome III inversion Payne.

The increase in chromosome I recombination observed in Cy Me females is unlikely to be an important confounding factor in the comparison of free and suppressed recombination in chromosomes II and III in Experiment 2. The contribution of chromosome I to total response is expected to be small in comparison with that of chromosomes II and III. Also, since the enhancement of recombination appears to be slight and to be at one end of chromosome I it is unlikely to occur between important bristle loci. In Experiment 1, chromosome I was not expected to contribute to selection response since it had been replaced by isogenic DF at the establishment of the lines.

ESTABLISHING SELECTION LINES

Experiment 1 : Twenty selection lines were established; 10 being selected for low (L) and 10 for high (H) sterno-pleural bristle number. In each direction 5 lines had free recombination (F) within chromosomes II and III and 5 had recombination suppressed (S). Lines were numbered 1 to 5 within each of the 4 direction x recombination (DxR) regimes: LF - Low Free; LS - Low Suppressed, HF - High Free and HS - High Suppressed. Each of the 10 F lines was reproduced by mating selected Cy Ubx males and + females and the 10 S lines by mating selected + males and Cy Ubx females each generation. In establishing the lines, chromosomes originated in 3 sources; chromosomes I and IV from the isogenic low score DF line, + chromosomes II and III from the Kaduna cage population and Cy and Ubx from a DF background stock. Chromosomes I and IV were controlled in this way to restrict response to chromosomes II and III. The series of matings to produce the desired genotypes is outlined in Figure 2. Since the Cy and Ubx chromosomes originated in one fly, two generations of multiplication were necessary prior to mating 1. Throughout the substitution process, effective population sizes were kept high by mating a large number of parents (> 300) in a large number of vials.

After establishment of the lines, selection intensities were 10 in 25 for each sex. Thus 25 flies of the following types were scored (i) F lines : Cy Ubx males and + females and (ii) S lines : + males and Cy Ubx females. From matings of selected parents the 4 segregants Cy, Ubx, Cy Ubx and + were expected to emerge in equal numbers. Of those segregants not selected as parents, 10 of each sex were scored. Scoring and selection are diagramed in Figure 3.

Selection lines were kept in half-pint milk bottle cultures. Parents/

1 Kaduna x DF/Y; Cy/DF; Ubx/DF; ci^D/DF

2 Kaduna x K/Y; Cy/K; Ubx/K; ci^D/K

3 DF/DF; Xa/DF; DF; DF/DF x K/Y; K/K; K/K; ci^D/K

4 DF/DF; Cy/DF; Ubx/DF; DF/DF x DF/Y; Xa/K; K ; ci^D/DF

5 DF/DF; Cy/K; Ubx/K; DF/DF x DF/Y; Cy/K; Ubx/K; DF/DF

* (a) DF/DF; K/K; K/K; DF/DF DF/Y; Cy/K; Ubx/K; DF/DF

(b) DF/DF; Cy/K; Ubx/K; DF/DF DF/Y; K/K; K/K; DF/DF

* (a) Used to establish Free recombination lines (F)

(b) " " " Suppressed " " (S)

Figure 2. Substitution of DF chromosomes I and IV; Kaduna wild chromosomes II and III and Cy and Ubx into the base population of Experiment I.

Free recombination

Parents	10 + females		10 Cy Ubx males	
Progeny	Cy	Ubx	Cy Ubx	+
males scored	10	10	25	10
select	-	-	10	-
females scored	10	10	10	25
select	-	-	-	10

Suppressed recombination

Parents	10 Cy Ubx females		10 + males	
Progeny	Cy	Ubx	Cy Ubx	+
males scored	10	10	10	25
select	-	-	-	10
females scored	10	10	25	10
select	-	-	10	-

Figure 3. Numbers of segregants and sexes scored and selected in the Free and Suppressed recombination lines of Experiment 1.

/Parents were mated and females allowed to lay for 3 days. Progeny were collected and sexes separated at 12 hour periods for the 4 days following first emergence. These were then separated into the 4 segregant classes and stored. The total number of females emerging over this period was counted and a sample of about 125 of each sex from each line was examined to determine the proportions of the 4 segregants comprising it.

Bristle scores were punched on tape each generation. A KDF 9 computer was programmed to summarise means and variances of data grouped into the following classes: (i) 2 directions of selection - High and Low, (ii) 2 degrees of recombination - Free and Suppressed, (iii) 2 sexes, (iv) 5 selection lines and (v) 4 segregants - Cy, Ubx, Cy Ubx and +. Experiment 1 was discontinued after 5 generations of selection when anomalies in the behaviour of the Ubx chromosome were discovered.

Experiment 2 : A second series of 20 selection lines was established using Me instead of Ubx as a suppressor of recombination in chromosome III. Both the Cy and Me chromosomes had originated in a single male. They were drawn from a line selected for low bristle score by Dr. A. Robertson in a similar recombination study carried out in 1963. The lines of Experiment 2 differed also from those of the first experiment in the nature of their chromosomes I and IV. They were sampled from the Kaduna population instead of DF. The lines were set up after 3 generations of multiplication of the Cy and Me chromosomes by backcrossing to Kaduna females. The selection procedure as outlined for Experiment 1 was then carried out for 17 generations. Lines were again designated LF(1 - 5); LS(1 - 5); HF(1 - 5) and HS(1 - 5). Selection was discontinued at generation 17 since all but the HF lines appear to have plateaued and some alteration had occurred in the Cy chromosome of several lines.

SELECTION RESPONSE

Results

Experiment 1 : The means of + (wild type) segregants, sexes pooled, are plotted for the 10 Free recombination (F) lines and the 10 Suppressed recombination (S) lines in Figs. 4 (a) and (b) for 5 generations of selection. Responses of + and Cy Ubx segregants pooled over lines within each of the 4 Direction x Recombination regimes appear in Figs. 4 (c) and (d). Mean scores of the 4 segregants Cy, Ubx, Cy Ubx and + at the beginning and end of selection are given in Table 4.

Gen	Seln. regime	Segregant Cy	Ubx	Cy Ubx	+
0	All	13.0±0.1	13.6±0.1	13.2±0.1	13.4±0.1
5	LF	10.5±0.1	11.3±0.2	11.3±0.1	11.0±0.1
"	LS	11.1±0.1	11.7±0.1	11.6±0.1	11.1±0.1
"	HF	15.7±0.1	17.6±0.2	16.2±0.1	16.2±0.1
"	HS	15.8±0.1	16.9±0.2	16.7±0.2	16.8±0.1

Table 4 Experiment 1. Mean scores of the 4 segregants averaged over lines within the 4 D x R regimes at the beginning and end of selection.

From a mean + score of 13.4±0.1 bristles in gen. 0 the High lines rose to 16.5±0.1 in gen. 5 and the Low lines fell to 11.0±0.1. In neither direction of selection was there a difference between the F and S lines at gen. 5. The low gen. 0 score of 13.4 compared with the usual score of 17 for Kaduna + flies is due to the substitution of Kaduna chromosomes I and IV for those of the low bristle score DF line. There is considerable/

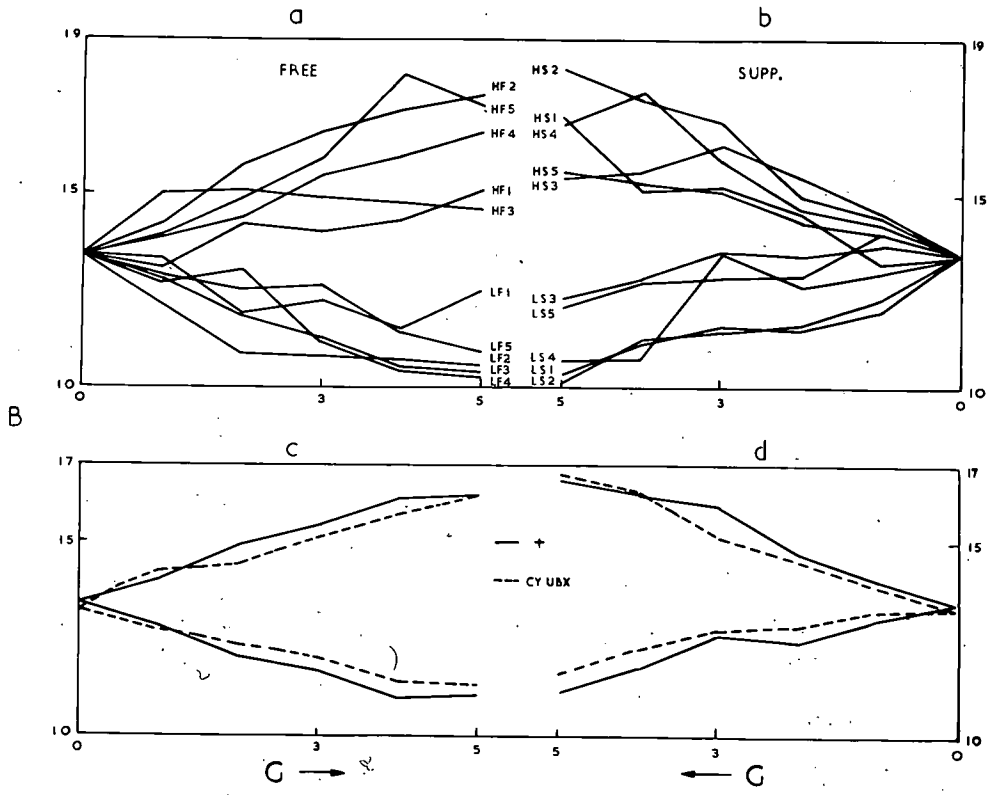


Figure 4 Expt. 1. Response in bristles (B) to 5 generations (G) of selection. + means for individual Free and Suppressed recombination lines plotted in (a) and (b). Response of + and Cy Ubx segregants pooled over lines plotted in (c) and (d).

/considerable variation among lines in mean + score at gen. 5. High lines ranged from 14.6 for HF3 to 18.2 for HS2 and the Low lines from 10.1 for LS2 to 12.5 for LF1. Linear regression coefficients of score on cumulative selection differential (realised heritabilities) pooled over the 10 High and 10 Low lines were calculated for the + and Cy Ubx segregants. These are given in Table 5 with similar values of the + and Cy Me segregants of Experiment 2 selected over the same period.

		Low	High
Expt. 1	+	0.38±0.04	0.40±0.04
	Cy Ubx	0.31±0.04	0.44±0.05
Expt. 2	+	0.22±0.03	0.49±0.04
	Cy Me	0.10±0.02	0.19±0.03

Table 5 Expts. 1 and 2. Realised heritabilities of + and suppressor heterozygote segregants over the first 5 gens. of selection. Estimates are pooled over the 10 lines within each direction of selection.

The only significant difference ($p < 0.05$) among the coefficients of Experiment 1 lies in the greater rate of response of Cy Ubx segregants in the High than the Low direction of selection. The slopes of + responses in both directions agree closely with the realised h^2 calculated for lines of Kaduna flies selected under similar conditions by Allan (1963). The replacement of + by DF chromosomes I and IV and the incorporation of Cy and Ubx into the lines evidently did little to alter response. A simple model is appropriate here to explain the expected response slopes of the 4 segregants.

Let selection change the average effects of + chromosomes II by d II, + chromosomes III by d III and the sum of the effects of chromosomes I and IV by dC. Suppressor chromosomes SII and SIII (e.g. Cy and Ubx) segregate in the selection lines with + chromosomes II and III. Rare recombination between these suppressor and + chromosomes when carried in females enables selection to change their effects dK2 and dK3. Then, summing over the chromosome complements, the changes in mean of the 4 segregant classes under selection can be written as follows:-

$$d\,(SII) = dII + 2dIII + dC + dK2$$

$$d\,(SIII) = 2dII + dIII + dC + dK3$$

$$d\,(SII\ SIII) = dII + dIII + dC + dK2 + dK3$$

$$d\,(+) = 2dII + 2dIII + dC$$

Thus, substituting Cy and Ubx for SII and SIII in the above model and assuming no changes dK2 and dK3 in Cy and Ubx, the expected change d (+) is twice d (Cy Ubx) since dC is zero the chromosomes I and IV being of isogenic DF origin. However, inspection of Figs. 4 (c) and (d) and comparison of realised h^2 for Cy Ubx and + in Table 5 show that the means of both segregants change at about the same rate under selection. This contrasts with a similar comparison in Table 5 of response in the lines of Experiment 2 where the realised h^2 of + was more than twice that of Cy Me. According to the model, twice the slope of the Cy Ubx response would be expected to exceed that of the + response if dK2, dK3 and $dC \neq 0$. This could result from recombination in Cy and Ubx with + chromosomes when carried through females or by the contamination of cultures with flies carrying foreign chromosomes I and IV. Further light is thrown on this later but these observations together with the difficulty of identifying/

/identifying Ubx phenotypes resulted in the discontinuation of Experiment 1.

Experiment 2 : In Figs. 5 and 6 are plotted the responses to 17 generations of selection of the + segregants in the Free and Suppressed recombination lines respectively. In Fig. 7 responses are plotted by pooling over lines within each of the 4 Direction x Recombination regimes. The break occurring in the HS response at gen. 11 is due to the dying out of one of the lines HS3. From gen. 12 to 17 averages are those of the 4 remaining HS lines. To check the repeatability of the apparently plateaued line HS4 it was split into HS4A and HS4B at gen. 11.

In Fig. 9 are plotted average responses of the Low lines together with those of Dr. Robertson. For the purposes of comparison these were designated Series 1 and Series 2 respectively. Means of F lines were calculated from scores on Cy Me males and + females and of S lines from + males and Cy Me females. These different estimates had to be used since only these flies were scored in the initial generations of the Series 2 lines. In pooling them it is assumed that sex difference is independent of genotype.

Average + scores of each of the 4 D x R regimes are given in Table 6 at generations 11 and 17.

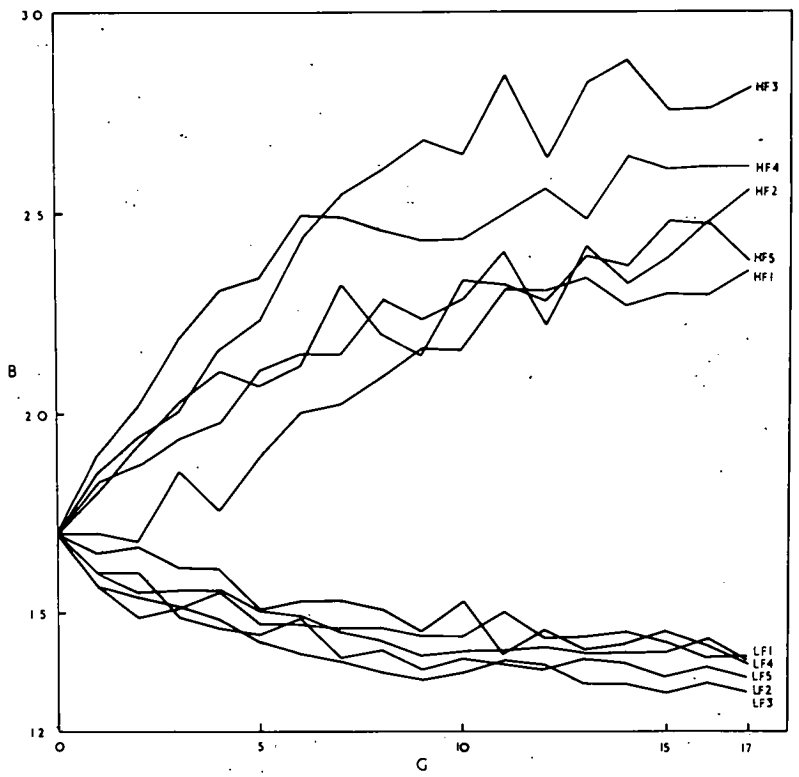


Figure 5 Expt. 2. Response to selection of the Free recombination lines. Generation (G) means are the average bristle scores (B) of + males and females.

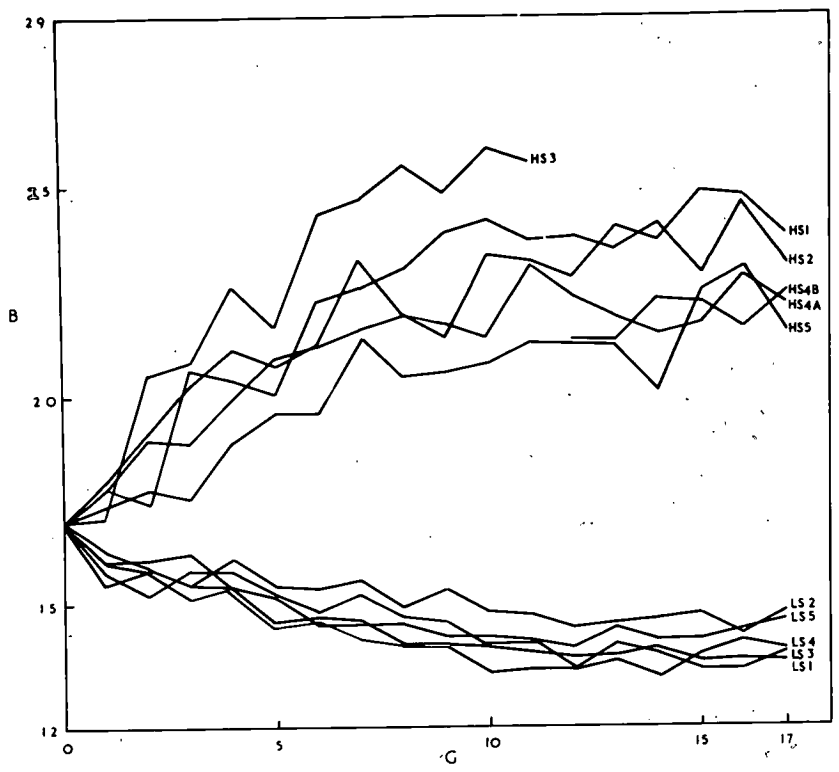


Figure 6 Expt. 2. Response to selection of the Suppressed recombination lines. Generation means are the average bristle scores (B) of ♦ males and females. At gen. 11 line HS3 was terminated and HS4 replicated.

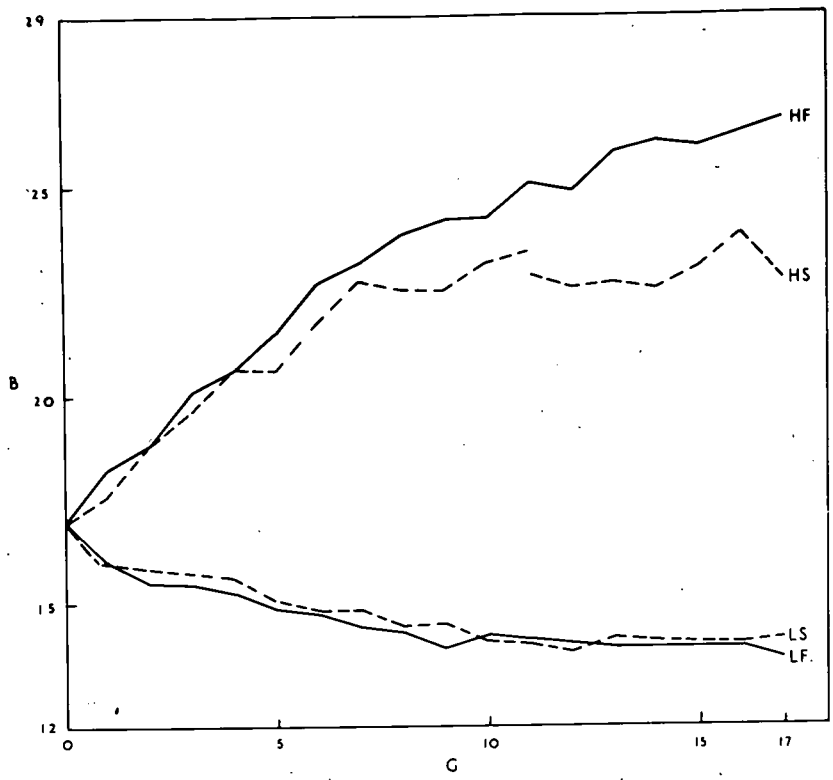


Figure 7 Expt. 2. Selection response. Generation (G) means are average + bristle scores (B) pooled over lines within the 4 Direction x Recombination classes: LF - Low Free; LS - Low Suppressed; HF - High Free and HS - High Suppressed.

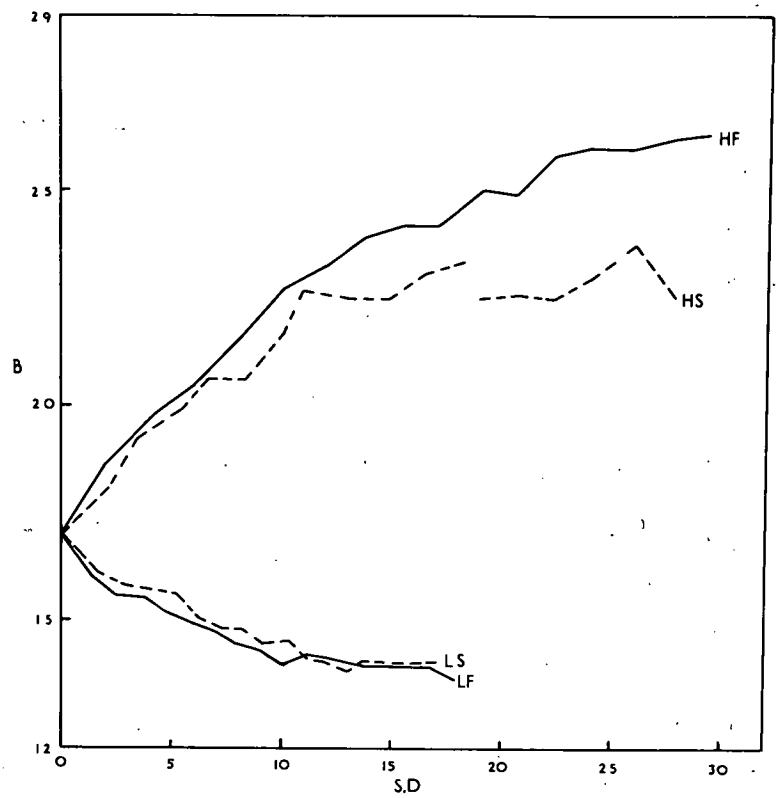


Figure 8. Expt. 2. Response to selection of + scores (B) pooled over lines within each of the 4 D x R regimes plotted against cumulative selection differential (S.D.).

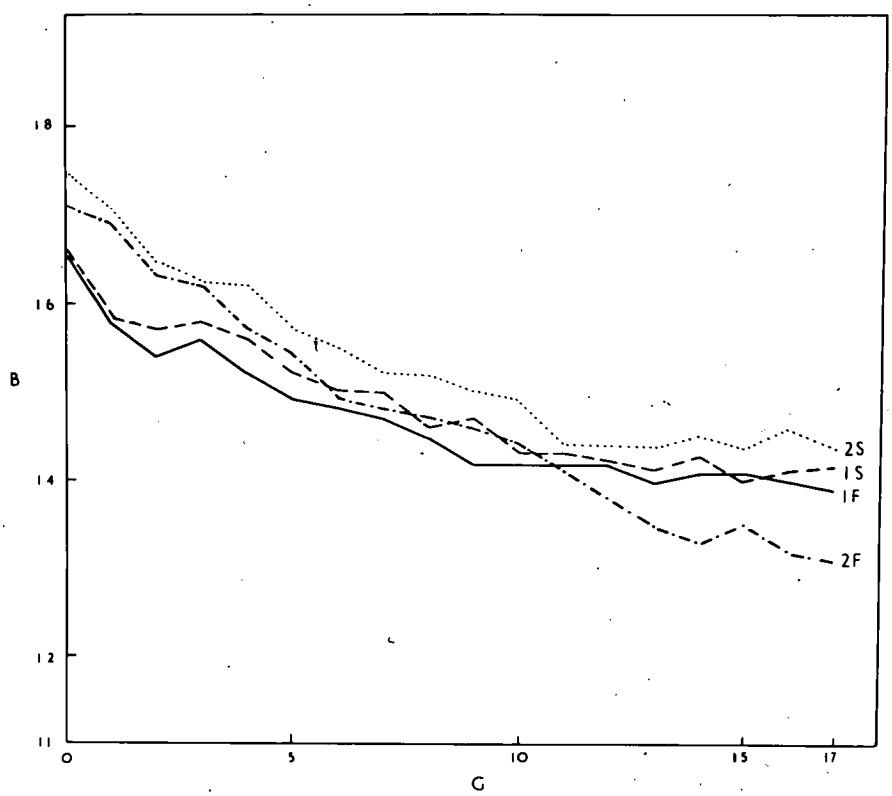


Figure 9 Response to selection in Series 1 and Series 2 Low, Free and Suppressed recombination regimes; 1F, 1S, 2F and 2S respectively. Generation (G) means are average bristle scores (B) of Cy Me males and + females for the F lines and + males and Cy Me females for the S lines.

Gen.	Free	High Suppressed	F - S*	P
11	25.0	23.4	+1.6±1.7	N.S
17	26.6	22.6	+4.0±1.2	0.001
		Low series 1		
11	14.1	14.0	+0.1±0.3	N.S
17	13.6	14.1	-0.5±0.3	N.S
		Low series 2		
11	14.0	14.5	-0.5±0.3	N.S
17	12.8	14.6	-1.8±0.3	0.001

* F - S : Free-Suppressed. Standard errors calculated from between line variances.

Table 6 Experiment 2. Comparison of + means of Free and Suppressed recombination lines after 11 and 17 generations of selection.

Suppression of recombination was apparently effective in reducing response at gen. 17 by 4.0 bristles in the High lines and 1.8 bristles in the Series 2 Low lines. However there was no difference between the Free and Suppressed Series 1 Low lines. Separation of the F and S responses of the High and Series 2 Low lines appears to have occurred between gens. 11 and 17.

At gen. 17 the range of + means for the HF lines was 23.6 to 28.1 and for the HS lines 21.5 to 23.8 bristles giving an overlap of the two ranges of only 0.2 bristles. However, line HS3 which had a mean score of 25.5 when it died out at gen. 11 was well inside the range for the HF lines. Mean + score ranges at gen. 17 for the Series 2 Low lines differ by almost one bristle. They are 12.5 to 13.5 for the LF lines and 14.2 to 15.2 for the LS lines.

From inspection of Figs. 6 and 7, plateauing in the S lines appears to have occurred before gen. 12. Thus selection limits in these lines were estimated by accumulating + means from gen. 12 to 17. These limits and the advances made from the base population before they were reached are shown in Table 7.

Advances are given in bristles and absolute and logarithmic phenotypic standard deviations. Phenotypic standard deviations are/

/are of + scores calculated within cultures at gen. 0. These were 1.87 (400 degrees of freedom) for Experiment 2 lines and 2.06(250 d.f.) for the Series 2 lines. The logarithmic transformation was used to overcome to some extent the association between mean and variance.

Table 7 shows the consequences to selection response of eliminating the contribution of genetic variance within chromosomes II and III by suppressing crossing over. Advance appears greater in the High direction of selection than the Low. In the HS lines it was approximately 3 phenotypic standard deviations and in the LS lines something less than 2. There is a close agreement between the advances of the Series 1 and 2 Low lines. The advances in Table 7 should overestimate those expected from utilising the variance among chromosomes II and III alone. From them, must be subtracted the contributions of chromosomes I and IV as well as that deriving from occasional recombination between suppressor chromosomes and their + homologues.

Half-lives : The number of generations elapsing before half the total selection advance had been achieved in the HS and LS lines was calculated. On a log. scale the means of + segregants at these half-lives were 19.7 and 15.4 for the HS and LS lines and the half lives were between 3 and 4 and between 4 and 5 generations respectively.

Realised heritabilities : Linear regression coefficients of response on cumulative selection differential (realised h^2) were calculated for the 4 segregants within each of the lines over the selection period of 17 gens. These are presented in Appendix Table 1. Since selection differentials were not available for the Series 2 Low lines, realised/

Selection regime	Gen. 0 bristles	Gen. 12-17 bristles	bristles	Advance s.d.*	log (s.d)
HS	17.0	23.2	+6.2±0.51	3.3	2.6
LS (Series 1)	17.0	14.0	-3.0±0.09	1.6	1.9
LS (Series 2)	17.8	14.7	-3.1±0.15	1.5	1.7

* s.d. : standard deviations

Table 7 Experiment 2. Estimated limits and advances in the + segregants of the Suppressed recombination lines. Advances measured in bristles and gen. 0 standard deviations of absolute and log scores.

/realised h^2 estimates could not be made. Responses of + means pooled over the 4 D x R regimes and plotted against cumulative s.d. are shown in Fig. 8. Estimates of the slopes of these responses are LF 0.16±0.01, LS 0.17±0.01, HF 0.32±0.01 and HS 0.25±0.01 so that over the 17 generations of selection, response in the High lines was about 1.5 that of the Low lines for the same amount of selection. The lower realised h^2 for the HS than for the HF lines merely reflected a reduced advance to the selection limit rather than a slower initial rate of response.

Since realised h^2 could not be found for the Series 2 lines, regressions of scaled + means on gen. number were calculated and compared with similar estimates on the Series 1 Low lines. Means were scaled using the transformation log (X - 6) of da Silva (1961) to remove the effect of mean on variance. Coefficients are presented in Table 8.

		Free	Suppressed
Low	Series 1	0.18±0.01	0.19±0.01
	Series 2	0.26±0.02	0.16±0.01

Table 8 Coefficients of linear regression of means of + segregants on generation number for the Series 1 and 2 low lines. The + means were transformed to logarithms.

As seen in Fig. 9 the average slope of the 2 F lines 0.26 is significantly greater ($p<0.01$) than the other three which do not differ among themselves. The continuation of response in the F lines of Series 2 after the F lines of Series 1 had apparently plateaued suggests that an excess of 0.77 units in the gen. 0 variance of the Series 2 over the Series 1 lines may have been genetic.

Generation means of the 4 segregants Cy, Me, Cy Me and + are plotted for the Free and Suppressed recombination lines in Figs. 10 and 11 respectively. Realised h^2 for these segregants can be substituted into the equations representing the contributions of chromosomes I to IV to total response already given for Experiment 1. These equations are then written as follows:-

(i) h^2 (Cy) = dII + 2dIII + dC + dK2

(ii) h^2 (Me) = 2dII + dIII + dC + dK3

(iii) h^2(CyMe) = dII + dIII + dC + dK2 + dK3

(iv) h^2 (+) = 2dII + 2dIII + dC

where the elements on the right hand side represent changes in units from one unit of selection in the average effects of + chromosomes II and III (dII, dIII), suppressor chromosomes Cy and Me (dK2, dK3) and + chromosomes I and IV (dC).

From these 4 equations, 4 sets of 3 independent simultaneous equations can be chosen. These are first solved for the F lines in both directions of selection by substituting in the appropriate realised h^2 estimates from Append. Table 1 and assuming that dK2 and dK3 are zero since Cy and Me are carried in males in these lines. This gives 4 estimates of dK2, dK3 and dC for the 4 sets of 3 equations. The same 4 sets are solved for the S lines in which dC is assumed to be the same as the corresponding set of equations solved for the F lines since the expected response in chromosomes I and IV is independent of suppression of recombination in chromosomes II and III. The sets of 3 equations for the S lines still have 4 unknowns so that solutions can be found for the sum of effects dK2 + dK3 and dII + dIII only.

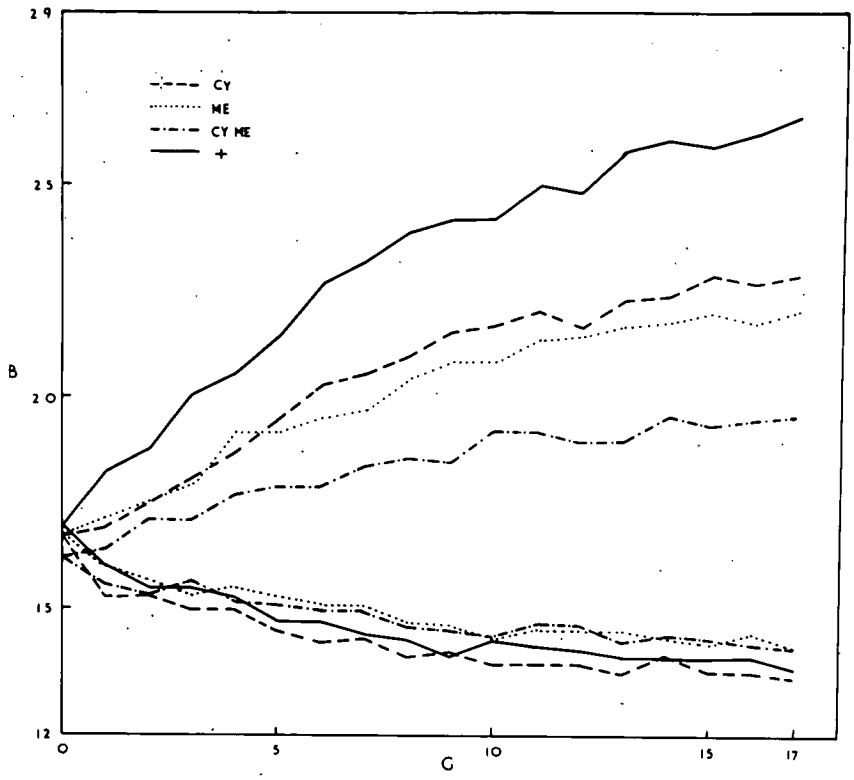


Figure 10 Expt. 2. Response to selection of the 4 segregants Cy, Me, Cy Me and + in the Free recombination lines. Generation (G) means are bristle scores (B) pooled over HF and LF lines.

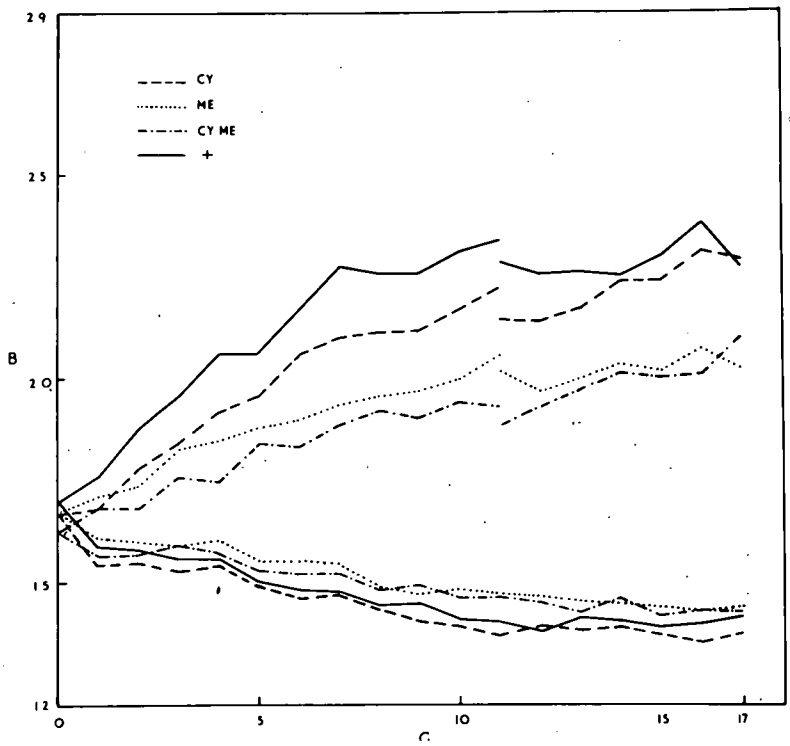


Figure 11 Expt. 2. Response to selection of the 4 segregants Cy, Me, Cy Me and + in the Suppressed recombination lines. Generation (G) means are bristle scores (B) pooled over HS and LS lines.

These responses in chromosome effects for the F and S lines were averaged over the estimates corresponding to each of the 4 sets and are presented in Table 9.

Selection regime	Chromosome response II dII	III dIII	II + III dII + dIII	I + IV dC	Cy + Me dK2 + dK3
LF	-0.01	-0.04	-0.05	-0.06	-
LS	-	-	-0.06	-0.06	-0.01
HF	+0.09	+0.12	+0.21	-0.10	-
HS	-	-	+0.12	-0.10	+0.08

Table 9 Experiment 2. Changes of chromosomal effects due to one unit of selection; estimated from realised $\underline{h}^2$ of the segregants Cy, Me, Cy Me and +.

Since they are calculated from realised $\underline{h}^2$ they should be largely free from the effects of scale. The following observations can be made.

(i) Chromosome III contributes more to response than chromosome II in both directions of selection.

(ii) The combined responses of chromosomes II and III are reduced by suppression of recombination in the High line but not in the Low.

(iii) Residual response dC is fairly high and negative in the Low lines indicating some contribution from chromosomes I and IV. In the High lines, on the other hand, dC is still negative suggesting a change in these chromosomes opposite in direction to that of selection. This apparent anomaly can be explained by dominance of the Me chromosome evidence for which is presented later. Slopes of the Cy Me and Me responses are less than would be expected from the model and the observed slopes of the Cy and + segregants.

(iv) From estimates of dK2 and dK3 it appears that Cy and Me have gained considerably in effect in the HS lines but almost negligibly in the LS lines through recombination with balanced + chromosomes in females.

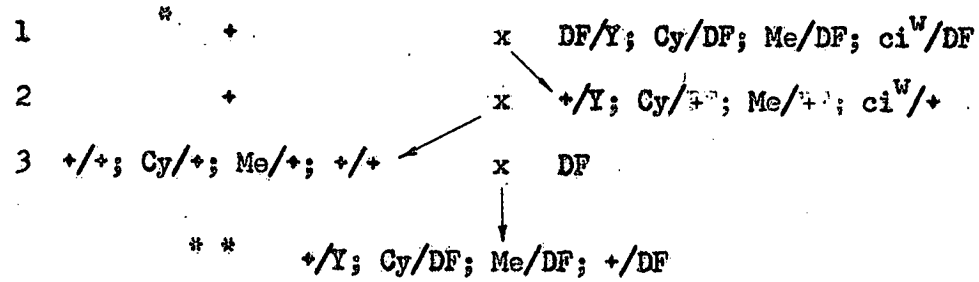
INDIVIDUAL CHROMOSOME RESPONSES

Chromosomes I and IV

Method

Experiment 1 : Since chromosomes I and IV of these lines had been substituted at the beginning of the experiment for those of isogenic DF they were not measured since they were not expected to contribute to response.

Experiment 2 : The first chromosomes of these lines were a sample of those in the Kaduna population and were expected to respond under selection. Their effects were measured at the beginning and end of selection by substituting them into a DF background as outlined in Fig. 12.



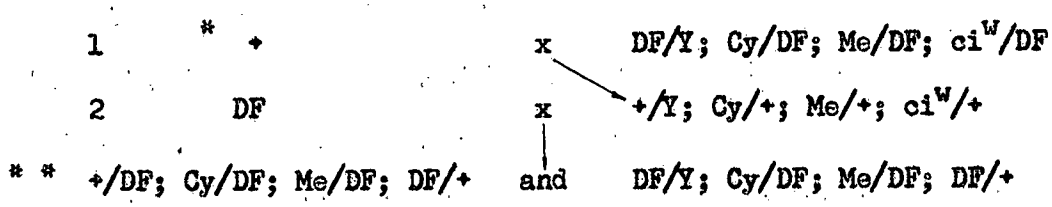
* + females from selected lines

* * males scored differed between lines in chromosomes I and IV

Figure 12 Experiment 2. Substitution of chromosomes I from selected lines into an isogenic background for measurement of change under selection.

The estimates of differences between lines in chromosome I effects as measured in the male offspring of mating 3 are confounded with those of chromosome IV.

To check on responses in chromosome IV, samples were extracted from the lines at the end of the experiment and substituted into an isogenic background for measurement. The substitution procedure is outlined in Fig. 13. In all matings a single bottle culture per selected line was used with 10 parents of each sex.



* + females sampled from selected lines

* * Male scores estimated chromosome IV effects

Female scores estimated heterozygous chromosome I effects

Figure 13 Substitution of chromosome IV from selected lines into an isogenic background for measurement of selection response.

Results

Experiment 2 : Appendix Table 2 shows the line means for substituted chromosomes I at the beginning and end of selection and of chromosome IV at the end of selection. The effects of chromosome I substitutions are summarised in Table 10. Differences are given between the effects of substituting first chromosomes (x) from (i) DF, (ii) All lines at gen. 0 and the (iii) High and (iv) Low lines at gen. 17 into the background X/Y; Cy/DF; Me/DF; +/DF.

Gen.	Chros. I Origin	Mean	Difference		p
0	(i) DF	11.05±0.06	(i) - (ii)	-0.86±0.08	0.001
"	(ii) All	11.91±0.05	(ii)- (iii)	+0.38±0.08	0.001
17	(iii) Low	11.53±0.06	(iii)- (iv)	-0.34±0.08	0.001
"	(iv) High	11.87±0.06	(iv)- (ii)	-0.04±0.08	N.S.

Table 10 Expt. 2. Measurement of response to selection of chromosomes I. Means are of first chromosomes sampled from DF, the base population and the High and Low lines and substituted into isogenic males.

At gen. 17 there was a difference of 0.34 bristles between the High and Low lines but none between the Free and Suppressed lines within directions of selection. Thus the slight enhancement of crossing over found in the presence of Cy and Me has not led to increased response. The greatest difference in Table 10 is that of 0.9 bristles between the first chromosomes of DF and all lines at gen. 0.

Although genetic change cannot be isolated from environmental change over the 17 generations of selection, the first chromosomes of the Low lines appear to have responded by about - 0.4 bristles and of the High lines not at all. At the end of the selection period no differences were found among lines in their chromosomes I when measured heterozygous with the DF first chromosome; the mean of all females scored being 12.04 ± 0.06. Males from the same mating which produced these females were scored to estimate between line differences in chromosome IV effects. No difference could be detected among the lines or the 4 D x R regimes so that the chromosome I changes measured were not confounded with changes in the fourth chromosome. The average of all males heterozygous selected chromosome IV/DF was 10.91±0.05 bristles. A sample of DF/Y; Cy/DF; Me/DF; DF/DF males was found to have a mean score of 10.14 ± 0.08 giving the effect of substituting a DF for a selected chromosome IV as + 0.77 ± 0.09 bristles.

A comparison of the effects of chromosome I in the High and Low lines with the difference between the means of + males in the High and Low lines indicates that this chromosome contributed only about 3% of the overall difference. Louw (1966) found that chromosome I accounted for 20% of the difference between a High (C3A) and a Low (DF) bristle line both originating from the Kaduna population. Of this difference 60% appeared to be due to a single high gene. The small difference observed between the first chromosomes of DF and those of the selected lines at the beginning and end of selection suggests that this gene must be rare in the Kaduna population since it was evidently not sampled at the establishment of these lines. From the means of males with High, Low and DF first/

/first chromosomes in Table 10 the expected difference between females heterozygous for chromosome I High/DF and Low/DF can be calculated as

$$(11.87 + 11.05)/2 - (11.53 + 11.05)/2 = 0.21 \pm 0.06$$

assuming additivity and dosage compensation. That this difference was not detected suggests a degree of dominance of the DF over the selected first chromosomes. This reflects the dominance of the DF over the C3A first chromosome found by Louw (1966).

Selected chromosomes II and III

Method

The change in effect of these chromosomes under selection has already been estimated from a consideration of the realised h^2 of the 4 segregant classes. These estimates, however, assume response to be linear over the 17 gens. of selection. This is clearly not the case for the HS lines which begin to plateau at about gen. 10. In addition to these estimates, the effects of substituting chromosomes II and III for their homologous suppressors SII and SIII was estimated in 2 ways for each generation of selection. This was done in the following way by finding the difference in bristle score between segregants emerging from the selection lines.

Chromosome II	estimate X	+	-	SII
	estimate Y	SIII	-	SII; SIII
Chromosome III	estimate X	+	-	SIII
	estimate Y	SII	-	SII; SIII

The regression of estimate X on Y (bXY) and the correlation between the two (rXY) was calculated for the lines of Experiment II over the 17 generations of selection. Homogeneity among lines for these estimates,/

/estimates, except for chromosome II in the Low lines, enabled them to be pooled within directions of selection. These are given in Table 11.

		Chromosome	
		II	III
LOW	b(XY)	N.S. *	+ 0.4
	r(XY)	N.S.	+ 0.4
HIGH	b(XY)	+ 0.5	+ 0.7
	r(XY)	+ 0.6	+ 0.8

* N.S. - Not significant ($p < 0.05$)

Table 11 Expt. 2. Agreement between effects of substituting selected chromosomes II and III into 2 genetic backgrounds, X and Y measured as the regression of X on Y (b(XY)) and correlation between X and Y (r(XY)).

Two points of interest arising from these estimates are: (i) r(XY) rises with the magnitude of X and Y mainly because their standard errors remain fairly constant. (ii) Y is always less than X i.e. a suppressor chromosome has a greater effect substituted into a + background than into a background possessing a non-homologous suppressor chromosome. The generally high correlation between the two substitutions X and Y illustrated additivity of chromosomes II and III in bristle effect and led to their being averaged to estimate the effects of chromosomes II and III.

Results

Experiment 1 : Table 12 shows the effects of chromosomes II and III substitutions at the beginning and end of selection. Since there was no difference between estimates for the Free and Suppressed recombination lines, they were pooled within directions of selection.

	Estimate *	Gen. 0 All lines	Gen. 5 High	Low
(i)	+ - Cy	+0.38±0.09	+0.74±0.14	+0.29±0.12
(ii)	Ubx - Cy Ubx	+0.36±0.09	+0.80±0.17	+0.04±0.12
** (iii)	+ - Cy (DF)	-	+0.68±0.11	+0.37±0.11
(iv)	+ - Ubx	-0.21±0.09	-0.74±0.17	-0.42±0.13
(v)	Cy - Cy Ubx	-0.23±0.09	-0.67±0.14	-0.67±0.11

* Estimates (i), (ii) and (iii) measure chromosome II and estimates (iv) and (v) chromosome III effects.

** Measurement of chros. II substituted into DF background.

Table 12 Experiment 1. Estimates of substitution effects of chromosomes II and III at the beginning and end of selection.

Averaging estimates (i) and (ii), chromosome II effects at gen. 0 were +0.37 ± 0.06 bristles. In 5 generations of selection they fell to +0.16±0.08 in the Low lines and rose to +0.77±0.10 in the High lines. Estimate (iii) measures response in chromosomes II by substitution into a DF background as outlined in Fig. 14. Responses were +0.68±0.1 for the High and +0.37±0.06 for the Low lines.

1 *	DF/DF; S/S; Ubx/S; DF/DF	x	DF/Y; Pm/DF; Sb/DF; DF/DF
2	DF/DF; Cy/DF; DF/DF; DF/DF	x	DF/Y; Pm/S; Ubx/DF; DF/DF
3	DF/DF; Cy/S; DF/DF; DF/DF	x	DF/Y; Cy/S; DF/DF; DF/DF
**	DF/DF; S/S; DF/DF; DF/DF		DF/Y; S/S; DF/DF; DF/DF
	DF/DF; Cy/S; DF/DF; DF/DF		DF/Y; Cy/S; DF/DF; DF/DF

* Sample of Ubx males from each selection line

** Measurement of second chromosome S homozygous and heterozygous for Cy in a DF background.

Figure 14 Experiment 1. Substitution of chromosomes II after 5 gens. of selection into an isogenic background for measurement.

Estimates (iv) and (v) for chromosome III averaged -0.22±0.06 at gen. 0 and fell to -0.54±0.06 in the Low lines at gen. 5. Unexpectedly, the effects of chromosome III in the High lines also declined to -0.70±0.10. The reason for this lies in the abnormally high scores of the Ubx and Cy Ubx segregants at gen. 5. This supports the previous observation based on realised h^2 that the bristle effect of the Ubx chromosome has been altered in both the HF and HS line through recombination with selected wild chromosomes.

Experiment 2 : The substitution effects of chromosomes II and III were averaged over the 2 backgrounds X and Y into which they were substituted and over the lines within each of the 4 D x R regimes and are presented for each generation of selection in Appendix Tables 3 and 4. They are also plotted against generation number in Figures 15 and 16. In the HF lines the chromosome II effect rose from 0.40±0.16 to 3.13±0.19 bristles after 17 gens. of selection while the chromosome III effect increased from 0.35±0.17 to 3.89±0.16 bristles over the same period. Corresponding changes in the Low direction could only be calculated for the Series 1 lines. They were, for the LF lines, 0.40±0.16 to 0.02±0.17 for chromosome II and 0.35±0.17 to -0.67±0.16 for chromosome III. In the Suppressed lines, selection limits for chromosomes II and III were estimated from inspection of Figs. 15 and 16. Except for chromosome II in the HS lines, estimates were derived by averaging over lines from gens. 11 to 17. The limit for chromosome II in the HS lines was estimated from gens. 7 to 11 because of apparent change in the effect of Cy through crossing over/

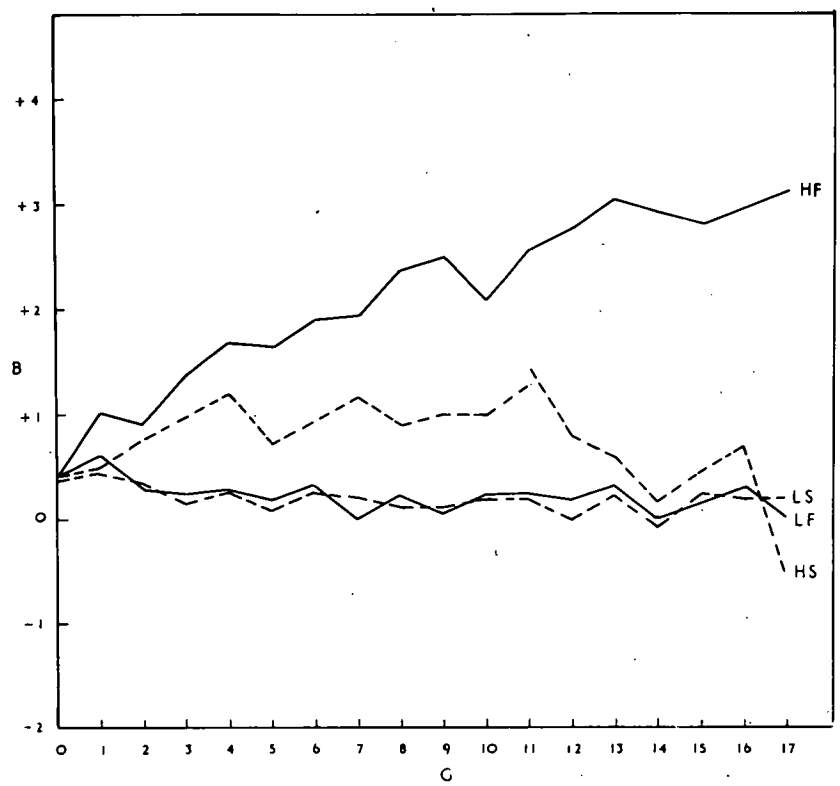


Figure 15 Expt. 2. Change under selection in the effect of substituting a single chromosome II for a homologous suppressor chromosome. Generation (G) means in bristles (B) are the average of substitution into 2 genetic backgrounds X and Y pooled over lines within the 4 D x R regimes.

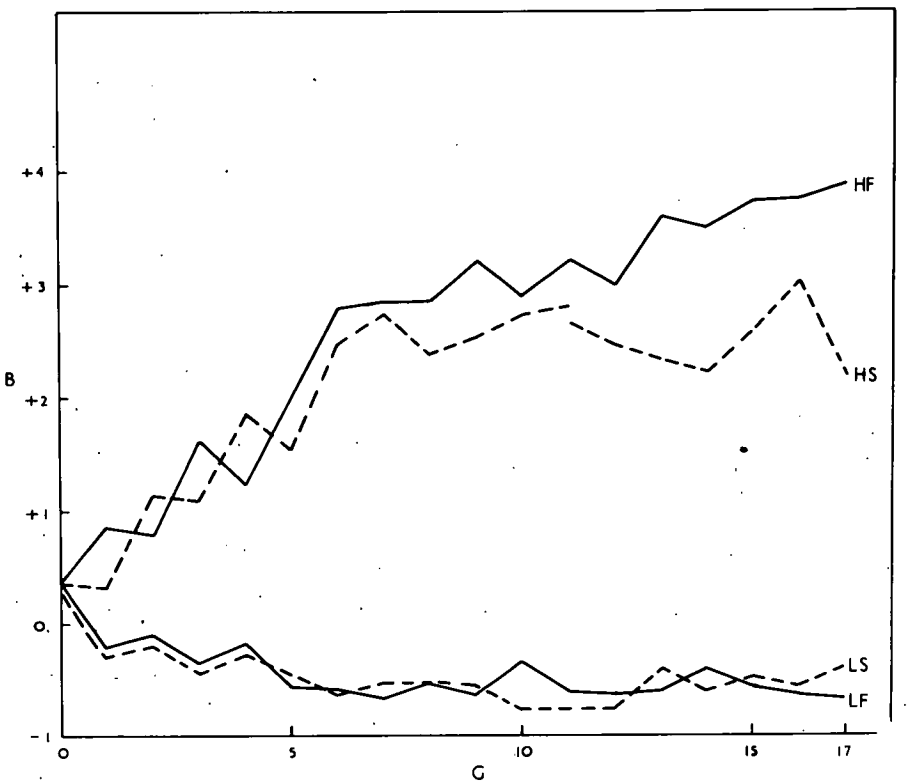


Figure 16 Expt. 2. Change under selection in the effect of substituting a single chromosome III for a homologous suppressor chromosome. Axes are the same as in Fig 15.

/over in the latter stages of selection. This limit was chosen since response seemed plateaued during this period. Cumulative means of the effects of chromosomes II and III were also estimated over gens. 11 to 17 for the Free recombination lines. These are clearly not limits for the HF lines but may be for the LF. Differences between gen. 0 and these later cumulative means are shown as advances for the 4 D x R regimes in Table 13.

As expected, the relative differences among the responses agree closely with those estimated from realised $\underline{h}^2$ in Table 9. An examination of responses for the LF and HF lines shows a higher contribution from chromosome III than chromosome II to total response in both directions. The ratio of chromosome III to chromosome II contributions is 3.9 for the LF and 1.3 for the HF lines. There is assymmetry of response for both chromosomes II and III. This is greater for chromosome II than chromosome III. Ratios of response in the High to that in the Low F lines are 10.3 for chromosome II and 3.4 for chromosome III. Advances in chromosomes II and III over the 17 gens. of selection are the same for the LF and LS lines. In the HS lines, on the other hand, advances in chromosomes II and III measured in this way were only 0.25 and 0.67 respectively of those in the HF lines.

(a)

DF/DF; Cy/+; Ubx/+; DF/DF x DF/Y; Pm/DF; Sb/DF; DF/DF

DF x DF/Y; Cy/DF; Ubx/DF; DF/DF

DF/Y; DF/DF; Ubx/DF; DF/DF *

* Ubx segregants measured over 5 gens. of backcrossing to DF.

(b)

+/+; Cy/+; Me/+; +/+ x DF/Y; Xa/DF; DF ; ci^W/DF

DF x +/Y; Cy/DF; Me/DF; ci^W/DF

DF x DF/Y; Cy/DF; Me/DF; ci^W/DF

DF/Y and DF/DF; Cy/DF; DF/DF; DF/DF **

** Both sexes of Cy and Me in DF were scored.

Figure 17 Measurement of suppressor chromosomes in a DF background at the end of selection. (a) Ubx from Expt. 1 and (b) Cy and Me from Expt. 2.

Seln.	Chromosome II	Chromosome III
LF	-0.24 ± 0.03	-0.93 ± 0.03
LS	-0.26 ± 0.04	-0.92 ± 0.04
HF	+2.48 ± 0.12	+3.18 ± 0.12
HS	+0.66 ± 0.11	+2.14 ± 0.11

Table 13. Experiment 2. Advances under selection in the effects of chromosomes II and III.

Suppressor chromosomes II and III

Method

A check was made to see if these had altered their effects through exchange with their wild homologues during selection. Over the 17 gen. selection period of Expt. 2 a total of 4250 potential parents of the Suppressed lines were scored whose Cy and Me chromosomes had derived from Cy Me mothers. Thus, with estimated recombination frequencies of 2% for Cy and 0.2% for Me, about 85 of these flies would be expected to carry an altered Cy and about 8 an altered Me chromosome.

As selection proceeded the difference in effect between the + chromosomes and their homologous suppressors increased. Thus, in the latter stages of selection, exchange of segments between a + chromosome and its homologous suppressor through rare crossing over in the S lines might be expected to produce a selectively advantageous suppressor and a disadvantageous + chromosome. Such an altered + chromosome should then be eliminated from and an altered suppressor incorporated into the S lines under selection.

That this has occurred, is suggested by the high score of Ubx segregants at the end of selection in Experiment 1 and the high values of dK2 + dK3 recorded in Table 9 for the HS lines of Experiment 2. To measure the bristle effects of the suppressor chromosomes, a sample from each selection line was substituted into a DF background as outlined in Figure 17 (a) and (b). An additional check on the integrity of the/

/the Experiment 2 suppressor chromosomes was made by examining the retention of recessive marker genes pr in Cy and ca in Me. This was done by sampling Cy and Me segregants from each line and backcrossing to the al sp and ru ca stocks respectively.

Results

Experiment 1 : The Ubx chromosome alone was measured due to the difficulty of distinguishing Cy from Cy Ubx segregants in the latter stages of selection. Mean scores of Ubx chromosomes substituted into DF were pooled over lines within the 4 D x R classes. They were HF 10.7±0.1, HS 10.6±0.1, LF 9.0±0.1 and LS 9.0±0.1. Clearly the Ubx chromosome has been altered since its derivation from a single male at the beginning of the experiment. Most likely, this alteration occurred during matings 4 and 5 of the substitution procedure of Figure 2 where both Cy and Ubx occurred together in females. These were the only opportunities for recombination in the Ubx chromosome in the HF lines since, during selection, suppressors were carried through males only.

Experiment 2 : The effects of Cy and Me chromosomes sampled from the 20 selection lines at gen. 17 and substituted into DF backgrounds are shown in Table 14. Estimates were pooled over lines within each of the 4 D x R selection regimes.

Selection regime	Suppressor chromosome	
	Cy	Me
LF	8.46±0.17	9.84±0.17
LS	8.36 "	9.89 "
HF	8.14 "	9.94 "
HS	8.89 "	9.87 "

Table 14 Expt. 2. Measurement of Cy and Me chromosomes sampled from the selection lines at gen. 17 and substituted into a DF background.

There were significant differences ($p < 0.01$) among the Cy but not among the Me means due to the high score of Cy in several of the HS lines. Evidently Cy has obtained a segment of high bristle effect through recombination with selected + chromosomes. This explains the apparent decline in the effect of chromosome II in the latter stages of selection shown in Fig. 15 due to the convergence of scores of Cy and non-Cy bearing segregants. This seems not to have occurred in all HS lines as is shown in Fig. 18. Here, the average chromosome II substitution effects are plotted for the last 11 generations of selection. The only lines apparently not affected are the replicated lines HS4A and HS4B. Replacement of the original Cy by the altered Cy chromosome appeared to be still continuing when the experiment was terminated at gen. 17 since the means of Cy and Cy Me segregants were increasing at a faster rate than those of the + and Me segregants, (Fig. 11). This illustrates how renewed response can result from a recombination/

/recombination event in a specific chromosome in the same way that Sismanidis (1942) was able to attribute accellerated responses to scutellar bristle selection to specific chromosome recombinations. Assays carried out on the retention of ca by the Me chromosomes in the Experiment 2 lines found no alteration of the Me chromosomes in this region. However, in the Series 2 Low lines ca was observed among the + segregants of one line after 14 gens. of selection indicating a selectively advantageous exchange between a + and a Me chromosome. In only one line HS1 was pr found to be absent from the Cy chromosomes after 17 gens. of selection. In this line all Cy chromosomes sampled were without pr and had their effects on bristle score increased indicating a complete replacement under selection of the original by the altered Cy chromosome.

As shown in the crossover tests of the Cy chromosome, all crossovers observed involved the region near pr and the centromere and most were single crossovers between the left and right arms. If a whole arm of the Cy chromosome had been exchanged with that of a + chromosome in this way, the relatively large change in the bristle effects of the Cy chromosomes observed in 3 of the HS lines would have been expected.

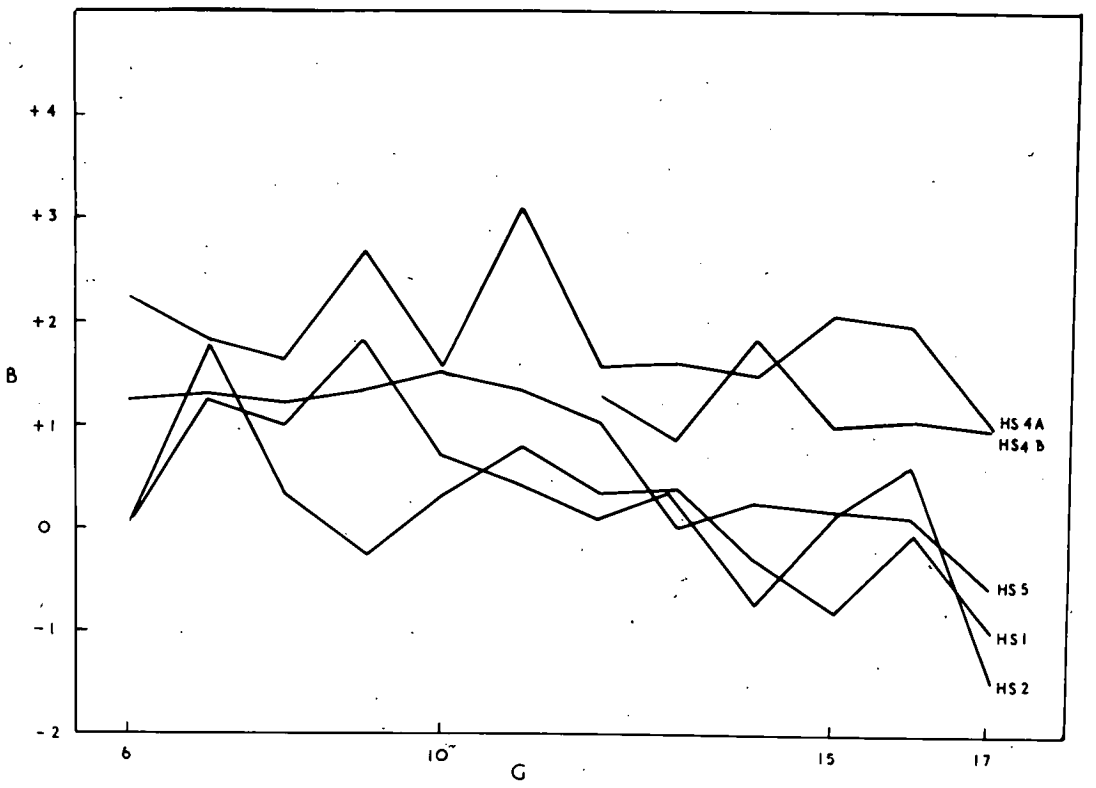


Figure 18 Expt. 2. Response in chromosome II substitution effect (bristles B) for the 5 HS lines from gen. 6 to gen. 17 (G) of selection.

VARIATION

Phenotypic variances These were calculated for the 4 segregant classes (Cy, Me, Cy Me and +) of the Experiment 2 lines for the 17 generations of selection. Variances of + segregants of all lines pooled over generations in 4 sections of the total selection period are shown in Appendix Table 5. In Table 15 are presented the variances of the 4 segregants pooled over lines at gen. 0 and for the 4 D x R regimes at gen. 17. The variances of the + segregants are again shown for the 4 regimes plotted against generation number in Fig. 19.

In the Low direction, variances of both Free and Suppressed recombination lines declined with the means as expected (Allan (1963)). Whilst variances did rise in the High lines, their association with generation mean was much less marked. As seen in Append. Table 5 wide differences occur among the variances of individual lines. In the 14 to 17 gen. period they ranged from 6.72 bristles^2 for HS1 to 3.80 for HS5. To eliminate the effect of mean on variance, coefficients of variation (C.V.) were calculated each generation. Figures 20 (a) and (b) plot the average C.V's for + segregants of the 4 D x R regimes throughout 17 gens. of selection. In both directions of selection there is a marked decline in C.V. particularly in the early stages of selection. Changes in C.V. for both Free and Suppressed Low lines are closely parallel throughout. In the High direction, however, there is a sharp rise in the C.V's of the Suppressed lines between gens. 11 and 17 which was largely due to an increase in variance of line HS1. This was one of the lines in which the Cy chromosome had undergone some recombination in the latter stages of selection.

Gen.	Seln. regime	Segregant			
		Cy	Me	Cy Me	+
0	All	2.91	2.63	2.29	3.48
17	LF	1.26	1.27	0.95	0.90
"	LS	1.26	1.07	1.21	0.99
"	HF	4.06	3.38	2.63	3.50
"	HS	5.76	4.20	5.11	5.59

Table 15 Expt. 2. Phenotypic variances of the 4 segregant classes at the beginning (gen. 0) and end (gen. 17) of selection. Values are pooled over lines within each of the 4 D x R regimes. The numbers of degrees of freedom are about 400 for gen. 0 and 128 for gen. 17 values.

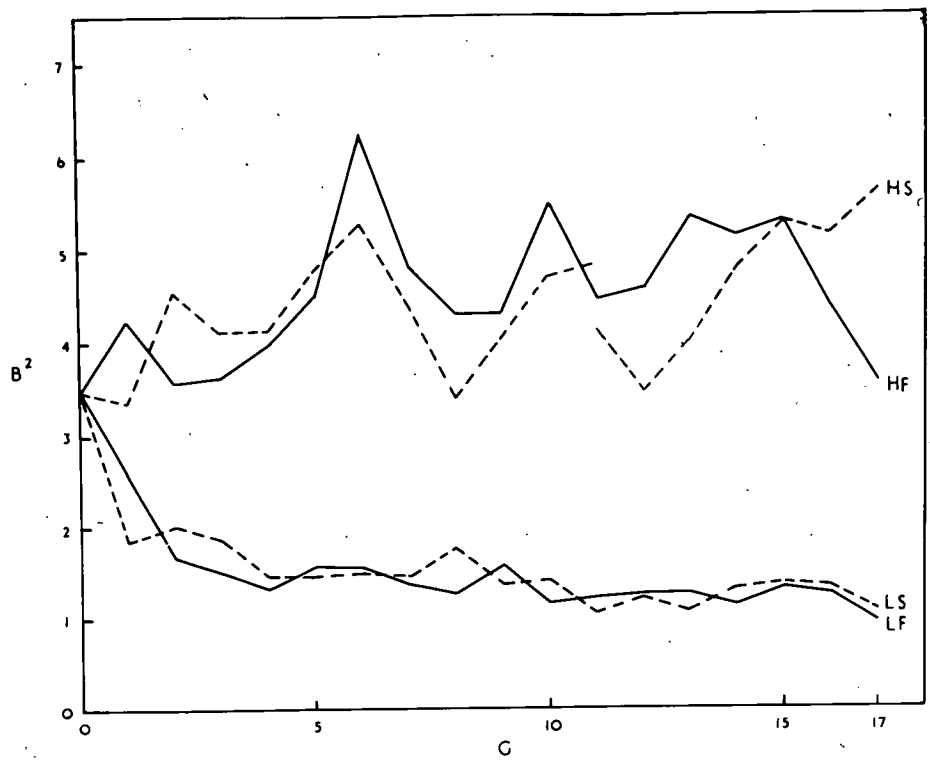


Figure 19 Expt. 2 Change in phenotypic variance of + segregants under selection. Generation (G) means are in bristles ^{2} (B^2) pooled over lines within each of the 4 D x R selection regimes.

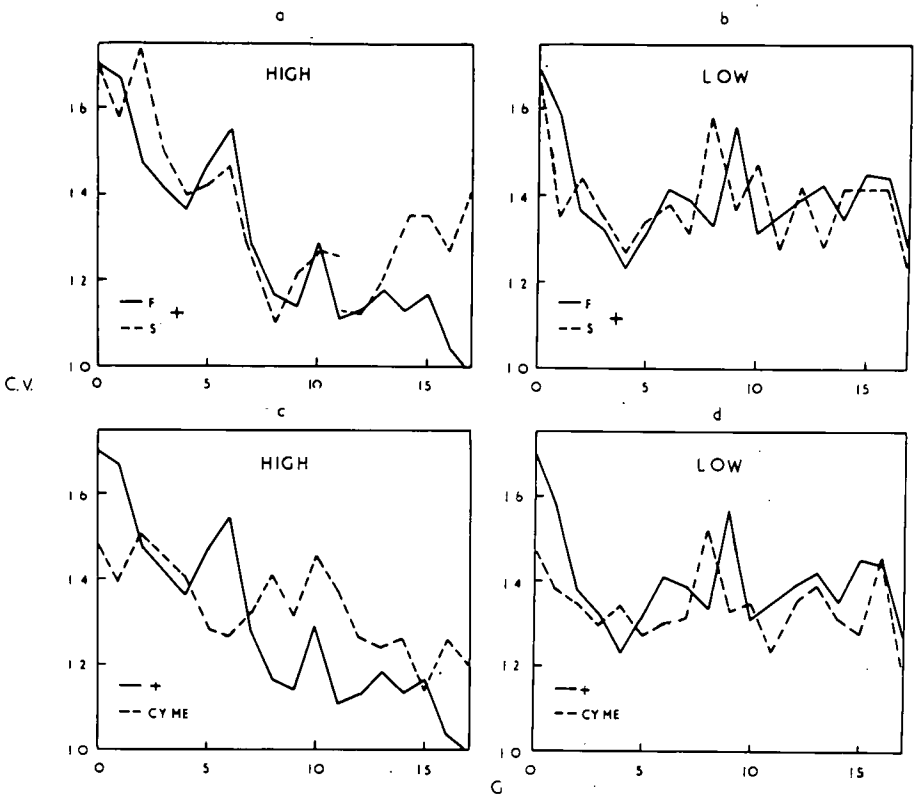


Figure 20. Expt. 2. Change in coefficient of variation (C.V.) over 17 generations (G) of selection. C.V's of + segregants in the Free (F) and Suppressed (S) lines are shown for High selection in (a) and Low in (b). C.V's for + and Cy Me segregants in the Free recombination lines only are compared for the High lines in (c) and the Low in (d).

Genetic variances It is shown in Appendix 2 that, assuming random mating and additivity of gene action, the substitution of a suppressor chromosome for one member of a pair of + chromosomes segregating in a line is expected to halve the contribution of that chromosome to total genetic variance. Thus one half the genetic variance due to that chromosome should be estimable from the difference between the variances of suppressor and + segregants since they share the same pool of + chromosomes. If, however, genes on the suppressor chromosome are dominant to their wild alleles, this substitution of the suppressor for the + chromosome will reduce its genetic variance by more than a half. Two independent estimates of the reduction in variance through substitution of + chromosomes II and III for their suppressor homologues in the unselected base population are given in Table 16.

	Estimate	Variance (B^2)
	Chromosome II	
(i)	+ - Cy	0.57
(ii)	Me - Cy Me	0.34
	mean	0.45
	Chromosome III	
(i)	+ - Me	0.85
(ii)	Cy - Cy Me	0.62
	mean	0.73

Table 16 Expt. 2. Estimates of half the genetic variance of chromosomes II and III. Estimates are based on the difference in variance between segregants in the unselected base population.

Bias through the correlation of mean and variance should be absent since Cy and Me segregants had the same score in this generation. The average reduction in variance effected by substituting + chromosome II for Cy was 0.45 units and chromosome III for Me, 0.73 units. A difference between estimates (i) and (ii) of 0.23 units estimates the interference of background genotype. Thus, summing over the substitution effects of chromosomes II and III gave 1.19 units as an estimate of half the genetic variance contributed by these chromosomes and an estimate of (2X1.19)/3.48 = 0.68 for the heritability of the sum of their effects. This is clearly too high considering the rate of initial selection response (realised h^2) which would also utilise chromosome I variance. One explanation is that the suppressor substitution, particularly that of chromosome III, reduces the variance by more than a half suggesting that the suppressor chromosomes have dominant alleles at some of the loci contributing to genetic variance in bristle score.

A further examination of the effect of suppressor chromosomes on variance was made by comparing the variances of the four types of progeny emerging from the following mating:

Kaduna x DF/Y; Cy/DF; Me/Ubx; DF/DF

Progeny were produced in 6 cultures each from 10 pairs of parents. All male parents were derived from a single male line and the Kaduna female parents were sampled from the cage. The mean scores and variances of males of the 4 progeny types pooled over cultures are presented in Table 17.

Progeny type	No.	mean	variance
DF/K; Ubx/K	224	15.4	2.39
DF/K; Me/K	189	14.7	1.85
Cy/K; Ubx/K	218	16.2	2.40
Cy/K; Me/K	216	15.3	1.50

Table 17 Effect on variance of + chromosomes II and III sampled from the Kaduna population (K) of balancing with suppressor chromosomes in a DF background.

A comparison of Ubx and Cy Ubx progeny with Me and Cy Me shows that Ubx heterozygotes are approximately 1.4 times more variable than Me heterozygotes. On the other hand, a comparison of Ubx with Cy Ubx and Me with Cy Me shows no effect of the substitution of Cy for DF on the variance of the + second chromosomes.

These observations support the conclusion that Me exhibits some dominance over the bristle effects of the + chromosomes. On the somewhat tenuous assumption that Ubx displays no such dominance, the substitution of Me for + homologues reduces variance due to the third chromosome by about 0.7 and not the expected 0.5. Correcting for this dominance, genetic variances of single chromosome II and III effects estimated from differences between segregants are now 0.45 and 0.51 and their heritabilities 0.26 and 0.29 respectively. These are still considered to be overestimates in view of the heritabilities of all chromosome effects realised under short term selection and shown in Table 5. These averaged 0.35 over both directions of selection. High values of 0.43 and 0.46 for the variances of chromosomes II and III were/

/were also obtained in the same way in the first selected generation. It seems probable that the variances of the suppressor heterozygotes have lower environmental components than those of the homozygotes from which they are subtracted, a commonly observed property of heterozygotes Lerner (1954).

In Figs. 20 (c) and (d) are plotted the mean coefficients of variation for the + and Cy Me segregants of the High and Low Free recombination lines. For both High and Low lines C.V's for Cy Me were initially lower than those for + segregants. However, after 2 or 3 generations these converged. Thence, in the Low lines they remained about equal to the end of the experiment but in the High lines the C.V's of the + segregants continued to decrease at a faster rate than those of the Cy Me segregants.

The convergence of C.V's for + and Cy Me segregants would be expected as that part of the genetic variance accounting for the difference between them is exhausted under selection. Two explanations can be invoked for the higher C.V's for Cy Me than + segregants at the end of selection in the High lines. These are (i) The C.V. overcorrects for the effect of mean on variance at high mean scores and (ii) the environmental variance of Cy Me segregants increased more rapidly than that of the + segregants as selection proceeded.

REPRODUCTIVE FITNESS

Viability Indexes

Method

From the findings of Latter and Robertson (1962) a reduction was expected in the viability of + flies due to inbreeding depression during selection. A viability component of fitness was measured each generation from the ratio of emergence of + flies to the emergence of flies heterozygous for + and suppressor chromosomes. Ratios were obtained for each line of Experiment 2 by counting the 4 segregants in samples of 125 of both sexes taken from all flies emerging over the first 4 days. This standard sampling period was necessitated by the findings presented in Appendix 3. This shows how the measured ratio of emergence of the 4 segregants Cy, Me, Cy Me and + is dependent upon which parent possesses the Cy and Me chromosomes and the length of time between first observed emergence and measurement.

The following ratios were calculated each generation to examine changes in the viability of zygotes homozygous + for chromosomes II and III alone and together.

1	Homoz. + chromosome II	/	Heterozygous + chromosome II
	i.e. + and Me	/	Cy and Cy Me
2	Homoz. + chromosome III	/	Heterozygous + chromosome III
	i.e. + and Cy	/	Me and Cy Me
3	Homoz. + chros. II and III	/	Heterozygous chroms. II and III
	i.e. +	/	Cy Me

Although they are not independent, their values give an indication of the separate and combined contributions of chromosomes II and III to viability change. These ratios are called Viability Indexes (V.I's). They are roughly analagous to the Competitive Indexes of Knight and Robertson (1957) who measured competition between zygotes to be tested and an isogenic marked tester stock as the ratio of their emergence from the same culture. The difference in this study lies mainly in the nature of the tester and the environments under which competition is measured. Tester zygotes are constant and differ from the tested only in the suppressor chromosomes which they carry and competition among zygotes includes a phase in a common maternal environment commencing at fertilization.

Results

The 3 estimates of V.I's for the Experiment 2 lines at the beginning, middle and end of the selection period are shown in Appendix Table 6. Estimates at the beginning were made from emergence counts in the unselected base population, in the middle by averaging counts from gens. 7 and 8 and at the end from gens. 16 and 17. The V.I's for each of these 3 points in the selection period pooled over lines within the 4 D x R regimes are plotted for chromosomes II, III and II + III in Fig. 21 (a), (b) and (c).

Fig. 21 (c) shows that flies homozygous + for chromosomes II and III declined in V.I. by about the same amount in the LF, HF and HS lines during selection. The V.I's of the LS lines, on the other hand, increased markedly over the same period. By inspection of Figs. 21 (a) and (b) it/

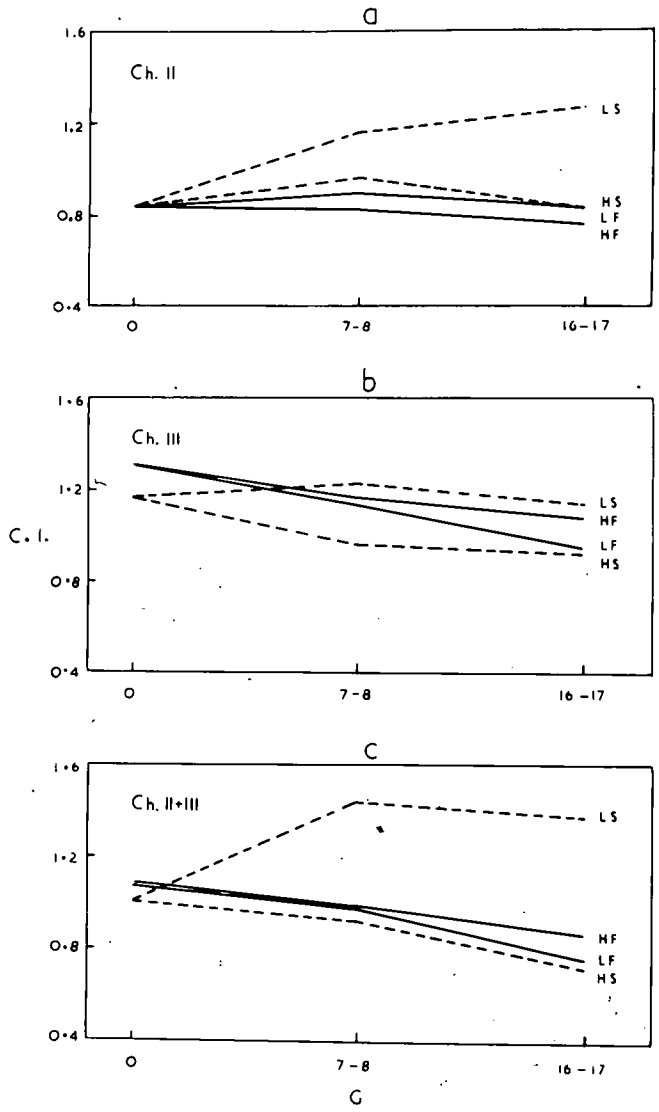


Figure 21 Expt. 2. Change in viability indexes (C.I.) for chromosomes II, III and II + III. C.I's are plotted at 3 points in the selection period and are pooled over lines within the 4 D x R selection regimes (LF, LS, HF, HS).

/it is seen that most of the decline in V.I's of the HS, LF and HF lines appears to have derived from a reduction in emergence of flies homozygous + for chromosome III. There was no significant decline in those homozygous + for chromosome II. The increase in V.I's of the LS lines resulted from an increase in the ratio of emergence of Non-Cy to Cy segregants as is seen from Fig. 21 (a).

The general uniformity of decline in V.I's among the HF, HS and LF lines regardless of direction of selection or degree of recombination suggests that most of the observed decline was due to inbreeding depression and little, if any, to unfavourable bristle viability associations resulting from pleiotrophy or linkage. The low V.I. of 0.31 for chromosomes II + III in line HS4 at the end of selection reflects a very low emergence of ~~Cy Me~~ + segregants possibly due to interaction between the two ~~suppressors~~ + Chromosomes of their effects on viability. The decline in the V.I's of the HF, LF and HS lines is less than that obtained in the sterno-pleural selection lines of Latter and Robertson (1962). This would be expected if a proportion of the loci causing inbreeding depression were on + chromosomes I and IV which are common to both tester and tested zygotes. Also, the spectrum of environments under which competition was measured in this study was slightly different from that of the study of Latter and Robertson (1962).

It is difficult to find an explanation other than pleiotropyy or linkage to account for the increase in V.I's of the LS lines during selection. It reflects a marked reduction in the number of Cy flies emerging. This is most marked for LS3 whose V.I. for chromosomes II + III rose to 2.57 at the end of selection; 3 times the mean of all lines.

To explain this unexpected result, a low viability recessive gene is proposed which is associated with low bristle effect through linkage or pleiotropy. This gene is present on the Cy chromosome and initially at low frequency among the + chromosomes. Suppose that its gene frequency changes from q to q + dq under one generation of selection. Before selection the frequency of homozygous recessives among + segregants is q^2 and among Cy segregants q since all Cy posses the gene. After selection the frequencies are $q^2 + 2qdq + dq^2$ among + segregants and q + dq among Cy segregants giving changes of $2qdq + dq^2$ and dq respectively. Thus the ratio of the rates of increase in frequency of homozygous recessives in the 2 segregants is $Cy/+ = dq/(2qdq + dq^2) = 1/(2q + dq)$ so that the increase in Cy > + when $q < 0.5 - dq/2$

and + > Cy when $q > 0.5 - dq/2$

If the viability of the segregants is a function of the frequency of the homozygous recessives and dq is small it would be expected that when q = 0 the rate of decline in viability of Cy would be greater than that of + segregants as q increased. This difference in rates would approach zero as q approached 0.5 and from q = 0.5 to q = 1.0 it would increase in the opposite direction as the viability of + segregants declined faster than that of Cy segregants. Such a gene in the LS lines might at worst be a lethal. In which case maximum frequency amongst + segregants would be 0.25 and in increasing to this frequency the observed more rapid decline in emergence of Cy than + segregants would be expected.

In Appendix 3 it is shown how the ratio of segregants emerging from matings of Cy Me and + parents depends upon the time of its measurement. It is possible that this ratio, measured over a standard period, might/

/might also be sensitive to fluctuations in rate of emergence caused by environmental differences between generations. These would then be confounded with the viability changes of interest in the V.I's. To check on this, rates of emergence were estimated from the number of females collected over a 4 day period from all lines each generation. These were pooled over lines within the 4 selection regimes and are presented in Append. Table 7. There was no systematic change over the selection period. Also, there was no difference between the first and second period at which V.I's were measured and only a slight increase in HF, LF and HS and a slight decrease in LS between the second and third period. From these observations, the measured V.I's are considered not to be biassed by rate of emergence.

Lethals

Method

An assay of lethal frequencies among chromosomes II and III in the lines of Experiment 2 was carried out using the series of matings outlined in Fig. 22 at two stages during the selection period. At gen. 5 chromosomes for assay were sampled at random from the lines within the 4 D x R regimes. At gen. 17 each line contributed a separate sample of 8 chromosomes II and III at mating 2 of Fig. 22. Subsequent losses however were fairly high so that the number actually assayed per line was much fewer. When more than one lethal was found in a line, identity tests were carried out by mating lethal heterozygotes inter se.

Results

The numbers of lethal and non-lethal chromosomes recovered in these tests are presented in Append. Table 8. The data are too few to give reliable estimates of lethal frequencies of individual lines or even of the 4 D x R regimes. However the following observations can be made.

(i) There is some evidence for an increase in lethal frequency between gens. 5 and 17. Lethal frequencies at gen. 5 were 10.5±4.0% for chromosome II and 8.5±4.0% for chromosome III and at gen. 17 they were 13.0±4.0% and 13.5±3.0% respectively. These increases should have accounted for part of the decline in the V.I's of the HF, HS and LF lines during selection. The assay technique would not have detected the lethal common to the + and Cy second chromosomes hypothesised to exist in the LS lines because of the use of Cy in mating 2 of Fig. 22.

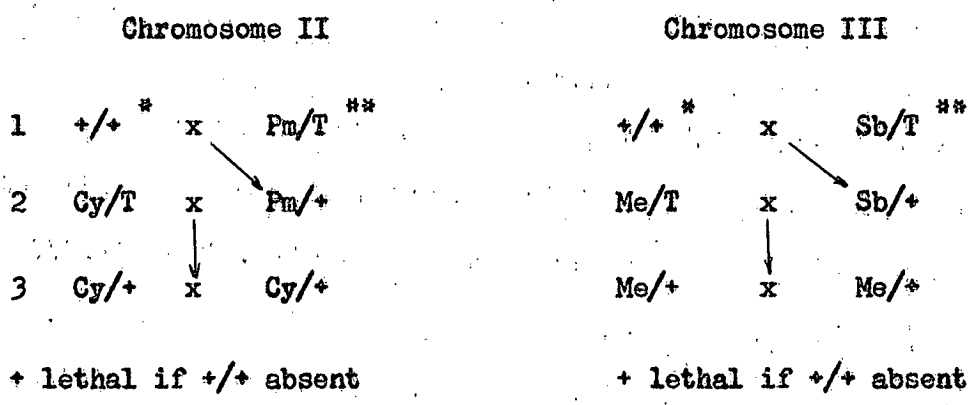


Figure 22 Expt. 2. Mating scheme for extracting and recording the frequency of lethal chromosomes II and III in the selection lines. Mating 1 was a mass mating and matings 2 and 3 single pair matings.

(ii) Of the 20 selection lines at gen. 17, 10 had at least one chromosome II lethal and 7 at least one chromosome III lethal. From identity tests it was found that where more than one lethal was sampled from a line, they were all identical. An examination of the V.I's for chromosomes II and III of all lines at gen. 17 in Append. Table 6 revealed none that approached 0.5. This value would be expected of a line held at the limit by the balancing of a lethal and non-lethal chromosome.

(iii) Averaging over chromosomes II and III at gen. 17, the percentages of lethals in the Low lines was 16.0±3.0 and in the High 10.7±3.0. The difference is not significant but seems to favour a higher frequency in the Low lines.

(iv) There was no difference between the Free and Suppressed lines in frequency of lethals at gen. 17.

III DISCUSSION

Selection response The experimental results show that suppression of recombination within chromosomes II and III has succeeded in reducing response in the Series 1 lines selected for high but not for low bristle score. A reduction in low bristle response was achieved however under suppression of recombination in the Series 2 set of selection lines derived from a separate population sampling. After transformation to logarithms, the ratio R of advances under free to those under suppressed recombination over the selection period were 1.5 for the High and 1.1 and 1.7 for the Series 1 and 2 Low lines respectively. These values of R probably underestimate the true reduction in response expected from a complete suppression of recombination within these two chromosomes for the following reasons: (i) A small contribution to the advance from which these R values were calculated was attributable to selection response in chromosome I, (ii) Limits were measured after only 17 gens. of selection at which time the Free recombination High and the Series 2 Low lines appeared to be continuing to respond to selection, (iii) There was clear evidence for recombination within the second chromosomes of the suppressed lines selected for high bristle score.

In explaining the behaviour under selection of lines in which recombination was suppressed it is recognised that, apart from a small contribution from chromosome I, total response should be the sum of responses of two systems undergoing Robertson's 'Normal' selection as described in the Introduction. These two systems are the sets of chromosomes II and III which were sampled from the Kaduna population/

/population in establishing the selection lines. Evidence for the additivity of the two systems appeared when changes under selection in the effects of chromosomes II and III were being measured and high correlations were observed between the effects of chromosomes of one system in two backgrounds whose genotypes differed at the second system. Other conditions required for the systems to agree with the 'Normal' selection models of Robertson are (i) a normal distribution of the effects of chromosomes implying a relatively high number of bristle loci on each ($n \doteq 10$), (ii) equality of frequencies q and effects of genes at these loci and (iii) linkage phases of bristle genes in equilibrium.

From studies in selection for sterno-pleural bristle number by da Silva (1961) and Allan (1963) and the relative positions on a log. scale of the means of the Kaduna population and limits observed in lines selected in both directions in this laboratory, it appears that the genes responsible for a high proportion of the variance in this character are additive and at intermediate frequencies in the Kaduna population. Robertson (personal communication) has estimated that such genes on chromosomes I, II and III contributed in the ratio 1 : 1.5 : 2 to an observed range between limits in both directions (D) of 18 bristles. These genes are responsible for a genetic variance ($6g^2$) of between 1.0 and 1.5 units in the base population. By subdividing both D and $6g^2$ in the proportions 1 : 1.5 : 2, from Wright's (1952) formula for the number of effective loci $n = D^2/8 6g^2$, an outside estimate of 10 bristle loci on both chromosomes II and III is obtained. This agrees with Louw's (1966) finding that the difference between a high and a low effect chromosome/

/chromosome III was due to the sum of the unequal effects of genes at at least 8 loci. Robertson (personal communication) deduced that genes at these loci were in linkage equilibrium in the Kaduna population since he found that relaxed selection lines appeared no less fit for their possession of an excess of coupling linkages so that he was unable to ascribe a natural selective advantage to repulsion linkages as hypothesised by Mather (1941). The condition for normal distribution of the chromosome II and III effects seems to be satisfied from the observed normality of the distribution of bristle scores in large samples of flies drawn from the Kaduna population.

Thus, from these considerations, it is concluded that the behaviour of the suppressed recombination lines can be largely explained in terms of 'Normal' selection operating on two independent chromosome systems. The free recombination lines, on the other hand, may be less like the computer models run by Robertson in comparison with the 'Normal' models for the calculation of R values. Distances between loci and individual gene effects on chromosomes II and III are unknown but are almost certainly unequal.

The two chromosome systems were examined separately to see if their contributions to overall response and behaviour under selection were in fact the same. As estimated from differences between segregant means, advances to the limit in the suppressed recombination Series 1 lines were about one half a genetic standard deviation for chromosome II in both directions and 2.1 and 1.7 standard deviations in the high and the low directions for chromosome III. Whilst these advances in chromosome III effect agree with, those in chromosome II are considerably less than/

/than expectations of about 2 standard deviations obtained by Robertson in his Monte Carlo selection runs with N = 10, i = 1 and h^2 = 0.20. This is partly the result of the suspected overestimation of the values of genetic variances of the chromosome systems and partly due to the effect that the observed crossing over in the Cy chromosome had on reducing the estimate of chromosome II response from the difference between Cy and non-Cy bearing segregants. There was no evidence that the measurement of chromosome III response was affected by crossing over in the same way.

Assuming that the estimate of chromosome III response is true, a second estimate can be made of chromosome II response in the HS lines unbiassed by any recombination change in the Cy chromosome. As already shown the advance in the + means of the HS lines can be represented by 2dII + 2dIII + dC where these terms represent the contributions of chromosomes II, III and I + IV to total change. Since dIII is assumed to be known with fair accuracy from the differences between segregants, and dC was found to be zero, then a solution can be found for dII. After conversion to logs. a value of 1.4 genetic standard deviations was calculated. This is in agreement with the estimate from segregant differences in lines HS4A and HS4B, the only HS lines whose Cy chromosomes appeared unchanged by recombination during selection. The ratios (R) of selection advances transformed to logs. under free and suppressed recombination are the following:

		High	Low
Chromosome II	(i)	3.4	1.0
	(ii)	1.4	
Chromosome III		1.3	1.0

Estimates (i) and (ii) of chromosome II response to high bristle number selection were made from (i) segregant differences and from (ii) a knowledge of chromosome III contribution to the response in + means. Estimate (ii) agrees most closely with expectations from the 'Normal' model. The additivity of the two chromosome systems is illustrated by the similarity of their separate R values to those of total response.

Differences in selection advance and R values are explicable in terms of the parameters q, n, N and h^2 where each of the 2 N segregating chromosomes of a system comprise n loci with genes at initial frequencies q and h^2 is the heritability of their effects in the base population. In Table 18 are given the probabilities (P) that at least one chromosome with the desired allele at all n loci is sampled to form the selection line and the advance (A) expected in the mean of the selection line upon the fixation of such a chromosome. These are given for each of two values of N, n and q. The initial genetic variance is the same for all cases.

2N (number of linkage groups) = 20

	n (number of loci) = 5		n = 10	
	P (Prob. best group)	A (Advance in std. dev)	P	A
q = 0.8	0.999	1.11	0.897	1.41
q = 0.2	0.005	4.47	0.002	6.32

2N = 10

	n = 5		n = 10	
	P	A	P	A
q = 0.8	0.981	1.11	0.679	1.41
q = 0.2	0.003	4.47	0.0002	6.32

Table 18 Probability (P) of sampling the best possible linkage arrangement of the n genes in establishing a selection line and the advance (A) in standard deviations expected from its fixation. (P) and (A) calculated for 2 values of N, n and q.

Although the values in Table 18 cannot be used to predict limits under 'Normal' selection, they do indicate how these three parameters can influence two of the components of selection advance. A halving of N and $\underline{n}$ affect very little either P or A. As expected, the highest probability of sampling the best linkage group and the lowest possible advance are associated with the highest N and lowest $\underline{n}$. Selection lines drawn from a population with $\underline{q}$ = 0.2 have a very much lower probability of possessing the best possible linkage group or chromosome than those from a population with q = 0.8. This is only partly compensated for by a higher expected advance when q = 0.2.

With 2N = 20 and $\underline{n}$ = 10 using computer simulation, Robertson (personal communication) investigated changes in R for different values of $\underline{q}$ and $\underline{h}^2$. His results are plotted in Fig. 23 and show that appreciable reductions in selection advance through suppression of recombination occur only at low values of $\underline{q}$ and high values of $\underline{h}^2$ and when in comparison with completely independent segregation.

Thus a knowledge of these parameters in the experimental population of this study seems necessary to an understanding of the behaviour observed under the two recombination regimes. This is obtained by examining the two chromosome systems in the Free recombination lines of Experiment 2. Although the additive genetic variances of the chromosome III and chromosome II systems were in the ratio of 1.13 in the base population, their ranges under selection for 17 gens. in both directions were in the ratio of 1.74. All that can be concluded from this is that the chromosome III system had a slightly higher initial genetic variance and perhaps more/

/more effective loci (n) than the chromosome II system. Estimates of h^2 for the sum of the two systems ranged from 0.35 from short term realised h^2 to 0.55 from segregant differences in the base population, so that the h^2 of each of the two chromosome systems is thought to be in the vicinity of 0.15 to 0.25. Another important observation from Experiment 2 is the assymetry of response in the two directions of selection observed in both chromosome systems. The ratios of responses in logs. of high to low selection was 4.5 for chromosome II and 1.6 for chromosome III. This suggests a directional gene frequency, greater for chromosome II than III and in favour of a higher q for low alleles in the base population. This is borne out by examining the log. means of the base population and the High and Series 1 Low lines after 17 gens. of selection. These means were 17, 26 and 14 respectively and give q and $1 - q$ estimates of 0.35 and 0.65. The true frequencies may be more extreme since only the Low but not the High lines had evidently reached their limits when Experiment 2 was terminated. In the Series 2 Low lines, started from a separate population sampling, the means of the base population and lower limit under free recombination approached 18 and 12 respectively. This, together with a higher initial realised h^2 than the Series 1 Low lines, suggests a more intermediate frequency of low and high bristle alleles in the base population.

The observed responses to selection under the two recombination regimes can best be explained by referring to Fig. 23. Assuming R values to be the same for both chromosome systems and $h^2 = 0.15$ to 0.25 with $q = 0.3$ for high and 0.7 for low alleles in Experiment 2 and $q = 0.5$ in the Series 2 Low lines the expected R values from the $h^2 = 0.20$ curve in Fig. 23 are/

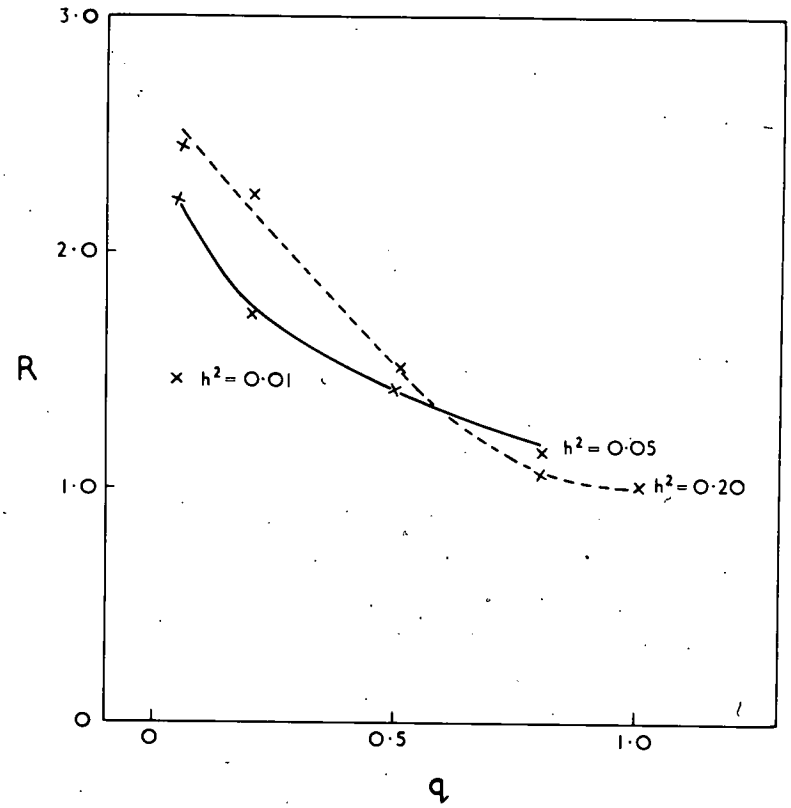


Figure 23 Ratio (R) of advance under Free recombination to that under 'Normal' selection of 20 linkage groups of 10 loci with favoured alleles at varying frequencies q. Values are plotted for 3 levels of h^2 of the linkage group effects.

/are 1.9 for high and 1.1 for low bristle selection in Experiment 2 and 1.5 for low bristle selection in the Series 2 lines. The observed R values of 1.5 for high and 1.0 for low in total response of Experiment 2 and 1.7 in the Series 2 Low lines are not inconsistent with these theoretical expectations. Lower values than those of the model would be expected in view of the appreciable linkage between loci even in the Free recombination lines. Also, the effective number (2N) of chromosomes segregating in each system is expected to be nearer 10 than the 20 used in Robertson's simulation studies.

Reproductive fitness The decline throughout the selection period in the Viability Indexes of the LF, HF and HS lines appears to result from inbreeding depression in emergence due to genes situated mainly on chromosome III. An increase in lethal frequency could have made some contribution to this decline but this was probably small since the increase was only about 4% between gens. 5 and 17.

Apart from the LS lines, there does not appear to be any evidence for bristle viability associations, through linkage or pleiotropy, undergoing correlated changes under selection. If such associations had been important in selection, a higher variance than was observed would have been expected among the Viability Indexes at the end of selection, particularly among lines where the chances of elimination of the associations would have been reduced by the suppression of recombination.

As seen from Appendix 4, natural selection against such bristle viability linkages favoured by artificial selection would be slight in/

/in lines whose suppressor chromosomes did not possess the same low viability genes. These linkages, if present, should then increase in frequency unhindered under artificial selection with a consequent reduction in Viability Indexes to values approaching 0.5. This was not observed in either the chromosomes II or III of any of the lines. In the LS lines, such bristle viability linkages were postulated to exist and to increase in frequency among the + chromosomes under artificial selection in the face of much stronger natural selection due to the balancing Cy chromosomes possessing the same low viability gene. (Appendix 4).

Since the mean bristle score of the HS lines advanced less than the HF lines over the experimental period, they would be expected to have a higher proportion of bristle gene linkages in repulsion. According to Mather (1941), this should confer a higher degree of internal balance on the suppressed lines and, in consequence, a higher fitness. If this did occur it failed to be reflected in higher Viability Indexes of these lines.

SUMMARY

Results are presented of response and changes of reproductive fitness in lines of Drosophila melanogaster selected for high and low sterno-pleural bristle number under two regimes of recombination frequency. Under one, recombination within chromosomes II and III occurred normally and under the other recombination was suppressed by balancing wild chromosomes II and III with marked suppressor chromosomes.

Lines were started using Cy as a chromosome II suppressor and Me and Ubx as chromosome III suppressors. Crossover tests detected a large increase in crossing over in Ubx in females in the presence of Cy. Carried in the same female Cy and Me produced 2.0% and 0.2% crossovers and caused a slight increase in chromosome I recombination frequency.

Conclusions are drawn from 2 series of lines using Cy and Me and established from 2 population samplings. Series 1 lines were selected for high and low bristle score and Series 2 for low score only. Selection was carried out for 17 generations during which time lines with suppressed recombination had plateaued, half-lives being between 3 and 5 generations. Estimated limits for these lines were for Series 1, 23 bristles for high and 14 for low and for Series 2, 14.5 for low. The ratios of advances over the selection period under free to that under suppressed recombination were for Series 1, 1.5 for high and 1.1 for low and for Series 2, 1.7 for low.

Individual chromosome responses were estimated for the Series 1 lines. There was no response in chromosome IV in either direction of selection and only a slight response in chromosome I in the low lines and none in the high. Chromosomes II and III contributed additively most of the total/

/total response. They accounted for about 40% of the initial variance with a number of loci fewer for chromosome II than III each with high bristle alleles at lower initial frequencies than low alleles. Selection advances in both chromosomes II and III were reduced to the same extent under suppression of recombination. Suppressor chromosomes were measured for change under selection. There was no detectable change in the Me chromosomes of any line but Cy chromosomes with effects altered by recombination were selected into some of the lines.

The results are consistent with expectations from a theoretical model of a multi-locus system whose selection limits are predictable from a knowledge of Nih, q and c where N is the effective population size, i the standardised selection differential, h^2 the heritability, q the initial gene frequency at each locus and c the distance between loci.

Changes in viability under selection were studied by comparing the emergences of the 4 segregant types of progeny and by lethal tests. In the suppressed recombination lines selected for low score there was evidence for a low viability-bristle gene linkage favoured by selection. In the other lines bristle-viability linkages were unimportant but inbreeding depression occurred in the emergence of flies possessing a pair of wild third chromosomes.

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APPENDIX 1

Tables

Selection line		Segregants Cy	Me	Cy Me	+
LF	1	0.15	0.08	0.08	0.11
	2	0.13	0.13	0.11	0.18
	3	0.17	0.13	0.12	0.20
	4	0.14	0.15	0.12	0.17
	5	0.16	0.14	0.11	0.14
Pooled		0.15±0.01	0.13±0.01	0.11±0.01	0.16±0.01
LS	1	0.14	0.16	0.12	0.19
	2	0.13	0.14	0.11	0.12
	3	0.22	0.16	0.15	0.21
	4	0.21	0.14	0.12	0.21
	5	0.13	0.11	0.09	0.13
Pooled		0.16±0.01	0.14±0.01	0.12±0.01	0.17±0.01
HF	1	0.24	0.21	0.15	0.31
	2	0.13	0.18	0.10	0.22
	3	0.32	0.19	0.11	0.40
	4	0.19	0.16	0.09	0.26
	5	0.26	0.23	0.13	0.42
Pooled		0.23±0.01	0.19±0.01	0.11±0.01	0.32±0.01
HS	1	0.32	0.14	0.16	0.28
	2	0.25	0.18	0.20	0.25
	3	0.45	0.24	0.25	0.41 *
	4	0.11	0.12	0.07	0.19
	5	0.24	0.13	0.16	0.20
Pooled		0.26±0.01	0.15±0.01	0.16±0.01	0.25±0.01

* generation 0 - 11

Appendix Table 1 Experiment 2. Linear regression coefficients of response on cumulative selection differential for the 4 segregants of each line over 17 generations of selection.

Selection line		Chromosome I gen. 0 (M)	Chromosome I gen. 17 (M)	Chromosome IV gen. 17 (F)	Chromosome IV gen. 17 (M)
LF	1	11.8	11.6	11.7	10.5
	2	12.0	11.7	11.8	10.8
	3	11.9	11.5	12.1	10.7
	4	11.5	11.5	12.1	10.8
	5	12.0	11.6	12.3	10.9
Mean		11.8±0.1	11.6±0.1	12.1±0.1	10.8±0.1
LS	1	11.8	11.3	11.8	10.7
	2	12.0	11.3	12.0	11.0
	3	11.9	11.8	11.8	11.1
	4	12.4	11.2	11.9	10.8
	5	11.9	11.6	11.8	11.0
Mean		12.0±0.1	11.4±0.1	11.8±0.1	10.9±0.1
HF	1	12.1	11.9	12.2	11.0
	2	12.2	11.9	11.9	11.2
	3	11.2	11.6	12.2	11.0
	4	11.6	12.2	12.3	11.2
	5	11.8	12.0	12.3	10.9
Mean		11.8±0.1	11.9±0.1	12.2±0.1	11.0±0.1
HS	1	11.9	12.3	11.7	11.0
	2	11.9	11.4	12.1	11.1
	3	12.1	11.8	12.2	10.7
	4	11.8	11.8	11.7	10.6
	5	12.1	11.8	12.6	11.1
Mean		12.0±0.1	11.8±0.1	12.1±0.1	10.9±0.1

Append. Table 2. Expt. 2. Measurement of chromosomes I and IV after substitution into isogenic males (M) and females (F). Samples of first chromosomes were taken from all selection lines at gens. 0 and 17 and fourth chromosomes from gen. 17 only.

	Selection regime			
Gen.	LF	LS	HF	HS
0	0.40	0.40	0.40	0.40
1	0.60	0.49	1.04	0.55
2	0.30	0.34	0.92	0.77
3	0.24	0.17	1.38	0.98
4	0.29	0.26	1.70	1.22
5	0.21	0.10	1.66	0.70
6	0.35	0.26	1.91	0.94
7	0.08	0.19	1.95	1.18
8	0.22	0.11	2.42	0.89
9	0.06	0.11	2.55	1.00
10	0.23	0.19	2.08	0.99
11	0.24	0.22	2.57	1.27
12	0.18	0.03	2.78	0.77
13	0.33	0.22	3.06	0.59
14	0	-0.09	2.93	0.17
15	0.14	0.23	2.80	0.45
16	0.27	0.19	2.94	0.68
17	0.02	0.21	3.13	-0.51

Append. Table 3 Experiment 2: Response to 17 gens. of selection in the bristle effects of chromosomes II substituted into 2 genetic backgrounds X and Y. Effects are averaged over lines of the 4 D x R regimes and the 2 backgrounds.

Gen.	Selection regime LF	LS	HF	HS
0	0.35	0.35	0.35	0.35
1	-0.22	-0.24	0.89	0.32
2	-0.11	-0.21	0.78	1.18
3	-0.35	-0.45	1.62	1.10
4	-0.20	-0.27	1.22	1.87
5	-0.59	-0.46	1.99	1.53
6	-0.59	-0.65	2.80	2.48
7	-0.68	-0.53	2.86	2.74
8	-0.55	-0.52	2.86	2.39
9	-0.65	-0.56	3.20	2.51
10	-0.35	-0.76	2.89	2.74
11	-0.59	-0.78	3.22	2.84
12	-0.63	-0.76	3.00	2.46
13	-0.61	-0.41	3.60	2.34
14	-0.39	-0.60	3.51	2.21
15	-0.56	-0.47	3.74	2.58
16	-0.64	-0.54	3.78	3.05
17	-0.67	-0.40	3.89	2.16

Append. Table 4 Experiment 2: Response to 17 gens. of selection in the bristle effects of chromosomes III substituted into 2 genetic backgrounds X and Y. Effects are averaged over lines of the 4 D x R regimes and the 2 backgrounds.

Seln. regime		Generations 1 - 5	6 - 9	10 - 13	14 - 17
LF	1	1.83	1.48	1.34	1.40
	2	2.25	1.17	1.16	0.99
	3	1.52	1.53	1.12	1.31
	4	2.11	1.75	1.60	1.27
	5	1.44	1.10	0.90	1.01
LS	1	1.19	1.61	1.14	1.39
	2	1.76	1.41	1.18	1.05
	3	1.18	1.58	1.08	1.32
	4	1.76	1.11	1.27	1.25
	5	2.46	1.44	1.37	1.19
HF	1	2.34	4.25	4.53	3.82
	2	5.58	4.57	5.52	6.01
	3	4.60	4.85	4.19	3.76
	4	3.66	5.11	4.22	5.11
	5	4.39	5.84	6.17	3.92
HS	1	3.35	3.24	3.46	6.72
	2	3.64	4.60	4.07	4.18
	3	5.83	6.02	6.54 (4.19)*	4.06 *
	4	3.94	4.06	3.97	5.08
	5	3.96	3.35	4.31	3.80

* These values are the phenotypic variances of HS4B which replaced HS3 at generation 11.

Append. Table 5 Expt. 2. Phenotypic variances of + segregants pooled over generations within 4 sections of the selection period. The average number of degrees of freedom for each value is 128.

Selection line	Gen. 0			Gen. 7 & 8			Gen. 16 & 17		
	Homozygous + chromosomes								
	II	III	II + III	II	III	II + III	II	III	II + III
LF 1	0.67	1.27	0.85	0.89	0.92	0.82	0.81	0.89	0.69
" 2	0.82	1.13	0.92	0.89	1.44	1.27	0.81	0.82	0.95
" 3	0.75	1.27	1.25	0.85	1.17	1.04	0.75	0.96	0.75
" 4	0.72	1.22	0.89	0.92	0.85	0.81	0.72	1.00	0.72
" 5	1.17	1.24	1.94	0.82	1.27	1.04	1.00	0.89	0.92
Pooled	0.82±0.08*	1.26±0.07	1.06±0.14	0.89±0.08	1.13±0.07	0.96±0.14	0.82±0.08	0.92±0.07	0.75±0.14
LS 1	1.08	1.25	1.13	1.00	1.04	1.08	1.22	1.32	1.56
" 2	0.92	1.13	1.04	1.38	1.13	1.63	1.08	0.89	0.92
" 3	0.82	1.27	1.04	1.44	1.38	1.94	1.94	1.32	2.57
" 4	0.75	1.17	0.92	1.38	1.50	2.03	1.50	0.89	1.32
" 5	0.82	1.44	1.17	0.81	1.17	0.92	0.89	1.22	1.13
Pooled	0.84±0.08	1.16±0.07	1.00±0.14	1.17±0.08	1.22±0.07	1.44±0.14	1.27±0.08	1.13±0.07	1.38±0.14
HF 1	0.92	1.22	1.13	0.80	1.13	0.81	0.82	1.13	0.96
" 2	1.08	1.22	1.32	0.92	1.17	1.08	0.85	1.08	0.89
" 3	0.85	1.25	0.85	0.85	1.13	0.96	0.72	1.27	0.96
" 4	0.72	1.38	1.25	0.82	1.17	0.96	0.69	1.04	0.72
" 5	0.75	1.44	1.08	0.82	1.17	0.96	0.75	0.96	0.72
Pooled	0.82±0.08	1.26±0.07	1.06±0.14	0.82±0.08	1.17±0.07	0.96±0.14	0.75±0.08	1.08±0.07	0.85±0.14
HS 1	0.82	1.04	0.85	1.13	0.82	0.92	0.82	1.08	0.89
" 2	0.92	1.13	1.04	1.08	0.75	0.85	0.96	0.89	0.89
" 3	0.82	1.08	0.92	1.13	1.32	1.50	0.69	1.27	0.89
" 4	0.69	1.27	0.92	0.95	1.22	0.81	0.95	0.96	0.31
" 5	0.85	1.13	1.25	0.85	0.85	0.75	0.96	0.82	0.75
Pooled	0.84±0.08	1.16±0.07	1.00±0.14	0.96±0.08	0.96±0.07	0.92±0.14	0.82±0.08	0.92±0.07	0.69±0.14

* Standard errors of V.I. estimated from between line variances.

Append. Table 6 Viability Indexes of zygotes homozygous wild type for chromosomes II, III and II + III measured at the beginning, middle and end of the selection process.

Gen.	LF	LS	HF	HS
0	156	163	138	124
1	167	185	153	163
2	141	170	145	157
3	161	167	156	143
4	144	127	144	117
5	193	191	242	170
6	154	101	164	119
7	126	147	122	114
8	176	179	159	134
9	123	122	147	103
10	163	149	141	129
11	116	139	111	107
12	157	139	136	147
13	148	112	128	119
14	139	106	137	154
15	184	123	206	134
16	183	146	185	150
17	137	129	137	119
Mean	154	144	153	134

Append. Table 7 Numbers of females emerging over 4 days following first emergence. Counts are averaged over lines within the 4 D x R selection regimes.

Seln. Line	Chromosome II No. sampled	Lethals	Chromosome III No. sampled	Lethals
Gen. 5				
LF	12	2	10	2
LS	12	1	13	1
HF	11	1	13	1
HS	16	2	7	0
Gen. 5 total	51	6	43	4
Gen. 17				
LF 1	4	0	5	1
2	3	1	4	3
3	4	0	3	1
4	0	0	5	0
5	5	0	4	0
Total	16	1	21	5
LS 1	5	0	3	0
2	3	1	3	0
3	2	0	5	5
4	1	0	3	0
5	2	0	4	1
Total	13	1	18	6
HF 1	4	1	5	0
2	3	0	6	0
3	3	1	6	0
4	0	0	4	0
5	1	0	5	1
Total	11	2	26	1
HS 1	4	1	3	0
2	1	0	5	0
3	4	1	4	0
4	6	2	3	0
5	5	1	3	1
Total	20	5	18	1
Gen. 17 total	60	9	83	13

Append. Table 8 Expt. 2. Numbers of lethal and non-lethal chromosomes II and III sampled from the selection lines at gens. 5 and 17.

APPENDIX 2

Comparison of expected genetic gains between selection with the same intensity (i) within heterozygous suppressor segregants (S) and (ii) within homozygous wild type segregants (+). Both segregants share the same pool of + chromosomes e.g. selection lines maintained by mating + males and Cy Me females.

Consider a locus with alleles A1 frequency p and A2 frequency q on + chromosomes segregating in a population with allele K on a balanced suppressor chromosome. With respect to this locus, genotypes, frequencies and effects within the + and S segregants are the following:

		+ Segregants			S Segregants	
(i)	Genotype	A.A.	$A.A_2$	A_2A_2	KA1	KA_2
(ii)	Freq.	p^2	2pq	q^2	p	q
(iii)	Effect (E)	+a	0	-a	$k + a/2$	$k - a/2$

and the frequency of A2(q) among the + alleles of these genotypes

(iv)	0	0.5	1.0	0	1.0

From (ii), (iii) and (iv) the covariances between q and E are the same for both segregants

(v) $\text{Cov.}(q,E) = -pqa$

The regressions of q on E are

(vi) $+b(q,E) = -pqa/\delta p1^2$ and $S\ b(q,E) = -pqa/\delta p2^2$

where $\delta p1^2$ and $\delta p2^2$ are the phenotypic variances of the + and S segregants respectively and are

(vii) $\delta p1^2 = \delta g1^2 + \delta e^2$ and $\delta p2^2 = \delta g2^2 + \delta e^2$

when $\delta g1^2$, $\delta g2^2$ and δe^2 are the genetic variances of the + and S segregants and the environmental variance respectively.

From (ii) and (iii) the genetic variances are

(viii) + $\sigma_{g1}^2 = 2pqa^2$ and S $\sigma_{g2}^2 = pqa^2$

The change in frequency of A2 (dq) within each of the 2 segregants is the product of the selection differential i σ_p and the regression of gene frequency on effect b(q,E)

(ix) + $dq1 = -ipqa/\sigma_{p1}$ and S $dq_2 = -ipqa/\sigma_{p2}$

Therefore the ratio of genetic change from selection within S to selection within + segregants is -

$$dq2/dq1 = \sigma_{p2}/\sigma_{p1} = \sqrt{2pqa^2 + \sigma_e^2 \,/\, pqa^2 + \sigma_e^2}$$

Since genetic gain is proportional to the coefficient of selection, this ratio is the same as that of the selection coefficients of A2 in the two segregants. It has a maximum value of $\sqrt{2}$ when $\sigma_e^2 = 0$ and when $\sigma_e^2 = \sigma_{g2}^2$ it is $\sqrt{1.5}$ and when $\sigma_e^2 = \sigma_{g1}^2$ it is $\sqrt{1.3}$.

Where parents of one sex are selected from S segregants and the others from + segregants as in the selection lines of this study

$$dq2/dq1 = 2\,\sigma_{p1}/(\sigma_{p1} + \sigma_{p2})$$

when dq2 is now the change expected from selecting within both segregants and dq1 from selecting parents of both sexes within + segregants. Calculated values of the ratio are 1.21 when $\sigma_e^2 = 0$, 1.11 when $\sigma_e^2 = \sigma_{g2}^2$ and 1.07 when $\sigma_e^2 = \sigma_{g1}^2$. Thus the gain from selecting the parents of one sex within S segregants is very small.

APPENDIX 3

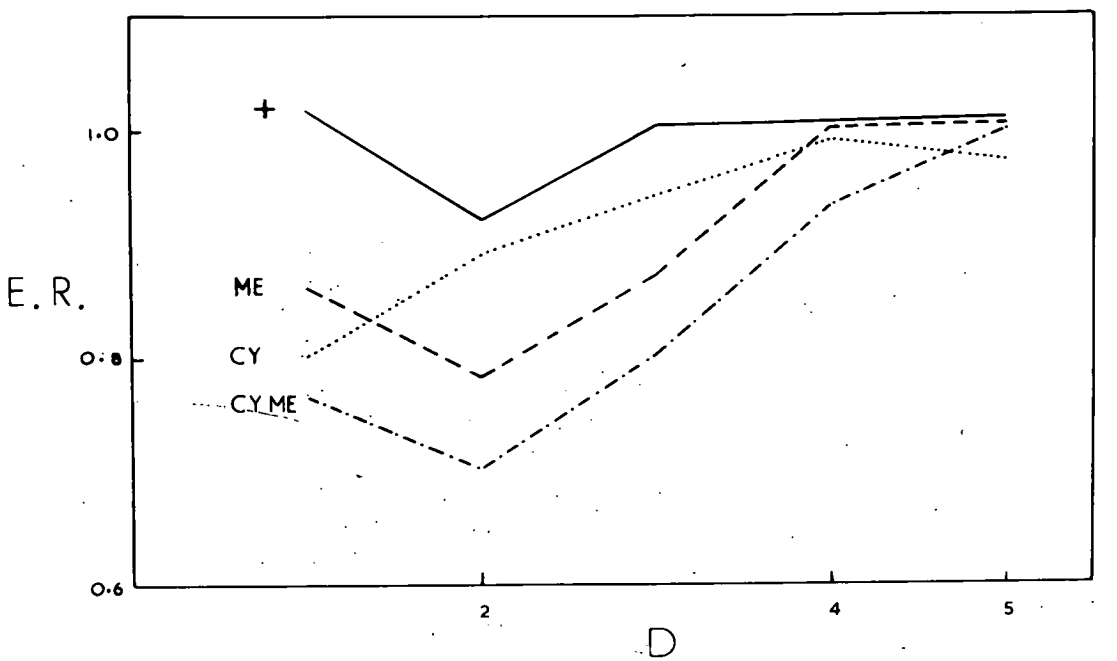
Differences between reciprocal crosses in the rates of emergence of progeny of 4 different genotypes.

Method

In Experiment 2 the Suppressed recombination lines were reproduced each generation from matings of + males and Cy Me females and the Free recombination lines from the reciprocal cross. From parental chromosome frequencies it was expected that equal numbers of Cy, Me, Cy Me and + progeny would be produced by both these crosses. The ratios of these 4 segregants were measured each generation to estimate changes in their relative fitnesses under selection. Therefore, it was necessary to determine the effect of direction of cross and time of measurement on the ratio of emergences of the 4 segregants in the absence of selection. Two $\frac{1}{2}$ pint cultures were set up in each of 6 successive generations, one from the mating of 10 + males with 10 Cy Me females and the other from the reciprocal cross. Each generation, + parents were obtained from large sub-cultures of the Kaduna population and Cy Me parents from the male parents in the previous generation. For each direction of the cross, cumulative totals were obtained of the 4 segregants emerging in the 5 successive 24 hour periods following first observed emergence.

Results

The ratios of cumulative totals of progeny from the Cy Me females to the + females (E.R.) averaged over the 6 generations are shown for the 5 successive periods (D) in Append. Fig. 1. The emergence of progeny from the Cy Me maternal cultures is delayed in comparison with that from the/



Append. Figure 1 Differences between reciprocal crosses of Cy Me and + in rates of emergence of the 4 progeny types; Cy, Me, Cy Me and +. Ratios of numbers emerging from Cy Me to + maternal cultures (E.R.) are calculated by accumulating counts over 5 successive days (D).

/the + cultures. The rate of emergence from the Cy Me females is slowest for all but the Cy segregants in the second 24 hour period but accellerates later so that by the fifth period, about the same number of each of the 4 segregants has emerged from the Cy Me as from the + maternal cultures. The initial retardation in emergence from Cy Me females is greatest for the Me and Cy Me segregants and least for the +.

The conclusion from this study is that, in estimating the relative viabilities of the 4 segregants from the ratio of their emergences, the period over which these are measured should be kept constant throughout selection and be at least 96 hours. Also, differences in these ratios can be expected between the Free and Suppressed recombination lines due to the direction of the cross alone.

APPENDIX 4

Selection against a high effect gene due to complete linkage with a recessive lethal under the mating conditions of this study.

Let the frequency of the high gene A (alternative allele a) be p in the suppressor parents and q in the + parents and let a proportion f of the suppressor chromosomes posses the lethal, then the distribution of offspring genotypes produced by mating suppressor (S) x + parents are as follows:

	SA	Sa	AA	Aa	aa
Lethal	fq	0	pq	0	0
Non-lethal	(1-f)q	1 - q	0	p+q - 2pq	(1-p)(1-q)

From this, it happens that the frequency of A among the + progeny is pq(2-p-q)/2(1-pq) less than the $^1/_2(p + q)$ expected from parental frequencies. If the lethal is present among the suppressor chromosomes then $f > 0$ and the frequency of A among the suppressor progeny is fq(1-q)/1-fq less than the q expected from parental frequencies. If $p = q = 0.5$ and the lethal is absent from the suppressor chromosome i.e. $f = 0$, then the expected total reduction in the frequency of the high chromosome is 0.084. If all suppressor chromosomes possess the lethal i.e. $f = 1$, then the reduction is 0.334. Thus, very little depression of viability would be expected to accompany selection for A when $f = 0$ but if $f = 1$ a measurable decline should result.