VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA*.
IX. CHROMOSOMAL ANALYSIS OF SCUTELLAR
BRISTLE SELECTION LINES¹

W. R. SCOWCROFT²

Department of Genetics, University of California, Davis

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Drosophila melanogaster, by reason of its small number of chromosomes, the lack of crossing over in the male, male hemizygoty for the 1st chromosome and the existence of inversion (dominant marked) chromosomes, provides a means of studying the chromosomal distribution of effective factors and the extent of the interactions between these factors.

PAYNE (1918) used a combination of backcrossing and recombination and found that the response to selection resulted from genetic changes in chromosomes 1 and 3. In lines selected for increased abdominal bristle number MATHER (1942) found that chromosome 2 played a larger part than had chromosome 3. In the low selection lines however, the major autosomes were of approximately equal importance. SISMANIDIS (1942) similarly attributed the majority of the response to selection for increased scutellar bristle number to the 2nd chromosome.

MATHER and HARRISON (1949) carried out an extensive assay of 12 abdominal bristle selection lines and the parents involved in producing these lines. The chaetae-producing potential of the three major chromosomes were different for each of the 12 lines. In general interaction between chromosomes 1 and 3 was favourable to the direction of selection relative to that in the unselected parent populations. The other interaction patterns however were heterogeneous.

ROBERTSON (1954) and ROBERTSON and REEVE (1953) analysed the chromosomal components of lines selected for large and small size by synthesising stocks which possessed all possible combinations of chromosomes from the two lines. Selection for large body size involved changes largely in chromosome 3 (ROBERTSON and REEVE 1953), while selection for small size produced effects mainly in the 1st (ROBERTSON and REEVE 1953; ROBERTSON 1954). In the large strain, the joint action of chromosomes 2 and 3 was greater than the sum of their individual effects.

The polygenic control of DDT resistance in *D. melanogaster* was suggested by the study of whole chromosome changes (KING and SØMME 1958). Resistance resulted from changes in all three major chromosomes but the apportionment amongst them was not the same for the two lines analysed.

The subdivision of genetic changes resulting from the effects of selection

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² Present address: Division of Plant Industry, CSIRO, Canberra, Australia.

demonstrate three important points not fully emphasized by selection studies or by the analysis of the components of genetic variance. First, interactions exist between segments on different chromosomes in both genetically heterogeneous unselected populations and in unselected inbred lines. Secondly, selection can alter interaction patterns and can also induce and utilize favourable interactions between segments on nonhomologous chromosomes. Chromosomal interactions, however, are only minimum estimates of the total interaction that exists in populations and selection lines. Since linkage aids in the preservation of favourable combinations of genes, a large portion of the single chromosome effects are probably due to intrachromosomal interactions as found by MATHER and HARRISON (1949), and KELLER and MITCHELL (1964). Finally, a feature of the results of chromosomal analyses is the demonstration of genetic heterogeneity between lines similarly selected for the same trait. Genes responsible for metric characters appear to be diffusely scattered throughout the genome and selection is opportunistic in deciding which portions of the genome will be utilized in eliciting a response.

In the research that follows, the technique of MATHER and HARRISON (1949) has been employed to analyse a number of related scutellar bristle selection lines. The response to selection in these lines has been reported by FRASER *et al.* (1965) and some of the results of the following analyses were briefly reported in the same publication.

MATERIALS AND METHODS

The responses of the scutellar selection lines that were analysed are shown in Figure 1. These lines were described in detail by FRASER *et al.* (1965). With the exception of line A15, the lines originated from stock 70 (A9, A4, A6, A21, A30) or from crosses of stock 70 with stock 71 (A1, A18) (see FRASER 1963). Line A15 was derived from wild females collected in Australia. Up to the 15th generation, selection in lines A1, A6 and A21 was for increased anterior bristles only; in lines A4 and A30 for increased intermediate bristles; in line A15 for anteriorly and posteriorly located bristles and in lines A9 and A18 for total number of scutellar bristles. Selection was practiced on females only. After the 15th generation selection was for total number of scutellar bristles regardless of position. Lines A1, A9 and A18 were crossed in all possible combinations at generation 26 to form the "crossed" line. Selection in this line was for both males and females with the highest scutellar number. At generation 40 another series of lines were established from the "crossed" line. In this set, selection was for a single scutellar value in females per line. Of this set, female scutellar lines AH5 and AH9 were analysed.

The inversion marked chromosomes used in the analyses were *CIB* or w^{m4} for the 1st chromosome; *In(2L+2R)Cy* for the 2nd and *Ubx¹⁹⁰* for the 3rd chromosome. Although these chromosomes do not suppress recombination to the extent found in other readily available inversion-marked chromosomes, they were chosen because they were the best compromise between the suppression of crossing over, ease of identification and the lack of major effect on scutellar bristles or on other macrochaetae on the thorax. The choice of the 1st chromosome was particularly limited since most of the chromosome 1 inversions involve breaks in the distal heterochromatin close to the scute locus, which usually results in a reduction of scutellar bristle number.

In every case the mating scheme was the same. Ten *CIB/+ Cy/+ Ubx/+* virgin females were mated to ten randomly chosen males of the selection line. A minimum of three and a maximum of four cultures were established per line. Ten virgin females of the constitution *CIB/'+' (or $w^{m4}/'+'$) *Cy/'+' Ubx/'+' (where '+' refers to chromosomes derived from the selection line concerned) were then mated to an equal number of males isolated from the selection line at the time the analysis was initiated. Again, three or four cultures were established**

FIGURE 1.—Response to selection for scutellar bristles in the A set of selection lines (derived from FRASER *et al.* (1965)).

per line. The female progeny from this cross were segregated on the basis of phenotype and each phenotypic class was scored for total number of scutellar bristles. In the cases where the w^{m4} inversion was used (A4, A6, A9, A21 and A30), the heterozygote, $w^{m4}/+$, could be distinguished from the homozygote, $+/+$ because these lines carried the white-honey (w^h) allele of the white locus. Each culture was scored on the 15th day after the matings were established.

Since the genotype of an individual is specified by its phenotype, subsequent reference to genotypes will be by phenotypes only. Individuals homozygous for a pair of selection line chromosomes will be designated as $+$, while individuals heterozygous for the balancer chromosome and the selection line chromosome will be specified by the balancer. For example, $CIB/+$, $Cy/+$ or $w^{m4}/+$, $Cy/+$, $Ubx/+$ genotypes will be referred to as $CIB\ Cy\ Ubx$ or $w^{m4}\ Cy\ Ubx$ respectively; $+/+$, $Cy/+$, $Ubx/+$ will be referred to as $+ Cy\ Ubx$ and so on for the rest of the segregating classes.

RESULTS

The mean scutellar bristle number of the eight segregating classes and of the generation from which the assayed chromosomes were taken are shown in Table 1 for each of the "A" set of selection lines. The scutellar number of the reconstituted selection line (the $+++$ phenotype) relative to the scutellar number of the selection line at the time of analysis provides a measure of the efficiency of the

TABLE 1
Scutellar bristle mean of females and their respective standard errors for the eight segregating phenotypes for each of the selection lines

Line	Scutellar mean of selection line†	Phenotypes								Generation†
		++	++Ubx	+Cy+	+CyUbx	CIB++	CIB+Ubx	CIBCy+	CIBCyUbx	
A1	6.90	6.36±0.10	4.52±0.06	6.24±0.09	4.59±0.06	4.76±0.07	4.00±0.00	4.46±0.06	4.02±0.01	23
A4*	4.80	4.75±0.25	4.53±0.09	4.35±0.10	4.40±0.06	4.33±0.21	4.34±0.09	4.30±0.13	4.16±0.04	25
A6*	5.10	5.18±0.17	4.70±0.08	4.72±0.12	4.35±0.06	4.62±0.16	4.36±0.06	4.63±0.09	4.17±0.04	25
A9*	7.40	7.11±0.16	4.98±0.09	6.88±0.12	4.59±0.05	6.66±0.15	4.60±0.07	6.19±0.11	4.50±0.05	27
A15	5.50	5.14±0.08	4.65±0.08	5.00±0.08	4.34±0.05	4.35±0.06	4.09±0.03	4.07±0.03	4.02±0.01	26
A18	6.70	6.41±0.10	4.37±0.04	6.20±0.10	4.26±0.04	4.82±0.09	4.03±0.02	4.60±0.06	4.00±0.00	24
A21*	5.10	4.34±0.07	4.55±0.09	4.53±0.07	4.31±0.04	4.45±0.11	4.29±0.05	4.32±0.06	4.17±0.03	26
A30*	5.10	4.15±0.08	4.30±0.05	4.43±0.12	4.13±0.03	4.11±0.05	4.21±0.04	4.12±0.04	4.06±0.02	23
"crossed"	7.35	7.42±0.09	4.92±0.06	7.05±0.08	4.60±0.06	5.42±0.08	4.14±0.03	4.95±0.07	4.06±0.02	37
AH5	5.95	6.06±0.09	4.29±0.06	5.91±0.10	4.25±0.05	4.50±0.08	4.02±0.01	4.46±0.06	4.00±0.00	47
AH9	8.28	8.34±0.12	5.39±0.07	7.92±0.10	4.85±0.07	6.71±0.08	4.52±0.05	5.68±0.08	4.17±0.03	47

* *w^{m4}* inversion used instead of the *CIB* inversion.

† At time of analysis—see Figure 1.

TABLE 2

The efficiency of the chromosomal analysis in terms of the ability of the reconstituted + + + phenotype to recover the selection advance

Line	Mean number of extra scutellar bristles		Efficiency [(A/B) $\times$ 100%] C
	In the selection line A	In + + + B	
A1	2.90	2.36	81.4
A4	0.80	0.75	93.8
A6	1.10	1.18	107.3
A9	3.40	3.11	91.5
A15	1.50	1.14	76.0
A18	2.70	2.41	89.3
A21	1.10	0.34	30.9
A30	1.10	0.15	13.6
"crossed"	3.35	3.42	102.1
AH5	1.95	2.06	105.6
AH9	4.28	4.34	101.40

technique (Table 2). The average efficiency of the technique was 81.2% but this was heavily biased by the low efficiency of the analysis for lines A21 and A30. Excluding these two values, the average efficiency of the analysis was 94.3%. With the possible exception of A21 and A30, the technique presumably does not alter the integrity of the assayed chromosomes.

The majority of the genetic changes resulting from selection appeared to be recessive since the bristle number of the triple heterozygote *Clb*/+⁺ *Cy*/+⁺ *Ubx*/+⁺ (or *w^{m4}*/+⁺ *Cy*/+⁺ *Ubx*/+⁺) was close to the mean scutellar number of the unselected stock 70 and stock 71—four bristles. Line A9 was the only one that appeared to carry dominant factors.

These 11 lines can be divided into four classes on the basis of their response to selection (Figure 1), the type of selection employed and/or the results of the chromosomal analyses (Table 1), thus: 1. Includes lines A1, A9 and A18 each of which had early accelerated responses to selection and which appeared to reach a limit around 6.8 bristles. 2. Includes the "crossed" line, in which the selected population was derived from the intercrossing of lines A1, A9 and A18, and lines AH5 and AH9 which were subpopulations derived from the "crossed" line in which selection was for a fixed number of scutellar bristles in females. 3. Includes A4, A6 and A15 which had a moderate response to selection resulting in a mean approximating 5.0 bristles at the time of analysis. 4. Includes A21 and A30 which had a response to selection similar to the Class 3 lines but in which a large portion of the selection advance was not recovered in the + + + phenotype of the chromosomal analysis (see Table 1).

Most of the genetic change resulting from selection appears to have been due to recessive factors since the triple heterozygote *Clb*/+⁺ *Cy*/+⁺ *Ubx*/+⁺ (or *w^{m4}*/+⁺ *Cy*/+⁺ *Ubx*/+⁺) had a mean of approximately four bristles. This then can be considered as the control level. Deviations from this control level resulting from the substitution of one or more selection line chromosomes reflects the

genetic changes that occurred in the substituted chromosomes in response to selection. The effect of selection on chromosome 1 therefore, is the difference in the average bristle number between the + *Cy Ubx* phenotype and *ClB Cy Ubx* (or *w^{m4} Cy Ubx*). Likewise the effect of selection on chromosome 3 is the difference between *ClB Cy* + (or *w^{m4}* etc.) and *ClB Cy Ubx* (or *w^{m4}* etc.). Similarly for chromosome 2. Interchromosomal interactions are then deviations from additivity of the single chromosome substitution effects. For example, the interaction between chromosomes 1 and 2 = (+ + *Ubx* - *ClB Cy Ubx*) - (1 effect + 2 effect) and so on for 1-3 and 2-3 interaction terms. The second order interaction component, 1-2-3, is the difference between + + + phenotype and the *ClB Cy Ubx* less the individual chromosome effects and the first order interactions.

Table 3 contains the results of the effects of each of the three major chromosomes alone and of interactions between the chromosomes for the A series of selection lines analysed. These are presented graphically in Figure 2.

Lines A1 and A18 had similar components contributing to selection advance. Both the 1st and 3rd chromosomes had an effect alone, and they interacted to produce an even greater effect. These two chromosomes accounted for almost all of the selection advance. In line A9, however, the 3rd chromosome alone accounted for the majority of the changes resulting from selection. This chromosome interacted with the 1st only slightly and to a lesser extent with the 2nd. In each of these three lines there was a negative second order interaction.

The lines of Class 2 ("crossed," AH5 and AH9) showed a qualitatively similar pattern to that of lines A1 and A18. In all cases the 1st and 3rd chromosomes accounted for the majority of the changes resulting from selection. The effect of selection for a mean of five bristles in females (line AH5) affected all components when compared to its parent line, "crossed." Particularly evident is the elimination of interactions involving chromosome 2. Selection for females with nine bristles, AH9, increased the component contributed by the 3rd and for the first time in these high level lines caused changes in the 2nd chromosome. Favorable genetic changes in these two chromosomes are also reflected in the increased 2-3 interaction component. The increase in the unfavorable second order interaction of AH9 over that of the parent "crossed" line suggests that natural selection opposed the favorable changes at the chromosomal and first order interaction levels.

The Class 3 lines are relatively dissimilar. Similar changes occurred in all chromosomes of A4 while in A6 the 3rd accounted for a larger portion of the genetic change than did either of the other two. Almost all of the single chromosome effects in line A15 involved chromosome 1 and interactions of 1 with 3 even though this latter chromosome had no effect alone.

The selection advance of line A21 involved genetic changes of essentially equal magnitude for all of the three major chromosomes, while in A30 the 2nd chromosome effect was more prominent than either the 1st or the 3rd. Interaction between 1 and 3 in line A30, however, was of considerable relative importance. The negative second order interaction in both Class 4 lines reflects the lower

TABLE 3
Contribution of the chromosomal components and of interchromosomal interactions for
each of the selection lines

Component	Selection line										
	A1	A4	A6	A9	A15	A18	A21	A30	*crossed'	AH5	AH9
A. Untransformed data											
1	0.58 (24.7)	0.24 (40.7)	0.18 (17.8)	0.09 (3.4)	0.32 (28.6)	0.26 (10.8)	0.14 (82.4)	0.07 (77.8)	0.54 (16.1)	0.25 (12.1)	0.68 (16.3)
2	-0.01 (-0.4)	0.18 (30.5)	0.19 (18.8)	0.10 (3.8)	0.07 (6.3)	0.03 (1.2)	0.12 (70.6)	0.15 (166.7)	0.08 (2.4)	0.02 (1.0)	0.35 (8.4)
3	0.45 (19.1)	0.14 (23.7)	0.46 (45.5)	1.69 (64.8)	0.05 (4.5)	0.60 (24.9)	0.15 (88.2)	0.06 (66.7)	0.89 (26.5)	0.46 (22.3)	1.51 (36.2)
1-2	-0.06 (-2.6)	-0.05 (-8.5)	0.16 (15.8)	0.29 (11.1)	0.24 (21.4)	0.08 (3.3)	0.12 (70.6)	0.02 (22.2)	0.24 (7.1)	0.02 (1.0)	0.19 (4.6)
1-3	1.20 (51.1)	-0.19 (-32.2)	-0.09 (-8.9)	0.60 (23.0)	0.61 (54.5)	1.34 (55.6)	0.07 (41.2)	0.24 (266.7)	1.56 (46.4)	1.20 (58.3)	1.56 (37.4)
2-3	0.31 (13.2)	-0.15 (-25.4)	-0.20 (-19.8)	0.37 (14.2)	0.21 (18.8)	0.20 (8.3)	-0.01 (-5.9)	-0.16 (-177.8)	0.39 (11.6)	0.02 (1.0)	0.68 (16.3)
1-2-3	-0.12 (-5.1)	0.42 (71.1)	0.31 (30.7)	-0.53 (-20.3)	-0.38 (-33.9)	-0.10 (-4.1)	-0.42 (-247.1)	-0.29 (-322.2)	-0.34 (-10.1)	0.09 (4.4)	-0.80 (-19.2)
B. Transformed data*											
1	2.35 (52.7)	0.65 (48.9)	0.40 (21.2)	0 (0)	1.60 (56.3)	1.87 (40.8)	0.40 (85.1)	0.37 (69.8)	1.40 (40.2)	1.69 (43.3)	1.50 (47.0)
2	0.11 (2.5)	0.48 (36.0)	0.56 (29.6)	0.33 (11.5)	0.68 (23.9)	0.70 (15.3)	0.40 (85.1)	0.70 (132.1)	0.22 (6.3)	0.47 (12.1)	1.10 (34.5)
3	2.14 (48.0)	0.34 (25.6)	1.12 (59.3)	2.13 (73.6)	0.60 (21.1)	2.55 (55.7)	0.44 (93.6)	0.40 (75.5)	1.83 (52.6)	2.21 (56.7)	2.56 (80.3)
1-2	-0.20 (-4.5)	-0.20 (-15.0)	0.39 (20.6)	0.43 (14.9)	-0.35 (-12.3)	-0.49 (-10.7)	0.06 (12.8)	-0.15 (-28.3)	0.18 (5.2)	-0.39 (-10.0)	-0.10 (-3.1)
1-3	-0.03 (-0.7)	-0.37 (-27.9)	-0.18 (-9.5)	0.55 (19.1)	0.41 (14.4)	-0.40 (-8.7)	0 (0)	0.23 (43.4)	0.85 (24.4)	-0.04 (-1.0)	-0.12 (-3.8)
2-3	0.43 (9.6)	-0.14 (-10.5)	-0.89 (-47.1)	-0.13 (-35.8)	0.27 (9.5)	0.59 (-12.9)	-0.27 (-57.4)	-0.78 (-147.2)	0.38 (10.9)	-0.52 (-13.3)	-0.99 (-31.0)
1-2-3	-0.34 (-7.6)	0.57 (42.9)	0.49 (25.9)	0.47 (16.3)	-0.37 (-13.0)	0.94 (20.5)	-0.56 (-119.1)	-0.24 (-45.3)	-1.38 (-39.7)	0.48 (12.3)	-0.76 (-23.8)

In parentheses are given the percentage contributions to selection advance of each of the chromosomal components and of interactions.
* Values are in standard deviations.

FIGURE 2.—The contribution to selection advance of the chromosomal components and of interchromosomal interactions for the A set of selection lines.

bristle number of the reconstituted +++ phenotype relative to that of the selection line at the time of the analysis.

The main difficulty in the genetic analysis of scutellar bristle number lies in the fact that it is a threshold character. As the mean of a population approaches four this threshold effect is magnified such that the validity of the comparison of means which may vary from 4 upward to 7 and 8 becomes tenuous (see Table 1). For this reason, the relative contribution of chromosomes and of interactions between chromosomes are biased to a greater or lesser extent subject to the scutellar means under comparison. A trait which is subject to threshold confounding can be treated on a scale which renders its distribution normal. The unit of measurement is the standard deviation of the distribution.

If the interactions found above are a function of the threshold at four bristles, then a probit transformation of the data to a normalized form will eliminate these interactions. The standard deviations separating the mean from the specified bristle class cut-off points are shown for each phenotype of each line analysed in Table 4. Negative values indicate that the mean falls within the top 50% of the distribution while positive values indicate that the mean is within the lower 50% of the distribution. The 5/6 cut-off point was used to estimate the probit intervals only in cases where at least one of the phenotypic classes did not contain individuals with four bristles.

In a similar manner to that used for the untransformed data, the contribution of each of the chromosomes and of interactions between chromosomes to selection advance can be computed from the transformed data. These estimates are shown in Table 3. The values for the chromosomal components alone estimate the number of standard deviations a given chromosome will elevate the mean of the selection line above the cut-off point specified in Table 4. Interaction components express, as in the case of the untransformed data analysis, deviations from addi-

TABLE 4

Means for each phenotype of each selection line in terms of standard deviations separating the mean and the specified cut-off point

Line	Phenotypes								Cut-off point for probit interval determination
	+++	++ Ubx	+ Cy +	+ Cy Ubx	CIB ++	CIB + Ubx	CIB Cy +	CIB Cy Ubx	
A1	-2.03	0.17	-2.03	0.08	-0.25	2.32*	0.29	2.43	4/5
A4	-0.32	0.08	0.39	0.36	0.43	0.53	0.67	1.01	4/5
A6	-0.91	-0.37	-0.36	0.58	0.19	0.42	-0.14	0.98	4/5
A9	-1.50	0.62	-1.30	1.38	-0.05	1.05	-0.75	1.38	5/6
A15	-0.73	0.18	-0.50	0.51	0.56	1.43	1.51	2.11	4/5
A18	-2.04	0.46	-1.48	0.67	-0.12	1.84	-0.01	2.54*	4/5
A21	0.51	0.12	0.14	0.58	0.41	0.58	0.54	0.98	4/5
A30	1.03	0.64	0.56	1.19	1.24	0.86	1.16	1.56	4/5
"crossed"	-0.95	0.73	-1.55	1.13	0.10	2.31	0.70	2.53	5/6
AH5	-1.45	0.68	-1.41	0.76	0.29	1.98	0.24	2.45*	4/5
AH9	-0.68	0.01	-1.43	1.01	-0.16	1.41	-0.05	2.51	5/6

* Minimum estimate.

tivity. Table 3 indicates that in general the magnitude of the chromosomal components relative to that of the interaction components are greater for the untransformed data.

A comparison of the chromosomal and interaction components, estimated from the transformed and untransformed data, can be made by considering each component in terms of its percent contribution to overall selection advance. The overall selection response for any one line is the difference between the + + + phenotype and the *CIB Cy Ubx* (or *w^{m4} Cy Ubx*) phenotype. Table 3 gives the percent contribution of each chromosome and of chromosomal interactions to the selection advance for each of the 11 "A" lines analysed for estimates based on the untransformed and transformed data respectively. With the exception of lines A21 and A30, the estimates of the percent contribution are compared in Figure 3.

In general, transformation of the data reduced the first and second order interaction components while the single chromosomal components were increased (Table 5). On an average the 1-2 and 1-3 positive interactions decreased to effectively zero after transformation while the 2-3 negative interaction component increased in magnitude after transformation.

In lines A1 and A18 the large positive 1-3 interaction found with the untransformed data appeared to be largely a result of the threshold at four bristles since this component is effectively eliminated by transformation. In line A9, with the exception of changing the sign and magnitude of the 2-3 and of the 1-2-3 interactions, the transformation has had little effect on the relative magnitude of the various components.

In the Class 2 lines ("crossed," AH5 and AH9) the 1-3 interaction component was reduced drastically by transformation, while contribution of the respective single chromosome components increased relative to the components estimated from the untransformed data. Relatively large second order interactions in the "crossed" line and in line AH9 are suggested by the transformed data.

Transformation, in the case of the Class 3 lines (A4, A6 and A15), altered the respective components only slightly over those estimated from the untransformed data. The largest single change occasioned by transformation was the reduction in the 2-3 interaction of line A15. Under both analyses all three major

TABLE 5

Average percent contribution of the components for all selection lines for the untransformed and transformed data

Component	Untransformed data (percent)	Transformed data (percent)
1	30.1	45.9
2	28.1	35.4
3	38.4	58.4
1-2	13.3	-2.8
1-3	53.9	4.5
2-3	-13.3	-29.5
1-2-3	-50.5	-11.9

FIGURE 3.—Percentage contribution of the chromosomal components and of interactions to selection advance for the untransformed data (solid vertical lines) and for the transformed data (dotted vertical lines) for the Class 1, 2, and 3 lines.

chromosomes were important in the determination of scutellar bristle number.

The greatest effect of transformation occurred in lines A21 and A30 of the Class 4 lines (see Table 3). The very large negative second order interaction and the positive 1-3 interaction estimated from the untransformed data were reduced quite drastically by transformation. The respective single chromosome components were not altered to any great extent.

DISCUSSION

The most striking feature of this analysis is that each line is genetically different from any other line in terms of the chromosomal components and chromosomal interactions. Line A9 of the Class 1 lines had a response pattern somewhat different to that of the other two lines, A1 and A18. This former line appeared to plateau early in the selection program and then underwent an accelerated response to selection (see Figure 1). Further, most of the genetic change that occurred in line A9 involved only the third chromosome. It is possible that the third chromosome of line A9 carried a polygenic system determining scutellar bristle number within which there had been two favorable recombinations. In lines A1 and A18, on the other hand, changes were involved in both the 1st and the 3rd chromosomes; the interaction between these two chromosomes appears to be a result of the threshold at four bristles.

The "crossed" line has retained those favorable changes which had occurred in A1, A9 and A18. The interaction component was not entirely eliminated by transformation, suggesting that favorable interactions can be built up by selection. Lines AH5 and AH9 differ on two main accounts. First, there has been a change in the magnitude of the 1st and 3rd chromosome components favorable to the direction of selection. In comparison to their parent line, "crossed," there has been a decrease in the two components in line AH5 and an increase in those components in AH9. Secondly, AH9 has utilized genetic variability that was contained within the 2nd chromosome; this has not been found in any of the other high level lines. The effects of selection and the chromosomal analyses both indicated the presence of a considerable amount of genetic variability in the "crossed" line.

The lines described by FRASER *et al.* (1965) as second-level lines, the Class 3 and Class 4 lines, are likewise genetically different. Each of the major chromosomes were favorably involved in selection response but their full potential was not realized because of unfavorable interactions, only part of which were removed by the transformation used. All three major chromosomes were involved in determining bristle number in A6 but the 3rd was of greater importance than the other two. Interactions were again major determinants of the scutellar number in line A6.

The response in A15 involved changes in the 1st chromosome. This is supported by FRASER *et al.* (1965) who found a major factor for scutellar bristles in the distal portion of the 1st chromosome. Interactions in this case can be explained on the basis of a threshold effect at four bristles.

The situation in the Class 4 lines, A21 and A30 is confounded by the low efficiency (Table 2) of the reconstituted + + + phenotype to recover the scutellar bristle number of the selection line. Since a large sample of chromosomes were taken from the selection line for assay, it is unlikely that the low efficiency resulted from homozygous lethality. It is possible that certain of the selection line chromosomes carried genes which were lethal in combination with the inversion marked chromosomes. If such is the case then the selection line chromosomes concerned presumably carried high scutellar potential factors. Since chromosome 4 was not controlled in this analysis, it is possible that a large portion of the genetic changes involved in the selection advance of A21 and A30 was located on the 4th. The extra scutellar bristle potential that was recovered in these lines indicates that all three major chromosomes were involved. Interactions, after threshold effects are removed, are important, particularly for the 2-3 component.

The striking feature of these chromosomal analyses is the heterogeneity across the various scutellar bristle selection lines. This explains the heterogeneity found by FRASER *et al.* (1965) in terms of different responses to selection. These A series of lines were each initiated from a single inseminated female and it is apparent that all of these females were genetically dissimilar even though they came from a population which was phenotypically invariant at four bristles. Selection has been able to extract genetic variability from a restricted base population and the response patterns indicate that the release of this variability can be either rapid (lines A1, A9 and A18) or slow (lines A4, A6, A15, A21 and A30).

All three major chromosomes were involved in response to selection. In general, chromosome 3 had a greater potential for increased scutellar bristles than the 1st and occasionally chromosome 2 played a role. Interactions between chromosomes to large extent can be accounted for by the threshold effect at four bristles. Those interactions remaining after transformation were in general unfavorable to the direction of selection; the full potential of the single chromosome effects was not realized.

The lines described by FRASER *et al.* (1965) as third level lines (A1, A9, A18, "crossed", AH5 and AH9) differ from the second level lines (A4, A6, A15, A21 and A30) in that the 2nd chromosome was not involved in selection advance of the third level lines, with the exception of line AH9. The second level lines in general have utilized variability on the second as well as that on the other two major chromosomes. It is somewhat contradictory that a greater response to selection was achieved by lines which utilized only a portion of the genome, whereas lines which utilized genetic variability in all three chromosomes realized a lesser response. In an experiment predicated upon the above results, NASSAR and FRASER (1965) found that restriction of the variability to one or other of the three major chromosomes led to a qualitatively greater response to selection than when the whole genome was allowed to remain variable. Assuming that complex genetic interactions are involved in the canalization at four bristles, it can be predicted that selection would have to reduce these interactions so that the additive genetic variance can be effectively utilized. Utilization of the genetic variability of the whole genome could possibly retain a residual amount of inter-

action because of the complexities involved. This residual interaction because of its role in the maintenance of phenotypic stability would reduce the effectiveness of selection. A reduction in the genetic variability by chance effects, as would be the case in some of the "A" lines as a result of the restricted base population, or by chromosomal manipulation as in the NASSAR and FRASER (1965) experiment, would reduce the interactions and allow a more efficient utilization of the additive genetic variance.

SUMMARY

A series of scutellar bristle selection lines was analyzed chromosomally to determine the genetic basis of response to selection. Selection lines which utilized genetic variability on the 1st and/or 3rd chromosomes had a greater response to selection than those which utilized genetic variability on all three major chromosomes. In general, interactions between chromosomes were favorable to the direction of selection in the high level lines, while in lines with the lower level response interactions tended to counter single-chromosome effects.

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