VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA**

XII. SELECTION IN *SCUTE* LINES

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Summary

Selection has been practised in *scute* lines for increased number of scutellar bristles. The substitution of sc^+ into these lines showed that the selection in *scute* had correlated effects on the number of extrascutellar bristles in *wild-type*. Crosses between *scute* and *wild-type* selection lines show that selection for extrascutellar bristles in *wild-type* has a correlated effect on the number of scutellar bristles in *scute*. This correlation is not complete; one component of the genetic system controlling the occurrence of extrascutellars does not have concomitant effects on the number of scutellar bristles in *scute*.

I. Introduction

The *scute* gene causes a reduction of the number of scutellar bristles which is accompanied by a marked increase of variability. Rendel (1959) found in lines segregating for sc^1 and sc^+ that selection for increased number of scutellar bristles in *scute* produced a correlated response of the number of extrascutellar bristles in *wild-type*. He concluded that the simplest explanation of these results is that a single system of modifier genes determines the number of scutellar bristles in both *scute* and *wild-type*. Fraser and Green (1964) found that substitution of sc^1 for sc^+ in lines which had been selected for extrascutellar bristles was epistatic to the selection response. They found no correlation between the number of extrascutellar bristles in *wild-type* and the number of scutellar bristles in *scute*, indicating that there are two sets of modifier genes: one acting on the expression of *scute*, the other acting on the expression of *wild-type*. Rendel (personal communication) has suggested that scaling effects may account for the discrepancy, due to modifiers having markedly greater effects with decrease of the number of scutellar bristles. In addition to this possibility there are some arithmetic errors in the Fraser and Green (1964) analysis, which indicate the possibility of a slight correlation between *scute* and *wild-type* expression. In view of this possibility, further experiments have been initiated to determine whether a real discrepancy exists between Rendel's and our results.

Fraser *et al.* (1965) have shown that the genetic control of the occurrence of extrascutellars is extremely complicated, involving marked heterogeneity of response to selection both between separate selection lines and at different times within selection lines. Fraser (1965) has also shown that the genetic control of the number of extrascutellars has complex dominance relations. If Rendel (1959) is correct in his deduction that a single genetic system modifies the expression of both *scute* and *wild-type*, then selection for increased number of scutellars in *scute* should be characterized by the

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same complex responses to selection, and the same pattern of dominance relations. The sc^1 gene therefore was introduced into the same base stock used by Fraser *et al.* (1965) for many of their experiments. This allowed a repeat of Rendel's (1959) experiment on the effect of selection in *scute* lines. The results of these experiments are presented and discussed in this paper.

II. Material and Methods

A sc^+w^h (line 70) played a major part in the origin of many of the selection lines studied by Fraser *et al.* (1965). Crosses were made of males of this line with female sc^1z. Males were then backcrossed to line 70, and an sc^1z stock formed. Four main

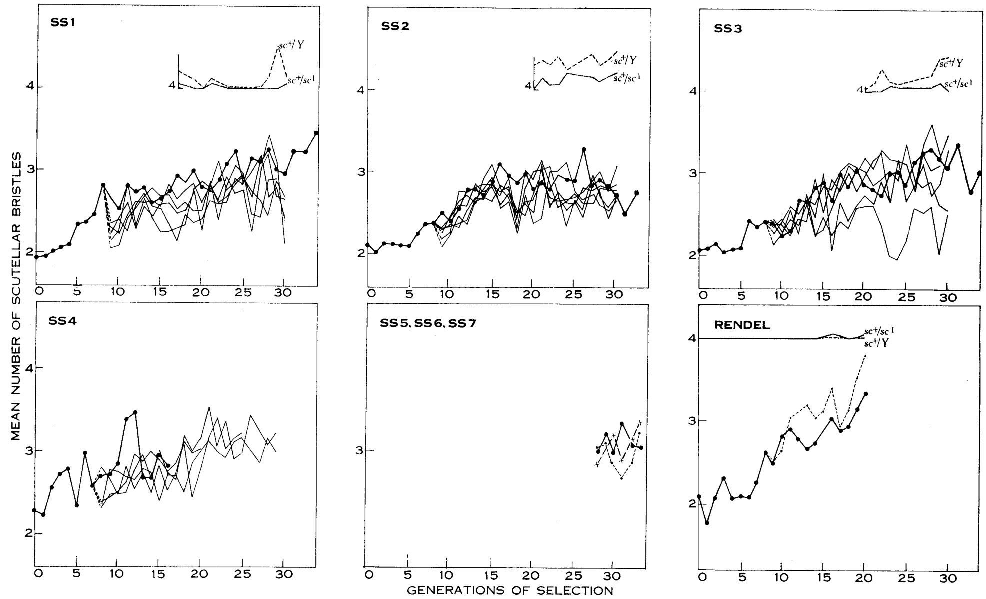

Fig. 1.—Mean scutellar number of sc^1/sc^1 females plotted against generation of selection for the SS main lines (———) and SS derived lines (———). The values for the sc^+/sc^1 and sc^+/Y genotypes are also shown.

selection lines for increased scutellar number were initiated from this stock. These are the SS1, SS2, SS3, and SS4 lines. Selection was restricted to females and no attempt was made to maintain a rigorously fixed population size or intensity of selection. Approximately six females were selected as parents from approximately 30 scored each generation. The lines were maintained in one-quarter pint bottles at 72°F. Several subsidiary experiments were initiated from these main lines.

A number of single female cultures were set up from the SS1–SS4 lines at the tenth generation. All of these were maintained as independent selection lines in vials for five generations. Selections were then made between these lines, within each group derived from a particular SS line, e.g. 15 inseminated females were taken from SS1 at the tenth generation, forming 15 selection lines, and the five lines with the greatest selection response were retained. The aim was to determine whether passage through an inbreeding bottleneck affected the response to selection and to allow comparison with the B set of lines of Fraser *et al.* (1965) in which each line was separated into three independent replicates at the seventh generation of selection. The lines derived from the main SS lines in this way are termed the "SS derived" lines.

Crosses were made at the fifteenth generation to introduce sc^+ into each of the SS1–SS4 lines as follows ($+^s$ = chromosomes II and III of SS line):

(1) sc^1z; $+^s$; $+^s$ (15th)	×	sc^+w^h; $Cy\ Ubx/Xa$
(2) sc^1z/sc^+w^h; $Cy/+^s$; $Ubx/+^s$	×	sc^1z; $+^s$; $+^s$ (16th)
(3) sc^1z; $+^s$; $+^s$ (17th)	×	sc^+z; $+^s$; $+^s$
(4) sc^+z/sc^1z; $+^s$; $+^s$	×	sc^1z; $+^s$; $+^s$ (18th)

These were maintained in permanent backcross to the SS selection lines.

Crosses were made between the SS lines to form three new lines: SS5 from SS1 and SS2, SS6 from SS2 and SS3, and SS7 from SS1 and SS3. The aim was to determine whether crossing could increase the realizable genetic variability.

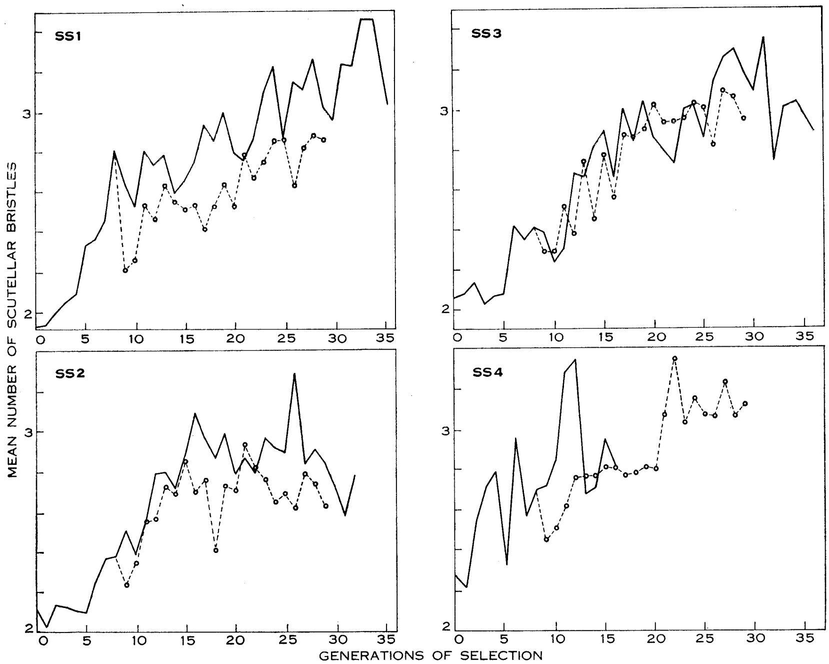

Fig. 2.—As for Figure 1, but with the separate derived lines averaged (- - - - - -).

III. Results and Discussion

The results for the main and derived SS lines are shown for females in Figure 1, as mean scutellar number plotted against generation of selection. The response to selection is similar to Rendel's (also shown in Fig. 1) in being slow and relatively homogeneous between generations. It differs from Rendel's in being less than he obtained. The main difference is that two of the SS lines reached a plateau at about 3 bristles. Rendel found no such restriction. Crosses between SS1, SS2, and SS3 to produce SS5, SS6, and SS7 did not have any marked effect on the effectiveness of selection. The long continued response to selection is in marked contrast to the heterogeneity of response found to selection for extrascutellars in *wild-type*. An interesting feature of these results is the close parallelism between the main and derived lines. This is shown in Figure 2 where the means over each set of derived lines are plotted for comparison with the results from the main lines. The SS1 derived lines dropped back about a third of a bristle, but then responded at very much the same rate as the main SS1 line. The SS2 derived lines reached a plateau similar to that which occurred in the main SS2 line. The comparison between the main and derived SS3 lines is very close. It would appear that the differences between the SS lines were effected before the ninth generation, and that the markedly different history of the main and derived lines did not have a major effect on the pattern of response.

TABLE 1

FREQUENCY DISTRIBUTION OF SCUTELLAR NUMBER IN sc^+/sc^1 AND sc^+/Y GENOTYPES OF THE SS MAIN LINES

Genotypes	Bristle Class	No. Scored in each Bristle Class		
		Line SS1	Line SS2	Line SS3
sc^+/sc^1	4	156	241	227
	5	2	24	7
	6	—	1	—
Mean No. of scutellar bristles		4·01	4·09	4·02
Mean over all lines		4·04		
sc^+/Y	4	141	163	187
	5	11	60	28
	6	—	5	—
Mean No. of scutellar bristles		4·07	4·30	4·13
Mean over all lines		4·16		

The results from the substitution of sc^+ into the SS main lines are given in Table 1 for the sc^+/sc^1 and sc^+/Y genotypes. Unfortunately, the substitution of sc^+ for sc^1 in the SS lines was not made until the fifteenth generation, and it is not possible to determine whether the extrascutellars found in sc^+/sc^1 and sc^+/Y are a correlated response, or a fortuitous feature of these stocks. The latter appears unlikely. Line 70 was prominent in the origin of the SS lines and many measurements have been made of the number of extrascutellars in this stock. The mean scutellar number of line 70 males ranged from 4·05–4·10. The mean scutellar number of sc^+/Y segregants from the SS lines is given for the last four generations in Table 1. It would appear that selection for increased scutellar number in *scute* has resulted in a correlated response in *wild-type*.

An interesting difference between these results and those of Rendel (1959) is that he found sc^+/sc^1 to have a greater frequency of extrascutellars than sc^+/Y; an opposite result was found in the SS lines where sc^{+}/Y had a greater frequency of extrascutellars than sc^{+}/sc^{1}.

In addition, the sc^{+}/Y expression found in the SS lines is greater than that found by Rendel (1959) in his lines, even though the *scute* expression is lower in the SS lines than in Rendel's (1959) lines. Clearly, any correlation between *scute* and *wild-type* expression is not simple and straightforward. This is further shown by comparisons between the SS lines—the *wild-type* expression is greater in SS2 than in SS1 and SS3, yet SS2 does not have a concomitantly different *scute* expression.

Fraser *et al.* (1965) found in crosses between extrascutellar *wild-type* selection lines that there was a marked regression below the mid-parent expectation, and Fraser (1965) found from a more extensive set of crosses that there were two qualitatively different responses in crosses between these lines. Three levels of response to selection

TABLE 2

MEAN SCUTELLAR NUMBERS OF sc^{1}/sc^{1} PROGENY OF A DIALLELIC SET OF CROSSES BETWEEN THE SS MAIN LINES AT THE NINTH GENERATION

Female Parent	Male Parent			
	Line SS1	Line SS2	Line SS3	Line SS4
Line SS1	*2·81*	2·22	2·65	2·63
Line SS2	2·50	*2·37*	2·45	2·67
Line SS3	2·51	2·54	*2·41*	2·72
Line SS4	2·54	2·48	2·67	*2·70*

were distinguished: first level (unselected), second level (moderate response), and third level (marked response). There was a marked regression in crosses between second-level lines and between most second- and third-level lines. This contrasts with crosses between third-level lines which showed only a slight regression below the mid-parent expectation. Crosses of both the second- and third-level lines with first-level lines showed a marked regression to the first level. The same recessivity of the second and third levels to the first level was found in crosses involving "inversion marked" chromosomes (Fraser *et al.* 1965; Fraser and Scowcroft 1965). A series of crosses were made between the SS lines at the ninth generation to determine their relation to the mid-parent expectation. The crosses were of four females with four males and 50 female and male progeny were scored. The results are given in Table 2. The results averaged over reciprocals are plotted against the mid-parent expectation in Figure 3. There was no-clear-cut pattern as was found in the crosses between extrascutellar *wild-type* lines. The response was similar to that found for the crosses between the third-level lines; namely, no marked deviation from the mid-point expectation.

A second set of crosses was made at the 34th generation between the SS1, SS2, and SS3 lines and a series of first-, second-, and third-level lines from the A set of extrascutellar lines (Fraser *et al.* 1965). The crosses were of sc^{1}/sc^{1} females (the SS lines) with sc^+/Y males (the A lines). Fifty male progeny were scored from each cross. The results are given in Table 3. The values of mean scutellar number at the beginning of selection and at the time the crosses were made are given in Table 3 for comparison.

There are several features of the comparisons of these crosses. Firstly, the crosses with the first-level lines are heterogeneous—the crosses with stock 73 show a marked reduction of scutellar number below the initial level of the SS lines, whereas the crosses with stocks 70 and 71 show a qualitatively less extreme reduction. It would appear possible that stock 73 contains an extremely strong negative component of scutellar number. This is not consistent with the results from crosses of stocks 70, 71, and 73 with extrascutellar selection lines, in which there was no indication that stock 73 contains an extremely strong negative component (see Fraser *et al.* 1965).

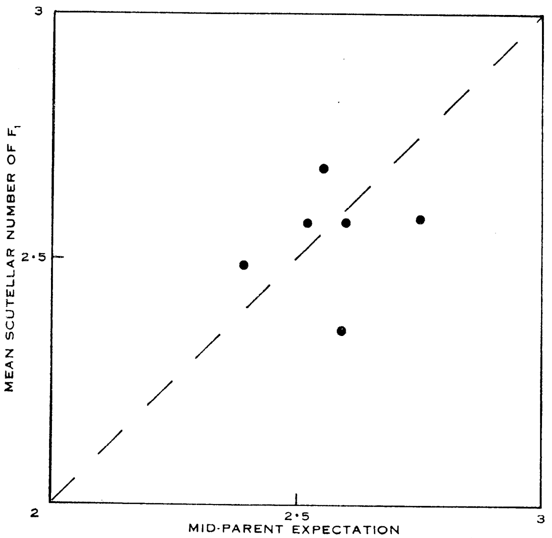

Fig. 3.—Mean scutellar numbers of the crosses between the SS lines plotted against the mid-parent expectation.

It is possible that stock 73 contains an autosomal dominant enhancer of *scute*. This will require extensive experimentation for its investigation. If stock 73 is considered as having unique features and eliminated from consideration here, then the crosses of the SS with first-level lines do not show a regression to unselected values, but are slightly below the average of the initial values and the values of the selection lines at the time of the crosses. If we assume that the *scute* expression of stocks 70 and 71 approximates to the initial values of the SS lines, then the crosses are in reasonable agreement with the mid-parent expectation. This contrasts markedly with the regression to the level of the unselected parent found in crosses between extrascutellar selection lines and stock 70, 71, and 73 (Fraser *et al.* 1965). The second feature of these crosses is the contrast between the crosses with unselected (first level) stocks and extrascutellar selected lines (second and third level). The crosses show a slight regression below the selected value of the SS lines. This contrast shows that the selection for increased scutellar number in *scute* and for extrascutellars in *wild-type* are analogous. This is in support of Rendel's hypothesis.

The third feature of these crosses is the lack of difference between the crosses with the second and third level selection lines. These lines differ markedly in their scutellar number, yet this difference is not reflected in their crosses with the SS lines. It would appear that the difference between the second- and third-level lines involves a genetic system which affects only the *wild-type* expression, having no effect on the *scute* expression.

TABLE 3

MEAN SCUTELLAR NUMBER OF sc^1/Y IN THE SS LINES INITIALLY AND AT GENERATION 34 OF SELECTION. THESE ARE GIVEN FOR COMPARISON WITH THE VALUES FOUND IN CROSSES OF THE SS LINES WITH FIRST-, SECOND-, AND THIRD-LEVEL EXTRASCUTELLAR LINES*

Crosses	Mean Scutellar No.			Mean over SS Lines and Crosses	Mean of Means
	Line SS1	Line SS2	Line SS3		
SS Lines					
Initial value	1·00	1·08	1·58	1·22	
Selected value (generation 34)	2·99	2·77	2·75	2·83	
First-level lines					
Stock 70	2·08	1·83	1·86	1·92	1·84
Stock 71	1·81	1·74	1·77	1·77	
Stock 73	0·46	0·76	0·42	0·54	
Second-level lines					
A4	2·97	2·58	2·59	2·71	2·51
A6	2·75	2·65	2·41	2·60	
A15	2·02	2·31	2·37	2·23	
Third-level lines					
A1	2·57	2·67	2·54	2·59	2·61
A9	2·68	2·70	2·55	2·64	
A18	2·49	2·69	2·67	2·61	

* See Fraser *et al.* (1965) for a description of these lines.

These results are in agreement with Rendel (1959) in the occurrence of a correlated response in *wild-type* to selection for increased number of scutellars in *scute*. This is further supported by the crosses between the SS lines and lines selected for extrascutellars in *wild-type*. These crosses show a greater scutellar number in sc^1/Y than do crosses of the SS lines with unselected *wild-type* lines, indicating that the selection for extrascutellars in *wild-type* involves the same genetic system as that on which selection has been practised in *scute*.

Other aspects of the data are not in agreement. Crosses of the SS lines with second-level extrascutellar lines do not differ from crosses of the SS lines with third-level extrascutellar lines. Erway (personal communication) has found that the third-level lines of the A set differ from the majority of the second-level lines, and from other third-level lines of the B set, in having marked increases of other main bristles.

It is reasonable to suggest that the third-level advance in the A set of lines involves a genetic system different from that involved in the advance to the second level. This is supported by the markedly different behaviour of second- and third-level lines in crosses between and within these classes: second × second and second × third crosses show a marked regression below the mid-parent, whereas third × third crosses do not show such a regression. This suggestion resolves the discordance between Rendel's and our results. An extensive set of crosses, involving the A set of lines has been made and their analysis should allow examination of the validity of this suggestion.

IV. References

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