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Correlated Responses of Different *scute* Genotypes to Long-term Selection for Increased Abdominal Bristle Number in *Drosophila melanogaster*

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Abstract

The first dose effect of sc^+ has been measured for abdominal bristle number in six replicate lines of *D. melanogaster* being selected upward for this character in the *sc* homo- and hemizygote. The within-line regression coefficient of the heterozygote on the *sc* homozygote showed considerable variation among the lines with a range of 0·47–1·22, indicating the dependence of gene action on genetic background. But, on the average, the effect of sc^+ was approximately additive for abdominal bristle number. From this average, the genetic correlation in the base population between the two genotypes was estimated to be considerably less than unity, which suggests some genetic variability that is dependent on the genotype of the major locus. A similar relationship was also obtained for the two male hemizygotes.

The sc^+ homozygote as well as the above genotypes were scored for abdominal and scutellar bristle number near the end of long-continued selection and the degree of dominance of sc^+ over *sc* assessed for each character. For abdominal bristle number, the degree of dominance was not altered significantly except in one line (Ua), where *sc* increased the bristle number in females only and was dominant over sc^+; the degree of dominance was apparently lowered for scutellar bristle number in all the lines, probably because selection had pulled the sc^+ homozygote and the heterozygote out of the four-bristle canalized zone.

Scutellar bristle number showed positive correlated response for all *scute* genotypes in each line except in Ua, but, when the five lines are compared, the relative amount of correlated response in one genotype does not necessarily correspond to that in another, suggesting interaction between the *scute* locus and genetic background for scutellar bristle number, at least in some lines.

Introduction

The number of bristles on abdominal sternites of *Drosophila melanogaster* is a character that has been extensively utilized in the experimental study of quantitative genetics, mainly for the reason that this character is well known to be relatively simple genetically and easy to score, at least in unselected populations. But, when the number of flies to be scored is large and/or the mean bristle number is doubled or tripled, as in many long-term selection lines (Jones *et al.* 1968), bristle scoring is no longer easy work. Therefore a mutant substantially reducing abdominal bristle number would be welcome in large-scale or long-term selection experiments if it does not entail any genetic complications of the character. The sex-linked mutant, *scute* (*sc*), appears to be a promising candidate for this purpose as the homo- and hemizygote for this gene have no more than half the number of bristles of the wild type in unselected populations. However, the effects this gene may have on the genetics of the character have not been examined until recently (Hammond 1973; Yoo 1974).

Realizing the possible advantage, Rathie (1969) introduced *sc* into a wild-type outbred strain as a part of the small chromosome segment carrying the mutant y^2,

which is very closely linked to *sc*, as well as *sc* itself. The additional mutant y^2 is quite useful, as it is a good marker for *sc* when the *scute* locus is segregating and it also makes it possible to distinguish reversion (or a similar mutational change) of *sc* from contamination by extraneous flies. But y^2 has little effect on abdominal bristle number compared with *sc*, and the notation of y^2 genotypes can be neglected when *scute* genotypes are under consideration for this character.

From an extensive genetic analysis of the *sc* population that Rathie (1969) started, Hammond (1973) concluded that the substitution of *sc* for sc^+ had only small effects on major genetic parameters and the gene action of *sc* was neither additive nor multiplicative, but somewhere between the two. If a similar gene action were observed also in selection lines, the results of selection experiments with the *sc* population might not be directly comparable with those of previous experiments done with a wild-type stock. Hence, if the *sc* population was to be used as a base population in selection experiments it appeared necessary to measure the effects of substitution of sc^+ for *sc* (inevitably including a small number of other loci adjacent to the *scute* locus) in selection lines derived from this population.

Rendel (1963) observed that the correlated response of abdominal bristle number to selection for scutellar bristle number differed for different amounts of selection and for different *scute* genotypes. He proposed a genetic model on the basis of simplified assumptions where various genetic correlations may be generated. Young and Sheldon (1965), in analysing lines selected for abdominal bristle number, and Sheldon and Milton (1972), in long-term selection lines for scutellar bristle number, found some difficulties in fitting their observations to Rendel's model. They performed selection in the wild type, while selection was primarily in the *sc* genotype in Rendel's (1963) experiment. As the former selection may be different from the latter in the effects on the genetic correlation between the two characters, although Rendel's model embraces both cases, more experimental evidence on correlated response to selection in the *sc* genotypes would be desirable.

In unselected populations, sc^+ is nearly but not completely dominant over *sc* for abdominal bristle number, whereas dominance is complete for scutellar bristle number. Rendel (1959) observed that a difference in scutellar bristle number between the heterozygote and the sc^+ homozygote was expressed when the influence of canalization was partly reduced by selection, and attributed the high degree of dominance to the canalization at four bristles of the wild type. A similar proposition that developmental canalization of the wild type results in dominance or that dominance is a form of canalization has been long expounded (Muller 1932; Plunkett 1932; Waddington 1957), but theoretical development and experimentation came about much later (Rendel 1967). On the other hand, if there were many specific genes whose effects were dependent on the genotype of another locus (major locus), as observed by Fisher and Holt (1944), genetic gain from selection in one genotype of the major locus would be expected to be larger than the correlated response in another genotype, possibly resulting in a change in the degree of dominance for some characters with little canalization, e.g. abdominal bristle number. Selection for abdominal bristle number, which may also affect the level of genetic background for scutellar bristle number, would then be expected to alter the degree of dominance in both characters but probably through different pathways.

In a long-term selection experiment for abdominal bristle number started with the *sc* population of Rathie (1969), subcultures segregating at the *scute* locus were main-

tained by continuous backcrossing to the main selection lines. By scoring the different *scute* genotypes for abdominal and scutellar bristle number we were able to study the effects of sc^+ on these characters, on correlated response in the latter and on the degree of dominance of sc^+ over *sc* for each.

Materials and Methods

Six lines of *D. melanogaster* were derived from the *sc* Canberra strain described by Rathie (1969) and were each selected for increased bristle number on one abdominal sternite, the fourth in males and the fifth in females, for more than 85 generations. The genetic correlation in bristle score between the two sternites within each sex was estimated to be unity in the selection lines (Yoo 1974) as well as in the base population (Hammond 1973). Out of 250 pairs scored 50 were selected as parents, and the lines were maintained in conditions similar to those described by Frankham *et al.* (1968). The particular code designations of the six lines are immaterial to the present discussion, but are used to allow cross-reference to other papers that are in preparation. At generation (G) 17 for lines Ua and Ub, G20 for lines CCa and CCb, and G22 for lines CRa and CRb a sample of males of the wild-type Canberra strain was mated to the 10 females next highest in bristle number to the 50 females selected for continuation of each selection line. In each subsequent generation, 10 heterozygote females from this subculture were backcrossed to the 10 *sc* males next highest to the 50 selected in each line (backcross 1 in Fig. 1). Four segregating genotypes (sc^+/sc, sc/sc, sc^+/Y and sc/Y) from this subculture were scored for abdominal bristle number in at least six generations at irregular intervals up to G87, starting at G21 for Ua and Ub and at G25 for the other lines.

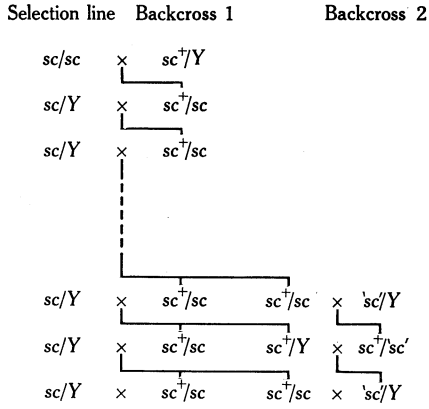

Fig. 1. Crossing procedures used to maintain subcultures segregating at the *scute* locus (backcross 1) and to substitute *sc* derived anew from the cage population ('*sc*') for *sc* in the selection lines (backcross 2).

In order to make sure that *sc* remained intact during selection, another backcrossing series (backcross 2 in Fig. 1) was started at G66 to allow substitution of the *scute* region of the *X* chromosome derived anew from the original cage population of the *sc* Canberra strain for that in each of the selection lines. These new cultures were backcrossed to backcross 1 every generation up to G78, when the *sc* homo- and hemizygote from backcross 2 were compared with those from backcross 1 for scutellar bristle number. They were very similar in mean and frequency distribution of bristle number in each line except in CCa, which was found to be nearly fixed for a probable mutant at or very close to the *scute* locus that reduced scutellar but increased abdominal bristle number considerably. Backcrossing was further extended to G87 in this line only, and the segregants of backcross 2 were scored instead of those of backcross 1 for scutellar and abdominal bristle number at G78 and G87.

Two matings were set up with flies from backcross 1, or from backcross 2 for CCa, and the progeny of phenotypically identifiable genotypes scored for abdominal and scutellar bristle number in

a generation between G81 and G87: viz. $sc^+/sc \times sc/Y$ (mating A) and $sc^+/sc \times sc^+/Y$ (mating B). As sc^+/sc^+ and sc^+/sc from mating B are not distinguishable, they were progeny-tested after being scored together with other genotypes. Similar matings were also set up with flies from the cage populations and the progeny scored at G89. These last data were taken as representing the common base population before selection was initiated.

Results

Change in the scute *Locus*

As the two mutants y^2 and *sc* had been intentionally introduced into the originally wild-type stock before starting the experiment, any visible mutations at these loci were eliminated whenever found. In addition it was necessary to exclude the possibility of *sc* mutating to an allele which may have escaped detection, for the relation between the *scute* locus and the genetic background that selection had brought about was of major interest. Backcross 2 was specifically designed to meet the need. Fig. 2 gives the comparison for each main selection line with backcross 1 and backcross 2 for scutellar bristle number, by which change at the *scute* locus may be disclosed. The *sc* homo- and hemizygotes were scored at G78 for backcrosses 1 and 2, while the main lines were scored later in G85 or G86 just before ending selection. The numbers of flies scored were not very large, ranging between 50 and 126 in each sex. As far as mean bristle number is concerned, the three cultures were very similar in each line except CCa, indicating that *sc* probably remained intact, though in some cases backcross 2 was not very close to backcross 1. In CCa, the *scute* locus (and the vicinity thereof) of the main line and of backcross 1 was clearly different from that of backcross 2 which harboured the original *sc*. As this difference maintained itself for a further 34 generations of backcrossing, it seems reasonable to conclude that mutation occurred at the *scute* locus during selection. Some details of the genetic nature of this mutant are given elsewhere (Yoo 1974). For this reason, therefore, backcross 2 was taken into consideration in place of the CCa backcross 1 after G58.

First Dose Effects of sc^+ *on Abdominal Bristle Number*

As selection was solely in the *sc* homo- and hemizygous main lines, the effects of sc^+ could not be measured until backcross 1 was started, by which time the selection program had advanced to some extent. Segregating genotypes were first scored after three to five generations of backcrossing, which may be assumed to have brought different *scute* genotypes into a roughly similar common genetic background except for the *X* chromosome. The number of flies scored was rather small with a range of 3–25 per genotype before G32, but about 50 flies were normally scored thereafter. Phenotypic variance was increased considerably in some selection lines, making it necessary to observe more individuals in the later stage of selection in order to roughly equalize the precision of genotype means estimated at different generations within a line.

In each selection line the generation means of the heterozygote were plotted against those of the *sc* homozygote and a linear regression fitted as shown in Fig. 3. The regressions are all significant, but there was a considerable amount of residual variation, except for Ua, as well as some curvilinearity, particularly in Ub and CCa. The curvilinearity seems to have been partly caused by the genetic background of the heterozygote being lower in bristle-producing activity than that of the *sc* homozygote

in early generations, when backcrossing was not performed long enough. Linear regressions were also fitted to the generation means of the wild type against those of

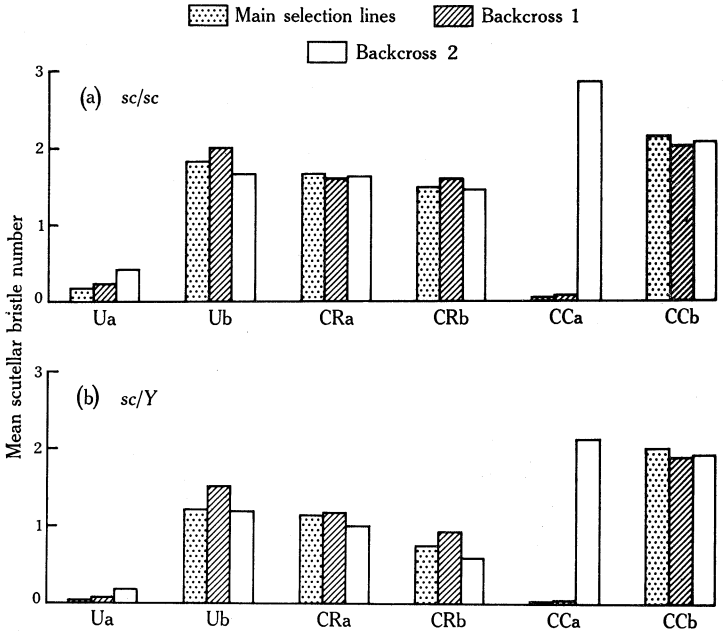

Fig. 2. Mean scutellar bristle numbers of main selection lines, backcross 1 and backcross 2. In main lines 50 flies were scored for each mean in G85 or G86, and 60–126 flies were scored in backcrosses 1 and 2 in G78.

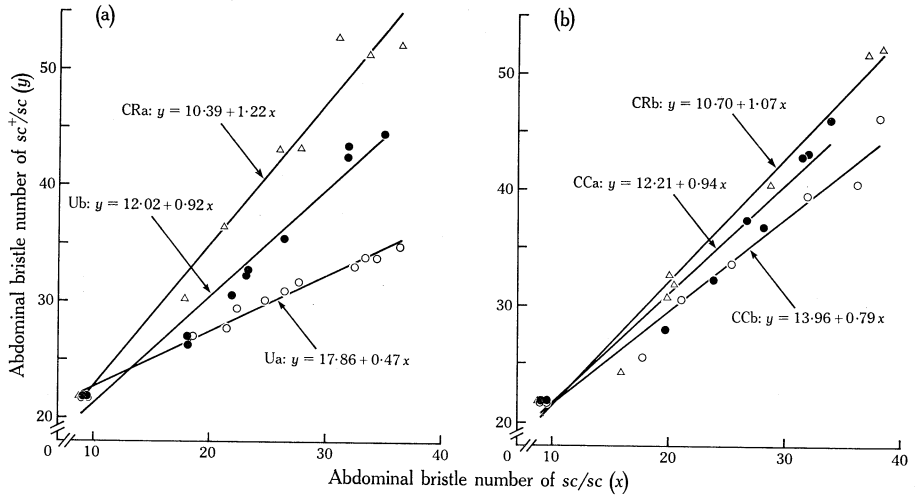

Fig. 3. Linear regression of sc^+/sc on sc/sc in lines Ua, Ub and CRa (*a*) and in lines CRb, CCa and CCb (*b*).

the *sc* hemizygote in males. The regression coefficients are significantly different among the five lines excluding Ua as well as among all six lines in each sex. They are therefore separately given in Table 1, together with their approximate standard errors.

If the effects of sc^+ in one dose were purely additive, the regression coefficient of one genotype on the other would be expected to be unity. In each sex, the regression coefficients are not significantly different from unity in Ub, CRb and CCa, while they are significantly larger and smaller than unity in CRa and CCb respectively. Ua is distinct from the others due to the much smaller regression coefficients in both sexes. The regression coefficients for the two sexes are not significantly different except in Ua.

Table 1. Regression coefficients of sc^+/sc on sc/sc, and of sc^+/Y on sc/Y, for abdominal bristle number

Line	$b \pm$ S.E. sc^+/sc on sc/sc	sc^+/Y on sc/Y	Line	$b \pm$ S.E. sc^+/sc on sc/sc	sc^+/Y on sc/Y
Ua	0·47±0·02**	0·55±0·03**	CRb	1·07±0·05	1·00±0·08
Ub	0·92±0·05	0·90±0·08	CCa	0·94±0·06	0·95±0·06
CRa	1·22±0·07*	1·22±0·07*	CCb	0·79±0·05**	0·81±0·05**

* Significantly different from 1·00 at $0{\cdot}01 < P < 0{\cdot}05$.
** Significantly different from 1·00 at $P < 0{\cdot}01$.

Degree of Dominance for Abdominal Bristle Number

The wild-type homozygote, as well as the other genotypes, were scored for abdominal and scutellar bristle number near the end of the selection program, when two or probably three lines were still responding to selection. Backcross 1 had been backcrossed to the main lines for 62 or more generations by then and the backcross 2 of CCa for 21 generations.

Table 2. Mean and phenotypic variance of the *sc* homozygote, the first (a_1) and second (a_2) dose effects of sc^+, and the degree of dominance (d) for female abdominal bristle number, together with standard errors

Line	Generation[A]	sc/sc Mean	σ_P^2	a_1	a_2	d
Base	0	9·49	2·86	12·31±0·31	0·90±0·33	0·932±0·023
Ua	81	34·24	8·02	−0·46±0·56**	−2·35±0·49**	0·164±0·168**
Ub	84	31·78	20·05	10·74±0·79	1·97±0·65	0·845±0·044
CRa	84	31·00	27·10	21·80±0·96**	2·74±0·73*	0·888±0·027
CRb	86	37·14	41·76	14·46±1·37	2·23±1·67	0·866±0·087
CCa	87	33·76	15·74	12·28±0·93	1·03±0·75	0·923±0·052
CCb	84	38·14	11·84	8·12±0·81**	0·73±1·23	0·918±0·128

[A] Generations of selection.
* Significantly different from the base value at $0{\cdot}01 < P < 0{\cdot}05$.
** Significantly different from the base value at $P < 0{\cdot}01$.

For abdominal bristle number, mean and phenotypic variance of the *sc* homozygote from backcross 1 are given in Table 2 to indicate the extent to which the genetic background has been shifted, as well as the difference between the heterozygote and the *sc* homozygote (i.e. the first dose effect of sc^+, a_1) and that between the wild-type homozygote and the heterozygote (i.e. the second dose effect of sc^+, a_2) for each of the six selection lines and the base population. The differences between genotypes were calculated within culture bottles, viz. the former from mating A and the latter from mating B.

The degree of dominance (d), defined as $d = a_1/(a_1+a_2)$, is also given in Table 2, together with its approximate standard error calculated from the variances of a_1 and a_2.

In CRa a_1 has been significantly increased, but a_2 is also significantly larger than the base, while the reverse is probably true in CCb. As a result, in both lines d is not significantly different from the base value of 0·932. Ub, CRb and CCa are not significantly different from the base in any of the parameters a_1, a_2 or d, though the values of d are considerably smaller in these lines. Ua is exceptional in that the *sc* homozygote does not differ significantly from the heterozygote in abdominal bristle number, while both the genotypes are now substantially higher than the wild-type homozygote. In other words, the original relationship between the two alleles with respect to abdominal bristle number and dominance has been reversed in females, *sc* now increasing the number of bristles and being dominant over sc^+. But the sc^+ hemizygote is still higher than the *sc* hemizygote in males, even though the difference between them has been decreased from 11·6 to 6·0 bristles. This unexpected relationship between the two alleles was further confirmed at G84 and even after 20 generations of relaxed selection, at G106. Selection lines as a whole showed a tendency to a lower degree of dominance than the base, though a_1 and a_2 have both drifted either side of the base value 'at random' in the sense that the six lines are more or less replicate populations.

Correlated Response in Scutellar Bristle Number

Fig. 4 shows the total correlated responses in scutellar bristle number for different *scute* genotypes. Mean bristle number before selection is expressed by the left end of a line and that after selection by the right end. Each right end is based on 50–70 observations in most cases for all genotypes other than sc^+/sc. As the mean of sc^+/sc from mating A was not exactly the same as that from mating B, the means of sc^+/sc^+ and of sc/sc were accordingly adjusted to be comparable, using as a base the average of the two sc^+/sc means. Consequently the number of observations for sc^+/sc is approximately doubled. Positive correlated response is quite apparent for all genotypes in each line except Ua. In general, difference between genotypes within a line appears to be largely dependent on the level of their means, being much less around the four-bristle class at which the development of scutellar bristle is strongly canalized. It may also be observed that, when different selection lines are compared, the relative amount of correlated response in one genotype does not correspond well with that in another. For example, CRa and CRb are very similar in the *sc* homo- and hemizygote, but obviously different from each other in other genotypes. A more evident contrast may be seen between CRb and CCb. Ua is qualitatively different from the others in showing negative correlated responses in the three lowest genotypes and none in the rest.

The first and second dose effects of sc^+ on scutellar bristle number were derived from the data given in Fig. 4, and the degree of dominance calculated as defined before. The values of these parameters are given in Table 3. The degree of dominance was evidently lower in the selection lines than in the base, principally because the sc^+ homozygote became higher than the heterozygote apart from change in the *sc* homozygote. The heterozygote and the sc^+ homozygote were well beyond the four-bristle class in CCa, displaying more correlated response than the *sc* homozygote, but the large difference between them lowered the degree of dominance. The negative correlated response in the *sc* homozygote of Ua was also weakly reflected in the

heterozygote, but not at all in the sc^+ homozygote, the degree of dominance being modified consequently. In the rest of the lines the correlated responses of the two homozygotes were larger than that of the heterozygote, the lowered a_1 and the raised a_2 resulting in a low degree of dominance.

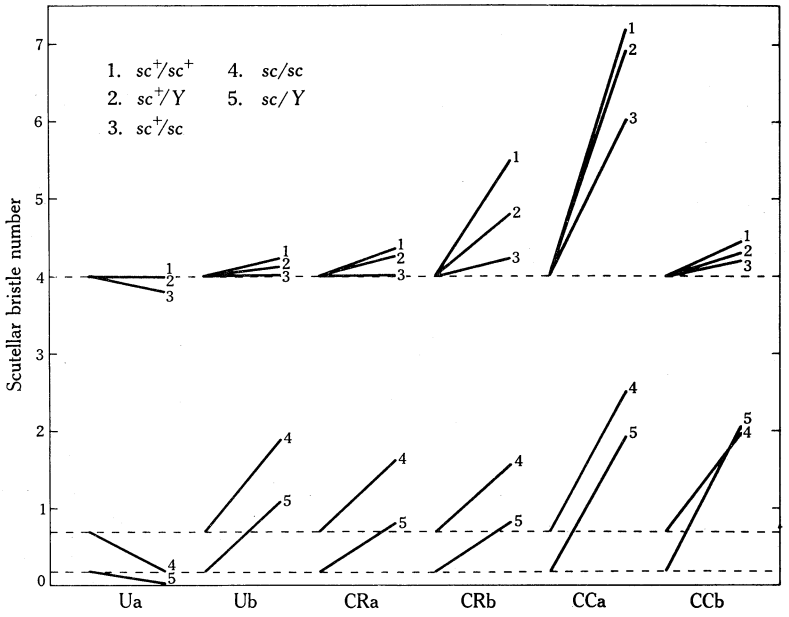

Fig. 4. Total correlated responses in scutellar bristle number for different *scute* genotypes. Left end of each thick line represents base population mean.

Also, Tables 2 and 3 show that the relative magnitude of correlated response in scutellar bristle number is hardly related to the response in abdominal bristle number when the selection lines are compared with each other. The relative change in the degree of dominance likewise shows no discernible relationship between the characters.

Table 3. The first (a_1) and second (a_2) dose effects of sc^+ and the degree of dominance (d) for female scutellar bristle number

Line	Generation	a_1	a_2	d	Line	Generation	a_1	a_2	d
Base	0	3·30	0·00	1·000	CRb	86	2·66	1·26	0·678
Ua[A]	84, 86	3·62	0·19	0·950	CCa	87	3·50	1·18	0·748
Ub	84	2·12	0·21	0·910	CCb	84	2·22	0·26	0·894
CRa	84	2·38	0·35	0·871					

[A] Scutellar bristles were not scored in G81 when abdominal bristles were; instead they were scored in G84 for the genotypes from mating A and in G86 for those from mating B.

Discussion

A few features of the selection experiment itself seem to be worth mentioning at the outset of this discussion. The experiment was originally designed to study the effects of population structure, in particular subdivision of a large population under

selection, on genetic improvement, and the details of this aspect are reported by Rathie (1974). It may be sufficient for the present purpose to point out that each selection line was started with equal contributions of 50 full-sib families common to all of the six lines, which were later manipulated similarly except for the first 17 generations when population structure treatments were imposed. Rathie (1974) concluded that the effects of population structure were negligible, if differences in selection differential among treatments were taken into account. Therefore the six selection lines may be regarded as replicate populations in the current experiment.

One of the salient points in this experiment is the variation of the first dose effect of sc^+, which was getting larger during selection, on abdominal bristle number among the replicate lines. For instance, the substitution of sc^+ for *sc* increased abdominal bristle number of the base population by 12·31, but the same substitution has brought about an estimated change of 6·61, 13·15 and 18·09 bristles in CCb, CRb and CRa respectively, when the bristle number of *sc*/*sc* went up to 35 in the later stage of selection. This kind of variation appears to be quite independent of the variation in selection response among the main lines, where selection has been actually practised, as mean abdominal bristle numbers of *sc*/*sc* (Table 2) have no discernible relationship with the regression coefficients of sc^+/*sc* on *sc*/*sc* (Table 1). Hence, the present finding, which would be difficult to observe in usual situations, provides another facet of diversities among replicate long-term selection lines (Yoo 1974).

The gene action of sc^+ might have been assumed to be non-additive if we had happened to observe selection lines like CRa or Ua, as their regression coefficients are significantly different from unity, while the reverse might have been assumed in some other cases. This probability demonstrates a danger of drawing conclusions on the mode of gene action from a small number of replicate populations. In fact, the gene action of sc^+ appears to be not only the property of the gene itself, but also of the population where it is observed.

After finding heterogeneity among regression coefficients, it may not be very meaningful statistically to consider an average situation over the lines. But, for the cases where we are forced to compare a selection experiment in *sc* stock to previous ones in sc^+ stock, and in order to gain an insight into the genetic nature of the base population, the mean of the regression coefficients ($\bar{b}$) and a rough estimate of genetic correlation ($\bar{r}$) between the two genotypes (Table 4) were calculated in two ways: firstly considering all the six lines and secondly excluding Ua, which is rather exceptional in various aspects as discussed in later paragraphs. The genetic correlations were calculated by regarding $\bar{b}$ as a regression of correlated response on direct response to selection, and by assuming the heritability of abdominal bristle number before selection in the heterozygote population to be of the same order as that in either of the two homozygote populations, which actually have similar heritability estimates in the base (Sheridan *et al.* 1968; Hammond 1973). Because the phenotypic variance of the heterozygote was not accurately estimated, that of the sc^+ homozygote was instead utilized in these calculations, but this would not mislead the conclusion reached as they were in fact very similar. Estimates of $\bar{b}$ and $\bar{r}$ for sc^+/sc^+ and *sc*/*sc* are not available, but they are likely to be much the same as those for sc^+/*sc* and *sc*/*sc*, because the ratio of the total increase (during selection) of bristle number in sc^+/sc^+ to that in *sc*/*sc* is quite similar to the values of $\bar{b}$ given in Table 4. In addition to the heterogeneity noted above, there is some possibility of bias in the estimates of $\bar{b}$, as

they were calculated from direct and correlated responses to long-term selection. This bias would be more likely in Ub and CCa, where curvilinearity of regression is evident. Therefore one should be cautious in regarding them as the estimates for the base population.

Table 4. Means of regression coefficients ($\bar{b}$), genetic correlation coefficients ($\bar{r}$) and coefficients of determination ($\bar{r}^2$) between two *scute* genotypes

	$\bar{b}$	$\bar{r}$	$\bar{r}^2$
Between sc^+/sc and sc/sc			
Including line Ua	0·902	0·736	0·542
Excluding line Ua	0·988	0·806	0·650
Between sc^+/Y and sc/Y			
Including line Ua	0·907	0·742	0·551
Excluding line Ua	0·978	0·800	0·640

From these calculations, it may be concluded that the effect of sc^+ substitution for *sc* is, on the average, approximately additive for abdominal bristle number during selection in the *sc* population. That the genetic correlation is considerably lower than unity clearly suggests that a large proportion of genetic variability in the base population apart from the *scute* locus is common to the *scute* genotypes, but that there is also a fair amount of genetic variability contributed by genes or gene combinations the effects of which depend upon the *scute* genotype.

It would be interesting to consider a few simplified genetic models for the genetic background of the base population with regard to abdominal bristle number. Firstly let us assume a simple situation where the genetic background consists of three types of genes: ordinary additive genes, modifiers of the *sc* homozygote and modifiers of the heterozygote. A modifier is supposed to produce an effect only in the genotype of the major locus being modified, but its effect is additive. Upward selection in the *sc* homozygote is expected to increase the frequency of active genes in the first two categories, but to be neutral to those in the last, resulting in a decreased effect of sc^+. This is not what was observed in the present experiment on the average, and the modifiers of the *sc* homozygote therefore may be rare or absent in the base. Nearly all the genetic variability in the *sc* homozygote population would then come from ordinary additive genes, while the coefficients of determination ($\bar{r}^2$) in Table 4 would indicate the proportion of genetic variability in the heterozygote population due to the ordinary genes, the rest being due to the modifiers of the heterozygote. Cocks (1954) gave 0·85 as an estimate of the coefficient of determination for abdominal bristle number between the wild type and the *sc* hemizygote of various populations. Although her estimate is not directly comparable to ours, both at least indicate the presence of genetic variability dependent on the *scute* genotype.

It should be mentioned that a similar argument can easily be developed in a more realistic model where the magnitude and direction of the effect of a gene are only partly dependent on the major locus genotype, viz. there seems to be lack of genes which have larger effects in the *sc* homozygote than in the heterozygote. Another simplified situation may be where all the genes comprising the genetic background have larger effects in the heterozygote (+ + or − −) than in the *sc* homozygote (+

or −). This model seems to be compatible with the ostensible 'scale effect' of *sc*, which decreases genetic variance as well as mean when substituted for sc^+ in the base population (Hammond 1973). But it is quite obvious that the effects of sc^+ should have increased with continuous upward selection if this were the correct model. Even though the limited data do not allow us to go into more details of the genetic make-up of the base population, it is quite certain that about 60% of the genetic variability is common to both the genotypes and the rest specific to the heterozygote, and that the selection lines differed in the effect of sc^+, because they included random samples of specific genes as well as ordinary genes. The sc^+ homozygote was quite similar to the heterozygote in many aspects of abdominal bristle number, probably bearing a similar relationship with the *sc* homozygote as the above. Again the similarity between the two sexes of the statistics given in Table 4 may lead to an equivalent argument for the two hemizygotes. With this postulation, selection in the wild type should be able to bring about a change in the effects of sc^+ relative to *sc* as it can capitalize on both kinds of genetic variability. In fact, Young and Sheldon (1965) observed increased and decreased effects of sc^+ in their high and low wild-type selection lines respectively, in accordance with expectation. A similar tendency may be found also in the high selection line of Haskell (1943), but not in the low selection line.

Observing that the substitution of sc^+ for *sc* at different levels of scutellar bristle number had similar effects on the total resource ('make') of scutellar and abdominal bristle, Rendel (1963) assumed that the effects of the *scute* alleles are essentially independent of genetic background in elaborating a genetic model for correlation between the above two characters. This view seems to be tenable in Ub, CRb and CCa, but the other lines suggest some interaction between genetic background and the *scute* locus, as was also found for scutellar bristle number by Sheldon and Milton (1972).

Rendel (1963), further assuming that scutellar and abdominal bristles share make and are therefore equitable, argued that the correlated response in one character to selection for the other could be in opposite directions for different *scute* genotypes initially, but it would become positive regardless of genotype with continued selection, because selection operates on the total amount of make and on make allocation factors. If the present results are to be interpreted in his theoretical framework, selection in the five lines (excluding Ua) would be thought to have advanced far enough to bring the correlation to the positive side, though it is not certain whether a transitional selection stage of opposite correlated responses occurred or not. A consistently positive correlation was also recently reported by Sheldon and Milton (1972).

The negative correlated responses in the *sc* genotypes (homo- and hemizygote) of Ua are ostensibly similar to those observed by Young and Sheldon (1965), who inferred that selection had resulted in a large change in make allocation but little in make itself. But a few differences should be noted that may not favour a similar inference: selection in the former was performed on *sc* genotypes to a more advanced stage than selection in the latter on sc^+ genotypes and the negative correlated response in the former is an exception rather than a rule. As selection when performed at a high level, i.e. in sc^+ genotypes, is expected to be more effective in altering make allocation than in increasing make, it may be different from selection at a low level.

Even though selection for abdominal bristle number was sufficiently powerful to pull the three highest genotypes (in both sexes) out of the canalized zone of the four-

scutellar-bristle class, the influence of canalization on phenotypic expression is still evident in all lines except CCa. In spite of this influence, some qualitative differences among the selection lines stand out. If the means of the *sc* genotypes are taken to indicate the levels of genetic background, CRa and CRb would appear to have quantitatively similar levels. But a qualitative difference is clearly manifested when *sc* is replaced by sc^+, suggesting that the similar levels of background have been attained in different ways. The difference may be due to epistasis between genetic background and the *scute* locus or due to the difference in sc^+ regulator(s) between the lines as postulated by Sheldon and Milton (1972). Again the high genetic background of CCb did not increase scutellar bristle number as much as the low one of CRb when sc^+ was present. Therefore there is an apparent interaction between genetic background and the major locus, which may violate one of the original assumptions in Rendel's (1963) model. The order, according to scutellar bristle number, among the five genotypes was consistently maintained within a line whenever a difference between genotypes was observed except between *sc*/*sc* and *sc*/*Y* in CCb, where the two genotypes are very similar. This unusual obliteration of sex difference was not observed for abdominal bristle number in this line. On the contrary, *sc*/*sc* showed proportionately more response than *sc*/*Y*, becoming even higher than sc^+/Y.

As the degree of dominance was estimated only once near the end of the experiment in the selection lines and in the base population, its overall trend during selection is not known. Also the large phenotypic variance in abdominal bristle number of the selection lines at this stage made it very difficult to measure the difference between genotypes accurately. Even though the wild-type allele tends to be less dominant over *sc* for abdominal bristle number in the selection lines as revealed by lower *d* values than the base value (Table 2), the evidence from individual lines other than Ua is by no means conclusive. Still, the results suggest that selection in the *sc* genotypes was not efficient in changing the first dose effect of sc^+ as mentioned above, and the modifiers of the heterozygote may have proportionately similar effects on the sc^+ homozygote. On the other hand, the selection brought about considerable change in the degree of dominance for scutellar bristle number, obviously because the selection increased the level of genetic background for scutellar bristle to an extent sufficient for the genotypes originally in the four-bristle class to pass the threshold, at least partly. In other words, selection for the typical quantitative character was more likely to change the degree of dominance for the correlated but canalized character than that for the selected character. This contrasting difference between the two characters is in accordance with the view that dominance becomes complete due to developmental canalization (Rendel 1959; cf. Waddington 1957).

In line Ua the dominance relationship for abdominal bristle number apparently has been altered during selection, but only with concurrent reversion of the effect *per se* on the character of *sc* relative to that of sc^+ in females. Assuming that the generation means of the sc^+ homozygote can be linearly regressed on those of the *sc* homozygote, the slope of the regression would be smaller than that for the heterozygote shown in Fig. 3, such that the former regression line crosses the latter one, resulting in a lower sc^+ homozygote than the heterozygote by G81. On the other hand, the difference between the heterozygote and the *sc* homozygote may have steadily decreased until it vanished, as suggested by the regression coefficient of the former on the latter being less than unity. An equivalent linear relationship, i.e. the decrease of the difference

between the two hemizygotes, was also observed in males, but the wild type was still much higher than *sc* when selection was terminated. This unusual change in abdominal bristle number appears to be superficially related to the negative correlated response in scutellar bristle number, but no intelligible genetic mechanism can be suggested to explain either observation at this stage. But it should be added that these changes may not have resulted from mutations at one or a few structural gene loci, as the whole process for abdominal bristle number was apparently continuous.

The characters measured in the experiment deserve the last comment. Though the wild-type allele is nearly but not completely dominant over the mutant *sc* for abdominal bristle number in the base population, it is not well understood whether the dominance has evolved due to the effect on abdominal bristle number or on other developmental functions with a secondary effect on the bristle number, and even whether the dominance has ever evolved or is just present as a physiological property of the alleles involved, as suggested by Wright (1929). On the other hand, the dominance of sc^+ over *sc* is almost complete for scutellar bristle number in the base population. There is a reasonable amount of evidence showing that the degree of dominance can be easily modified by moving the level of genetic background outside the canalized zone(s) (Rendel 1967), but conclusive experimental evidence supporting the contrary argument that dominance can evolve through developmental canalization is still to come (Ohh and Sheldon 1970). The peripheral nature of the relationship between abdominal bristle number and reproductive fitness (Robertson 1955) tempts one to relate the dominance in this character to the effects of the genes on other genetically related and reproductively important characters, in particular scutellar bristle number, which has been shown to be under the influence of relatively strong natural selection (Latter 1963). This proposition rests on Rendel's (1963) suggestion that the two characters may be controlled by a common genetic system. That is, dominance for abdominal bristle would have been a by-product of that evolving for scutellar bristle, the latter becoming more complete than the former with developmental canalization. But it is considered difficult in this proposition to reconcile the fact that the degree of dominance for the latter tends to be lower than that for the former when the influence of canalization on the latter is partly removed.

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