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# Decanalization of scutellar bristle number in *Drosophila*

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SUMMARY

A major difference in developmental stability has been demonstrated between two populations produced by artificial selection for supernumerary scutellar bristles. The test system involves the substitution of an X-ray induced partial revertant of $sc^1$ for the wild-type allele at the *scute* locus, enabling direct comparisons to be made of the degree of canalization at the wild-type level of expression of the character. One population is comparable with the unselected Canberra stock in stability, though it differs appreciably in mean bristle number: the other population shows a marked reduction in the level of regulation of bristle number variability. The alleles responsible for the reduced level of canalization are rare in the base population, and are of particular importance in the determination of limits to directional selection. Their effects on developmental stability have been shown to depend on the activity of the allele at the *scute* locus.

## 1. INTRODUCTION

The concept of canalization was introduced by Waddington (1957) to describe the way in which development is regulated to produce a constant phenotype in a genetically heterogeneous population. Scutellar bristle development in *Drosophila melanogaster*, for example, results in a regular pattern of four bristles, despite the existence of considerable *potential* genetic variability in wild-type populations (Rendel, 1967). The degree of canalization of this phenotype is most directly measured by the proportion of the population having four bristles, or by the related statistic, 'the span of the four-bristle class', obtained by probit transformation (Fig. 1). The probit transformation has the desirable property of giving a measure of developmental regulation which is independent of changes in mean bristle number (Falconer, 1960).

The degree of canalization of the four-bristle scutellar phenotype has been shown to be influenced by allelic substitutions at the *scute* locus (Table 1). The mean span of the four-bristle class in two wild-type populations, viz. Oregon-RC and Canberra, is approximately 5·4 in females; in flies homozygous for the *scute* alleles $sc^{+59k}$ and $sc^{+60e}$ (revertants of $sc^1$), the corresponding probit intervals are 4·9 and 4·5 respectively, and females of an unselected stock with four doses of $sc^1$ have a four-bristle class span of 4·4 (Scowcroft, Green & Latter, 1968).

The degree to which the level of canalization in wild-type stocks can be altered by artificial selection has not yet been established. Young (1967) reported negative

results in attempts to increase or decrease canalization of scutellar bristle number at four, using an ingenious system of selection in a population segregating for $sc^1$. Rendel, Sheldon & Finlay (1966) have shown that a new level of canalization, at a mean bristle number of two, can be produced by selection in a homozygous $sc^1$ stock. Stability of bristle number in this stock is due to a negative interaction between anterior and posterior sites on the same side of the fly (Rendel, 1965): if an anterior bristle is present, the probability of a posterior bristle on the same side is greatly reduced, and vice versa. This interaction is much less pronounced in an unselected $sc^1$ stock.

Table 1. *Degree of canalization of the four-bristle scutellar phenotype in females of unselected stocks differing at the* scute *locus*

| *Scute* allele | Mean bristle number | Proportion with four bristles | Span of four-bristle class in probit units | Reference* |
|---|---|---|---|---|
| $sc^+$ (Oregon-RC) | 4·02 | 0·983 | 5·48 ± 0·14 | (1) |
| $sc^+$ (Canberra) | 4·02 | 0·981 | 5·40 ± 0·17 | (2) |
| $sc^{+59k}$ | 4·01 | 0·984 | 4·88 ± 0·18 | (3) |
| $sc^{+60e}$ | 4·08 | 0·924 | 4·48 ± 0·13 | (3) |
| $sc^1$ (four doses) | 3·86 | 0·875 | 4·43 ± 0·29 | (3) |

* (1) Sheldon, Rendel & Finlay (1964); (2) Latter (unpublished); (3) Scowcroft, Green & Latter (1968).

In this paper, we report the occurrence of a genotype produced by artificial selection, which greatly reduces the level of canalization at four scutellar bristles, and examine its interaction with allelic substitutions at the *scute* locus. The genotype is derived from a wild-type population designated SH1, which has a complex history of selection for increased scutellar bristle number (Latter, 1970).

## 2. MATERIAL AND METHODS

The response to selection for high scutellar bristle number in the Canberra population normally ceases when the number of bristles present at the anterior, interstitial and posterior sites total approximately eight. In exceptional lines, however, total bristle number at these sites may be increased by selection to more than eleven. Bristle number variability is far greater in these exceptional lines than in those plateaued at the eight-bristle level. It has been concluded from indirect evidence that the increase in variance is due to allelic substitutions which affect the degree of *regulation* of bristle development (Latter, 1970).

The allele $sc^{+60d19}$ ($sc^{60d}$) reduces total bristle number so that the degree of canalization at four bristles can be directly measured in populations with vastly different mean bristle numbers. In this paper, comparisons are made of three populations following this major gene substitution: (i) the Canberra base population, an unselected wild-type stock; (ii) line SB9, derived from the Canberra population by selection for high scutellar bristle number, which plateaued at a mean close

to eight bristles;* and (iii) line SH1, also derived from the Canberra stock by selection, with a mean of almost thirteen bristles* (Latter, 1970). The $sc^{60d}$ allele is an X-ray induced partial reversion of $sc^{1}$ produced by Dr M. M. Green. The substitution was effected by taking a recombinant gamete with a single crossover between $sc^{60d}$

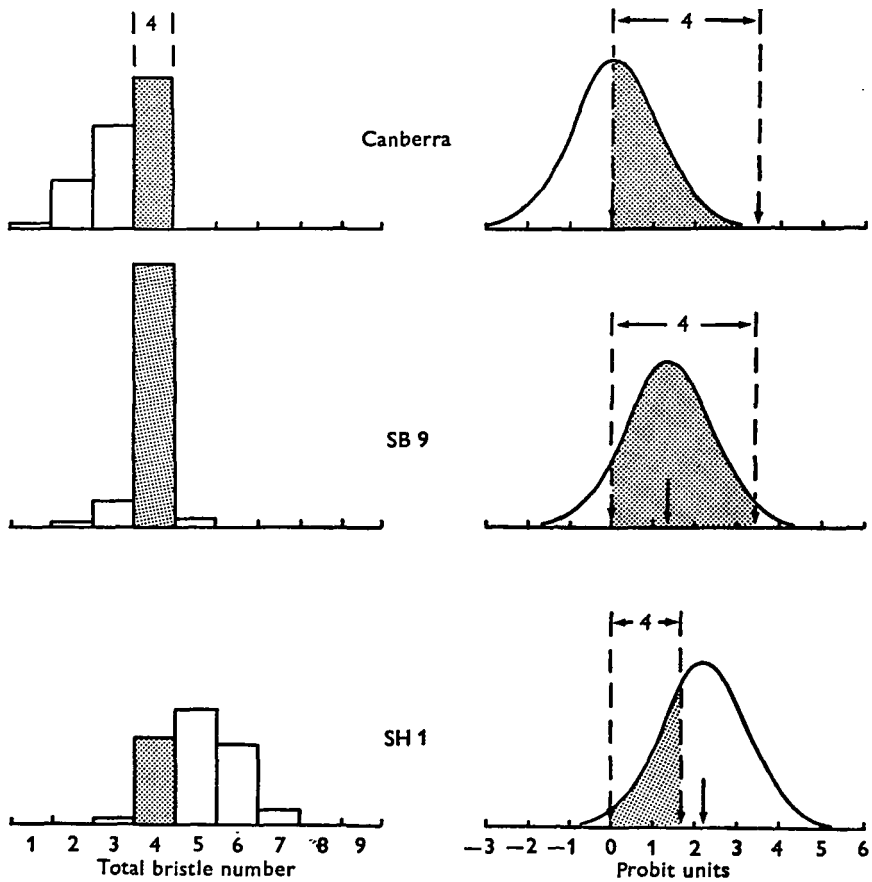


Fig. 1. Frequency distributions of total scutellar bristle number in the $sc^{60d}$ substituted populations, and the corresponding transformed distributions plotted relative to the 3/4 threshold as origin. Shaded areas represent the proportion of the population with the normal four-bristle phenotype.

and the *white* locus, a distance of 1·5 map units. Simultaneously, the second and third chromosomes of the respective populations were conserved by the use of inversion marked chromosomes. Two backcrosses were made in each case to improve the sample of second and third chromosomes in the substituted populations.

* Line SB9 here refers to Scl/10/R48/S7/R108j/S30/R9; line SH1 is (Sc1/10/R48/S29 × Sc2/31) R48/S22/R55 (Latter, 1970).

## 3. RESULTS

The three populations following $sc^{60d}$ substitution differ significantly in mean bristle number (Table 2), but all have an appreciable proportion of flies with four bristles (Fig. 1). Direct comparison of the probit distances spanned by the four-bristle class in lines SB9 and SH1 (Table 2) shows SH1 to be significantly lower than SB9 in this measure of developmental regulation. The span of the 'five-bristle class' in substituted SH1, i.e. $0{\cdot}99 \pm 0{\cdot}03$, is little different from that characteristic of the Canberra base population (Latter, 1964).

Table 2. *Scutellar bristle number distributions and probit intervals in females of the* $sc^{60d}$ *substituted populations*

| Bristle class | Canberra | Line SB9 | Line SH1 |
|---|---|---|---|
| | (*a*) Bristle number distributions | | |
| 0 | 6 | — | — |
| 1 | 80 | 1 | — |
| 2 | 810 | 11 | — |
| 3 | 1761 | 137 | 36 |
| 4 | 2510 | 1446 | 782 |
| 5 | — | 33 | 1042 |
| 6 | — | — | 726 |
| 7 | — | — | 150 |
| 8 | — | — | 5 |
| Means | $3{\cdot}29 \pm 0{\cdot}01$ | $3{\cdot}92 \pm 0{\cdot}01$ | $5{\cdot}07 \pm 0{\cdot}02$ |
| Wild-type means | $4{\cdot}02 \pm 0{\cdot}01$ | $8{\cdot}10 \pm 0{\cdot}05$ | $12{\cdot}70 \pm 0{\cdot}15$ |
| | (*b*) Probit intervals | | |
| 3 | $0{\cdot}99 \pm 0{\cdot}02$ | $1{\cdot}11 \pm 0{\cdot}10$ | — |
| 4 | 3·52* | $3{\cdot}38 \pm 0{\cdot}08$ | $1{\cdot}70 \pm 0{\cdot}06$ |
| 5 | — | — | $0{\cdot}99 \pm 0{\cdot}03$ |

* Minimum estimate.

A wild-type fly normally has two anterior and two posterior scutellar bristles, and it has been reported that these two component regions of the scutellum are to some extent subject to differential control (Scowcroft *et al.* 1968). Robertson (1965) has, in addition, questioned the use of the probit transformation in the analysis of total bristle number, suggesting that control of development should be examined at the level of the individual bristle site. We have therefore calculated the necessary statistics on this basis (Table 3), and shown the corresponding transformed distributions in Fig. 2. The conclusions from this analysis are (i) that the reduced level of regulation in SH1 inferred from Table 2 applies to bristles in both the anterior and posterior regions; line SB9 appears to be comparable with the Canberra population from which it was derived: and (ii) that the $sc^{60d}$ populations show no clear-cut evidence of a higher degree of canalization of posteriors by comparison with anteriors, in contrast to the observations of Scowcroft *et al.* (1968) for populations carrying $sc^{60e}$ or $sc^{59k}$.

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Table 3. *Probit intervals spanned by the 'one-bristle per site' class for anterior and posterior scutellar sites in the* $sc^{60d}$ *substituted populations (Fig. 2)*

| Site | Population | Mean bristle number per site | | Probit intervals in $sc^{60d}$ substituted populations '1' bristle/site |
|---|---|---|---|---|
| | | $sc^{+}$ | $sc^{60d}$ | |
| Anterior | Canberra | 1·01 ± 0·01 | 0·92 ± 0·01 | 4·23 ± 0·11 |
| | SB9 | 2·74 ± 0·03 | 1·02 ± 0·01 | 4·50 ± 0·20 |
| | SH1 | 3·91 ± 0·03 | 1·53 ± 0·01 | 2·94 ± 0·22 |
| Posterior | Canberra | 1·00 ± 0·01 | 0·77 ± 0·01 | 4·35* |
| | SB9 | 1·04 ± 0·01 | 0·94 ± 0·01 | 4·52 ± 0·31 |
| | SH1 | 1·63 ± 0·02 | 0·97 ± 0·01 | 3·62 ± 0·07 |

* Minimum estimate.

## 4. DISCUSSION

This experiment was designed to test an hypothesis advanced by Latter (1970) to account for the observed increase in bristle number variability in a selection line of exceptionally high mean (SH1). It was proposed that particular allelic substitutions, distinguishing this population from other selection lines plateaued at a lower level (SB9 being a typical representative), are responsible for a breakdown of some aspect of developmental regulation. The test system involves the use of a partial revertant of $sc^{1}$, denoted $sc^{60d}$, which enables direct comparisons to be made of developmental stability at mean bristle numbers comparable with that of wild-type stocks (Fig. 1).

Figs. 1 and 2 provide convincing evidence that SB9 is comparable with the Canberra wild-type stock in developmental regulation in the presence of $sc^{60d}$, though it is appreciably higher in mean for both anterior and posterior bristles. Response to selection in the Canberra population from four bristles to eight is therefore due primarily to genes which increase bristle number without change in the normal processes of regulation. Line SH1, on the other hand, can be seen from the two figures to be drastically reduced in developmental stability in the presence of $sc^{60d}$.

The transformed distributions in Figs. 1 and 2 have been graphed with the 3/4 threshold as origin for total bristle number, and the 0/1 threshold as origin for bristle number per site. It is to be expected *a priori* that a history of selection for *supernumerary* bristles should be without effect on the threshold mechanism concerned with the absence or presence of the normal bristle complement. If this is so, the difference in canalization between the selected populations SH1 and SB9 can be seen to be due to a marked reduction in the concentration of substrate necessary for extra-bristle initiation. The alleles responsible are recessive, in contrast to the genes of predominantly additive effect accumulated in most selection lines (Latter, 1966, 1970), and are apparently rare in the Canberra base population since they are fixed in only a small proportion of plateaued lines.

We have seen that comparisons of developmental stability based on total bristle

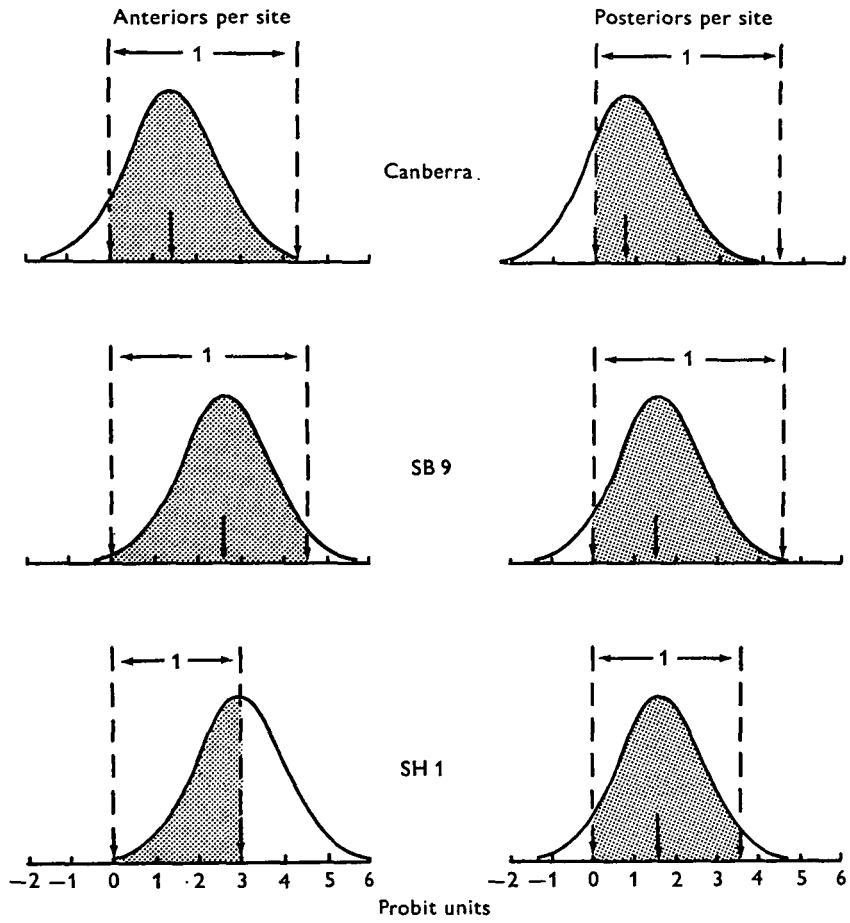


Fig. 2. Transformed distributions of bristle number per site in the $sc^{60d}$ substituted populations, plotted relative to the 0/1 threshold as origin. Shaded areas represent the proportion of the population with one bristle per site.

Table 4. *The degree of canalization of anterior bristle number per site, estimated for different* scute *alleles in three genetic backgrounds*

| Genetic background | *Scute* allele | Mean bristle number/site | Level of canalization* | Reference† |
|---|---|---|---|---|
| I. Canberra | $sc^{+}$ | 1·01 ± 0·01 | 6·32 ± 0·18 | (1) |
| (unselected) | $sc^{60d}$ | 0·92 ± 0·01 | 4·23 ± 0·11 | (2) |
| II. Selection | $sc^{1}$ | 0·79 ± 0·02 | 3·44 ± 0·25 | (1) |
| line SB9 | $sc^{60d}$ | 1·02 ± 0·01 | 4·50 ± 0·20 | (2) |
| III. Selection | $sc^{1}$ | 1·04 ± 0·01 | 3·30 ± 0·10 | (1) |
| line SH1 | $sc^{60d}$ | 1·53 ± 0·01 | 2·94 ± 0·16 | (2) |

* Measured as the span of the 'one bristle per site' class.
† (1) Latter & Scowcroft (unpublished). (2) This study.

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number are substantially the same as those derived from a single-site analysis, and the latter may often be possible when flies with a total of four scutellar bristles are rare. Table 4 summarizes a number of single-site estimates of stability for anterior bristles, which indicate the importance of the *scute* locus in the determination of the level of regulation of the 'one bristle per site' phenotype (cf. Table 1). The substitution of $sc^{60d}$ into the unselected wild-type background can clearly be seen to reduce the level of canalization at the anterior sites, and the two *scute* alleles $sc^{1}$ and $sc^{60d}$ interact with the genetic backgrounds of lines SB9 and SH1 in the determination of developmental stability. The difference between the two *sc* genotypes in span of the one-bristle class in the background of SB9, viz. $1{\cdot}06 \pm 0{\cdot}32$, differs significantly from that in the SH1 background of $-0{\cdot}36 \pm 0{\cdot}19$, implying that the combination of an active *scute* allele *and* the genetic background of SB9 (or Canberra) is necessary for stability.

The decanalizing alleles incorporated into line SH1 by artificial selection may operationally be described as regulators of the activity of the *scute* locus in the determination of developmental stability. The genes concerned are of major importance in the determination of the ultimate limits to artificial selection (Latter, 1970), and have obvious relevance to the genetic model of regulation of development proposed by Rendel (1967). If it proves technically possible to locate and manipulate the important factors individually, the genetic system involved will merit further detailed study.

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