VARIATION OF SCUTELLAR BRISTLES IN DROSOPHILA XVI. MAJOR AND MINOR GENES

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THE prime questions posed in genetic research are "what is the gene and how does it act to affect the phenotype" with much less attention given to the questions "what is the genotype and how does it determine the phenotype". Geneticists interested in the genetic basis of continuously varying characters have to a large degree been involved in the second approach, attempting to describe the nature of systems of genes, rather than the identification of individual elements of such systems. MATHER (1943) suggested that the genes involved in such quantitative variation are essentially different from genes involved in discontinuous variation, coining the terms "polygene" and "oligogene" for the two types. Such a division presents operational difficulties since some effects of a particular gene may be small and subject to considerable environmental variation, i.e., polygenic; whereas other effects of the same gene may be large with little environmental variation, i.e., oligogenic (WADDINGTON 1943). However, the difficulty of an operational definition does not disprove MATHER's suggestion. RENDEL (1968 *op. cit.* p. 49) states, "In my view he [MATHER] is correct and they [polygenes and oligogenes] are distinct, though I do not believe that they are the only two types which need to be distinguished. A major gene is a gene usually with large effects, and it is regulated. I suppose it corresponds to MATHER's major [oligogene] gene and that it is a structural gene . . .". RENDEL goes on to develop the concept of inducible structural genes with galaxies of regulator genes controlling the activity of the structural genes, as a model for the genetic system controlling the number of scutellar bristles. He considered the scute locus to be a structural gene, regulated by an assortment of minor genes, either in the repressor sense, or in a competitive sense. He states (*ibid.* p. 65), "This [major] gene, either by replicating itself or competing with minor genes for ribosomes or by some other means under genetic control, establishes itself in competition with a number of minor genes . . .". Our analysis of the same character led to essentially the same type of model, but we were and still are reluctant to apply the details of molecular genetics (FRASER, ERWAY and BRENTON 1968; MILLER and FRASER 1968; FRASER 1968).

Our model is based on two major loci: scute (*sc*) and extravert (*xvt*) (which is probably an allele of polychaetoid (*pyd*)) whose expressions are modified by two sets of modifier genes: the α and β modifiers, respectively. Mutations at the scute locus result in a reduction of the number of scutellar bristles below the norm

of four, whereas mutations at the extravert locus result in an increase of the number of scutellar bristles above the norm. Substitution of *sc* for sc^+ suppresses *xvt* and the β modifiers (MILLER and FRASER 1968). The substitution of *xvt* for xvt^+ suppresses the expression of the α modifiers in the presence of sc^+ (FRASER 1968). This latter feature was based on a fairly intricate comparison of parent, F_1 and F_2 values in a series of crosses between lines differing in the α and β modifiers. MILLER and FRASER (1968) suggested that a test of the interactions between *sc*, *xvt*, α and β could be made by maintaining *xvt/xvt* lines in segregation for *sc* and sc^+, selecting in separate lines for increase and decrease of the number of scutellar bristles, separately in scute and non-scute segregants. The present paper details the results of such a test.

MATERIALS AND METHODS

A series of selection lines was formed from crosses between the A1, A9 and A18 extra-scutellar selection lines (FRASER *et al.* 1965). These three lines are all *xvt/xvt* and each has been maintained in a y^+sc^+ and y^1sc^1 version. Crosses were made between a y^+sc^+ version of one of the three lines, and a y^1sc^1 version of one of the other two lines, e.g., y^1sc^1(A1) $\times$ y^+sc^+(A9). Selection was only practiced in males: y^1sc^1/Y in one set of lines, and y^+sc^+/Y in another set of lines. Selected males were mated to $y^+sc^+/y\ sc^1$ unselected females from the same culture maintaining segregation for sc^+ and sc^1. The identification of such heterozygous females could be made on body color in lines in which the selected male parents were y^1sc^1/Y, since the two types of females produced are yellow and non-yellow, respectively. The identification of heterozygous females required progeny testing in lines in which the selected male parents were y^+sc^+/Y.

Four types of selection lines were established: high and low for scutellar numbers in y^1sc^1/Y, and high and low for scutellar numbers in y^+sc^+/Y. Twenty-five males in each culture were scored and the 5 most extreme in the requisite direction retained as parents.

The crosses involving lines A1 and A9 did not show any response to selection—these were discarded and attention concentrated on the lines from the crosses of A1 with A18, and A9 with A18. Replicate selection lines from these crosses showed very similar responses, so these were amalgamated after five generations of selection. The results were clear-cut and very little additional insight would have been gained by a statistical analysis.

RESULTS AND DISCUSSION

The mean numbers of scutellar bristles in sc^1 and sc^+ males are shown in Figure 1 for the four types of selection lines in the two initial crosses.

Consider first the selection lines in which selection was practiced on sc^1/Y (the scute selection lines). The selection produced a steady response leading to a difference between the high and low lines of the order of 0.5 bristles in the A1–18 lines, and of the order of 1.0 bristles in the A9–18 lines. These selection responses in sc^1/Y males were not paralleled by analogous differences in the sc^+/Y males of the same lines. Differences between high and low lines of sc^+/Y are small and show no consistent change with generation of selection. It would appear that the genetic difference of the α system produced by selection is either not manifested in sc^+/Y or it is not transmittted to this genotype. The latter involves either very close linkage of the α genes with sc^1, or very strong lethality interactions of the α genes with sc^+. Both are unlikely, and we can conclude that

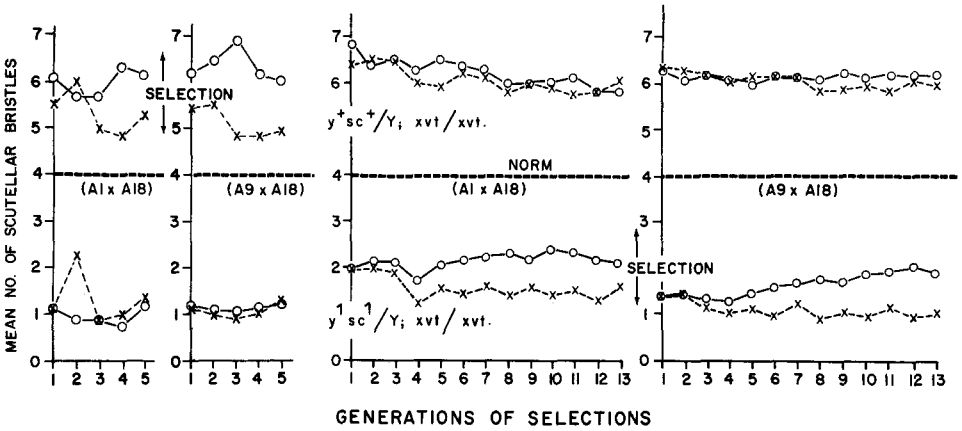

FIGURE 1.—Mean number of scutellar bristles is shown plotted against generation of selection for the $y+sc+/Y$ progeny and for the y^1sc^1/Y progeny. In the two left graphs selection was practiced only in $y+sc+/Y$: circles-high lines, crosses-low lines. In the two right graphs selection was only practiced in y^1sc^1/Y: circles-high lines, crosses-low lines.

the lack of difference between high and low lines of the sc^+/Y males is due to a suppression of the α system of modifiers. RENDEL (1959) and FRASER (1966) have shown that the effects of selection in sc^1/Y are not suppressed in sc^+/Y and, therefore, we must consider a non-scute locus as the suppressor. All of our lines are xvt/xvt and it is possible that the suppression of α modifiers is consequent from this homozygosity. MILLER and FRASER (1968) have shown that xvt is not expressed (in its effect on scutellar bristles) in sc^1/Y or sc^1/sc^1. In our experiment two types of males occur: $sc^1/Y;xvt/xvt$ and $sc^+/Y;xvt/xvt$. It appears that sc^1 suppresses xvt in the former, allowing selection for scutellar bristles to focus on the modifiers of sc^1, whereas xvt/xvt suppresses the expression of these same modifiers in the latter genotype.

Two types of females segregate in the scute selection lines: sc^1/sc^1 and $sc^+/sc.^1$ The difference between the high and low lines in sc^1/sc^1 parallels that produced in sc^1/Y. The results for sc^+/sc^1 differ between the lines from the A9–18 cross and those from the A1–18 cross. In the former there is a consistent difference between the high and low lines which although smaller than that in sc^1/Y is in the same direction. In the latter, the differences between high and low lines are small and erratic, being overall generations in the opposite direction; i.e., the high line has the lowest number of scutellar bristles in sc^+/sc^1. It would appear that the suppression of the α modifiers by xvt is at least partly manifested in sc^+/sc^1. A feature of the suppression of xvt by sc^1 is that this is manifested in sc^+/sc^1 but to a reduced degree—the effects of xvt on other bristles are suppressed, but the effect on scutellar bristles is only reduced (ERWAY, personal communication; FRASER, ERWAY and BRENTON 1968).

Figure 1 also contains the results for the selection lines in which selection was practiced on sc^+/Y (the non-scute selection lines). The progeny testing necessary in these lines increased the generation interval, and only five generations of se-

lection were completed. Selection was effective, producing differences of the order 1.0–1.5 bristles in sc^+/Y. Apart from the second generation of the low lines in the A1–18 crosses, no differences were found in sc^1/Y, corroborating the results of MILLER and FRASER (1968) that the expression of the β system of modifiers is suppressed in sc^1/Y and sc^1/sc^1. The effort of identifying sc^+/sc^1 was not undertaken since MILLER and FRASER (1968) have shown that the β modifiers of *xvt/xvt* are not completely suppressed by sc^+/sc^1. Their width and intensity of expression are reduced but not suppressed.

CONCLUSIONS

The model of two oppositely acting major loci (*sc* and *xvt*), each with a separate set of modifiers (α and β modifiers) is supported by the above data. The two parts of this system are connected by suppressive effects: *sc* suppresses *xvt* and the β modifiers, and *xvt* suppresses the α modifiers.

Other loci can be included in this model. The gene suppressor of Hairy wing (*su-Hw*) is a suppressor of scute. LEA (personal communication) has results indicating that the suppression of *sc* by *su-Hw* does not fully remove the suppression of *xvt* by *sc*. These results, if confirmed, would show that the scute locus has two parts: one part which is suppressed by *su-Hw*, acting directly on bristle development, and another part, which is not similarly suppressed by *su-Hw*, acting on the *xvt* locus.

Another gene, Scutoid (*Sco*), results in a decrease of the numbers of scutellar bristles. LEA (personal communications) has results showing the modifiers of *sc* also affect *Sco*. The relationship of *Sco* to *xvt* needs to be investigated to determine whether *Sco* is a suppressor of *xvt*. The gene, tufted (*tft*), results in a very marked increase of the number of scutellar bristles—the scutellum of tufted flies is densely packed with bristles. It is possible to imagine the tufted locus as a regulator of a locus determining the upper limit of the number of scutellar bristles. Mutations at the tufted locus remove the repression, and bristle development proceeds at an unregulated pace. The relationship of *tft* to *xvt* needs to be investigated. It should be possible to develop this network of interactions (KAUFMAN 1969) such that quantitative computer models can be constructed and then tested to determine whether stable states occur.

SUMMARY

Selection for increased and decreased numbers of scutellar bristles was practiced on *xvt/xvt*; sc^1/Y or *xvt/xvt*; sc^+/Y males, in lines segregating for sc^1 and sc^+. The responses to selection showed the occurrence of two systems of modifiers—one acting at the *xvt/xvt* level of bristle number, and the other acting at the *sc* level of bristle number.

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