

Selection for a threshold character in *Drosophila*

III. Genetic control of variability in plateaued populations*

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1. SUMMARY

An analysis of populations of *Drosophila melanogaster* which had ceased to respond to selection for increased scutellar bristle number has disclosed the existence of an overall negative genetic correlation between replicate lines in the frequency of the two major component bristle types, viz. anteriors and posteriors. Negative phenotypic correlations among component bristle sites have also been detected *within* populations. A model involving competition among sites for the available resources of a particular limiting substrate is therefore proposed. Genetic changes have been effected in exceptional populations which lead either to an increase in the rate of production of the limiting substrate, or to a lowering of the concentration of the substrate necessary for bristle initiation. The allelic substitutions concerned are recessive, and have been described as *decanalizing* alleles in view of their effects on both bristle number variability and a measure of developmental regulation at individual anterior sites. Genetic variation has also been demonstrated for the mean allocation of resources to each of the four component bristle types, viz. anteriors interstitials, posteriors and apicals. A brief discussion is given of the implications of the model for breeding practice in domestic species.

2. INTRODUCTION

Earlier papers in this series (Latter, 1964; 1966) have described the short-term response to artificial selection for increased scutellar bristle number in the Canberra strain of *D. melanogaster*. In wild-type populations of this species almost all individuals have two anterior and two posterior macrochaetae on the scutellum. Occasional flies are found with an additional bristle, usually located in the vicinity of one of the anterior sites in stocks raised at 25 °C; more rarely, individuals occur in which one of the four normal bristles is completely missing.

Selective breeding from those individuals with extra bristles leads readily to an increase in the mean bristle number of the population. The initial response has been shown to be a linear function of the accumulated selection differential, if the population mean is plotted on a probit scale to allow for the threshold

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nature of character (Latter, 1964). This period of linear response (phase I) is sufficient to raise the incidence of individuals with extra bristles to almost 100%. Estimates of the probit distances spanned by the bristle number classes indicate that the standard deviation of the population, measured on the underlying scale, is essentially constant over this period. The same is true of the difference in mean between the two sexes.

Continued selection in populations with at least 20 pairs of parents per generation has been shown to give a regular pattern of two consecutive phases of linear response in the mean (Latter, 1966). There is at the same time a continuous decline in reproductive fitness due to reduced fecundity and rate of development, and to an increase in the incidence of sterile females. There is little evidence of non-additive genetic effects on the probit scale throughout phases I and II. Backcrosses to the base population give hybrids of precisely intermediate mean (Latter, 1966), and chromosome substitutions show the two major autosomes to be almost additive in effect (Latter, 1970).

The present paper is concerned with the results of selection continued beyond phase II. In almost all populations a plateau is reached at a mean of 8–10 bristles in females, but some exceptional populations reach higher levels. The nature of these limits to selection is examined, and a model proposed which takes into account variation at individual bristle sites. A feature of the model is the hypothesis that in populations plateaued at the mean level of 8–10 bristles potential genetic variation exists which is expressed only in particular genetic backgrounds, i.e. that the level of variability is genetically controlled (Scowercroft & Latter, 1970).

3. SELECTION LIMITS IN LARGE POPULATIONS

Fig. 1 illustrates the pattern of response observed in populations with a large number of breeding individuals each generation. The two lines concerned, viz. Sc2 and Sc3, were subjected to continuous directional selection over a period of approximately 50 generations, finally reaching a mean level in females of 8.7 and 8.1 bristles respectively. The theory of selection limits developed by Kimura (1957) and Robertson (1960) leads us to expect the long-term behaviour of such populations to depend in particular on the value of $N_e\bar{i}$ where N_e is the effective breeding size of the population in each generation and \bar{i} denotes the standardized selection differential. Over the first ten generations of selection in Sc2 and Sc3, the mean values of $N\bar{i}$ were close to 70 and 45 respectively, where N is the *actual* number of parents used. Over the remainder of their selection history, both lines had mean values of $N\bar{i}$ equal to 60.

Population means have been plotted in Fig. 1 on a probit scale appropriate for total scutellar bristle number counted on both sides of the animal (Latter, 1966). The pattern of response on this scale is similar to that shown by other model quantitative traits which have been studied in moderately large populations, e.g. abdominal hair number (Clayton & Robertson, 1957) and body size (Robertson, 1955). However, the total response in Fig. 1 is only 5 phenotypic standard deviations, or approximately 8 additive genetic standard deviations.

The predominant bristle pattern in both Sc2 and Sc3 at the plateau level is one with 3 bristles per anterior site, and a single bristle at each posterior site, to give a total of 8 bristles. The asymmetrical distribution of bristle number in population Sc2/51 (Fig. 1) is due primarily to individuals with 4 bristles at one or both of the anterior sites. Relaxation of selection at this point led to the elimination of individuals with 4 bristles per anterior site within nine generations.

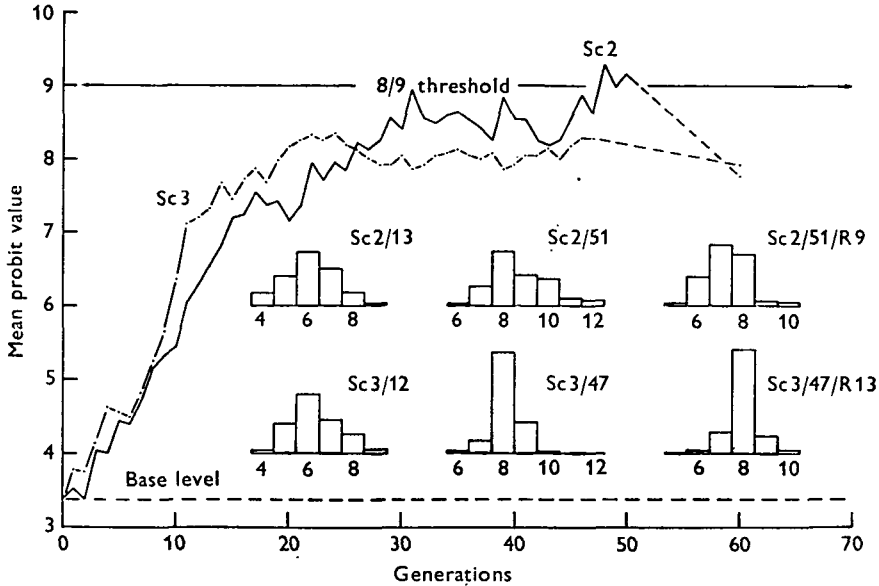


Fig. 1. The response to continuous selection for increased scutellar bristle number in females of lines Sc2 and Sc3, plotted in probit units. Frequency distributions of bristle number in representative generations are also shown, the designation Sc2/51/R9 corresponding to 51 generations of selection in line Sc2, followed by 9 generations of random mating under crowded conditions.

Relaxation and renewed selection

An antagonism between artificial and natural selection has been a characteristic feature of response in the four selection lines Sc1–Sc4 which were initiated directly from the Canberra base population (Latter, 1963, 1966). As shown in the previous section, two of these lines kept under continuous selection for about 50 generations ceased to respond at mean probit values less than 9.0 (Fig. 1). For comparison, Table 1 summarizes the behaviour of 15 lines initiated from populations stabilized by a long period of natural selection under crowded conditions, giving the mean probit values and phenotypic standard deviations of bristle number at the selection limits.

The series of lines designated SA1–5 were maintained each generation by 20 pairs of selected parents; the series SB1–10 all with the same origin, involved 10 pairs per generation. The selection intensity was the same in both series, viz. 20/100 and 10/50 respectively. The average selection limit in the SA series is of

the order of 9.5, compared with 9.0 in the SB series. Four individual lines reached mean probit values of 10.0 or greater, viz. SA1, SA5, SB3 and SB10: two of these lines show a phenotypic standard deviation of bristle number which is considerably in excess of that of all other lines, viz. SA1 and SB10.

Table 1. Selection limits reached by lines initiated from stabilized populations

Selection line	Stabilized population		Selection limit			
	Origin*	Mean probit value	Generation	Mean probit value	Standard deviation**	Reference
SA1	Sc1/10/R48	5.6	SA1/40	10.7	1.41 ± 0.05	Fig. 2
SA2	Sc1/10/R76	5.4	SA2/33	8.4	0.89 ± 0.07	Fig. 4
SA3	Sc2/16/R14	5.8	SA3/33	8.9	0.95 ± 0.09	Fig. 4
SA4	Sc1/10/R48/S7/R112a	5.0	SA4/32	9.4	0.92 ± 0.09	Fig. 4
SA5	Sc1/10/R48/S7/R112b	5.0	SA5/32	10.1	1.08 ± 0.11	Fig. 4
SB1	Sc1/10/R48/S7/R108	a 5.5	SB1/30	8.8	0.97 ± 0.05	
SB2		b 5.5	SB2/30	9.0	0.83 ± 0.04	
SB3		c 5.5	SB3/30	10.0	0.88 ± 0.04	
SB4		d 5.5	SB4/30	8.6	0.89 ± 0.04	
SB5		e 5.5	SB5/30	8.9	0.94 ± 0.04	
SB6		f 5.5	SB6/30	8.4	0.83 ± 0.04	Fig. 7
SB7		g 5.5	SB7/30	9.1	0.94 ± 0.05	
SB8		h 5.5	SB8/30	8.4	0.85 ± 0.04	
SB9		j 5.5	SB9/30	8.6	0.85 ± 0.04	
SB10		k 5.5	SB10/30	10.1	1.28 ± 0.04	Fig. 7

* Sc1/10 denotes 10 generations of selection in line Sc1; R, random mating without selection under crowded conditions; S, renewed artificial selection for high bristle number; BS, selection for low bristle number. ** Standard deviation of total number of scutellar bristles in females.

Figs. 2 and 3 document the behaviour of line SA1 in the approach to the selection limit. The following aspects of the response are worthy of note: (i) relaxation of selection in the vicinity of the 8/9 threshold leads to a loss of almost 50% of the realized response; (ii) the segregating locus or loci responsible for this loss on relaxation of selection have apparently been fixed in the line between the 14th and 18th generation, the population thereafter being stable under natural selection; (iii) the resultant populations show marked fluctuations in mean from one generation to the next at the plateau level, i.e. following SA1/15; and (iv) the transition from one level of variability to the next occurs over a period of no more than 5 generations, i.e. between generations 10 and 14 (Fig. 3).

Despite the stability of SA1 under natural selection at the plateau level back selection is effective in reducing both mean bristle number and the variability displayed (Fig. 2). The high phenotypic standard deviation of SA1 at the selection limit cannot therefore be accounted for by a model involving a locus, or loci, whose effect is simply to enhance the level of *environmental* variance among individuals in the population. If such a model were appropriate, reverse selection might be

effective in reducing mean bristle number, but the high variability characteristic of SA1/25 would be expected to be retained.

Crosses among plateaued lines

Since the exceptionally high variability of populations SA1 and SB10 at their respective plateaux is apparently related to their high mean bristle numbers (Table 1), it might be expected that renewed selection following intercrossing of plateaued lines would produce populations of both high mean and variance. In general this expectation is not realized. Random intercrossing of plateaued lines of the SB series (Table 1 and Fig. 7), followed by 25 generations of random mating, and thereafter 20 generations of directional selection, has resulted in populations all with mean probit value less than 10.5, and phenotypic standard deviation consistently less than 1.0 (B. D. H. Latter, unpublished).

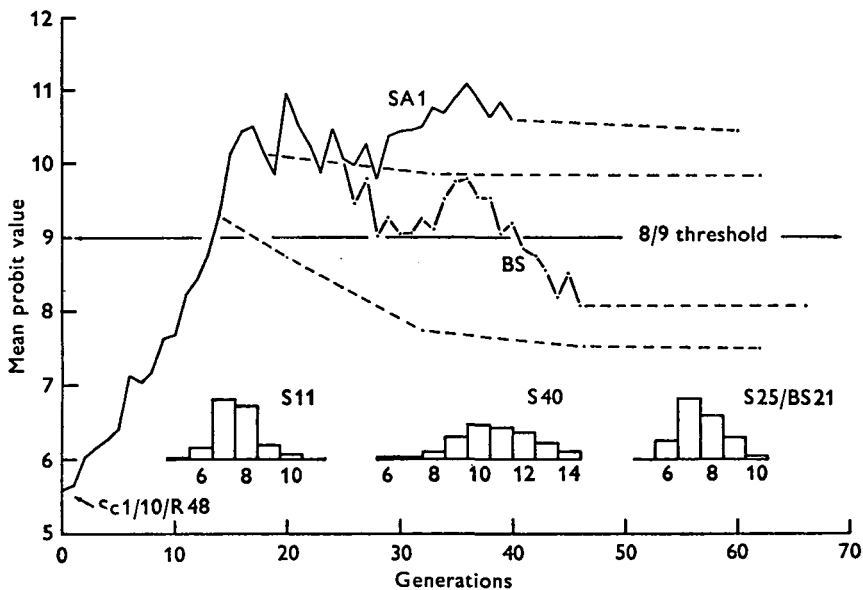


Fig. 2. Response to selection in line Sc1 following 48 generations of natural selection: S and BS denote selection for high bristle number and back selection respectively. Broken lines indicate a period of random mating under crowded conditions. Frequency distributions of bristle number in representative generations are also shown.

An exception to this general rule is illustrated in Fig. 4. Lines SA2 and SA3 are independently derived from the Canberra population. Their behaviour on relaxation of selection at generation 21 suggests the existence in each line of genetic variation for bristle number which (i) is stable under natural selection; (ii) responds little to forward selection, yet gives a rapid response to back selection. The crossing of these two lines, followed immediately by artificial selection (SH2, Fig. 4) enabled the population mean to be increased to a level comparable with SA1. An identical regime involving two other unrelated plateaued populations, viz.

Sc2/51/R9/S10 and Sc4/25/R10/S10, gave no response in the mean over a 10 generation period of selection.

Crosses involving the high variability line SA1 are of particular interest (Table 2). The difference of more than two phenotypic standard deviations (probit units) distinguishing SA1/29 from Sc2/31 proves to be almost completely recessive: crosses

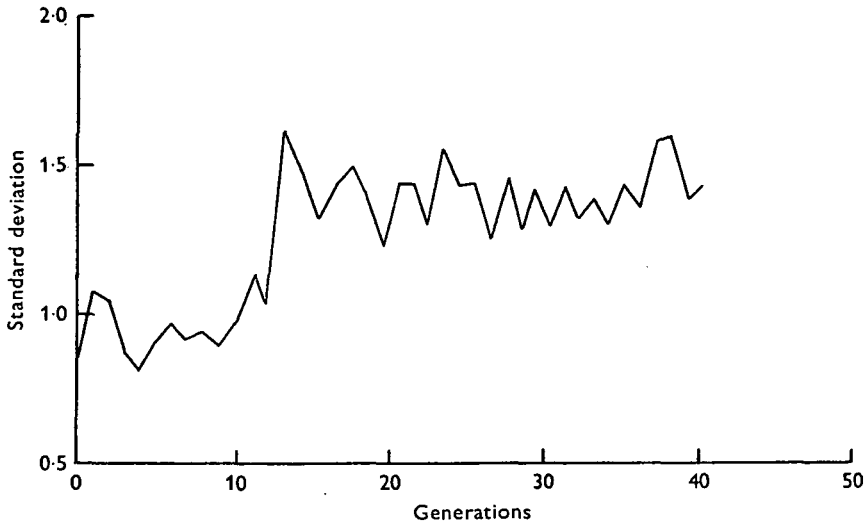


Fig. 3. Phenotypic standard deviation in females of selection line SA1, measured on the bristle number scale.

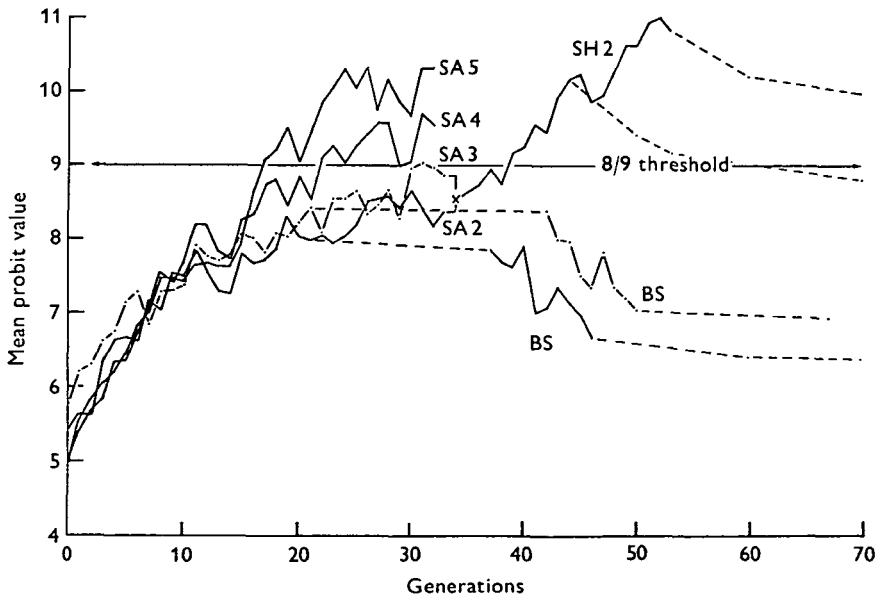


Fig. 4. Response patterns in populations stabilized under natural selection (cf. Tables 1, 3). Broken lines indicate populations maintained under crowded conditions without artificial selection, as in previous figures. BS denotes back selection.

to populations of lower mean value, i.e. Sc1/10/R80 and Canberra base, show SA1/29 and Sc2/31 to be almost indistinguishable as parents as far as the cross means are concerned (last two columns, Table 2). The hybrid populations are likewise indistinguishable in the phenotypic standard deviation of bristle number. It should be emphasized here that crosses involving two populations with means below the 8/9 threshold rarely show evidence of departure from additivity when expressed in terms of mean probit value (Latter, 1966). The estimated hybrid mean of 6.3 ± 0.12 for the cross Base \times Sc2/31 (Table 2) represents a statistically significant departure from the mid-parental value of 5.8 ± 0.09 , but the deviation is of a minor order.

Table 2. Mean probit values of hybrid populations derived from the plateaued lines Sc2 and SA1*

	Parental populations			
	Base	Sc1/10/R80	Sc2/31	SA1/29
Base	<i>3.4 ± 0.08</i>	—	6.3 ± 0.12	6.4 ± 0.09
Sc1/10/R80	—	<i>5.5 ± 0.13</i>	7.0 ± 0.08	7.1 ± 0.08
Sc2/31	—	—	<i>8.1 ± 0.16</i>	8.2 ± 0.12
SA1/29	—	—	—	<i>10.5 ± 0.07</i>

* Reciprocal hybrids have been combined using female scores only: parental mean probit values in females are italicized in the table.

Two independent lines of evidence indicate that the difference in mean between populations Sc2/31 and SA1/29 cannot be due to a single recessive gene: (i) the means of the reciprocal F_1 's do not differ significantly in females, whilst their male sibs differ by only 0.7 probit units: both autosomal and sex-linked genes are therefore involved, (ii) selection in the hybrid population, following 48 generations of random mating, resulted in a linear response in the mean on the probit scale for 22 generations: this selection line has been designated SH1 (Table 3). The resultant population, SH1/22 has a modal bristle number in females of 13, and a mean probit value of approximately 12.5 (Fig. 6). The difference of 4 probit units between SH1/22 and SB2/16 for example, has been shown to be almost completely recessive (Latter, 1970).

The simplest model to account for these phenomena is one involving a threshold mechanism, which may possibly be involved in the genetic control of development in wild-type individuals. No such threshold is discernible from observations of the distribution of total scutellar bristle number within populations (Fig. 1), and a more penetrating analysis based on component bristle types is therefore essential. The next section is concerned with this aspect of the study.

4. VARIATION IN BRISTLE NUMBER AT INDIVIDUAL SITES

Bristles on the scutellum can be classified with little ambiguity into four types, viz. anterior, interstitial, posterior and apical (Fig. 5). Supernumerary bristles occurring on the scutellum in unselected wild-type populations are usually anterior

bristles, though apicals may also be found. Extra posterior or interstitial bristles are extremely rare in natural populations. A study of populations containing multiple doses of three different *scute* alleles has led Scowcroft, Green & Latter (1968) to conclude that the degree of canalization of the normal phenotype, i.e. one bristle per site, may be considerably greater for posterior bristles than for anteriors.

Table 3. *Origin of selection lines derived from intercrosses of plateaued populations*

Selection line	Hybrid population from which derived*
SH1	(SA1/29 × Sc2/31) R48
SH2	(SA2/33 × SA3/33) R1

* Sc2 is a selection line derived directly from the Canberra population:
The origin of SA1, SA2 and SA3 is given in Table 1.

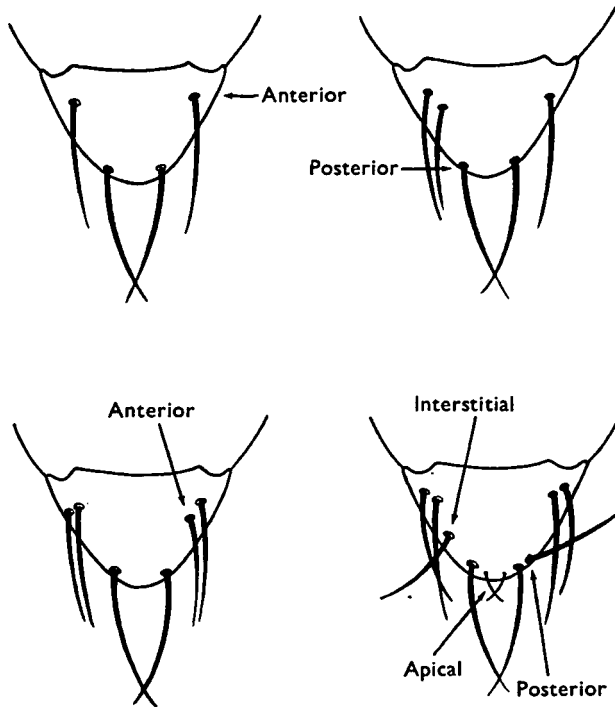


Fig. 5. Bristle types classified according to site and orientation. The prime basis for classification is the location of the bristle socket; classification of a bristle located approximately mid-way between the anterior and posterior sites is based on location and orientation.

Fig. 6 illustrates the bristle number variation of individual sites for each of four selection lines from Fig. 4, together with the population of high total bristle score (SH1/22) whose origin is given in Table 3. The following important points should be noted from the frequency distributions: (i) line SA2 shows a distribution of

bristle types which is characteristic of most populations at a plateau level below the 8/9 threshold: a high proportion of flies are found with three bristles per anterior site, and one per posterior site, to give a total of 8 bristles; interstitial bristles are rare, and apicals are found with a frequency of approximately 18%; (ii) comparison of SA2 with SH1 shows all four bristle types to be involved in the higher total bristle score of SH1: particularly striking is the high incidence of extra *posterior* bristles in SH1, and a high frequency of individuals with four or more bristles per anterior site; (iii) the frequency distributions of SA4, SA5, and SH2 indicate that

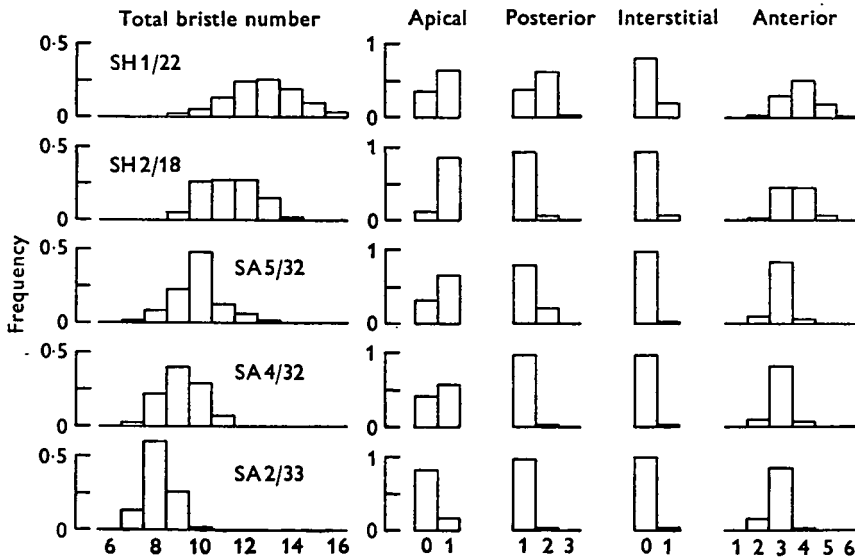


Fig. 6. Distributions of total bristle number in females of five representative populations of mean greater than 8, and frequencies of the four component bristle types expressed on a single site basis (cf. Tables 1, 3).

the component bristle types are to some extent genetically independent: SA4 owes its superiority over SA2 almost entirely to an increase in the frequency of apicals, SA5 to apicals and posteriors, and SH2 to apicals and anteriors. To obtain more definitive information on the behaviour of individual bristle types under selection for total scutellar bristle number, the SB series of ten replicate selection lines initiated from Sc1/10/R48/S7/R108 (Table 1) has been studied in detail at the limits to selection (Fig. 7).

It has previously been emphasized that selection in the base population for total bristle number on the scutellum places most emphasis on selection for anterior bristles, and all populations in Table 4 have a mean number of bristles per anterior site in the range 2.5-3.0. Two significant facts emerge from a comparison of the ten plateaued replicate lines: (i) all four bristle types have higher mean values in every replicate than are found in the base population; (ii) genetic sampling and selection for higher bristle number has resulted in highly significant genetic

differences among lines in the *apportionment* of total bristle number to the component sites.

The between-line correlations of Table 5 indicate the extent to which this apportionment of total bristle number can be considered to be a process of competition for the available resources of a particular substrate. Differences in the mean number of apical bristles are the primary cause of differences among the replicate

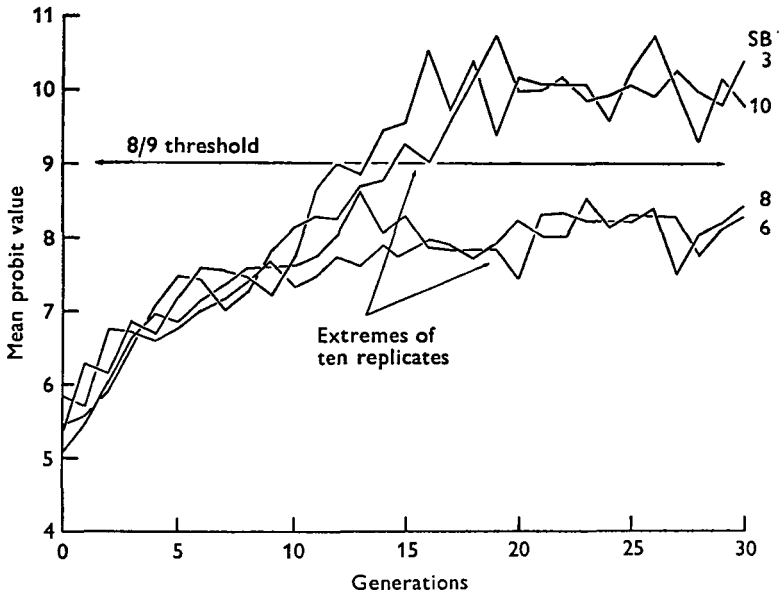


Fig. 7. Response patterns of the most extreme of the ten replicate populations in the SB series (Table 1). Selection was based on total scutellar bristle number, and the resulting bristle patterns in the plateaued lines are described in Tables 4, 5, 6.

Table 4. Mean numbers of bristles per site, for each of four component bristle types, in the plateaued SB series of ten replicate lines

(Table 1, Fig. 7.)

Selection line	Anteriors	Interstitials	Posteriors	Apicals
SB1/30*	2.67 ± 0.04	0.11 ± 0.02	1.20 ± 0.02	0.20 ± 0.02
SB2/30	2.49 ± 0.03	0.16 ± 0.02	1.47 ± 0.03	0.22 ± 0.02
SB3/30	2.86 ± 0.03	0.08 ± 0.01	1.06 ± 0.01	0.63 ± 0.02
SB4/30	2.74 ± 0.03	0.04 ± 0.01	1.05 ± 0.01	0.23 ± 0.02
SB5/30	2.78 ± 0.03	0.02 ± 0.01	1.01 ± 0.01	0.36 ± 0.02
SB6/30	2.84 ± 0.03	0.06 ± 0.01	1.05 ± 0.01	0.12 ± 0.02
SB7/30	2.82 ± 0.04	0.11 ± 0.02	1.18 ± 0.02	0.25 ± 0.02
SB8/30	2.82 ± 0.03	0.04 ± 0.01	1.04 ± 0.01	0.11 ± 0.02
SB9/30	2.74 ± 0.03	0.03 ± 0.01	1.04 ± 0.01	0.26 ± 0.02
SB10/30	3.00 ± 0.03	0.10 ± 0.02	1.10 ± 0.01	0.68 ± 0.02

* The lines were scored on five or more consecutive generations, during which flies were maintained without selection under optimal conditions. Standard errors are based on the variability among means of these consecutive generations.

lines in total bristle number, and the mean number of apicals is not significantly correlated with that of any of the other three bristle types (Table 5). The anteriors and posteriors are *negatively* correlated between lines at the plateau, despite the fact that both components have shown a positive overall response to selection. The table also suggests that the bristles classified as interstitial are closely related to posterior bristles, despite their obvious displacement from the normal posterior sites on the scutellum. The matrix of correlation coefficients relating a, i, and p bristles, viz. -0.37 , -0.72 , and 0.89 , has a determinant which is close to zero ($+0.03$): the coefficients are not of great accuracy, each having only 8 degrees of freedom, but the data suggest something close to a linear relationship among the means of these three bristle types.

Table 5. *Between-line correlations based on the mean counts for component bristle types and total bristle number, calculated from the data of Table 4*

	Anterior (a)	Interstitial (i)	Posterior (p)	Apical (ap)
Total (t)	0.44	0.48	0.19	0.89**
Anterior (a)	—	-0.37	-0.72^*	0.54
Interstitial (i)	—	—	0.89**	0.10
Posterior (p)	—	—	—	-0.15

*, ** Significant at 0.05, 0.01 level respectively (D.F. = 8).

Genetic control of variability

It has been shown that some selection lines are characterized by a high level of phenotypic variability at the selection limit, e.g. SA1, SH1, but no evidence has been presented to indicate that this increase in bristle number variability is due to a reduced level of developmental regulation. In fact, I know of no such evidence from any recorded study of selection response in experimental populations. Two observations in the present study are relevant to this question: (i) *negative* phenotypic correlations between sites on the scutellum have been detected *within* plateaued populations, providing additional support for a model involving competition among sites for limiting substrate; and (ii) estimates of the span of a chosen bristle number class, based on scores of individual anterior sites, show the increased variability in bristle number to be due partly to impaired developmental regulation.

The evidence for a negative phenotypic relationship among component sites on the scutellum, within populations which have ceased to respond to directional selection for total bristle number, is presented in Table 6. The measure of site interaction (γ) represents twice the sum of the covariances of bristle number at the 8 individual sites on the scutellum (cf. Fig. 5), and significant interaction has been detected in each of the five populations with the highest means. Line SB10 is exceptional in having a significant *positive* estimate of site interaction, and it is this line which has previously been noted as having a phenotypic standard deviation far greater than that of any of the other nine lines (cf. Table 1). Replicates

SB1, 2, 3, and 7 show the type of interaction which would be anticipated if a genetically determined upper limit were imposed on the level of a particular substrate which is limiting at this level of bristle number. Progress to higher levels under selection would then require a genetic modification of this fixed upper limit; if this is the correct interpretation, it must be concluded that directional selection for total bristle number alone rarely brings about the necessary change, other than as a chance phenomenon.

Table 6. *Within population variability, for each of four component bristle types, in the plateaued SB series of ten replicate lines*

Selection line	Variance of bristle number per site				Measure of site interaction** (γ)
	Anteriors (σ_a^2)	Interstitials (σ_i^2)	Posteriors (σ_p^2)	Apicals (σ_{ap}^2)	
SB1/30	0.273	0.098	0.162	0.159	-0.463
SB2/30	0.269	0.131	0.242	0.174	-0.934
SB3/30	0.202	0.071	0.061	0.234	-0.340
SB4/30	0.216	0.034	0.050	0.177	+0.021
SB5/30	0.202	0.017	0.012	0.229	+0.128
SB6/30	0.228	0.060	0.050	0.107	-0.198
SB7/30	0.275	0.093	0.143	0.185	-0.494
SB8/30	0.187	0.042	0.040	0.100	-0.070
SB9/30	0.183	0.031	0.041	0.195	-0.119
SB10/30	0.246	0.090	0.089	0.215	+0.187
Approximate S.E.*	± 0.019	± 0.018	± 0.012	± 0.013	± 0.092

* Standard errors have been estimated in the same way as described for Table 5.

** $\gamma = \sigma_i^2 - 2\{\sigma_a^2 + \sigma_i^2 + \sigma_p^2 + \sigma_{ap}^2\}$, where σ_i^2 is the variance in total bristle number. The overall mean value of γ is -0.228 ± 0.029 .

In Table 7 are given a number of estimates of the span of the '3 bristles per anterior site' class, for populations at different levels of phenotypic variability for bristle number on the scutellum as a whole. It can be seen from the table that increased variability is associated with a reduction in the span of this particular class, which is the only 'single-site' class observable in all the populations. This observation is of particular importance, since it establishes the fact that variability in total bristle number is not wholly determined by the mean frequencies of additional bristles at the component sites. Variability at the individual site level, measured by a statistic which is independent of the mean, has increased in lines of high bristle number variability. The additional response to selection in these populations is due mainly to the occurrence of individuals exceeding the 3/4 threshold for bristles per anterior site, and the 1/2 threshold for bristles per posterior site (Fig. 6).

Table 7. Estimates of mean probit distances spanned by the '3 bristles per anterior site' class in females

Population	Mean probit value	Phenotypic standard deviation*	Span of '3' class
SA2/33**	8.4	0.89 ± 0.07	2.98 ± 0.12
SA4/32	9.4	0.92 ± 0.09	2.93 ± 0.13
SA5/32	10.1	1.08 ± 0.11	2.59 ± 0.13
SH2/18	10.9	1.17 ± 0.12	1.83 ± 0.13
SA1/40	10.7	1.41 ± 0.05	1.76 ± 0.09
SH1/22	12.8	1.52 ± 0.10	1.67 ± 0.09

* Of total scutellar bristle number in females.

** Estimates of the parameters in this table are based on a number of separate estimates obtained in consecutive generations maintained under optimal conditions.

5. DISCUSSION

The selection lines involved in this study have shown many of the complexities characteristic of populations at a plateau under directional selection (Falconer, 1960). A comparatively simple threshold model appears to be adequate to account for the observations we have made, and can be justified in this instance by the behaviour of the separate components of total bristle number, which are readily observed. Component analyses are often difficult or impossible in selection experiments concerned with conventional quantitative variables, and scutellar bristle number is therefore particularly suited to this line of investigation.

Robertson (1959*a, b*) has demonstrated qualitative differences between two components of body size in *Drosophila*, viz. cell size and cell number, in their responses to selection, inbreeding and environmental stress. Waddington (1952) has speculated that all quantitative genetic and environmental variation is subject to some degree of genetic control, to the extent that the developmental and physiological processes concerned are regulated. If the separate components of a chosen metric trait are subject to different systems of regulation in the process of development, observations of a single quantitative phenotype may be inadequate to suggest an appropriate mechanistic model of behaviour at the limits to selection.

The selection limits described in this paper are of particular interest in that exceptional populations are characterized by a high level of bristle number variability, e.g. SA1/40 with a mean probit value of 10.7, and SH1/22 at a mean level of about 12.8 (Tables 1, 7). Reverse selection in SA1/25 has been shown to reduce the level of variability to that observed in almost all the plateaued populations of this study. Outcrossing to lines of mean probit value of the order of 8.0–8.5 shows the genes responsible for high mean and variance in lines SA1 and SH1 to be almost completely recessive.

In plateaued populations of normal variability, negative correlations between component bristle types have been demonstrated, though the information recorded to date does not indicate which particular components are involved

(Table 6). It has also been shown that anterior and posterior bristle means are negatively correlated between replicate selection lines at the limits to selection (Table 5). These observations lead us to suggest the following model as the basis of a working hypothesis capable of experimental test and modification.

The Model

1. Bristle development at the component sites on the scutellum involves a process formally analogous to the allocation of available resources of a particular substrate produced during development. Bristle frequencies at component sites will therefore show negative correlations within a population whenever the product concerned is limiting in the process of bristle formation.

2. Selection for total scutellar bristle number in the base population leads to an increase in the frequency of bristles at all component bristle sites, so that this particular substrate does not appear to limit total bristle number in the unselected population. This corresponds to phase I of the response pattern (Latter, 1966), i.e. a period of linear response in the mean on the probit scale.

3. The mean allocation of these resources to each of the four bristle types, anteriors, interstitials, posteriors and apicals is genetically determined, and genetic sampling may produce differences between selection lines in component bristle frequencies, at a given level of total bristle number.

4. Genetic control is exercised over the *limit* to which these particular resources can be pushed under selection. The most consistent manifestation of this limit is that the number of anterior + interstitial + posterior bristles rarely exceeds a total of 8. As the resources of the critical substrate become limiting, a period of reduced rate of response in total bristle number is observed (phase II), during which opposition due to natural selection is intensified, and a reduction in the level of additive genetic variance can be detected (Latter, 1966).

5. Further response to selection is conditional upon allelic substitutions which lead either (i) to an increase in the rate of production of the limiting substrate, or (ii) to a lowering of the concentration of the substrate necessary for bristle initiation. The available evidence does not enable us to choose between these alternatives. The allelic substitutions concerned are recessive, and will be described as '*decanalizing*' alleles in view of their effects on both bristle number variability and the measure of developmental regulation at individual anterior sites.

The foregoing model is similar in some respects to that proposed by Rendel (1967). He has demonstrated negative correlations between anterior and posterior sites in selected populations homozygous for the sex-linked mutant *scute*, in which mean total scutellar bristle numbers are *less* than the normal four (Rendel, 1965). We have here found that the same phenomenon may be exhibited in wild-type stocks at mean total bristle numbers in the vicinity of eight. Evidence has been presented elsewhere (Scowcroft & Latter, 1970) which suggests that the decanalizing alleles involved in the present model may correspond to a system of one or more regulators controlling the activity of a major gene, possibly the *scute* locus. A detailed hypothesis involving regulation of the activity of the *scute* locus has been

advanced by Rendel (1968) to account for phenotypic invariance in unselected wild-type populations.

Fraser (1967) has proposed a model of genetic control of scutellar bristle number which involves two major genes, each with a set of modifiers, to account for the non-additive genetic behaviour of some of his extensive set of selection lines. The correspondence between his results and ours is not yet apparent. It is known however, that the allele which he has designated *x-vert* is not present in the high bristle number population SH1/22.

As far as breeding practice is concerned, the implications of the model presented in this paper are twofold. Continued directional selection alone may be ineffective in disrupting systems which regulate some of the developmental processes being modified, unless the limiting process can be identified and subjected to separate selection pressure in a plateaued population. Subdivision of the total breeding population into a number of isolates may be the only practicable way of concentrating the genes required for progress beyond such a threshold, capitalizing on accidents of genetic sampling by subsequent between-line selection. A similar inference can be drawn from the observations of Hosgood, MacBean & Parsons (1968). Our experiments also support the suggestion of Rendel (1963) that negative genetic correlations between component traits may be generated by selection, thereby restricting progress in the short-term. But the behaviour of the populations under selection in this study indicates that appropriate allelic substitutions may sufficiently alter the developmental or physiological processes involved that quite different genetic relationships among the components are induced.

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