SELECTION FOR AN ALMOST INVARIABLE CHARACTER IN *DROSOPHILA*[1]

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(With Four Text-figures)

1. Meristic characters

Most quantitative characters, such as stature, body weight, growth rate or pigment content, vary continuously between wide limits. By means of these characters, individuals may be classified into a number of categories limited only by the accuracy of the measuring instrument used. Any phenotypic variability in a population, whether it be heritable or non-heritable, is detectable, and, what is more, is subject to the action of selective forces.

There is, however, another kind of quantitative character, in which variation is discontinuous. This includes the meristic characters, such as vertebra number or chaeta number, in which total expression is variable only by varying the number of units which it contains. The number of vertebrae or chaetae must be an integral number, since fractions of a unit are impossible. This discontinuity in variation has, in the past, led to certain difficulties in understanding how natural selection can act to produce adaptive and evolutionary changes in such characters, since phenotypic variability is frequently not observable, except perhaps in very large samples. Fisher (1930) has, however, pointed out that genetic variability may be present even though it is not detected phenotypically. He suggests that the observable distribution should be regarded as a natural example of a normally distributed variation grouped in equal intervals, which may be large as compared with the standard deviation. If the unit of grouping were, for example, eight times the standard error, only about one individual in fourteen thousand would be expected to depart from the common type. On this view genetic variability fully adequate to permit adaptive and evolutionary changes would be present even though the phenotypes are almost invariable.

Evidence that the situation is, in fact, much as Fisher suggests has been obtained in two ways. One, in the direct assay of genetical potentialities of a series of individuals by diallel crosses (Schmidt, 1919); which, however, is of limited value when the character in question varies but rarely. The second, and more powerful, method is by selection. Of the selection experiments on meristic characters two require special mention for their bearing on the present study. The first of these was carried out by Payne (1918) who selected for increased number of macrochaetae on the scutellum of *Drosophila melanogaster*. This is almost invariably four in both wild and laboratory flies (see Table 1), but starting off with two aberrant five-bristled females mated to normal males Payne raised the mean number of bristles to nine in thirty generations. This clearly shows that considerable heritable variability is hidden under the almost complete uniformity of this meristic character.

The second experiment was conducted by Mather (1941), who selected for both increase and decrease in the number of chaetae on the ventral abdominal surface of *D. melanogaster*.

[1] Part of a thesis approved for the degree of Doctor of Philosophy in the University of London.

This character, though meristic, is far from invariable in natural material, and hence the masking effect of the discontinuous variation is small. Mather was able to show that even when the phenotype is variable, a still greater amount of variability is hidden in the genotype, in the form of balanced polygenic combinations. Marked selective changes are made possible by recombination, which unbalances the combinations and permits segregation to release this hidden, or potential, variability.

The masking effect on variability of discontinuous variation, combined with the storage of variability in polygenic combinations would enable the phenotypic expression to be constant in spite of the presence of a considerable quantity of heritable variation, i.e. of a large potential change with selection. In order to obtain further information on this point, especially with respect to the way in which heritable variability is stored, it was decided to reinvestigate the response to selection of scutellar chaeta number, and to carry out certain tests, as will be described later, on the lines resulting from such selections.

2. THE SELECTION EXPERIMENTS

The frequency of extra scutellar macro-chaetae among the stocks at the John Innes Horticultural Institution was found to be very low. Of eight stocks counted (Table 1) five contained no flies with additional chaetae. Two others have less than 1% of five bristled females, and, in one case, an equally small proportion of abnormal males, in the other case no abnormal male. The eighth stock gave four females with five chaetae out of sixty-one examined, while sixty males were all normal. The frequency of extra chaetae is higher in female than in males, as was observed by Payne, but is very low even in this sex.

Table 1. *Frequency of flies with extra-scutellar macro-chaetae in eight stocks*

	Females		Males	
Stock	Total	No. with extra chaetae	Total	No. with extra chaetae
yw	61	4	60	0
B	149	1	186	1
BB	242	2	244	0
y^{36e}	80	0	83	0
fB^1B^1	140	0	123	0
gvl	196	0	100	0
$\hat{ff} \times +$	173	0	181	0
$\hat{yy} \times wmf$	33	0	30	0

Selection lines were started from two stocks, *yw* and *B*. The line from the *B* stock died out after seven generations, during which no persistent increase of chaeta number with selection had occurred. A normal female from the seventh generation was mated to a normal male of the line *yw* C (see below) to give the hybrid line $B \times yw$.

Three matings were used for the initiation of lines from the *yw* stock. All were of five-bristled females by normal males, the female in the first mating probably not being virgin. This would make little difference, however, since all the *yw* stock males were four-bristled.

Seven brother-sister single-pair matings were set up from the progeny of this first pair, selection for high chaeta number being exercised. These each gave rise to a separate selection line, of which, however, three were soon lost or discarded because of sterility. The remaining four are the lines *yw* A–D. Lines *yw* E–F came from the second stock

mating and lines *yw* G–J from the third. A male of *yw* C was used in the development of the hybrid line (see above).

The flies with most scutellar chaetae were, in every generation, selected as parents of the next. All matings were single-pair brother-sister, and were made in tubes. Two days after mating the flies were transferred to new tubes and allowed to lay for two days, before being placed into further laying tubes for a like period. From two to four matings were made of each line in each generation, but only the successful one with the most extreme parents was used for continuing the line. All flies were raised in the incubator at 25° C. More flies were counted from the early than from the later generations. This was partly deliberate and partly due to the onset of sterility.

The results of selection from the *yw* stock are shown in Figs. 1 and 2. Fig. 1 shows the behaviour of the four lines, *yw* A–D, obtained from the first pair selected from stock.

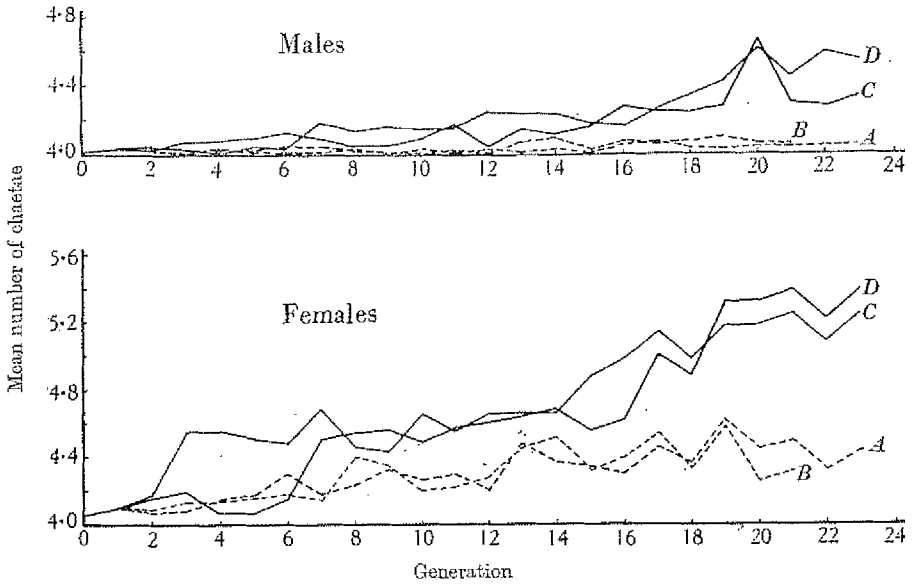

Fig. 1. The response to selection of lines *yw* A–D.

Males and females are given separately, the males always showing a smaller average departure from the normal number of four scutellar chaetae. It will be seen that the behaviour of the males parallels that of the females, but is less easy to interpret because of the smaller departures. Hence our discussion will refer especially to the female data. In Fig. 2, which gives the lines (excepting *yw* J, which is reserved for special discussion) derived from the second and third selected pairs, males are entirely omitted as being in agreement with, and less informative than, females.

Let us first consider the lines *yw* A–D, which are all derived from the single five chaetae stock female, whose progeny constitute selected generation 1 ($S1$) in Fig. 1. These four lines fall very clearly into two pairs. A and B show little advance with selection until generation 5 ($S5$) after which the mean number of chaetae rises slightly but soon becomes stable, or nearly so, at approximately 4·3 or 4·4. These two lines show identical behaviour, but differ sharply from C and D. This latter pair shows an early and marked rise into a mean chaeta number of 4·5, after which no great response to selection occurs before $S14$.

Between $S14$ and $S19$ both C and D show another sharp rise to a mean of approximately 5·2 chaetae, again becoming stable for the last four generations of the experiment. After $S7$ these two lines are as nearly identical in behaviour as lines A and B, but they differed before this time. C shows its first advance in $S3$, while in D this rise was delayed until $S7$. When D did advance, however, the rise was exactly equal to that obtained four generations earlier in C.

These remarkable results are confirmed by the later selections *yw* E–I (Fig. 2). E and F, obtained by selection from the same pair of stock flies, are identical so far as they were continued. F showed a sharp rise not found in E, in its last generation, but such rises have been observed elsewhere as chance fluctuations, e.g. line C at $S7$. Lines G–I were all derived from the third stock pair and fall into two classes, I and G, which were alike in behaviour, except for a short-lived, and presumably chance peak at $S6$ in I, and H,

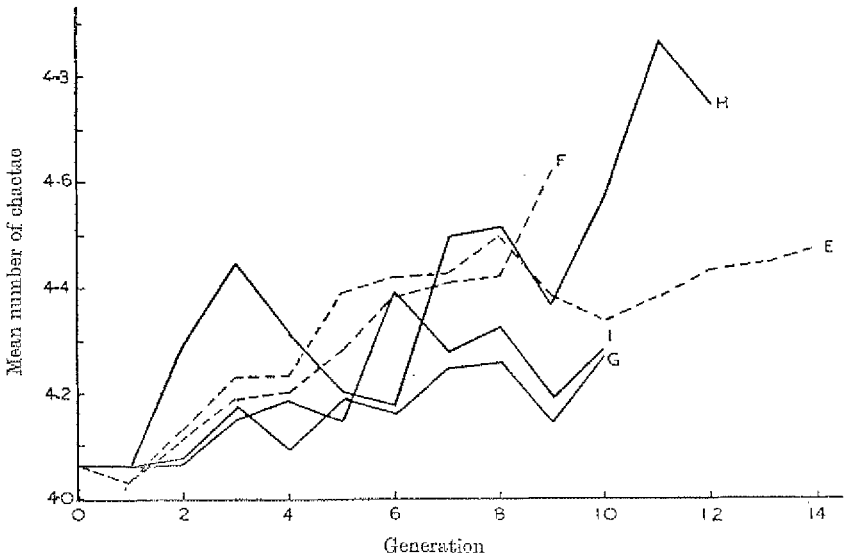

Fig. 2. The response to selection of lines *yw* E–I. Only the female results are shown.

which from the first has a much higher mean chaetae number than either I or G. There is a disturbing trough at $S5$–6 in H, but this does not persist and so can most likely be ascribed to chance.

Thus all these nine selected lines appear to follow from the first, one or other of a limited number of paths. Their differences in response, even as late as $S19$ are not fortuitous. They are apparently consequences of differences established from the first. Even when the two like lines C and D differ by four generations in the time of their first rise, the magnitude of the responses to selection, when they do occur, is exactly the same. The meaning of these facts will be discussed later.

The hybrid line, $B \times yw$, was initiated by an interstock cross. Its behaviour is shown graphically in Fig. 3. The line responded to selection from the very beginning, but the response was most rapid from $S3$ to $S7$. After $S7$ the rise in chaeta number was slower. It should be noted that the total response in this line was nearly three chaetae in females against a maximum of just under 1·5 in the *yw* C and D. Nor is it clear that response had ceased when the hybrid line was terminated at $S18$.

One further remark must be made about this line. At $S7$ a Notch mutation was detected. This was, of course, lethal in males and hence was maintained in heterozygous females. Fig. 3 shows that Notch flies always had an average of nearly two more chaetae than their normal sisters. Hence Notch females exclusively were used as parents in each generation, with the consequence that the condition persisted for the remainder of the experiment. The average of all females, whether Notch or not, is taken as the chaetae number characteristic of this line. Linkage tests showed that this effect on chaeta number was inseparable from the Notch mutation.

The line *yw J* (Fig. 4) was unique in that back selection was practised in $S8$. It responded steadily to selection for increased chaeta number until $S6$, after which no further advance was obtained in the females, though the males showed signs of a slight advance. The back selection was commenced when a male with only three chaetae was found in $S8$. Mated to a normal sister this gave the first generation in the back selection

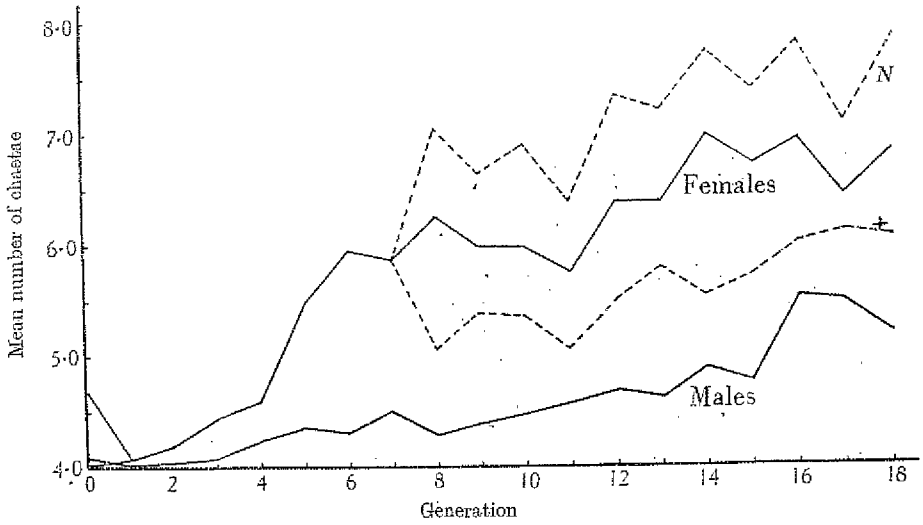

Fig. 3. The response to selection of the hybrid line $B \times yw$. The solid line for females is the average of all flies of this sex. The dotted lines, marked N and +, are the averages of Notch and not-Notch females taken separately.

line. This also contained a three-chaeta male which was again mated to a normal sister, but no flies with less than four chaetae were observed afterwards, all the matings being of normal by normal. Thus it is unlikely that the flies with subnormal chaeta number were due to a scute mutation as was first suspected. If this had been the case, many scute progeny should have appeared in the second generation, when, in actual practice, none were found.

The back selection line fell sharply at first; but the fall was less rapid later, though it seemed to persist until the end of the experiment. By this time the back selection line had almost returned to the chaeta number of the original *yw* stock. Reselection for increased chaetae, was commenced at $S14$, and this new selection line showed a sharp rise, at least in females, for a short time. It appeared to become stable later, though at a mean number of chaetae lower than that of the original selection line, from which it was separated by six generations of back selection.

3. ANALYSES OF THE SELECTED LINES

In order to elucidate further the nature of the responses to selection, certain of the lines were tested at various times in the hope of determining which chromosomes were responsible for the phenotypic changes. The tests were made by the method which Mather (1942*a*) described for the detection of chromosomes which have responded to selection.

The lines *yw* A–D and the hybrid line were tested in that way. The hybrid line will require some special discussion, but the tests of *yw* lines were all alike. The tester stock was *Cy/Pm*; *H/In* 3 (*R*) *Mo Sb sr*, females of which were mated to *yw* males from the line and generation to be tested. *Cy Sb* daughters of this mating were backcrossed to further *yw* males from the same selected line, and either of the same or the next generation. Neglecting the relatively rare cross-overs between *y* and *w*, eight classes of flies were found in each sex in the next generation, viz. (I) *yw*, (II) +, (III) *yw Cy*, (IV) *Cy*,

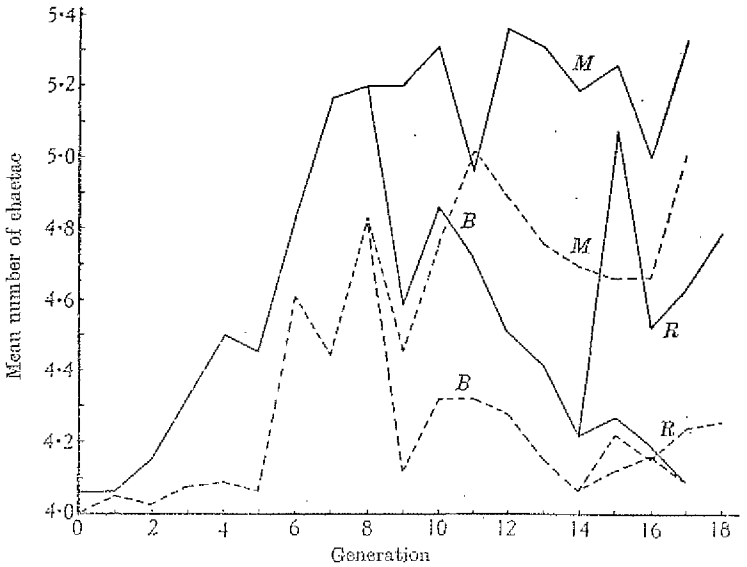

Fig. 4. The response to selection, back selection and reselection in the line *yw* J. *M* indicates the main selection line, *B* the back selection line and *R* the reselection line. The main and reselection lines are selected for increased, and the back selection line for decreased numbers of scutellar macrochaetae.

(V) *yw Sb*, (VI) *Sb*, (VII) *yw Cy Sb*, (VIII) *Cy Sb*. If no effective crossing-over occurred in the mother, the chromosomes in class (I) would all have been derived ultimately from the *yw* line, while class (VIII) would have received one number of each chromosome pair from the *yw* line and one from the tester stock. All the other classes would receive either one or both of each chromosome pair from *yw*, the remainder coming from the tester stock. These latter could be detected by examination of the flies' phenotype. Thus a + fly gets only an *X* from the tester, *yw Cy* and *yw Sb*, a II and a III respectively and *Cy* and *Sb*, an *X* and II and an *X* and III from the tester. *yw Cy Sb* has both a II and a III but not an *X* from the tester.

Actually, of course, effective recombination occurs freely between the *X* chromosomes, and to some extent between the III chromosomes, though hardly at all between the II chromosomes, in mothers of the above constitution. Hence, though the test is very efficient for chromosome II, it is less so for chromosome III and less still for the *X*. Even so, however, the results of the various tests proved to be very informative.

The data were analysed in the way described by Mather. The difference between the chaeta means of all *Cy* and all non-*Cy* flies, irrespective of their constitution for the other chromosomes was taken as a measure of the difference in effect between the tester and tested chromosome II. *Sb* as against not-*Sb* measured the difference attributable to chromosome III, though, of course, this detectable difference was less than the true one by virtue of the recombination in III *L*. Lastly, part of the *X* chromosome difference is measured by not-*yw* as compared with *yw*. This type of analysis is strictly sound only if equal numbers of flies of all eight marked classes have their chaetae counted. These numbers were not always quite equal in the present analyses but the differences were sufficiently small not to cause any serious misjudgment. The consistency of the results bears further witness to their trustworthiness. The tester chromosome value was subtracted from the tested chromosome value in all cases. So a positive difference indicates greater chaeta producing power of the chromosome from the *yw* lines as compared with its homologue from *Cy*/*Pm* : *H*/*Sb*. It should be observed that only those genes of the *yw* lines which are not fully dominant to their allelomorphs in the tester will be detected in these analyses.

Table 2 gives the differences associated with each chromosome found by this technique, for the *yw* stock and the various selection lines in different generations. It will be observed that the *S*19 flies of *yw* D were analysed in two separate tests. The two sets of results are

Table 2. *Differences in chaeta-producing power of tested chromosomes from their homologues in the tester stock*

		Chromosome					
		X		II		III	
Line	Generation	♀	♂	♀	♂	♀	♂
yw stock	*S*0	0·015	0·000	0·038	0·000	0·008	0·000
yw A	*S*19	−0·110	−0·013	0·265	0·044	0·037	−0·011
yw B	*S*20	0·037	−0·003	0·256	0·007	0·013	0·000
yw C	*S*13	0·095	−0·020	0·401	0·110	0·052	0·037
	*S*21	0·076	0·010	0·761	0·208	0·366	0·113
yw D	*S*14	−0·004	−0·035	0·448	0·154	—	—
	*S*19 first test	0·015	0·013	0·692	0·210	0·467	0·090
	*S*19 second test	0·141	−0·020	0·834	0·449	0·227	0·094
B × *yw*	*S*12 first test	—	—	0·754	0·372	0·509	0·197
	*S*12 second test	—	—	0·806	0·381	0·474	0·102
	*S*12 third test	—	—	0·951	0·384	0·563	0·240
	*S*17	—	—	0·940	0·526	1·100	0·385

broadly in agreement, except for a remarkable value for the *X* chromosome given by the females of the second test. This is so out of keeping with the rest of the results that it must be treated with great reserve. Chromosome III was not tested at *S*14 of *yw* D, as progeny were obtained from *H* mothers only. As *H* itself reduces the number of scutellar chaetae, all *H* flies were rejected and their non-*H* sibs used for assaying chromosomes *X* and II.

The next step in the analysis is now possible. The differences of Table 2 were obtained by comparing the tested chromosome with a tester which was the same in all the analyses. So the various tested chromosomes may themselves be compared via this common tester. Thus the *yw* stock chromosome II differed from the *Cy* tester by 0·038 as measured in females, whereas chromosome II from *yw* A, generation *S*19, gave an equivalent figure of 0·265. So *yw* A has a chromosome II which gives on the average in females 0·265 − 0·038, or 0·227, chaetae more than that of the parental stock. The corresponding difference as

expressed in males is 0·044 − 0·000 or 0·044. The differences obtained in this way are set out in Table 3, from which it is possible to see to which chromosomes the selective responses are due.

Table 3. *Changes in the mean chaeta-producing power of various chromosomes in the* yw *lines*

		Chromosome					
		X		II		III	
Line	Generations	♀	♂	♀	♂	♀	♂
yw A	1–19	−0·125	−0·013	0·227	0·044	0·029	−0·011
yw B	1–20	0·022	−0·003	0·218	0·007	0·005	0·000
yw C	1–13	0·080	−0·020	0·363	0·110	0·044	0·037
	13–21	−0·019	0·030	0·360	0·098	0·314	0·076
yw D	1–14	−0·019	−0·035	0·410	0·154	—	—
	14–19 first test	0·019	0·048	0·244	0·056	—	—
	14–19 second test	0·145	0·015	0·386	0·295	—	—
	1–19 first test	—	—	—	—	0·459	0·090
	1–19 second test	—	—	—	—	0·219	0·094

The *X* chromosome shows little evidence of change. In *yw* D it gives a value of 0·145 for change in females from *S*14 to *S*19, in one test, but this is belied by the females of another test and also by the males. In the case of *yw* A the *X* chromosome appears to have moved against selection to the extent of giving a difference of −0·125 in females. Here again, however, the males provide no confirmatory evidence. It thus appears likely that no significance should be attached to this negative difference. In view of the nature of the test it should be noted that these remarks apply only to the left end of the chromosome, the right end being inadequately tested.

Chromosome II shows response to selection in every case, in females, and this is confirmed by the behaviour of the males in all but two cases, *yw* B and the first test *yw* D *S*14–19. We may conclude that the second chromosome has changed during every stage tested.

Chromosome III shows no change in lines A and B, and no change before *S*13 in line C. After *S*13, however, it responded to selection in this last line. In line D this chromosome responded before *S*19 but was not tested at *S*14. In view, however, of the great similarity in behaviour of lines C and D, it seems not unreasonable to suppose that chromosome III did not change before *S*13 in line D.

The remarkable similarity of lines A and B and of lines C and D noted in § 2, is rendered even more striking by the results of the analysis. A and B change only in chromosome II, the responses being equal. This chromosome must then be responsible for the noticeable response of generations *S*4 to *S*8 in these lines. In C and D the equal early selective responses are also due to chromosome II, but the difference is larger than in A and B, as would be expected from Fig. 1. Chromosome II continued to change markedly after *S*13 and *S*14, but at least a part of the later response (*S*14–*S*17) must be attributed to chromosome III. We can thus analyse the response curve into its constituent parts.

The tests of chromosomes II and III were conducted in the $B \times yw$ line in the same way as in the four *yw* lines. The results are given in Table 2. It is clear that chromosome II had changed markedly, even as compared with *S*14 of the *yw* C line from which it was descended. There is some indication of a smaller change in this chromosome between *S*12 and *S*17. Chromosome III showed a change before *S*12, and another of nearly equal

magnitude after that generation. The later response in this line would thus appear to be due more to chromosome III than to chromosome II; while the earlier one was due more to II than to III.

The *X* chromosome could not be followed in this line in the crosses to the *Cy/Pm* tester. It was, however, possible to recognize changes which occurred before *S*4, because the early generations segregated for *yw* and *B*. Though parents were chosen solely on the basis of chaeta number, *B* had vanished by *S*4, but *yw* and + chromosomes persisted until *S*7, after which point the Notch mutation introduced a variation in the mating system. This made it impossible for either of these chromosomes to be lost. It thus appears that the right end of the original *B* chromosome was less effective in producing extra chaetae than was the homologous part of the *yw* chromosome. Hence it was eliminated by selection. But the left ends of both original chromosomes had equal effects and both persisted in the experiment in combination with the not-*B* right end. This interpretation was borne out by the effects of the various recombinant classes in the early generations of the experiment. Whether the left ends of the chromosomes changed during the experiment, in the way that the autosomes changed, it is impossible to say. The persistent equivalence of the + and *yw* homologues suggests that they did not do so; but this cannot mean that this part of the *X* chromosome carries no polygenes affecting chaeta number, for Payne found such genes in his experiments.

4. The storage of variability

The extent to which any of the lines would respond to selection is clearly governed by the amount of genetical variability available to the action of selection. This variability was not apparent in the flies from which the selection lines were started, so it must either have been stored in the original material in such a way that it had no effect on the phenotype or it must have arisen by mutation during the course of the experiments.

The latter explanation is ruled out by the nature of the responses. In the first place the hybrid line responded more than did any of the *yw* lines. This is inexplicable on the mutation view, but would be expected on the alternative storage hypothesis, as we shall see later. Secondly, it is clear from the behaviour of the various *yw* lines that each fell into a category whose selective properties was constant from the beginning. A and B were alike but differed sharply from C and D whose responses were of equal magnitude even though occurring a few generations apart. There is no sign of the unpredictable behaviour which would be an inevitable outcome of mutation. Finally, the tests described in § 3 show that particular responses are ascribable to particular chromosomes. This would indeed be a remarkable finding if the variation, upon which the selective response depended, were mutational.

We are thus left with the view that the variability was present in the original material, but stored in the genotypes in such a way that little trace of it was detectable in the phenotype. The meristic nature of the character must be able to cover some of the variability, as shown in § 1, but this fails to account for the responses being attributable to changes in particular chromosomes. As these changes accompanied the periods of marked response, the greater part of the variability must have been stored in some way by the genic organization of the chromosomes themselves. The character itself being clearly under polygenic control, we have, in fact, a case of balanced polygenic combinations of the kind described by Mather (1941).

A balanced polygenic combination consists of a number of polygenes, within a chromosome, some acting in a way tending to increase the manifestation of the character, the rest tending to decrease it. The proportions of the two kinds are balanced so that the total effect of all the linked polygenes is near to the optimum effect for the chromosome in the wild. Addition of either + or − polygenes would move the effect away from this optimum, and, in the wild, would lead to a selective disadvantage. Thus there is a natural selection for maintenance of this balance. Recombinations with homologous combinations can destroy the balance of + and − polygenes, release variability and permit advances with selection in experiment.

The behaviour of the various selection lines is in full accord with, indeed in its broad outlines is predictable from, the theory of polygenic combinations. In the first place the original material would not be expected to show any great phenotypical variation, because this would be correlated with variation in the balance of the combinations. It would occur only to the extent to which the total effects of the different combinations in one or more chromosomes depart from the optimum. Such departure must in general be too small to produce observable variation in a meristic character showing discontinuous grades of expression. Each chromosome, *X*, II and III, will be balanced independently of the rest and so inter-chromosome recombination, which would release stored variability in the first generations of the experiment, will have little effect. The reshuffling of separately balanced components cannot lead to unbalance.

When, however, homologous but distinct combinations come together in a zygote, effective intra-chromosome recombination will occur, and unbalance will be brought about by the reassortment of the constituent + and − polygenes. This will release the stored variability, which will then be manifest in the phenotypes, and selection becomes operative. Now clearly this unbalancing process in any chromosome must depend on two distinct things, heterozygosity for the various combinations and the relation of crossing-over to the heterozygous genes. The former is essential for recombination to be effective, the latter for recombinations of the polygenes to occur at all.

To deal with the second agent first, it is clear that any pair of combinations in a heterozygote will have its own characteristic relations of gene distribution with regard to the places where crossing-over occurs. Thus each pair will have its own characteristic rate and total magnitude of variability release. Some will be able to release but little variability and that slowly. Others will show quicker release, others greater total release and so on. Some may not be able to release any variability at all.

With a limited number of parents, such as was used in these experiments, the number of possible heterozygous pairs of combinations in any chromosome is limited. A given selection line will start with flies having one or other of this limited range of alternatives and so each line will respond to selection in one or other of a limited number of ways. The fate of the line is decided before selection starts, by the organization of its polygenic combinations. Furthermore the different chromosomes, *X*, II and III, will each have its own combinations and hence its own characteristic behaviour, which will be repeated in all lines starting from parents of like constitution. So we can see why the lines A and B, C and D, etc., showed identical responses to selection, and why the responses were attributable to changes, or as is now clear recombination, in particular chromosomes. Such a result was inevitable in an experiment of this kind, from the properties of polygenic combinations.

There remains the question of heterozygosity to be considered. It is obvious that the more polygenes there are heterozygous, the greater will be the chance of any crossing-over leading to effective recombination, unbalance, variability release and selective response. This is why the hybrid line shows greater response to selection, correlated with change in all its tested chromosomes, than does any of the *yw* lines. An inter-stock cross is likely to have more heterozygous polygenes than a line developed from one of the parental stocks.

It would seem likely, however, that, as the *yw* selection lines were not only propagated exclusively by brother-sister mating but also rigorously selected, homozygosis should set in early in the experiments. Actually, marked responses to selection were still obtained after eighteen or nineteen generations in some of these lines (Fig. 1). It has been concluded that these responses were not due to mutational variability, and so it is necessary to suppose that heterozygosis has persisted throughout the experiment. The line *yw* J affords some evidence on this point (Fig. 4). Back selection was begun at *S* 8. It was immediately effective, even though continuation of the former type of selection was ineffective in the same material. So flies with genetically low chaeta numbers must have been segregating out, though there was no corresponding segregation in the high direction. This clearly implies dominance of the polygenes controlling chaeta production.

Dominance, however, is not sufficient in itself to account for the results, for it does not explain why heterozygosity was present after so many generations of brother-sister mating. This is most easily accounted for by assuming that heterozygous flies had a higher average chaeta number than homozygotes, i.e. showed heterosis in the direction of selection. Granted dominance of the polygenes this is not an unlikely state of affairs (see Mather, 1942*b*).

The back selection line in *yw* J was continued for some generations and then a new high selection was taken from it. This reselection was effective but did not succeed in reaching the chaeta number attained by the original selection line from which the back selection was made. The reselection bears much the same relation to the back selection as the latter does to the original selection. Its behaviour can be accounted for by dominance of the low polygene allelomorphs in the same way that the back-selection results required dominance of the high allelomorphs. This introduces the difficulty, however, that dominance is apparently in one direction in one case and in the opposite direction in another. No final answer can yet be given to this question, but Mather (1942*b*) has reviewed evidence suggesting that different polygenes may differ in the direction of their dominance. Whether this alone will be sufficient to account for the behaviour of back-selection lines cannot yet be decided. The postulation of interaction between polygenes should certainly be adequate for this purpose, but further investigations are necessary before this subject can profitably be discussed in more detail.

Whatever the detailed behaviour of the individual polygenes may prove to be, it is, however, clear that the phenotypic stability of meristic characters hides genetic variability sufficient to permit great advances with selection. The nature of the response of such characters to selection is governed by the organization of the balanced polygenic combinations by means of which this potential variability is stored.

5. SUMMARY

The number of scutellar chaetae in *Drosophila melanogaster* is normally four. Very rarely flies, usually females, are observed to have five chaetae. Starting with such aberrant flies, selection was practised for increased chaeta number in lines derived from the *yw* stock and from a hybrid material of $B \times yw$. All lines were maintained by brother-sister matings. The selection curves showed short periods of rapid response and long periods of near stability.

The various *yw* lines fell into a limited number of classes according to their response to selection. Within a class the lines behaved either identically or nearly so. Sometimes a response would occur at slightly different times in two like lines, but even when this happened, the magnitude of the response was constant. Lines in different classes gave different response curves. The hybrid line was unlike any of the *yw* lines and responded much more to selection.

Tests showed that each response in the various lines could be attributed to changes in a particular chromosome or chromosomes. Like *yw* lines showed changes of the same magnitude in the chromosomes. In the *yw* material the *X* chromosome never changed and chromosome III in some lines only, but chromosome II responded always. The *X* was not tested in the hybrid line, but both autosomes were found to show large responses.

These results show that genetic variability for chaeta number was present as differences between balanced polygenic combinations in the original material. Phenotypic stability was combined with genotypic variability. The response of any line to selection was conditioned by the organization of the combinations which it carried and hence was characteristic. The limited number of classes into which the *yw* lines fell was determined by the limited number of different combinations present in the *yw* stock.

Back selection and reselection in one *yw* line afforded evidence that polygenes show dominance, possibly some in the direction of high and others in the direction of low manifestation. Polygenic interaction may also be necessary to explain these results.

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