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Canalization Of Scutellar Bristles In Pyd And Pyd H Populations Of Drosophila Melanogaster.

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CANALIZATION OF SCUTELLAR BRISTLES IN

PYD AND PYD H POPULATIONS OF DROSOPHILA MELANOGASTER

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By

Rita Kathleen Bryson

B.S., The University of New Mexico, 1971

THESIS

Submitted in Partial Fulfillment of the
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ABSTRACT OF THESIS

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ABSTRACT

In most wild-type populations of Drosophila melanogaster the number of scutellar bristles is almost constant at four in spite of environmental variations and genetic differences among individuals. The mutant genes pyd and h disrupt this developmental canalization by adding extra bristles to the scutellum.

A common genetic background was provided for homozygous pyd and pyd h genotypes, forming two base stocks. These stocks possessed a greater mean number of scutellar bristles, variance, and sensitivity to three different temperatures (18 C, 21 C, and 28 C) than the wild-type stock from which their background genotype was obtained. From each base stock a high and a low selection line and an unselected control line were derived. Selection for scutellar bristles was suspended after ten generations.

In general, the response to selection, realized heritability, variance, and temperature sensitivity were greater in the high lines and lower in the low lines than in their respective control lines. These results supported an initial hypothesis that pyd is a mutant allele of a structural gene controlled by regulator genes and that its modifiers are not controlled. However, the results did not rule out the possibility that the wild allele of pyd is a regulator gene. The response to selection in probits, which measure an underlying variable, and the realized heritability estimates were no greater in pyd h lines than in pyd lines in most cases, indicating no more genetic variability was revealed by the addition of h to pyd. Either the two genes interrupt the same metabolic pathway or the development of scutellar bristles is modified by polygenes that are not locus-specific. But the combination

of pyd and h was probably more susceptible to environmental influences than pyd alone.

Dorsocentral bristles, also canalized at four, were scored along with all counts of scutellar bristles. The responses to selection and changes in variance and temperature sensitivity for dorsocentral bristles were similar to these measures for scutellar bristles. It was concluded that the two bristle systems share some developmental pathways.

In the F_1 and F_2 generations of crosses between the pyd high and low lines and between the pyd h high and low lines, most means were lower than the midparent expectations, and the means of reciprocal crosses were different. These facts indicated that at least part of the selection advance was due to genes with non-additive effects. It was hypothesized that a sex-linked suppressor that affected both bristle types was present in the pyd and pyd h low lines.

Selection for number of dorsocentral and scutellar bristles also altered their size, shape, and distribution.

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INTRODUCTION

Taxonomic distinctions are based on those characteristics that tend to be constant within a taxon and that vary between taxa. The development of these characters is regulated so that the same phenotype results almost all the time, even in the presence of environmental fluctuations and genetic variability. This mechanism ensures the development of optimal phenotypes even under suboptimal conditions. Waddington (1942) first termed this developmental canalization.

If a character is not canalized, phenotypic differences occur among the members of a wild-type population of a species due to isoalleles of major genes and to segregation of polygenes, or genes with small individual effects. Variations may also be caused by such environmental factors as temperature, light, and crowding, so that the population displays a continuous range of phenotypes for that characteristic. The level of expression of the character in any one individual is dependent upon the interaction of genetic and environmental factors during development. However, the development of canalized characters is buffered against these variations so that, within a certain range, differences in genetic make-up and in the environment are not reflected phenotypically. The distribution of phenotypes in the population is truncated, with most of the individuals falling into one phenotypic class.

The number of bristles on the scutellum of Drosophila melanogaster is canalized at four in wild-type populations. There are two anterior and two posterior bristles, slightly curved, which occur at fixed positions on the scutellum. Ninety-five per cent or more of wild-type flies have this pattern (Fraser, 1963). Figure 1 is a dorsal view of the thorax of a wild-type fly.

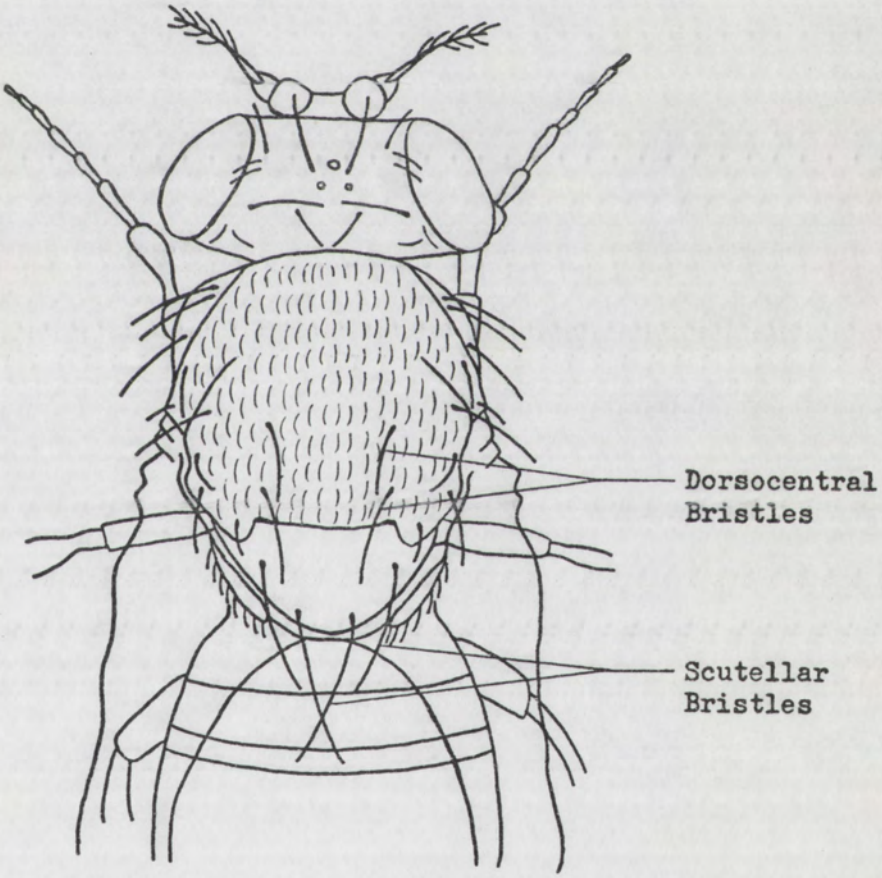


FIGURE 1. Dorsal view of the thorax of Drosophila melanogaster.

Hidden genetic differences among the members of a population can be exposed under conditions of stress. The underlying variations are exhibited phenotypically in individuals having more or fewer bristles than the standard number of four.

There are three major means by which normal canalized development can be disrupted. The first of these is long continued selection of rare individuals with extra or missing bristles. Selection for extra scutellar bristles in wild-type populations has been studied by Fraser (1963), Latter (1964, 1966, 1970), Fraser et al. (1965), and Sheldon (1968). Lines were developed with means much greater than four and with a large amount of variability around the means.

Environmental stress is a second factor that can disrupt normal canalized development. Sheldon (1968) and Pennycuik and Fraser (1964) found that the relative frequencies of anterior and posterior bristles of flies grown on a food medium fortified with yeast differ from the corresponding values obtained for flies grown on standard media. The effects of different thermal treatments have been studied by Ives (1939), Pennycuik and Fraser (1964), Fraser, Erway, and Brenton (1968), and Sheldon (1968). Although temperature can alter the mean number of scutellar bristles in wild-type populations, the changes are small compared to those in mutant populations. In general, the development of canalized characters is resistant to environmental influences. For example, the posterior crossvein is another species characteristic of D. melanogaster. Waddington (1953) has shown that extreme temperature shocks during early development are necessary to disrupt canalization and thereby produce breaks in the vein.

Mutation of a major gene involved in bristle development is a third

way normal canalized development can be disrupted. The sex-linked recessive gene scute (sc) reduces the number of bristles at many bristle sites, including scutellar bristles. In sc populations there is a marked increase in phenotypic variance over the wild type, and sc males have a lower mean number of bristles than females. Rendel (1959) selected for increased numbers of scutellar bristles in lines segregating for sc. Each generation sc males (sc/Y) that had the highest bristle counts were mated to heterozygous females (sc^+/sc). This selection procedure maintained four genotypes in the population: sc/Y, sc^+/Y, sc/sc, and sc^+/sc. Rendel found that the effectiveness of selection and the sex dimorphism decreased as the population mean approached four. Increasing numbers of the sc/Y and sc/sc flies were accumulating in the four-bristle class while none with five bristles appeared. At the same time, the mean of the wild-type flies (sc^+/Y and sc^+/sc) did not change significantly from four during the selection procedure. After 15 generations of selection, some sc^+/Y and sc^+/sc flies with five and six bristles began to appear. By probit transformation of the data, Rendel obtained estimates of the amount of genetic change, or change in the amount of an underlying variable, that produced the changes in mean bristle number. He found that it took approximately the same amount of genetic change to go from two to three, three to four, or five to six bristles. But to go from four to five bristles required eight times as much genetic change.

Rendel (1962) termed the variable underlying the development of scutellar bristles "Make." In a later work (Rendel, 1967) the concept of Make was expanded to include all genetic and environmental influences that interact to produce the phenotype. Make is, therefore, the resultant

of all forces contributing to the development of scutellar bristles. Make may be contributed to by major or minor genes, pH, time, temperature, and many other factors. Thus, the study of the relationship between the phenotype and those factors, some of which are unknown, that bring about the development of the phenotype is greatly simplified. If Make is plotted against the possible phenotypes of an uncanalized character, a straight line results. There is a direct relationship between the underlying variable and phenotypic expression. A graph of Make against the possible phenotypes of a canalized character is sigmoidal. There is a region, called the canalized plateau or zone, within which Make may change without producing corresponding changes in the phenotype. Figure 2 (redrawn from Rendel, 1967) is a graph of mean scutellar bristle number against Make and was based on data from several different stocks and genotypes.

Rendel, Sheldon, and Finlay (1965) extended this hypothesis, and some of their main conclusions were as follows. The developmental system of scutellar bristles is regulated through control of the major gene at the sc locus. The control of major gene activity by a set of regulatory genes is exercised to fix the level of the total product of the developing system--major gene, polygenic background, and environment. The means of unselected sc populations are lower than those of wild-type populations because sc is a less-effective structural gene than its wild allele. Scutellar bristles are not canalized in unselected sc populations because the level of Make for most individuals is too low to come under the influence of the regulatory genes. Minor genes, the source of the underlying genetic variability, are not controlled. As the mean increases above four in selected populations (sc or wild-type) and is moved farther

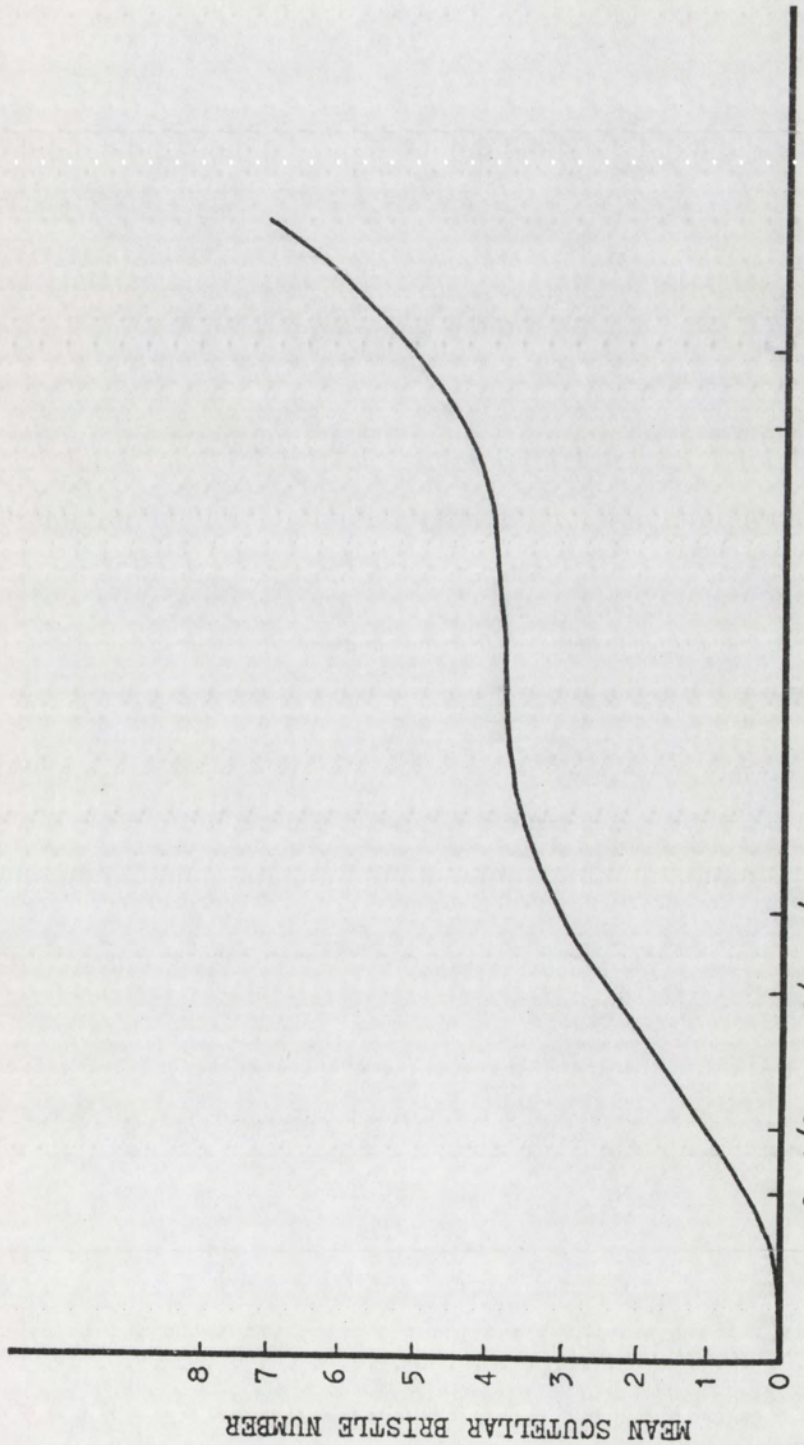


FIGURE 2. Mean scutellar bristle number plotted against Make.

from the canalized zone, the variance increases as major gene activity exceeds the limit of the regulatory system, and minor gene activity becomes more effective and is expressed. Thus canalization decreases as the mean bristle number increases.

Other investigators have studied the canalization of scutellar bristles and have drawn conclusions that differ from those of Rendel and his colleagues. Fraser et al. (1965) selected for increased numbers of scutellar bristles in wild-type stocks and found heterogeneous results between different selection lines and between generations within any one given line. Fraser (1965) made crosses between these lines and found some dominance relations and a complex pattern of interactions. Whereas selection in the presence of sc produces a correlated response in wild-type flies (Rendel, 1959; Fraser, 1966), selection in the presence of the wild allele of sc does not produce a correlated response in sc flies in the same population (Fraser and Green, 1964). From these experiments Fraser concluded that there are at least two multigenic systems operating to determine the number of scutellar bristles. One operates in the presence of the sc allele; the other operates in the presence of the wild allele. Further studies showed that three of Fraser's (1965) selection lines were homozygous for an autosomal recessive factor that markedly increases the number of scutellar, dorsocentral, and vertical bristles. Miller and Fraser (1968) termed this factor extra-verticals (x-vert). Substitution of sc for sc^+ in x-vert lines resulted in the suppression of x-vert and its modifiers (termed β-modifiers), but did not affect the modifiers of sc (termed α-modifiers). Additional experiments (Fraser, 1967) showed that the α system is suppressed in sc^+/sc^+; x-vert/x-vert genotypes and enhanced in sc/sc; $x\text{-}vert^+/x\text{-}vert^+$ and

sc/sc; x-vert/x-vert genotypes. The β system is enhanced in sc^+/sc^+; x-vert/x-vert genotypes and suppressed in sc/sc; $x\text{-}vert^+/x\text{-}vert^+$ and sc/sc; x-vert/x-vert genotypes. Several other mutant genes have been studied in relation to these two systems and a model of interactions worked out (Fraser, 1971). Figure 3 diagrams the suppression and expression relationships. Crowded conditions in cultures suppresses x-vert (Fraser, Erway, and Brenton, 1968), as does the mutant gene Scutoid (Sco). Sco is an autosomal dominant that behaves similarly to sc. By suppressing sc, the suppressor of Hairy wing ($su(Hw)^2$) partially removes the suppression of x-vert by sc.

Still other hypotheses besides the two major ones described have been advanced to explain canalization of scutellar bristles (Robertson, 1965; Latter, 1970). Because Rendel's methods and ideas are the most widely accepted, they were used as the basis of this investigation. According to Rendel, the mutation of a major gene affecting the number of scutellar bristles shifts the mean of the population out of the canalized range, so that the effects of segregating minor genes and of the environment are revealed. However, Rendel worked with sc, which decreases the mean number of bristles. Scute is the only mutant gene affecting scutellar bristles that has been studied extensively. No mutant genes that increase the number of scutellar bristles have been studied in relation to Rendel's model of canalization. It is possible that a major gene of this type would be a structural gene regulated in a similar manner as sc. If this were true, the primary difference between this gene and sc is that it would shift the population mean out of the canalized zone in the opposite direction. Segregation of minor genes, which would not be controlled, would be revealed in an increased population variance.

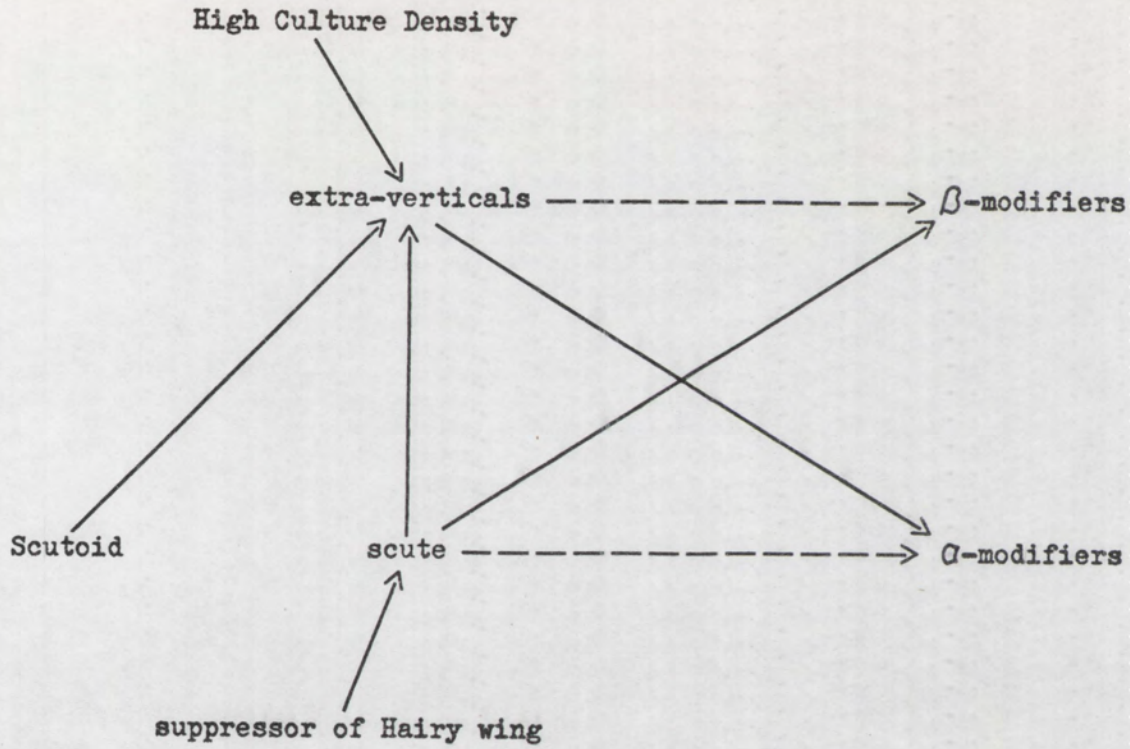


FIGURE 3. Fraser's model of canalization of scutellar bristles involving two systems of modifiers.

Selection for increased and decreased numbers of scutellar bristles should then be effective. One might expect the selection response and sex dimorphism to decrease as the mean approached four in a low selection line. Selection for increased numbers of scutellar bristles should be more effective according to Rendel's model. As the mean increased and the major gene activity exceeded the bounds of the control mechanism, more of the minor gene activity would be expressed phenotypically and could be acted upon by selection.

Resistance to environmental fluctuations and low population variance are characteristics of a canalized system, presumably because the level of Make for most of the individuals in the population does not override the controlling genotype. Sensitivity to temperature variation has been used as a criterion for canalization (Rendel and Sheldon, 1960; Rendel, Sheldon, and Finlay, 1966; Lee and Fraser, 1969). A low selection line that contains a mutant gene increasing the number of scutellar bristles should be less sensitive to different temperatures than a high selection line. This is because the level of Make for more individuals would be low enough to be brought under the influence of the regulatory system. Differences in the level of Make at different temperatures would not be reflected phenotypically as readily in a population with a mean close to four than in a population with a higher mean. For similar reasons, the variance of a high selection line should be greater than that of a low selection line. More of the major gene effect would override the control mechanism, and the activity of a larger number of minor genes would be expressed.

One might expect that if one mutant gene shifts the development of scutellar bristles out of the range that is canalized, then two mutant

genes would shift development even farther from the canalized zone. The assumption is that the two mutant genes act in the same direction, both either increasing or decreasing scutellar bristle number. The reason for this is that different mutant genes are likely to have separate systems of modifiers, which may or may not overlap (Haskell, 1943; Cocks, 1954; Kindred, 1967). One mutant gene would expose one set of modifiers and a second mutant gene would expose additional modifiers. Therefore, a doubly mutant population should be less canalized--have a higher variance and greater sensitivity to temperature variation--than a singly mutant population because, according to Rendel, modifying genes are not controlled. This population should also show a greater response to selection for both increased and decreased numbers of scutellar bristles. It would possess a greater amount of genetic variability expressed as phenotypic variability on which selection could act.

The present study is an attempt to test the validity of the foregoing hypotheses. There are numerous genes that affect bristle number in D. melanogaster. It was necessary to find two mutants, both of which increase the mean number of scutellar bristles over the normal number of four. The mutant genes polychaetoid and hairy meet this criterion. Homozygous polychaetoid populations and populations homozygous for both polychaetoid and hairy were studied in relation to the effects of these genes on canalization of scutellar bristles. The effects were measured by the response to selection for increased and decreased numbers of bristles, sensitivity to different temperatures, and population variance.

Many bristle mutants disturb the development of several different types of bristles. As mentioned earlier, mutant genes of the sc series remove bristles from other sites in addition to reducing the number of

scutellar bristles. Rendel (1963) and Young and Sheldon (1965) studied the correlation between scutellar bristles and another bristle type in populations segregating for sc. Polychaetoid also increases the mean number of other types of bristles besides scutellar bristles. Selection for scutellar bristles may modify the development of another bristle system that is similarly affected by polychaetoid.

Wild-type flies have four dorsocentral bristles on the dorsal side of the thorax, anterior to the scutellum (see Figure 1). There are two anterior and two posterior bristles, which occur at fixed positions. The effects of selection for scutellar bristles on dorsocentral bristles would depend on any changes in the total amount of bristle-making resources common to both and on any changes in the proportion allotted to each bristle system (Rendel, 1963). A change in total resources would generate a positive correlation; a change in the distribution of resources would generate a negative one. The net correlation would be the result of the combination of these two tendencies. Selection for scutellar bristles might also change the degree of canalization--temperature sensitivity and variance--of dorsocentral bristles. The particular outcome would depend upon how much of the background genotype or modifiers of scutellar bristles and the regulatory genes of scutellar bristles affect dorsocentral bristles. In the present study the effects of selection for scutellar bristles on dorsocentral bristle development in the polychaetoid and polychaetoid-hairy populations were measured by the changes in mean dorsocentral bristle number, sensitivity to different temperatures, and population variance.

MATERIALS AND METHODS

All flies were grown on a standard cornmeal-agar medium. Except for the temperature studies at 18 C and 28 C, experiments were conducted at 21±1 C in a room provided with continuous light.

Two stocks, one homozygous for the mutant gene polychaetoid and the other homozygous for hairy, were obtained from the California Institute of Technology. Polychaetoid (pyd) is an autosomal recessive (3-39.0; Lindsley and Grell, 1968) that adds extra bristles to most normal bristle locations. Its maximum effect is on dorsocentral bristles, but scutellar, presutural, humeral, and other bristles are also affected (Neel, 1940). The mutant gene hairy (h), also an autosomal recessive (3-26.5; Lindsley and Grell, 1968), adds hairs where they are not normally present--along the wing veins, on the scutellum, pleurae, and on top of the head (Neel, 1941). It slightly increases the mean scutellar bristle number and occasionally adds extra bristles to other normal bristle locations. These two genes interact super-additively to increase greatly the mean number of scutellar bristles in populations homozygous for both h and pyd (Neel, 1941). Figure 4 shows diagrams of the thoraces of representative h, pyd, and pyd h flies.

A stock carrying both h and pyd in the homozygous condition was synthesized. Reciprocal crosses were made of the h and pyd stocks, and the offspring were allowed to interbreed. Seven genotypes, including four crossover categories, were possible in the resulting progeny. Of these, approximately 50 males and 50 females phenotypically pyd were taken and crossed. These included pyd h^+/pyd h^+ and the indistinguishable pyd h^+/pyd h crossover genotypes. Double homozygotes were extracted from the offspring. Figure 5 diagrams the synthesis of the pyd h stock.

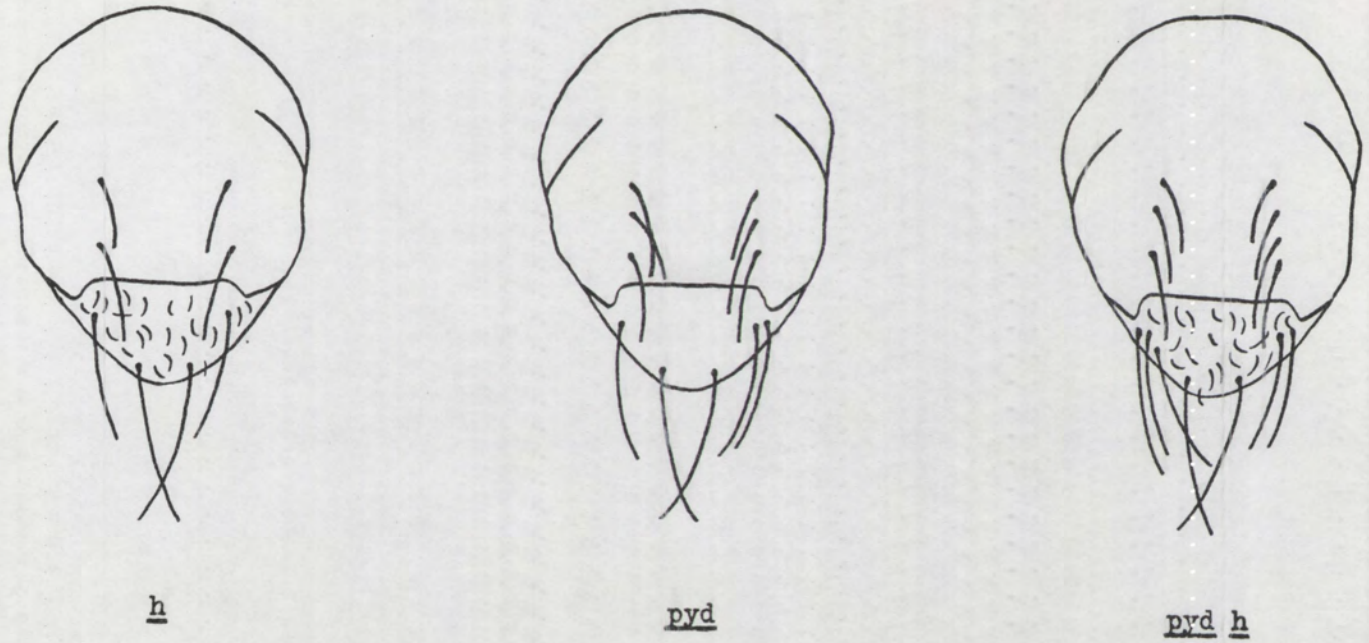


FIGURE 4. Thoraces of representative h, pyd, and pyd h flies.

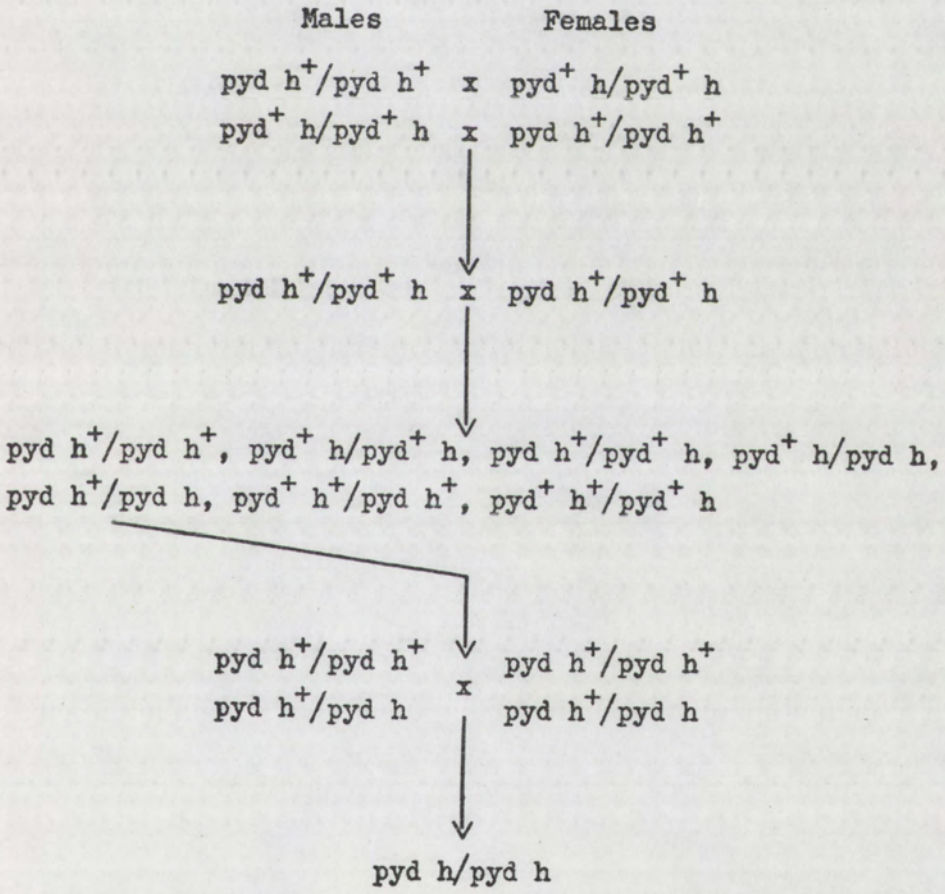


FIGURE 5. Synthesis of the pyd h stock.

In a selection experiment it is essential to use stocks that have a high amount of genetic variability. Otherwise, selection is ineffective because most of the phenotypic variance is due to environmental influences that are not heritable. Stocks such as pyd and h were expected to have low amounts of genetic variability because they had been maintained in a laboratory for many generations, with transfers of relatively few flies each generation.

To alleviate this problem, it was necessary to provide a genetically heterogeneous background for the homozygous pyd and pyd h genotypes. A highly heterozygous wild stock was synthesized by mixing four different wild-type laboratory stocks. Three of these, Canton-S, Lausanne-S, and Urbana-S, were standard wild-type laboratory stocks. The fourth, Albuquerque Wild, was a stock derived from a sample of flies collected in Albuquerque, New Mexico, in 1964 and since maintained in the laboratory. Each wild-type stock may have had a high degree of homozygosity and, therefore, a low amount of genetic variability, but the stocks should have differed with respect to the alleles that were homozygous. A mixture of the four stocks would thus result in a stock possessing a high amount of genetic variability.

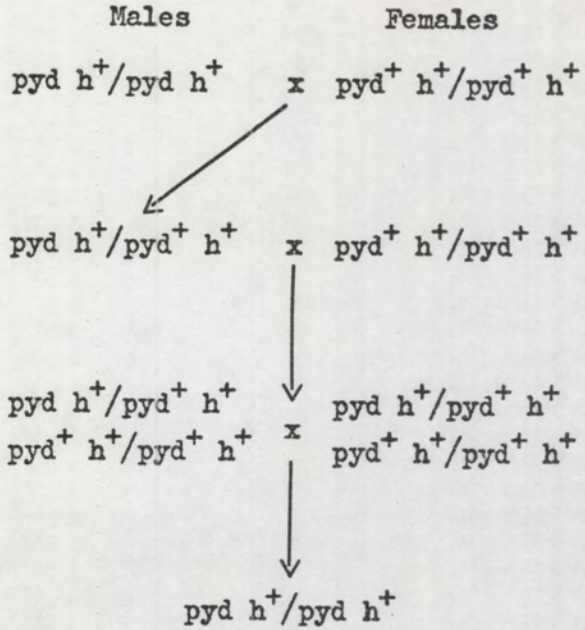
The homozygous pyd and pyd h genotypes were placed against the heterozygous background from the synthesized wild-type stock. Twenty wild-type females were crossed to 10 mutant males in each of 10 one-half pint culture bottles. Twenty male offspring were backcrossed to 20 females from the wild-type stock, again in each of 10 bottles. The progeny of the backcross were allowed to interbreed in large numbers. From the next generation 40 male and 40 female homozygous mutant flies were extracted to form pyd and pyd h populations with approximately

75 percent of their background genotypes from the wild-type stock of mixed origin. This procedure is diagrammed in Figure 6.

One technical difficulty encountered was distinguishing pyd h^+/pyd h^+ and pyd h/pyd h genotypes from pyd^+ h^+/pyd h^+ and pyd^+ h/pyd h genotypes, respectively. Heterozygous pyd flies occasionally show extra bristles (Neel, 1941). To ensure that both the pyd and pyd h stocks were homozygous for pyd, only flies with strongly expressed phenotypes were chosen.

The pyd and pyd h stocks with the mixed-wild background will be referred to as the base stocks. Two selection lines, high and low, and one unselected control line were derived from each of the two base stocks. The following selection procedure was applied. From each base stock 50 males and 50 virgin females were scored for dorsocentral and scutellar bristle number. The 10 males and 10 females with the highest scutellar counts were chosen as parents of the first generation of the high selection lines. The 10 pairs with the lowest scutellar counts were selected as parents of the first generation of the low selection lines. Ten males and 10 females were taken at random from the two base stocks as parents of the first generation of the two control lines. In each succeeding generation, 50 males and 50 virgin females from the high and low lines were scored, and the 10 highest or 10 lowest of each sex were selected as parents of the next generation. The two control lines were not sampled, but 10 males and 10 females were chosen randomly each generation as parents of the next generation. After 10 generations selection was discontinued, and the control lines, in addition to the high and low lines, were scored for dorsocentral and scutellar bristles. Figure 7 outlines the selection procedure.

The tenth generation of the six resulting lines (pyd control, low,



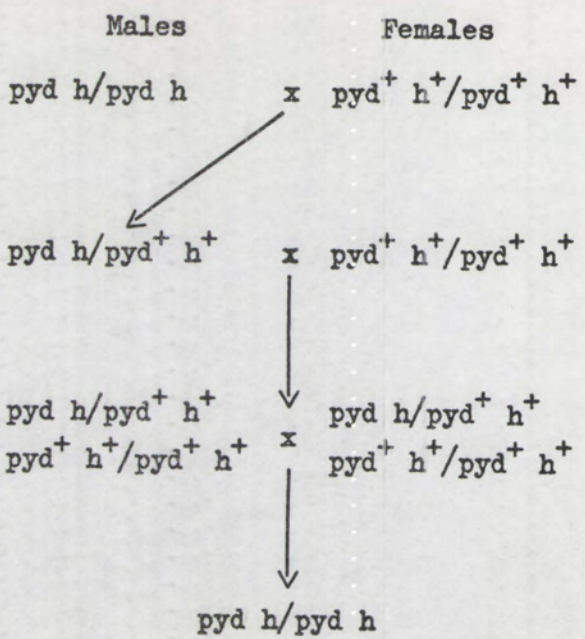
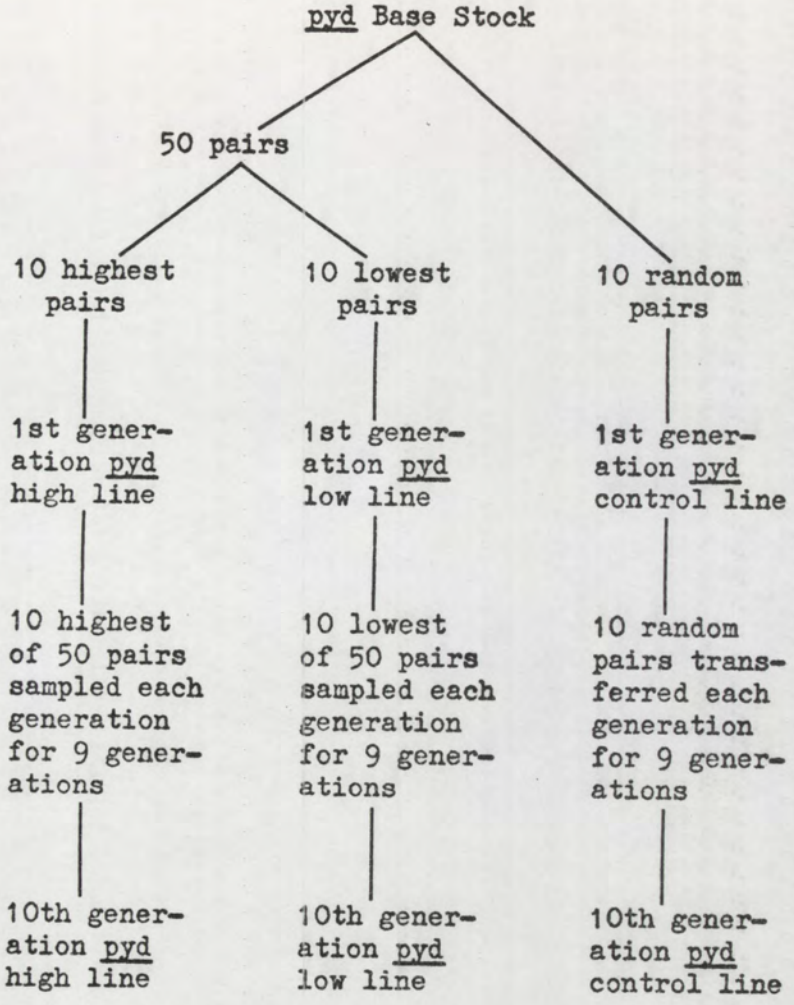


FIGURE 6. Procedure followed to place the homozygous pyd and pyd h genotypes against a common genetic background.



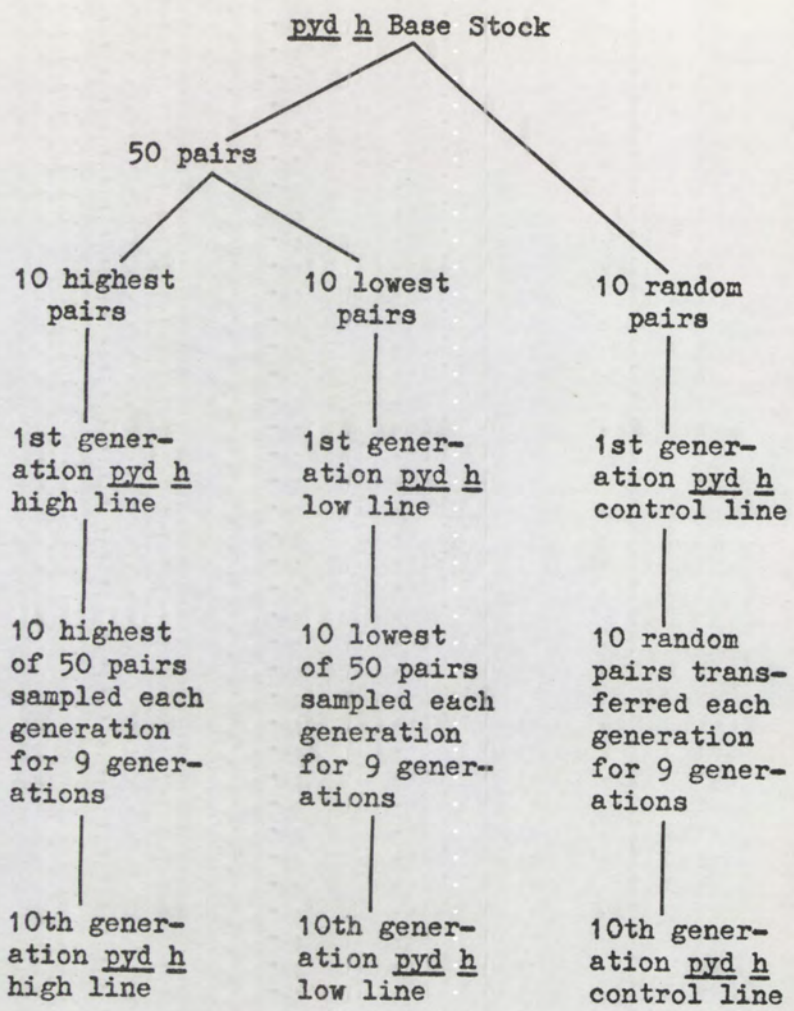


FIGURE 7. Selection procedure.

high; pyd h control, low, high) was tested for the effect of different temperatures on bristle development. The pyd and pyd h base stocks and the wild-type stock were tested soon after they were synthesized. Three temperatures were employed: 18 C, 21 C, and 28 C. Twenty pairs of flies from each line were placed into each of two one-half pint culture bottles per temperature. Fifty male and 50 female offspring from each bottle were scored for dorsocentral and scutellar bristles. Incubators provided with continuous light were used to maintain temperatures at 18±1 C and 28±1 C.

An estimate of the number of loci with additive effects contributing to the development of dorsocentral and scutellar bristles should reflect the amount of genetic variability in a population for these characters. One way to obtain a rough estimate of the number of loci, or effective factors, is from the following equation (Falconer, 1960):

$$n = \frac{R^2}{8(\sigma_A^2)}$$

n is the number of factors; R equals the total range between the means of a high and a low selection line; σ_A^2 is the additive genetic variance in the original population. The additive genetic variance is estimated from the difference between the F_1 and F_2 phenotypic variances from a cross of the two selection lines. This formula is based on the comparison of the total range produced by selection with the amount of genetic variance in the original population. It is assumed that the genes at all the loci involved have approximately equal additive effects. A small number of genes will then produce less total response to selection than a large number. If only a few loci contribute to the development of a

character, the genetic variance will be large because a greater proportion of the population will have the extreme genotypes.

In order to obtain estimates of the number of factors, reciprocal crosses were made between the tenth generation pyd high and low lines and between the tenth generation pyd h high and low lines. For each reciprocal cross 10 pairs of flies were mated in each of five one-half pint culture bottles. The F_1 generations were mated in like manner to form the F_2 generations. One hundred males and 100 females were scored for dorsocentral and scutellar bristles in the F_1 and F_2 generations of each original reciprocal cross.

RESULTS

Response to Selection

Selection resulted in some unexpected changes in the development of the flies and in the conformation of scutellar bristles. As selection proceeded, the generation time of the high lines increased, and fewer flies developed each generation. Extra bristles are usually positioned near one of the four normal sites (Neel, 1940); but in the pyd and pyd h high lines in later generations, one or two bristles on some flies occurred so far out of place that they were in the middle of the scutellum. Some of the bristles were curved upwards at sharp angles and were much thicker than those of the unselected control lines. Figure 8 shows some examples of scutellar bristle patterns in the four selection lines. The generation time of the low lines did not change appreciably. Some of the bristles on many pyd low line flies were short and thin. In later generations, flies with only three scutellar bristles began to appear. From the seventh generation on, flies in the pyd h low line appeared regularly with some of their scutellar bristles extremely small and twisted. In general, selection in the low lines brought about a reduction in bristle size, whereas in the high lines bristle size increased.

Selection was successful in both increasing and decreasing the mean number of scutellar bristles in the pyd and pyd h lines. The generation means of the four selection lines and two control lines and their responses to selection are given in Table 1 and summarized in Figures 9 and 10. It can be seen that the control line means did not change much from the original means in the base stocks (generation 0). For any given line, the mean number of bristles of males was always less than that of

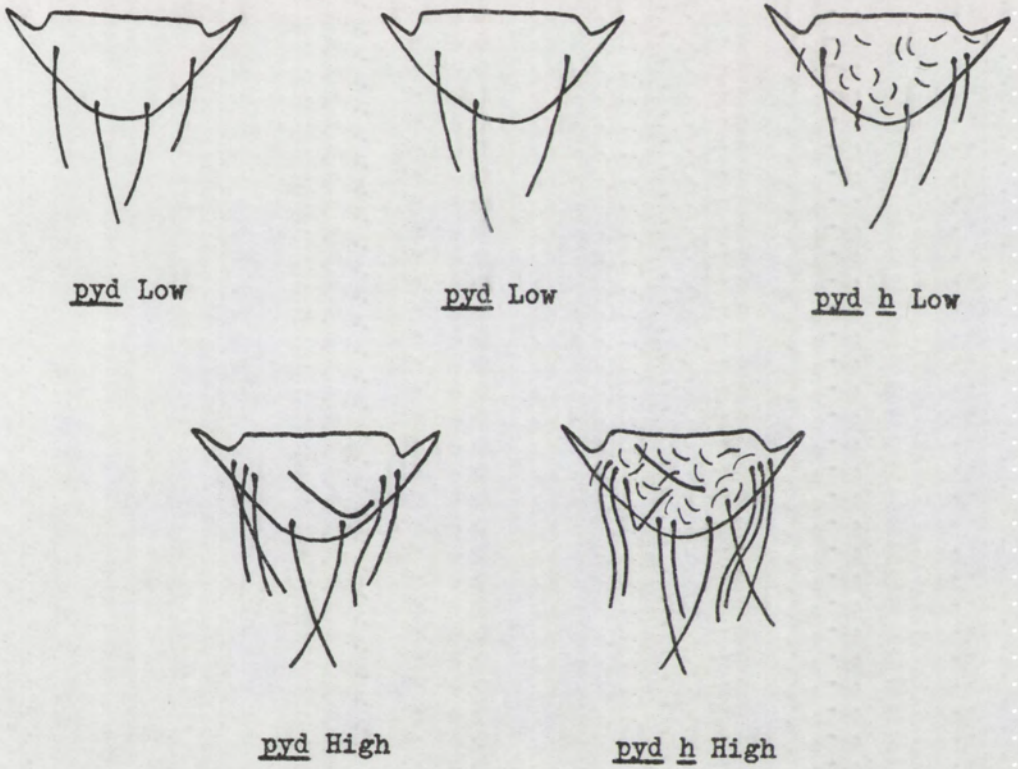


FIGURE 8. Examples of scutellar bristle patterns found in the four selection lines.

TABLE 1. Mean scutellar bristle number in the control, low, and high lines and the responses to selection

Generation Number	Low Males	Low Females	High Males	High Females	Control Males	Control Females
			pyd Lines			
0	4.78	5.42	4.78	5.42	4.78	5.42
1	4.70	5.54	5.14	6.06	-	-
2	4.50	5.10	5.26	6.18	-	-
3	4.90	5.30	5.50	6.32	-	-
4	4.48	5.16	5.62	6.60	-	-
5	4.42	4.98	5.80	7.04	-	-
6	4.34	5.06	6.18	6.96	-	-
7	4.24	4.64	6.52	7.52	-	-
8	4.36	4.68	6.72	7.80	-	-
9	4.10	4.38	7.08	8.12	-	-
10	4.18	4.40	7.52	9.14	4.72	5.18
Response	-0.60	-1.02	+2.74	+3.72	-0.06	-0.24
			pyd h Lines			
0	6.82	7.88	6.82	7.88	6.82	7.88
1	6.50	7.48	7.46	8.52	-	-
2	6.58	7.46	7.40	9.24	-	-
3	6.28	7.02	8.04	9.58	-	-
4	5.66	6.64	8.32	9.90	-	-
5	5.80	6.28	8.70	10.34	-	-
6	5.98	6.28	9.02	10.76	-	-
7	5.66	6.32	9.28	10.56	-	-
8	5.56	6.14	9.06	10.82	-	-
9	5.76	6.20	9.64	11.44	-	-
10	5.40	6.02	10.40	11.94	6.56	7.66
Response	-1.42	-1.86	+3.58	+4.06	-0.26	-0.22

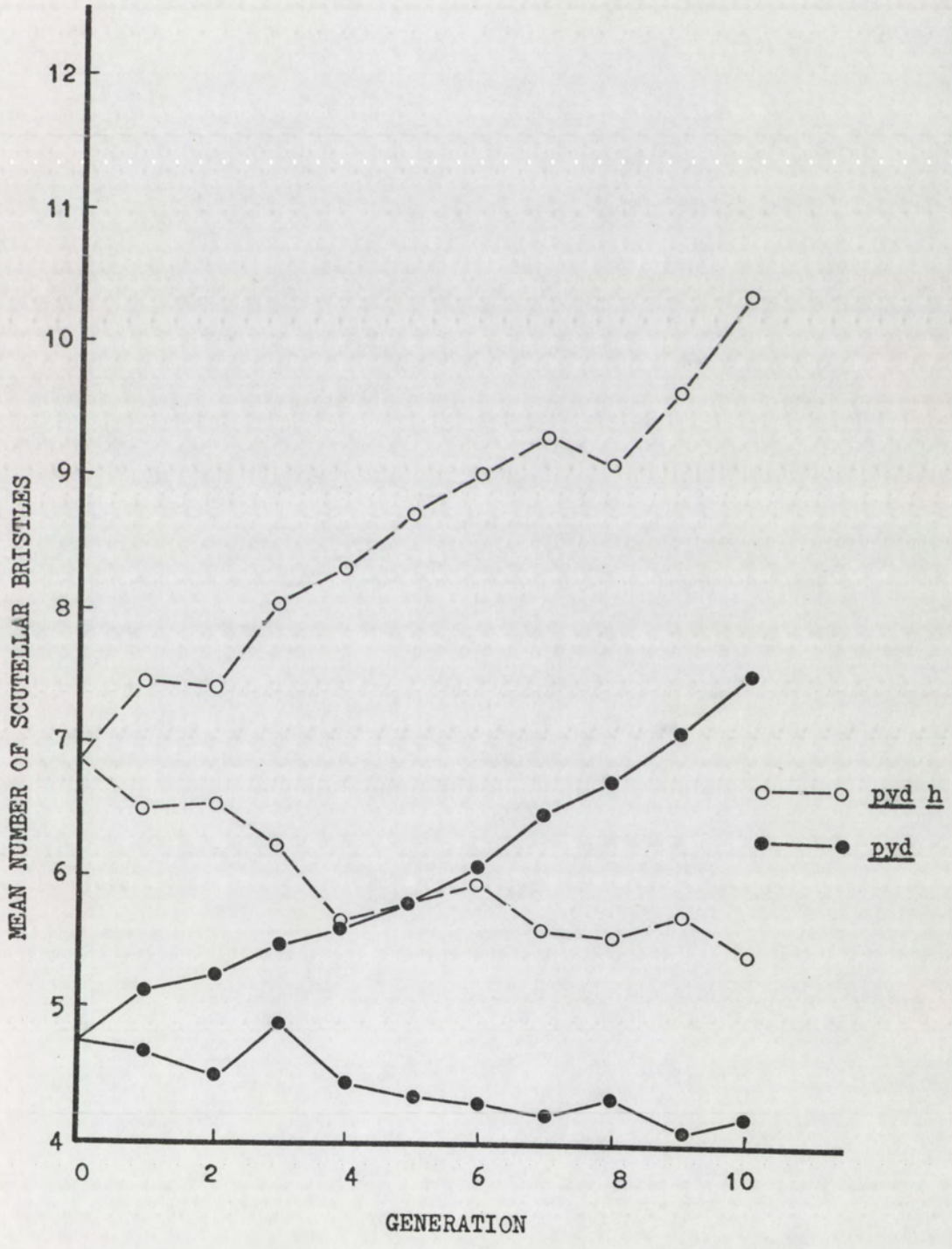


FIGURE 9. Mean number of scutellar bristles plotted against generation of selection for high and low line males.

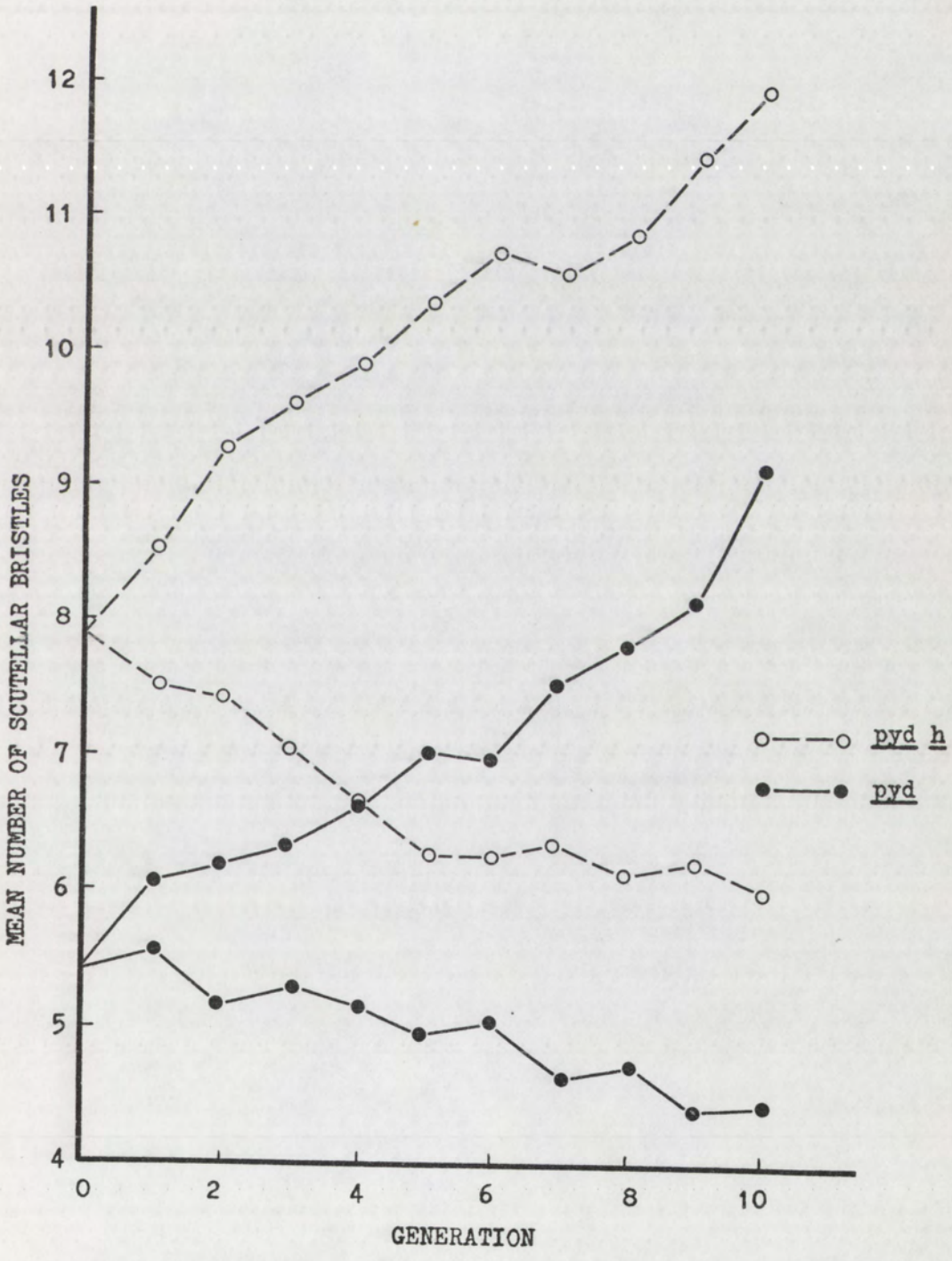


FIGURE 10. Mean number of scutellar bristles plotted against generation of selection for high and low line females.

females, as is the case in sc and selected wild-type populations. This sex dimorphism decreased in the low lines and increased in the high lines. The responses to selection were also greater in the pyd and pyd h high lines than in their respective low lines. Low pyd males and females changed by 0.60 and 1.02 bristles respectively, high pyd males and females by 2.74 and 3.72. Low pyd h males and females changed 1.42 and 1.86 bristles, high pyd h males and females 3.58 and 4.06. Selection response in the pyd h high and low lines was greater than in the pyd high and low lines. The divergences of the pyd h high and low males and females were, respectively, 5.00 and 5.92; the divergences of pyd high and low males and females were 3.34 and 4.74. A test of significance was performed to see if the separation of the pyd h high and low lines was significantly different from the separation of the pyd lines. The mean difference between individuals of the tenth generation pyd h high and low samples was calculated. The same was done for the pyd tenth generation samples. The t-tests of the difference between the means showed that the pyd h mean differences were significantly greater than the pyd mean differences for both males and females. The t-values are given in Table 2.

Next, the realized heritability was calculated for the four selection lines. Heritability is the proportion of the phenotypic variance that is due to genetic differences among individuals. Quantitative characters in a population with a large amount of genetic variability have a relatively high degree of heritability. Therefore, a greater selection gain is possible in a population with a high heritability coefficient. One way to estimate heritability is from the effectiveness of selection. Heritability measured from a selection experiment in this manner is termed the realized heritability. The mean scutellar bristle

TABLE 2. Divergence of the high and low lines

Scutellar Bristles	Males	Females
pyd	3.34	4.74
pyd h	5.00	5.92
t-value	4.990**	2.806**
Dorsocentral Bristles	**Males**	**Females**
pyd	1.98	2.66
pyd h	3.14	3.90
t-value	2.740**	2.618*

*P < 0.05

**P < 0.01

number each generation (response to selection) was plotted against the cumulated selection differential (see Figures 11 and 12). The selection differential is the difference between the mean of the selected parents and the mean of the entire sample from which they were taken. Realized heritability was estimated from the regression of response on the cumulated selection differential. This method of estimating heritability and others may be found in Falconer (1960).

The realized heritability estimates of the four selection lines are given in Table 3. The values for each sex and of the same type of selection line (high or low) were tested for significant differences with t-tests. The heritability of pyd h was found to be significantly greater than that of pyd only in low line females. Considering high line females, the heritability of pyd h was significantly less than that of pyd. Heritability realized by selection was greater in the high than in the low lines, except for pyd h females. The differences were obvious, and, therefore, no t-tests were run on the high-low pairs.

As mentioned previously, realized heritability is a measure of the effectiveness of selection. The realized heritability estimates have shown that selection was equally effective in pyd and pyd h for males, less in pyd h than pyd for high females, and less in pyd than pyd h for low females. However, Figures 9 and 10 and the tests of significance performed on the divergences of the high and low lines indicated that selection was more effective in pyd h than pyd in all cases. This apparent contradiction can be partially resolved by use of the probit transformation.

Differences in the response to selection between different genotypes can be eliminated when measured in standard deviation units, or probits

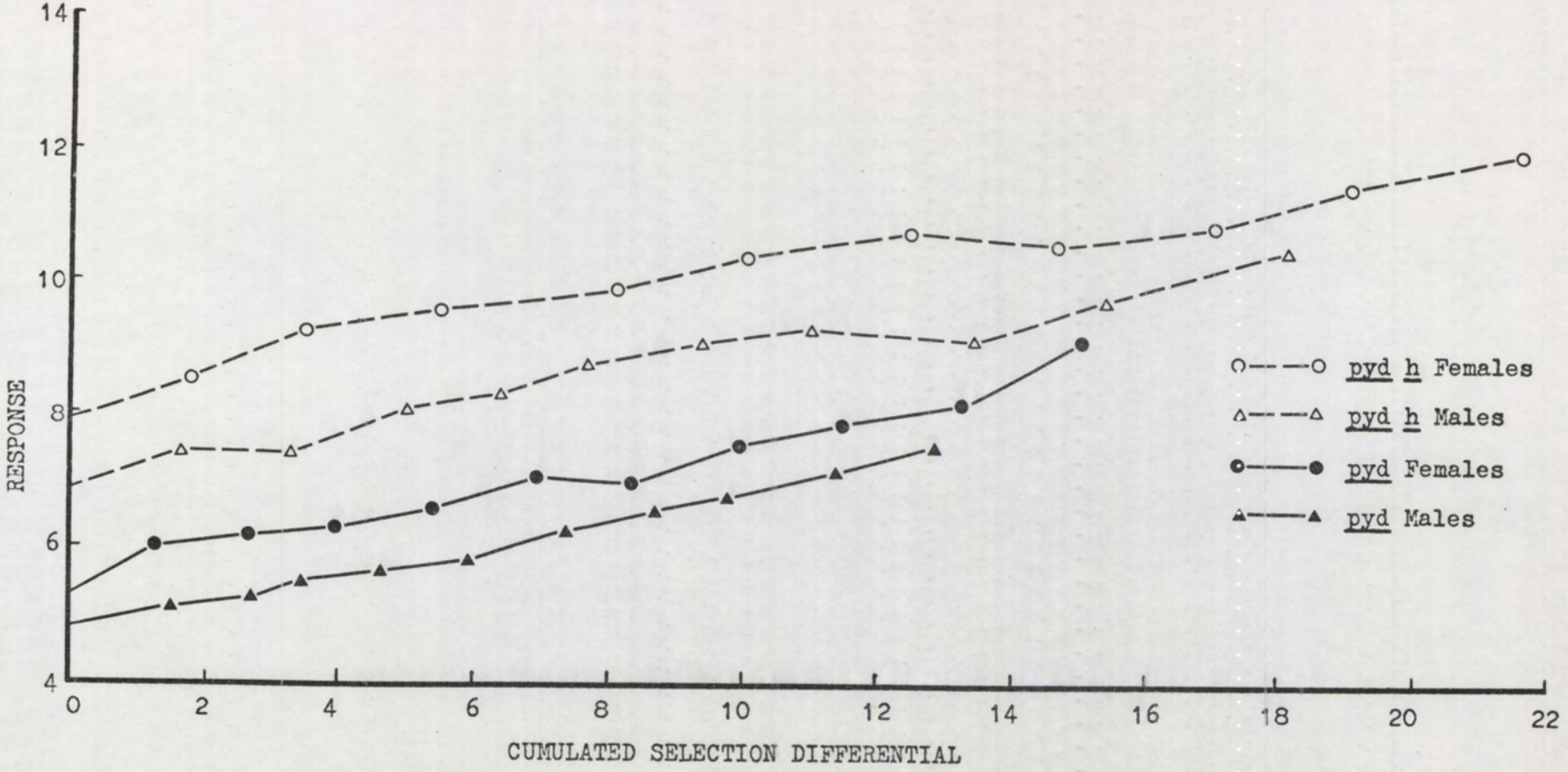


FIGURE 11. Response to selection plotted against cumulated selection differential for the high lines.

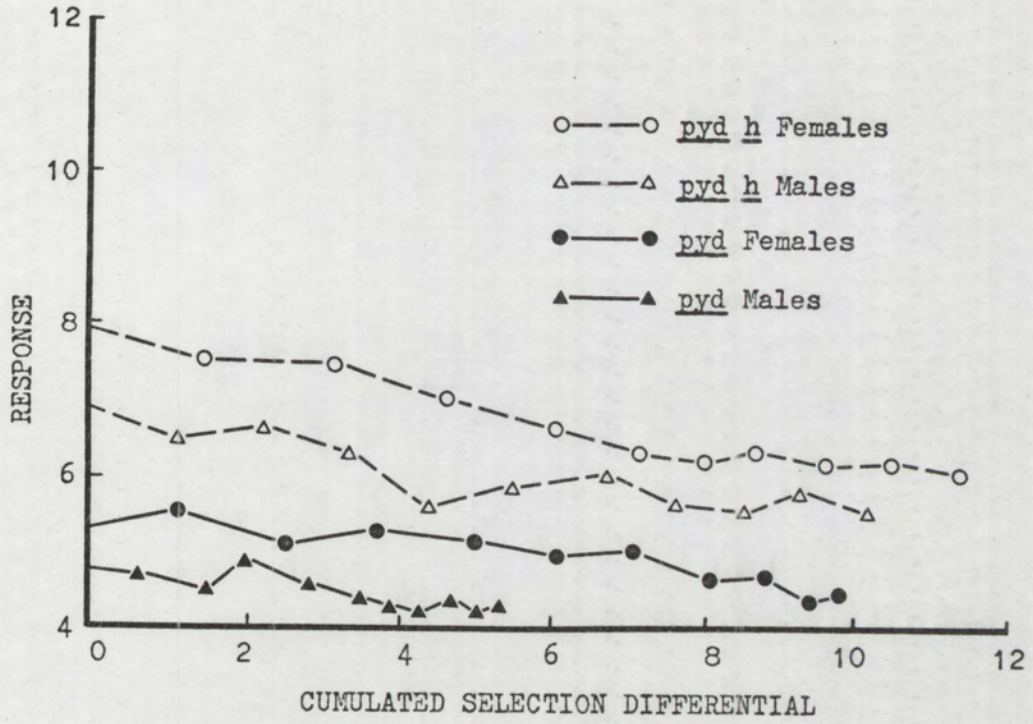


FIGURE 12. Response to selection plotted against cumulated selection differential for the low lines.

TABLE 3. Realized heritability estimates for scutellar bristles

Low Lines	Males	Females
pyd	0.124	0.108
pyd h	0.124	0.169
t-value	0.000	3.041**
High Lines	**Males**	**Females**
pyd	0.206	0.211
pyd h	0.180	0.162
t-value	1.527	2.336*

*P < 0.05

**P < 0.01

(Rendel, 1959). It is assumed that the underlying variable of scutellar bristle development, or Make in Rendel's terminology, is normally distributed. The phenotype is not normally distributed because it is canalized. The probit transformation converts a distribution of phenotypes into a normal distribution of the underlying variable. Figure 13 is a diagram of how the probit transformation changes the distribution of a population (redrawn from Rendel, 1962). The percentage of the population cut off by each class boundary is transformed into a probit value. A probit is a standard deviation unit to which five has been added to make all values positive. The differences between class boundaries on the left-hand scale in Figure 13 are represented as differences in Make in standard deviation units on the right-hand scale.

A few preliminary calculations were necessary before the responses to selection in standard deviations of Make could be determined. First, the number of individuals in each bristle class was pooled over generation (from the base stock through the tenth generation) for the four lines separately. This gave sample sizes of 550 for males and for females (50 per generation). The percentage of every sample falling into each bristle class was calculated, and a probit value from a table of probits (Fisher and Yates, 1963) was assigned to each class boundary, or threshold. The distance in standard deviations spanned by any one bristle class was calculated from the difference between its upper and lower boundaries. The class widths of the four lines are given in Table 4. It can be seen that, except for the six-bristle class of the pyd h low line and the seven-bristle class of the pyd low line, the class widths did not differ appreciably among lines. Omitting these values, the class widths were averaged over sex and line. The overall mean class

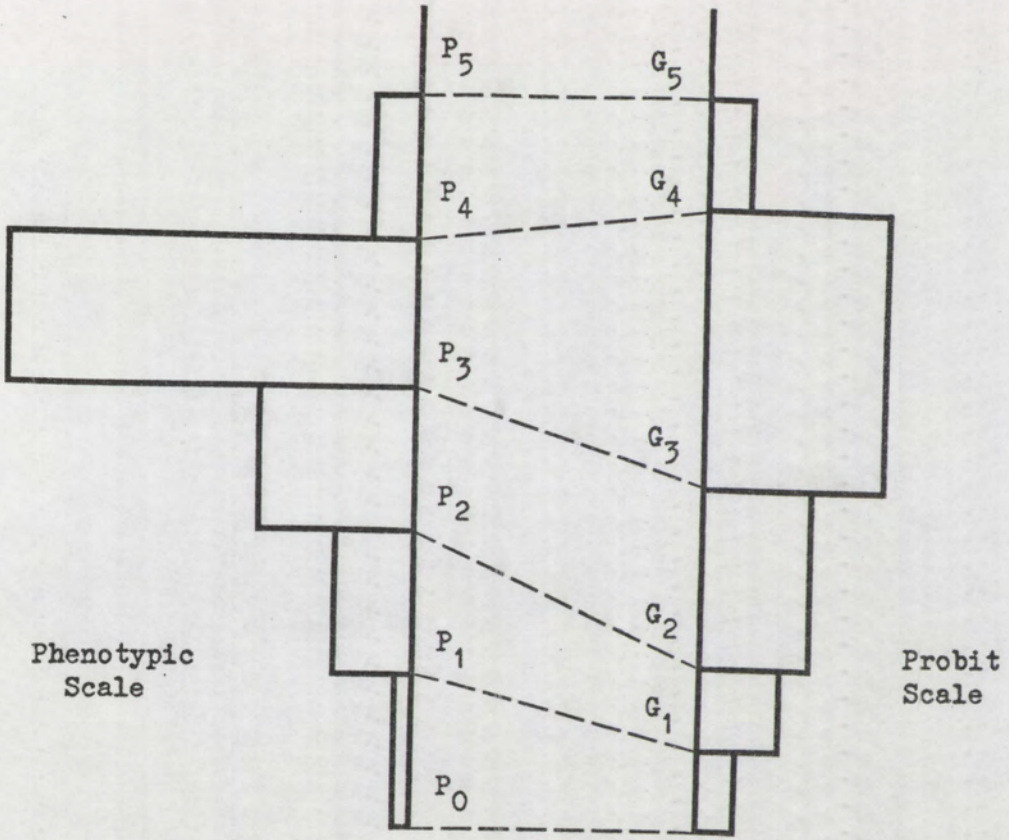


FIGURE 13. The distribution of a population, skewed on the phenotypic scale with equal class intervals (P), and almost normal on the probit scale, where the class intervals are measured in standard deviations of Make (G).

TABLE 4. Estimates of the widths of scutellar bristle classes in probits and the level of Make at each threshold

		Bristle Class										
Line	Sex	4	5	6	7	8	9	10	11	12	13	14
pyd Low	M	2.68	1.09	0.88								
	F		1.10	0.91	1.30							
pyd High	M		0.86	0.81	0.74	0.64	0.45	0.39				
	F		0.89	0.86	0.62	0.55	0.54	0.55				
pyd h Low	M		1.11	1.40	0.67	0.69	0.55					
	F		1.17	1.41	0.74	0.69	0.59					
pyd h High	M			1.02	0.70	0.65	0.62	0.49	0.60	0.31	0.39	0.24
	F				0.70	0.58	0.52	0.50	0.52	0.44	0.41	0.47
Mean Class Widths		2.68	1.04	0.90	0.70	0.63	0.54	0.48				

	Threshold							
	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11
Level of Make	0	2.68	3.72	4.62	5.32	5.95	6.49	6.97

widths tended to decrease with an increase in bristle number. The width of the four-bristle class was 2.68σ, the widest. The notation X/X in Table 4 denotes a particular class boundary. For example, 4/5 indicates the threshold or boundary between the four- and five-bristle classes. The 3/4 threshold was chosen as the zero point on the scale. The level of Make at any threshold above this is the sum of the class widths below it. For example, the amount of Make at the 6/7 threshold is 4.62σ, the sum of the four-, five-, and six-bristle class widths. These calculations were necessary to standardize over all four lines the level of Make at each threshold.

Next, the probit values at each threshold in the base stock (generation 0) and tenth generation samples were determined. The probits are given in Table 5. Because the width of the six-bristle class of the pyd h low line (1.40σ) was greater than that of the other lines, it was necessary to correct the probit value at the 6/7 threshold in the base stock and tenth generation of this line. If this correction had not been made, the pyd h low line could not have been compared with the other lines on the same scale (Rendel, 1967). The corrected probit values are ones that would have been obtained had the width of the six-bristle class been 0.90σ (the mean of this class for the other lines) instead of 1.40σ. There was no need to correct the 7/8 threshold of the pyd low line because the seven-bristle class did not occur in the base stock or tenth generation of this line.

Probits measure the distance in standard deviations between the mean of a distribution and a chosen cut off point (Rendel, 1967). Because five is added to all values, the mean lies at 5.00σ instead of zero. Once the distance between the mean and a particular class boundary

TABLE 5. Scutellar bristle probit values in generations 0 and 10 of the four selection lines

Line	Generation	Sex	Threshold 3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11
pyd	0	M		5.00	5.77	6.55				
		F		3.92	5.20	6.08				
pyd Low	10	M	2.95	5.92	7.05					
		F		5.47	6.55	7.05				
pyd High	10	M				4.23	5.05	5.99	6.55	6.75
		F				3.45	4.01	4.59	5.25	6.08
pyd h	0	M			3.59	4.49	5.46	6.24	6.44	
		F				4.01	4.80	5.47	6.08	
pyd h Low	10	M		3.82	5.00	5.90				
		F		2.95	4.01	4.91	6.04			
pyd h High	10	M					2.95	3.72	4.48	5.00
		F					2.95	3.59	3.92	4.36

was known, the mean of a sample with respect to that class boundary could be determined from Table 4. The mean in the base stock and in the tenth generation of each line was estimated from several class boundaries, and these numbers were averaged for more accuracy. The response to selection in standard deviation units for any given line was the difference between the mean Make in the base stock and the mean in the tenth generation. The estimates of mean level of Make and the responses to selection are given in Table 6.

An example may clarify the above method of calculation. The pyd h low line tenth generation males will be considered. From Table 5 the probit value at the 4/5 threshold was 3.82σ. This value indicated the mean was 1.18σ above the 4/5 threshold. From Table 4 the standardized amount of Make at the 4/5 threshold was 2.68σ. Adding 1.18σ to 2.68σ gave 3.86σ as the mean Make estimated from the 4/5 threshold. The probit value of 5.00σ at the 5/6 cut off indicated the mean was at the 5/6 threshold. From Table 4 the level of Make at the 5/6 threshold was 3.72σ. At the 6/7 cut off the probit value of 5.90σ indicated the mean was 0.90σ below the 6/7 threshold. Subtracting 0.90σ from 4.62σ, the standard amount of Make at the 6/7 threshold, gave 3.72σ. These three estimates, 3.86σ, 3.72σ, and 3.72σ, were averaged. The mean Make for the tenth generation pyd h low males was then 3.77σ. This number was subtracted from 4.98σ, the mean level of Make in the base stock, to give 1.21σ as the response to selection for males in this line.

Most of the responses to selection in standard deviations corresponded with the realized heritability estimates. The response of the high lines was greater than that of the low lines (see Table 6). There was very little difference in the response of pyd and pyd h males.

TABLE 6. Scutellar bristle Make in generations 0 and 10 of the four selection lines and the responses to selection in σ

			Threshold								
Line	Generation	Sex	3/4	4/5	5/6	6/7	7/8	8/9	9/10	10/11	Average Make
pyd	0	M		2.68	2.95	3.07					2.90
		F		3.76	3.52	3.54					3.61
pyd Low	10	M	2.05	1.76	1.67						1.83
		F		2.21	2.17	2.57					2.32
pyd High	10	M				5.39	5.27	4.96	4.94	5.22	5.16
		F				6.17	6.31	6.36	6.24	5.89	6.19
pyd h	0	M			5.13	5.13	4.86	4.71	5.05		4.98
		F				5.61	5.52	5.48	5.41		5.50
pyd h Low	10	M		3.86	3.72	3.72					3.77
		F		4.73	4.71	4.71	4.28				4.61
pyd h High	10	M					7.37	7.23	7.01	6.97	7.14
		F					7.37	7.36	7.57	7.61	7.48

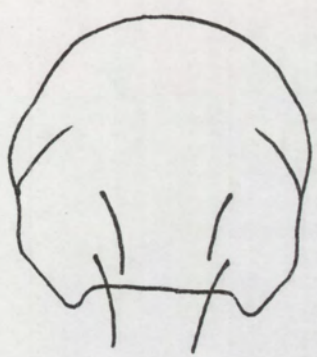
Response to Selection

Sex	pyd Low	pyd High	pyd h Low	pyd h High
M	1.07	2.26	1.21	2.16
F	1.29	2.58	0.89	1.98

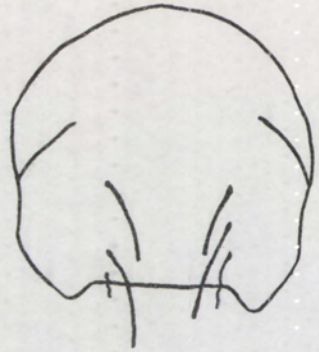
The response of pyd h high females, 1.98σ, was less than that of pyd high females, 2.58σ, as was expected from the realized heritability estimates. However, whereas the realized heritability of pyd h low females was greater than the estimate for pyd low females, the response to selection of pyd h low females, 0.89σ, was less than the response of pyd low females, 1.29σ. The probit transformation was thus able to correct for most, but not all, of the discrepancy between the response to selection in bristles and the realized heritability.

Selection for scutellar bristles produced similar changes in dorsocentral bristles. In the high lines there were many extra bristles, most of which appeared to be the result of hypertrophy of hairs normally found on the thorax. There were fewer extra dorsocentral bristles in the low lines. In the pyd h low line some of the bristles were extremely small and twisted, as were some of the scutellar bristles. Figure 14 shows a few examples of dorsocentral bristle patterns.

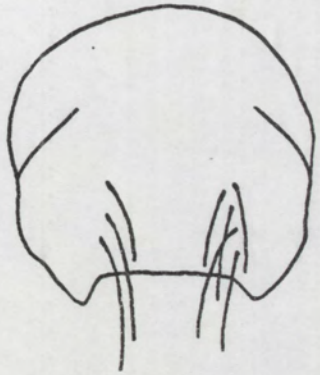
The generation means of dorsocentral bristles in the four selection lines and the responses to selection are given in Table 7 and summarized in Figures 15 and 16. It is interesting to note that the pyd h control line means after ten generations (males, 7.30; females, 9.28) were much higher than the original means in the pyd h base stock (males, 6.22; females, 7.46). Also, dorsocentral bristles of the pyd control line females decreased more than they did in the low line females. The response of the high lines was greater than the response of the low lines. Low pyd males and females changed by 0.20 and 0.48 bristles, high pyd males and females by 1.78 and 2.18 bristles. Low pyd h males and females changed 0.70 and 0.94 bristles, high pyd h males and females 2.44 and 2.96 bristles. The divergence of the pyd h high and low lines was



pyd Low



pyd h Low



pyd High

pyd h High

FIGURE 14. Examples of dorsocentral bristle patterns found in the four selection lines.

TABLE 7. Mean dorsocentral bristle number in the control, low, and high lines and the responses to selection

Generation Number	Low Males	Low Females	High Males	High Females	Control Males	Control Females
			pyd Lines			
0	5.90	7.04	5.90	7.04	5.90	7.04
1	6.38	7.06	6.34	7.54	-	-
2	5.74	7.00	6.30	7.06	-	-
3	6.52	7.26	6.42	7.20	-	-
4	6.32	7.18	6.50	7.48	-	-
5	6.48	7.26	6.32	7.22	-	-
6	6.24	7.12	6.60	7.52	-	-
7	6.86	7.72	6.50	7.42	-	-
8	6.34	7.20	7.56	8.56	-	-
9	5.98	6.84	7.00	8.32	-	-
10	5.70	6.56	7.68	9.22	5.84	6.40
Response	-0.20	-0.48	+1.78	+2.18	-0.06	-0.64
			pyd h Lines			
0	6.22	7.46	6.22	7.46	6.22	7.46
1	6.52	8.14	6.82	7.60	-	-
2	6.24	7.04	6.84	7.70	-	-
3	6.04	6.64	6.94	7.70	-	-
4	5.86	6.96	7.18	8.60	-	-
5	6.00	6.72	7.32	8.20	-	-
6	6.08	6.84	7.04	9.10	-	-
7	5.88	6.40	6.94	8.40	-	-
8	5.86	6.62	7.84	9.90	-	-
9	5.42	6.22	8.14	9.94	-	-
10	5.52	6.52	8.66	10.42	7.30	9.28
Response	-0.70	-0.94	+2.44	+2.96	+1.08	+1.82

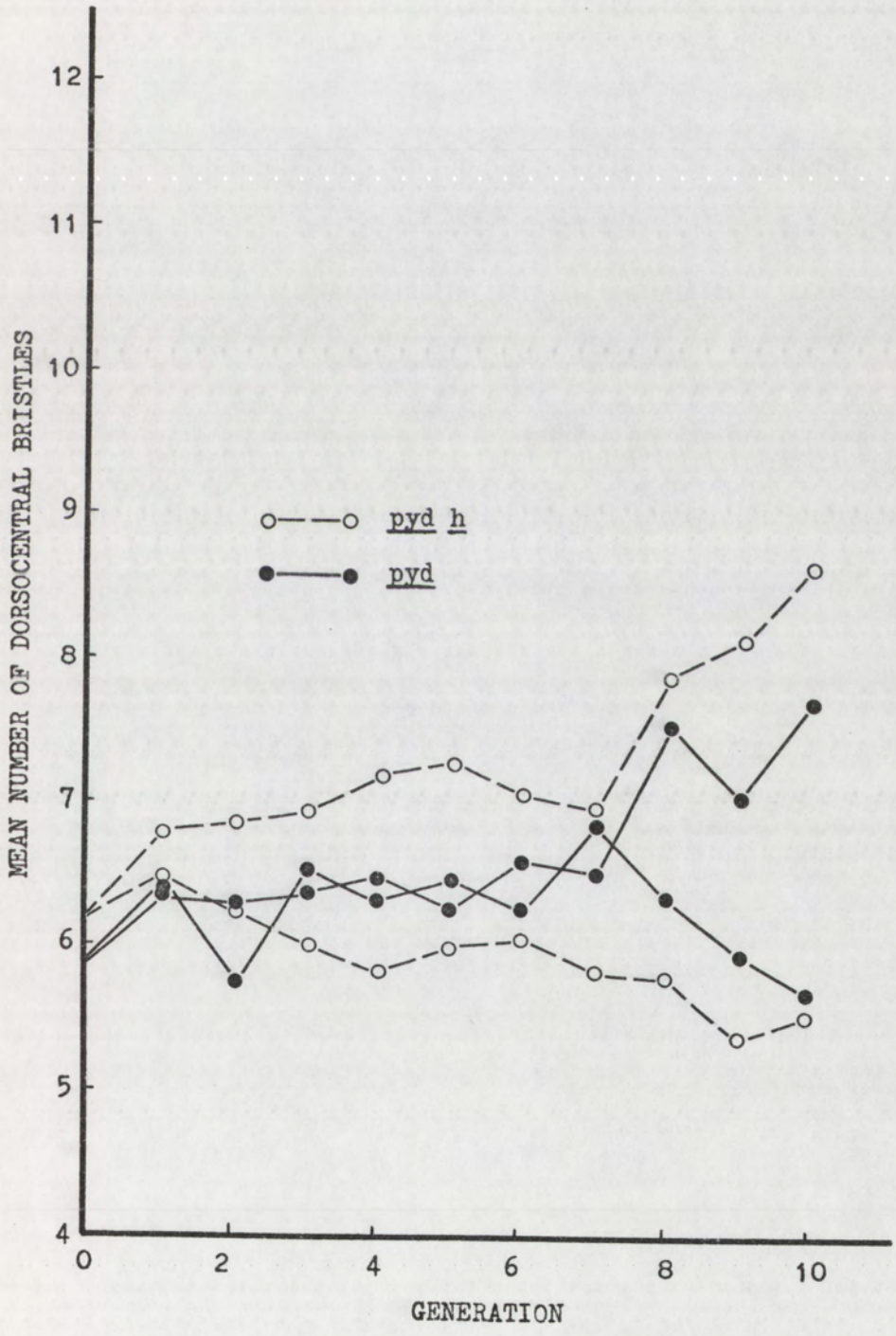


FIGURE 15. Mean number of dorsocentral bristles plotted against generation of selection for high and low line males.

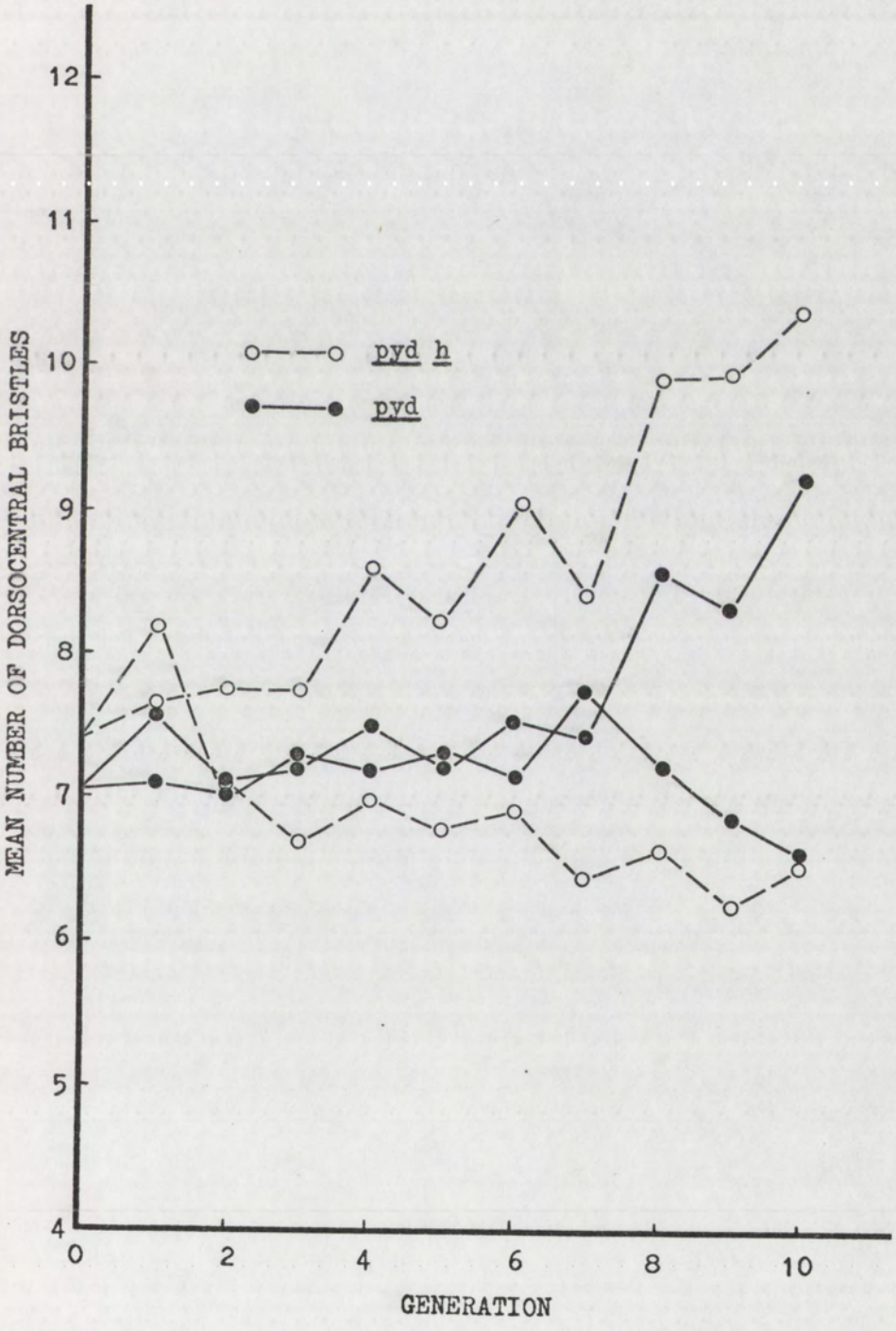


FIGURE 16. Mean number of dorsocentral bristles plotted against generation of selection for high and low line females.

significantly greater than the divergence of the pyd high and low lines, as was found for scutellar bristles (see Table 2). But the response of dorsocentral bristles was less than the response of scutellar bristles in all cases. In fact, the pyd high and low dorsocentrals did not diverge at all until the eighth generation of selection. The mean dorsocentral bristle number was always greater in females than in males, but the sex dimorphism decreased in the low lines and increased in the high lines.

The dorsocentral bristle data were transformed into probits in the same manner as was done for scutellar bristles. Table 8 gives the average amounts of dorsocentral Make in the base stocks and tenth generations and the responses to selection. The responses to selection in standard deviation units followed the pattern of response in bristles. High lines changed more than low lines, pyd h lines more than pyd lines. These results could not be compared to realized heritability because this parameter was not determined for dorsocentral bristles. Selection was not directly applied to dorsocentral bristles, and, therefore, no selection differential could be calculated.

There was a lack of correlation between dorsocentral and scutellar bristles in the base stocks. The correlation coefficients are given in Table 9. The pyd and pyd h control, low, and high lines were not significantly different from their respective base stocks in most cases. In general, correlation in the high lines was more positive than correlation in the low lines. However, the high and low coefficients were significantly different only in pyd females and pyd h males, where the low line values were negative.

Sensitivity to Different Temperatures

The samples of 50 flies that were taken from each of the two bottles

TABLE 8. Average dorsocentral bristle Make in generations 0 and 10 of the four selection lines and the responses to selection in σ

Line	Generation	Sex	Average Make
pyd	0	M	1.33
		F	2.24
pyd Low	10	M	1.05
		F	1.88
pyd High	10	M	2.61
		F	3.54
pyd h	0	M	1.50
		F	2.50
pyd h Low	10	M	0.90
		F	1.80
pyd h High	10	M	3.26
		F	4.14

Response to Selection

Sex	*pyd* Low	*pyd* High	*pyd h* Low	*pyd h* High
M	0.28	1.28	0.60	1.76
F	0.36	1.30	0.70	1.64

TABLE 9. Coefficients of correlation between dorsocentral and scutellar bristles

	pyd		pyd h	
Line	Males	Females	Males	Females
Base Stock	-0.021	0.057	0.276	0.178
Control	0.152	0.075	0.392	0.396
High	0.376	0.472	0.317	0.271
Low	0.284	-0.093	-0.155	0.065

at each temperature were pooled prior to calculating the mean bristle number. Plots of mean dorsocentral and scutellar bristle number against temperature are shown in Figures 17, 18, 19, and 20 for all lines. There was an inverse relationship between temperature and mean dorsocentral and scutellar bristle number in most lines.

Sensitivity to different temperatures was measured by the magnitude of the difference between the lowest and highest mean number of bristles at the three temperatures. For all lines, the means and the difference between the lowest mean and highest mean are given in Tables 10 and 11. It can be seen that temperature had very little effect on mean bristle number in the wild-type stock, and that placing the pyd and pyd h homozygous genotypes against the wild-type background greatly increased the temperature sensitivity. The response of scutellar bristles to different temperatures was not the same in the pyd and pyd h selection lines. Among pyd lines scutellar bristles were most sensitive in the high line, least in the low line, with the control line intermediate. But among pyd h lines, fluctuation of mean scutellar bristle number was greatest in the control line, least in the high line, with the low line intermediate. The sensitivity of the pyd h high line was much less than the sensitivity of the pyd high line, whereas the pyd control and low lines showed less response to temperature than the corresponding pyd h lines. In almost all lines scutellar bristles were not as sensitive to temperature as were dorsocentral bristles. Considering dorsocentral bristles, there appeared to be little difference between pyd and pyd h lines. For both genotypes the high lines exhibited the greatest sensitivity to different temperatures, the low lines the least, and the control lines intermediate.

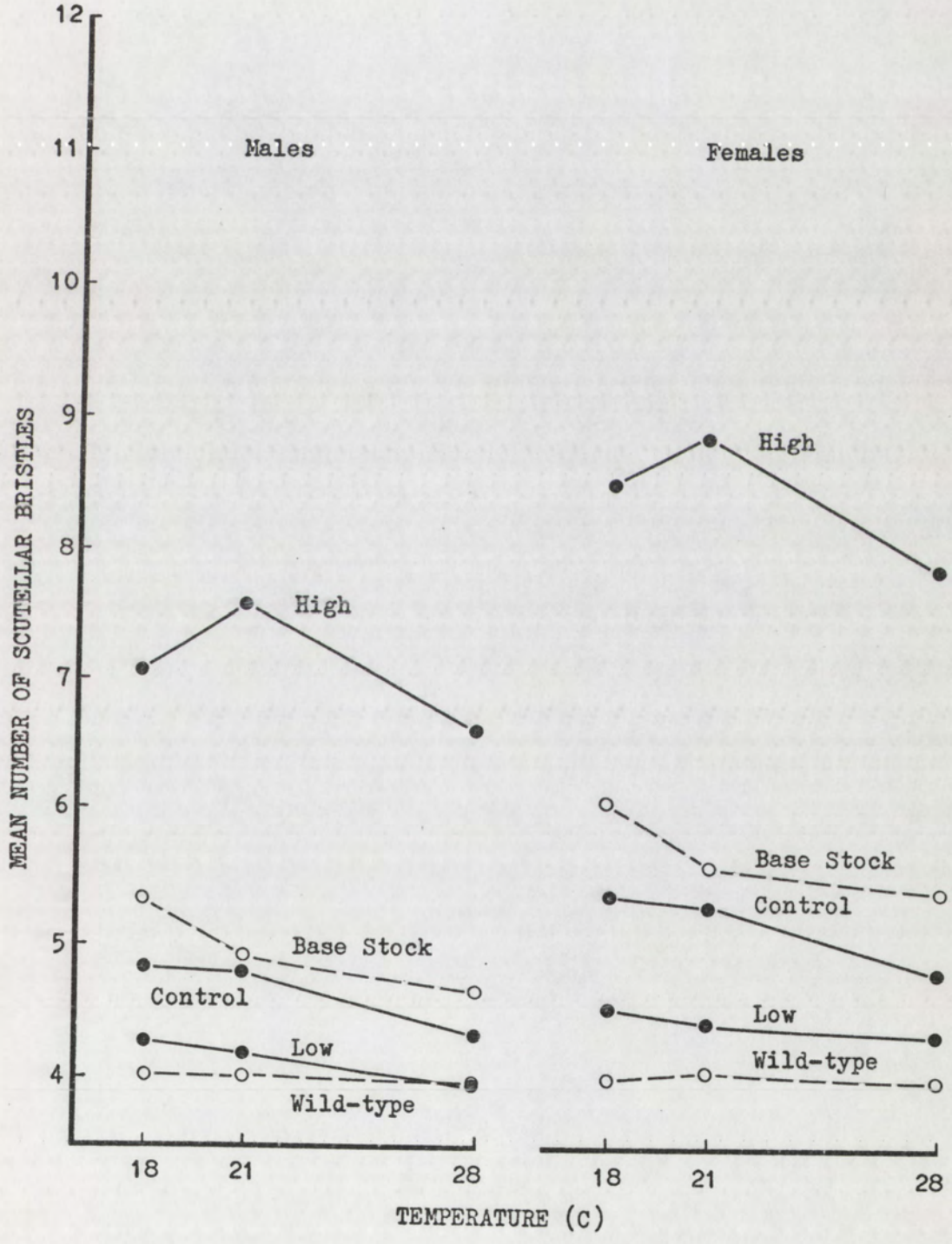


FIGURE 17. Mean number of scutellar bristles in the pyd lines and the wild-type stock plotted against temperature.

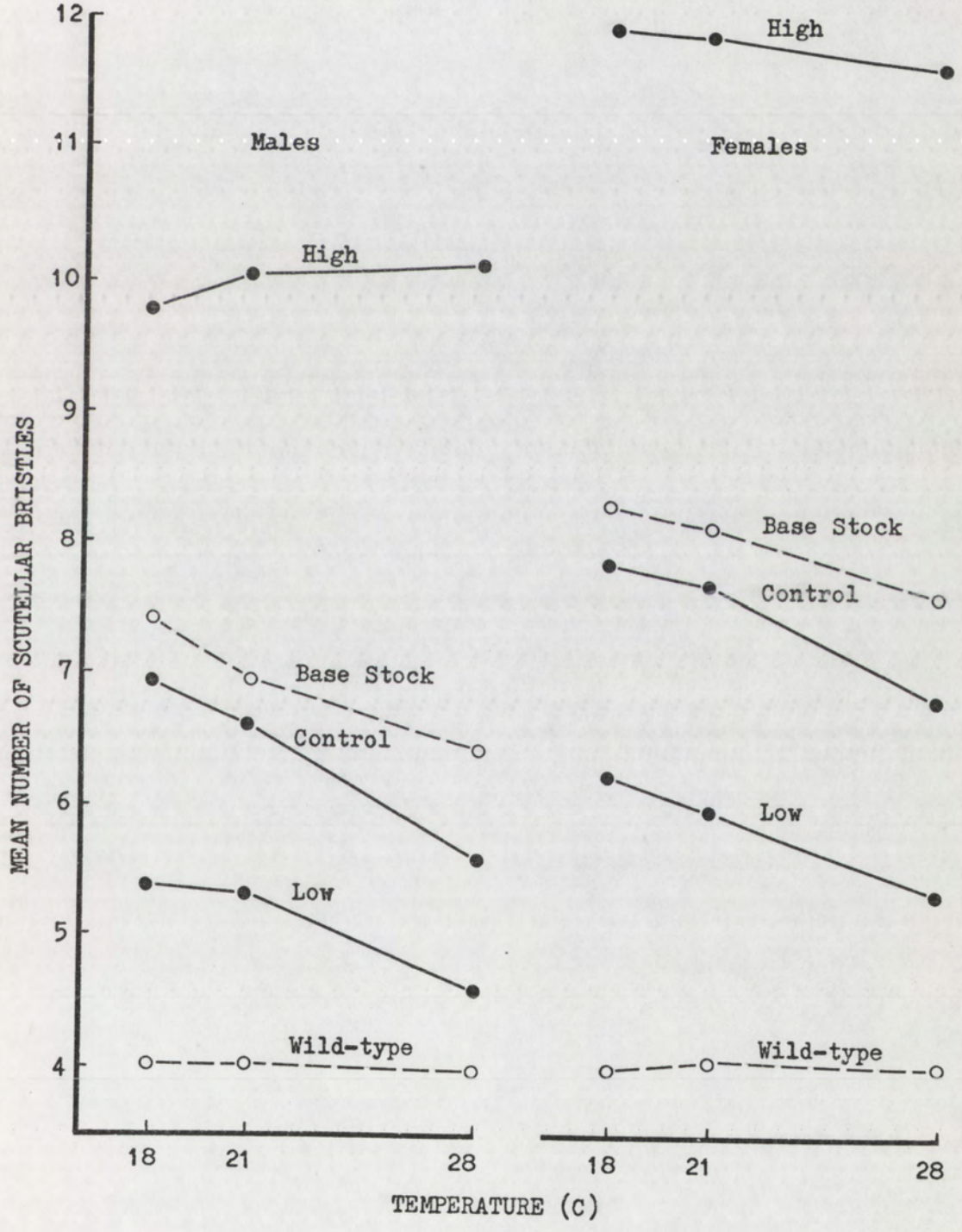


FIGURE 18. Mean number of scutellar bristles in the pyd h lines and the wild-type stock plotted against temperature.

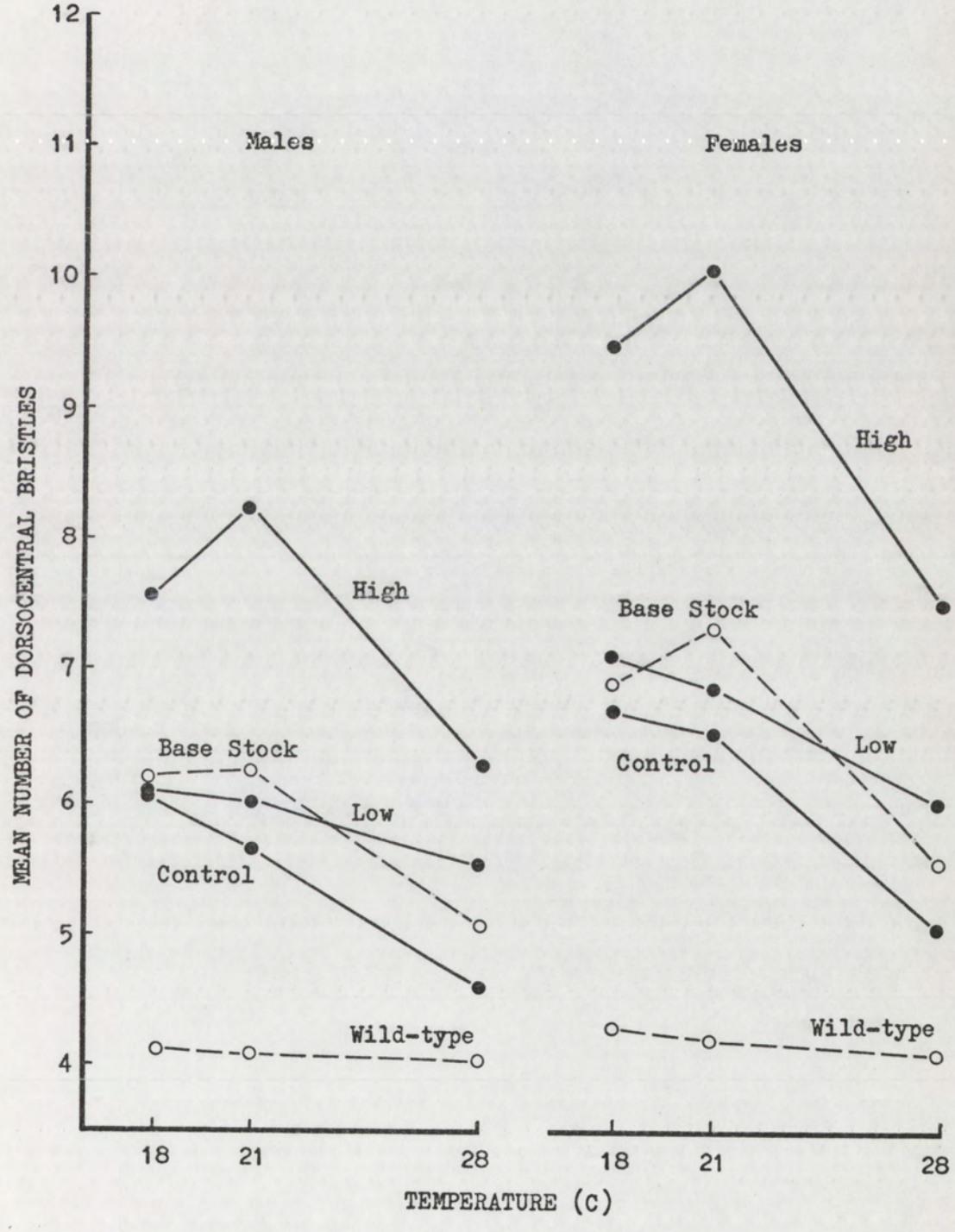


FIGURE 19. Mean number of dorsocentral bristles in the pyd lines and the wild-type stock plotted against temperature.

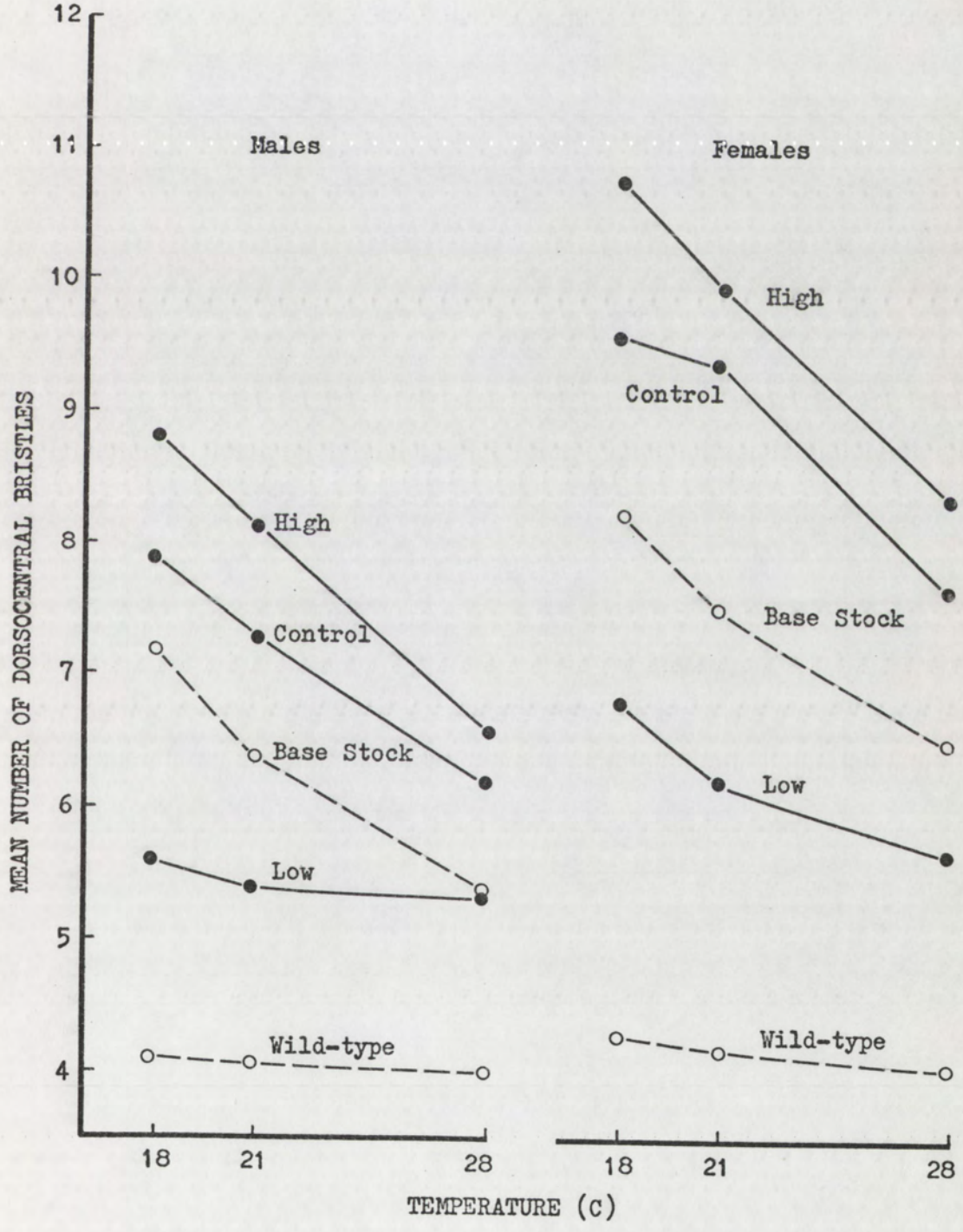


FIGURE 20. Mean number of dorsocentral bristles in the pyd h lines and the wild-type stock plotted against temperature.

TABLE 10. Mean scutellar bristle number at 18 C, 21 C, and 28 C and the difference between the lowest and highest mean

		pyd				pyd h			
Line	Temp. (C)	Males	Diff.	Females	Diff.	Males	Diff.	Females	Diff.
	18	7.05		8.50		9.81		11.93	
High	21	7.57	0.99	8.89	1.03	10.06	0.34	11.87	0.24
	28	6.58		7.86		10.15		11.69	
	18	4.27		4.52		5.43		6.25	
Low	21	4.18	0.28	4.39	0.20	5.35	0.81	5.99	0.91
	28	3.99		4.32		4.62		5.34	
	18	4.82		5.36		6.99		7.86	
Control	21	4.80	0.52	5.30	0.58	6.63	1.36	7.70	1.00
	28	4.30		4.78		5.63		6.86	
	18	5.35		6.08		7.42		8.33	
Base Stock	21	4.90	0.64	5.62	0.70	6.98	0.97	8.15	0.68
	28	4.71		5.38		6.45		7.65	
	18	4.01		4.01					
Wild-type	21	4.01	0.01	4.05	0.04				
	28	4.00		4.02					

TABLE 11. Mean dorsocentral bristle number at 18 C, 21 C, and 28 C and the difference between the lowest and highest mean

		pyd				pyd h			
Line	Temp. (C)	Males	Diff.	Females	Diff.	Males	Diff.	Females	Diff.
	18	7.56		9.44		8.78		10.76	
High	21	8.22	1.96	10.06	2.59	8.16	2.19	10.00	2.42
	28	6.26		7.47		6.59		8.34	
	18	6.03		7.08		5.60		6.79	
Low	21	5.98	0.53	6.91	1.09	5.41	0.31	6.22	1.10
	28	5.50		5.99		5.29		5.69	
	18	6.02		6.67		7.91		9.58	
Control	21	5.66	1.47	6.51	1.65	7.31	1.71	9.40	1.92
	28	4.55		5.02		6.20		7.66	
	18	6.17		6.91		7.22		8.23	
Base Stock	21	6.22	1.18	7.29	1.80	6.40	1.85	7.50	1.71
	28	5.04		5.49		5.37		6.52	
	18	4.09		4.27					
Wild-type	21	4.07	0.07	4.18	0.23				
	28	4.02		4.04					

Population Variance

The samples taken from the populations raised at 21 C for the temperature studies were used to estimate the population variances of dorsocentral and scutellar bristles. The two replicates were pooled to give sample sizes of 100. The variances of the four selection lines, two unselected control lines, base stocks, and wild-type stock are given in Table 12. Tests of significance were run between pyd and pyd h scutellar bristle variances within each type of line. Tests were also run in pairs among the lines within pyd or pyd h. Control-low, control-high, high-low, and base stock-wild-type stock comparisons were made. The same was done for dorsocentral bristle variances.

The F-ratios are given in Tables 13 and 14. The pyd h high line scutellar bristles were more variable than the pyd high line scutellar bristles; the base stocks were not significantly different. Scutellar bristles in the pyd h control and low lines were in general more variable than those in the pyd control and low lines (see Table 13), but significant differences were found for only one sex in these lines. There were no significant differences between pyd and pyd h dorsocentral bristle variances, except for the control lines where pyd h was more variable than pyd. Table 14 shows that for both dorsocentral and scutellar bristles almost all the differences in variances between the control and low, control and high, and high and low lines, and between the base stocks and wild-type stock were highly significant. The general pattern was base stock > wild-type stock; high > control > low. Only a few exceptions to this were found, all involving dorsocentral bristles.

Crosses between the High and Low Lines

The F_1 and F_2 means and the expected midparent values of the crosses

TABLE 12. Variances of dorsocentral and scutellar bristles

Scutellar Bristles	pyd		pyd h	
Line	Males	Females	Males	Females
High	1.742	2.099	2.946	3.791
Low	0.190	0.341	0.513	0.515
Control	0.687	0.717	1.023	1.323
Base Stock	0.596	0.905	0.868	1.361
Wild-type	0.010	0.048		
Dorsocentral Bristles	**pyd**		**pyd h**	
Line	Males	Females	Males	Females
High	3.749	5.168	2.944	3.535
Low	1.373	1.456	0.972	1.244
Control	0.954	1.121	1.630	2.485
Base Stock	1.446	1.562	1.556	1.828
Wild-type	0.086	0.190		

TABLE 13. F-ratios of pyd and pyd h dorsocentral and scutellar bristle variances

Scutellar Bristles		
Lines Tested	Males	Females
Highs	1.691*	1.806**
Lows	2.700**	1.510
Controls	1.489	1.845**
Base Stocks	1.456	1.504
Dorsocentral Bristles		
Lines Tested	Males	Females
Highs	1.273	1.462
Lows	1.413	1.170
Controls	1.709*	2.217**
Base Stocks	1.076	1.170

*P < 0.05

**P < 0.01

TABLE 14. F-ratios between lines for dorsocentral and scutellar bristle variances

Scutellar Bristles	pyd		pyd h	
Lines Tested[1]	Males	Females	Males	Females
C-H	2.536**	2.927**	2.880**	2.865**
C-L	3.616**	2.103**	1.994**	2.569**
L-H	9.168**	6.155**	5.743**	7.361**
W-B	59.600**	18.854**	86.800**	28.354**
Dorsocentral Bristles	**pyd**		**pyd h**	
Lines Tested[1]	Males	Females	Males	Females
C-H	3.930**	4.610**	1.806**	1.423
C-L	1.439	1.299	1.677*	1.998**
L-H	2.731**	3.549**	3.029**	2.842**
W-B	16.814**	8.221**	18.093**	9.621**

[1] C=Control, H=High, L=Low, W=Wild-type, B=Base Stock

*$P < 0.05$

**$P < 0.01$

between the high and low selection lines are given in Table 15. The midparent expectations are the averages of the high and low parental means. The F_1 and F_2 means should be close to these averages if the major differences between the high and low lines were due to genes with additive effects. Most of the F_1 and F_2 means were lower than the midparent expected values. This was true for both types of bristles, males and females, pyd and pyd h genotypes. The means of reciprocal crosses were different in most cases. These two results may reflect a pattern of interactions that will be discussed later.

The reciprocal F_1 and F_2 samples were pooled to obtain estimates of the number of factors contributing to the development of dorsocentral and scutellar bristles. The estimates are given in Table 16. These values were much smaller than what might be expected for a character with an underlying variable that is continuously distributed. The number of loci contributing to the formation of abdominal bristles in D. melanogaster has been estimated by the same method to be 99, and the number for thorax length, 59 (Falconer, 1960). Falconer used the data from previous experiments (Robertson, 1955; Clayton and Robertson, 1957) to calculate these values. The method employed estimates the number of genes with additive effects. However, there appeared to be some non-additive interactions in all lines--the means were lower than expected and reciprocal crosses were different, as mentioned above. The estimates were, therefore, probably distorted, and no attempt was made to draw conclusions from these data.

TABLE 15. F_1 and F_2 means of the crosses between the high and low selection lines and the expected midparent values

	pyd		pyd h	
Scutellar Bristles	Males	Females	Males	Females
Midparent Expected	5.85	6.77	7.90	8.98
F_1				
H Males x L Females	4.55	5.78	6.78	8.25
L Males x H Females	5.70	6.22	7.80	8.64
F_2				
H Males x L Females	5.07	5.65	6.77	7.91
L Males x H Females	5.38	6.60	7.24	8.49
	pyd		pyd h	
Dorsocentral Bristles	Males	Females	Males	Females
Midparent Expected	6.69	7.89	7.09	8.47
F_1				
H Males x L Females	5.71	7.35	6.23	8.04
L Males x H Females	6.77	7.59	7.35	8.24
F_2				
H Males x L Females	6.21	7.30	6.52	7.76
L Males x H Females	6.84	8.17	6.88	8.37

TABLE 16. Estimates of the number of factors contributing to the development of dorsocentral and scutellar bristles

	pyd		pyd h	
Bristles	Males	Females	Males	Females
Scutellar	5.23	2.85	5.37	4.35
Dorsocentral	2.61	0.92	2.17	4.02

DISCUSSION

Effect of pyd on the Development of Scutellar Bristles

The manner in which pyd disrupts the canalization of development of scutellar bristles supports the hypothesis that it is a mutant allele of a major structural gene controlled by regulator genes and that its modifiers are not controlled. Most of the differences between the high and low lines produced by selection were in complete agreement with the expectations. For example, the sex dimorphism decreased in the low lines and increased in the high lines. Furthermore, the responses to selection were greater in the high than in the low lines when measured phenotypically in bristles and also when measured on the underlying scale in probits. There are, however, other possible causes for an asymmetrical response between high and low selection lines. Falconer (1960) lists some of the more common ones. Heritability was estimated in order to measure the relative amounts of genetic variability expressed in the different lines. In general, the values obtained were as expected--more modifying genes were revealed in the high than in the low lines.

The highly significant differences in the variances of scutellar bristles among the control, low, and high selection lines were also in agreement with the expected results, as were the results of the temperature studies in most cases. Selection usually results in an increase in the homozygosity of the genetic background as the favored alleles are fixed. The development of individuals possessing a high degree of homozygosity is less buffered against environmental fluctuations than is the development of individuals possessing a high degree of heterozygosity (Lerner, 1954). The fact that the low lines showed a decrease

in variance and a decreased sensitivity to different temperatures compared with the control lines lends support to the hypothesis that a regulatory system was present and functioning. The number of parents used each generation was the same for all lines, thus restricting the genetic variability to the same degree. Therefore, any genotypic differences among the control, low, and high lines must have been due primarily to different frequencies of minor genes accumulated by selection. The increased temperature sensitivity in the pyd high line and increased variance in both high lines were consequently most likely due to the overriding of the control mechanism by the greater activity of the minor genes in these lines, rather than to an increase in homozygosity. The pyd h high line was expected to show the greatest sensitivity to different temperatures because the development of the flies in this line was the most disturbed of all the lines. It would be difficult to explain the apparent insensitivity to temperature variation of this line.

Low variance, low sex dimorphism, and insensitivity to temperature variation are all characteristics of a canalized system. It could be interpreted that a change in these characteristics was brought about by a change in the canalizing genotype. However, it is unlikely that merely changing the mean of a population would act on all the developmental pathways necessary to change all of these characteristics. Kindred (1965) found that in sc lines selection for reduced sensitivity to different temperatures, although successful, did not change the canalization of scutellar bristles because the within-bottle variance did not change. Druger (1967) obtained the same results from a similar experiment and concluded that the lack of response to temperature was achieved by a different metabolic pathway than the within-bottle variance.

Lee and Fraser (1969) found that selection for decreased sex dimorphism in sc lines did not reduce the sensitivity to different temperatures. Only selection for reduced variance around a mean of two scutellar bristles in sc lines has succeeded in changing the entire canalizing genotype (Rendel and Sheldon, 1960; Rendel, Sheldon, and Finlay, 1966). The low variance lines they developed possessed low sex dimorphism and were insensitive to temperature variation. It is doubtful that the presence of these characteristics of canalization in the pyd low line was the result of a change in the canalizing genotype. Rather, this was more likely the result of the mean having been brought low enough so that control by the canalizing genes was no longer exceeded by the majority of flies in the population.

Although the results obtained in the present study support the hypothesis that pyd is a mutant allele of a major gene subject to control, similar results could have been obtained if pyd were a mutant allele of a regulator gene. Assuming the pyd locus was concerned with control, stronger regulation would have been selected for in the low lines and weaker regulation in the high lines. Falk (1963) stated that genes whose normal alleles are responsible for not producing a particular phenotypic effect are probably involved in a controlling system. He proposed a model of regulation of bristle number analogous to the operon of Jacob and Monod (1961). Hairy wing (Hw) is a mutant gene that adds extra hairs and bristles to various sites. The mutant achaete (ac) removes the posterior dorsocentral bristles and nearby hairs (Lindsley and Grell, 1968). Hw^+ is the operator; ac^+ and sc^+ are two structural genes of the operon. The operator can be repressed by the product of the regulator gene, which he says is possibly h^+ or pyd^+. However, no

work has been done to confirm this, and certainly further studies would be necessary to determine the mode of action of pyd.

Comparison of pyd and pyd h Lines

The expected effects of pyd and h together on scutellar bristle development compared with the effect of pyd alone were based on the assumption that h would reveal additional modifying genes. But the comparisons of the responses to selection on the underlying scale and the realized heritability estimates between pyd and pyd h lines indicated that no more genetic variability was uncovered by pyd h than pyd. The greater response to selection of pyd h in bristles may be explained by the decreasing widths of the bristle classes as the mean increased. Because the means of the pyd h lines were larger to begin with, they may have gone through more bristle classes than the pyd lines, but the classes were narrower on the underlying scale, making the response appear to be greater on the phenotypic scale. In other words, apparently less increase of bristle Make was necessary to form an additional bristle as the mean was shifted farther from the canalized zone. It might be mentioned here that the estimates of heritability and response to selection in probits were limited in accuracy by the relatively small sample sizes. The lack of correspondence between these two measures for pyd h low females could be due to this factor.

Although pyd h evidently did not reveal more genetic variability than pyd, this does not necessarily mean that development was no more disturbed in the presence of two mutant genes. That the variance and temperature sensitivity of scutellar bristles was greater in pyd h than pyd lines in many instances may indicate that the double homozygote was nevertheless more susceptible to environmental influences. The phenotypic

variance is the sum of the variance due to genetic factors and the variance due to environmental fluctuations (Falconer, 1960). The addition of h to pyd probably increased the phenotypic variance by enlarging the environmental component of the overall variance.

There are two possible explanations for the finding that pyd h revealed no more genetic variability than pyd. If pyd and h affected the same biochemical pathway, they would probably reveal the same modifiers. Kindred (1967) worked with several mutant genes affecting vibrissae in the mouse. She suggested that the mutant genes Tabby and Ragged interrupted different metabolic pathways because the modifiers of Tabby did not alter the expression of Ragged. The two mutants apparently were modified by different genes. Lee and Fraser (1969), from work on D. melanogaster, postulated that high polygenic overlap between non-allelic genes indicates the greater importance of general modifying genes in the development of a character. Locus-specific modifiers would be more important when there was a low degree of polygenic overlap. General modifying genes affecting the development of scutellar bristles would be consistent with Rendel's contention that modifiers are not controlled. They are probably just background genes with primary effects on other genetic systems, and if they are controlled at all, they are controlled with respect to those systems (Rendel, 1967).

Dorsocentral Bristles

The hypotheses made concerning the canalization of scutellar bristles could not predict the effects selection would have on dorsocentral bristles. However, because the major phenotypic effect of pyd is on dorsocentral bristles (Neel, 1940), it was therefore not surprising that selection on the modifiers of pyd changed the mean number of dorsocentral

bristles in the same direction as the mean number of scutellar bristles. The two bristle systems most likely share some of the developmental pathways modified by the genes on which selection acted. It also appeared that selection for scutellar bristles succeeded in bringing about a change in the canalization of dorsocentral bristles, considering that their variance and temperature sensitivity decreased in the low lines and increased in the high lines in most instances. Apparently the number of dorsocentral bristles is canalized by a mechanism resembling the one that canalizes the number of scutellar bristles. The two types of bristles could be controlled by the same or by different regulatory systems.

Because the coefficients of correlation between dorsocentral and scutellar bristles in the control, low, and high lines were not significantly different from the base stock coefficients, nothing definite could be concluded concerning what effect selection had on the partitioning of bristle resources between the two systems. Selection was practiced for only 10 generations, a relatively short period of time. Further selection could have caused the differences found to become significant.

Crosses between the High and Low Lines

The results of the crosses between the high and low selection lines were not as expected for either dorsocentral or scutellar bristles. It was anticipated that the means of reciprocal crosses and the F_1 and F_2 means would be about the same as the midparent values, and that estimates of the number of factors in the pyd and pyd h base stocks would be obtained. However, these expectations were based on the assumption that the genes accumulated by selection had additive effects. The disagreement

between reciprocal crosses could have been due to the presence of a sex-linked factor or to cytoplasmic inheritance. Because most of the means were lower than the expected midparent values, it appeared that either the modifying genes did not have additive effects or that their expression was suppressed. Suppressor genes are well-known in D. melanogaster. One example of a suppressor is su(Hw)^2, which suppresses many different mutant genes and is, therefore, termed a super-suppressor. This gene can restore almost completely the canalization of scutellar bristles in sc lines (Lee, 1970).

The lowered F_1 and F_2 means and the disparity of the results from reciprocal crosses can be explained by the presence of a sex-linked suppressor in both the pyd and pyd h low lines. Further tests would have to be made to confirm this, but a pattern of interactions was worked out that was fully supported by the data obtained in this study. The distribution of the high and low X chromosomes in the P_1, F_1, and F_2 generations of the reciprocal crosses is diagrammed in Figure 21. The F_1 males from a high males by low females cross received their X chromosomes from the low parental line; F_1 males from a low males by high females cross received their X chromosomes from the high parental line. F_1 females received one X chromosome from the high and one from the low line. In the F_2 generation there was a mixture of genotypes. Males were X^HY and X^LY, while females were X^HX^H and X^LX^H or X^LX^L and X^LX^H, depending on whether the initial female parents were from a high or low line. The hypothetical suppressor was consistent--dorsocentral and scutellar bristles, males and females, pyd and pyd h were all affected. Figure 21 may be compared with the means in Table 15. The X^HY F_1 males always had a greater mean number of dorsocentral and scutellar bristles

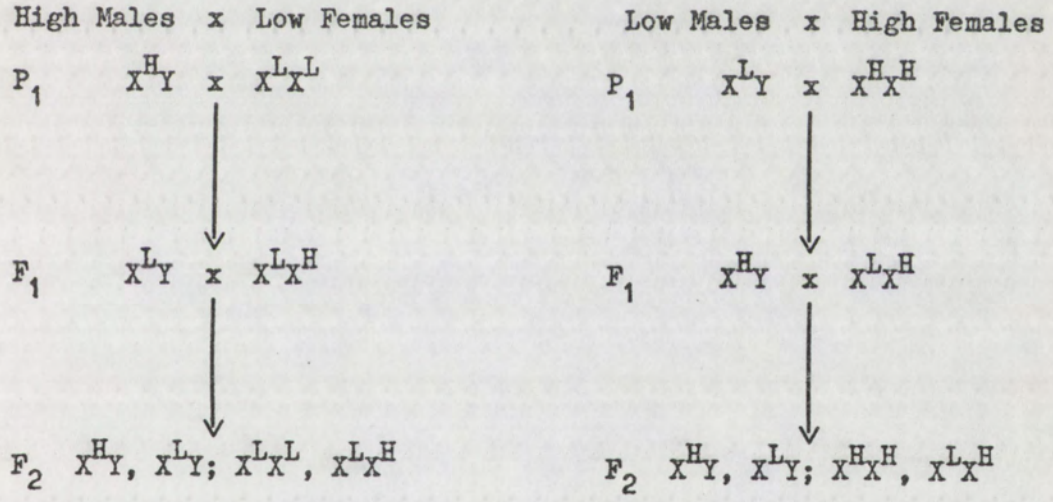


FIGURE 21. Distribution of high and low X chromosomes in the P_1, F_1, and F_2 generations.

than X^LY F_1 males. The X^LX^L and X^LX^H F_2 females always had a lower mean number of bristles than X^HX^H and X^LX^H F_2 females. For example, considering pyd scutellar bristles, the X^HY mean was 5.70; the X^LY mean was 4.55, more than one bristle difference. The X^LX^L and X^LX^H class mean was 5.65; the X^HX^H and X^LX^H class mean was 6.60. The midparent expectations were 5.85 for males and 6.77 for females. Thus, according to this model, a factor or factors residing on the X^L chromosomes acted to reduce the mean number of bristles.

It is possible that selection in the low lines, rather than increasing the frequency of genes with negatively additive effects, resulted in the increased frequency of genes that suppressed pyd. The mutant gene x-vert, which is an integral part of Fraser's model of canalization of scutellar bristles, is probably an allele of pyd (Fraser, Erway, and Brenton, 1968; Lee, 1970). Scute, which is sex-linked, suppresses x-vert (Miller and Fraser, 1968), as mentioned previously. The phenotypic effects of pyd and x-vert are similar, and it is conceivable that weak sc^+ isoalleles accumulated in both the pyd and pyd h low lines and suppressed pyd. This is only speculation, but it would explain the general suppression of the pyd phenotype.

Pleiotropic Effects

The factors accumulated by selection apparently had pleiotropic effects. This would account for the fact that some attributes of bristle development besides number were depressed in the low lines and magnified in the high lines. The extreme reduction in size and distorted shape of some of the dorsocentral and scutellar bristles in the pyd h low line were probably produced by genetic factors that were peculiar to this line and that disturbed both bristle-forming systems similarly.

The fact that fewer flies developed and the developmental time increased in the high lines indicated that the development of the flies in general and not just bristle development was disrupted. It is known that fitness components such as viability and fertility usually decrease when normal development is disrupted by artificial selection. Dobzhansky (1970) has reviewed much of the literature pertaining to this phenomenon.

The actual cause of the changes in bristle number was probably a change in the amount of tissue capable of forming bristles. There is an area of bristle-forming potential around a normal bristle site (Neel, 1940). In pyd populations Neel observed that most extra bristles arose near a normally situated bristle. As distance from the normal sites increased in any direction, bristle size and incidence decreased. The area that normally gives evidence of being capable of forming bristles must have spread in the high lines, as some bristles, especially extra scutellar bristles, were very far-removed from normal bristle locations. In the low lines some tissue areas must have lost the capability of forming bristles.

The canalization of development of dorsocentral and scutellar bristles thus includes the adjustment of all phenotypic characteristics to a specified norm. Evidently not only number but also conformation and position are involved. The bristle-forming system directing the constant expression of all these features must of necessity be complex.

SUMMARY

That pyd is a mutant allele of a structural gene controlled by regulator genes and that its modifiers are not controlled was supported by the responses to selection, temperature sensitivity, and variance of the pyd and pyd h lines. However, these findings did not rule out the possibility that pyd is a mutant allele of a regulator gene. Adding h to pyd apparently did not reveal more modifying genes, but the combination of pyd and h probably disturbed development more, and therefore was more subject to environmental fluctuations than pyd alone.

The results of the crosses between the high and low lines indicated that genes with non-additive effects had been accumulated by selection. To explain the differences between reciprocal crosses and that the F_1 and F_2 means were lower than the midparent expectations, it was hypothesized that a sex-linked suppressor was present in the low lines. Besides number, selection also affected other bristle characteristics such as size, shape, and distribution. In general, bristle development was depressed in the low lines and exaggerated in the high lines.

Scutellar bristles evidently share some of their developmental pathways with dorsocentral bristles, so that selection for scutellar bristles resulted in similar changes in both bristle systems.

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