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GENOTYPE X ENVIRONMENT INTERACTIONS IN DROSOPHILA MELANOGASTER

The University of Oklahoma PH.D. 1983

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GENOTYPE X ENVIRONMENT INTERACTIONS IN *DROSOPHILA MELANOGASTER*

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

FRED B. SCHNEE

Norman, Oklahoma

1983

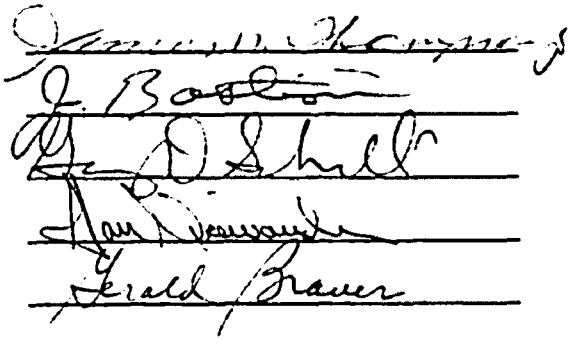
GENOTYPE X ENVIRONMENT INTERACTIONS

IN DROSOPHILA MELANOGASTER

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF ZOOLOGY

By



ACKNOWLEDGMENTS

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PREFACE

The statistical techniques of biometrical genetics have been used extensively to study the relationship between genotype and environment in quantitative traits such as sternopleural bristle number in Drosophila melanogaster. While many interesting results have stemmed from this work, the mechanism of genotype x environment interaction is still poorly understood. Polygene mapping represents an alternative to the more commonly used biometrical genetic approach to the study of quantitative traits. While polygene mapping has proved to be a powerful tool in the resolution of polygenic systems, it has never been applied to the study of genotype x environment interactions. In this dissertation research, the organization of polygenes affecting temperature-sensitivity was examined in lines of D. melanogaster selected at 18°, 25° and 29°C for increased or decreased bristle number.

This study is written in two sections. The first examines the response of lines selected for increased or decreased bristle number at 18°, 25° and 29°C and analyzes the chromosomal architecture associated with each of these lines. The second is a study of the intrachromosomal

distribution and number of polygenic loci on chromosome 3 in each of the tested lines. Both sections are written in a style suitable for publication in Genetics. Data and analyses not included for publication are provided for reference in Appendices I-IV. In addition, a paper which stemmed from a related project is included as Appendix V. This paper is now in press in Evolution.

GENOTYPE X ENVIRONMENT INTERACTIONS IN *DROSOPHILA MELANOGASTER*

CHAPTER I

CONDITIONAL POLYGENIC EFFECTS IN THE STERNOPLEURAL BRISTLE SYSTEM OF *DROSOPHILA MELANOGASTER*. I. RESPONSE TO SELECTION AND WHOLE CHROMOSOME ANALYSIS

ABSTRACT

The chromosomal architecture of genotype x temperature interactions was investigated in lines of *Drosophila melanogaster* selected for increased or decreased sternopleural bristle number at 18°, 25° and 29°C. In general such interactions were found to have a stabilizing effect on the sternopleural bristle number phenotype. In addition, the polygenic modifiers of the sternopleural phenotype studied, mean bristle number and response to temperature, were found to be separable at the chromosomal level. While chromosome 3 had the largest effect on mean bristle number, chromosome 2 was most important in determining the temperature effect at 29°C.

INTRODUCTION

During development, the relationship between a genotype and the environment is plastic and is dependent, at least in part, upon the polygenic makeup of an organism. Biometrical geneticists have developed sophisticated techniques for the study of genotype x environmental interactions in quantitative traits (for reviews, see Freeman 1973; Mather and Jinks 1981). Most of these approaches are directed towards the prediction of selection responses in different environments. The specific genetic architecture of genotype x environmental interactions has, however, received comparatively little attention.

Connolly and Jinks (1975) examined the architecture of the conditional effects associated with temperature and growth rates in Schizophyllum commune and found directional dominance to be an important component. In Drosophila melanogaster, Gibson (1970) has shown that the magnitude of interactions between chromosomes varies with culture temperature, and Caligari and Mather (1975) have found that the genes chiefly responsible for producing the genotype x environmental interaction in the sternopleural bristle system of D. melanogaster are carried on chromosome 2.

While these studies are important, additional work aimed at the identification and location of specific loci is needed.

Polygene mapping, first described by Thoday (1961), has proved to be profitable for identifying loci involved in quantitative traits (see reviews in Thompson and Thoday 1979). Furthermore, work by Spickett (1963) and others demonstrated that this technique is useful in the resolution of specific polygenic interactions, indicating its potential value in the study of genotype x environmental interactions.

The first step in mapping is the localization of polygenes to a specific chromosome. In this study, 12 lines of D. melanogaster were selected for increased or decreased sternopleural bristle number at either 18°, 25° or 29°C. Whole chromosome substitutions at each temperature allowed those chromosomes associated with genotype x temperature interactions to be identified. The interactions we found suggest that temperature-dependent effects may act as a stabilizing force on the phenotype of quantitative traits.

MATERIALS AND METHODS

The base stock used in the selection procedure was produced by intercrossing four isofemale strains (OK-1505, OK-1513, OK-1520 and OK-1526) collected in Noble, Oklahoma, in May 1979.

Lines were raised on a standard cornmeal, molasses, yeast and agar medium seeded with live yeast (Ashburner and Thompson 1979). Temperature was maintained in incubators set at $29\pm0.5^{\circ}$, $25\pm0.5^{\circ}$ and $18\pm0.5^{\circ}$C. Selection on sternopleural bristle number was carried out at each of these temperatures in replicate high and low lines. Five pairs of parents were selected from 20 pairs counted each generation. In addition, an unselected control line was maintained by random mating at each temperature.

We will refer to each selection line by a code indicating the direction of selection, the replicate number and the temperature at which it was selected. For example, the replicate-1 line, selected for high bristle number at 25° will be referred to as the High-1-25 line. Similarly, the replicate-2 line, selected at 18°C for reduced bristle number, will be called the Low-2-18 line.

At generation S-8 the incubator used to hold lines at

18°C failed. Selection was resumed at 18° after lines spent two generations at 25° under relaxed selection.

The heterozygous effects of chromosomes 2 and 3 were measured by crossing males from a test selection line to an inbred standard stock that carried the recessive eye color mutants brown (bw, 2-104.5) and scarlet (st, 3-44.0). This standard was made isogenic with balancer chromosomes before it was used in whole chromosome assays. The F_1 males were backcrossed to the bw;st standard. The eye color of each of the four F_2 classes allowed the identification of its chromosomal makeup. For example, scarlet-eyed flies (+/bw; st/st) carried a single chromosome 2 from the tested line, while brown-eyed flies (bw/bw; +/st) carried a single chromosome 3. Red-eyed flies (+/bw; +/st) carried both a tested second and third chromosome, allowing the inter-chromosomal interaction to be quantified. The reconstituted bw;st class acted as an internal control to which the other three classes could be contrasted. Fifty flies from each class were counted for each whole chromosome assay. Each of the whole chromosome assays was carried out at 18°, 25° and 29°C, so that the effects of a single autosome could be isolated and measured in contrasting environments. Selection lines were inversion-free.

The results of the whole chromosome assays were tested for significance by a six-way factorial analysis of variance (Sokal and Rohlf 1981). The six factors tested in this

analysis were temperature, chromosome 2, chromosome 3, the chromosome 2 x chromosome 3 interaction, sex, and replicate variation.

RESULTS

The effects of temperature on sternopleural bristle number in the base stock, from which all selection lines originated, was measured by raising flies at 18°, 25° and 29°C. The mean and standard error for sternopleural bristle number of 100 flies at each of these temperatures was 19.05±1.67, 17.56±1.77 and 16.34±1.92, respectively. An analysis of variance revealed a significant ($P < 0.05$) temperature effect, in which bristle number increases as temperature decreases.

Responses to selection are shown in Figures 1-3. Only the data for males are shown for simplicity, since female responses were identical except for having a higher mean bristle number. All lines responded to selection for both decreased and increased bristle number at all temperatures. Selection responses at 25° and 29° were similar, except that sternopleural bristle number was higher at 25°. At these two temperatures the selection lines responded steadily to selection, reaching a plateau by about generation 35.

At the time selection was terminated, the 18° lines had achieved a smaller response than the other lines. This can be explained, in large part, by the shorter period of

selection caused by the extended generation time at low temperature. The 18° lines also tended to show a higher replicate variance than did lines selected at 25° or 29°. This variance is most evident in the low lines, in which the Low-2 replicate responded to a greater degree than did the Low-1 line. The higher variance may be related to the incubator failure at S-8, which caused a reduction in population size and thus could have contributed to drift in polygene allele frequencies.

Analysis of whole chromosome effects allowed us to measure the phenotypic influences of chromosome 2 and 3 isolated from the 18°, 25° and 29° selection lines (Tables 1 and 2). In all cases, the effect of chromosome 3 was the largest, with chromosome 2 showing a significant, though smaller, effect. The chromosome 2x3 interaction was more variable, but in general had the smallest effect (Table 3).

Chromosomes which were involved in genotype x environment interactions will have effects which are dependent upon the environment. In this experiment, such temperature-dependent effects were identified by replicating the same chromosome at 18°, 25° and 29°. If the phenotype associated with a chromosome was significantly different at one temperature than at another, as determined by an analysis of variance, a temperature-dependent effect was considered to be associated with the tested chromosome.

Several temperature-dependent effects were found for the

chromosomes surveyed. Although smaller, but significant, temperature-dependent effects were associated with chromosome 2 and the 2x3 interaction, the largest temperature x genotype interaction was traceable to chromosome 3. For example, in those lines selected for increased bristle number at 25° and 29°, the influence of chromosome 3 on bristle number was significantly smaller ($P < 0.001$) when flies were raised at 18° (see Table 2).

In some cases, however, the effect of chromosome 2 was more important than chromosome 3 in determining the responses to different temperatures. For example, chromosome 2 of the high lines selected at 29° caused a significant increase in bristle number at 29° relative to its effect at 25°. Chromosome 3 from these replicate lines had no statistically significant genotype x temperature interactions at these temperatures. Thus, temperature-dependent polygene effects may be distributed throughout the genome, though in these lines they appear to be most common on chromosome 2.

The temperature at which selection had been carried out often played an important role in determining the magnitude and direction of temperature-dependent effects. For example, both of the replicate lines selected for increased bristle number at 29° carried second chromosomes whose effects were greatest at 29°. Similarly, chromosome 3 of the Low-2-18 line reduced bristle number most effectively at 18°. Thus, selection at a given temperature tended to favor chromosomes

whose effect was greatest at the temperature in which it was selected.

The only exception to this trend was shown by chromosome 3 of the High-1-25 line. In this case, the greatest effect was found at 29° rather than 25°. The large change at 29° was not found in its replicate, however, suggesting that genetic differences may have been produced by random fixation.

A positive association was found between the magnitude of the 2x3 interaction and temperature. For example, the Low-1-25 line had a significant ($P < 0.05$) positive 2x3 interaction at 25°, while at 18° a significant ($P < 0.05$) negative interaction was found.

The bw;st line was used in the whole chromosome assays as a standard against which the influences of chromosome 2 and 3 of each selection line could be contrasted. Both the base stock used to initiate all of the selection lines and the bw;st standard showed the typical inverse relationship to temperature. With few exceptions, however, temperature-dependent effects showed the opposite relationship. The chromosome 2x3 interaction tended to increase bristle number with increasing temperature. At 18° the 2x3 interaction in the High-2-18 line had no significant effect, but at 29° it significantly increased bristle number by an average of 0.72 bristles ($P < 0.001$). Most lines showed genotype x environment interactions associated with chromosome 2 or 3

which increased bristle number at increasing temperatures. In the High-1-25 line, for example, the third chromosome significantly decreased bristle number by an average of 2.81 bristles when raised at 18° ($P < 0.001$).

While genotype x temperature interactions that opposed the effect of temperature were common, genotype x temperature interactions that enhanced the effect of temperature were not. For example, a temperature-dependent effect was found in the Low-2-18 line which significantly reduced bristle number at 18°. Yet, no temperature-dependent effects were found at 18° which increased sternopleural bristle number. Thus, the trend associated with genotype x temperature interactions was to oppose the effect of temperature, by increasing sternopleural bristle number with increasing temperature.

DISCUSSION

Sternopleural bristle number is believed to be under stabilizing selection (Barnes 1968; Parsons 1973; Caligari and Mather 1980). Since bristle development is sensitive to environmental conditions, shifts in temperature can act as a destabilizing influence, by shifting bristle number away from its optimum. The ability of Drosophila to adapt to a change in the environment is in large part determined by its ability to maintain control of its phenotype. Strains which show significant genotype x environment interactions will also, by definition, differ in their relative phenotypic stability. An inverse relationship between bristle number and temperature was found in both the selection line base stock and the bw;st standard used to determine genotype x temperature effects. A similar response has been reported several times in the literature (e.g. Rasmuson 1958; Parsons 1961; Caligari and Mather 1975), indicating that an inverse relationship between temperature and sternopleural bristle number is the typical response in Drosophila. While bristle number decreased with increasing temperature, most temperature-dependent chromosomal effects showed the opposite relationship. As a result, those genotypes which exhibited

temperature effects maintained a more stable phenotype.

Temperature-dependent effects which oppose the destabilizing action of temperature and thus maintain an optimum bristle number can be postulated to have an adaptive value. The largest and most common genotype x environment effects in this study were those which tended to negate the effect of temperature upon bristle number. This may indicate that conditional genes which increase bristle number at higher temperatures play an important role in the long-term adaptability of the Drosophila genome.

Caligari and Mather (1975) found that, while chromosome 3 had the largest effect on mean sternopleural bristle number, chromosome 2 had the largest influence upon the response to temperature. In our study, chromosome 3 had the largest effect on mean bristle number and usually determined the response to temperature at 18° and 25°. Yet, chromosome 2 was generally most important in determining the response at 29°. In the High-1-29 line, for example, chromosome 3 played the largest role in determining the response at 25°. At 29°, however, chromosome 3 had no significant temperature effect. Under the same conditions, chromosome 2 had a significant temperature-dependent influence which increased bristle number by an average of 0.84 bristles ($P < 0.001$). Thus, while the results of Caligari and Mather (1975) point out that genes responsible for determining mean bristle number are not necessarily linked to those genes that

determine response to temperature, our results show that the genes which determine response at one temperature are not always linked to those which determine response at another temperature. This is indicative of a genetic system that is quite flexible in its response to temperature. Such flexibility would be expected particularly in ectothermic organisms such as Drosophila, which lack physiological mechanisms to maintain temperature within homeostatic limits.

The linkage relationships of polygenic factors within a chromosome represent still another aspect of the architecture of a genome. In this study, some third chromosomes had a significant effect upon both the mean sternopleural bristle number and the response this developmental system showed towards shifts in temperature. At the whole chromosome level, we have found that the correlation between these two aspects of the bristle phenotype often breaks down. The next step is to see whether these two phenotypic components can also be separated at the intrachromosomal level. Polygene mapping of selected third chromosomes will be reported in a subsequent paper.

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TABLE 1

Effects of second chromosomes on sternopleural bristle number[a]

Line	Selection temperature	Effect present at:			
		All temperatures	18° only	25° and 29°	29° only
High-1	18	0.75***	--	--	--
High-2	18	0.99***	--	--	--
High-1	25	0.83***	--	1.38***	--
High-2	25	0.87***	--	0.58*	--
High-1	29	1.31***	--	1.02***	0.84***
High-2	29	0.89***	--	0.78***	0.40*
Low-1	18	-0.54***	--	--	--
Low-2	18	-0.88***	--	--	--
Low-1	25	-0.81***	--	--	--
Low-2	25	-1.14***	--	--	--
Low-1	29	-0.64***	--	--	--
Low-2	29	-1.28***	--	--	--

TABLE 1 continued

[a]The magnitudes are shown for second chromosomes isolated from high and low selection lines tested at 18°, 25° and 29°C. Magnitudes are calculated as the difference in sternopleural bristle number between the experimental and standard chromosomes. Significance levels are determined from analyses of variance; dashes represent non-significant effects.

* $0.05 > P > 0.01$; *** $P < 0.001$

TABLE 2

Effects of third chromosomes on sternopleural bristle number[a]

Line	Selection temperature	Effect present at:			
		All temperatures	18° only	25° and 29°	29° only
High-1	18	1.66***	--	--	--
High-2	18	1.49***	--	--	--
High-1	25	1.58***	--	2.81***	0.42*
High-2	25	2.33***	--	2.32***	--
High-1	29	2.03***	--	2.33***	--
High-2	29	2.08***	--	2.04***	--
Low-1	18	-0.35***	--	--	--
Low-2	18	-1.05***	-0.52*	--	--
Low-1	25	-1.50***	--	-0.54*	--
Low-2	25	-1.67***	--	-0.40*	--
Low-1	29	-1.11***	--	--	--
Low-2	29	-1.42***	--	-0.43*	--

TABLE 2 continued

[a]The magnitudes are shown for third chromosomes isolated from high and low selection lines tested at 18°, 25° and 29°C. Magnitudes are calculated as the difference in sternopleural bristle number between the experimental and standard chromosomes. Significance levels are determined from analyses of variance; dashes represent non-significant effects.

* $0.05 > P > 0.01$; *** $P < 0.001$

TABLE 3

Effects of 2x3 chromosome interactions on sternopleural bristle number[a]

Line	Selection temperature	Effect at:		
		18°	25°	29°
High-1	18	0.00	0.11	0.55***
High-2	18	0.09	0.18	0.23
High-1	25	0.32*	0.69***	0.72***
High-2	25	-0.11	0.41**	0.25
High-1	29	0.18	0.74***	0.61***
High-2	29	0.22	0.51**	0.72***
Low-1	18	0.23	0.09	-0.15
Low-2	18	-0.24*	0.01	0.27
Low-1	25	-0.36**	0.19	0.36**
Low-2	25	-0.10	0.24	0.47***
Low-1	29	0.10	0.08	0.31*
Low-2	29	0.02	0.22	0.24*

TABLE 3 continued

[a]The magnitudes are shown for 2x3 chromosome interactions isolated from high and low selection lines tested at 18°, 25° and 29°C. Significance levels are determined from analyses of variance.

* 0.05 > P > 0.01; ** 0.01 > P > 0.001; *** P < 0.001

LEGENDS

Figure 1. -- Male responses to selection at 18°C.

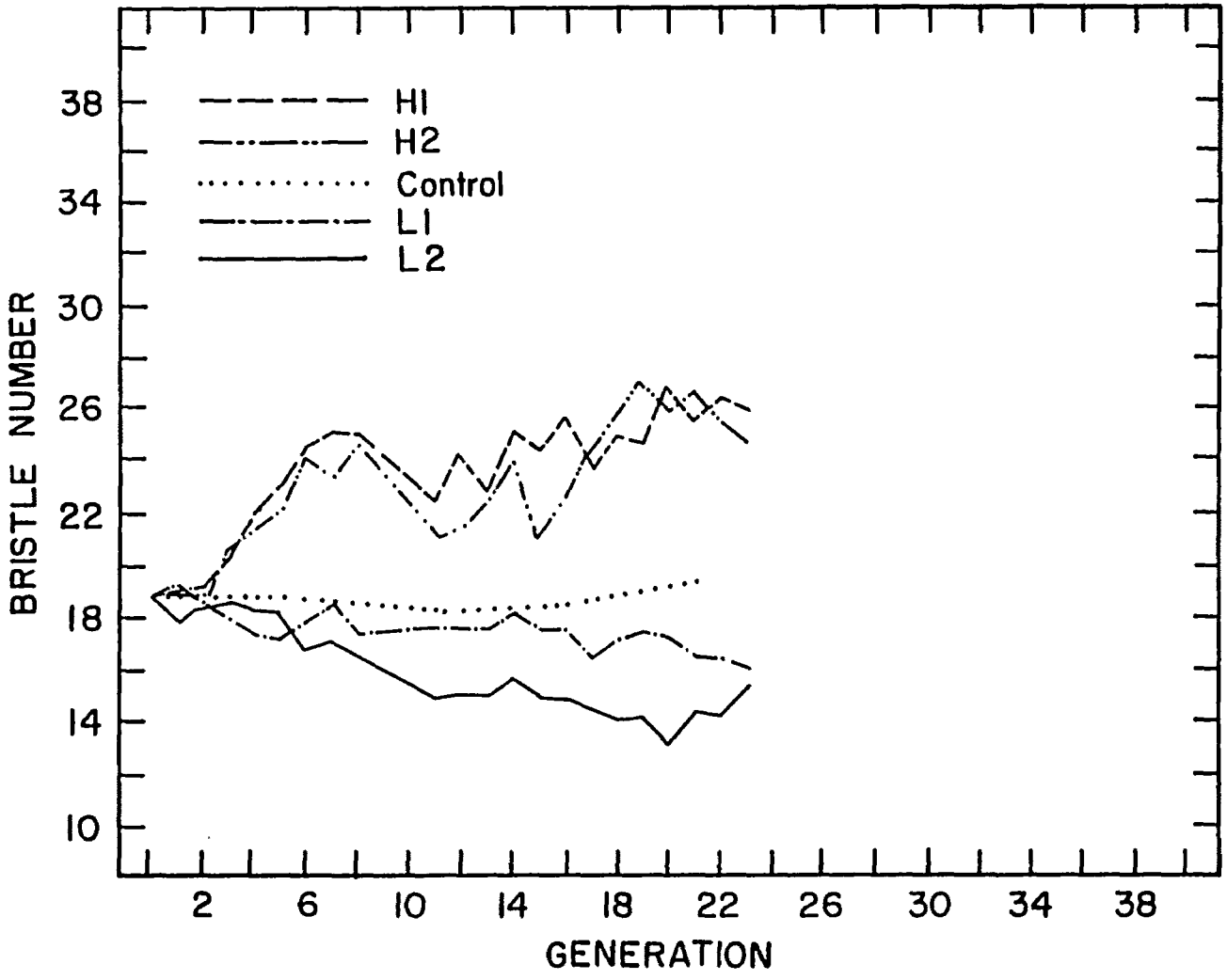
H1, High-1-18; H2, High-2-18; L1, Low-1-18; L2, Low-2-18.

Figure 2. -- Male responses to selection at 25°C.

H1, High-1-25; H2, High-2-25; L1, Low-1-25; L2, Low-2-25.

Figure 3. -- Male responses to selection at 29°C.

H1, High-1-29; H2, High-2-29; L1, Low-1-29; L2, Low-2-29.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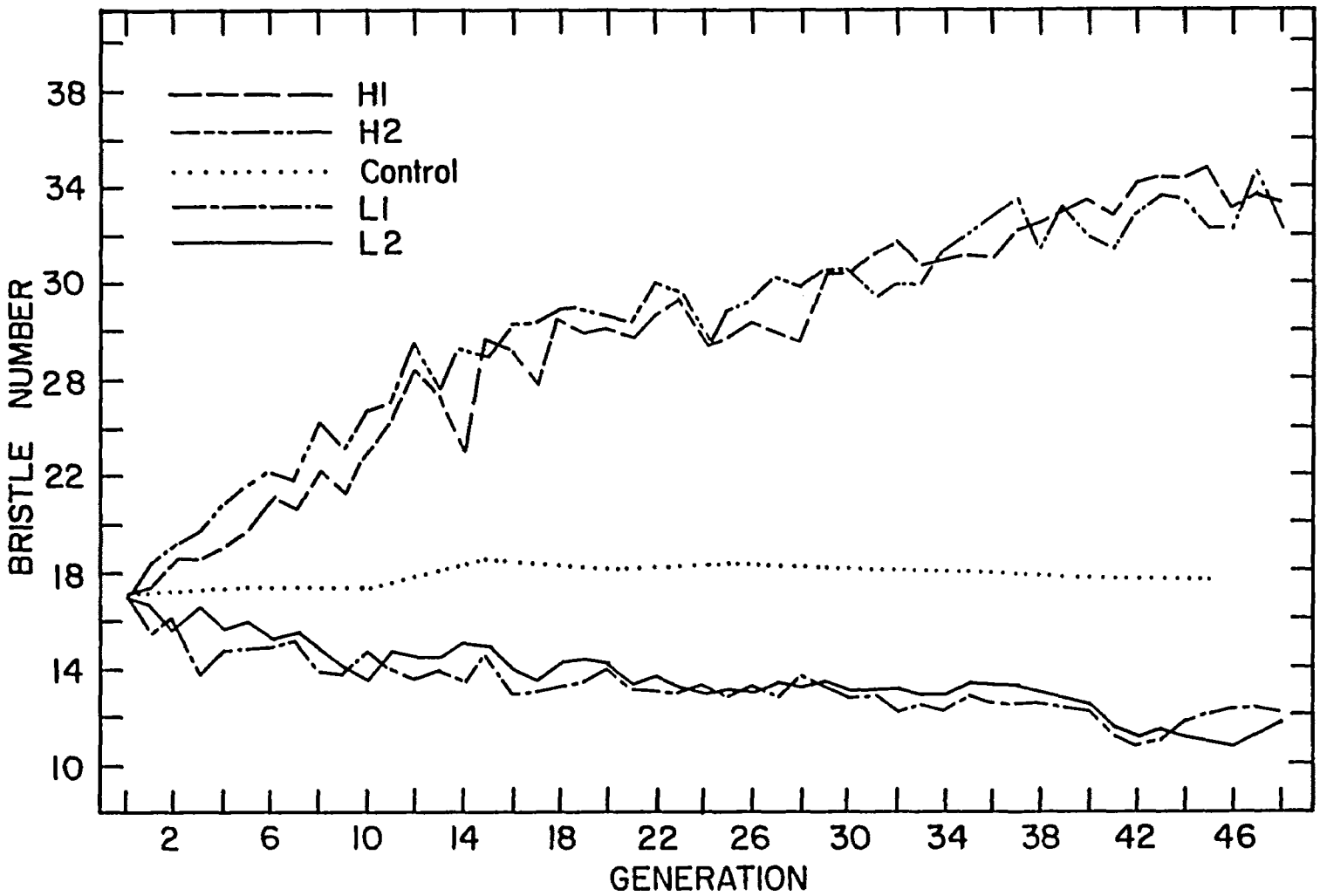
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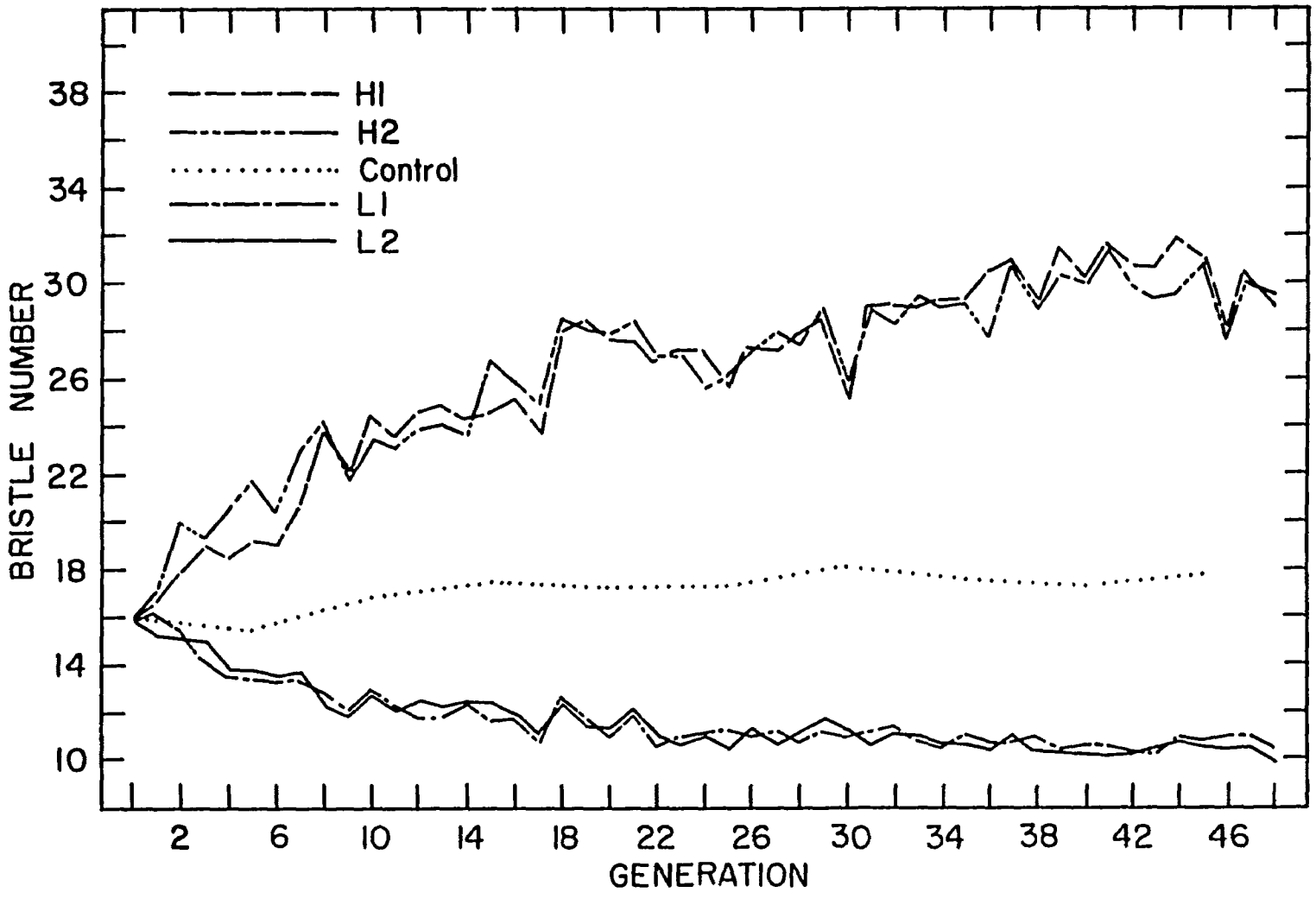
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GENERATION

CHAPTER II

CONDITIONAL POLYGENIC EFFECTS IN THE STERNOPLEURAL BRISTLE SYSTEM OF DROSOPHILA MELANOGASTER. II. POLYGENE MAPPING

ABSTRACT

The intrachromosomal architecture of third chromosomes isolated from lines of Drosophila melanogaster selected for high or low sternopleural bristle number was examined at 18° and 25°C. Two components of sternopleural bristle development, bristle number and temperature-sensitivity, were often found to be determined by different regions of chromosome 3. In many cases, however, there was tight linkage between the polygenic loci which determine these two characteristics. In one of the low selection lines, further study was possible and a temperature-dependent polygenic locus was mapped. It is suggested that genotype x environmental interactions be thought of in terms of conditional polygenic effects. Such conditionality may be one of the means by which polygenic variation is maintained within a population in the face of selection for an optimum phenotype.

INTRODUCTION

The degree of expression of quantitative traits is commonly influenced by environmental factors, such as temperature. Yet, the magnitude and direction of environmental effects is, in turn, dependent upon the genotype. Studies designed to investigate genetic effects of whole chromosomes have revealed much about the basic architecture and possible evolutionary significance of genotype x environment interactions. For example, it is often found that heterokaryotypes display greater phenotypic stability in a variable environment than do homokaryotypes (see Parsons 1975, for review). This is also true for other measures of genetic heterozygosity (e.g. Lerner 1954; Thoday 1956).

Many simple quantitative characters have served as experimental models in the study of polygenic expression. For example, the sternopleural bristle system in Drosophila melanogaster has been used extensively, because it is readily scored, it appears to be under stabilizing selection as a sensory-related system (e.g. Barnes 1968; Parsons 1973; Caligari and Mather 1980), and it is phenotypically sensitive to environmental influences (Parsons 1961). One interesting

observation is that the polygenes that have the greatest effect upon bristle number are not always identical to those that have the greatest effect upon environmental sensitivity. Caligari and Mather (1975) have shown, for example, that chromosome 3 carried the major modifiers of bristle number, while chromosome 2 had the greatest influence upon the overall response of the system to temperature. In a similar way, Schnee and Thompson (1984b) found that the genetic control of response to temperature can be different at 18° and 29°.

Linkage relationships between factors involved in genotype x environment interactions often indicate the relative importance of immediate versus future fitness (Mather 1942). Furthermore, linkage studies can be used to distinguish between correlated effects and pleiotropy of factors on a given chromosome. Schnee and Thompson (1984b) found chromosomes that affect sternopleural bristle number as well as the response of this developmental system to temperature. Studies of the intrachromosomal architecture of such chromosomes could reveal whether these components of a quantitative system are due to a single polygenic locus (Thompson and Thoday 1974) or to separate loci with different effects.

In our study, we isolated individual third chromosomes from lines selected for increased or decreased bristle number at 18°, 25° and 29°C. Recombinational mapping of

polygenic loci allowed us to investigate the linkage relationships of factors that affect sternopleural bristle number at 18° and 25°. While a relatively tight linkage between response to temperature and bristle number was found in some chromosomes, in most instances the factors that affect bristle number and those that affect response to temperature appeared to occupy separate sites on chromosome 3.

MATERIALS AND METHODS

All of the selection lines used in this experiment were derived from a common base stock, which was produced by intercrossing four isofemale strains (OK-1505, OK-1513, OK-1520 and OK-1526) collected in Noble, Oklahoma, in May 1979. Lines were selected for either decreased or increased sternopleural bristle number at 18°, 25° or 29°C. Each selection line will be referred to by its direction of selection, replicate number and the selection temperature. Thus, the High-1-25 line refers to replicate-1 of the lines selected for increased sternopleural bristle number at 25°. A more detailed description of these selection lines can be found in Schnee and Thompson (1984b).

The recessive markers used for mapping bristle number modifiers were dumpy (dp, 2-13.0) and brown (bw, 2-104.5) on the second chromosome; and veinlet (ve, 3-0.2), scarlet (st, 3-44.0), rough (ro, 3-91.1), and claret (ca, 3-100.7) on the third chromosome. Mutants are described in more detail in Lindsley and Grell (1968).

All flies were raised on a standard cornmeal, molasses, yeast and agar medium seeded with live yeast (Ashburner and Thompson 1979). Temperature was maintained in incubators

set at 18±0.5°, 25±0.5° and 29±0.5°C.

Males from each selection line were crossed to females from an isogenic bw;st stock in order to extract single third chromosomes for study. A single heterozygous male (+/bw; +/st) from each cross was backcrossed to bw;st females to produce a stock of flies which carried both a second and a third test chromosome. Since each of these stocks originated from a single male, each line is homogeneous with respect to the test chromosomes it carries. These stocks were maintained by backcrossing +/bw; +/st males to bw;st females each generation.

The effect that various segments of chromosome 3 had on bristle number was tested by crossing +/bw; +/st test males to an inbred standard dp; ve st ro ca line (Figure 1). The dumpy females heterozygous for chromosome 3 were isolated (dp/dp; + + + +/ve st ro ca). These females were backcrossed to standard dp; ve st ro ca males in replicates at 18° and 25°. The offspring produced from this cross were then scored for their sternopleural bristle number. The recessive markers carried by these offspring allowed the classification of each region of chromosome 3 with respect to its test or standard chromosome origin. For example, the + + ro ca recombinant carries polygenic loci from the selected chromosome to the left of ro and loci of standard strain origin from the region of ro to the right tip of the chromosome.

Progeny testing of the Low-2-29 ve + + + and + st ro ca recombinant classes was carried out by backcrossing individual recombinant males to standard dp; ve st ro ca females, in order to produce multiple copies of each recombinant chromosome. In this way, random environmental effects tend to be averaged out, permitting a more accurate estimate of the polygenic makeup of a given chromosome. Approximately 20 recombinant chromosomes of each class were progeny tested. Tests of each recombinant were carried out at both 18° and 25°, so that the differential effects of temperature could be evaluated.

A principal assumption of progeny testing is that heterozygous males do not produce recombinant chromosomes. This allows the testing of the same chromosome, unaltered, for several generations. Male recombination is, however, known to occur in some strains of Drosophila at fairly high levels (Thompson and Woodruff 1978). To test for the presence of male recombination, males heterozygous for test and standard third chromosomes were crossed to dp;ve st ro ca females and the progeny were scored for recombinants. Although recombination was found to occur at low levels (approximately 0.1% when clusters are taken into account), it did not pose a serious problem in these assays, since any recombinants produced by male crossing over could be detected by means of the recessive markers carried by the standard and could be discarded.

All analyses of variance were carried out using individual degree of freedom comparisons of means for unequal sample sizes (Sokal and Rohlf 1981). Test cited in the results are those for male data only, unless otherwise indicated.

The standard deviation used in determining map distances was calculated as $(\underline{p} \times \underline{q} \times \underline{n})^{0.5}$, where $\underline{n}$ is the sample size and $\underline{p}$ and $\underline{q}$ are the frequency of recombinants which involved a crossover to the right and left, respectively, of the polygenic locus being mapped.

Mapping requires that each progeny test line be classified into "high" or "low" groups. Clustering analyses were used to provide an independent confirmation of our visual interpretation of the progeny test results. The difference between the mean of each progeny test line and the mean of each internal control (dp; ve st ro ca) standard, for two generations at 25°C, was used to calculate a distance matrix. Cluster analysis was done by the Unweighted Pair Group Method Using Arithmetic averages (UPGMA) using NT-SYS, a package of multivariate statistical programs (Rohlf, Kishpaugh and Kirk 1979).

RESULTS

Schnee and Thompson (1984b) found that chromosome 3 carried factors that altered sternopleural bristle number. In addition, these same chromosomes often influenced the response that the sternopleural system showed to changes in temperature. For example, flies carrying chromosome 3 of the High-1-25 line produced both a significant increase in bristle number (on average 1.58 bristles, $P < 0.001$) and a significantly reduced response to temperature changes. While the bw;st standard used in these tests increased by an average of 1.46 bristles when shifted from 25° to 18°, those lines carrying the test chromosome increased by only 0.72 bristles. The association of these two effects, bristle number and response to temperature, could be explained in several ways. If temperature sensitivity varies greatly among loci, one might expect to find some polygenic loci affecting bristle number while other might have a greater role in the response to temperature. Alternatively, a single locus might act upon both aspects of bristle number variability and might, therefore, be considered a pleiotropic locus. In either of these two cases, the question becomes one of linkage, in that two very closely linked loci will be

unresolvable from a single pleiotropic locus.

Recombinational mapping has been used by Spickett (1963), Davies (1971) and others as a powerful tool in the resolution of correlated polygenic effects associated with a single chromosome. The technique examines various classes of recombinant chromosomes to determine whether the correlated effects are traceable to the same or to different regions of a chromosome.

Flies carrying test chromosomes were crossed to the standard inbred line dp; ve st ro ca which carries recessive markers distributed along chromosome 3 (Figure 1). Bristle numbers were counted in males and females from each of the resulting parental and recombinant chromosome classes (Tables 1 and 2). Recombinational mapping was carried out for 12 third chromosomes isolated from lines selected for increased or decreased sternopleural bristle number at 18°, 25° or 29°. The breeding program tested replicate chromosomes at 18° and 25° so that it was possible to score each of the recombinant chromosomes for its effect on bristle number and its relative response to temperature.

The results of the High-2-29 line are summarized in Figure 2. The data are consistent with the hypothesis that one or more polygenic loci having significant effects on bristle number are located between veinlet and scarlet. All recombinants which carried the veinlet-scarlet region of the High-2-29 chromosome had high mean sternopleural bristle

numbers (for example, pooling 18° and 25° scores from Tables 1 and 2, + + ro ca and + + + ca were not significantly different from the + + + + parental, $F_{1,330} = 0.00$ and $F_{1,275} = 0.88$, respectively). The complementary chromosome classes (ve st + + and ve st ro +) had low bristle numbers like the ve st ro ca standard ($F_{1,304} = 1.71$ and $F_{1,206} = 0.35$, respectively).

Response to temperature is indicated by the slopes of the lines in Figure 2 and is quantified by the bar graphs on the figure. The factor or factors determining response to temperature also appear to map to the region between veinlet and scarlet. The + + + +, + + ro ca and + + + ca classes show a small increase (about one bristle or less) when shifted from 25° to 18°. In contrast, the ve st ro ca, ve st + + and ve st ro + classes show large increases (about two bristles) when subjected to a similar temperature shift. These differences were generally significant, though limited samples sometimes obscured the relationship. In High-2-29 recombinant females, for example, bristle numbers in the ve st + + class were significantly different from those in + + + + ($P < 0.05$), but were not significantly different from the ve st ro ca standard. The reciprocal class (+ + ro ca) was significantly different from only the ve st ro ca standard ($P < 0.001$). Thus, in the High-2-29 line, the major polygenic modifiers of mean sternopleural bristle number and those determining the overall response to

temperature lie in the same region of chromosome 3.

The pattern of results found for the Low-2-29 line (Figure 3) is similar to that described for High-2-29. The recombinant chromosomes which carry the region between veinlet and scarlet from the Low-2-29 chromosome are low in bristle number (mean bristle numbers at 25°, for example: + + + +, 14.55; + + ro ca, 14.63; + + + ca, 14.56) and show a high response to temperature (+ + + +, 3.42; + + ro ca, 3.16; + + + ca, 3.51). On the other hand, those chromosomes which carry both the veinlet and scarlet markers are high in bristle number (ve st ro ca, 18.32; ve st + +, 18.39; ve st ro +, 18.71) and low in their response to temperature (ve st ro ca, 1.85; ve st + +, 1.87; ve st ro +, 2.39). The ve + + + and + st ro ca classes are intermediate for both characters. This is consistent with the view that the factors responsible for bristle number and response to temperature lie within the same region of chromosome 3.

Figure 4 shows the results of mapping chromosome 3 from the High-1-25 line. The pattern for mean sternopleural bristle number is the same as that found for the High-2-29 line, again pointing to the importance of the ve-st region in influencing bristle number. Response to temperature, however, is different. This difference can be seen best in the female data in which the + st ro ca class (mean bristle number = 20.88 at 25°) is significantly different from the ve st ro ca standard (mean = 18.63 at 25°) in average bristle

number ($F_{1,252}$ = 27.54, $P < 0.001$). Yet, the + st ro ca class is not significantly different from the standard in its response to temperature ($F_{1,252}$ = 0.91). This difference can be explained by hypothesizing that the polygenic loci determining response to temperature and those determining bristle number occupy different sites on chromosome 3 of the High-1-25 line. Analysis of response to temperature of the various classes of chromosomes reveals that those carrying the st and ro markers are high in their response to temperature (that is, a temperature shift produces a large change in bristle phenotype), while those carrying the scarlet-rough region of the High-1-25 chromosome show a small response. Thus, for the High-1-25 chromosome, the genetic loci determining mean sternopleural bristle number appear to lie between veinlet and scarlet, while those that influence the sensitivity to temperature are located between scarlet and rough.

While the results from the High-2-29 and Low-2-29 lines suggest that there is relatively tight linkage between the modifiers of these separate components of the bristle phenotype, most of the lines in which mapping was carried out seem to confirm the loose linkage typified by the High-1-25 line. Of the five other lines displaying significant differences from the standard in their response to temperature (High-2-25, Low-1-25, Low-2-25, High-1-29 and Low-2-18), all displayed a pattern of loose linkage.

In the Low-2-29 line, the ve + + + class showed an intermediate mean bristle number (16.05 at 25°). Since a crossover can occur anywhere between veinlet and scarlet, some ve + + + recombinants will carry the polygenic allele that reduces bristle number in the Low-2-29 chromosome and some will not (ve L + + + if recombination is between ve and the low factor; ve H + + + if recombination is to the right of the polygenic locus). The ve + + + class is, therefore, intermediate because the chromosomes are heterogeneous with respect to polygenic alleles. In order to map the low factor, one must be able to classify each ve + + + chromosome into "high" and "low" categories unambiguously. Phenotypic classification in the original recombinational mapping test would be based upon independent samples of one fly, and it thus becomes impossible to distinguish genetic effects from environmental noise. One way of overcoming this problem is progeny testing, which allows the genotype of a given recombinant male to be replicated exactly over several generations. In this way the effect of each initial recombinant chromosome can be examined in a large number of individuals. A large sample size allows the effect of the environment to be averaged out and assists in the classification of each recombinant chromosome with respect to its effect on bristle number.

The Low-2-29 ve + + + and + st ro ca recombinants were tested for two generations at 25° and one generation at 18°.

The results of the ve + + + progeny test at 25° are seen in the first two lines below the histogram in Figure 5. Two groups of recombinant chromosomes can be distinguished. The tests of the + st ro ca chromosomes also revealed two groups of recombinant chromosomes, confirming that the recombinants were heterogeneous in polygenic makeup. The progeny tests of + st ro ca are similar to those in Figure 5, but are not illustrated since viability difficulties prevented further tests at 18°.

The frequencies of the high and low recombinant classes can be used to map the polygenic locus determining bristle number. The classification of each recombinant was confirmed using cluster analysis. A total of 23 out of 31 recombinants (74%) could be classified as having been produced by a crossover between the ve locus and the polygenic locus affecting bristle number. Since the map distance between ve and st is approximately 43.8 cM, the bristle locus is estimated to be 74% of this distance to the right of ve. The bristle determining locus can thus be located at 32.6± 2.3 cM. In keeping with the rules of nomenclature for polygenic loci (Thompson and Thoday 1974), this locus will be referred to as PL(3)sp^{fs}, for sternopleural bristle-fahrenheit sensitive.

That a temperature-dependent effect is associated with this factor is seen in the tests of the recombinant line at 18° (Figure 5). While the two classes are still distinct,

the magnitude of the difference between the two groups is smaller. Thus, the relative effect of $\underline{PL(3)sp^{fs}}$ on bristle development is reduced at 18°. This could explain the increased response to temperature associated with chromosome 3 of the Low-2-29 line. Since the effect of this locus is reduced at 18°, the increase in sternopleural bristle number due to a reduction in temperature will be even greater. Temperature sensitivity of the locus, therefore, enhances the natural environmental effect. It is, however, impossible to eliminate the alternative hypothesis that the temperature-dependent effect could be due to a locus tightly linked to the bristle-determining locus.

DISCUSSION

Mather (1943) presented the first unified theory relating linkage to evolution, though the origin of his ideas can be traced back as early as Bridges (1922) and Fisher (1930). Mather's theory of balanced polygenic combinations addressed the dual problems of fitness and adaptability. In the short term, organisms are faced with the immediate problem of adapting to their own unique niche. In this sense, selection should favor similar phenotypes which show maximum fitness, and any heterogeneity in genotypes may produce offspring with relatively lower fitness. In the long term, however, variability is needed if the population is to retain the ability to adapt to an unpredictably changing environment. Mather's solution to this apparent contradiction was to propose that the chromosome consisted of a balanced polygenic architecture. In this view, stabilizing selection should produce chromosomes with tightly-linked alternating "+" and "-" loci which would produce an optimum phenotype of high fitness. Such a chromosome would maintain variability, since it contained both high and low factors, though variation would only be released slowly by recombination.

While this view represents one answer to the paradox of long term versus short term adaptability, one must realize that it is only one of many possible solutions. For example, in the case of environmental cycles that are short relative to the generation time of a species, loose linkage relationships would allow more rapid responses of the genome to the environment. In this sense, linkage relationships may give an indication of the relative importance of short term fitness versus long term needs of a particular species.

In our study we found loose linkage between factors affecting sternopleural bristle number and those that influenced the response of this system to temperature. This type of architecture implies a strategy of flexibility in which the factors influencing these components of bristle development can be manipulated rapidly by natural selection to meet the problems posed by unpredictable changes in temperature.

Parsons (1975) has related the genetic variability of a species having a broad niche, such as D. melanogaster, to those that prefer a more restricted set of environmental conditions, such as D. simulans. In general, D. melanogaster was found to have more chromosomal variability than D. simulans. Our results confirm that the D. melanogaster genome is flexible in that selection can produce a wide variety of responses. At one level this is seen in the variation of these lines both in their mean bristle number

and in their temperature sensitivity (Schnee and Thompson 1984b). At another, it is seen in terms of linkage relationships which allow either a slow or fast release of this variation. While it is tempting to explain the variability found in our experiments in terms of phenotypic plasticity of D. melanogaster, additional experiments are needed to demonstrate this. For example, it would be interesting to examine the linkage relationships in the more temperature-limited D. simulans. One would expect to find tight linkage between bristle and temperature-sensitive factors. Unfortunately, the markers needed for precise polygene mapping in D. simulans are not readily available. In addition, one might predict that the frequency of temperature-sensitive polygenic alleles will change seasonally to match the changing environmental temperatures.

Clearly, the D. melanogaster genome can be characterized as being flexible in its response to temperature. Our results from mapping within a chromosome and those reported by Caligari and Mather (1975) at the interchromosomal level point to an independence among factors determining bristle number and the response to temperature. Polygenic loci having the greatest effect upon bristle development can be different at 18° and 25° (Schnee and Thompson 1984b). Furthermore, Caligari and Mather (1980) studied 18 outbred lines derived from a Texas population and found that natural populations show genetic heterogeneity for polygenic loci

affecting the development of sternopleural bristles. The fact that our selection lines originated from a base stock which had only recently been taken from the wild confirms their findings.

The genetic basis of the response an organism shows to changes in the environment can be viewed in several ways. In biometrical genetics it is approached statistically in terms of a genotype x environment interaction. It is also profitable, however, to relate this phenomenon to conditional genetic effects (Schnee and Thompson 1984a). Conditional mutations are well documented in Drosophila and can often be understood at the molecular level (Suzuki et al. 1976). That conditional effects are also associated with polygenic loci in the sternopleural bristle system is implied by the temperature-dependent effects found for the chromosomes surveyed, and it is demonstrated by the response PL(3)sp^{fs} showed at 18° and 25°. There is no evidence to suggest that the nature of conditional expression of major genes is different from that in polygenic systems. Thus, genotype x environment interactions can perhaps best be thought of in terms of conditionally expressed polygenes.

Furthermore, conditional polygenes present certain implications about the variation found in polygenic systems. Schnee and Thompson (1984a) found polygenes in the scute system of D. melanogaster which could be characterized as being neutral under certain environmental conditions. At

both the chromosomal (Schnee and Thompson 1984b) and the intrachromosomal level, conditional neutrality may also play a role in the sternopleural bristle system. If conditional polygenes do not significantly affect bristle phenotypes in certain environmental conditions, they can be maintained in these circumstances with a minimum effect upon the genetic load. Conditional neutrality can thus represent a means by which an optimum phenotype can be maintained in the presence of potential genetic variability.

Thoday and Thompson (1976) have pointed out that some polygenes may have an effect on phenotypic variation and yet not be directly involved in the development of the character. The fact that the polygenic influence on temperature-sensitivity can be separated from that altering bristle number demonstrates that some polygenes have an indirect effect upon sternopleural bristle development. Genotype x environment interaction will, then, be determined by the conditional polygenes which a particular strain carries. Temperature-dependent polygenes, on the other hand, will affect bristle number, but will play only an indirect role in determining the genotype x environment interaction.

The $\underline{PL(3)sp^{fs}}$ locus maps to 32.6 cM on chromosome 3. It is interesting to note that Thoday, Gibson and Spickett (1964) have also mapped a polygenic locus affecting sternopleural bristle number ($\underline{PL(3)sp^{t2}}$) to approximately this same position. While it would be interesting to test

whether these bristle modifiers are allelic, the $\underline{PL(3)sp^{t2}}$ locus is no longer in stock. However, the apparent clustering of loci in this region, in spite of the small number (less than 12) of polygenes that have been mapped precisely, suggests that only a limited number of polygenic loci can alter the development of sternopleural bristles significantly.

In the few cases in which the variation of sternopleural bristle number between strains has been examined by polygene mapping, it has been found that only a few loci account for the majority of the phenotypic variance (Spickett and Thoday 1962; Wolstenholme and Thoday 1963; Thoday, Gibson and Spickett 1964; Gibson and Thoday 1966). Our results confirm this and indicate that the variation found for genotype x environment interactions can also depend upon relatively few polygenic loci. It is clear that polygenic systems are not as amorphous as was once thought and that similar studies of polygenic architecture should be helpful in understanding complex developmental systems.

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TABLE 1

Average male and female sternopleural bristle numbers at 25°C in each recombinant class produced by mapping a third chromosome extracted from three selected lines[a]

Recombinant class	Line		
	High-1-25	High-2-29	Low-2-29
+ + + +	21.72±2.53 (150)	22.00±2.31 (169)	14.55±1.67 (80)
ve st ro ca	18.35±2.03 (139)	18.37±2.03 (167)	18.32±1.78 (72)
ve + + +	20.15±2.32 (150)	20.35±2.49 (166)	16.05±2.20 (76)
+ st ro ca	19.57±2.12 (140)	19.76±2.08 (157)	17.01±1.63 (68)
ve st + +	18.71±1.91 (145)	18.53±2.18 (171)	18.39±1.66 (75)
+ + ro ca	21.20±2.23 (144)	21.85±2.31 (163)	14.63±1.26 (61)
ve st ro +	18.07±1.70 (64)	18.37±1.90 (81)	18.71±1.39 (26)
+ + + ca	21.82±2.25 (116)	21.50±2.01 (114)	14.56±1.54 (34)

[a]Mean bristle numbers ± s.d. is given; N is shown in parentheses.

TABLE 2

Average male and female sternopleural bristle numbers at 18°C in each recombinant class produced by mapping a third chromosome extracted from three selected lines[a]

Recombinant class	Line		
	High-1-25	High-2-29	Low-2-29
+ + + +	21.90±2.00 (176)	22.63±2.32 (169)	17.97±1.52 (57)
ve st ro ca	20.14±1.64 (123)	20.23±1.71 (142)	20.17±2.10 (59)
ve + + +	20.66±1.67 (155)	21.70±1.98 (170)	18.59±1.62 (51)
+ st ro ca	21.25±1.73 (117)	20.78±1.79 (136)	19.72±1.73 (45)
ve st + +	20.15±1.16 (153)	20.54±1.65 (158)	20.26±1.60 (50)
+ + ro ca	22.21±1.82 (147)	22.54±2.06 (165)	17.79±1.38 (36)
ve st ro +	19.49±1.55 (47)	20.30±1.52 (64)	21.10±1.22 (10)
+ + + ca	22.01±2.42 (93)	22.34±1.80 (95)	18.07±2.02 (13)

[a]Mean bristle numbers ± s.d. is given; N is shown in parentheses.

LEGENDS

Figure 1. -- Breeding program for recombinational mapping tests. Males heterozygous for chromosomes 2 and 3 of the selection line are mated to inbred marker strain females. The heterozygous males are backcrossed, and females showing the dumpy phenotype are crossed to standard strain males at 18° and 25°C. The recombinants produced from this cross are scored for their sternopleural bristle number.

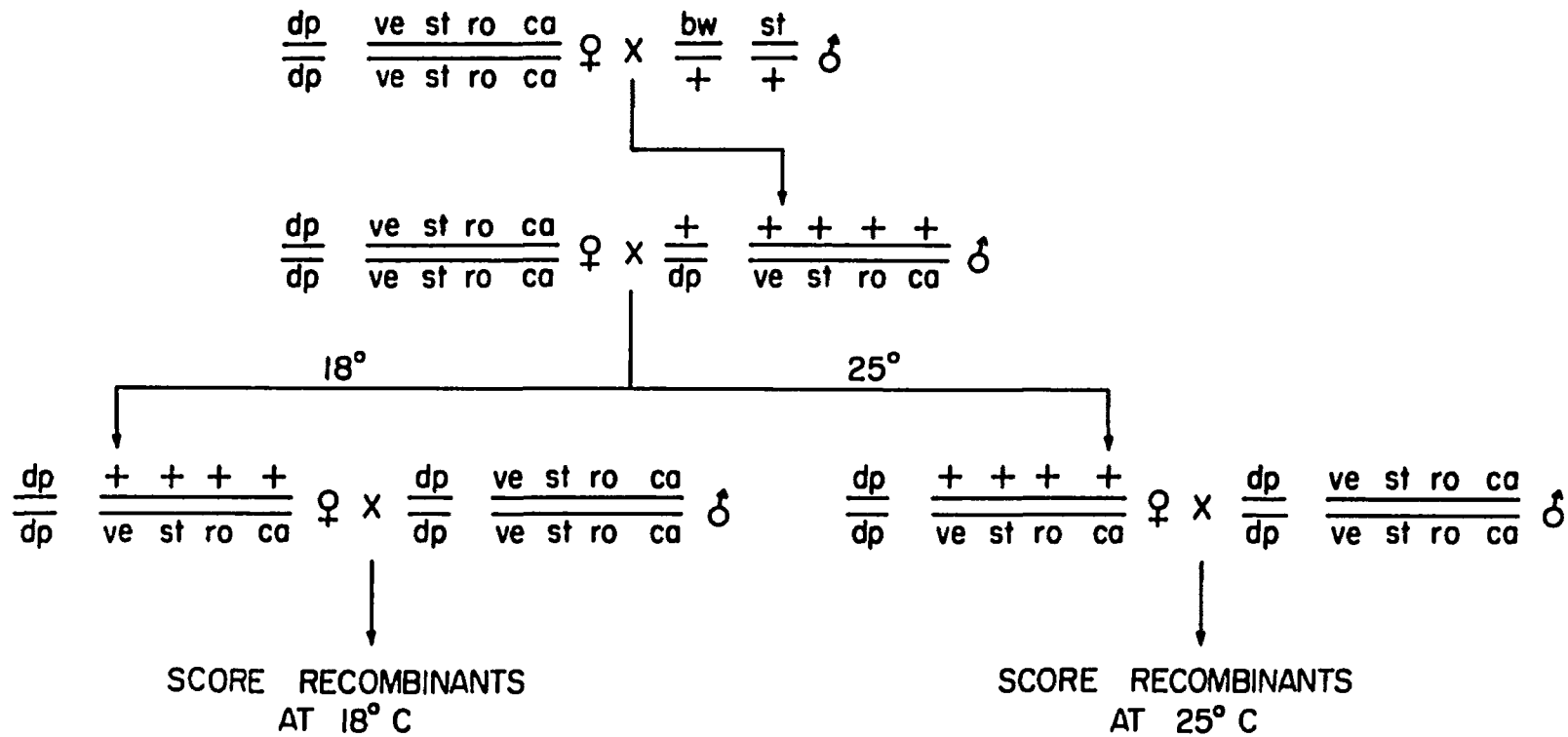
Figure 2. -- High-2-29 average male and female sternopleural bristle number at 25° and 18°C in each recombinant class produced by mapping chromosome 3. White areas of the recombinant chromosomes indicate regions that are derived from the selection line chromosome, black indicates regions derived from the standard chromosome and dotted areas indicate regions in which crossing over occurred. Bar graphs show the magnitude of changes in mean sternopleural bristle number due to a shift in temperature from 25° to 18°C.

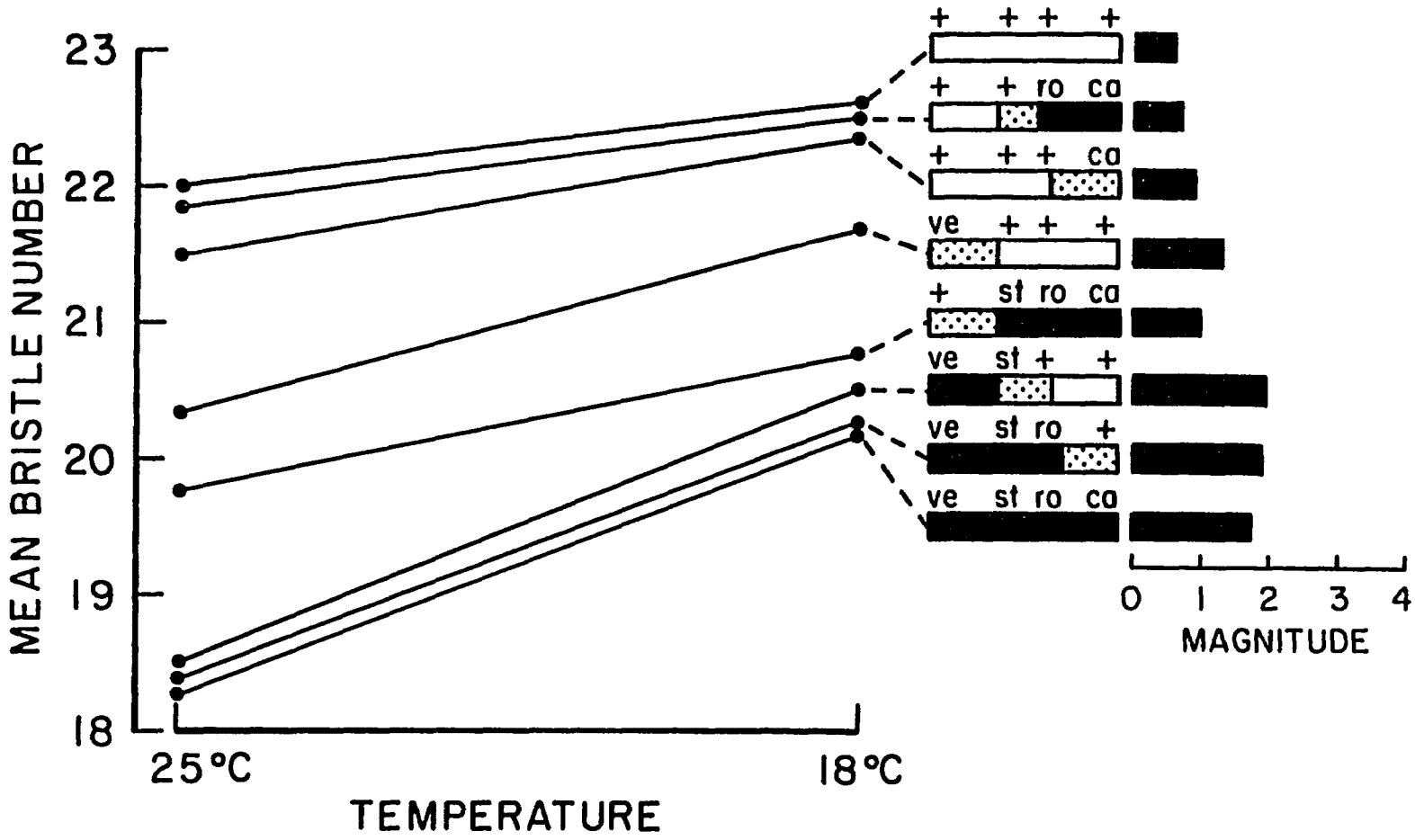
Figure 3. -- Low-2-29 average male and female bristle

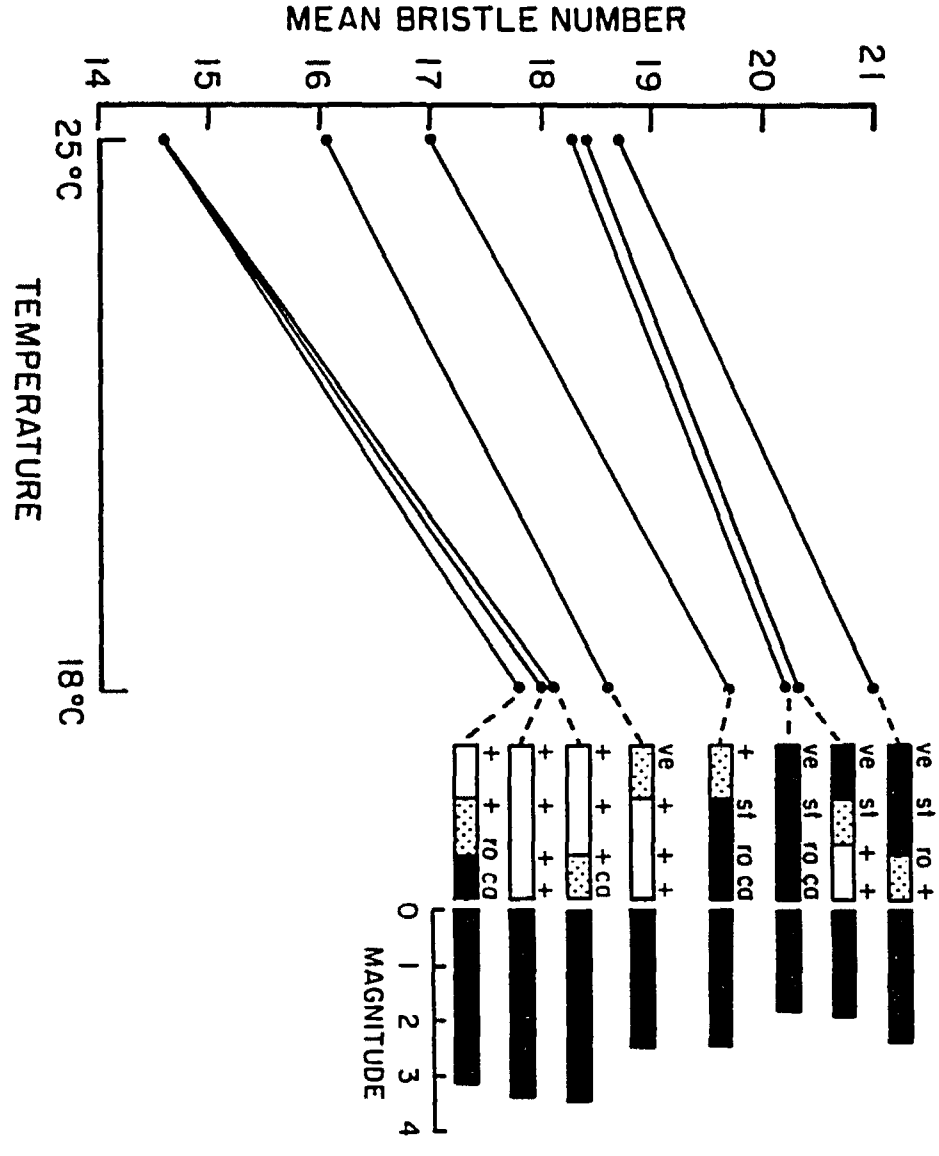
number at 25° and 18°C.

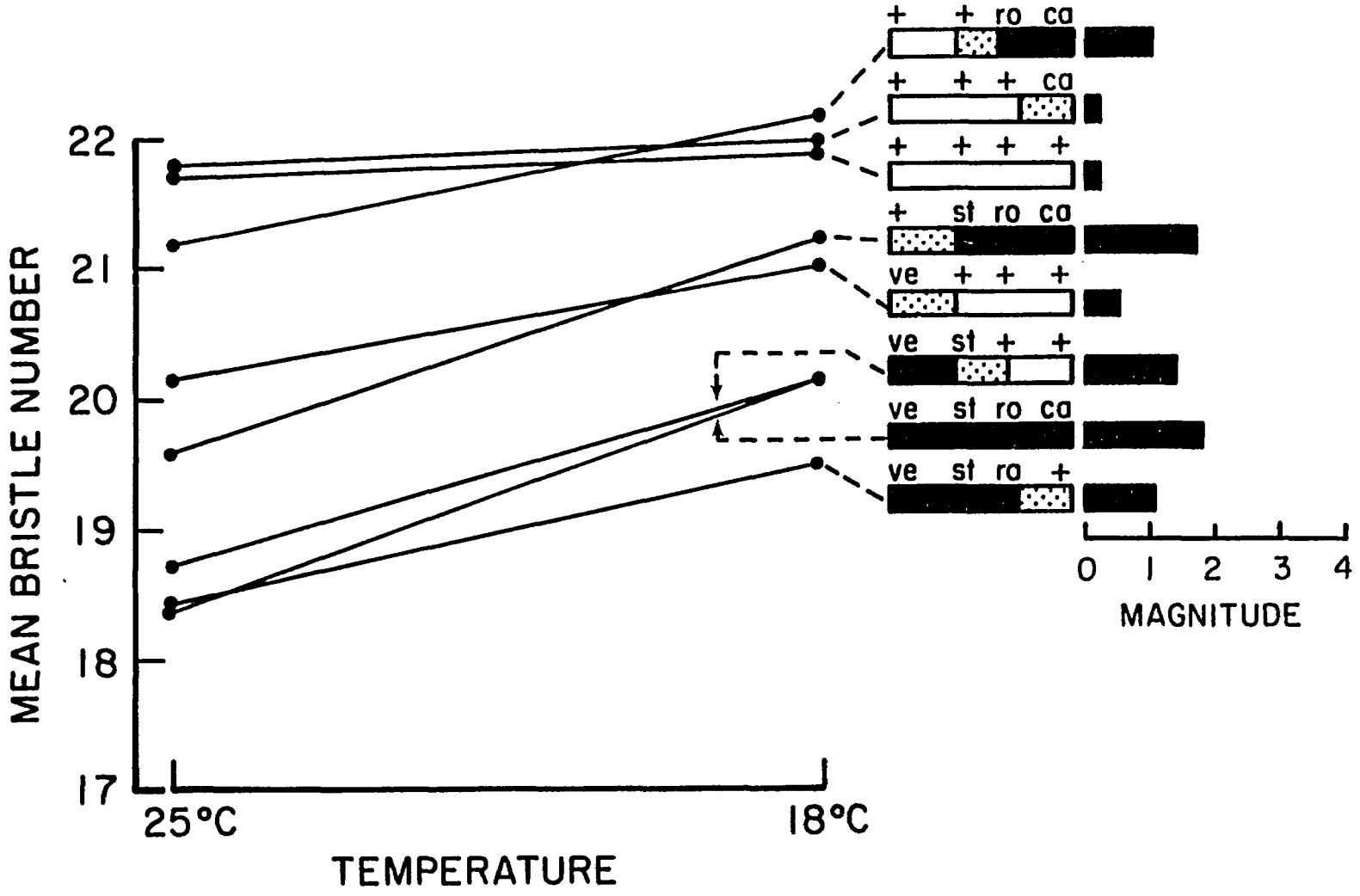
Figure 4. -- High-1-25 average male and female bristle number at 25° and 18°C.

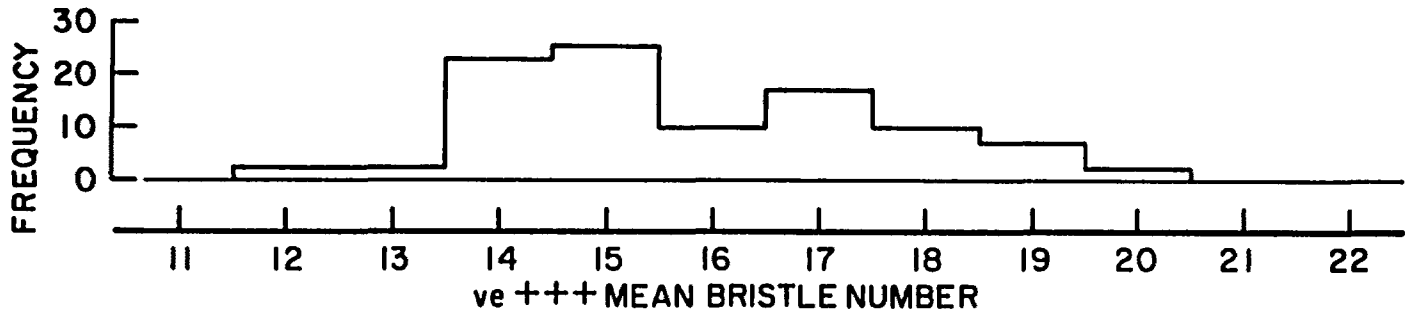
Figure 5. -- Progeny test of ve + + + recombinant males for two generations (PT1 and PT2). Following PT2, each line was tested for two generations at 18°. Dashed lines denote recombinants which had been classified as ve H + + + based on their response at 25°. See text for further explanation.

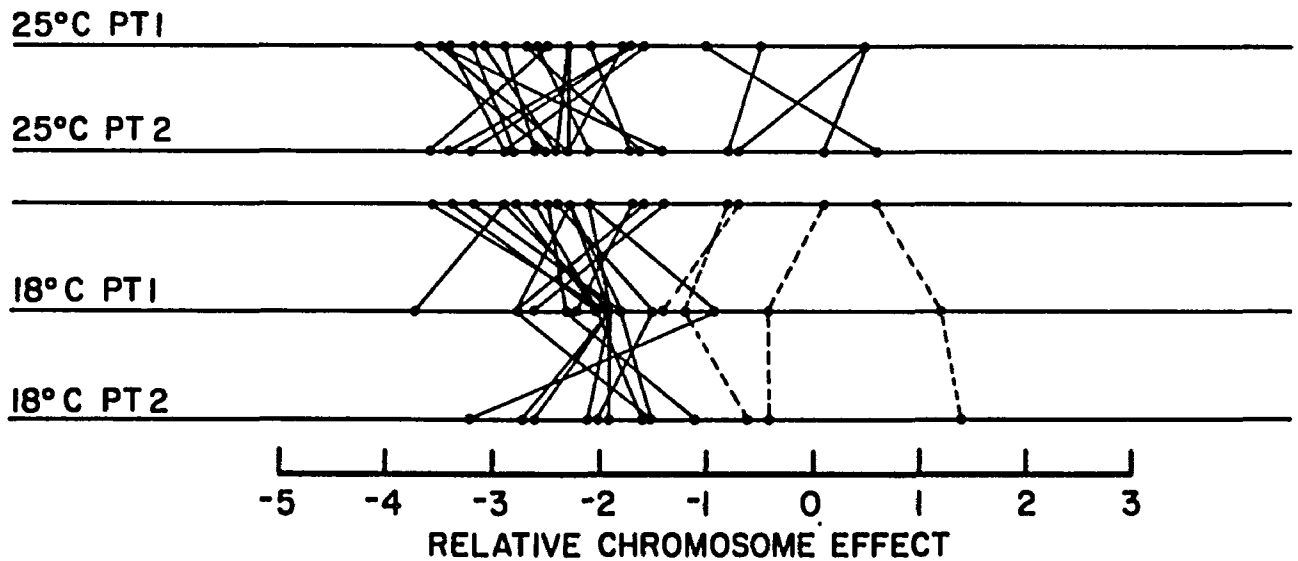

dp / dp ve st ro ca / ve st ro ca ♀ X bw / + st / + ♂
dp / dp ve st ro ca / ve st ro ca ♀ X + / dp + + + + / ve st ro ca ♂
18°
25°
dp / dp + + + + / ve st ro ca ♀ X dp / dp ve st ro ca / ve st ro ca ♂
dp / dp + + + + / ve st ro ca ♀ X dp / dp ve st ro ca / ve st ro ca ♂
SCORE RECOMBINANTS AT 18° C
SCORE RECOMBINANTS AT 25° C


MEAN BRISTLE NUMBER
23
22
21
20
19
18
25°C
18°C
TEMPERATURE
+ + + +
+ + ro ca
+ + + ca
ve + + +
+ st ro ca
ve st + +
ve st ro +
ve st ro ca
0 1 2 3 4
MAGNITUDE


MEAN BRISTLE NUMBER
14
15
16
17
18
19
20
21
25°C
TEMPERATURE
18°C
ve st ro +
ve st + +
ve st ro cg
+ st ro cg
ve + + +
+ + + cg
+ + + +
+ + + ro cg
0 1 2 3 4
MAGNITUDE


MEAN BRISTLE NUMBER
22
21
20
19
18
17
25°C
18°C
TEMPERATURE
+ + ro ca
+ + + ca
+ + + +
+ st ro ca
ve + + +
ve st + +
ve st ro ca
ve st ro +
0 1 2 3 4
MAGNITUDE


FREQUENCY
30
20
10
0
11
12
13
14
15
16
17
18
19
20
21
22
ve +++ MEAN BRISTLE NUMBER


25°C PT1
25°C PT2
18°C PT1
18°C PT2
-5
-4
-3
-2
-1
0
1
2
3
RELATIVE CHROMOSOME EFFECT

APPENDICES

APPENDIX I

Summaries of recombinational mapping of third chromosomes from each of the selection lines. Tables present the magnitude and significance of changes in bristle number due to chromosome region and assay temperature. In addition, I include a figure summarizing cluster analysis used to confirm the assignment of high and low categories in ve + + + recombinants produced in polygene mapping of Low-2-29.

Table 1. Magritude of the effects of High-1-25 recombinart male third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Stardard			ve st ro ca as Stardard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	163	-	-	-	1.20***	2.34***	-0.57
ve st ro ca	134	1.20***	-2.34***	0.57	-	-	-
ve + + +	148	0.75***	-1.45***	0.12	1.32***	0.88***	-0.45
+ st ro ca	133	1.16***	-1.23***	0.53	1.11***	1.11***	-0.04
ve st + +	148	1.11***	-2.31***	0.48	1.67***	0.08	-0.10
+ + ro ca	143	1.07***	-0.01	0.44	1.64***	2.33***	-0.13
ve st ro +	60	0.95***	-2.59***	0.31	1.51***	-0.26	-0.26***
+ + + ca	112	0.26	-0.23	-0.37	0.83***	2.11***	-0.94***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 2. Magnitude of the effects of High-1-25 recombinant female third chromosomes at 18° and 25°C, or sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	163	-	-	-	0.76***	2.78***	-1.03***
ve st ro ca	128	0.76***	-2.78***	1.03***	-	-	-
ve + + +	157	- 0.07	-1.35***	0.21	0.96***	1.42***	-0.82***
+ st ro ca	124	0.69***	-1.56***	0.97***	1.73***	1.22***	-0.06
ve st + +	150	0.51*	-2.43***	0.78***	1.53***	0.35*	-0.25
+ + ro ca	148	0.11	-0.21	0.39	1.15***	2.58***	-0.64***
ve st ro +	51	0.35*	-3.15***	0.62***	1.37***	-0.37	-0.41***
+ + + ca	97	0.11	0.44	0.39	1.14***	3.22***	-0.64***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 3. Magritude of the effects of High-2-25 recombirant male third chromosomes at 18° and 25°C, or sternopleural bristle number, usirg the + + + + or ve st ro ca parental classes as stardards.

		Effect Usirg:					
		+ + ro + as Stardard			ve st ro ca as Stardard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + ro +	143	-	-	-	1.64***	2.75***	-1.23***
ve st ro ca	105	1.64***	-2.75***	1.23***	-	-	-
ve + ro +	122	0.95***	-0.86***	0.54***	2.18***	1.89***	-0.69***
+ st ro ca	102	1.34***	-2.10***	0.92***	2.57***	0.64***	-0.30
ve st ro +	125	1.05***	-3.32***	0.63***	2.27***	-0.58	-0.59
+ + ro ca	137	0.80***	0.05	0.39	2.03***	2.80***	-0.83***

Significarce levels determined from analysis of variarce,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 4. Magritude of the effects of High-2-25 recombirant female third chromosomes at 18° ard 25°C, on sterropleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Usirg:					
		+ + ro + as Stardard			ve st ro ca as Standard		
Recombirart	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + ro +	152	-	-	-	0.64***	3.43***	-0.46***
ve st ro ca	99	0.64***	-3.43***	0.46***	-	-	-
ve + ro +	131	0.00	-1.12***	-0.17	0.46**	2.31***	-0.63***
+ st ro ca	118	0.53	-2.90***	0.35***	0.99***	0.53**	-0.10
ve st ro +	125	0.51	-3.32***	0.33***	0.96***	0.11	0.02
+ + ro ca	114	0.06	-0.12	-0.12	0.51***	3.31***	-0.58***

Significarce levels determined from analysis of variarce,

* 0.05 > p > 0.01; ** 0.01 > p > 0.001; *** p < 0.001

Table 5. Magnitude of the effects of Low-1-25 recombinant male third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	164	-	-	-	2.88***	-1.76***	0.55***
ve st ro ca	136	2.88***	1.76***	-0.55***	-	-	-
ve + + +	159	3.03***	0.57*	-0.40*	2.48***	-1.18***	0.16
+ st ro ca	135	2.84***	1.70***	-0.60***	2.28***	-0.06	-0.04
ve st + +	156	2.92***	0.86***	-0.51**	2.37***	-0.90***	0.05
+ + ro ca	145	3.32***	0.78***	-0.11	2.76***	-0.97***	0.45***
ve st ro +	47	3.03***	1.25***	-0.41***	2.47***	-0.51*	0.15***
+ + + ca	81	3.29***	0.63*	-0.15***	2.73***	-1.12***	0.41

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 6. Magnitude of the effects of Low-1-25 recombinant female third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	165	-	-	-	2.14***	-2.02***	0.05
ve st ro ca	131	2.14***	2.02***	-0.05	-	-	-
ve + + +	156	2.46***	0.89***	0.18	2.32***	-1.13***	0.32
+ st ro ca	135	2.42***	1.73***	0.15	2.29***	-0.30*	0.28
ve st + +	158	2.16***	1.34***	-0.11	2.03***	-0.68***	0.03
+ + ro ca	157	2.92***	0.66***	0.65***	2.78***	-1.37***	0.78***
ve st ro +	61	2.36***	1.75***	0.09***	2.23***	-0.27*	0.23**
+ + + ca	74	2.54***	0.44	0.27	2.41***	-1.58***	0.41

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 7. Magritude of the effects of Low-2-25 recombirant male third chromosomes at 18° and 25°C, on sternopleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	102	-	-	-	2.74***	-1.76***	0.18*
ve st ro ca	74	2.74***	1.76***	-0.18*	-	-	-
ve + + +	102	2.60***	0.48	-0.32	2.42***	-1.28***	-0.14
+ st ro ca	83	2.76***	1.36***	-0.16	2.58***	-0.40	0.02
ve st + +	92	2.55***	1.11***	-0.35	2.37***	-0.64*	-0.19
+ + ro ca	94	3.11***	0.38	0.19	2.93***	-1.38***	0.37**
ve st ro +	13	1.53***	0.47	-1.38***	1.35***	-1.29***	-1.21***
+ + + ca	36	3.10***	-0.04	0.19***	2.92***	-1.80***	0.37***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 8. Magnitude of the effects of Low-2-25 recombinant female third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	106	-	-	-	2.29***	-1.79***	0.36*
ve st ro ca	83	2.29***	1.79***	-0.36*	-	-	-
ve + + +	104	2.12***	0.41	-0.52*	1.77***	-1.38***	-0.17
+ st ro ca	75	2.30***	1.39***	-0.35**	1.94***	-0.40	0.00
ve st + +	99	2.04***	1.09***	-0.61**	1.68***	-0.70**	-0.25
+ + ro ca	99	2.52***	0.55*	-0.13	2.17***	-1.24***	0.23
ve st ro +	25	2.75***	0.44*	0.10***	2.39***	-1.35*	0.45**
+ + + ca	41	2.43***	0.62*	-0.22***	2.08***	-1.17**	0.14*

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 9. Magnitude of the effects of High-1-29 recombirant male third chromosomes at 18° and 25°C, on sterropleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	87	-	-	-	1.94***	3.03***	0.65
ve st ro ca	61	1.94***	-3.03***	-0.65	-	-	-
ve + + +	74	1.87***	-1.19***	-0.71*	1.22***	1.84***	-0.06
+ st ro ca	62	2.56***	-1.13***	-0.03	1.91***	1.90***	0.62
ve st + +	78	2.65***	-2.52***	0.07	2.00***	0.50	0.71**
+ + ro ca	81	2.24***	0.59	-0.35	1.59***	3.62***	0.30*
ve st ro +	24	2.48***	-2.22***	-0.10***	1.84***	-0.80	0.55
+ + + ca	45	2.87***	0.63	0.28*	2.22***	3.65***	0.93

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 10. Magnitude of the effects of High-1-29 recombinant female third chromosomes at 18° and 25°C, or sterropleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	90	-	-	-	1.12***	3.57***	-0.35**
ve st ro ca	82	1.12***	-3.57***	0.35**	-	-	-
ve + + +	82	1.04***	-1.76***	0.27	1.39***	1.81***	-0.08
+ st ro ca	77	0.80**	-2.14***	0.03	1.15***	1.43***	-0.32*
ve st + +	88	0.81**	-3.24***	0.04	1.16***	0.33	-0.31
+ + ro ca	85	0.83**	-0.14	0.06	1.18***	3.42***	-0.29**
ve st ro +	38	0.62***	-3.60***	-0.15	0.97***	-0.03	-0.50**
+ + + ca	51	0.43	-0.43	-0.34	0.78***	3.14***	-0.69***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 12. Magnitude of the effects of High-2-29 recombinant female third chromosomes at 18° and 25°C, on sterropleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	170	-	-	-	0.97***	3.15***	-0.58**
ve st ro ca	165	0.97***	-3.15***	0.58**	-	-	-
ve + + +	152	0.41	-1.40***	0.02	0.99***	1.75***	-0.55**
+ st ro ca	145	0.53*	-2.20***	0.14	1.10***	0.95***	-0.43**
ve st + +	169	0.93***	-2.89***	0.54*	1.51***	0.26	-0.04
+ + ro ca	166	0.07	-0.20	-0.32	0.65**	2.95***	-0.90***
ve st ro +	83	0.89**	-3.41***	0.50	1.46***	-0.27	-0.08*
+ + + ca	102	0.41	-0.56	0.02	0.98***	2.59***	-0.56***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 11. Magritude of the effects of High-2-29 recombirant male third chromosomes at 18° and 25°C, or sterropleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	168	-	-	-	1.52***	2.88***	-0.66**
ve st ro ca	144	1.52***	-2.88***	0.66**	-	-	-
ve + + +	166	1.56***	-1.18***	0.69**	2.22***	1.70***	0.04
+ st ro ca	148	1.12***	-1.89***	0.26	1.78***	0.99***	-0.40*
ve st + +	160	1.70***	-2.65***	0.83***	2.36***	0.22	0.18
+ + ro ca	162	1.24***	-0.02	0.38	1.90***	2.85***	-0.28
ve st ro +	62	1.67***	-2.52***	0.80	2.33***	0.35	0.15**
+ + + ca	107	1.06***	-0.22	0.02	1.72***	2.65***	-0.46***

Significance levels determined from analysis of variarce,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 13. Magnitude of the effects of Low-1-29 recombinant male third chromosomes at 18° and 25°C, on sterropleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	47	-	-	-	2.69***	-2.19***	0.45
ve st ro ca	41	2.69***	2.19***	-0.45	-	-	-
ve + + +	42	2.66***	1.08*	-0.47	2.21***	-1.11*	-0.02
+ st ro ca	25	2.22***	1.64***	-0.92**	1.77***	-0.55	-0.47
ve st + +	33	2.21***	2.05***	-0.93**	1.76***	-0.13	-0.47
+ + ro ca	35	3.35***	0.82	0.22	2.91***	-1.37***	0.67
ve st ro +	8	2.67***	2.79***	-0.47***	2.22***	0.60	-0.02*
+ + + ca	16	2.82***	1.01	-0.32***	2.37***	-1.18	0.13

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 14. Magritude of the effects of Low-1-29 recombirant female third chromosomes at 18° and 25°C, on sterropleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Usirg:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	49	-	-	-	1.87***	-1.20*	0.00
ve st ro ca	42	1.87***	1.20*	0.00	-	-	-
ve + + +	45	2.07***	0.19	0.20	2.06***	-1.01	0.20
+ st ro ca	39	1.25***	1.07*	-0.62	1.24**	-0.12	-0.62
ve st + +	47	1.73***	1.58***	-0.14	1.72***	0.38	-0.13
+ + ro ca	45	2.15***	0.32	0.16	2.14***	-0.88*	0.28
ve st ro +	17	2.07***	1.75***	0.20	2.07***	0.55	0.21
+ + + ca	14	2.12***	0.00	0.25	2.12***	-1.20*	0.26

Significance levels determined from analysis of variarce,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 15. Magnitude of the effects of Low-2-29 recombinant male third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	109	-	-	-	2.61***	-2.66***	1.07***
ve st ro ca	86	2.61***	2.66***	-1.07***	-	-	-
ve + + +	101	3.06***	1.09***	-0.62**	1.99***	-1.57***	0.45*
+ st ro ca	67	3.11***	2.11***	-0.57***	2.04***	-0.56*	0.50
ve st + +	93	2.88***	2.87***	-0.80***	1.81***	0.20	0.27
+ + ro ca	73	3.03***	0.03	-0.65***	1.96***	-2.64***	0.42
ve st ro +	20	2.98***	3.63***	-0.70***	1.91***	0.96	0.37*
+ + + ca	33	3.41***	0.76	-0.26***	2.35***	-1.90***	0.80

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 16. Magnitude of the effects of Low-2-29 recombirant female third chromosomes at 18° and 25°C, on sterropleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Usirg:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	118	-	-	-	2.39***	-3.02***	0.58***
ve st ro ca	99	2.39***	3.02***	-0.58***	-	-	-
ve + + +	102	2.49***	0.78**	-0.49**	1.91***	-2.25***	0.09
+ st ro ca	91	2.80***	2.27***	-0.18***	2.22***	-0.76***	0.41
ve st + +	96	2.37***	2.90***	-0.61***	1.79***	-0.13	0.02
+ + ro ca	85	2.99***	-0.26	0.01	2.40***	-3.29***	0.59***
ve st ro +	33	2.66***	3.35***	-0.31***	2.08***	0.33	0.27**
+ + + ca	35	3.22***	-0.10**	0.24***	2.64***	-3.12***	0.83

Significance levels determined from analysis of variarce,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 17. Magnitude of the effects of High-1-18 recombirant male third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Stardard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	170	-	-	-	2.16***	3.32***	-0.48***
ve st ro ca	129	2.16***	-3.32***	0.48***	-	-	-
ve + + +	144	0.87***	0.19	-0.81***	1.36***	3.52***	-1.29***
+ st ro ca	128	1.18***	-1.64***	-0.50	1.66***	1.68***	-0.98***
ve st + +	74	0.94***	-0.59	-0.74***	1.42***	2.73***	-1.22***
+ + ro ca	18	0.71***	-2.15***	-0.97***	1.19***	1.17**	-1.46***
ve st ro +	0	-	-	-	-	-	-
+ + + ca	10	0.84***	-1.09	-0.84***	1.32***	2.24***	-1.32***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 18. Magnitude of the effects of High-1-18 recombinant female third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	170	-	-	-	1.50***	3.57***	0.55
ve st ro ca	167	1.50***	-3.57***	-0.55	-	-	-
ve + + +	170	1.91***	-1.49***	-0.13	1.37***	2.09***	0.42
+ st ro ca	158	1.87***	-3.42***	-0.18*	1.32***	0.15	0.37
ve st + +	87	1.70***	-1.74***	-0.35	1.15***	1.83***	0.20
+ + ro ca	46	1.84***	-3.79***	-0.21	1.29***	-0.22	0.34
ve st ro +	8	2.89***	-3.51***	0.84***	2.34***	0.06	1.39
+ + + ca	10	2.12***	-0.08	-0.08***	1.57***	3.49***	0.63*

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 19. Magritude of the effects of High-2-18 recombirart male third chromosomes at 18° and 25°C, or sterropleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Usirg:					
		+ + + + as Standard			ve st ro ca as Stardard		
Recombirart	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	81	-	-	-	2.46***	1.68***	-0.06
ve st ro ca	63	2.46***	-1.68***	0.06	-	-	-
ve + + +	70	2.59***	-0.24	0.20	2.65***	1.43***	0.18
+ st ro ca	58	1.94***	-0.32	-0.45*	2.01***	1.36***	-0.51*
ve st + +	64	2.07***	-0.92**	-0.32	2.13***	0.75*	-0.39
+ + ro ca	65	2.64***	0.43	0.25	2.70***	2.10***	0.18
ve st ro +	25	1.67***	-1.26**	-0.72***	1.73***	0.41	-0.79***
+ + + ca	42	2.15***	0.23	-0.24*	2.22***	1.90***	-0.31*

Significarce levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 20. Magnitude of the effects of High-2-18 recombinant female third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	77	-	-	-	1.04***	1.85***	-0.57*
ve st ro ca	71	1.04***	-1.85***	0.57*	-	-	-
ve + + +	73	1.00***	-0.83**	0.53	1.58***	1.02***	-0.04
+ st ro ca	71	0.80*	-1.22***	0.33	1.37***	0.63**	-0.24
ve st + +	78	1.19***	-1.19***	0.72**	1.77***	0.65*	0.15
+ + ro ca	73	0.73*	-0.29	0.26	1.30***	1.56***	-0.31
ve st ro +	30	1.23*	-1.49***	0.77	1.81***	0.36	0.19
+ + + ca	37	2.44***	0.97	1.97	3.01***	2.82***	1.40*

Significance levels determined from analysis of variance.

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 21. Magnitude of the effects of Low-1-18 recombirant male third chromosomes at 18° and 25°C, or sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	169	-	-	-	2.08***	-1.20***	0.23*
ve st ro ca	145	2.08***	1.20***	-0.23*	-	-	-
ve + + +	158	2.31***	0.66***	0.00	2.08***	-0.54	0.23
+ st ro ca	129	2.40***	0.87*	0.09	2.17***	-0.33*	0.32
ve st + +	152	2.41***	0.68**	0.10	2.18***	-0.52*	0.32*
+ + ro ca	135	2.19***	0.56	-0.11*	1.96***	-0.64***	0.11
ve st ro +	56	2.61***	0.63	0.30*	2.38***	-0.57***	0.53
+ + + ca	81	2.47***	0.50	0.16**	2.24***	-0.70***	0.39

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 22. Magnitude of the effects of Low-1-18 recombinant female third chromosomes at 18° and 25°C, or sterropleural bristle number, using the + + + + or ve st ro ca parental classes as stardards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Stardard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	163	-	-	-	1.84***	-0.57	-0.40
ve st ro ca	143	1.84***	0.57	0.40	-	-	-
ve + + +	153	1.66***	0.20	0.22	2.06***	-0.37	-0.18
+ st ro ca	127	1.76***	0.32	0.32	2.16***	-0.24	-0.08
ve st + +	152	2.03***	0.24	0.59	2.43***	-0.33	0.19
+ + ro ca	135	1.80***	0.37	0.36	2.21***	-0.20	-0.04
ve st ro +	60	2.03***	0.32	0.59	2.43***	-0.24**	0.19***
+ + + ca	72	1.75***	0.49	0.31*	2.16***	-0.07	-0.09***

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 23. Magritude of the effects of Low-2-18 recombirart male third chromosomes at 18° and 25°C, on sterropleural bristle number, usirg the + + + + or ve st ro ca parental classes as standards.

		Effect Usirg:					
		+ + + + as Stardard			ve st ro ca as Stardard		
Recombirant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	73	-	-	-	2.12***	-1.48***	-0.05
ve st ro ca	69	2.12***	-1.48***	0.05	-	-	-
ve + + +	64	2.54***	0.51	0.47	2.59***	-0.96***	0.42*
+ st ro ca	55	1.83***	1.52***	-0.25**	1.87***	0.04	-0.30
ve st + +	63	1.35***	1.27***	-0.73***	1.39***	-0.20	-0.78*
+ + ro ca	55	2.82***	0.29	0.75	2.87***	-1.19***	0.70*
ve st ro +	11	1.61***	2.80***	-0.47***	1.66***	1.32**	-0.51**
+ + + ca	26	2.99***	0.92	0.91	3.03***	-0.56***	0.86

Significarce levels determined from analysis of variarce,

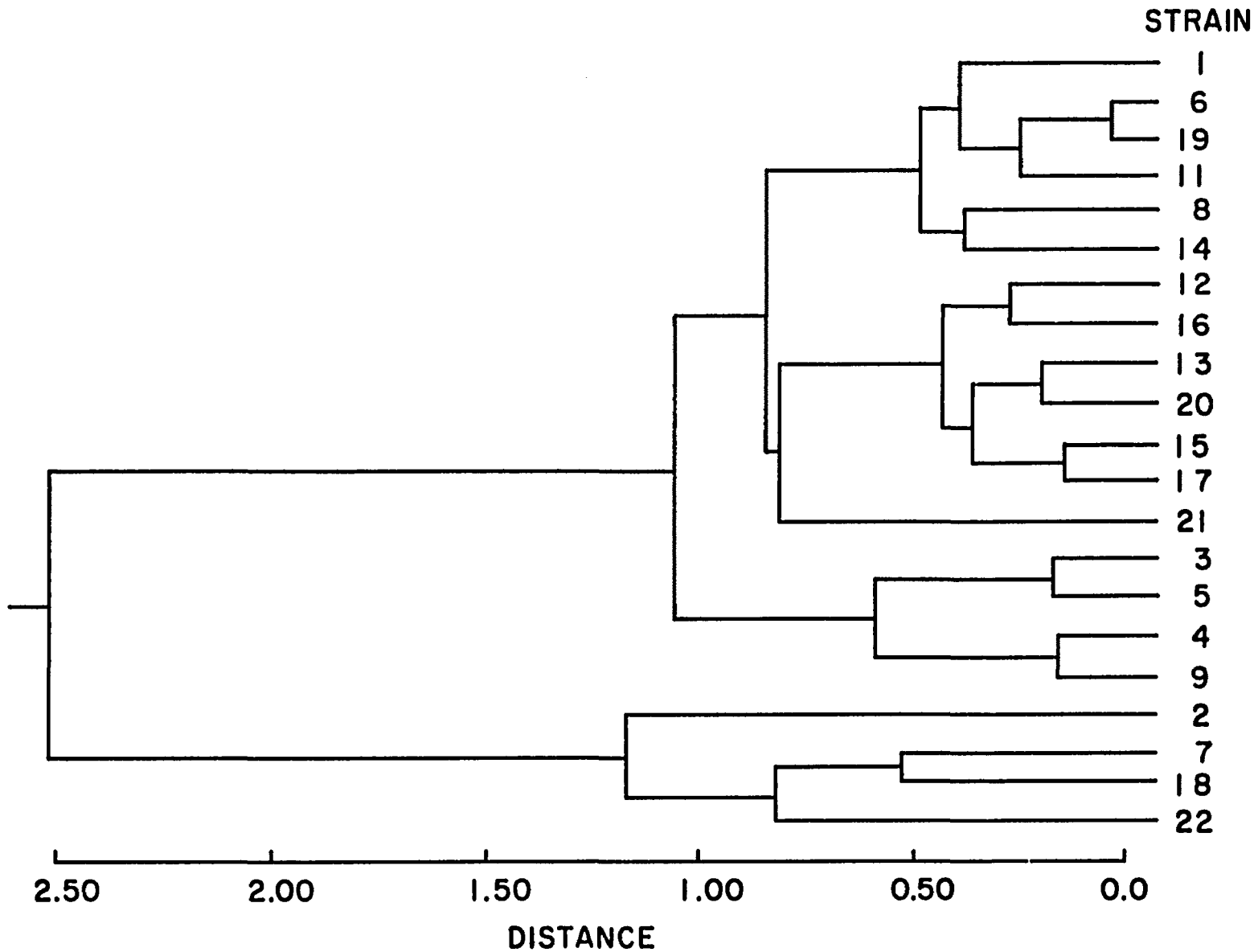
* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 24. Magnitude of the effects of Low-2-18 recombirant female third chromosomes at 18° and 25°C, on sternopleural bristle number, using the + + + + or ve st ro ca parental classes as standards.

		Effect Using:					
		+ + + + as Standard			ve st ro ca as Standard		
Recombinant	N	Temperature	Chromosome	C x T	Temperature	Chromosome	C x T
+ + + +	69	-	-	-	1.54***	-1.85***	-0.01*
ve st ro ca	68	1.54***	1.85***	0.01*	-	-	-
ve + + +	72	1.78***	0.51	0.25	1.79***	-1.34***	0.24*
+ st ro ca	57	1.97***	1.76***	0.44	1.98***	-0.09	0.43
ve st + +	70	1.44***	1.65***	-0.09	1.45***	-0.20	-0.10
+ + ro ca	63	1.99***	0.17	0.46	2.00***	-1.67***	0.45**
ve st ro +	20	1.47***	2.31***	-0.06	1.48***	0.46	-0.07*
+ + + ca	18	1.93***	0.28	0.40	1.94***	-1.57***	0.39

Significance levels determined from analysis of variance,

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$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DISTANCE

APPENDIX II

X chromosome and maternal effects in the High-25 and Low-25 replicate lines assayed at 18°, 25° (which was also the selection temperature), and $29^{o}C$.

Table 1. Effect of X Chromosome at 18°, 25°, and 29°C in lines selected for increased or decreased sternopleural bristle number.

	18°		25°		29°	
Line	N	X Chromosome	N	X Chromosome	N	X Chromosome
High-1-25	98	0.25	100	2.58***	90	1.58***
High-2-25	69	1.85***	83	2.49***	95	3.46***
Low-1-25	90	-1.01**	99	-1.48***	98	-0.94***
Low-2-25	49	0.05	100	-0.90***	90	-0.42

Significance levels are from t-tests of males taken from reciprocal crosses using bw;st as the standard.

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

Table 2. Maternal effect at 18°, 25°, and 29°C in lines selected for increased or decreased sterropleural bristle number.

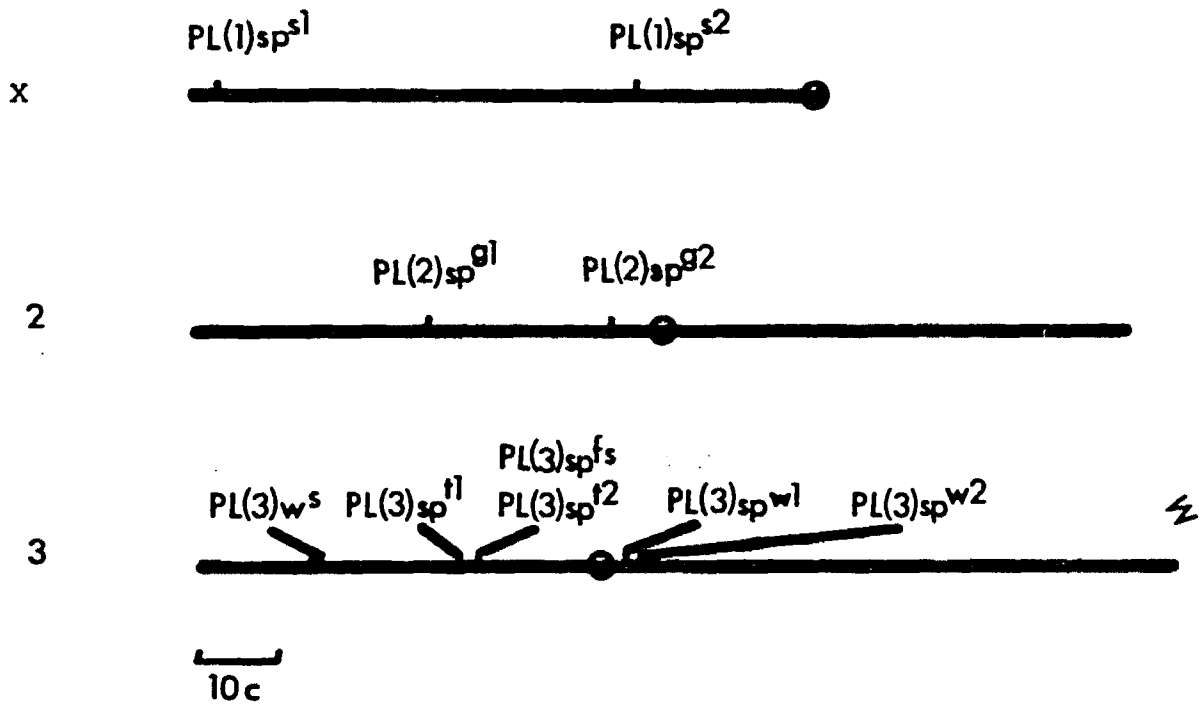
	18°		25°		29°	
Line	N	Maternal	N	Maternal	N	Maternal
High-1-25	100	0.58*	98	0.14	89	0.22
High-2-25	60	0.43	88	0.68	91	2.45***
Low-1-25	89	0.27	100	-0.48*	100	-0.28
Low-2-25	60	0.15	100	-0.38	90	0.08

Significance levels are from t-tests of females taken from reciprocal crosses using bw;st as the standard.

* $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$

APPENDIX III

Map of the known polygenic loci that affect the development and phenotypic variance in sternopleural bristles in *Drosophila melanogaster*. See Thompson and Thoday (1974) for references to original descriptions of all except *PL(3)sp*^{fs}.


PL(1)sp^s1
PL(1)sp^s2
X
PL(2)sp^g1
PL(2)sp^g2
2
PL(3)sp^fs
PL(3)w^s
PL(3)sp^t1
PL(3)sp^f2
PL(3)sp^w1
PL(3)sp^w2
3
10c

APPENDIX IV

Summary of biometrical analyses carried out on a High (P1) and Low (P2) sternopleural bristle selection line tested at 25° and 29°C. These data were presented at the American Society of Zoologists annual meeting in Dallas, Texas, in 1981.

ABSTRACT

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THE GENOME CAN RESPOND TO SELECTION IN DIFFERENT ENVIRONMENTAL CONDITIONS BY INVOLVING DIFFERENT GENETIC LOCI OR BY MODIFYING GENETIC INTERACTIONS. THE GENETIC ARCHITECTURE OF TWO STERNOPLEURAL BRISTLE SELECTION LINES IN DROSOPHILA MELANOGASTER (HIGH AND LOW) WAS STUDIED AT TWO TEMPERATURES (25° AND $29^{o}C$). THE ANALYSIS OF BRISTLE VARIATION WAS DONE BOTH BY BIOMETRICAL SCALING TESTS AND BY WHOLE CHROMOSOME ASSAYS AS USED IN POLYGENE MAPPING. AT BOTH TEMPERATURES, THE SCALING TESTS REVEALED A STRICTLY ADDITIVE SYSTEM FOR BOTH THE HIGH AND THE LOW SELECTION LINES. ON THE OTHER HAND, WHEN TESTED AT $25^{o}C$, THE WHOLE CHROMOSOME ASSAY OF THE HIGH LINE REVEALED A SIGNIFICANT INTERACTION ($P < 0.05$) BETWEEN CHROMOSOMES 2 AND 3. THIS INTERACTION IS LOST WHEN THE ASSAY OF THE SAME LINE IS DONE AT $29^{o}C$. IN ALL CASES, THE LARGEST EFFECT WAS ASSOCIATED WITH CHROMOSOME 3. THESE RESULTS INDICATE THAT THE RELATIONSHIPS AMONG GENES CAN CHANGE WITH ENVIRONMENT AND POINT OUT THE DISCREPANCIES WHICH CAN OCCUR BETWEEN BIOMETRICAL ANALYSES AND POLYGENE MAPPING.

SUPPORTED BY NIH GRANT RO1-GM-24809-03.

AVERAGE STERNOPLEURAL BRISTLE NUMBER AT 29°C AND AT 25°C ($\bar{x} \pm$ S.D)

Generation	29°C	25°C
P1	26.88 ± 1.68	28.65 ± 2.54
P2	12.95 ± 1.05	14.10 ± 1.07
F1	18.56 ± 2.61	19.05 ± 1.73
B1	21.04 ± 3.15	22.34 ± 3.76
B2	14.88 ± 1.90	17.06 ± 1.84
F2	17.73 ± 3.84	20.30 ± 3.60

BIOMETRICAL PARAMETERS FOR STERNOPLEURAL BRISTLE VARIATION

Parameter	29°C		25°C	
	Value ± S.D.	t	Value ± S.D.	t
m	18.98		23.77	
[d]	6.96 ± 1.0	7.04 ***	7.27 ± 1.4	5.28 ***
[h]	-4.58 ± 38.0	-0.12	-9.17 ± 38.5	-0.24
[i]	0.94 ± 17.0	0.05	-2.40 ± 16.6	-0.14
[j]	-1.61 ± 7.6	-0.21	4.00 ± 8.8	-0.45
[k]	4.17 ± 22.0	0.19	4.45 ± 22.5	0.20

APPENDIX V

Manuscript describing conditional neutrality of polygene effects in the scute bristle system of Drosophila melanogaster. This paper has been accepted and is in press in Evolution.

Conditional Neutrality of Polygene Effects

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In Press: Evolution

The complex genetic structure of natural populations poses an almost endless series of challenges to our powers of measurement and theoretical analysis. A case in point is the long-standing controversy between "selectionists", who propose that the high levels of genetic variation in nature are maintained by natural selection, and "neutralists", who account for it in terms of genetic drift and mutation pressure (Dobzhansky, 1970; Kimura, 1968). The controversy remains unresolved because unambiguous evidence favoring one or other view is extremely difficult to obtain, in spite of the fact that investigators generally concentrate upon genetic loci whose products and, to some extent, developmental functions are fairly well understood.

The problem is compounded, however, when one turns to quantitative variation. All populations show segregation for large numbers of polygenic loci which influence the expression of traits playing a major role in adaptation. Yet, individual polygenic loci are seldom distinctly separable from other loci or from environmental effects (Thompson and Thoday, 1979). Furthermore, our estimate of their selective importance is mainly based upon the degree to which they modify a particular phenotype. Thus, the problem of evaluating selection versus neutrality is strongly biased in favor of selection, in the sense that one only observes those polygenic loci that have a phenotypic effect and, given that effect, they must have at least a potential importance in natural populations, as artificial selection experiments amply demonstrate.

A more direct approach to trying to understand the value of

specific polygenic variants, therefore, is to try to identify polygenic loci which have no observable phenotypic effects under certain conditions. These could be considered "conditionally neutral", in the sense that their overt phenotypic expression is dependent upon the developmental context. This hypothesis is based upon the idea that environmental conditions can affect the biochemical characteristics of development so that some polygenic loci are more effective modifiers of the trait under one set of conditions (e.g., high temperature) and less so, or totally ineffective, under another (e.g., low temperature). We have used modifiers of scutellar bristle formation in Drosophila melanogaster to investigate this possibility.

Experimental Design

Polygenic systems often behave differently in different environments, and the scutellar bristle system of Drosophila is a useful model for studying this interaction. Pennycuik and Fraser (1964) have shown, for example, that the average scutellar bristle number in D. melanogaster increases as culture temperature is reduced. Yet, artificial selection can alter, or even reverse, the relationship between bristle number and temperature (Kindred, 1965; Druger, 1967), confirming that the expression of this interaction has a genetic component. The nature of this genotype x temperature interaction, however, is not well understood. Our prediction is that somewhat different loci are being selected under different temperature regimes.

To test this, we studied the differences in genetic architecture that are associated with the response of scutellar bristle number to artificial selection in two temperatures: 25°C, the normal culture temperature, and 29°C, which is near the upper limit for this species (Ashburner and Thompson, 1978). Here we are not really trying to explain the selection response per se. Rather, selection is simply an efficient means of pulling together the linked loci that either increase or decrease phenotypic expression so that they can be dealt with as homogeneous chromosomal units. The relative effectiveness of selected polygenic modifiers was estimated by assaying the phenotypic effects of isolated whole chromosomes at both 25° and 29°C. This enabled us to see, at least at the whole chromosome level, whether the same genes and interactions are expressed under different environmental conditions.

The simplest hypothesis is that polygenic loci will have qualitatively similar effects under a range of environmental conditions. The stipulation of "qualitatively" similar effects is necessary, because scaling due to environment-related changes in development may alter the phenotype quantitatively. Similarity therefore becomes our null hypothesis, and demonstrable differences, such as changes in sign (e.g., increasing rather than decreasing) or the statistically significant loss of phenotypic effects, would be evidence against this null hypothesis.

The sex-linked recessive mutation scute (sc, 1-0.0) was used to uncover segregating polygenic modifiers of scutellar bristle formation. Under normal conditions, the number of scutellar

bristles is canalized at four and modifiers are cryptic. Artificial selection was carried out in replicate High and Low lines in which five pairs of parents were selected from 20 pairs counted each generation.

Lines were maintained on a standard cornmeal, molasses, yeast, agar medium seeded with live yeast. Temperature was maintained in incubators set at 25±0.5°C or 29±0.5°C. A yellow body color mutation was included in the scute lines as a marker to identify possible contaminants. As expected, no contamination of selection lines was observed during the course of any experiments.

Heterozygous whole chromosome effects were measured using a chromosome substitution breeding program (Figure 1) in which inbred standard chromosomes were marked with the recessive eye color mutants brown (bw, 2-104.5) and scarlet (st, 3-44.0). For these experiments, however, the critical point is that a single autosome can be isolated from a selection line and be replicated so that its phenotypic effects can be measured under contrasting environmental conditions.

Results and Discussion

Responses for 20 generations of selection in two replicates are shown in Figure 2 (male data only; female responses were similar, except for having a slightly higher mean bristle number as is typical for this sex). Temperature itself accounted for only about 0.3 bristle difference in males (0.5 in females), with 25° flies being larger and generally having more bristles than those

at 29° (c.f., Parsons, 1961).

All lines responded well in both temperatures, but the most interesting comparison is among High lines. In spite of quantitative differences among replicates, it is clear that the 25° lines responded more rapidly than did the 29° lines and achieved a significantly higher mean bristle number. This contrast between 25° and 29° responses provides at least indirect evidence that different genetic effects are involved. If the genes selected at one temperature were also functionally important at the other temperature, one would expect the responses to be essentially the same. While two replicates are not conclusive, they encourage more definitive studies along these lines.

Furthermore, lines selected at 18° (Schnee, unpublished) showed an even faster response than did the 25° lines. Thus, there appears to be an inverse correlation between the rate of change in bristle number and the culture temperature. These results are similar to those reported by Gibson (1970), who selected for extra bristles in a set of non-scute lines cultured at different temperatures. He found that interchromosomal interactions differed among lines, indicating that the apparent genetic architecture of a trait can vary significantly when expression is measured in different environmental situations (see also Jinks and Connolly, 1975; Connolly and Jinks, 1975). The next step is to determine whether differences among lines are due to quantitatively different expression of the same genes in altered environments or to different genes playing the primary role at each temperature.

Using a standard whole chromosome substitution breeding program

(e.g., Thompson, 1975), the phenotypic effects of single chromosomes isolated from the 25° and 29° selection lines could be measured (Table 1) and compared to the expression each had in the alternate temperature (Table 2). In general, the response of the High lines at both temperatures could be accounted for by third chromosome loci increasing bristle number, while in the Low lines, both of the autosomes carried loci significantly reducing bristle number. The negative effect of chromosome 2 in the High 1 (25°) line and the positive effect associated with chromosome 3 in the Low 2 (29°) line are probably examples of accidental fixation of alleles caused by founder effects in the establishment of the lines. High 2 (25°) apparently carried recessive modifiers. In contrast to the results of Gibson (1970), no interchromosomal interactions were significant.

On the surface, therefore, the response of the sc selection lines at 25° and 29° appears to be roughly equivalent at the whole chromosome level. The error of this interpretation is shown by the data in Table 2, which summarizes the phenotypic effects of chromosomes tested in the alternate temperature. Seven of the 16 temperature shifts resulted in the complete loss of a significant phenotypic effect. The second chromosome alleles reducing bristle number in the Low lines at both 25° and 29°, for example, showed no effect when that same chromosome was tested at 29° and 25°, respectively. In these instances, polygenic alleles were only effective at the temperature in which selection occurred.

Even more striking, however, are examples such as that provided by the High 2 (25°) line in which polygenic alleles increasing bristle number were expressed at the alternate temperature (29°),

but apparently did not contribute to the genetic variation available for selection to act upon at 25°.

A comparable situation has been discussed by Wallace (1981) drawing upon a study by Druger (1962), in which body size in D. pseudoobscura was selected at 16° and at 25°, then tested at the alternate temperature. The response of some lines was consistent with the hypothesis that gene loci causing a reduction in body size were active at high temperatures but inactive at low ones, and vice versa for loci increasing body size. The "silent" loci were unaffected by selection and, thus, caused a partial loss of the earlier response when they were "activated" in the temperature shift.

When environmental conditions change, it is not really surprising to find that chromosome effects will be different and, in some cases, have an even greater influence than under the original selection conditions. Environmental changes can alter the physiological nature of the trait and, thus, influence the paths by which it can be readily modified. This is probably especially true of temperature in an ectothermic invertebrate, such as Drosophila. Loci acting upon the new critical biochemical steps become subject to selection pressures, while others may remain essentially neutral under these conditions. Thus, "neutral" polygenic loci may accumulate more or less passively until the appropriate conditions arise for their expression (c.f., Thoday, 1975). Clearly, neither selective advantage nor neutrality must be permanent.

Summary

Replicate outcrossed scute bristle lines of Drosophila melanogaster were selected for high and for low scutellar bristle number at 25° and at 29°C. Single second and third chromosomes were then isolated from each line using a breeding program that allowed us to replicate a given chromosome and test its phenotypic effects upon bristle number at each of the experimental temperatures. Several examples were found in which a chromosome lost its effect under the alternate temperature, supporting the hypothesis that specific loci or sets of loci can be phenotypically silent under certain environmental conditions.

Such conditional neutrality in polygene x temperature interactions is, therefore, one way to account for the robustness of the genetic system in dealing with diverse, unpredictable selection pressures. Even strong selection for phenotypic change under one set of conditions does not necessarily exhaust the genetic variation that might be uncovered under other conditions.

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Table 1. Magnitude of phenotypic effects associated with heterozygous whole second and third chromosomes isolated from replicated High and Low scutellar number selection lines.

Line	25°C			29°C		
	2	3	2x3	2	3	2x3
High 1	-0.35***	0.60***	0.09	0.08	0.19**	0.04
High 2	-0.03	-0.03	-0.05	0.00	0.22***	0.07
Low 1	-0.36***	-0.28***	0.01	-0.19**	-0.35***	0.05
Low 2	-0.32***	-0.49***	0.19	-0.27***	0.04	0.14

** $0.01 > p > 0.001$; *** $p < 0.001$

Table 2. Qualitatively different whole chromosome effects when isolated whole chromosomes are tested under different environmental conditions.

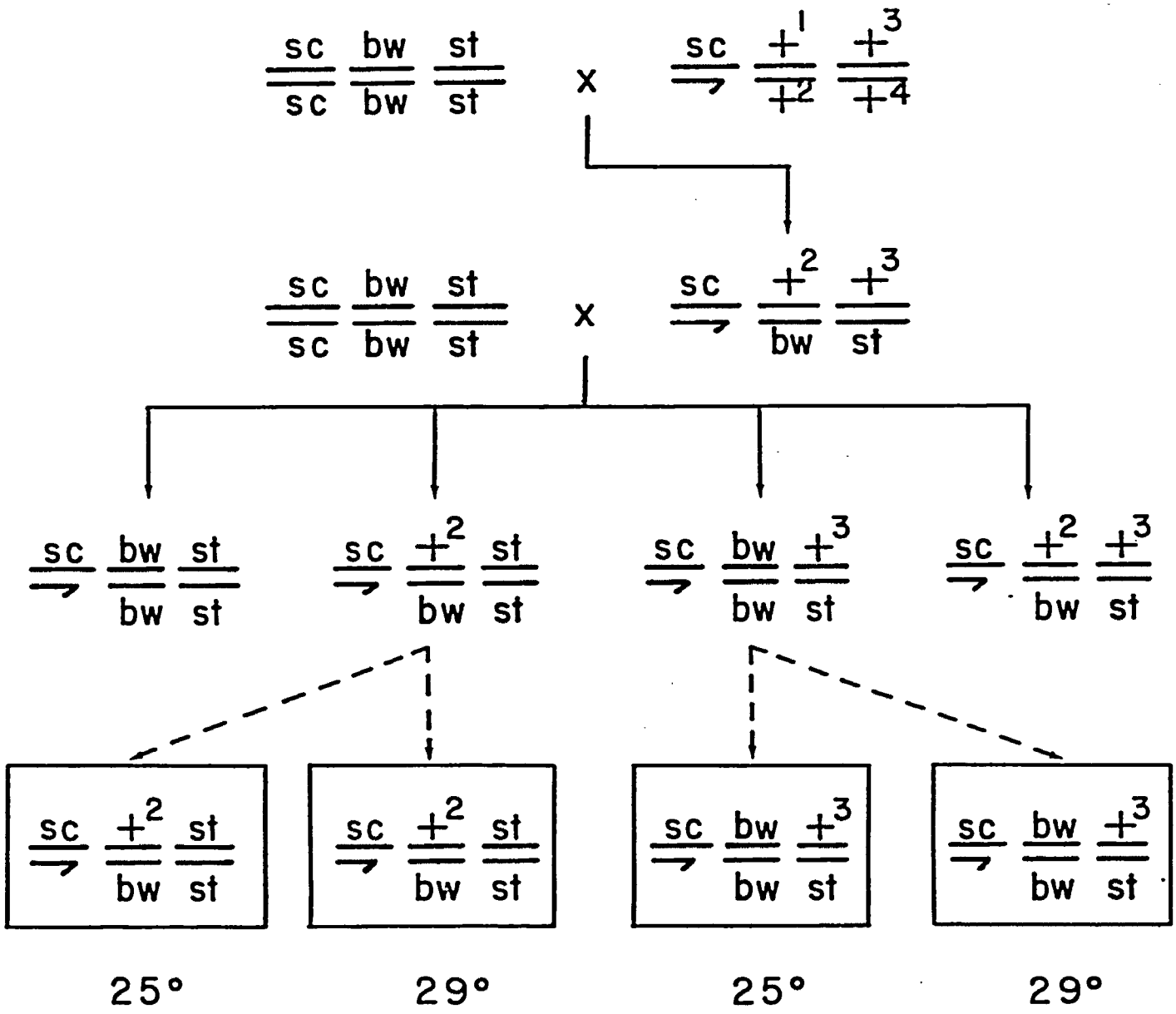
Selection Line	Chromosome Tested	Effect at Selected Temperature	Effect at Alternate Temperature
High 1 (25°)	2	-0.35***	-0.15
Low 2 (25°)	2	-0.32***	-0.04
High 1 (29°)	2	0.08	0.38***
Low 2 (29°)	2	-0.27***	-0.11
High 2 (25°)	3	-0.03	0.11***
Low 1 (25°)	3	-0.28***	-0.04
High 2 (29°)	3	0.22***	0.05

Significance levels are determined from analyses of variance, ***, $p < 0.001$.

Legends

Figure 1. Breeding program for the isolation of single heterozygous autosomes from a selection line. Selected males are mated to inbred marker strain females. Each F_1 male carries one of the second and one third chromosome from the selection line. These males are then test crossed singly to the marker strain, yielding all combinations of selected and marker chromosomes (only males illustrated here, but both sexes were scored). Males carrying a particular isolated second or third autosome can then be test crossed again, thus replicating the tested chromosome so that its effect can be compared in different temperatures. Males are indicated by the J-shaped Y chromosome, and the four primary autosomes are numbered for individual identification.

Figure 2. Responses to selection for High and Low scutellar bristle number in sc lines selected at 25° and 29°C. The control line measurements are indicated by solid circles.


sc bw st / sc bw st
x
sc +1 +3 / +2 +4
sc bw st / sc bw st
x
sc +2 +3 / bw st
sc bw st / bw st
sc +2 st / bw st
sc bw +3 / bw st
sc +2 +3 / bw st
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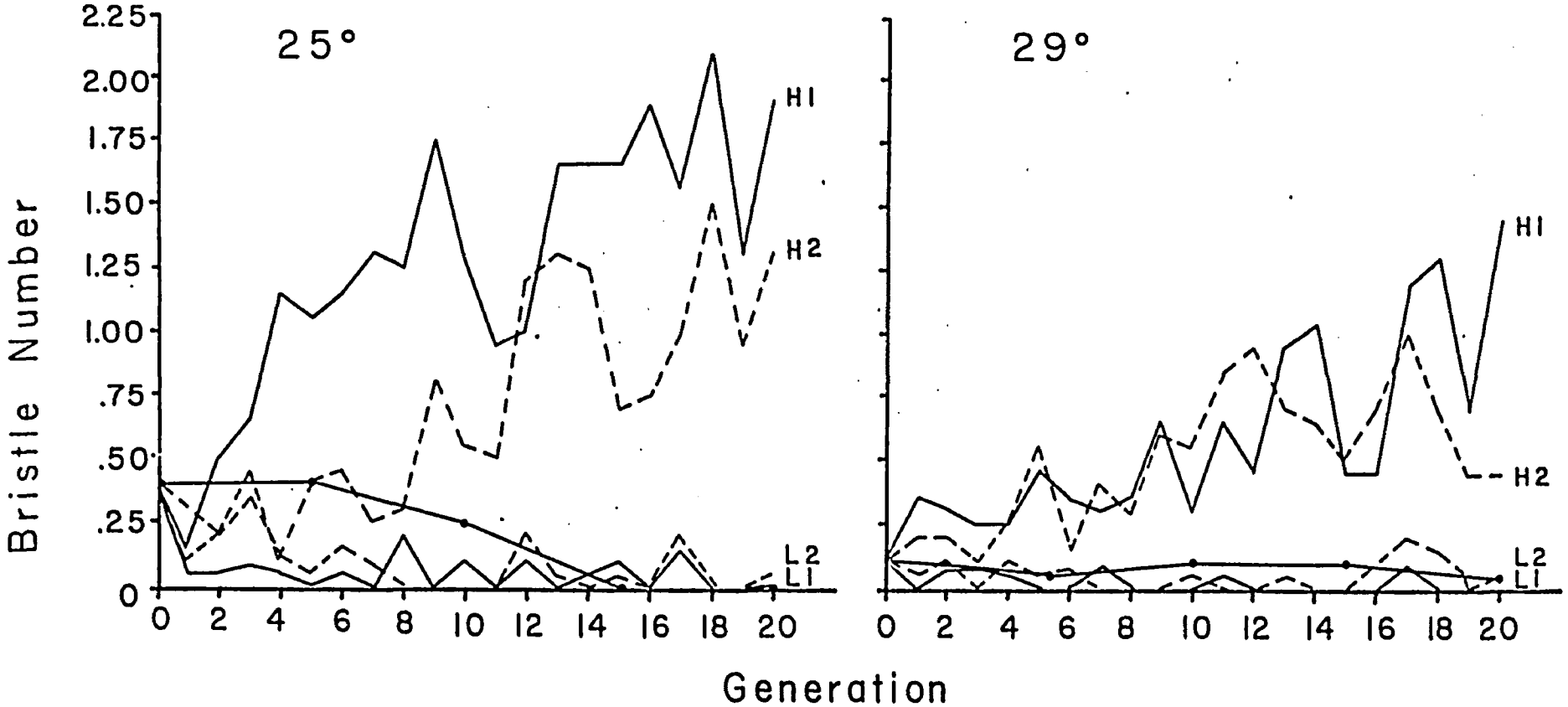
25°
29°
25°
29°


25°
29°
H1
H2
L2
L1
Bristle Number
Generation
2.25
2.00
1.75
1.50
1.25
1.00
.75
.50
.25
0
0 2 4 6 8 10 12 14 16 18 20