VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA*

XIV.* EFFECTS OF TEMPERATURE AND CROWDING†

By A. S. FRASER,‡§ L. ERWAY,‡ and W. BRENTON‡

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Summary

Several lines of *D. melanogaster* which were selected for increased numbers of scutellar bristles have been analysed for their response to temperature and larval density. Genetic data are summarized which indicates that two different polygenic systems have been separately involved in the selection responses. The one system, designated as the α-modifiers, has been involved in the presence of *scute*$^+$ and shows a correlated response in the presence of *scute* alleles. The other system, designated as the β-modifiers, has been involved in several lines which also possess a major gene, provisionally called *extra-vert*. This gene is a chromosome III recessive which manifests itself by increasing the number of dorsocentral and vertical as well as scutellar bristles. The effects of temperature and larval densities permit a further discrimination between these two genetic systems involved in bristle determination. A model is presented for the interaction of these two systems.

I. INTRODUCTION

Studies have been made of the effects of temperature during development on the number of scutellar bristles in *Drosophila* (Child 1935; Ives 1939; Rendel and Sheldon 1960; Pennycuik and Fraser 1964). Results have differed between genotypes, and between bristles located on different regions of the scutellum. Rendel and Sheldon (1960) found that increasing temperature resulted in a decreasing number of scutellar bristles in *scute* stocks. This contrasted with the marked increase in the number of extra scutellar bristles that they found in *non-scute* stocks. These extra (supernumerary) scutellar bristles were small and located in the posterior region of the scutellum. Pennycuik and Fraser (1964), studying a *non-scute* line, found that the occurrence of extra scutellar bristles had a negative temperature coefficient for bristles located close to the anterior scutellar bristles, contrasting with a positive temperature coefficient for bristles located adjacent to the posterior scutellar pair. Bristles located between the anterior and posterior scutellar bristles, i.e. interstitially located extra scutellar bristles, were at a maximum at intermediate temperatures. Rendel and Sheldon (1960) concluded from their studies that the *scute* gene interferes with a developmental system controlling the addition and subtraction of scutellar bristles at the four normal sites. This developmental system, they concluded, is controlled by a set of genes having a negative temperature coefficient. They contrasted this with another developmental system controlling the occurrence of posteriorly located extra scutellar bristles, i.e. bristles controlled by genes having a

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‡ Department of Animal Husbandry, University of California, Davis, California 95616.

§ Present address: Biological Sciences Department, University of Cincinnati, Ohio 45202.

positive temperature coefficient. The concept of a multigenic system being separable into a number of systems of genes has been frequently discussed (see Fraser 1953; Waddington 1962).

Fraser and Green (1964) and Fraser (1965, 1966) have shown that the control of the number of scutellar bristles is genetically heterogeneous, involving several systems of genes, thus extending Rendel and Sheldon's conclusions (1960). Erway (unpublished data) has shown that the marked increase of scutellar bristles found in some of the lines selected for extra scutellar bristles is due to a recessive, autosomal gene *extra-vert* (*x-vert*). Miller and Fraser (1967) have shown that *scute* alleles are epistatic to *x-vert*, i.e. little if any of the effect of *x-vert* on scutellar bristles shows up in the presence of the *scute* alleles. He has also shown that *scute* alleles are epistatic to a system of modifiers (termed the β-modifiers) which determine the degree of *x-vert* expression, including a range of lines whose means for scutellar bristle number are 4·5–10 in the presence of *scute*$^+$. Moreover, data has been obtained that *x-vert* is also epistatic to the α-modifiers (Fraser, unpublished data). The crosses involved *x-vert* and *non-x-vert* lines whose scutellar bristle number means overlapped considerably.

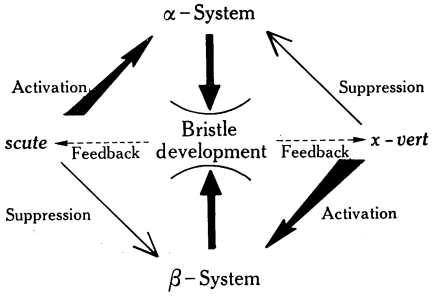

Fig. 1.—A proposed model for the relationships between two major bristle genes and their respective sets of genetic modifiers. These two systems interact epistatically to control bristle development.

The F_2 progeny of these crosses were segregated on the basis of the penetrance of *x-vert*. Although the effect of the α-modifiers showed up in the presence of *x-vert*$^+$, there was little or no difference in the mean scutellar bristle number in the presence of *x-vert*. This complex scheme of interactions is illustrated in Figure 1. It involves two main loci, *scute* and *x-vert*, each of which is modified by their respective separate systems, the α- and β-modifiers, the overall effect on bristle development being dependent on the status of the main loci.

Comparisons of genotypes at different temperature treatments should be a useful tool in the further analysis of this character. Waddington (1953), Milkman (1955), and Mohler (1965) have demonstrated the utility of this approach in analyses of genes affecting crossveins in the wings of *Drosophila*. Temperature is just one aspect of the environment that could be useful in this regard. Other aspects of the environment, e.g. culture density, can also be easily controlled and it is feasible to consider that comparisons over such a range of environments should allow a much more complete description of a genetic system than could be obtained in the absence of such comparisons. The present paper involves an examination of this thesis for a number of *non-scute* lines that were selected for increased number of scutellar bristles (Fraser 1963, 1965; Fraser *et al.* 1965; Scowcroft 1966).

II. Materials and Methods

The selection lines used in this study have been taken from a more extensive set of lines which had been selected for increased number of scutellar bristles. Five lines were used in the first part of the study (A1, A4, A6, A9, and A21). Lines A1 and A9 have been shown by Erway (unpublished data) to be homozygous for *x-vert*. This gene, in addition to causing an increase in the number of scutellar bristles, also causes increases in the number of other bristles of which the dorsocentral and vertical ones are the most diagnostic. Lines A6 and A21 do not contain *x-vert*, but they do have an increased number of scutellar bristles over that found in unselected lines. (This increase is much less than that found in the *x-vert* lines.) Lines A6 and A21 do not have concomitant increases in the numbers of dorsocentral and vertical bristles. The fifth line, A4, was included because of its anomalous features. In crosses with *x-vert* lines A4 produces F_1 progeny whose scutellar bristle number means only partially approached the mid-parent expectations which were satisfactorily met by all other *x-vert* × *x-vert* crosses. When A4 was crossed with *non-x-vert* lines the means for scutellar bristle number regressed markedly toward the unselected level as was the case for all *x-vert* × *non-x-vert* crosses (Fraser *et al.* 1965). Erway has shown (unpublished data) that A4 is polymorphic for the *extra-vert* syndrome, but this does not necessarily demonstrate polymorphism at the *x-vert* locus. It is possible that A4 is polymorphic for a suppressor of *x-vert*, a point for which some of the data below may be relevant.

Cultures of the five lines were formed at three levels of crowding specified by the number of pairs of parents (4, 8, and 16) and maintained at three temperatures (18, 22, and 29°C) in quarter-pint bottles. Four replicate cultures were produced, and 50 females were scored for scutellar, dorsocentral, and vertical bristle number in each culture. These are referred to as "parent-density experiments".

A second set of experiments was made with two *x-vert* lines (A1 and A9) involving densities specified by numbers of eggs. Adults were allowed to lay eggs in Petri dishes containing regular media coloured with grape juice. Eggs were collected with a spatula, counted, and placed in 1-in. vials containing a constant amount of media. The first "egg-density experiment" involved 10 replicates of each of three densities (50, 250, and 500) for both lines. The collected eggs varied in age by as much as 12–14 hr. The second egg-density experiment involved five replicates for each of six densities (50, 100, 150, 200, 250, and 500) for A1 only since A9 was found to be relatively insensitive to density. The eggs collected for this experiment varied in age by as much as 8–9 hr. The progeny of each vial were separately counted by sex over the entire period of eclosion, thus providing a measure of the effect of density on viability. Thirty males and 30 females from each vial were individually scored and recorded for the number of bristles at the three positions, scutellar, dorsocentral, and vertical. On this basis, the penetrance of *x-vert* (arbitrarily defined as the presence of either extra dorsocentral or vertical bristles or both) could be scored in individual flies, as well as the overall mean for each of the bristle positions. All of the egg-density experiments were conducted at room temperature (23 ± 1°C).

III. Results

(*a*) *Effects of Temperature and Parent Density*

The means of numbers of scutellar, dorsocentral, and vertical bristles, averaged over temperature treatments, are given in Table 1, and allow comparison between the three levels of parent density. It is evident that differences of parent density do not result in changes of the mean numbers of these three types of bristles. The differences of parent density did, however, result in marked changes of the cultures; higher densities resulted in markedly smaller flies. The absence of any effect of parent density allows the data to be accumulated over such treatments giving a greater basis of accuracy for comparisons between temperature treatments. The mean numbers of

scutellar, dorsocentral, and vertical bristles averaged over parent-density treatments are given in Figure 2. There are several noteworthy features of these data:

(1) dorsocentral and scutellar bristles have negative temperature coefficients contrasting with vertical bristles which have a positive temperature coefficient;

(2) a clear distinction can be made between the *x-vert* lines A1 and A9, and the *x-vert*$^+$ lines A6 and A21 for all three types of bristles at all three temperatures. This distinction is somewhat confounded by the increased mean number of dorsocentral bristles in line A21 at 18°C; *x-vert*$^+$ lines rarely show extra dorsocentral bristles at any temperature;

(3) the "polymorphic" line A4 is intermediate between the *x-vert* and *x-vert*$^+$ levels of expression for all but vertical bristles at 18°C.

TABLE 1

EFFECTS OF PARENT DENSITY ON BRISTLE NUMBER

Mean number of scutellar, dorsocentral, and vertical bristles were averaged over replicate crosses and temperature treatments

Line	Four Parents			Eight Parents			Sixteen Parents		
	Scutellar	Dorso-central	Vertical	Scutellar	Dorso-central	Vertical	Scutellar	Dorso-central	Vertical
A1	7·33	5·38	7·19	7·49	5·36	6·80	7·40	5·53	6·69
A9	7·66	5·86	6·41	8·08	5·63	7·36	7·85	5·31	7·20
A4	5·82	4·64	6·66	6·04	4·98	6·65	6·00	4·66	6·55
A6	4·75	4·16	6·00	4·75	4·14	6·00	4·68	4·08	6·00
A21	4·85	4·40	6·01	4·69	4·44	6·03	4·70	4·62	6·05
Means	6·08	4·89	6·35	6·16	4·91	6·57	6·10	4·84	6·49

In (3) the line A4 mean is *not* different from that of the *x-vert* lines. This casts some doubt on the hypothesis that line A4 is polymorphic for *x-vert*/*x-vert*$^+$. It is more probable that this line is homozygous for *x-vert* and polymorphic for a suppressor of *x-vert* which is inactive at 18°C. The frequency distributions of number of vertical bristles for the A4 line are given in Figure 3 with those of the two *x-vert* lines for comparison. The percentage penetrance of *x-vert* for each line at each temperature is as follows:

Line	18°C	22°C	29°C
A1	27·7	69·5	78·7
A9	38·3	81·0	95·3
A4	34·8	44·0	42·0

The effect of temperature on the form of the distribution is most marked between 18 and 22°C. The effects of increasing temperature from 22 to 29°C are much smaller by comparison. The *x-vert* lines show a shift towards a nearly normal distribution for vertical bristle number with increase of temperature. This contrasts with the behaviour of the "polymorphic" line A4. The distribution of vertical bristles in line

A4 does not differ from that found in the *x-vert* lines at 18°C, but with increasing temperature their distribution becomes bimodal. This can be explained by approximately half of the individuals showing the *non-x-vert* syndrome, and the other half showing the *x-vert* range of number of vertical bristles. Erway has shown that the

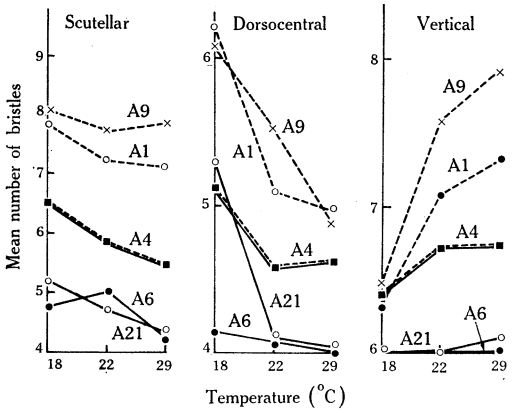

Fig. 2.—Mean number of bristles at each of three body positions plotted for five lines over three temperatures. Lines A1 and A9 are homozygous for *x-vert*; line A4 is polymorphic for the genetic ability to express the *x-vert* phenotype; and lines A6 and A21 are homozygous for *x-vert*$^+$.

bimodality is due to segregation of a genetic factor which was previously considered to be *x-vert*. The present data indicate the need for an extension of his analysis in terms of a segregation for a suppressor of *x-vert*. Chromosomal analyses of the A series of lines by Scowcroft (1966) support this possibility since the A4 line did not contain the predominant third-chromosome component characteristic of *x-vert* lines. In this respect line A4 was almost unique in that it had a major component requiring the interaction of chromosomes I, II, and III.

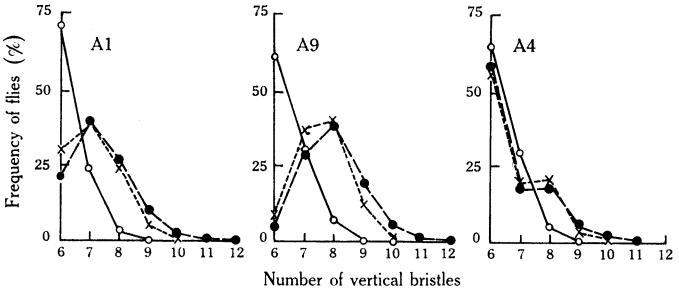

Fig. 3.—Percentage frequency of flies plotted against their respective number of vertical bristles. The distribution at 18°C (○), 22°C (×) and 29°C (●) is shown for lines A1, A9, and A4.

The prime objective of our studies has been the analysis of variation of number of scutellar bristles, and in this regard the variation of temperature during development does not appear to offer any advantages since the differences between lines in mean number of scutellar bristles do not change to any marked degree with change of temperature. This contrasts with the marked line × temperature interactions

found for dorsocentral and vertical bristles. However, the *x-vert* syndrome involves increases of all three types of bristles, and there is a possibility of discriminating between an *x-vert* and an *x-vert*$^+$ component of increased number of scutellar bristles by use of the concomitant effects of this gene on *vertical* bristles and the interaction of this effect with temperature. The joint distributions of scutellar and vertical

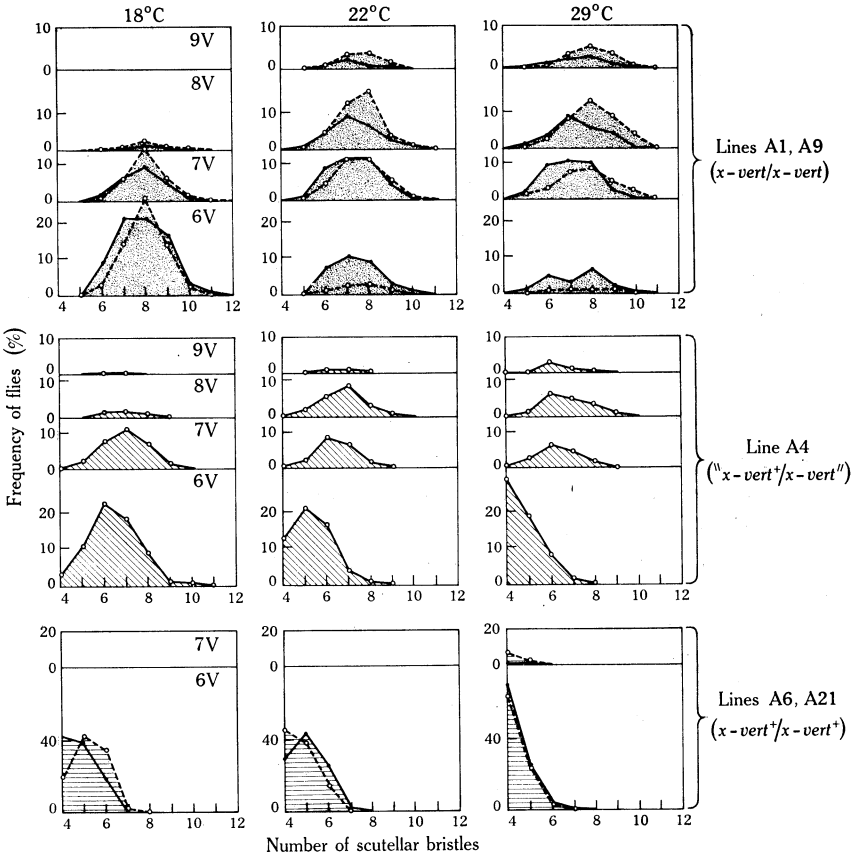

Fig. 4.—Effect of temperature on scutellar and vertical bristles plotted for each of the three genotypes with respect to *x-vert*. The joint distribution includes the percentage of all flies scored for any one line at one temperature. Flies were separated according to the number of vertical bristles (6V = norm).

bristles are shown in Figure 4, for the *x-vert* lines A1 and A9, the *x-vert*$^+$ lines A6 and A21, and the A4 line. (The latter is referred to as polymorphic for *x-vert* and *x-vert*$^+$; this reference is to the syndrome rather than to the gene.)

The joint distributions of scutellar and vertical bristle number show a marked difference between the *x-vert* and *x-vert*$^+$ lines (A1 and A9 *v.* A6 and A21) such that these are qualitatively separable, particularly at the higher temperatures. The *x-vert* distribution shows little, if any, correlation of scutellar with vertical bristle number and, although there is a marked increase of vertical bristles with increase

of temperature, there is only a slight effect of temperature on the number of scutellar bristles. The *x-vert*$^+$ distribution shows a marked shift into the zone of four scutellar bristles with increasing temperature. This shift is greater than appears from a consideration of the means (see Fig. 2). The differences between the *x-vert* and *x-vert*$^+$ distributions are clearly illustrated in the A4 line which is polymorphic for this syndrome. There are two shifts of the joint distribution with increasing temperature: (1) the distribution of scutellar bristle number of flies with six vertical bristles (the

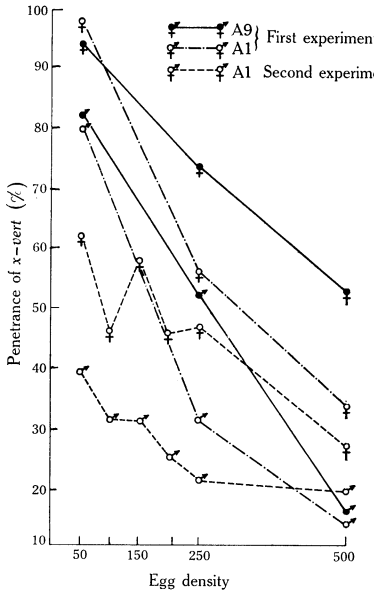

Fig. 5

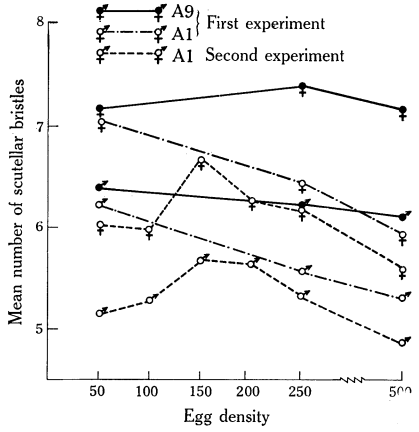

Fig. 6

Fig. 5.—Percentage of flies with *x-vert* expression is plotted at different levels of egg density.
Fig. 6.—Mean number of scutellar bristles for lines A1 and A9 plotted for various levels of egg density.

norm) shifts towards the zone of four scutellar bristles, and (2) there is a shift towards an increased frequency of flies with more than six vertical bristles that is not correlated with any marked changes of their scutellar bristle number. The comparison of the joint distributions of scutellar and vertical bristle numbers at three temperatures allows an almost complete discrimination between the increased number of scutellar bristles caused by *x-vert* and the β-system of modifiers and that due to another genetic system. Essentially the same phenomenon can be found for the effects of *x-vert* and *x-vert*$^+$ on dorso central and scutellar bristles within line A4 at the three temperatures.

(*b*) *Effects of Egg Density*

The results of Pennycuik and Fraser (1964) and the present data show that differences of parent density cause little, if any, significant changes of scutellar, dorsocentral, or vertical bristle number. This would appear to terminate any interest in culture density as a useful treatment in the analysis of bristle number. However,

unpublished data obtained by Erway and Brenton indicate that culture density does affect bristle development. *Extra-vert* genotype lines were crossed with line 70 (*x-vert*$^+$) to establish population cages with equal allelic frequencies at this locus. The frequency of flies with the *x-vert* expression in these cages was extremely low in the very first generations under the cage conditions, indicating that either very strong selection was operating against *x-vert* or that the cage conditions were resulting in a suppression of the *x-vert* phenotype. Samples of flies were extracted from the cages, placed in quarter-pint culture bottles, and allowed to lay eggs for 1 day. The frequency of *x-vert* flies which developed from these cultures closely approximated the expected values (25% homozygous *x-vert* with 50–70% penetrance). A series of tests has

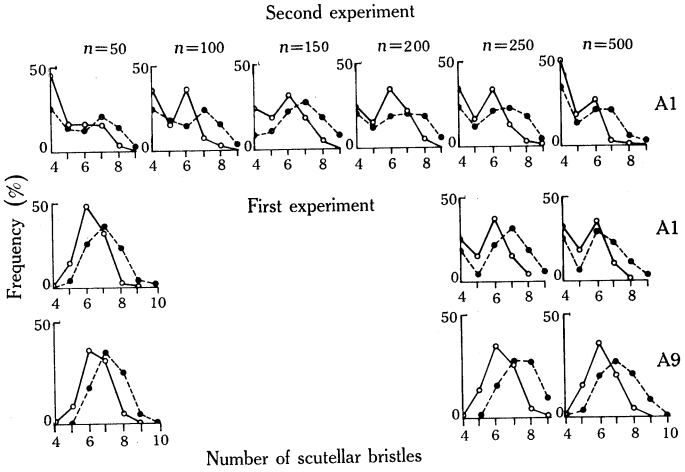

Fig. 7.—Effect of egg density on the mean number of scutellar bristles in male (○) and female (●) flies.

shown that the high densities developed under the cage conditions do suppress the development of the *x-vert* phenotype. Culture density was considered to be the most probable factor operative in the cages. A series of experiments was performed to test this hypothesis involving cultures established from known numbers of eggs.

In the first series of such cultures 50, 250, and 500 eggs were placed in 1-in. vials. Emerging adults were scored for scutellar, dorsocentral, and vertical bristle number. The results (Fig. 5) show a marked effect of egg density on the penetrance of *x-vert*. Both lines A1 and A9, show the reduction in penetrance of *x-vert* which contrasts with the effect of egg density on mean number of scutellar bristles (Fig. 6). There is a marked reduction of mean scutellar bristle number with increasing density in A1, and little if any effect in A9. A further point of difference between the lines is that the frequency distribution of scutellar bristle number becomes increasingly bimodal with increasing egg density in line A1. This is illustrated in Figure 7. The bimodality is apparent only for the scutellar bristles of line A1. The distributions of vertical and dorsocentral bristles approximated a normal distribution only under the most ideal conditions for *x-vert* expression (females at low density of the first egg-density experiment; also Fig. 3). The distributions for both of these bristles

were highly skewed in the direction of the normal number for males at all densities and for females at high densities.

The second set of cultures of the A1 line was established for egg counts of 50, 100, 150, 200, 250, and 500. The results, shown in Figures 5, 6, and 7, are analogous to the first set of cultures except that the low penetrance for dorsocentral and vertical bristles and the bimodality of scutellar bristle number is apparent at the lowest density of 50 eggs. All three sets of data (Figs. 5, 6, and 7) indicate that the second experiment provided a generally reduced *x-vert* penetrance and lower means for scutellar bristle number. The age and consistency of the media may be the uncontrolled and critical factor in determining whether a density effect is observed. However, one variable was changed between the first and second experiment that may contribute to the differences. The maximum range in age of collected eggs was reduced from 14 to 9 hr, a fact which may accentuate any critical stage of larval competition. In any event it appears that the low density of the second set of cultures did not approach the conditions for maximum performance as observed in the first set.

The bimodality of the frequency distribution of scutellar bristle number in the A1 line has not been observed previously in normal quarter-pint cultures (see Fig. 4). This phenomenon has been noted only in high egg-density cultures. It is possible that the bimodality is caused by a genetic polymorphism of sensitivity to culture density. Genetic tests will be needed to examine this possibility. Any genetic difference which may contribute to the bimodality of scutellar bristle number or to the presence of extra dorsocentral or vertical bristles under high egg-density conditions cannot be due to polymorphism at the *x-vert* locus, nor to the modifier of *x-vert* which has been postulated for line A4. Line A1 is homozygous for *extra-vert*, and it does not show the bimodality for scutellar bristle number at high temperature that was demonstrated for line A4 (see Fig. 4). Additional data indicating that temperature and larval density are affecting two separate aspects of the *x-vert* syndrome is not included. The density data of A1 has been plotted as a joint distribution of scutellar and vertical bristle number as in the manner of Figure 4. Whereas increased temperature further discriminates between the two genetic components of A4, increased density of A1 larvae reduces the extra vertical classes together with the bimodality for scutellar bristles. The interpretation is that increased density interacts with the genotype to effectively switch off the ability to express *x-vert* at the three bristle positions.

It is apparent that the experiments involving differences of parent density did not impose sufficiently high culture densities to allow detection of an effect on bristle development. It appears that effects of culture density on bristle development depend not so much on the total density of a culture but rather on the density within a limited age range. Very limited observations suggest a reason for some of the apparent discrepancy between parent and egg density. Four quarter-pint bottles for each of three parent densities for line A1 were set up. The parents were dumped after 24 hr and then the progeny were counted until they had all emerged. The scores were remarkably uniform about the following means: 5 pairs of parents averaged 50 progeny with an average *x-vert* penetrance in females of 70%; 25 pairs of parents averaged 190 progeny with an average *x-vert* penetrance in females of 40%; and 50 pairs of parents averaged 140 progeny with an average *x-vert* penetrance in females of 80%. It would appear,

therefore, that conditions of parental crowding can affect the rate of egg laying, such that it is not possible to achieve sufficiently high densities of eggs of more or less synchronous ages to produce a reduction of *x-vert* penetrance equivalent to that found in the egg-density experiments.

IV. Discussion

The study of two major loci, *scute* and *x-vert*, each with effects on various bristles (scutellar, dorsocentral, and vertical) has provided a means of discriminating between systems of genetic modifiers. Manipulation of environmental conditions has increased this ability to discriminate. The ability to modify gene expression either by selection of genetic modifiers or by environmental manipulation is by no means new. Several reports are particularly relevant to the studies described herein. Morgan (1915) described the effect of wetness of the media on the penetrance of *abnormal abdomen*. Older and dryer media produced nearly all flies with normal abdomen. A similar effect was described for *eyeless* (Morgan 1929) and for *antennaless* (Gordon and Sang 1941; Sang 1961). The role of temperature and condition of the media on the penetrance and expressivity of *crippled* (Komai 1926) is remarkably parallel to some effects of *x-vert*. *Crippled* is a recessive chromosome II mutant affecting either the hind or middle limb. Which of the two limbs is affected depends on the condition of the media, the defects being qualitatively different for the two limbs. Temperature, time of emergence, and size of the brood affect its expression. Unfortunately, the effect of these environmental factors were not quantified. The effect of temperature and density on the expression of *Curly* and *curled* were quantified and studied for their interactions (Nozawa 1956*a*, 1965*b*). High larval densities obtained either by parent density or by egg density reduced the *Curly* expressivity. The degree of *Curly* expressivity had a positive correlation with temperature. Separate studies of *curled* show similar responses to environment but at a much lower level of expression. The interaction of these two mutants was additive and, moreover, it was shown that they both had the same temperature effective period (the last day of the pupal stage).

Waddington (1955) conducted a genetic analysis of lines derived from his "genetic assimilation" (Waddington 1953) of variation for crossveins of the wing. In this analysis he found that genetic factors for deficiencies of crossveins and for extra crossveins were distinct from each other. Some F_1 progeny between the two types of strains exhibited both gaps and extra bits of crossveins, indicating that the "quantity of cross-vein" is not "causally homogeneous". He also produced evidence that the two types of factors interact with each other in a manner to "suppress the expression" of each other. This type of genetic interaction is remarkably similar to that for bristles described in the introduction and described in detail by Miller and Fraser (1968). Whereas Waddington (1955) concluded that the normal range of environmental variation produced little effect on the development of crossveins, no effort was made to further distinguish these two systems by more extreme environmental manipulation.

A significant addition which the present paper makes is the usefulness of environmental manipulation to distinguish between two different genes or genetic systems

affecting the same character. For example, difficulties which have been encountered in scoring for *x-vert* at high densities and at room temperature can easily be avoided by using low densities and high temperature.

Other unpublished data indicates that *x-vert* is probably allelic to *polychaetoid*. Further studies will be necessary to determine the relationship of these two genes and their sensitivities to environmental and genetic modification. Neel (1940) studied the effects of temperature and nutritional levels on the relationship between body size and dorsocentral bristle number for *polychaetoid* and for *Dichaete*. He was able to remove most of the effect of temperature on bristle number by correcting for body size, but his measurement involved only the dorsocentral bristles. From the present data on *x-vert* one might expect the effect of *polychaetoid* on vertical bristles to show a positive temperature coefficient despite the obvious reduction in body size at higher temperatures. This observation should emphasize the usefulness of measuring several of the manifold effects of a gene over a wide range of environmental conditions. Increasing temperature or larval density both reduce *x-vert* expression on scutellar and dorsocentral bristles, but the effect on vertical bristles is opposite for the two treatments. This suggests that the effect of *x-vert* on vertical bristles must be independent of body size. This is very similar to the data of Pennycuik and Fraser (1964) which indicate that temperature and culture density can have differential effects for bristles on the scutellum. Anterior scutellar bristles have a negative temperature coefficient whereas posterior scutellar bristles have a positive temperature coefficient. High culture density reduced the number of anterior scutellar bristles at all temperatures but had no effect on posterior scutellar bristles.

The distinction between parent density and egg density emphasizes the necessity to know the biology of the organism. The assumption is often made that parent density will automatically result in an equivalent egg or larval density. Two facts are obscured by such an assumption: (1) a several fold increase in the number of parents does not necessarily result in a proportional increase in the number of eggs laid; and (2) the same egg density accumulated over long periods is not as effective in larval competition as that obtained for eggs of a more uniform age.

The number of bristles at any particular position in Drosophilidae is so constant as to be a taxonomic feature. The number of scutellar bristles is normally maintained at four (dorsocentrals also four and verticals six) by a process of developmental canalization (Rendel 1959; Fraser *et al.* 1965). Whatever processes contribute to this canalization almost completely suppress the expression of either genetically or environmentally caused variability. Such a regulatory process must involve a "measurement" of the potential effectiveness of a genetic or environmental stress for modifying bristle development, and it must also involve a corresponding "reaction" to suppress the potential deviation of development due to that stress. The researches of this group (Fraser, Erway, Miller, Brenton, and Lee) have led to the model of genetic control of bristle development shown in Figure 1. The present results, showing the sensitivity of the *x-vert* gene to conditions of temperature and culture density, suggest that this may be part of the "canalizing" mechanism (involving measurement and reaction), with the α- and β-modifiers as the "canalized" mechanism.

The antagonistic effects of two major loci involved in bristle development appear to be consistent with ideas of what a buffered system should involve (see Waddington 1955).

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