Analyses of some Genes from Abdominal Bristle Number Selection Lines in Drosophila melanogaster

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Summary. Effects on abdominal bristle number were determined for three mutations, scabrous-like, dark hairy margin and scabrous, and for some second chromosome recessive lethal genes prevalent in various irradiated and unirradiated selection lines derived from an outbred population. The relationship between the effect of a lethal gene on a quantitative character and the equilibrium frequency of the lethal in a line selected for that character was examined.

Recently it has been suggested that a large proportion of the response in selection lines may be due to effects of a relatively small number of genes (Spickett and Thoday 1966, Robertson 1966). In Drosophila, special techniques, such as chromosomal analysis using marked inversion stocks, have long been used in the study of the genetics of quantitative characters, e.g. Mather (1942), Sismanidis (1942), Robertson and Reeve (1953), Fraser and Scowcroft (1965) and Scowcroft (1966). In the last decade methods have been developed which, although laborious, enable individual loci affecting metric characters to be studied and mapped. Thoday (1961) outlined a scheme for locating polygenes and measuring their effects. This method has been used for detailed analyses of sternopleural bristle number selection lines by Thoday, Gibson and Spickett (1964) and Spickett and Thoday (1966). Inter-varietal chromosome substitution lines can be used for similar analysis of quantitative characters in wheat, e.g. Law (1966, 1967).

On a less sophisticated level, the basis of the response in selection lines can be at least partly revealed by an examination of the effects of visible mutants which reach high frequencies. In a group of irradiated and unirradiated lines derived from the Canberra population, an outbred strain of Drosophila melanogaster, Hollingdale and Barker (1971) found three mutants which became prevalent in different lines which were being selected for increased abdominal bristle number. Lethal analysis of the same lines revealed several recessive lethals present at high frequencies. These three visible mutants and some of the second chromosome lethals were studied in some detail, to determine why they had become prevalent.

Methods and Results

1. scabrous-like (scal)

This is a recessive semi-lethal, semi-sterile mutant on chromosome II, mapped at 11.7 ± 0.3 centi-Morgans (Barker and Hollingdale 1970). Females are almost completely sterile. In homozygotes the eyes are roughened, and slightly bulging; bristle number is increased (see later); the wings are abnormal, tending to be broad, slightly spread and curved, with disturbed venation — longitudinal vein L II is irregular and the posterior crossvein is abnormal, sometimes with a section missing, sometimes with an extra piece of vein associated with it. Wing effects tend to be more pronounced in females. Emergence was delayed in the line in which this mutant was found (line SO.2, unirradiated, Hollingdale and Barker 1971).

When a mutant with a phenotype similar to scabrous (Lindsley and Grell 1968) was first discovered in line SO.2, an attempt was made to establish a subline lacking the mutant. This was unsuccessful as the mutant gene was retained in the subline even though flies with the mutant phenotype were excluded before selecting individuals with high abdominal bristle number. The subline was terminated after three generations of selection. The scabrous-like segregants in the final generation had abdominal bristle numbers of 45.2 ± 0.7 and 37.6 ± 0.5 for the fifth sternite in females and the fourth sternite in males respectively; the corresponding means for wild-type segregants were 34.7 ± 0.2 and 28.1 ± 0.2. The mutant also increases scutellar bristle number; the scabrous-like segregants had an average of 6.5 bristles in females and 5.7 in males compared with 4 bristles in wild-type flies.

At generation 61, wild-type flies from line SO.2 were scored for abdominal bristle number and individually progeny tested to determine their genotypes at the scabrous-like locus, by mating scored flies with
a scal/Cy stock. In a culture with no scabrous-like progeny and less than twenty non-Cy progeny the SO.2 parent was classed as semi-sterile; its genotype at the mutant locus could not be determined. (Twenty wild-type progeny was an arbitrary limit, chosen because occasionally cultures were found with about this number of wild-type progeny and one scabrous-like offspring.) This introduced a bias, important only for SO.2 females, since the heterozygote class included cultures with less than twenty non-Cy progeny, whereas the homozygote wild-type class did not. However, as shown in Table 1, mean bristle number of semi-sterile females was intermediate between the means for heterozygotes and wild homozygotes and the gene frequency in females, 33.4%, was similar to that in males, 33.7%. The over-estimate of the heterozygote effect of scabrous-like in females was therefore unlikely to be large.

scabrous-like thus became prevalent in selection line SO.2 because of a sizable heterozygote effect on bristle number (0.7 standard deviations for females, 0.5 for males) and was maintained at a high frequency for more than thirty generations despite the sterility of mutant homozygote females. The equilibrium between natural and artificial selection prevented the frequency of scabrous-like rising much above the maximum expected for a lethal gene, and although mutant females were not deliberately discarded, they were never sufficiently numerous to create difficulty in maintaining the line.

2. dark hairy margin (dhm)

This is a recessive mutant on chromosome III, mapped at 43.2 centiMorgans (Barker and Hollingdale 1970). In homozygotes, the whole wing appears darker than wild-type, wing veins are thicker and the margin more hairy; bristle number is increased (see later); wings tend to spread slightly and in some cultures wing abnormalities reduce viability. The mutant became fixed in line SO.3 (unirradiated, Hollingdale and Barker 1971).

At generation 38 all selected flies in line SO.3 were dark hairy margin phenotype, so a subline, SO.3+, was initiated using a random sample of wild-type flies from line SO.3 mated to a random sample of dark hairy margin flies. In subsequent generations mutant homozygotes were discarded from the subline before selecting for abdominal bristle number under the same selection regime used in SO.3. Mean bristle numbers in line SO.3 and its subline SO.3+ are shown in Figure 1; bristle number means in sublines after five generations of relaxation of selection are also included. Although SO.3+ was considerably below SO.3 for some time, prevention of fixation of dark hairy margin did not limit the response of SO.3+. Over the last generations, the mean of SO.3+ was increasing faster than the mean of SO.3.

Table 1. Effect of scabrous-like, scal, on bristle number in line SO.2 at generation 61; \( x \) = mean abdominal bristle number (fifth sternite in females, fourth in males), \( n \) = scored and progeny tested

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Females</th>
<th></th>
<th>Males</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>+/scal*</td>
<td>42.7 ± 0.3</td>
<td>82</td>
<td>34.3 ± 0.3</td>
<td>87</td>
</tr>
<tr>
<td>+/+</td>
<td>40.8 ± 0.4</td>
<td>42</td>
<td>32.9 ± 0.4</td>
<td>42</td>
</tr>
<tr>
<td>Semi-sterile</td>
<td>41.5 ± 0.4</td>
<td>32</td>
<td>32.0 ± 0.1</td>
<td>10</td>
</tr>
<tr>
<td>Sterile</td>
<td>44.8 ± 0.8</td>
<td>4</td>
<td>34.8 ± 1.2</td>
<td>10</td>
</tr>
</tbody>
</table>
| Frequency of scal | 33.4% | 33.7% | 1.4 ± 0.5 | 2.6%
| Heterozygote effect | 1.9 ± 0.5 | 1.4 ± 0.5 |      |
| Phenotypic standard deviation | 2.9 | 2.6 |  

* Genotype at the scabrous-like locus in fertile, wild-type individuals was determined by examining their progeny for scabrous-like segregants.

![Image](image-url)

Fig. 1. Response of line SO.3 and its subline SO.3+ to selection for increased abdominal bristle number. Broken lines indicate periods of relaxation of selection.

The effect of this gene on abdominal bristle number was examined by progeny testing flies scored for bristle number. A relaxed selection subline taken from line SO.3 at generation 29 and grown under normal culture conditions for one generation was used for the first progeny test. A second progeny test was carried out using flies from generation 40 of subline SO.3+. Results of both progeny tests are given in Table 2. The dark hairy margin homozygotes were higher in abdominal bristle number than wild-type flies but of the four estimates of heterozygote effect only that for females from line SO.3+ differed significantly from zero. This estimate, 1.1 ± 0.5 bristles, is about half the phenotypic standard deviation for wild-type females of line SO.3+ at the time of the progeny test. This small heterozygote effect must have been sufficient to account for retention of the mutant in subline SO.3+, and its initial increase in frequency in selection line SO.3. The mutant also increased scutellar bristle number;