THE INTERACTION OF SOME WING MUTANTS IN *DROSOPHILA MELANOGASTER*

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INTRODUCTION

THE combination effects of many gene mutations in *Drosophila* seem to be cumulative and roughly proportional to the effect of each single gene. "Disproportionate" combination effects have also been described qualitatively by BRIDGES (1919), BRIDGES and MOHR (1919), LEBEDEFF (1935), and others.

The discovery that two well known sex-linked genes of *Drosophila melanogaster*, bifid and Beadex, produce a striking disproportionate combination effect on wing shape and size permitted a quantitative study of this phenomenon.

MATERIALS

Bifid, symbol *bi*, influences the venation of the wing. All the longitudinal veins are fused at the base of the wing, and the fourth longitudinal vein may fail to reach the margin. A notch may be present in the margin of the wing. The latter feature is very rarely present in the bifid stocks used in this experiment.

Beadex, symbol *Bx*, is represented by a multiple allelic series producing scalloped wings of approximately normal length. The alleles used, in ascending order, are: *Bx^r*, *Bx¹*, *Bx²*, *Bx³*, and *Bx^J*.

EXPERIMENTAL

A single male with aberrant wings was found by PROFESSOR VICTOR JOLLOS in a culture which had been kept on Pike's Peak. This male was mated to *Bx^J* females. In the F_2 , a number of males with very short, scalloped wings appeared. This new "small wing" type was given to the author for analysis.

It was found that the "small wing" type contained bifid and Beadex-J. Linkage data indicated that the interaction of these two factors produced "small wings." On this view, the original aberrant parental male was bifid. Crossing over produced the F_2 bifid Beadex-J, small wing, males.

This was confirmed by using an unrelated stock of bifid containing the mutant ruby eyes. The loci of bifid, ruby, and Beadex on the X chromosome are 6.9, 7.5, and 59.4, respectively. A bifid ruby female was crossed with a Beadex-J male. All the F_2 crossovers that were ruby and Beadex-J were also bifid and "small wing," if one omits the rare double crossovers. Similar results were also obtained when bifid flies extracted from

a bifid cut-6 garnet-2 bobbed stock were crossed with a Beadex-2 stock.

The interaction of bifid with different Beadex alleles was tested by crossing bifid ruby females to Bx^r , Bx^1 , Bx^2 , and Bx^3 males, respectively. The three F_1 and the three F_2 cultures made for each Bx allele yielded identical results. F_1 females heterozygous for Bx^r or Bx^1 were phenotypically normal, although only Bx^r is ordinarily recessive. The bifid ruby stock must contain modifiers suppressing the dominance of Bx^1 .

Two types of scalloped wings were present in the F_2 males of all four series, and in the females of the Bx^2 and the Bx^3 series: a Beadex type, and a non-Beadex type. Bifid venation was invariably absent in the former, and invariably present in the latter. All the scalloped wing F_2 females of the Bx^r and the Bx^1 series were bifid and non-Beadex in type. Since the corresponding F_1 females had normal wings, Bx^r and Bx^1 are at least incompletely dominant in the presence of homozygous bifid. All the other Beadex alleles tested are dominant. However, all bifid Beadex wings are progressively smaller in the following order: heterozygous Beadex female, homozygous Beadex female, Beadex male.

The accompanying photographs illustrate the difference between the different types of wings in the male. In the Beadex wing, the scalloping is roughly parallel to the long axis. The posterior margin of the wing is always more scalloped than the anterior costal margin, which is frequently normal in the less extreme alleles (figures 1-5).

The bifid Beadex wing is highly variable in shape and size. This made a qualitative comparison of bifid wings containing different Beadex alleles impossible. The scalloping is oblique to the long axis. Both the posterior and the costal margins are equally scalloped at the distal end. In contrast to Beadex, both length and width are greatly reduced.

Large vesicles are frequently formed in Beadex and in bifid Beadex wings during their expansion. Such wings become very crumpled and reduced in length, and have been disregarded in this study.

A qualitatively new type of wing has been produced by the crosses of three different bifid stocks with five different Beadex alleles. It is difficult to see how this disproportionate combination effect could result merely from the summation of the known effects of bifid and Beadex. Quantitative data should permit a decision concerning this point.

Such data were obtained from a single pair mating of a bifid ruby female with a Beadex-1 male, and a bifid ruby female with a Beadex-3 male. The parental stocks were inbred, and all cultures were kept in the same incubator at 25°C. The wings were removed from the F_2 males appearing during the first six days of the culture, and mounted on slides.

All measurements were taken from camera lucida drawings made at a magnification of 47.6 times. Length measurements were taken to a tenth

of a millimeter with an error of less than 0.2 millimeters. Wing areas were measured with a planimeter set so that 25 square centimeters equalled 0.261 planimeter units. The error was small since ten measurements of a normal wing gave a mean of 0.332 with a standard deviation of 0.0017.

Distal length was measured as a straight line connecting the end of the third longitudinal vein with the intersection of the fourth longitudinal vein by the posterior crossvein. The continuation of this line to the proximal margin gave the proximal length. Total length represents the

TABLE 1
Bx³ Series. Means and Standard Errors.

CLASS	AREA	TOTAL LENGTH MM	DISTAL LENGTH MM	PROXIMAL LENGTH MM	CROSSVEIN INTERVAL MM
+	0.2887* ±(0.0031)**	81.89 (0.51)	45.85 (0.32)	36.01 (0.33)	17.45 (0.19)
bi	0.2765 ±(0.0032)	80.59 (0.54)	44.39 (0.38)	36.09 (0.36)	16.81 (0.18)
Bx ³	0.2497 ±(0.0039)	86.37 (0.61)	51.05 (0.41)	35.17 (0.38)	16.13 (0.20)
bi Bx ³	0.1539 ±(0.0034)	65.81 (1.40)	38.19 (1.04)	27.51 (0.43)	11.74 (0.18)

* The mean of 50 wings.

** The standard error of this mean.

sum of proximal and distal lengths. The crossvein interval was measured on the fourth longitudinal vein. The area measured represents the wing surface distal to a perpendicular line intersecting the first costal break. No width measurements were attempted, since width is so variable in the individual bifid Beadex wing.

The means and standard errors of the measurements are given in tables 1 and 3. All values are based on fifty wings. Tables 2 and 4 give the quotients of the differences between means divided by the standard errors of the differences. The fourth difference tested is that between the experimental value of bifid Beadex and the value which would result from a summation of the effects of bifid and Beadex. Thus, in table 1, the sum

EXPLANATION OF FIGURES 1-5

FIGURE 1.—Bifid. $\times 42$

FIGURE 2.—Beadex¹. $\times 42$

FIGURE 3.—Beadex³. $\times 42$

FIGURE 4.—Bifid Beadex¹. $\times 42$

FIGURE 5.—Bifid Beadex³. $\times 42$

FIGURES 1-5. (See opposite page for description.)

TABLE 2
Bx³ Series. Difference/Error.

DIFFERENCE	AREA	TOTAL LENGTH	DISTAL LENGTH	PROXIMAL LENGTH	CROSSVEIN INTERVAL
+ - bi	2.7	1.8	2.9	0.2	2.5
+ - Bx ³	7.8	5.7	10.0	1.7	4.7
+ - bi Bx ³	29.2	10.8	7.0	15.7	22.0
Additive*	10.3	10.5	8.8	8.7	8.1

* The sum of the first two differences minus the third difference.

of the differences in area of bifid and Beadex-3 from normal is equal to 0.0122 plus 0.0390 or 0.0512. The experimental difference between bifid Beadex-3 and normal is 0.1348. The difference between 0.0512 and 0.1348 is 0.0836. Table 2 shows that this difference is 10.3 times its error.

The measurements of the mutants differ significantly from normal in the following respects: The area and distal length of bifid are smaller. The crossvein interval and the area of Bx³ are smaller, while the total and distal length are larger. In Bx¹, all the measurements except distal length are smaller. Bi Bx³ and bi Bx¹ are smaller than normal in all respects.

TABLE 3
Bx¹ Series. Means and Standard Errors.

CLASS	AREA	TOTAL LENGTH MM	DISTAL LENGTH MM	PROXIMAL LENGTH MM	CROSSVEIN INTERVAL MM
+	0.3290 ± (0.0026)	85.87 (0.45)	47.53 (0.28)	38.31 (0.29)	18.31 (0.18)
bi	0.2973 ± (0.0025)	81.34 (0.40)	44.04 (0.31)	37.31 (0.22)	16.63 (0.10)
Bx ¹	0.2939 ± (0.0022)	83.37 (0.29)	47.58 (0.22)	35.85 (0.23)	16.41 (0.16)
bi Bx ¹	0.2323 ± (0.0027)	75.09 (0.72)	43.34 (0.54)	31.85 (0.36)	13.68 (0.16)

All the values of bi Bx³ are significantly smaller than those expected from a simple additive effect of bifid and Beadex-3. This is also true in the bi Bx¹ wings in regard to area, total and proximal length, and possibly the crossvein interval. The values for bi Bx³ are lower than those for bi Bx¹ in all cases. Thus, the areas of the bi Bx³ and the bi Bx¹ wings are respectively 53.3 percent and 70.6 percent of the normal wing area. However, none of the differences are statistically significant with the numbers available.

There are also other features of the bifid Beadex wing which cannot be explained by a simple additive effect of bifid and Beadex. In the Bx^1 series, only 12 out of 71 Bx^1 wings had scalloped costal margins, while all 63 bi Bx^1 wings had scalloped costal margins. A similar difference was present in the venation of bifid and bifid Beadex wings in both series. In bifid wings, the fourth longitudinal vein failed to reach the margin in 4 out of 167 wings (2.4 percent). This characteristic feature of bifid was observed in 121 out of 179 bifid Beadex wings (67.6 percent), although the other classes of F_2 wings were normal in this respect. The failure of the fifth longitudinal vein to reach the margin in Beadex wings remained unaltered in bifid Beadex wings.

TABLE 4
Bx¹ Series. Difference/Error.

DIFFERENCE	AREA	TOTAL LENGTH	DISTAL LENGTH	PROXIMAL LENGTH	CROSSVEIN INTERVAL
$+ - bi$	8.8	7.5	8.3	2.8	8.0
$+ - Bx^1$	10.4	4.7	0.1	6.6	7.9
$+ - bi Bx^1$	25.6	12.7	6.9	14.0	19.3
Additive	4.8	3.2	0.9	4.3	2.6

Less extensive tests of the interaction of bifid with other sex-linked genes producing scalloped wings were made. The mutants cut-6 and scalloped were used. Qualitative examination revealed no difference between cut-6 and bifid cut-6 male wings. The bifid scalloped combination is more difficult to evaluate qualitatively, since scalloped itself is extremely variable. On the whole, bifid scalloped male wings seemed to be more reduced than scalloped wings.

The disproportionate interaction of bifid with scalloped is not as striking as that of bifid with Beadex, in regard to size and shape of the wing. The results of this combination on venation, however, parallel those of the latter. It was found that 0, 8.7, 15.7, and 83.3 percent respectively, of the normal, the bifid, the scalloped, and the bifid scalloped wings had the fourth longitudinal vein interrupted, in a total of 336 wings.

DISCUSSION

GOLDSCHMIDT (1935) has studied the development of Beadex, cut, and other mutants producing scalloped wings. He found that their development was characterized by peripheral degeneration. Our data indicate that other factors are also involved in producing the characteristic dimensions of Beadex and bifid Beadex wings.

The crossvein interval region is not affected by scalloping, nor presumably by peripheral degeneration. It is, however, considerably reduced

in Beadex and bifid Beadex wings. The factors responsible for this decrease do not seem to influence the distal length. Thus, in Bx^3 wings, the distal length, and consequently the total length, are greater than normal. In bifid Beadex wings, the crossvein interval is proportionately more reduced than the distal length.

The interaction of bifid and Beadex seems to be fairly specific. The combinations of other wing mutants with Beadex, reported by CSIK (1934), do not have disproportionate effects. The bifid cut-6 combination effect is also not disproportionate. The description of the original bifid stock by MORGAN and BRIDGES (1915) and the results of the bifid scalloped combination indicate that bifid may act disproportionately with other genes besides Beadex.

The methodological usefulness of disproportionate effects is necessarily limited. The type of interaction with bifid may, however, serve to differentiate between wing mutants whose development and phenotypes are similar, such as Beadex and cut-6.

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SUMMARY

1. Combinations of bifid with five different Beadex alleles produce a qualitatively new type of reduced wing.
2. This disproportionate combination effect is quantitatively much greater than a simple summation of the independent effects of bifid and Beadex.
3. Bifid also interacts disproportionately with scalloped, but not with cut-6.
4. Peripheral degeneration cannot be the only aberrant factor involved in the formation of Beadex and bifid Beadex wings.

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