NOTES AND COMMENTS

A BALANCED LETHAL SYSTEM IN THE FLOUR BEETLE, *TRIBOLIUM CASTANEUM*

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1. INTRODUCTION

Balanced lethal systems are well known in both plants and animals. From the classical example involving the chromosome complexes of *Oenothera* (Cleland, 1936) to the intricate marked inversion stocks of various *Drosophila* species, these systems have wide use and application both in nature and in the laboratory.

This note describes a balanced lethal system in the flour beetle, *Tribolium castaneum*, an organism which has recently become popular for use in population genetics research. It is the first recorded case of a balanced lethal system in the Coleoptera.

2. MATERIALS AND METHODS

The *Sa-2* gene of *T. castaneum* is one of several alleles at the *Sa* (Short antenna) locus in linkage group VII (Dawson and Sokoloff, 1964). It is dominant with recessive lethal effects; i.e. *Sa-2/Sa-2* individuals die in embryonic or early larval stages. Heterozygotes are characterised by a reduction and/or fusion of antennal segments and a variable deformation of the tibiae.

In the course of studies with *Sa-2* (hereafter referred to as *Sa*), a number of inbred lines propagated by brother × sister mating were established. After 13 generations the progeny of one of these lines were found to be all mutant instead of the expected ratio of 2 mutant: 1 wild type. Several of the female offspring were mated individually to wild type males, and all crosses produced some + offspring. This indicated that the parental females were *Sa/+* and that the + chromosome carried a recessive lethal gene. Such a lethal would have to be either located quite close to *Sa* or involved in an inversion including the *Sa* locus.

A definitive test for the presence of a lethal gene on the + chromosome in an *Sa/+* individual is easily made by use of another dominant gene with recessive lethal effects, fused tarsi and antennae (*Fta*). The latter is located in the same linkage group as *Sa* and, in heterozygous combination with *Sa*, produces a dominant synthetic lethal (Sokoloff, 1964). Thus a mating between *Sa+/++* and *+Fta/++* individuals has an expectation of progeny which are phenotypically *Fta*, *Sa* and wild type in equal proportions. If the *Sa* parent were carrying a recessive lethal in the + chromosome which was close enough to the *Sa* locus to effectively eliminate crossing over, the *Fta* progeny (which would carry the lethal) could be mated to other beetles from the balanced lethal strain. The resulting offspring should then be ½ *Fta* and ½ *Sa*, since the *Fta/Sa* and lethal/lethal individuals would die. Any wild type progeny would be the result of crossovers between *Sa* and *l* and/or *Fta* and *l*, and the data could thus be used to estimate the distances between these genes as an aid in locating the position of the lethal.

The distance between *Sa* and the lethal was estimated more precisely from the results of a number of matings involving parents from the balanced lethal strain. Wild type progeny from such matings would be expected to have resulted from

crossovers between *Sa* and the lethal. Since cases of mild expression of *Sa* closely resemble wild type, all progeny which appeared to be normal were mated to wild type individuals from a standard laboratory strain. If no *Sa* beetles were found among the offspring of the latter matings, the tested parent was assumed to be wild type.

All matings were carried out in large shell vials or in creamers containing a standard mixture of stone-ground whole wheat flour enriched with five per cent brewer's yeast. The cultures were kept in an incubator maintained at 29° C. and 60 per cent. relative humidity.

3. RESULTS

When males heterozygous for the *Fta* gene were crossed to females from the *Sa* strain thought to carry the lethal gene, the distribution of progeny phenotypes was as follows: 15 +, 20 *Fta*, 23 *Sa*. This approximates the 1:1:1 distribution expected if *Fta/Sa* results in a synthetic lethal (Sokoloff, 1964); $\chi^2 = 2 \cdot 30$, $0 \cdot 5 < P < 0 \cdot 25$. Backcrosses of *Fta* females (now carrying the lethal) to males from the same *Sa* strain yielded the following progeny: 123 *Fta*, 119 *Sa*, 12 +. The presence of a lethal factor is thus verified, since a 1:1:1 ratio would again be expected if there were none.

TABLE 1

Expected frequencies of gametes and viable progeny phenotypes from the mating
Sa++/+1+ X ++Fta/+1+, where *X* and *Y* are the respective crossover frequencies for
the Sa-1 and 1-Fta regions

	$\dfrac{1-Y}{2}$ + + Fta	$\dfrac{Y}{2}$ + + +	$\dfrac{Y}{2}$ + l Fta	$\dfrac{1-Y}{2}$ + l +
$\dfrac{1-X}{2}$ Sa + +		$\dfrac{Y(1-X)}{4}$ Sa		$\dfrac{(1-X)(1-Y)}{4}$ Sa
$\dfrac{X}{2}$ + + +	$\dfrac{X(1-Y)}{4}$ Fta	$\dfrac{XY}{4}$ +	$\dfrac{XY}{4}$ Fta	$\dfrac{X(1-Y)}{4}$ +
$\dfrac{X}{2}$ Sa l +		$\dfrac{XY}{4}$ Sa		
$\dfrac{1-X}{2}$ + l +	$\dfrac{(1-X)(1-Y)}{4}$ Fta	$\dfrac{Y(1-X)}{4}$ +		

The distances between *Sa* and *l* (X) and between *l* and *Fta* (Y) were estimated by the maximum likelihood method (*e.g.* Bailey, 1961). Table 1 lists the classes of viable offspring by phenotype, from which the expected frequencies of *Sa*, *Fta* and + are easily calculated. If second order and higher terms in the equations resulting from the maximum likelihood procedure are ignored, estimates of $2 \cdot 8 \pm 2 \cdot 5$ and $5 \cdot 8 \pm 2 \cdot 4$ units are obtained for X and Y respectively.

It is not possible from these data to determine the position of the lethal gene in relation to *Sa* and *Fta*. However, if these two markers are indeed 18 units apart as reported by Sokoloff (1965), it is probable that the order of the genes is *Sa-l-Fta*.

Data from 16 productive matings between beetles from the balanced lethal strain can be used to estimate the distance between *Sa* and the lethal. Table 2 gives the classes of viable progeny resulting from such matings. A total of 1000 offspring were obtained, of which six were shown to be + by progeny tests as previously described. Another eight normal-appearing adults were found, but these either could not be progeny tested or produced no offspring.

TABLE 2

Expected frequencies of gametes and viable progeny phenotypes from mating two parents of genotype Sa+/+l, *where X is the crossover frequency between* Sa *and* 1

	$\dfrac{1-X}{2}$ Sa +	$\dfrac{X}{2}$ Sa l	$\dfrac{X}{2}$ + +	$\dfrac{1-X}{2}$ + l
$\dfrac{1-X}{2}$ Sa +			$\dfrac{X(1-X)}{4}$ Sa	$\dfrac{(1-X)^2}{4}$ Sa
$\dfrac{X}{2}$ Sa l			$\dfrac{X^2}{4}$ Sa	
$\dfrac{X}{2}$ + +	$\dfrac{X(1-X)}{4}$ Sa	$\dfrac{X^2}{4}$ Sa	$\dfrac{X^2}{4}$ +	$\dfrac{X(1-X)}{4}$ +
$\dfrac{1-X}{2}$ + l	$\dfrac{(1-X)^2}{4}$ Sa		$\dfrac{X(1-X)}{4}$ +	

Both parents were $Sa+/+l$, and from this double intercross seven of the sixteen zygotic combinations are lethal. If simultaneous crossovers in both parents are ignored, the maximum likelihood estimates for the distance between *Sa* and l are 0.60 ± 0.24 and 1.40 ± 0.38 units, depending on whether there were 6 or actually 14+ individuals. These values are in agreement with the estimate of 2.88 ± 2.50 units from the previous experiment.

More precise estimates for the *Sa-l* distance may also be obtained by maximum likelihood, but their determination requires solution of a fifth order equation. The equation was solved for the quadratic case and yielded estimates of 0.59 ± 0.24 and 1.39 ± 0.37, values very close to those obtained by the first method.

It should be noted that crossing over in the two sexes is not equal for genes located in this linkage group (Johnson, 1966). Hence the estimated map distances obtained in the present study should be considered as approximations only.

Whereas the possibility exists that the lethal was associated with a chromosome inversion, a linkage test indicated that the distance between

Sa and chestnut (Eddleman and Bell, 1963) had not changed. Thus it is probable that the *Sa* gene has not been involved in an inversion, at least of very great size.

The data clearly indicate the presence of a balanced lethal system in this species of flour beetles. In addition to being useful in genetic studies once sufficient genetic markers become available, the lethal gene also serves a useful immediate purpose. In order to maintain the *Sa* stock, it is necessary to select mutant individuals at frequent intervals. With the balanced lethal system present in the stock, it can be maintained for a considerable length of time without having to be selected. Furthermore, it might be possible to balance an *Fta* strain with the same lethal, particularly if it is located between *Sa* and *Fta*.

4. SUMMARY

A balanced lethal system is described in linkage group VII of the flour beetle, *Tribolium castaneum*. Short antenna (*Sa*), a dominant gene with recessive lethal effects is located from 0·5 to 3 units from an autosomal lethal.

5. REFERENCES

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THE PROBABILITY OF SURVIVAL OF A NEW MUTANT IN A FLUCTUATING ENVIRONMENT

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1. INTRODUCTION

THE classical treatment of the problem of the probability of survival of a favourable new mutant has always supposed that the population in which the mutation occurs is of constant size. This may well be the most commonly occurring situation, but two other cases at least deserve some attention. These are, firstly, the case where the population size undergoes cyclic fluctuations, and secondly the case where the population size is initially small and then grows fairly rapidly until it reaches an equilibrium value, where it levels off. In this paper we derive survival probabilities under each of these circumstances.