ELEMENTS CAUSING MALE CROSSING OVER IN *DROSOPHILA MELANOGASTER*[1]

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ABSTRACT

A second chromosome line of *Drosophila melanogaster* (Symbol: *T-007*) has previously been shown to be responsible for the induction of male recombination. In the present investigation, the genetic elements responsible for this phenomenon have been partially identified and mapped. A major element (Symbol: *Mr*, for *M*ale *r*ecombination) locates on the second chromosome between the *pr* (2L-54.4) and *c* (2R-75.5) loci and is responsible for the large majority of male recombination. In addition, there appear to be "secondary elements" present which have the ability to induce male recombination in much reduced frequencies and which are diluted out through successive backcross generations when *Mr* is removed by recombination. The possible nature of these "secondary elements" is discussed.

IT has been generally assumed that crossing over is absent in Drosophila males, despite the fact that only a relatively small number of species have been adequately tested. Notable exceptions to the aforementioned assumption include certain strains of *Drosophila ananassae* (KIKKAWA 1937; HINTON 1970; MORIWAKI and TOBARI 1973) and *Drosophila willistoni* (FRANCA, DA CUNHA and GARRIDO 1968).

MORGAN first reported the absence of crossing over in male *Drosophila melanogaster* (MORGAN 1912, 1914), and this observation has since been confirmed by numerous investigators. It was not until recently that a natural population of *Drosophila melanogaster* was found to contain genetic elements that could give rise to male recombination (HIRAIZUMI 1971; HIRAIZUMI *et al.* 1973). They reported that a large percentage of the second chromosome lines isolated from a natural population in southern Texas were able to undergo male recombination, although in frequencies much lower than those in females. Since this first report, a number of other investigators have observed similar phenomena in *Drosophila melanogaster* isolated from natural populations in numerous geographical locations including: Florida (VOELKER 1974), North Carolina (BROADWATER *et al.* 1973), Ohio (WADDLE and OSTER 1974), Oklahoma (WOODRUFF and THOMPSON, personal communication), Pennsylvania (YAMAGUCHI and MUKAI 1974), several New England populations maintained in the laboratory for less than 10 years (KIDWELL and KIDWELL 1975), Cambridge, England (WOODRUFF, personal communication), and Australia (SVED 1974).

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In addition to the induction of male recombination, males heterozygous for the second chromosomes, isolated by HIRAIZUMI, were found to show segregation frequencies from heterozygous male parents much lower than the Mendelian expectation of 0.50. SLATKO and HIRAIZUMI (1973) further showed that these chromosome lines acted as "mutator strains", as evidenced by increased frequencies of *X* and second chromosome recessive lethals, visible mutations, and mosaics.

One conspicuous absence from previous studies concerned the identity of the genetic elements responsible for the induction of the male recombination phenomenon. The purpose of the present study is to report on this aspect.

MATERIALS AND METHODS

Strains of *Drosophila melanogaster* used for the present study are listed as follows.

1. *cn bw*: A standard second chromosome line marked with two recessive eye color mutants, *cn* (cinnabar eye color, 2R-57.5) and *bw* (brown eye color, 2R-104.5). Homozygous flies, *cn bw/cn bw*, show white eye color.
2. *In(2L+2R) Cy; cn² bw*: A second chromosome line with two large inversions, one in the left and the other in the right arm. This chromosome carries the dominant marker *Cy* (Curly wing) and two recessive eye color mutants, *cn²* (an allele of *cn*) and *bw*. Homozygous lethal, this line will be abbreviated as *Cy*.
3. *al dp b pr c px sp*: A second chromosome line marked with seven recessive markers, *al* (aristaless, 2L-0.01), *dp* (dumpy wing, 2L-13.0), *b* (black body color, 2L-48.0), *pr* (purple eye color, 2L-54.4), *c* (curved wing, 2R-75.5), *px* (plexus wing vein, 2R-100.5), and *sp* (speck, 2R-107.0). This line will be abbreviated as *apl* in this report.
4. *T-007*: One of the second chromosome lines that showed male recombination in the frequency of about 1% between *cn* and *bw*. This line was isolated from a natural population in Harlingen, Texas. Males collected from the natural population were first mated to *C(1)DX, y f; cn bw* females (to replace their *Y* chromosomes) and progeny males were then backcrossed to *cn bw* females for nine generations before being kept as a balanced stock, *T-007/Cy*. *T-007* is associated with recessive lethality.

A standard cornmeal-agar food, supplemented with proprionic acid as a mold inhibitor, was used throughout these experiments. The age of all flies at the time of matings was usually less than six days. Parents were kept in a vial for seven days and then discarded. Progeny were counted through the nineteenth day from the date of mating. All experiments were carried out at room temperature, 23°–24°.

EXPERIMENTS AND RESULTS

Mapping of the elements causing male recombination: The *T-007* second chromosomal line has been kept in our laboratory as a balanced stock after many generations of backcross matings (see MATERIALS AND METHODS) which selected only for the second chromosome. It is apparent that at least one major element causing male recombination must locate on the second chromosome, as all other chromosomes would have been diluted out during the course of the backcross matings initiated in 1971. The second chromosome of this line was thus examined in order to map the position of the elements responsible for male recombination. The mating scheme used for this purpose is shown in Figure 1 (A).

Initially, *T-007/Cy* males were mated to *apl* females. From this mating, virgin F_1 *T-007-apl* females were selected and backcrossed to homozygous *apl* males. Among the progeny of these matings were individuals bearing various recombi-

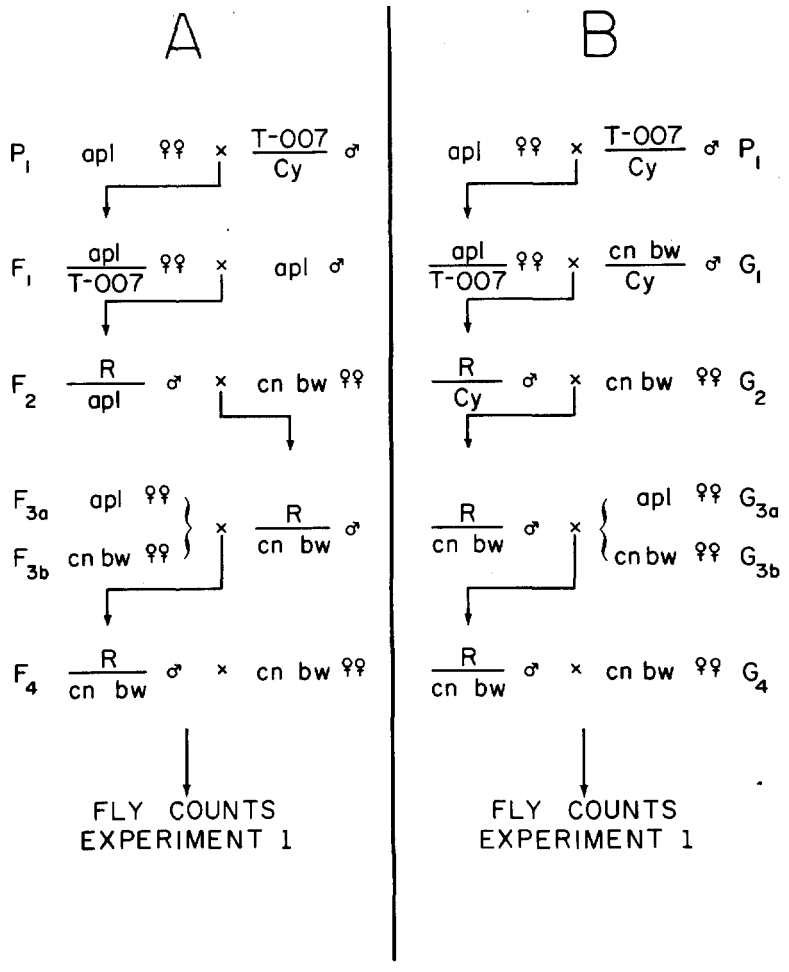

FIGURE 1.—A. Mating scheme utilized to isolate recombinant chromosome types (R) generated between the *apl* and *T-007* second chromosomes, including isolation of the presumptive non-recombinant chromosomes of the genotype + + + + + + +, and to subsequently test them for the ability to induce male recombination between the second chromosome right arm markers *cn* and *bw*. B. Mating scheme utilized to isolate the presumably non-recombinant chromosomes of the *al dp b pr c px sp* genotype, and to subsequently test them for the ability to induce male recombination between *cn* and *bw*. For full details consult text.

nant chromosomes which were generated in the heterozygous F_1 females. These recombinant chromosomes were then assayed for the presence or absence of the ability to induce male recombination between the two recessive markers *cn* and *bw*. This was done as follows: The F_2 males of the appropriate recombinant genotypes were individually mated to *cn bw* females, and from each of these matings, F_3 males were isolated. All F_3 males collected from each F_2 mating were phenotypically "wild type" but genotypically either *apl/cn bw* or *recombinant chromosome type/cn bw*. It was therefore necessary to double-mate individual F_3 male

progeny from *each* original F_2 recombinant male first to *apl* females (F_{3a} in Figure 1(A)) to select males of the appropriate genotypes and then to *cn bw* females (F_{3b} in Figure 1(A)) to isolate a larger number of *recombinant chromosome type/cn bw* males. The F_4 males were genotypically heterozygous for *cn bw* and the identical "recombinant chromosome" present in the F_2 parental males. These heterozygous males were then mated to *cn bw* females to test for the presence of the ability to induce male recombination. By this scheme, each of the individually isolated recombinant genotypes could be tested for the ability to induce male recombination between *cn* and *bw*, and in addition, it was possible to obtain a fairly large number of F_4 males (i.e., replications) for each individually isolated recombinant chromosome.

It should be noted that from this mating scheme it is also possible to isolate the presumptive non-recombinant chromosomes of the + + + + + + + + genotype (= *T-007*), but impossible to isolate the non-recombinant *apl* chromosomes. This is due to the fact that in the F_2 matings in Figure 1(A), it is impossible to distinguish the *apl* chromosome derived from the F_1 females and the *apl* chromosome from F_1 males. For the purpose of isolating the non-recombinant *apl* chromosomes, an alternative mating scheme was used, which is shown in Figure 1(B). The results of these matings, designated as Experiment 1, are summarized in Table 1.

Table 1 includes the results obtained for the 12 recombinant and 2 presumptive non-recombinant genotypes (Type numbers 1–14) generated in the *T-007/apl* heterozygous females, which were tested for the ability to induce male recombi-

TABLE 1

Male recombination frequencies between the cn *and* bw *loci for the twelve recombinant and two presumptive non-recombinant chromosome types generated in* T-007/apl *heterozygous females*

Group	Type number	Recombinant chromosome type	Total no. of lines isolated	N_1*	N_2†	Avg. no. replic. per line	Avg. no. progeny per line	Rec. freq. between *cn* and *bw*
	1	+ + + + + + + +	19	0	19	28.5	1682	0.0097
	2	*al* + + + + + + +	4	0	4	31.5	1727	0.0100
A	3	*al dp* + + + + + +	9	0	9	21.3	1399	0.0079
	4	*al dp b* + + + + +	6	0	6	32.2	1874	0.0098
	5	*al dp b pr* + + +	10	6	4	43.5	2235	0.0018
	6	*al dp b pr c* + +	6	3	3	19.2	1323	0.0005
	7	*al dp b pr c px* +	5	2	3	44.0	2199	0.0012
B	8	*al dp b pr c px sp*	21	9	12	25.0	1612	0.0009
	9	+ *dp b pr c px sp*	4	0	4	18.0	1330	0.0019
	10	+ + *b pr c px sp*	9	2	7	24.4	1930	0.0020
	11	+ + + *pr c px sp*	7	0	7	27.6	1585	0.0025
	12	+ + + + *c px sp*	11	1	10	41.2	2187	0.0061
C	13	+ + + + + *px sp*	10	0	10	22.5	1471	0.0063
	14	+ + + + + + *sp*	4	0	4	25.5	1393	0.0102

* Number of lines which did not induce any male recombination.
† Number of lines which induced some male recombination. For further details, consult text.

nation between the second chromosome right arm markers *cn* and *bw*. For each recombinant chromosome type isolated (F_2 or G_2 males in Figure 1), a number of independently isolated chromosome lines were collected (designated as "Total number of lines isolated" in Table 1). For each independently isolated chromosome line, a number of replications were made (corresponding to the F_4 or G_4 males, Figure 1). The average number of replications and the average number of subsequent progeny scored for each chromosome line are shown for each recombinant chromosome genotype. Additionally, the number of independently isolated recombinant chromosome lines showing male recombination induction are listed, along with the recombination frequency (measured between *cn* and *bw*) averaged for all lines of each recombinant chromosome type. For example, in Group B, 21 independent (F_2) males with the *al dp b pr c px sp* genotype (type number 8) were isolated. For *each* of the 21 lines, the number of replications (F_4 males) averaged 25.0 and the number of progeny (averaged for the 21 lines) was 1612. Of the 21 lines, 12 induced some male recombination. The recombination frequency between *cn* and *bw*, averaged for all 21 lines, was 0.0009 (almost 0.1%).

Because the phenomenon of male recombination seems to be of largely premeiotic origin (HIRAIZUMI *et al.* 1973), any computations of average recombination frequencies must take into consideration the occurrence of clustering. Although a deviation in the distribution of recombinants among males from the Poisson expectation was statistically significant, the degree of clustering was generally small. In addition there were no large differences, with respect to clustering, between the 14 recombinant chromosome types. For all practical purposes, therefore, the use of a simple average recombination frequency is permissible, neglecting the small clustering effect.

The recombinant chromosome types listed in Table 1 have been organized into three groups (Groups A to C). It can be seen that with respect to the ability to induce male recombination, the three groups can be classified into two sets. The first set (Groups A and C) induces a relatively higher frequency of male recombination than the second set (Group B). The recombinant types in the first set (Groups A and C) have only one region in common: the pr^+ region derived from the *T-007* chromosome. Conversely, those recombinant chromosome types in the second set contain the *pr* region from the *apl* chromosome. Note that of a total of 63 chromosomes carrying the pr^+ region which were tested, only one (of the type $+ + + + c\ px\ sp$) did not induce any male recombination. All of these observations seem to suggest that one major element responsible for the induction of male recombination is located near, and probably to the right of, the pr^+ locus in the *T-007* chromosome.

As was mentioned previously, practically all (i.e., 62 out of 63) of the recombinant chromosomes carrying the pr^+ region from *T-007* induced male recombination. If one assumes that only a single element is responsible for male recombination induction, the majority of the complementary recombinant chromosome types (which carry the *pr* region from the *apl* chromosome) should not induce male recombination. However, this does not appear to be the case; the

majority (40 out of 58) show the induction of male recombination, although in markedly reduced frequencies. These results suggest that in addition to the major element located near the *pr*+ region of the *T-007* chromosome, there must be at least one additional "secondary element" present which is also responsible for the induction of male recombination. If a single "secondary element" which can induce low levels of male recombination is assumed, then by examination of the lines in Group B (lines not carrying *pr*+ from *T-007*), it should be possible to localize this element. The assumption of a single second locus would necessarily imply the existence of two distinct classes of male recombination in this group.

It might appear, by preliminary inspection, that a "secondary element" may be present around the *al*+ locus, since 18 out of the 20 recombinant chromosome types with *al*+ (types 9, 10, and 11) showed some male recombination. It can also be seen, however, that this single "secondary element" model does not entirely explain the observed results, since more than half (22 out of 42) of the remaining recombinant types (types 5, 6, 7, and 8) also show some male recombination induction.

One other interesting observation from the data in Table 1 that pertains to the analysis of the "secondary elements" concerns the presumptive non-recombinant chromosome of the genotype *al dp b pr c px sp*. Flies of this type carry all seven mutant markers, and therefore have the same genotype as the standard *apl* chromosome, except for the possible occasional occurrence of double crossover events (in the *T-007/apl* females) between any two adjacent markers. Also, possible single crossover events outside of the *al* and *sp* markers (to the left of *al* or to the right of *sp*) might occur such that the tip of the left or right arm of *T-007* could be transferred to the "non-recombinant" chromosome. The frequency of such undetected double crossovers should be very low, as should be the frequency of recombination outside the two end markers, considering their map positions relative to the tips of the chromosome arms. A total of 21 *al dp b pr c px sp* "non-recombinant" chromosomes were tested for the ability to induce male recombination, as shown in Table 1. Of the 21 lines tested, 12 showed the ability to induce male recombination. This frequency (60%) is too high to be explained by the occurrence of double crossing over between any two adjacent markers, or by single crossover events outside the end markers (*al* and *sp*).

It should be stated here that neither the *apl* chromosome nor the *cn bw* chromosome induces any male recombination. From the mating *apl/cn bw* ♂ × *cn bw* ♀, 7656 progeny were scored and no recombinants were observed. Similarly, from the mating *apl/cn bw* ♂ × *apl* ♀, 4471 progeny were scored, and again, no recombinants were found. Thus, the *cn bw* chromosome and the *apl* chromosome do not contain genetic elements which can cause male recombination.

These results suggest that in addition to the presence of the major locus for male recombination induction, "secondary elements" must be present which can induce low levels of male recombination. Since the *T-007* second chromosomal line was originally kept by repeated backcross matings to *cn bw*, only the originally isolated second chromosome remains in the *T-007/Cy* stock. Any genetic elements located on any other chromosome would have been diluted out.

Thus, there must be an association between the "secondary elements" and the *T-007* second chromosome. We will return to reconsider these "secondary elements" later.

Many of the chromosome lines included in Table 1 were discarded after the completion of Experiment 1. Several of the lines, however, were kept by repeated backcross matings through males to *cn bw* females. After six generations of these backcross matings, these lines were re-examined for the ability to induce male recombination. The results of these matings, designated as Experiment 2, are shown in Table 2.

Experiment 2 was originally designed to obtain some confirmation of the results presented in Table 1. The results, however, provided much more important information than a mere confirmation. Whereas the data presented in Table 1 is a summary of *all* independently isolated chromosome *lines* of a given geno-

TABLE 2

Comparisons of male recombination frequencies for several recombinant chromosome types between Experiment 1 and Experiment 2

Group	Recombinant chromosome type	Line number	Experiment 1			Experiment 2		
			No. F_4 males tested	No. progeny scored	Rec. freq. between *cn* and *bw*	No. males tested	No. progeny scored	Rec. freq. between *cn* and *bw*
A	+ + + + + + +	8	50	2421	0.0050	20	935	0.0011
	+ + + + + + +	9	50	2690	0.0126	17	858	0.0163
	+ + + + + + +	11	47	1964	0.0041	20	1087	0.0055
	+ + + + + + +	13	47	2298	0.0083	19	926	0.0088
	al + + + + + +	3	48	2175	0.0092	14	739	0.0149
	al + + + + + +	4	49	2388	0.0101	20	1184	0.0042
	al dp b + + + +	2	44	2109	0.0079	20	1271	0.0047
	al dp b + + + +	5	47	2532	0.0122	20	1306	0.0100
	Mean				0.0087			0.0082
B	*al dp b pr c* + +	4	20	890	0.0000	20	1267	0.0000
	al dp b pr c px sp	8	17	942	0.0000	20	1214	0.0000
	al dp b pr c px sp	9	20	980	0.0000	20	1333	0.0000
	Mean				0.0000			0.0000
C	*al dp b pr c px sp*	7	20	1007	0.0020	30	2033	0.0000
	al dp b pr c px sp	10	47	2424	0.0017	30	2093	0.0000
	al dp b pr c px sp	11	20	909	0.0022	29	1741	0.0000
	al dp b pr c px sp	12	40	1749	0.0017	30	2102	0.0000
	+ *dp b pr c px sp*	3	20	942	0.0032	40	2694	0.0000
	+ *dp b pr c px sp*	4	20	920	0.0011	40	2410	0.0000
	+ + + *pr c px sp*	3	48	2275	0.0004	40	2874	0.0000
	Mean				0.0018			0.0000

For full details, consult text.

type, the data in Table 2 is presented so that for each *individual line* of a given genotype, direct comparisons can be made between the results obtained in Experiment 2 (after 6 generations of backcross matings).

Before examining the results presented in Table 2, one aspect which first should be considered concerns any change in the "recombinant chromosome genotype" due to male recombination which could have occurred during the six generations of backcross matings to the *cn bw* females. Any recombination between the *cn* and the *bw* loci could be detected by phenotype. In fact, such recombinants were occasionally found and eliminated during the stock-keeping procedures. Since the *cn bw* chromosome does not carry any markers in the left arm, male recombination in the left arm could not be detected in this manner. Before experiment 2 was performed, a check was made for the presence of the left arm markers characteristic for each of the "recombinant chromosome" lines. This screening was done by mating the heterozygous males, (*recombinant chromosome type /cn bw*), to *apl* females and examining the phenotypes of the progeny flies. This works efficiently for the lines carry the left arm end marker, *al*, but does not work for lines such as $+++++$ *c px sp*, which lack left arm markers. Consequently, there is the small possibility of undetected male recombination in the left arm of such genotypes. In addition, there is no way to detect any double crossover events which might have occurred between any two adjacent markers, or single crossover events outside of the two end markers, *al*, and *sp*. The possibility of such undetected male recombination should be very small, however, since the frequency of male recombination is generally low. Based upon these considerations, it seems probable that a large majority (presumably all) of the "recombinant chromosome" lines tested in Experiment 2 still maintained the same genotypes originally present when they were tested in Experiment 1.

In Table 2, the recombinant chromosome types are divided into three groups (Groups A, B, and C). Group A includes those lines which carry the pr^+ region from *T-007* and which induced relatively higher frequencies of male recombination in Experiment 1 (Mean = 0.0087). When retested after six generations of backcross matings, these lines continued to induce male recombination in comparable frequencies (Mean = 0.0082).

As mentioned previously, several lines tested in Experiment 1 failed to induce male recombination. With only one exception, these were restricted to lines which carry the *pr* region from the *apl* chromosome. Group B in Table 2 lists such lines, i.e., those lines which induced no male recombination in Experiment 1 and which were retested in Experiment 2. It can be seen that those lines which were unable to induce male recombination in Experiment 1 remained unable to do so when retested after the six backcross generations.

The most interesting observation from the date presented in Table 2 concerns those lines which are included in Group C. These are the lines which carry the *pr* region from the *apl* chromosome and which showed relatively lower frequencies of male recombination in Experiment 1. When these lines were retested after six generations of backcross matings, none was able to induce male recombination any longer. In these genotypes, the ability to induce male recombination is now very much reduced.

Because there was a previous suggestion that the "major element" responsible for the induction of male recombination locates between the *pr*+ and *c*+ loci in the *T-007* chromosome, the two complementary recombinant chromosome types generated between these two markers (i.e., + + + + *c px sp* and *al dp b pr* + + +) were examined separately from the recombinant types listed in Table 2. The results from the matings designed to retest these two recombinant types for the ability to induce male recombination after the six generations of backcross matings are shown in Table 3.

Table 3 is analogous to Table 2 (in design and intention), with the exception that only the two complementary recombinant chromosome types, + + + + *c px sp* and *al dp b pr* + + +, are considered. Group A includes those lines which induced relatively higher frequencies of male recombination in Experiment 1. It can be seen that these lines have retained the ability to induce male recombination when retested after six generations of backcross matings. It is interesting to note that both of the complementary genotypes are represented in this group, as expected if the "major element" locates between the *pr*+ and *c*+ regions of the *T-007* chromosome.

Group B in Table 3 includes those lines which induced no recombination in Experiment 1. The lines included in this group are still unable to induce male recombination, analogous to the data presented for Group B in Table 2.

Group C in Table 3 contains a single representative. This line induced relatively lower male recombination in Experiment 1; but when retested after the 6 generations of backcross matings, this line was found to be unable to induce

TABLE 3

Comparisons of male recombination frequencies for the al dp b pr + + + *and* + + + +c px sp *recombinant chromosome types between Experiment 1 and Experiment 2*

Group	Recombinant chromosome type	Line number	Experiment 1			Experiment 2		
			No. F_4 males tested	No. progeny scored	Rec. freq. between *cn* and *bw*	No. males tested	No. progeny scored	Rec. freq. between *cn* and *bw*
A	+ + + + *c px sp*	5	50	2266	0.0013	20	1063	0.0019
	+ + + + *c px sp*	6	37	2491	0.0129	20	1336	0.0112
	+ + + + *c px sp*	7	47	2975	0.0064	20	1348	0.0052
	al dp b pr + + +	4	20	1960	0.0034	40	2557	0.0023
	al dp b pr + + +	10	50	2716	0.0056	30	1972	0.0076
	Mean				0.0059			0.0056
B	*al dp b pr* + + +	2	45	2104	0.0000	30	1819	0.0000
	al dp b pr + + +	3	50	2328	0.0000	20	1142	0.0000
	al dp b pr + + +	8	40	2630	0.0000	20	1330	0.0000
	al dp b pr + + +	9	40	2390	0.0000	20	1477	0.0000
	Mean				0.0000			0.0000
C	*al dp b pr* + + +	1	21	1900	0.0046	30	1660	0.0000

For full details, consult text.

male recombination any longer. This line thus acts similarly to those lines included in Group C in Table 2.

These results seem to indicate that the maintenance of the ability to induce male recombination is due to a single element located between pr^+ and c^+ in the *T-007* chromosome, as some of the lines of the genotype *al dp b pr* + + + still maintain the ability to induce male recombination in Experiment 2, and thus still carry the "major element". This element may locate nearer to pr^+ in the *T-007* chromosome, although the number of lines tested is too few to determine its position accurately. When a chromosome carries this element, to which we give the name *Mr* (for *M*ale *r*ecombination), this genotype has the ability to exhibit similar levels of male recombination through successive generations. As was pointed out previously, *Mr* is not the only element; there seem to be other "secondary elements" present which can induce male recombination in much reduced frequencies. Results of Experiment 2 indicate that the action of such "secondary elements" is rather transient, inducing male recombination for only a few generations.

DISCUSSION

The male recombination system in *Drosophila melanogaster* appears to be a complex system in which one major element, *Mr*, is responsible for the large majority of male recombination. *Mr* locates between the pr^+ and c^+ loci in the *T-007* chromosome, possibly nearer to the pr^+ locus. In addition to this major element, there seem to be other "secondary elements" present whose abilities to induce male recombination are much less than that of *Mr* and whose effects are "diluted out" through successive backcross generations.

It is obvious that the elements responsible for male recombination must be associated with the second chromosome. However, this does not preclude the fact that this strain of *Drosophila melanogaster* could have had elements located on other chromosomes. Because the original isolation selected only the second chromosome, the influence of the other chromosomes is unknown. In fact, VOELKER (1974) and WADDLE and OSTER (1974) have obtained results that indicate that when both second and third chromosomes are extracted simultaneously from males isolated from "natural populations", a higher frequency of male recombination is observed than if just the original second chromosome or the original third chromosome is present.

At the present time, little data is available concerning the nature of the transitory "secondary element" effect. It was mentioned previously that neither the *apl* chromosome nor the *cn bw* chromosome induces male recombination (*apl/cn bw* males × *cn bw* females—7656 progeny, 0 recombinants; *apl/cn bw* males × *apl* females—4471 progeny, 0 recombinants). Thus, it is unlikely that either one of these stocks carries *Mr* or any "secondary elements" that can induce male recombination.

It is possible to envision that during backcrossing to *cn bw*, modifiers (which could be interpreted as "secondary elements") from the *apl* stock were being diluted out. This would imply, however, that the *apl* stock must behave differ-

ently than the *cn bw* stock. Neither of these stocks induces male recombination, nor does either of these stocks show any type of suppression or enhancement phenomenon. It is reasonable to conclude that the loss of "modifiers" (originally present in the *apl* stock) or the gain of "suppressors" (originally present in the *cn bw* stock) are not likely explanations for the evanescent "secondary element" effect.

Ruling out these possibilities, the simplest explanation for this phenomenon rests with the *T-007* genotype itself. It is interesting to note that this temporal "secondary element" effect could be the explanation for the speculations concerning transposable elements (HIRAIZUMI *et al.* 1973; KIDWELL and KIDWELL 1973; VOELKER 1974; WADDLE and OSTER 1974) that have been advanced in order to explain some unusual aspects of this system.

A number of other possible speculations concerning the transitory "secondary element" effect can be made. This phenomenon could perhaps most easily be explained by assuming that the "secondary elements" are products of *Mr*; however, one must consider the fact that the temporal effects are manifest for several generations. Obviously, a simple protein product of *Mr* is an unlikely candidate. In fact, there is no *a priori* reason to assume that the "secondary elements" are physical particles. *Mr* may induce some change in its homolog, which is temporal. This is similar in a number or respects to the paramutation phenomenon seen in a number of organisms (for recent review, see BRINK 1973) and/or ribosomal DNA "magnification" seen in *Drosophila melanogaster* (RITOSSA 1968; TARTOF 1974).

It is our feeling that a number of the previously mentioned speculations are experimentally testable. Investigations into this aspect of the male recombination system are the subjects for future studies.

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