PARAMETERS OF MALE AND FEMALE RECOMBINATION INFLUENCED BY THE *T-007* SECOND CHROMOSOME IN *DROSOPHILA MELANOGASTER*[1]

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ABSTRACT

The *T-007* second chromosome line of *Drosophila melanogaster*, previously shown to contain genetic elements responsible for male recombination induction, appears to affect several parameters of recombination in females. In *T-007* heterozygous females, the distribution of recombination (but not the total frequency) is changed from that observed in control females; relative increases are observed in the more proximal regions of the second, third and *X* chromosomes, while relative decreases are observed more distally. These changes are paralleled by altered coefficient of coincidence values and in an increased nondisjunction frequency of second chromosomes. The distribution of recombination in females is strikingly similar to that observed in males as measured along the second and third chromosomes, and the frequency of nondisjunction of the *X* and *Y* chromosomes is increased in *T-007* heterozygous males. Based upon these results and responses to the effect of structurally rearranged heterologues (the "interchromosomal effect"), it is suggested that *T-007* affects the preconditions for meiotic exchange in females. It is not yet known if elements responsible for these effects are the same elements responsible for the numerous other traits associated with the *T-007* second chromosome.

SINCE the first reports of MORGAN (1912, 1914), it has generally been assumed that crossing over does not occur in Drosophila males, despite the fact that only a relatively small number of species have been adequately tested. Since the first report of spontaneous male recombination induced by chromosomes isolated from a natural population of *D. melanogaster* (HIRAIZUMI 1971), chromosomes with similar properties have been recovered in high frequencies from natural populations in world-wide locations, including the United States (WADDLE and OSTER 1974; VOELKER 1974; KIDWELL and KIDWELL 1975; CARDELLINO and MUKAI 1975; YAMAGUCHI, CARDELLINO and MUKAI 1976; WOODRUFF and THOMPSON 1977; GREEN 1977), Australia (SVED 1976), Greece (GIANNOPOLUS and PELECANOS, personal communication), Japan (MINAMORI and SUGIMOTO

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1973), Yugoslavia and Taiwan (YAMAGUCHI 1976), Israel (GREEN 1977), and Russia (GOLUBOVSKY, IVANOV and GREEN 1977). Of the 150 second-chromosome lines isolated from southern Texas, about 30% showed the ability to induce male recombination (HIRAIZUMI 1971). In addition, where frequency estimates have been made in other studies with similarly isolated chromosomes from natural populations, 30% to 100% of the chromosomes tested were associated with male recombination induction, mutation induction, reduced transmission frequencies of wild chromosomes from heterozygous males and, often, other anomalous phenomena such as altered male and female fertility. A recent resampling of a southern Texas population undertaken in March, 1975, has shown that about 50% of the second and 50% of the third chromosomes isolated can induce male recombination (MATTHEWS and HIRAIZUMI 1978). Thus, the system not only appears to be spread world wide, but also is in relatively high frequencies.

One second chromosome line (Symbol: *T-007*) originally isolated by HIRAIZUMI (1971) has been extensively analyzed in this laboratory. Previous reports have indicated that male recombination can be induced in frequencies of about 3.5% along the second chromosome and about 2% along the third chromosome (HIRAIZUMI *et al.* 1973; SLATKO and HIRAIZUMI 1973). Preliminary data suggested that the *T-007* second chromosome may also influence other parameters of the recombination process in males and females (SLATKO and HIRAIZUMI 1975). Since these preliminary reports, a large body of data has been accumulated; it is the purpose of this report to extend these observations and describe our further analysis of this genetic system.

MATERIALS AND METHODS

Stocks of *Drosophila melanogaster* used for the present study are listed as follows (for complete description, see LINDSLEY and GRELL 1968): Chromosome *2* markers include *al* (aristaless, *2L*-0.01), *dp* (dumpy, *2L*-13.0), *b* (black, *2L*-48.5), *pr* (purple, *2L*-54.4), *cn* (cinnabar, *2R*-57.5), *lt* (light, *2L*-55.0), *stw*^{3} (straw, *2R*-55.1), *c* (curved, *2R*-75.5), *px* (plexus, *2R*-100.5), *bw* (brown, *2R*-104.5), and *sp* (speck, *2R*-107.0). Chromosome *3* markers include *ru* (roughoid, *3L*-0.0), *h* (hairy, *3L*-26.5), *Gl* (Glued, *3L*-41.4), *th* (thread, *3L*-43.2), *st* (scarlet, *3L*-44.0), *cu* (curled, *3R*-50.0), *Sb* (Stubble, *3R*-58.2), *sr* (stripe, *3R*-62.0), *e*^{s} (ebony-sooty, *3R*-70.7), and *ca* (claret, *3R*-100.7). *X*-chromosome markers include *y*^{2} (yellow, *1*–0.0), *cv* (crossveinless, *1*–13.7), *v* (vermilion, *1*–33.0), *f* (forked, *1*–56.7) and *car* (carnation, *1*–62.5).

Wild type strains

Tokyo: A standard wild-type second-chromosome line that has been kept by backcross matings, through males, to *cn bw* females for more than 15 years.

Canton-S: A standard wild-type line derived from wild flies collected in Canton, Ohio, by C. B. BRIDGES.

T-007: One of the second chromosome lines isolated from a natural population in Harlingen, Texas, in February, 1970. An individual (captured) male was mated to *C(1)DX, y f*; *cn bw* (double-*X*) females. By this mating, the *Y* chromosome from the natural population was replaced by the *Y* chromosome from the *C(1)DX, y f*; *cn bw* stock. A single progeny male from the parental mating was selected and backcrossed to *cn bw* females. The backcross matings were repeated for a total of ten backcross generations, selecting for only the wild derived second chromosome. Because the *T-007* chromosome contains a recessive lethal, the stock is now kept as a balanced lethal stock, *T-007/In(2L+2R), Cy cn*^{2} *bw*. *T-007* heterozygous males charac-

teristically show about 3.5% male recombination along the second chromosome (with about 1% between *cn* and *bw*) and about 1.5% male recombination along the third chromosome.

Special chromosome stocks

C(2L); C(2R): A chromosome line in which the second chromosome is now present as essentially two complementary metacentric isochromosomes, due to a presumptive translocation-type event and joining of breakpoints on opposite sides of homologous centromeres. The isochromosomes are both reversed metacentrics (*RM*).

C(1)DX, In(1)dl-49—In(1)sc^8, y f: A laboratory stock containing two *X* chromosomes attached in a tandem acrocentric configuration. *C(1)DX* females must carry a *Y* chromosome to survive, and the *C(1)DX/Y* females will produce sons that inherit their *X* chromosomes from their father and their *Y* chromosomes from their mother. This stock is commonly referred to as "double-*X*."

In(3LR)TM3, Sb, Ser: A third chromosome line associated with a series of complex, overlapping inversions, such that recombination is suppressed throughout the entire chromosome. This chromosome is marked with two dominant markers, *Sb* (Stubble, 3–58.2) and *Ser* (Serrate, 3–92.5).

y+Y (*synonym*: sc^8·Y): A laboratory stock in which the tip of the *In(1)sc^8 X* chromosome, including *y+* (the wild-type allele of *y*) is now present on the tip of the long arm of the *Y* chromosome.

For control matings, Canton-S or Tokyo laboratory chromosomes were utilized instead of wild chromosomes recently isolated from natural populations because of the suspect nature of the latter (see KIDWELL 1977). A standard cornmeal-agar food was used for all experiments. Flies used for experimental matings were usually less than six-days old. Unless otherwise indicated, a single male was mated to a harem of virgin females (the number depending upon the fecundity and viability of the females used, usually two to four females for most stocks). Virgin females were collected within eight hours after eclosion. Matings and egg laying were allowed to proceed for seven days, and then parents were discarded. Progeny were counted through the 19th day from the date of mating. All experiments were carried out at room temperature, 24°.

RESULTS

The frequencies and distributions of recombination in T-007 *heterozygous males and females along the second, third, and* X *chromosomes*

Preliminary data had suggested that male recombination could occur along the second chromosome (HIRAIZUMI 1971) and, in somewhat lower frequencies, along the third chromosome (HIRAIZUMI *et al.* 1973) in *T-007* heterozygous males. Because it was of interest to determine both the frequency and the distribution of recombination in these males, experiments were performed by placing multiply marked second or third chromosomes into the *T-007* male genotype. The first experiment was performed using *T-007/apl* (*apl*: *al dp b pr c px sp*) heterozygous males. These males were backcrossed to *apl* females, and the frequency of male recombination for each marked interval was obtained. In addition, the centromeric region of the second chromosome was marked with *pr cn*, and the frequency of male recombination in this interval was obtained by mating *T-007/pr cn* males × *pr cn* females. The frequencies of male recombination along the second chromosome thus obtained are presented in Table 1.

Since the markers along the second chromosome are unevenly spaced, it was necessary to adjust the observed recombination frequencies to make proper

TABLE 1

Distribution of recombination frequencies in T-007 *heterozygous males along the (A) second chromosome and (B) third chromosome*

(A)

	al-dp	*dp-b*	*b-pr*	*pr-cn*	*cn-c*	*c-px*	*px-sp*	Total progeny
Male recombination frequency (A)	0.0031	0.0070	0.0033	0.0044*	0.0083	0.0054	0.0023	8958
Control female recombination frequency (B)	0.1287	0.3003	0.0383	0.0098†	0.1650	0.2560	0.0581	2168
R (= A/B)	0.0241	0.0233	0.0862	0.4490	0.0503	0.0211	0.0396	

(B)

	ru-h	*h-th*	*th-st*	*st-cu*	*cu-e*^{s}	*e*^{s}*-ca*	Total progeny
Male recombination frequency (A)	0.0010	0.0051	0.0000	0.0024	0.0037	0.0012	5900
Control female recombination frequency (B)	0.2610	0.2000	0.0090	0.0503	0.2400	3.3170	1749
R (= A/B)	0.0038	0.0255	0.0000	0.0477	0.0154	0.0038	

The male recombination frequencies were obtained as stated in the text.
* From the mating *T-007/pr cn* males × *pr cn* females, 1604 progeny scored.
† From the mating *Tokyo/pr cn* females × *pr cn* males, 3660 progeny scored.

comparisons among regions. This was performed by dividing the observed frequency of male recombination in a given interval by the frequency of control recombination observed in the corresponding interval. To simplify the following discussions, we will refer to this ratio as R. In order to obtain control recombination frequencies, *apl/Tokyo* females were mated to *apl* males (and *pr cn/Tokyo* females to *pr cn* males), and the frequencies of recombination along the second chromosome were scored. These frequencies are presented in Table 1. It should be mentioned that, in both the male and control female matings, the recombination frequency for the *cn–c* region was computed by subtracting the frequency of recombination observed between *pr* and *cn* from the frequency of recombination observed between *pr* and *c*.

Frequencies of male recombination along the third chromosome in *T-007* heterozygous males were similarly measured by backcrossing *T-007/+*; *rucuca/+* males to *rucuca* females (*rucuca*: *ru h th st cu sr e*^{s} *ca*). These frequencies are presented in Table 1, along with the results of control matings, *Tokyo/rucuca* females × *rucuca* males. It should be noted that no recombinants were observed between *th* and *st*, in *T-007/rucuca* males, presumably because of the relatively short map distance between them. The R values were tabulated, as mentioned previously, and these results are presented in Table 1.

From the data presented in Table 1, it can be seen that there is a recombination frequency of about 3.38% along the second chromosome, and about 1.34% male recombination along the third chromosome in *T-007* heterozygous males. Despite the lower total recombination for the third chromosome relative to the second

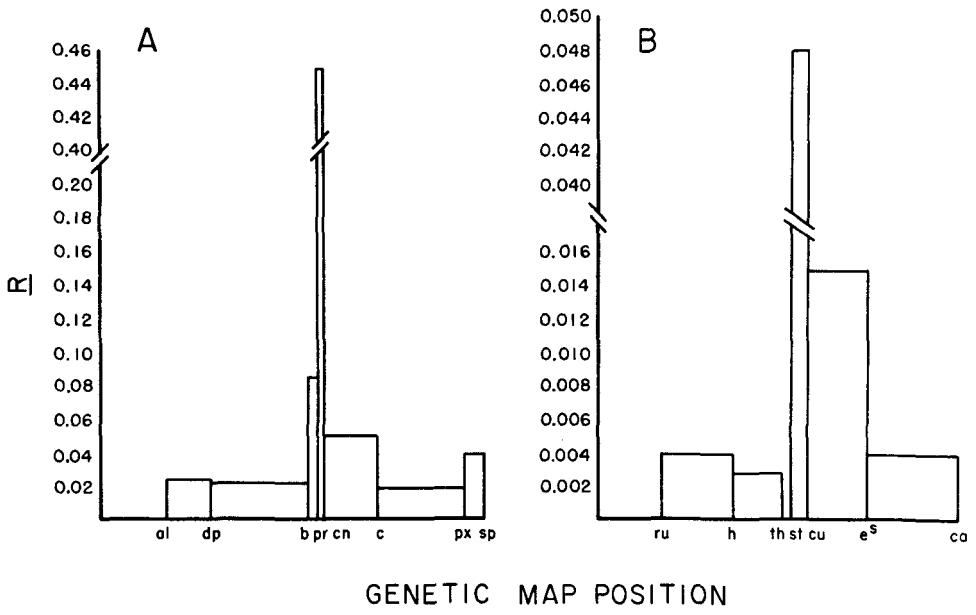

FIGURE 1.—Distribution of R values for *T-007* heterozygous males (A) along the second chromosome and (B) along the third chromosome.

chromosome, it is interesting to compare the distribution of R values along each of these two chromosomes. Figure 1(A) portrays the distribution of R values along the second chromosome; Figure 1(B) portrays the distribution along the third chromosome. It can be seen that both distributions are remarkably similar, with increases observed in the centromeric regions. For both distributions, the R values were heterogeneous among regions ($\chi^2_6 = 244.5$, $p < 0.01$ for the second chromosome; $\chi^2_5 = 60.34$ $p < 0.01$ for the third chromosome).

Previous reports (SLATKO and HIRAIZUMI 1975) had suggested that frequencies and distributions of recombination in *T-007* heterozygous females might also be altered. Accordingly, *T-007/apl* heterozygous females were backcrossed to *apl* males, and recombination frequencies were obtained for all six regions along the second chromosome. The data for the experimental matings (*T-007/apl* females mated to *apl* males) and the control matings (*Tokyo/apl* females mated to *apl* males) are shown in Table 2, together with the data that directly measured the *pr–cn* interval (by mating *T-007/pr cn* females to *pr cn* males in the experimental set). The R values obtained for all intervals of the second chromosome were computed by the methods mentioned previously. In both the experimental and the control sets, the frequency of recombination for the *cn–c* interval was computed by subtracting the frequency of recombination observed in the *pr–cn* region from that observed in the *pr–c* region.

The frequencies of recombination along the third chromosome in *T-007* heterozygous females were similarly examined by mating *T-007/+*; *rucuca/+* females to *rucuca* males. Recombination frequencies were computed for the six

TABLE 2

Distribution of recombination in T-007 *heterozygous females along the (A) second and (B) third chromosomes*

(A)

	al-dp	*dp-b*	*b-pr*	*pr-cn*	*cn-c*	*c-px*	*px-sp*	Total progeny
T-007 female recombination frequency (A)	0.0735	0.2891	0.1168	0.0474*	0.2002	0.1985	0.0465	2217
Control female recombination frequency (B)	0.1287	0.3003	0.0383	0.0098†	0.1650	0.2560	0.0581	2168
R (= A/B)	0.5711	0.9627	3.050	4.8367	1.2133	0.7754	0.8003	

(B)

	ru-h	*h-th*	*th-st*	*st-cu*	*cu-e*^{s}	*e*^{s}*-ca*	Total progeny
T-007 female recombination frequency (A)	0.2165	0.2388	0.0103	0.1289	0.2720	0.3341	1838
Control female recombination frequency (B)	0.2607	0.1995	0.0091	0.0503	0.2401	0.3168	1749
R (= A/B)	0.8305	1.197	1.1319	2.5626	1.1329	1.0546	

The female recombination frequencies were obtained as stated in the text.
* From the mating *T-007/pr cn* females × *pr cn* males, 3819 progeny scored.
† From the mating *Tokyo/pr cn* females × *pr cn* males, 3660 progeny scored.

marked intervals. The control frequencies of recombination were obtained by scoring matings of *Tokyo/rucuca* females to *rucuca* males. The R values for each of these intervals were computed and are shown in Table 2. For each chromosome, the R values were heterogeneous among regions ($\chi^2_5 = 200.5$, $p < 0.01$ for the second chromosome; $\chi^2_5 = 77.26$, $p < 0.01$ for the third chromosome).

The distributions of R values in *T-007* heterozygous females along the second and third chromosomes (listed in Table 2) are portrayed in Figure 2. With respect to the second chromosome, it can be clearly seen that the value of R is much higher in the centromeric (*pr–cn*) region than in the more distal regions. The recombination frequency observed in this region (in the *T-007* heterozygous females) is about 4.8-fold more than that observed in the control females. A similar situation, although less pronounced, can also be seen with respect to the third chromosome. Altogether, these results indicate that in *T-007* heterozygous females, recombination frequencies are increased in the centromeric regions of both the second and the third chromosomes.

The distribution of R values along the X chromosome was also examined in *T-007* heterozygous females by mating *y cv v f car*/+ + + + +; *T-007*/+ females to *y cv v f car* males. The control recombination frequencies were obtained by mating *y cv v f car*/+ + + + +; Tokyo (or Canton-S/+) females to *y cv v f car* males. These frequencies are presented in Table 3.

It can be seen that recombination frequencies in *T-007* heterozygous females are relatively lower in the more distal regions of the X chromosome (*y–cv* and *cv–v*) and are relatively higher in the more proximal regions (*v–f* and *f–car*).

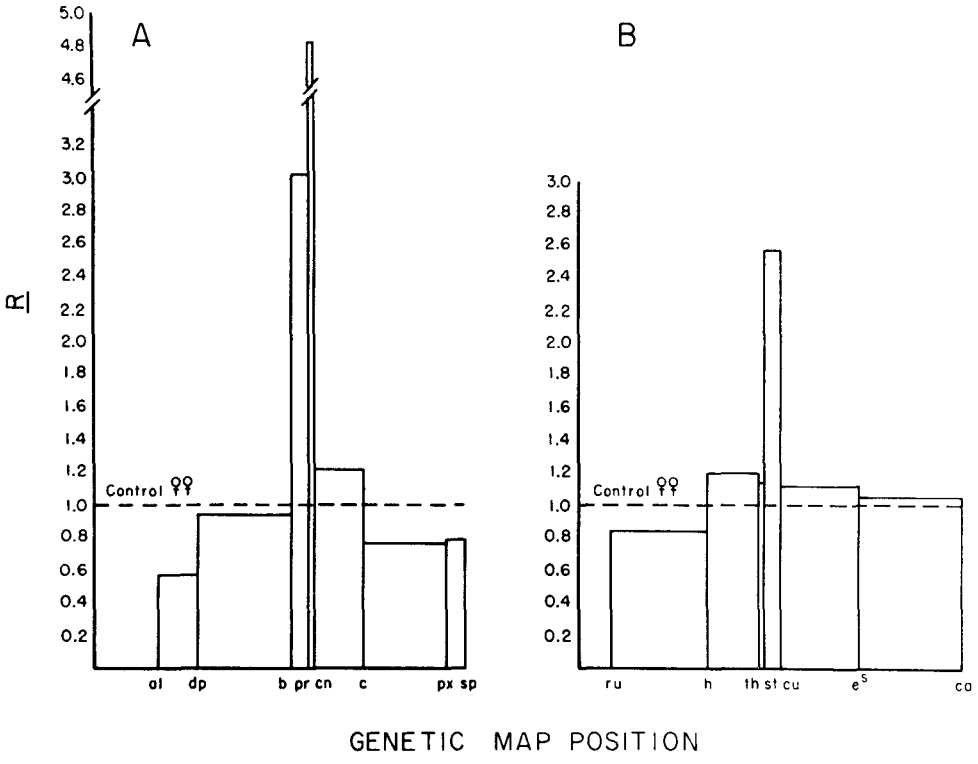

FIGURE 2.—Distribution of R values in *T-007* heterozygous females (A) along the second and (B) along the third chromosome.

The R values are highly significantly heterogeneous among regions ($\chi^2_3 = 19.4$, $p < 0.01$). This result is similar to that found for the second and for the third chromosome.

In *T-007* heterozygous females, the total map length was found to be about 97.3 for the second chromosome, about 120.1 for the third chromosome, and about 57.0 for the X chromosome, a total genetic map length of about 274.3 centimorgans. The corresponding length, as measured in control females was 263.9

TABLE 3

Distribution of recombination frequencies in + + + + +/y cv v f car; T-007/+ *females along the* X *chromosome*

	y-cv	*cv-v*	*v-f*	*f-car*	Total progeny
T-007 female recombination frequency (A)	0.0643	0.1514	0.2329	0.1216	2319
Control female recombination frequency (B)	0.0752	0.1976	0.2223	0.1113	4134
R (= A/B)	0.8550	0.7662	1.0477	1.0925	

Female contribution frequencies for each interval were determined as stated in the text.

centimorgans. Thus, the total frequency of recombination in *T-007* heterozygous females and in control females appears to be about the same, and increases in the frequencies of recombination in centromeric regions in the *T-007* heterozygous females are counterbalanced by apparent decreases in recombination frequencies in the more distal regions.

As was shown earlier, the relative increase in recombination frequency along the second chromosome in *T-007/apl* heterozygous males and females was largely confined to the *pr–cn* region. It was of interest to further subdivide this region and examine the distribution of recombination within these narrower, subdivided intervals. To perform these experiments, three marker chromosome stocks were utilized: *lt stw*^{3} *c*, *pr cn c*, and *pr stw*^{3}. *T-007/Cy* males were mated to marker chromosome females and from these parental matings, F_1 males or females of the genotype *T-007*/marker chromosome were selected and backcrossed to the marker chromosome stock. Control frequencies of female recombination were obtained by mating Canton-S/marker chromosome females to marker chromosome males. The matings performed in each of these experiments were carried out in half-pint milk bottles, placing 40 parental flies per bottle. Parents were transferred through four broods (three days, two days, two days, two days) for a total of nine days, and then discarded; progeny were scored for 19 days after inception of the matings.

From these matings, the frequency of recombination could not be directly measured in all intervals of the map, due to overlapping of markers in the batteries of matings. In fact, for only two regions, *lt-stw*^{3} and *cn–c*, are the frequencies of recombination measured directly. The frequencies of recombination for the other regions are based upon subtractions of various subsets of the data. For example, the frequency of recombination between *pr* and *lt* was calculated as the frequency of recombination observed between *pr* and *stw*^{3} (directly obtainable from the matings) minus the frequency of recombination between *lt* and *stw*^{3} (directly obtainable from the matings). Similarly, the frequency of recombination between *stw*^{3} and *cn* was calculated as the frequency of recombination between *pr* and *cn* minus the frequency of recombination between *pr* and *stw*^{3}. This estimation method was considered to be more accurate than the alternative method available (*stw*^{3}*–c* minus *cn–c*) because these relatively shorter regions should have a lower frequency of undetected double crossovers.

The frequencies of recombination observed in the control (Tokyo/marker chromosome) female matings, the *T-007*/marker chromosome female matings and the *T-007*/marker chromosome male sets of matings were utilized to construct linear recombination maps. These three maps are shown in Figure 3. It can be seen that in *T-007* heterozygous males, a recombination frequency of 0.59% is observed between *pr* and *cn*, and approximately 1.30% recombination is observed between *pr* and *c*. These frequencies are very close to those presented earlier (see Table 1). In *T-007* heterozygous females, the corresponding recombination frequencies are approximately 3.51% between *pr* and *cn*, and about 26.32% between *pr* and *c*. These frequencies are slightly different from, but comparable to, the data observed previously (see Table 2).

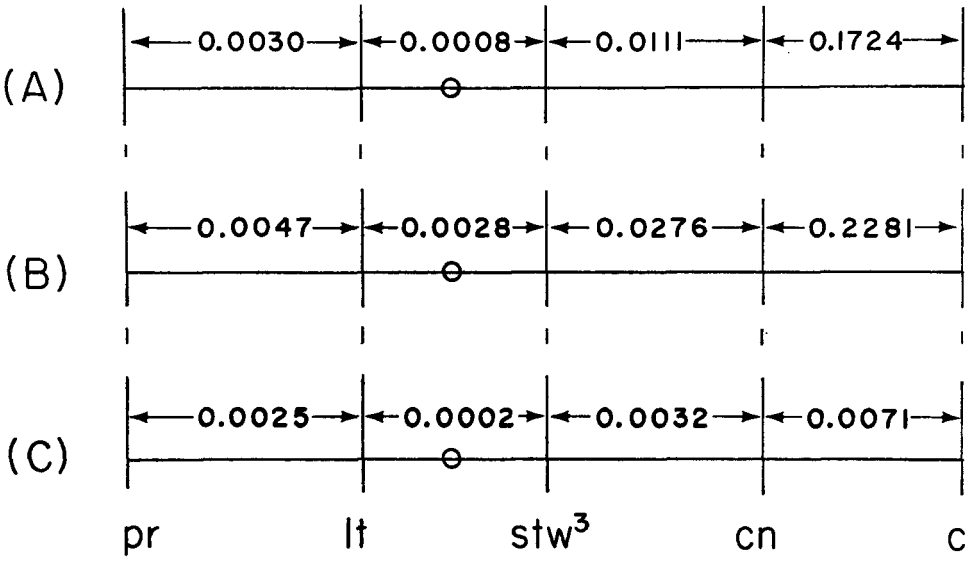

FIGURE 3.—Recombination maps generated in (A) control matings (Tokyo/marker chromosome females × marker chromosome males), and in experimental matings—(B) *T-007*/marker chromosome females × marker chromosome males;—(C) *T-007*/marker chromosome males × marker chromosome females. Computation of recombination frequencies from these matings are described in the text.

With respect to *T-007* heterozygous females, recombination frequencies are significantly increased over control frequencies in the *lt–stw*^{3} region ($\chi^2_1 = 11.25$, $p < 0.01$) and in the *stw*^{3}*–cn* region ($\chi^2_1 = 38.0$, $p < 0.01$), while no difference was observed for the *pr–lt* region ($\chi^2_1 = 1.56$, $p > 0.05$). No attempt was made to analyze statistically the recombination frequencies in *T-007* heterozygous males because the recombination frequencies for several of the regions were based upon estimates, and because the frequencies of recombination present in these subdivided intervals were very low. However, from inspection of the data, it seems fair to conclude that the frequency of recombination in these males, in terms of the *R* values defined earlier, is much higher in the *pr–lt* interval than in either the *lt–stw*^{3} or *pr–stw*^{3} intervals. It should be noted, however, that there is as much relative recombination in the largely heterochromatic *lt–stw*^{3} interval as there is in the more distal euchromatic regions (*e.g.*, the *R* values are comparable, see Figure 1).

It has been known since the early works of MATHER (1938, 1939) that a discrepancy exists between the cytological (*e.g.*, salivary and metaphase maps) and the meiotic (*i.e.*, standard female recombination) map. This discrepancy is largely due to the dearth of standard female recombination in the centromeric heterochromatin, and to a "telomeric" effect. It was of interest to compare the meiotic, mitotic and cytological maps to the maps for *T-007*-induced male recombination.

Utilizing the data in LINDSLEY and GRELL (1968), BECKER (1976) and latest available cytological data, meiotic recombination, salivary gland chromosome and metaphase chromosome maps were constructed. Mitotic maps were constructed from the data of WHITTINGHILL (1955). The *T-007* male and female recombination maps were constructed from the data presented in Tables 1, 2, and Figure 3.

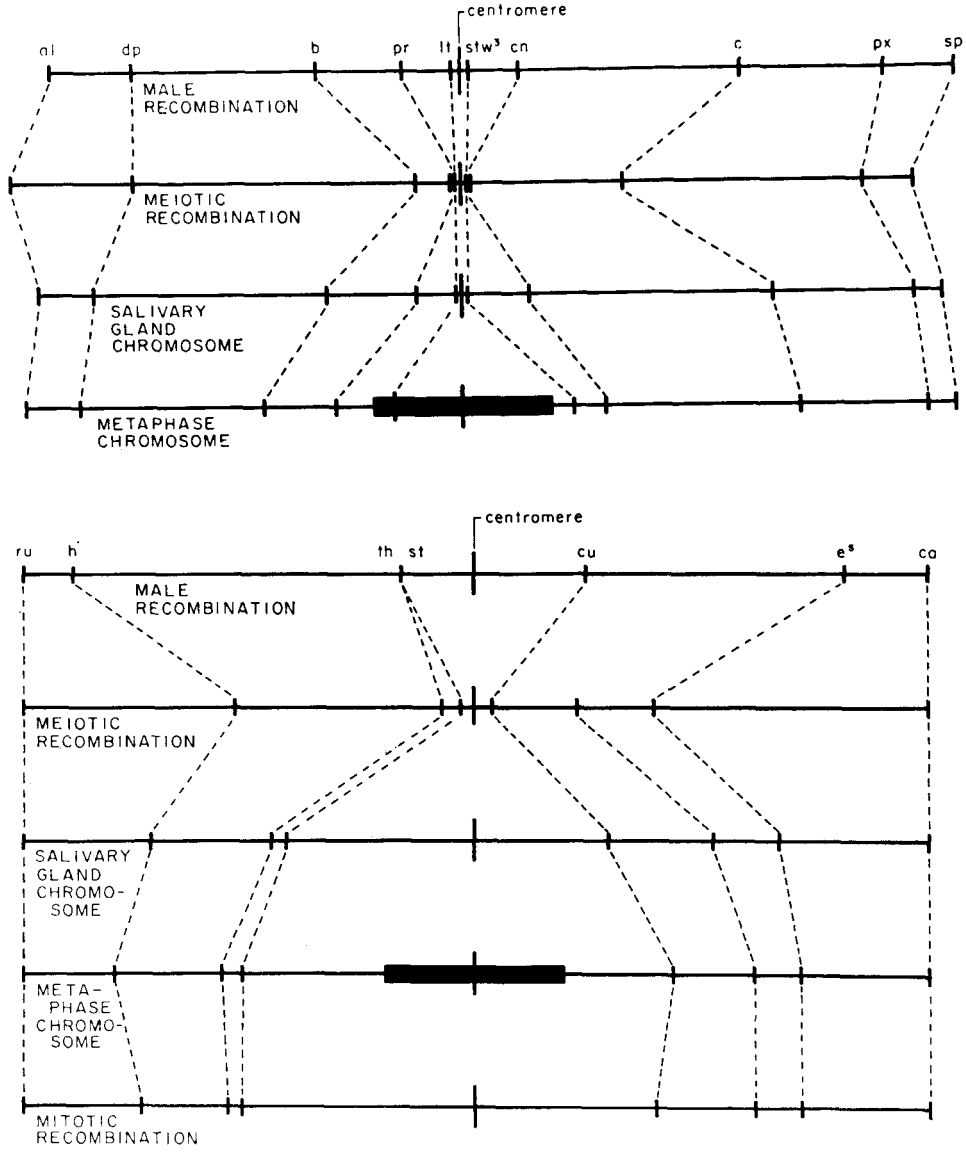

FIGURE 4.—Comparisons of recombination and cytological maps for the second chromosome (top panel) and for the third chromosome (bottom panel). Descriptions concerning derivations of the maps, are given in the text.

These maps for the second and for the third chromosome are shown in Figure 4. It can be seen that the *T-007* male recombination maps agree more closely with the salivary gland and metaphase maps than with the control meiotic recombination maps. The *T-007* male recombination map also closely resembles the mitotic recombination map, with a slight discrepancy in the centromeric region, where the majority of mitotic recombination occurs. These results indicate that the recombination events induced in *T-007* heterozygous males are, in general, more nearly proportional to actual chromosome length than to standard female recombination.

Nondisjunction

It was of interest to examine another parameter characterizing the meiotic process in males and females, nondisjunction. Nondisjunction was measured for the second chromosome in males and females, and for the *X* and *Y* chromosomes in males.

Nondisjunction of the second chromosome was measured in control males by mating Tokyo/*cn bw* males to *C(2L), dp*; *C(2R), px* females. Viable progeny will be regularly produced from these matings under two conditions: (1) When nondisjunction of second chromosomes occurs in the Tokyo/*cn bw* males such that both the Tokyo and the *cn bw* chromosomes are present in a sperm (a disomic sperm), and when this sperm fertilizes a nullosomic egg, the zygote will retain a full diploid, (patroclinous) normal sequence second chromosome set; and (2) When nondisjunction of second chromosomes occurs in the Tokyo/*cn bw* males such that the sperm is nullosomic, and when this sperm fertilizes a disomic egg (which would be *C(2L), dp*; *C(2R), px*), the resulting zygote also will retain a full diploid (matroclinous) chromosomal complement.

From 43 matings of one Tokyo/*cn bw* male to three *C(2L), dp*; *C(2R), px* females (for nine days), two exceptional (surviving nondisjunctional) progeny were observed. As the frequency of nondisjunction is commonly measured in terms of the number of eggs produced from the matings, it was necessary to perform egg counts from these matings. The average number of eggs produced by the *C(2L), dp*; *C(2R), px* females in these matings was 284.6 per mating. The frequency of control nondisjunction in the control Tokyo/*cn bw* males thus becomes two exceptional progeny divided by the product of 43 matings times 284.6 eggs per mating, which equals 0.000163, or 0.163 exceptions per 1,000 eggs.

In the experimental set, *T-007/cn bw* males were mated to *C(2L), dp*; *C(2R), px* females. From 138 matings (one male and three females mated for nine days), 17 exceptional progeny were observed. The frequency of second chromosome nondisjunction in *T-007/cn bw* males is thus 17/(138)(270.4), which equals 0.000456, or 0.46 exceptions per 1,000 eggs. Thus, *T-007/cn bw* males show an approximate 2.8-fold increase in the frequency of second chromosome nondisjunction over control frequencies, although this difference is not statistically significant ($\chi_1^2 = 2.05$ $p > 0.05$). In the experimental matings, of the 17 exceptional progeny, only three were *C(2L), dp*; *C(2R), px*, indicating that the

majority of these exceptions were due to disomic sperm produced in the *T-007/cn bw males*. In the control set, both exceptional progeny were *C(2L), dp; C(2R), px*, providing little information on the tendency of the production of nullosomic sperm, as opposed to disomic sperm.

With respect to nondisjunction of second chromosomes in control Tokyo/*cn bw* females, the reciprocal cross was utilized; Tokyo/*cn bw* females were mated to *C(2L), dp; C(2R), px* males. From 128 matings of one Tokyo/*cn bw* female to three *C(21), dp; C(2R), px* males (for nine days), five exceptional progeny observed, and from 65 matings of three Tokyo/*cn bw* females to three *C(2L), dp; C(2R), px* males for nine days, one exceptional progeny was observed. The average number of eggs produced in the second set (three Tokyo/*cn bw* females) was 344.1 eggs per mating. Thus, in the first set, the observed frequency of nondisjunction was 5/(128)(158), or five exceptions out of 20,224 eggs, and in the second set, the observed frequency of nondisjunction was 1/(65)(344.1), or one exception out of 22,366 eggs. Pooling the results from these two sets, six exceptional progeny were observed out of 42,590 eggs, or 0.141 exceptions per 1,000 eggs. This control frequency agrees with those obtained in other laboratories (0.1–0.2 exceptions per 1,000 eggs; BAKER and HALL 1976). Of the six exceptional progeny, all were dp^+ px^+, indicating that the exceptional progeny were the result of disomic eggs.

In the experimental matings, three *T-007/cn bw* females were mated to three *C(2L), dp; C(2R), px* males for nine days. From these matings 91 exceptional progeny were observed out of 173 matings. The average number of eggs produced per mating was 301.05, and thus, the frequency of observed second chromosome nondisjunction in *T-007/cn bw* females was 91/(173)(301.05), which is 0.00175, or 1.75 exceptions per 1,000 eggs.

T-007/cn bw females appear to show an approximate 12-fold increase in nondisjunction over control frequencies. This difference is statistically significant ($\chi^2_1 = 59.66$, $p < 0.01$). Of the 91 exceptional progeny, 85 were *C(2L), dp; C(2R), px*, indicating that the majority of exceptional progeny observed were due to the production of nullosomic eggs.

Nondisjunction of the sex chromosome pair in males was also examined. For the control set, y/y^+Y males were mated to *C(1)DX*, y f/Y; *cn bw* females. From these matings, nondisjunction in the y/y^+Y males can be determined to have occurred by the presence of y^+ f^+ males, y f females and y f^+ females, as opposed to the presence of y f^+ males and y^+ f females (the products of regular disjunction). It should be noted that the presence of y^+ f^+ males and y f females indicates a first division nondisjunction event, and the presence of y f^+ females and y f females indicates a second division nondisjunction event. Because y f females will arise in both cases, a comparison of the frequency of y^+ f^+ males with the frequency of y f^+ females observed may indicate the division at which nondisjunction events primarily occur.

In the control series, y/y^+Y males mated to *C(1)DX/Y*, y f; *cn bw* females, two nondisjunctional progeny were observed out of 4,217 progeny (0.00047), or

0.47 exceptions per 1,000 sperm. This control value is similar to those previously reported in other laboratories (BAKER and HALL 1976). One exceptional progeny was a $y\ f^+$ female, and the other was a $y^+\ f^+$ male.

In the experimental set, the matings were y/y^+Y; *T-007/cn bw* males × *C(1)DX*, $y\ f/Y$; *cn bw* females; 17 nondisjunctional progeny were observed out of 8,627 progeny (0.000197), or 1.97 exceptions per 1,000 sperm. These results, a four-fold increase in nondisjunction of the *X* and *Y* chromosomes in the experimental set, are statistically significant ($\chi^2_1 = 4.29$, $p < 0.05$). Of the 17 nondisjunctional progeny, three were $y^+\ f^+$ males, three were $y\ f$ females, and 11 were $y\ f^+$ females. Thus, the majority of nondisjunction events appear to occur at the second meiotic division.

It might be suggested that male recombination events, occurring between homologous regions of the y^+ *Y* and y *X* chromosomes might give rise to progeny that could negate the above conclusions. While such recombination events have been shown to occur in low frequencies (LINDSLEY 1955), they would give rise to + + males, + + females and/or $y\ f$ females in the above matings. However, the largest class of presumptive nondisjunction progeny, y + females, still suggests that the events are second division nondisjunction events. Experiments designed to determine specifically whether such *X* and *Y* recombination is increased in *T-007* males are in progress, but the lack of clustering of such resulting phenotypes in the matings described above (each exception was from an independent parental male) suggests that there was no increase in male recombination events.

Finally, it should be mentioned that none of these nondisjunction experiments directly measures the absolute frequency of nondisjunction. Corrections can be introduced to account for unobservable classes, but these corrections often rely upon various assumptions, such as equal viabilities and equal segregations, which may not be the case.

Interchromosomal effects

It has been known for many years that the frequency of recombination in normal females can be increased by the structural heterozygosity of nonhomologous chromosomes, termed the "interchromosomal effect" by STURTEVANT (1919) (for recent reviews, see LUCCHESI and SUZUKI 1968; LUCCHESI 1976). Because the "interchromosomal effect" is thought to act by altering preconditions for meiotic exchange, a response of *T-007* to the "interchromosomal effect" might be considered as evidence that *T-007* is involved in the alteration of the preconditions for meiotic exchange.

A set of experiments had indicated that the multiply inverted third chromosome *In(3LR)TM3* showed a definite "interchromosomal effect" in control females, as measured along the second chromosome. Accordingly, two sets of experimental matings were performed. In the first, males carrying the *T-007* second chromosome were mated to *al dp cn bw*; *In(3LR)TM3*/+ females. From these parental matings, F_1 virgin *T-007/al dp cn bw* females were selected and backcrossed to *al dp cn bw* males. In addition, individual F_1 virgin *T-007/al*

TABLE 4

Recombination frequencies observed in T-007/al dp cn bw; +/+ *females and in* T-007/al dp cn bw; In(3LR), TM3/+ *females, as measured across the second chromosome*

Region	*T-007/al dp cn bw*; +/+*	*T-007/al dp cn bw*; *In(3LR)TM3*/+†
al-dp	0.0754 (125)	0.1518 (196)
dp-cn	0.3675 (609)	0.4051 (523)
cn-bw	0.4212 (698)	0.4609 (595)

The number of recombinants observed in each region are presented in parentheses.
* 1657 progeny scored.
† 1291 progeny scored.

dp cn bw; *In(3LR)TM3*/+ female sibs were selected and backcrossed to *al dp cn bw* males. Recombination frequencies in both sets of matings were scored between the second chromosome markers *al*, *dp*, *cn*, and *bw*.

Results of these matings are presented in Table 4. It can be seen that *T-007*-induced female recombination appears to be affected by the "interchromosomal effect" of *In(3LR)TM3*, as all three regions measured in these experiments show increased frequencies of recombination. The distribution of recombination in the *T-007/al dp cn bw*; *In(3LM)TM3*/+ females is significantly different from that of *T-007/al dp cn bw*; +/+ females ($\chi^2_5 = 25.5$, $p < 0.01$).

To determine whether or not there is an "interchromosomal effect" upon second chromosome recombination in *T-007* males, *T-007/cn bw*; +/+ males were mated to *cn bw* females in the control set, while in the experimental matings, *T-007/cn bw*; *In(3LR)TM3*/+ male sibs were mated to *cn bw* females. Recombination frequencies were scored between *cn* and *bw* in both sets. Results of this experiment indicate that there appears to be no "interchromosomal effect" upon observed frequencies of male recombination. The recombination frequency observed in the control set was 0.0087 (56 recombinants were observed out of 6.424 progeny). This frequency is comparable to frequencies expected between these markers, as reported previously by HIRAIZUMI (1971). In the experimental matings, the observed frequency of recombination was 0.0055 (19 recombinants were observed among 3,467 progeny). The frequencies of recombination in the two sets were not significantly different ($\chi^2_1 = 3.12$, $0.05 < p < 0.10$), and thus there appears to be no "interchromosomal effect" upon male recombination induction. A similar conclusion has been reached by WOODRUFF, SLATKO and THOMPSON (1978).

DISCUSSION

SANDLER *et al.* (1968) have theorized that mutants affecting meiosis in Drosophila females which cause both altered distributions of recombination with alterations in interference values (*e.g.*, the probabilities of double crossover events with respect to map distances) may be considered as mutants that affect the preconditions (*e.g.*, meiotic homologous chromosome pairing) for meiotic exchange and disjunction. From the recombination data in *T-007* heterozygous

females and in the comparable controls, it was possible to examine interference data along the second, third, and *X* chromosomes, as measured by coefficient of coincidence values. Standard errors were computed by the methods of KOJIMA (1961), and regional comparisons were performed using the maximum likelihood "scoring method" of FISHER (1935) (see BAILEY 1961).

Thirty-six paired combinations of regions were examined in the control (Tokyo heterozygous female) and experimental (*T-007* heterozygous female) matings. Coefficient of coincidence values (± 1 standard error) for adjacent regions are presented in Table 5. Generally, these values are higher in *T-007* females than in the control females. However, it can be seen that not all combinations of paired regions show higher coefficient of coincidence values in *T-007* females. Several regions failed to show this effect and, in fact, several regions showed lower coefficient of coincidence values in *T-007* females than in control females. No pattern is readily apparent in terms of the regions involved or in terms of regions that show the most altered distributions of recombination (*e.g.*, centromeric or telomeric regions). A very similar pattern was observed and reported by KIDWELL (1977). These results, and the presence of an "interchromosomal effect" upon *T-007*-induced female recombination further suggest that *T-007* appears to influence meiotic recombination in females *via* effects upon the preconditions for exchange and disjunction (CARPENTER and SANDLER 1974).

TABLE 5

Coefficient of coincidence values (including ± 1 standard error) observed in control and T-007 *heterozygous females, for adjacent regions*

2nd chromosome regions	Control (+/*apl* ♀)	Experimental (*T-007*/*apl* ♀)
(*al-dp*) – (*dp-b*)	0.0298 ± 0.030	0.531 ± 0.009
(*dp-b*) – (*b-pr*)	0.321 ± 0.011	0.467 ± 0.005
(*b-pr*) – (*pr-c*)	0.966 ± 0.056	0.952 ± 0.011
(*pr-c*) – (*c-px*)	0.330 ± 0.003	0.550 ± 0.004
(*c-px*) – (*px-sp*)	0.124 ± 0.004	0.049 ± 0.002
3rd chromosome regions	Control (+/+; +/*rucuca* ♀)	Experimental (*T-007*/+; +/*rucuca* ♀)
(*ru-h*) – (*h-th*)	0.319 ± 0.003	0.379 ± 0.003
(*h-th*) – (*th-st*)	0.000	0.640 ± 0.119
(*th-st*) – (*st-cu*)	4.600 ± 3.808	0.000
(*st-cu*) – (*cu-e*^{s})	0.752 ± 0.030	0.880 ± 0.010
(*cu-e*^{s}) – (*e*^{s}-*ca*)	0.556 ± 0.003	0.650 ± 0.003
X chromosome regions	Control (*y cv v f car*/+++++ ♀)	Experimental (*y cv v f car*/+++++; *T-007*/+ ♀)
(*y-cv*) – (*cv-v*)	0.190 ± 0.003	0.180 ± 0.008
(*cv-v*) – (*v-f*)	0.440 ± 0.002	0.620 ± 0.006
(*v-f*) – (*f-car*)	0.060 ± 0.001	0.030 ± 0.004

For complete details, consult text.

With respect to *T-007* males, the genetic recombination maps agree more closely with the mitotic recombination maps than with the control female meiotic recombination maps. This suggests that the male recombination events are perhaps largely mitotic in origin, agreeing with the Poisson distribution analysis, which indicated that male recombination was of largely premeiotic origin (HIRAIZUMI *et al.* 1973). The lack of an interchromsomal effect upon male recombination induction also agrees with this interpretation, as it has been shown that there is a lack of an interchromosomal effect upon spontaneous or irradiation induced male and female gonial recombination (WHITTINGHILL 1955; PARKER 1948; RAMEL 1962).

However, there are two puzzling aspects of this situation. First, while there may be a slight increase in second chromosomal centromeric heterochormatic male recombination (as evidenced by *lt–stw*^{s} male recombination frequencies), it is apparent from Figure 3 that the majority of the large frequency of male recombination occurs outside of the *lt–stw*^{s} interval, in the *pr–lt* interval. Thus, while the male recombination map agrees closely with the mitotic recombination map, a discrepancy apparently exists between the two mechanisms, with respect to heterochromatic recombination induction. Further research concerning this discrepancy is in progress.

Secondly, HENDERSON, WOODRUFF and THOMPSON (1978) have recently shown that meiotic chromosome breakage, attributable to male recombination events, occurs in primary and secondary spermatocytes of a "male recombination" strain of *D. melanogaster* (symbol: OK-1) in OK-1/*In(2LR)* heterozygous males. This suggests that a large fraction of the recombination in these males occurs meiotically. However, Poisson distribution analysis of observed recombinants per male indicates that a majority of the recombination events occur premeiotically (*e.g.*, in gonial cells) (WOODRUFF and THOMPSON 1977). Thus, either both meiotic and premeiotic recombination occur frequently, or some "event" leading to meiotic breakage is a premeiotic one. These two hypotheses are difficult to distinguish experimentally; however, gonial breakage has not been observed, despite extensive experimental observations (HENDERSON, WOODRUFF and THOMPSON 1978).

Based upon the results presented in this report, *T-007* appears to be similar to several of the "meiotic mutants" isolated in Drosophila and several other organisms (reviewed by BAKER *et al.* 1976a). Recent attempts to categorize these meiotic mutants with respect to various biochemical processes, such as mutagen sensitivity, repair deficiency, and/or with various processes such as mitotic and meiotic chromosome instability or mitotic recombination, have been partially successful in determining the possible molecular functions of some of these mutants (BAKER *et al.* 1976b). What roles *T-007* may play in these processes are the interesting subjects for future studies.

The diversity of genetic effects induced by the *T-007* chromosomal line is rather large. Previous reports have implicated *T-007* as being responsible for male recombination induction (HIRAIZUMI *et al.* 1973), distorted transmission frequencies of second chromosomes from heterozygous males (HIRAIZUMI 1977),

somatic and germ line mutator activities (SLATKO and HIRAIZUMI 1973), X-ray sensitivity (SLATKO 1973), and reduced male fertility (HIRAIZUMI 1977). Results presented in this report indicate that *T-007* also affects several additional meiotic parameters in males and females.

Numerous chromosome lines responsible for male recombination induction show meiotic effects that are similar to those discussed in this report. These include altered distributions of relative recombination frequencies in males and females, altered coefficient of coincidence values, increased nondisjunction frequencies, and responses to "interchromosomal effects" (WOODRUFF and THOMPSON 1978; KIDWELL 1977). In addition, these same chromosome lines have been shown to be responsible for other anomalous genetic phenomena, such as distorted transmission frequencies from heterozygous males, increased frequencies of male and female infertility and sterility, mutator activities, etc.

While it has previously been assumed that all of these effects are the result of a single genetic system, it is now becoming necessary to re-evaluate this assumption. Many isolated chromosome lines appear to be heterogeneous with respect to the array of particular effects produced. For instance, with respect to male sterility, *T-007* heterozygous males show no evidence of increased sterility (HIRAIZUMI 1971). WOODRUFF and THOMPSON (1978) and SVED (1976) have also obtained evidence indicating no male sterility in their "male recombination" lines, whereas KIDWELL and KIDWELL (1975) found a high percentage of male sterility in their "male recombination" lines. With respect to female sterility, *T-007* heterozygous females show no evidence of increased sterility, but WOODRUFF and THOMPSON (1978) and SVED (1977) do find increased sterility; KIDWELL, KIDWELL and SVED (1977) found increased sterility in some lines and not in others. These discrepancies extend to include distorted transmission frequencies and some meiotic effects, such as nondisjunction (M. M. GREEN, personal communication).

Despite the correlations (which imply underlying relationships) among several of the phenomena associated with these strains (for example, mutation, transmission frequency and male recombination, SLATKO and HIRAIZUMI 1973; mutation and sterility, KIDWELL, KIDWELL and SVED 1977, etc.), it has been suggested that chromosomes now present in natural populations may be associated with several different genetic elements, each with its own effect(s) (SLATKO 1976). In one particularly interesting example, GREEN (1977) has shown that the HAIFA-12 "male recombination" chromosome is associated with a bristle mutation that confers female sterility and reduced male and female viability.

Mapping experiments designed to localize the genetic elements responsible for the numerous genetic effects associated with these "male recombination" chromosomes have, in general, not been successful. In the case of the *T-007* chromosome line, regions containing genetic elements causing male recombination have been partially identified (SLATKO and HIRAIZUMI 1975; SLATKO 1978; MATTHEWS *et al.* 1978). We are currently investigating whether or not these elements are also responsible for the other phenomena associated with this

chromosome. This analysis, although tedious, is necessary for the complete determination of why such chromosomes are present in surprisingly high frequencies in world-wide natural populations of *Drosophila melanogaster*.

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