GENETIC MODIFICATION OF RECOMBINATION RATE IN *TRIBOLIUM CASTANEUM*

ANDREW A. DEWEES

Department of Biology, Sam Houston State University, Huntsville, Texas 77340

Manuscript received April 9, 1975
Revised copy received July 17, 1975

ABSTRACT

Asymmetrical responses were obtained in a replicated study of 15 generations of two-way selection for recombination rate between the ruby (*rb*) and jet (*j*) loci in *Tribolium castaneum*. Recombination rates in the two replicate high lines increased from an average of 0.22 in the base populations to an average of 0.42 at generation 15. Recombination rate pooled over the 15 generations of selection in each low line was significantly less than the control but there was no clear downward trend in response to selection for decreased recombination rate. The realized heritabilities were 0.16 ± 0.03 and 0.17 ± 0.02 in the two high lines, and were not significantly different from zero in the two low lines. Selection was based on crossing over in *cis* females only; however, rates measured in *cis* males after 12 generations showed the same response patterns as female rates. Similar response patterns were also determined for recombination measured in *trans* males and females at generation 18 following three generations of relaxed selection. The distribution of recombination rates measured in backcross beetles [$(H \times L) \times H$ and $(H \times L) \times L$] at generation 12 indicated polygenic control with those genes decreasing recombination rate being dominant. Detailed analysis of recombination rates in F_1's produced by interline crosses at generation 15 confirmed the directional dominance findings. Under a polygenic model of recombination modifiers in which low recombination is dominant to high, average recombination rates will increase as inbreeding progresses, thus providing a mechanism for the production of new gene combinations in small populations.

THE prediction that linkage intensity can be modified by natural selection was first proposed by FISHER (1930) and later studied in more detail through the theoretical treatment of two-locus fitness models by KIMURA (1956), NEI (1967), TURNER (1967), BODMER and FELSENSTEIN (1967), KARLIN and FELDMAN (1970), FELDMAN (1972) and FELDMAN and BALKAU (1973). These studies suggest that linkage between genes can be tightened under certain epistatic fitness models, thus increasing average population fitness. In conflict with the buildup of adaptations to the immediate environment, partially attainable through restriction of recombination, is the flexibility required for the buildup of adaptations to new environments that can be met through the release of genetic variability by increased recombination due to crossing over (DARLINGTON 1939; MATHER 1943). Because of its role in adjusting the frequencies of gene combinations, recombination between linked genes is expected to exhibit considerable genetic variability for the action of natural selection.

Several investigators have attempted, with varying degrees of success, to modify the recombination rate between linked loci by artificial selection in Drosophila (GOWEN 1919; DETLEFSEN and ROBERTS 1921; PARSONS 1958; ACTON 1961; MUKHERJEE 1961; MOYER 1964; KALE 1968; CHINNICI 1971a; KIDWELL 1972a; VALENTIN 1973a; and ABDULLA and CHARLESWORTH 1974), in fungi (PRITCHARD 1955; CALEF 1957; LANDNER 1974) and in the lima bean (ALLARD 1963). With the exception of the studies of CHINNICI (1971a), KIDWELL (1972a) and ABDULLAH and CHARLESWORTH (1974), previous attempts to change recombination rates by selection were initiated in base populations restricted in variability and were carried out under selection schemes that resulted in high rates of inbreeding. Moreover, none of the previous studies included an unselected control concurrent with the selection lines and few were replicated.

The present study was designed to estimate the amount and type of genetic variability in a population on which selection may act to change recombination rates. Two-way selection for recombination rate in the flour beetle (*Tribolium castaneum*) was initiated from a large random-mating base population having a broad genetic background. Two replications of the selection lines and the control lines were maintained with a minimum of inbreeding for 15 generations. Preliminary reports have been previously presented (DEWEES 1970, 1973).

MATERIALS AND METHODS

Tests of recombination rates were made in two-point testcrosses with the recessive genes for ruby eye color (*rb*) and jet body color (*j*), which are in linkage group V of *Tribolium castaneum*. Recombination in this region has been previously reported as 33% in males and 21% in females (DEWEES 1967).

Initiation of the base population: The mating scheme used to establish the base populations and selection lines is shown in Figure 1. To establish a large random-mating base population with considerable genetic variation, beetles from the ruby-jet stock were mass-mated in reciprocal crosses of 50 males and 50 females to Purdue University + Foundation Stock, a synthetic wild-type stock derived from crosses of eight different laboratory strains (BRAY, BELL and KING 1962). The ruby-jet stock was derived from crosses of the two mutant strains ruby (DEWEES 1964) and jet (PARK 1954). One hundred F_1 male and 100 F_1 female progeny were collected from each parental cross and mass-mated to produce the F_2 generation. Reciprocal crosses of F_2 wild-type and F_2 ruby-jet beetles were then set up in pair matings from which 30 of each reciprocal cross were determined to be of the desired testcross (+ +/*rb j X rb j*/*rb j*). Two F_3 males and females of both parental genotypes (non-recombinants) were obtained from each of the 60 F_2 matings. The F_3 generation was then established by placing these beetles together in two mass matings each of 120 males and 120 females representing the two reciprocal testcrosses. Thereafter until the F_{10} generation two reciprocal mass matings consisting of 120 males and 120 females mated in a two-point testcross were carried out. The parents of each testcross were composed of an equal number of individuals produced by each of the two reciprocal crosses of the preceding generation. The purpose of these 10 generations of random testcross matings was to establish a base population (generation 0 of selection) approaching genetic equilibrium for modifiers of recombination rate and also to maintain the appropriate testcross genotypes in the resulting base population.

Two replications of the base population were established using non-recombinant progeny taken from two consecutive egg collections of the tenth generation of random mating. Each replication of the base population consisted of 50 testcrosses in which the two marker genes were linked in coupling in the female parents (+ +/*rb j* ♀ *X rb j*/*rb j* ♂). Fifty reciprocal crosses

were also set up in each replication to measure crossing over in the male; however, all selection was based on crossing over in females.

The initiation of selection and control lines: From 30 of the 50 testcross matings in each replication of the base population in which pupae were sexed, the five matings having the highest percent crossing over and the five having the lowest percent crossing over were used to establish generation 1 of the high and low selection lines, respectively (see Figure 1). The criterion of selection throughout the study was percent recombination in the female based on her progeny produced in the first seven days of egg laying. Four virgin + +/*rb j* females and four virgin *rb j*/*rb j* males were then obtained in a second seven-day egg collection from each of the five selected testcrosses and mated in all possible combinations to form the 20 testcrosses of generation 1. Full-sib matings were avoided. In subsequent generations of selection the same scheme was followed, which involved testing the recombination rates of 20 females and selecting the five matings from which non-recombinant progeny were used to establish the next generation. In

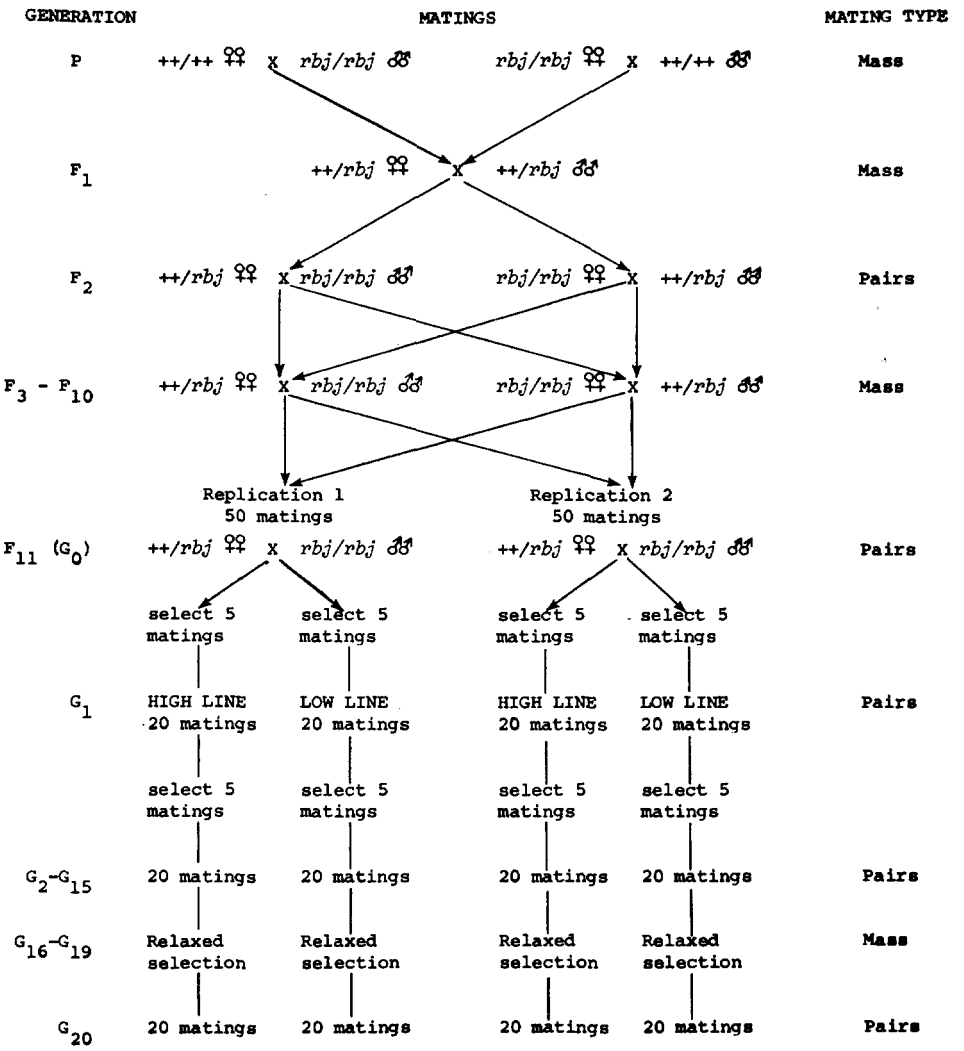

FIGURE 1.—Mating scheme for the initiation of the base populations and selection lines.

each replication a control line was established and maintained as a mass mating of 60 + +/*rb j* females and 60 *rb j*/*rb j* males initially supplied in equal numbers from 30 testcrosses of the base population, and thereafter chosen at random from the control population of the previous generation. Both replications, each consisting of the control line and the high and low selection lines, were maintained concurrently.

The beetles were cultured on the standard diet of 95% whole wheat flour and 5% dried brewer's yeast and kept in a Jamesway Incubator Model 252 maintained at 35° and 70% relative humidity. Standard errors for estimates of pooled recombination rate were computed according to COCHRAN (1963). The arcsin transformation of recombination rates (arcsin $\sqrt{p}$) was analyzed in all statistical tests to meet the assumption of normality.

RESULTS

The base populations: The two replications of the base population (generation 0 of selection) consisted of 50 testcross matings from which two seven-day egg collections were taken and recombination rates computed. Analyses of the variation among and within matings and estimates of repeatability of recombination rate are presented in Table 1. Since selection was based on recombination rates measured in *cis* females, the base population analyses were restricted to this sex. There was significant variation among the testcross mean recombination rates in both replications. The repeatability of .56, measured as the mean intraclass correlation coefficient, represents an upper estimate of the heritability of this trait. The mean rates of recombination between the *rb* and *j* loci measured in the base population females were 0.23 ± 0.009 and 0.21 ± 0.008 for replications one and two, respectively.

Selection response: Generation means resulting from 15 generations of two-way selection for recombination rate are plotted in Figure 2. The selection line means represent recombination rates pooled over 20 testcross matings. The recombination rates of the two control lines were pooled since there was no significant difference between them. Although the response to selection for increased recombination rate was initially most rapid for replication one (R1H), both high lines showed their greatest response during the first 10 generations and both appeared

TABLE 1

Analyses of variance of recombination rates in* cis *females in the base populations*

Source of variation	df	Mean squares	Variance components	Repeatability
Replication 1:				
Between matings	44	32.625**	11.455	.541
Within matings	45	9.715	9.715	
Totals	89		21.170	
Replication 2:				
Between matings	48	25.870**	9.477	.578
Within matings	49	6.916	6.916	
Totals	97		16.393	

* Based on the arcsin transformation of recombination rates.
** Significant at the .01 level.

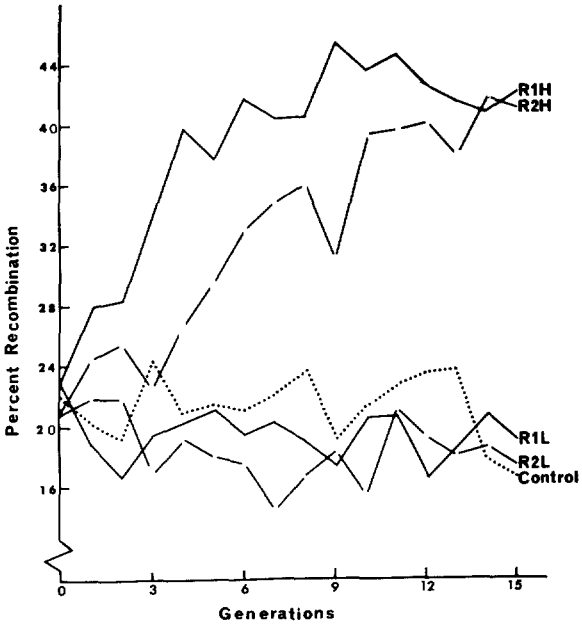

FIGURE 2.—Total recombination rates for the high (H) and low (L) lines in each replication (R1 and R2) and for the pooled control plotted over the 15 generations of two-way selection.

to plateau near 42% recombination with little or no progress the last five generations of selection. After five generations of relaxed selection, during which beetles within each selection line were randomly testcrossed *en masse*, recombination rates were again measured and found to exhibit little or no change (Table 2). The results prior to relaxed selection represent an approximate doubling of recombination rate in response to selection; however, the actual percent crossing over is underestimated because even-numbered, multiple crossover events are not detected as recombinants. HALDANE's (1919) mapping function, which assumes no interference,

$$d = -\frac{1}{2}\ln(1-2p)$$

expresses the actual rate of crossing over d as a function of the recombination

TABLE 2

Selection line recombination rates in cis *females at generation 20 following five generations of relaxed selection*

Selection line	Pooled recombination rate ± standard error	Number of matings	Total number of individuals
1 High	.392 ± .024	16	735
1 Low	.248 ± .023	18	920
2 High	.415 ± .021	20	1340
2 Low	.210 ± .014	20	1270

rate p. The average rate of crossing over computed by this function increased from 0.29 in the base population to 0.92 after 15 generations of selection.

Although the recombination rates averaged over the 15 generations of selection in both low lines (R1L and R2L) were significantly less than the pooled control mean ($P<.01$ for paired comparisons between the means of each low line and the pooled control), there was no clear downward trend in response to selection for decreased recombination rate. The control values during the last two generations of selection were actually lower than the low line recombination rates.

The regression of generation means (arcsin transformation) on generations for each selection line further points out the asymmetrical response to selection obtained for this character (Table 3). The high line regression coefficients were significantly greater than zero and resulted in a pooled average increase in recombination of 1.3% per generation. The low line regression coefficients, although negative, were not significantly different from zero.

The generation means were also regressed on the cumulative selection differentials to determine if the asymmetrical responses were due to unequal amounts of selection in the high and low lines (see last column in Table 3). These regression coefficients, which are measures of realized heritability, clearly show that the cause of asymmetry is not acting through the selection differentials. The averages of the high and low line selection differentials in degrees per generation were 4.03 and −4.29 for replication one and 4.86 and −4.65 for replication two. This type of asymmetrical selection response can be attributed to directional dominance where those genes that decrease recombination rates are generally dominant over their alleles. Additional evidence for this hypothesis will be presented later in this section.

Recombination in males: There was a 10% to 20% deficiency in the number of beetles in the *rb j* parental class compared to the number of wild-type parentals produced from the testcrosses (Table 4). Since this deficiency results in a small overestimate of recombination rate of about the same magnitude in both the base populations and selection lines, no attempt was made to correct these estimates. However, among beetles produced from the reciprocal testcrosses (*rb j*/+ + ♂ ×

TABLE 3

Summary statistics for 15 generations of two-way selection for recombination rates in cis *females*

Selection line	Average change in percent recombination per generation	Regression coefficients for the regression of generation means on:	
		Generations	Cumulative selection differential*
1 High	1.16	.69 ± .14†	.161 ± .029
2 High	1.44	.88 ± .08	.170 ± .017
1 Low	—.04	—.03 ± .07	.007 ± .017
2 Low	—.07	—.06 ± .08	—.004 ± .020

* Measure of realized heritability.
† Standard error of regression coefficient.

TABLE 4

Distribution of the numbers of testcross progeny for the two base populations (generation 0) and the selection lines (generations 1 to 15)

Line	Parentals		Recombinants		Total	Number of matings	Average number of progeny per 7-day egg collection*
	++	rbj	rb+	+j			
1 Base	3881	3434	1102	1123	9540	45	106
1 High	6071	5486	3536	3545	18638	281	66
1 Low	10241	8473	2151	2311	23176	283	82
2 Base	4299	3524	1028	1033	9884	49	101
2 High	9376	8261	4528	4586	26751	282	95
2 Low	10248	8241	2103	2103	22695	274	83

* The progeny from each single-pair mating were produced in two consecutive seven-day egg collecting periods for the base populations and in one seven-day period for the selection lines.

rb j/rb j ♀) in the base population there was a 60% reduction in the number of *rb j/rb j* beetles compared to + +/*rb j* and, in addition, a 30% reduction in the number of + *j*/*rb j* beetles compared to *rb* +/*rb j* beetles. The percentage hatch of eggs produced by + +/+ +, + +/*rb j*, and *rb j*/*rb j* generation 12 females each mated to *rb j*/*rb j* males was 92%, 70% and 47%, respectively. The deficiency in the number of jet beetles, therefore, appeared to be associated with a reduced egg hatch, particularly among eggs having maternally-derived jet cytoplasm. Because of the inviability of jet-containing genotypes, selection was based on recombination measured in + +/*rb j* females only. Recombination rates in males were measured in generations 0 and 12 of selection and were corrected for the jet deficiencies by omitting the *rb j*/*rb j* and + *j*/*rb j* offspring classes from the computations. Because of the disproportionate reduction in the viabilities of the two jet classes and the variable nature of these reductions among matings, alternative methods of viability correction which do not require loss of data were not appropriate (BAILEY 1961). A comparison of the male and female recombination rates after an apparent plateaued response to selection (generation 12) shows the same asymmetrical response pattern in males as in females; however, the degree of divergence between the high and low selection lines is not as great for male recombination rates (Table 5). The recombination rates are based on two consecutive seven-day egg collections in the male selection lines and base populations and on single 12-day egg collections in the female selection lines. The sex differences in recombination rates observed in generation 0 of selection confirm previous findings for this linkage group (DEWEES 1967).

Recombination in trans *heterozygotes:* Although the selection scheme necessitated that all measures of recombination rate during the selection study be made in female *cis* heterozygotes, recombination rates in *trans* heterozygotes were determined from crosses initiated from generation 18 following three generations of relaxed selection. The appropriate *trans* testcross genotypes were produced from reciprocal mass matings betweeen beetles of the two recombinant classes (+ *j*/*rb j* × *rb* +/*rb j*) from generation 18. Within each selection line 16 matings

TABLE 5

Recombination rates measured in female and male cis *heterozygotes for the base populations and selection lines following 12 generations of selection*

Sex	Line	Pooled recombination rate ± standard error	Number of matings	Total number of individuals
Females	1 Base	.233 ± .009	45	9540
	1 High	.428 ± .015	18	1125
	1 Low	.167 ± .016	19	1637
	2 Base	.209 ± .008	49	9884
	2 High	.403 ± .014	20	2396
	2 Low	.194 ± .009	19	2012
Males*	1 Base	.306 ± .011	47	3876
	1 High	.402 ± .015	11	371
	1 Low	.266 ± .016	18	1220
	2 Base	.299 ± .011	43	3601
	2 High	.387 ± .017	24	1728
	2 Low	.263 ± .012	19	1551

* The jet and ruby-jet classes are not included in the computations of male recombination rates.

of each reciprocal testcross ($+\ j/rb + \times rb\ j/rb\ j$) were set up so that recombination rates were measured in both sexes (Table 6). The control lines were discontinued prior to generation 18; therefore, recombination rates in unselected beetles were not available for comparisons with the selected lines. It is clear from Table 6 that recombination rates measured in *trans* configuration continued to be divergent in the high and low selection lines, the greatest divergence being in females, the sex in which selection was carried out. These results generally agree with male and female recombination rates measured in *cis* heterozygotes of generation 12 as previously shown in Table 5; however, there appears to be less differentiation between the replication 1 high and low selection lines for the *trans* than for the *cis* arrangement.

Backcross results: Backcrosses in generation 12 were made to determine whether factors with major effects were responsible for the selection response. High and

TABLE 6

Recombination rates measured in female and male trans *heterozygotes at generation 18*

Sex	Line	Pooled recombination rate ± standard error	Number of matings	Total number of individuals
Females	1 High	.356 ± .015	16	1139
	1 Low	.186 ± .010	15	1179
	2 High	.350 ± .023	15	1125
	2 Low	.132 ± .009	16	1858
Males*	1 High	.462 ± .024	16	489
	1 Low	.387 ± .033	15	447
	2 High	.410 ± .022	16	510
	2 Low	.285 ± .023	15	701

* The jet and ruby-jet classes are not included in the male rate computations.

low line beetles in each replication of generation 12 were crossed to produce F_1 beetles which in turn were backcrossed to beetles from both the high and low parental lines. Recombination rates based on offspring produced in seven-day egg collections were then measured in *cis* backcross females. The histograms for the four resulting frequency distributions are shown in Figure 3. In none of the four backcross sets is there indication of segregation of a single factor having a major effect on recombination rate. All backcross distributions appear to be unimodal, indicating polygenic control of recombination rate.

If those genes that cause a decrease in recombination rate are generally dominant, a possibility suggested by the asymmetrical selection response, then the variance of this trait should be lower in the (L × H) × L backcrosses than in the (H × L) × H backcrosses. Heterozygous dominant and homozygous recessive genotypes would result from segregation in (H × L) × H backcrosses, whereas segregation in (L × H) ×L backcrosses would result in more uniform genotypes in which only the dominant genes are expressed. One-tail F-tests of the transformed variable (arcsin $\sqrt{p}$) indicated a significant difference between the backcross variances of replication 1 ($F_{40, 46} = 2.02$; $0.01 < P < 0.025$) but no significant difference between the replication 2 variances ($F_{34, 55} = 1.1$; $0.5 < P < 0.75$).

A comparison of the backcross means, indicated by arrows on the abscissa of Figure 3, with the means of the high and low selection lines of generation 12 (Table 5) provides an additional check of the directional dominance hypothesis. If those alleles that decrease recombination rate are dominant, then the (L × H) × L backcross means should be similar to the low line means since the "high"

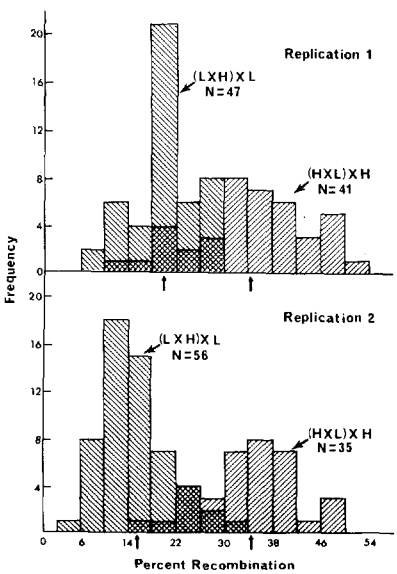

FIGURE 3.—Histograms of percent recombination measured in backcross *cis* females following 12 generations of selection (N = number of females tested in each backcross group).

alleles are concealed in backcross heterozygotes. The observed values of the backcross mean and low line (generation 12) mean pooled over replications were 0.180 and 0.177, respectively ($t_{139} = 0.73$; $0.4 < P < 0.5$), thus supporting the directional dominance hypothesis. By the same reasoning the pooled (H × L) × H backcross mean should be considerably less than the pooled high selection line mean, which was the case—the former was 0.342 and the latter was 0.416 ($t_{112} = 4.5$; $P < 0.001$).

Interline F_1 crosses: All possible crosses (+ +/*rb j* ♀♀ × *rb j*/*rb j* ♂♂) between the four selection lines were made in mass matings following 15 generations of selection. Recombination rates based on seven-day egg collecting periods were then measured in 15 testcrosses (+ +/*rb j* ♀ × *rb j*/*rb j* ♂) which were set up in each of the resulting 16 lines (four parental and 12 F_1 lines). The pooled recombination rates and their standard errors are presented in Table 7 where the four parental lines are represented on the main diagonal and the two goups of reciprocal F_1 lines are above and below the diagonal. Selected single degree of freedom comparisons of the 16-line means were determined for the transformed variable arcsin $\sqrt{p}$. Since the number of successful crosses per line varied from 13 to 15, it was necessary to use a weighted orthogonal analysis (Li 1964, p. 410). As indicated in Table 8, the first comparison, which contrasts high and low selection line means (1H and 2H *versus* 1L and 2L), accounts for about 40% of the between-line sum of squares. The second comparison shows no significant difference between reciprocal crosses (those means above the diagonal *versus* those below the diagonal in Table 7). The third comparison (1H × 1H, 1L × 1L, 2H × 2H and 2L × 2L, *versus* all H × L F_1 crosses) measures the deviation of the mean F_1 recombination rate (0.217) from the mean of the high and low parental lines (0.285) and, therefore, measures directional dominance of genes controlling recombination rate. This comparison is highly significant and verifies the previously supported hypothesis

TABLE 7

Total recombination rates in cis *females for the selection lines and F_1 reciprocal crosses after 15 generations of selection*

	Male parent line			
	1H	1L	2H	2L
1H	.355	.241	.331	.225
	.019*	.014	.016	.011
1L	.225	.182	.229	.147
	.013	.015	.014	.011
2H	.355	.225	.393	.236
	.013	.012	.017	.011
2L	.198	.160	.166	.211
	.011	.012	.011	.014

* Standard error of pooled recombination rate.

TABLE 8

Analysis of between-line variation in recombination rates for the selection lines and reciprocal F_1 crosses following 15 generations of selection

Source of variation	df	Sum of squares	Mean squares
All lines	15	5254.44	350.30**
High *vs.* Low	1	1973.34	1973.34**
Reciprocal crosses	1	26.06	26.06
Dominance	1	670.06	670.06**
$(R_i \times R_j)$ *vs.* $(R_i \times R_i)$	1	261.27	261.27**
Error	213	4213.08	19.78
Total	228	9467.52	

** Significant at $P<.01$.

that dominant genes decrease recombination and their recessive alleles increase recombination. The fourth comparison in Table 8, although non-orthogonal to the others, also measures directional dominance and is highly significant. It contrasts the mean of the four parental lines, 1H, 1L, 2H and 2L, with the mean of the reciprocal F_1 crosses between the two high lines (1H × 2H and 2H × 1H) and between the two low lines (1L × 2L and 2L × 1L). The means of the reciprocal crosses between the two low lines (1L × 2L and 2L × 1L) are both less than the means of the two low parental lines (Table 7). Apparently selection in the two low lines has fixed slightly different sets of dominant genes that reduce recombination rate so that in the 1L × 2L F_1 beetles these two sets of genes act together to further reduce the recombination rate. The same reasoning correctly predicts that the mean recombination rate of 1H × 2H F_1 crosses should be less than the mean rate of the two high selection lines (Table 7).

DISCUSSION

The observed asymmetrical response to selection suggests that recombination rate in the ruby-jet region of *Tribolium castaneum* is under the control of multiple genetic factors which exhibit directional dominance. Genes that increase recombination are predominantly recessive and account for the rapid and progressive increase in recombination rate observed in both high lines, whereas their dominant alleles decrease recombination and account for the small response to selection in the low lines. This type of asymmetry could also result from directional gene frequencies in the base populations (FALCONER 1960); however, this is not likely since the base populations used in this study were formed from crosses of diverse genetic strains. Much of the genetic variability in such populations is due to genes at intermediate frequencies. The strongest evidence favoring directional dominance as the cause of the asymmetrical response comes from the detection of significant dominance effects in the interline crosses and backcrosses.

In previous studies of selection for recombination rate the direction and magnitude of response has depended on the amount of variability in the initial

population and the degree of inbreeding permitted during selection. Care was taken in the preparation of the base populations used in this study to assure maximum initial variability for the action of selection. Inbreeding was minimized through the avoidance of full-sib matings. WRIGHT's coefficient of inbreeding, F, as determined by the following random mating formula (CROW and KIMURA 1970):

$$F_t = 1/2N + (1 - 1/N)\ F_{t-1} + 1/2N\ F_{t-2}$$

after 15 generations ($t = 15$) of selecting five families ($N = 10$) was 0.495 less the contribution due to full-sib matings. Although F is not small, the similarity of the response patterns observed in the two replications favors selection rather than random drift as the major force in this study.

Chromosomal rearrangements affect recombination rates (SCHULTZ and REDFIELD 1951; LUCCHESI and SUZUKI 1968) and might, therefore, partially account for the response of this trait to selection. The incorporation of inversions in lines subjected to selection for reduced recombination has been reported in Drosophila by KIDWELL (1972a) and indirectly indicated in the studies of DETLEFSEN and ROBERTS (1921) and MOYER (1964). Only CHINNICI (1971a) and ABDULLAH and CHARLESWORTH (1974) have reported response to selection for decreased recombination in lines lacking cytologically detectable inversions. The detection of inversions is not practicable in Tribolium; however, it is unlikely that the base populations contained inversions in the ruby-jet region. Selection for reduced recombination would favor inversion heterozygotes and result in a drastic decrease in recombination rate. There was no general downward trend in response to selection for decreased recombination. The fact that recombination rates in *trans* females at generation 18 in the high and low lines were similar to rates in *cis* females, the arrangement and sex in which all selection was based, argues against inversions in the ruby-jet region and for the existence in these lines of recombinagenic genes having similar effects on both *cis* and *trans* arrangements. Chromosomes heterozygous for inversions and translocations sometimes increase crossing over in non-homologous chromosomes (SCHULTZ and REDFIELD 1951) and could partially account for the large response to selection observed in both high selection lines. However, the evidence from the selection line backcrosses indicated several genetic factors with small effects on recombination rate. It is likely that these are polygenic factors and not chromosomal rearrangements.

Varied results have been reported from previous studies of selection for recombination rate. In studies of *D. melanogaster* yielding little or no response to selection (GOWEN 1919; PARSONS 1958; ACTON 1961), the base populations were restricted in their variability and high levels of inbreeding were allowed. More recently VALENTIN (1973a) in a short-term, two-way selection study of two linkage regions in *D. melanogaster* was able to demonstrate a small but significant divergence between high and low lines after six generations for one of the regions. No significant differences between lines were obtained for the second region, although both lines exhibited a drastic reduction in recombination due to

the incorporation of a recessive third chromosome gene which greatly reduced recombination rates (VALENTIN 1973b). Significant symmetrical response to two-way selection indicative of polygenic control of recombination rate has been reported for *D. melanogaster* (CHINNICI 1971a, b) and for *Aspergillus nidulans* (PRITCHARD 1955; CALEF 1957). The type of asymmetrical response obtained in the present study has also been reported in short-term studies in the lima bean by ALLARD (1963) and in Neurospora by LANDNER (1974), and in a long-term study in *D. melanogaster* by KIDWELL (1972a), who reported an approximate doubling of recombination rate between Glued (*Gl*) and Stubble (*Sb*) in response to upward selection but no response to downward selection. However, in a related study of simulated natural selection for decreased recombination in the same linkage region, a significant downward response was observed in four of six lines (KIDWELL 1972b). In general, selection for recombination rate has been successful, particularly in well-designed studies, but it does not appear, *a priori*, possible to predict the direction of greatest response.

Dominance of recombinagenic genes in the direction of decreased recombination, as observed in this study, has also been reported by KIDWELL (1972a). Although CHINNICI (1971a) reported "codominance" of genes affecting recombination, crosses between his high and low selection lines produced recombination rates in the F_1 which were less than the average rates of the two parent lines and less than the base population rates, thus suggesting partial dominance in the direction of reduced recombination. In addition, STAMBERG and KOLTIN (1973) stated that for all of the "fine" control genes so far identified in the fungi *Schizophyllum commune* and *Neurospora crassa*, low frequency of recombination is dominant to high. These studies provide considerable evidence that this kind of gene action is widespread in nature, although evidence exists for partial dominance in the opposite direction for recombination rates in Drosophila (LAW 1961; LAWRENCE 1963) and for chiasma frequencies in rye (REES and THOMPSON 1956) and in barley (GALE and REES 1970).

Under a polygenic model of recombination modifiers in which low recombination is dominant to high, average recombination rates in small populations will increase as inbreeding progresses due to the increase in homozygosity of recessive alleles. The increased variability resulting from the proposed model provides the flexibility required by small populations for occupying new or changing environments. On the other hand high heterozygosity in large outbread populations results in minimum recombination of linked genes, thus preserving favorable gene combinations which allows for the stability of populations. PANDEY (1972) summarized much of the evidence for this kind of gene control of recombination and outlined the evolutionary significance of the modification of both intergenic and intragenic recombination. Additional evidence supporting the predictions under this model comes from studies of the relationship between mating system and chiasma frequency in plants. GRANT (1958), HARINARAYANA and MURTY (1971) and ZARCHI *et al.* (1972) reported higher chiasma frequencies in inbred populations than in outbred populations; however, REES and THOMPSON (1956) observed the reverse relationship. Genetic control of recombination rates is

obviously important in the adjustment of genotypes to changing environments, but additional information is needed concerning the existence and mode of action of recombinagenic genes in natural populations.

This work was supported by Faculty Research grants from Sam Houston State University. The expert technical assistance of Miss Karen Becak is gratefully appreciated. Dr. A. E. Bell kindly read the manuscript and made helpful comments.

LITERATURE CITED

Abdullah, N. F. and B. Charlesworth, 1974 Selection for reduced crossing over in *Drosophila melanogaster*. Genetics **76:** 447–451.

Acton, A. B., 1961 An unsuccessful attempt to reduce recombination by selection. Am. Naturalist **95:** 119–120.

Allard, R. W., 1963 Evidence for genetic restriction of recombination in the lima bean. Genetics **48:** 1389–1395.

Bailey, N. T. J., 1961 *Introduction to the Mathematical Theory of Genetic Linkage*. Clarendon Press, Oxford.

Bodmer, W. F. and J. Felsenstein, 1967 Linkage and selection: theoretical analysis of the deterministic two locus random model. Genetics **57:** 237–265.

Bray, D., A. E. Bell and S. C. King, 1962 The importance of genotype by environment interaction with reference to control populations. Genet. Res. **3:** 282–302.

Calef, E., 1957 Effects on linkage maps of selection of crossovers between closely linked markers. Heredity **11:** 265–279.

Chinnici, J. P., 1971a Modification of recombination frequency in Drosophila. I. Selection for increased and decreased crossing over. Genetics **69:** 71–83. ——, 1971b Modification of recombination frequency in Drosophila. II. The polygenic control of crossing over. Genetics **69:** 85–96.

Cochran, William G., 1963 *Sampling Techniques*. 2nd edition. John Wiley and Sons, New York.

Crow, J. F. and M. Kimura, 1970 *An Introduction to Population Genetics Theory*. Harper and Row, New York.

Darlington, C. D., 1939 *The Evolution of Genetic Systems*. Cambridge University Press, London and New York.

Detlefsen, J. A. and E. Roberts, 1921 Studies on crossing over. I. The effect of selection on crossover values. J. Exptl. Zool. **32:** 333–354.

Dewees, A. A., 1964 Variation in a "wild" population of *Tribolium castaneum*. Tribolium Inform. Bull. **7:** 55–56. ——, 1967 Sex differences in recombination values for linkage group V of *T. castaneum*. Tribolium Inform. Bull. **10:** 89–90. ——, 1970 Two-way selection for recombination rates in *Tribolium castaneum*. Genetics **64:** s16–s17 (Abst.) ——, 1973 Modification of recombination frequency in *Tribolium castaneum*. Genetics **74:** s62–s63 (Abst.)

Falconer, D. S., 1960 *Introduction to Quantitative Genetics*. Ronald Press, New York.

Feldman, M. W., 1972 Selection for linkage modification. I. Random mating populations. Theoret. Pop. Biol. **3:** 324–346.

Feldman, M. W. and Beverley Balkau, 1973 Selection for linkage modification. II. A recombination balance for neutral modifiers. Genetics **74:** 713–726.

Fisher, R. A., 1930 *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

GALE, M. D. and H. REES, 1970 Genes controlling chiasma frequency in *Hordeum*. Heredity **25**: 393–410.

GOWEN, J. W., 1919 A biometrical study of crossing over. On the mechanism of crossing over in the third chromosome of *Drosophila melanogaster*. Genetics **4**: 205–250.

GRANT, V., 1958 The regulation of recombination in plants. Cold Spring Harbor Symp. Quant. Biol. **23**: 337–363.

HALDANE, J. B. S., 1919 The combination of linkage values, and the calculation of distance between the loci of linked factors. J. Genet. **8**: 299–309.

HARINARAYANA, G. and B. R. MURTY, 1971 Cytological regulation of recombination in *Pennisetum* and *Brassica*. Cytologia **36**: 435–448.

KALE, P. G., 1968 Spontaneous crossing over in the males of *Drosophila ananassae*: Two-way selection for recombination values. Japan. J. Genet. **43**: 27–31.

KARLIN, S. and M. W. FELDMAN, 1970 Linkage and selection: Two locus symmetric viability model. Theoret. Pop. Biol. **1**: 39–71.

KIDWELL, M. G., 1972a Genetic change of recombination value in *Drosophila melanogaster*. I. Artificial selection for high and low recombination and some properties of recombination-modifying genes. Genetics **70**: 419–432. ——, 1972b Genetic change of recombination value in *Drosophila melanogaster*. II. Simulated natural selection. Genetics **70**: 433–443.

KIMURA, M., 1956 A model of genetic system which leads to closer linkage by natural selection. Evolution **10**: 278–287.

LANDNER, L., 1974 Genetic control of recombination in *Neurospora crassa*. III. Selection for increased and decreased recombination frequency. Hereditas **78**: 185–200.

LAW, C. N., 1961 Recombination in the X-chromosome of *Drosophila melanogaster*. Nature **191**: 1180–1181.

LAWRENCE, M. J., 1963 Control of crossing-over in the X-chromosome of *Drosophila melanogaster*. Heredity **18**: 27–46.

LI, J. C. R., 1964 *Statistical Inference*. Edwards Brothers, Inc., Ann Arbor.

LUCCHESI, J. C. and D. T. SUZUKI, 1968 The interchromosomal control of recombination. Ann. Rev. Genet. **2**: 53–86.

MATHER, K., 1943 Polygenic inheritance and natural selection. Biol. Rev. **18**: 32–64.

MOYER, S. E., 1964 Selection for modification of recombination frequency of linked genes. Ph.D. thesis. University of Minnesota. Diss Abstract **25**: 1508–1509.

MUKHERJEE, A. S., 1961 Effect of selection on crossing over in the males of *Drosophila ananassae*. Am. Naturalist **95**: 57–59.

NEI, M., 1967 Modification of linkage intensity by natural selection. Genetics **57**: 625–641.

PANDEY, K. K., 1972 Origin of genetic variation: regulation of genetic recombination in higher organisms—a theory. Theoret. Appl. Genet. **42**: 250–261.

PARK, T., 1954 Experimental studies of inter-species competition. II. Temperature, humidity and competition in two species of *Tribolium*. Physiol. Zool. **27**: 177–238.

PARSONS, P. A., 1958 Selection for increased recombination in *Drosophila melanogaster*. Am. Naturalist **92**: 255–256.

PRITCHARD, R. H., 1955 The linear arrangement of a series of alleles of *Aspergillus nidulans*. Heredity **9**: 343–371.

REES, H. and J. B. THOMPSON, 1956 Genotypic control of chromosome behavior in rye. III. Chiasma frequency in homozygotes and heterozygotes. Heredity **10**: 409–424.

SCHULTZ, J. and H. REDFIELD, 1951 Interchromosomal effects on crossing over in *Drosophila*. Cold Spring Harbor Symp. Quant. Biol. **16**: 175–197.

STAMBERG, J. and Y. KOLTIN, 1973 Genetic control of recombination in *Schizophyllum commune*: evidence for a new type of regulatory site. Genet. Res. **22:** 101–111.

TURNER, J. R. G., 1967 On supergenes. I. The evolution of supergenes. Am. Naturalist **101:** 195–221.

VALENTIN, J., 1973a Selection for altered recombination frequency in *Drosophila melanogaster*. Hereditas **74:** 295–297. ——, 1973b Characterization of a meiotic control gene affecting recombination in *Drosophila melanogaster*. Hereditas **75**: 5–22.

ZARCHI, Y., G. SIMCHEN, J. HILLEL and T. SCHAAP, 1972 Chiasmata and the breeding system in wild populations of diploid wheats. Chromosoma **38:** 77–94.

Corresponding editor: R. W. ALLARD