EFFICIENCY OF SELECTION FOR INCREASED OR DECREASED RECOMBINATION*

There is a large amount of evidence that linkage intensity is under genetic control (see Bodmer and Parsons, 1962; Nei, 1967). However, the results of selection experiments on recombination value in Drosophila are not necessarily consistent. Detiezen and Roberts (1921), Parsons (1958), and Mukherjee (1961) reported the effectiveness of selection for reduced or increased recombination, while Gowen (1919) and Acton (1961) were not able to change recombination value by artificial selection. It seems, therefore, worthwhile theoretically to study the efficiency of such a selection in the presence of modifier genes for recombination.

The selection schemes so far employed can be divided into two categories. One is that due to Parsons (1958) and designed to increase recombination value. This scheme consists of three mating steps as given in Figure 1. The other is a family selection, in which a large number of families are raised by pair matings and a family showing a low or high recombination value is selected. All the workers other than Parsons (1958) used this scheme with a slight modification in individual cases.

Let us first consider Parsons' scheme. Suppose that a pair of allelic genes, $M$ and $m$, located on an autosomal chromosome, control the recombination

* This work was supported in part by a grant from the Scientific Research Fund of the Ministry of Education, Japan.
value between two loci A and B, and that the recombination values of
genotypes MM, Mm, and mm are r2, r1, and r0, respectively. For simplicity,
we assume that the A and B loci are located on a chromosome different
from that of the M locus. Let P, Q, R and S, T, U be the initial frequencies
of genotypes MM, Mm, mm in the female and male populations, respec-
tively, so that the initial gene frequency of M is p0 = P + 1/2Q in the
female and q0 = S + 1/2T in the male. The types and frequencies of female
gametes in the step 1 mating in Figure 1 are shown in Table 1.

<table>
<thead>
<tr>
<th>Modifier Genotype</th>
<th>Frequency</th>
<th>Gametes Produced</th>
</tr>
</thead>
<tbody>
<tr>
<td>MM</td>
<td>P</td>
<td>AB: (1 - r2)/2, Ab: r2/2, aB: (1 - r0)/2</td>
</tr>
<tr>
<td>Mm</td>
<td>Q</td>
<td>AB: (1 - r2)/2, Ab: r1/2, aB: (1 - r0)/2</td>
</tr>
<tr>
<td>mm</td>
<td>R</td>
<td>AB: (1 - r2)/2, Ab: r0/2, aB: (1 - r0)/2</td>
</tr>
</tbody>
</table>

In the step 2 mating only the genotypes Ab/ab and aB/ab are used. The frequencies of MM, Mm, and mm in each of these two groups are given by
p0'q0, p0'(1 - q0) + (1 - p0')q0, and (1 - p0')(1 - q0), respectively, in
both the male and female populations, where p0' is (Pr2 + 1/2Qr1)/(Pr2 +
Qr1 + Rr0). Hence, the gene frequency of M becomes

\[ p_2 = p_0'q_0 + \frac{p_0'q_0 + (1 - p_0')q_0}{2}. \]

The genotype frequencies with respect to the loci A and B in the offspring
from the step 2 mating do not depend on the recombination value, so that
the gene frequency of M does not change from step 2 to step 3. From step
3 to step 1 in the next cycle, however, selection is again conducted, and the
gene frequency of M in the group of AB/ab or ab/ab in step 1 of the next
cycle becomes

\[ p_3 = p_3'p_1 + \frac{1}{2}[p_1(1 - p_1) + (1 - p_1)p_1], \]

where

\[ p_1' = \frac{p_2r_2 + p_2(1 - r_2)r_1}{p_2r_2 + 2p_2(1 - p_2)r_1 + (1 - p_2)^2r_0}. \]

Hence, the amount of change in gene frequency per one cycle of selection,
that is, three generations, is given by \( \Delta p = p_2 - p_0 \). Figure 2 shows the
values of \( \Delta p \) for various initial gene frequencies in the case of \( r_2 = 0.08;\)
\( r_1 = 0.08, 0.05, \) or \( 0.02; \) and \( r_0 = 0.02 \), where \( p_0 = q_0, P = p_0^2, Q =
2p_0(1 - p_0), \) and \( R = (1 - p_0)^2 \) are assumed. It is seen from this figure
that this type of selection is quite effective if the initial gene frequency is
in the range of 0.1-0.9. In Parsons' experiment the recombination value
between loci b and pr on the second chromosome in D. melanogaster increased from 0.049 to 0.074 by three cycles of selection. Numerical com-
putations have shown that this amount of change in the recombination
value is quite reasonable, if the environmental and chance variation is small and if modifier genes with a relatively large effect are segregating. This type of selection is not, however, so effective when one wants to reduce recombination, as seen from Figure 2.

![Diagram showing the effects of high and low selection on gene frequency changes.](image)

Fig. 2.—Amounts of change in the modifier-gene frequency per one cycle of selection (three generations) in Parsons' selection scheme. The abscissa represents the initial gene frequency (see text). The curves recessive, additive, and dominant stand for the cases of \( r_n = 0.08, r_s = 0.02, r_c = 0.02 \), \( r_n = 0.08, r_s = 0.05, r_c = 0.02 \), and \( r_n = 0.08, r_s = 0.08, r_c = 0.02 \), respectively.

The same formulation as the above can be made for the family selection, and it can be shown that the family selection is very effective if recombination-modifying genes with a large effect exist and if selection is made among a large number of families. Namely, if a pair of alleles are segregating and \( n \) families are raised by pair matings, the probability of obtaining at least one family from the mating \( MM \times MM \) is \( 1 - (1 - PS)^n \). Therefore, if \( PS \) and \( n \) are sufficiently large, the modification of recombination value can be completed even in a single generation. In reality, of course, such a favorable condition does not appear to exist. On the contrary, the effect of selection is generally diluted by environmental and chance variation. The number of modifier genes (loci) may also be large.
Indeed, the result of the selection experiment by Detlefsen and Roberts (1921) indicates that the selection for recombination is essentially the same as the selection for ordinary quantitative characters. In one selection line they reduced the recombination value between loci \( w \) and \( w^b \) on the X-chromosome from 28.6% to 9.7% in the first 10 selection cycles (one cycle consisted of two generations). The so-called selection differential was negative (surprisingly!) in some generations but accumulated to 43.3% or units. Therefore, the heritability of recombination value in this case is estimated to be about 44%. Acton (1961) reproduced the same type of selection experiment with loci \( c^r \) and \( u^g \) on the second chromosome, but he was unable to reduce the recombination value. In his case, the accumulated selection differential in the first 10 selection cycles was 43.8 units. It seems, therefore, that his original stock had little genetic variation with respect to the recombination value. Gowen (1919) was also unable to change the recombination value between \( a^s \) and \( ro \) on the third chromosome, but, as he stated, his stock again appears to have had little genetic variation. In this sort of experiment it is very important to examine whether the original stock has enough genetic variation.

Finally, it should be mentioned that the effectiveness of artificial selection does not necessarily indicate the effectiveness of natural selection in modifying recombination values. For natural selection to be effective, there must be intergenic interaction or epistasis between the loci of which the recombination value is to be modified, as shown by Nei (1967). Further, even if there is epistasis, the amount of change in the modifier-gene frequency per generation is generally much smaller under natural selection than under artificial selection.

LITERATURE CITED


MAsATOshI NE1
YOKO IMAIZUMI

DIVISION OF GENETICS
NATIONAL INSTITUTE OF
RADIOLOGICAL SCIENCES
9-1, 4-chome, ANAGAWA, CHIBA
JAPAN
June 16, 1967