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Selection and Recombination in *Drosophila melanogaster*[1]

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Summary. Artificial selection for wing length in *Drosophila melanogaster* resulted in changed crossing-over frequencies between three marker genes on the 2nd chromosome, *b, cn* and *vg*.

The results suggest that artificial selection is a causal agent in producing the observed changes; moreover it is suggested that the modifications in cross-over frequency are controlled by extra-nuclear factors.

Introduction

Recombination is the mechanism by which a large amount of the variability present in a population is made available, and therefore influences the outcome of natural and artificial selection.

There is a large amount of evidence that linkage intensity is under genetic control (see: Bodmer and Parsons, 1962; Nei, 1967; Lindsley et al. 1968); in particular there is evidence, however scanty, suggesting that control over recombination is polygenic (Detlefsen and Roberts, 1922; Parsons 1958; Mukherjee 1961).

In order to determine whether changes in recombination values may have some importance in evolutionary processes, it would seem interesting to investigate if these changes could be related to those induced in quantitative characters. In fact, selecting for a quantitative character also produces changes in the genotypic structure outside the genetic basis of the character considered; these changes could result in modified recombination values either as a correlated response or a casual one. When a correlation is detectable between a selected measurable character and specific recombination values, it seems safe to assume that some kind of interdependence exists between selection and recombination.

Material and Methods

A disruptive selection for wing length was performed on flies heterozygous at the loci *b* (brown), *cn* (cinnabar) and *vg* (vestigial) on the second chromosome, derived from a cross between a Canton strain and a strain carrying the three recessive markers in the homozygous condition. Within each selection line in each selection generation non-recombinant heterozygous flies were crossed with homozygous recessives. Two selected lines were obtained:

1. selection in plus direction,
P = heterozygous ♀♀ crossed to homozygous ♂♂
2. selection in minus direction
M = heterozygous ♀♀ crossed to homozygous ♂♂.

Measurements were taken of the wing length in all four lines considered, and counts of the cross-over frequencies were made in lines where the heterozygous females were selected.

The following crosses were performed in order to study the genetic control of the recombination between *b, cn,* and *vg* loci:

a) backcrosses of female flies from the selected lines with the parental stock carrying the markers *b, cn,* and *vg*.

b) crosses between flies belonging to lines selected in different directions.

Results

The percentage of non-recombinant flies at each generation of selection is shown in fig. 1. While selection for short wing does not influence the cross-over frequency in the portion of the second chromosome considered, the percentage of non-recombinant flies increases when wing length is selected for in the plus direction.

When the two recombination intervals between the marker genes, *b, cn* and *cn, vg*, are considered separately, it may be seen (table 1) that the frequency of crossover is modified only in the former one when plus-variant flies are selected for wing length. This kind of localization of the modified crossover frequency is similar to that found by Parsons (1958) while performing a selection directly on recombination frequency. No differences are observed between the two intervals considered when selection for short wing is made.

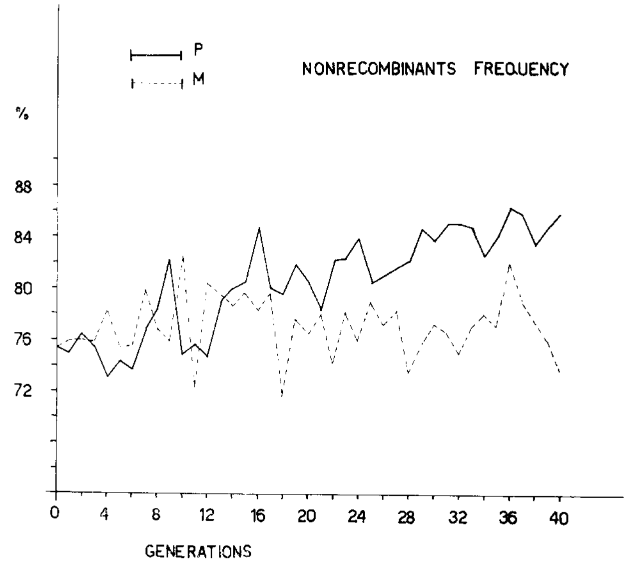

Fig. 1. Percentage of non-recombinant flies scored at different selection generations

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Table 1. *Regression coefficient values of the crossover percentage on generation of selection in the two different directions*

Phenotypes	Plus		Minus	
	b	*t*	*b*	*t*
+ + +; bcnvg	0.3054	8.007**	0.0178	0.403
b + +; + cnvg	−0.1906	8.099**	0.0445	1.346
bcn +; + + vg	−0.0078	0.274	0.0072	0.188

** = $P < 0.001$.

Table 2. χ^2 *values for the comparisons between expected and observed crossover frequency in progenies of backcrosses between heterozygous females from selected lines and homozygous b cn vg flies*

Cross	*b* + +; + *cn vg*	*b cn* +; + + *vg*
Plus × Parental Strain	18.48***	0.001
Minus × Parental Strain	3.38	3.83*
Plus × Minus	8.90**	0.10
Minus × Plus	0.16	10.97***

* = *P* between 0.05 and 0.01
** = *P* between 0.01 and 0.001
*** = *P* less than 0.001.

The results obtained by crossing heterozygous females from the two selected lines with *b, cn, vg* marked males either from the parental strain or from the other selected line are shown in table 2.

In progenies from plus-selected females the frequency of *b* + + and + *cn vg* flies is lower than that expected while the products of the crossing-over in the *cn, vg* interval appear in the expected percentage; this suggests that both crosses give results similar to those observed in the population studied under selection. In progenies from minus-selected females the frequency of *b cn* + and + + *vg* flies is significantly higher than that expected, while crossovers produced by crossing-over in the contiguous interval (*b, cn*) are present in the expected frequency. These results differ from those observed in progenies from plus-selected heterozygous females, where the changes in crossover frequency are different from those obtained from minus-selected females crossed with *b, cn, vg* males from the same selected population.

The comparison between the reciprocal crosses, plus × minus and minus × plus (table 2), suggests that the observed changes in crossover frequency are determined by extra-nuclear factors.

Discussion

When it is considered that selection was performed for wing length on flies which were non-recombinant in respect of the three marker genes, one might expect that there should have been some selective pressure favouring genotypes with decreased recombination values. This assumption could explain a decrease in crossover frequency between the marker genes which should be similar in both selected lines (plus- and minus-selected flies). The differences in recombination observed when comparing plus- and minus-selected lines suggest that the modifications of crossover frequency may be the direct or indirect result of the selection performed on wing length. This view is strengthened by the evidence that changes in recombination values seem to be determined by extra-nuclear factors. In fact these findings rule out the possibility that the observed changes in crossover frequency are determined by the selection of modifier genes linked to the genes determining wing length.

A further complication is produced by the fact that variation in crossover frequency is not detectable in the minus-selected line; this suggests the existence of nucleus-cytoplasm interactions in determining the recombination frequency. It seems, therefore, that the selection performed for wing length is effective in modifying extra-nuclear effects which influence the crossover frequency; in other words, these results suggest that selection for wing length is a causal agent in modifying the recombination values in at least one region (*b* — *v g*) of the second chromosome of *Drosophila melanogaster.*

If the relationship between selection and recombination suggested above is of general occurrence it is possible to envisage a new mechanism of self-regulation of selection.

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