Change of the crossing-over frequency in *Drosophila* during selection for resistance to temperature fluctuations

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Abstract

Significant differences among cage populations of *Drosophila* in the dynamics of linkage disequilibrium for marker loci *b, cn* and *vg* of chromosome 2 have been found at optimum and extreme temperatures. Fifteen generations of selection under extreme conditions considerably increased recombination frequency in the *cn-vg* region and over the whole of the *b-vg* interval. From the data obtained it is inferred that recombination--promoting alleles with intermediate expression in the heterozygous state are responsible for these changes.

Introduction

Natural populations are characterized by a dynamical equilibrium between the factors increasing and decreasing variability (Mayr, 1970; Zhuchenko, 1980). It is believed that in a homogeneous environment natural selection, as soon as the population reaches an equilibrium, should promote the tightening of linkage between the interacting loci for fitness (Fisher, 1930). In other words, if a species evolves to increase the mean fitness then the process is most likely to be accompanied by a decline in the recombination frequency. Hence the question arises as to why this process did not result in the population achieving the zero level of recombination, i.e. 'why does the genome (genotype) not congeal?' (Turner, 1967).

Maynard Smith (1978) singles out three types of models to explain recombination maintenance in a population: sib competition, random linkage disequilibrium, and selection in varying environments.

Despite the abundance of theoretical models, the problem of the possibility of the recombination controlling system (rec-system) reorganization during selection for adaptive characters has virtually not been worked out experimentally. Exceptions can be found in the work of Flexon and Rodell (1982) on recombination frequency (rf) increase in large autosomes of *D. melanogaster* during direct selection for DDT resistance; our data on recombination frequency changes in chromosome 2 of *D. melanogaster* in a population cultured under variable temperature conditions (Zhuchenko *et al.*, 1983); experiments of Lobashev *et al.* (1973) with the same object, and of Harinarayana and Murthy (1971) with mustard.

.The results presented in this paper can be regarded as experimentally substantiating Maynard Smith's hypothesis (1980) that in a linked polygenic system directional selection with a changing optimum provides an increase in rec⁺-allele concentration with the corresponding increase in recombination frequency, i.e. reorganization of the genetic system of recombination regulation.

Material and methods

The dynamics of population changes was studied on two model populations of *D. melanogaster* (control and experimental) over 40 generations. The populations had been obtained by crossing heter-

ozygotes (b, cn, vg × Domodedovo-18) and were subsequently maintained by random mating in acrylic glass boxes (40 × 25 × 25 cm) containing 30 open vials (10 × 2.5 cm) each. The control population (C) was cultured at an optimum temperature of 25 ± 0.5°C. The experimental population (T) was maintained with the range of diurnal fluctuations of temperature increasing with generations from 21 to 29°C at the beginning of the experiment and from 15 to 32°C at the end of it.

The population size, phenotype frequency, linkage disequilibrium, and correlation between linked markers were being studied throughout the experiment. The χ^2 of the 2 × 2 table for absolute frequency values of four phenotypic classes was used to estimate interlocus correlations (R). The correlation between the allelic states of linked loci was determined from $R = \sqrt{\chi^2/N}$, where N is the sample size. Based on the phenotype frequencies in each generation, the population allelic concentration and D values for each pair of loci (on the assumption of panmixia) were estimated by the maximum likelihood method (Turner, 1968).

This approach allowed one to obtain R and D values by the average scoring of about 1500 flies per generation per variant (600 minimum and 3200 maximum). For direct estimation of D values based on population gamete frequencies, the data in the literature usually refer to small samples, not exceeding 150-200 individuals, due to much effort required by this method. Therefore, notwithstanding the advantages offered by direct estimation of D values, the significance of the data is considerably reduced due to statistical fluctuation. For indirect estimation based on scoring phenotype frequencies, a bias of estimates is possible when initial assumptions are not realized (e.g. in case of limitations on panmixia). Nevertheless, the conclusions obtained in this case, preliminary as they are, are characterized by high stability.

Recombination frequency was estimated for hybrid females in F_1, F_{26} and F_{39}. The F_1 heterozygotes developed at optimum temperature (25 ± 0.5°C) in the C variant and at temperature with diurnal fluctuations (from 15 ± 1°C to 29 ± 1°C) in the T variant. Backcross progenies (the first four 3-day broods) of both populations developed under optimum conditions. Phenotypically normal virgin females were selected from C and T populations in F_{26} and crossed with b, cn, vg test males (1♀ × 2♂)

under the same conditions. Considering possible effects of temperature on cross-over rate, half of the T females in F_{26} were maintained at optimum conditions (designated as TC) and the other half under the same conditions as the whole of the T population (designated as TT); the control (CC) was cultured under standard conditions. In the progeny of the above cross identification for marker loci was performed in families segregating for no less than two markers. To determine the recombination frequency for the C and T populations of F_{39}, phenotypically normal virgin females were crossed with males of the b, cn, vg line (1♀F_{39} × 2♂b, cn, vg). Phenotypically normal virgin females (+++/b, cn, vg) were selected from the progeny of this cross for which rf was estimated based on the examination of six 3-day broods of F_b.

Due to high amplitude of temperature variations the females in the F_6 generation of the T-population became sterile, and we could not obtain the F_7 progeny. To continue the experiment the variant T was reestablished from the F_{10} of the C-population. Therefore, the actual divergence between T and C flies for recombination frequency is caused by differences in their external conditions starting with F_{11} zygotes.

Results and discussion

Figure 1 shows the dynamics of D for both regions of the b, cn, vg interval. On the whole, the D variation pattern in the control population is in approximate agreement with the dynamics expected in the absence of selection. In population T, during the first three generations D and R were decreasing much faster, and starting approximately with generation 20, slower than in the control population with the difference being highly significant in a number of generations. It is interesting to note that despite relatively high cross-over rates between marker loci, significant deviations of D and R values from zero are observed as late as generations 30-35. Stable differences between populations T and C in the dynamics of correlation between markers can probably be regarded as an indication that there is selection for resistance to temperature variation. In view of this, it is also interesting that during the first four generations (till the death of population T) this selection favoured normal al-